Soil biochemical and chemical changes in relation to mature spruce *(Picea abies)* forest conversion and regeneration

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Summary – Zusammenfassung

To investigate soil changes from forest conversion and regeneration, soil net N mineralization, potential nitrification, microbial biomass N, L-asparaginase, L-glutaminase, and other chemical and biological properties were examined in three adjacent stands: mature pure and dense Norway spruce (*Picea abies* (L.) Karst) (110 yr) (stand I), mature Norway spruce mixed with young beech (*Fagus sylvatica*) (5 yr) (stand II), and young Norway spruce (16 yr) (stand III). The latter two stands were converted or regenerated from the mature Norway spruce stand as former. The studied soils were characterized as having a very low pH value (2.9 – 3.5 in 0.01 M $CaCl_2$), a high total N content (1.06 – 1.94 %), a high metabolic quotient (qCO_2) (6.7 – 16.9 g CO_2 kg^{-1} h^{-1}), a low microbial biomass N (1.1 – 3.3 % of total N, except LOf_1 at stand III), and a relatively high net N mineralization (175 – 1213 mg N kg^{-1} in LOf_1 and Of_2, 4 weeks incubation). In the converted forest (stand II), C : N ratio and qCO_2 values in the LOf_1 layer decreased significantly, and base saturation and exchangeable Ca showed a somewhat increment in mineral soil. In the regenerated forest (stand III), the total N storage in the surface layers decreased by 30 %. The surface organic layers (LOf_1, Of_2) possessed a very high net N mineralization (1.5 – 3 times higher than those in other two stands), high microbial biomass (C, N), and high basal respiration and qCO_2 values. Meanwhile, in the Oh layer, the base saturation and the exchangeable Ca decreased. All studied substrates showed little net nitrification after the first period of incubation (2 weeks). In the later period of incubation (7 – 11 weeks), a considerable amount of NO_3-N accumulated (20 – 100 % of total cumulative mineral N) in the soils from the two pure spruce stands (I, III). In contrast, there was almost no net NO_3-N accumulation in the soils from the converted mixed stand (II) indicating that there was a difference in microorganisms in the two types of forest ecosystems. Soil microbial biomass N, mineral N, net N mineralization, L-asparaginase, and L-glutaminase were correlated and associated with forest management.

Chemische und biochemische Veränderungen der Bodeneigenschaften durch Verjüngung und Waldumbau eines Fichtenaltbestandes

Um die durch den Waldumbau und die Regeneration bedingten Standortsveränderungen zu untersuchen, wurden die Netto-Stickstoffmineralisierung, die potenzielle Nitrifikation, der mikrobiell gebundene Stickstoff (Nmic), L-Asparaginase, L-Glutaminase sowie weitere chemische und biologische Parameter an drei benachbarten Standorten untersucht: Standort I, reiner Fichtenaltbestand (*Picea abies* (L.) Karst –110 Jahre); Standort II, Fichtenaltbestand mit Buchenunterbau (*Fagus sylvatica* – 5 Jahre); Standort III, reine Fichtenaufforstung (16 Jahre). Die Standorte II und III entstanden infolge des Waldumbaus aus reinen Fichtenaltbeständen. Die untersuchten Böden sind gekennzeichnet durch sehr niedrige pH-Werte (pH(H_2O) 3,7 – 4,2, pH ($CaCl_2$) 2,9 – 3,5), hohe Gesamtstickstoffgehalte (1,06 – 1,94 %), hohe metabolische Quotienten (6,7–16,9g CO_2 kg^{-1} h^{-1}), geringe N_{mic}-Gehalte (1,1 – 3,3 % des Gesamt-N, ausgenommen LOf_1 von Standort III) und eine relativ hohe N-Nettomineralisation (175 – 1213 mg N Kg^{-1} in LOf_1 und Of_2, nach 4 Wochen Inkubation). Am Standort II nahm das C : N-Verhältnis und der qCO_2 im LOf_1-Horizont deutlich ab, wohingegen der Gehalt an austauschbarem Ca sowie die Basensättigung im Mineralboden geringfügig zunahmen. Am Standort III nahm der N-Vorrat (Auflagehumus + Mineralboden 0 – 10 cm) um 30 % ab. In den LOf_1- und Of_2-Lagen des Auflagehumus dieses Standortes traten eine hohe N-Nettomineralisation (1,5- bis 3fach höher als in den Standorten I und II), hohe Gehalte an mikrobiell gebundenem C und N, eine erhöhte Basalatmung sowie erhöhte qCO_2-Werte auf. In den Oh-Lagen hingegen nahm die Basensättigung ab. Alle untersuchten Standorte zeigten in der ersten Periode der Inkubation (0 bis 2 Wochen) eine geringe Netto-Nitrifikation. An den Standorten I und III fand in der späteren Periode (7. bis 11. Woche) eine Anreicherung an NO_3 (20 – 100 % des gesamten mineralischen N-Vorrates) statt. Im Gegensatz dazu wurde am Standort II keine NO_3-N- Anreicherung festgestellt. Dies deutet auf einen Unterschied in der Zusammensetzung der mikrobiellen Gemeinschaften in den zwei verschiedenen Forstökosystemen hin. Nmic, N-Nettomineralisation, L-Asparaginase und L-Glutaminase korrelieren miteinander und zeigen eine enge Beziehung zu den Bewirtschaftungsformen.

Key words: Norway spruce / soil nitrogen / N mineralization / biochemical soil properties / forest management PNSS P109/4B

1 Introduction

Due to the intensive forest management practices, pure coniferous stands dominate most forests in middle Europe where the original forests were presumably mixed forest with both coniferous and deciduous tree species (*Reinhard* and *Makeschin*, 2001). Numerous studies have showed that pure spruce and pine forests in Europe cause a decrease of soil buffer capacity, soil degradation and reduce the biodiversity of the whole forest ecosystem (*Van Breemen* et al., 1987; *Pederson* and *Bille-Hansen*, 1995; *Rennenberg* et al., 1998). In addition, with the progress of industrialization, there is a danger of increasing atmospheric N deposition in forest ecosystems (*Gundersen*, 1995). Many studies have shown that nitrogen no longer seems to be the growth limiting factor in many places and that excess N from deposition may cause nutrient leaching, acidification, and nutritional imbalances of forest vegetation (e.g. *Tietema* et al., 1992; *Gundersen*, 1995; *Rennenberg* et al., 1998) and finally impacts the sustainability of the entire ecosystem.

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The current study was an investigation in which soil biochemical and chemical properties, especially those related to soil nitrogen cycling, were compared in adjacent ecosystems under different management in Eastern Germany. The main objectives of this study were: 1) to compare the soil biochemical changes, especially soil properties concerned with nitrogen cycling, after conversion and regeneration of a pure, even-aged mature spruce stand and 2) to evaluate the effects of forest conversion and regeneration.

2 Material and methods

2.1 Site description

The study sites were located in the Ecological Monitoring Station (50°59′ N, 13°34′ E), Tharandt Forest, Germany. The altitude of the study sites is 380 m asl with an average annual temperature of 7.6 °C and 820 mm of precipitation. The soil is derived from glacial sediments on rhyolite. The soil type is a Dystric Cambisol (FAO) with a sandy-loamy texture. The indigenous vegetation in this area is a mixed forest with multiple storeys that consists of spruce, beech, fir, and maple (*Bitter* et al., 1998). Due to the deep impact of anthropogenic activities (management, heavy atmospheric deposition, etc.), pure, even-aged spruce forests now dominate this area, resulting in a decrease in forest diversity, an increase in forest damage (sensitivity to the environmental change), and a deterioration in soil fertility (*Nebe* and *Fiedler*, 1985; *Bitter* et al., 1998). Therefore, the development of methods to properly manage pure and mature coniferous forests in this area have become a very essential issue.

In the study area, three adjacent stands were selected: stand I, mature spruce stand (*Picea abies* [L.] KARST.), 110 yr., 720 trees ha^{-1}, average height 27.5 m, average dia. at 1.3 m height 38.2 cm, canopy density 0.8, mor humus; stand II, a mature spruce stand interplanted with young beech (*Fagus sylvatica* L.), spruce 540 trees ha^{-1}, canopy density 0.6, the height and dia. were as in stand I, young beech 5 yr, 2.2 m height, 1000 trees ha^{-1}, humus type as stand I; stand III, a young spruce stand, 16 yr, 1200 trees ha^{-1}, average height 7.2 m, average dia. at 1.3 m height 6.4 cm. Stand III was regenerated after clear cutting the former mature spruce stand as in the stand I and II. Stand II was transformed by thinning and interplanting young beech trees in mature spruce stand. All studied soils were limed with 4100 kg ha^{-1} calcite in 1954 and 547 kg ha^{-1} Ca in 1985. Because the three studied stands had very similar initial soil conditions (for detailed information see *Nebe* and *Fiedler* 1985), we assumed that the main soil properties differences among studied forests were caused by forest management.

2.2 Soil sampling and preparation

From each stand, soil samples were taken in early October 1999 (late growing season). In each stand, a 20 × 25 m sample plot was selected. These selected sample plots had similar topography and initial soil conditions. Along two diagonals of the sample plot, 15 soil cores (20 × 20 cm, at least 1 m away from nearest tree) were systematically taken. The cores were divided into LOf_1, Of_2, Oh layers, and 0–10 cm mineral soil. According to the German classification, LOf_1 consists of up to 10 %, Of_2 10–70 %, and Oh >70 % fine fragments, respectively. Three composite soil samples, each consisting of 5 cores, were taken. Soil samples were immediately transferred to the laboratory, where living plant material and coarse roots were removed by hand, then sieved (mesh size 2 mm for mineral, 5 mm for organic layer) and stored at 4 °C in plastic bags. For bulk chemical analyses, the samples were dried at 65 °C (organic soil) or 105 °C (mineral soil) and ground with a grinder. Other measurements were done using fresh material. All analyses were carried out within one month after sampling.

2.3 Net N mineralization and potential net nitrification

An anaerobic incubation procedure was used to determine both N mineralization (*Keeney* and *Bremner*, 1966; *Alef*, 1991) and potential net nitrification (*Alef*, 1991). For net N mineralization incubation, 10 g (mineral soil) or 5 g (organic layer) of fresh soil (3 replicates) was put into a polyethylene bottle (250 ml) and soil samples were wetted to field water capacity. The incubation bottle was closed with an air-tight cap and incubated at 25 °C. Meanwhile, the control (2 replicates) was put into a freezer at –16 °C. After 0, 1, 2, 4, 7, 9, and 11 weeks of incubation, the cumulative mineral N (NH_4-N, NO_3-N) was extracted in 100 ml of 1 M KCl solution by 1 h shaking. The samples were then filtered and NH_4-N and NO_3-N concentrations were measured using a flow injection analyzer (Skalar). The cumulative mineral N was calculated from the difference of mineral N (sum of NH_4-N and NO_3-N) in the incubated soil and control on the basis of the dried soil weight at different incubation periods. For potential net nitrification incubation, the same procedures were adopted as above, except 300 μg $(NH_4)_2SO_4$-N (in 1 ml solution) was added in both the controls and incubation samples.

2.4 Soil microbial N and C, soil basal respiration, L-asparaginase and L-glutaminase activity

The fumigation-extract method (FEM) was used for soil microbial C and N determination (*Vance* et al., 1987). Three sub-samples of fresh material (50 g for mineral soil, 20 g for organic layers) were extracted with 200 ml of 0.5 M K_2SO_4. The samples were shaken for 40 min and filtered. Simultaneously, three other sub-samples of soil were fumigated with ethanol-free chloroform for 24 h at 25 °C and then extracted. The total organic C and N in the extractants were immediately determined by Multi-NC-Analyzer (Jena Analytik). The differences in organic C and N of the extracts between fumigated and not fumigated soils (FE-C, FE-N) were shown for microbial biomass comparison. For an evaluation of the proportions of microbial biomass C and N in the soil, the flushes were converted to microbial C and N by the following formulas: $C_{mic} = 2.63 \times$ FE-C (mg C kg^{-1}), $N_{mic} = 1.85 \times$ FE-N (mg N kg^{-1}) (*Alef*, 1991; *Brookes* et al., 1985).

Soil basal respiration was determined by the Isermeyer method (*Alef*, 1991). A total of 20 g (mineral soil) or 10 g

organic soil (3 replicates) was placed in Schott bottles. The bottles were put into the incubator at 25 °C for 24 h. Soil-evolved CO_2 was absorbed by 0.05 N NaOH solution and then the absorbed CO_2 was determined by titration with 0.05 N HCl. The results were expressed as mg CO_2 kg^{-1} h^{-1}. In order to compare the physiological status of soil organisms, the metabolic quotient (qCO_2) was further calculated:

$$qCO_2 = \frac{Basal\ respiration\ (mg\ kg^{-1}\ \ h^{-1})}{Microbial\ biomass\ C}$$

(*Anderson* and *Domsch*, 1993)

Soil L-asparaginase and L-glutaminase were determined according to the description by *Frankenberger* and *Tabatabai* (1991a, 1991b). Briefly, 5 g fresh soil was placed in a flask treated with 0.2 ml of toluene and 9 ml of THAM buffer. The flask was swirled for a few seconds to mix the contents, and then added 1 ml 0.5 m L-asparagine solution, and the flask was swirled again for a few seconds. The flask was stopped and incubated at 37 °C for 2 h. After incubation, ca. 35 ml KCl-Ag_2SO_4 solution was added and the accumulated NH_4^+-N in the incubated sample was determined by the distillation method (*Keeney* and *Bremner*, 1966). To perform controls, the procedure for the assay of L-asparaginase was followed but the 1 ml of 0.5 m L-asparagine solution was added after the addition of the KCl-Ag_2SO_4 reagent. The difference in accumulated NH_4^+-N between incubated samples with and without the addition of L-asparaginase was used to evaluate enzyme activity. For determination of L-glutaminase activity, 1 ml 0.5 m L-glutamine was added into the sample instead of L-asparaginase. The other procedures were the same as for L-asparaginase determination.

2.5 Other analyses

Soil pH was measured in the suspension with 1:2.5 (mineral soil) and 1:10 (organic soil) of soil and distilled water (or 0.01 M $CaCl_2$), respectively. The total C and N content were determined using the combustion method with an automated CHN analyzer (Foss Heraeus Vario EL). For exchangeable K, Ca, Mg, Na, Al, Fe, Mn, and H, dried soil samples (2.5 g) were extracted with 100 ml 1 M NH_4Cl. The H^+ was determined using an electrode pH meter. The other cations were determined by ICP-OES with K by AAS. Effective cation exchange capacity (CEC_{eff}) was expressed as the sum of charges of the extractable cations {K + Na + Ca + Mg + Al + Fe + Mn + H}.

Preliminary examination of the data revealed that most of the data showed the non-homogeneity of variances, and the data were log-transformed if necessary to fulfil the assumptions of variance analysis. Pare-wise comparisons were made using Tukey's HSD test. The Pearson correlation was used for correlation analysis. All statistics were computed using STATISTICA (*StatSoft Inc.*, 1995).

3 Results

3.1 General soil characteristics

The total thickness of the organic layer decreased in the order of stand I > stand II > stand III (Tab. 1). The organic C contents in LOf_1 and Of_2 under mature spruce were significantly higher than those in the other stands, but not for the total N. Most of the soil layers in stand I and III showed higher C : N ratios than in stand II. The soil reaction in the three stands ranged from 3.7 to 4.3 (H_2O) and 2.9 to 3.5 ($CaCl_2$), respectively. There were no differences in pH values in the Of_2 and Oh layers in stand I and II whereas in stand III, the pH of the Of_2 layer was the lowest. In mineral soil, the pH (H_2O) in stand II was significantly higher than in stand III.

Extractable Al and Ca were the dominant cations (Tab. 2), which accounted for 12.7 – 49.4 % and 9.2 – 57.6 % of total exchangeable cations in organic horizons, respectively, and 61.4 – 79.3 % and 5.2 – 14.4 % of the total cations in the 0 – 10 cm mineral soil layer, respectively. The percentage of extractable Ca decreased with soil depth whereas the percentage of extractable Al increased. These two variables showed a close negative correlation (r = –0.85, $P < 0.001$).

Table 1: Soil characteristics of studied stands (average values, n = 3).
Tabelle 1: Bodeneigenschaften der untersuchten Standorte (Mittelwerte, n = 3).

Stand	Layer	TS[a] (cm)	OW/BD[b] ($g\,cm^{-3}$)	C_{org}[c] (%)	N_t[d] (%)	C : N ratio	pH	
							(H_2O)	($CaCl_2$)
Stand I	LOf_1	2.2	0.36	50.3a	1.82ab	27.6a	4.1abe	3.3acf
	Of_2	3.5	0.43	42.1b	1.89ab	22.3b	3.9ac	3.1bceghi
	Oh	1.6	0.51	25.8c	1.08c	24.1ac	3.8cd	3.3abdf
	0–10 cm	–	0.92	4.37A	0.18A	24.9ad	4.2efi	3.5f
Stand II	LOf_1	2.3	0.33	41.5b	1.96a	21.2e	3.9adf	3.3afg
	Of_2	3.0	0.37	34.1e	1.68bdf	20.3e	3.7cg	3.0bei
	Oh	1.5	0.46	28.1c	1.28e	22.0cde	3.9adfgh	3.3abf
	0–10 cm	–	0.94	4.59A	0.20A	23.0cdef	4.3bi	3.5af
Stand III	LOf_1	1.5	0.43	41.7b	1.94ad	21.5cde	4.0acf	3.2ab
	Of_2	3.3	0.29	39.1be	1.57bf	24.9af	3.7ch	2.9i
	Oh	0.9	0.35	27.7c	1.06c	26.2abf	4.1fi	3.4f
	0–10 cm	–	0.99	5.62B	0.21A	27.2ab	4.0adfg	3.3afh

[a] Thickness of soil layer. [b] Organic soil weight per unit or bulk density. [c] Total organic C. [d] Total N

Table 2: Soil extractable cations (1 M NH_4Cl) of studied forests (average values, n = 3).
Tabelle 2: Extrahierbare Kationen (1 M NH_4Cl) der untersuchten Standorte (Mittelwerte, n = 3).

Stand		Extractable cations (cmol kg^{-1})								CEC_{eff}	Bs [a] (%)	Al [b] (%)	Ca [c] (%)
		K	Ca	Mg	Na	Fe	Mn	Al	H				
Stand I	LOf_1	0.85	14.1	1.47	0.19	0.28	2.47	3.1	2.0	23.5	70.7	12.7	57.6
	Of_2	0.70	8.4	1.37	0.20	0.49	0.93	8.8	4.6	25.6	41.8	34.6	33.0
	Oh	0.47	4.5	0.65	0.16	0.38	0.43	9.0	2.7	18.3	31.1	49.4	25.1
	0–10 cm	0.11	0.7	0.07	0.08	0.20	0.22	7.6	0.6	9.6	9.9	79.3	7.0
Stand II	LOf_1	1.22	5.2	1.20	0.23	0.56	2.33	4.2	2.7	17.7	44.9	23.7	29.8
	Of_2	0.42	4.0	0.55	0.17	0.84	0.42	7.3	2.4	18.1	39.4	40.3	33.1
	Oh	0.42	6.9	0.65	0.21	0.78	1.39	11.3	3.3	25.0	32.8	45.4	27.6
	0–10 cm	0.43	2.3	0.57	0.19	1.50	0.13	9.9	1.1	16.1	21.3	61.4	14.4
Stand III	LOf_1	1.60	6.1	1.43	0.25	1.40	0.63	7.3	4.7	22.9	38.4	32.2	26.4
	Of_2	0.89	3.9	0.95	0.22	1.73	0.24	11.7	5.3	24.9	23.8	47.1	15.5
	Oh	0.90	1.6	0.41	0.09	1.71	0.10	7.3	5.3	16.9	15.1	42.9	9.2
	0–10 cm	0.91	0.6	0.11	0.09	0.90	0.02	8.0	1.4	11.2	8.5	70.9	5.2

[a] Percentage of base cations account for effective cation exchange capacity (CEC_{eff}). [b] Percentage of exchangeable Al.
[c] Percentage of exchangeable Ca

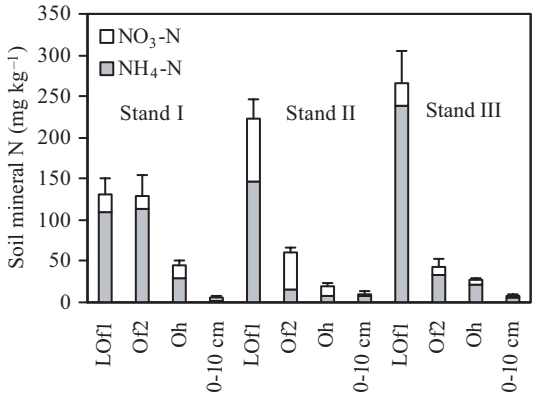

Figure 1: Cumulative mineral N (NH4-N, NO3-N) during soil incubation. Bars represent 1 S.D. of 3 replicates.
Abbildung 1: Mineralischer Stickstoff (NH_4-N, NO_3-N) (kumulativ) während der Inkubation. Balken stellen 1 S.D. von 3 Wiederholungen dar.

3.2 Soil mineral N and microbial C, N

The mineral N in organic layers ranged from 35 – 266 mg N kg^{-1} (Fig. 1) whereas in the mineral soil, this value was less than 10 mg N kg^{-1}. In organic layers of pure spruce stands (I and III), NH_4-N concentrations were much higher than NO_3-N, especially in the LOf_1 and Of_2 layers. In contrast, Of_2 and Oh in stand II had higher NO_3-N concentrations. The soil microbial C and N concentrations in organic layers in stand I and II had a similar vertical distribution (Tab. 3). However, these values in mineral soil were significantly higher in stand II than in stand I. In stand III, both, microbial C and N were significantly higher than these in comparable layers in the other two stands.

Table 3: Comparison of microbial C, N (Cmic, Nmic), L-asparaginase (L-asp) and L-glutaminase (L-glu) activities, basal respiration (BR), and metabolic quotient (qCO_2) in different soil layers of studied stands.
Tabelle 3: Vergleich von mikrobiellem C und N (Cmic, Nmic), L-Asparaginase- (L-asp) und L-Glutaminase (L-glu)-Aktivitäten, Basalatmung (BR) und metabolischen Quotienten (qCO_2) in den Bodenhorizonten der Standorte.

Stand	Layer	C_{mic}	N_{mic}	C_{mic} : N_{mic}	L-asp	L-glu	BR	qCO_2
		(mg kg^{-1})			(mg NH_4-N kg^{-1} h^{-1})		(mg CO_2-C kg^{-1} h^{-1})	
I	LOf_1	4140a[a]	366a	11.4abc	46.4a	827.2a	75.4a	18.2a
	Of_2	3010bf	267b	11.3abc	43.3a	391.6b	27.1bh	9.1b
	Oh	1780cd	169c	10.5bc	6.4c	377.2b	21.5b	12.3ab
	0–10 cm	170A	14A	12.3a	3.6A	211.2AB	2.8A	16.4a
II	LOf_1	4315a	410a	10.6b	42.5a	736.6af	50.6a	11.8bc
	Of_2	3222b	260bd	12.5ac	47.8a	518.5c	24.9b	7.8b
	Oh	1772d	160c	11.2abc	8.8c	293.6d	9.9c	5.6de
	0–10 cm	396B	29B	13.9d	8.1B	186.6B	5.6B	14.0ab
III	LOf_1	9092e	1069e	8.5e	99.2d	1255.6e	160.1d	17.7ab
	Of_2	3683ab	309abd	11.9abc	48.5a	750.2a	26.8b	7.3d
	Oh	2540f	246bd	10.4ab	21.9e	601.0cf	11.5c	4.5e
	0–10 cm	479C	35C	13.8d	11.1C	241.3B	5.8B	12.2la

[a] In each column, values not marked with the same letter are significantly different ($p < 0.05$)

3.3 Net N mineralization and potential nitrification

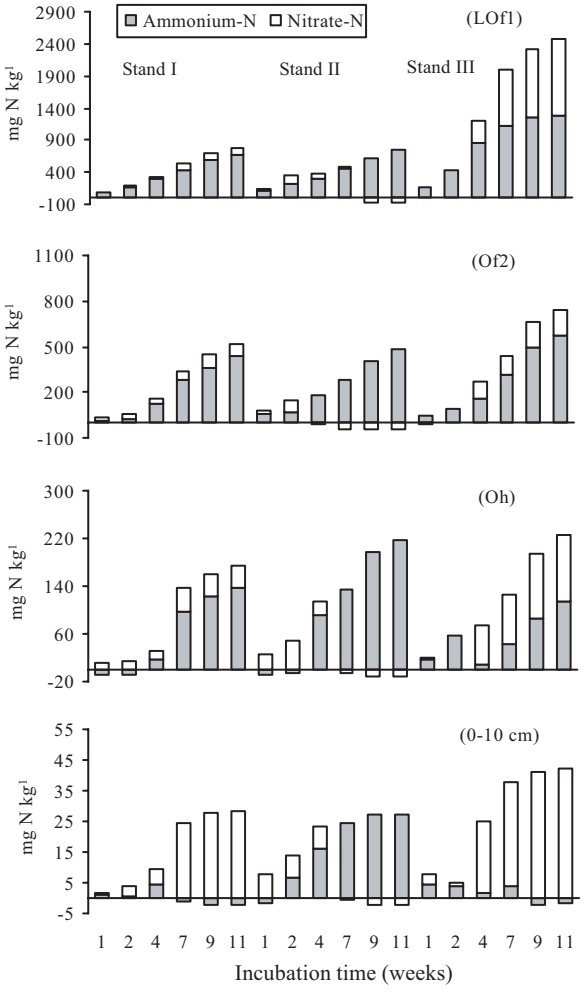

Figure 2: Composition of cumulative mineral N during soil incubation.
Abbildung 2: Zusammensetzung des mineralischen Stickstoffs während der Inkubation (kumulativ).

During the incubation, all substrates continuously accumulated mineral N (NH_4-N + NO_3-N) indicating that N mineralization was higher than N immobilization (Fig. 2). Organic horizons in the young spruce stand (III) had significantly higher cumulative N than those from the other stands. This was seen especially in the LOf1 layer where the amount of cumulative mineral N during 11 weeks incubation was three times more than seen in other stands. Although substrates from stands I and II under mature spruce with/without beech had quite similar magnitude of accumulated N during 11 weeks incubation, the two upper organic layers from stand II showed a changeable net N mineralization rate: high (0–2 weeks) – low (2–7 weeks) –high again (7–11 weeks). Net N mineralization rate of substrates from stand I remained relatively constant.

The composition of the cumulative N pattern during incubation was associated with forest types (Fig. 3). At the beginning (2 weeks) in samples from pure spruce stands (I, III), there was very little or no net NO_3-N accumulated in the incubated samples. However, in the later phase of incubation, there was a considerable amount of NO_3-N accumulated in the incubated samples, especially in mineral soils. In contrast, soils from the mixed stand (II) showed some NO_3-N accumulation at the beginning of incubation, however, no net NO_3-N accumulation occurred in the later phase.

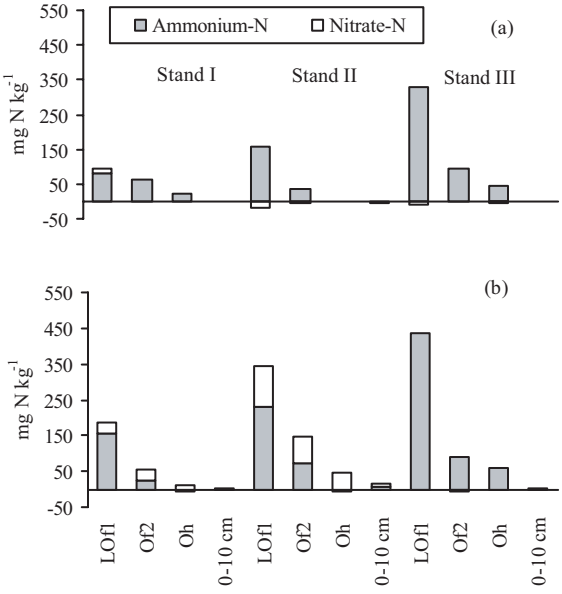

Figure 3: Comparison of cumulative mineral N and its composition during incubation (a) with addition of $(NH_4)_2SO_4$, and (b) without addition.
Abbildung 3: Vergleich von mineralischem Stickstoff (kumulativ) und dessen Zusammensetzung während der Inkubation (a) mit $(NH_4)_2SO_4$ und (b) ohne $(NH_4)_2SO_4$.

Fig. 3 shows the results of mineral N with/without enriched NH_4-N after two weeks of incubation. It was surprising to see that the addition of NH_4-N did not stimulate the nitrification rates. On the contrary, the cumulative NO_3-N in samples with the addition of NH_4-N decreased or was not observed. Meanwhile, in comparison with substrates without the addition of ammonium, the total cumulative N was lower except in Of_2 layers of spruce stands (I and III), in which N mineralization did not change.

3.4 L- asparaginase and L-glutaminase activities, basal respiration, and metabolic quotient (qCO_2)

Soil L-asparaginase activities in LOf_1 and Of_2 layers were almost one order of magnitude higher (43–99 mg NH_4-N kg^{-1} h^{-1}) than those in Oh and 0–10 cm mineral layers (3.6–22 mg NH_4-N kg^{-1} h^{-1}; Tab. 3). The L-glutaminase activities were also much higher in the LOf_1 and Of_2 than in Oh and 0–10 cm but the decreased gradient from Of_2 to 0–10 cm layer did not change as drastically as L-asparaginase activities. The two amidohydrolases significantly correlated (r = 0.82). All soil layers of the young spruce stand showed significantly higher activities than in the comparable layers in other stands.

Soil basal respiration showed high variability within the three replicates. The coefficients of variation were between 43 and 89 %. The soil basal respiration value was much higher in LOf_1 than in underlying layers (Tab. 3), especially in stand III. The metabolic quotient (qCO_2) values in different layers at site I were usually higher than those found at the other two sites (with the exception of LOf_1 at site III).

3.5 Relationships among soil chemical and biochemical properties

Using a simple correlation method and data from different soil layers in different studied stands (n = 12), it was revealed that soil total N concentrations positively correlated with the soil CEC_{eff} (r = 0.782, P = 0.006), basal respiration (r = 0.746, P = 0.006), initial mineral N (r = 0.674, P = 0.014), soil microbial biomass C (r = 0.764, P = 0.008), microbial N (r = 0.652, P = 0.021), extractable Ca (r = 0.725, P = 0.010), L-asparaginase activity (r = 0.761, P = 0.006), L-glutaminase activitiy (r = 0.728, P = 0.005), and cumulative N (11 weeks of incubation; r = 0.854, P = 0.005). Soil total N was found to be negatively correlated with the percentage of exchangeable Al^{3+} (r = –0.904, P = 0.001). The microbial biomass (C, N) was more closely correlated with the two amidohydrolases activities and basal respiration (r > 0.930, P < 0.001) than organic C and total N. The C : N ratios and qCO_2 values had no significant correlation with other soil parameters.

4 Discussion

4.1 Soil acidity

The studied soils showed very acidic conditions, especially in the organic layers (Tab. 1; *De Boer* et al., 1992; *Priha* and *Smolander*, 1999). In the LOf_1 layer of stand I, exchangeable Al was lower and exchangeable Ca higher than the comparable layers in other stands (Tab. 2). This may be the result of low biological activity and a thick litter layer in pure mature spruce stand which reduce the mobility of exchangeable Ca (Tab. 1, 3). In the mineral soil (0–10 cm) layers, the converted forest (stand II) showed some increment in base saturation, exchangeable Ca, and CEC_{eff}. However, due to the short conversion time, these improvements were very limited.

4.2 Soil organic C, total N, and microbial C, N

On an area basis, the total N storage in the surface layers (sum of organic layers and 0–10 cm mineral) decreased by 10 and 30 % in converted forest and regenerated forest, respectively (Tab. 4). However, the microbial biomass (C, N) increased especially in the mineral soil (0 – 10 cm). In comparison to other coniferous stands in the temperate zone, the total N content in the studied soils were higher with overall lower C : N ratios (*Martikainen*, 1984; *Tietema* et al., 1992; *Berg* and *Verhoef*, 1998), especially in the organic layers in stand II and III (Tab. 1). Meanwhile, the ratios of $C_{mic} : C_{org}$ and $N_{mic} : N_t$ (0.39 – 0.94 % and 0.8 – 2.3 %, respectively, except values in the LOf_1 at stand III, Tab. 4) in studied soils were very low, which were usually 0.8 – 2.0 % and 2.0 – 8.0 % (*Wardle*, 1998; *Priha* and *Smolander*, 1999), respectively. These results may reflect the high environmental stresses (*Lang* and *Jagnow*, 1986; *Walters* and *Joergensen*, 1991) due to the long-term and high S and N atmospheric deposition (27.5 kg N, 35.4 kg S $ha^{-1}yr^{-1}$ in throughfall of stand I, data are averages from 1992 to 1998. (*Wickel* and *Zimmermann*, 1998)) and long-term monoculture of spruce (*Bartels* et al., 1999). The high qCO_2 values also confirmed this soil condition (Tab. 3; *Anderson* and *Domsch*, 1993). When comparing stand I to stand II, it was observed that the $C_{mic} : C_{org}$ and $N_{mic} : N_t$ ratios increased slightly (Tab. 4) which may indicate a tendency towards improvement. After regeneration, these two ratios increased considerably. However, if the soil conditions in both, mature and young pure stands are com-

Table 4: Vertical distribution of total organic C (C_{org}), total N (N_t), and microbial C (C_{mic}), N (N_{mic}), expressed on an area basis, in different layers of studied stands (kg ha^{-1}).
Tabelle 4: Vertikale Verteilung vom gesamten organischen Kohlenstoff (C_{org}), Gesamtstickstoff (N_t) und mikrobiell gebundenem C (C_{mic}) bzw. N (N_{mic}) in (kg ha^{-1}).

		LOf_1	Of_2	Oh	0–10 cm	Total
Stand I	C_{org}	39837	63361	21053	40204	164455
	N_t	1441	2845	881	1656	6823
	C_{mic} [a]	328(0.82)	453(0.71)	145(0.69)	156(0.39)	1083(0.66)
	N_{mic}	29.0(2.0)	40(1.4)	14(1.6)	13(0.8)	96(1.4)
Stand II	C_{org}	31499	37851	19389	43146	131885
	N_t	1487	1865	883	1880	6116
	C_{mic}	328(1.0)	358(0.94)	122(0.63)	372(0.86)	1180(0.89)
	N_{mic}	31(2.1)	29(1.6)	11(1.3)	27(1.5)	98(1.6)
Stand III	C_{org}	26897	37419	8726	55638	128679
	N_t	1251	1502	334	2079	5167
	C_{mic}	586(2.2)	352(0.94)	80(0.92)	474(0.85)	1493(1.2)
	N_{mic}	69(5.5)	30(2.0)	8(2.3)	35(1.7)	141(2.7)

[a] data in parentheses are percentage of $C_{mic} : C_{org}$ or $N_{mic} : N_t$.

pared, it could be inferred that the soil disturbance during regeneration operations and soil physical condition improvements, such as the increase of soil temperature due to the low vegetation coverage (*Mai* and *Fiedler*, 1989), were the main causes of change.

4.3 Soil potential N mineralization and nitrification

Soil N mineralization is the key process regulating the N cycle in forest ecosystems (*Aber*, 1989; *Ross* et al., 1999). In our studied soils, net N mineralization during incubation was relatively high although the pH values were very low (Fig. 2, Tab. 2). The measured values were similar to the results of *Tietema* et al. (1992) in N-saturated acidic forests in the Netherlands. In their study, the cumulative mineral N (incubating an intact soil core in the laboratory) after 4 weeks of incubation was in the range of 203 to 1380 mg N kg^{-1} in L and Of layer, and 62 to 177 mg N kg^{-1} in the Oh. In our study, the surface organic layers of young regenerated forest showed very high net N mineralization during the incubation. The initial soil mineral N was high as well, which could provide a possibility for nitrification and N mobilization (*Tietema* et al., 1992; *Ste-Marie* and *Pare*, 1999).

During the 11 weeks of incubation, the LOf_1 from the young spruce stand (III) accumulated the highest mineral N content (Fig. 2). However, this might not mean that the potential mineralizable N was higher in this layer than that in the other two stands. According to the cumulative N tendency at different times, it can be extrapolated that net N mineralization of LOf_1 from the mature spruce stand after 11 weeks of incubation still showed a higher rate, whereas the LOf_1 layer from the young spruce stand gradually decreased. When comparing the cumulative N in LOf_1 and Of_2 layers from the mature spruce with/without beech, similar amounts of cumulative mineral N after 11 weeks of incubation was noticed. However, the overall tendency during the whole incubation period appeared to be quite different. Cumulative N in the LOf_1 from stand II showed a higher rate in the first 2 weeks, afterwards (2 to 7 weeks) it stagnated and then after 7 weeks increased again. Presumably, this mineralization pattern was caused by the different organic sources from different tree species, i.e. litter from beech is generally considered a more easily decompozable organic matter, while litter from spruce is relatively resistent. If models were used to predict potential soil N mineralization in stand II, a two-pool model might have better reflected the actual situation (*Eller* and *Bettany*, 1988; *Campbell* et al., 1994).

Nitrification in acidic forests seems to be complex and not yet totally understood. Some studies have noticed little or no net nitrification occurring during incubation of acidic forest soils (low pH and possible allelochemical inhibitors) (*Olson* and *Reiners*, 1983; *Tietema* et al., 1992). Other studies (*Van Breemen*, 1987; *De Boer* et al., 1992) have shown that nitrifying activities can occur in very acidic forest soil environments with a low pH value of 3 to 4. *De Boer* et al. (1992) and *Martikainen* (1984) attributed the nitrification in acidic forest soil to chemolithotrophic bacteria. Other researchers (e.g., *Lang* and *Jagnow*, 1986; *Papen* et al., 1991; *Ste-Marie* and *Pare*, 1999) have suggested that heterotrophic nitrifying microorganisms may be more important for nitrification than autotrophic nitrifiers in acidic forest soils. *Mai* and *Fiedler* (1989) compared the nitrifier numbers in soils under mature (stand I) and young spruce (stand III) in 1988, and found that there were very low autotrophic nitrifier numbers in both stands. However, our anaerobic incubation result showed (Fig. 2) that in the later phase of incubation, a relatively high proportion of NO_3-N, especially in Oh and 0–10 cm, accumulated in the samples from pure spruce stands (I, III). On the contrary, the soils from the mixed stand (II) had almost no cumulative NO_3-N after 7 weeks of incubation. This result may reflect the difference in microorganism communities associated with different forest types. During the later phase of incubation, it was assumed that the oxygen concentration was very low in the tightly capped incubation bottle, which created unfavorable autotrophic nitrification conditions (*Papen* et al., 1991; *De Boer* et al., 1992; *De Boer* and *Kowalchuk*, 2001). Thus, we believe that the high proportion of NO_3-N in the incubated soils from the pure spruce stands (I, III) was caused by heterotrophic nitrification. Our potential nitrification experiment also confirmed that almost no autotrophic nitrification occurred during a short-term incubation (2 weeks), even with the addition of NH_4-N (Fig. 3). These results may indicate that the low pH values prohibited autotrophic nitrification. However, for the pure spruce stand, the potential heterotrophic nitrification could be high, especially under anaerobic conditions.

4.4 Relationships among soil properties

Adams and *Martin* (1984) concluded from a literature review that mineralization of organic N occurs in the entire pH range but the rate decreases progressively below a value of 6. In our study, although the substrates had very low pH values, net N mineralization showed high mineralization activities, so it would seem that other site factors also had a considerable impact on N mineralization. The high net N mineralization from the soil under the young spruce may be attributed to enhanced soil temperature and moisture content during forest regeneration (*Mai* and *Fiedler*, 1989) as well as to a higher litter quality in the growing stand (*Nadelhoffer*, et al., 1983; *Berg*, 2000).

In comparison to other study results, the soil metabolic quotients (qCO_2) in our study were high (4.5 – 18.2 mg CO_2-C g^{-1} h^{-1}) (Tab. 3). *Walters* and *Joergensen* (1991) determined that the qCO_2 values in beech forests ranged from 1.4 to 2.6 mg CO_2-C kg^{-1} h^{-1}. The qCO_2 value in a spruce stand in Finland (*Priha* and *Smolander*, 1999) was rather high (1.29–13.9 mg kg^{-1} h^{-1}). They attributed this high value to high organic acid and sugar concentrations in the spruce litter. The qCO_2 value reflects the physiological status of soil microorganisms; a high value means that soil microbial activity is in low efficiency, and the soil microorganisms usually live under environmental stress (*Anderson* and *Domsch*, 1993). According to our results (Tab. 3), the layers such as LOf_1 and 0 – 10 cm soil layer from stand I and III, which had high qCO_2 values, usually were characterized by low pH value, high C : N ratios, and a high percentage of exchangeable Al. Therefore, it may be assumed that the soil organisms in these layers suffer from high environmental stress.

This study also showed soil microbial biomass C and N correlated negatively with the percentage of exchangeable Al and positively with the percentage of exchangeable Ca. These results were consistent with other studies (*Walters* and *Joergensen*, 1991). *Raubuch* and *Beese* (1993) showed that soil microbial biomass had an exponential decrease with depth and was positively correlated to the exchangeable Ca^{2+}, Mg^{2+}, and Ca : Al and negatively correlated to Al^{3+}. Soil microbial biomass C and N were also highly correlated with other soil nitrogen indexes (initial mineral N concentration, accumulated N during the incubation, L-asparaginase, L-glutaminase activity, and microbial C). These results may mean that microbial biomass can be taken as a comprehensive index for studying forest soils.

L-asparaginase and L-glutaminase are two of the most important enzymes involved in hydrolysis of native and added organic N to soils, which specifically act on C-N bonds in linear amides other than peptides (*Frankenberger* and *Tabatabai*, 1991a; 1991b). Unfortunately, until now very few studies have been reported on their activities in forest soils. This study showed that although these two enzymes were significantly correlated with other parameters such as total N, initial mineral N, microbial C and N, and N mineralization, their vertical distributions were different. L-glutaminase activity decreased significantly with soil depth (except Of_2 and Oh layers in stand I) (Tab. 3), while L-asparaginase activity in LOf_1 and Of_2 layers showed similar magnitude (except stand III), but in Oh layer the L-asparaginase activity was much less than in organic layers above it. Meanwhile, in mineral soil, L-asparaginase activity increased significantly after regeneration or conversion but L-glutaminase activity did not differ significantly after regeneration or conversion.

4.5 Soil properties and forest management

Soil nutrition availability and transformation changes have been attributed to chemical and physical conditions that regulate the activity of soil microbes (*Vitousek* and *Matson*, 1985; *Priha* and *Smolander*, 1999). Forest management can deeply impact soil chemical and physical conditions, which then further impact the soil nutrition pool and transformation (*Piccolo* et al., 1994; *Bauhus* et al., 1998). Soils in the mature spruce stand showed a high organic C and N content in the LOf_1 and Of_2 layers as well as low pH and CEC_{eff} values (Tab. 1 and 2). From stand I to stand II (forest conversion), the soil acidity was not significantly improved due to the short conversion period, yet the soil C : N ratios and qCO_2 values decreased, while base saturation in the mineral soil (0 – 10 cm) increased which provided a precondition for further improvement. When shifting from mature to young spruce stands after clear cutting, soil microbial biomass and net N mineralization increased. In the mineral soil (0 – 10 cm), soil acidity and Al saturation tended to increase, pH decreased, and environmental stress to soil microorganisms also increased (high qCO_2 value).

Although the spruce is usually taken as an acid adapted tree species in the temperate zone, it is clear that acidic soil conditions are disadvantageous for soil microbial activities and soil biodiversity. In order to improve acidic soil conditions, some researchers propose a liming practice (*Kreutzer*, 1995). It is recognized that liming, as a rule, simulates soil mineralization and nitrification through an increase in soil pH and availability of Ca and Mg cations (*Martikainen*, 1984; *Mai* and *Fiedler*, 1989). However, the long-term effect of liming for the stability of the whole ecosystem is still a matter of question. The stands in this study had been limed twice in the past 46 years. According to the reports available, after liming the soil pH initially increased (significantly) (*Mai* and *Fiedler*, 1989) but returned to initial levels after 4 years. In this study, extractable Ca and Mg in the surface organic layers (LOf_1, Of_2) accounted for more than 20 % of the total exchangeable cations (Tab. 2) which could be attributed to liming. However, in the mineral soil this value was still very low. On the contrary, soil extractable Al content was very high in Oh and mineral soil (0 – 10 cm), where exchangeable Al accounted for 42.9 to 79.3 % of the total extractable cations. Ca : Al and Mg : Al ratios were very low at ratios less than 1 : 15 and 1 : 20, respectively (Tab. 2). The high percentage of exchangeable Ca can be a simulation for Al leaching from the upper soil layer and deposits in the Oh and 0 – 10 cm mineral layers (*Kreutzer*, 1995). These results suggest that overspread liming in forest soil may result in a negative impact on soil fertility. Transformation to a mixed forest (as stand II) could be a rational option.

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