Methane-limited methanotrophy in tidal freshwater swamps

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[1] We investigated the relationship between CH_4 production and oxidation in two tidal freshwater wetland forests in order to determine whether CH_4 oxidation efficiency was limited by O_2 or CH_4. Methane oxidation was measured in situ over a 16-month period with bi-monthly applications of the inhibitor CH_3F. Oxidation consumed 52 ± 10 and 81 ± 9% of diffusive CH_4 emissions on the two sites. Methane oxidation rates were linearly related to gross CH_4 emissions on both sites ($r^2 = 0.96$), demonstrating the process was CH_4-limited. This interpretation is consistent with the fact that the apparent activation energies for the potential CH_4 production and oxidation differed by <4 kJ mol^{-1}. Apparent activation energies calculated from field emissions data were also similar for the two processes. The high CH_4 oxidation efficiency on these sites may be attributed to relatively low rates of methane production, a deep oxidizing zone (5–10 cm), and low cover of understory vegetation capable of CH_4 transport. If our results are typical of forested wetlands, CH_4 oxidation efficiency in forested wetlands will not change in response to soil warming. *INDEX TERMS:* 1890 Hydrology: Wetlands; 0322 Atmospheric Composition and Structure: Constituent sources and sinks; 0315 Atmospheric Composition and Structure: Biosphere/atmosphere interactions; 4235 Oceanography: General: Estuarine processes; *KEYWORDS:* methane emissions, methane oxidation, temperature responses, forested wetland, global warming, methanogenesis

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1. Introduction

[2] Methanotrophic bacteria substantially reduce methane emissions from natural and agricultural wetlands and thereby limit the global wetland source to ~175 Tg yr^{-1} [*Schlesinger*, 1997]. The wetland methanotrophy sink has been estimated to consume between 40% [*King*, 1996] and 70% [*Reeburgh et al.*, 1993] of gross CH_4 production (100–400 Tg yr^{-1}). Because these estimates exceed the rate that CH_4 is currently increasing in the atmosphere (40 Tg yr^{-1}), climate-induced changes in CH_4 oxidation rates have the potential to influence the atmospheric burden of this greenhouse gas. The extent to which CH_4 emissions will increase with future soil warming will be determined in part by changes in the efficiency of CH_4 oxidation.

[3] There are at least two mechanisms by which soil warming could cause a larger increase in CH_4 production than CH_4 oxidation, and thereby increase net CH_4 emissions proportionally more than gross CH_4 production. If methanotrophy is limited by O_2 availability and, provided that factors such as radial oxygen loss and water-table depth do not change, rising temperature will stimulate CH_4 production but not oxidation. Root-associated methanotrophy is O_2-limited in certain emergent aquatic macrophytes such as *Phragmites australis* [*van der Nat and Middelburg*, 1998], *Sparganium eurycarpum* [*King*, 1996], and *Typha latifolia* [*Lombardi et al.*, 1997]. Because >75% of the diffusive CH_4 efflux can pass through plants [*Shannon and White*, 1994; *Chanton and Dacey*, 1991; *King*, 1996], in many cases methane oxidation should also be O_2-limited on an ecosystem basis.

[4] Alternatively, CH_4 oxidation rates may be limited by CH_4 concentration [e.g., *Gilbert and Frenzel*, 1998]. In such cases, both CH_4 production and oxidation will increase, but not necessarily at the same rate. CH_4 oxidation efficiency could decline if methanogenesis increased faster with temperature than methanotrophy. Indeed, methanotrophy is generally less sensitive to temperature than methanogenesis. Apparent activation energies for CH_4 oxidation range from 20 to 80 kJ mol^{-1} compared to the range 50–450 kJ mol^{-1} for CH_4 production [*Dunfield et al.*, 1993]; Q_{10} values average 1.9 and 4.1, respectively [*Segers*, 1998]. A lower activation energy for CH_4 oxidation versus production would produce temperature-induced changes in net emissions greater than those predicted from the activation energy of CH_4 production alone [*Dunfield et al.*, 1993]. These two mechanisms could occur simultaneously in different parts of an ecosystem (e.g., soil surface versus rhizosphere), and each would cause the proportion of CH_4 production consumed by oxidation to decline with increasing temperature as observed in a temper-

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ate marsh [*Lombardi et al.*, 1997] and a boreal fen [*Popp et al.*, 2000].

[5] The design of our study was intended to minimize the influence of seasonal fluctuations in water-table depth on CH_4 oxidation. Although few in situ measurements of CH_4 oxidation in relation to water-table depth have been reported [*King*, 1996], there is abundant indirect evidence of a relationship between these variables [*Roulet and Moore*, 1995; *Sundh et al.*, 1995; *Kettunen et al.*, 1999]. Tidal freshwater wetlands provide a unique environment for separating the effects of water-table depth and temperature. Unlike most temperate and tropical wetland ecosystems, seasonal variations in water-table depth are minor and regular flooding ensures that the maximum depth of the aerobic zone is fairly stable.

[6] Our objectives were to: (1) quantify the size of the CH_4 oxidation sink in two temperate swamp forests, (2) quantify seasonal changes in CH_4 oxidation as a proportion of gross production (i.e., CH_4 oxidation efficiency), and (3) compare the temperature responses of CH_4 production and oxidation as an explanation for changes in CH_4 oxidation efficiency.

2. Methods

2.1. Study Sites

[7] The White Oak is a low-gradient, blackwater, coastal plain river located in southeastern North Carolina [*Megonigal*, 1996]. Atlantic tides propagate upriver about 30 km causing floodplain soils to be alternately flooded and exposed twice daily, except during some neap tides. The upper reaches of the tidal zone are fresh water (salinity <0.5‰) and floodplain soils are dominated by methanogenic respiration [*Kelley et al.*, 1990]. We established two sites in the tidal fresh-water zone of this river. The Upper site was farthest from the ocean and 6 km upstream of Haywood Landing; the Lower site was 2 km downstream of the Upper site and 0.4 km upstream of Goldhaber's Island, the site of previous studies on CH_4 dynamics [*Kelley et al.*, 1990, 1995]. Soils are mapped as Dysic, thermic Typic Medisaprists at the Lower site [*Barnhill*, 1992] and Euic, thermic Typic Medisaprists at the Upper site [*Barnhill*, 1981]. They are characterized by 1–2 m thick accumulations of muck containing 20% organic carbon.

[8] Freshwater tidal wetlands on the White Oak River are primarily forests mixed with patches of marsh. *Fraxinus caroliniana* dominates both sites, but *Nyssa sylvatica* var. *biflora* is also important at the Lower site where it contributes 52% of the wood production [*Megonigal*, 1996]. Both forests support scattered *Taxodium distichum* trees that are several meters taller than the forest canopy. The herbaceous layer at the Lower site is dominated by highly flood-tolerant species such as *Orontium aquaticum* and *Peltandra virginica*, while the Upper site is dominated by relatively less flood-tolerant species of *Sorus* and *Aster*. Basal area, leaf litterfall, and herbaceous production on the two sites are similar, but wood production is 116% greater at the Upper site [*Megonigal*, 1996]. In total, these features suggest that the Upper site is drier than the lower site [*Christensen*, 1988; *Megonigal et al.*, 1997].

[9] On each site, we established a single 100-m transect parallel to the river channel and 12 m inland. Twenty plots, separated by >1 m distance, were located in topographic depressions. A boardwalk and 2 m-long elevated ramps approaching each plot minimized soil disturbance during sampling.

2.2. Methane Emissions

[10] Methane emissions were measured with static chambers made from polyethylene containers. The containers were modified by riveting a 33 × 47-cm frame of 2.5-cm aluminum angle stock to the mouth. Between the container and frame was a layer of 0.5-cm thick closed-cell neoprene foam gasket and silicone sealant. A second strip of foam outside the frame provided a temporary seal to permanently installed bases that extended 5 cm into the soil. A 2 kg-weight ensured good contact between the chamber and base. A set of 64-l chambers fit with 0.5-l s^{-1} brushless fans (one per chamber) was used during the growing season to accommodate 75-cm high plants. Sets of 38 or 27-l chambers without fans were used in the winter. The duration of the flux measurements ranged from 1 hour in summer to 10 hours in winter, yet headspace [CH_4] rarely rose above 10 $\mu l\ l^{-1}$. The headspace was sampled five times per flux measurement through a rubber septum with plastic syringes. Rubber bands between the syringe barrel and plunger maintained positive pressure on the sample in case of a leak. All fluxes were measured during neap tides when the soil surface was exposed (i.e., at low tide).

[11] In situ CH_4 oxidation rates were measured on eight dates over a 13-month period using the CH_3F-block technique [*Oremland and Culbertson*, 1992]. Each estimate began with a pre-treatment flux measurement made simultaneously on all the plots in a transect. Next, the soils and plants in 10 of the 20 chambers were exposed to 1.5% CH_3F for 12 hours. The chambers were usually vented for about 1 hour before measuring post-treatment emissions. However, the chambers were not vented twice during the winter when low CH_4 emission rates demanded long incubation periods. The other 10 plots were treated the same but received ambient air. A permanent, random assignment of the treatments was made at the beginning of the study, so that control plots were never exposed to CH_3F.

[12] Net CH_4 emissions from the control plots were measured monthly. When this coincided with the CH_4 oxidation experiments, net emission rates were calculated as the mean of pre- and post-treatment measurements from control plots. On the final sampling date, CH_4 emissions on the control plots were measured before and after removing the vegetation. Plants were cut 2 cm below the soil surface and the exposed stem was buried by gently covering it with muck.

[13] In field trials, CH_3F increased CH_4 fluxes after 6 hours of treatment. Post-treatment samples of plant stems contained 0.2 ± 0.1% CH_3F (mean ± SD) and soils contained 0.1 ± 0.1% CH_3F at 3 cm below the surface. In laboratory incubations (details are given subsequently), 0.15% CH_3F completely inhibited potential CH_4 oxidation, but CH_4 production was not inhibited at levels up to 1.5% CH_3F. These levels effectively inhibit CH_4 oxidation in other systems [*Oremland and Culbertson*, 1992; *Epp and Chanton*, 1993]. Although CH_3F often inhibits methanogenesis in laboratory incubations, it does not necessarily inhibit in situ CH_4 emissions, which depend more on pore

water [CH_4] than instantaneous CH_4 production [*King*, 1996; *Lombardi et al*., 1997]. Methylfluoride does not affect photosynthesis or stomatal conductance at the levels we used [*Epp and Chanton*, 1993; *King*, 1996], and its effects on methanotrophy are quickly reversible [*Epp and Chanton*, 1993; *van der Nat and Middelburg*, 1998].

[14] Dissolved CH_4 in pore water was determined on samples drawn from polyvinylchloride wells (2.5-cm diameter × 20-cm deep) at seven locations on each site and on three samples drawn directly from the river. At low tide, the wells were emptied and allowed to refill twice before immediately taking a 5-ml sample by syringe. Dissolved CH_4 was stripped into a 5-ml headspace of ambient air by vigorous shaking for 2 min.

[15] Methane and CH_3F were analyzed on a Varian 3700 gas chromatograph with a flame ionization detector, a Porapak Q 80/100 mesh column at 50°C, and a He carrier at 30 ml min^{-1}. Because of the remote field location, gas samples were stored for 3 to 5 days before they were analyzed. Recovery of CH_4 standards stored in syringes during field measurements was 94 ± 4% (mean ± SD).

2.3. Environmental Measurements

[16] Water-table depth, air temperature, and soil temperature at 10 and 50 cm were recorded at 30-min intervals on a Campbell data logger. Water-table depth was measured in one 60-cm well per transect with differential pressure transducers referenced to the atmosphere [*Keeland et al.*, 1997]. Air and soil temperatures were measured with thermocouples.

[17] The depth at which the soil profile became reducing was determined on two occasions with steel rods placed adjacent to the plots for 8 weeks [*Bridgham et al.*, 1991]. Redox potential profiles were measured monthly in a single plot on each transect as described by *Faulkner et al.* [1989].

2.4. Potential CH_4 Production and Oxidation

[18] Soil cores were collected in late October 1995 from 10 locations on each transect. Cores were extracted in 7.6-cm (i.d.) by 30-cm deep PVC sleeves with a piston corer. Compaction was generally <1 cm at the Lower site and <2 cm at the Upper site. The cores were flooded with river water and capped for transportation to Duke University.

[19] Soils were processed in a glove box with an atmosphere of 95% N_2 and 5% H_2. The chamber atmosphere was circulated through columns of Drierite and molecular-sieve to remove humidity, and activated charcoal to remove organic toxins that may have been introduced with the purge gas. Molecular oxygen concentrations were always <1% and normally <0.2%.

[20] To determine down core patterns of potential CH_4 production, cores were cut into four depth intervals (0–5, 5–10, 10–20, and 20–30 cm), then randomly paired to give five composite samples per depth per site. We added 40 g of wet soil and 40 ml of degassed, deionized water to 250-ml canning jars, then removed most of the fine roots from the resulting slurry. The jars were sealed while inside the chamber using canning lids fit with a septum and flushed with 1 l of high-purity N_2 to remove H_2. Jars for CH_4 oxidation potentials were prepared similarly outside the chamber.

[21] Aerobic jars had an initial headspace [CH_4] of 1200 μl l^{-1} and a final [CH_4] of 500 μl l^{-1}, which was above the level at which CH_4 oxidation became concentration-dependent in these soils. The oxidation study was completed 4 days after the soil was collected. Potential rates of CH_4 production were measured in separate anaerobic jars over a 3-day period beginning 8 days after collection. Before beginning the flux measurements, the headspace and soil solution were purged with 1 l of high-purity N_2. Jars in both experiments were continuously agitated on a linear shaker bath at 22°C. The headspace was sampled at least five times for each flux determination.

[22] In November 1995, a second collection of 10 soil samples per site (surface 10 cm only) were returned to the glove box, sieved through a 2.4-mm screen, and combined into a single composite sample for each site. Our intent was to minimize variation between sub-samples in order to isolate the influence of temperature on microbial activity. The jars were prepared as previously described except that aerobic jars had an initial headspace [CH_4] of 2000 μl l^{-1}. Two replicate jars per site were randomly assigned to water baths at the following nominal temperatures: 0°, 6°, 12°, 18°, 24°, 30°, and 36°C. Aerobic jars were incubated on linear shakers, but not anaerobic jars because CH_4 degassing was not diffusion-limited in comparisons of static and shaken-incubations. All incubations were completed within 16 days of soil collection.

[23] The influence of [CH_3F] on CH_4 production and oxidation was assessed in the laboratory using methods similar to those described for the temperature response studies. Jars were amended with CH_3F at headspace concentrations of 0, 0.0015, 0.015, 0.15, and 1.5%. Methane production and consumption were measured in the presence of CH_3F.

2.5. Methane Oxidation Calculations and Statistics

[24] Methane fluxes were calculated using regression analysis [*SAS Institute*, 1987] applied to the linear portion of CH_4 concentration versus time. Most fluxes were calculated from 5-points, but never from fewer than 3 points. Net CH_4 emissions were calculated using regression slopes with r^2 values >0.90 (80% of measurements). Slopes with $r^2 <$ 0.90 and y-intercepts $\leq$ 4 μl l^{-1} were assigned a value of one-half the detection limit, while slopes with higher intercepts and $r^2 < 0.90$ were deleted on the assumption that chamber placement had caused ebullition. To increase the sample size in the CH_4 oxidation experiments, we used a less conservative lower-limit for r^2 of 0.60 ($0.60 \leq r^2 < 0.90$ in 8% of observations). The detection limit ranged from 0.4 to 0.02 mg m^{-2} d^{-1} depending on chamber size and measurement interval.

[25] Significant changes in pre-treatment versus post-treatment CH_4 emissions were assessed with paired t-tests [*SAS Institute*, 1987]. The tests were one-sided because CH_3F was expected to either increase CH_4 emissions or have no effect. We accounted for the increased probability of a significant difference due to repeated t-tests with Bonferroni's correction [*Day and Quinn*, 1989]. For a one-tailed t-test the corrected α-values for a 0.05 significance level were 0.0063 for the Lower site and 0.0071 for the Upper site. A significant increase in flux from both the treated and control plots would suggest a cause other than CH_3F, such as a temperature increase or soil disturbance. Two-sided paired t-tests were used to analyze the plant removal experiment.

[26] Methane oxidation efficiency was calculated two ways. Plot-weighted oxidation used the pre-treatment and post-treatment fluxes on a per-plot basis

$$\text{Plot-wise methane oxidation} = 1 - \left(\frac{\text{pre} - \text{treatment flux}}{\text{post} - \text{treatment flux}}\right) \quad (1)$$

[27] Because CH_4 oxidation was calculated for each plot separately, both low-flux and high-flux plots were weighted the same. In this case, CH_4 oxidation efficiency was calculated as the average of equation (1) across all treated plots, regardless of the direction of the change. Plot-wise oxidation had either a normal or $\log_e$-normal distribution as determined by the Shapiro-Wilk Statistic [*SAS Institute*, 1987].

[28] Oxidation was also calculated using values of CH_4 emissions averaged across the treated plots

$$\text{Flux-Weighted Methane Oxidation} = 1 - \left(\frac{\overline{X}\text{pre} - \text{treatment flux}}{\overline{X}\text{post} - \text{treatment flux}}\right) \quad (2)$$

[29] In this case, CH_4 oxidation was weighted in favor of the plots with the largest absolute fluxes, yielding the best estimate of site-wide methane oxidation efficiency. The two equations were compared using a two-sided paired *t*-test of flux-weighted oxidation versus mean plot-wise oxidation.

[30] Comparisons of potential CH_4 production and oxidation across depths were made with a one-way analysis of variance [*SAS Institute*, 1987] and the Least-Significant-Difference test at $\alpha = 0.05$. Values were $\log_e$-normalized when necessary. Proc Reg in SAS was used to fit flux data to linear and Arhennius temperature models.

3. Results

3.1. Hydrology and Dissolved Methane

[31] The Lower site was typically inundated twice per day. The soil surface was exposed to the atmosphere for a few hours each day during spring tides and for periods of 1 or 2 days during neap tides, totaling about 40% of the year (Figure 1). The Upper site was inundated twice per day during spring tides, but had longer periods of subaerial exposure totaling 60% of the year. Water-table depth variation on these tidally flooded sites did not have a seasonal pattern (Figure 1). In contrast, soil temperature at 10 cm varied seasonally from 3° to 32°C with a maxima in July and minima in January [*Megonigal*, 1996].

[32] Redox potential profiles in June indicated the soils were Fe-reducing below 10 cm (Figure 2). In January, the measurement interval was shortened, and the data suggested that the oxidizing/reducing interface was no deeper than 5 cm on the Upper site and perhaps at 10 cm at the Lower site. However, the depth of rust on steel rods was not significantly different between the sites. These data and detailed seasonal [CH_4] profiles from a nearby site [*Kelley et al.*, 1995] suggest that aerobic CH_4 oxidation begins at a depth of 5–10 cm.

[33] Dissolved CH_4 in shallow groundwater (10–20 cm deep) averaged 3 and 23 μM on the Lower and Upper sites, respectively. Concentrations varied seasonally from <1 to 224 μM.

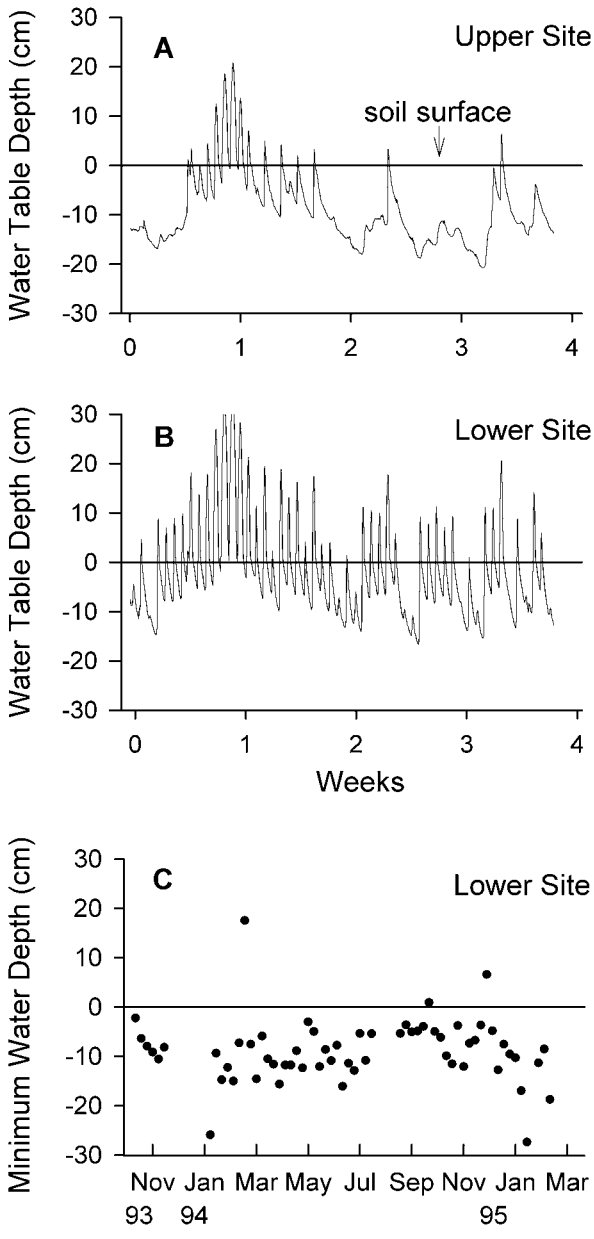

Figure 1. Water-table depth at two sites (a, b) on the White Oak River over a spring-neap tide cycle from 20 March to 16 April, 1994. (c) 7-day averages of minimum water-table depth on the Lower site over an annual cycle.

3.2. Net Methane Emissions

[34] There was considerable temporal and spatial variation in net CH_4 emissions. The highest emissions occurred between June and October, reaching a peak mean flux of 17 mg CH_4 m^{-2} d^{-1} on the Upper site in July (Figure 3). The distribution of fluxes on the Upper site was strongly skewed by a single control plot with consistently high emissions (maximum >200 mg CH_4 m^{-2} d^{-1}) that contributed >50% of the annual emissions from all control plots. Thus the median is a better estimate of central tendency for net emissions (Figure 3). Unless stated otherwise, this plot was eliminated

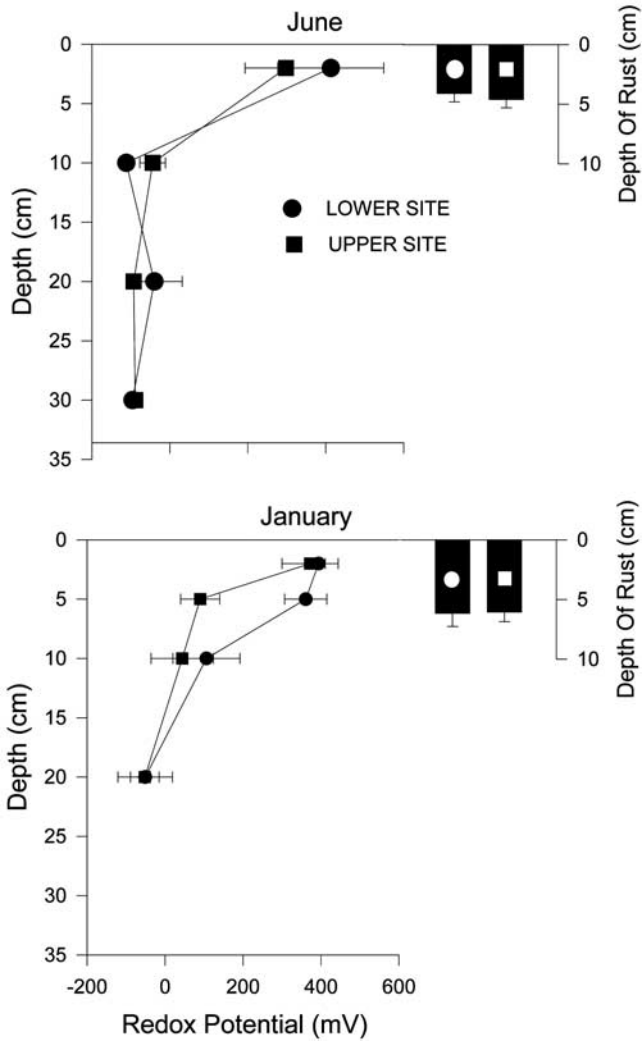

Figure 2. Estimates of O_2 penetration depth during summer and winter for two study sites. Redox potential is an instantaneous estimate of O_2 penetration, while steel-rod oxidation depths are an integrated estimate (30-day periods). Data are means ± 1 SE.

from the calculation of methane oxidation rates. Net emissions from the Lower site were generally greater than the Upper site. Net methane emissions on the control plots was measured with and without plants on one occasion at the end of the study. There was no significant effect of plants on CH_4 emissions.

3.3. Methane Oxidation

[35] Methane emissions increased significantly following application of CH_3F in 14 of 15 trials ($P < 0.007$; Appendix A). The exception occurred on a date when soil temperature was 7.5°C; there was no response to CH_3F at the Lower site and a significant increase in control-plot emissions at the Upper site. Several control plots were net sinks of atmospheric CH_4 in January, reaching subambient headspace concentrations (data not shown).

[36] On the Lower site, gross CH_4 emissions (i.e., during CH_3F inhibition) increased from 5.4 ± 6.2 mg CH_4 m^{-2} d^{-1} during the period from October to May, to 18.5 ± 31.3 mg CH_4 m^{-2} d^{-1} (mean ± SD, $n = 40$) during the summer (see also Appendix A). The seasonal variation in gross emissions on the Upper site was similar (5.6 ± 16.6 and 22.1 ± 54.0 mg CH_4 m^{-2} d^{-1}, respectively, $n = 48$). There were no significant differences between the sites for either period of the year.

[37] Methylfluoride treatment increased methane emissions by 52 ± 29% on the Lower site and 79 ± 24% on the Upper site (mean ± SD, $n = 70$, calculated plot-wise), a significant difference of 27% ($P < 0.0001$). When calculated on a flux-weighted basis, oxidation consumed 51 ± 15 and 76 ± 16% of gross CH_4 emissions at the two sites, respectively ($n = 6–7$). There was no significant difference in CH_4 oxidation efficiency calculated on a plot-wise or flux-weighted basis ($P = 0.12$). Because ebullition, hydrologic export, and emissions from trees were not measured, these figures may overestimate the proportion of total methane production consumed by oxidation. There was no clear relationship between ambient soil temperature and methane oxidation efficiency (Figure 4).

[38] Combining data from the two sites, CH_4 oxidation increased linearly as a function of gross CH_4 emissions ($r^2 = 0.96$, Figure 5). The regression intercept was not significantly different from zero. Based on the slope of this line, 73% of gross emissions were oxidized across a broad range of CH_4 production rates, soil temperature and plant cover.

3.4. Potential CH_4 Production and Oxidation

[39] Potential CH_4 oxidation rates varied significantly across depths ($P = 0.001$), but not across sites (Table 1). Peak rates occurred at the soil surface. In comparison, CH_4 production potential was lower and more variable (Table 1). Potential production peaked at 5–10 cm on the Lower site and at 10–20 cm at the Upper site, but there were no significant differences across depths or sites.

[40] Potential CH_4 production increased monotonically with temperature from near 0° to 36°C, but potential CH_4 oxidation rates declined between 30° and 36°C [*Megonigal*, 1996]. All the CH_4 production jars incubated in the 18°C water bath ($n = 4$) deviated markedly from the temperature

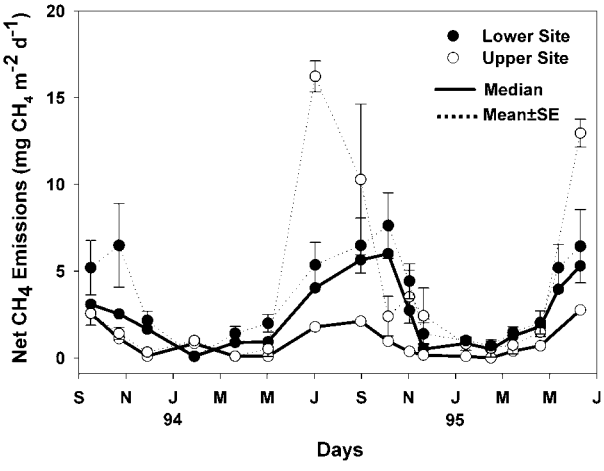

Figure 3. Net CH_4 emissions from two sites on the White Oak River, NC. Each point represents 7–20 observations in the absence of CH_3F. Data are means ± 1 SE.

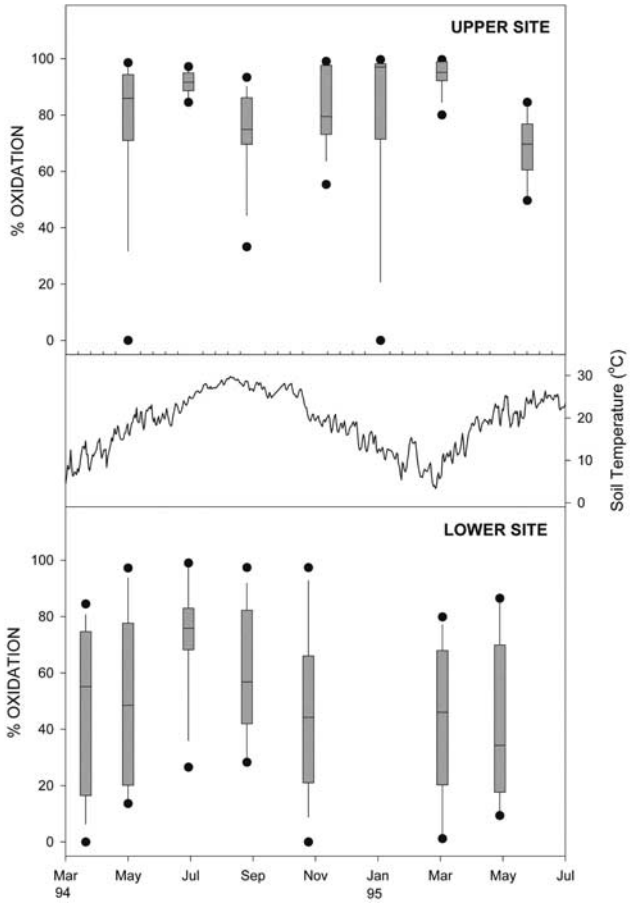

Figure 4. Quantile box plots of percent CH_4 oxidation in 14 experiments with a significant increase in CH_4 emissions following treatment with CH_3F. Horizontal lines inside each box are the median, box boundaries are the 25th and 75th percentiles, and points are minimum and maximum values.

relationships fit to the remaining data (Figure 6), suggesting there was an unidentified problem with the water bath. Thus the 18° and 36°C samples were not used for regression modeling.

[41] The temperature-response curves fit both a linear and an Arhennius model in all cases ($P < 0.03$, adjusted-$r^2 > 0.67$). Potential CH_4 production was explained better by an Arhennius model (adjusted-$r^2 \geq 0.97$) than a linear model (adjusted-$r^2 \leq 0.77$) on both sites. For CH_4 oxidation, the two models produced nearly identical fits at the Upper site (adjusted-$r^2 = 0.94$), but the linear model fit best for the Lower site (adjusted-$r^2 = 0.97$ versus 0.87).

[42] Temperature-response curves for CH_4 production and oxidation were remarkably similar within a given site. At the Lower site, apparent activation energy (E_a) calculated from the Arhennius plots (Figure 6) was 73.9 kJ mol^{-1} for production and 77.0 kJ mol^{-1} for oxidation; values for the Upper site were 59.7 and 60.0 kJ mol^{-1}, respectively. To facilitate comparisons with other studies, we used the Arhennius equations to calculate apparent Q_{10} values over the range 10°–20°C. At the Lower site, Q_{10} was 2.4 for both oxidation and production; at the Upper site Q_{10} was 2.9 for oxidation and 3.1 for production. Applying a linear model to the CH_4 oxidation data produced Q_{10} values that were lower than those for production, but the difference was <0.8 units (linear model oxidation $Q_{10} = 1.9$ and 2.4 on the Lower and Upper sites, respectively).

[43] Temperature response functions were also fit to in situ CH_4 emissions data. The Arhennius model consistently explained field emissions better than the linear model, but the relationships were significant only at the Lower site ($P \leq 0.004$, $n = 7$). The E_a for net emissions at the Lower site was 85 kJ mol^{-1} ($Q_{10} = 3.4$), a value similar to potential CH_4 oxidation and production as determined in laboratory soil incubations. The E_a for gross emissions and CH_4 oxidation were higher than laboratory incubations would suggest (120 and 141 kJ mol^{-1}, respectively; $Q_{10} = 5.6$ and 7.7). Although the fit of the Arhennius model on the Upper site was not significant, there was a trend ($P < 0.10$) for $E_a \leq 80$ ($Q_{10} \leq 3$), which is similar to those produced by the laboratory soil incubations.

4. Discussion

[44] Methanotrophic bacteria significantly reduced diffusive CH_4 emissions from two temperate wetland forests during all the seasons of the year. Emissions were reduced by 52% on the Lower site and 79% on the Upper site. These figures are lower than estimates made in the same general area by a different method (86–96%; *Kelley et al.*, [1995]), and higher than estimates for two bottomland hardwood forests in Florida (46%; *Happell and Chanton*, [1993]). Our estimates fall within the range of previous estimates from forested wetland soils (Table 2). Although few direct in situ estimates of CH_4 oxidation exist, it seems that CH_4 oxidation efficiency is higher in wetland forests than marshes. Because herbaceous plants can tolerate wet sites better than woody

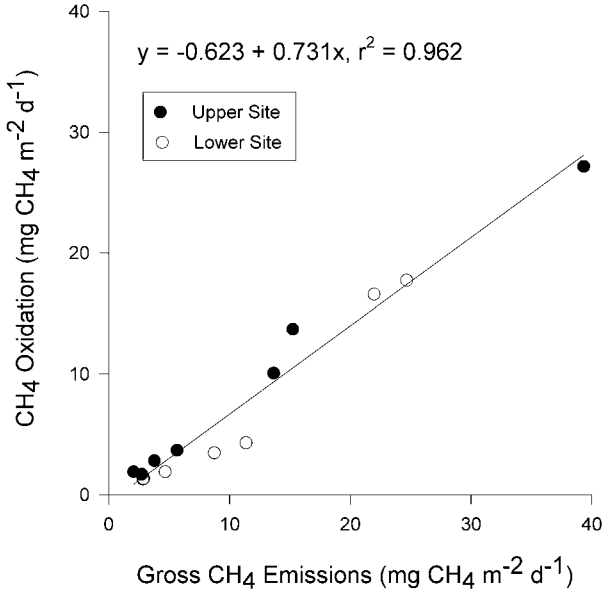

Figure 5. Relationship between rates of gross CH_4 emission (post-CH_3F treatment) and CH_4 oxidation using data from experiments that yielded a significant increase in emissions. Each point is the mean of 8–10 replicates.

Table 1. Potential Production and Oxidation of CH_4 in Soils From Two Tidal Freshwater Swamps on the White Oak River, North Carolina[a]

		Potential CH_4 Production, nmol g^{-1} d^{-1}			Relative CH_4	Potential CH_4 Oxidation, μmol g^{-1} d^{-1}			Relative CH_4
Site	Depth	Mean	SE	Median	Production	Mean	SE	Median	Oxidation
Lower	5	43.14[b]	23.50	8.74	1.0	3.41[b]	0.45	3.28	1.0
	10	33.20[b]	13.95	26.95	12.3	2.75[b]	0.07	2.74	0.9
	20	12.74[b]	3.50	11.92	1.9	1.63[c]	0.35	2.00	0.5
	30	3.85[b]	0.92	3.69	1.0	1.01[c]	0.35	1.09	0.3
Upper	5	13.61[b]	4.71	8.75	1.0	3.45[b]	0.26	3.66	1.0
	10	4.19[b]	1.21	3.64	0.5	2.83[c]	0.18	2.68	0.8
	20	37.81[b]	28.03	14.65	2.7	1.85[d]	0.18	1.90	0.5
	30	18.51[b]	10.72	16.28	1.5	0.72[e]	0.20	0.62	0.2

[a] Relative CH_4 production and oxidation were normalized to rates in the top 5 cm section of individual core-pairs; values are the mean of five ratios. Means with different superscripts are significantly different ($P = 0.05$) in comparisons across depths within a site.

plants, this difference may reflect higher O_2 availability on sites with a relatively deep aerobic-anaerobic interface.

[45] Net CH_4 emissions, understory plant cover, and soil temperature varied substantially over the study period, yet percent CH_4 oxidation was relatively constant (Figure 5). Two previous studies interpreted a warm-season decline in percent CH_4 oxidation as evidence suggesting that the process was O_2-limited [*King*, 1996; *Lombardi et al.*, 1997], although other explanations were also offered. The linear relationship between CH_4 oxidation and gross CH_4 emissions in our study suggests that oxidation rates were CH_4-limited, as reported for rice microcosms [*Gilbert and Frenzel*, 1995, 1998; *Bosse and Frenzel*, 1998].

[46] Provided methanotrophy was CH_4-limited rather than O_2-limited, percent CH_4 oxidation should have varied seasonally if methanotrophs and methanogens exhibited large differences in their temperature response characteristics. In the present study, apparent Q_{10} values for these processes determined in laboratory incubations were similar within a given site, suggesting that CH_4 production and oxidation changed with temperature at approximately the same rate (Figure 6). Thus the temperature-response curves for methane production and oxidation are consistent with our observation of a season-independent rate of CH_4 oxidation, and the view that oxidation was CH_4-limited.

[47] It is useful to consider differences between this study and previous studies that reported O_2-limited methanotrophy. *Lombardi et al.* [1997] quantified CH_4 oxidation in the rhizosphere while we quantified the process in both the rhizosphere and soil surface simultaneously. It is possible that those systems were CH_4-limited on an ecosystem (i.e., ground-area) basis even though the rhizosphere was O_2-limited. This was not the case for sites studied by *King* [1996] and *Popp et al.* [2000] because they determined that 70–90% of CH_4 emissions passed through plants. Similarly, rhizosphere oxidation at our sites could have been O_2-limited even though the ecosystem was CH_4-limited overall. This would have required a large fraction of diffusive emissions to pass across a CH_4-limited soil surface versus an O_2-limited rhizosphere. In a single trial at the end of our study, there was no significant difference in CH_4 emissions in the presence or absence of plants. Although we do not consider one trial definitive, when considered in the context of sparse herbaceous plant cover and a 5–10-cm deep CH_4-oxidizing zone, it is possible that plants are not the dominant pathway for CH_4 ventilation at our sites.

[48] Methanotrophy may be CH_4-limited at these sites because of low CH_4 production, high CH_4 oxidation, or a combination of these factors. Potential CH_4 production rates were lower than 80% of the values reported in the literature [*Segers*, 1998], while potential CH_4 oxidation was lower than 60% of the values. Median emissions at our sites peaked at about 6 mg CH_4 m^{-2} d^{-1} compared to a median of 72 mg CH_4 m^{-2} d^{-1} for swamps in the literature [*Le Mer and Roger*, 2001]. We did not determine K_m values for CH_4 oxidation, but [CH_4] drops rapidly within 5–10 cm of the soil surface to levels that may limit oxidation in the uppermost portion of the profile even during the summer [*Kelley et al.*, 1995].

[49] There are reasons to suggest that these soils have a higher capacity to oxidize CH_4 than many other sites that have been studied. Despite year-round tidal flooding, the soil surface is exposed 40% of the year at the Lower site and 60% of the year at the Upper site. This difference of 20% appears to be ecologically important because the Upper site had a 27% higher CH_4 oxidation capacity ($P < 0.0001$, Appendix A), a deeper peak depth of CH_4 production (Table 1), and fewer highly flood-tolerant plant species in the understory than the Lower site. The fact that the depth

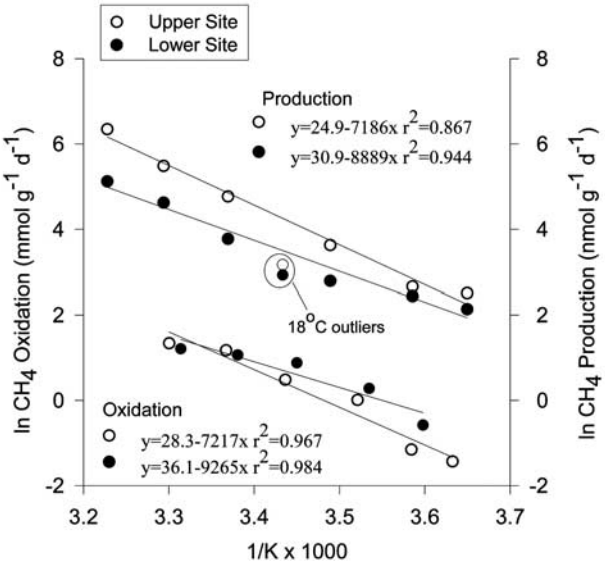

Figure 6. Arhennius plots of potential CH_4 production and oxidation as a function of temperature for two sites on the White Oak River, NC.

Table 2. Field Estimates of the CH_4 Oxidation Efficiency of Wetland Soils

Environment	Method	Percent Oxidation[a]	Citation
Freshwater tidal swamp (Lower site)	CH_3F-block	52 ± 29	this study
Freshwater tidal swamp (Upper site)	CH_3F-block	79 ± 24	this study
Freshwater tidal swamp (UF-NB)	difference[b]	86 ± 21	*Kelley et al.* [1995]
Freshwater tidal swamp (UF-FB)	difference[b]	89 ± 16	*Kelley et al.* [1995]
Freshwater tidal swamp (GI-NB)	difference[b]	91 ± 7	*Kelley et al.* [1995]
Freshwater tidal swamp (GI-FB)	difference[b]	96 ± 6	*Kelley et al.* [1995]
Bottomland hardwood swamp	O_2/N_2, 2M picolinic acid[b]	46 ± 24	*Happell and Chanton* [1993]
Cypress-Tupelo Swamp, floodwater	bottle incubations	50	*Pulliam* [1993]
Freshwater *Typha latifolia* marsh	CH_3F-block	47 ± 17	*Epp and Chanton* [1993]
Freshwater marsh, peat surface	C_2H_2-block	43	*King* [1996]
Freshwater marsh, rhizosphere	C_2H_2-block	27 ± 6	*King* [1996]
Freshwater marsh, *Sagittaria lancifolia* rhizosphere	CH_3F-block	19 ± 8	*Lombardi et al.* [1997]
Freshwater marsh, *Pontederia cordata* rhizosphere	CH_3F-block	22 ± 22	*Lombardi et al.* [1997]
Freshwater marsh, *Typha latifolia* rhizosphere	CH_3F-block	55 ± 18	*Lombardi et al.* [1997]
Rice rhizosphere	CH_3F-block	0	*Denier van der Gon and Neue* [1996]
Temperate *Sphagnum* bog, July to Aug.	soil CH_4 profiles	89	*Fechner and Hemond* [1992]
Temperate *Sphagnum* bog, Oct. to Nov.	soil CH_4 profiles	24	*Fechner and Hemond* [1992]
Carex-dominated fen	isotope mass balance	20 ± 11	*Popp and Chanton* [1999]
Carex-dominated fen	CH_3F-block	15 ± 15	*Popp et al.* [2000]
Carex-dominated fen	difference[b]	78 ± 12	*Popp et al.* [2000]

[a] Errors are standard deviations.
[b] Calculated as the difference between potential CH_4 production and net CH_4 emissions.

distribution of potential CH_4 oxidation rates was virtually the same on the two sites is expected because transient differences in water-table depth influence potential CH_4 production more strongly than oxidation [*Roulet et al.*, 1993]. Previously studied sites were normally inundated or ponded for most of the year [*King*, 1996; *Lombardi et al.*, 1997; *Popp et al.*, 2000].

[50] Sparse understory plant cover in our forested sites may raise CH_4 oxidation efficiency by forcing CH_4 to diffuse through a relatively thick oxidizing zone, rather than through plants, before escaping to the atmosphere. Understory cover averaged 39% at the Lower site and 35% at the Upper site, whereas marshes can be expected to have 100% cover. A related consideration is that some understory species in forested wetlands may not efficiently transport gases [*Dacey and Klug*, 1979; *Shannon et al.*, 1996], a property that is species specific [*Calhoun and King*, 1997]. Most understory species at the Upper site were not characteristic of extremely wet habitats. Species such as *P. virginica* that are known to efficiently conduct gases [*Frye et al.*, 1994; *Chanton et al.*, 1992] occurred in just 30% of plots at the Upper site compared to 90% of plots at the Lower site.

[51] Net consumption occurred on 3 of 10 plots at the Lower site and 4 of 10 plots at the Upper site ($r^2 > 0.95$) on a day when the mean soil temperature was 3°C at 10 cm, the coldest sampling day in the study. In each case, headspace [CH_4] began at ambient levels and fell to subambient levels. Other flux estimates between the months of November and May also produced negative fluxes, but the initial and final CH_4 concentrations in the headspace were slightly above ambient (>1.9 $\mu l\,l^{-1}$), and the possibility cannot be dismissed that the chambers had small leaks or were returning to a pre-disturbance equilibrium [*Conrad*, 1994]. Rates of net CH_4 oxidation were low (−2.3 to −0.9 mg CH_4 m^{-2} d^{-1}), as would be expected in a soil with high moisture and low temperatures. Wetlands have been observed to switch from net sources to net sinks of atmospheric CH_4, but always in response to a deepening of the water table [*Roulet et al.*, 1993; *Happell and Chanton*, 1993; *Shannon and White*, 1994; *Pulliam*, 1993; *Harriss et al.*, 1982]. These sites apparently switched to net CH_4 sinks in response to changes in temperature.

5. Implications and Conclusions

[52] Natural and agricultural wetlands contribute 40% of CH_4 emissions to the atmosphere, yet this amount represents just 30–60% of the CH_4 they produce because of microbial CH_4 oxidation. Our results suggest that future soil warming will not change CH_4 oxidation efficiency on sites where the temperature-response characteristics of methanogens and methanotrophs are similar, and oxidation is CH_4-limited. It remains to be determined whether these characteristics are typical of certain classes of wetland ecosystems such as temperate and tropical swamps.

[53] We propose that CH_4 oxidation efficiency is generally higher in wetland forests than marshes because forests occupy drier positions on the landscape, and CH_4 limitation develops in response to a relatively deep aerobic zone. It follows that wetland forests are more likely than marshes to be CH_4-limited. About 60% of global wetlands are forested bogs or forested swamps [*Matthews and Fung*, 1987].

[54] Methanotrophy at these sites may be CH_4-limited in part because the soils are weak producers of CH_4. However, our data suggest that CH_4 limitation could also occur on sites that support high rates of CH_4 production. Estimates of flux-weighted and plot-wise CH_4 oxidation efficiency were statistically similar because the plots with high rates of CH_4 emission also had high rates of oxidation. Additional in situ studies in forested wetlands are needed to establish the generality of our observations. Projecting the effects of rising temperature on methane cycling in wetland soils will also require models that account for temperature-dependent changes in gas diffusion rates, gas transport through plants, methanotroph population sizes, and O_2 competition from microbes or chemical oxidation.

Appendix A

Table A1. Paired *t*-Tests of In Situ Methane Emissions Before and After Exposure to Either Ambient Air (Control) or 1.5% CH_3F (Treated)[a]

Date	Treat	*n*	Pre-Treatment Flux, mg CH_4 m^{-2} d^{-1}	Post-Treatment Flux, mg CH_4 m^{-2} d^{-1}	*P*-value[b]	Flux-Weighted Oxidation, %	Plot-Wise Oxidation, %
			Lower Site				
March 3, 1994	Air	4	1.21 (1.33)	1.02 (1.39)	0.8202	...	ns
	CH_3F	10	1.53 (1.63)	2.89 (2.53)	0.0026	47.0	48.9 (30.8)
May 3, 1994	Air	10	1.48 (2.20)	3.19 (2.70)	0.0232	...	ns
	CH_3F	10	2.75 (2.68)	4.67 (3.11)	0.0006	41.1	50.0 (30.4)
June 30, 1994	Air	10	5.89 (5.99)	5.61 (5.17)	0.7664	...	ns
	CH_3F	10	5.36 (6.13)	21.96 (29.97)	0.0001	75.6	72.3 (22.1)
Aug. 27, 1994	Air	10	6.72 (7.58)	5.83 (5.21)	0.8945	...	ns
	CH_3F	10	6.92 (7.92)	24.66 (45.12)	0.0001	71.9	59.9 (24.7)
Oct. 29, 1994	Air	10	3.37 (3.51)	4.65 (4.62)	0.8256	...	ns
	CH_3F	10	5.26 (4.86)	8.74 (7.44)	0.0011	39.8	46.5 (9.8)
Jan. 10, 1995	Air	10	1.10 (1.44)	0.74 (0.66)	0.9800	...	ns
	CH_3F	10	1.08 (1.07)	1.06 (0.92)	0.5710	...	ns
March 9, 1995	Air	9	1.43 (1.38)	1.47 (2.02)	0.0305	...	ns
	CH_3F	10	1.52 (1.09)	2.83 (2.00)	0.0029	46.3	43.7 (28.0)
May 5, 1995	Air	10	3.79 (3.83)	2.91 (2.85)	0.3827	...	ns
	CH_3F	10	7.05 (7.55)	11.36 (9.62)	0.0010	37.9	43.4 (28.8)
			Upper Site				
May 1, 1994	Air	9	0.19 (0.19)	0.10 (0.00)	0.1878	...	ns
	CH_3F	10	0.94 (2.64)	3.78 (7.11)	0.0006	75.1	75.7 (29.1)
June 30, 1994	Air	9	6.43 (7.50)	1.64 (1.67)	0.0167	...	ns
	CH_3F	8	1.51 (2.01)	15.23 (11.95)	0.0001	90.1	91.5 (4.4)
Aug. 27, 1994	Air	9	3.17 (2.92)	5.70 (9.76)	0.2884	...	ns
	CH_3F	10	12.14 (25.49)	39.32 (81.84)	0.0001	69.1	73.3 (16.8)
Nov. 13, 1994	Air	9	0.36 (0.47)	0.75 (1.66)	0.4436	...	ns
	CH_3F	10	3.57 (9.52)	13.65 (35.33)	0.0001	73.8	82.6 (14.1)
Jan. 8, 1995	Air	8	0.18 (0.25)	0.50 (0.48)	0.0018	64.0	75.3 (28.1)
	CH_3F	10	1.01 (3.09)	2.72 (5.08)	0.0006	62.9	79.5 (23.7)
March 11, 1995	Air	9	2.63 (5.70)	3.23 (4.69)	0.0112	...	ns
	CH_3F	9	0.14 (0.26)	2.06 (2.79)	0.0001	93.2	94.1 (6.0)
June 2, 1995	Air	9	7.14 (8.00)	3.06 (2.18)	0.0186	...	ns
	CH_3F	9	1.96 (1.78)	5.65 (3.92)	0.0001	65.3	68.6 (11.6)

[a] Values are means (SD).

[b] Probability that the pre-treatment:post-treatment flux ratio was significantly different from zero in a paired *t*-test. Based on Bonferonni's Correction, *P*-values <0.0063 at the Lower Site and <0.0071 at the Upper Site are significantly different at $\alpha = 0.05$; ns = no significant difference.

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References

Barnhill, W. L., *Soil Survey of Jones County, North Carolina*, p. 98, USDA Soil Conservation Service, Washington, D.C., 1981.

Barnhill, W. L., *Soil Survey of Onslow County, North Carolina*, p. 139, USDA Soil Conservation Service, Washington, D.C., 1992.

Bosse, U., and P. Frenzel, Methane emissions from rice microcosms: The balance of production, accumulation and oxidation, *Biogeochemistry*, *41*, 199–214, 1998.

Bridgham, S. D., S. P. Faulkner, and C. J. Richardson, Steel rod oxidation as a hydrologic indicator in wetland soils, *Soil Sci. Soc. Am. J.*, *55*, 856–862, 1991.

Calhoun, A., and G. M. King, Regulation of root-associated methanotrophy by oxygen availability in the rhizosphere of two aquatic macrophytes, *Appl. Environ. Microbiol.*, *63*, 3051–3058, 1997.

Chanton, J. P., and J. W. H. Dacey, Effects of vegetation on methane flux, reservoirs, and carbon isotopic composition, in *Trace Gas Emissions by Plants*, edited by T. D. Sharkey, E. A. Holland, and H. A. Mooney, pp. 65–92, Academic, San Diego, Calif., 1991.

Chanton, J. P., G. J. Whiting, W. J. Showers, and P. M. Crill, Methane flux from *Peltandra virginica*: Stable isotope tracing and chamber effects, *Global Biogeochem. Cycles*, *6*, 15–31, 1992.

Christensen, N. L., Vegetation of the southeastern coastal plain, in *North American Terrestrial Vegetation*, edited by M. G. Barbour, and W. D. Billings, Cambridge Univ. Press, New York, 1988.

Conrad, R., Compensation concentration as critical variable for regulating the flux of trace gases between soil and atmosphere, *Biogeochemistry*, *27*, 155–170, 1994.

Dacey, J. W. H., and M. J. Klug, Methane emission from lake sediment through water lilies, *Science*, *203*, 1253–1255, 1979.

Day, R. W., and G. P. Quinn, Comparisons of treatments after an analysis of variance in ecology, *Ecol. Monogr.*, *59*, 433–463, 1989.

Denier van der Gon, H. A. C., and H.-U. Neue, Oxidation of methane in the rhizosphere of rice plants, *Biol. Fertil. Soils*, *22*, 359–366, 1996.

Dunfield, P., R. Knowles, R. Dumont, and T. R. Moore, Methane production and consumption in temperate and subarctic soils: Response to temperature and pH, *Soil Biol. Biochem.*, *25*, 321–326, 1993.

Epp, M. A., and J. P. Chanton, Rhizospheric methane oxidation determined via the methylfluoride inhibition technique, *J. Geophys. Res.*, *98*, 18,413–18,422, 1993.

Faulkner, S. P., W. H. Patrick Jr., and R. P. Gambrell, Field techniques for measuring wetland soil parameters, *Soil Sci. Soc. Am. J.*, *53*, 883–890, 1989.

Fechner, E. J., and H. F. Hemond, Methane transport and oxidation in the unsaturated zone of a *Sphagnum* peatland, *Global Biogeochem. Cycles*, *6*, 33–44, 1992.

Frye, J. P., A. L. Mills, and W. E. Odum, Methane flux in *Peltandra virginica* (Araceae) wetlands: Comparison of field data with a mathematical model, *Am. J. Bot.*, *81*, 407–413, 1994.

Gilbert, B., and P. Frenzel, Methanotrophic bacteria in the rhizosphere of rice microcosms and their effect on porewater methane concentration and methane emission, *Biol. Fertil. Soils*, *20*, 93–100, 1995.

Gilbert, B., and P. Frenzel, Rice roots and CH_4 oxidation: The activity of bacteria, their distribution and the microenvironment, *Soil Biol. Biochem.*, *30*, 1903–1916, 1998.

Happell, J. D., and J. P. Chanton, Carbon remineralization in a North Florida swamp forest: Effects of water level on the pathways and rates of soil organic matter decomposition, *Global Biogeochem. Cycles*, *7*, 475–490, 1993.

Harriss, R. C., D. I. Sebacher, and F. D. Day Jr., Methane flux in the Great Dismal Swamp, *Nature*, *297*, 673–674, 1982.

Keeland, B. D., J. F. Dowd, and W. S. Hardegree, Use of inexpensive pressure transducers for measuring water levels in wells, *Wetlands Ecol. Manag.*, *5*, 121–129, 1997.

Kelley, C. A., C. S. Martens, and J. P. Chanton, Variations in sedimentary carbon remineralization rates in the White Oak River estuary, North Carolina, *Limnol. Oceanogr.*, *35*, 372–383, 1990.

Kelley, C. A., C. S. Martens, and W. I. Ussler, Methane dynamics across a tidally flooded riverbank margin, *Limnol. Oceanogr.*, *40*, 1112–1129, 1995.

Kettunen, A., V. Kaitala, A. Lehtinen, A. Lohila, J. Alm, J. Silvola, and P. J. Martikainen, Methane production and oxidation potentials in relation to water table fluctuations in two boreal mires, *Soil Biol. Biochem.*, *31*, 1741–1749, 1999.

King, G. M., In situ analyses of methane oxidation associated with the roots and rhizomes of a bur reed, *Sparganium eurycarpum*, in a Maine wetland, *Appl. Environ. Microbiol.*, *62*, 4548–4555, 1996.

Le Mer, J., and P. Roger, Production, oxidation, emission and consumption of methane by soils: A review, *Eur. J. Soil Biol.*, *37*, 25–50, 2001.

Lombardi, J. E., M. A. Epp, and J. P. Chanton, Investigation of the methyl fluoride technique for determining rhizospheric methane oxidation, *Biogeochemistry*, *36*, 153–172, 1997.

Matthews, E., and I. Fung, Methane emission from natural wetlands: Global distribution, area, and environmental characteristics of sources, *Global Biogeochem. Cycles*, *1*, 61–86, 1987.

Megonigal, J. P., Methane production and oxidation in a future climate, Ph.D. dissertation, 151 pp., Duke Univ., Durham, NC, 1996.

Megonigal, J. P., W. H. Conner, S. Kroeger, and R. R. Sharitz, Aboveground production in southeastern floodplain forests: A test of the subsidy-stress hypothesis, *Ecology*, *78*, 370–384, 1997.

Oremland, R. S., and C. W. Culbertson, Importance of methane-oxidizing bacteria in the methane budget as revealed by the use of a specific inhibitor, *Nature*, *356*, 421–423, 1992.

Popp, T. J., and J. P. Chanton, Methane stable isotope distribution at a *Carex* dominated fen in north central Alberta, *Global Biogeochem. Cycles*, *13*, 1063–1077, 1999.

Popp, T. J., J. P. Chanton, G. J. Whiting, and N. Grant, Evaluation of methane oxidation in the rhizosphere of a Carex dominated fen in north central Alberta, Canada, *Biogeochemistry*, *51*, 259–281, 2000.

Pulliam, W. M., Carbon dioxide and methane exports from a southeastern floodplain swamp, *Ecol. Monogr.*, *63*, 29–53, 1993.

Reeburgh, W. S., S. C. Whalen, and M. J. Alperin, The role of methanotrophy in the global methane budget, in *Microbial Growth on C1 Compounds*, edited by J. C. Murrell and D. P. Kelly, pp. 1–14, Intercept, Andover, UK, 1993.

Roulet, N. T., and T. R. Moore, The effect of forestry drainage practices on the emissions of methane from northern peatlands, *Can. J. For. Res.*, *25*, 491–499, 1995.

Roulet, N. T., R. Ash, W. Quinton, and T. Moore, Methane flux from a drained northern peatlands: Effect of a persistent water table lowering on flux, *Global Biogeochem. Cycles*, *7*, 749–769, 1993.

SAS Institute, *SAS/STAT Guide for Personal Computers*, version 6 edition, SAS Institute, Cary, NC., 1987.

Schlesinger, W. H., *Biogeochemistry: An Analysis of Global Change*, Academic, San Diego, Calif., 1997.

Segers, R., Methane production and methane consumption: A review of processes underlying wetland methane fluxes, *Biogeochemistry*, *41*, 23–51, 1998.

Shannon, R. D., and J. R. White, A three-year study of controls on methane emissions from two Michigan peatlands, *Biogeochemistry*, *27*, 35–60, 1994.

Shannon, R. D., J. R. White, J. E. Lawson, and B. S. Gilmour, Methane efflux from emergent vegetation in peatlands, *J. Ecol.*, *84*, 239–246, 1996.

Sundh, I., C. Mikkelä, M. Nilsson, and B. H. Svensson, Potential aerobic methane oxiation in *Sphagnum*-dominated peatland—Controlling factors and relation to methane emission, *Soil Biol. Biochem.*, *27*, 829–837, 1995.

van der Nat, F. J. W. A., and J. J. Middelburg, Seasonal variation in methane oxidation by the rhizosphere of *Phragmites australis* and *Scirpus lacustris*, *Aquat. Bot.*, *61*, 95–110, 1998.

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