A three-year study of controls on methane emissions from two Michigan peatlands

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Abstract. We investigate temporal changes in methane emissions over a three-year period from two peatlands in Michigan. Mean daily fluxes ranged from 0.6–68.4 mg CH_4 m^{-2} d^{-1} in plant communities dominated by *Chamaedaphne calyculata*, an ericaceous shrub, to 11.5–209 mg CH_4 m^{-2} d^{-1} in areas dominated by plants with aerenchymatous tissues, such as *Carex oligosperma* and *Scheuchzeria palustris*. Correlations between methane flux and water table position were significant at all sites for one annual cycle when water table fluctuations ranged from 15 cm above to 50 cm below the peat surface. Correlations were not significant during the second and third annual periods with smaller water table fluctuations. Methane flux was strongly correlated with peat temperatures at −5 to −40 cm (r_S = 0.82 to 0.98) for all three years at sites with flora acting as conduits for methane transport. At shrub sites, the correlations between methane flux and peat temperature were weak to not significant during the first two years, but were strong in the third year.
Low rates of methane consumption (−0.2 to −1.5 mg CH_4 m^{-2} d^{-1}) were observed at shrub sites when the water table was below −20 cm, while sites with plants capable of methane transport always had positive net fluxes of methane. The methane oxidizing potential at both types of sites was confirmed by peat core experiments. The results of this study indicate that methane emissions occur at rates that cannot be explained by diffusion alone; plant communities play a significant role in altering methane flux from peatland ecosystems by directly transporting methane from anaerobic peat to the atmosphere.

Introduction

Estimates of methane emissions from northern peatlands are based on a small but growing database of annual studies that have addressed seasonal and spatial variations in methane flux from peatlands. Variations in net flux may be due to a number of often interrelated factors, including temperature (Crill et al. 1988; Moore et al. 1990; Whalen & Reeburgh 1992; Dise et al. 1993), water levels (Svensson & Rosswall 1984; Sebacher et al. 1986; Moore et al. 1990; Dise et al. 1993), and plant communities (Whalen & Reeburgh 1988, 1990a; Yavitt & Lang 1990; Whiting & Chanton 1992). Methane generated in anaerobic sediments can be emitted to the atmosphere by internal transport through vascular aquatic plants and emergent vegetation (Dacey & Klug 1979; Chanton & Dacey 1991; Whiting & Chanton 1992). Methane oxidation in aerobic and anaerobic sediments can also account for the variability in net
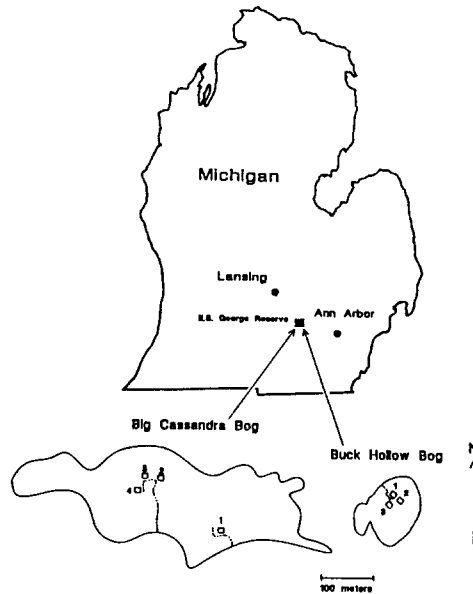
Fig. 1. Location map of E.S. George Reserve and diagrams of Buck Hollow Bog and Big Cassandra Bog showing locations of flux chamber sites.

methane emissions from wetland ecosystems (Moore et al. 1990; Yavitt et al. 1990a; Fechner & Hemond 1992).

While recent studies have characterized some of the factors that affect methanogenesis, little is known about the internal processes that control methane emissions from peatlands of the northern temperate zone. In addition, few studies have measured methane flux and its controlling variables from peatlands over several annual cycles (e.g. Whalen & Reeburgh 1992; Dise et al. 1993). In this study we investigate methane fluxes from two peatland ecosystems in southern Michigan, USA, over a period of three years. We attempt to characterize the spatial and temporal variability of methane emissions from several distinct plant communities within the two peatlands. In addition, the influences of factors such as water levels, temperature, and methane oxidation on the variability of methane emissions within and between peatland ecosystems were monitored to determine their effects on methane fluxes and on methane within the saturated peat.

Materials and methods

Field sites

The field sites were located in southern Michigan on the Edwin S. George Reserve, a University of Michigan field station (Fig. 1). The local topography is a result of glacial outwash and moraines deposited during glacial retreats, with soils composed primarily of sand and gravel. The permanent sampling stations from which we conducted this study were located in two peatlands, Buck Hollow Bog and Big Cassandra Bog (42°27′ N, 84°01′ W). Both ombrotrophic peatlands are located in closed, kettle-hole or ice-block depressions that were formed as the glaciers receded. The peat deposits are grounded, without a floating mat or subsurface open water; the mean pH of Buck Hollow Bog and Big Cassandra Bog were 4.2 and 3.9, respectively.

Buck Hollow is an open peatland covered by a wet lawn of *Sphagnum* species, out of which grows a dense cover of *Scheuchzeria palustris*, an arrow-grass. Other vascular plants of lesser dominance that are interspersed throughout the sphagnum lawn include cranberries (*Vaccinium oxycoccos*), cottongrass (*Eriophorum virginicum*) and small (<30 cm in height) leatherleaf shrubs (*Chamaedaphne calyculata*). In Buck Hollow, three flux chambers were grouped in a triangular pattern approximately 10 m apart to assess the natural variation in methane flux from the sphagnum-*S. palustris* wet lawn covering the majority of the peatland. In contrast to Buck Hollow Bog, Big Cassandra Bog exhibits hummock-hollow microtopography dominated by sphagnum and *Polytrichum* mosses and covered by a dense stand of *C. calyculata*. Sites 1, 2, and 3 were located in the *C. calyculata*-sphagnum community dominating the majority of the peatland surface. Site 4 was located in a 100 m^2, central area of the peatland dominated by a dense stand of *Carex oligosperma* in a wet sphagnum lawn.

Collection and analysis of methane and environmental parameters

Measurements of net methane fluxes were made using static chambers, consisting of a permanent aluminum base (0.25 m^2), a removable midsection and a plexiglass top (Whalen & Reeburgh 1988). Mylar sheets were used to shade the chambers on sunny days. We constructed boardwalks leading to all sites to minimize disturbance to the peatlands. Gas samples for methane were collected from a boardwalk with syringes connected to the chamber lid with tubing and luer connectors. All gas samples were collected in 10 cm^3 plastic or glass syringes with butyl rubber plungers equipped with plastic stopcocks, and were analyzed within 3–4 days of collection.

We sampled all sites at 10 to 14 day intervals during periods of high flux, and at 3–4 week intervals during colder periods. Each time series of flux measurements from a chamber consisted of 4–8 samples taken at intervals of 5 to 15 minutes during summer high fluxes to several hours during the winter; complete time series ranged from 30 minutes to over 24 hours. Methane fluxes were calculated by determining the slope of the least squares regression line of methane concentration change in the flux chamber vs. time. Time series with coefficients of determination (r^2 values) less than 0.900 were rejected; these non-linear series occurred in about 6% of our flux measurements and may have resulted from peat disturbance during sampling when the peat was highly enriched with methane near the surface. Slopes not significantly different from zero ($p < 0.05$) were reported as a time series with a flux = 0 mg CH_4 m^{-2} d^{-1}. In general, the detection limit for positive and negative fluxes was $\pm$ 0.1 mg CH_4 m^{-2} d^{-1}. Methane was analyzed on a Shimadzu GC-14A gas chromatograph with a flame ionization detector.

Porewaters were collected with Hesslein-type diffusion 'peepers' (Hesslein 1976). The cells of the lucite peepers were covered with a 0.2 μm membrane (Gelman HT-200). The peepers were initially inserted into the peat after making an incision in the peat with a sharp knife, allowed to equilibrate with the peat porewaters for 3–4 weeks, then removed for sampling. Porewaters were collected from each cell with a glass syringe, which was immediately capped with a luer plug after sampling. All porewater samples were stored at 4 °C until analyzed within 3–4 days. Dissolved methane concentrations in porewaters were determined by the phase equilibration technique (McAuliffe 1971). Analysis for headspace methane was by GC/FID as described in the previous section. The detection limit for porewater methane was 0.1 μM.

At each site, peat temperatures were measured at 10 intervals to a depth of 1 m by using thermocouples threaded through a length of insulated, 5.1 cm dia PVC pipe permanently inserted into the peat. Temperatures at the various peat depths were initially measured every 3–4 weeks by attaching the thermocouple leads to an Omega hand-held temperature meter. At various times throughout the study, we attached a Campbell CR-10 datalogger to the thermocouples at each site; the datalogger was programmed to sample temperatures every 10 minutes and record the hourly mean temperature.

Water table elevations were determined with perforated standpipes (7.6 cm dia. PVC) permanently inserted into the peat at each site to 1 m depth. Using a 'dipstick' technique, we determined water table elevations to within ± 0.5 cm at 3–4 week intervals. All elevations were calculated relative to a fixed datum on firm land because peat surfaces can alternatively rise and fall due to fluctuating water tables which cause expansion and contraction of the peat (Roulet 1991). In subsequent references to water table and peat temperature

elevations, the reference point is the peat surface, with positive and negative elevations taken as above and below the peat surface, respectively.

Hourly precipitation data for the study period was obtained with either a raingauge located on the George Reserve about 0.5 km from each peatland, or a second collector located in Gregory MI, 5 km NW of the peatland sites. Long-term precipitation data was obtained for the period 1948–1980 for Howell MI, located 8 km N of the study sites. The mean annual rainfall for this period was 76.1 cm. Annual precipitation for 1991, 1992, and 1993 was 74.2, 92.0, and 86.7 cm, respectively, deviating from the 1948–1980 mean by −2.6, +20.9, and +6.0 percent.

Methane oxidation and plant enclosure experiments

The potential for methane oxidation in unsaturated peat was assessed with peat cores removed from Buck Hollow Bog and site 1 in Big Cassandra Bog. Cores were obtained in September 1992 with 6.75 cm dia. PVC pipe sharpened at one end, cut into three sections representing the 0–10, 10–20, and 20–30 cm depth intervals in the peat, and sealed on the bottom with a rubber stopper. Procedures for time series experiments to measure methane consumption were similar to those of other investigators (Whalen & Reeburgh 1990b; Whalen et al. 1990). All experiments were conducted at room temperature (22 °C). Oxidation rates were determined by least squares regression of the natural logarithm of methane concentration (ppmv) vs. time, after allowing sufficient time (>0.5 hr) for equilibration of the injected methane with the peat core. Acetylene, a known inhibitor of methane-oxidizing bacteria (Bédard & Knowles 1989), was added to peat samples in separate experiments to confirm that methane consumption was mediated by microbial activity. Samples of the headspace were analyzed for methane by GC/FID as previously described.

Direct emissions of methane from several plant species common to both peatlands were measured by sealing plants, *in situ*, in containers of fixed volume (5 to 12 L). Chambers were rendered airtight by gently taping an inverted polypropylene skirt to the plant base and filling any voids between the plant and the skirt with a viscous cornstarch gel. The skirt was then attached to the container with a threaded connector. Accumulation of methane inside each chamber was measured by sampling the chamber air through an attached stopcock with a 5 mL glass syringe at various time intervals. Gas samples were analyzed for methane as previously described for flux chambers. The enclosed plants were then harvested and dried to constant mass at 105 °C; emissions were normalized to the dry biomass enclosed in each chamber. Methane accumulation was significant and linear in all plant enclosures ($p < 0.05$, $r^2 > 0.99$).

Statistical analyses

The flux distributions from each site were tested for normality and equal variance, both before and after logarithmic transformations, using the Kolomogorov-Smirnov and Levene tests, respectively ($p < 0.05$). Assumptions of normality and equal variance were not satisfied after logarithmic transformations of the data; therefore, nonparameteric tests were used for statistical analyses (Sokal & Rohlf 1981). Differences between flux distributions at the various sites were determined with the Friedman repeated measures ANOVA on ranks test, and paired multiple comparisons were calculated with Dunn's test. Correlations between methane flux and environmental factors were conducted using Spearman's rank order test. Annual fluxes were determined by integration of individual flux curves over the three annual periods.

Results

Methane fluxes, water levels, and peat temperatures

Methane fluxes in the two peatland ecosystems exhibited large variability within and between sites. Mean fluxes were usually higher than median values, indicating distributions skewed toward higher rates. Methane fluxes at the three chambers in Buck Hollow Bog were highest, and were not significantly different from each other ($p < 0.05$), indicating a high degree of spatial homogeneity (Fig. 2a). Fluxes varied seasonally, with the highest fluxes (491–1445 mg CH_4 m^{-2} d^{-1}) emitted between late May and July. Summer fluxes declined rapidly below 200 mg CH_4 m^{-2} d^{-1} by late August 1991, but declined more slowly in 1992 and 1993, reaching 200 mg CH_4 m^{-2} d^{-1} by early October. Positive methane fluxes were observed year round, including periods of ice cover (2.4–42 mg CH_4 m^{-2} d^{-1}).

We also observed seasonal variations, as well as interannual differences, in the elevation of the water table in Buck Hollow (Fig. 2b). During the dry 1991 summer, the water table declined to -18 cm in late September, and remained below the peat surface from mid-June through early November. The water table remained at or above the peat surface for most of 1992 and 1993, declining briefly to -6 cm from late June to early July 1992. Mean daily temperatures at depths of -5, -40, and -100 cm in Buck Hollow Bog followed seasonal changes in air temperature, with the surface peat layers more susceptible to short-term and extreme temperature fluctuations (Fig. 2c). In Buck Hollow Bog, the correlation between methane flux and peat temperature was always stronger than the flux-water table correlation, both for each annual cycle and for the combined three-year data set (Table 1).
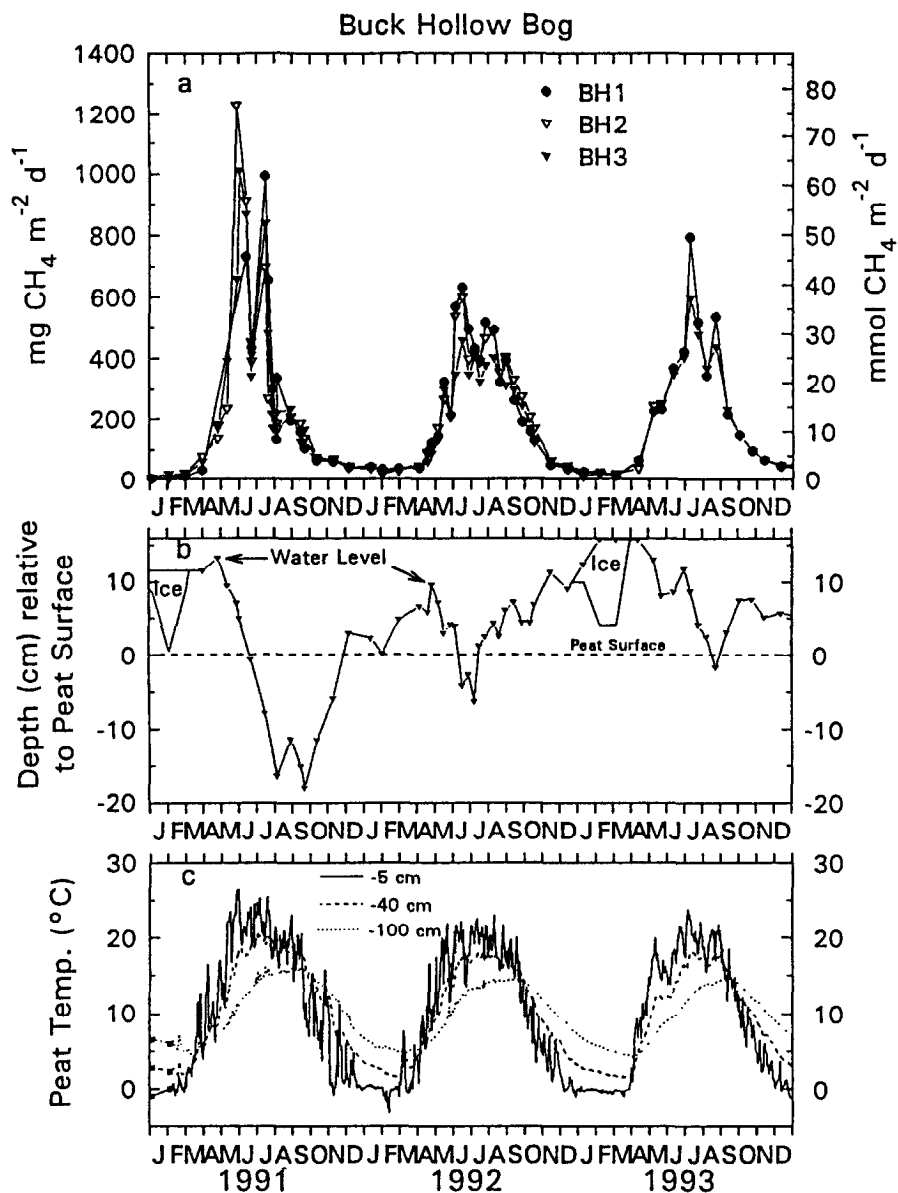
Fig. 2. a) Methane fluxes from Buck Hollow Bog. BH1, 2, and 3 are individual flux chambers located approx. 10 m apart; b) water table position in Buck Hollow Bog; c) peat temperatures at 5, 40 and 100 cm below the peat surface in Buck Hollow Bog. Square symbols represent discrete temperature measurements taken in 1/91 and 2/91; lines without symbols represent daily mean temperatures.

Big Cassandra Bog, site 1
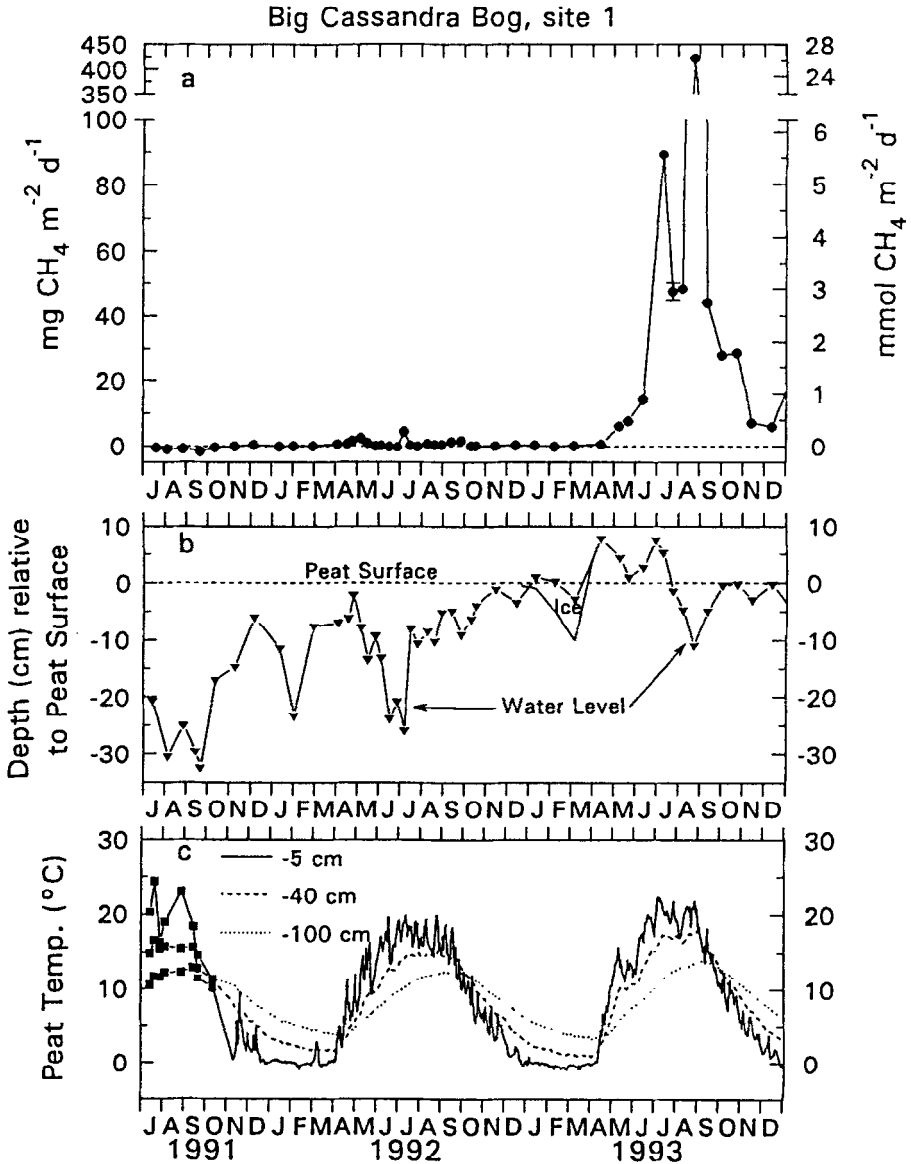
Fig. 3. a) Methane fluxes from Big Cassandra Bog, site 1. Error bars represent ±1 SD of the mean of duplicate time series from one chamber during one day; b) water table position in Big Cassandra Bog, site 1; c) peat temperatures at 5, 40 and 100 cm below the peat surface in Big Cassandra Bog, site 1. Square symbols represent discrete temperature measurements taken from 7/91 to 11/91; lines without symbols represent daily mean temperatures.

Table 1. Spearman's correlation coefficients (r_S) for relationships between CH_4 flux and peat temperature (to -40 cm) or water table position for sites in Buck Hollow (BH) and Big Cassandra (BC) Bogs[1].

Site	Temperature				Water table (May–Sep)			
	1991	1992	1993	All	1991	1992	1993	All
BH	0.88(−15)	0.90 (−5)	0.97 (−5)	0.84 (−5)	0.80	−0.51	NS	0.20
BC1	–	NS	0.96(−20)	NS	–	NS	NS	0.77
BC2	0.63(−15)	NS	0.96(−40)	0.57(−20)	0.79	NS	NS	0.70
BC3	0.62(−20)	NS	0.92(−40)	0.58(−20)	0.79	NS	NS	0.67
BC4	0.86(−20)	0.82(−40)	0.98(−15)	0.70(−20)	0.74	NS	NS	0.76
BC1234	0.69(−20)	0.40(−70)	0.86(−40)	0.65(−20)	0.70	0.52	NS	0.66
All sites	0.74(−20)	0.72(−20)	0.82(−20)	0.72(−20)	0.58	0.39	NS	0.34

[1] All correlation coefficients are significant at $p < 0.05$. Values in parentheses indicate depths below peat surface for best fit-temperature data. NS denotes not significant ($p > 0.05$).

Methane fluxes at all sites in Big Cassandra Bog were significantly less than the three sites in Buck Hollow Bog ($p < 0.05$). In addition, fluxes from site 1 were significantly less ($p < 0.05$) than fluxes from sites 2, 3, and 4 in Big Cassandra Bog. When we began monitoring site 1 in July 1991, methane fluxes were negative, indicating net methane consumption (Fig. 3a). Methane consumption reached a maximum of -1.5 mg CH_4 m^{-2} d^{-1} in late September 1991 and shifted to net methane emission with the onset of winter. During 1992, methane flux at site 1 remained low, ranging between -0.3 and 4.5 mg CH_4 m^{-2} d^{-1}. The two years of low flux coincided with a low water table that never reached the peat surface and was frequently below -20 cm (Fig. 3b). In contrast to 1991 and 1992, methane fluxes in 1993 reached a maximum of 450 mg CH_4 m^{-2} d^{-1}, and generally ranged between 15–90 mg CH_4 m^{-2} d^{-1} throughout the summer. The water table during 1993 was frequently at or above the peat surface. Peat temperatures at -5 cm in site 1 (Fig. 3c) reached a maximum of $+20$ to $+25$ °C in July and August, and declined to near 0 °C during the winter months. Similar to Buck Hollow, peat at lower depths was buffered from temperature extremes. The correlation between methane flux and temperature was not significant in 1992, but strong in 1993, while the flux-water table correlation was not significant for both annual cycles (Table 1).

Methane fluxes from sites 2 and 3 in Big Cassandra Bog were not significantly different ($p > 0.05$), but were significantly lower than sites in Buck Hollow Bog and intermediate to fluxes from sites 1 and 4 in Big Cassandra

Big Cassandra Bog, sites 2 & 3
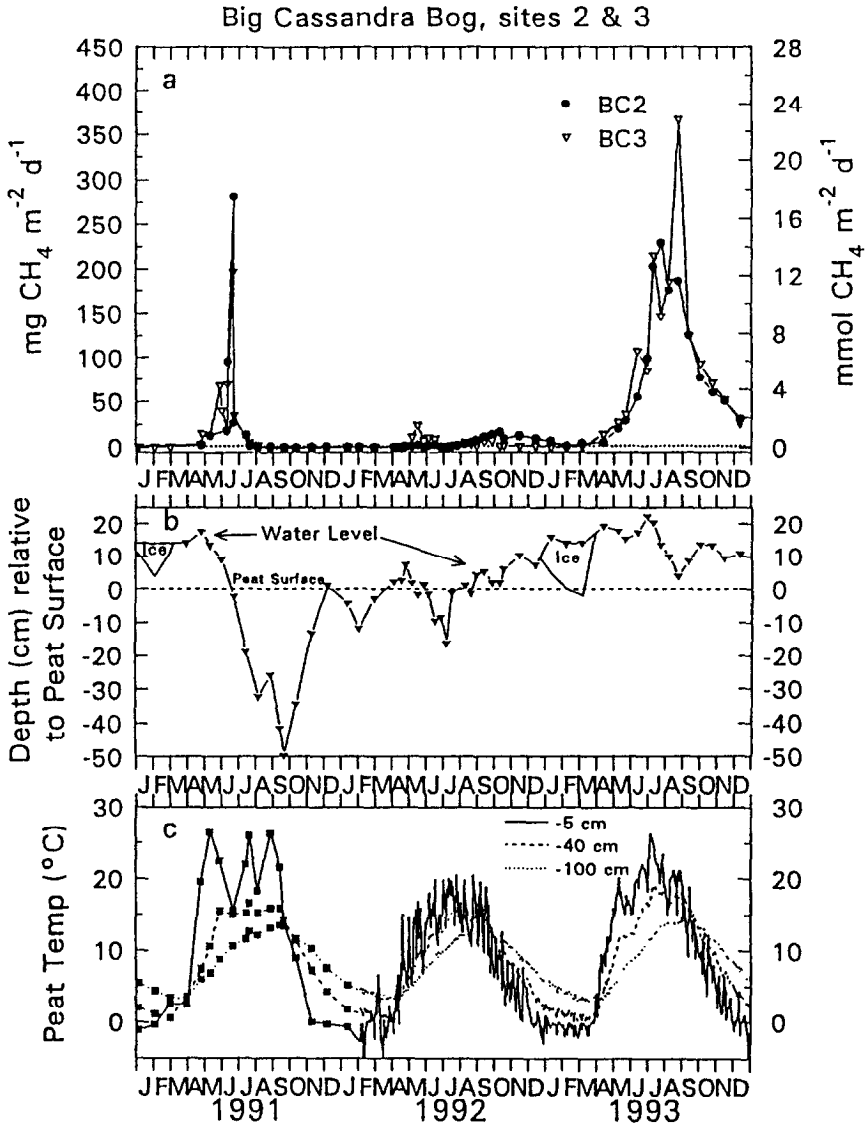
Fig. 4. a) Methane fluxes from Big Cassandra Bog, sites 2 and 3. Error bars represent ±1 SD of the mean of duplicate time series from each chamber during one day; b) water table position in Big Cassandra Bog, sites 2 and 3; c) peat temperatures at 5, 40 and 100 cm below the peat surface in Big Cassandra Bog, sites 2 and 3. Square symbols represent discrete temperature measurements taken from 1/91 to 1/92; lines without symbols represent daily mean temperatures.

Bog. The inter-annual variations in fluxes from these two sites were significantly different ($p < 0.05$) for the three year period (Fig. 4a). During 1991, fluxes reached a maximum of 281 mg CH_4 m^{-2} d^{-1} in mid-June 1991, and decreased sharply in the fall coincident to the rapidly declining water table. Similar to site 1, we observed negative fluxes (-0.1 to -1.6 mg CH_4 m^{-2} d^{-1}) at site 2 and 3 during the fall of 1991. Methane fluxes from sites 2 and 3 remained below 25 mg CH_4 m^{-2} d^{-1} through 1992, but increased to 100–250 mg CH_4 m^{-2} d^{-1} in the 1993 summer.

Water table fluctuations at sites 2 and 3 (as well as site 4) were greater than other sites in both peatlands (Fig. 4b), declining to a minimum at -50 cm in late September. As with other sites, summer peat temperatures at -5 cm fluctuated the most (between $+15$ and $+27$ °C), while at greater depths summer temperatures ranged between $+10$ and $+17$ °C (Fig. 4c). Correlations between methane flux and temperature at sites 2 and 3 were similar, ranging from moderate to strong in 1991 and 1993, to not significant in 1992. In contrast, the flux-water table correlation at the two sites was strongest in 1991, and not significant in the two subsequent annual cycles (Table 1).

Methane fluxes from site 4 in Big Cassandra Bog were significantly greater ($p < 0.05$) than sites 1, 2, and 3. Fluxes from site 4 increased to 75 mg CH_4 m^{-2} d^{-1} by late June 1991, then decreased precipitously to less than 5 mg CH_4 m^{-2} d^{-1} by October, coinciding with a rapid decline in the water table below the peat surface (Fig. 5a,b). During 1992, fluxes at site 4 increased to 101 mg CH_4 m^{-2} d^{-1} by mid-June, and then dropped ten-fold to 10 mg CH_4 m^{-2} d^{-1} by early July as the water table declined to -16 cm. In contrast to the 1991 summer, methane fluxes quickly rebounded to 70–90 mg CH_4 m^{-2} d^{-1} through September 1992 when water levels returned to the peat surface in mid-July. Unlike sites 1, 2, and 3, we did not observe negative methane fluxes at the *Carex*-dominated site 4 on any sampling date. The extreme fluxes observed during 1993 at site 4 coincided with the only period when the water table was consistently above the peat surface for the entire summer. Peat temperatures at site 4 (Fig. 5c) were similar to those at sites 2 and 3, with surface peats (-5 cm) exhibiting greater seasonal fluctuations in temperature than deeper (-40, -100 cm) peats. The correlations at site 4 between methane flux and peat temperature, like Buck Hollow Bog, were strong for the three annual cycles, while the flux-water table correlations ranged from not significant to moderately strong (Table 1).

Porewater profiles of dissolved methane

Representative porewater profiles of dissolved methane for Buck Hollow Bog and sites 1 and 4 in Big Cassandra Bog are shown in Fig. 6a–i. Note the effects of fluctuations in the water table on the depth of the dissolved methane
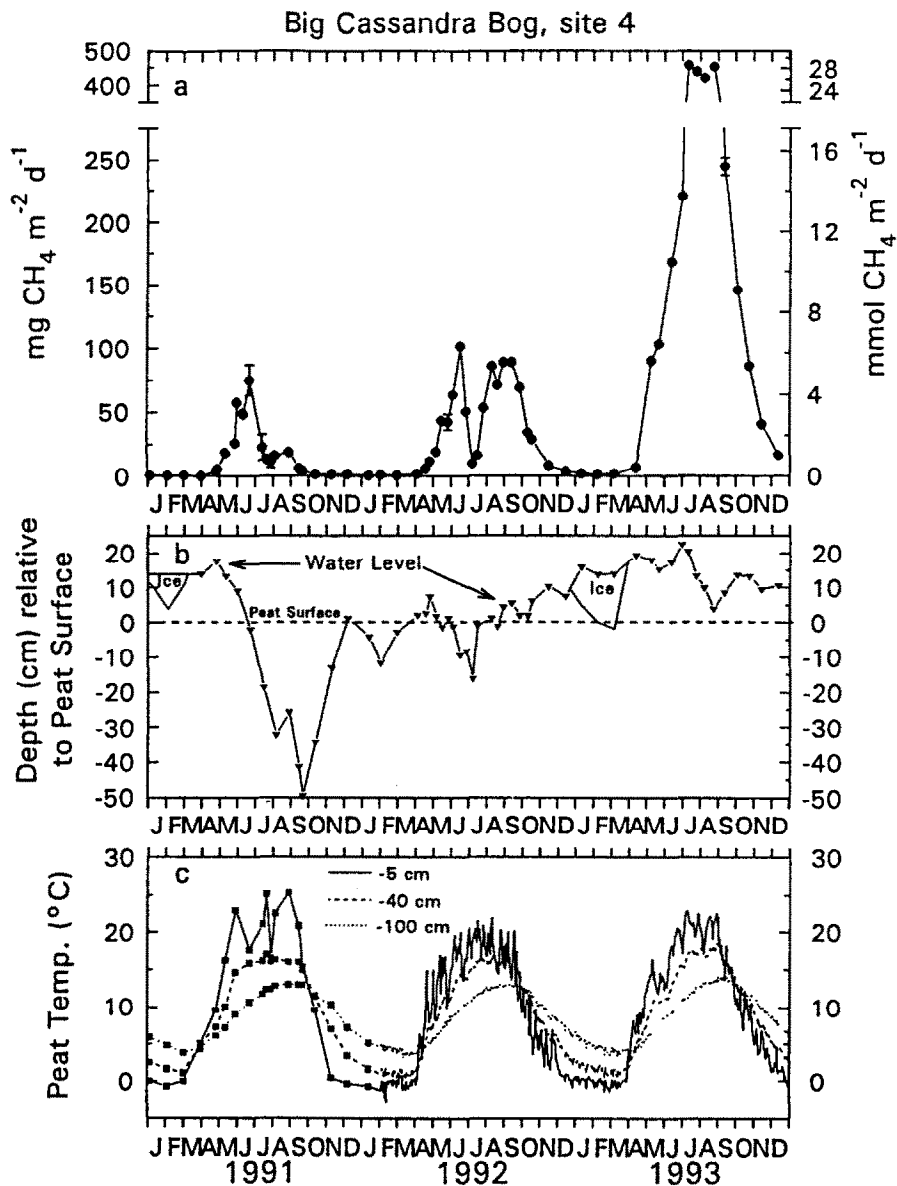
Fig. 5. a) Methane fluxes from Big Cassandra Bog, site 4. Error bars represent ±1 SD of the mean of duplicate time series from one chamber during one day; b) water table position in Big Cassandra Bog, site 4; c) peat temperatures at 5, 40 and 100 cm below the peat surface at Big Cassandra Bog, site 4. Square symbols represent discrete temperature measurements taken from 1/91–2/92; lines without symbols represent daily mean temperatures.

BUCK HOLLOW BOG

BIG CASSANDRA BOG, site 1

BIG CASSANDRA BOG, site 4
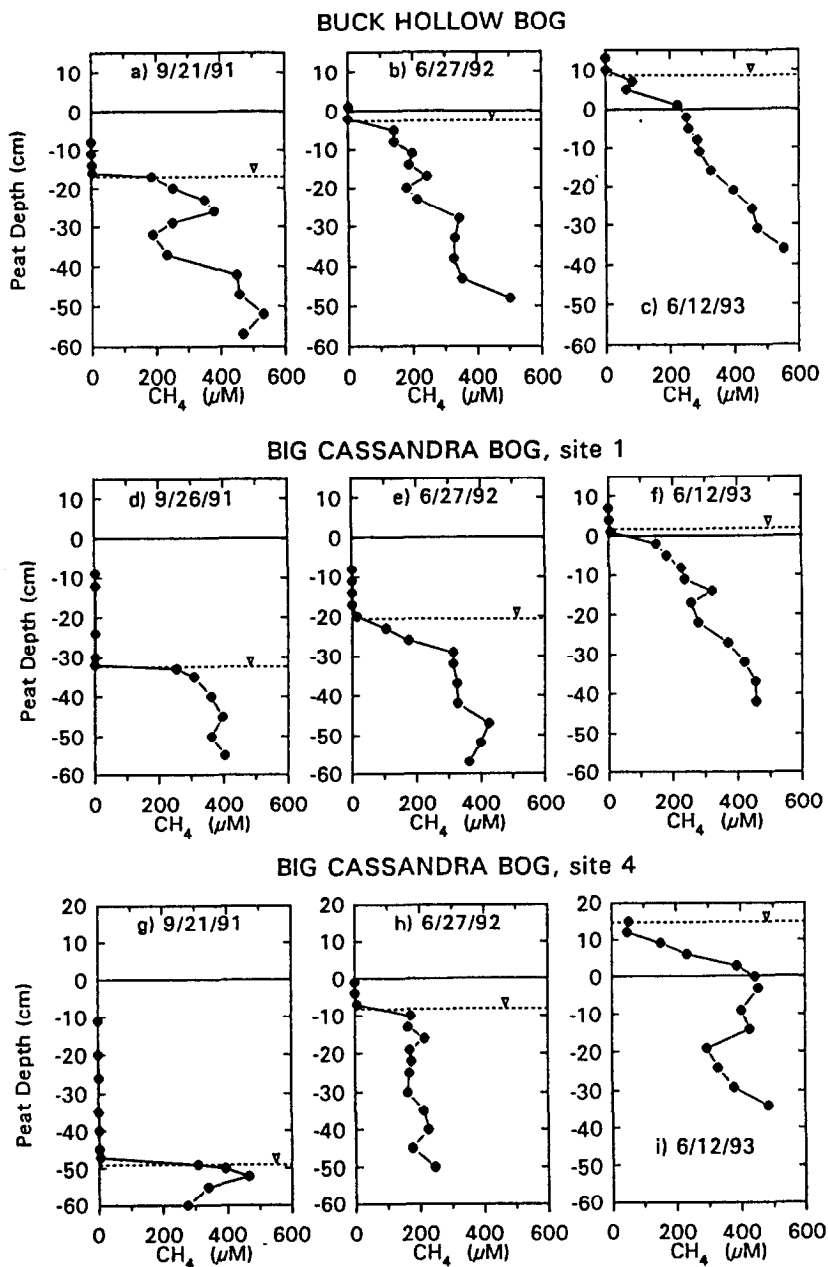
Fig. 6. Porewater concentrations (μM) of dissolved methane in; a–c) Buck Hollow Bog; d–f) Big Cassandra Bog, site 1, and; g–i) Big Cassandra Bog, site 4. The solid horizontal line at 0 cm represents the peat surface, while the dotted line and triangle indicate the water table position on that date.

Table 2. Mean daily methane fluxes from Buck Hollow and Big Cassandra Bogs.[1]

Site	Annual period		
	1991	1992	1993
BH	209 (±2)	187 (±16)	183 (±8)
BC1	–	0.6	38.0
BC23	11.4 (±0.6)	4.3 (±1.2)	68.4 (±7.3)
BC4	11.5	29.5	130

[1] Values are daily means for annual fluxes in mg CH_4 m^{-2} d^{-1}. All mean daily fluxes were determined by integration of the flux curve over the annual period. Values for Buck Hollow Bog (BH) represent means of three replicate chambers (±1 SD) in 1991 and 1992, and two chambers in 1993. BC23 represents the mean (±1 SD) of single chambers at sites 2 and 3 in Big Cassandra Bog.

pool and the shape of the concentration gradient. During the dry summer of 1991, the dissolved methane pool at all sites was located as much as 18 to 50 cm below the peat surface due to the low water table (Fig. 6a,d,g). The methane concentrations increased to 300–400 μM within several cm below the water table, indicating a net flux of methane from the saturated peat into the unsaturated zone. By the summer of 1992, the water table had increased to near the peat surface; methane accumulated in porewater closer to the peat surface (Fig. 6b,e,h). This trend continued in 1993, when the water table and the methane pool were near or above the peat surface (Fig. 6c,f,i).

Methane oxidation in peat cores

We observed methane consumption in aerobic peat cores obtained from Buck Hollow Bog and site 1 in Big Cassandra Bog in September 1992 (Fig. 7). First-order methane consumption was observed in all experiments, as indicated by least-squares regression of the decrease in the natural logarithm of methane concentration with time ($r^2 > 0.99$, $p < 0.001$, in all experiments). In the Buck Hollow core sections, methane concentrations were depleted to a threshold of 0.45 ppmv. The sections from site 1 in Big Cassandra Bog did not reach threshold values in the time allowed for the experiments, but concentrations in the 10–20 and 20–30 cm sections were depleted to below 0.90 ppmv. Acetylene additions to separate cores completely arrested methane consumption, confirming that the decrease in methane was a result of microbial oxidation.
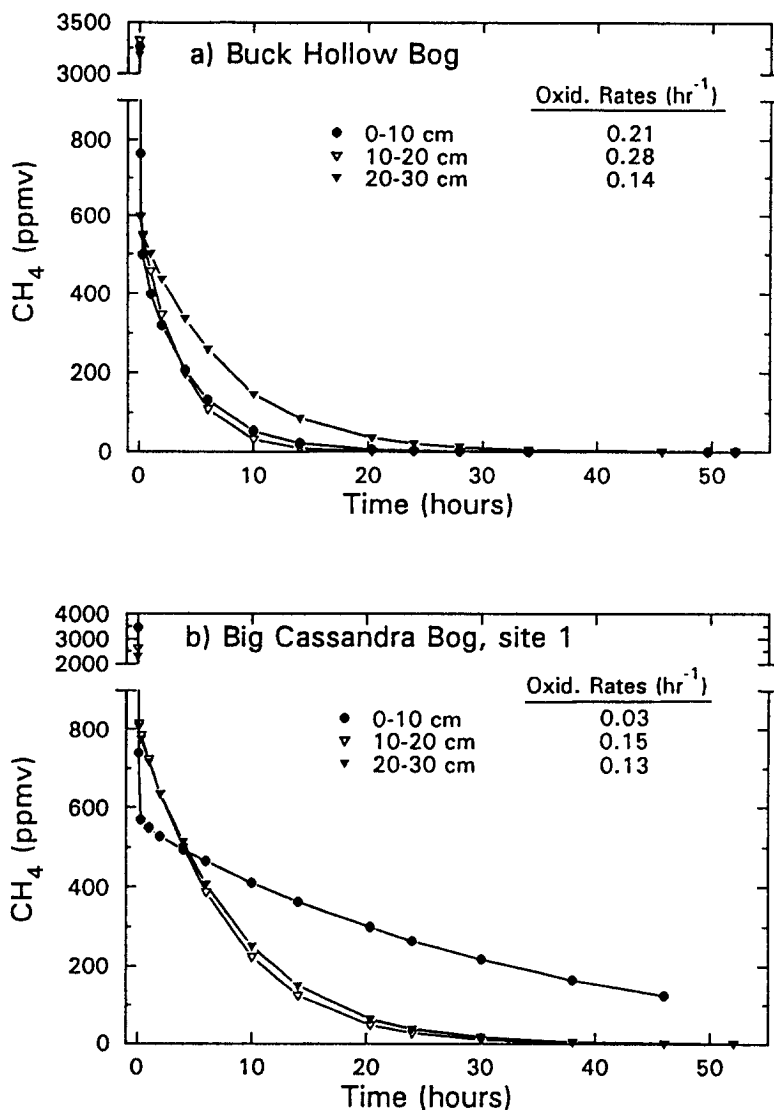
Fig. 7. Methane consumption in peat cores from a) Buck Hollow Bog; b) Big Cassandra Bog, site 1. The oxidation rates are first-order constants for each core section calculated from the slope of the natural logarithm of CH_4 concentration (ppmv) vs. time. Cores were obtained in September 1992.

Annual fluxes

Mean daily fluxes were determined by integration of the time series data for methane flux encompassing the three annual cycles (Table 2). Buck Hollow Bog had the highest and most consistant mean daily fluxes (183–209 mg CH_4

m^{-2} d^{-1}), whereas mean fluxes at all sites in Big Cassandra Bog exhibited large interannual differences. Site 1 in Big Cassandra Bog had the lowest mean flux (0.6 mg CH_4 m^{-2} d^{-1}), nearly three orders of magnitude less than mean fluxes in Buck Hollow. The high mean daily flux for 1991 at sites 2 and 3 combined (11.4 mg CH_4 m^{-2} d^{-1}) was a result of high fluxes observed during early June 1991, despite the negative fluxes observed later in the summer (Fig. 4a). The mean daily flux for 1992 at sites 2 and 3 was significantly lower (4.3 mg CH_4 m^{-2} d^{-1}, $p < 0.05$). We observed the opposite trend at site 4 in Big Cassandra Bog; the 1991 mean daily flux (11.5 mg CH_4 m^{-2} d^{-1}) was significantly lower than the 1992 mean daily flux (29.5 mg CH_4 m^{-2} d^{-1}). In 1993, mean fluxes from all sites in Big Cassandra Bog were significantly higher ($p < 0.05$) than means fluxes in either 1991 or 1992.

Discussion

Relationships between methane flux and environmental parameters

In this study, a strong correlation between methane flux and peat temperature was observed in Buck Hollow Bog and Big Cassandra Bog site 4 ($r_S = 0.82$–0.98) for 1991 (Table 1). The flux-temperature correlation at these two sites was always stronger than the flux-water table correlation (not significant -0.80). The water table in Buck Hollow Bog did not decline as much in 1991 as the Big Cassandra sites (-18 cm vs. -32 to -50 cm, respectively), thus the stronger correlation between flux and temperature is probably due to the small effect of the water table on the balance of methane production and oxidation, as has been observed at other wet sites (Wilson et al. 1989; Whalen & Reeburgh 1992). The vascular plants at Buck Hollow Bog and site 4 in Big Cassandra Bog (*S. palustris* and *C. oligosperma*) may have mitigated the effects of the low water table on methane flux by bypassing the large zone of aerobic peat and transporting methane through roots and stems directly to the atmosphere (Chanton & Dacey 1991; Whiting & Chanton 1992).

In contrast, fluxes at sites 2 and 3 in Big Cassandra Bog were more strongly correlated with water table position ($r_S = 0.79$) than with temperature ($r_S = 0.62$–0.63) during 1991 (Table 1). These sites were dominated by the woody shrub, *C. calyculata*. Positive correlations between methane flux and water level have been observed in other investigations where the water table frequently declines below the peat surface (Moore et al. 1990; Whalen & Reeburgh 1990; Dise et al. 1993). The pattern of declining methane flux in response to a declining water table position is demonstrated particularly well in our study by the 1991 mid-summer 'crash' in methane flux that was observed at sites 2, 3, and 4 in Big Cassandra Bog (Figs. 4, 5). There also appears to be a threshold at -15 cm; below this depth methane fluxes within
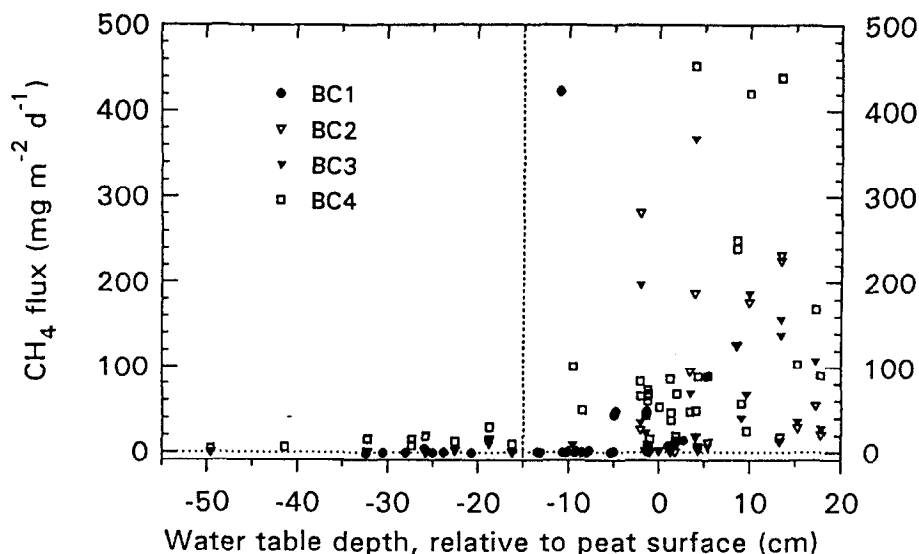
Fig. 8. Water table depth (cm) vs. methane flux for sites for sites 1, 2, 3, and 4 in Big Cassandra Bog (May–September data). Methane fluxes to the left of the vertical dashed line at -15 cm were significantly less ($p < 0.05$) than fluxes to the right of the line.

individual sites are significantly less ($p < 0.05$) than when the water table is above -15 (Fig. 8). Moore & Roulet (1993) obtained results similar to our field observations by manipulating water levels in peat columns obtained from bogs and fens. Methane fluxes were greatest when the water table declined from the peat surface to -20 cm, but fluxes decreased rapidly as water levels continued to declined from -20 to -50 cm. Conversely, methane flux remained near zero until the water level was raised to near the peat surface. These findings are also similar to our results from sites 1–4 in Big Cassandra Bog. When water levels rose to the peat surface following the 1991 dry period, methane fluxes were the lowest we observed during the three year study, with net methane consumption (negative flux) frequently observed at sites 1, 2, and 3 (Figs. 3a, 4a).

Our field results, as well as the laboratory studies of Moore & Roulet (1993) indicated that a sustained decline in the water table affects methane flux in several ways. As the water table initially declines below the peat surface, the methane gradient is probably steep and high methane fluxes can continue because methane production and consumption have not been affected. When the water reaches -15 to -20 cm, the oxic-anoxic interface has moved below shallow zones of methane production, adversely affecting methanogenic populations. Aerobic methane-oxidizing (methanotrophic)

bacteria can also become established in the deepening zone of aerobic, unsaturated peat and significantly deplete methane diffusing from the saturated peat.

In 1992 and 1993, the correlation between methane flux and temperature remained strong at Buck Hollow Bog and site 4 in Big Cassandra Bog (r_S 0.82–0.98, Table 1). However, the correlations between methane flux and water table or temperature for the shrub sites (sites 1, 2, and 3 in Big Cassandra Bog) in 1992 were not significant. These findings are consistent with the hypothesis that temperature affects the short-term metabolic processes that generate methane, while water table position has both short- and long-term effects that control methanogenic and methanotrophic populations within a site (Yavitt et al. 1990b; Dise et al. 1993; Moore & Roulet 1993). The rapid, or short-term effects of water table changes were most evident during 1991 at sites 1, 2, and 3 in Big Cassandra Bog, when the water table declined below −15 to −20 cm. As the zone of aerobic, unsaturated peat increased, fluxes of methane at these sites became negative, indicating consumption of methane diffusing upward from saturated peat as well as consumption of atmospheric methane diffusing into the upper, aerobic peat. The long-term consequences of the large, unsaturated zone are evident the following year. Methane fluxes remained low in 1992, and fluxes did not increase significantly until the 1993 summer, two years after the low water conditions. The long-term effects may be caused by a reduction in the population of methanogenic bacteria during the long period of low water levels, followed by low temperatures that inhibited the regrowth of bacterial populations. Other possibilities for long-term effects include changes in the availability of methanogenic substrates, as well as changes in supply of alternate electron acceptors, such as sulfate.

Relationships between diffusive and plant transport of methane

There are three major mechanisms for methane transport from the saturated zone: molecular diffusion, ebullitive transport, and direct transport through the aerenchymatous tissues of vascular plants. Diffusive flux is defined by Fick's first law;

$$F = -\Phi \cdot D \cdot \frac{dC}{dz}$$

where F is the diffusive flux, Φ is the porosity of the peat matrix in the zone of interest (approx. 0.90–0.95 in surface peats), D is the molecular diffusion coefficient for methane in water (1.62×10^{-5} cm^2 s^{-1} at 20 °C, Jähne et al. 1987), and dC/dz is the concentration gradient of porewater methane. We determined dC/dz from the steepest slope of the methane gradient directly below the air-water interface (Fig. 6).
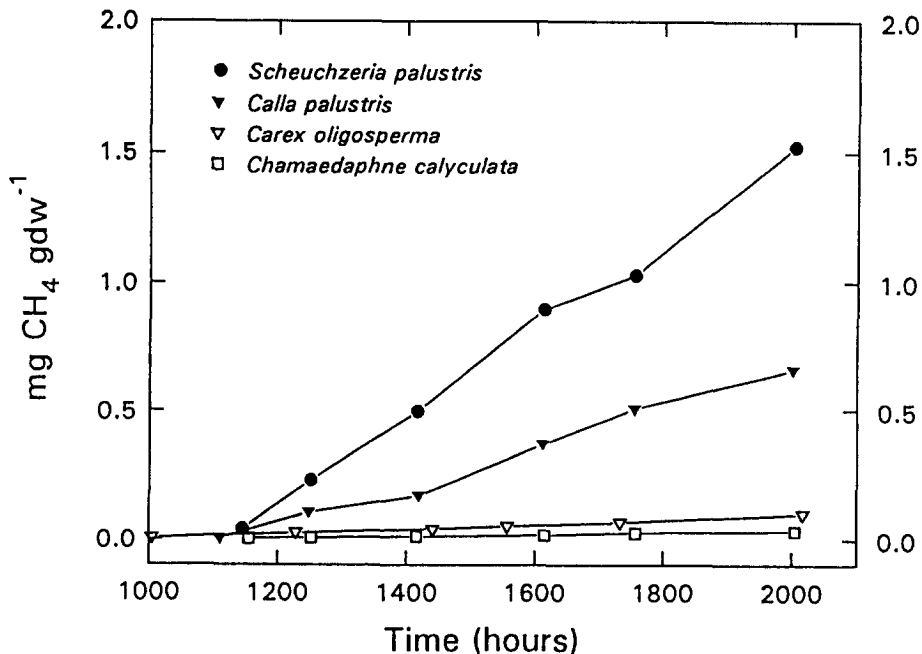
Fig. 9. Mass of methane emitted from vascular plants common to Buck Hollow Bog and Big Cassandra Bog as a function of time of day. Mass of methane at each time interval is normalized to the dry weight (gdw) of each plant enclosed in a chamber. All measurements were taken in May 1992.

The proportion of diffusive flux contributing to net flux from Buck Hollow Bog was 25% during the low water period in September 1991 (Fig. 6a). In 1992 and 1993, diffusive flux during the growing season was less than 5% of the net flux from the peat surface (Fig. 6b, 6c). These determinations were supported by our plant enclosure experiments; high rates of methane transport (4.17 mg CH_4 gdw^{-1} d^{-1}) occurred through the aerenchymatous stems of *S. palustris* (Fig. 9), which is enhanced by its deep rhizosphere extending to greater than 80 cm below the peat surface. Although not directly measured, ebullition appeared to be a minor component of net flux except during late May–early June. Therefore, we estimate that direct methane emissions from *S. palustris* can account for as much as 75% of the net methane flux from Buck Hollow during the growing season, with the remaining 25% contributed by ebullition and diffusion.

In contrast, methane flux at site 1 in Big Cassandra Bog is limited to diffusive or ebullitive flux. Our plant enclosures of *C. calyculata*, the dominant vascular plant species at site 1, indicated that very low rates of methane were emitted through the stems and leaves of this woody shrub (0.09 mg CH_4 gdw^{-1} d^{-1}, Fig. 9). Diffusive fluxes for 1991 and 1992, calculated from the

porewater profiles of methane, indicate that more methane diffused from the saturated zone than was emitted to the atmosphere (Fig. 6d,e). However, in 1993, a year of high water tables and high flux at site 1 (note that fluxes were still 10 times less than in Buck Hollow Bog), the diffusive flux based on the dissolved methane profile (20 mg CH_4 m^{-2} d^{-1}) was similar to the net flux measured with the chamber method (14 mg CH_4 m^{-2} d^{-1}). This suggests that the majority of methane emitted from site 1 is from diffusion, and that methane oxidation exerts a stronger influence on the net flux of methane from this site.

C. oligosperma, the dominant vascular plant at site 4 in Big Cassandra Bog, is also a significant methane emitter relative to *C. calyculata* (0.22 mg CH_4 gdw^{-1} d^{-1} vs. 0.09 mg CH_4 gdw^{-1} d^{-1}, Fig. 9). Whiting & Chanton (1992) have also observed direct emissions of methane from *Carex* spp. When we compare flux chamber measurements with calculations of diffusive fluxes from methane gradients during the growing season (Fig. 6g–i), the percentage of net flux from transport through *C. oligosperma* appears to increase as the water table rises. The roots of *C. oligosperma* extend 20–30 cm below the peat surface at Big Cassandra Bog, unlike the greater than 80 cm penetration of *S. palustris* rhizomes in Buck Hollow Bog. When the water table declines below 20–30 cm, as during the summer and fall of 1991, the ability of *C. oligosperma* to transport methane to the atmosphere is reduced because its roots no longer extend into the pool of dissolved methane below the water table. On 9/21/91, the water table at site 4 in Big Cassandra Bog had declined to −50 cm, and the methane flux, as calculated from the diffusion gradient (Fig. 6g), was 9 to 12 mg CH_4 m^{-2} d^{-1}. The net flux from the static chamber on the same date was 4 mg CH_4 m^{-2} d^{-1}, indicating that 55% to 67% of the methane diffusing upward from the saturated zone below −50 cm was consumed, presumably by methanotrophic bacteria, before reaching the peat surface. As the water table increased in 1992 and 1993 (Fig. 6h and 6i, respectively), the percentage of net flux due to direct emissions through *C. oligosperma* increased from 30–60% in 1992 to 82–95% in 1993.

Methane oxidation

The high rates of methane consumption observed in the peat core experiments (Fig. 7) are an indication that significant methane consumption occurs at sites dominated by plants capable of transporting methane (e.g. Buck Hollow Bog, Big Cassandra Bog site 4), as well as at sites devoid of these plants (Big Cassandra Bog sites 1, 2, and 3). In addition, our peat core experiments and field results indicate that populations of methane-consuming bacteria are likely to be affected by water table conditions specific to individual sites. For instance, at site 1 in Big Cassandra Bog, the water table was frequently

positioned below -30 cm in 1991 and 1992. Therefore, the largest populations of methane-oxidizing bacteria were probably located in the aerobic peat directly above the methane pool diffusing upward from the saturated zone. Our laboratory experiments support this hypothesis, as the first-order consumption rate constants in the -10 to -20 cm, and -20 to -30 cm core sections (0.15 and 0.13 hr^{-1}, respectively) were four to five times higher than the 0 to -10 cm section (0.03 hr^{-1}). Conversely, the consumption rate constants in the 0 to -10 cm and -10 to -20 cm sections from Buck Hollow (0.21 and 0.28 h^{-1}, respectively) were higher than the rate constant from the -20 to -30 cm section of peat core (0.14 hr-1). These results indicate that methane-consuming bacteria may not become established in peats which are saturated with water (and anaerobic) throughout the year, i.e. below -20 cm for the duration of the study in Buck Hollow. It appears that they do thrive in peats that fluctuate between unsaturated (largely aerobic) and saturated (anaerobic) conditions. Our results are supported by other research showing that significant proportions of methane diffusing from the saturated zone of peatlands through the unsaturated zone can be oxidized (Fechner & Hemond 1992).

Methane oxidation at sites 1, 2, and 3 in Big Cassandra Bog was evident from the negative fluxes observed during low water periods. The effect of methane oxidation on net fluxes at Buck Hollow and site 4 in Big Cassandra Bog was not as evident due to the positive fluxes maintained at these sites at all times. Nevertheless, during low water periods the ability of plants such as *S. palustris* and *C. oligosperma* to transport methane can be partially offset by methane consumption in the unsaturated peat so that the net flux is significantly reduced. The lowering of the water table from $+5$ cm to -18 cm between June and late September 1991 coincided with an eight-fold decline in methane flux from Buck Hollow Bog. Additionally, mean daily methane fluxes for September 1991 (water table between -12 and -18 cm) and September 1992 and 1993 (water table between $+1$ and $+7$ cm) were 136 and 223–317 mg CH_4 m^{-2} d^{-1}, respectively (significantly different at $p < 0.05$), suggesting that changes in methane fluxes for different years but the same months was due to methane oxidation.

Annual fluxes

We compared the annual fluxes from this study with reported values for other North American wetlands (Table 3). The annual flux for Buck Hollow is among the highest values reported, and is intermediate to the methane flux from beaver ponds in West Virginia (Yavitt & Lang 1990b), and S-4 bog (an open bog) and Junction Fen in Minnesota (Dise 1992). The water table positions at these sites were either at or above the peat/soil surface for major

Table 3. Annual methane flux for peatland sites in North America.[1]

Reference	Site	Annual flux ($g CH_4 m^{-2} yr^{-1}$)	Latitude
Yavitt et al. 1990b	West Virginia, USA;		39°07′–39°34′ N
	shrub wetlands	−0.13	
	other wetlands	2.2	
	beaver ponds	91	
This study	Michigan, USA;		42°27′ N
	2 temperate bogs		
	Buck Hollow	66.9–76.3	
	Big Cassandra		
	site 1	0.2–13.9	
	site 2 and 3	1.6–25.0	
	site 4	4.2–47.3	
Roulet et al. 1992	Ontario, Canada;		45°04′ N
	low boreal forest		
	wetland sites	1.63	
	beaver ponds	7.6	
	conifer swamps	0.18	
	thicket swamps	4.7	
	mixed swamps	1.7	
	bogs	1.7	
	fens	0.36	
Dise et al. 1993	Minnesota, USA;		47°32′ N
	S-2 bog	10	
	S-4 bog	43	
	Junction Fen	66	
Lansdown et al. 1992	Washington, USA		47°35′ N
	Kings Lake Bog	35.5	
Moore & Knowles 1990	Quebec, Canada;		
	temp. domed bogs	0.1	45°33′ N
	temperature swamps	1.2–4.7	45°32′ N
	subarctic fens	1.3–9.9	54°48′ N
Moore et al. 1990	Quebec, Canada;		54°48′ N
	subarctic/boreal fens	10.4	
Whalen & Reeburgh 1992	Alaska, USA; tundra		64°52′ N

Table 3 cont'd

Reference	Site	Annual flux (g CH$_4$ m^{-2} yr^{-1})	Latitude
	Eriophorum	10.3	
	Carex	17.6	
	Moss	2.5	
	Black Holes	7.4	
Sebacher et al. 1986	Alaska, USA; bogs, fen and boreal marsh	11.2	65°–70°20' N

[1] All studies were seasonal and conducted at fixed sites, except for Sebacher et al. (1986), which was conducted along a transect over several days.

portions of the year. In contrast, annual fluxes from Big Cassandra Bog are more comparable to the low boreal bogs of Ontario (Roulet et al. 1992) as well as peatland sites with shrubs in West Virginia (Yavitt et al. 1990b). However, we emphasize that the Big Cassandra sites demonstrate the large variability in annual flux which can occur in systems with a highly dynamic water table (Table 2).

Our results, as well as those of others, indicate that plant communities exert a primary influence on methane flux (Table 3). For example, Whalen & Reeburgh (1992) observed higher annual methane fluxes on sites dominated by *Eriophorum* and *Carex* (10.3–17.6 g CH$_4$ m^{-2} yr^{-1}) compared to plots without vascular plants (2.5–7.4 g CH$_4$ m^{-2} yr^{-1}). The role of plants as direct conduits for gas exchange can also obscure latitudinal (or climatic) influences on methane flux; thus, annual fluxes from sites in Alaska that are dominated by vascular sedges (Whalen & Reeburgh 1992) can be much higher than sites without methane-transporting plants at lower latitudes and higher peat temperatures (Yavitt et al. 1990b; Roulet et al. 1992; this study). In addition to direct transport of methane through plants, there are several other mechanisms by which plant communities can affect annual methane fluxes in peatland ecosystems. The quality of organic carbon providing substrates for methanogenesis has been cited as a reason for differing fluxes among plant communities (Yavitt & Lang 1990; Valentine et al. 1994). For instance, Yavitt & Lang (1990) found higher rates of methane production in peat obtained from bogs lacking shrub growth. Peat with shrub growth had a higher amount of acid-insoluble carbon, suggesting that the more refractory carbon was not as rapidly converted to labile substrates for methanogens. The acid-insoluble

organic matter is primarily derived from lignin, and requires woody plant tissue for its formation. The differing methane fluxes in our systems support these findings. The highest annual fluxes were observed at Buck Hollow and Big Cassandra site 4, where the decomposition of *S. palustris* and *C. oligosperma* is likely to provide more labile substrates than the refractory organic matter derived from the ericaceous shrubs dominating the ground cover at sites 1, 2, and 3 in Big Cassandra Bog, where annual fluxes were low (Table 2).

Plant communities may also control methane fluxes in peatland ecosystems through indirect effects on the water table (Nichols & Brown 1980). The hummock-hollow microtopography at sites 1, 2 and 3 in Big Cassandra Bog exposes more surface area of moss to the atmosphere, and evaporation from the moss layer may be increased over that in Buck Hollow Bog, where a flat, sphagnum lawn is prevalent. The increased rates of water loss from evaporation in Big Cassandra Bog may lead to greater declines in the water table during periods of low rainfall. In turn, the lower water table provides a deeper zone for methane oxidation to occur within the moist, aerobic peat above the water surface. The effects of lowered water table also include lower methane production and methane flux for at least a year following the return of saturated conditions. Reduction in methanogenic bacteria in upper peat layers from extended aerobic conditions appears to require long periods (>1 yr) of saturation to revive methane production.

Conclusions

Our results indicate that several environmental factors, as well as processes related to the plant communities, are responsible for regulating the spatial and temporal variations in methane emission from the two peatland ecosystems. The factors which are clear from our study include: 1) water table position and peat temperature, which account for some of the among- and within-site variability in methane flux, both seasonally and over several annual cycles; 2) methane oxidation in the aerobic surface layers of peat; 3) the transmission of methane directly to the atmosphere by plants. Our results show that certain vascular plant communities obscure the effect of water table on methane emissions by serving as conduits which circumvent the zone of fluctuating water table. It is also likely that plants control the quantity and quality of substrates from decaying plant tissues and from root exudates that are available to methanogenic bacteria. Future investigations should continue to address the short and long-term effects of physical parameters, such as temperature and water levels, while also attempting to determine the interrelationships between physical parameters and vascular plant communities as they affect methane flux from peatland ecosystems.

Acknowledgements

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