

Environmental Factors Controlling Methane Emissions from Peatlands in Northern Minnesota

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Controls on methane emission from peatlands in northern Minnesota were investigated by correlation to environmental variables and by field manipulation. From September 1988 through September 1990, methane flux measurements were made at weekly to monthly intervals at six sites in the Marcell Experimental Forest, northern Minnesota (two open bog sites, two forested bog sites, a poor fen, and a fen lagg). Flux was related to water table position and peat temperature with simple correlations at individual sites and multiple regression on all sites together. The effect of water table was also investigated experimentally in "bog corrals" (open-ended metal enclosures set in the peat) in which water table was artificially raised to the surface in the driest peatland.

→ Temperature largely controlled variation in flux within individual ecosystems at Marcell, but hydrology distinguished between-site variation. Water table position, peat temperature, and degree of peat humification explained 91% of the variance in log CH₄ flux, predicted annual methane emission from individual wetlands successfully, and predicted the change in flux due to the water table manipulation. Raising the water table in the bog corrals by an average of 6 cm in autumn 1989 and 10 cm in summer 1990 increased emission by 2.5x and 2.2x, respectively. Just as expanding the scale of investigation from a single habitat in a wetland to several wetlands necessitates incorporation of additional variables to explain flux (water table, peat characteristics), modeling flux from several wetland regions, if possible, will require the addition of climate parameters.

INTRODUCTION

An increase in the concentration of atmospheric methane, documented through ice core analyses as beginning about 400 years ago and recently (since 1970) accelerating to a rate of about 1% per year, has engendered a number of studies to better quantify global methane sources and sinks (summaries by *Aselmann and Crutzen* [1989]), *Mathews and Fung*, [1987], and *Cicerone and Oremland* [1988]. After carbon dioxide, methane is the most important radiatively active ("greenhouse") gas, adsorbing infrared radiation strongly in the 7.66 μm band. Methane accounts for an estimated 12% of total greenhouse warming [*Hansen et al.*, 1989] and since concentrations of the gas are increasing at twice the rate of carbon dioxide, its relative importance is expected to increase in the future. Natural wetlands are one of the major sources of atmospheric methane, contributing an estimated 15-20% to the global budget [*Aselmann and Crutzen*, 1989; *Mathews and Fung*, 1987].

Beyond identifying sources and sinks of methane, mitigation of emissions depends on understanding the factors that control its production and consumption. Temperature, water table position, and substrate nutrient quality have all been shown to affect methane flux from northern peatlands [e.g., *Roulet et al.*, 1992; *Crill et al.*,

1988; *Moore and Knowles*, 1989; *Harris and Sebacher*, 1981], but the relationships are far from straightforward. In different studies some or even all of these factors have had no effect on flux. Most studies assess the effects of the environmental correlates individually; to our knowledge, only one [*Roulet et al.*, 1992] has examined the interacting effects of both temperature and water table simultaneously. Since there are very few studies of flux over a full annual cycle [e.g. *Whalen and Reeburgh*, 1992], possible seasonal shifts in controls may be missed. Finally, inferring causality from statistical correlations between flux and environmental variables is hampered by a scarcity of experimental data on the effect of the variables individually.

In this study, methane emission was measured for 2 years from five different peatland ecosystems (six sites) in northern Minnesota and correlated with peat temperature, water table position, and degree of peat humification. The relationship established between flux and these factors was compared to results from a field manipulation experiment in which the water table was artificially raised in three experimental plots within the driest peatland. It was also used to test if annual methane emission from a site could be successfully predicted by knowing only peat temperature and water table position. The aim of this project was to distinguish the main factors that influence methane flux within single wetlands and among different wetlands in a region.

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METHODS

Study Sites

The study peatlands are located within Marcell Experimental Forest (USDA Forest Service) in northern Minnesota (47° 32' N, 93° 28'

W). The region is characterized by small upland watersheds forested with aspen (*Populus tremuloides*) and birch (*Betula papyrifera*) surrounding peaty lowlands [Verry, 1975; Boelter and Verry, 1977]. The lowlands contain both nutrient-poor bogs, which are fed by precipitation, and fens, which receive some mineral nutrients from groundwater or subsurface flow (and thus support a more diverse flora). Black spruce (*Picea mariana*) and tamarack (*Larix laricina*) are common in the forested bogs, as are sedges (*Carex spp.*) and alder (*Alnus rugosa*) in the fens. Both bogs and fens at Marcell have a ground cover of sphagnum, in particular *Sphagnum angustifolium*, *Sphagnum capillifolium*, and *Sphagnum magellanicum*.

Mean annual temperature at Marcell (1961-1990) is 3.1 °C and mean annual precipitation is 77 cm, of which about 30% is snow. Average summer (June to August) temperature for 1988, 1989, and 1990 was 2.7 °C, 0.9 °C, and 0.9 °C warmer, respectively, than the 1961 to 1990 summer average of 17.4 °C. Total precipitation for 1988, 1989, and 1990 was 18% above average, average, and 23% below average, respectively. The summers of 1988 and 1989 were

wet and the summer of 1990 was very dry (7 cm total precipitation in July and August). Record wet months occurred in August and September of 1988 and June of 1989, and record warm months occurred in June and July of 1988 and January of 1990.

The three peatlands selected for intensive study were Bog S-2, a 3-ha perched bog completely forested with black spruce and ringed by an alder fen (referred to as the fen lagg), Bog S-4, a partially open 8-ha bog with a small central pond, and Junction Fen, a weakly minerotrophic, open 5-ha fen. The sites are described in detail elsewhere [Crill et al., 1988; Dise, 1993]. Fluxes were measured at weekly to monthly intervals from a 35-cm-high sphagnum bog hummock ("collar 3"), a bog hollow ("collar 4"), and a depression in the fen lagg ("collar 5") in Bog S-2, from two locations on a floating sphagnum mat near the open water in Bog S-4 ("collar 1" and "collar 2"), and one location in the carex/sphagnum community of Junction Fen ("collar 6"). The sites at collars 1 and 3 were identical to those used in an April to June 1986 survey of methane flux at Marcell [Crill et al., 1988]; collars 2 and 4 were located near sites measured in that earlier study.

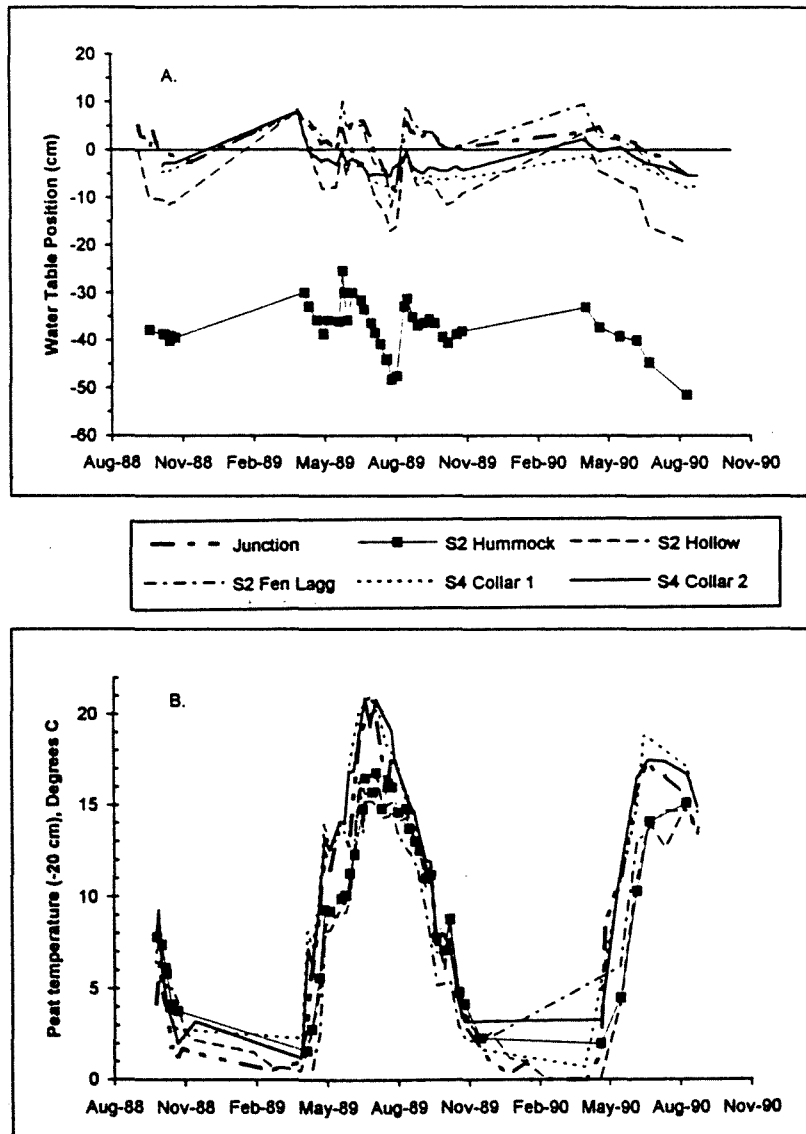


Fig. 1. (a) Water table position (peat surface at hollows is equal to 0) and (b) 20-cm peat temperature, Marcell Experimental Forest survey sites, September 1988 to September 1990. Symbols show measurement dates for hummock site.

Flux Measurements

Methane flux from five of the six sites (hereafter called "survey sites") was measured at monthly intervals in the winter, and weekly to fortnightly intervals during the rest of the year, from September 1988 to September 1990. Measurements at the S-2 fen lagg began 8 months later than the others, in May 1989. Sampling was most frequent in the year April 1989 to April 1990. Flux was measured in the field by fitting an aluminum chamber (dimensions 63 x 64 x 37 cm) over an aluminum collar set into the site. Head space samples from the chamber were taken every 4 min for 20 min with 60-ml plastic syringes, resulting in five grab samples. Samples were analyzed with a Shimadzu Mini 2 gas chromatograph with a flame ionization detector, attached to a Hewlett-Packard HP-3390A integrator. Methane flux was calculated from the slope of the concentration change over time corrected to the surface area covered by the chamber and the "effective volume" of the chamber (total volume of chamber reduced by the volume occupied by the peat surface and any standing water, or water equivalent of the snow in winter). The regression coefficient and the intercept (near ambient CH_4) were used as checks on the measurement; approximately 10% of the measurements were rejected. Methane concentrations increased linearly in the chambers over periods of 2-47 hours in 10 test measurements spanning all four seasons [Dise, 1991]. This method is also in good agreement with both flow-through chamber techniques [Crill *et al.*, 1988; Bartlett *et al.*, 1988] and tower-based estimates integrating over a larger area [Bartlett *et al.*, 1989; Verma *et al.*, 1992].

Within-site variability was evaluated from June through October 1989 by measuring weekly flux from four replicate collars in Junction Fen (including collar 6) and Bog S-2 (including collar 4). These measurements were repeated monthly during the snow-free season for the rest of the study. Coefficients of variation averaged

33% for replicates in Bog S-2 (range 10-82%) and 45% in Junction Fen (range 18-82%), somewhat lower than the values of 50-100% commonly reported. The survey site fluxes were consistently within the range of the other replicates [Dise, 1993].

Bog corrals

To isolate the influence of hydrology on methane flux, a field experiment was designed to manipulate water level within a subsection of Bog S-2. Three "bog corrals," open-ended, square, 11 gauge sheet metal enclosures (dimensions 1.2 x 1.2 x 1.5 m), were installed in January 1989 by chain sawing the outline of the corral in the frozen peat and hammering the corral vertically into the peat until only 30 cm was exposed above the surface. Lateral drainage was thus cut off and because the lower peat is quite dense, vertical drainage was very slow. One collar was installed in a hollow in each corral. After 1 month of background CH_4 measurements, water level in the corrals was raised to the surface on July 8, 1989, and kept there through November. Surface water level was maintained as needed by adding bog water from an adjacent well or removing pooled rainwater. These adjustments were small (± 1 cm) and only infrequently made (every 1 to 2 weeks); the experiment was largely self-sustaining. Three other hollow sites in S-2 were established as controls, and all six were measured weekly. The bog corral experiments were repeated on a limited schedule the following year.

Ancillary Measurements

At each sampling site, temperature was measured using an Omega HH-72T thermistor with a thermocouple probe at the end of a 50-cm tube. A temperature profile at surface, 2, 10, 20, 30, and 40 cm was recorded for all survey sites, and temperatures at surface

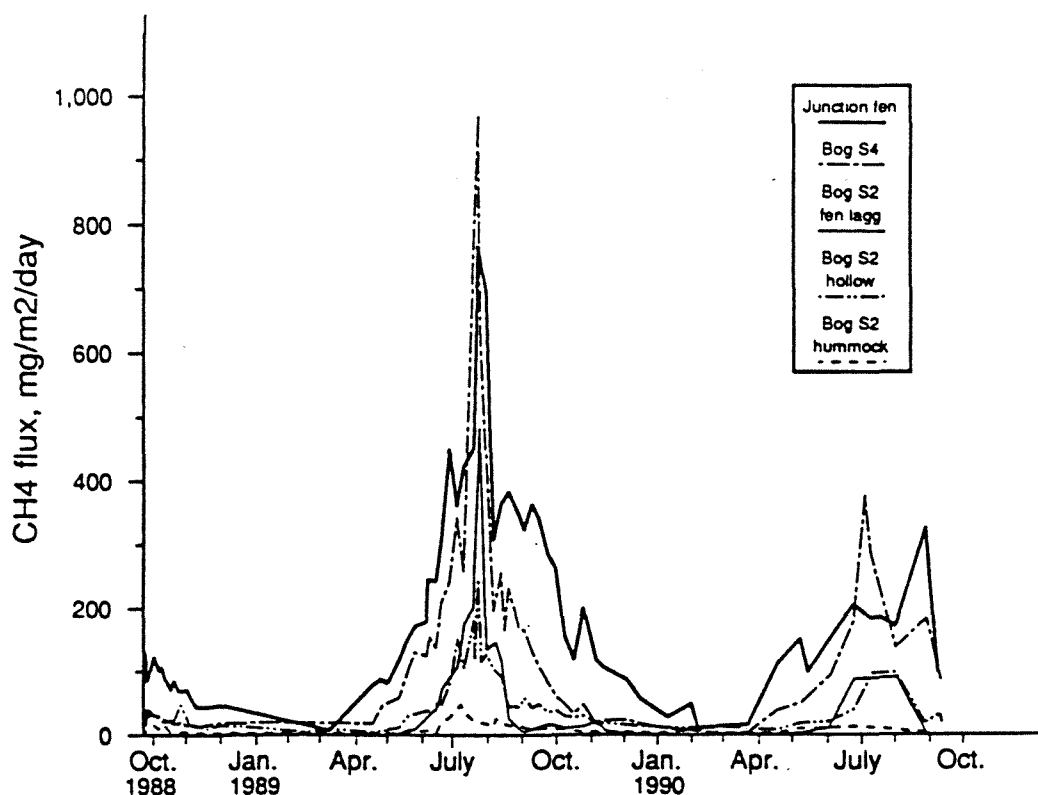


Fig. 2. Methane flux, survey sites, September 1988 to September 1990, from Dise [1993].

and 10 cm were recorded for the bog corral and control sites. Water table depth was determined during each flux sampling by referencing the water line to a stake in small wells dug at each of the sites. All water table measurements are reported as relative to the peat surface at hollows. Pore water samples were extracted manually at the desired depth through a stainless steel tube fitted onto the stop cock of a 60-cm³ plastic syringe. Dissolved methane was stripped from the sample in the lab by introducing an equal volume of air and shaking the sample for 5 minutes [Crill et al., 1988]. Headspace concentrations were corrected for CH₄ in the air. Gas samples were also collected from the submerged stems of water arum (*Calla palustris*) at the fen lagg site using a 60-cm³ syringe equipped with a needle. The sample was drawn by piercing the underwater stem and pulling air from the central pith. Samples of 20-40 cm³ could regularly be collected from the plants in this way.

Data Analyses

Annual fluxes were calculated by integrating daily fluxes over the year. Stepwise multiple linear regression was used to relate methane flux to environmental variables. Since a logarithmic transformation normalized the data and greatly reduced variance heteroscedasticity [Sokal and Rohlf, 1981], log (CH₄ flux + 1) was used as the dependent variable (a value of 1 was added to each flux before transformation because the data include some zero values). Independent variables in the stepwise regression were peat temperature (surface, 2, 10, 20, 30, and 40 cm), water table position from the peat surface in each collar, 3-week running average water table, 1 month running average water table, year of measurement (dummy variable; Devore and Peck [1986]), season (dummy variable), bog versus fen (dummy variable), and Von Post

TABLE 1. Relationships among Methane Emission (mg CH₄ m⁻² d⁻¹), Peat Temperature, and Water Table Position, Marcell Experimental Forest sites

Site	Regression	N.	r ²
Bog S-2-hummock	log (flux+1) = 0.042(T20) + 0.609	43	0.50
	log (flux+1) = 0.0509(T20) + 0.025(MWT) + 1.44	29	0.59
Bog S-2-hollow	log (flux+1) = 0.054(T10) + 1.04	59	0.74
Bog S-2-fen lagg	log (flux+1) = 0.085(T10) + 0.476	31	0.38
Bog S-4-collar 1	log (flux+1) = 0.082(T20) + 0.995	45	0.84
Bog S-4-collar 2	log (flux+1) = 0.069(T20) + 1.08	41	0.88
Junction Fen	log (flux+1) = 0.059(T30) + 1.60	52	0.71

T is the peat temperature at the depth (cm) at which the best-fit regression line was obtained. MWT is the one-month running mean water table. All regression lines are significant at $p < 0.01$.

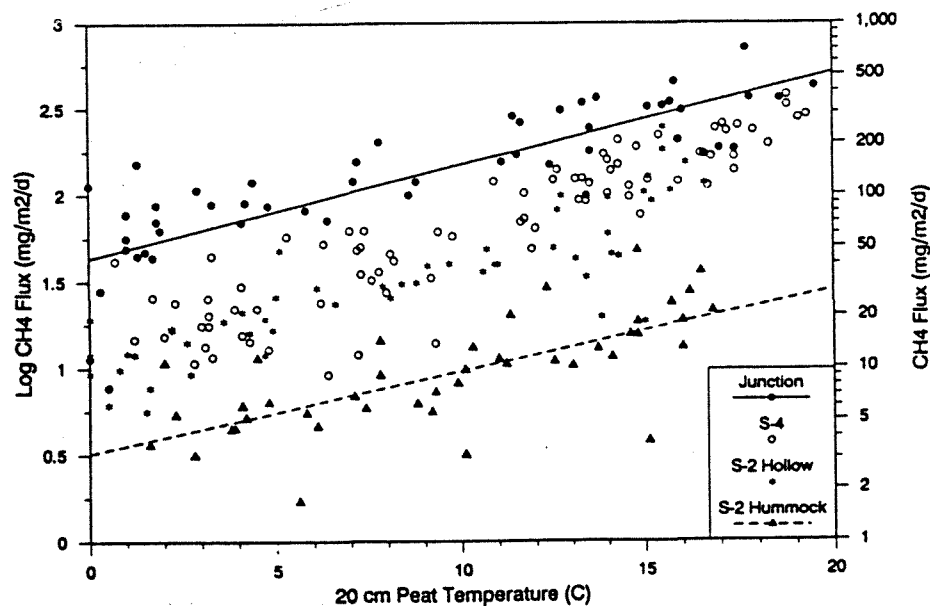


Fig. 3. Peat temperature versus log CH₄ flux, survey sites. Regression lines for Junction Fen and Bog S-2-hummock are shown.

humification scale (ranked variable, *Sokal and Rohlf* [1981]). The last variable is an index of the degree of peat decomposition [*Staneck and Silc*, 1977]. It differentiates peat types on the basis of evidence from intact plant structures, clarity of pore water, and muckiness; the range is from completely unhumified and muck free (1) to completely humified (10). In this study, the index ranged from 2 in Junction Fen to 4 in Bog S-2.

RESULTS

Seasonal Trends in Environmental Variables

Water table position for all six sites showed the same annual pattern, with high spring levels declining through the summer and fall, except for a fairly sharp increase in early fall 1989 (Figure 1a). The five different ecosystem types could be segregated by water table into three groups: Junction Fen and the S-2 fen lagg were the wettest, the hummock site in Bog S-2 was the driest, and the S-2-hollow and S-4 sites were intermediate. The fact that the S-4 sites are on a floating mat is clearly shown by the water table pattern, as the amplitude of the drop in summer water table is only about half that of the other sites.

Peat temperatures could be segregated into two broad categories: the cooler sites in the forested Bog S-2 and the warmer sites in the open S-4 bog and Junction Fen (Figure 1b). Temperature differences between open and forested sites were most

pronounced in July, when they amounted to 2°-3°C at 20 cm depth. Subsurface peat temperature was a lagged (1-2 weeks at 20 cm) and dampened record of air temperature. Temperature at 10 cm in the S-2 bog corrals averaged about 1° warmer than the controls in the summer and 1° cooler than the controls in the autumn, perhaps due to heat conduction by the corrals.

Methane Flux From Survey Sites

Detailed descriptions of spatial and temporal patterns of methane emission from the survey sites are presented elsewhere [*Dise*, 1991, 1993]. In brief, emission differed significantly among the three peatlands (S-2, S-4, Junction) and among the three different habitats within S-2 (hummock, hollow, lagg). The magnitude of seasonal fluxes consistently followed the rank order Junction > Bog S-4 > Bog S-2 hollow > Bog S-2 hummock, paralleling the gradient from wettest to driest site (Figure 2). Flux peaked in mid-July at all sites in 1989, then gradually decreased through fall and winter. Emission was 30-40% lower in 1990 and showed no pronounced summer peak. Methane was emitted all year, including winter, by all sites except the fen lagg. One negative flux (methane consumption) was recorded from the 320 survey site measurements over 2 years: a value of -0.8 mg CH₄ m⁻² d⁻¹ measured from the S-2 fen lagg on August 31, 1990. Annual

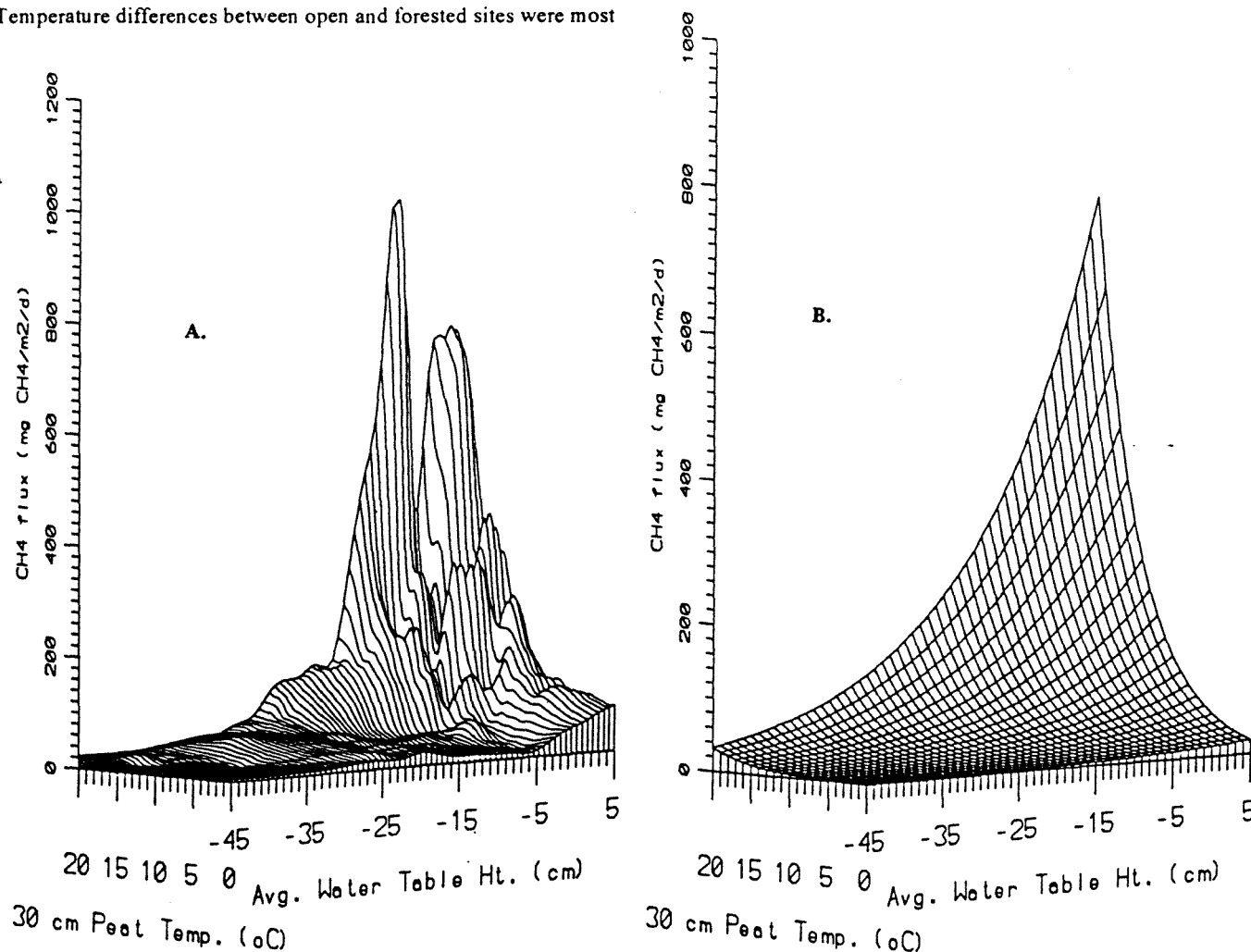


Fig. 4. Methane flux versus peat temperature (30 cm) and water table height (monthly running average). (a) Survey data (Kriging interpolation used to create surface). Peaks in surface curves are July pulses of methane in Junction Fen and Bog S-4. (b) Regression model of the survey data (model C in Appendix).

flux (April 1989 to April 1990) ranged from 3.5 g CH₄ m⁻² in Bog S-2 to 65.7 g CH₄ m⁻² in Junction Fen.

Correlative Studies

At each location CH₄ flux correlated closely with temperature (Table 1). Only in the dry Bog S-2 hummock did addition of water table position improve the correlation significantly. The temperature correlation was highest in Bog S-4 ($r^2 = 0.88$) and lowest in the S-2 marginal fen ($r^2 = 0.38$), where significant fluxes are, we believe, controlled primarily by plant transport (discussed below). The value of Q_{10} over the range 5 °- 15 °C for spring, summer, and fall averaged 5.1, being lowest (2.9) at 20 cm in the dry Bog S-2 hummock and highest (7.9) at 10 cm in the Bog S-2 fen lagg. Similar values have been reported during spring thaw from subarctic fens in Quebec [Moore and Knowles, 1990]. The Q_{10} estimates from this study were lower than Crill *et al.*'s [1988] values of 5.4 to 13 for the same sites at Marcell, but their study was conducted during a warm and wet spring and early summer, when emission rates were high and increasing relatively rapidly. Restricting our data to the same dates as their study gave comparable Q_{10} values. When fluxes were split by season, temperature was again, with the exception of the S-2 hummock (in summer), the only factor that correlated significantly with methane flux. It is thus apparent that in the individual peatlands studied at Marcell, any effect of water table on flux is masked by the overriding influence of temperature.

The effect of a second factor became evident only when all of the sites were considered together (Figure 3). The regression lines between log flux and temperature were approximately parallel among sites and distinct: at any given temperature, drier sites had lower fluxes than wet sites. This relationship became obvious with a multiple regression (Figure 4); although CH₄ flux at individual survey sites correlated only to temperature, water table position became the most important correlate when data from five sites (excluding the S-2 marginal fen) were pooled. The best fit multiple linear regression was

$$\log(\text{CH}_4 + 1) = 0.0214(\text{MWT}) + 0.0765(\text{T30}) - 0.154(\text{VP}) + 1.63$$

$$R^2 = 0.91 \quad n = 141 \quad p < 0.0001$$

where flux was in units of mg CH₄ m⁻² d⁻¹, MWT was the monthly running mean water table (measured once a week) in centimeters, T was °C at 30 cm depth, and VP was the Von Post humification scale value at 30 cm (model "A" in Appendix). Water table position accounted for 62% of variance, temperature 26%, and humification only 2%, perhaps because it did not differ much among locations. Water table position and temperature were uncorrelated in the model ($r^2 = 0.02$). The same model resulted from either forward inclusion (in which variables are entered into an initially empty model one at a time until the best fit model results) or backward deletion (where variables are sequentially deleted from an initially full model) and with randomly split halves of the data. When VP was left out of the multiple regression, vegetation type (bog or fen) became significant and also accounted for 2% of variance. When water table position measured on the same day as flux was used (rather than monthly running mean water table), the R^2 value dropped only slightly, to 0.88, although the standard deviation was higher ($n = 196$, $p < 0.0001$, model B in Appendix). Similar regression models were developed with slight variations in the independent variables for specific applications (in Appendix).

As expected, a split-data model did well in predicting methane emission from the other half of the data set ($r^2 = 0.91$, $n = 71$, $p < 0.0001$, Appendix model D used), with no apparent variance heterogeneity (Figure 5a). Back transforming to actual fluxes reduced the predictive value of the equation ($r^2 = 0.75$) due to increasing variability with increasing magnitude of fluxes. Prediction of the geometric mean flux for each site, however, was excellent ($r^2 = 0.97$, Figure 5b). The predictive value of similar regression models generated from the survey data declined with first, temporal, and then, spatial distance from the Marcell data. Thus a regression generated from 1989 data worked well in predicting 1990 fluxes ($r^2 = 0.78$, $n = 19$, $p < 0.0001$, model E used), but the 1988 to 1990 data regression performed less well with Marcell data from 1986 [Crill *et al.*, 1988] ($r^2 = 0.69$, $n = 54$, $p < 0.0001$, model F used) and least with data from quite different boreal peatlands in Alaska [Sebacher *et al.*, 1986; S. Whalen, unpublished data (1990)] ($r^2 = 0.15$, $n = 36$, $p < 0.02$, model G used).

Water Table Manipulation

The influence of hydrology on methane emission at individual sites was demonstrated experimentally in the bog corrals (Figure 6). Fluxes from corrals and controls were not significantly different during the pre-treatment period and in the days immediately following. Raising and maintaining the water table in Bog S-2 at the peat surface from July 8 onward led, after a lag of more than 3 weeks, to distinctly higher CH₄ fluxes (approximately double the controls). Between August 8 and November 7, 1989, total flux from enclosures was 9.5 g CH₄ m⁻². In controls, where water table averaged 6.1 cm beneath the peat surface, flux was 3.8 g CH₄ m⁻², 40% of the enclosure flux. In 1990 (May 9 to August 31), flux from the corrals was 15.7 g m⁻² versus 7.1 g m⁻² from the controls (45% lower), with the average water table difference at 10.4 cm. Paired t tests indicated these flux differences were highly significant both years ($p < 0.02$). Although, as previously discussed, no relation between flux and water table position was found in the S-2 hollow site, water table height accounted for 34% of the variation in flux (in addition to 38% due to temperature) when considering the corrals and controls together in S-2. The fact that water table position became an important correlate with flux in S-2 hollows only when the bog corral data were included suggests that the part of the bog isolated by the corrals had, in effect, become a distinct habitat.

Since only 10-cm peat temperature was measured in the manipulation experiments, a new regression model was developed from survey data to test flux predictions (using 10-cm temperature instead of 30-cm temperature, Appendix model H). This model, generated from all the 1989 to 1990 survey data but not using corral/control data, successfully predicted both the geometric mean fluxes and the total fluxes from the corrals and controls in 1989 and 1990 (Figure 5b). It also reproduced the overall patterns of both the autumn decline in flux and the effect of the water table height (Figure 7), although the latter was not exactly replicated: the regression model predicted fluxes to be less responsive to the water table change than actually observed and more responsive to temperature (corrals were slightly warmer than controls in summer and cooler than controls in late autumn). This is not surprising considering the model is based on flux data from several different peatlands including wet ones (where the flux response to temperature changes is more pronounced than in S-2). The regression coefficients represent an averaging of responses from the different sites.

Estimating Annual Emission

Annual emission of methane at Marcell has been closely approximated by multiplying the geometric mean summer (June to August) methane flux by a time period of about 175 days [Dise, 1993]. We used this relationship together with the regression to predict annual methane flux from individual sites as follows: log flux was estimated from the regression for each site during each day between June 1 and August 31 in which water table and 30-cm peat temperature measurements were available. Geometric mean summer flux was calculated by computing the antilog of the average of those values for each site, and finally, annual flux was

estimated by multiplying the geometric mean flux by 175. The result was compared to annual fluxes calculated by integration of measured values. To avoid predicting fluxes from a model calibrated on those same fluxes, we used two approaches: (1) a split-data technique to calculate annual flux from April 1, 1989 to March 31, 1990 (model D in Appendix used) and (2) a model using data from the first year to predict annual flux from the second year (model E used). Since, with the first approach a model generated from one year was used to predict fluxes from that same year, within-site variability due to climate or biology was low and predicted flux was very close to measured flux (means of 27.9 and 31.5 g CH₄ m⁻² yr⁻¹, respectively, Table 2). In the second case,

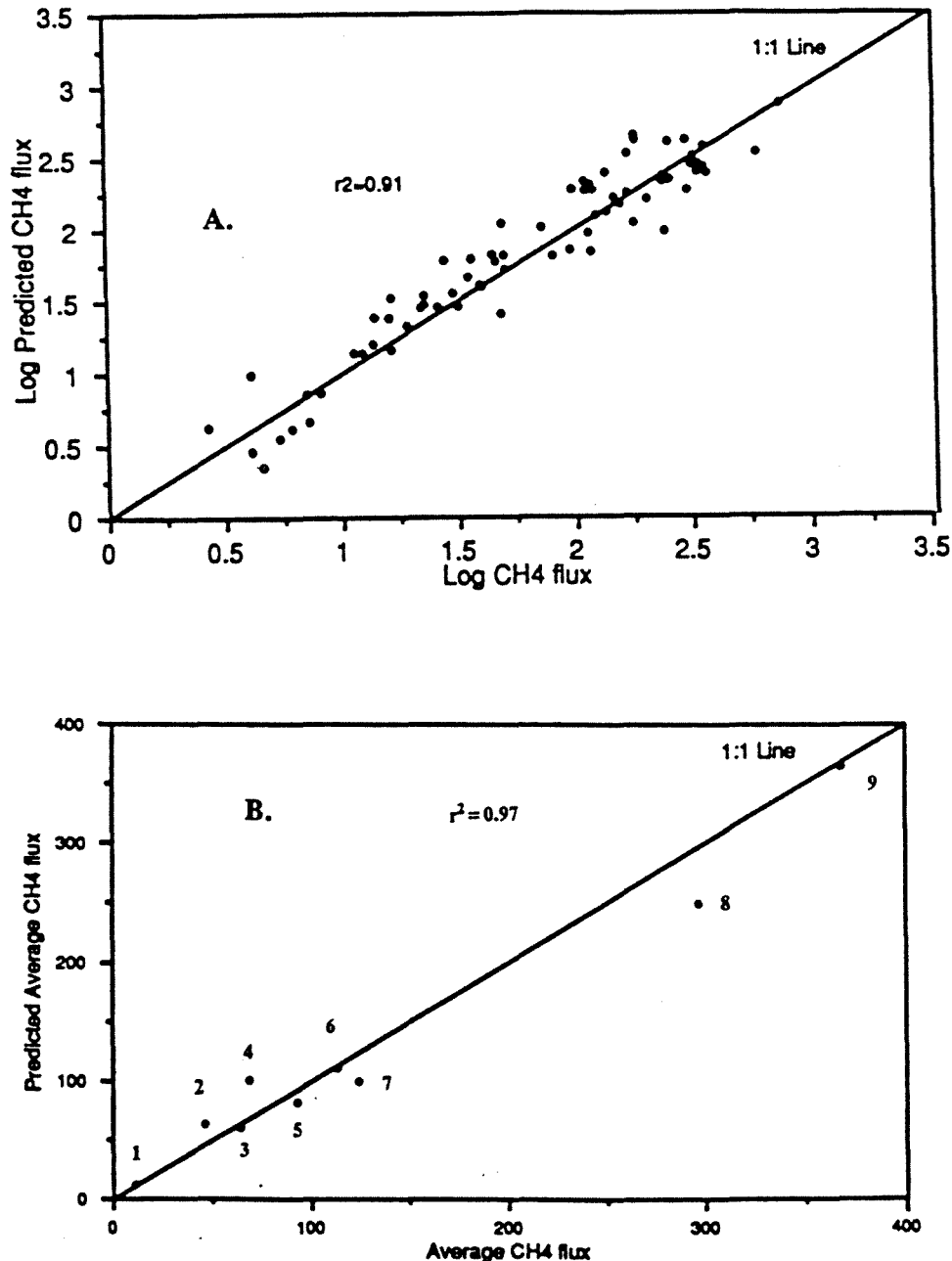


Fig. 5. Predicted versus measured methane flux, split data set (model D in Appendix; model H for bog corrals and replicate collars). (a) Log flux, survey sites. (b) Geometric mean flux, May to November 1989 (except where noted). Sites are (1) Bog S-2 hummock, (2) Bog S-2 replicate collars, (3) Bog S-2 hollow, (4) Bog S-4 collar 2, (5) Bog S-2 bog corrals, (6) Bog S-4 collar 1, (7) Bog S-2 bog corrals (May to August 1990), (8) Junction Fen, and (9) Junction Fen replicate collars (June to September 1989).

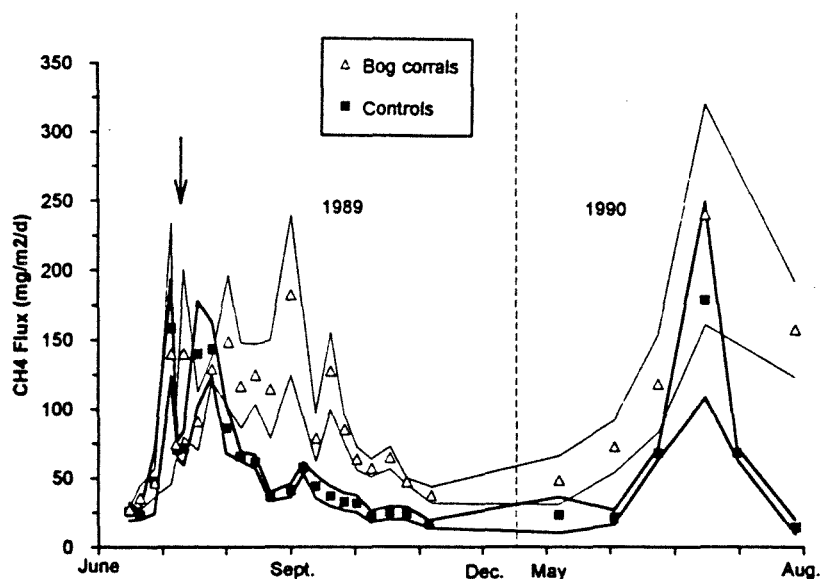


Fig. 6. Methane emission from S-2 bog corrals and controls, June 1989 to August 1990. Each point is the mean of 2-3 measurements, boundary lines are ± 1 standard error of the mean. Arrow indicates start of experiment on July 8, 1989.

data generated from a wet year were used to predict flux from a dry year: as expected, predicted flux ($28.8 \text{ g CH}_4 \text{ m}^{-2} \text{ yr}^{-1}$) was about one third higher than measured flux ($21.2 \text{ g CH}_4 \text{ m}^{-2} \text{ yr}^{-1}$). Predictions for the wet sites were poorest because the model incorporated summer pulses in Junction and S-4 that were not observed the second year. Fluxes from the drier Bog S-2 were again predicted very well. It is clear that additional influences on flux from wet sites, not accounted for in the regression, need further investigation. These may include population dynamics of methanogens under optimal conditions, pulses of increased flux tied to a lowering of the water table [e.g., Moore et al., 1990; Dise, 1993] or decreases in atmospheric pressure [e.g., Mattson and Likens, 1990; N.J. Shurpali et al., Seasonal distribution of methane flux in a Minnesota peatland measured by eddy correlation, submitted to *Journal of Geophysical Research*, 1993], ebullition, or the release of plant exudates as substrates for methanogenesis.

Special Case: Plant Transport

The pattern of annual methane emission from the fen lagg was unique among the six sites. Significant fluxes occurred only from early June to late August, but during those 3 months such a large amount of methane was emitted (11.2 g m^{-2} or 90% of total annual flux) that the annual flux estimated from the lagg was very close to that of the hollow site in S-2, which emitted methane all year. A near-total cessation of methane emission occurred in the lagg in early September despite an autumn water table consistently at or slightly above the surface.

The unusual pattern of fluxes from this site and the relatively poor relationship between flux and either temperature or water table suggested that methane fluxes in the lagg may be strongly influenced by other factors. A likely candidate is emission through emergent macrophytes. Significant methane emission began in the lagg only when shoots of *Calla palustris* emerged in early May (Figure 8). Fluxes declined sharply with this plant's senescence in late August, suggesting that it provided conduits for CH_4 transport. By allowing rapid passage through the many layers of surface-matted leaves and vegetation, as well as bypassing potential surface

oxidation [Chanton and Dacey, 1992], methane was probably released much faster than by diffusion alone. Transport of methane has been shown in numerous aquatic plants including cultivated rice [Cicerone and Shetter, 1981], *Typha latifolia* (cattail) [Holzapfel-Pshorn and Seiler, 1986; Sebacher et al., 1985], *Nuphar luteum* (yellow water lily) [Sebacher et al., 1985], and *Peltandra virginica* (arrow-aram) [Sebacher et al., 1985]. In the fen lagg, three measurements of methane concentration in submerged *Calla* stems averaged $916 \text{ mg CH}_4 \text{ m}^{-3}$, within the range of concentration for those plants ranked highest in methane transport in one study [Sebacher et al., 1985]. Also supporting the transport hypothesis is the observation that pore water methane concentration (30 cm) in the lagg increased sharply in mid-September after the *Calla* died, a change that was not paralleled in the S-2 hollow site [Dise, 1991]. This suggests that a significant temperature drop occurred (methane solubility increases with decreasing temperature), a large amount of organic substrate became available, and/or a major loss mechanism was discontinued. Temperature changes alone (13.5° to 11.6° from August 1 to September 13) were insufficient to account for the pore water [CH_4] increase, and we feel that the elimination of the main loss mechanism was the reason for the buildup. Similarly, Wilson et al. [1989] reported a large springtime decrease in pore water methane concentration in a Virginia swamp accompanied by the emergence of the arrow-aram *Peltandra* which could not be attributed solely to a temperature increase [Chanton and Dacey, 1992].

In the autumn, after the senescence of the *Calla*, some methane may be released from this site by ebullition [Holzapfel-Pshorn and Seiler, 1986; Chanton and Dacey, 1992]. Since it is highly unlikely that such episodic release would be detected from weekly chamber measurements, it is quite possible that the annual flux calculated from this site is an underestimate.

DISCUSSION

This study used both correlation and experimentation to suggest possible controls on methane emission in Minnesota peatlands. That a significant correlation between flux and peat temperature

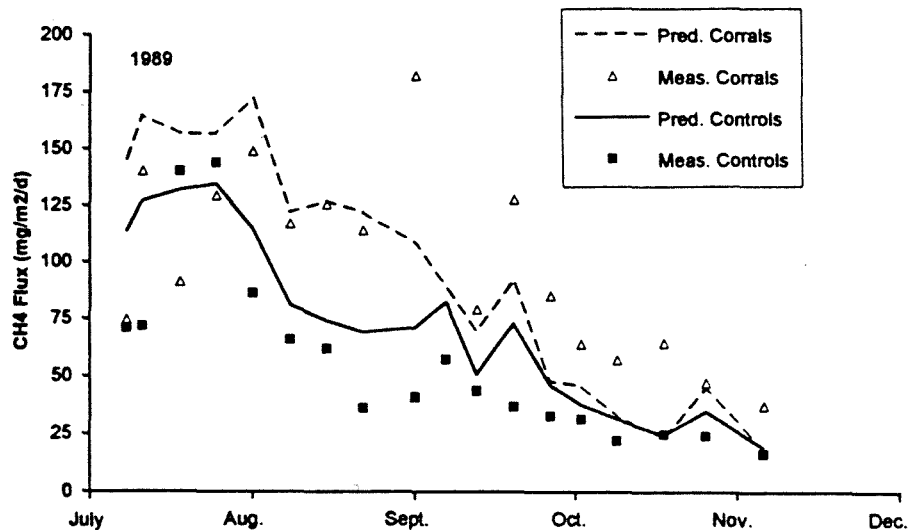


Fig. 7. Test of regression model (model H in Appendix) with bog corral data, 1989. First data points are at start of experiment on July 8, 1989.

was found in the survey sites strongly suggests that methane emission in Marcell is dominated in individual ecosystems over short time periods (days to weeks) by temperature in the 10 to 30-cm zone (Table 1). Similar relationships between flux and temperature were found in an earlier study at Marcell [Crill *et al.*, 1988], as well as in other studies in Canada [Moore and Knowles, 1990] and Alaska [Bartlett *et al.*, 1992]. The statistical analysis suggested, somewhat surprisingly, that the controls on flux do not change over the course of the year. Regardless of season, temperature was the only important correlate with flux in individual sites, and water table was the major correlate among sites. This suggests that seasonal shifts in CH_4 flux controls at Marcell do not occur and implies that in other areas a measurement program of

several months may be adequate to establish the important environmental controls on flux.

The very strong relationship found between flux and the combined variables of water table and temperature across sites suggests that these environmental factors may be considered potential tools for estimating emission remotely [Matson and Vitousek, 1990] as well as for incorporation into climate change models. Evaluating this possibility would require a thorough review of existing empirical studies on flux in peatlands together with the few process-oriented investigations to resolve conflicting information about the important controls on methane emission. It remains unclear, for example, why correlations with environmental variables are higher at Marcell than those reported to date in other

TABLE 2: Comparison of calculated versus predicted total annual methane emission, Marcell Experimental Forest Peatlands, April 1989 to April 1990

Site	Annual Methane Emission, $\text{g CH}_4 \text{ m}^{-2}$			
	April 1989 to April 1990		Sept. 1989 to Sept. 1990	
	Calc.	Pred. (<i>N</i> , 95% c.i.)	Calc.	Pred. (<i>N</i> , 95% c.i.)
Bog S-2, hummock	3.5	3.2 (6, 2.0-5.1)	2.5	2.4 (2, -)
Bog S-2, hollow	13.8	12.4 (9, 8.6-17.9)	10.2	9.6 (3, 6.2-15.0)
Bog S-4	43.1	37.8 (7, 25.4-57.1)	28.0	43.3 (6, 36.1-51.8)
Junction Fen	65.7	58.1 (6, 34.1-98.9)	43.9	59.9 (5, 45.6-78.6)
Mean	31.5	27.9	21.2	28.8

Regression equation between $\log \text{CH}_4$ flux (dependent variable) and water table, 30-cm peat temperature, and Von Post humification index (independent variables) used. Regression model C used for April 1989 to 1990 predictions; model D used for September 1989 to 1990 predictions (in Appendix). Calc. is flux estimate calculated by integration. Pred. is predicted estimate. *N* is the number of data points used in prediction. C.i. is the confidence interval.

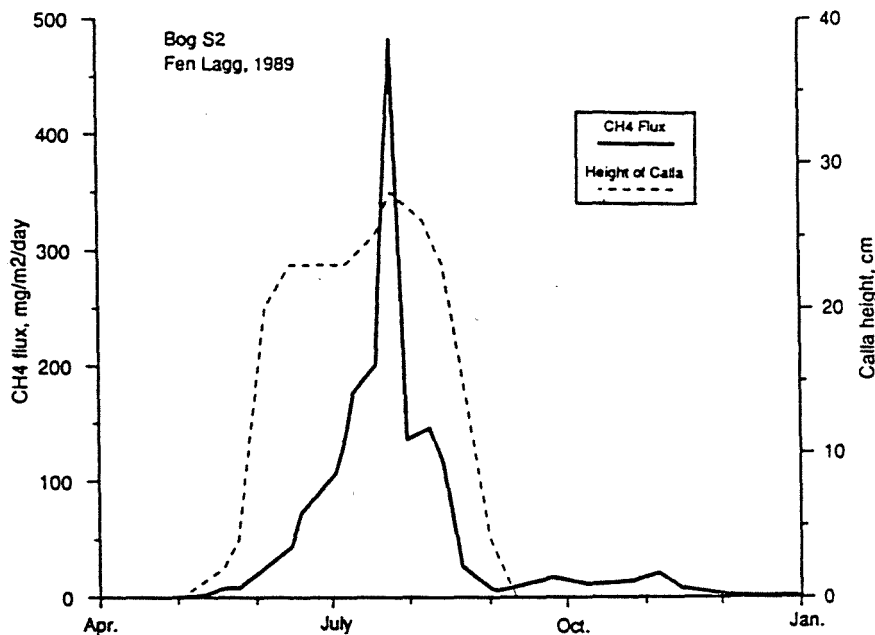


Fig. 8. Methane emission from the S-2 fen lagg site and height of *Calla palustris* at the site, April 1989 to January 1990.

investigations. It is encouraging that a similar but weaker relationship was also found among flux, water table and temperature in low boreal peatlands in Ontario ($R^2 = 0.49$) [Roulet *et al.*, 1992], indicating this simple modeling approach may be applicable to a wider region.

A second critical requirement for remote estimates is to determine how the relationship may be best expressed in a way that lends insight into processes and is a starting point for regional extrapolation. Roulet *et al.* [1992] used mean (May to October) values of flux, peat temperature (10 cm) and water table from 24 sites in their model ($n = 24$) instead of the actual measurements made from each day as we have ($n = 141$, model A or $n = 196$, model B). The advantages of their approach are that day-to-day fluctuations in emission (which can be large) due to unknown factors are reduced in importance and that using broad correlations may be the only way to apply such a model to a large region. The disadvantage is that it becomes increasingly more difficult to relate models to actual processes (and therefore to have confidence in predictions) as the data they are based on are more and more lumped. This is especially true for the processes involved in methane emission which are probably related to flux nonlinearly. Regardless of the variables used, "scaling up" a regression to incorporate different wetland regions, if at all possible, would require regionally determined climate parameters in the model: the regression generated from a low boreal region such as Marcell is useless to predict Alaska fluxes. Finally, as illustrated by the fen lagg, these across-site relationships among emission, water table and temperature may be only valid where diffusive flux through the peat can be assumed. Methane emission from areas such as rice paddies, cattail marshes or lakeshores may be most closely related to the life cycle of the emergent macrophytes.

To conclude, in these peatlands, CH_4 flux was dominated locally by peat temperature in the 10 to 30-cm zone (Table 1). Expansion of the spatial scale from individual locations to several distinct habitats within three wetlands, however, revealed the importance of water table position as the overriding factor influencing flux regionally (Figures 3 and 4). These relationships suggest two

different phenomena: a long-term effect of hydrology upon the balance of methanogenic and methanotrophic bacteria population sizes and a short-term effect of temperature upon their metabolic rates. Additional influences, especially on wetter sites which may have sporadic summer pulses, can only be identified with multi-year studies in a region.

APPENDIX: REGRESSION MODELS, MARCELL 1988-1990 METHANE FLUX SURVEY

- MWT 1 month (five values) running mean water table position
(relative to peat hollow surface), range +5 to -45 cm.
- T30 30 cm peat temperature, range 4.5 to 20.0 °C.
- VP Von Post Humification Index value, range 2 to 4.
- WT water table height, range +8 to -51.5 cm.

Full Models

Model A

Using running mean water table

$$\begin{aligned} \text{Log}(\text{CH}_4 \text{ flux}+1) &= 0.0214(\text{MWT}) + 0.0765(\text{T30}) \\ &\quad - 0.1544(\text{VP}) + 1.627 \\ R^2 &= 0.91; \text{ s.d.} = 0.1728; n = 141 \end{aligned}$$

Model B

Using water table measured on same date as flux measurement:

$$\begin{aligned} \text{Log}(\text{CH}_4 \text{ flux}+1) &= 0.0173(\text{WT}) + 0.0634(\text{T20}) \\ &\quad - 0.2226(\text{VP}) + 1.958 \\ R^2 &= 0.88; \text{ s.d.} = 0.2016; n = 196 \end{aligned}$$

Model C

Von Post not included (for Figure 4b)

$$\text{Log}(\text{CH}_4 \text{ flux}+1) = 0.0271(\text{MWT}) + 0.0779(\text{T30}) + 1.177$$

$$R^2 = 0.88; \text{ s.d.} = 0.1919; n = 141$$

Split Model

Model D

Developed on a randomly generated subsample of the entire data set, then used to predict methane concentration from the other subsample:

$$\text{Log}(\text{CH}_4 \text{ flux}+1) = 0.0213(\text{MWT}) + 0.0772(\text{T30})$$

$$- 0.1707(\text{VP}) + 1.680$$

$$R^2 = 0.92; \text{ s.d.} = 0.1665; n = 71$$

Regressions Used for Prediction of Flux at Other Sites and at Marcell in Different Years:

Model E

Regression using only 1988 to 1989 data (to predict 1990 methane fluxes at Marcell):

$$\text{Log}(\text{CH}_4 \text{ flux}+1) = 0.0202(\text{MWT}) + 0.0796(\text{T30})$$

$$- 0.1873(\text{VP}) + 1.700$$

$$R^2 = 0.92; \text{ s.d.} = 0.1591; n = 124$$

Model F

Regression on full data set using 10-cm temperature and same-day (not average) water table (to predict 1986 methane fluxes at Marcell):

$$\text{Log}(\text{CH}_4 \text{ flux}+1) = 0.0167(\text{WT}) + 0.0578(\text{T10})$$

$$- 0.2296(\text{VP}) + 2.021$$

$$R^2 = 0.87; \text{ s.d.} = 0.2083; n = 207$$

Model G

Regression on full data set using 10 cm temperature, no VonPost (to predict Alaska fluxes)

$$\text{Log}(\text{CH}_4 \text{ flux}+1) = 0.0277(\text{MWT}) + 0.0557(\text{T10}) + 1.437$$

$$R^2 = 0.86; \text{ s.d.} = 0.2142; n = 141$$

Model H

Regression on full data set using 10-cm temperature (to predict bog corral fluxes)

$$\text{Log}(\text{CH}_4 \text{ flux}+1) = 0.0215(\text{MWT}) + 0.0557(\text{T10})$$

$$- 0.1772(\text{VP}) + 1.929$$

$$R^2 = 0.89; \text{ s.d.} = 0.1905; n = 154$$

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