Pergamon

Soil Biol. Biochem. Vol. 28, No. 10/11, pp. 1271–1281, 1996

PII: S0038-0717(96)00139-3
0038-0717/96 $15.00 + 0.00

MOISTURE AND TEMPERATURE SENSITIVITY OF CH_4 OXIDATION IN BOREAL SOILS

S. C. WHALEN*† and W. S. REEBURGH
Department of Earth System Science, University of California, Irvine, CA 92717-3100, U.S.A.

(Accepted 4 June 1996)

Summary—We used laboratory experiments to evaluate CH_4 uptake kinetics and the influence of soil moisture and temperature on rates of CH_4-oxidation by boreal soils at *in situ* CH_4 concentrations. Two upland forest sites (AS2 and BS2) were atmospheric CH_4 sinks; a bog site (LB) was an atmospheric CH_4 source characterized by distinct depth zonation of CH_4 production and consumption. Apparent half-saturation constants (K_s) for CH_4-oxidation showed relatively well-adapted communities. The K_s for the high CH_4-source soil (LB) was 1.1 μM, about 10-fold higher than values for CH_4-sink soils (AS2 and BS2), 37 and 124 nM. Experiments assessing the individual effects of moisture and temperature on CH_4-oxidation indicated that moisture was the primary control in CH_4-sink soils at AS2 and BS2, while temperature was more important in CH_4-source soil at LB. A combination of the highest moisture content and lowest temperature for each soil gave the lowest CH_4-oxidation rates in experiments evaluating the interactive effects of these two variables. Conversely, a soil moisture content close to the optimum identified in moisture dependence experiments combined with the highest soil temperature consistently gave the highest CH_4-oxidation rate. Copyright © 1996 Elsevier Science Ltd

INTRODUCTION

A contemporary increase in the concentration of atmospheric CH_4 is well-documented (Houghton *et al.*, 1995) and the magnitudes and ranges of major budgetary terms are becoming better refined (e.g. Fung *et al.*, 1991). Within this context, there is a growing awareness of the need to augment source strength studies with an improved understanding of atmospheric and biospheric CH_4 chemistry and their linkages (Prinn, 1994).

Microbial CH_4-oxidation in aerobic soils and sediments adjacent to anaerobic zones of production has long been acknowledged as a modulator of CH_4 flux to the atmosphere (reviewed by King, 1992; Mancinelli, 1995; King, 1992; Mancinelli, 1995). However, recent field studies point to an additional role of CH_4-oxidation in the atmospheric CH_4 budget. Well-drained, geographically heterogeneous soils show a widespread, consistent ability to serve as atmospheric CH_4 sinks (Seiler *et al.*, 1984; Steudler *et al.*, 1989; Born *et al.*, 1990; Keller *et al.*, 1990; Whalen and Reeburgh, 1990a; Yavitt *et al.*, 1990, 1995; Crill, 1991; Mosier *et al.*, 1991, 1993; Whalen *et al.*, 1991; Striegl *et al.*, 1992; Koschorreck and Conrad, 1993; Tate and Striegl, 1993; Castro *et al.*, 1993, 1994, 1995; Keller and Reiners, 1994). Tropospheric reaction with hydroxyl radicals (OH) was once considered to be the only important sink for atmospheric CH_4 (Cicerone and Oremland, 1988). However, studies of CH_4-oxidation in well-drained soils point to a sink strength that is about 7% of the annual global destruction by OH radicals (Dörr *et al.*, 1993).

Methane-oxidation is important in the atmospheric CH_4 budget. Reeburgh *et al.* (1993) estimate that nearly 60% of the 1188 Tg CH_4 produced y^{-1} from anthropogenic and natural sources is oxidized microbially adjacent to the zone of production or in soils functioning as atmospheric CH_4 sinks. Process-level studies (Whalen *et al.*, 1990; Nesbit and Breitenbeck, 1992; Adamsen and King, 1993; Dunfield *et al.*, 1993; King and Adamsen, 1992) and many of the field investigations cited above have identified soil moisture and temperature as key controls on CH_4-oxidation in soils. The relative importance and interactive effects of these regulators remains uncertain. Moreover, the kinetics of CH_4 uptake by soil microbes subsisting on atmospheric CH_4 are poorly characterized.

The boreal forest is circumpolar and occupies >8% of the earth's continental surface (Lieth, 1975). This region presently plays a major role in the atmospheric CH_4 budget. It is characterized on one extreme by well-drained forest soils that consume atmospheric CH_4 (Whalen *et al.*, 1991) and on the other by poorly-drained bog soils that are point sources of CH_4 emission to the atmosphere (Whalen and Reeburgh, 1990b). The future role of the boreal

*Present address: Department of Environmental Science and Engineering, Rosenau Hall CB #7400, University of North Carolina, Chapel Hill, NC 27599-7400, U.S.A.
†Author for correspondence.

forest in the atmospheric CH_4 budget is uncertain. Geophysical climate change models predict significant alterations in temperature and precipitation for this region (Mitchell *et al.*, 1990). Accurate prediction of future trends in soil CH_4-oxidation in this and other regions as a result of altered climate and land use change requires an improved understanding of the physiology and controls of this microbial process.

Our laboratory study was aimed at assessing CH_4 uptake kinetics and the moisture and temperature sensitivity of CH_4-oxidizing microbial communities in boreal soils. Further, we have examined the interactive effects of moisture and temperature on rates of CH_4-oxidation in these soils. Our objective was to better understand the physiological characteristics of CH_4-oxidizing communities in boreal soils and important factors that regulate CH_4-oxidation.

MATERIALS AND METHODS

Following from our aims, we selected soils from sites that we expected to represent extremes with respect to CH_4-oxidizing communities. Two sites were in well-drained forest soils that were atmospheric CH_4 sinks (Whalen *et al.*, 1991). The other site was a peat bog that showed a net CH_4 flux to the atmosphere and had distinct soil zones of CH_4 production and oxidation (S. C. Moosavi, unpubl. M.S. thesis, University of New Hampshire, 1994). Our goal in moisture and temperature dependence experiments was to evaluate the response of CH_4-oxidation at *in situ* CH_4 concentrations. Therefore, experiments involving upland forest soils were done at the present atmospheric CH_4 concentration of $1.7\ \mu l\ l^{-1}$ CH_4 (i.e. free-air atmosphere) and experiments with bog soil were made in a CH_4-amended atmosphere that gave zero-order (substrate-saturated) rates of CH_4-oxidation.

Site description and sample collection

Soils were collected on 10 occasions during the summers of 1993 and 1994 from the Bonanza Creek Experimental Forest (BCEF) and Lemeta Bog, both near Fairbanks Alaska (64°N, 148°W).

Soils within BCEF are a well-drained, stone-free micaceous loess and show slight morphological development. Samples were collected from two sites along the successional sequence of the boreal forest. The intermediate successional stage was represented by a south-facing aspen (*Populus tremuloides*; site AS2) community with a 3–5 cm floor of leaf litter and an insignificant understory. The advanced successional stage was represented by a north-facing black spruce (*Picea mariana*; site BS2) stand with a continuous ground cover of feather mosses (*Pleurozium* spp. and *Hylocomium* spp.) invaded by lowbush cranberry (*Vaccinium vitis-idaea*) and lichens. The organic horizon extends to about 10 cm. These upland sites have no soil zone of methanogenesis and are atmospheric CH_4 sinks (Whalen *et al.*, 1991). Thus, the CH_4-oxidizing community is normally exposed to CH_4 concentrations at or below the atmospheric level ($\sim 1.7\ \mu l\ l^{-1}$). A complete site description is given in Van Cleve *et al.* (1991).

Lemeta Bog (LB) is a poorly-drained, open stand of stunted black spruce with an undergrowth of *Sphagnum* invaded by Labrador tea (*Ledum palustre*), cloudberry (*Rubus chamaemorus*) and lowbush cranberry. The maximum thaw depth is < 1 m with peat extending to permafrost. Most areas within the bog show net CH_4 emission to the atmosphere (Moosavi, 1994). Samples were collected from drained, aerobic peat overlying a water-saturated anaerobic zone of methanogenesis. Thus, CH_4 oxidizers are normally exposed to uptake-saturating concentrations of CH_4. This site is fully described in Luken and Billings (1985) and Funk *et al.* (1994).

Bulk soil samples were collected from the zone of maximum CH_4-oxidation (10-20 cm at AS2 and BS2; 20-30 cm at LB) with a trowel (BS2 and AS2) or serrated knife (LB), after removal of topsoil with a stainless-steel coring apparatus (AS2 and BS2; Whalen *et al.*, 1992) or serrated knife (LB). Samples were returned to the laboratory within 2 h. Individual samples from each site were composited (~5 kg total), sieved (AS2 and BS2 only; < 4 mm grain size), homogenized with a garden trowel, and stored at 4°C in foil-covered polyethylene tubs until experiments were begun (within 24 h of sample collection).

Soil physical and chemical properties

Physical and chemical properties were determined for each soil composite according to standard methods (Carter, 1993). Soil moisture was measured gravimetrically by oven-drying at 105°C (AS2 and BS2) or 85°C (LB) and organic content was determined by loss on ignition (550°C) of oven-dried samples. Gravimetric water holding capacity (WHC) was determined as the difference in weight between water-saturated and oven-dried soils. Soil pH was measured potentiometrically on soil-deionized water pastes (ratio 1:1 to 1:2).

Experimental

Experiments were performed in ~1-liter Mason jars modified for syringe sampling of the headspace gas (Whalen *et al.*, 1990). Equal-sized aliquots of homogenized soil composites (100 to 200 g field-moist samples; mass dependent on site) were dispensed into Mason jars. A soil property (e.g. moisture content) was adjusted within each jar to yield one or two jars exposed to each treatment condition and the microbial communities were conditioned for 8–12 h in a free-air atmosphere to the altered environment. All experiments involved time-course

measurement (every 0.5 to 1 h) of the headspace CH_4 concentration in jars incubated statically for 6 to 12 h. Jar headspaces for AS2 and BS2 soils were equilibrated with a free-air atmosphere (~1.7 μl CH_4 l^{-1}) to approximate *in situ* CH_4 concentrations and sampling commenced immediately upon sealing. Headspace CH_4 concentrations in jars with LB soil were adjusted to concentrations previously determined to give zero-order CH_4 consumption (amended atmosphere experiments; +600 to 1200 μl CH_4 l^{-1}) and to simulate the *in situ* CH_4 concentration. Zero-order (substrate-saturated) oxidation was indicated by a linear time-course for decrease in the headspace CH_4 concentration. These soils were conditioned at the selected moisture or temperature conditions for an additional 2 h after CH_4 addition before zero time (T_0) headspace samples were withdrawn.

The moisture response of CH_4-oxidation at room temperature (~25°C) was determined at soil moisture contents above and below those of field-moist soils. Soil moisture was incrementally increased by application of a fine mist of deionized water to the soil with simultaneous stirring. Moisture content was decreased by spreading a thin layer of soil over a foil sheet followed by exposure to ambient or slightly elevated (5°C) temperatures in a convection oven. Soils were periodically consolidated, weighed and redistributed to promote even drying over a 2 to 6 h period. Soil moisture content is expressed as a percentage of water holding capacity (% of WHC) to facilitate comparisons of relative degree of wetness for and among soil samples.

The substrate-saturated temperature response of CH_4-oxidation (LB soil) was evaluated at roughly 7°C increments from 5°C to 42°C. We did not expect a pronounced temperature influence on CH_4-oxidation rates at atmospheric CH_4 concentrations (AS2 and BS2 soil). To better detect a response, we eliminated any influence of jar-to-jar variability in microbial community composition and activity by assessing CH_4-oxidation in duplicate samples from each site that were exposed to 4, 16 and 28°C (random order) over three successive days.

The large number of samples required to assess the interactive effect of soil moisture and temperature on CH_4-oxidation forced us to limit the scope of these experiments. The interactive effect was determined only across the range of soil temperatures (~4 to 20°C) and % of WHCs (~30 to 70%) normally encountered in the field at each site. In contrast, experiments assessing the individual effects of these variables spanned a greater range of values.

Progress curves (17 to 37 h) for CH_4 depletion versus time were used to determine values of the kinetic parameters for CH_4-oxidation (K_s = apparent half-saturation constant; V_{max} = maximum oxidation rate) by the microbial consortium at each site. Experiments were conducted at room temperature on a single field-moist soil composite from each site.

Methane analysis

Headspace CH_4 determinations were made by flame ionization detection gas chromatography with a precision of < 1% (Whalen *et al.*, 1991). Calibration gases are relatable to mixtures obtained from the National Institute of Standards and Technology.

Statistical analyses and calculations

Substrate-saturated rates of CH_4-oxidation (ng CH_4 g^{-1} dw of soil; dw = dry weight) in moisture, temperature and moisture-temperature experiments involving LB2 soil were calculated from linear regression of headspace CH_4 concentration versus time for amended atmosphere experiments. First-order rate constants for CH_4-oxidation, k (h^{-1}), were calculated from linear regression of ln-transformed concentration versus time data in experiments involving a free-air atmosphere (AS2 and BS2 soils). To facilitate comparison of CH_4-oxidation rates among sites, these data are expressed as the rate of CH_4-oxidation at 1.5 μl CH_4 l^{-1} (ng CH_4 g^{-1} dw of soil). This is a typical concentration in the air-filled pore space near the soil surface at AS2 and BS2 (Whalen *et al.*, 1992).

Values for kinetic constants for CH_4-oxidation (K_s and V_{max}; defined above) were estimated from the integrated solution for the Michaelis-Menten model (Robinson, 1985):

$$V_{max}t = S_o - S_t + K_s\ln(S_o/S_t) \quad (1)$$

where S_o and S_t are the headspace CH_4 concentrations at start of the experiment and at time = t, respectively. Data for CH_4 concentration versus time in progress curve experiments was directly fitted to equation (1) by a quasi-Newton method, using the SYSTAT program package (SYSTAT Inc. Evanston, Illinois). Values of K_s are expressed as aqueous-phase concentrations (nM) by applying Bunsen solubility coefficients (Yamamoto *et al.*, 1976) to gas-phase CH_4 concentrations.

Statistical analyses (α = 0.05) follow Zar (1984). Experiments assessing community response to multiple treatment conditions for a manipulated variable through time-course analysis of change in substrate concentration often involve compromises with regard to sampling frequency and replication. This is particularly true where rates of activity cannot be determined from time-linear observations, as in experiments assessing k at very low substrate concentrations. We often directed our efforts toward firmly establishing the CH_4-oxidation rate in a single sample at each treatment condition by making multiple observations of headspace CH_4 concentration closely spaced in time for each time-course experiment used in rate determinations. Values for

r^2 in linear regression equations used to determine substrate-saturated CH_4-oxidation rates or k exceeded 0.95 in nearly all cases. Use of relatively large, homogenized soil samples (100 to 200 g) for each treatment minimized the potential effect of sample-to-sample differences in the size of the microbial community on CH_4-oxidizing activity. In cases where CH_4-oxidation rate determinations were made on replicate samples, coefficients of variation averaged only 6.8%. In concert, high values of r^2 for regression equations used to determine CH_4-oxidation rates and low coefficients of variation when rate determinations were made on replicate samples suggest that a single rate determination gave a true measure of the response of CH_4-oxidation to the manipulated variable. Associations between manipulated variables and rates of CH_4 consumption calculated from time-courses were analyzed by best fit relationships (highest r^2), which were either linear or polynomial regressions.

RESULTS

Soil properties

Some soil properties differed between the forest and bog (Table 1). Bog soil (LB) was lower in pH and higher in organic content and WHC compared with forest soils (AS2 and BS2). However, soils at BS2 and LB2 were most similar with respect to % of WHC at the time of sample collection, as data ranged from about 40–80% at both sites, vs 13–46% at AS2. Gravimetric moisture content increased with increasing percent organic matter, with data averaging about 11, 40 and 500% at AS2, BS2 and LB.

Moisture response experiments

Methane-oxidation rates in moisture response experiments for the two forest soils were similar (Fig. 1). Data ranged from 0.01 to 0.92 ng CH_4 g^{-1} dw h^{-1} for AS2 (n = 7) and from 0.01 to 1.35 ng CH_4 g^{-1} dw h^{-1} for BS2 (n = 6). Rates of CH_4-oxidation were generally 1000-fold higher in LB soil than in the forest soils, due to the higher concentration of headspace CH_4, larger communities of CH_4-oxidizing bacteria or both (Fig. 1). Data ranged from 360 to 1330 ng CH_4 g^{-1} dw h^{-1} (n = 7). A polynomial function provided the best fit to the moisture (M) response of the CH_4-oxidation rate (V) at each site. These relationships give optimum water contents (% of WHC; $dV/dM = 0$) of 21, 27 and 50% for CH_4-oxidation in AS2, BS2 and LB soils, respectively. The % of WHCs for field-moist soils were 13, 45 and 45% for AS2, BS2 and LB, respectively, with the difference between the ambient and optimum % of WHC ranging from −8% at AS2 to +18% at BS2.

Although the moisture response of CH_4-oxidation may partly depend on the CH_4 concentration, the study sites can be expected to experience a relatively narrow range of CH_4 concentrations. Soils at AS2 and BS2 are constantly exposed to sub-atmospheric CH_4 concentrations (< 1.7 μl l^{-1}), while LB soil is subject to CH_4 concentrations that are more variable, but saturate the CH_4-oxidizing capability of the microbial community. Hence, the data for % of WHC collected through the summers of 1993 and 1994 (Table 1) and the moisture dependence relationships for CH_4-oxidation (Fig. 1) were used for a one-dimensional analysis of the seasonal (June through August) influence of soil moisture on rates of CH_4-oxidation in these soils. The moisture response of CH_4-oxidation is predicted to range over factors of 2.6, 5.0 and 1.6 at AS2, BS2 and LB.

Temperature response experiments

Site-wise comparison of CH_4-oxidation rates in temperature response experiments shows that rates were most similar for the two forest soils, in agreement with results of moisture response experiments. Nonetheless, rates were about four-fold higher at BS2 than AS2, with data ranging from 2.71 to 4.29 ng CH_4 g^{-1} dw h^{-1} (n = 6) and 0.73 to 1.18 ng CH_4 g^{-1} dw h^{-1} (n = 6) at the two respective sites (Fig. 2). Rates of CH_4 oxidation were 2–3 orders of magnitude higher in LB soil (range: 2727–4473 ng CH_4 g^{-1} dw h^{-1}; n = 14) than in forest soils (Fig. 2), also in agreement with moisture dependence data. The data indicate a linear response in CH_4 consumption to changing temperature in a free-air atmosphere for forest soils. Slopes for regression equations were significantly different between forest soils, indicating a greater temperature influence on CH_4-oxidation for soil from BS2 than AS2. A polynomial provided the best fit to the temperature (T) response for CH_4-oxidation (V) under substrate-saturated conditions for LB soil (Fig. 2). However, the temperature range tested was greater than the range investigated for forest soils. The data indicate an optimum temperature, T_{opt},

Table 1. Water holding capacity and field range of values for soil properties at three boreal study sites at the time of sampling

Site	*WHC*[a]	*%WHC*	*% Organic Matter*[b]	*pH (H_2O)*
AS2	65	13–46	2.6–4.6	5.2–5.8
BS2	72	44–72	5.7–13.3	4.4–5.1
LB	711	40–82	88–94	3.6–4.0

[a]WHC = water holding capacity ((g H_2O g^{-1} dry weight soil) ×100).
[b]loss on ignition at 550°C.

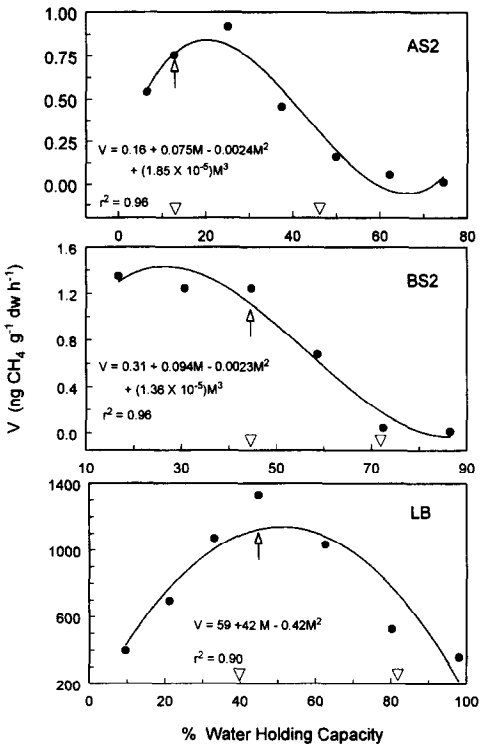

Fig. 1. Methane oxidation rate at room temperature as a function of percent of water holding capacity for boreal soils. Methane oxidation rates for AS2 (top) and BS2 (middle) soils were calculated for 1.5 µl CH_4 l^{-1} from first-order rate constants, while CH_4 oxidation rates for LB soil (bottom) were directly measured in time-course experiments. Polynomial functions are fitted to the data from each site. Arrows indicate the percent of water holding capacity for each soil at the time of sample collection. Open triangles on abscissa indicate maximum and minimum percent of water holding capacity observed *in situ* during the study.

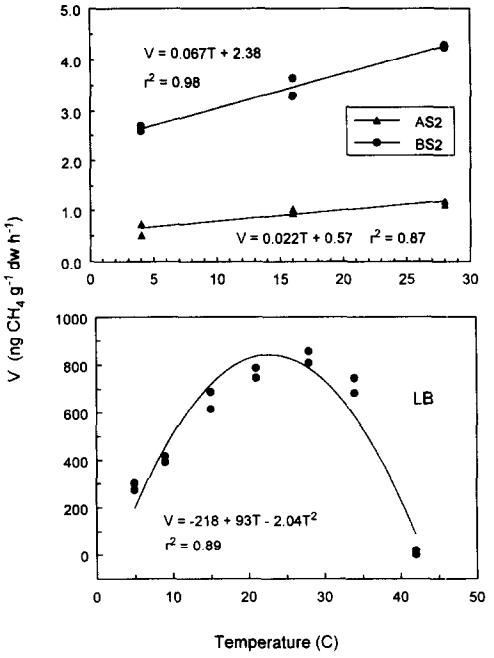

Fig. 2. Methane oxidation rate as a function of temperature for boreal soils. Methane oxidation rates for AS2 (top) and BS2 (middle) soils were calculated for 1.5 µl CH_4 l^{-1} from first-order rate constants, while CH_4 oxidation rates for LB soil (bottom) were directly measured in time-course experiments. A linear (AS2 and BS2) or polynomial (LB) function is fitted to the data from each site.

($dV/dT = 0$) of about 23°C for substrate-saturated CH_4-oxidation in LB soil.

Soils at the depth of sample collection varied in temperature from 6–21°C at AS2, 4–18°C at BS2 and 4–13°C at LB during June through August. Thus, T_{opt} for LB soil was 10°C higher than the maximum *in situ* soil temperature. The relationships from Fig. 2 indicate that the temperature response of CH_4-oxidation will range over factors of 1.5 and 1.4 for AS2 and BS2 soil. Data from Fig. 2 suggest a linear relationship between CH_4-oxidation rate and temperature ($V = 30.7T + 138$; $r^2 = 0.96$; $n = 6$) for LB soil over the range 4–13°C; the temperature response of CH_4-oxidation will range over a factor of 2.1. Thus, soil moisture exerted greater control on rates of CH_4-oxidation than temperature in the forest soils over the range of values observed for these environmental measures during this investigation. Conversely, soil temperature was more important than moisture in regulating CH_4 consumption in the bog soil.

Moisture-temperature interactions

Results of experiments assessing the interactive effects of moisture and temperature on CH_4-oxidation over the general ranges of values observed *in situ* for these variables at each site (Fig. 3) agree qualitatively with results from experiments evaluating their individual effects (Figs 1 and 2). Rates of CH_4-oxidation at each site are within the range observed for experiments described above, with rates for LB soil >100-fold higher than rates for forest soils. The data for AS2 and BS2 indicate a modest decline in the CH_4-oxidation rate with decreasing temperature over the entire range of % of WHC, but a rapid decrease in the CH_4-oxidation rate as soil moisture approached the highest values of % of WHC observed during this investigation. In contrast, the data for LB show a pronounced temperature effect on rates of CH_4-oxidation and a less prominent decline in CH_4 consumption at high values of % of WHC.

Maximum observed rates of CH_4-oxidation in moisture-temperature experiments corroborate well the data from experiments analyzing the individual effects. The maximum rates of CH_4-oxidation for AS2, BS2 and LB soil (Table 2) were 0.85, 1.10 and 706 ng g^{-1} dw h^{-1}, respectively. For each soil, the maximum oxidation rate occurred at the highest test temperature, as predicted in Fig. 2. The % of WHC

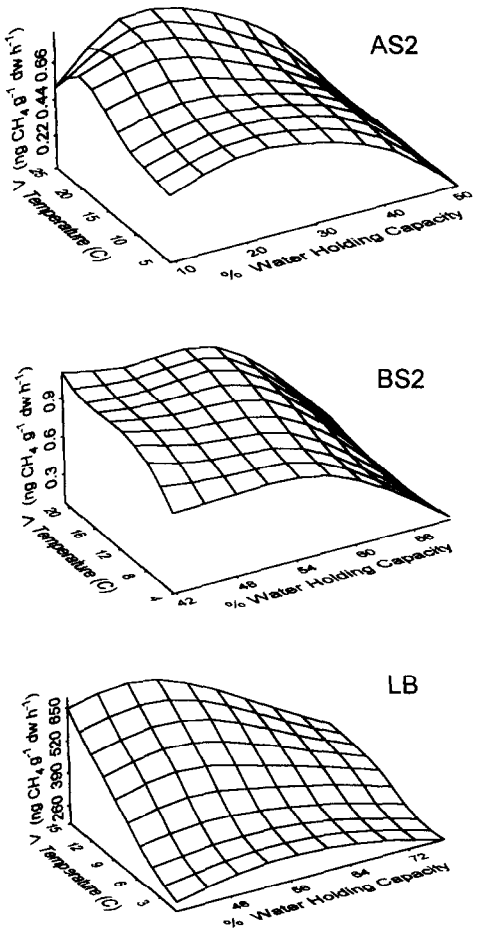

Fig. 3. Methane oxidation rates as a function of moisture-temperature interactions for boreal soils. Methane oxidation rates for AS2 (top) and BS2 (middle) soils were calculated for 1.5 μl CH_4 l^{-1} from first-order rate constants for each moisture-temperature combination. Methane oxidation rates for LB soil (bottom) were directly measured in time-course experiments for each moisture-temperature combination.

at the highest rate of CH_4-oxidation for AS2 and LB are close to the optimum % of WHC identified in moisture dependence experiments (cf. Table 2 and Fig. 1). The moisture content at the maximum rate of CH_4 oxidation for BS2 in moisture-temperature experiments exceeded the optimum % of WHC for CH_4-oxidation by this soil in moisture dependence experiments. Nonetheless, results between these experiments with BS2 soil are consistent, as the % of WHC for field-moist soils (Table 1) always exceeded the optimum of 27%. The lowest % of WHC tested in moisture-temperature experiments (42%; Table 2) gave the highest rate of CH_4-oxidation and corresponds with the lowest % of WHC observed *in situ* at BS2 during our study (Table 1).

The combined influence of adverse temperature and moisture conditions resulted in a severe reduction in rates of CH_4-oxidation for all soils. The minimum rate of CH_4-oxidation was consistently observed with the combination of the highest % of WHC and lowest temperature tested (Table 2). The ratio of maximum-to-minimum rate of CH_4-oxidation in moisture-temperature dependence experiments gives an indication of the potential combined influence of these factors on CH_4-oxidation during June through August at each site. Methane-oxidation rates may vary seasonally by factors of 42, 11 and 3.9 at AS2, BS2 and LB due to moisture–temperature interactions.

Methane-oxidation kinetics

Differences in rates of CH_4-oxidation between forest and bog soils can be attributed to experimental conditions (free-air versus amended atmosphere experiments). However, kinetic constants (Table 3) derived from progress curves for the decrease in headspace CH_4 for soils initially exposed to uptake-saturating concentrations point to fundamental differences in microbial populations between site types. Values of K_s and V_{max} for AS2 and BS2 were reasonably similar, but were roughly an order of magnitude lower than the data for LB.

DISCUSSION

Rates of microbial activity depend on enzymatic processes and their environmental modulators. Our moisture manipulation experiments were made at headspace CH_4 concentrations that approximate *in situ* amounts. Thus, they provide the first direct evidence for moisture sensitivity of CH_4-oxidation rates in boreal soils that represent extreme environments with respect to *in situ* CH_4 concentrations.

Table 2. Maximum and minimum rates of CH_4 oxidation observed in moisture-temperature dependence experiments, corresponding values of soil moisture and temperature and range of moistures and temperatures tested for each soil

Site	*CH_4 oxidation rate (ng g^{-1} dw h^{-1})*						*Range tested*	
	Max.	*% WHC*	°C	*Min.*	*% WHC*	°C	*% WHC*	°C
AS2	0.85	20	25	0.02	51	4	9–51	4–25
BS2	1.10	42	21	0.10	70	4	42–70	4–21
LB	706	53	15	183	77	1	41–77	1–15

WHC = water holding capacity ((g H_2O g^{-1} dry weight soil) ×100).

Table 3. Kinetics of CH_4 oxidation by field-moist composites of boreal soil

Site	$nM\ CH_4$		$ng\ CH_4\ g^{-1}\ dw\ h^{-1}$	
	K_s	95% CI[a]	V_{max}	95% CI
AS2	37	31–44	12	11–13
BS2	124	110–137	137	131–143
LB	1090	1020–1070	3570	3370–3770

[a]95% confidence interval.

Methane-oxidizing bacteria at AS2 and BS2 are normally exposed to a free-air atmosphere, while those at LB are consistently subjected to uptake-saturating concentrations of CH_4. These results (Fig. 1) imply a moisture sensitivity of CH_4-oxidation by the local microbial communities in all boreal soils across a 1000-fold range of *in situ* substrate concentrations.

Results from moisture dependence experiments at forest sites (Fig. 1) corroborate the results of field studies in soils that show only a zone of CH_4 oxidation (no methanogenesis) and are atmospheric CH_4 sinks. Seasonal investigations have reported an inverse correlation between soil moisture and CH_4-oxidation rates in forested (Keller *et al.*, 1986; Steudler *et al.*, 1989 Whalen *et al.*, 1991; Koschorreck and Conrad, 1993; Lessard *et al.*, 1994; Castro *et al.*, 1995 Sitaula *et al.*, 1995) and unforested soils (Mosier *et al.*, 1991, 1993; Koschorreck and Conrad, 1993; Keller and Reiners, 1994), but these data necessarily include any temperature effect. No field data exist for moisture dependence of CH_4-oxidation under uptake-saturating conditions. Methane is produced and oxidized simultaneously and in close proximity in these environments (e.g. Sundh *et al.*, 1994), and the observed CH_4 flux reflects the net effect of these two processes.

Laboratory studies of the moisture dependence of CH_4-oxidation are few, often involve amended atmospheres and give variable results. In accord with our data, Adamsen and King (1993) showed an inverse relationship between gravimetric soil water content (range 20–50%) and CH_4-oxidation by coniferous soil composites at a headspace concentration of 10 μl CH_4 l^{-1} while Yavitt *et al.* (1995) generally found that the lowest rate of CH_4 consumption at both 51 and 1.7 μl CH_4 l^{-1} was associated with the highest soil moisture content (variable among samples) in composites of hardwood forest soils. In contrast, Nesbit and Breitenbeck (1992) reported a relative insensitivity of CH_4-oxidation to soil moisture (25 and 75% water-filled pore space) for swamp and forest soils at 100 μl CH_4 l^{-1}. Differences in the moisture response of CH_4-oxidation among these studies may be related to the physiological characteristics of the extant microbial communities and experimental CH_4 concentration. King and Schnell (1994) reported a CH_4 concentration-dependent response of NH_4^+–N inhibition of CH_4-oxidation in forest soils normally exposed to a free-air atmosphere. Our experiments at *in situ* CH_4 level-concentrations probably gave the most reliable measure of the moisture response of CH_4-oxidizing microbial communities in the boreal soils tested.

The observed negative relationship between soil moisture and CH_4-oxidation rates in many field studies involving atmospheric CH_4 consumption is generally attributed to diffusion limitation of substrate supply as soil moisture increases (Dörr *et al.*, 1993). Data for AS2 (Fig. 1) suggest that water stress control of CH_4-oxidation must also be considered. Increasing the % of WHC from a field-moist 13% to 25% resulted in a 22% increase in the CH_4-oxidation rate. Field observations point to water stress control of CH_4-oxidation under some circumstances. Dry tropical forest (Keller *et al.*, 1990), desert (Striegl *et al.*, 1992) and grassland (Mosier *et al.*, 1991) soils all showed enhanced CH_4-oxidation when soil water content was naturally or artificially increased. Physiological stress is an acknowledged, but poorly understood control of CH_4-oxidation (Adamsen and King, 1993). Process-oriented studies of CH_4-oxidation in soil should include water stress as well as diffusion limitation in moisture response experiments, as regional changes in climate may include a reduction in soil moisture content.

Present susceptibility of CH_4-oxidizing bacteria to water stress may vary among environments, and altered soil moisture regimes under future climatic conditions may not have intuitively obvious effects on microbial consumption of atmospheric CH_4. Percent of WHC for AS2 soil varied from 13 to 20% during 1993 and from 26 to 46% in 1994. Local June through August precipitation in 1993 and 1994 was 56% and 92% of the 30 year mean (NOAA, 1993, 1994). Thus, data in Fig. 1 suggest that water stress may be an important control on CH_4-oxidation at AS2 only in an abnormally dry year under the present climate. However, a long-term reduction in summer soil moisture predicted for this region in some general circulation models (Mitchell *et al.*, 1990) may lead to chronic water stress and a reduced sink strength for AS2 and similar sites. In contrast, % of WHC at BS2 exceeded the calculated optimum of 27% even during the abnormally dry summer of 1993 (Table 1) and Fig. 1 predicts that this site will increase in sink strength during a protracted period of reduced precipitation. Other forested areas may react to a long-term re-

duction in soil moisture in a fashion similar to BS2. Castro *et al.* (1995) observed that the highest monthly average rate of CH_4 consumption in temperate forest soils coincided with the lowest soil moisture content recorded in 6 years of study and suggested that this region may increase in sink strength with a reduction in soil moisture.

A subsurface maximum of CH_4-oxidizing activity in the mineral forest soil zone has been commonly observed (Whalen *et al.*, 1992; Adamsen and King, 1993; Koschorreck and Conrad, 1993; Bender and Conrad, 1992; Schnell and King, 1994) and has been attributed to NH_4^+ inhibition in surface, organic soils (King and Schnell, 1994). Avoidance of water stress may be an added benefit, as the only report of a surface maximum in CH_4-oxidizing activity (Whalen and Reeburgh, 1990a) involved tundra soil that receives almost daily precipitation. Ecosystem level responses to altered climate may include a shift in the zone of maximum CH_4-oxidizing activity to accommodate changes in soil moisture. Downward displacement will avoid cell desiccation as soils dry, but will also increase the diffusional path length for CH_4. This potential response of CH_4-oxidizing communities to drier conditions climate is unexplored and must be considered in assessing potential effects of altered climate.

The range in response of CH_4-oxidation rates to soil moisture and temperature conditions that bracket field observations suggests that for the June through August period soil moisture (diffusion) is the primary environmental control on CH_4-oxidation in our forest soils and temperature is of secondary importance. This is consistent with field data (Castro *et al.*, 1994) from a temperate forest where a moisture–CH_4 flux relationship developed during a watering experiment at nearly constant soil temperature was used to accurately predict ($r^2 = 0.75$) measured fluxes in previous seasons where soil temperatures ranged over ~20°C. Other seasonal field studies show a weak temperature correlation for atmospheric CH_4-oxidation across ecosystems (Steudler *et al.*, 1989; Born *et al.*, 1990; Crill, 1991; Koschorreck and Conrad, 1993; Castro *et al.*, 1993, 1995; Tate and Striegl, 1993; Crill *et al.*, 1994; Sitaula *et al.*, 1995), but these observations include a variable moisture effect.

Methane-oxidation rates by soils from AS2 and BS2 increased by only 80 and 61% with a temperature increase from 4 to 28°C (Fig. 2). This linear and limited response of CH_4-oxidation in a free-air atmosphere by our forest soils compares favorably with studies that have isolated the temperature effect on CH_4-oxidation. Linear increases of about 35% (King and Adamsen, 1992) and 55% (Lessard *et al.*, 1994) in the rate of CH_4-oxidation by forest soils have been reported over the temperature ranges 0–30°C and 6–17°C, respectively. Differences in the relative response of CH_4-oxidation to temperature change among investigations are likely related to interactions among gas-phase transport, soil–water gas exchange and enzymatic activity, but the data clearly point to a lesser role for temperature than moisture as a control of CH_4-oxidation in a free-air atmosphere.

The zero-order temperature response for CH_4-oxidation by LB soil showed a greater relative rate increase for an incremental increase in temperature than soils from forest sites over the *in situ* range of soil temperatures (Fig. 2). These data point to greater enzymatic control of microbial CH_4-oxidation in this high source CH_4 soil than in forest soil exposed only to atmospheric CH_4. Accordingly, the range in response of CH_4-oxidation rates to soil moisture and temperature conditions that span field observations indicates that for the June through August period soil temperature exerts a greater influence than moisture on CH_4-oxidizing activity. The T_{opt} of 23°C agrees closely with the 20 to 25°C reported by Dunfield *et al.* (1993) for CH_4-oxidation in other subarctic peats incubated at 1000 μl CH_4 l^{-1}, but is somewhat lower than zero-order values of 38°C and 31°C reported for cultures of *Methylomonas rubra* (King and Adamsen, 1992) and landfill cover soils (Whalen *et al.*, 1990), respectively. These T_{opt} values for natural soil samples all exceed the highest *in situ* summer soil temperatures.

Our moisture–temperature experiments (Fig. 3) were designed to assess interactions between enzymatic (temperature) and diffusive (moisture) control of CH_4-oxidation as opposed to individual effects (Figs 1 and 2). Data for forest soils confirm the general dominance of diffusive control of atmospheric CH_4-oxidation under field conditions and are in agreement with a similar laboratory study of moisture–temperature interactions (Schimel *et al.*, 1993) where moisture controlled CH_4-oxidation by upland tundra soil composites ranged from 5 to 15°C and from 25% to 200% of WHC.

The shape of the three dimensional contour plot for CH_4-oxidation in high source CH_4 bog soil (LB) differs distinctly from similar plots for atmospheric CH_4 consumption by forest soils (Fig. 3). A greater temperature response and less precipitous decline at elevated soil moisture contents are evident. This corroborates results of experiments testing the individual effects of moisture and temperature (Figs 1 and 2) and provides further evidence for increased control of CH_4-oxidation by enzymatic activity at LB and similar, high source CH_4 environments. High latitude bogs are important point sources of atmospheric CH_4 (Whalen and Reeburgh, 1990) and this region is projected to experience warmer temperatures and a possible reduction in summer soil moisture under an altered climate (Mitchell *et al.*, 1990). Our data (Fig. 3) predict accelerated rates of CH_4-oxidation, largely in response to warmer tem-

peratures. However, Q_{10}s for substrate-saturated CH_4-oxidation (1.3–2.3) in peat (Dunfield *et al.*, 1993; Crill *et al.*, 1994; Nedwell and Watson, 1995) are decidedly lower than Q_{10}s for methanogenesis (5.3–20) in peat (Dunfield *et al.*, 1993; Nedwell and Watson, 1995). Neglecting other potential ecosystem-level effects of altered climate on ecosystems (e.g. change in aerobic-to-anaerobic soil zones), CH_4 emission from northern bogs may therefore increase as a result of the greater temperature sensitivity of methanogenesis than CH_4-oxidation.

The apparent half-saturation constant for CH_4-oxidation in LB soil (Table 3) agrees well with similar data for microbial communities in high source CH_4 environments. Soils from a landfill cover (Whalen *et al.*, 1990) and subarctic (Dunfield *et al.*, 1993) and arctic (Whalen *et al.*, 1996) peatland showed K_s values in the 1.0–6.2 μM range. Temperate peat had somewhat higher K_s values, 14 to 45 μM (Nedwell and Watson, 1995). Forest soil values of K_s (Table 3) are in accord with the 30 to 51 nM reported for temperate cambrisols that consume atmospheric CH_4 (Bender and Conrad, 1992).

The V_{max} for LB soil was lower than previous reports for comparable environments. The dry mass-based V_{max} from Table 3 is 380 ng CH_4 g^{-1} ww h^{-1} for field-moist soil, compared with 800 ng g^{-1} ww h^{-1} in subarctic peat (Dunfield *et al.*, 1993) and 2500 ng g^{-1} ww h^{-1} in landfill topsoil (Whalen *et al.*, 1990). In contrast, V_{max} for the forest samples (Table 3) agrees closely with the 11 to 58 ng g^{-1} dw h^{-1} reported for cambrisols (Bender and Conrad, 1992).

Values for kinetic constants undoubtedly reflect complex interactions between the environment and enzyme systems. Moreover, V_{max} depends on community vigor and size. Experimental design and curve fitting procedure also influence reported kinetic values (e.g. Robinson and Tiedje, 1982). The relatively narrow range in K_s and V_{max} values for three cambrisols (Bender and Conrad, 1992) under different management practices and these two boreal soils from different successional stages is therefore noteworthy. These two studies are the first to evaluate kinetic constants for high affinity (Bender and Conrad, 1992) CH_4-oxidizing communities. Overall, values for kinetic constants in these boreal soils point to CH_4-oxidizing communities that are fine-tuned to assimilate CH_4 at *in situ* concentrations.

In summary, methanotrophs in subsurface zones of boreal soils are physiologically well-adapted for CH_4 consumption over a broad range of *in situ* substrate concentrations. Soil moisture and temperature affect rates of CH_4 consumption in these soils by influencing substrate supply and rates of enzyme activity, respectively. Rates of CH_4-oxidation are more temperature-sensitive in high source CH_4 bog soils and more moisture-sensitive in forest soils that consume atmospheric CH_4. Our results give insight into the influence changing environmental conditions may have on CH_4-oxidation in boreal soils. Ultimately, interactions among these factors will influence the locus and extent of the CH_4-oxidizing zone in boreal soils and will determine the future importance of this region in the atmospheric CH_4 budget.

Acknowledgements— This work was supported by the U.S. Environmental Protection Agency and the National Institute for Global Environmental Change. The Bonanza Creek Long Term Ecological Research Program is supported by the National Science Foundation. Chad Staiger assisted in field and laboratory analyses.

REFERENCES

Adamsen A. P. S. and King G. M. (1993) Methane consumption in temperate and subarctic forest soils: rates, vertical zonation, and responses to water and nitrogen. *Applied and Environmental Microbiology* **59,** 485–490.

Bender M. and Conrad R. (1992) Kinetics of CH_4-oxidation in oxic soils exposed to ambient air or high CH_4 mixing ratios. *FEMS Microbiology Ecology* **101,** 261–270.

Born M., Dörr H. and Levin I. (1990) Methane consumption in aerated soils of the temperate zone. *Tellus* **42B,** 2–8.

Carter M. R. (Ed.) (1993) *Soil Sampling and Methods of Analysis.* Lewis, Boca Raton.

Castro M. S., Steudler P. A., Melillo J. M., Aber J. D. and Millham S. (1993) Exchange of N_2O and CH_4 between the atmosphere and soils in spruce-fir forests in the northeastern United States. *Biogeochemistry* **18,** 119–135.

Castro M. S., Melillo J. M., Steudler P. A. and Chapman J. W. (1994) Soil moisture as a predictor of methane uptake by temperate forest soils. *Canadian Journal of Forest Research* **24,** 1805–1810.

Castro M. S., Steudler P. A., Melillo J. M., Aber J. D. and Bowden R. D. (1995) Factors controlling atmospheric methane consumption by temperate forest soils. *Global Biogeochemical Cycles* **9,** 1–10.

Cicerone R. J. and Oremland R. S. (1988) Biogeochemical aspects of atmospheric methane. *Global Biogeochemical Cycles* **2,** 299–327.

Crill P. M. (1991) Seasonal patterns of methane uptake and carbon dioxide release by a temperate woodland soil. *Global Biogeochemical Cycles* **5,** 319–334.

Crill P. M., Martikainen P. J., Nykänen H. and Silvola J. (1994) Temperature and N fertilization effects on methane-oxidation in a drained peatland soil. *Soil Biology & Biochemistry* **26,** 1331–1339.

Dörr H., Katruff L. and Levin I. (1993) Soil texture parameterization of the methane uptake in aerated soils. *Chemosphere* **26,** 697–713.

Dunfield P., Knowles R., Dumont R. and Moore T. R. (1993) Methane production and consumption in temperate and subarctic peat soils: response to temperature and pH. *Soil Biology & Biochemistry* **25,** 321–326.

Fung I., John J., Lerner J., Matthews E., Prather M., Steele L. P. and Fraser P. J. (1991) Three-dimensional model synthesis of the global methane cycle. *Journal of Geophysical Research* **96D,** 13033–13065.

Funk D. W., Pullman E. R., Peterson K. M., Crill P. M. and Billings D. W. (1994) Influence of water table on carbon dioxide, carbon monoxide and

methane fluxes from taiga bog microcosms. *Global Biogeochemical Cycles* **8,** 271–278.

Houghton J. T., Meira Filho L. G., Bruce J., Lee H., Callandar B. A., Haites, E., Harris N. and Maskell, K. (Eds) (1995) *Climate Change, 1994. Radiative Forcing of Climate Change and An Evaluation of the IPCC IS92 Emission Scenarios.* Cambridge University Press, Cambridge.

Keller M. and Reiners W. A. (1994) Soil-atmosphere exchange of nitrous oxide, nitric oxide, and methane under secondary succession of pasture to forest in the Atlantic lowlands of Costa Rica. *Global Biogeochemical Cycles* **8,** 399–409.

Keller M., Kaplan W. A. and Wofsy S. C. (1986) Emission of N_2O, CH_4 and CO_2 from tropical forest soils. *Journal of Geophysical Research* **91D,** 11791–11802.

Keller M., Mitre M. E. and Stallard R. F. (1990) Consumption of atmospheric methane in soils of central Panama: effects of agricultural development. *Global Biogeochemical Cycles* **4,** 21–27.

King G. M. (1992) Ecological aspects of methane-oxidation, a key determinant of global methane dynamics. *Advances in Microbial Ecology* **12,** 431–468.

King G. M. and Adamsen A. P. S. (1992) Effects of temperature on methane-oxidation in forest soil and pure cultures of the methanotroph *Methylomonas rubra*. *Applied and Environmental Microbiology* **58,** 2758–2763.

King G. M. and Schnell S. (1994) Effect of increasing atmospheric methane concentration on ammonium inhibition of soil methane consumption. *Nature* **370,** 282–284.

Koschorreck M. and Conrad R. (1993) Oxidation of atmospheric methane in soil: Measurement in the field, in soil cores and in soil samples. *Global Biogeochemical Cycles* **7,** 109–121.

Lessard R., Rochette P., Topp E., Pattey E., Desjardens R. L. and Beaumont G. (1994) Methane and carbon dioxide fluxes from poorly drained adjacent cultivated and forest sites. *Canadian Journal of Soil Science* **74,** 139–146.

Lieth H. (1975) Primary production of the major vegetation units of the world. In *Primary Productivity of the Biosphere* (H. Lieth and R. H. Whittaker, Eds), pp. 203–214. Springer, New York.

Luken J. O. and Billings W. D. (1985) The influence of microtopographic heterogeneity on carbon dioxide efflux from a subarctic bog. *Holarctic Ecology* **8,** 306–312.

Mancinelli R. L. (1995) The regulation of methane oxidation in soil. *Annual Reviews of Microbiology* **49,** 581–605.

Mitchell, J. F. B., Manabe S., Tokioka T. and Meleshko V. (1990) Equilibrium climate change. In *Climate Change. The IPCC Scientific Assessment* (J. T. Houghton, G. J. Jenkins and J. J. Ephraums, Eds), pp. 131–172. Cambridge University Press, New York.

Moosavi, S. C. (1994). *Controls on methane flux from an Alaskan boreal wetland.* M.S. Thesis, University of New Hampshire.

Mosier A., Schimel D., Valentine D., Bronson K. and Parton W. (1991) Methane and nitrous oxide fluxes in native, fertilized and cultivated grasslands. *Nature* **350,** 330–332.

Mosier A. R., Klemedtsson L. K., Sommerfeld R. A. and Musselman R. C. (1993) Methane and nitrous oxide flux in a Wyoming subarctic meadow. *Global Biogeochemical Cycles* **7,** 771–784.

Nedwell D. B. and Watson A. (1995) CH_4 production, oxidation and emission in a U.K. ombotrophic peat bog: Influence of SO_4^{2-} from acid rain. *Soil Biology & Biochemistry* **7,** 893–903.

Nesbit S. P. and Breitenbeck G. A. (1992) A laboratory study of factors influencing methane uptake by soils. *Agriculture, Ecosystems and Environment* **41,** 39–54.

National Oceanographic and Atmospheric Administration (NOAA) (1993) *Local climatological data, Fairbanks, Alaska. Annual summary with comparative data report.* Asheville, NC.

National Oceanographic and Atmospheric Administration (NOAA) (1994) *Local climatological data, Fairbanks, Alaska. Annual summary with comparative data report.* Asheville, NC.

Prinn R. G. (1994) The interactive atmosphere: global atmospheric-biospheric chemistry. *Ambio* **23,** 50–61.

Reeburgh W. S., Whalen S. C. and Alperin M. J. (1993) The role of methylotrophy in the global methane budget. In *Microbial Growth on C1 Compounds* (J. C. Murrell and D. P. Kelly, Eds), pp. 1–14. Intercept Ltd., Andover, U.K.

Robinson J. A. (1985) Determining microbial kinetic parameters using nonlinear regression analysis. Advantages and limitations in microbial ecology. *Advances in Microbial Ecology* **8,** 61–114.

Robinson J. A. and Tiedje J. M. (1982) Kinetics of hydrogen consumption by rumen fluid, anaerobic digestor sludge and sediment. *Applied and Environmental Microbiology* **44,** 1374–1384.

Schimel J. P., Holland E. A. and Valentine D. (1993) Controls on methane flux from terrestrial ecosystems. In *Agricultural Ecosystem Effects on Trace Gases and Global Climate Change* (L. A. Harper *et al.*, Eds), pp. 167–182. Soil Science Society of America, Madison, WI.

Schnell S. and King G. M. (1994) Mechanistic analysis of ammonium inhibition of atmospheric methane consumption in forest soils. *Applied and Environmental Microbiology* **60,** 3514–3521.

Seiler W., Conrad R. and Scharffe D. (1984) Field studies of methane emission from termite nests into the atmosphere and measurements of methane uptake by tropical soils. *Journal of Atmospheric Chemistry* **1,** 171–176.

Sitaula B. K., Bakken L. R. and Abrahamsen G. (1995) CH_4 uptake by temperate forest soil: effect of N input and soil acidification. *Soil Biology & Biochemistry* **27,** 871–880.

Steudler P. A., Bowden R. D., Melillo J. M. and Aber J. D. (1989) Influence of nitrogen fertilization on CH_4 uptake in temperate forest soils. *Nature* **341,** 314–316.

Striegl R. G., McConnaughey T. A., Thorstenson D. C., Weeks E. P. and Woodward J. C. (1992) Consumption of atmospheric methane by desert soils. *Nature* **357,** 145–147.

Sundh I., Nilsson M., Granberg G. and Svensson B. H. (1994) Depth distribution of microbial production and oxidation of methane in northern boreal peatlands. *Microbial Ecology* **27,** 253–265.

Tate C. M. and Striegl R. G. (1993) Methane consumption and carbon dioxide emission in tallgrass prairie: effects of biomass burning and conversion to agriculture. *Global Biogeochemical Cycles* **7,** 735–748.

Van Cleve K., Chapin F. S. III, Dyrness C. T. and Viereck L. A. (1991) State factor control of element cycling in taiga forests. *BioScience* **41,** 78–88.

Whalen S. C., Reeburgh W. C. and Reeburgh W. S. (1990a) Consumption of atmospheric CH_4 by tundra soils. *Nature* **346,** 160–162.

Whalen S. C., Reeburgh W. C. and Reeburgh W. S. (1990b) A methane flux transect along the trans-Alaska pipeline haul road. *Tellus* **42B,** 237–249.

Whalen S. C., Reeburgh W. S. and Barber V. A. (1992) Oxidation of methane in boreal forest soils: a comparison of seven measures. *Biogeochemistry* **16,** 181–211.

Whalen S. C., Reeburgh W. S. and Kiser K. S. (1991) Methane consumption and emission by taiga. *Global Biogeochemical Cycles* **5,** 261–273.

Whalen S. C., Reeburgh W. S. and Reimers C. E. (1996) Control of tundra methane emission by microbial oxidation. In *Landscape Function: Implication for Ecosystem Response to Disturbance. A Case Study in Arctic Tundra* (J. F. Reynolds and J. D. Tenhunen (Eds)). Springer, New York.

Whalen S. C., Reeburgh W. S. and Sandbeck K. A. (1990) Rapid methane-oxidation in a landfill cover soil. *Applied and Environmental Microbiology* **56,** 3405–3411.

Yamamoto S., Alcauskas J. B. and Crozier T. E. (1976) Solubility of methane in distilled water and seawater. *Journal of Chemical and Engineering Data* **21,** 78–80.

Yavitt J. B., Downey D. M., Lang D. E. and Sextone A. J. (1990) CH_4 consumption in two temperate forest soils. *Biogeochemistry* **9,** 39–52.

Yavitt J. B., Fahey T. J. and Simmons J. A. (1995) Methane and carbon dioxide dynamics in a northern hardwood ecosystem. *Soil Science Society of America Journal* **59,** 796–804.

Zar J. H. (1984) *Biostatistical Analysis.* Prentice Hall, Englewood Cliffs, NJ.