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Methane Consumption in Temperate and Subarctic Forest Soils: Rates, Vertical Zonation, and Responses to Water and Nitrogen†

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Rates of methane consumption were measured in subarctic coniferous and temperate mixed-hardwood forest soils, using static chambers and intact soil cores. Rates at both sites were generally between 1 and 3 mg of CH_4 m^{-2} day^{-1} and decreased with increasing soil water contents above 20%. Addition of ammonium (1 μmol g of $soil^{-1}$) strongly inhibited methane oxidation in the subarctic soils; a lesser inhibition was observed for temperate forest samples. The response to nitrogen additions occurred within a few hours and was probably due to physiological changes in the active methane-consuming populations. Methane consumption in soils from both sites was stratified vertically, with a pronounced subsurface maximum. This maximum was coincident with low levels of both nitrate and ammonium in the mixed-hardwood forest soil.

Terrestrial environments cover less than 30% of the earth's surface but play a major role in the composition and dynamics of atmospheric trace gases. For example, about 50% of the total global CO_2 production occurs in terrestrial environments (24). An even higher percentage of the atmospheric methane burden originates from terrestrial sources, including wetlands, ruminants, rice paddies, natural gas leakage, landfills, and biomass burning (4, 8, 15). In addition, terrestrial environments are the only known net biological atmospheric methane sinks. Though largely ignored in the past, soils are now considered an important component of global methane dynamics, consuming 5 to 50 Tg of methane $year^{-1}$ (2, 8), an amount comparable to 1 to 10% of the total global emission.

Atmospheric methane oxidation was first described by Harriss et al. (9) for surface peats in the Great Dismal Swamp and then later by Born et al. (2), Crill (7), Keller et al. (12–14), King and Adamsen (19), Steudler et al. (26), and Yavitt et al. (31) for various temperate and tropical forests. Seiler et al. (25) and Mosier et al. (23) observed uptake in grasslands, and King et al. (20) and Whalen and Reeburgh (28) reported consumption for tundra soils.

Collectively, these studies have established ranges of rates as well as some of the controls of atmospheric methane consumption. For instance, temperature is a relatively minor determinant, while diffusive gas transport in the soil atmosphere and the water content of the soil matrix are critical factors (e.g., see references 2, 7, 19, and 29). Soil nitrogen content and land use practices have also been identified as important controls, though the mechanisms by which these factors are expressed are unclear (12–14, 23, 26).

We report here aspects of atmospheric methane consumption (oxidation) in temperate and subarctic forest soils. Both of these soil types are globally significant as methane sinks. In contrast to previous reports on the consumption of other atmospheric trace gases, e.g., hydrogen and carbon monoxide, we show that the maximum rates of methane uptake are localized below the soil surface. In addition, we show that methane consumption in subarctic forest soils may be more sensitive to nitrogen inhibition than consumption in temperate forests.

MATERIALS AND METHODS

Site description and sample collection. Soils were collected from several sites within a subarctic spruce-lichen woodland and an elevated tundra site near Schefferville, Quebec, Canada (SCH; 54°43′N, 66°42′W). The woodlands were generally similar and characterized by a vegetation of *Picea mariana*, *Picea glauca*, *Ledum groenlandicum*, *Betula glandulosa*, and a thick mat of the reindeer lichen, *Cladonia alpestris* (22). In addition, soils were collected from a temperate mixed forest of pine, *Pinus strobus*, and hardwood, *Quercus rubra*, adjacent to the Darling Marine Center, Walpole, Maine (DMC). Additional details on this site have been described previously (19). At both the SCH and DMC sites, soil cores were obtained by using polyvinyl chloride (inner diameter, 10 cm) or acrylic (inner diameter, 6.3 cm) tubes. When intact cores were desired for experimental incubations, the upper organic layers of the soils were cut with a serrated knife around the circumference of the core tubes, which were subsequently pushed into the mineral soil horizon. When only specific subsurface horizons were desired, the organic layers were removed by hand and the underlying mineral soils were collected in 36-mm acrylic core tubes.

Depth profiles of methane and methane consumption. Depth profiles of soil gases at the DMC site were obtained by using handmade stainless-steel needles (outer diameter, 0.16 cm; inner diameter, 0.08 cm) fitted with plastic luer-lock hubs. The needle tips were inserted to specific depths in the soil, and approximately 1 ml of the soil air was sampled with a syringe after the syringe and needle were flushed by collecting and discarding a similar volume of the soil atmosphere. The samples were returned to the laboratory immediately after collection (<15 min); the sampling needles were re-

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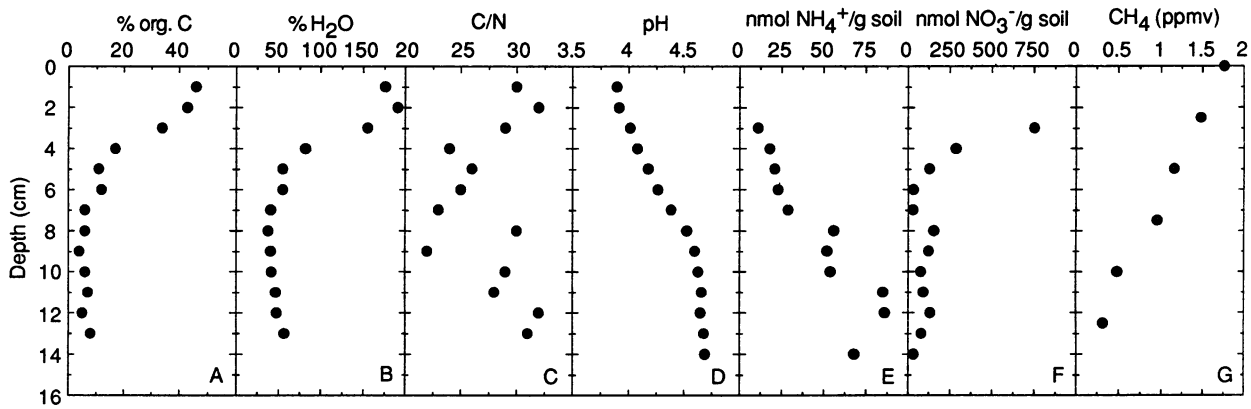

FIG. 1. Soil characteristics for cores obtained from a mixed-hardwood–conifer forest adjacent to the DMC. (A) Percent (wt/wt) organic carbon; (B) % (wt/wt) water; (C) C/N ratio; (D) pH; (E) ammonium (nmol g [wet weight]$^{-1}$); (F) nitrate plus nitrite (nmol g [fresh weight]$^{-1}$); (G) methane (ppm).

placed with a gas chromatography needle, and the syringe contents were analyzed as described below.

Rates of atmospheric methane oxidation were determined by using a static chamber technique. Polyvinyl chloride or acrylic tubes (9-cm inner diameter) were inserted into the soils described above and sealed after approximately 0.5 h with polyvinyl chloride caps or green neoprene stoppers, respectively. The headspace volumes were approximately 1,000 cm^3. The tubes were covered as necessary with aluminum foil to minimize solar heating. Headspace methane concentrations were measured at intervals up to 72 h, using 1-cm^3 samples. Since atmospheric methane consumption was first order, oxidation rates were calculated by regression analysis of logarithmically transformed concentration data.

Intact soil cores were sectioned into 1- to 3-cm slices (about 30 cm^3 of soil) to measure methane oxidation as a function of soil depth. The slices were placed with minimal disturbance into 120-ml screw-cap glass jars that were sealed with rubber stoppers. Consumption of atmospheric methane was monitored over time at 23 to 25°C.

Effects of nitrogen and moisture. The effects of various inorganic nitrogen sources on methane consumption were determined with soils obtained from >5-cm depth; the soils were sieved (2-mm mesh), and 10 g (fresh weight) was added to 60-cm^3 screw-cap bottles. For the SCH samples, 1-ml solutions of 5 or 10 mM ammonium sulfate or 10 mM ammonium chloride or sodium nitrate were distributed uniformly on the surface of the soils. The bottles were sealed with butyl rubber stoppers, and methane (ultra high purity) was injected to a final concentration of about 10 ppm. For the DMC samples, 1-ml solutions of ammonium chloride, sodium chloride, or sodium nitrate were added to the soils and methane concentrations were initially ambient (about 1.7 ppm).

The effect of soil moisture on atmospheric methane consumption in the DMC forest was examined by gently adding 20, 40, and 60 ml of tap water to intact cores. These volumes corresponded to 6.4, 12.8, and 19.2 mm of precipitation and represented additions of about 10, 20, and 30% of the water initially in the cores over the upper 10 cm. To examine the effects of soil moisture on the methane consumption in the most active horizon, various volumes of deionized water were added to SCH soils collected and manipulated as described above. The actual water contents of the treated soil were determined after incubation with 10 ppm of methane at ambient laboratory temperature.

Nitrogen and methane analyses. Ammonium and nitrate-plus-nitrite contents of the DMC soils were determined after extracting soil samples with either 1 N KCl or deionized water for 0.5 h at room temperature. The extracts were centrifuged prior to further processing. Ammonium in the KCl extract was determined by using the indophenol method (21) and an LKB Ultraspec 4050 spectrophotometer. The nitrate-plus-nitrite content of the deionized water extract was analyzed by the method of Velghe and Claeys (27). In addition, the pH of the deionized water extracts was measured with a Beckman Ionanalyzer (Beckman Instruments, Inc.). Total carbon and nitrogen contents of unextracted soils were determined by using an elemental analyzer (Carlo Erba model 1106). Soil water content was determined after drying for approximately 2 days at 60°C (DMC) or 24 h at approximately 80°C in an oven with circulating air (SCH). The two drying methods give comparable results.

Methane was analyzed with a Shimadzu 14A gas chromatograph and a flame ionization detector operated at 150°C. Methane was separated with a Porapak Q column (1 m by 3-mm outside diameter) in series with a wide-bore capillary column (DB-1; 30 m by 0.53-mm outside diameter; J&W Scientific, Inc.). The nitrogen carrier flow rate was 20 ml min^{-1} at 40°C. The detector response was standardized with "certified master gas" standards (Scott Specialty Gases) containing either 0.861 ppm (±2%) or 100.4 ppm (±1%) of methane in nitrogen. The detection limit for methane was 0.1 ppm. The coefficient of variation for replicate injections of the 0.861-ppm standard was 4%.

Nitrapyrin (99% purity; Hach Chemicals) was prepared by the method of King (16) at a concentration of 760 μM. Methane standards and ultra-high-purity methane were obtained from Scott Specialty Gases; acetylene was obtained from AGA, Århus, Denmark. All other chemicals were of reagent-grade purity and were obtained from various commercial suppliers.

RESULTS

Soil characteristics. The soils from DMC showed pronounced variations with increasing soil depth for a number of parameters (Fig. 1). Organic carbon decreased from about 40% in the litter layer to <10% in the deeper mineral soil

TABLE 1. Methane consumption in intact cores and chambers

Site	Rate (mg of CH_4 m^{-2} day^{-1}) ± 1 SE[a]
SCH	
Forest sites	
Site 1	0.53 ± 0.14 (6)
Site 2	0.27 ± 0.14 (7)
Site 3	1.57 ± 0.07 (3)
Subarctic tundra	3.34 ± 0.96 (2)
DMC	2.70 ± 0.12 (5)

[a] Replicate number is given in parentheses. Rates from SCH were obtained during July 1990, and those from DMC were obtained in June 1991.

TABLE 2. Methane consumption in SCH soils amended with various nitrogenous substrates[a]

Substrate added (μmol g of $soil^{-1}$)	Rate constant (h^{-1})	Threshold (ppm)
None[b]	0.041 ± 0.009	1.2 ± 0.1
$(NH_4)_2SO_4$, 0.5	0.016 ± 0.003	3.1 ± 0.5
$(NH_4)_2SO_4$, 1.0	0.002 ± 0.002	5.3 ± 0.4
NH_4Cl, 1.0	0.003 ± 0.003	4.9 ± 0.2
$NaNO_3$, 1.0	0.010 ± 0.003	3.9 ± 0.4

[a] Rate constants were measured by following methane uptake 2 h after substrate addition; threshold values are defined as the methane concentrations remaining after >30 h of incubation. $n = 3$.
[b] Deionized water.

horizons; C/N ratios varied between about 25 and 35, with no clear pattern. Soil pH increased smoothly from <4 to about 4.7, with maxima occurring at depths of >8 cm. Nitrate plus nitrite decreased from about 750 to ≤100 nmol g^{-1} in the upper 6 cm; ammonium concentrations ranged from about 12 to 37 nmol g^{-1} at depths of <6 cm but increased abruptly to values in excess of 70 nmol g^{-1} at depths of >10 cm.

Methane consumption rates. Soils from all of the forest sites consumed atmospheric methane, typically at rates of <3 mg m^{-2} day^{-1} (Table 1); rates at the tundra site exceeded values in the SCH forest soils by about threefold, but were comparable to values from the DMC forest. The disappearance of methane from the gas phase of the static chambers and core samples used to estimate rates at all sites was a first-order process; this allowed for calculation of a first-order uptake constant and estimation of uptake rates by using a concentration of 1.7 ppm. The relaxation time, the time required for chamber headspace and soil pore gas concentrations to equilibrate, was <10 min (data not shown). Thus, rates were not underestimated because of a disequilibrium between the soil and chamber gas phases.

Depth profiles indicated that little or no net methane consumption occurred in the upper, organic horizons; in fact, methane production was occasionally observed in these near-surface soils (Fig. 2A and B). At soil depths in excess of 5 cm, net methane consumption was observed (Fig. 2A and B). In the SCH soils, consumption rate constants increased with depth to the underlying rock substratum (Fig. 2A), the depth of which generally limited cores to approximately 10 to 15 cm in depth. In the DMC soils, maximal consumption was observed at a depth of 6 to 7 cm (Fig. 2B). An integrated consumption rate was calculated from the rate constants for specific depths and the in situ methane concentrations (Fig. 2B). The resulting rate, 6.4 ± 0.2 mg m^{-2} day^{-1} (mean ± standard deviation; $n = 5$) exceeded rates for intact cores (2.6 ± 0.3 mg m^{-2} day^{-1}; $n = 5$) incubated at 10°C during the same period (19).

Effects of nitrogen and soil moisture. Methane consumption in mineral soils from SCH was significantly inhibited by additions of either ammonium or nitrate (Table 2). Ammonium sulfate decreased uptake rate constants by 61 to 95%, with an apparent dose-related effect; ammonium chloride inhibited uptake (93%) more effectively than a comparable concentration of the sulfate salt. The effect of sodium nitrate, a decrease in uptake of 76%, was not statistically different from the effects of comparable ammonium sulfate concentrations. In addition, all nitrogen treatments increased the threshold for methane oxidation to supra-atmospheric levels (>3 ppm) with the consequent loss of the capacity for consumption of atmospheric methane (1.7 ppm). Additions of 6 ppm of 1% acetylene or 0.1 μmol of nitrapyrin g of $soil^{-1}$ (not shown) completely inhibited consumption as well.

Ammonium chloride inhibited methane consumption in DMC soils within about 2 h, but the effect was less pronounced than for SCH soils (Fig. 3, Table 2). Likewise, sodium nitrate had a weaker inhibitory effect in the DMC

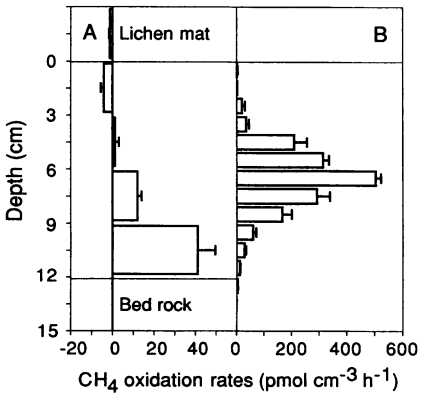

FIG. 2. Methane consumption versus depth in soil slices from SCH (A) and DMC (B). Data are means of triplicate samples, and error bars represent ±1 standard error.

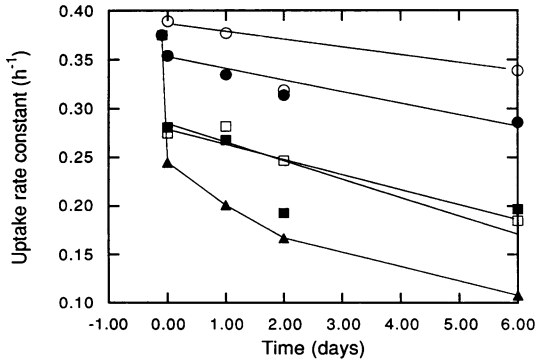

FIG. 3. Effects of added ammonium chloride (▲), sodium chloride (□), and sodium nitrate (■) relative to controls with no additions (○) or equal volumes of deionized water (●) in DMC soils. All substrates were added at final concentrations of 1 μmol g^{-1} to 10-g soil samples. Data are means of triplicate rate constants ($hour^{-1}$) for each treatment at varied intervals before or after substrate addition.

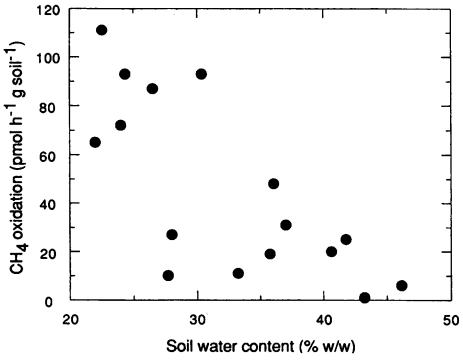

FIG. 4. Methane consumption rates versus water content for soils from the mineral horizon of a conifer forest near Schefferville, Quebec, Canada.

samples. Though the effect of sodium nitrate was significantly different from that of the controls ($P < 0.05$), it did not differ statistically from that of a comparable concentration of sodium chloride ($P > 0.1$). The relative inhibition by ammonium chloride but not sodium nitrate or sodium chloride also increased during the initial 48 h after addition but remained more constant thereafter (Fig. 3). In contrast to the SCH soils, nitrogen addition did not significantly affect thresholds for methane uptake (all <0.1 ppm) or eliminate the capacity for uptake of atmospheric methane.

In soils from SCH, rates of methane consumption were inversely proportional to water content over a range of 20 to 50% (Fig. 4). When soils were water saturated, rates were reduced >90% compared with values at about 20 to 25% water. An even more dramatic effect of water addition was noted for intact cores from the DMC forest site. Methane consumption was unaffected by water additions corresponding to about 6 mm of precipitation. However, an addition corresponding to a total of 13 mm of precipitation diminished consumption by 50%, and additions corresponding to a total of 19 mm of precipitation completely inhibited uptake (Fig. 5).

DISCUSSION

In this study, rates of atmospheric methane consumption are about 1 mg of CH_4 m^{-2} day^{-1} for the subarctic lichen woodland sites and about 3 mg m^{-2} day^{-1} for an elevated tundra site. Comparable values have been reported for Alaskan tundra (28) and temperate forests (26), respectively.

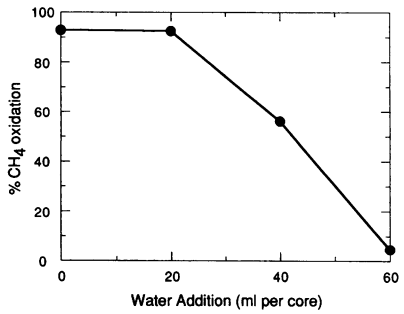

FIG. 5. Effect of water additions on methane consumption in intact cores from the DMC. The addition of 20, 40, or 60 ml of water corresponded to precipitation of approximately 6, 13, or 19 mm.

Lower values for tundra have been reported by King et al. (20) and for temperate forests by Keller et al. (12). Born et al. (2) have found little seasonal variability in methane uptake rates within various soil types in Germany, but substantial variability among different sites with a range from 0.2 mg m^{-2} day^{-1} in a clay soil to 3.5 mg m^{-2} day^{-1} in a sandy soil. These variations may be attributed to a combination of factors, including soil moisture, pH, litter layer thickness, nitrogen inputs, and vertical zonation of methane uptake.

In general, methane consumption at the DMC and SCH sites occurred at soil depths of >3 cm, with maximum rates at 7 to 9 cm. This subsurface maximum was associated with the mineral soil horizon and relatively low organic matter and water contents. In contrast, net methane production was observed in the upper, organic-rich 3 cm of the SCH soils. Though generally oxic, these soils may have contained locally anoxic microzones supporting methanogenesis. Methane consumption may have occurred in the surface soils as well, but at rates less than those for methane production. A different depth profile has been reported by Whalen and Reeburgh (28), who observed maximum rates just beneath the uppermost vegetated zone of a tundra soil. Whalen et al. (29) have also reported a subsurface maximum for methane consumption in a landfill soil, but this pattern may be explained by the presence of a subsurface source of methane.

Subsurface maxima for forest soils are more enigmatic since methane is derived from the atmosphere, or in some cases from low rates of endogenous production in zones coincident with or above those for methane consumption (Fig. 2) (32). The low rates or even absence of net methane consumption in surface soils and litter raises a number of questions about the distribution and activity of soil methanotrophs. Are methanotrophs limited to subsurface horizons by biotic factors, such as predation, competition for nutrients, or responses to suboptimal nutrient concentrations? Does methanotroph distribution reflect a preference for some parameter associated with the mineral-rich soils? Does the presence of clays in the subsurface horizons promote growth or survival relative to the upper, more organic-rich horizons? Answers to these questions are important because the depth distribution of methanotrophs is a key rate-limiting factor since methane transport is determined by diffusion. It is also important to stress the fact that soil methane consumption may occur in a relatively small zone (e.g., see Fig. 2) (7), which in spite of its subsurface location may render the process particularly sensitive to anthropogenic as well as natural disturbances. For example, changes in water regimens, temperature, and land use can all have a disproportionate effect on the soil horizons encompassing active methanotrophs.

The disparity between the chamber and depth integrated uptake rates for the DMC forest (2.6 and 6.4 mg m^{-2} day^{-1}, respectively) could be due to differences in the field and laboratory incubation temperatures (about 10 and 22 to 25°C, respectively) and errors in the soil methane concentrations used for calculating integrated uptake. Temperature differences probably contribute only a small amount to the observed disparity since King and Adamsen (19) have found a Q_{10} of 1.2 for this site. Likewise, errors in soil methane concentrations are probably minimal. While such errors could originate from a number of sources, the observation of field concentrations of ≤0.3 ppm indicates a maximum error of perhaps 0.3 ppm if the true minima were zero. Such an absolute error would result in <20% overestimates of the depth integrated rate and thus account for only part of the

observed 246% difference with respect to chamber rates. A potentially greater error might result from the incubation procedure used for the depth profiles, which exposed small soil slices to the atmosphere. This would increase diffusive transport and potentially stimulate uptake. Consequently, depth profiles of methane consumption based on the use of undisturbed soil slices may provide an accurate reflection of the relative distribution of activity, but perhaps a less reliable estimate of total areal consumption.

At all depths, atmospheric methane uptake appears very sensitive to soil moisture content (12, 23, 26). The low consumption rates for soils with approximately 50% water agree with results of Whalen et al. (29), who also reported maximal methane consumption at 11%. Keller et al. (14) have reported a ninefold increase in consumption after addition of 50 ml of water to 300 g of desiccated soil. Similarly, Conrad and Seiler (5, 6) have noted that water contents of approximately 5 to 11% result in maximal uptake of atmospheric hydrogen and carbon monoxide. The sensitivity of methane consumption to water content likely results in significant short-term temporal variability in uptake in response to precipitation as well as long-term variability in conjunction with changing patterns of precipitation on regional and global scales.

The effects of water content are expressed through two factors: (i) soil-atmosphere gas exchange; (ii) physiological responses to water stress. Others (2, 19, 29) have emphasized the importance of diffusive transport as a regulatory factor and described the relationship between soil void volume and water content (10). Much less is known about the relationship between methane uptake and water stress, which is a function of the chemical potential of soil water (or soil water activity; see references 3 and 10 for pertinent reviews). Low water potentials can substantially limit bacterial activity, particularly at values of <-1 MPa. Results from preliminary studies with pure cultures (*Methylosinus trichosporium* OB3b and *Methylomonas rubra*) indicate relatively little tolerance for moderate stress (18). Thus, the optimum soil water content for methane consumption must reflect a balance between the relationship between rates of gas transport and physiological stress. Data from Whalen et al. (29) provide a clear example of this balance in a landfill soil.

In addition to soil water content, methane uptake is particularly sensitive to nitrogen additions. Although the amounts used in this study (1 μmol g of soil^{-1}) correspond to inputs of <20 kg of N ha^{-1}, the effects are notable, including an immediate decrease in uptake rates and loss of the capacity for atmospheric methane consumption in the SCH soils. The stronger effect of ammonium in SCH than DMC soils merits further attention since the results indicate a greater sensitivity of subarctic forests to nitrogen inputs.

In earlier studies, Mosier et al. (23) and Steudler et al. (26) have reported less marked but significant decreases in atmospheric methane consumption rates days, months, or even years after nitrogen fertilization. The rapidity of the response in this study suggests that the mechanisms for short-term inhibition of uptake probably involve physiological (e.g., metabolic) phenomena. For example, consumption could have decreased because of the inhibitory effect of ammonia on methane monooxygenase (see Bédard and Knowles [1]). The ammonium amendments would have raised ammonia concentrations to levels more than 25 to 147 times those for methane (assuming a pK_a for ammonium protonation of 9.3, a soil pH of 4, and equilibrium of the soil with 1.7 to 10 ppm of methane). The enhanced inhibition of ammonium chloride for >48 h after addition raises the possibility of other responses as well, e.g., population changes. Such changes may contribute to the longer-term effects observed by others (23, 26).

While the effects of ammonium additions could be expressed via methanotrophs or ammonia-oxidizing bacteria, there is at present no convincing evidence supporting a significant role for ammonia-oxidizing bacteria in soil methane consumption. Previously reported rates of methane consumption by ammonia-oxidizing bacteria necessitate unrealistically high population densities to account for typically observed consumption rates (17). Moreover, consumption of atmospheric methane by ammonia-oxidizing bacteria remains undocumented, even though Jones and Morita (11) did observe slow uptake rates at about 3 ppm of methane. Thus, some uncertainty remains over the actual mechanisms by which ammonia inhibition is expressed.

The effects of sodium nitrate and sodium chloride are also difficult to explain, since no direct inhibitory effects on methanotrophs have been documented previously for the concentrations used here. In fact, extant pure cultures of methanotrophs grow readily in media containing 10 mM levels of either salt. The rapid response time is inconsistent with indirect effects based on interactions with other components of the soil microflora, but such effects cannot be ruled out. Direct effects could be due to release of ammonium from clays in the soil by sodium ion exchange. More detail analyses of nitrogen dynamics are required to resolve the mechanisms of inhibition. The importance of understanding the linkage between nitrogen dynamics and methane consumption is emphasized by the fact that the maximum values for methane uptake in the DMC soils occur in a depth interval at which both nitrate and ammonium are relatively low (Fig. 1). The concentrations of nitrate and ammonium in this interval are less than values reported by Mosier et al. (23) for fertilized soils in which methane consumption was apparently inhibited. Above and below the interval, nitrate and ammonium, respectively, increase to potentially limiting levels.

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