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Journal

Chemosphere - Global Change Science, 2(2)

ISSN

1465-9972

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Publication Date

2000-09-23

DOI

10.1016/S1465-9972(00)00003-9

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Effect of nitrogen fertilization on atmospheric methane oxidation in boreal forest soils

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Received 7 May 1999; accepted 9 September 1999

Importance of this Paper: The “greenhouse” gas CH₄ is increasing in atmospheric concentration. Oxidation by methanotrophic bacteria in upland soils is the only biological sink for atmospheric CH₄. Methanotrophs are inhibited by high soil N, raising concern that the contemporary worldwide increase in atmospheric N deposition will decrease soil CH₄ oxidation. The boreal forest occupies 13% of the earth’s continental surface and is important in atmospheric CH₄ oxidation. We studied atmospheric CH₄ oxidation in fertilized boreal forest plots to determine the N sensitivity of the methanotrophic community and conclude that increased N deposition will not alter the rates of CH₄ oxidation in these soils.

Abstract

Field plots of aspen and black spruce in the Alaskan boreal forest were fertilized repeatedly with nitrogen during the 1993 summer growing season, and weekly determinations of the influence of fertilization on atmospheric CH₄ oxidation were made with static chambers. Repeated fertilization with (NH₄)₂SO₄ solution or nutrient media used to culture methanotrophic or nitrifying bacteria gave a total addition of 140 or 580 kg N ha⁻¹. Time-integrated CH₄ oxidation was not significantly different in fertilized soils versus watered controls because CH₄ oxidation was localized in a subsurface soil zone that was probably not penetrated by surface-applied aqueous phase fertilizer. Insensitivity of CH₄ oxidation by these soils to a high rate of N fertilization and the low current rate of atmospheric N deposition suggest that future increases in atmospheric N deposition will not alter the sink strength of high latitude boreal forest soils in the atmospheric CH₄ budget. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Methane oxidation; Forests; Nitrogen fertilization

1. Introduction

The atmospheric concentration of the radiatively important greenhouse gas CH₄ has shown a well-documented, contemporary increase (Houghton et al., 1996). Methane is second only to CO₂ as a greenhouse gas and contributes approximately 20% to global warming

(Bouwman, 1990). Microbial oxidation in well-drained soils is the only identified biological sink for atmospheric CH₄ and accounts for 3% to 9% of total annual atmospheric CH₄ destruction (Prather et al., 1996). This is similar in magnitude to the current atmospheric increase of 37 Tg CH₄ yr⁻¹ (Houghton et al., 1996). Consequently, alterations of the soil sink strength are a significant determinant of the rate of change in the atmospheric CH₄ concentration (Prather et al., 1996) and absence of this sink will cause the atmospheric CH₄ concentration to increase at 1.5 times the current rate (Duxbury, 1994).

Methanotrophic bacteria are generally considered to be responsible for atmospheric CH₄ oxidation (Conrad,

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1996; King, 1997), although NH_4 -oxidizing bacteria are capable of oxidizing CH_4 at rates lower than methanotrophs (Jones et al., 1984; Bedard and Knowles, 1989). Hence, soils with high nitrification rates show low CH_4 oxidation because CH_4 oxidation is dominated by nitrifiers (Castro et al., 1995; Steudler et al., 1996).

Influences on rates of atmospheric CH_4 oxidation in well-drained soils include soil temperature, moisture and N status (reviewed by King, 1992, 1997; Mancinelli, 1995) as well as land use patterns (Ojima et al., 1993; Willison et al., 1995; Hudgens and Yavitt, 1997; Boecyx et al., 1998). Forest plots experimentally fertilized with N frequently show depressed atmospheric CH_4 oxidation relative to unfertilized controls (Steudler et al., 1989; King and Schnell, 1994; Sitaula et al., 1995). Consequently, the well-documented worldwide increase in atmospheric N deposition on terrestrial and aquatic environments (Matthews, 1994; Galloway et al., 1995) may result in a decrease in atmospheric CH_4 oxidation by upland forest soils (Castro et al., 1995).

The boreal forest occupies 13% of the earth's continental surface (Schultz, 1995), and upland boreal forest soils are important in atmospheric CH_4 consumption (Whalen et al., 1991). Agriculture is expanding worldwide (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). Since boreal forests are generally unsuitable for this land use, upland soils of this region will 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 microbial community response to global change, including increased atmospheric N deposition.

This study was aimed at determining the impact of increased N input on atmospheric CH_4 oxidation by boreal forest soils and to qualitatively determine the relative importance of methanotrophs and nitrifiers in oxidizing CH_4 in these soils. We experimentally fertilized plots with $(\text{NH}_4)\text{SO}_4$ solution to simulate increased atmospheric N input. Further, we attempted to enhance populations of nitrifiers or methanotrophs in additional plots by fertilizing with liquid media used to culture these microbial groups. The rate of CH_4 oxidation in treated plots was compared with that of watered controls.

2. Materials and methods

2.1. Site description

Field sites were located along a successional sequence in Bonanza Creek experimental forest (64°N, 148°W) near Fairbanks, Alaska. 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 sites have no soil zone of methanogenesis and are atmospheric CH_4 sinks (Whalen et al., 1992).

2.2. Experimental

Methane flux determinations were made using the static chamber technique (Whalen et al., 1991). Each chamber consisted of a skirted aluminum base permanently seated in the soil and a removable aluminum lid that utilized a water-filled channel for a seal. Lids were equipped with an o-seal fitting to allow syringe sampling of headspace gas and fitted with a capillary bleed to equilibrate with atmospheric pressure. Eight bases were deployed in June 1993 at each site. Methane fluxes were determined at each chamber on 8 July (Calendar day (CD) 189). Soils enclosed within two randomly selected bases at each site were then amended with 2-L of one of the following: (a) a growth medium for methanogens (King and Adamsen, 1992); (b) a growth medium for nitrifiers (De Boer et al., 1991); (c) $(\text{NH}_4)_2\text{SO}_4$ in deionized water; or (d) deionized water only. Methane oxidation was measured weekly from CD 194 through CD 243. Fertilization with the assigned treatment immediately followed each CH_4 flux determination. Fertilization added 73 kg NO_3^- -N ha^{-1} (methanogen medium) or 18 kg NH_4^+ -N (nitrifier medium and $(\text{NH}_4)_2\text{SO}_4$ treatment) to these soils on a weekly basis.

2.3. Methane analysis

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

2.4. Statistical analyses and calculations

Area-based rates of CH_4 oxidation were calculated from the time-linear decrease in CH_4 concentration in the chamber headspace during a 0.75 h deployment. Day rates of CH_4 oxidation for each chamber were time-integrated over the experimental period and treatment means within each site were compared by single factor analysis of variance. Data satisfied assumptions of normality and homoscedasticity without transformation. A significance level of $\alpha = 0.05$ was used.

3. Results and discussion

Day-rates of CH₄ oxidation at AS2 varied over a factor of about 1.6 (0.46–0.76 mg m⁻² d⁻¹) during the study period (Fig. 1). Time-integrated rates of CH₄ oxidation varied from 29.2 to 32.3 mg m⁻² and were not significantly different across treatments. Day-rates of CH₄ oxidation at BS2 were somewhat higher and less variable than for AS2 (Fig. 1). Methane oxidation rates varied over a factor of 1.3, from 0.69 to 0.89 mg m⁻². Time-integrated rates of CH₄ oxidation varied from 36.8 to 40.1 mg m⁻² and were not significantly different across treatments. The temporal pattern of CH₄ oxidation was generally similar across treatments within each site. This probably reflects changes in soil moisture, which controls diffusion of CH₄ to the zone of oxidation, and hence is a primary determinant of rates of atmospheric CH₄ oxidation by soils (King, 1997). Increased N input to forests can increase the fine root biomass (Magill et al., 1997), which may decrease air-filled porosity and limit rates of diffusion and atmospheric CH₄ oxidation. Any increase in fine root biomass in response to fertilization here had no impact on

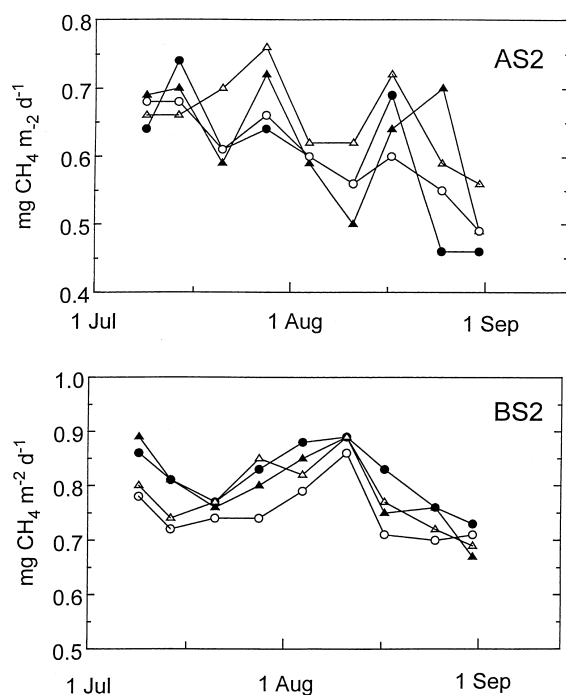


Fig. 1. Methane oxidation at sites AS2 and BS2 in response to fertilization with nitrifier medium (▲), methanotroph medium (○), (NH₄)₂SO₄ solution (△) or deionized water (●). Each point represents the mean rate of CH₄ oxidation from duplicate chambers for each treatment. Standard deviations averaged 0.06 and 0.17 mg CH₄ m⁻² d⁻¹ at AS2 and BS2, respectively. Error bars are eliminated for clarity.

soil–atmosphere gas exchange, as time-integrated rates of CH₄ oxidation did not differ significantly between control and fertilized plots at either site. The generally higher rates of CH₄ oxidation at BS2 than at AS2 is consistent with the higher gas-filled porosity at BS2 (Whalen et al., 1992), which allows for more rapid diffusion of atmospheric CH₄ into the soil.

The N load from repeated fertilization totaled about 140 kg NH₄⁺-N ha⁻¹ for plots treated with (NH₄)₂SO₄ and the nitrifier medium and about 580 kg NO₃⁻-N ha⁻¹ for plots fertilized with the methanotroph medium. Atmospheric CH₄ oxidation at both sites was unaffected by fertilization at these levels, which is consistent with a similar observation for a boreal spruce forest fertilized for three years with NH₄NO₃ at 60 kg N ha⁻¹ (Gulledge et al., 1997). However, most studies report inhibition of atmospheric CH₄ oxidation in N-fertilized forest soils. Pine forests fertilized with NH₄NO₃ at 30 and 90 kg N ha⁻¹ gave CH₄ oxidation rates that were 85% and 62%, respectively, of unfertilized controls (Sitaula et al., 1995), while a temperate softwood forest amended with the same fertilizer at 120 kg N ha⁻¹ showed a CH₄ oxidation rates that were 67% of unfertilized controls (Steudler et al., 1989). Urea fertilization of a pine plantation (180 kg N ha⁻¹) resulted in a 5- to 20-fold decrease in atmospheric CH₄ oxidation relative to controls (Castro et al., 1995), while application of urea, KNO₃ or NH₄Cl to forested peatland soils at 100 kg N ha⁻¹ significantly depressed CH₄ oxidation (Crill et al., 1994). Finally, fertilization of a mixed oak–pine forest with only 10 kg NH₄Cl-N ha⁻¹ inhibited atmospheric CH₄ oxidation by about 20% relative to control plots (King and Schnell, 1994).

Sensitivity of atmospheric CH₄ oxidation in forest soils to N fertilization may relate to the position of the CH₄ oxidizing community in the soil column. Maximum rates of atmospheric CH₄ oxidation are found 10–20 cm below the soil surface at both sites, and 91% and 98% of depth-integrated CH₄ oxidation at AS2 and BS2 occurs at soil depths >10 cm (Whalen et al., 1992). Hence, it is likely that liquid fertilizer additions did not penetrate to the active CH₄ oxidizing zone. Other studies also point to the locus of the CH₄ oxidizing zone as a key determinant of soil sensitivity to N fertilization. Surface localization of fertilizer in conjunction with a subsurface zone of CH₄ oxidation was offered as a possible explanation for the lack of a fertilizer effect on CH₄ oxidation in a humisol amended with 100 kg ha⁻¹ urea-N (Dunfield et al., 1995), while addition of NH₄Cl, KNO₃ and urea-N at this same level all inhibited CH₄ oxidation in forest peat soils where CH₄ oxidation was largely restricted to the 0–5 cm zone.

Nitrifiers are frequently located in the organic, NH₄⁺-rich surface layers of forest soils (Lensi et al., 1991; Schnell and King, 1994; Castro et al., 1995), suggesting that the NH₄⁺-N and nitrifier medium solutions

contacted this component of the microbial community. Methane is co-oxidized along with NH_4^+ -N by nitrifying bacteria (Bedard and Knowles, 1989) and urea-N fertilization (rapidly hydrolyzed to NH_4^+ -N; Zhengping et al., 1996) in pine forest soil has been demonstrated to reduce atmospheric CH_4 oxidation by shifting the relative importance of methanotrophs and nitrifiers (Castro et al., 1995). Hence, insensitivity of CH_4 oxidation at AS2 and BS2 to amendment with NH_4^+ -N or the nitrifier medium suggests that methanotrophs are primarily responsible for CH_4 oxidation in these soils. This is consistent with the observation that nitrifying activity is low in other boreal forest soils (Gulledge et al., 1997). In contrast to the nitrifier medium, the methanotroph medium probably never reached the target organisms. Hence, the rate of CH_4 oxidation was uninfluenced by this treatment.

Increased atmospheric N deposition is not likely to reduce rates of atmospheric CH_4 oxidation in boreal forest soils. The loading rate of 140 kg N ha^{-1} for repeated fertilization with NH_4^+ -N solution or nitrifier medium is 70-fold higher than the estimated annual deposition (wet plus dry) of 2 kg N ha^{-1} for remote continental areas (Galloway, 1993). Moreover, experimental conditions were considerably more favorable than natural rainfall for delivery of nutrients to the active methanotrophic zone located at $>10 \text{ cm}$ below the soil surface. Each of the eight fertilizations simulated a 2.7 cm , high N rainfall while total annual precipitation at these study sites is 30 cm equally divided between rain and snow, and no single rain event exceeded 2 cm during the year this study was conducted (NOAA, 1993). Additionally, chamber bases extended to a depth of about 15 cm below the soil surface, ensuring that fertilizer did not move laterally following application. In concert, low annual precipitation and subsurface localization of the zone of atmospheric CH_4 oxidation ensure that any realistic increase in atmospheric N deposition will not alter the sink strength of upland boreal forest soils in the atmospheric CH_4 budget.

Acknowledgements

This work was supported by the US 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 laboratory and field analyses.

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