PERGAMON

Short communication

Interactive effects of tree species and soil moisture on methane consumption

Oleg V. Menyailo[a,b,*], Bruce A. Hungate[b]

[a]*Institute of Forest SB RAS, Krasnoyarsk 660036, Russian Federation*
[b]*Department of Biological Sciences and Merriam Powell Center for Environmental Research, Northern Arizona University, Flagstaff, AZ 86001, USA*

Abstract

Methane consumption by temperate forest soils is a major sink for this important greenhouse gas, but little is known about how tree species influence CH_4 uptake by soils. Here, we show that six common tree species in Siberian boreal and temperate forests significantly affect potential CH_4 consumption in laboratory microcosms. Overall, soils under hardwood species (aspen and birch) consumed CH_4 at higher rates than soils under coniferous species and grassland. While NH_4^+ addition often reduces CH_4 uptake, we found no effect of NH_4^+ addition, possibly because of the relatively high ratio of CH_4-to-NH_4^+ in our incubations. The effects of soil moisture strongly depended on plant species. An increase in soil moisture enhanced CH_4 consumption in soils under spruce but had the opposite effect under Scots pine and larch. Under other species, soil moisture did not affect CH_4 consumption. These results could be explained by specific responses of different groups of CH_4-oxidizing bacteria to elevated moisture.

Methane is an important greenhouse gas, contributing roughly 20% to observed and predicted global warming (IPCC, 2001). Boreal and temperate forest upland soils are important biological sinks for atmospheric CH_4 (Wahlen and Reeburgh, 1996). While some soil microbial C and N transformations (N-mineralization, nitrification, denitrification, C-respiration) are strongly affected by tree species in Siberian boreal forests (Menyailo et al., 2002b), the effects of tree species on CH_4 oxidation remain largely unstudied. The influence of tree species on the fluxes of greenhouse gases is a critical question in soil science and biogeochemistry, especially given increasing interest in artificial afforestation in Europe, North America and Russia as a way to reduce net CO_2 emissions (Schulze et al., 2002). Additionally, the species composition of boreal forests is likely to change in response to climate and atmospheric change. Pastor and Post (1988) suggested that changes in temperature and precipitation resulting from increasing atmospheric CO_2 concentrations will cause a northward

migration of the hardwood–conifer forest border in North America. Thus, a better understanding of the effects of different species on soil processes is needed to predict how such human-induced and natural changes in species composition will alter ecosystem processes, including soil CH_4 consumption.

Increased N deposition from the atmosphere and altered soil water content could also have important effects on CH_4-oxidizing bacteria (Steudler et al., 1989; Wahlen and Reeburgh, 1996). These effects may be interactive because of varying sensitivities of CH_4-oxidizing bacteria to these factors. The aim of this work is to determine the interactive effects of tree species, soil moisture, and N addition on soil CH_4 consumption.

We assessed the influence of boreal forest species on soil CH_4 consumption in the Siberian artificial afforestation experiment, in which six common boreal forest tree species have been grown under common garden conditions for the past 30 yr. Because this experiment began with initially uniform soils, and all plots are exposed to the same climatic conditions, differences in soil properties that arise over time can be fully attributed to the effects of plant species (Wedin and Tilman, 1990).

---

* Corresponding author. Address: Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011-5640, USA. Tel.: +1-928-523-0432; fax: +1-928-523-0925.

E-mail address: menyailo@hotmail.com (O.V. Menyailo).

The research plots are located 50 km northwest from Krasnoyarsk and were established by the Laboratory of Soil Science of the Institute of Forest, Siberian Branch of the Russian Academy of Sciences (Menyailo et al., 2002a). The upper 0–50 cm of soil of a 1.5 ha area were removed, mechanically homogenized to minimize vertical and spatial heterogeneity of chemical, physical and biological properties, and subsequently returned to the site prior to experimental planting. In 1971–1972, 2–3 yr old seedlings of spruce (*Picea abies*), birch (*Betula pendula*), Scots pine (*Pinus sylvestris*), aspen (*Populus tremula*), larch (*Larix sibirica*) and Arolla pine (*Pinus cembra*) were sown into individual plots, each occupying 2400 m^2. An area of 9600 m^2 was left for grassland as a control, and the soil under grass was not mechanically homogenized. The region is characterized by continental climatic conditions with average rainfall 500 mm yr^{-1}, average daily summer temperature of 20 °C (at 12:00), depth to permafrost 70–170 cm and soil temperature to 20 cm depth in winter −4 to −14 °C, in summer 10–12 °C. The soil is the grey forest type according to the Russian Soil Classification System and Greyzem according to FAO (1990). Litterfall is asynchronous among the six study species, so soil samples were collected in August, to avoid the possible influence of fresh litter. In August 2001, each plot was sub-divided into three parts: A, B and C. From each sub-plot, two trees were randomly chosen and four soil samples were taken at 50 cm apart of the stem of each tree. In the grassland plot, three sub-plots (each of 2 m^2) were chosen along the forest plantation; at each sub-plot six soil samples were taken from 0 to 10 cm depth. Soil samples from each sub-plot were mixed. The total number of soil samples was 21: six species plus grassland by three subplots. The six tree species can be separated into three groups according to their effects on net N mineralization, net nitrification and denitrification. All these activities were highest under Arolla pine and larch, intermediate under deciduous aspen and birch, and

lowest beneath spruce and Scots pine (Menyailo et al., 2002b). These groups correspond to those based on the chemical properties (pH, C, C-to-N ratio): soils under Arolla pine and larch had the highest pH and C content and intermediate C-to-N ratios, birch and aspen have intermediate values of pH and C and the lowest C-to-N ratios, and spruce and Scots pine have the lowest pH and C and the highest C-to-N ratio (Menyailo et al., 2002a). Thus, tree species caused significant changes in soil N transformations by modifying the amount and quality of soil organic matter and soil pH and the differences in CH$_4$ oxidation activity under different species are very likely.

We incubated three replicate soil samples from each of the six tree species (and grassland) with two amounts of soil water content (60 and 90% of water-holding capacity) and two rates of N addition (none added or addition of 66 mg N kg^{-1} soil as NH$_4$Cl, corresponding to approximately 200 kg N ha^{-1}) in a complete factorial design. In each replicate incubation, 10 g of soil were placed in 250 ml flasks and CH$_4$ was added to a concentration of 10 ml l^{-1}; incubations were conducted at room temperature (approx. 25 °C).

The decline in CH$_4$ concentration was measured during 6 d of incubation. Each day, 1 ml of the headspace was sampled by syringe and injected to 20 ml filled with He and sealed glass flask to store 1–4 h before concentration measurements by SRI gas chromatograph with FID and Porapak Q column (2 m), injection volume was 5 ml. The rate of CH$_4$ oxidation was calculated using linear regression and expressed as nmol CH$_4$ g dw^{-1} h^{-1}. The distribution of the rates was tested for normality. Three-way ANOVA was computed with soil moisture, species and N as independent variables. Where the main effect or interactions were significant ($P < 0.05$), Tukey's post hoc comparisons were used to determine significant pairwise contrasts.

Methane consumption varied from approximately 1–5 nmol CH$_4$ g dw^{-1} h^{-1} (Fig. 1). Tree species strongly
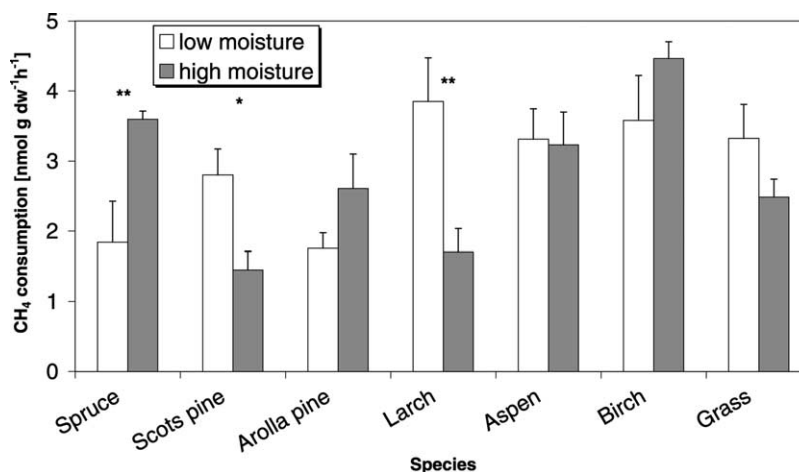

Fig. 1. Rate of CH$_4$ consumption measured under six tree species and grassland at two moisture contents (60 and 90% WHC). The initial concentration of CH$_4$ was 10 ml l^{-1}. Because N addition had no effect, means and standard errors were calculated across N treatments ($n = 6$). Asterisks show the significance of the soil moisture effect by different species: **$P < 0.010$; *$P < 0.050$.

Table 1
Results of three-way ANOVA's test with species, moisture and N as independent variables and CH_4 consumption rate as dependent variable. Significant effects ($P < 0.05$) are in bold

	df effect	F	P-level
Species	**6**	**4.276**	**0.004**
Moisture	1	0.310	0.582
N	1	0.359	0.554
Species × moisture	**6**	**4.873**	**0.002**
Species × N	6	1.285	0.296
Moisture × N	1	0.302	0.587
Species × Moisture × N	6	0.312	0.925

affected CH_4 consumption ($P = 0.004$, Table 1). Overall, birch had higher values than coniferous species and grassland ($P < 0.05$). Aspen had higher values than Scots pine ($P = 0.033$) and Arolla pine ($P = 0.043$). N addition did not affect CH_4 consumption ($P > 0.05$). Other authors reported inhibition of CH_4 oxidation by NH_4^+ addition (Steudler et al., 1989), promotion due to additional N supply for biomass growth (Bodeller et al., 2000), and no effect of N addition (Wahlen and Reeburgh, 2000). King and Schell (1994) reported a CH_4 concentration-dependant response to NH_4^+-N inhibition of CH_4-oxidation in forest soils normally exposed to a free-air atmosphere, with the inhibitory effect of NH_4^+ diminishing with increasing CH_4 concentration. The responses we observed may be explained by a similar phenomenon, in that initial concentrations of CH_4 were very high (10 ml l^{-1}), masking any inhibitory effect of N additions.

While the main effect of soil moisture had no significant effect on CH_4 oxidation ($P > 0.05$), the interaction between species and moisture was significant ($P = 0.002$). Increased soil moisture enhanced CH_4 consumption in soils under spruce ($P = 0.009$) but reduced CH_4 consumption under Scots pine ($P = 0.04$) and larch ($P = 0.002$). Under other species soil moisture did not affect CH_4 consumption ($P > 0.05$). Previous studies of the effects of soil moisture on CH_4 consumption also show varying responses. For example, Adamsen and King (1993) showed an inverse relationship between gravimetric soil water content and CH_4-oxidation in coniferous soil composite, and Yavitt et al. (1995) also found that the lowest rate of CH_4 consumption was associated with the highest soil water content in composite of hardwood forest soil. In contrast, Nesbit and Breitenbeck (1992) found that CH_4 oxidation was relatively insensitive to soil moisture (25 and 75% water-filled pore space) for swamp and forest soils. Wahlen and Reeburgh (1996) explained such differences in response to moisture by the physiological characteristics of the extant microbial communities and by differences in initial CH_4 concentrations. In our incubation experiment, soils were exposed to equal CH_4 concentration; thus, differences in microbial communities under different tree species is one plausible reason for different

responses to soil moisture. Both methanotrophs and nitrifying bacteria are capable of CH_4 oxidation (Conrad, 1995), and the proportion of these groups is likely to vary among different soils (Gulledge et al., 1997). Thus, the different responses to soil moisture may be explained by plant species effects on the relative abundances of methanotrophs and nitrifiers and by differing sensitivities of these groups to soil moisture. For example, Menyailo et al. (2002b) have shown that net nitrification is highest under larch and lowest under spruce and Scots pine. If nitrifying bacteria were mostly responsible for CH_4 consumption under larch, the increase in moisture resulted in inhibition of nitrification activity and decline in CH_4 consumption. It is more difficult to explain variation in response to increased moisture due to greater activity of methanotrophs under spruce and Scots pine, as the response was different (Fig. 1). This may be due to (a) the lack of a relationship between net nitrification rate and actual CH_4 oxidation by nitrifying bacteria or (b) different response to increased moisture by different groups of methanotrophs.

These results provide evidence that the future predictions of CH_4 uptake in boreal and temperate forests should consider changes in tree species composition together with changes in soil moisture regimes. However, if, as predicted, global warming causes birch to replace coniferous species, potential CH_4 uptake will be higher regardless of soil moisture changes.

Acknowledgements

References

Adamsen, A.P.S., King, G.M., 1993. Methane consumption in temperate and sub arctic forest soils: rates, vertical zonation, and responses to water and nitrogen. Applied and Environmental Microbiology 56, 485–490.

Bodeller, P.L.E., Roslev, P., Henckel, T., Frenzel, P., 2000. Stimulation by ammonium-based fertilizers of methane oxidation in soil around rice roots. Nature 403, 421–424.

Conrad, R., 1995. Soil microbial processes involved in production and consumption of atmospheric trace gases. In: Gwynfryn Jones, J., (Ed.), Advances in Microbial Ecology, Plenum Press, New York, pp. 207–250.

FAO. (1990). Soil Map of the world, revised legend, FAO, Rome, Italy.

Gulledge, J., Doyle, A.P., Schimel, J.P., 1997. Different NH_4^+ inhibition patterns of soil CH_4 consumption: a result of distinct CH_4 oxidizer populations across sites? Soil Biology & Biochemistry 29, 13–21.

IPCC, 2001. In: Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J., Dai, X., Maskell, K., Johnson, C.A. (Eds.), Climate Change 2001. The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the

Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, UK.

King, G.M., Schell, S., 1994. Effect of increasing atmospheric methane concentration on ammonium atmospheric of soil methane consumption. Nature 370, 282–284.

Menyailo, O.V., Hungate, B.A., Zech, W., 2002a. Tree species mediated soil chemical changes in a Siberian artificial afforestation experiment. Plant and Soil 242, 171–182.

Menyailo, O.V., Hungate, B.A., Zech, W., 2002b. The effect of single tree species on soil microbial activities related to C and N cycling in the Siberian artificial afforestation experiment. Plant and Soil 242, 183–196.

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

Pastor, J., Post, W.M., 1988. Response of northern forests to CO_2-induced climate change. Nature 334, 55–58.

Schulze, E.-D., Valentini, R., Sanz, M.-J., 2002. The long way from Kyoto to Marrakesh: implications of the Kyoto protocol negotiations for global ecology. Global Change Biology 8, 505–518.

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

Wedin, D.A., Tilman, D., 1990. Species effects on nitrogen cycling: a test with perennial grasses. Oecologia 84, 433–441.

Wahlen, S.C., Reeburgh, W.S., 1996. Moisture and temperature sensitivity of CH_4 oxidation in boreal soils. Soil Biology & Biochemistry 28, 1271–1281.

Wahlen, S.C., Reeburgh, W.S., 2000. Effect of nitrogen fertilization on atmospheric methane oxidation in boreal forest soils. Chemosphere—Global Change Science 2, 151–155.

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