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Nitrogen mineralization peaks under closed canopy during the natural forest development cycle of an old-growth temperate spruce forest

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Abstract

- **Context** Old-growth forests with natural forest development and complex stand structure have become extremely rare in Central Europe. Changes of biogeochemistry and the N cycle across a full forest development cycle are not well understood.
- **Aims** We tested the hypothesis that net N mineralization and the relative importance of nitrification are increasing with proceeding forest development from regeneration to decay stages.
- **Methods** In an unmanaged old-growth spruce forest, we measured net ammonification and nitrification rate in the five forest development stages in 2 years using the intact soil core incubation method.
- **Results** Net N mineralization (and ammonification) rates were higher in the closed stands of the optimum and over-mature stages than in the more open decay and regeneration stages. Only a small proportion of NH_4^+ was oxidized to NO_3^- in the studied acidic soils.
- **Conclusion** Lower N mineralization in the more open than the closed patches of this natural forest is unexpected, contrasting with the findings from artificial gaps. Possible reasons

are reduced litter supply and lower canopy N interception in gaps in this forest under exposure to high N deposition. Further studies in other old-growth forests are needed to better understand the mechanisms causing long-term change in N cycling with forest development.

- **Key message** Nitrogen mineralization was higher in the optimum and over-mature stages with closed canopy than in the more open decay and regeneration stages of an unmanaged old-growth forest with high atmospheric nitrogen load, in contrast to published experiments with artificial gaps.

Keywords Nitrogen cycle · Nitrification · Ammonification · Old-growth forest · *Picea abies* · Gaps

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Contribution of the co-authors MH and CL designed the study, CB conducted the field and laboratory work, MJ, MH, HFJ supervised the work, MJ coordinated the research project, CB, MJ, HFJ, CL and MH wrote the paper.

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1 Introduction

Ammonification and nitrification are major nitrogen (N) transformation processes in soils providing readily available ammonium (NH_4^+) and nitrate (NO_3^-) for plant uptake. Both pathways of N supply depend on abiotic (soil temperature, moisture, and chemistry) and biotic factors (litter chemistry and decomposer activity) but are also influenced by vegetation structure and plant productivity through canopy openness and the amount of litter mass (Prescott 2002). Several studies reported higher N mineralization rates in gaps than in the forest interior due to higher soil temperatures and higher soil moisture as a consequence of reduced transpiration (e.g., Prescott 2002; Bagherzadeh et al. 2008); however, others found no difference or lower rates in the gap (e.g., Bauhus et al. 2004). The $\text{NO}_3^-/\text{NH}_4^+$ ratio of N supply was often higher in the soil of coniferous forest gaps than in the forest interior (Hart et al. 1994; Prescott et al. 2003) due to reduced litter mass and thus lower C availability in the gap (Hart et al. 1994). The gap effect on soil N supply is relevant for managed forests because mineral N availability may vary with

management intensity in clear-cutting, shelterwood, or selective cutting regimes (Schmidt et al. 1996). Much less is known about variation in N supply with natural gap dynamics in unmanaged old-growth forests, particularly in the decay stage with open canopies and abundant deadwood influencing N mineralization and nitrification.

As most temperate natural forests have cyclic successional age dynamics forming different forest development stages (Korpel 1995; Stöcker 1997), this natural forest dynamics creates a structurally heterogeneous vegetation pattern with coexistence of dense and open patches (Stöcker 2002) and contrasting microclimatic conditions in the different development stages. Further, the amount of deadwood as a source of decomposable organic matter varies across the forest development cycle (Harmon 2009; Jacob et al. 2013). Deadwood influences soil N dynamics by acting as a net N sink in the initial phase of decay while representing a net N source in later stages (Laiho and Prescott 2004; Spears et al. 2003). This structural heterogeneity in natural forests may also influence N mineralization, plant N uptake and thus the balance between supply and plant demand at the stand level over long time spans.

The productivity of most temperate and boreal forests is limited by low N availability (Vitousek et al. 1997), and acidic coniferous forests have generally been considered to have a tight N cycle with almost all mineralized N taken up by roots (Vestgarden et al. 2004). However, increasing atmospheric N deposition has reduced the growth limitation of temperate forests by N in many regions, and at sites with high atmospheric N input, forest soils can even become saturated with N (Aber et al. 2003). This factor must be considered when examining the dynamics of N transformation processes across the natural forest development cycle. The interception of N and other substances from atmospheric sources increases with the size of the intercepting canopy surface area (Lovett and Lindberg 1993; Hauck and Runge 2002) and thus may increase with tree age and stand density in the early stages of stand development (Rothe and Mellert 2004). Elevated N deposition increases not only the plant available N pool, but may also lead to increased N mineralization (Peréz et al. 1998) revealing complex interactions between atmospheric and soil N fluxes.

Norway spruce (*Picea abies* (L.) H. Karst.) is one of the two economically most important tree species in Central Europe's forestry sector. Many studies have addressed the N cycle and N mineralization in planted spruce stands (e.g., Persson and Wirén 1995), but not much is known about N mineralization in natural old-growth spruce forests, especially in the decay stage. Since over-mature and decaying trees are unique elements of old-growth forests that are lacking in managed forests, we asked how the natural stand development, especially with the presence of over-mature and decay stages might influence net N mineralization and nitrification.

With a comparative study in all five forest development stages (regeneration to decay) of a natural mountain spruce forest, we tested the hypotheses that (i) the soil in patches with over-mature and decaying spruce trees supports higher N mineralization rates than soil in the younger forest development stages due to more favorable abiotic conditions, and (ii) an increasing proportion of the released NH_4^+ is oxidized to NO_3^- when canopy closure decreases from early to late stages of the forest development cycle. We further asked whether these expected patterns would persist under chronic N deposition as is characteristic for most parts of Central Europe and the study region.

2 Material and methods

2.1 Study site

The study was carried out in the Harz Mountains in Central Germany with Mt. Brocken as the highest peak (1,142 m a.s.l.). The study site was chosen in a natural old-growth Norway spruce stand of the *Calamagrostio villosae-Piceetum* community (temperate mountain spruce forests; Ditttrich et al. 2013) located on the eastern slope of Mt. Brocken at elevations between 930 and 1,000 m a.s.l. This forest stand of c. 300 ha in the core protection zone of Harz National Park is one of the last remaining unmanaged old-growth forests in Central Europe. Since the early Middle Ages (ca. 800 AD), the area was reserved as a hunting ground for the nobility and clergy (Schade 1926). The forest was banned from logging and forest pasture and was never exploited for charcoal production during medieval times (Kortzfleisch 2008), a widespread forest use practice in that time. Due to low human influence and the fact that the studied spruce stand has not been used for timber harvesting for several centuries, the stand follows natural stand dynamics from the regeneration through the optimum to the decay stage. A typical cycle is thought to last for about 300 years and is dominated only by spruce (Stöcker 1997). We installed 25 plots of 10 m × 10 m size in order to cover the whole spectrum of stages of the forest development cycle, considering the five development classes of Stöcker (1997) (Table 1), each being replicated five times. Dendrochronological evidence shows that the oldest trees are more than 280 years old (Hauck et al. 2012). The plots were chosen in a stratified random selection procedure in order to exclude patches with blanket bog formation and shallow Leptosols on boulders. The climate on Mt. Brocken is characterized by an annual mean temperature of 3–3.5 °C, annual precipitation of 1,600 mm year⁻¹, 130 to 170 days with snow cover, and more than 300 fog days (Glässer 1994). The bedrock is granite and the dominant soil type Stagnic Cambisol (IUSS Working Group WRB 2006). Soils were highly acidic and strongly affected by slope water and locally

Table 1 Structural attributes (based on Stöcker 1997, modified) and stand characteristics of the five forest development stages on Mt. Brocken

	A Regeneration	B Initial	C Optimum	D Over-mature	E Decay
Number of tree individuals	Low to high, increasing	Very high, decreasing	High, stable	High, decreasing	Medium to low, decreasing
Canopy cover	Low, steadily increasing	Medium to high, closure of gaps	High, closure of gaps	Decreasing, gap formation	Medium to low, decreasing
Tree mortality	Low	Medium	Low	Medium-high	High
Deadwood	Remaining from decay phase	Small-sized wood debris	Increasing	Increasing in canopy layer	Dead trees dominate
Canopy stratification	Very few mature trees and offspring	Heterogeneous structure	Low variance in tree height	Low variance in tree height	Disintegration of canopy layer
Tree size, age structure	Saplings dominate	Medium-sized trees, low variance	Tall to medium-sized trees, low variance	Tall trees, low variance	Tall (dead) trees and saplings
Tree vitality	Very high	High	Stagnating-decreasing	Low	Low, dieback
Tree regeneration	Abundant	Medium-low, partly suppressed	Very low, suppressed	Low, partly suppressed	Starting in groups
Stem density of live trees (N ha ⁻¹)	40±40 a	960±289 b	480±66 ab	380±37 ab	0
Mean tree height of live trees (m)	3.2 a	6.6±0.2 a	22.5±1.4 b	22.3±0.8 b	–
Mean dbh of live trees (cm)	7.6 a	12.4±0.6 a	43.2±3.3 b	48.6±1.3 b	–
Total deadwood (m ³ ha ⁻¹)	351±101 a	156±39 a	50±8 a	242±89 a	1,280±319 b
Herb layer (cover in %) ^a					
<i>Deschampsia flexuosa</i>	36±6 a	23±5 a	39±6 a	46±11 a	28±11 a
<i>Calamagrostis villosa</i>	23±9 a	21±6 a	25±6 a	20±6 a	41±8 a
<i>Galium saxatile</i>	21±12 a	7.5±3.7 a	2.2±1.8 a	5.4±2.7 a	12±3 a
<i>Vaccinium myrtillus</i>	12±8 a	21±10 a	9.3±4.9 a	17±5 a	9.0±5.8 a
<i>Picea abies</i>	1.0±0.4 a	1.3±0.8 a	1.2±0.9 a	0.7±0.2 a	0.5±0.1 a

Within a row, means sharing the same letter, do not differ significantly ($P < 0.05$, Kruskal–Wallis test)

^a Dominating herb layer species according to Dittrich et al. (2013)

also by waterlogging. The dominant humus form was mor-like moder (Zanella et al. 2011). The mass of standing deadwood differed significantly with highest values in the decay stage (about 200 Mg C ha⁻¹) and lowest values in the optimum stage (2 Mg C ha⁻¹), while the mass of lying deadwood showed no significant differences (Jacob et al. 2013).

2.2 Measurement of N mineralization and nitrification rates

In situ rates of net N ammonification and net nitrification were determined by the intact soil core incubation technique (Hart et al. 1994) using stainless steel cylinders of 6.5 cm inner diameter and 40 cm length with both ends open to rain, drainage, and evaporation. In the mostly shallow soil profiles, we investigated the topsoil (0–10 cm) (excluding the humus) and the lower 10–20 cm horizon. In 2009, samples were taken at each plot corner (at 3.5 m distance from the plot corner for avoiding edge effects) and in the center of the 25 plots resulting in five replicate samples per plot, soil depth, and sampling period (500 samples in total: 25 plots × 2 depths × 2 periods × 5 replicates). In 2010, a reduced sampling design was applied with samples collected only in the plot center

(only one replicate per plot, soil depth, and sampling period, i.e., 100 samples in total). The cylinders were installed for two 30-day intervals in summer (July/August) and autumn (September/October) of 2009 and 2010, thereby covering most of the short growing season on cool Mt. Brocken (Table 2). A second set of cylinders with soil cores extracted in direct vicinity of the incubated ones was returned to the laboratory immediately after installing the cylinders for determining the inorganic N stocks at the beginning of the

Table 2 Mean daily temperature and precipitation totals during the four incubation periods in the summers and autumns of 2009 and 2010

Year	Season	Temperature (°C)	Precipitation (mm day ⁻¹)	Incubation period (days)
2009	Summer	12.4±0.5	4.3±1.2	28
	Autumn	8.2±0.6	5.1±1.4	30
2010	Summer	15.2±0.8	1.6±0.6	28
	Autumn	6.8±0.5	5.0±1.7	41

Calculations are based on daily data of the German National Meteorological Service (Deutscher Wetterdienst, Offenbach, Germany) recorded on top of Mt. Brocken

incubation. The material was kept cool during the transport (about 3–4 h). In the laboratory, a few drops of chloroform were added for retarding microbial growth, and the soil samples were immediately extracted with 150 ml 0.5 M K_2SO_4 solution using a ratio of soil to K_2SO_4 solution of approximately 1:3. The samples were shaken for 1 h, the solution subsequently passed through a cellulose filter (3 μm , Sartorius, Göttingen, Germany), and stored at -18°C . The NH_4^+ and NO_3^- concentrations in the filtrate were measured photometrically with a SAN^{++} continuous flow injection analyzer (Skalar Analytical B.V., The Netherlands). NO_3^- concentrations were measured using the copper-cadmium reduction method (Skalar method 461–000), the NH_4^+ concentrations with the Berthelot reaction method (Skalar method 155–000). Daily rates of net ammonification and net nitrification (unit: mg N kg^{-1} dry soil day^{-1}) were calculated as the difference of the NO_3^- -N or NH_4^+ -N concentrations at the beginning and the end of the incubation period ($t_1 - t_0$), divided by the days of field incubation. The sum of net ammonification and net nitrification rate was termed daily net N mineralization rate.

2.3 Characterization of soil properties

For characterizing soil physical and chemical properties, additional soil samples were taken at four depths (0–10; 10–20; 20–40; and 40–60 cm) from the centre of each plot. Total concentrations of C and N were measured with a C/N analyzer (Vario EL III, Elementar, Hanau, Germany) after the samples had been dried (70°C , 48 h), sieved (fraction < 2 mm), and milled. The effective cation exchange capacity was determined by percolating 2.5 g fresh soil material with 100 ml 0.2 N BaCl_2 solution that was subsequently analyzed using ICP-OES (Optima 5300 DV, Perkin Elmer, Waltham, Massachusetts, USA). Base saturation was calculated as the percentage of Ca, K, Mg, and Na ions in the effective cation exchange capacity. The soil pH (H_2O) and pH (KCl) (1 N KCl) values were measured with an InLab 413 glass electrode (Mettler-Toledo, Greifensee, Switzerland) in saturated soil suspensions consisting of 10 g fresh fine soil (mineral soil), or 5 g of the organic layer, in 25 ml demineralized water. Soil bulk density and the water content of the soil were determined by the difference of fresh and dry weight after drying at 105°C for 48 h. Particle size distribution and the relative abundance of different fractions were analyzed by sedimentation. Canopy closure was measured by hemispherical photography (Coolpix 8400, Fisheye converter UR-E16; Nikon, Tokio, Japan).

2.4 Statistical analyses

Arithmetic means and standard errors are presented throughout the paper. Statistical analyses were carried out using R software (version 2.10.1). All data sets were tested for normal distribution with the Shapiro–Wilk test and with Levene's test

for homogeneity of variances. Since the data on N conversion rates, C/N ratio, and N stocks were not normally distributed, we tested for significance of differences between the five different forest development stages using the Kruskal–Wallis rank sum test combined with the two-sample Mann–Whitney *U*-test (with Bonferroni-correction and a corrected level of significance of $P \leq 0.005$) for subsequent pairwise comparisons for cases where the Kruskal–Wallis rank sum test showed significant differences. To test for significant differences between the forest development stages in the normally distributed parameters pH and base saturation, we used one-way analysis of variance (ANOVA) with a significance level of $P \leq 0.05$. Pearson correlation coefficients were calculated for analyzing the relationship between total N, pH, and net N mineralization rate. Multiple regression analysis was calculated with SAS software (version 9.1) with stepwise forward variable selection to investigate the influence of the soil chemical parameters on the net N mineralization rate in the two different soil depths.

3 Results

3.1 Soil chemical characteristics

All plots were characterized by high soil acidity, with the pH ranging from 3.6 to 4.0 (in H_2O) and 3.0 to 3.6 (in KCl) (Table 3). Soil texture was dominated by sand and silt (51 % sand, 36 % silt, and 13 % clay), and the mean soil depth to the bedrock was 54 ± 1 cm (data not shown). The mean depth of the organic layer (20 ± 2 cm) exhibited a statistically insignificant trend ($P = 0.47$) for higher values in the optimum stage (C) and lower values in the regeneration (A) and the decay (E) stages than in the initial (B) and over-mature (D) stages (Table 3). Total N content, C/N ratio, pH value, and base saturation in the upper soil profile did not differ between the five forest development stages (Table 3). Canopy closure was significantly lower in the decay (E) stage (74 %) than in the initial (B), optimum (C), and over-mature (D) stages (85–91 %). The soil water content in summer and autumn was highest in the uppermost soil layer (0–10 cm) and decreased with soil depth. At 0–10 cm, a (statistically insignificant) trend for lower soil water content in the optimum (C) and over-mature (D) stages than in the other development stages existed; in the 10–20 cm horizon, the soil contained more water in the optimum (C) than in the regeneration (A) stage.

3.2 Net N mineralization rate

The concentration of NH_4^+ in the topsoil (0–10 cm; K_2SO_4 extraction) ranged between 20 and 70 mg N kg^{-1} dry soil in the four measuring periods; it was much lower at 10–20 cm (Table 4: t_0 figures). The NO_3^- concentration was 2 to 10

Table 3 Soil chemical and physical characteristics at two soil depths (0–10; 10–20 cm) of the topsoil together with canopy closure in the five forest development stages (A, regeneration; B, initial; C, optimum; D, over-mature; E, decay stage)

	A	B	C	D	E
Depth of organic layer [cm]	16.8±3.7 a	19.4±6.8 a	25.2±2.4 a	20.0±1.3 a	17.4±2.6 a
0–10 cm					
pH (H ₂ O)	3.7±0.0 a	3.8±0.2 a	3.7±0.1 a	3.6±0.1 a	3.8±0.1 a
pH (KCl)	3.2±0.1 a	3.3±0.2 a	3.2±0.1 a	3.0±0.1 a	3.2±0.1 a
N _t [kg ha ⁻¹]	4,273±365 a	5,033±110 a	3,744±627 a	3,996±657 a	4,802±189 a
C/N ratio	19.9±0.6 a	19.8±1.0 a	23.6±3.8 a	21.0±1.5 a	20.0±0.9 a
Base saturation [%]	12.3±4.0 a	11.1±3.9 a	11.9±4.7 a	13.4±4.8 a	11.1±2.9 a
Water content [%]	74.0±2.2 a	71.1±1.7 a	67.5±3.9 a	67.4±2.6 a	74.9±0.9 a
10–20 cm					
pH (H ₂ O)	4.0±0.1 a	3.9±0.3 a	3.9±0.0 a	3.7±0.1 a	3.8±0.1 a
pH (KCl)	3.6±0.1 a	3.5±0.2 a	3.4±0.1 a	3.3±0.2 a	3.4±0.1 a
N _t [kg ha ⁻¹]	3,339±1,491 a	6,807±2,451 a	5,209±1,599 a	3,135±646 a	5,019±2,183 a
C/N ratio	19.1±1.7 a	20.7±2.4 a	19.5±0.7 a	17.7±0.9 a	18.1±1.4 a
Base saturation [%]	6.6±2.4 a	7.1±2.3 a	5.5±1.6 a	5.3±1.3 a	4.4±0.6 a
Water content [%]	33.7±4.9 a	48.1±5.3 ab	53.0±4.4 b	36.1±3.9 ab	45.3±4.9 ab
Canopy closure [%]	81.5±3.6 ab	90.5±2.1 a	90.0±0.7 a	85.4±1.5 a	74.3±2.4 b

Means (±SE) followed by the same letter within a row do not differ significantly ($P \leq 0.05$, [Kruskal–Wallis rank sum test for N_t, C/N ratio, water content and canopy cover; ANOVA for pH and base saturation])

N=5 plots per stage

times smaller than the NH₄⁺ concentration with values in the range between 0 (not detectable) to 10 mg N kg⁻¹ in the topsoil. The spatial and temporal variations tended to be higher for NO₃⁻ than for NH₄⁺ with peak NO₃⁻ concentrations observed in summer 2010 (up to 38 mg N kg⁻¹).

In the topsoil (0–10 cm), net N mineralization rate showed a consistent trend for higher values in the optimum and over-mature stages with high canopy closure (stages C–D) compared to the more open development stages, especially the decay stage (E) (Fig. 1). These trends were statistically significant for the 0–10 cm layer, but persisted only partly at 10–20 cm depth. In all four measuring periods, the optimum (C) and over-mature (D) stages showed the highest N supply rates of all stages. Net N mineralization was significantly lower in 2009 than in 2010 ($P \leq 0.01$; except for the 10–20 cm layer in autumn; data not shown), but with a similar pattern among the five forest development stages and was significantly higher in summer than in autumn ($P \leq 0.01$; data not shown). At 0–10 cm depth, nitrification rate was very low and N mineralization rate thus largely equalled ammonification rate (Fig. 1). At 10–20 cm depth, the relative importance of nitrification was higher and more than 60 % of the NH₄⁺ released by mineralization in summer was oxidized to NO₃⁻; nitrification accounted for 35 % of net N mineralization in autumn. However, the absolute rates of ammonification and nitrification were about ten times smaller at 10–20 cm depth than at 0–10 cm (Fig. 1). Multiple regression analysis showed that pH (KCl) had a significant ($P \leq 0.05$) and total N a marginally significant influence ($P = 0.07$) on net N mineralization rate at 0–10 cm soil depth (Table 5). At 10–20 cm depth, we found significant effects of the C/N ratio ($P \leq 0.01$) and base saturation ($P \leq 0.05$) on net N mineralization rate.

4 Discussion

In the studied old-growth spruce forest, net N mineralization rate was significantly higher in the optimum and over-mature stages (C, D) with highest canopy closure than in the more open decay stage. N supply also tended to be lower in the early (A and B) than the optimum and over-mature stages (difference only partly significant). This result does not confirm our first hypothesis that net N mineralization increases with proceeding forest development resulting in highest mineralization rates in the open decay stage, as is implied by some earlier work on N mineralization comparing gaps with the forest interior (Prescott et al. 1992; Scharenbroch and Brockheim 2007; Bagherzadeh et al. 2008). Elevated N mineralization rates in gaps as compared to the forest interior have been explained in lowland spruce forests with more favorable microclimatic conditions, i.e., higher solar radiation and higher temperatures, and also higher soil moisture (Scharenbroch and Brockheim 2007). In the mountain spruce forest on Mt. Brocken, the cold and wet environment with approximately 5 months of snow cover, high annual precipitation, and low temperatures even in summer (Glässer 1994) creates very moist and acidic soil conditions, which may hamper soil biological activity and the breakdown of organic material. Development stages with a warmer soil in summer and partial drying of the very wet soil, which would be more favorable for decomposer activity, are virtually absent from the studied high elevation forest where canopy cover remains fairly high (74 %) even in the decay stage due to the abundance of standing dead spruce trees. In this moist environment, partial soil drying through canopy transpiration by mature spruce trees might be more important for decomposer activity than

Table 4 Initial concentrations of NO_3^- and NH_4^+ in the cylinders (t_0) and at the end of the incubation period (t_1) in the each two seasons in 2009 and 2010 at two soil depths (0–10 cm; 10–20 cm) in the five development stages (A, regeneration; B, initial; C, optimum; D, over-mature; E, decay)

			A	B	C	D	E	P value	
NO₃[−] (mg N kg^{−1})									
Summer 2009	0–10 cm	t ₀	1.5±0.8	3.1±1.8	1.5±0.6	0.9±0.5	4.2±0.8	*	
		t ₁	5.2±5.3	15.3±8.1	11.7±2.3	27.0±4.6	31.7±5.3	***	
	10–20 cm	t ₀	0.8±0.1	1.3±0.5	1.6±0.3	1.1±0.2	2.4±0.6	*	
		t ₁	6.0±1.8	6.8±2.2	8.9±1.1	13.1±1.8	14.2±2.9	*	
	0–10 cm	t ₀	0	0	0	0	2.0±1.9		
		t ₁	0	0	0.1±1.1	0	0		
	10–20 cm	t ₀	1.1±0.5	2.1±0.8	0.4±0.4	0.8±0.4	2.8±0.9		
		t ₁	4.5±1.2	6.1±1.1	3.1±0.9	6.2±1.0	6.4±1.2	*	
	0–10 cm	t ₀	3.3±6.3	38.0±26.4	21.4±25.2	25.2±21.0	26.4±23.3		
		t ₁	31.8±10.3	33.0±8.6	31.4±10.1	36.5±16.4	58.1±12.4		
	10–20 cm	t ₀	0.7±1.7	10.9±7.8	3.8±5.1	1.7±3.8	6.9±4.7		
		t ₁	13.7±4.9	19.3±5.3	23.7±2.8	18.5±5.4	36.7±4.6	*	
	0–10 cm	t ₀	0	0	0	0	0		
		t ₁	16.0±9.3	11.2±6.3	9.8±6.7	13.8±5.6	18.3±6.8		
	10–20 cm	t ₀	0	0	0	0	0		
		t ₁	5.2±3.1	3.5±2.8	2.1±1.7	4.2±2.3	6.1±2.3		
	NH₄⁺ (mg N kg^{−1})								
	Summer 2009	0–10 cm	t ₀	52.0±4.8	62.1±6.1	65.2±6.0	61.8±5.5	70.1±16.5	
t ₁			156.3±28.9	114.9±18.3	192.1±15.1	182.3±22.2	77.9±10.5	***	
	10–20 cm	t ₀	10.6±1.4	13.3±1.2	14.3±1.2	13.1±1.0	10.3±0.67	***	
		t ₁	35.0±17.2	12.5±1.4	17.3±2.8	15.9±2.0	7.4±0.78	***	
	0–10 cm	t ₀	52.7±7.1	69.3±12.1	68.2±7.7	58.7±4.2	55.7±6.4		
		t ₁	107.9±22.7	86.6±7.5	164.5±33.4	161.8±22.2	91.6±25.3	***	
	10–20 cm	t ₀	6.4±0.9	7.8±0.5	11.6±3.1	8.4±0.7	6.9±0.5	***	
		t ₁	15.8±3.9	10.7±1.1	21.8±5.0	19.6±2.6	9.5±1.9	***	
	0–10 cm	t ₀	40.5±13.5	59.2±5.6	64.8±11.0	53.2±5.7	34.2±4.5		
		t ₁	116.8±39.7	247.0±29.9	246.3±22.2	251.4±34.3	117.4±18.2	**	
	10–20 cm	t ₀	5.9±1.1	6.8±0.56	5.4±0.62	6.8±0.97	9.6±3.0		
		t ₁	9.9±1.1	14.6±3.3	15.9±3.4	16.6±1.9	14.0±3.9		
	0–10 cm	t ₀	22.2±2.4	31.8±3.1	29.3±4.5	35.9±6.5	30.5±9.4		
		t ₁	100.3±34.1	176.1±61.5	189.6±37.0	146.3±23.3	53.7±9.7		
	10–20 cm	t ₀	5.7±0.7	5.9±0.4	6.4±0.4	8.8±1.8	8.2±2.2		
		t ₁	9.6±2.1	16.1±2.4	29.6±10.5	12.6±1.7	8.3±0.8		

Given are means (±SE). Significant differences between the means in a row are marked with asterisks (* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$; Kruskal–Wallis rank sum test; $N=5$)

0 stands for ‘not detectable’

Fig. 1 N conversion rates at two soil depths (a, b=0–10 cm; c, d=10–20 cm) of the topsoil in the five forest development stages (A, regeneration; B, initial; C, optimum; D, over-mature; E, decay stage) of both sampling years (2009 and 2010); error bars represent the standard error

increased light transmission to the ground and soil warming on sunny days in gaps.

The atmospheric N deposition in the study area is another factor that could explain higher N mineralization rates in dense coniferous stands than in the more open forest stages. In the study area, measured deposition rates ranged between 27 kg N ha⁻¹ year⁻¹ in open areas and 47 kg N ha⁻¹ year⁻¹ in closed forest stands where deposition is increased due to canopy interception (Böhlmann et al. 2005). These deposition rates clearly exceed the critical loads of 10–20 kg N ha⁻¹ year⁻¹, which has been assumed for boreal and temperate coniferous forests (Achermann and Bobbink 2003). Several studies found increased N mineralization rates in areas with elevated N deposition (e.g., Pérez et al. 1998; Rowe et al. 2012), which were

of the mean, *small Latin letters* indicate significant differences between N mineralization rate, *capital letters* between the ammonification rates, and *Greek letters* between the nitrification rates; $N=5$ ($P \leq 0.05$, Kruskal–Wallis rank sum test)

probably caused by shifts in the composition of the soil microbial community (Zechmeister-Boltenstern et al. 2011). In general, saprophytic fungi are dominating over bacteria in the decomposer community of acidic soils due to the generally higher acid tolerance of the former (Rousk et al. 2009). However, Lauber et al. (2008) showed that the abundance of fungal taxa was more strongly related to the C/N ratio and the total P content of the soil than to soil pH itself. At our study sites with pH (KCl) values below 3.3, it is likely that both ammonification and nitrification are mainly conducted by acid-tolerant fungi. Nevertheless, our correlation analysis showed that N mineralization rate was in both soil horizons mainly dependent on pH, base saturation and the C/N ratio assuming that even small changes in soil pH and C/N ratio may influence net N mineralization rate at this site.

Besides the control by abiotic factors, N mineralization should vary across the forest development stages with changing litter supply and possibly also with variation in plant N demand. Spruce needles are relatively poor in N, but rich in lignin causing thus slower leaf litter decomposition than in most broad-leaved trees and herbaceous understory plants. Nevertheless, input of fresh spruce needles might be an influential factor for N mineralization in the studied forest, because the assumed variation in needle litter input matches with

Table 5 Results of multiple regression analyses for soil chemical parameters predicting net N mineralization rate

	Predictor	F value	P value
N mineralization rate: 0–10 cm ($R^2=0.33$; $P=0.02$)	pH (KCl)	7.44	0.01
	Total N	3.58	0.07
N mineralization rate: 10–20 cm ($R^2=0.39$; $P=0.03$)	C/N	9.32	0.007
	Base saturation	6.36	0.02

measured N mineralization rates across the forest development cycle. The lower net N mineralization rate in the decay stage could be due to reduced input of fresh organic material, mainly spruce needles, and a resulting shortage of organic C and N. Variation in herb litter supply is an unlikely explanation because the herb and cryptogam layers did not differ significantly in their structure between the forest development stages (Dittrich et al. 2013).

Deadwood was probably not a major N source in the open (late and early) forest development stages of our study site. Deadwood in the early stages of decay has been shown to act as a transient N sink, rather than a source as one might intuitively expect, since N is immobilized by wood-inhabiting fungi (Boddy and Watkinson 1995; Herrmann and Prescott 2008). Even over the entire span from tree death to complete wood decomposition, the contribution of deadwood decay to the N supply of the vegetation is low given the low decomposition rates in cold coniferous forests (Harmon 2009). Accordingly, Hart (1999) estimated that the net N release from decaying deadwood contributed only by about 4–6 % to the estimated plant N demand in an old-growth conifer forest of the Pacific Northwest of North America.

A likely higher fine root abundance of *Picea abies* in the optimum and over-mature stages as compared to the decay stage might also contribute to the lowered N mineralization rate in the latter stage, as Colin-Belgrand et al. (2003) found higher net N mineralization in the rhizosphere of *P. abies* than in soil with lower root density. These authors assumed that this effect was caused by differences in the quality of the available carbon in rhizosphere and non-rhizosphere soil.

The rapid decrease in N mineralization rate with soil depth is likely to result primarily from lowered temperature (and perhaps decreased base saturation), since C/N ratio and soil moisture were generally more favorable at 10–20 than 0–10 cm depth. Sajedi et al. (2012) could also show that the soil oxygen level is a restricting factor for biological processes and thus the availability of N in old-growth forests, which could be an explanation of the decreased N mineralization with soil depth also in our case. Similarly, other authors found more than 75 % of net N mineralization in temperate acid forest soils to occur in the uppermost 0–10 cm layer (e.g., Persson and Wirén 1995).

The figures of net N mineralization rate obtained from the field incubation in the montane spruce forest studied by us ($0.23\text{--}0.91\text{ kg N ha}^{-1}\text{ day}^{-1}$) fit rather well with literature data of net N mineralization in other European spruce stands (0.33, Jussy et al. 2004; 0.36, Šantrůčková et al. 2009; and $0.10\text{--}0.29\text{ kg N ha}^{-1}\text{ day}^{-1}$, Persson and Wirén 1995); however, they are in the upper range of reported values. We suggest that the relatively high measured N mineralization rates may result from the rather high N deposition on Mt. Brocken.

Our data may even underestimate the production of NO_3^- , since the cylinders allowed water percolation during the

incubation period and thus the leaching of highly mobile NO_3^- ions in periods of high rainfall. Thus, local differences in the amount of throughfall and percolating water in this structurally heterogeneous forest may have influenced the measured NO_3^- concentrations in the soil cylinders to a certain extent. This could be one explanation of the rather high spatial variation found in the actual NO_3^- concentrations in the cylinders across the plots and in apparent net nitrification rates. In the absence of important NO_3^- -preferring species in this ecosystem, NO_3^- could also be subjected to frequent leaching in the soil outside the incubation cylinders when rainfall is high. Norway spruce, the only abundant tree species in our plots, and *Calamagrostis villosa*, one of the most abundant grass species in the understory, are known to prefer NH_4^+ over NO_3^- as mineral N source (Ellenberg and Leuschner 2010). This adaptation fits to the dominance of NH_4^+ over NO_3^- in the soils on Mt. Brocken.

5 Conclusions

N mineralization markedly differed between the development stages of this old-growth spruce forest, thereby increasing the spatial and temporal heterogeneity of N availability. In contrast to lowland spruce forests, N mineralization was lower in the more open patches than in the closed forest patches, which might be attributable to reduced litter supply, lower canopy N interception, and perhaps less drained soils due to reduced canopy transpiration. Our results demonstrate that the gap dynamics in natural forests have a profound influence on forest biogeochemistry. If it turns out that reduced mineral N supply in the decay stage of old-growth forests is a characteristic phenomenon, this could be a hint to a biogeochemical feedback at the ecosystem level leading to increased mineral N supply when plant (tree) demand is high- and down-regulation through reduced litter supply when tree uptake is low. Analyses of the spatial and temporal variability of soil microbial activity and additional N transformation measurements with the ^{15}N pool dilution technique in this old-growth forest would provide further insights into the effects of the forest development cycle on N mineralization.

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