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REGULAR ARTICLE

# Variability of soil N cycling and $N_2O$ emission in a mixed deciduous forest with different abundance of beech

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**Abstract** The mixture of other broadleaf species into beech forests in Central Europe leads to an increase of tree species diversity, which may alter soil biochemical processes. This study was aimed at 1) assessing differences in gross rates of soil N cycling among deciduous stands of different beech (*Fagus sylvatica* L.) abundance in a limestone area, 2) analyzing the relationships between gross rates of soil N cycling and forest stand N cycling, and 3) quantifying $N_2O$ emission and determining its relationship with gross rates of soil N cycling. We used $^{15}N$ pool dilution techniques for soil N transformation measurement and chamber method for $N_2O$ flux measurement. Gross rates of mineral N production in the 0–5 cm mineral soil increased across stands of decreasing beech abundance and increasing soil clay content. These rates were correlated with microbial biomass which, in turn, was influenced by substrate quantity, quality and soil fertility. Leaf litter-N, C:N ratio and base saturation in the mineral soil increased with decreasing beech abundance. Soil mineral N production and assimilation by microbes were tightly coupled, resulting in low $N_2O$ emissions. Annual $N_2O$ emissions were largely contributed by the freeze-thaw event emissions, which were correlated with the amount of soil microbial biomass. Our results suggest that soil N availability may increase through the mixture of broadleaf species into beech forests.

**Keywords** Broadleaf tree species · Gross N mineralization · Gross nitrification · Litter quality · Microbial assimilation of N · Nitrous oxide emission · $^{15}N$ pool dilution

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## Introduction

Natural forest vegetation in Central Europe is unique due to the widespread occurrence of near-monospecific

beech forests in which this single species occupies 80–100% of the canopy area. In limestone areas of Central Europe, the use and management of beech forests often resulted in an mixture of different proportions of other broadleaf species and an increase of tree species diversity. Changes in tree species or even the mixture of species can have a pronounced influence on various chemical, physical, and biological soil properties due to species-specific differences in nutrient uptake, litter chemistry, root activity, canopy interception and growth (Alriksson and Eriksson 1998; Binkley and Giardina 1998). The composition of the forest canopy was shown to influence the understory vegetation (Mölder et al. 2008), soil nutrient status (Dijkstra 2003; Guckland et al. 2009), mineralization processes (Raulund-Rasmussen and Vejre 1995; Son and Lee 1997), soil acidity (Binkley and Valentine 1991; Reich et al. 2005), composition and activity of soil fauna and microflora (Saetre et al. 1999; Neirynck et al. 2000; Cesarz et al. 2007), and soil structure (Graham et al. 1995).

Soil nitrogen dynamics are directly affected by litter quality (e.g. Taylor et al. 1991; Prescott 2002; Inagaki et al. 2004; Miyamoto and Hiura 2008) and soil conditions (Bengtsson et al. 2003; Booth et al. 2005; Kooijman et al. 2008). Distinctive differences were found between conifers and hardwood species with regard to their effects on stocks, distribution and mineralization rates of soil N (Jerabkova et al. 2006; Joshi et al. 2006; Inagaki et al. 2004). In addition, $N_2O$ emissions were significantly higher in deciduous than in coniferous forests (Ambus et al. 2006; Butterbach-Bahl et al. 2002). Even within deciduous forests, differences in broadleaf species affect soil N dynamics through their differences in litter chemistry and their effects on soil chemistry. The dominance of broadleaf species in hemlock-hardwood stands was shown to increase the rate of net mineralization and nitrification as a result of improved litter quality (Ferrari 1999). Species-related differences in litterfall fluxes of elements (Ca, Mg, K, P and N) and in soil acidification were observed under canopies of different deciduous species (Nordén 1994a, b). Soil biology, especially earthworm biomass, was also influenced by deciduous tree species (Neirynck et al. 2000; Cesarz et al. 2007). In general, beech litter was found to decompose more slowly than the litter of other Central European deciduous tree species (Wise and Schäfer 1994).

From our previous study in a broadleaf mixed forest with beech, ash (*Fraxinus excelsior* L.), lime (*Tilia cordata* Mill. and/or *T. platyphyllos* Scop.), hornbeam (*Carpinus betulus* L.), and maple (*Acer pseudoplatanus* L. and/or *A. platanoides* L.), we found that surface soil acidity, C and N accumulation in the humus layer, and leaf litter C:N ratio increased with increasing abundance of beech (Guckland et al. 2009). Differences in the redistribution of nutrients and alkalinity via leaf litter were identified as important factors that contributed to this beech effect. These results suggest that the abundance of beech might also affect processes of soil N transformation in deciduous mixed forests and thus in N availability to plants and microbes. In the present study, we report on the soil N dynamics in this broadleaf mixed forest. Three stands with different beech abundance were studied. We hypothesized that soil N transformation rates and thus $N_2O$ losses increase with decreasing beech abundance. Our objectives were i) to assess differences in gross rates of soil N cycling among stands of different beech abundance, ii) to analyze the relationships between gross rates of soil N cycling and forest stand N cycling, and iii) to quantify $N_2O$ emission and assess its relationship with gross rates of soil N cycling. To our knowledge, this study is the first to investigate differences in soil N cycling across a range of beech abundance in a European mixed deciduous forest.

## Materials and methods

### Site description

The study was conducted in mature stands of deciduous forest in the Hainich National Park, Thuringia, Germany. The site has an elevation of 350 m a.s.l.. The mean annual temperature is 7.5°C and the mean annual precipitation is 670 mm. The geological substrate is Triassic limestone covered with 60–70 cm loess. The soil type is a Stagnic Luvisol (FAO (1998) classification) with some of the characteristics given in Table 1. The soil exhibits stagnic properties during winter and spring but is quite dry during summer. The forest has a history of at least 200 years. This has not been managed since 1990; before that time it had been used for military training since the 1960s. In 1997, it became a national

**Table 1** Soil properties at different depths of the stands with different beech abundance. Means (±1 SE) followed by a different letter indicate significant differences among stands (one-way ANOVA with Tukey HSD test at $P \leq 0.05$). Samples from 0 to 5 cm and 5 to 10 cm were taken directly from six plots established for $N_2O$ flux determination ($n=6$), and subsoil samples (10 to 20 cm and 20 to 30 cm) were taken from three points ($n=3$) of a 12 m×12 m grid established on each stand (Guckland et al. 2009)

| Stand | Beech abundance (% of tree basal area) | Soil depth (cm) | pH | Base saturation (%) | Texture (Clay/Silt/Sand)(%) | Bulk density (g $cm^{-3}$) |
|---|---|---|---|---|---|---|
| A | 89 | 0–5 | 4.5 (0.1)$^{b}$ | 48 (1)$^{b}$ | 15$^{c}$ / 82 / 3 | 0.8 (0.03) |
| | | 5–10 | 4.3 (0.02)$^{b}$ | 19 (1)$^{b}$ | 14$^{c}$ / 83 / 3 | 1.2 (0.1) |
| | | 10–20 | 4.2 (0.1)$^{c}$ | 19 (19)$^{b}$ | 14$^{c}$ / 83 / 3 | 1.3 (01) |
| | | 20–30 | 4.3 (0.1)$^{c}$ | 15 (3)$^{c}$ | 14$^{c}$ / 82 / 4 | 1.5 (0.1) |
| B | 59 | 0–5 | 5.4 (0.2)$^{a}$ | 91 (4.1)$^{a}$ | 23$^{b}$ / 75 / 2 | 0.9 (0.02) |
| | | 5–10 | 5.0 (0.2)$^{a}$ | 77 (7)$^{a}$ | 23$^{b}$ / 74 / 3 | 1.0 (0.2) |
| | | 10–20 | 5.2 (0.5)$^{b}$ | 71 (24)$^{a}$ | 21$^{b}$ / 77 / 2 | 1.2 (0.05) |
| | | 20–30 | 6.1 (0.6)$^{b}$ | 94 (6)$^{b}$ | 24$^{b}$ / 73 / 24 | 1.5 (0.04) |
| C | 42 | 0–5 | 5.7 (0.2)$^{a}$ | 97 (4.7)$^{a}$ | 31$^{a}$ / 66 / 3 | 1.0 (0.03) |
| | | 5–10 | 5.8 (0.3)$^{a}$ | 97 (1)$^{a}$ | 31$^{a}$ / 65 / 4 | 1.0 (0.1) |
| | | 10–20 | 5.8 (0.7)$^{a}$ | 94 (4)$^{a}$ | 32$^{a}$ / 65 / 3 | 1.3 (0.2) |
| | | 20–30 | 6.9 (0.3)$^{a}$ | 100 (0)$^{a}$ | 45$^{a}$ / 53 / 2 | 1.4 (0.1) |

park. Different forest ownerships have generated a small-scale stand mosaic of species-poor, beech-dominated forest patches and stands with up to 14 deciduous tree species per hectare that are all growing under similar climatic conditions on the same geological substrate (limestone covered by loess). Clay content in the upper 30 cm of the loess layer varied between 14 and 45%. Our study is a part of a long-term project on biogeochemical cycles and biotic interactions in stands with decreasing abundance of beech and conversely with increasing tree species diversity. Three stands were selected with decreasing beech abundance (expressed as percentage of total tree basal area, Table 1): stand A is dominated by beech (89% of the tree basal area), stand B is a three-species stand with beech (59%), ash (13%), and lime (19%) as predominant species, and stand C is covered with beech (41%), ash (31%), lime (15%), hornbeam (4%) and maple (9%) as dominant species. Soil clay content was higher in the mixed stands of deciduous tree species than in the beech-dominated stand (Table 1). All stands grow on nearly flat terrain (slope≤3%).

## Soil and litter sampling

In each stand, three transects were randomly selected and on each transect two plots (5×5 m each) were established, totalling to 6 plots per stand. Measurements of soil N cycling, $N_2O$ emissions and soil properties were conducted on these plots. The distance between plots in one stand ranged from 10 to 50 m. Gross and net rates of N transformation were determined in November 2006 and April 2007 using intact soil cores from the upper 5 cm of the mineral soil. Five soil cores (diameter of 8 cm, height of 5 cm) were taken with stainless-steel cylinders on each plot, with approximately 1 cm distance between cores. The cores were transported to the laboratory and stored at 4°C overnight prior to measurements the following day. Additional soil cores from 0 to 5 cm and 5 to 10 cm were taken at each plot for general physical and chemical characteristics. Leaf litter was collected starting from September 2005 to December 2005 at monthly intervals, described in detail by Guckland et al. (2009). Five litter collectors (surface area of 0.29 $m^2$) were randomly distributed along each of the three transects per plot. In addition, we sampled 12 points within a 12×12 m grid per stand using a circular frame (sampled surface of 300 $cm^2$) for measurements of total N and organic C in the organic layer with a frame.

## Analysis of leaf litter, organic layer and mineral soil

Leaf litter dry matter was determined gravimetrically after drying to constant mass at 60°C. Leaf litter from all

litter collectors of the same transect was combined resulting in three pooled samples per stand. These pooled samples were ground and analyzed for total C and N using CNS Elemental Analyzer (Elementar Vario EL, Hanau, Germany) and base cations (Ca and Mg) by pressure digestion in concentrated $HNO_3$ (König and Fortmann 1996) followed by analysis of the digests using Inductively Coupled Plasma-Atomic Emission Spectrometer (ICP-AES; Spectro Analytical Instruments, Kleve, Germany).

For the organic layer and mineral soil, total organic C and N from ground samples were determined as mentioned above. Soil pH was measured in a suspension with distilled $H_2O$ (5 g of soil to 15 mL of $H_2O$). Cation exchange capacity (CEC) of the mineral soil was determined by percolating 2-mm sieved soil samples with 100 ml of 1 M $NH_4Cl$ for 4 h (König and Fortmann 1996) and measuring cations in percolates using ICP-AES. Base saturation was calculated as percentage base cations (Na, K, Ca and Mg) of the CEC. Soil texture was determined using the sieving and pipette method (Schlichting et al. 1995). Soil bulk density was determined by soil core method.

## Gross N transformation rates, microbial biomass, and net N transformation rates

We used the $^{15}N$ pool dilution technique and calculation procedures as described in details by Davidson et al. (1991) and Hart et al. (1994). Two intact cores of each plot were injected with $(^{15}NH_4)_2SO_4$ solution (for gross N mineralization and $NH_4^+$ consumption rates) and another two cores were injected with $K^{15}NO_3$ solution (for gross nitrification and $NO_3^-$ consumption rates). Each soil core received five 1-mL injections, containing 25 μg N $mL^{-1}$ with 95% $^{15}N$ enrichment. One core of each labeled pair was broken up immediately, mixed in a plastic bag, and a subsample was extracted with 0.5 mol $L^{-1}$ $K_2SO_4$ solution (1:5 dry soil mass to solution ratio) ten minutes after $^{15}N$ injection ($T_0$). Mineral N extraction was done by shaking the samples for 1 hour and filtering them through $K_2SO_4$-prewashed filter papers. The $T_0$ cores were used to correct for the reactions that occur immediately after addition of $^{15}NH_4^+$ and $^{15}NO_3^-$. The other core of the $^{15}NH_4^+$-labeled pair was incubated for 1 day at 10°C ($T_1$). For the $^{15}NO_3^-$-labelled cores, a test conducted prior to measurement showed no detectable change in the $NO_3^-$ concentration and $^{15}NO_3^-$ after 1 day of incubation, and hence we incubated these cores for 2 days at 10°C ($T_1$). The $T_1$ cores were then extracted with 0.5 mol $L^{-1}$ $K_2SO_4$ as described above. Microbial assimilation of $NH_4^+$ was calculated as the difference between gross $NH_4^+$ consumption and gross nitrification rates (Davidson et al. 1991). Microbial assimilation of $NO_3^-$ was determined by the appearance of $^{15}N$ in the $CHCl_3$-labile microbial biomass, using the nonlinear model described by Davidson et al. (1991). About 25 g soil of the $T_1$ $^{15}NO_3^-$-labeled samples were fumigated with $CHCl_3$ for 5 days and then extracted with 0.5 mol $L^{-1}$ $K_2SO_4$ as described above.

Part of the extracts was used for analysis of $NH_4^+$ and $NO_3^-$ concentrations using continuous flow injection colorimetry (Cenco/Skalar Instruments, Breda, Netherlands). $NH_4^+$ was determined by Berthelot reaction method (Skalar Method 155–000) and $NO_3^-$ by copper-cadmium reduction method ($NH_4Cl$ buffer but without ethylenediamine tetraacetic acid; Skalar Method 461–000). The rest of the extracts was use for $^{15}N$ analysis by diffusion of $NH_4^+$ (from the $^{15}NH_4^+$-labeled cores) and of $NO_3^-$ (from the $^{15}NO_3^-$-labeled cores). For the fumigated $T_1$ $^{15}NO_3^-$-labeled samples, part of the extract was used for persulfate digestion for determination of $^{15}N$ enrichment in extractable organic N pool (Corre et al. 2007), needed for the calculation of microbial assimilation of $NO_3^-$. The same diffusion procedure and blank correction were followed as described in our earlier works (Corre et al. 2003; Corre and Lamersdorf 2004; Corre et al. 2007). $^{15}N$ was analyzed using isotope ratio mass spectrometry (Finigan MAT, Bremen, Germany).

Microbial biomass C and N were determined from the $T_1$ $CHCl_3$-fumigated and the corresponding unfumigated samples. Organic C content of the $K_2SO_4$ extracts was analyzed by UV-enhanced persulfate oxidation using a Dohrmann DC-80 carbon analyzer with an infrared detector (Rosemount Analytical Division, Santa Clara, California, USA). The organic N content of the extracts was determined by persulfate digestion (Corre et al. 2007), followed by colorimetric analysis of $NO_3^-$ (as above). Microbial biomass C and N were calculated as the difference in extractable organic C and persulfate-N between the fumigated and unfumigated soils divided by $k_C$=0.45 and $k_N$=0.68 for 5-day fumigated samples (Brookes et al. 1985).

The remaining one soil core was used to estimate net N mineralization and net nitrification rates. The soil in the core was cut vertically into two parts. One part was removed from the core ($T_0$) and the half that remained in the core was incubated for 14 days at 10°C ($T_1$). The $T_0$ and $T_1$ soil samples were extracted with 0.5 mol $L^{-1}$ $K_2SO_4$ solution and the extracts were analyzed for $NH_4^+$ and $NO_3^-$ contents as described above. Net N mineralization and nitrification rates were calculated as the difference between $T_1$-and $T_0$-$NH_4^+$ and $NO_3^-$ concentrations, respectively.

## Calculation of mean residence time

The mean residence time (MRT) specifies the average length of time an N atom resides in a given pool; a low MRT indicates a rapid turnover of the N pool. The calculation of MRT (N pool ÷ flux rate) assumes that the N pool is at steady state and that the flux is equal to the rate of input to that pool. MRT was calculated for the following N pools: a) total N in the organic layer using leaf litter-N as input flux rate, b) $NH_4^+$ and $NO_3^-$ pools in the 0-5 cm mineral soil using gross N mineralization and gross nitrification as input flux rates, respectively, and c) microbial biomass N using $NH_4^+$ + $NO_3^-$assimilation as input flux rate.

## $N_2O$ fluxes, soil temperature, moisture content, and extractable N

$N_2O$ fluxes were measured biweekly from September 2005 to September 2007. On each plot, one permanent chamber base (0.04 $m^2$ area, 0.15 m height, and inserted into the soil to 0.10 m depth) was installed three weeks before the start of measurements. Soil $N_2O$ fluxes were measured using vented static chambers (total volume 9.25 L). The cover was kept on the chamber base for one hour during which four gas samples were taken (0, 20, 40 and 60 minutes after closure) and stored in pre-evacuated glass containers with teflon-coated stopcock. Gas samples were analyzed using a gas chromatograph (GC 6000, Carlo Erba Instruments/ Thermo Fisher Scientific, Milan, Italy) equipped with an electron capture detector and an autosampler system (Loftfield et al. 1997). Gas fluxes were calculated from linear regression of concentrations versus time for each chamber, corrected with measured air temperature and air pressure (Ruser et al. 1998). Zero fluxes (no change in concentration) were included. During periods with snow cover (thickness of the snow cover was ≤10 cm) chambers were carefully installed on the base frames without removing the snow. The annual $N_2O$ losses were approximated by applying the trapezoid rule on time intervals between measured flux rates, assuming constant flux rates per day.

Simultaneous to $N_2O$ flux measurements, soil temperature (at 5 cm depth) was measured and soil samples were taken from 0–5 cm mineral soil (except from January to March 2006 when the ground was frozen) for measurements of soil moisture content and extractable N. Soil moisture content was determined gravimetrically by oven-drying at 105°C for one day and expressed as water-filled pore space (WFPS) using the measured bulk density and assuming a particle density of 2.65 g $cm^{-3}$ for mineral soil. Extractable N was determined from the soils extracted with 0.5 mol $L^{-1}$ $K_2SO_4$ and the extracts analyzed for $NH_4^+$, $NO_3^-$ (as above) and total N by continuous flow injection colorimetry (UV-persulfate oxidation followed by hydrazine sulfate reduction; Skalar Method 473-000).

## Statistical analyses

For soil N transformation rates, differences between the two sampling dates (November 2006 and April 2007) for each stand were tested using Paired-samples T test. If there were no significant differences between sampling dates, we used the means of both sampling dates for further analyses; if otherwise, analysis was conducted separately for each sampling date. We used Kruskal-Wallis H test with multiple comparison extension to assess differences among stands (A, B, and C) when assumptions of normality and homogeneity of variance were not met. For parameters that showed normal distribution and homogenous variance, differences among stands were evaluated using one-way analysis of variance with Tukey HSD test. Spearman rank correlation was used to test relationships among soil N cycling parameters and controlling factors. Linear regression analysis was conducted to relate gross rates of mineral N production in the soil to annual leaf litter N input and C:N ratio using the mean values per transect.

All tests were considered significant at $p \leq 0.05$ and were conducted with STATISTICA 7.1.

## Results

### Leaf litter, organic layer and mineral soil

The annual leaf litter input, concentrations and stocks of Ca, Mg and N, and leaf litter quality (C:N ratio) increased with decreasing beech abundance and increasing soil clay content. This was paralleled by decreasing mass, total N stocks and turnover time of total N pool in the organic layer (Table 2). Similarly, soil pH, base saturation (Table 1), concentrations and stocks of Ca, Mg and total N increased while C:N ratio decreased (Table 2) in the upper mineral soil with decreasing beech abundance. Clay content correlated with soil pH ($r$=0.82, $p$<0.01, $n$=18), base saturation ($r$=0.85, $p$<0.01, $n$=18) and total N ($r$= 0.87, $p$<0.01, $n$=18) in 0–5 cm mineral soil.

### Gross rates of N transformation, N pools and mean residence time of N pools

Gross rates of soil N transformation and N pools (except for $NH_4^+$) did not differ between sampling dates in all stands. Gross N mineralization rates in the 0–5 cm mineral soil increased with decreasing beech abundance (Fig. 1). These values result in annual gross N mineralization rates of 450, 700 and 1030 kg N $ha^{-1}$ $yr^{-1}$ for stands A, B and C, respectively, assuming constant rates throughout the year. Gross $NH_4^+$ assimilation rates were comparable and correlated with gross N mineralization rates (Fig. 1, Table 3). Gross nitrification rates were 5–14% of gross N mineralization rates, and also increased with decreasing beech abundance (Fig. 1). Gross nitrification rates were correlated with gross N mineralization rates, while microbial assimilation rates of $NO_3^-$ were correlated with and as high as gross nitrification rates (Fig. 1, Table 3). All N transformation processes were positively correlated with microbial N which, in turn, was positively correlated with total N, total C, pH and base saturation across stands (Table 3). Annual gross rates of N mineralization and nitrification were correlated with N input via leaf litter and leaf litter C:N ratio (Fig. 2).

$NH_4^+$ concentrations were lower in November 2006 than in April 2007, and in April 2007 $NH_4^+$

**Table 2** Dry mass, nutrient concentrations and nutrient stocks in the leaf litter, organic layer and 0–5cm mineral soil of the investigated stands with different abundance of beech. Means (±1 SE) followed by a different letter indicate significant differences among stands (one-way ANOVA with Tukey HSD test at $P \leq 0.05$)

| | Stand/ % beech | Dry mass | Ca | | Mg | | Total N | | C:N ratio | N turnover time[#] (year) |
|---|---|---|---|---|---|---|---|---|---|---|
| | | (Mg $ha^{-1}$) | (kg $Mg^{-1}$) | (kg $ha^{-1}$) | (kg $Mg^{-1}$) | (kg $ha^{-1}$) | (kg $Mg^{-1}$) | (Mg N $ha^{-1}$) | | |
| Annual leaf litterfall* ($n$=3) | A / 89 | $3.0^{b}$ (0.1) | $12.1^{c}$ (0.3) | $36.2^{c}$ (1.0) | $1.1^{c}$ (0.05) | $3.6^{c}$ (0.2) | $7.0^{c}$ (0.1) | $0.021^{c}$ (0.001) | $70^{a}$ (0.9) | |
| | B / 59 | $4.0^{a}$ (0.3) | $21.3^{b}$ (0.5) | $85.1^{b}$ (2.3) | $1.33^{b}$ (0.04) | $5.3^{b}$ (0.2) | $8.9^{b}$ (0.3) | $0.036^{b}$ (0.003) | $55^{b}$ (2.0) | |
| | C / 42 | $4.7^{a}$ (0.1) | $22.7^{a}$ (0.4) | $106.9^{a}$ (2.0) | $1.59^{a}$ (0.06) | $7.5^{a}$ (0.3) | $10.9^{a}$ (0.3) | $0.051^{a}$ (0.004) | $45^{c}$ (1.0) | |
| Organic layer ($n$=12) | A / 89 | $25.4^{a}$ (2.2) | n.d. | n.d. | n.d. | n.d. | $10.8^{b}$ (1.1) | $0.28^{a}$ (0.02) | 29 (1.1) | 13 |
| | B / 59 | $12.6^{b}$ (0.9) | n.d. | n.d. | n.d. | n.d. | $11.6^{ab}$ (1.3) | $0.15^{b}$ (0.01) | 29 (1.2) | 4 |
| | C / 42 | $7.4^{c}$ (0.6) | n.d. | n.d. | n.d. | n.d. | $12.5^{a}$ (1.6) | $0.09^{b}$ (0.01) | 27 (0.6) | 2 |
| 0–5cm mineral soil ($n$=6) | A / 89 | $461^{a}$ (39) | $0.66^{c}$ (0.1) | $0.3^{c}$ (0.03) | $0.05^{c}$ (0.01) | $0.02^{c}$ (0.01) | $1.7^{b}$ (0.1) | $0.8^{b}$ (0.01) | $18^{a}$ (0.8) | |
| | B / 59 | $411^{ab}$ (39) | $2.09^{b}$ (0.3) | $0.9^{b}$ (0.17) | $0.11^{b}$ (0.02) | $0.05^{b}$ (0.01) | $2.4^{ab}$ (0.1) | $1.1^{ab}$ (0.04) | $14^{b}$ (0.3) | |
| | C / 42 | $432^{b}$ (22) | $4.54^{a}$ (0.7) | $1.9^{a}$ (0.26) | $0.18^{a}$ (0.02) | $0.08^{a}$ (0.00) | $3.8^{a}$ (0.4) | $1.5^{a}$ (0.11) | $14^{b}$ (0.3) | |

* Data collected by M. Jacob, Department of Plant Ecology, University of Göttingen

[#] N turnover time in the organic layer was calculated by dividing mean N pool with the mean annual leaf litter-N input, assuming a steady state condition

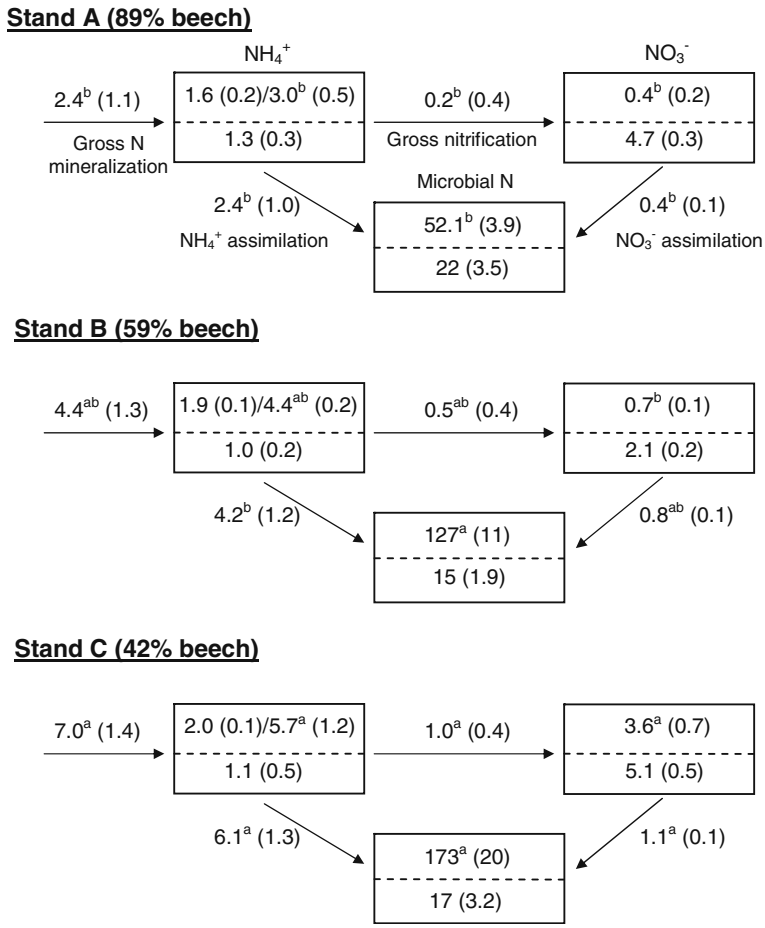


**Fig. 1** Gross rates of N transformation (mg N $kg^{-1}$ $d^{-1}$), N pools (mg N $kg^{-1}$, upper numbers in boxes) and mean residence time (d, lower numbers in boxes). For each parameter, means (±1 SE, $n$=6) followed by a different letter indicate significant differences among stands (Kruskal-Wallis H-test with multiple comparison extension at $p \leq 0.05$). $NH_4^+$ pool is given separately for November 2006 (first values) and April 2007 (second values) since for each stand these sampling periods differed (Paired-samples T-test at $p \leq 0.05$)

levels increased with decreasing beech abundance. $NO_3^-$ concentrations and microbial biomass N also increased with decreasing beech abundance. The $NH_4^+$ pool MRT was about 1 day, $NO_3^-$ pool MRT was 2–5 days, and microbial N MRT was 2–3 weeks; these did not differ among stands (Fig. 1).

## Net rates of N transformation

The net N release differed between the two sampling dates (Fig. 3). In November 2006, negative values of net N mineralization and nitrification rates (except for stand B, although this was not different from zero; One-sample T test at $p$=0.35) were observed in the 0-5 cm mineral soil, implying that microbial N assimilation exceeded mineral N production. In April 2007, we observed positive values of net rates of N transformation in all stands (Fig. 3). Net N mineralization and nitrification rates were negatively correlated with microbial C:N ratio ($r$=−0.47, $p$<0.05, $n$=36, and $r$=−0.42, $p$<0.05, $n$=36, respectively). The mean microbial C:N ratio across stands was significantly higher in November (9.2±0.8) than in April (7.8±0.4).

## $N_2O$ flux rates and soil factors

The emission rates of $N_2O$ ranged from −31.4 to 167.8 μg $N_2O$-N $m^{-2}h^{-1}$ but most (75%) of the measured fluxes did not differ from zero (Fig. 4a). The highest $N_2O$ emissions occurred between February and March 2006 when there was intermittent freezing and thawing of the soil. These emissions accounted 90%, 94% and 46% of the total emissions during the first year in stands A, B and C, respectively. Peak emissions during this freeze-thaw period were correlated with mean microbial biomass N ($r$=0.61, $p$<0.01, $n$=18). Annual $N_2O$ emissions increased with decreasing beech abundance (0.11±0.11, 0.19±0.16, and 0.40±0.23 kg $N_2O$-N $ha^{-1}yr^{-1}$ in stands A, B, and C respectively; $p$=0.02). Soil

**Table 3** Spearman rank correlation coefficients among gross rates of N transformations, N pool sizes and soil properties in 0–5 cm mineral soil ($n$=18)

| | $NH_4^+$ assimilation | Gross nitrification | $NO_3^-$ assimilation | $NH_4^+$ * | | $NO_3^-$ | Microbial N | Total N | Total organic C | pH | Base saturation |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Nov 2006 | Apr 2007 | | | | | | |
| | | mg N $kg^{-1}$ $d^{-1}$ | | | | mg N $kg^{-1}$ | | | mg C $kg^{-1}$ | | % |
| Gross N mineralization (mg N $kg^{-1}$ $d^{-1}$) | 0.89** | 0.50* | 0.66** | 0.14 | 0.11 | 0.67** | 0.61** | 0.72** | 0.59* | 0.60** | 0.60** |
| $NH_4^+$ assimilation (mg N $kg^{-1}$ $d^{-1}$) | | 0.42 | 0.77** | 0.02 | 0.13 | 0.55* | 0.63** | 0.62** | 0.55* | 0.54* | 0.51* |
| Gross nitrification (mg N $kg^{-1}$ $d^{-1}$) | | | 0.63** | -0.10 | 0.62** | 0.74** | 0.81** | 0.68** | 0.71** | 0.62** | 0.62** |
| $NO_3^-$ assimilation (mg N $kg^{-1}$ $d^{-1}$) | | | | 0.56* | 0.55* | 0.73** | 0.81** | 0.81** | 0.85** | 0.64** | 0.68** |
| $NH_4^+$ * Nov 2006 (mg N $kg^{-1}$) | | | | | 0.28 | 0.19 | 0.19 | 0.41 | 0.19 | -0.51* | 0.42 |
| $NH_4^+$ * Apr 2007 (mg N $kg^{-1}$) | | | | | | 0.54* | 0.60** | 0.45 | 0.51* | -0.46 | 0.40 |
| $NO_3^-$ (mg N $kg^{-1}$) | | | | | | | 0.68** | 0.78** | 0.87** | 0.65** | 0.72** |
| Microbial N (mg N $kg^{-1}$) | | | | | | | | 0.85** | 0.77** | 0.73** | 0.72** |
| Total N (mg N $kg^{-1}$) | | | | | | | | | 0.89* | 0.74** | 0.79** |
| Total organic C (mg C $kg^{-1}$) | | | | | | | | | | 0.61** | 0.67** |
| Soil pH | | | | | | | | | | | 0.97** |

* Correlation for $NH_4^+$ pool was conducted separately for the corresponding months because $NH_4^+$ levels differed between these sampling periods (Fig. 1)

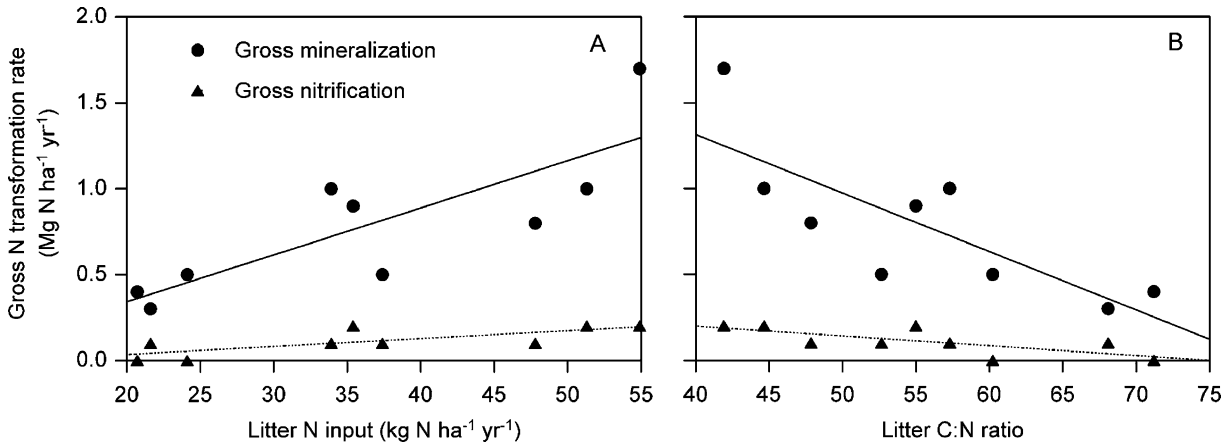


**Fig. 2** Regression analysis between annual gross N mineralization and nitrification rates using the mean values for each transect ($n$=9; three transects per stand) **a** annual leaf litter-N input (gross N mineralization=0.03x–2.6, $r^2$=0.61, $p$=0.007; gross nitrification=0.005x–0.06, $r^2$=0.51, $p$=0.018) and **b** leaf litter C:N ratio (gross N mineralization=−0.03x+2.7, $r^2$=0.56, $p$=0.012; gross nitrification=−0.01x+0.4, $r^2$=0.46, $p$=0.026)

extractable N was dominated by organic N (ranging from 8–14 mg N $kg^{-1}$ across stands) and constituted less $NH_4^+$ (3.4–4.0 mg N $kg^{-1}$) and $NO_3^-$ (0.9–2.0 mg N $kg^{-1}$); these did not differ among stands and exhibited no seasonal variability (Fig. 4b). We found no correlations between $N_2O$ flux rates and extractable N, WFPS (Fig. 4c) or soil temperature (Fig. 4d).

## Discussion

### Leaf litter quality and soil fertility

The increasing leaf litter N input and decreasing organic layer mass and N turnover time in the organic layer suggest faster litter decay across stands with decreasing beech abundance. The turnover time of litter N in the organic layer does not necessarily reflect litter mineralization since it does not provide information on the form and fate of C and N losses from the forest floor. The faster turnover of litter N in the organic layer of the mixed stands (stands B and C) than in the beech stand (stand A) can be explained by differences in litter quality. The higher recalcitrance of beech litter is probably due to the lower nutrient contents, higher C:N ratio (Table 2) and higher lignin:N ratio (Jacob et al. 2009; Jacob 2010) compared to litter of the other deciduous tree species. Lignin:N ratio is known to be a key factor determining dynamics of litter decomposition (Taylor et al. 1991; Scott and Binkley 1997; Goh

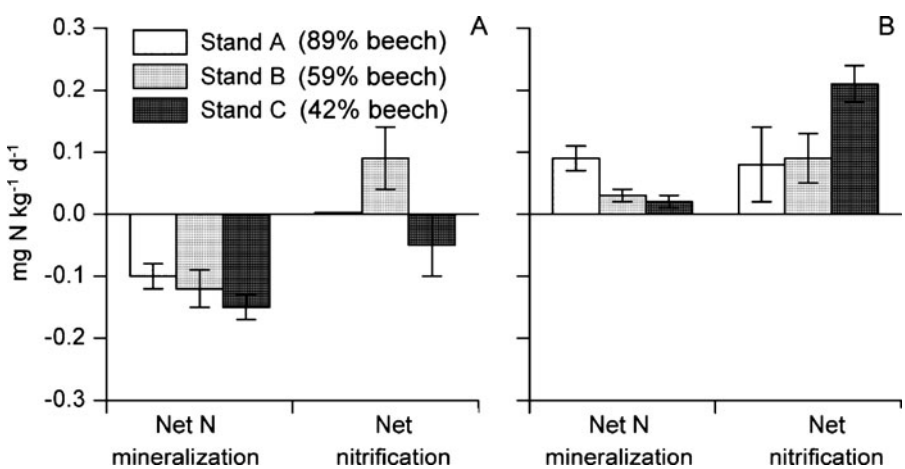


**Fig. 3** Net rates of N transformation in **a** November 2006 and **b** April 2007

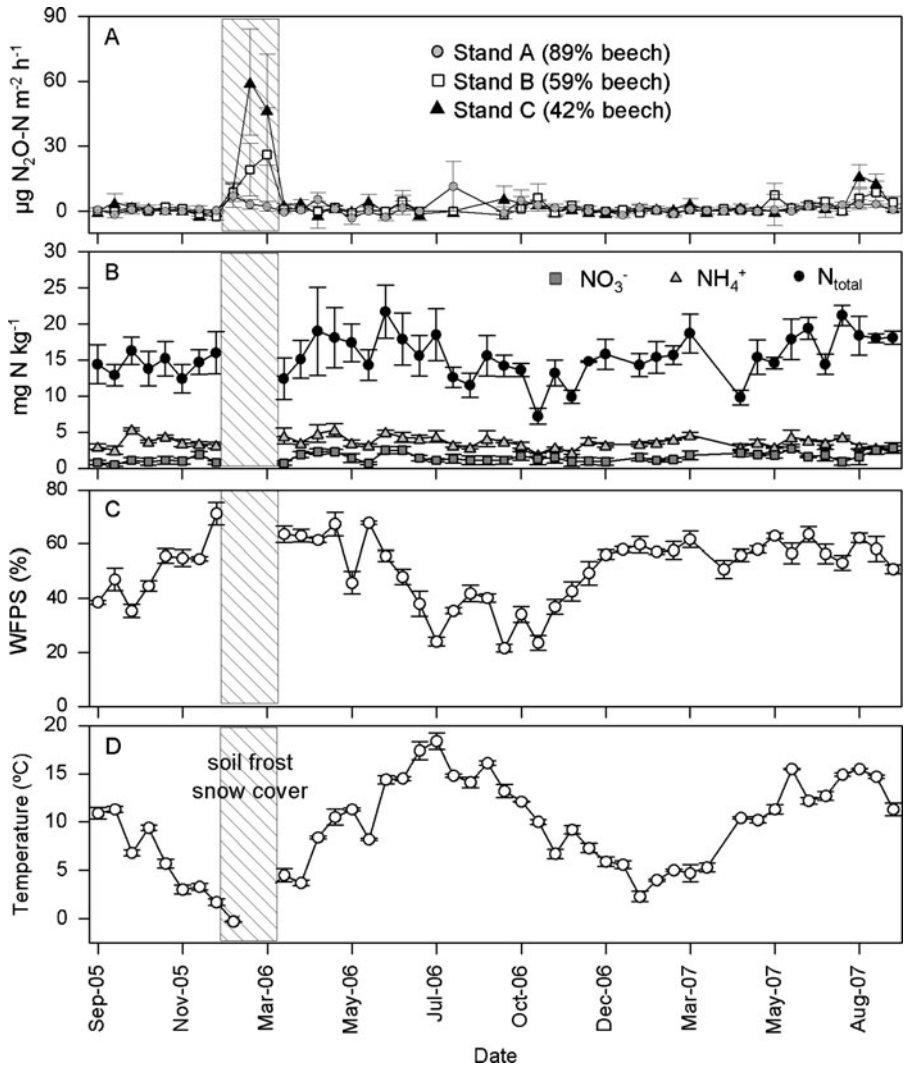


**Fig. 4** Means of **a** $N_2O$ fluxes (±1 SE, $n$=6), **b** extractable N, **c** water-filled pore space (WFPS), and **d** soil temperature at 0–5 cm mineral soil measured in stands with different abundance of beech during the 2-yr study period. Extractable N, WFPS and soil temperature are presented as means across the three stands ($n$=18) because these parameters did not differ among stands in all sampling dates. The hatched period represents the time with a continuous snow cover (thickness of snow cover was ≤10 cm)

and Totua 2004). Our findings supported other studies that showed beech litter decomposition to be slower than litter of other broadleaf tree species with the exception of oak (Wise and Schäfer 1994; Finzi et al. 1998; Neirynck et al. 2000). The increased leaf litter quality with decreasing beech abundance was also paralleled by increased soil fertility (i.e., low acidity, high base saturation, large stocks of Ca, Mg and N, and low C:N ratio) in the upper mineral soil. In a related study, we have shown that the abundance of beech and tree species-related differences in magnitude of soil-tree nutrient cycling have contributed to the differences in surface soil acidification and base cation stocks (Guckland et al. 2009). In their study, the influence of soil texture on the soil-tree nutrient cycling feedback could not be separated. The correlation of clay content with measures of soil fertility suggests that the higher clay contents in the mixed stands with high leaf litter quality may also have augmented the retention of nutrients released from litter decomposition. In view of these beech-related feedbacks on litter quality and soil biochemical conditions, we investigated how the microbially-mediated soil N transformation rates differ across sites of different beech abundance. We also like to point out that the analyzed stands differed in soil clay content and that it was not possible to clearly separate effects of clay content and beech abundance.

## Gross rates of N transformation

The gross N mineralization rates measured in this study were comparable to the rates measured in other

beech forests on Lithic Dystrochrept soils (Verchot et al. 2001; Geßler et al. 2005) and beech-oak forests on Dystric Cambisol soils (Bengtsson et al. 2003). Corre et al. (2003) reported lower gross $NH_4^+$ transformation rates in a Dystric Cambisol mineral soil under beech in Central Germany that has a more acidic soil and lower base cation stocks than our study site. Median gross rates of N mineralization in a mixed beech-oak stand on a Dystric Cambisol soil in Sweden were 2–6 folds higher than ours (Bengtson et al. 2006). Their large spatial variability was explained by tree species impact and variations in soil moisture and temperature.

Our study showed that the increasing gross N transformation rates with decreasing beech abundance were correlated with microbial N (Fig. 1, Table 3). In turn, microbial N was correlated with measures of soil fertility (Table 3), suggesting the indirect influence of soil biochemical conditions on gross N transformation rates. The high leaf litter quality and improved soil fertility supported larger microbial biomass in the mixed stands than in the beech stand (Fig. 1). The link between microbial biomass and gross N transformation rates is attributed to the role of microbial biomass size in driving the cycling of nutrients in the soil (Knops et al. 2002). In addition, the correlations among annual gross N mineralization and nitrification rates with annual leaf litter N input and leaf litter C:N ratio across stands (Fig. 2) also suggest the influence of substrate quantity and quality on gross rates of mineral N production. Thus, the increasing N availability (measured by gross N transformation rates) with decreasing beech abundance were influenced both by the increases in microbial biomass size and substrate availability.

Microbial assimilation of $NH_4^+$ was a larger fate of produced $NH_4^+$ than nitrification (Fig. 1). A similar $NH_4^+$-dominated soil N cycle was also reported by Bengtsson et al. (2003) and Corre et al. (2007) for different deciduous and spruce forests. Our results showed that nitrifiers were poor competitors for $NH_4^+$ and the produced $NO_3^-$ was largely assimilated by microbial biomass. Despite longer MRT of $NO_3^-$ than of $NH_4^+$ pool (Fig. 1), $NO_3^-$ concentrations were lower than $NH_4^+$ concentrations (Figs. 1 and 4). The closely-coupled $NH_4^+$ cycling, low rates and closely-coupled $NO_3^-$ cycling, and fast turn over of microbial biomass indicated efficient retention of mineral N in the soil.

## Net rates of soil N cycling did not reflect soil N availability

Net N transformation rates are the net result of the production and consumption of $NH_4^+$ and $NO_3^-$. The net assimilation of mineral N by microbial biomass (i.e., negative rates of net N mineralization and nitrification) observed in November 2006 was possibly due to a flash of C inputs from litterfall, setting high demand for microbial assimilation of N. Support for this comes from the high microbial C:N ratio in autumn, indicating high assimilation of C, and from the negative correlations between microbial C:N ratios and net N mineralization and nitrification rates. Low or absence of net release of mineral N in forest soils following litterfall in autumn was also observed in other beech stands (Gasche et al. 2002; Geßler et al. 2005). The net production (positive rates) of mineral N in April 2007 suggests low microbial consumption relative to production of mineral N. This was supported by the higher $NH_4^+$ concentrations in spring than in autumn (Fig. 1) and the high proportion of net nitrification to net N mineralization rates in the mixed stands with high $NH_4^+$ levels (Fig. 3). Studies have shown that microbial production and consumption of mineral N do not vary commensurately across seasons, which may result in unrelated net and gross rates of N transformation processes (Davidson et al. 1992; Corre et al. 2002). Our results suggest that the net N cycling rates were influenced by microbial consumption as driven by flashes of C input and did not reflect the patterns of soil N availability across stands.

## $N_2O$ emission

Annual $N_2O$ emissions from the different stands were generally low, which reflect the efficient retention of N through the closely-coupled soil N cycling in our sites. These values were comparable to the estimated $N_2O$ emission from deciduous forest soils in Germany with an average of 0.37 kg $N_2O$-N $ha^{-1}yr^{-1}$ (Schulte-Bisping et al. 2003). Studies have shown that emissions were smaller in coniferous stands than in broadleaf stands (Butterbach-Bahl et al. 1998; Butterbach-Bahl et al. 2002; Borken and Beese 2006), which were suggested to be caused by smaller gross rates of N mineralization and nitrification in

coniferous than broadleaf stands (Ambus et al. 2006). There is little information on the influence of different deciduous tree species on $N_2O$ emission. Our results show that increasing annual $N_2O$ emissions with decreasing beech abundance were related to the winter emissions during a freeze-thaw period. These emissions increased with the amount of soil microbial biomass.

It should be stressed that the observed differences in $N_2O$ emissions among stands originated from a short pulse of activity during intermittent freezing and thawing. The contribution of freeze-thaw $N_2O$ emissions to annual $N_2O$ loss supported previous findings in agricultural and forest ecosystems that frost periods are of crucial importance in estimating annual $N_2O$ emissions from temperate terrestrial ecosystems (Flessa et al. 1995; Papen and Butterbach-Bahl 1999; Teepe et al. 2000). Our results suggest that the magnitude of freeze-thaw $N_2O$ emissions might be influenced by the microbial biomass size, which increased with decreasing abundance of beech and increasing soil fertility. This claim is supported by the results of Papen and Butterbach-Bahl (1999) who showed that increased $N_2O$ emissions from forest soils during frost periods were fuelled by easily degradable substrate derived from dead microbial biomass. Sterilization experiments showed that $N_2O$ emissions during freeze-thaw cycles originate from microbial N transformation (Röver et al. 1998), and Teepe et al. (2001) pointed out that $N_2O$ production in frozen soil layers may originate from denitrification in thin liquid water films surrounding the soil matrix.

## Conclusions

This study has shown that abundance of beech in mixed deciduous forests can have a pronounced effect on the stand and soil N cycling. These effects of beech abundance have probably also been augmented by the coincidentally high clay contents in stands with low beech abundance. Across stands of decreasing beech abundance, leaf litter-N input, leaf litter quality, turnover time of total N pool in the organic layer, soil fertility and microbial biomass increased, which the latter in turn resulted to a positive feedback of N cycling in the mineral soil. Gross N transformation rates in the mineral soil increased with decreasing beech abundance. The produced $NH_4^+$ was largely assimilated by the microbial biomass. Net N cycling rates did not reflect the trends of gross N cycling rates because microbial production of mineral N did not vary commensurately with microbial consumption of mineral N across stands and seasons. Both $NH_4^+$ and $NO_3^-$ cycling were closely-coupled and resulted to an efficient retention of mineral N in the soil. This efficient N retention was reflected by the generally low $N_2O$ emissions. Annual $N_2O$ emissions were mainly contributed by the freeze-thaw event emissions, which were correlated with the amount of microbial biomass. Our results suggest that increasing the tree species diversity in beech stands growing on limestone areas by the mixture of valuable broadleaf tree species may enhance rates of N cycling in the stand and within the soil. Moreover, we like to point out that other factors, which were not addressed in this study, may influence net and gross rates of soil N turnover in stands with different deciduous tree species. Among those are for example tree species-dependent differences of rooting depth, light penetration through the canopy and timing of litterfall.

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