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S.C. Whalen

Influence of N and non-N salts on atmospheric methane oxidation by upland boreal forest and tundra soils

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Abstract The short-term (24 h) and medium-term (30 day) influence of N salts (NH_4Cl, $NaNO_3$ and $NaNO_2$) and a non-N salt (NaCl) on first-order rate constants, k (h^{-1}) and thresholds (C_{Th}) for atmospheric CH_4 oxidation by homogenized composites of upland boreal forest and tundra soils was assessed at salt additions ranging to 20 μmol g^{-1} dry weight (dw) soil. Additions of NH_4Cl, $NaNO_3$ and NaCl to 0.5 μmol g^{-1} dw soil did not significantly decrease k relative to watered controls in the short term. Higher concentrations significantly reduced k, with the degree of inhibition increasing with increasing dose. Similar doses of NH_4Cl and NaCl gave comparable decreases in k relative to controls and both soils showed low native concentrations of NH_4^+-N ($\leq$1 μmol g^{-1}dw soil), suggesting that the reduction in k was due primarily to a salt influence rather than competitive inhibition of CH_4 oxidation by exogenous NH_4^+-N or NH_4^+-N released through cation exchange. The decrease in k was consistently less for $NaNO_3$ than for NH_4Cl and NaCl at similar doses, pointing to a strong inhibitory effect of the Cl^- counteranion. Thresholds for CH_4 oxidation were less sensitive to salt addition than k for these three salts, as significant increases in C_{Th} relative to controls were only observed at concentrations $\geq$1.0 μmol g^{-1} dw soil. Both soils were more sensitive to $NaNO_2$ than to other salts in the short term, showing a significant decrease in k at an addition of 0.25 μmol $NaNO_2$ g^{-1} dw soil that was clearly attributable to NO_2^-. Soils showed no recovery from NaCl, NH_4^+-N or $NaNO_3$ addition with respect to atmospheric CH_4 oxidation after 30 days. However, soils amended with $NaNO_2$ to 1.0 μmol $NaNO_2$ g^{-1} dw showed values of k that were not significantly different from controls. Recovery of CH_4-oxidizing ability was due to complete oxidation of NO_2^--N to NO_3^--N. Analysis of soil concentrations of N salts necessary to inhibit atmospheric CH_4 oxidation and regional rates of N deposition suggest that N deposition will not decrease the future sink strength of upland high-latitude soils in the atmospheric CH_4 budget.

Key words Methane oxidation · Nitrogen fertilization · Ammonium · Tundra soil · Upland boreal soil

Introduction

A contemporary increase in the atmospheric concentration of the radiatively important greenhouse gas CH_4 is well documented (IPCC 1996). CH_4 currently contributes approximately 20% to global warming (Bouwman 1990), but on a mass basis has a global warming potential 56 times that of CO_2 in a 20-year time horizon (IPCC 1996). Microbial oxidation in well-drained soils is the only identified biological sink for atmospheric CH_4 and accounts for 3–9% of total annual atmospheric CH_4 destruction (Prather et al. 1995). This is similar in magnitude to the current atmospheric increase of 37 Tg CH_4 $year^{-1}$ (IPCC 1996). Consequently, alterations of the soil sink strength are a significant determinant of the rate of change in the atmospheric CH_4 concentration (Prather et al. 1995) and absence of this sink will cause the atmospheric CH_4 concentration to increase at 1.5 times the current rate (Duxbury 1994).

Influences on rates of atmospheric CH_4 oxidation include soil temperature, moisture and N status (King 1992, 1997; Mancinelli 1995) as well as land use patterns (e.g. Ojima et al. 1993; Willison et al. 1995; Hudgens and Yavitt 1997; Boeckx et al. 1998). Results of studies assessing the influence of N fertilization on CH_4 consumption in aerobic soils give conflicting results between soils, the form and mass of N applied and the duration of inhibition (e.g. Nesbit and Breitenbeck

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S.C. Whalen (✉)
Department of Environmental Science and Engineering,
CB 7400, University of North Carolina, Chapel Hill,
NC 27599-7400, USA
e-mail: steve_whalen@unc.edu
Tel.: +1-919-9669895
Fax: +1-919-9667911

1992; Adamsen and King 1993; Hütsch et al. 1993, 1994; Dunfield et al. 1995). N fertilization frequently reduces soil CH_4 consumption (e.g. Steudler et al. 1989; Mosier et al. 1991; King and Schnell 1994a). However, some studies report no effect of N fertilization (Bronson and Mosier 1993; Tate and Striegl 1993; Flessa et al. 1995; Delgado and Mosier 1996) or even a stimulatory effect on CH_4 consumption (Knightly et al. 1995; Christensen et al. 1997; Börjesson and Nohrstedt 1998; De Visscher et al. 1999) and induction of CH_4 oxidizing activity (Bender and Conrad 1995). Further, positive correlations has been observed between NH_4^+ concentration and CH_4 consumption (Goldman et al. 1995) and between soil fertility and CH_4 consumption (Castro et al. 1995) for temperate forest soils. Clearly, the relationship between soil N and oxidation of atmospheric CH_4 in aerobic soils is not straightforward and broad generalizations across ecosystems are not possible.

The tundra and boreal forest are circumpolar and occupy ~17% of the earth's continental surface (Schultz 1995). These regions presently play a major role in the atmospheric CH_4 budget. Upland forest and tundra soils consume atmospheric CH_4 (Whalen et al. 1991), while poorly drained areas emit CH_4 to the atmosphere (Whalen and Reeburgh 1992). The fraction of the earth's terrestrial surface under agriculture is increasing (Adams et al. 1990) and agricultural soils have lower area-based rates of CH_4 consumption than aerated forests, shrublands and savannah (reviewed by King 1997). Inasmuch as tundra and boreal forests are generally unsuitable for this land use, aerated soils of these regions may be critical in slowing future increases in atmospheric CH_4. Accurate prediction of future trends in soil CH_4 oxidation in these high-latitude soils requires an improved understanding of the physiology and controls of this microbial process.

Anthropogenic alteration of the global N cycle has resulted in a worldwide increase in atmospheric N deposition on terrestrial and aquatic environments (Matthews 1994; Galloway et al. 1995). Increased N input may affect rates of CH_4 oxidation in high-latitude soils.

Consequently, this laboratory study was aimed at assessing the N sensitivity of microbial communities oxidizing atmospheric CH_4 in representative tundra and boreal forest soils. In particular, the immediate influence of different forms of N and non-N salts and mass of salt applied on rates and thresholds for CH_4 oxidation and the recovery of CH_4-oxidizing activity after 30 day were determined.

Materials and methods

Field sites

Soils were collected in September 1995 from representative boreal forest (BS2) and upland tundra T3 sites in Alaska. Sites BS2 and T3 are located in the Bonanza Creek Experimental Forest (64°N, 148°W) and in the Arctic Long Term Experimental Research area near Toolik Lake (68°N, 149°W), respectively. Site BS2 is a north-facing black spruce (*Picea mariana*) 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. Soils are a well-drained, stone-free micaceous loess. Site T3 is a moderately exposed, south-facing sandstone outcrop on a late Wisconsin moraine. Moss (*Sphagnum* spp.), avens (*Dryas octopetala*), willow (*Salix* spp.) and lichens (*Cetraria* spp., *Cladonia* spp.) dominate the plant community. A 2-cm organic layer overlies soils that are a sandy loam rich in rock fragments. Bedrock occurs at a depth of 10–20 cm. These sites have no soil zone of methanogenesis and are atmospheric CH_4 sinks (Whalen et al. 1991 and unpublished data).

Experimental

Bulk soils were collected from the zone of maximum CH_4-oxidizing activity at BS2 (10–20 cm) and T3 (5–15 cm). Soils were sieved (4 mm mesh) and homogenized and the influence of N salts ($NaNO_3$, $NaNO_2$, NH_4C1), a non-N salt consisting of the counterions of the selected N salts (NaCl), and concentration (0.25, 0.5, 1, 2, 5, 10 and 20 μmol N or NaCl g^{-1} dw soil) on the threshold and rate of CH_4 oxidation were assessed. Reduced concentrations of $NaNO_2$ (0.025, 0.05, 0.075, 0.10, 0.15, 0.20 and 0.25 μmol N g^{-1} dw soil) were also tested. The high (0.25–20 μmol N g^{-1} dw soil) and low range (0.025–0.25 μmol N g^{-1} dw soil) $NaNO_2$ additions were designated experiments A and B, respectively. Ten grams dry weight equivalent of soil was added to each of several 160-cm^3 serum vials. One milliliter of deionized H_2O (control) or chemical solution was evenly spread over the surface of soils to give three replicates for controls and each N or NaCl concentration listed above. Perforated foil was placed on the tops of serum vials to allow air exchange between the headspace and the atmosphere and samples were acclimated overnight (~12 h) at room temperature with no evaporative water loss. On the following morning, all vial headspaces were equilibrated with the laboratory atmosphere (~1.9 μl CH_4 l^{-1}) for 2 h and experiments to assess the short-term effect of N amendment commenced by sealing the vials with butyl stoppers. Immediately after sealing and at 1.5-h intervals to 4.5 h, 3 cm^3 N_2 was injected into each vial and a 3-cm^3 sample was immediately removed for CH_4 analysis. Following the 4.5-h sampling, each vial was re-equilibrated with the laboratory atmosphere and sealed. A sample was withdrawn after 24 h to measure the threshold for CH_4 oxidation (C_{Th}). Previous experience (Whalen et al. 1992) indicated that after this time headspace CH_4 concentrations would be reduced to the point where these soils would not consume additional CH_4. Vials remained sealed and headspaces were adjusted to 10 μl CH_4 l^{-1}.

Samples were stored at 15 °C (a typical summer soil temperature; Whalen et al. 1991) for 30 days. Headspaces of randomly chosen controls were analyzed for CH_4 at 2- to 4-day intervals and when concentrations were reduced to 1 μl CH_4 l^{-1} all vials were flushed and headspaces were readjusted to 10 μl CH_4 l^{-1}. At 30 days, time courses for CH_4 consumption were again assessed as described above (experiment B for $NaNO_2$ excluded) to give a measure of the medium-term effect of these salts on CH_4 oxidation. Following this second time course, the triplicate samples for each level and form of salt added were composited and analyzed for NO_3^--N + NO_2^--N (hereafter referred to as NO_3^--N), NO_2^--N and NH_4^+-N.

Methane analysis

CH_4 was measured using a Shimadzu GC8A flame ionization detection gas chromatograph fitted with a 0.5-ml sample loop. Gases were separated on a 1-m molecular sieve 5A column operated at 70 °C with an N_2 (33 ml min^{-1}) carrier. The gas chromatograph was calibrated with commercial CH_4-air blends following verification of stated concentrations with National Institute of Standards and Technology standards. The precision of analysis expressed as a coefficient of variation for 10 replicate injections of standards (1.01–9.23 μl CH_4 l^{-1}) was 0.3%. The detection limit was 0.05 μl CH_4 l^{-1}.

Soil physicochemical properties

Extractable (2M KCl; 10:1 volume/soil wet weight) NO_3^--N, NO_2^--N and NH_4^+-N were determined by the copperized cadmium reduction, modified Griess-Ilosvay and indophenol blue methods, respectively (Keeney and Nelson 1982), following sample filtration through a Whatman no. 42 filter. Soil pH was measured potentiometrically on 1:2 soil-deionized water slurries equilibrated for 24 h. Gravimetric water-holding capacity (WHC) was determined as the difference in weight between water-saturated and oven-dried (105 °C) soils. Organic content was determined as loss on ignition (550 °C) of oven-dried soils. Soil texture was assessed hydrometrically and total N and total C were determined by dry combustion (Carlo Erba NA 1500 Elemental Analyzer). Cation exchange capacity was determined by the NH_4OAc method (Thomas 1982).

Statistical analyses and calculations

All CH_4 concentrations were corrected for dilution by added N_2 and the effect of previous sampling (Breitenbeck 1990) in time course experiments and first-order rate constants for CH_4 oxidation, k (h^{-1}), were calculated from linear regression of ln-transformed data for concentration versus time. The influence of concentration on k and C_{Th} was evaluated by single-factor analysis of variance (ANOVA) for each salt. Multiple comparisons of treatment means were performed by Tukey's honestly significant difference procedure. Treatments that totally inhibited CH_4 oxidation were excluded from the ANOVA and were simply assumed to differ significantly from other treatments. The remaining data satisfied assumptions of normality and homoscedasticity without transformation. Statistical analyses were performed using the SYSTAT (SYSTAT Inc. Chicago, Ill.) statistical package for personal computers. A significance level $\alpha = 0.05$ was used for all tests.

Results

Soils at both sites were acidic and generally comparable with respect to measured chemical properties (Table 1). Most of the inorganic N was as NH_4^+-N. Site T3 soils were relatively wetter (52% WHC) than BS2 soils (29% WHC at the time of collection). Liquid amendments during experimentation increased soil moisture to 66% and 41% WHC for T3 and BS2 soils, respectively. The major difference between soils related to texture, as BS2 was predominantly silt while T3 showed a high sand content.

Soils from T3 showed more vigorous CH_4 oxidation than soils from BS2. First-order rate constants for CH_4 oxidation by watered controls were higher for all treatments by a factor of 3 for T3 than for BS2 soils (Tables 2, 3).

Addition of NH_4Cl or NaCl at ≤ 0.5 μmol g^{-1} dw soil did not significantly decrease k with respect to controls in either soil in short-term response experiments (Tables 2, 3). Similar data for $NaNO_3$ showed no effect at ≤ 1.0 μmol N g^{-1} dw soil and ≤ 0.5 μmol N g^{-1} dw soil for BS2 and T3 soils, respectively. Thus, there was no clear indication of greater sensitivity of k to any of these salts at additions to at least 0.5 μmol g^{-1} dw soil. Following the onset of inhibition of CH_4 oxidation by these three salts (72–89% of control values of k), the degree of inhibition increased with increasing dose in all cases. However, there was no clear evidence of consistently greater relative inhibition (i.e. lower % of control) by NH_4Cl than NaCl at comparable doses for either soil. In contrast, relative inhibition was consistently greater for NH_4Cl and NaCl than $NaNO_3$ at comparable doses from 1.0 to 20 μmol g^{-1} dw soil for both soils.

Table 1 Physicochemical characteristics of boreal forest (BS2) and arctic tundra (T3) soils

Characteristic	BS2	T3
pH (H_20)	4.5	4.2
WHC (% dry weight)[a]	80	66
% WHC[b]	29	52
Organic matter (% w/w)	7.4	8.4
Total C (% w/w)	2.2	3.0
Total N (% w/w)	0.12	0.17
NH_4^+ (μmol N g^{-1} dw)	0.8	1.0
NO_3^- (μmol N g^{-1} dw)	0.0	0.1
Sand/silt/clay (%)	9/88/3	69/26/5
CEC[c]	15.8	12.3

[a] Water holding capacity

[b] Field-moist soils

[c] Cation exchange capacity (mEq 100 g^{-1} dw at pH 7)

In contrast to the other salts, the lowest level of added $NaNO_2$ in experiment A (0.25 μmol g^{-1} dw soil) significantly decreased k relative to controls in both soils (Tables 2, 3). An additional experiment (B) involving lower additions of $NaNO_2$ showed that k values for concentrations up to and including 0.25 μmol N g^{-1} dw soil were not clearly distinguishable from controls in both soils. Collectively, the results of experiments A and B indicate that the onset of inhibition of CH_4 oxidation by $NaNO_2$ occurs at or slightly above 0.25 μmol $NaNO_2$ g^{-1} dw soil.

The highest concentration of NH_4Cl and NaCl tested (20 μmol g^{-1} dw soil) terminated CH_4 oxidation for BS2 soil (Table 2). However, k for this dose was 23–25% of controls for T3 soils, pointing to a lower sensitivity to high additions of these salts (Table 3). Likewise, T3 soil was less sensitive to high levels of $NaNO_2$ addition in experiment A. The k value was reduced to zero at 1.0 μmol $NaNO_2$ g^{-1} dw soil in T3 soil compared with 0.5 μmol $NaNO_2$ g^{-1} dw soil in BS2 soil. Soils were essentially identical in sensitivity to $NaNO_3$ additions in excess of 5.0 μmol g^{-1} dw soil.

Soil from T3 showed generally lower values for C_{Th} after addition of NH_4Cl, $NaNO_3$ or NaCl at comparable doses than soil from BS2 in short-term response experiments (Tables 4, 5). Values for C_{Th} and k were equally sensitive to high level $NaNO_2$ addition (experiment A), as the significant changes in both occurred at the same

Table 2 Mean ($n=3$) first-order rate constants (k) for CH_4 oxidation and (% of control) for BS2 soil as a function of form and concentration of added salt. First-order rate constants were determined about 12 h after salt addition. Values of k followed by the same letter within each column do not differ significantly

Concentration (μmol g^{-1} dw)[a]	k (h^{-1})				
	NH_4Cl	$NaNO_3$	$NaNO_2$ (A)	$NaNO_2$ (B)	NaCl
0 (0) control	0.065 a	0.055 a	0.061 a	0.052 a	0.051 a
0.25 (0.025)	0.065 (100) a	0.054 (98) a	0.009 (15) b	0.055 (106) a	0.053 (104) a
0.5 (0.05)	0.058 (89) ab	0.055 (100) a	0.000 (0)	0.048 (92) ab	0.053 (104) a
1.0 (0.075)	0.051 (78) b	0.052 (95) a	0.000 (0)	0.049 (94) ab	0.040 (78) b
2.0 (0.10)	0.039 (60) c	0.040 (73) b	0.000 (0)	0.056 (108) a	0.038 (75) b
5.0 (0.15)	0.021 (32) d	0.028 (51) c	0.000 (0)	0.050 (96) ab	0.017 (33) c
10.0 (0.20)	0.016 (25) d	0.021 (38) cd	0.000 (0)	0.045 (87) ab	0.000 (0)
20.0 (0.25)	0.000 (0)	0.016 (29) d	0.000 (0)	0.042 (81) b	0.000 (0)

[a] Concentrations in parentheses are for $NaNO_2$ (B), while those not in parentheses are for all other amendments

Table 3 Mean ($n=3$) first-order rate constants (k) for CH_4 oxidation and (% of control) for T3 soil as a function of form and concentration of added salt. First-order rate constants were determined about 12 h after salt addition. Values of k followed by the same letter within each column do not differ significantly

Concentration (μmol g^{-1} dw)[a]	k (h^{-1})				
	NH_4Cl	$NaNO_3$	$NaNO_2$ (A)	$NaNO_2$ (B)	NaCl
0 (0) control	0.242 a	0.223 a	0.203 a	0.208 a	0.196 a
0.25 (0.025)	0.240 (99) a	0.218 (98) a	0.147 (72) b	0.203 (98) a	0.203 (104) a
0.5 (0.05)	0.231 (95) a	0.219 (98) a	0.041 (20) c	0.205 (99) a	0.201 (103) a
1.0 (0.075)	0.185 (76) b	0.198 (89) b	0.000 (0) d	0.198 (95) a	0.141 (72) b
2.0 (0.10)	0.143 (59) c	0.169 (76) c	0.000 (0) d	0.212 (102) a	0.106 (54) c
5.0 (0.15)	0.105 (43) d	0.122 (55) d	0.000 (0) d	0.201 (97) a	0.097 (50) c
10.0 (0.20)	0.083 (34) e	0.088 (39) e	0.000 (0) d	0.194 (93) a	0.088 (45) c
20.0 (0.25)	0.055 (23) f	0.065 (29) f	0.000 (0) d	0.195 (94) a	0.049 (25) d

[a] Concentrations in parentheses are for $NaNO_2$ (B), while those not in parentheses are for all other amendments

Table 4 Mean ($n=3$) threshold for CH_4 oxidation (C_{Th}) by BS2 soil as a function of form and concentration of added salt. Threshold values followed by the same letter within each column do not differ significantly

Concentration (μmol g^{-1} dw)[a]	C_{Th} (μl CH_4 l^{-1})				
	NH_4Cl	$NaNO_3$	$NaNO_2$ (A)	$NaNO_2$ (B)	NaCl
0 (0) control	0.21 a	0.22 a	0.24 a	0.24 a	0.30 a
0.25 (0.025)	0.20 a	0.20 a	1.56 b	0.26 a	0.34 a
0.5 (0.05)	0.17 a	0.23 a	1.81 c	0.29 a	0.29 a
1.0 (0.075)	0.21 a	0.23 a	1.78 c	0.39 ab	0.43 a
2.0 (0.10)	0.38 b	0.33 b	1.79 c	0.47 b	0.52 a
5.0 (0.15)	1.00 c	0.48 c	1.81 c	0.42 b	1.05 b
10.0 (0.20)	1.40 d	0.71 d	1.80 c	0.31 ab	1.39 c
20.0 (0.25)	1.71 e	0.95 e	1.81 c	0.43 b	1.70 d

[a] Concentrations in parentheses are for $NaNO_2$ (B), while those not in parentheses are for all other amendments

concentration of $NaNO_2$ within each soil. Otherwise, C_{Th} was frequently less sensitive than k to concentration of added salts. Values of C_{Th} for BS2 soil became significantly higher with respect to controls at 2.0 μmol g^{-1} dw soil for NH_4Cl and $NaNO_3$ and at 5.0 μmol g^{-1} dw soil for NaCl. Similarly, a significant increase in C_{Th} relative to controls was not observed for T3 soil until concentrations of NH_4Cl, $NaNO_3$ and NaCl were ≥ 5.0 μmol g^{-1} dw soil.

Determinations of k 30 days after salt additions (medium-term effect) showed no clear evidence of recovery from salt amendment, with the exception of the high (experiment A) $NaNO_2$ addition experiment (Tables 6, 7). Values of k for NH_4Cl, $NaNO_3$ and NaCl addition were not significantly different from controls for concentrations as high as 0.25–1.0 μmol g^{-1} dw soil, depending on the soil and salt added. The medium-term effect of NH_4Cl, $NaNO_3$ and NaCl additions appeared

Table 5 Mean ($n=3$) threshold for CH_4 oxidation (C_{Th}) by T3 soil as a function of form and concentration of added salt. Threshold values followed by the same letter within each column do not differ significantly

Concentration (μmol g^{-1} dw)[a]	C_{Th} (μl CH_4 l^{-1})				
	NH_4Cl	$NaNO_3$	$NaNO_2$ (A)	$NaNO_2$ (B)	NaCl
0 (0) control	0.06 a	0.10 a	0.17 a	0.18 a	0.19 a
0.25 (0.025)	0.07 a	0.11 a	0.32 b	0.17 a	0.15 a
0.5 (0.05)	0.09 a	0.12 a	0.65 c	0.19 ab	0.17 a
1.0 (0.075)	0.09 a	0.13 a	1.81 d	0.17 a	0.17 a
2.0 (0.10)	0.10 a	0.12 a	1.82 d	0.17 a	0.20 a
5.0 (0.15)	0.13 ab	0.13 a	1.80 d	0.17 a	0.17 a
10.0 (0.20)	0.19 b	0.13 a	1.80 d	0.22 b	0.28 b
20.0 (0.25)	0.41 c	0.23 b	1.81 d	0.18 a	0.32 b

[a] Concentrations in parentheses are for $NaNO_2$ (B), while those not in parentheses are for all other amendments

Table 6 Mean ($n=3$) first-order rate constants (k) for CH_4 oxidation and (% of control) for BS2 soil as a function of form and concentration of added salt 1 month after salt addition. Values of k followed by the same letter within each column do not differ significantly

Concentration (μmol g^{-1} dw)	k (h^{-1})			
	NH_4Cl	$NaNO_3$	$NaNO_2$	NaCl
0 (control)	0.059 a	0.059 a	0.062 a	0.059 a
0.25	0.038 (65) ab	0.050 (85) a	0.052 (84) ab	0.058 (98) a
0.5	0.045 (76) a	0.032 (54) b	0.051 (82) ab	0.054 (92) a
1.0	0.037 (63) ab	0.036 (61) b	0.047 (76) ab	0.039 (66) b
2.0	0.024 (41) b	0.029 (49) b	0.038 (61) b	0.041 (69) b
5.0	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)
10.0	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)
20.0	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)

Table 7 Mean ($n=3$) first-order rate constants (k) for CH_4 oxidation and (% of control) for T3 soil as a function of form and concentration of added nutrient 1 month after nutrient addition. Values of k followed by the same letter within each column do not differ significantly

Concentration (μmol g^{-1} dw)	k (h^{-1})			
	NH_4Cl	$NaNO_3$	$NaNO_2$	NaCl
0 (control)	0.223 a	0.212 a	0.202 a	0.190 a
0.25	0.186 (83) ab	0.177 (83) a	0.207 (102) a	0.195 (103) a
0.5	0.200 (90) ab	0.172 (81) a	0.200 (99) a	0.196 (103) a
1.0	0.168 (75) bc	0.164 (77) a	0.218 (108) a	0.075 (39) b
2.0	0.139 (62) c	0.126 (59) b	0.184 (91) a	0.078 (41) b
5.0	0.000 (0)	0.000 (0)	0.000 (0)	0.032 (17) c
10.0	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)
20.0	0.000 (0)	0.000 (0)	0.000 (0)	0.000 (0)

to be greater than the short-term effect at high concentrations. Doses ≥ 5.0 μmol g^{-1} dw soil for these salts totally inhibited CH_4 oxidation in both soils, except for NaCl amendment to T3, where only the 10.0 and 20.0 μmol N g^{-1} dw soil additions gave no CH_4 oxidation.

In contrast to the medium-term response to the other salt additions, CH_4 oxidation recovered from the lowest amendments in the high-level $NaNO_2$ addition experiment. Values of k for additions of ≤ 1.0 μmol $NaNO_2$ g^{-1} dw soil (BS2) and ≤ 2.0 μmol $NaNO_2$ g^{-1} dw soil (T3) were not significantly different from controls. Nonetheless, concentrations ≥ 5.0 μmol $NaNO_2$ g^{-1} dw soil still fully inhibited CH_4 oxidation.

The point of total inhibition for salts was sharply defined in most cases in these medium-term experiments (Tables 6, 7), unlike the gradual decrease in k with increasing dose that was characteristic for most salt amendments in short-term response experiments (Tables 2, 3). With the exception of NaCl for T3 soil, k ranged from 41% to 91% of controls at the dose immediately preceding that which effected total inhibition of atmospheric CH_4 oxidation.

Nutrient analysis of soils following the 30-day determination of k indicated that all of the NO_2^--N in the high-level $NaNO_2$ addition experiment (experiment A) had been nitrified to NO_3^--N. N transformations were minimal in both soils for all other treatments. Observed concentrations were within 10% of expected concentrations (added N plus native N) for each form and level of N if no transformations are assumed.

Discussion

The three-fold higher values of *k* consistently observed for T3 soil relative to BS2 soil (Tables 2, 3, 6, 7) likely stems from differences in soil texture (Table 1) and size of the resident methanotroph populations. Bender and Martin (1994) reported a higher oxidative capacity for fine sand than for silt and clay due to facilitated diffusion and preference of methanotrophs for the coarser-grained soil fractions.

Inhibition of atmospheric CH_4 oxidation by NH_4^+ salts has been demonstrated to involve competitive interactions between CH_4 and CH_4 monooxygenase as well as the toxic effects of NO_2^- and other intermediates (King and Schnell 1994b; Schnell and King 1994). The reported inhibition of atmospheric CH_4 oxidation by other N and non-N salts (Nesbit and Breitenbeck 1992; Crill et al. 1994; Knightly et al. 1995; Nedwell 1996) may involve multiple mechanisms that include desorption of bound NH_4^+-N (King and Schnell 1998), a decrease in soil water potential (Schnell and King 1996) or other non-specific salt effects (Gulledge and Schimel 1998).

At concentrations at and above the point of inhibition of CH_4 oxidation by NH_4Cl and NaCl in my short-term response experiments (generally ≥ 1.0 μmol g^{-1} dw soil) with both soils, the degree of inhibition increased with increasing dose (Tables 2, 3) and the relative degree of inhibition was not consistently greater for NH_4Cl than NaCl at comparable doses. Observations of a similar or greater decrease in CH_4 consumption by equimolar concentrations of a non-NH_4^+-salt than an NH_4^+ salt tested in parallel have often been interpreted (e.g. Gulledge et al. 1997; MacDonald et al. 1997) to indicate no effect of added NH_4^+-N, and have prompted MacDonald et al (1997) to question the competitive inhibition theory. Thus, results here suggest that an ionic effect rather than competitive NH_4^+-N inhibition depresses CH_4 oxidation in the NH_4Cl addition experiment. Desorption of bound NH_4^+-N likely had little effect on CH_4 oxidation in NaCl-treated soils. Although cation exchange capacities are low, exchangeable NH_4^+-N concentrations are only ≤ 1 μmol N g^{-1} dw soil in unamended soil (Table 1).

The short-term response of CH_4 oxidation to $NaNO_3$ amendment was remarkably similar to that for NH_4Cl and NaCl addition (Tables 2, 3). Onset of inhibition occurred at a common dose and the degree of inhibition increased with increasing dose. However, the degree of inhibition for a $NaNO_3$ was consistently less than for NH_4Cl and NaCl at a similar dose. King and Schnell (1998) reported that common anions including Cl^- and NO_2^- can vary in their effect on NH_4^+-N adsorption and desorption, and therefore have differing influences on atmospheric CH_4 oxidation. Again, the low level of exchangeable NH_4^+-N in the study soils suggests little increased availability on salt addition. Gulledge and Schimel (1998) reported a severe inhibitory effect of Cl^- salts in particular on CH_4 oxidation in soils from varied environments, including a boreal forest birch stand low in exchangeable NH_4^+-N. Thus, the observation of lower inhibition of CH_4 oxidation by $NaNO_3$ than NaCl and NH_4Cl at similar doses may stem simply from a more severe non-specific salt effect associated with the Cl^- counter-anion.

More severe inhibition in CH_4 oxidation at low CH_4 concentrations by NO_2^--N than NH_4^+-N at comparable doses in both soils (Tables 2, 3) is consistent with a similar report (Schnell and King 1994) for an acid forest soil that showed 59% and 42% inhibition following addition of $NaNO_2$ and NH_4Cl, respectively, at 1 μmol N g^{-1} fresh weight (fw) soil. Otherwise, Hütsch (1998) reported 84% inhibition of CH_4 oxidation in a loamy arable soil within 24 h after $NaNO_2$ addition at 2.9 μmol N g^{-1} fw soil. The soils in this study are apparently extremely sensitive to NO_2^--N, as concentrations similar to those tested in these other studies gave total inhibition of CH_4 oxidation. Moreover, inhibition was clearly due to NO_2^-, as the effect was evident at doses where equinormal NaCl and other N salts had no influence on CH_4 oxidation relative to controls.

Thresholds for atmospheric CH_4 consumption by controls (Tables 4, 5) are consistent with other reports from high-latitude environments (Whalen et al. 1991, 1992) and elsewhere (Whalen et al. 1990; Yavitt et al. 1990; Koschorreck and Conrad 1993; Bender and Conrad 1993, 1995) that generally show values of 0.1 to 0.3 μl CH_4 l^{-1} for C_{Th}. The data showing a short-term increase in C_{Th} at high doses of all salts is in general agreement with the only other study assessing the influence of exogenous N on this parameter. There, Adamsen and King (1993) reported supra-atmospheric values of C_{Th} (>3 μl CH_4 l^{-1}) for a forest soil exposed to 10 μl CH_4 l^{-1} and amended with various NH_4^+ and NO_3^--N salts at 1–2 μmol N g^{-1} fw soil. With the exception of $NaNO_2$, C_{Th} here appears to be less sensitive than *k* in both soils to salt amendment from the standpoint that values differ significantly from controls at higher doses within each treatment. Inasmuch as C_{Th} is probably a manifestation of the overall physiological status of methanotrophs as influenced by environmental conditions (King 1997), this observation of reduced sensitivity of C_{Th} than *k* to salt addition cannot be generalized. However, information concerning the sensitivity of C_{Th} to salt addition and changes in soil physicochemical variables is essential to predicting the future sink strength for the soil consumptive term in the atmospheric CH_4 budget because C_{Th} can clearly be a determinant of overall CH_4 consumption.

With the exception of $NaNO_2$, soils showed no evidence at 30 days for recovery of *k* from the effect of any salt addition. Studies that report the medium-term (days to months) influence of similar amendments give variable results. Nesbit and Breitenbeck (1992) and Schnell and King (1994) found persistent inhibition a month or more following addition of NH_4Cl to forest soils at 7 μmol N g^{-1} fw soil and 1 μmol N g^{-1} dw soil, respectively. Similarly, Priemé and Christensen (1997) reported continued inhibition of CH_4 oxidation in forest soil to 27 days in response to 1.2 μmol g^{-1} dw soil amendment with NH_4Cl-N, KNO_3-N and KCl while Hütsch et al. (1996) observed complete suppression of CH_4 oxidation to 7 days in a sandy arable soil amended with 16.8 μmol $(NH_4)_2SO_4$-N g^{-1} dw soil. Otherwise, data from Bronson and Mosier (1994) show either no difference or some decrease (~15%) in the degree of inhibition between 6 and 12 days for NH_4Cl, KNO_3 or NH_4NO_3 added to grassland soils at 1.8 μmol N g^{-1} dw soil.

The medium-term recovery of *k* in soils amended with $NaNO_2$ at doses as high as 2 μmol g^{-1} dw soil (Tables 6, 7) is clearly related to the complete oxidation of NO_2^--N to NO_3^--N. Hütsch (1998) also reported contemporaneous oxidation of exogenously added NO_2^- (2.9 μmol N g^{-1} dw soil) and a decrease in the inhibitory effect of the added substrate from 84% immediately after application to 41% after 48 h. Further, Dunfield and Knowles (1995) observed complete reversibility of NO_2^- inhibition of CH_4 oxidation accompanied by the return of NO_2^--N to background levels 70 h after addition to humisol slurries. The low accumulation of NO_3^--N in NH_4Cl-treated soils after 30 days and the complete recovery of NO_3^--N as NO_3^--N in $NaNO_2$-treated soils indicates that NH_4^+-N oxidation is the rate-limiting step in nitrification in these soils and is consistent with the observation by Gulledge et al. (1997) for other boreal forest soils that nitrifiers are slow in consuming NH_4^+-N. Rapid oxidation of exogenous NO_2^--N and undetectable levels of NO_2^--N in NH_4Cl-amended soils indicate that NO_2^--N will not inhibit in situ atmospheric CH_4 oxidation in these soils.

Partial (Hütsch 1998) or complete (Dunfield and Knowles 1995) recovery from NH_4^+-N addition has been associated with high rates of nitrification. Except for NO_2^--N oxidation, rates of microbial N transformation were low in the soils in this study and concentrations of NO_3^--N and NH_4^+-N were essentially static for 30 days following amendment. Thus, the observations that: (1) the normality at which *k* was significantly lower than controls was reasonably similar for NH_4Cl, $NaNO_3$ and NaCl amendments in both short- and medium-term experiments; (2) the normality of salt addition that elicited the onset of inhibition essentially did not change over 30 days; (3) NO_2^--N oxidation in soils from experiment A resulted in recovery of CH_4 oxidation to levels comparable to other treatments; and (4) complete inhibition of CH_4 oxidation at 30 days at a level that was markedly similar among treatments all suggest that the inhibitory effects on CH_4 oxidation observed here for all treatments in both the short and medium term (exception: short-term $NaNO_2$ addition in experiment A) was due primarily to a salt influence.

N fertilization experiments of forest plots frequently show depressed levels of CH_4 consumption relative to unfertilized controls (e.g. Steudler et al. 1989; Sitaula et al. 1995) causing concern that increased atmospheric N deposition may result in a decrease in atmospheric CH_4 consumption by upland soils (Castro et al. 1995). However, changes in soil CH_4 consumption may be an artifact in response to heavy N-fertilizer application rather than the natural reaction of the system to chronic, low-level atmospheric N deposition (Butterbach-Bahl et al. 1998). Thus, it may be equally as instructive to determine whether inhibitory levels of N can be achieved in these soils through atmospheric deposition. Data here can be unambiguously interpreted to indicate that NH_4^+ and NO_3^- salts do not inhibit CH_4 oxidation regardless of the mechanism in either the short or medium-term at concentrations at least to 0.5 μmol N g^{-1} dw (Tables 2, 3, 6 and 7). These concentrations represent 62% and 50% increases over prefertilization NH_4^+-N levels for BS2 and T3 soils, respectively (Table 1). Assuming annual precipitation of 30 cm at both sites (Whalen et al. 1991; Kling et al. 1992), a soil bulk density of 0.91 g cm^{-3} (Whalen et al. 1992), an average inorganic-N (NH_4^+-N plus NO_3^--N) concentration of 5 μmol l^{-1} in bulk precipitation (Galloway et al. 1984; Whalen and Cornwell 1985; Bormann et al. 1989) and distribution of the entire atmospheric N load homogeneously in a subsurface, 10-cm zone of CH_4 oxidation (Whalen et al. 1992), annual atmospheric N loading will be 0.016 μmol N g^{-1} dw soil. A doubling of this annual load will represent 6% of the inorganic-N concentration necessary to inhibit atmospheric CH_4 oxidation. This simplistic analysis does not consider the influence of increased atmospheric deposition on N turnover, which may be more important than absolute concentration in determining sensitivity of atmospheric CH_4 oxidation to increased N loading (Mosier et al. 1991). Nonetheless, it suggests that substantial increases in atmospheric N deposition and N delivery to the active methanotrophic zone without plant assimilation will be necessary to inhibit atmospheric CH_4 oxidation in these soils. This corroborates a previous report (Whalen et al. 1991) that showed no effect of N fertilization (1:1 mix of urea-N and $(NH_4)_2SO_4$ up to 20 g N m^{-2} $year^{-1}$) on CH_4 oxidation in field plots at BS2.

In conclusion, NH_4C1, $NaNO_3$ and NaCl salts had no effect on atmospheric CH_4 oxidation by upland boreal forest and tundra soils in the short or medium term at amendments to 0.5 μmol g^{-1} dw soil. Inhibition at higher amendments (to 20 μmol g^{-1} dw soil) is probably due largely to a nonspecific salt effect and *k* appears to be more sensitive than C_{Th} to salt addition in the short-term. Soils were extremely sensitive to $NaNO_2$ addition, but recovered the ability to oxidize atmospheric CH_4 after 30 days, when the exogenously supplied NO_2^--N had been oxidized to NO_3^--N. In contrast, suppression of CH_4 oxidation remained constant over 30 days in soils amended with high levels of NH_4Cl, $NaNO_3$ and NaCl. Increased atmospheric N loading will likely not diminish the CH_4-oxidizing capability of these soils.

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