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Stand age and tree species affect N_2O and CH_4 exchange from afforested soils

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Abstract. Afforestation of former agricultural land is a means to mitigate anthropogenic greenhouse gas emissions. The objectives of this study were (1) to assess the effect of oak (*Quercus robur*) and Norway spruce (*Picea abies [L.] Karst.*) stands of different stand ages (13–17 and 40 years after afforestation, respectively) on N_2O and CH_4 exchange from the soil under these species and (2) identify the environmental factors responsible for the differences in gas exchange between tree species of different ages. N_2O and CH_4 fluxes (mean $\pm$ SE) were measured for two years at an afforested site. No species difference was documented for N_2O emission (oak: 4.2 ± 0.7 µg N_2O-N $m^{-2}\,h^{-1}$, spruce: 4.0 ± 1 µg N_2O-N $m^{-2}\,h^{-1}$) but the youngest stands (1.9 ± 0.3 µg N_2O-N $m^{-2}\,h^{-1}$) emitted significantly less N_2O than older stands (6.3 ± 1.2 µg N_2O-N $m^{-2}\,h^{-1}$). CH_4 exchange did not differ significantly between tree species (oak: -8.9 ± 0.9, spruce: -7.7 ± 1) or stand age (young: -7.3 ± 0.9 µg CH_4-C $m^{-2}\,h^{-1}$, old: -9.4 ± 1 µg CH_4-C $m^{-2}\,h^{-1}$) but interacted significantly; CH_4 oxidation in the soil increased with stand age in oak and decreased with age for soils under Norway spruce. We conclude that the exchange of N_2O and CH_4 from the forest soil undergoes a quick and significant transition in the first four decades after planting in both oak and Norway spruce. These changes are related to (1) increased soil N availability over time as a result of less demand for N by trees in turn facilitating higher N_2O production in older stands and (2) decreasing bulk density and increased gas diffusivity in the top soil over time facilitating better exchange of N_2O and CH_4 with the atmosphere.

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1 Introduction

Afforestation is viewed as a means to mitigate rising atmospheric concentrations of CO_2 because forest ecosystems can store atmospheric carbon in the long term. However, afforestation also affects the dynamics of other strong greenhouse gases, such as methane (CH_4) and nitrous oxide (N_2O) and it has been widely documented that forest ecosystems display higher rates of CH_4 oxidation and smaller emissions of N_2O fluxes compared to agricultural land (Allen et al., 2009; McNamara et al., 2008; Tate et al., 2007).

Lower emissions of N_2O in forest soils are related to the availability of N in the soil. Compared to fertilised agricultural soils the availability and input of inorganic N is generally lower in forest soils and the potential to produce N_2O in forests is lower than in agricultural soils (Liu and Greaver, 2009).

The larger CH_4 uptake rates in forest soils have been attributed to both physical and biogeochemical changes in the soil environment following afforestation that favour methanotrophic bacteria. Thus, diffusion of CH_4 into the soil has been proposed as a primary constraint on CH_4 oxidation rate in soils (Ball et al., 1997) and it is generally accepted that the porosity of forest soils is larger than in agricultural soils, thereby providing a soil environment more suited for CH_4 uptake. Furthermore, it has been documented that the methanotrophic community responsible for consumption of CH_4 is sensitive to disturbance of the soil; thus the CH_4 uptake capacity recovers only slowly to pre-cultivation levels in afforested soils (Prieme et al., 1997). This has recently been demonstrated in a field based study of GHG exchange in a Canadian afforestation chronosequence (Peichl et al., 2010). Also, it is recognised that CH_4 uptake in soils is further suppressed by high levels of available mineral nitrogen (N) in the soil as well as atmospheric deposition of N (Butterbach-Bahl et al., 1998; Reay and Nedwell, 2004; Steudler et al., 1989).

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Thus, the combined effect of larger oxidation of atmospheric CH_4 and lower N_2O emissions in forests suggests a significant mitigation potential of land-use change from cropland to forest.

In recent years afforestation in Europe has focused increasingly on native deciduous species rather than conifers (Mather, 2000). Partly, because deciduous forests have a higher potential for recharge of groundwater reservoirs (Christiansen et al., 2006, 2010) than coniferous forests, but also out of concern for biodiversity and recreational value of forested landscapes (The Danish Forest and Nature Agency, 1999). It is well documented that the deposition of atmospheric inorganic N is larger in coniferous than in deciduous forests in Europe (Gundersen et al., 2009; Rothe et al., 2002). The effect of forest type on N_2O fluxes is unclear. It has been reported that coniferous stands emitted more N_2O than adjacent deciduous stands (Bowden et al., 1991; Oura et al., 2001). A pure European beech stand in southern Germany forest emitted 4 to 5 times more N_2O compared to an even-aged Norway spruce stand, although the combined $NO + N_2O$ emissions were largest from the soil under the Norway spruce (Papen and Butterbach-Bahl, 1999). Moreover, a study for a wide range of European forest soils revealed that the N_2O emissions were highest in deciduous forests, but these forests were also situated on generally more nutrient rich soils (Ambus et al., 2006). Hence, soil N status rather than forest type could be the main driver responsible for the magnitude of N_2O emissions (Liu and Greaver, 2009). Therefore, coniferous stands receiving more N than adjacent deciduous forests on similar soils and under the same climate would potentially release more N_2O because the N availability in the soil will be higher.

It has also been suggested that conversion of hardwood forests to Norway spruce and pine plantations would decrease CH_4 oxidation potential in the soil because of the higher N deposition in coniferous forests (Borken et al., 2003). Other studies have also documented that CH_4 uptake in the soil under stands of deciduous tree species is higher than for soils under adjacent coniferous stands because of lower diffusion capacity due to the presence of an organic horizon under conifers and the influence of tree species on the composition of the methanotrophic community (Borken et al., 2006; Butterbach-Bahl and Papen, 2002; Menyailo and Hungate, 2003).

Afforestation and the shift in tree species composition from conifers to deciduous species in the future forests of Europe will represent an important change in the land use with consequences for the greenhouse gas budgets and climate impact of forests (Borken et al., 2003). However, there is a need to increase our knowledge of greenhouse gas fluxes from terrestrial ecosystems in general by including the development over time in order to understand the climate impact of the given ecosystem, including forests (Anderson-Teixeira and DeLucia, 2011). An aspect of afforestation that has not received much attention is the effect of stand development on the fluxes of N_2O and CH_4 from soils (Ball et al., 2007; Peichl et al., 2010; Prieme et al., 1997). These studies suggest that CH_4 oxidation increases over time, but opposite trends for N_2O have been reported. However, comparative studies of the exchange of N_2O and CH_4 in differently aged stands of common European tree species exposed to the same land use history and environmental conditions are to our knowledge missing. Thus, it is relevant to assess how GHG exchange in coniferous and deciduous forests can be expected to develop over time and investigate how GHG exchange relates to soil and ecosystem factors in the contrasting forest types. We therefore studied CH_4 and N_2O fluxes for a two year period in two differently aged monoculture stands of oak (*Quercus robur L.*) and Norway spruce (*Picea abies [L.] Karst.*) planted on the same former arable soil and exposed to the same climate. The main objectives of the study were to (1) assess the effect of tree species and stand age on CH_4 and N_2O exchange and (2) identify the environmental factors responsible for the differences in GHG exchange between tree species of different ages.

2 Materials and methods

2.1 Study sites

This study was conducted in Vestskoven (55°41′ N, 12°21′ E); a former intensively cultivated area located 15 km west of Copenhagen, Denmark. The conversion from agriculture to forest commenced in 1967 and evenly aged stands of Norway spruce and oak were established over the years. Thus, Vestskoven represents a unique area to study the influence of afforestation in different stages of stand development with different species located on the same soil type and climate. Four stands were studied in Vestskoven: two monoculture stands of Norway spruce planted in 1969 (S-69) and 1997 (S-97) and two monoculture stands of oak planted in 1970 (O-70) and 1993 (O-93). All stands were located within an area of $1 \times 3\,km^2$ (supplementary material, Fig. S-1).

The soils are moist Mollic Hapludalfs (Soil Survey Staff, 1998) with a texture of sandy loam developed from glacial calcareous till deposits. There were signs of pseudogley in the O-70, S-97 and S-69 stands (L. Vesterdal, personal communication; Vesterdal et al., 2002). Soil and stand characteristics for the four stands are given in Table 1. The topography in the area is flat (elevation 18–27 m) and the climate is temperate with a mean annual temperature of 7.7 °C and a mean annual precipitation of 625 mm for the period 1960–1990 (Danish Meteorological Institute, 2000). The groundwater level was 3–4 m below the surface (Erntsen, 2005).

Table 1. Stand characteristics at Vestskoven of the, organic carbon (C) pool, C/N ratio, soil pH and bulk density of the top 25 cm of the mineral soil. Atmospheric mineral nitrogen (N) deposition and mineral NO_3^- leaching and mean NO_3-N concentrations in the soil water below the root zone are given for the entire stand. Nitrogen fluxes and concentration data represented the period from April 2001 to March 2002. Data from Hansen et al. (2007); Ritter et al. (2003); Vesterdal et al. (2002).

		C (Mg ha^{-1})			C/N ratio			Soil pH ($CaCl_2$)			Bulk density (g cm^{-3})			N deposition	NO_3^- leaching	NO_3-N 90 cm[a]
Stand	Plot	0–5	5–15	15–30	0–5	5–15	15–30	0–5	5–15	15–30	0–5	5–15	15–30	kg N ha^{-1} yr^{-1}	kg N ha^{-1} yr^{-1}	mg l^{-1}
O-93	A	17.1	28.8	33.2	13.4	12.0	11.4	7.1	7.0	6.6	1.39	1.61	1.57	6.8		0.03
	B	14.8	28.9	26.9	11.9	11.5	12.2	4.9	4.7	4.6	1.38	1.59	1.57	9.7	2	4.7
	C	15.9	30.3	23.2	11.3	11.1	11.6	6.0	5.9	5.7	1.35	1.49	1.54	8.3		8.1
O-70	A	20.4	24.2	17.7	13.3	10.2	10.5	4.6	4.9	5.4	1.28	1.52	1.63	9.6		23
	B	19.4	23.5	18.1	13.4	10.7	11.0	4.7	4.8	5.6	1.15	1.43	1.51	–	7	–
	C	15.9	21.9	17.1	12.1	10.1	10.5	4.8	5.1	6.0	1.23	1.55	1.69	10.7		15
S-97	A	13.2	27.5	20.7	10.7	10.5	11.2	5.9	5.8	5.9	1.35	1.50	1.48	13.0		2.5
	B	13.9	25.5	19.9	10.5	10.1	10.9	5.9	5.8	6.0	1.45	1.51	1.63	11.2	0	4.9
	C	17.1	30.5	20.0	10.6	10.1	11.0	5.7	5.6	5.6	1.51	1.48	1.57	10.6		1.1
S-69	A	14.9	19.0	13.6	12.5	10.3	9.7	4.1	4.7	5.6	1.34	1.59	1.73	27.0		73
	B	18.7	19.8	14.4	16.1	10.2	10.3	3.9	4.4	4.8	1.36	1.66	1.69	21.3	13	17
	C	17.1	18.8	16.2	14.1	10.1	9.7	4.0	4.5	5.1	1.36	1.53	1.66	19.2		18

Mineral soil C/N ratios in 0–5 cm were generally higher in the older stands, but differences between the stands were less distinct below 5 cm (Table 1). Similarly, soil pH was consistently lower in the older stands in 0–15 cm (Hansen et al., 2007; Ritter et al., 2003) (Table 1). Furthermore, both N deposition, NO_3^- leaching and NO_3-N concentration in soil water below the root zone was largest in the soil under Norway spruce stands and N deposition increased with stand age for both species though most pronounced for Norway spruce (Hansen et al., 2007) (Table 1).

2.2 Field design

In each stand three plots (50 m^2) were established in a previous chronosequence study of the carbon (C) (Vesterdal et al., 2002) and N cycle (Hansen et al., 2007). At each plot three closed static chambers to measure GHG fluxes were installed with a maximum distance of 2–5 m apart. The minimum distance between individual plots was: 35 m (O-93), 120 m (O-70), 70 m (S-97) and 120 m (S-69). The plots were not subject to edge effects as they were placed >100 m from the forest edge (supplementary material, Fig. S1).

In this study design we only have one replicate of each treatment/stand that somewhat limits interpretation of the statistical analyses and observed differences among stands could be inherited from natural differences or different treatments under the previous agricultural use. However, a previous investigation including more stands and ages revealed homogeneous soil condition across the area as indicated by similar soil chemical properties in the lower parts of the old plough layer which are less likely influenced by species and age differences (Ritter et al., 2003). Further it was shown in Vesterdal et al. (2002) that soil texture and indicators of soil development in profiles for the S-97 and S-69 stands (representing the extremities of the study area) were similar. For the four stands chosen for this study, variations in soil properties displayed in Table 1 were as large within and between stands of same age. Considering the soil homogeneity in the area and the relative large distances as well as soil differences between plots within a stand, we believe that the plots can be assumed as replicates in the analysis of GHG data.

2.3 Field measurements

Measurements of GHG fluxes were conducted on a monthly basis in a period of two years from February 2008 to April 2010. At each sampling occasion volumetric soil water content (Theta probe ML2x, Delta T Devices, UK) and soil temperature (model 550B, UEi, Beaverton, Oregon, USA) in 0–5 cm beside each static chamber was also measured. In total 131 to 144 measurements of GHG fluxes, volumetric soil water content and soil temperature were conducted for each stand. The net soil surface exchange of CH_4 and N_2O was measured on a monthly basis with closed static chambers that were installed in permanent locations throughout the study period. The chamber collar (inner diameter of 30.5 cm) was inserted 10 cm in the soil and chamber volumes ranged from 5 to 9 l. At each measurement a lid was placed on top of the collar and sealed with a silicon rubber ring wrapped around the edge of the lid ensuring gas-tight conditions. Chamber headspace samples were withdrawn with 60 ml plastic syringes through a butyl rubber septum in the middle of the lid at times 0, 30, 60 and 120 min. In March 2009 the enclosure time was reduced to 60 min and samples taken every 20th minute. At each headspace sampling the syringe was used to mix the headspace by pumping three times before fully filling the syringe. Pressure changes in a manually sampled chamber headspace has been reported to lead to overestimation of the estimated diffusive flux (Bekku et al., 1995), but we did not observe any changes in headspace concentrations that could be attributed to mass flow caused by depressurisation of the chamber headspace. Headspace samples were transferred to non-evacuated 2.7 ml crimped vials with a butyl rubber septum by flushing the vial with 58 ml of the sample in the syringe and pressurising the vial with the remaining 2 ml.

2.4 Gas chromatography and calculation of gas fluxes

Gas samples were analysed on a Shimadzu GC-2014 gas chromatograph (Shimadzu, Kyoto, Japan) equipped with electron capture and flame ionisation detectors set at 300 °C and 200 °C, respectively. The carrier gas was 100 % N_2 with a flow rate of 25 ml min^{-1}. Methane and N_2O were analysed in separate columns set in a constant oven temperature of 40 °C. The column used for CH_4 was a 60/80 Carboxen 1000 (15 ft, 1/8 in). For N_2O an 80/100 Hayesep Q (2.5 m, 1/8 in) column was used. A syringe extracted 1.6 ml sample from the vial and injected 0.75 ml into each column used for CH_4 and N_2O.

All gas fluxes were calculated by linear regression. Analyses of the measurement series resulting in an R^2 value above 0.85 was accepted for flux calculation. It was observed that for regression analyses resulting in R^2-values below 0.85 the increase or decrease of N_2O and CH_4 concentrations did not follow a distinct trend and fluxes were therefore considered to be close to zero and set to a zero flux. For N_2O 151 out of 559 flux measurements were considered as zero fluxes. For CH_4 139 out of 545 flux measurements were considered as zero fluxes. Fluxes were expressed as μg N_2O-N m^{-2} h^{-1} or μg CH_4-C m^{-2} h^{-1}.

2.5 Soil sampling and laboratory analyses of extractable mineral nitrogen

One core of mineral soil in 0–15 cm was sampled next to each chamber with a cylinder (Ø 5 cm) in April 2011. The soil core from adjacent to each chamber was divided in the field into 0–5 cm and 5–15 cm sections and were kept intact and cooled until analysis. For each plot intact soil cores were

pooled by the respective depth segments to form one composite sample representing that plot. A total of 3 samples for each depth segment per stand were analysed giving in total 24 samples from two depths that were used to describe the variation in extractable mineral N between the stands. We considered the level of extractable N and the proportion of NO_3^-/NH_4^+ to be an indicator of the soil N status.

Pooled soil samples were homogenised and sieved (<2 mm) to remove stones. Living and dead roots were removed by hand. Immediately after sieving pooled soil samples for 0–5 and 5–15 cm were extracted with 20 ml 1 M KCl and 0.1 M KCL for determination of the concentration of extractable NH_4-N (mg kg^{-1} dry soil) and NO_3-N (mg kg^{-1} dry soil), respectively.

Soil and KCl solution were shaken for 1 h and subsequently centrifuged for 10 min at 2000 rpm. The supernatant was filtered through a 0.45 µm filter. Extracts were kept cool at 4–5 °C and dark before analysis 1–2 days after extraction. Before analysis all extracts were degassed in an ultrasonic bath at room temperature. Ammonium and NO_3-N were analyzed by flow injection analysis on a PE Lambda 2 UV/VIS Spectrometer (Perkin-Elmer, Waltham, MA, USA) with a detection limit of 0.05 mg NH_4-N L^{-1} and 0.01 mg NO_3-N L^{-1} equipped with a 18 µm Suprasil flow cell.

2.6 Statistics

For all statistical analyses the SAS software version 9.2 (SAS Institute Inc., Cary, North Carolina, USA, 2008) was used and significance was accepted at $p \leq 0.05$. Effects of tree species, stand age (young/old) and tree species x stand age interaction were tested separately on time series of log-natural transformed N_2O ($\ln(N_2O + 18)$) ($n = 559$) and CH_4 ($\ln(CH_4+80)$) ($n = 545$) fluxes, soil water content and soil temperature by repeated measures ANOVA using the Mixed procedure in SAS. Data were log-transformed to comply with the assumptions of the statistical test, variance homogeneity between groups and normal distribution of residuals. For the analyses concerning N_2O and CH_4 fluxes the model formulation included tree species and stand age as class variables, soil water content and soil temperature as numeric independent variables. Tree species and stand age were included as class variables to test for significant effects of these variables on soil water content and soil temperature. Stand differences in soil water content, soil temperature and log-natural transformed fluxes of N_2O and CH_4 were also tested by the repeated measures ANOVA with stand name as the only class variable in the model. The chamber represented the subject repeated over time and the plot was used to account for the random variation of the tested parameter in the repeated measure analyses.

The effect of tree species ($n = 6$) and stand age ($n = 6$) (class variables) on average plot concentration (mg kg^{-1} dry soil) of total extractable mineral N ($NH_4^+ + NO_3^-$) and the percentage of NO_3-N to total extractable mineral N ($\%NO_3^-$) for 0–15 cm and mineral soil bulk density in 0–5 cm, was tested separately using the Mixed procedure in SAS. Differences in average plot concentrations of the same parameters as above between individual stands ($n = 3$) were also tested using the mixed procedure with only the stand name defined

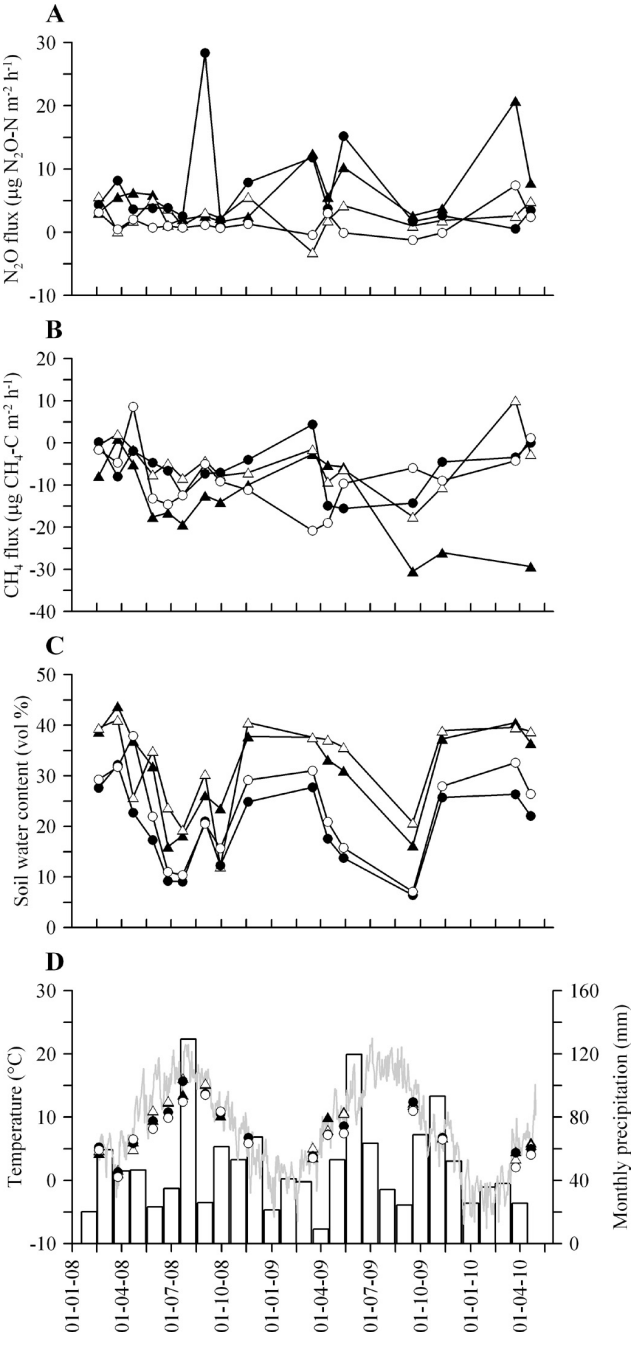

Fig. 1. Stand average **(A)** N_2O flux (µg N_2O-N m^{-2} h^{-1}), **(B)** CH_4 flux (µg CH_4-C m^{-2} h^{-1}), **(C)** soil water content (vol%) and **(D)** soil temperature (°C) in 0–5 cm (symbols), monthly precipitation in mm (bars) and average daily temperature in °C (grey line). Spruce 1969 (●), Spruce 1997 (○), Oak 1970 (▲), Oak 1993 (△).

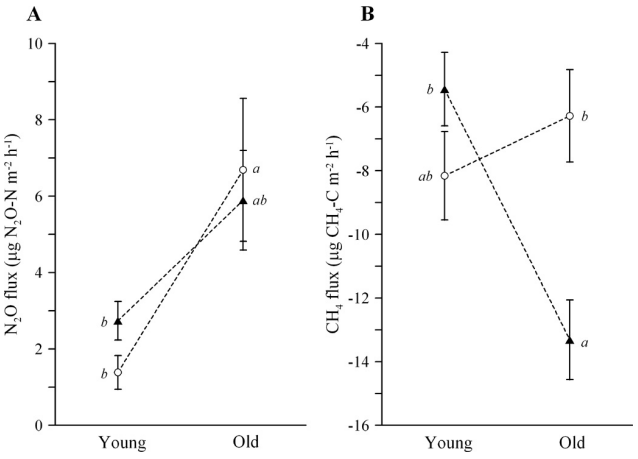

Fig. 2. Stand comparison of **(A)** soil water content (vol%), **(B)** soil temperature (°C) and **(C)** soil bulk density (g cm^{-3}) in 0–5 cm. Error bars (± std. error of the mean) represent the temporal variation. Different letters indicate significant difference ($p < 0.05$). Oak (▲) and Norway spruce (○). Dashed lines are included for clarification and do not represent regression lines.

as class variable. The p-values of multiple comparisons between stands were adjusted by the Bonferroni method, by multiplying the p-value by the number of comparisons. Using the mineral soil bulk density and the time series for soil water content and air temperature the effective diffusion (D_s) for CH_4 and N_2O (D_s, $cm^2\ s^{-1}$) was estimated according to the method by (Borken et al., 2003). The effect of tree species ($n = 6$) and stand age ($n = 6$) was tested similarly to the abovementioned soil factors.

The relationship between plot mean N_2O and CH_4 fluxes, respectively, and mineral soil pH, bulk density, soil organic C pool and C/N ratio of the mineral soil in a depth of 0–5 cm was tested using backward linear stepwise regression.

3 Results

3.1 Abiotic soil properties

Soil water content displayed a similar temporal trend for all investigated stands, with highest soil water content during winter and early autumn and a minimum during summer (Fig. 1c). Soil water ranged from a maximum of 44 vol% in the O-70 stand to a minimum of 6 vol% in the S-69 stand (Fig. 1c). Furthermore, the two oak stands had higher soil water content than the Norway spruce stands (Fig. 1c). Only the O-70 stand showed a notable variation of mean soil water content within the stand of around 10 vol% while the spatial variation of the mean soil water content within the other stands did not exceed 5 vol%. The repeated measures ANOVA showed that the average soil water content was significantly ($p = 0.004$) higher in oak (31.5 ± 0.6 vol%) compared to Norway spruce (21.3 ± 0.6 vol%) which was also reflected in the stand comparison (Fig. 2a). Younger stands had a significantly ($p = 0.02$) higher mean soil water content (27.3 ± 0.7 vol%) than older stands (25.6 ± 0.7 vol%). The soil water content of the S-97 stand was significantly ($p = 0.045$) higher than for the S-69 stand (Fig. 2a).

Soil temperature ranged from a minimum of 0.5 °C in winter to maximum 16 °C in summer and displayed similar temporal variation as the average air temperature, although the amplitude of air temperature was larger, ranging from −6 to 23 °C (Fig. 1d). The spatial variation of soil temperature was similar for all investigated stands at a maximum of 0.5 °C. The monthly precipitation for this area in the investigation period ranged from 9 mm to 130 mm and monthly precipitation >100 mm was only observed in the summer months (Fig. 1d). The oak stands had a significantly ($p = 0.0127$) higher soil temperature (8.6 ± 0.3 °C) than the Norway spruce stands (7.8 ± 0.2 °C), but there was no significant effect of stand age ($p = 0.32$) or species × age interaction ($p = 0.21$) even though soil temperature increased with stand age in oak and decreased in Norway spruce (Fig. 2b). The stand comparison only revealed a marginal significant difference ($p = 0.04$) in soil temperature between the two young stands (Fig. 2b).

The average bulk density of the oak stands (1.32 ± 0.04 g cm^{-3}) was significantly ($p = 0.008$) lower compared to the Norway spruce stands (1.42 ± 0.03 g cm^{-3}). Furthermore, the average bulk density was significantly ($p = 0.001$) lower in older stands (1.30 ± 0.04 g cm^{-3}) compared to younger stands (1.43 ± 0.02 g cm^{-3}). The stand comparison showed that the bulk density was significantly lower in the O-70 stand compared to both of the younger stands (Fig. 2c). However, the bulk density was not significantly different between the young stands or compared to the S-69 stand (Fig. 2c). The soil bulk density decreased in the same manner with stand age in both tree species (Fig. 2c).

3.2 N_2O exchange

The stand mean N_2O fluxes ranged between −3 to 30 µg N_2O-N m^{-2} h^{-1} during the period of investigation and did not display any pronounced seasonal trend (Fig. 1a). However, the highest observed N_2O flux in the S-69 stand was observed during summer and the highest N_2O flux in the O-70 stand was measured in the early spring after a long period of subzero air temperatures (Fig. 1a). Uptake of N_2O was observed for the majority of chambers in all stands and constituted around 15 % of all chamber measurements of N_2O fluxes. Uptake of N_2O occurred at all times of year and there was a tendency towards more occasions of N_2O uptake in the O-93 and S-97 stands. The highest maximum N_2O fluxes were also observed in the O-70 (166 µg N_2O-N m^{-2} h^{-1}) and S-69 (202 µg N_2O-N m^{-2} h^{-1}) stands. The spatial variation of N_2O fluxes at stand level was highest in the youngest stands (351 % and 5600 % for O-93 and S-97, respectively) in contrast to consistent lower spatial variation

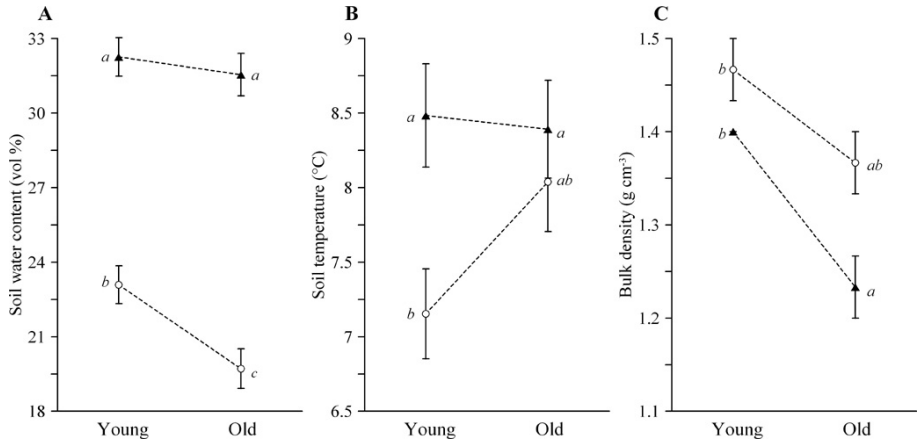

Fig. 3. Stand comparisons of average **(A)** N_2O fluxes (µg N_2O-N $m^{-2}\,h^{-1}$) and **(B)** CH_4 fluxes (µg CH_4-C $m^{-2}\,h^{-1}$). Error bars (± std. error of the mean) represent the temporal variation. Different letters indicate significant difference ($p < 0.05$). Oak (▲) and Norway spruce (○). Dashed lines are included for clarification and do not represent regression lines.

in the older stands (181 % 10 and 228 % for O-70 and S-69, respectively) (supplement, Table S1). The repeated measures ANOVA indicated that there was a significant effect of tree species. However, the mean values of N_2O fluxes for the oak (4.2 ± 0.7 µg N_2O-N $m^{-2}\,h^{-1}$) were identical to the average N_2O fluxes for the Norway spruce forests (4.0 ± 1.0 µg N_2O-N $m^{-2}\,h^{-1}$). Young stands (1.9 ± 0.3 µg N_2O-N $m^{-2}\,h^{-1}$) had a significantly ($p < 0.0001$) lower average N_2O flux than older stands (6.3 ± 1.2 µg N_2O-N $m^{-2}\,h^{-1}$). Furthermore, N_2O fluxes were positively related to soil water content ($p < 0.0001$) and soil temperature ($p < 0.0001$). The stand comparison indicated that the average N_2O fluxes of the S-97 stand and the O-93 stand were significantly ($p = 0.003$ and $p < 0.001$, respectively) lower than the S-69 stand (Fig. 3a).

3.3 CH_4 exchange

The stand mean CH_4 fluxes ranged between −30 to 9 µg CH_4-C $m^{-2}\,h^{-1}$ and were mostly negative and only above zero during winter and early spring (Fig. 1b). The highest uptake of CH_4 was consistently observed for the O-70 stand while the rest of the stands did not display any pronounced differences over time (Fig. 1b). There was a weak tendency towards higher uptake of CH_4 during summer periods and less during winter (Fig. 1b). Emission of CH_4 was observed for all chambers predominantly in spring and autumn and constituted around 15 % of all CH_4 flux measurements. Maximum CH_4 emission was observed for the S-97 stand (66 µg CH_4-C $m^{-2}\,h^{-1}$). The O-70 had the lowest number of CH_4 emission events. The spatial variation was lowest in the 20 O-70 (113 %) stand and highest in O-93 stand (2200 %) and no trend with stand age was observed (supplement, Table S1). Methane uptake did not differ significantly ($p = 0.12$) between oak (-8.9 ± 0.9 µg CH_4-C $m^{-2}\,h^{-1}$) and Norway spruce forests (-7.7 ± 1 µg CH_4-C $m^{-2}\,h^{-1}$). Neither did older stands (-9.4 ± 1 µg CH_4-C $m^{-2}\,h^{-1}$) have significantly ($p = 0.097$) higher CH4 uptake than in younger stands (-7.3 ± 0.9 µg CH_4-C $m^{-2}\,h^{-1}$). However, there was a strong significant ($p = 0.001$) tree species × stand age interaction. Thus, the Norway spruce and oak stands displayed opposite trends in the development of average CH_4 fluxes with forest age (Fig. 3b). Average CH_4 uptake did not differ among spruce stands whereas the CH_4 uptake of the O-70 stand forest was significantly and higher than in the O-93 stand ($p = 0.003$) and S-69 stand ($p = 0.026$) (Fig. 3b).

3.4 Relation between greenhouse gas exchange and soil properties

According to the backward linear regression analysis plot average fluxes of N_2O were not related to any of the tested variables soil pH, bulk density, soil organic C pool or C/N ratio although bulk density described the variation of N_2O fluxes best among the variables. There was an indicated ($p = 0.11$) negative relationship between N_2O and bulk density. The plot average CH_4 fluxes was positively related only to bulk density ($p = 0.011$) according to the backward regression analysis. The estimated model was able to explain 49 % of the variation in CH_4 fluxes.

Furthermore, according to the repeated measures ANOVA individual chamber N_2O fluxes were positively related to soil water content ($p < 0.0001$) and soil temperature ($p < 0.0001$) and also indicated a positive relationship ($p = 0.07$), albeit not significant, between individual chamber fluxes of CH_4 and soil water content. Thus, CH_4 uptake (negative flux) would increase with decreasing soil water content. Individual chamber fluxes CH_4 were not related to soil temperature ($p = 0.40$).

4 Discussion

4.1 N_2O exchange

The measured N_2O fluxes for the young stands of oak and Norway spruce were low compared to the range of observed N_2O fluxes for European forests, but N_2O fluxes of the oldest stands at Vestskoven were comparable to N_2O fluxes measured in a mature beech forest in Denmark (mean $\pm$ SE: 9.1 ± 1.7 µg N_2O-N $m^{-2}\,h^{-1}$) (Pilegaard et al., 2006). The observed spatial and temporal variation of N_2O fluxes stress the importance of measuring the exchange over a long period as well as having a sufficient spatial coverage of the specific tree species in order to capture the natural spatial variation. The temporal resolution of our dataset was too low to identify individual freeze-thaw or rewetting events that might cause the N_2O emission to increase rapidly from the soil (Goldberg and Gebauer, 2009).

The analysis of repeated N_2O flux measurements did indicate that fluxes from the soil were significantly higher under Norway spruce compared to oak, but the measured average N_2O emission under oak and Norway spruce was similar. We attribute the seeming statistical effect of tree species to the large temporal and spatial variation. However, the significant effect of stand age on N_2O fluxes is in accordance with the study of (Ball et al., 2007) who found higher N_2O emissions in 30-year old stands compared to 20-year old stands of Sitka spruce. The higher fluxes in the older stands were attributed to better aeration of the soil due to deeper groundwater table that facilitated more efficient release of substrate necessary for N_2O production (Ball et al., 2007).

Including all measurements from all four stands, N_2O fluxes were positively related to soil water content as is widely accepted (Davidson et al., 2000). However, we observed that the annual average soil water content was significantly higher in the younger stands than in older stands. Thus, the observed increase of N_2O fluxes with stand age must also be ascribed to other factors related to the soil environment than soil hydrology, such as diffusivity of gas in the soil and the N status of the soil under the different stands.

Nitrous oxide fluxes have been reported to increase with decreasing soil pH because the nitrous oxide reductase enzyme is inhibited at low soil pH (Weslien et al., 2009). We did not find a relation between soil pH and N_2O fluxes even though the soil pH at Vestskoven is decreasing with stand age (Table 1, Ritter et al., 2003). The lack of a pH effect over stand development is attributed to that other soil factors exerted a stronger control on the N_2O emissions in the differently aged stands. Thus, the indicated negative relationship with bulk density we found could point to that the more dense soils in the younger stands would lower soil diffusivity and in turn limit the physical exchange of N_2O. This assumption was confirmed by the significantly higher estimated effective diffusion coefficient for N_2O in the older stands. For CH_4, restriction of diffusion into the soil has been reported to hamper CH_4 exchange (Dörr et al., 1993) and we suggest that the same phenomenon is partly responsible for the lower N_2O emission in younger stands. In addition the lower exchange capacity from the more compact soil in the younger stands will lead to longer retention time of N_2O in the soil increasing the likelihood of reduction of N_2O to N2 especially if the soil water content is high. This would in turn lower the net N_2O emission.

We also did not find any relationship between N_2O fluxes and mineral soil C/N ratio even though it has been shown that the mineral soil C/N ratio is a general predictor of N_2O fluxes across European forests (Pilegaard et al., 2006) with higher N_2O fluxes at low C/N. However, given the narrow range of C/N ratios between our plots (10–14) other biotic factors related to N uptake in trees likely exert a more important control on substrate availability for N_2O production in these differently aged stands than what the differences in C/N ratio indicate.

In an earlier study of N budgets in Danish afforestation chronosequences, including our stands at Vestskoven, it was shown that soil water NO_3^- concentration decreased below detection limit in newly afforested agricultural soils and slowly increased with stand age to a lower level than that expected for agricultural soils in the same area (Hansen et al., 2007). The lower NO_3^- concentrations in young stands were attributed to the high demand for mineral N of the young trees and undergrowth and yet lower input from atmospheric deposition. In older stands a lower N demand combined with higher atmospheric deposition of N would produce higher NO_3^- concentrations in the soil water (Hansen et al., 2007). This explanation could help to understand why we observed significantly lower N_2O emissions in younger afforested soils and increased emissions with stand age. As we did not observe any consistent effect of tree species on N_2O emissions we suggest that the tree species affect the N_2O emissions indirectly by influencing the soil N status differently, because N availability (extractable N (Fig. 4) and subroot zone NO_3-N concentrations (Table 1)) in general was higher in the soil under Norway spruce than oak. There was a positive relationship between past NO_3^- leaching (Hansen et al., 2007) and our mean annual N_2O fluxes (Fig. 5). This relationship can only serve as qualitative indicator that observed soil N status changes over time result in increased N availability and hence larger N_2O emissions. However, we believe the difference in NO_3^- leaching between young and older stands is still valid today because the young stands (less than 20 years) are still expected to be in the phase of high N demand by plants, i.e. low leaching below the root zone (Hansen et al., 2007). Hence, we suggest that as the stands become older than 40 years the tree species will exert the dominant control on soil development, N availability and hence the magnitude of N_2O emissions. However, given the short time period of 40 years of our study this effect of tree species on soil N status is not dominant yet. The consistently higher atmospheric N deposition leading to enhanced

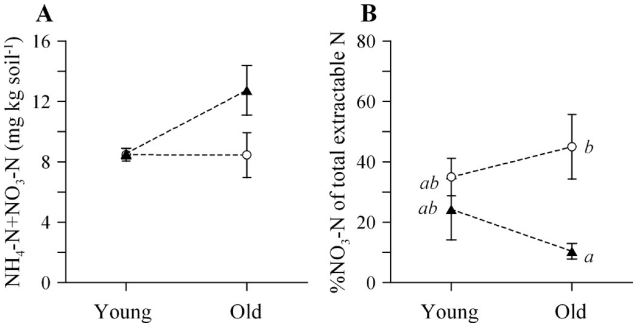

Fig. 4. Stand averages of total extractable mineral N (mg N (NH_4-N + NO_3-N) kg^{-1} dry soil) **(A)** in the top 0–15 cm of the mineral soil, **(B)** the percentage of NO_3-N to total extractable mineral N in the top 0–15 cm of the mineral soil. Error bars represent the standard error of the mean. Oak (▲) and Norway spruce (○). Significant differences between stands marked with different letters. Dashed lines are included for clarification and do not represent regression lines.

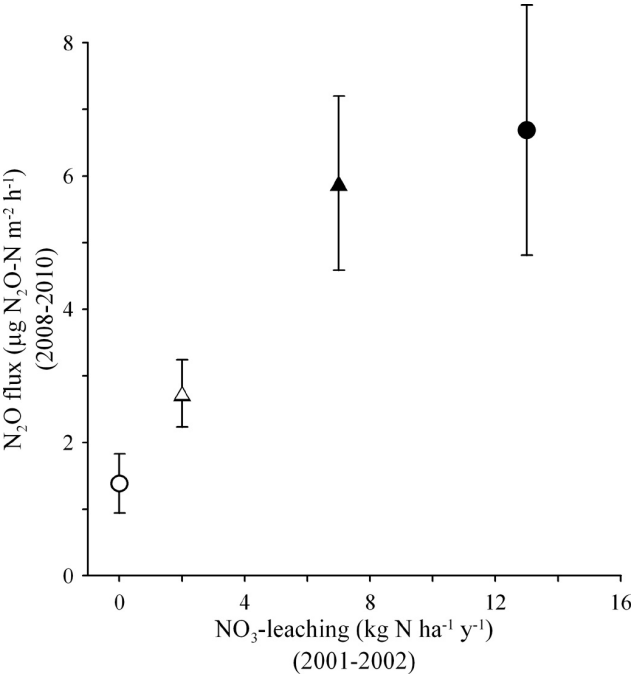

Fig. 5. Relationship between stand average N_2O flux and estimated NO_3^- leaching from Hansen et al. (2007). Norway spruce 1969 (●), Norway spruce 1997 (○), Oak 1970 (▲), Oak 1993 (△).

N availability in the soil as observed for coniferous forests in Denmark (Gundersen et al., 2009) represent an important tree species effect that can induce different potentials to produce N_2O in the soil over the forest rotation. However, in order to confirm this hypothesis more direct investigations of in situ measurements of N_2O net exchange in a longer age sequence are needed than what we had available.

4.2 CH_4 exchange

The CH_4 uptake rates we measured were lower compared to recently published rates for European forests (Fig. 2b) (mean ± SE: -46 ± 20 µg CH_4-C m^{-2} h^{-1}, Skiba et al., 2009). The stands we studied were all younger compared to the stands in Skiba et al. (2009) (46–100 years) and it can not be ruled out the CH_4 oxidation at Vestskoven might increase as the stands mature. We found increasing CH_4 uptake in all the stands during the summer of 2008 coinciding with lower soil water content and higher soil temperature. These findings are in line with previously reported CH_4 fluxes from soils displaying a similar seasonal variation (e.g. Butterbach-Bahl and Papen, 2002; Guckland et al., 2009). However, during the rest of the period the temporal variation of CH_4 exchange was weak and detecting any seasonality of fluxes at stand level was hampered by the low measurement frequency and the large spatial variation.

In situ measured CH_4 uptake rates increased with stand age after afforestation (Ball et al., 2007; Peichl et al., 2010). Similarly, we measured an increase in CH_4 oxidation between the O-70 and the two younger stands (Fig. 2b). However, due to the significant interaction between species and age, the overall effect of both tree species and stand age was masked by the different development of CH_4 fluxes with stand age for the different species.

It has been suggested that diffusion of CH_4 into soil exerts a strong control on CH_4 uptake in forest soils whereas soil temperature only has a minor influence (Dörr et al., 1993; King and Adamsen, 1992). More importantly, we found that bulk density was the only soil physical factor that could explain the variation of average plot CH_4 fluxes between the stands. This is in line with finding for a range of European forest soils (Ball et al., 1997). However, the S-69 stand had the lowest uptake of CH_4 of all stands while at the same time displaying the highest effective diffusion.

The development of an organic horizon, especially under coniferous species, can lower the CH_4 oxidising capacity in the soil by functioning as a diffusion barrier (Dong et al., 1998). The accumulation of litter material in the forest floor was much smaller under oak compared to Norway spruce stands at Vestskoven both in young and older stands (Vesterdal et al., 2002). However, we did observe similar CH_4 exchange rates in S-97, S-69 and O-93 indicating that the presence of an organic horizon was less important to restrict diffusion in the young stands. Furthermore, recent studies have shown that removal of the organic horizon did not significantly affect CH_4 oxidation in the soil under coniferous forests (Borken and Beese, 2006; Peichl et al., 2010). It is also suggested that CH_4 oxidation can be inhibited by organic compounds that are present in the organic horizons under coniferous stands (Amaral and Knowles, 1998). Thus, the soil methanotrophs in the S-69 might have been exposed to a higher level of inhibition from organic compounds

released from the well-developed organic horizon than in the O-70 supporting the significantly lower CH_4 oxidation in S-69 (Fig. 2b). This chemical inhibition of methanotrophs might not be as effective in the younger stands since it can be expected that the methanotrophic community is less well-developed than in the older stands (Prieme et al., 1997).

Even though no soil chemical or DIN fluxes at stand level could be significantly related to the plot average CH_4 fluxes the level of mineral N could still influence the dynamics of CH_4 uptake. It is widely recognised that soil mineral N inhibits microbial CH_4 uptake because of a competition between enzymatic turnover of mineral N species and CH_4 in the soil (e.g. Reay and Nedwell, 2004; Steudler et al., 1989). Ammonium has been suggested as an inhibitor of CH_4 oxidation in methanotrophic bacteria (Dunfield and Knowles, 1995) because the similarities between CH_4 and NH_4^+ may trigger a competition for the active site of the methane monooxygenase enzyme involved in the process. However, according to our extraction measurements of mineral N, NH_4^+ content was highest in O-70 (Fig. 4b) and inhibition by NH_4^+ do not fit well with our observations of CH_4 oxidation (Fig. 2b). Prolonged exposure to high levels of mineral N was suspected to inhibit certain genera of CH_4 oxidising soil bacteria and over time lead to different capacities to oxidise CH_4 in the soil (Borken et al., 2003). It was recently shown that methanotrophic diversity and abundance was lower in soils under Norway spruce than in soils under European beech (Degelmann et al., 2010). It could be hypothesised that the larger input of mineral N by atmospheric deposition in the soil under the S-69 stand (Hansen et al., 2007, Table 1) in combination with the organic compounds could function to inhibit methanotrophs in contrast to the O-70 stand thereby supporting the divergent development of CH_4 oxidation in the soil under oak and Norway spruce after the first four decades after afforestation (Fig. 2b).

5 Summary and conclusion

We found that N_2O emissions increased significantly with stand age of the forest, but there was no effect of tree species in the first four decades after planting. For CH_4 no effect of stand age or species was found but a significant interaction between tree species and stand age was found, e.g. CH_4 uptake increased in the soil under oak but remained constant under Norway spruce. Our results also showed that oak and Norway spruce stands affected the soil environment differently in the first four decades after planting with regard to both soil physical factors and nutrient status that regulated the emission of N_2O and the soil oxidation capacity of CH_4. However, in the period we measured, 15–17 years after planting N_2O emissions were low as well as the CH_4 oxidation rates. We attribute the small fluxes to low N availability because of high plant demand of N and restriction of diffusion by high bulk density and high soil moisture content in these recently afforested soils. In this first phase (between 17 to 40 years) of the forest establishment, as we studied, differences of N_2O and CH_4 exchange between oak and Norway spruce were not detected. Thus, we conclude that during the first four decades after planting of trees on former agricultural (1) increased N availability in the soil due to lower N demand from trees after four decades since afforestation supports higher N_2O emission from the soil in both oak and Norway spruce and (2) the soil bulk density decreases with time under both forest types enhancing the exchange of N_2O to the atmosphere and oxidation of CH_4 in the soil.

Supplementary material related to this article is available online at: http://www.biogeosciences.net/8/2535/2011/bg-8-2535-2011-supplement.pdf.

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