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.

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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).
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 m². An area of 9600 m² 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 m²) 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 CH₄ 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 NH₄Cl, 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 CH₄ was added to a concentration of 10 ml l⁻¹; incubations were conducted at room temperature (approx. 25°C).

The decline in CH₄ 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 CH₄ oxidation was calculated using linear regression and expressed as nmol CH₄ 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 CH₄ g dw⁻¹ h⁻¹ (Fig. 1). Tree species strongly...
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 soil moisture conditions, CH$_4$ consumption 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.

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