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### Permalink

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### Journal

Geomicrobiology Journal, 17(3)

### ISSN

0149-0451

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### Publication Date

2000-07-01

### DOI

10.1080/01490450050121198

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## Methane Oxidation, Production, and Emission at Contrasting Sites in a Boreal Bog

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*Boreal peatlands, a major source of atmospheric CH<sub>4</sub>, are characterized by a rapidly fluctuating water table position and meter-scale variations in relief. Regional and ecosystem-based studies show that water table position generally controls CH<sub>4</sub> emission from boreal peatlands by influencing the relative extent of the zones of CH<sub>4</sub> oxidation and production within the peat profile. We used a combined field and laboratory study to assess the influence of local hydrology on the short-term dynamics of CH<sub>4</sub> production, oxidation, and emission from sites in an Alaskan boreal peatland that were characterized by temporarily (site LB1A) and permanently (LB2) water-saturated subsurface peat during the thaw season. The two sites contrasted sharply with respect to the dynamics of CH<sub>4</sub> cycling. Site LB1A, which showed low CH<sub>4</sub> concentrations in pore water (<2 μM) and unsaturated peat (<2.6 nM), consumed both atmospheric CH<sub>4</sub> and CH<sub>4</sub> diffusing upward from the saturated zone for a net flux of -0.9 mg CH<sub>4</sub> m<sup>-2</sup> d<sup>-1</sup>. In contrast, LB2 had pore water CH<sub>4</sub> concentrations, 300 μM and emitted CH<sub>4</sub> at 69 mg m<sup>-2</sup> d<sup>-1</sup>. Roughly 55% of the CH<sub>4</sub> diffusing upward from the saturated zone at LB2 was oxidized in transit to the peat surface. Methane oxidation potentials (V<sub>ox</sub>) were maximum in the 10-cm zone immediately above the local water table at both sites but were greater on a dry mass (dw) basis at LB2 (498–650 ng CH<sub>4</sub> g<sub>dw</sub><sup>-1</sup> h<sup>-1</sup>) than at LB1A (220–233 ng CH<sub>4</sub> g<sub>dw</sub><sup>-1</sup> h<sup>-1</sup>). Methane production potentials (V<sub>p</sub>) were low (<2 ng CH<sub>4</sub> g<sub>dw</sub><sup>-1</sup> h<sup>-1</sup>) at LB1A, but the maximum at LB2 (139 ng CH<sub>4</sub> g<sub>dw</sub><sup>-1</sup> h<sup>-1</sup>) was spatially coupled with the maximum V<sub>ox</sub>. Methanogens exposed to O<sub>2</sub> produced no CH<sub>4</sub> in a subsequent 48 h anoxic incubation, whereas methanotrophs incubated anoxically oxidized CH<sub>4</sub> vigorously within 20 h of return to an oxic environment, indicating that the former are more sensitive than the latter to adverse O<sub>2</sub> conditions. Experiments with <sup>14</sup>CH<sub>4</sub> showed that ~71% of assimilated <sup>14</sup>CH<sub>4</sub> was respired as <sup>14</sup>CO<sub>2</sub>. Respiration by methanotrophs contributes at most ~1.1–1.7% (molar basis) of gross ecosystem respiration (15.6–17.9 mg CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>) at these sites.*

**Keywords** boreal bog, methane oxidation, methanogenesis, peatlands

A 1% annual increase in the atmospheric concentration of the radiatively important trace gas CH<sub>4</sub> over the last 200 years is well documented (Houghton et al. 1996), and CH<sub>4</sub> currently

Received 29 February 2000; accepted 1 May 2000.

This research was supported by the U.S. Environmental Protection Agency and the National Institute for Global Environmental Change.

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contributes ~20% to global warming (Bouwman 1990). The relative importance of CH<sub>4</sub> as a greenhouse gas is expected to increase, given that, on a mass basis, CH<sub>4</sub> has a global warming potential 56 times that of CO<sub>2</sub> in a 20-year time horizon (Houghton et al. 1996).

Wetlands are the largest natural source of atmospheric CH<sub>4</sub>, contributing 110 Tg annually, or 20% of the total emission from all sources (Fung et al. 1991). High-latitude (>45°N) peatlands emit 38 Tg of CH<sub>4</sub> annually (Bartlett and Harriss 1993) and are therefore particularly important in the atmospheric CH<sub>4</sub> budget. Methane emission from peatlands depends in part on the balance between methanogenesis in an anaerobic, subsurface zone and CH<sub>4</sub> oxidation by methanotrophs in an overlying, aerobic layer (Whalen and Reeburgh 1992; Whalen et al. 1996). Dissolved O<sub>2</sub> profiles in peatlands indicate that the oxic zone extends from the surface of the water saturation or a few centimeters below (Benstead and Lloyd 1994; Nedwell and Watson 1995; Whalen et al. 1996). Water table position therefore serves as an indicator of the relative extent of the zones of CH<sub>4</sub> production and oxidation. Accordingly, CH<sub>4</sub> emission from peatlands has been positively correlated with water table position through repeated measurements in individual wetlands (e.g., Crill et al. 1988; Moore et al. 1990; Shannon and White 1994) or by regional comparisons of mean CH<sub>4</sub> fluxes and water table positions (reviewed by Bubier and Moore 1994).

Peatlands are characterized by surface heterogeneity and fluctuating water table position (Clymo and Pearce 1995). In particular, differences in relief and microtopography within a specific high-latitude peatland underlain by permafrost may result in local water table fluctuations ranging from near zero on a seasonal scale to 30 cm over hours to days (Whalen and Reeburgh 1992; Moosavi et al. 1996). This results in differences in the thermal regime, nutrient cycling, plant community composition, and organic matter production on a scale of several meters (Waddington and Roulet 1996). Consequently, studies documenting the generalized relationship between wetland CH<sub>4</sub> emission and water table position at the ecosystem to regional scale lack the temporal and spatial resolution necessary to assess the short-term (days) impact of this environmental variable on the dynamics of methanogenesis and CH<sub>4</sub> oxidation. Nonetheless, there is a growing awareness of the need to augment studies of source strengths with process-level investigations at finer spatiotemporal scales, both to improve our understanding of present climates and to forecast more accurately future trends in the concentration of atmospheric CH<sub>4</sub> (Prinn 1994).

The overall aim of this investigation was to examine the short-term dynamics of CH<sub>4</sub> production and oxidation in a high-latitude peat bog in response to water table position. We selected for study two sites that seasonally showed zones of permanently or transiently water-saturated peat. We combined field observations of CH<sub>4</sub> and CO<sub>2</sub> emission and peat CH<sub>4</sub> profiles with a laboratory study of the extant potentials for CH<sub>4</sub> production and oxidation, the short-term (≤ 2-day) response of these potentials to water table fluctuation, and the distribution of end products (biomass and CO<sub>2</sub>) of <sup>14</sup>CH<sub>4</sub> oxidation. We expected higher rates and potentials for CH<sub>4</sub> production at the permanently inundated site, but higher rates and potentials for CH<sub>4</sub> oxidation at the transiently saturated site.

## Methods

### Field Sites

The study site, Lemeta Bog, is a high boreal wetland complex located near Fairbanks, Alaska (64°53'N, 147°30'W). The plant community changes along a moisture gradient from paper birch (*Betula papyrifera*) and grasses in dry areas of the bog margin to a floating mat of *Carex* spp. and *Sphagnum* in the wettest areas. Moosavi et al. (1996) have given a complete description. We selected for study two sites that best represent the plant community and

hydrologic conditions of the wetland complex. The dry bog site (LB1A) was characterized by an overstory of black spruce (*Picea mariana*) and tamarak (*Larix laricina*) with an undergrowth of *Sphagnum* invaded by Labrador tea (*Ledum palustre*), cloudberry (*Rubus chamaemorus*), lowbush cranberry (*Vaccinium vitis-idaea*), and blueberry (*Vaccinium uliginosum*). The wet site (LB2) was dominated by *Sphagnum* interspersed with cloudberry, blueberry, Labrador tea cotton grass tussocks (*Eriophorum vaginatum*), and *Carex* spp. Peat extended to permafrost at both sites, and our experiments were conducted in late summer (August) of 1994, when thaw depths were maximum (43 and 63 cm at LB1A and LB2, respectively). Site LB1A is drained to permafrost except during rainfall when the bottom several centimeters of the thaw layer are water-saturated for a few days. In contrast, at LB2 a water-saturated zone persists immediately above the thaw layer throughout the summer and may extend to within 10 cm of the peat surface for several days after rainfall.

### **Field Sampling**

Following from our experimental aims, we made single determinations of CH<sub>4</sub> and CO<sub>2</sub> flux as well as depth distributions of temperature and CH<sub>4</sub> in peat each site. Thereafter, we destructively sampled the peat at the exact location where these measurements were made to assess rates, potentials, and depth distributions of CH<sub>4</sub> oxidation and production in a controlled laboratory environment.

Methane and CO<sub>2</sub> flux determinations were made by using the static chamber technique (Whalen and Reeburgh 1992). Each chamber consisted of a skirted aluminum base seated in the peat and a removable aluminum lid that utilized a water-filled channel for a seal. Lids were equipped with an O-seal fitting to allow syringe sampling of the headspace gas and fitted with a capillary bleed to equilibrate with atmospheric pressure. Following flux measurements, the depth distributions of temperature and CH<sub>4</sub> concentration were determined at 5-cm intervals to 40 (LB1A) or 45 cm (LB2) in the peat isolated by each aluminum chamber base. Temperature was measured with a portable thermistor probe. Methane samples were collected through the unsaturated zone (<32 cm at LB1A, <23 cm at LB2) with 30-mL polyethylene syringes fitted with a two-way stopcock and a removable steel tube (1 mm [i.d.] × 1 m long). Similarly, 30-mL pore water samples were collected into 60-mL polyethylene syringes in the saturated zone. The following day, peat within each aluminum chamber base was sampled to 40 cm with a 15-cm-diameter stainless steel coring apparatus. Each 40-cm core was cut horizontally into eight 5-cm sections that were then divided into triplicate subcores (6.7 cm in diameter × 5 cm long) by using a plastic tube. A single subcore from each depth interval in the saturated zone was immediately placed in a Mason jar (capacity ~1 L), amended with 180 mL of pore water from that depth, and sealed under ultrapure N<sub>2</sub>. Additionally, one subcore from each 5-cm depth interval in the lower unsaturated zone (15–30 cm at LB1A, 10–20 cm at LB2) was amended with 180 ml of composite pore water and sealed under N<sub>2</sub>. All other core sections from both the saturated and unsaturated zones were sealed in Mason jars under ambient atmosphere for transport to the laboratory.

### **Laboratory Studies**

All laboratory experiments were conducted on the 6.7-cm-diameter × 5-cm-long core sections in 1-L Mason jars capped with lids fitted with a septum for syringe sampling of the headspace gas. Core sections used for CH<sub>4</sub> oxidation experiments were disjoined and spread at the bottom of the jars before experimentation to avoid any limitation of diffusion and to prevent formation of anoxic zones. During experimentation, all jars were maintained in a

controlled temperature environment within  $\pm 1^\circ\text{C}$  of the temperature at the depth of sample collection. Headspace  $\text{CH}_4$  concentrations were adjusted to a concentration that had been shown previously to give zero-order kinetics ( $600 \mu\text{l L}^{-1}$ ; Whalen and Reeburgh 1996), and the resulting reduction in concentration was monitored by hourly sampling over an 8-h time course. Immediately after determination of the  $\text{CH}_4$  oxidation potential, a single subcore from each sample depth was randomly selected for assay for the end products of  $\text{CH}_4$  oxidation in a single endpoint experiment. Each sample was equilibrated in an ambient air atmosphere and amended with microliter quantities of biogenically produced  $^{14}\text{CH}_4$  (Daniels and Ziekus 1983) tracer ( $3.5 \text{ kBq}$ ; specific activity  $2005 \text{ kBq mol}^{-1}$ ). Experiments were terminated after a 6-h incubation in the dark by adding  $2 \text{ cm}^3$  of acetylene (Bedard and Knowles 1989). Jar headspaces were flushed with He into a stripping/oxidation line where  $^{14}\text{CO}_2$  was trapped directly and  $^{14}\text{CH}_4$  was trapped as  $^{14}\text{CO}_2$  after combustion. Soils were freeze-dried and assayed by dry combustion for  $^{14}\text{C}$  incorporated into microbial biomass. The radioactivity of all samples was determined by liquid scintillation spectrometry. The remaining core section from each depth interval was analyzed for pH, organic content, bulk density, particle density, and percent water-filled pore space. Methodological details of radiocarbon experiments and physicochemical assays are given in Whalen and Reeburgh (1992) and Whalen et al. (1992).

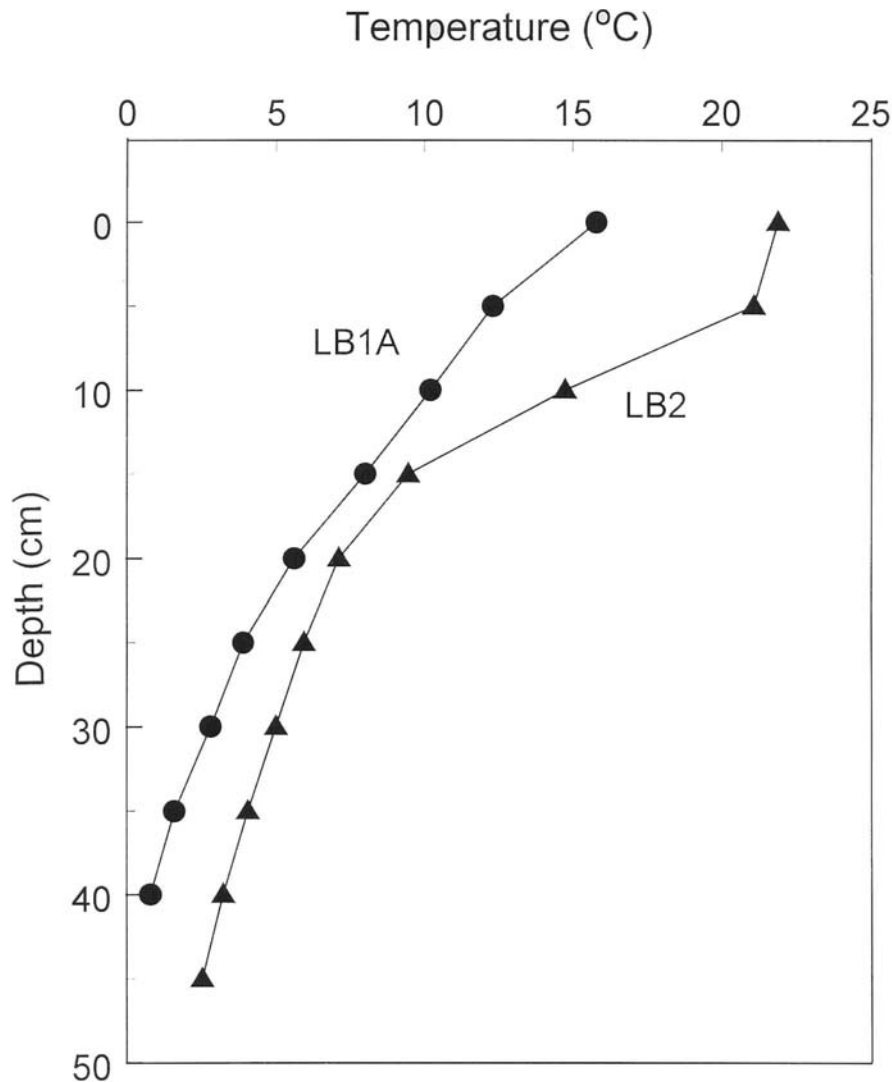
Methane production was determined for the core sections amended with pore water and sealed with  $\text{N}_2$  in the field. On return to the lab, the pore water was stripped of  $\text{CH}_4$  by bubbling with  $\text{N}_2$  for 1 h, the jars were resealed under ultrapure  $\text{N}_2$ , and the time course for  $\text{CH}_4$  accumulation was measured over 54 h. Cores were allowed to drain for 20 h in an ambient air atmosphere and resealed in Mason jars. Headspaces were adjusted to  $\text{CH}_4$  contents of  $\sim 20 \mu\text{l L}^{-1}$ , and the time course for change in  $\text{CH}_4$  concentration was determined over the next 45 h to assess the ability of methanotrophs to resume activity after temporary anoxia. Finally, cores were rewetted with pore water and made anoxic as described above, after which the time course for  $\text{CH}_4$  accumulation was reassessed for 48 h to evaluate the ability of methanogens to resume  $\text{CH}_4$  production after transient exposure to an ambient atmosphere. This switch between oxic and anoxic conditions was intended to simulate a rapid drop and rise in the water table position, respectively.

### *Gas Analysis and Calculations*

Methane was stripped from pore water samples by equilibration with an equal volume of ultrapure  $\text{N}_2$  (McAuliffe 1971). Methane and  $\text{CO}_2$  determinations were made by flame ionization and thermal conductivity gas chromatography, respectively, with a precision of  $< 1\%$  in both cases (Whalen et al. 1992). Calibration gases were related to standards from the National Institute for Technology and Standards. Soil  $\text{CH}_4$  in the unsaturated zone is expressed as the equilibrium aqueous-phase concentration calculated with Bunsen solubility coefficients (Yamamoto et al. 1976) so that data from both the unsaturated and waterlogged zones can be presented in comparable units. Details of all calculations, including integration of dry mass-normalized ( $\text{g}_{\text{dw}}^{-1}$ ) rates of microbial activity in individual core sections to yield area-based ( $\text{m}^{-2}$ ) rates, are given in Whalen et al. (1992) and Whalen and Reeburgh (1992).

### **Results**

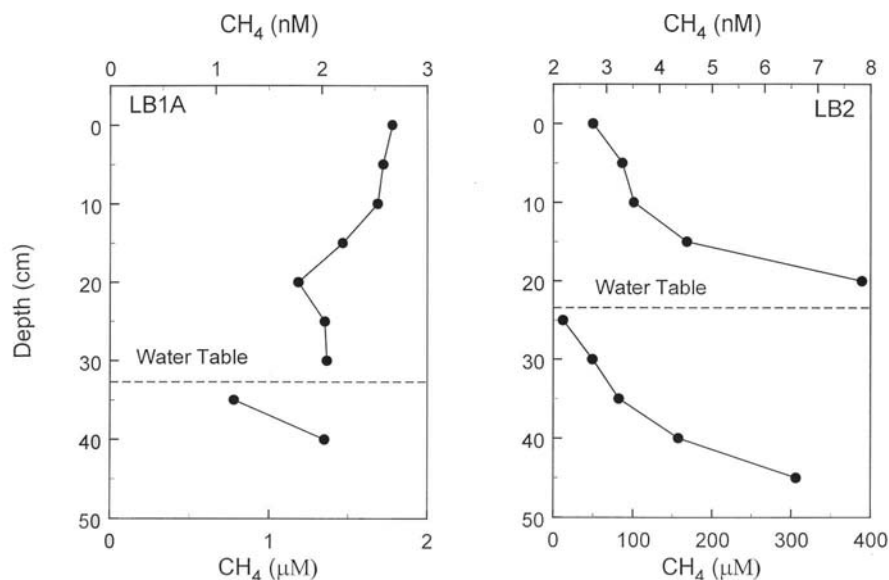
The two sampling sites were similar with respect to pH, organic content, and percent air-filled pore space in the unsaturated zone. The pH of core sections varied from 3.7 to 4.7, and the organic content varied from 88% to 96% (average 93%). No depth-dependent



**FIGURE 1** Peat temperature distributions at sites LB1A and LB2 in Lemeta Bog.

trends were noted for either variable. Bulk density increased with depth at both sites, from  $\sim 0.02 \text{ g cm}^{-3}$  in the 0- to 5-cm zone to  $0.25 \text{ g cm}^{-3}$  in the 35- to 40-cm zone. The percentage of air-filled pore space decreased from  $\sim 81\%$  in the 0- to 5-cm zone at both sites to 43% (LB1A) and 25% (LB2) just above the saturated zone. Peat temperatures decreased with increasing depth at both sites (Figure 1). Relatively lower temperatures at LB1A, especially in the surface peat, were due to shading by the larch and black spruce overstory, which was absent at LB2.

The two sites showed distinctly different depth distributions for  $\text{CH}_4$  (Figure 2). The  $\text{CH}_4$  concentration in the unsaturated zone of LB1A was lowest (1.8 nM) at 20 cm, and increased slightly with increasing distance both above and below this depth. Methane concentrations in the unsaturated zone were also in the nanomolar range, but decreased steadily to the peat surface. Methane concentrations in the saturated zone were three and five orders of magnitude greater than concentrations in the unsaturated zone at LB1A and LB2,



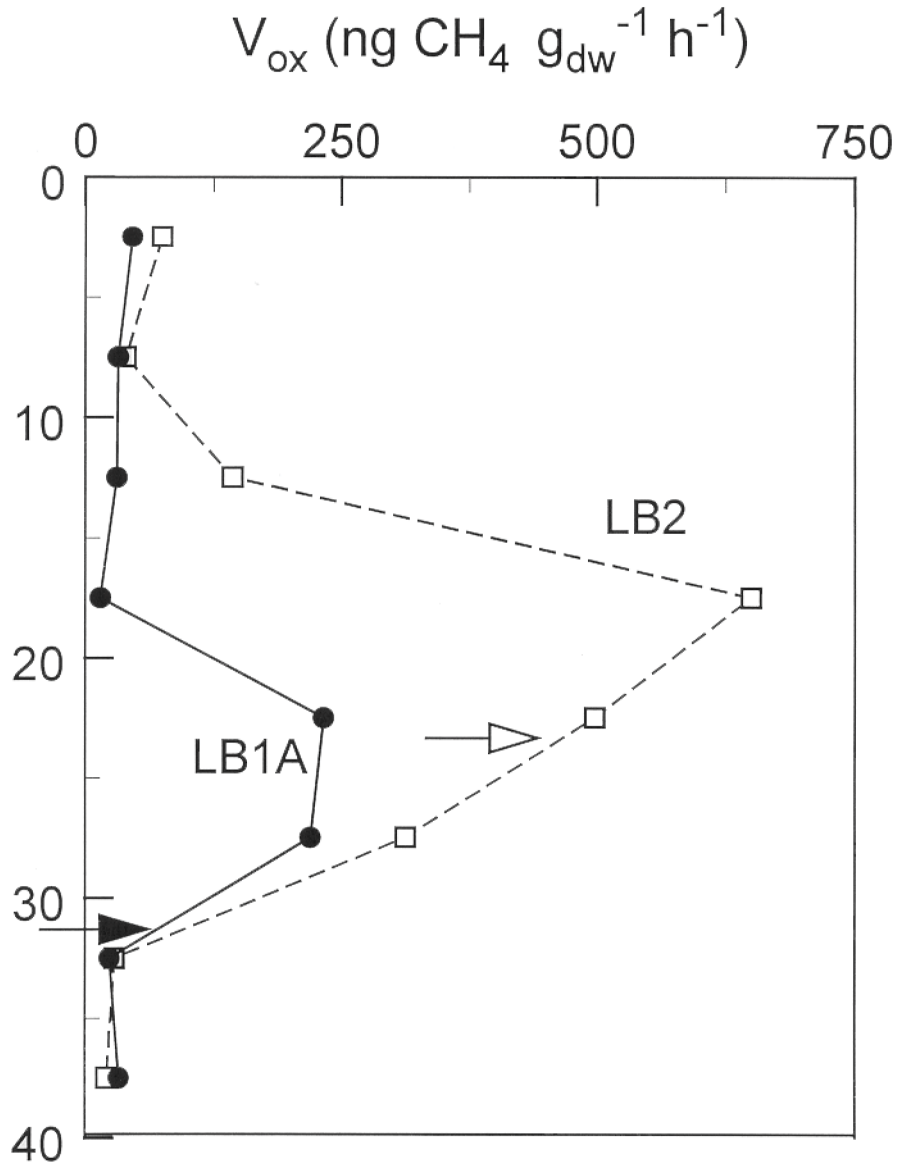
**FIGURE 2** Peat  $\text{CH}_4$  distributions at sites LB1A and LB2 in Lemeta Bog. Each value for the unsaturated zone is the calculated aqueous-phase  $\text{CH}_4$  concentrations in equilibrium with the measured  $\text{CH}_4$  concentration in the air-filled pore space at the temperature of the depth of sample collection. Note the change in scale for  $\text{CH}_4$  concentrations between the unsaturated and saturated zones.

respectively. Thus,  $\text{CH}_4$  concentrations in the saturated zone at LB2 were  $\sim 100$ -fold higher than at LB1.

Methane fluxes in static chamber experiments differed in both sign and magnitude between sites. The flux at LB1A ( $-0.9 \text{ mg of CH}_4 \text{ m}^{-2} \text{ d}^{-1}$ ) indicated consumption of atmospheric  $\text{CH}_4$ , whereas that at LB2 ( $69 \text{ mg of CH}_4 \text{ m}^{-2} \text{ d}^{-1}$ ) indicated net  $\text{CH}_4$  emission from the peat surface to the atmosphere. In contrast to  $\text{CH}_4$ , fluxes of  $\text{CO}_2$  were reasonably similar between sites. Carbon dioxide emission in static chamber experiments was  $15.6$  and  $17.9 \text{ g m}^{-2} \text{ d}^{-1}$  at LB1A and LB2, respectively.

Depth distributions of  $\text{CH}_4$  oxidation potential ( $V_{\text{ox}}$ ) were similar between sites; that is, the greatest rates were observed in a 10-cm horizon of the unsaturated zone immediately above the local water table (Figure 3).  $V_{\text{ox}}$  values in this horizon were about threefold greater at LB2 than at LB1A, ranging from  $498$  to  $650 \text{ ng of CH}_4 \text{ g}_{\text{dw}}^{-1} \text{ h}^{-1}$  at the former and from  $220$  to  $233 \text{ ng of CH}_4 \text{ g}_{\text{dw}}^{-1} \text{ h}^{-1}$  at the latter. Methane oxidation potentials in deep (30–40 cm), water-saturated peat were similar at both sites ( $21$  to  $33 \text{ ng of CH}_4 \text{ g}_{\text{dw}}^{-1} \text{ h}^{-1}$ ) and an order of magnitude or more lower than the  $V_{\text{ox}}$  immediately above the saturated zone. Methane oxidation potentials in surface peat (0–10 cm) were roughly comparable at both sites ( $32$  to  $75 \text{ ng of CH}_4 \text{ g}_{\text{dw}}^{-1} \text{ h}^{-1}$ ) and slightly higher than values deep in the saturated zone.

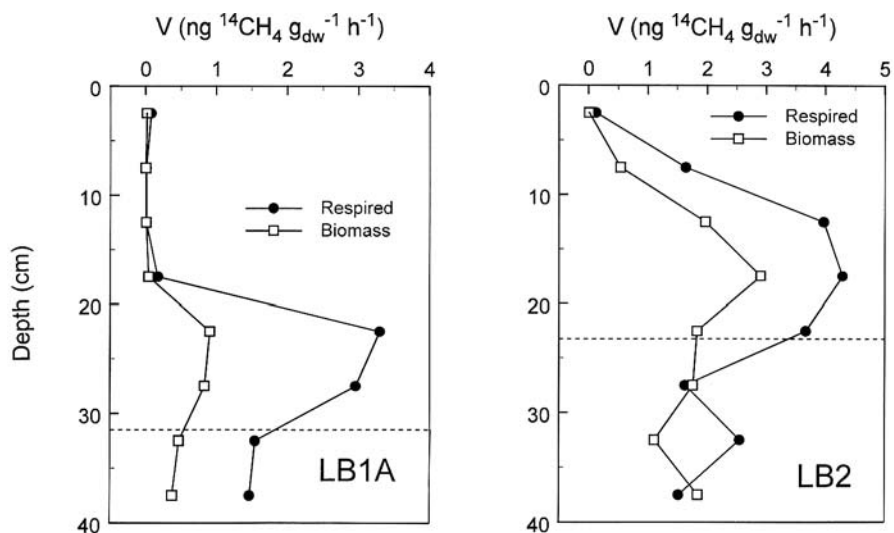
Depth profiles for oxidation of  $^{14}\text{CH}_4$  (Figure 4) were similar to those for  $V_{\text{ox}}$  (Figure 3), in that a subsurface maximum was observed in the unsaturated zone just above the water table at both sites. The fraction of assimilated radiocarbon that was respired ranged from 45% to 98% (mean  $\pm$  SD:  $71\% \pm 4\%$ ) for the 16 core sections exposed to  $^{14}\text{CH}_4$ . Fractional respiration showed no pattern with respect to depth at either site and was not significantly different between sites. Mass balances for each core section showed full recovery ( $100\% \pm 7\%$ ; mean  $\pm$  SD) of added label as  $^{14}\text{C}$ -biomass,  $^{14}\text{CO}_2$ , and unassimilated  $^{14}\text{CH}_4$ .



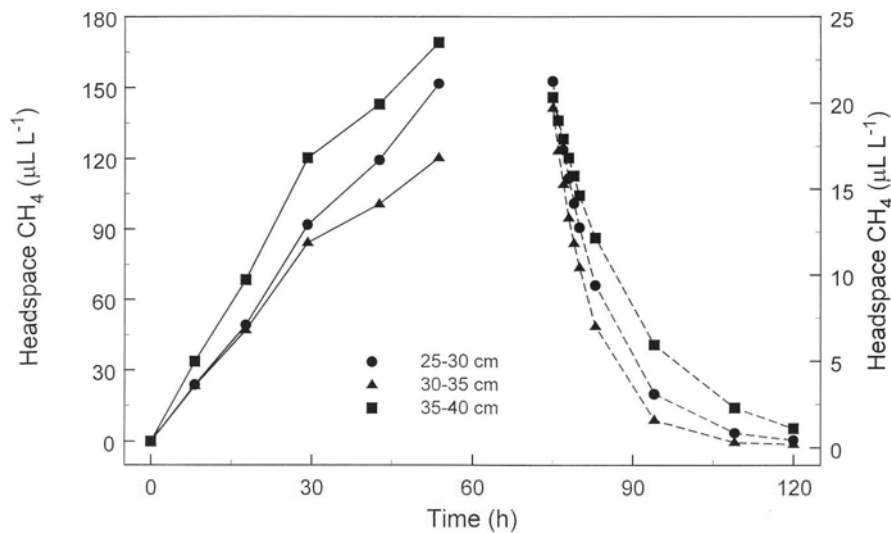
**FIGURE 3** Depth distribution of CH<sub>4</sub> oxidation potential ( $V_{ox}$ ) in cores collected from two sites in Lemeta Bog. The mean  $V_{ox}$  of duplicate subcores is plotted at the midpoint of each 5-cm sampling interval. Error bars are eliminated for clarity, but the standard deviation averaged 21%. The water table position is indicated by solid (LB1A) and open (LB2) arrows.

Experiments assessing the depth distribution of potential CH<sub>4</sub> production ( $V_p$ ) at LB1A showed extremely limited  $V_p$  in 5-cm core sections from 25 to 40 cm (0.1 to 0.2 ng of CH<sub>4</sub> g<sub>dw</sub><sup>-1</sup> h<sup>-1</sup>) and no  $V_p$  at the higher peat horizons tested (15 to 25 cm). In contrast,  $V_p$  for 5-cm core sections from 20 to 40 cm deep at LB2 ranged from 32 to 139 ng of CH<sub>4</sub> g<sub>dw</sub><sup>-1</sup> h<sup>-1</sup>, and modest  $V_p$  values (4 to 10 ng of CH<sub>4</sub> g<sub>dw</sub><sup>-1</sup> h<sup>-1</sup>) were still evident in higher (10 to 20 cm) peat horizons. Methane began accumulating without lag in all core sections showing  $V_p$  at both sites (e.g., Figure 5).

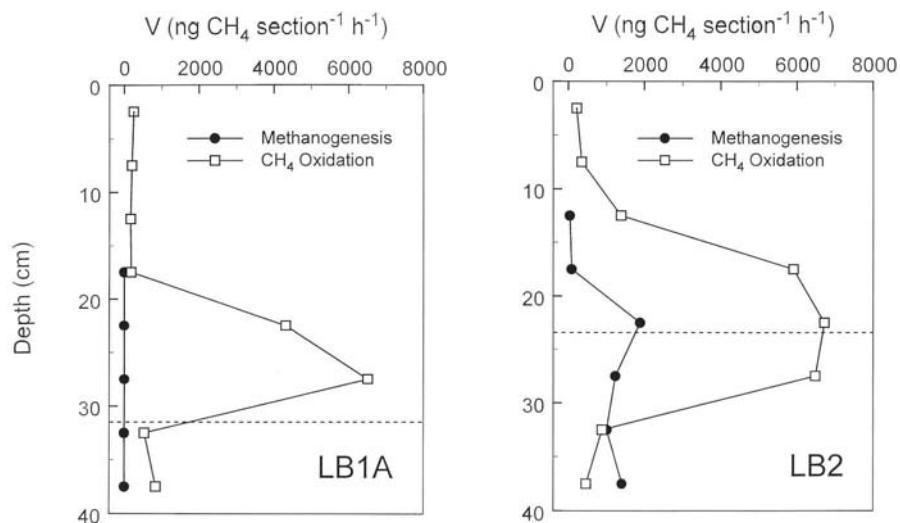




**FIGURE 4** Depth distributions of  $^{14}\text{CH}_4$  consumption (V) in cores from two sites in Lemeta Bog, showing the partitioning of assimilated radiocarbon into respiration ( $^{14}\text{CO}_2$ ) and microbial biomass. Values of V are plotted at the midpoint of each 5-cm depth interval. Horizontal dashed lines indicate the water table position.



**FIGURE 5** Time courses for  $\text{CH}_4$  production (left) and oxidation (right) in selected 5-cm core sections (from site LB2 in Lemeta Bog) that were alternately made anoxic and oxic. Methane production by anoxic core sections plus pore water was measured for 54 h. Core sections were drained for 20 h in an oxic environment and then amended with  $\sim 20 \mu\text{l L}^{-1}$   $\text{CH}_4$ , after which the time course for  $\text{CH}_4$  oxidation was determined for 45 h. Not shown: no  $\text{CH}_4$  was produced over 48 h by continued incubation of core sections rewetted and made anoxic at 120 h.



**FIGURE 6** Depth distribution of  $\text{CH}_4$  oxidation and production potentials in cores collected from two sites in Lemeta Bog. Methane oxidation and production potentials for an entire 6.7-cm-diameter  $\times$  5-cm-long core section are plotted at the midpoints of each depth interval. Horizontal dashed lines indicate the water table position.

Core sections from the saturated zone of LB2 that were incubated anaerobically in pore water in experiments assessing  $V_p$  showed vigorous  $\text{CH}_4$  oxidation after draining for 20 h in an ambient air atmosphere and subsequent exposure to a  $\text{CH}_4$  headspace of  $\sim 20 \mu\text{l L}^{-1}$  (Figure 5). Headspace  $\text{CH}_4$  concentrations decreased to  $< 1 \mu\text{l L}^{-1}$  (subatmospheric) within 45 h for all core sections. Core sections from the saturated zone of LB1A (30–40 cm) behaved similarly when drained and exposed to  $\text{CH}_4$  in an oxic environment (data not shown). Core sections from both sites that were subsequently rewetted with pore water and again rendered anaerobic showed no  $\text{CH}_4$  production over the next 48 h (data not shown).

When the total dry peat mass in each 5-cm core section was considered, LB1A showed low  $V_p$  throughout the peat profile but a high  $V_{ox}$  in the unsaturated zone immediately above the water table (Figure 6). In contrast, LB2 showed both high  $V_p$  and high  $V_{ox}$  at the interface of the saturated and unsaturated peat. The area-based  $\text{CH}_4$  oxidation potential ( $\Sigma V_{ox}$ ) of  $153 \text{ mg m}^{-2} \text{ d}^{-1}$  at LB2 was  $\sim 1.5$  times the value of  $91 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$  calculated for LB1A. Site-wise differences were even more pronounced for area-based  $\text{CH}_4$  production potentials ( $\Sigma V_p$ ), where  $\Sigma V_p$  was 39 and  $< 1 \text{ mg of CH}_4 \text{ m}^{-2} \text{ d}^{-1}$  for LB2 and LB1A, respectively. Thus,  $\Sigma V_{ox}$  exceeded  $\Sigma V_p$  at both sites.

## Discussion

The two experimental sites were reasonably similar at comparable depths with respect to pH, percent organic matter, temperature, bulk density, and percent air-filled porosity in the unsaturated zone. However, differences in local hydrology on a scale of meters (continuous [LB2] versus transient [LB1A] presence of a saturated zone during the thaw season) yielded distinct site-wise differences in  $\text{CH}_4$  oxidation and production potentials,  $\text{CH}_4$  fluxes, and peat  $\text{CH}_4$  profiles.

Peat  $\text{CH}_4$  concentrations in the unsaturated zone at LB1A (Figure 2) were consistently at or below the aqueous-phase concentration ( $\sim 2.5 \text{ nM}$ ) in equilibrium with atmospheric

CH<sub>4</sub> (1.8 μl L<sup>-1</sup>), whereas CH<sub>4</sub> concentrations in the saturated zone clearly exceeded this value. Thus, peat in the unsaturated zone of LB1A consumed not only atmospheric CH<sub>4</sub>, but also all of the CH<sub>4</sub> diffusing upward from the saturated zone. This corroborates well the measured CH<sub>4</sub> flux of -0.9 mg m<sup>-2</sup> d<sup>-1</sup> and also agrees with data from similar sites within this bog ("dry sites"; Moosavi et al. 1996) that oscillate between net CH<sub>4</sub> emission and consumption at low rates throughout the thaw season.

In contrast to LB1A, LB2 showed net CH<sub>4</sub> emission to the atmosphere. The measured CH<sub>4</sub> flux of 69 mg m<sup>-2</sup> d<sup>-1</sup> is consistent with the 1992 and 1993 seasonal averages of 72 and 43 mg m<sup>-2</sup> d<sup>-1</sup> reported by Moosavi et al. (1996) for similar sites ("wet sites") within this bog. Methane concentrations as great as 306 μM in the saturated zone and nanomolar concentrations immediately above in the unsaturated zone suggest intense CH<sub>4</sub> oxidation at the interface of these two peat horizons (Figure 2). Moreover, the concave upward CH<sub>4</sub> profile in the unsaturated zone (Figure 2) suggests continued oxidation of the CH<sub>4</sub> diffusing upward to the peat surface. Using a stagnant film model for gas transfer and assuming a film thickness of 200 μm at the water table surface (Whalen et al. 1996), we estimate a CH<sub>4</sub> flux of 152 mg m<sup>-2</sup> d<sup>-1</sup> from the water table surface to the unsaturated zone. Comparing this estimated flux with the measured emission from the peat surface implies consumption of 83 mg of CH<sub>4</sub> m<sup>-2</sup> d<sup>-1</sup> in the unsaturated zone. Thus, we estimate that 55% of the CH<sub>4</sub> emitted from the water table surface is oxidized while diffusing upward through the unsaturated zone. Our estimate for the fractional oxidation of CH<sub>4</sub> at LB2 is somewhat less than that for other wet peats (King et al. 1990; Yavitt et al. 1990; Fenchner and Hemond 1992), which show ~70% to 90% oxidation of available CH<sub>4</sub>. However, our estimate is based on a single observation, and fractional oxidation clearly depends on the position of the water table. Harriss et al. (1982) observed that temperate swamp soils may function seasonally as a source or a sink for atmospheric CH<sub>4</sub>, depending on the water table position.

Methane oxidation potential is generally considered to provide a relative measure of the methanotrophic biomass because measurements are made at uptake-saturating CH<sub>4</sub> concentrations (Sundh et al. 1994). Our observation of the greatest V<sub>ox</sub> immediately above the saturated zone (Figures 3 and 6) compares favorably with other studies in peatlands, which show the most activity in a similar zone or in anaerobic peat within several centimeters below the local water table (Bubier et al. 1993; Lien et al. 1993; Sundh et al. 1993, 1994, 1995; Nedwell and Watson 1995; Moore and Dalva 1997; Saarnio et al. 1997; Watson et al. 1997; Kettunen et al. 1999). Methanotrophs remain viable after an extended period of anoxia (King 1996). Thus, variability between studies in the location of the greatest V<sub>ox</sub> probably best reflects the average seasonal condition where CH<sub>4</sub> and O<sub>2</sub> supplies are adequate rather than the water table position at the time of sampling.

Our ranges for V<sub>ox</sub> (15–650 ng of CH<sub>4</sub> g<sub>dw</sub><sup>-1</sup> h<sup>-1</sup>) and Σ V<sub>ox</sub> (91–153 mg of CH<sub>4</sub> m<sup>-2</sup> d<sup>-1</sup>) are generally lower than data for other peatlands. Reported values of V<sub>ox</sub> range from <1 to 10,390 ng of CH<sub>4</sub> g<sub>dw</sub><sup>-1</sup> h<sup>-1</sup> for various Canadian wetlands (Moore and Knowles 1990; Bubier et al. 1993; Moore and Dalva 1997) and from 1280 to 5120 ng of CH<sub>4</sub> g<sub>dw</sub><sup>-1</sup> h<sup>-1</sup> for a Finnish pine fen (Saarnio et al. 1997), whereas we calculate values as great as 23,000 ng of CH<sub>4</sub> g<sub>dw</sub><sup>-1</sup> h<sup>-1</sup> for an English blanket bog from data given by McDonald et al. (1996). Reported values of Σ V<sub>ox</sub> range from 40 to 22,100 mg of CH<sub>4</sub> m<sup>-2</sup> d<sup>-1</sup> for Swedish boreal peatlands (Sundh et al. 1994, 1995) and from 191 to 607 mg of CH<sub>4</sub> m<sup>-2</sup> d<sup>-1</sup> for the Finnish pine fen already mentioned (Saarnio et al. 1997). However, unlike those studies, which were conducted at room temperature, our values were obtained at the in situ peat temperatures. We previously reported an optimum temperature of 23°C for substrate-saturated CH<sub>4</sub> oxidation in these peats (Whalen and Reeburgh 1996). However, temperatures at the depths of the greatest V<sub>ox</sub> and Σ V<sub>ox</sub> values were ~5–7°C (cf. Figures 1, 3, and 6), indicating that much greater rates are possible at room temperature.

Our data for LB2 indicating that the locations for the  $V_{ox}$  and  $V_p$  maxima are spatially similar (Figure 6) agree with other reports for peat environments that show proximity or overlap of these potentials (Bubier et al. 1993; Sundh et al. 1993, 1994; Nedwell and Watson 1995; Moore and Dalva 1997; Saarnio 1997; Edwards et al. 1998; Kettunen et al. 1999). Our values of  $<1\text{--}139$  ng of  $\text{CH}_4$   $\text{g}_{\text{dw}}^{-1} \text{h}^{-1}$  for  $V_p$  are similar to the ranges of  $0\text{--}270$ ,  $8\text{--}121$ , and  $1\text{--}58$  ng of  $\text{CH}_4$   $\text{g}_{\text{dw}}^{-1} \text{h}^{-1}$  given by Magnusson (1993), Moore and Knowles (1990), and Bubier et al. (1993), respectively, for Swedish *Sphagnum* peats, a subarctic Canadian fen, and 12 Canadian peatland sites. However, our data are generally lower than those from other peatland studies that used similar methodology to measure  $V_p$ . Methane production potentials averaged 129 and 3640 ng of  $\text{CH}_4$   $\text{g}_{\text{dw}}^{-1} \text{h}^{-1}$  in a comprehensive study of Canadian wetlands (Moore and Dalva 1997) and a Minnesota fen (Williams and Crawford 1984), respectively. Values for  $V_p$  ranged from  $\sim 100$  to 2288 ng of  $\text{CH}_4$   $\text{g}_{\text{dw}}^{-1} \text{h}^{-1}$  for samples collected below the water table in a fen (Saarnio et al. 1997) and in two mires (Kettunen et al. 1999) in Finland and from 70 to 10,400 ng of  $\text{CH}_4$   $\text{g}_{\text{dw}}^{-1} \text{h}^{-1}$  in a temperate bog (Yavitt et al. 1987). As with  $V_{ox}$ , our values for  $V_p$  probably would have been higher if they had been determined at room temperature because rates of methanogenesis are notably temperature-dependent (e.g., Dunfield et al. 1993).

Here, and in most of the studies cited above,  $V_{ox} > V_p$ . However, the two values are not directly comparable (Sundh et al. 1994; Moore and Dalva 1997). The latter involves no addition of methanogenic substrate and therefore gives  $\text{CH}_4$  production from endogenous substrate only for a methanogenic community that is probably substrate-limited (Valentine et al. 1994; Yavitt et al. 1997; Bergman et al. 1998).

The presence of a viable methanotrophic community in anoxic Lemeta Bog peat is clearly illustrated by the resumption of  $\text{CH}_4$  oxidation on a time scale of  $<1$  day after exposure to ambient air atmosphere (Figure 5). We cannot discount an even shorter response time, because  $\text{CH}_4$  consumption measurements were not initiated until 20 h after  $\text{O}_2$  reintroduction. Rapid recovery of  $\text{CH}_4$  oxidizing activity after anoxia has previously been attributed to reactivation of the indigenous population by  $\text{O}_2$  (King 1996; Edwards et al. 1998); the response time is too rapid to involve the germination of cysts and spores, which may take days (Whittenbury et al. 1970). Vegetative cells were probably responsible here also. King et al. (1990) attributed a reduction in post- to preanoxia relative  $\text{CH}_4$  oxidizing potential in a Danish wetland sediment to the co-occurrence of populations that recover slowly (days) and those that recover rapidly after reexposure to  $\text{O}_2$ . The relative importance of these two functional groups in Lemeta Bog is unclear. However, the highly dynamic water table position favors the development of a methanotrophic population capable of rapid recovery from anoxia, and the consumption of  $20 \mu\text{l L}^{-1}$   $\text{CH}_4$  to subatmospheric concentrations ( $1 \mu\text{l L}^{-1}$ ) within 48 h by reoxygenated samples (Figure 5) clearly points to a vigorous population of anoxia-tolerant methanotrophs. A rapid response capability to  $\text{O}_2$  reintroduction may be widespread for at least part of the methanotrophic community in peat. Yavitt et al. (1990) reported immediate  $\text{CH}_4$  consumption for surface peats in a temperate bog, but a lag of 12 h for peats 30 to 40 cm deep. Edwards et al. (1998) and McDonald et al. (1996) detected  $\text{CH}_4$ -oxidizing activity throughout 30-cm-deep cores from a UK blanket bog after  $\leq 2$  h exposure to air, whereas King et al. (1990) reported immediate  $\text{CH}_4$  oxidation by anoxic subtropical peats incubated with  $\text{O}_2$ , and Roslev and King (1996) observed  $\text{CH}_4$  oxidation by anoxic temperate marshland peat 1 to 7 h after  $\text{O}_2$  addition.

We are unaware of other studies analyzing the immediate impact of a change in the  $\text{O}_2$  environment on  $V_p$  and  $V_{ox}$  simultaneously. Although the time course for recovery of methanogenic activity after exposure to  $\text{O}_2$  is uncertain, the absence of  $\text{CH}_4$  production for 48 h after samples were again made anaerobic clearly points to a greater short-term sensitivity by methanogens than methanotrophs in Lemeta Bog to adverse conditions

with respect to  $O_2$ . Studies assessing the influence of  $O_2$  exposure on methanogenesis in environmental samples are few and give conflicting results. In general agreement with our data, Ratering and Conrad (1998) observed that  $CH_4$  production in slurries of an Italian rice soil was completely inhibited by a 48-h exposure to air and that this inhibition persisted for 30 days. Similarly, Öquist and Sundh (1998) found that a 40-day exposure of boreal bog peat to air resulted in a 1-week delay in  $CH_4$  production in surface samples and complete inhibition of methanogenesis in deep peat (50 to 55 cm) during the subsequent 27-day anoxic incubation. In contrast, Schutz et al. (1989) observed that incubation of paddy soil in air for 6 h had no effect on methanogenesis, whereas Mayer and Conrad (1990) demonstrated  $CH_4$  production in previously air-dried paddy soil within 2 days after being placed in an anaerobic atmosphere. Clearly, efforts to model peatland  $CH_4$  emission will benefit from an improved understanding of the apparent hysteresis and recovery of activity by methanogens in the response to a shift from oxic to anoxic conditions that will accompany a rising water table.

The low  $CH_4$  concentration in pore water at the infrequently flooded LB1A site (Figure 2) is consistent with demonstrated  $O_2$  sensitivity of Lemeta Bog methanogens (Figure 5). However, relatively high  $V_{ox}$  in the 20- to 30-cm-deep horizon (Figure 3) suggests that the residence time of pore water during periodic flooding is sometimes sufficient to allow for methanogenesis. Insofar as aerobic decomposition in normally unsaturated peat reduces the availability of methanogenic precursors during periods of anoxia (Sundh et al. 1994; Kettunen et al. 1999), it is likely that rates of  $CH_4$  production at LB1A are always less than at LB2 and that the  $CH_4$  oxidizers efficiently intercept upwardly diffusing  $CH_4$  such that the net flux to the atmosphere is near zero. The observation that similar sites in Lemeta Bog alternate between weak  $CH_4$  emitters and consumers throughout the thaw season (Moosavi et al. 1996) supports this contention. Low  $V_p$  in core sections from 25 to 40 cm deep at LB1A ( $0.1$  to  $0.2$  ng of  $CH_4$   $g_{dw}^{-1} h^{-1}$ ) may reflect not only poor substrate quality but also the recent history of the site, in that the time between saturation and sampling may have been insufficient to activate or develop the methanogenic community fully.

Both methanogens and methanotrophs probably are attached to peat particles and remain in the same layer of the peat matrix despite water table fluctuations (Kettunen et al. 1999). Given the high  $O_2$  sensitivity of methanogens in this peat, the fact that the greatest values of  $V_p$  and  $V_{ox}$  at LB2 overlap in space is enigmatic (Figure 6). However, anaerobic microzones supporting methanogenesis can persist in seemingly dry peat (Öquist and Sundh 1998), although peat higher in the profile is generally more readily decomposed (e.g., Hogg 1993). Consequently, the locus of  $V_p$  probably reflects a balance between  $O_2$  tolerance and substrate supply. Methanotrophs not only are able to withstand extended periods of anoxia but also are capable of functioning at dissolved  $O_2$  concentrations as low as  $0.1$  mg  $L^{-1}$  (Rudd et al. 1976). Hence, the spatial coupling of  $V_p$  and  $V_{ox}$  is not surprising. Spatial overlap of aerobic respiration and methanogenesis is a well-established component of the  $CH_4$  production process in ecosystems that are characterized by changing  $O_2$  conditions (Wagner et al. 1999).

Recovery of  $71\% \pm 4\%$  of assimilated  $^{14}CH_4$  as  $^{14}CO_2$  (Figure 4) indicates that most of the  $CH_4$  carbon consumed by the peat microbial community was used for energy rather than biomass. Studies assessing the relative allocation of assimilated  $CH_4$  give highly variable results. In agreement with our data, Yavitt et al. (1988, 1990) reported a respiratory loss of 78–85% of assimilated  $CH_4$  for Appalachian peatlands, and Whalen et al. (1992) showed a 60% loss for boreal forest soils. However, other terrestrial environments show less loss to respiration. Roughly 30% of assimilated  $CH_4$  was respired by landfill cover soils (Whalen et al. 1990; Jones and Nedwell 1993) and by a cultivated humisol (Megraw and Knowles

1987). Freshwater and marine ecosystems also show a wide range for respiratory loss of CH<sub>4</sub>, 39–98% (summarized in Whalen et al. 1990). Differences among studies may reflect differences among CH<sub>4</sub>-oxidizing communities or among their physiological states (Megraw and Knowles 1987). Assuming that 71% of  $\Sigma V_{ox}$  is respired, we calculate (molar basis) as an upper limit that 1.1–1.7% of the observed respiratory CO<sub>2</sub> flux in static chamber measurements is the result of CH<sub>4</sub> oxidation. Thus, although CH<sub>4</sub> oxidation serves as an important modulator of CH<sub>4</sub> emission from Lemeta Bog to the atmosphere, it contributes little to the gross ecosystem respiration.

In conclusion, this study demonstrates that meter-scale differences in local hydrology in a boreal bog may give sharp contrasts in CH<sub>4</sub> production and oxidation, which result in highly variable atmospheric CH<sub>4</sub> fluxes on a similar scale. The methanotrophic and methanogenic communities show spatial overlap, but respond on different time scales to the changes in peat O<sub>2</sub> status that may result from rapid changes in water table position. Process-oriented studies such as these will allow mechanisms underlying CH<sub>4</sub> fluxes to be better incorporated into models to improve our predictive capabilities regarding peatland response to future climates. Future study should be directed toward better understanding of the O<sub>2</sub> sensitivity of methanogenesis in these ecosystems.

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