



Microbial nitrogen turnover in soils under different types of natural forest

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Abstract

Microbial nitrogen (N) turnover was compared among 12 forest stands with a natural vegetation composition. They comprised six typical forest types in the eastern part of Austria, including oak and beech forests, spruce–fir–beech forests, floodplain and pine forests. The aim was to provide a reference basis for measurements in managed, especially disturbed or damaged forest ecosystems. We measured total C- and N-concentrations in soil, extractable NO_3^- and NH_4^+ concentrations, microbial biomass N, nitrogen mineralisation potential and potential N_2O production in soil. As indicators of NH_4^+ availability and NO_3^- translocation into deeper soil horizons, accumulation of NH_4^+ and NO_3^- on resin bags was evaluated. Differences between the forest stands in potential N turnover were related to the size of the total N stores in soil and to vegetation composition. N mineralisation potential and microbial biomass were generally higher in the spruce–fir–beech, floodplain and pine forests with large N pools than in the oak and beech forests with lower N pools. Fastest N turnover was found in soils of a virgin spruce–fir–beech forest situated on nutrient-rich bedrock. Mineralisation potentials in these soils doubled averages in the other soils. N_2O production rates measured by an intact soil core-incubation method varied widely among the forest stands and were highest (up to $170 \mu\text{g N}_2\text{O-N m}^{-2} \text{h}^{-1}$) in soils of an oak–hornbeam and a woodruff–beech forest situated close to the city of Vienna, probably as a result of high atmospheric N input. Within the study sites, the soil moisture content was the factor mainly responsible for seasonal and microscale variability in N_2O production rates.

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1. Introduction

The capacity of forest soils for nitrogen (N) retention and transformation has recently received attention because of possible N enrichment of forest ecosystems following elevated atmospheric N deposition (Johnson,

1992; Abrahamsen and Stuanes, 1998). Excess N which cannot be held within the system may adversely affect the environment by leaching of nitrate into the groundwater or emission of N_2O into the atmosphere. Microorganisms occupy a dominant role in all major N cycling processes, and N uptake by soil microorganisms has been found to be critical for regulating the N balance of forest ecosystems (Stark and Hart, 1997; Zogg et al., 2000).

Rates of microbial N uptake and turnover may vary considerably among heterogeneous types of forest

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which exist within landscapes (Vitousek et al., 1982). It is well known that soil (Reich et al., 1997) and vegetation characteristics (Priha and Smolander, 1999; Wang and Fernandez, 1999) influence forest N cycling, but the understanding of the underlying soil–plant–microbial relationships is incomplete. Effects of plant species composition on forest N cycling are of particular relevance for measures in forest management, which typically involve alterations in soil and vegetation properties. By their influence on soil N cycling, management practices which favour certain species may improve ecosystem stability and resilience. Reintroduction of native tree species into degraded forests can promote soil nutrient cycling and may contribute to forest restoration.

Our objective was to observe forest type related effects on N cycling processes in forests with a natural vegetation composition. Several types of forest are present within a comparatively small area in the eastern part of Austria, where they form the natural vegetation cover in correspondence with site conditions. For the present study 12 forest stands were selected, representing six forest types, which include forests dominated by oak and beech as well as spruce–fir–beech forests, floodplain and pine forests. Our aims were: (1) to compare N pool sizes and N transformation rates in soils under different types of natural forest; (2) to examine how N losses via N_2O production were linked to environmental factors and to other N cycling properties; (3) to explore the relationships between vegetation characteristics, soil properties and microbial N processes in these forest ecosystems; (4) ultimately, by assessing the characteristics of the N cycling processes in natural forest stands, we strove to provide reference data for future investigations in managed, especially degraded or damaged forests.

2. Material and methods

2.1. Study sites and sampling design

The 12 forest stands studied include oak–hornbeam forests, woodruff–beech forests, acidophilous beech forests, spruce–fir–beech forests, floodplain forests and Austrian pine forests. These forest types comprise the zonale vegetation types found in the region (i.e. oak

and beech forests) and additionally include two azonale vegetation types typical of dry and wet sites (i.e. pine and floodplain forests). The zonale vegetation types are distributed along a thermal gradient: oak–hornbeam forests are favoured by warm and dry conditions and are succeeded by beech forests and further by spruce–fir–beech forests towards colder and wetter climates. Each forest type was represented by two stands. Site characteristics and the geographical location of the stands which are all situated in the eastern region of Austria are given in Table 1.

At all sites, the composition of the plant communities is considered to be natural, which means that it has not been changed by human interference. The sites Rothwald and Neuwald are virgin forests. Vegetation characteristics of the study sites are shown in Table 2. Soils were classified according to FAO nomenclature (1994), plant associations were determined by relevés and classified according to Mucina et al. (1993). Corresponding stands of the acidophilous beech forests, the floodplain forests and the pine forests have the same soil types, while those of the oak–hornbeam forests, the woodruff–beech forests and the spruce–fir–beech forests are found on different soil types.

Soils were sampled in spring and autumn 1997 and 1998. Within the forest stands, transects of 50 m were established. Ten soil samples were taken from the mineral layer (0–10 cm) at sampling points set at 5 m intervals. In addition, three intact soil cores (5 cm high, 7.5 cm diameter) were taken close to each sampling point, resulting in 30 soil cores per site and sampling date. At the different sampling dates, the transects were shifted 1 m forward to guarantee undisturbed sampling. The soil cores and the soil samples were taken to the laboratory in cooling boxes.

In spring 1998, resin bags containing ion-exchange resins (IER, 4 mg Dowex IX8 pract. and 4 mg Amberlite IR 120 pract.) were placed under soil cores (10.5 cm depth, 9 cm diameter) which were taken from each sampling point. The resin bags and the soil cores were enclosed in close-fitting PVC pots and were then returned to the same holes from which the cores had been taken. In autumn 1998, the resin bags were removed. Nitrate accumulated on the resins was analysed as a measure of nitrate translocation into deeper soil horizons. IER ammonium gave a measure of ammonium availability in the surrounding soil.

Table 1
Site characteristics of the forest stands under study^a

Forest type	Site ^b	Geographical location (latitude: N, longitude: E)	Elevation (m a.s.l.)	Annual climate data		Soil type	Geology
				Temp. (°C)	Ppt. (mm)		
Oak–hornbeam	JE	48°11'N, 16°13'E	325	8.8	643	Dystric Planosol	Laab formation
	K	47°58'N, 16°41'E	270	8.7	593	Calcaric Planosol	Micashist/limestone
Woodruff–beech	JB	48°11'N, 16°13'E	320	8.8	643	Dystric Planosol	Laab formation
	Kl	48°07'N, 16°03'E	510	7.6	768	Dystric Cambisol	Laab formation
Acidophilous beech	D	48°24'N, 15°32'E	500	7.6	613	Dystric Cambisol	Gföhl gneiss
	S	48°32'N, 15°33'E	550	7.4	631	Dystric Cambisol	Gföhl gneiss
Spruce–fir–beech	R	47°46'N, 15°07'E	1035	5.5	1759	Chromic Cambisol	Dolomite
	N	47°46'N, 15°32'E	995	5.8	1262	Stagnic Luvisol	Sandstone
Floodplain	M	48°00'N, 16°42'E	160	9.7	582	Calcaric Fluvisol	Recent clay
	B	48°08'N, 16°33'E	160	9.7	534	Calcaric Fluvisol	Recent clay
Austrian pine	St	47°53'N, 16°02'E	640	7.0	668	Rendzic Leptosol	Dolomite
	Me	47°59'N, 16°10'E	475	8.2	554	Rendzic Leptosol	Dolomite

^a Climate data include mean annual temperature (Temp.) and total annual precipitation (Ppt.) from long-term averages given by the Hydrographisches Zentralbüro im Bundesministerium für Land- und Forstwirtschaft (1994) and Harlfinger and Knees (1999).

^b JE: Johannser Kogel oak, K: Kolmberg, JB: Johannser Kogel beech, Kl: Klausen-Leopoldsdorf, D: Dürnstein, S: Saubrunn, R: Rothwald, N: Neuwald, M: Müllerboden, B: Beugenu, St: Stampftal, Me: Merkenstein.

2.2. Soil chemical and microbiological methods

The soil samples were stored at -20°C and prior to analysis were sieved to 2 mm. Percent total soil carbon (C_t) and total soil nitrogen (N_t) were analysed after dry combustion. Percent organic carbon (C_{org}) was calculated by subtracting carbonate content from C_t . Soil

pH was measured in CaCl_2 by glass electrode (soil:0.01 M $\text{CaCl}_2 = 1:5$). NH_4^+ -N was determined in 2 M KCl-extracts by a modified indophenol reaction according to Kandeler (1996a). NO_3^- -N in 2 M KCl-extracts was measured colorimetrically as NO_2^- -N after enzymatic reduction using the test kit by Mannheim–Boehringer (Cat. No. 1746081). For the

Table 2
Vegetation characteristics of the forests studied (for abbreviations of study sites see Table 1)

Site	Forest community	Main tree species
JE	Carpinion	<i>Carpinus betulus</i> L., <i>Quercus petraea</i> Liebl., <i>Quercus cerris</i> L., <i>Acer campestre</i> L., <i>Ulmus glabra</i> Huds
K	Carpinion	<i>Q. petraea</i> Liebl., <i>C. betulus</i> L., <i>Fagus sylvatica</i> L.
JB	Eu–Fagenion	<i>F. sylvatica</i> L., <i>C. betulus</i> L.
Kl	Hordelymo–Fagetum	<i>F. sylvatica</i> L.
D	Luzulo–Fagenion	<i>F. sylvatica</i> L.
S	Luzulo–Fagenion	<i>F. sylvatica</i> L.
R	Adenostylo glabrae–Fagetum	<i>F. sylvatica</i> L., <i>Abies alba</i> Mill., <i>Picea abies</i> Karsten
N	Cardamino trifoliae–Fagetum	<i>F. sylvatica</i> L., <i>A. alba</i> Mill., <i>P. abies</i> Karsten
M	Pruno–Fraxinetum	<i>Fraxinus excelsior</i> L., <i>Alnus glutinosa</i> Gaertn., <i>Prunus padus</i> L., <i>A. campestre</i> L., <i>Salix alba</i> L.
B	Fraxino–Populetum	<i>Populus alba</i> L., <i>Acer negundo</i> L., <i>F. excelsior</i> L.
St	Euphorbio saxatilis–Pinetum nigrae	<i>Pinus nigra</i> Arnold
Me	Euphorbio saxatilis–Pinetum nigrae	<i>P. nigra</i> Arnold

core-IER method (Binkley and Hart, 1989), the resin bags were extracted twofold with 1.59 M HCl. After neutralisation with NaOH, NO_3^- -N was measured colorimetrically as NO_2^- -N after reduction with copper sheathed granulated zinc (Kandeler, 1996d). NH_4^+ -N was determined according to Kandeler (1996a) as described above. Nitrogen mineralisation potential was determined by anaerobic incubation of soil samples for 7 days at 40 °C (Kandeler, 1996b). Microbial biomass N was analysed as ninhydrine-reactive N by a fumigation-extraction technique as described by Hackl et al. (2000b) and calculated as

ninhydrine-reactive N \times 3.1. Urease activity was measured according to Kandeler (1996c).

2.3. Gas flux measurements

The intact soil cores were stored at 4 °C for not more than 4 days. After adjustment to room temperature they were incubated for the measurement of N_2O and CO_2 production. Each soil core was enclosed in a 500 ml gas-tight glass-jar and kept at 25 °C for 24 h in 1997 and for 6 h in 1998, after ensuring that increases in concentration were linear (Fig. 1a and b). At the

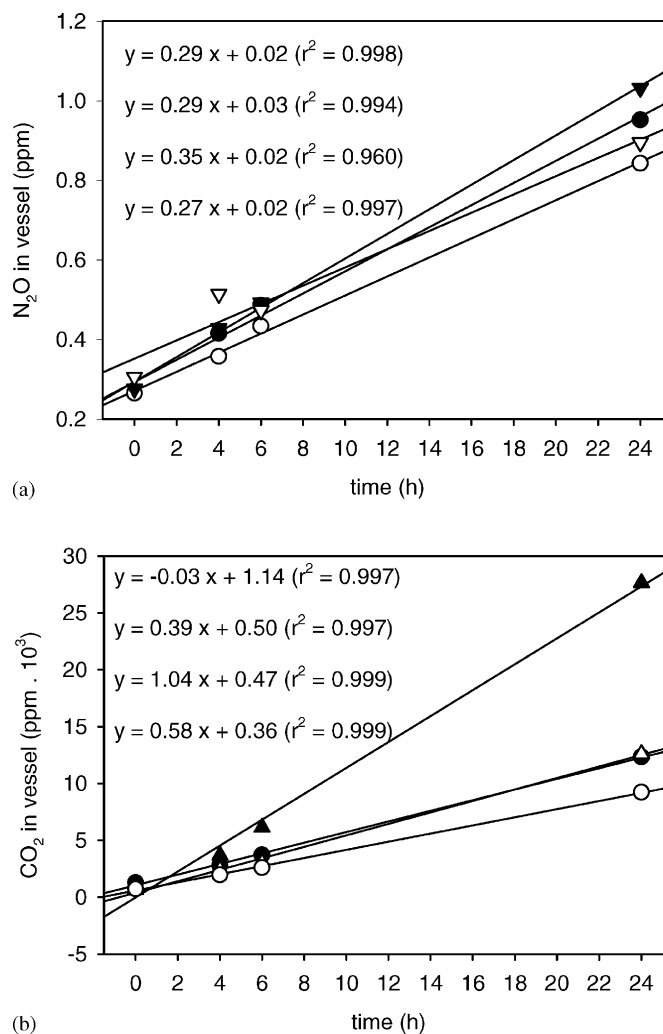


Fig. 1. Regression analyses of N_2O (a) and CO_2 (b) production rates from soils of four representative soil cores of the sampling site “Klausen-Leopoldsdorf” measured at intervals of 4, 6 and 24 h. Regression equations are set in the order of the values at 24 h.

beginning and at the end of the incubation period gas samples were taken. With a gas-tight syringe, head space air of the vessels was transferred into evacuated 10 ml glass vials which were then stored under water until analysis. Gas samples were analysed by gas chromatography using a ^{63}Ni electron capture detector for N_2O (injector: 120 °C, detector: 330 °C, oven: 30 °C, carrier gas: N_2 ; Zechmeister-Boltenstern, 1994) and TCD for CO_2 (injector: 60 °C, detector: 150 °C, oven: 80 °C, carrier gas: helium).

2.4. Statistical analysis

Statistica 5, Version 97 was used for statistical processing of data. As homogeneity of variances of the data was not ensured, the non-parametrical Mann–Whitney U -test was used to test for significant differences in soil chemical and soil microbiological parameters among sampling dates, forest types and sites. Correlations between N_2O production rates and soil chemical and microbiological variables were determined using Spearman's rank correlations.

Stepwise linear regression analyses were used to explore the relationships between nitrogen transformation rates, forest type and soil variables and between plot means of N_2O production rates and soil variables. For this procedure, N_2O production rates

were log-transformed whenever data were not normally distributed.

3. Results

Soil chemical data of the 12 forest soils were in a wide range and are presented in Table 3.

Nitrogen mineralisation potential and urease enzyme activity were measured as indicators of microbial N transformation. Both parameters were positively correlated with the amount of microbial biomass N ($r^2 = 0.71$ and 0.69 , respectively; $P < 0.05$), which indicates the size of the microbial N pool.

The interplay of microbial biomass N, N mineralisation potential and urease enzyme activity gave evidence that gradual differences existed among the forest stands in potential N turnover (Table 4). In the N-rich soils of the floodplain forests and the spruce–fir–beech stand Rothwald potential N mineralisation rates were significantly higher (up to $31.2 \mu\text{g NH}_4\text{-N g}^{-1}$ per day) than in the other forest soils and urease activity was also high (up to $122.7 \mu\text{g NH}_4\text{-N g}^{-1} \text{ h}^{-1}$). These soils contained large amounts of microbial biomass N, reaching up to $241.3 \mu\text{g N g}^{-1}$. In the pine forest soils, the content of microbial biomass N was also high (261.0 and $163.5 \mu\text{g N g}^{-1}$), while mineralisation rates were somewhat lower (17.3 and

Table 3
Soil chemical and microbial characteristics of the forest stands studied^a

Forest type	Site	pH (CaCl_2)	Organic C (%)	Total soil N (%)	C/N	Resin bag (mg m^{-2} per day)	
						$\text{NO}_3\text{-N}$	$\text{NH}_4\text{-N}$
Oak–hornbeam	JE	4.2 ± 0.2	5.04 ± 0.34	0.22 ± 0.01	23.4 ± 0.6	n.d.	n.d.
	K	5.2 ± 0.3	4.23 ± 0.21	0.20 ± 0.01	21.0 ± 0.4	17.7 ± 14.7	1.91 ± 0.7
Woodruff–beech	JB	4.6 ± 0.1	4.38 ± 0.31	0.19 ± 0.01	22.5 ± 0.8	n.d.	n.d.
	KI	4.0 ± 0.0	4.36 ± 0.32	0.33 ± 0.02	13.1 ± 0.4	27.0 ± 3.5	0.48 ± 0.3
Acidophilous beech	D	4.6 ± 0.1	9.45 ± 1.34	0.35 ± 0.04	26.9 ± 0.7	20.5 ± 4.2	0.78 ± 0.3
	S	3.2 ± 0.0	7.03 ± 0.56	0.30 ± 0.02	23.5 ± 0.5	7.1 ± 2.6	1.39 ± 0.6
Spruce–fir–beech	R	5.3 ± 0.4	16.00 ± 2.38	0.94 ± 0.15	17.1 ± 1.1	37.5 ± 3.7	0.99 ± 0.4
	N	3.8 ± 0.1	6.46 ± 0.63	0.38 ± 0.03	16.9 ± 0.7	22.5 ± 2.1	0.42 ± 0.1
Floodplain	M	6.9 ± 0.0	5.46 ± 0.34	0.47 ± 0.02	11.7 ± 0.4	21.9 ± 2.8	0.03 ± 0.0
	B	7.0 ± 0.0	3.92 ± 0.13	0.23 ± 0.01	17.2 ± 0.5	18.6 ± 9.3	0.05 ± 0.0
Austrian pine	St	7.2 ± 0.1	16.99 ± 2.69	0.61 ± 0.09	28.0 ± 1.0	11.7 ± 2.1	0.46 ± 0.2
	Me	7.2 ± 0.0	9.64 ± 0.63	0.26 ± 0.02	37.0 ± 2.0	8.4 ± 1.4	0.10 ± 0.0

^a Values represent means of 10 subsamples (\pm S.E.). For abbreviations of study sites see Table 1.

Table 4

Microbial nitrogen mineralisation potential, urease activity and microbial biomass nitrogen in soils of the forest stands studied^a

Forest type	Site	N mineralisation potential ($\mu\text{g NH}_4\text{-N g}^{-1}$ per day)	Urease activity ($\mu\text{g NH}_4\text{-N g}^{-1} \text{h}^{-1}$)	Microbial biomass N ($\mu\text{g N g}^{-1}$)
Oak–hornbeam	JE	12.47 (1.74) de	43.17 (3.92) d	39.37 (8.02) ef
	K	15.01 (2.69) cde	57.92 (7.52) d	90.16 (14.43) cd
Woodruff–beech	JB	9.57 (0.83) e	54.70 (3.74) d	64.40 (11.37) de
	KI	11.54 (1.86) de	82.91 (9.06) abc	110.81 (11.95) c
Acidophilous beech	D	8.77 (0.84) e	51.36 (6.56) d	101.35 (16.61) c
	S	1.81 (0.24) f	24.28 (2.65) e	29.46 (4.10) f
Spruce–fir–beech	R	31.16 (7.24) ab	122.65 (25.05) ab	241.27 (49.99) ab
	N	15.29 (0.54) c	56.03 (6.96) cd	86.22 (10.25) cd
Floodplain	M	21.85 (1.14) b	102.56 (5.33) a	175.47 (12.33) ab
	B	26.93 (2.33) a	70.15 (2.80) bc	154.89 (7.77) b
Austrian pine	St	17.29 (2.22) cd	99.22 (17.72) ab	260.97 (45.36) a
	Me	14.88 (1.57) cd	63.15 (4.37) bc	163.46 (18.63) ab

^a Values represent means of 10 subsamples (S.E.). Different letters indicate significant differences between sites at $P \leq 0.05$. For abbreviations of study sites see Table 1.

14.9 $\mu\text{g NH}_4\text{-N g}^{-1}$ per day). Soils of the floodplain and the pine forests as well as the spruce–fir–beech forest Rothwald contained significantly higher amounts of microbial biomass N than the soils of the other forests which were mainly composed of beech and oak. In the oak and beech forests, also N turnover was generally slower. The slowest N turnover rates were measured in soils of an acidophilous beech forest (Saubrunn), which showed low mineralisation and urease activity (1.8 $\mu\text{g NH}_4\text{-N g}^{-1}$ per day and 24.3 $\mu\text{g NH}_4\text{-N g}^{-1} \text{h}^{-1}$, respectively) as well as a small microbial N pool of only 29.5 $\mu\text{g N g}^{-1}$. Soils of this site were most acidic and poor in nutrients.

Microbial N parameters were all affected by the size of the total N store: N mineralisation potential, microbial biomass N and urease activity were significantly correlated with total soil N ($r^2 = 0.64, 0.67$ and 0.51 , respectively) at $P < 0.05$. By regression analysis of microbial N parameters the following regression equations were obtained at $P < 0.05$:

- microbial biomass N = 0.277 N mineralisation potential + 0.635 total soil N ($r^2 = 0.730$);
- urease activity = 0.409 N mineralisation potential + 0.464 N total soil N ($r^2 = 0.653$);
- N mineralisation potential = 0.444 biomass N + 0.344 total soil N ($r^2 = 0.569$).

As indicators of on site-N processes, accumulation of NO_3^- and NH_4^+ on IER bags was measured (Table 3). No data are available for the Johannser Kogel sites, because the resin bags were destroyed by wild boars. The amount of IER-nitrate gives a measure of NO_3^- availability as well as NO_3^- translocation through the upper soil horizon and was greatest in the spruce–fir–beech forest Rothwald. In all forest soils, even the acidic beech forest soils and the pine forest soils, considerable amounts of NO_3^- were found on the resin bags. NH_4^+ availability was high in the acidic beech forest soils and the Rothwald and was very low in the floodplain forests.

Huge differences existed between the forest sites in concentrations of KCl-extractable NO_3^- and NH_4^+ (Fig. 2). In soils of the acidophilous beech forests, mineral N was strongly dominated by ammonium, and nitrate concentrations were always low. At somewhat lower ammonium concentrations, nitrate was also low in soils of the pine forests. Soils of the floodplain forests, by contrast, were high in nitrate and low in ammonium. In the oak–hornbeam and the woodruff–beech forests, varying concentrations of soil nitrate and ammonium were measured. Highest concentrations of mineral N were found in the spruce–fir–beech forest Rothwald.

Nitrous oxide (N_2O) production rates at the four sampling times are presented in Fig. 3. At nearly all

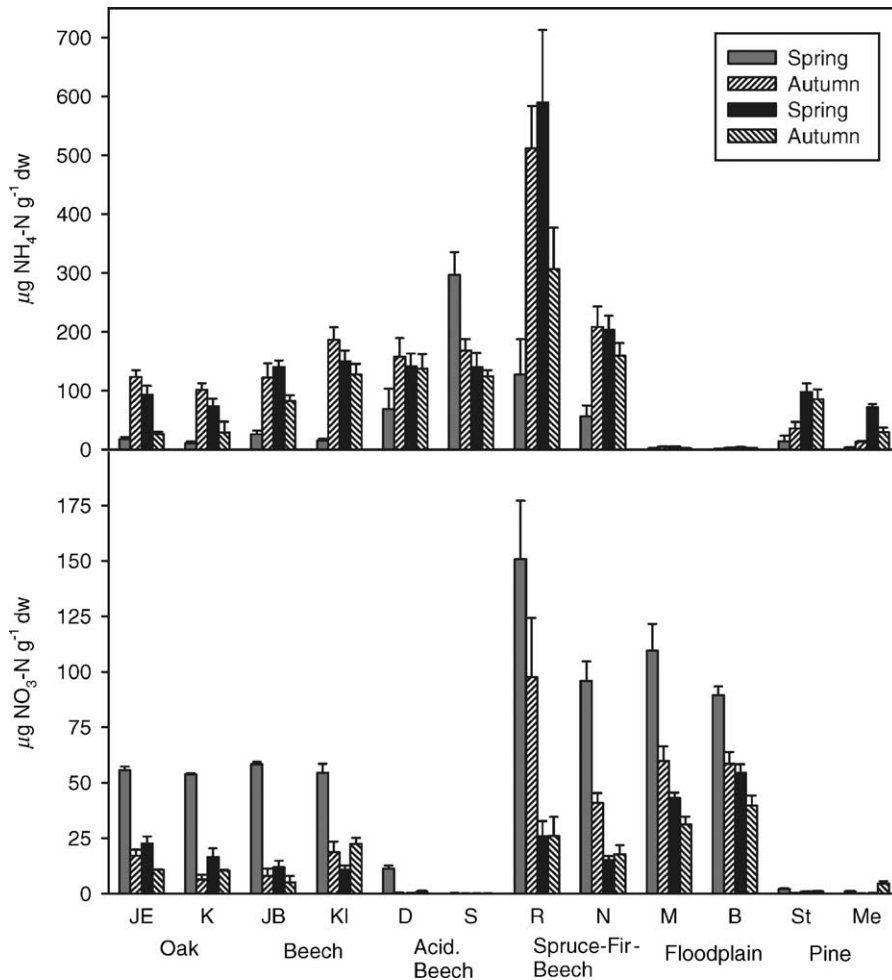


Fig. 2. Concentrations of KCl-extractable ammonium and nitrate in the soils of the 12 forest stands studied. Measurements were done in spring and autumn of two subsequent years. Mind the different scaling of the axes. Values represent means of 10 subsamples, error bars are standard errors. Each forest type (oak, beech, acidophilous beech, spruce–fir–beech, floodplain and pine forest) is represented by two study sites.

sites, N_2O production rates varied considerably across the seasons. Only in soils of the spruce–fir–beech forest Neuwald N_2O production rates were relatively uniform at the four sampling times. Significant differences in N_2O production rates between the sampling times at the individual sites are indicated by different letters in Fig. 3.

Throughout the sampling period, N_2O production rates were low in soils of the acidophilous beech forests and the Austrian pine forests, which also had low soil nitrate concentrations. Lowest N_2O production occurred in soils of the pine forest Stampfltal.

In 1997 N_2O production rates from soils of this site were significantly lower than those measured in soils of the other sites. In 1998 they were significantly different from all other sites except the other pine forest, Merkenstein, and in autumn also the acidophilous beech forest Dürnstein. N_2O production rates from soils of the spruce–fir–beech forests ($4.3\text{--}39.4 \mu\text{g } N_2O\text{-N m}^{-2} \text{ h}^{-1}$) were of similar magnitude as from soils of the floodplain forests ($1.75\text{--}57.08 \mu\text{g } N_2O\text{-N m}^{-2} \text{ h}^{-1}$). Highest N_2O production up to $170 \mu\text{g } N_2O\text{-N m}^{-2} \text{ h}^{-1}$ occurred in soils of an oak–hornbeam forest and a woodruff–beech forest

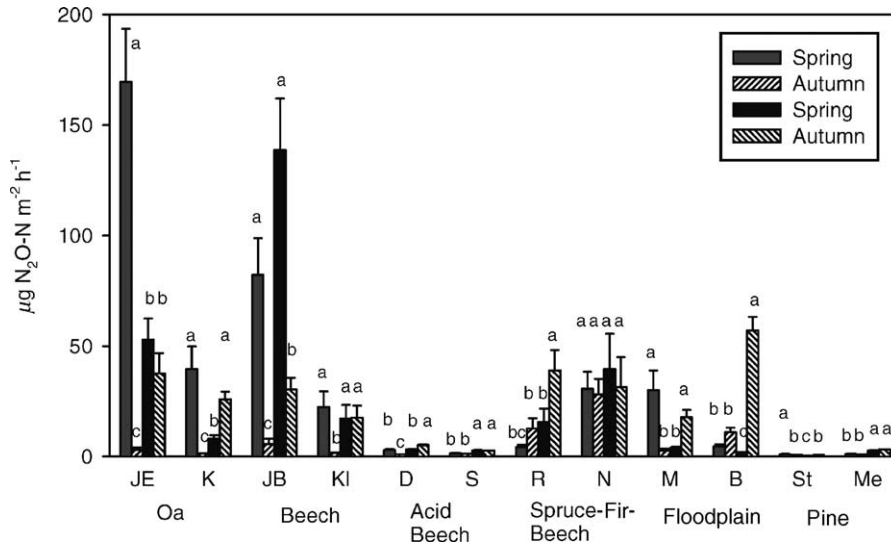


Fig. 3. Potential N₂O production in soils of the 12 forest soils studied. Measurements were done in spring and autumn of two subsequent years. Values are derived from means of 30 soil cores, error bars represent standard errors. Different letters indicate significant differences between sampling dates within sites at $P \leq 0.05$. For abbreviations of forest types see Fig. 2.

situated on the mountain Johannser Kogel (Fig. 3). In spring 1997, N₂O production rates were significantly higher from soils of the oak–hornbeam forest Johannser Kogel than from all other forest soils. N₂O production rates from the woodruff–beech forest differed from those of the oak–hornbeam forest

but nevertheless were significantly higher than N₂O production rates from soils of the other sites. In spring 1998, N₂O production rates were highest from soils of this woodruff–beech forest, when significantly lower rates were measured in all other forest soils.

Table 5

Spearman’s rank correlation coefficients between N₂O production rates and soil chemical parameters within individual sampling sites, including data from all sampling dates (only significant correlations are shown)

Forest type	Site	Soil moisture	pH	NO ₃ -N	CO ₂
Oak–hornbeam	JE	0.784****		0.580***	
	K	0.765****		0.476**	
Woodruff–beech	JB	0.806****		0.388*	
	KI	0.637****			
Acidophilous beech	D				0.652****
	S		0.809****	−0.472**	0.688****
Spruce–fir–beech	R		−0.345*		0.447**
	N				
Floodplain	M	0.569***			
	B	0.576***		0.352*	0.389*
Austrian pine	St		0.375*		−0.390*
	Me	0.666****	−0.637****	0.483**	0.683****

* $P < 0.05$.
 ** $P < 0.01$.
 *** $P < 0.001$.
 **** $P < 0.0001$.

While at the two sites representing a singular forest type N_2O production rates were significantly different at most sampling occasions, they were influenced by soil parameters in a similar way (Table 5). For instance, N_2O production was mainly influenced by soil moisture and soil nitrate in soils of the oak–hornbeam and the woodruff–beech forests and was highly correlated with CO_2 production in soils of the acidophilous beech forests. In soils of the floodplain forests, N_2O production was strongly influenced by soil moisture.

4. Discussion

4.1. Microbial N transformation

Gradual differences existed in potential nitrogen turnover across the 12 forest stands (Table 4). It appeared that differences in N transformation rates were related both to the size of the total N stores in soil and to vegetation composition. An overall feature of our results was that the microbial biomass was not equally efficient in transforming and immobilising N at sites of varying N supply.

It is generally assumed that N cycling is more rapid on N-rich forest sites, because vegetation on these sites produces litter with higher N-concentrations. Consequently, N availability on N-rich sites successively increases while it decreases on poor sites (Gosz, 1981; Prescott et al., 2000). In support of this hypothesis, the highest soil N content as well as highest microbial N transformation rates were measured in the spruce–fir–beech stand Rothwald. Extractable N in these soils was extraordinarily high (127–589 and 26–151 $\mu\text{g NO}_3\text{-N g}^{-1}$), and mineralisation potentials doubled averages in the other soils (31.2 $\mu\text{g N g}^{-1}$ per day versus 14.1 $\mu\text{g N g}^{-1}$ per day). Microbial biomass was 2.5 times higher than averages in the other soils. Soils of this site were the most nutrient-rich of all, which is partly an effect of the geological substrate, dolomite. Lower nutrient concentrations as well as lower N transformation rates were found in soils of the other spruce–fir–beech stand, Neuwald, which is situated on sandstone with slow nutrient release.

The Rothwald site is part of Austria's largest virgin forest area. There, nitrogen availability may be generally high due to effects of stand age, causing lower N

uptake by trees in mature versus younger forests (Johnson, 1992), and to long-term nutrient accumulation in the absence of harvesting. Since precipitation is typically high in this montane forest, microbial processes may be particularly favoured by the high soil water content. Thus, stand history and climatic conditions may further contribute to the high N supply and turnover in soils of the Rothwald site.

Except for the Rothwald site, which was characterised by outstanding site conditions, forests of the same forest type showed similarities in their N cycling properties. Previous studies on forest N cycling have found that microbial N transformations were associated with vegetation properties. N transformation rates and the content of microbial biomass were higher in soils of birch stands than in soils of spruce and pine stands (Priha and Smolander, 1999). At a smaller local scale, aspects of forest vegetation dominated by sugar maple were characterised by higher soil N availability than aspects dominated by oak and beech (Peterjohn et al., 1998). The varying quality and degradability of the leaf litter of different tree species were mainly regarded as the underlying causes for these findings.

In deciduous forests, lower rates of litter decomposition are commonly observed from oak and beech than from elder, ash, maple or cherry trees (Mayer, 1984). This might explain why soil N contents and N turnover rates were lower in the oak and beech forests than in the floodplain forests, which were mainly composed of ash, elder, maple and poplar trees. Soils of the floodplain forests were rich in organic material, originating from episodic flooding events. In addition to the nutrients returned by fast litter decomposition, high allochthonous C-supply may provide favourable conditions for soil microorganisms, resulting in high microbial biomass values and fast nutrient turnover.

In spite of the higher litter quality commonly attributed to deciduous than to coniferous tree species (Stump and Binkley, 1993; Priha and Smolander, 1999), N mineralisation rates were lowest in the oak and beech forests and not in those forests dominated by coniferous tree species, i.e. the pine forests. While coniferous forest soils are often characterised by low soil pH (Sjöberg and Persson, 1998; Ross et al., 1999), the two pine forests in the present study are situated on nutrient-rich dolomite, resulting in high soil pH values. Probably, the high soil pH at these sites renders conditions more favourable for litter

decomposition and mineralisation than otherwise observed for pine-litter. While in situ-N mineralisation might be hampered by the low soil water content of the pine forest soils, mineralisation potentials are likely to display higher values, since they are measured under water-saturated conditions. As indicated by amounts of sugars and amino acids in the soil organic matter, substrate availability for microorganisms was especially high in the pine forest soils (Hackl et al., 2000b), which were restricted to only a small layer wherein microbial activity and soil nutrients were concentrated. Thus, high substrate availability may be responsible for the fast N turnover in these soils.

Beside differences in microbial N turnover, the efficiency of N uptake by herbaceous plants varied among the forest stands. This was revealed by data on nitrate accumulation on IER, which represents the amount of nitrate percolating through the upper soil horizon with the soil water (Binkley and Hart, 1989). In spite of the low content of extractable soil nitrate at the acidophilous beech stand Dürnstein, considerable amounts of nitrate were translocated onto the resin bags. This was probably a result of low microbial N immobilisation as well as low N uptake by the scarce herbaceous layer at this site. By contrast, nitrate seemed to be effectively retained by microorganisms and plant roots in the floodplain forests, which had large microbial biomass pools and a dense undergrowth-vegetation.

4.2. N_2O production

Potential N_2O production from soil was measured to make clear how much nitrogen was prone to losses as gas. Additionally, nitrate concentrations in topsoil were determined. Nitrate may easily be leached into deeper soil horizons or be lost as N_2O during denitrification. In soils of two forest types—the acidophilous beech forests and the pine forests—only small amounts of nitrate were produced, so that almost all mineralised nitrogen remained in the immobile ammonium form. Accordingly, neither of these forest types showed any significant N_2O production during the study.

The acidophilous beech forests were generally poor in nitrogen, which is indicated by low mineralisation rates and small microbial N pools. The pine forests, by contrast, had rather high mineralisation potentials.

While in many coniferous forest soils nitrate production by autotrophic nitrification is hampered by low soil pH (Persson et al., 1989), conditions in these pine forest soils were not unfavourable to autotrophic nitrifiers. However, nitrifiers are typically weak competitors for available ammonium against heterotrophs and plant roots (Van Miegrot et al., 1992). Thus, we assume that plant roots and heterotrophic decomposers were highly efficient in immobilising ammonium in these soils, and thereby retained N within the system. High contents of microbial biomass in the pine forest soils may be indicative of a high capacity for microbial N uptake. N cycling has also been considered tight in a Siberian *Pinus sylvestris* forest, where N was rapidly metabolised and only trace amounts of nitrate were produced (Ross et al., 1999).

Comparing N_2O production rates from the 12 forest sites, we found that only those soils, which were generally high in nitrate, had a potential for significant N_2O production. Highest N_2O production rates were produced in soils of an oak–hornbeam and a woodruff–beech stand situated on the mountain Johannser Kogel. High N_2O production at the Johannser Kogel stands may be caused by high atmospheric N input, because the stands are located close to the city area of Vienna and thus are directly exposed to high N loads. High N_2O production rates occurred in spring of both years, possibly as a result of high N deposition rates during winter combined with low N uptake by herbaceous plants in early springtime. As they are not so strongly influenced by urban deposition, the two other sites of the same forest types always produced less N_2O .

Soil moisture was the factor most frequently responsible for microsite differences and seasonal variations in N_2O production from the forest soils. Variability in N_2O production within sites was also related to soil pH, soil nitrate content and CO_2 production. However, the relative importance of these factors was different for the various forest types (Table 5). N_2O production was mainly affected by soil moisture and nitrate in the oak–hornbeam and woodruff–beech forests, and was linked to CO_2 production in the acidophilous beech forests. In the floodplain forests, variability in N_2O production was largely controlled by soil moisture. Although environmental factors in most cases had a similar impact

within the same forest type, the influence of specific site characteristics was also evident. For instance, N_2O production on the microscale was strongly determined by the soil pH at the Saubrunn site, which had the most acidic soils (Table 3). The high soil pH in soils of the Merkenstein site might inhibit N_2O in favour of N_2 production, which is expressed by an inverse relationship between N_2O production and soil pH (Table 5). A decrease in the $N_2O:N_2$ ratio with increasing pH has previously been found in beech forest and pasture soils (Struwe and Kjølter, 1994; Stevens et al., 1998). N_2O production was related to microbial respiration not only in the acidophilous beech forests but also at the pine forest site Merkenstein. Apparently, severe limitations were acting upon microbial activity at these sites. While in the acidophilous beech forests microbial activity was likely to be inhibited by low soil pH, in the latter it may have been restricted by the low soil moisture content.

5. Conclusions

Our results make evident that N cycling of the forest stands was related to site-specific conditions, including soil and vegetation type as well as climatic conditions and stand history. N cycling was tight in acid beech forests where microbial activity was limited by low soil pH. Indigenous pine forests on calcareous bedrock showed high microbial N storage. N turnover in these soils could be activated by raising the soil moisture content. Concerning N losses from soil via N_2O production, it appeared that high nitrate availability was a principal prerequisite for substantial N_2O production to occur. It was suggested that elevated N_2O production rates at sites situated close to the city area of Vienna may have been triggered by high atmospheric N deposition. Variability in N_2O production within sites and seasons was most strongly related to the soil moisture content.

As was shown, large N pool sizes and high amounts of N cycled within the system did not necessarily entail high N losses. Rather, it was implied that it was not amounts but the turnover rates of N and hence the size and activity of the microbial biomass that were critical for the N balance of the forests studied. These findings are not only relevant in terms of ecosystem research, but might also have implications for issues of

forest management. Our data suggest that microbial growth and activity are especially promoted in ecosystems where the nutrient supply for the soil microorganisms is high, which is the case when sufficient degradable plant material is available. Such conditions are sought after in sustainable forestry, which aims at maintaining ecosystem functioning by low impact management and the preservation or reintroduction of native tree species. We suggest that data obtained in natural forests may be set in comparison with those measured in the corresponding planted stands where they may provide reference data for the ecological evaluation of management measures.

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