Chapter 18

TREE SPECIES EFFECTS ON POTENTIAL PRODUCTION AND CONSUMPTION OF CARBON DIOXIDE, METHANE, AND NITROUS OXIDE: THE SIBERIAN AFFORESTATION EXPERIMENT

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ABSTRACT

Changes in tree species composition could affect how forests produce and consume greenhouse gases, because the soil microorganisms that carry out these biogeochemical transformations are often sensitive to plant characteristics. We examined the effects of thirty years of stand development under six tree species in Siberian forests (Scots pine, spruce, arolla pine, larch, aspen and birch) on potential rates of soil CO_2 production, N_2O-reduction and N_2O production during denitrification, and CH_4 oxidation. Because many of these activities relate to soil N turnover, we also measured net nitrification and N mineralization. Overall, the effects of tree species were more pronounced on N_2O and CH_4 fluxes than on CO_2 production. Tree species altered substrate-induced respiration (SIR) and basal respiration, but the differences were not as large as those observed for N transformations. Tree species caused similar effects on denitrification potential, net N mineralization, and net nitrification, but effects on N_2O reduction were idiosyncratic, resulting in a decoupling of N_2O production and reduction. CH_4 oxidation was affected by tree species, but these effects depended on soil moisture: increasing soil moisture enhanced CH_4 oxidation under some tree species but decreased it under others. If global warming causes deciduous

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species to replace coniferous species, our results suggest that Siberian forests would support soil microbial communities with enhanced potential to consume CH_4 but also to produce more N_2O. Future predictions of CH_4 uptake and N_2O efflux in boreal and temperate forests need to consider changes in tree species composition together with changes in soil moisture regimes.

INTRODUCTION

Natural biological processes are critical regulators of exchanges of greenhouse gases between the biosphere and atmosphere, particularly for carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O). The processes mediating these exchanges change in direct response to altered temperature, precipitation, and other aspects of global change. However, the indirect effects of global change on exchanges of greenhouse gases are not well understood, particularly the impacts of altered distributions of plant species, a widely predicted (and likely ongoing) consequence of the Earth's changing climate. Because plant species have strong and idiosyncratic influences on ecosystem properties that regulate fluxes of greenhouse gases, their effects on these fluxes are likely to be large and individualistic, in some cases amplifying and in others counteracting the direct influences of global climate change. Furthermore, afforestation in northern latitudes is increasingly considered to be a viable way to increase the terrestrial carbon sink, helping to mitigate global climate change. The effects of such efforts on biosphere-atmosphere exchanges of N_2O and CH_4, however, have not been considered. Because CH_4 has 200 times and N_2O 290 times the climate forcing potential of CO_2, tree species that increase CO_2 uptake but enhance emissions of these more potent greenhouse gases could actually do more harm than good, creating a net positive feedback to global warming (Figure 1).

The effects of tree species are thus important to know because global change will alter species composition of forests, changing ecosystem processes and greenhouse gas fluxes. The direction and magnitude of these effects are unknown. The areal extent of artificial afforestation (conversion of grassland to forestry) is also likely to increase substantially in the coming decades. To maximize the sink strength of these landscapes for greenhouse gases, the effects of individual tree species needs to be clarified across a broad range of sites and environmental conditions.

Artificial afforestation experiments provide an opportunity to identify explicitly the influences of individual tree species on soil microbial processes related to production and consumption of greenhouse gases. These "common garden" experiments are initially homogenous in microbial, chemical, and physical properties, and trees are of the same age (Wedin and Tilman, 1990, Binkley, 1994, Menyailo et al., 2002a). Only a few artificial afforestation

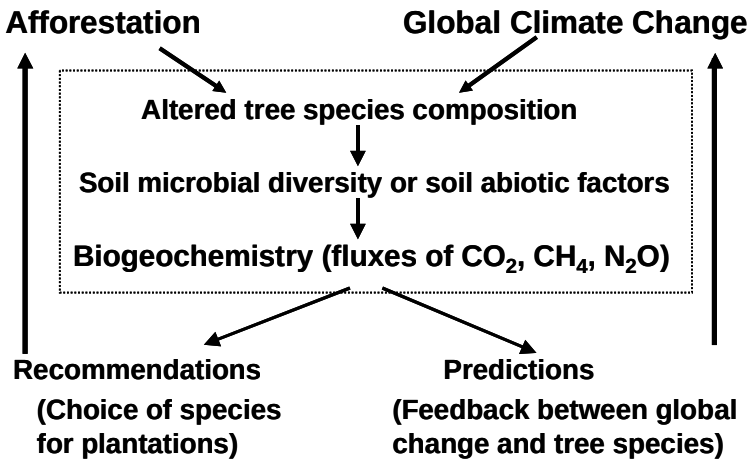

Figure 1. Conceptual scheme showing feedback between climate change and tree species composition in forests. The box in the center shows the hypothesized influences of tree species on the fluxes: either through changes in soil abiotic factors or through changes in microbial community structure and composition.

experiments have examined microbiological processes, and results have been inconsistent. In some cases, no distinct species effect was found after 23-24 years of stand growth (Priha and Smolander, 1997; Scott 1998). By contrast, in another experiment tree seedlings caused changes in C transformation activities in soil after only 4 months of growth (Priha et al., 1999b). The effects of tree species in the Siberian Afforestation Experiment (see other chapters in this volume) on microbial transformations of CO_2, CH_4 and N_2O were presented in a number of publications (Menyailo and Huwe, 1999, Menyailo et al., 2002b, Menyailo and Hungate 2003), here we synthesize the most important results.

THE SIBERIAN AFFORESTATION EXPERIMENT

The research plots (Figure 2) are located 50 km Northwest of Krasnoyarsk and were established by the Laboratory of Soil Science of the Institute of Forests, 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 y old seedlings of Norway spruce (*Picea abies, = Picea obovata*), birch (*Betula pendula*), Scots pine (*Pinus sylvestris*), aspen (*Populus tremula*), larch (*Larix sibirica*) and arolla pine (*Pinus cembra*) were planted into monoculture plots, each occupying 2400 m^2. An 600 m^2 area was left for grassland as a control, and

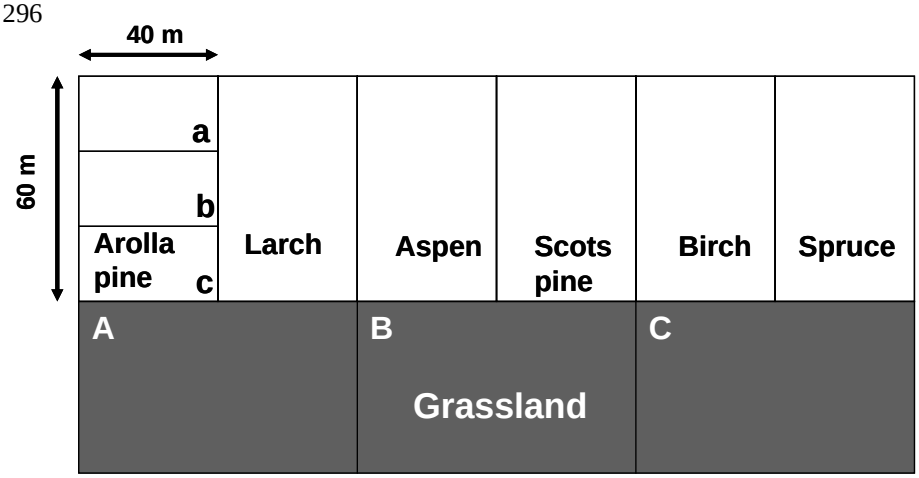

Figure 2. Layout of the Siberian afforestation experiment, organized by laboratory of soil science of the Institute of Forest SB RAS in 1971-1972 y under idea of Prof. N.V. Orlovsky.

the soil under grass was not mechanically homogenized. The region is characterized by continental climatic conditions with average rainfall 500 mm $year^{-1}$, average daily summer temperature of 20 ^{o}C (at noon), depth to permafrost 70-170 cm and soil temperature to 20 cm depth in winter -4^{o} to -14^{o}, in summer 10^{o} to 12^{o}. The soil is the gray forest type according to the Russian Soil Classification System and Greyzem according to FAO (FAO, 1990). Litterfall is asynchronous among the six study species (Mukhortova, this volume), so soil samples were collected in August to avoid the influence of fresh litter. In August 2001, each plot was sub-divided into three parts: A, B and C (as shown in Figure 2). 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 the 0-10 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.

STUDY OF MICROBIAL ACTIVITIES

Denitrification potential

Five grams of soil were placed in glass flasks (25 ml) and pre-incubated at 28^{o}C for 3 days to initiate microbial activity. Thereafter, 5 ml of distilled water with KNO_3 and glucose were added to each sample. The resulting concentrations of nitrate and glucose were 100 µg NO_3-N g^{-1} soil and 100 µg glucose-C g^{-1} soil. The flasks were closed with air-tight rubber stoppers and fixed with clamps. Anaerobic conditions were induced by exchanging the gas phase with helium for 15 min. Acetylene (2.5 ml of C_2H_2,10% v/v) was then

added to inhibit N_2O-reductase, and prevent catalysis of N_2O to N_2. All samples were incubated for 24 hours, then a sample of headspace gas was taken from each flask for determination of N_2O using gas chromatography (Shimadzu 14A, N_2 carrier gas, equipped with an electron capture detector (ECD ^{63}Ni), Menyailo and Huwe, 1999). The sample volume was 1 ml. The results were expressed as mg N_2O-N kg^{-1} dry soil day^{-1}.

Potential N_2O reduction

From each of the 63 soil samples, 4 sub-samples were used to measure potential N_2O reduction. As above, five grams of soil were placed in glass flasks (25 ml) and pre-incubated at 28 ^oC for 3 days to initiate microbial activity. Thereafter, 5 ml of distilled water with glucose were added to each sub-sample. The resulting concentration of glucose was 100 mg C kg^{-1} soil. The flasks were closed with air-tight rubber stoppers and fixed with clamps. Anaerobic conditions were induced by exchanging the gas phase with helium for 15 min. After removing O_2 from the flasks, 1 ml of N_2O was added to two sub-samples as a final electron acceptor. To another two sub-samples, 1 ml of N_2O and 2.5 ml of C_2H_2 (10% v/v) were added. The last series of sub-samples were necessary to estimate abiotic N_2O consumption by soil (e.g., dissolution in water). One ml of the headspace from each flask was sampled at 0 h, 24 h and 48 h, in order to analyze for N_2O concentration as described above. Biotic N_2O consumption rates were calculated as the difference between changes in N_2O concentration between C_2H_2 treated and untreated samples. For the first incubation day, the following formula was used:

$$N_2O \text{ reduction rate} = (B_0 - B_{24}) - (A_0 - A_{24})$$

where B_0 is the initial concentration of N_2O in flask without C_2H_2, B_{24} is the concentration of N_2O in this flask after 24 h incubation, A_0 is the initial concentration of N_2O in flask with C_2H_2 and A_{24} is the concentration of N_2O in this flask after 24 h of incubation. For the second incubation day, the analogous formula was used substituting concentrations of N_2O at 24 h as initial and at 48 h instead of 24 h. As the rate of N_2O consumption was linear during two days of incubation, mean values were calculated and expressed as mg N_2O-N $kg^{-1}day^{-1}$.

Net N-mineralization and net nitrification

Approximately 15 g were extracted with 1M KCl (1:5) to determine the initial concentration of ammonium (NH_4^+-N) and nitrate (NO_3^-N) with a flow injection analyzer (Lachat). Additionally, 15 g from each soil sample were

placed in plastic flasks (150 ml), moistened to 60% of water-holding capacity, sealed with stoppers and incubated at 28 ^{o}C for 30 days. To avoid anaerobic conditions, the flasks were opened every 3 days for 5 min. On day 30, soil samples were analyzed for NH_4^+-N and NO_3^--N as described above.

Net mineralization rate was calculated as the difference in [NO_3^- + NH_4^+] before and after the incubation and was expressed as mg (NO_3^- + NH_4^+)-N kg^{-1} 30 $days^{-1}$. Net nitrification was calculated as the difference in [NO_3^-] before and after the incubation and was expressed as mg NO_3^--N kg^{-1} 30 $days^{-1}$.

Basal and substrate-induced respiration

To study basal respiration, 5 g of soil were placed in a 25 ml-flask. Water was added to achieve 60% of water-holding capacity. The flasks were closed with rubber stoppers, fixed with clamps and incubated at 28 ^{o}C for 3 days. Afterwards, flasks were open for 30 min to allow aeration, sealed and incubated at the same temperature for 24 h. A gas sample of the headspace (1 ml) from each flask was taken for analysis of CO_2 concentrations using gas chromatography as described above. For substrate-induced respiration, five grams of soil were placed in 25 ml-flasks and moistened with distilled water. The flasks were closed with rubber stoppers, fixed with clamps and pre-incubated at 28 ^{o}C for 3 days. Thereafter, flasks were open and a water solution with glucose as a C-source was added to obtain 60% water holding capacity and 100 mg glucose-C kg^{-1} soil. Soil samples were then incubated for 24 hours and 1 ml of the headspace air of each flask was sampled and analyzed for CO_2 as described above. The results were expressed as g CO_2-C $kg^{-1}day^{-1}$.

Methane oxidation

We incubated three replicate soil samples from each of the six tree species with two amounts of soil water content (60 and 90% of water-holding capacity). 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 (2m), injection volume was 5 ml. The rate of CH_4 oxidation was calculated using linear regression and expressed as nmol CH_4 g dry $soil^{-1}$ h^{-1}.

RESULTS AND DISCUSSION

N_2O production and consumption via denitrification

Denitrification potential (N_2O production) showed high variation and ranged from 5.8 to 15 mg N_2O-N kg^{-1} day^{-1} (Figure 3). Rates differed significantly among species ($P<0.001$), with highest N_2O production under arolla pine and larch. Production of N_2O under arolla pine and larch was significantly higher than beneath spruce, Scots pine and birch, where the lowest N_2O production was measured. Aspen had a lower N_2O production than larch ($P=0.025$) and higher than spruce ($P=0.017$), and in the same range as under Scots pine, arolla pine and birch.

Potential N_2O reduction varied from 4.6 to 13.7 mg N_2O-N kg^{-1} day^{-1} and values were comparable to those observed for N_2O production (Figure 3), indicating that neither NO_3^- nor N_2O was a limiting substrate in our incubation experiments. N_2O reduction was significantly affected by trees species ($P<0.001$). As for N_2O production, the highest rate of N_2O reduction was found under arolla pine and larch, significantly higher than under all other species ($P<0.035$). In contrast to N_2O production, low values of N_2O reduction were found under deciduous species aspen and birch, significantly lower than beneath spruce, arolla pine and larch.

Soil emissions of N_2O depend on the rates of both N_2O production (due mainly to denitrification) and consumption (N_2O-reduction), so the ratio of these processes is indicative of the potential ratio of N_2O/N_2 in the denitrification end products. The ratio of N_2O production-to-N_2O reduction may indicate conditions of species and environment that will produce the greatest rates of N_2O production. We found higher ratios of these two steps of denitrification under deciduous species than under conifers. We propose that higher N_2O fluxes should be observed under birch and aspen than under conifers, in accord with Butterbach-Bahl et al. (1997, also Butterbach-Bahl and Kiese, this volume). Pastor and Post (1988) found that changes in temperature and precipitation resulting from an increase of atmospheric CO_2 concentrations caused a northward migration of the hardwood-conifer forest border in North America. Such migration of the hardwood forests is likely to also occur in Russian Siberia. Based on our results, replacing conifers by deciduous species may double the ratio of N_2O/N_2 as end products of denitrification. Potential denitrification in Siberia was even higher than in the tropical forest soils (Menyailo et al., 2002b), the main terrestrial N_2O source (Matson et al., 1990), indicating that the microbial community in temperate forest zone can potentially produce higher amounts of N_2O. By changing environmental conditions due to global changes, atmospheric N deposition or forest fires, which increase soil inorganic N, temperate forests will likely play an increasingly important role in the global N_2O budget.

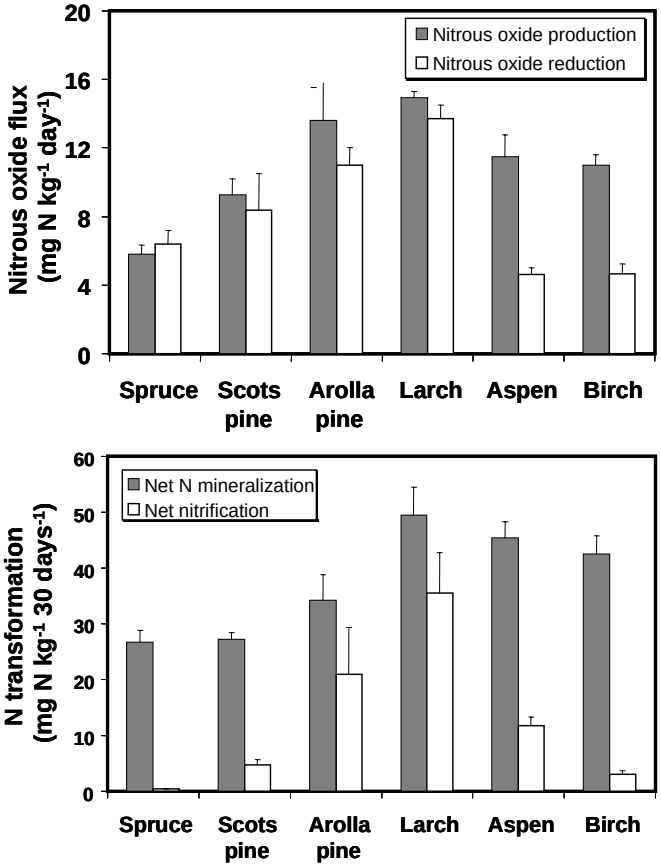

Figure 3. Potential rate of N_2O production (upper), measured in anaerobic conditions with addition of nitrate, glucose and acetylene and potential rate of N_2O reduction (anaerobic conditions, glucose and N_2O additions). Net N mineralization (lower) in 30 days aerobic incubation at constant soil moisture (60% WHC) and temperature regime (28 ^{o}C) and net nitrification.

Net N mineralization and nitrification

Inorganic N is important factor regulating the fluxes of greenhouse gases in many ways. We expected that the differences in net N mineralization and net nitrification might be helpful to explain the variation in the processes of greenhouse gas transformations. Mean values for net N mineralization ranged from 27 to 50 mg (NO_3^- + NH_4^+)-N kg^{-1} 30 $days^{-1}$ (Figure 3). The highest rate of net N mineralization was found under larch. Larch and arolla pine increased N mineralization significantly compared to spruce (P<0.001) and Scots pine (P=0.004), where the lowest rate was found. N mineralization under larch was also significantly higher than that under birch (P<0.001) and aspen (P=0.003).

Among all of the measured activities, net nitrification was most strongly affected by tree species (P<0.001), with means ranging over 2 orders of magnitude from 0.35 to 35.6 mg NO_3^--N kg^{-1} 30 $days^{-1}$ (Figure 3). Net nitrification tended to vary among species in the same order as net N mineralization: low activities of both processes occurred under spruce und Scots pine, intermediate values were found under aspen and birch, and the highest rates occurred under larch and arolla pine.

The contribution of net nitrification to net N mineralization depended strongly on tree species. Net nitrification constituted the smallest part of net N mineralization under spruce, just 1-3%. By contrast, net nitrification contributed to 90-100% of net N mineralization under larch and arolla pine, indicating that almost all of the net increase in inorganic N was due to NO_3^- accumulation.

CO_2 production from soil heterotrophic microorganisms

Soil respiration is the major source of ecosystem CO_2 efflux, and much of the efflux from the soil comes from heterotrophic microbes. Basal respiration (without glucose addition) varied within a very narrow range: 65 to 87 mg CO_2-C kg^{-1} day^{-1} (Figure 4). Tree species significantly (P=0.009) influenced basal respiration rate. arolla pine, larch and aspen increased basal respiration rates compared to Scots pine (P<0.020) and birch (P=0.010). Basal respiration under birch was significantly lower than under spruce (P=0.041). Even though the species effects were significant, the differences among species were not as large as for N transformations.

As expected, substrate-induced respiration (SIR) through glucose addition caused a 3-fold increase in respiration (Figure 4). SIR was also influenced by tree species (P<0.001). Arolla pine and larch increased SIR compared to other species (P<0.050). Intermediate values of SIR were found beneath spruce, aspen and birch. The lowest value was found under Scots pine, where SIR was significantly lower than under all other species (P<0.050). Overall, the effects of species on SIR were similar to effects on basal respiration rate.

The Siberian afforestation experiment showed that while effects of tree species on C respirations were significant, the differences among species were much smaller than the effects on N transformations. These results are in accord with other laboratory incubation studies (Scott 1998), and field measurements of CO_2 evolution (Paré, cited by Côté et al., 2000) which indicated no difference between coniferous and deciduous stands. Mikola (1985) studied 30- to 50 year-old spruce and birch forests growing on originally approximately similar sites and found no difference in soil respiration. Also no differences in CO_2 flux were found between an agricultural and forest soil, while much larger N_2O was produced in the agricultural field (van Bachove et al., 2000). These results support our

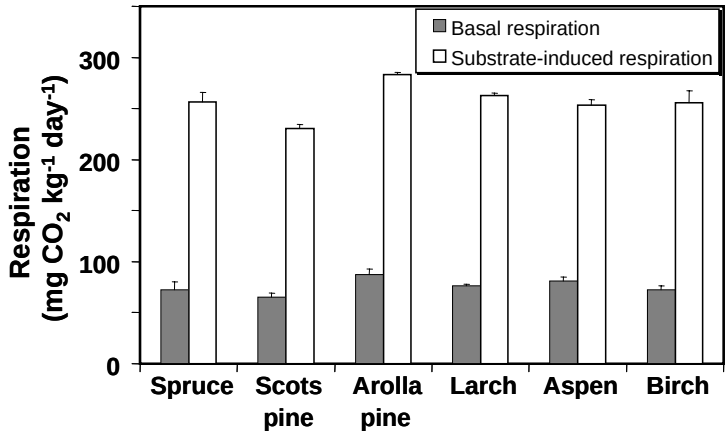

Figure 4. Activity of basal respiration in soil samples beneath six tree species (N=3) measured as CO_2 production during 24 h incubation at 60% of WHC and 28 ^{o}C and substrate-induced respiration (SIR) in the same soil samples measured as described above but with addition of glucose.

conclusion about stronger effects of tree species on N than on C transformation processes. However, this contrasts to other study where tree seedlings of three species (pine, spruce and birch) were growing under greenhouse conditions for four months and no differences between species were found on net N mineralization, nitrification and denitrification, while species did affect C mineralization (Priha et al., 1999b). Clearly, seedling studies cannot be used reliably to predict patterns in forests.

CH_4 oxidation

Temperate and boreal forest upland soils are a significant sink of atmospheric CH_4. Methane consumption in our soils varied from approximately 1 to 5 nmol CH_4 g^{-1} h^{-1} (Figure 5). Tree species strongly affected CH_4 consumption (P=0.004). Overall, birch had higher values than coniferous species (P<0.05). Aspen had higher values than Scots pine (P=0.033) and arolla pine (P=0.043). 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 showed varying responses. For example, Adamsen and King (1993) showed an inverse relationship between gravimetric soil water content and CH_4-oxidation in coniferous soil, and Yavitt et al. (1995) also found that the lowest rate of CH_4 consumption was associated with the highest soil water content in

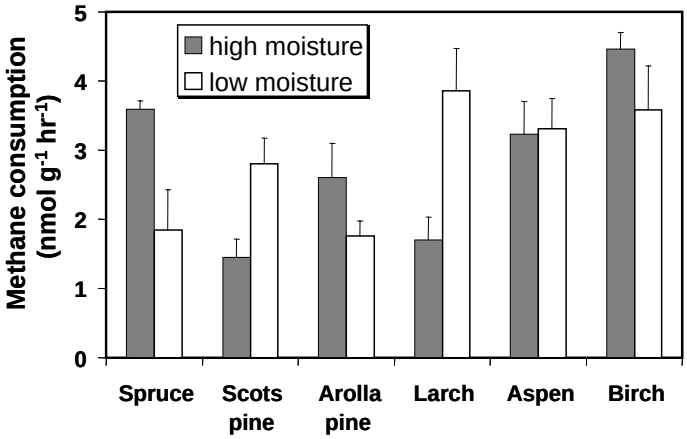

Figure 5. Rate of CH_4 consumption measured under the six tree species at two moisture contents (60 and 90% WHC). The initial concentration of CH_4 was 10 ml l^{-1} (n=6). The significant effects of soil moisture were observed beneath spruce and larch (P<0.010) and Scots pine (P<0.05).

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, we have shown that net nitrification is highest under larch and lowest under spruce and Scots pine (Menyailo et al., 2002b, and this work). 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 (Figure 5). 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

global warming causes birch to replace coniferous species, potential CH_4 uptake will be higher regardless of soil moisture changes.

CONCLUSIONS

We have shown strong effects of tree species on soil microbiological processes responsible for the fluxes of greenhouse gases. The species effects are much larger than were previously reported (Priha et al., 1999a,b). Both species and depth had larger effects on N transformations than on C transformations. Denitrification potential varied under different species in the same way as did net N mineralization and net nitrification, while N_2O reduction rate did not. This caused a large difference between N_2O production and reduction rates under deciduous species. We predict that deciduous species will produce more N_2O in the field than conifers and that Siberian forests will produce more N_2O if global climate change results in changes in species composition. The rate of CH_4 oxidation is affected by tree species, but this effect interacts strongly with soil moisture. 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. Nevertheless, if, as predicted, global warming causes deciduous species to replace coniferous species, the uptake of CH_4 will be higher.

ACKNOWLEDGMENTS

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