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Partitioning of ^{15}N-labeled ammonium and nitrate among soil, litter, below- and above-ground biomass of trees and understory in a 15-year-old *Picea abies* plantation

NINA BUCHMANN[1], GERHARD GEBAUER & ERNST-DETLEF SCHULZE

Universität Bayreuth, Lehrstuhl Pflanzenökologie, Postfach 10 12 51, 95440 Bayreuth, Germany; [1] *present address: Department of Biology, University of Utah, Salt Lake City, Utah 84112, USA*

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Abstract. The partitioning of nitrogen deposition among soil, litter, below- and above-ground biomass of trees and understory vegetation was investigated in a 15-year-old *Picea abies* (L.) Karst. plantation in the Fichtelgebirge, Germany, by labeling with 62 mg of ^{15}N tracer per square meter in March 1991. Ammonium and nitrate depositions were simulated on five plots each, by labeling with either ^{15}N-NH_4^+ or ^{15}N-NO_3^-, and the ^{15}N pulse was followed during two successive growing seasons (1991 and 1992). Total recovery rates of the ^{15}N tracer in the entire stand ranged between 93 and 102% for both nitrogen forms in 1991, and 82% in June 1992. $\delta^{15}N$ ratios increased rapidly in all compartments of the ecosystem. Roots and soils (to 65 cm depth) showed significant ^{15}N enrichments for both ^{15}N-treatments compared to reference plots. Newly grown spruce tissues were more enriched than older ones, but the most enriched $\delta^{15}N$ values were found in the understory vegetation. Although spruce trees were a much larger pool (1860 g biomass/m^2) than understory vegetation (*Vaccinium myrtillus* 333 g/m^2, *Calluna vulgaris* 142 g/m^2, *Deschampsia flexuosa* 22 g/m^2), the ericaceous shrubs and the perennial grass were a much greater sink for the ^{15}N label. Eight months after labeling, 9% of the ammonium and 15% of the nitrate label were found in the understory. *P.abies* retained only 3% of the ^{15}N-ammonium and 7% of the ^{15}N-nitrate. The main sink for both ^{15}N tracers was the soil, where 87% of the ammonium and 79% of the nitrate tracer were found. The organic soil horizon (5-0 cm depth) contained 63% of the ^{15}N-ammonium and 46% of the ^{15}N-nitrate suggesting strong immobilization by microorganisms of both N forms. Eight months after tracer application, about 16% of both ^{15}N-tracers was found below 25 cm soil depth. This 16% corresponds well to a 20% decrease in the recovery of both ^{15}N tracers after 15 months and indicates a total loss out of the ecosystem. Highly enriched $\delta^{15}N$ values were found in fruit bodies of fungi growing in reference plots (no ^{15}N addition), although soils did not show increased $\delta^{15}N$ ratios. No transfer of ^{15}N-tracer between fungi and spruce or understory vegetation was apparent yet.

Introduction

Studies of forest decline in the Fichtelgebirge, NE-Bavaria, Germany (Schulze et al. 1989) demonstrate the important role of high atmospheric nitrogen (N) deposition in the unbalanced nutrition of *Picea abies* (Norway spruce) stands growing on acidic soils. In a 30-year-old stand, surplus N stimulated growth and caused deficiency of phloem-mobile elements such as magnesium (Oren et al. 1988a). However, a nearby 10-year-old spruce stand showed low foliar concentrations of N and no growth increase despite a total N deposition of about 3 × ambient (Buchmann et al. 1995a). The question of whether competition for nitrogen between Norway spruce saplings and the understory vegetation masked the response of spruce trees to this increased N deposition could not be answered. Therefore, knowledge about partitioning of N deposition among different compartments of the ecosystem, including all members of the plant community, seems critical to understand the varying responses of adjacent forest stands to similar disturbances such as elevated atmospheric N inputs.

The widespread observation that forest decline in Central Europe was followed by increased nitrate concentrations in runoff and subsequently in ground water (Hauhs & Wright 1986; Hauhs et al. 1989) was also verified in the Fichtelgebirge (Hantschel 1987; Türk 1992; Durka & Schulze 1992). Durka et al. (1994) showed that between 10 and 40% of the nitrate in spring waters came directly from atmospheric nitrate deposition without microbial interactions. However, no quantitative information is available about the pathway of atmospheric ammonium deposition. Under conditions where ammonium deposition almost equals the nitrate input (Hantschel 1987; Türk 1992), microbial transformations in the soil and uptake patterns of the dominant vegetation might influence the internal cycling of each form of N differently. For example, the importance of nitrate retention by soil microorganisms, and the preferential use of one N form over the other by different plant species are not yet fully known. Two to four times higher ammonium than nitrate uptake was found for Norway spruce by Buchmann et al. (1995b) whereas Nadelhoffer et al. (1995) found after labeling field plots with ^{15}N-nitrate, that red spruce showed lower rates of nitrate assimilation than American beech and other deciduous species.

To understand the fate of ammonium-N and nitrate-N deposition in forest stands we conducted a ^{15}N tracer experiment in a young *P.abies* plantation in the Fichtelgebirge, Germany. Tracing the two N species within an ecosystem using ^{15}N is advantageous because the system's natural N level is relatively unaltered. By labeling throughfall with either ^{15}N-ammonium or ^{15}N-nitrate in March 1991, we were able (1) to follow the partitioning of added ^{15}N among soils, litter, and above- and below-ground biomass of spruce trees

and understory vegetation during two successive growing seasons (1991 and 1992), (2) to identify major sinks within the vegetation and soils for both N forms, and (3) to investigate the competition between the dominant tree species and the understory vegetation.

Material and Methods

Study site and stand characteristics

The study site was located near Wülfersreuth (670 m) in the Fichtelgebirge, northeast-Bavaria, Germany (50°N latitude, 12°E longitude, see Schulze et al. 1989). The mean annual air temperature is 5.9 °C, the mean annual precipitation is 1072 mm (Oren et al. 1988b). The total bulk precipitation during the seven-month 1991 growing season (April–October) was 512 mm, which was approximately equal to the long-term average for summer precipitation between April and September (493 mm; Türk 1992). The nutrient-poor soil is a Spodo-Dystric Cambisol ('podsolierte Braunerde') developed from phyllite. The average soil pH is 3.9, and C/N ratios in the upper 30 cm (organic and mineral soil) are around 30 (for more details, see Buchmann et al. 1995b). During 1991, the mean molar ammonium to nitrate ratio in the main rooting horizon (0-25 cm depth) was 9:1 (Buchmann et al. 1995b).

The tracer study was conducted in a 15-year-old *Picea abies* (L.) Karst. plantation established on a windfall area with 14% slope facing SW. In spring 1991, the *P.abies* trees were 3.6±0.06 m tall (n = 225), with a living crown radius of 1±0.01 m and an average spacing of 1.67 ± 0.01 m. Cation supply was low but did not seem to inhibit growth (Buchmann et al. 1995b). The stand density was 0.4 stems m^{-2} and the leaf area index was 7.8. Due to an open canopy of *P.abies* (ground cover 66±2%, n = 15), a dense understory layer with ericaceous dwarf shrubs and grasses was present. The understory was dominated by *Vaccinium myrtillus* L., *Calluna vulgaris* L. Hull and *Deschampsia flexuosa* (L.) Trin. (35±3%, 17±3%, and 38±3% ground cover, respectively). Both dwarf shrubs have evergreen twigs, but leaves of *C.vulgaris* are evergreen whereas leaves of *V.myrtillus* are deciduous. *D.flexuosa* is a perennial grass. Fifteen plots (2 treatments and a reference with 5 replicates of 40-70 m^2 plots) were established in 1990. Plots were randomly distributed in the study area and separated from each others by a 3 m-buffer zone to avoid cross-contamination after tracer addition. Ground cover of all species in all 15 plots was estimated in spring 1991. No significant differences in stand characteristics, such as age, height and crown radius of trees, average distance between trees, and ground cover of all species,

were apparent among treatments at the beginning of the experiment (lowest $P = 0.12$).

Biomass measurements for Norway spruce were made in spring of 1990 (Buchmann 1993). Ten representative trees, 12 to 15 years old, 2.17 to 4.85 m tall, with an average spacing of 0.75 to 2.06 m, were used to develop allometric relationships. All 10 trees were separated into whorls, main and subsidiary branches. The number, length (total, needled, non-needled), diameter and bark thickness of the stem and all branches were measured. Each branch was then divided into different age classes. After drying for 48 h at 70 °C, needles and twigs were separated and dry weights recorded. Parameters that are easily measured in the field, such as absolute height and crown area were used to estimate the biomass of an individual tree (see Appendix 1). These parameters were measured for all 225 study trees in March 1991 (15 plots with 15 study trees each). Biomass data for newly grown tissues (0-year-old foliage and twigs, and stems) were collected at each individual sampling time, together with biomass data for the understory vegetation. Bark biomass was estimated after determination of the bark density (0.29 g/cm^3) and the bark volume of all study trees. To convert biomass per tree into tree biomass per plot or per m^2, the biomass of spruce tissues (needles, twigs, bark and stem wood) was summed for all 15 study trees per plot. To account for non-study trees in each plot, an average biomass per compartment was calculated (from n = 225) and added to the already known biomass of the study trees within a plot.

Understory biomass was determined at each sampling time (see below) by harvesting five 25 x 25 cm squares with 100% coverage by the different species. Leaves and branches of *D.flexuosa* and *C.vulgaris* were dried and weighed. Branches and leaves of *V.myrtillus* were separated before dry weight was measured. These values were then corrected for the actual ground cover of each species in each plot.

Total root biomass of Norway spruce was not directly measured to avoid soil disturbance, but data from allometric relationships between above- and below-ground biomass of young, open-canopy coniferous stands were used for root biomass estimation (Schulte-Bisping & Murach 1984: total root biomass = 29% of above-ground biomass; Vogt et al. 1987: fine root biomass = 27% of needle biomass). Roots with diameters <10 mm were estimated from biomass relationships of a 12-year-old spruce stand in the Hils mountains, Germany (fine and large roots = 50% of total root biomass, Schulte-Bisping & Murach 1984). Biomass of understory roots was estimated using data from Scandinavia and the Netherlands (Persson 1983; Fiala 1989; Aerts et al. 1992).

Table 1. Annual rainfall and atmospheric deposition (in g m^{-2} 7-month growing $season^{-1}$) in 1991 compared to the experimental treatments in March 1991 and the average long-term inputs between April and September (g m^{-2} 6-month $period^{-1}$, Türk 1992).

	Treatment additions	Deposition 5/91-10/91		Long-term average	
		Above the canopy	Below the canopy	Above the canopy	Below the canopy
mm	0.5	512	356	493	370
pH	nd	4.4	5.1	4.4	4.2
NH_4–N	0.06	0.35	0.18	0.54	0.74
NO_3–N	0.06	0.54	0.24	0.64	0.81
SO_4–S	<0.001	0.50	0.54	0.99	1.89
K	0.007	0.12	0.18	0.54	1.52
Mg	0.001	0.02	0.03	0.10	0.19

^{15}N *labeling*

In March, 1991, fifteen plots (two treatments and a reference with five plots as replicates) were treated with nitrogen solutions of 62 mg $^{15}N/m^2$ by simulating soil N input as a 0.5 L/m^2 rain event (Table 1). Highly enriched $^{15}NH_4Cl$ tracer (95%) was added as the ^{15}N-ammonium treatment to five plots, and 99% enriched $K^{15}NO_3$ tracer was applied to the five plots of the ^{15}N-nitrate treatment. The addition rate of ^{15}N tracers was calculated to increase the total ^{15}N pool of the ecosystem by 5% (Buchmann et al. 1995b). Non-enriched NH_4NO_3 (62 mg N/m^2) was added to the five reference plots. Lower branches of spruce trees were lifted from the ground to avoid foliar ^{15}N uptake during application. Spraying of tracer on dormant stems and branches of the dwarf shrubs (*C.vulgaris*, *V.myrtillus*) could not be avoided. The dominant grass *D.flexuosa* is a perennial species but new leaves had not emerged at this time. Plants might have taken up ^{15}N during tracer application, but the extent of above-ground uptake seemed to be small (Buchmann et al. 1995b). The comparison of water and nutrient input between the treatments and the natural atmospheric deposition shows that we avoided fertilizer effects (Table 1).

Sampling and analyses

All 15 plots were sampled six times during 1991 (March, April, June, July, September and November) and two times in 1992 (April and June). Five soil cores were taken (2 cm in diameter, 70 cm long) and five different cores for root sampling (7.5 cm in diameter, 20 cm long) at randomly chosen locations. Soil cores were divided into 6 soil depths (5–0, 0–5, 6–15, 16–25,

26–45, and 46–65 cm depth) and combined to form one composite sample per plot and per depth. Needles and twigs of different age classes, wood and bark of twigs and the stem were sampled from three randomly selected spruce trees per plot. Samples were taken from 6-year-old branches in the sun crown because they carried the highest percentage of twig (17%) and needle (18%) biomass. Leaves and twigs of the three understory species were collected at five different locations in each plot. Only green leaves were sampled for the grass *D.flexuosa*; app. 20 cm long twigs of the dwarf shrubs were cut and separated into leaves and wood for *V.myrtillus*. Three litter traps (0.15 m^2 each) were placed in two different positions in each plot (two below the canopy, one among the trees). Fruit bodies of fungi growing in all 15 plots were collected once in September 1991. Litter was collected monthly and separated into different litter fractions (spruce buds, needles and twigs, understory litter, and undefined).

Composite samples per plot of each sample type (except litter) were used for further analyses. Because the two different locations of the litter traps resulted in different litter amounts ($P < 0.001$, Buchmann 1993) these traps were analyzed separately and an area-weighted average was used for statistical analyses. After drying (70 °C for 48 h) and either grinding (plants and fungi) or sieving (soils, diameter <2 mm), the total N concentrations and the isotopic composition were determined by using an on-line-system combining an elemental analyzer (CARLO ERBA NA 1500) for Dumas combustion of the samples, and a FINNIGAN MAT delta E gas isotope mass spectrometer. Tissues of understory vegetation were rinsed with distilled water before drying to avoid measurement of ^{15}N deposited on or adsorbed at cuticles or bark.

Bulk precipitation was collected weekly from 10 collectors across the entire stand. Collectors consisted of funnels attached to the top of spruce trees with collecting bottles located below the crown and in the shade. Throughfall was collected weekly from three collectors in each plot. Two collectors were placed below the crown and one in the free space among the trees. Significant differences in rain volume and ion concentrations existed for throughfall collectors in different positions, therefore area weighted averages were calculated for throughfall deposition (Buchmann 1993). Ammonium and nitrate concentrations in the precipitation samples were measured by using a Flow Injection Analyzer (QuickChemAE, Lachat). Cations (potassium K^+, magnesium Mg^{++}) and sulfur (S) were determined in all samples with an ICP emission-spectrometer (JY 38P, Instruments S.A. Jobin-Yvon) after pressure digestion with HNO_3 at 160 °C for 6 h (Schramel et al. 1980, 1982).

N and ^{15}N calculations and tracer recovery

The N pools of the plant compartments were calculated by multiplying N concentrations with biomass for each sampling time. Natural ^{15}N abundance is noted in δ units (equation 1):

$$\delta^{15}N = (R_{Sample}/R_{Standard} - 1) * 1000 \quad (1)$$

where $R = {}^{15}N/{}^{14}N$ and atmospheric N_2 is the standard. The absolute ratio (R) of a sample is defined by rearrangement of Equation (1) (compare Boutton 1991) as:

$$R_{Sample} = {}^{15}N/{}^{14}N = (\delta^{15}N/1000 + 1) * R_{Standard} \quad (2)$$

^{15}N enrichment is either noted in δ units or as ^{15}N frequency in atom% (Equation (3)):

$$atom\% = F_{Sample} * 100 \quad (3)$$

where the fractional abundance F_{Sample} is defined by

$$F_{Sample} = {}^{15}N/({}^{15}N + {}^{14}N) = R_{Sample}/(R_{Sample} + 1) \quad (4)$$

^{15}N concentrations ($[^{15}N]$) in plant and soil materials were calculated separately for each plot and sampling time (Equation (5)) and corrected for natural ^{15}N abundance by subtracting the natural ^{15}N concentrations measured in the reference plots (mean from n = 5). ^{15}N concentrations of soil and plant materials were converted to an area basis, ($^{15}N/m^2$), by using Equations (6) and (7).

$$[{}^{15}N] = atom\% / 100 * [N] \quad (5)$$

with [N] = N concentration.

$$\text{Soil samples: } {}^{15}N/m^2 = [{}^{15}N] * d_B * h \quad (6)$$

with h = horizon depth and d_B = bulk density for the different soil horizons of an adjacent stand (Hantschel 1987).

$$\text{Plant samples: } {}^{15}N/m^2 = [{}^{15}N] * bio/m^2 * c \quad (7)$$

with bio/m^2 = biomass per unit ground area and c = ground cover

The total recovery rates after the ^{15}N-ammonium treatment varied between 81 and 101% in 1991, the first year of the experiment, and was 80% in 1992, the second year. After the ^{15}N-nitrate treatment, the total recovery ranged between 88 and 107% in 1991, and was 83% in 1992. The plot-to-plot

variations of total recovery rates were larger for the ^{15}N-nitrate (1 s.e. = 16% in 1991) than for the ^{15}N-ammonium treatment (1 s.e. = 10% in 1991), similar to the pattern observed for the δ^{15}N ratios.

Statistics

The independent sampling of all compartments of the stand was achieved by using random numbers for individual spruce trees and each square meter of a plot (for understory vegetation, roots and soil sampling). The statistical analyses of stand characteristics, biomass, δ^{15}N, N concentration, and N and ^{15}N budgets were done using analyses of variance with treatment, species, tissue, tissue age or depth as main factors (SPSS-PC+^{TM}, Norusis 1990). When the interaction term was not significant at the 0.05 level, the data were combined and analyzed together. The least-significant-difference-test (multiple-range-test, $LSD_{0.05}$) was used to separate among the means.

Results

Stand characteristics

Prior to treatment, above- and below-ground biomass in the ^{15}N application and reference plots were not significantly different ($P > 0.05$, Table 2). At the beginning of the growing season understory biomass (497 g/m^2) accounted for 27% of the stand's above-ground biomass while spruce accounted for the remaining 73% (1860 g/m^2). Although understory biomass almost doubled during the summer of 1991 (959 g/m^2), standing biomass never differed among the two treatments and the reference (Table 2). All species started the next year with a standing biomass similar to their July values (Buchmann 1993).

Natural nitrogen deposition via throughfall

Nitrogen input by bulk deposition and by throughfall was measured during the growing season in 1991. During these 7 months (April to October), total N deposition above the canopy was 0.89 g N/m^2 and thus exceeded the ^{15}N addition by a factor of 14 (see Table 1). Less than 50% of this N reached the soil surface as throughfall (0.42 g N/m^2) which still exceeded the ^{15}N addition by a factor of 7. The ratio of ammonium and nitrate in precipitation was 2:3 and remained fairly stable (Fig. 1) despite canopy interception and co-deposition of NH_3 and SO_2 gases (Burkhard 1994). K^+ and Mg^{++} deposition in throughfall increased compared to the bulk precipitation, indicating either

Table 2. Biomass (g/m^2) of *P.abies* and understory species at the beginning of the growing season, in April 1991. Above-ground biomass (except spruce stem) is also given for July 1991. Means and standard errors are given (n = 5 for the different treatments, n = 15 for the stand).

	^{15}N–NH_4^+ treatment plots	^{15}N-NO_3^- treatment plots	Reference plots	P^*	Stand
April 1991					
Above-ground	2414±214	2320±245	2338±191	.95	2357±117
P.abies	1900±244	1865±317	1815±200	.97	1860±139
needles[1]	647± 82	657±104	644± 66	.99	649± 46
twigs[2]	505± 65	511± 84	502± 52	.99	506± 37
stem wood	595± 84	542±111	510± 75	.81	549± 50
stem bark	153± 15	156± 25	160± 16	.97	157± 10
V.myrtillus[3]	367± 44	260± 39	373± 36	.12	333± 25
C.vulgaris	127± 47	173± 63	125± 20	.72	142± 26
D.flexuosa	20± 2	21± 4	25± 3	.57	22± 2
Roots[4]	357± 32	357± 44	361± 26	.99	358± 19
P.abies	260± 33	259± 43	253± 27	.99	257± 19
V.nyrtillus	21± 4	13± 2	19± 2	.17	18± 2
C.vulgaris	15± 6	21± 8	15± 2	.73	17± 3
D.flexuosa	61± 5	65± 11	74± 10	.57	66± 5
Total	2771±245	2677±289	2699±216	.96	2716±135
July 1991					
P.abies					
needles[5]	777± 82	791±104	778± 66	.99	782± 46
twigs[6]	547± 65	554± 84	543± 52	.99	548± 37
V.myrtillus					
twigs	515± 62	345± 55	523± 59	.30	467± 36
leaves	100± 12	71± 11	101± 10	.12	91± 7
C.vulgaris	225± 84	308±112	222± 36	.72	252± 46
D.flexuosa	136± 12	144± 24	166± 22	.57	149± 11

* *P*-values represent the results of one-way analyses of variance with treatment as main factor.
[1] 1 to 9 yr-old.
[2] 1 to 11 yr-old.
[3] twigs only.
[4] fine and large roots (diameter < 10 mm).
[5] 0 to 9 yr-old.
[6] 0 to 11 yr-old.

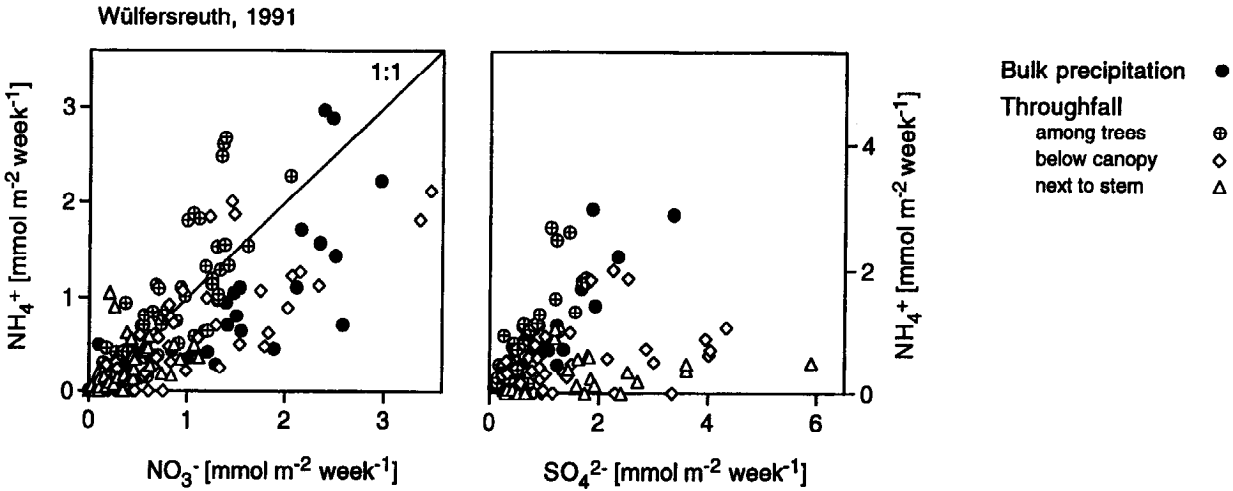

Figure 1. Relationships between nitrate or sulfate deposition and ammonium input in bulk precipitation and throughfall collected weekly from April through November 1991. Throughfall collectors were placed in three positions within each plot, among the trees, below the canopy and next to the tree stems. Area-weighted weekly averages are presented.

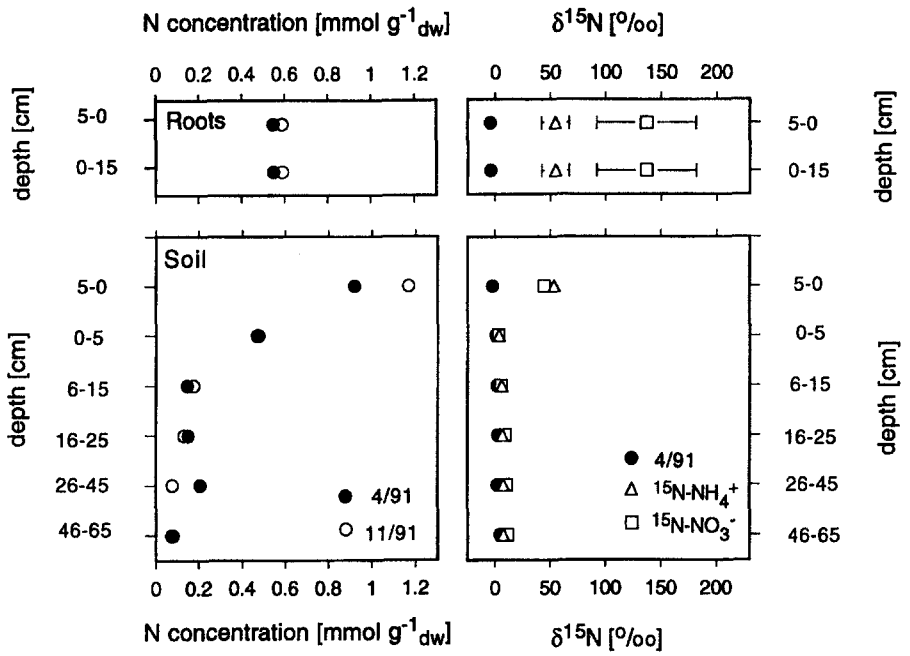

Figure 2. Nitrogen concentrations and $\delta^{15}N$ of soil and roots in April and November 1991. Means and standard errors are given (± 1 s.e.). n = 15 for the stand mean of N concentration and $\delta^{15}N$ in April and November 1991. n = 5 for $\delta^{15}N$ for both, the $^{15}N\text{-}NH_4^+$ and $^{15}N\text{-}NO_3^-$ treatment in November 1991. Symbol is larger than the error bar where error bar is absent.

dry deposition or leaching. Although the water volume decreased due to canopy interception, total sulfate deposition was higher below than above the canopy (Table 1) and the range of weekly deposition was larger in throughfall than in bulk precipitation (Fig. 1). One explanation for this observation could be that dry deposition on foliage was washed down and eventually measured as soil input.

N concentrations and $\delta^{15}N$ in different compartments of the ecosystem

Total N concentrations in the soil (Fig. 2) decreased with increasing depth for all three treatments ($P = 0.82$ for treatment as main factor) and showed no significant changes during the growing season 1991 ($P = 0.66$ for time as main factor). Prior to the tracer treatments, natural $\delta^{15}N$ ratios increased with depth from −2.2‰ in the organic horizon to +4.2‰ in 65 cm depth. No differences existed among the different plots. Tracer applications increased the $\delta^{15}N$ ratios in the organic horizon to 53‰ in the ^{15}N-ammonium and to 45‰ in the ^{15}N-nitrate plots (November 1991). Eight months after the tracer application, $\delta^{15}N$ in the deeper horizons (0.46 to 0.65 m depth) increased

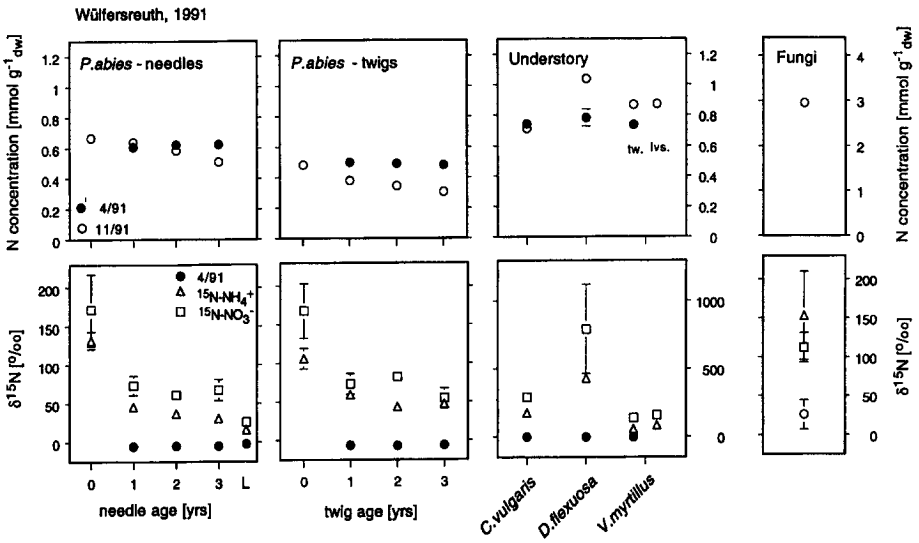

Figure 3. Nitrogen concentrations and $\delta^{15}N$ of different functional groups of organisms in the Norway spruce stand in April and November 1991 (except for fungi which were sampled in September 1991). Means and standard errors are given (± 1 s.e.). n = 15 for the stand mean of N concentration and $\delta^{15}N$ in April and November 1991. n = 5 for $\delta^{15}N$ for both, the ^{15}N-NH_4^+ and ^{15}N-NO_3^- treatment in November 1991. Symbol is larger than the error bar where error bar is absent.

from +4.2‰ to +7.3‰ in the ^{15}N-ammonium plots. A significantly higher increase from +4.2‰ to +11.0‰ was found on ^{15}N-nitrate plots.

Roots < 10 cm diameter for all plant species showed low N concentrations during the study period (Fig. 2). The mean $\delta^{15}N$ value of roots in 0–15 cm soil depth was −4.4‰ in April 1991, prior to the treatments, reflecting the isotopic signature of the surrounding soil in the main rooting horizon. After 8 months, $\delta^{15}N$ values increased after the ^{15}N-treatments to 55‰ (^{15}N-ammonium plots) and 137‰ (^{15}N-nitrate plots). The variability of the isotope signal was higher after the ^{15}N-nitrate treatment than after the ^{15}N-ammonium addition (1 s.e. 45.0‰ vs. 13‰, n = 5 each).

Mean foliar N concentration in spruce needles was 0.6 mmol N/g_{dw} during the 1991 growing season (Fig. 3). Despite these low N concentrations, tree and foliage growth of *P.abies* did not seem to be affected (Buchmann et al. 1995b). Natural $\delta^{15}N$ values were negative and increased slightly with needle age (−5.31‰ in 1-yr-old to −4.45‰ in 4-yr-old needles). Similar patterns were reported for older needles in other coniferous stands by Gebauer & Schulze (1991) and Gebauer & Dietrich (1993). After the tracer applications, the most enriched $\delta^{15}N$ ratios were found in 0-yr-old foliage (139‰ after the ^{15}N-ammonium additions and 210‰ after the ^{15}N-nitrate additions). A

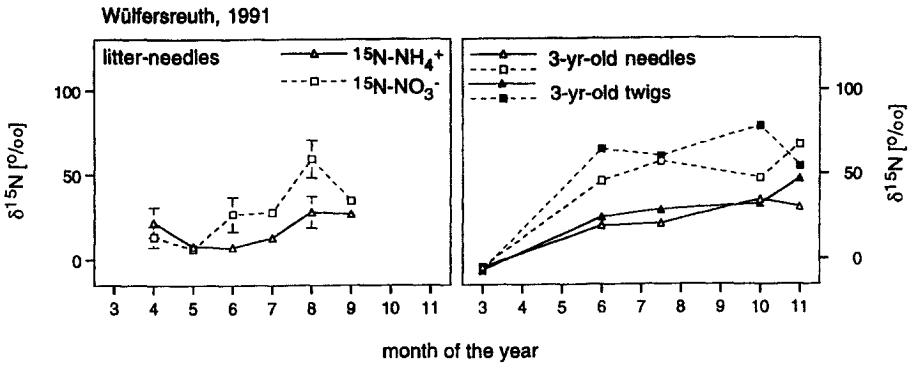

Figure 4. $\delta^{15}N$ of needle litter and 3-year-old needles and twigs during March and November 1991. Means and standard errors are given (± 1 s.e.; n = 5). Symbol is larger than the error bar where error bar is absent.

strong negative relationship between needle age and ^{15}N enrichment was found in needles and twigs during both growing seasons (Buchmann et al. 1995b). N concentrations were lower but $\delta^{15}N$ values were higher in twigs than in needles of the same age class ($P < 0.001$ for tissue type as main factor, except for 0-yr-old foliage). However, the seasonal course of tracer uptake was similar for both tissues (Fig. 4). N concentrations were significantly higher in twig bark (0.5 mmol N/g_{dw}) than in woody tissues (0.2 mmol N/g_{dw}), and $\delta^{15}N$ values of wood (73‰) were more positive than those of bark (50‰, $P < 0.001$, Buchmann 1993). Stem bark had similar N concentrations as twig bark (0.5 mmol N/g_{dw}), but $\delta^{15}N$ values of stem bark were more positive than those of twig bark prior to the tracer application (+2.35‰) and increased steadily during the 1991 growing season from 28‰ in June to 42‰ eight months later (means for both tracer applications, n = 10). The rapid uptake by spruce of the applied tracers could be seen one month after the ^{15}N application in the litter traps ($P = 0.03$, Fig. 4). Because up to 87% of the annual litterfall in 1991 consisted of spruce needles, $\delta^{15}N$ in litter increased throughout the growing season to become almost as positive as those of old spruce needles (Figs. 3 & 4).

All three understory species showed similar N concentrations of around 0.75 mmol N/g_{dw} in April 1991 (Fig. 3), which was higher than in spruce tissues. In November 1991, the grass *D.flexuosa* and the dwarf shrub *V.myrtillus* showed increased N concentrations whereas *C.vulgaris* did not change significantly. Prior to tracer application, natural $\delta^{15}N$ values of dormant twigs were negative, −2.34‰ for *C.vulgaris* and −4.87‰ for *V.myrtillus*. The grass *D.flexuosa* had a mean $\delta^{15}N$ value of −3.36‰. Leaves of *V.myrtillus* showed N concentrations similar to twigs but retained more ^{15}N

than twigs. After 8 months, the nitrogen isotopic composition of *V.myrtillus* leaves was 83‰ for the ^{15}N-ammonium treated plants and 158‰ for the ^{15}N-nitrate plants. The δ^{15}N values of twigs of the dwarf shrub *V.myrtillus* were less positive than those of leaves, with values of 55‰ in ^{15}N-ammonium treated plots and 137‰ in ^{15}N-nitrate treated ones. δ^{15}N of *C.vulgaris* increased to 174‰ on ^{15}N-ammonium treated plots and to 292‰ on ^{15}N-nitrate plots. The most enriched δ^{15}N values were measured for *D.flexuosa*, where δ^{15}N increased from −3.36‰ to 429‰ after ^{15}N-ammonium addition and to 792‰ after ^{15}N-nitrate addition. However, above-ground uptake into evergreen leaves cannot fully be excluded. As seen in the other compartments, the ^{15}N-nitrate plots showed higher variability than the ^{15}N-ammonium plots.

At all sampling times, soils and plants in reference plots did not exhibit any sign of ^{15}N enrichment due to adjacent ^{15}N-treated plots. However, nitrogen isotopic composition of fruit bodies of fungi (*Dermocyte semisanguinea*, *Dermocyte spec.*, *Hygrophoropsis aurantiaca*, *Lactarius spec.*, *Paxillus involutus*) in the reference plots ranged between +7 and +63‰ in September 1991, 6 months after tracer application (Fig. 3). In ^{15}N-treated plots, δ^{15}N ratios were even more enriched and ranged from 71 to 404‰ in ^{15}N-ammonium plots and from 32 to 183‰ in ^{15}N-nitrate plots. Nitrogen concentrations in fungi were the highest among all investigated tissues (Fig. 3). Fungi were the only compartment of the ecosystem in which the ammonium tracer yielded higher ^{15}N enrichments than the nitrate tracer.

N and ^{15}N budgets of the P.abies stand 8 months after tracer application

The total amount of nitrogen stored in the understory vegetation was as high as in spruce trees (Table 3) despite the smaller understory biomass (see Table 2). Both spruce and understory species accounted for about 10 g/m^2 or 44% of the nitrogen found in plant compartments (Table 3). Due to its higher biomass, the dwarf shrub *V.myrtillus* contained more then twice the amount of N per unit ground area than *C.vulgaris* (6.7 g N/m^2 vs. 3.0 g N/m^2). The grass *D.flexuosa* accounted for only 3% of the understory N (0.3 g N/m^2). Because biomass per ground area was different among these three species (see Table 3), N taken up by *C.vulgaris* was lowest (9.32 mg N/g dry weight), was intermediate for *V.myrtillus* (12.06 mg N/g) and was greatest for *D.flexuosa* (14.53 mg N/g) (Fig. 3, November 1991). The largest N pool in the ecosystem was the soil. More than 98% of all nitrogen stored in this ecosystem was found in the soil profile, more than 10% in the organic horizon alone (5-0 cm).

The ^{15}N partitioning of both ^{15}N tracers in the Norway spruce stand did not follow the total N distribution (Table 3). While only 1.5% of the total N was found in plant tissues (23.7 g N/m^2), 16% of the ^{15}N-ammonium and 25% of the ^{15}N-nitrate tracers were detected in the above- and below-ground biomass

Table 3. Nitrogen and ^{15}N tracer budget for the *P.abies* stand 8 months after tracer application (November 1991). Percentage values were calculated for nitrogen with the entire stand as 100% and for the ^{15}N treatments with the tracer input as 100%. Means and standard errors are given (n = 15 for the nitrogen budget, n = 5 for each of the ^{15}N treatments). nd = not detectable.

			^{15}N tracer retained			
	Nigrogen		^{15}N-NH_4^+		^{15}N-NO_3^-	
	g/m^2	%	mg/m^2	%	mg/m^2	%
P.abies	10.48±0.82	0.65	2.09±0.35	3.4±0.6	4.19±0.99	6.5±1.6
needles + twigs[1]	9.21±0.66	0.58	1.95±0.42	3.2±0.7	3.80±0.98	6.1±1.6
stem bark	1.06±0.11	0.07	0.14±0.04	0.2±0.1	0.39±0.11	0.6±0.2
stem wood	0.21±0.02	0.01	nd	nd	nd	nd
Understory:	10.04±0.81	0.63	5.64±1.15	9.1±1.9	9.65±1.53	14.8±2.5
V.myrtillus	6.72±0.67	0.42	2.71±0.81	4.4±1.3	3.27±0.76	5.0±1.2
C.vulgaris	3.00±0.67	0.19	2.50±1.32	4.0±2.1	4.86±2.00	7.5±3.2
D.flexuosa	0.32±0.03	0.02	0.43±0.06	0.7±0.1	1.52±0.49	2.3±0.8
Litter	0.21±0.02	0.01	0.014±0.001	0.03±0.01	0.02±0.01	0.04±0.02
Roots[2]	2.95±0.19	0.18	0.63±0.33	1.0±0.2	2.14±2.18	3.5±1.6
Plant totals	23.68±0.67	1.47	8.37±1.0	13.5±2.0	16.0±0.75	24.8±3.2
Soil:	1576±193	98.53	54.0±3.7	87.1±7.6	48.9±6.1	78.9±9.0
organic horizon	164±8	10.25	38.8±10.1	62.6±0.1	28.7±14.0	46.3±0.1
mineral soil[3]	1412±185	88.28	15.2±4.0	24.5±0.1	20.2±3.8	32.6±0.1
Stand	1600	100	62.37	100.5	64.90	103.7

[1] 0- to 11-yr-old foliage.
[2] roots with diameter < 10 mm.
[3] 0–65 cm depth.

of plants. Labeling the soil N input with ^{15}N tracer simulates throughfall deposition. Therefore retention of the ^{15}N tracers by any compartment of the ecosystem will reflect the relative partitioning of ammonium and nitrate-N input entering the soil. 87% of the tracer input in ^{15}N-ammonium treated plots and 79% in ^{15}N-nitrate treated plots were retained in the soil, mainly in the organic horizon (Table 3), where 63% of the ammonium and 46% of the nitrate label were found. Only 25% of the ^{15}N-ammonium and 33% of the ^{15}N-nitrate were transported into mineral horizons (0–65 cm depth) at the end of the 1991 growing season. However, 16% of both the ^{15}N-ammonium and the ^{15}N-nitrate tracers was found below 25 cm by November 1991, eight months after the tracers were applied. This 16% corresponds to a decreased

recovery rate of about 20% from 94% to 80% for ^{15}N-ammonium and from 100% to 83% for ^{15}N-nitrate until June 1992, 15 months after labeling and might indicate loss to groundwater.

Among the plant compartments, the understory vegetation was the main sink for ^{15}N. 9% of the ^{15}N-ammonium and 15% of the ^{15}N-nitrate input were retained by the understory. Similar amounts of ^{15}N-ammonium were taken up by the two ericaceous dwarf shrubs *V.myrtillus* and *C.vulgaris* (4%, Table 3), but ^{15}N-nitrate uptake was higher for *C.vulgaris* (7.5%) than for *V.myrtillus* (5.0%). Only between 1 and 2% of the tracers were retained by the grass *D.flexuosa*. However, ^{15}N-concentrations were much higher for the grass than for both dwarf shrubs (Fig. 3). Despite higher biomass and ground cover, *P.abies* retained less ^{15}N than the understory vegetation (Table 3). Only 3% of the ammonium tracer and 7% of the nitrate tracer were assimilated in spruce tissues, mainly in needles and twigs. Negligible amounts of the tracers (less than 0.05%) were detected in the litterfall of 1991, which was mainly composed of spruce needles. Incorporation into plant roots accounted for 1% of the ^{15}N-ammonium and 4% of the ^{15}N-nitrate input.

Seasonality of ^{15}N retention

The temporal variability of the ^{15}N retention among the different compartments of the ecosystem (Fig. 5) did not change the overall distribution pattern described above. ^{15}N retention in the soil remained stable at approximately 79% in the first year and dropped to 70% in 1992 for the ^{15}N-ammonium tracer. Recovery rates averaged 72% and decreased to 64% during the second summer in the ^{15}N-nitrate treated plots. ^{15}N retention in spruce tissues increased slightly during the growing season 1991 from 2.5% in June to 3.4% in November, and to 3.6% in June 1992 in the ^{15}N-ammonium treated plots. ^{15}N-nitrate treated plots showed a similar trend with increasing ^{15}N retention from June 1991 (6.2%) to November 1991 (6.5%) to June 1992 (6.9%). The temporal pattern was different for the understory vegetation. ^{15}N uptake increased between June and July 1991, from 8.8 to 14.5% in ^{15}N-ammonium treated plots and from 19.4 to 23.4% in ^{15}N-nitrate treated plots. Due to litter fall, ^{15}N retention by the plants decreased in November 1991. 9.1% of ^{15}N-ammonium and 14.8% of ^{15}N-nitrate was stored in the understory vegetation at the end of the season. Percentages of ^{15}N input stored during the second summer were lower than for the previous summer, 6.3% for ^{15}N-ammonium and 11.9% for ^{15}N-nitrate treated plots.

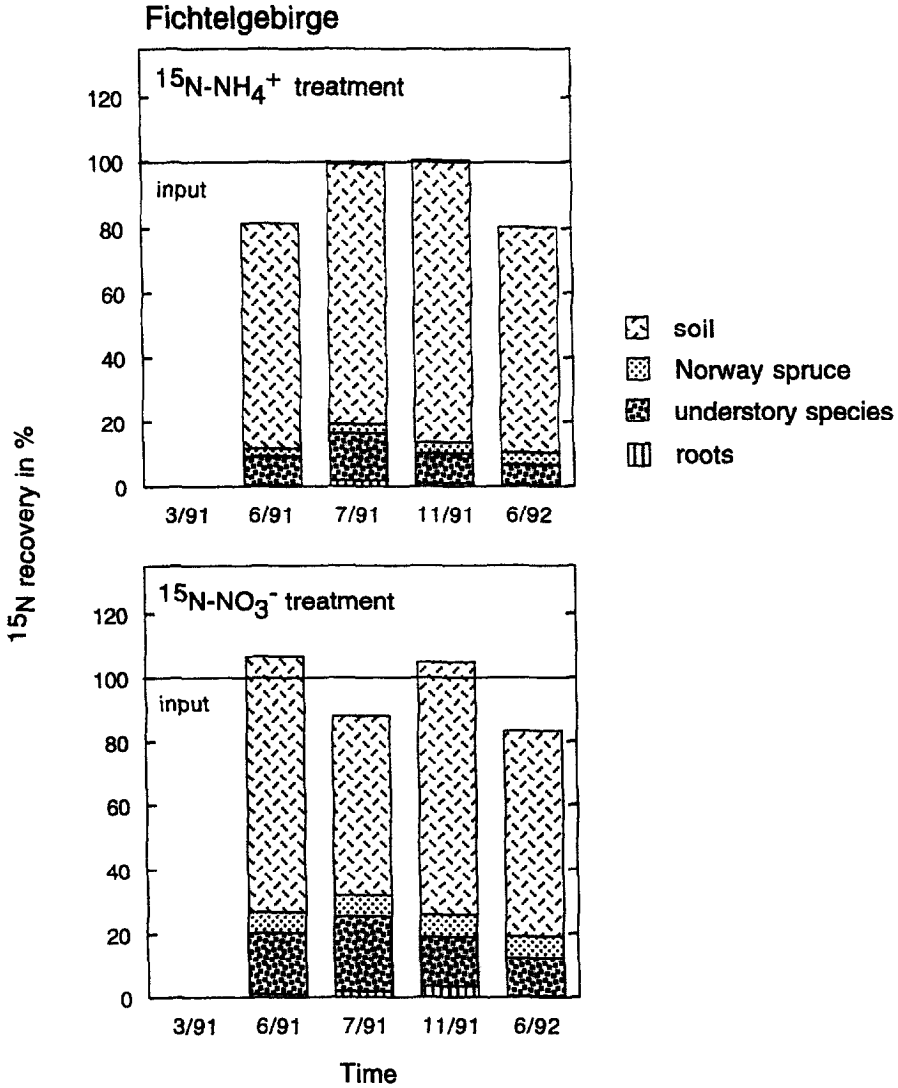

Figure 5. Seasonal changes of the ^{15}N recovery rates in different compartments of the stand, 3 to 15 months after the ^{15}N-ammonium (top) and the ^{15}N-nitrate treatments (bottom). Soil includes organic and mineral horizons to 0.65 m depth. All tissues of spruce and the understory species are summed up and presented in the individual bars. Roots are combined for all four species and represent fine roots only.

Discussion

Labeling the soil N input with ^{15}N-ammonium and ^{15}N-nitrate, thus avoiding canopy interception, enabled us to follow the pathways of nitrogen deposition

in a *P.abies* plantation and to determine the major sinks for wet N deposition for both inorganic forms of N. The retention of ^{15}N-ammonium and ^{15}N-nitrate among different compartments of the stand reflects the relative partitioning of ammonium and nitrate-N deposition as influenced by physico-chemical and physiological processes of the internal nitrogen cycle within the ecosystem. However, it should be clearly stated that the partitioning of ^{15}N-ammonium and ^{15}N-nitrate tracers, applied in equal molar quantities, does not directly represent the total N uptake by the vegetation. Because the ammonium tracer was diluted 9:1 in the soil solution, this dilution factor has to be considered before calculating total N uptake (Buchmann et al. 1995b).

During two growing seasons, the largest sink for the ^{15}N label was the soil, where between 79 and 87% of the simulated N input was found after 8 months. Nadelhoffer et al. (1992) report similar results for a ^{15}N-ammonium tracer study in a hardwood mixed forest where 67% of the ^{15}N-input was found in the surface soil (0-5 cm) after one growing season. These results are consistent with the model of Aber et al. (1991) who modeled the fate of N under "nitrogen saturation" conditions and predicted that a large percentage would be held in the soil organic matter. Eight months after tracer application, we found 46 to 63% of the ^{15}N tracers in the organic horizon, suggesting high microbial N immobilization. Nadelhoffer et al. (1995) reported that the forest floor retained about 30% more ^{15}N-nitrate than the 0-5 cm mineral soil, probably due to soil micro-organisms. This pattern was also found with soil cores held under controlled moisture and temperature conditions (Coûteaux & Sallih 1994) where retention of inorganic N tracers was highest in the organic horizons of six different coniferous forest soils, and was mainly stored as organic nitrogen. In a short-term experiment, Groffman et al. (1993) traced ammonium and nitrate in a temperate forest in Michigan, USA. They found higher immobilization rates for ammonium (60%) than for nitrate (48%) in well-drained forest soils and concluded that the key factor regulating the fate of ammonium and nitrate was microbial biomass. In accordance with Groffman et al. (1993), we found more ammonium than nitrate in the organic horizon (63 vs. 46% of the input). Higher immobilization of ammonium and also adsorption onto exchange sites of organic matter and clay minerals retains more ammonium, whereas nitrate is lost to the groundwater. This could be seen after 8 months, when more nitrate than ammonium tracer was found in deeper soil horizons (33% vs. 25% of the input), indicating nitrate leaching and loss from the ecosystem (Hantschel 1987; Türk 1992; Durka et al. 1994). After 15 months, tracer amounts decreased in the organic horizon while total ^{15}N amounts in the mineral soil remained almost constant. Volatilization of ammonia and denitrification (Schmitt 1994) cannot account for the observed differences due to the very low pH values in these soils. However, Preston &

Mead (1995) suggested that the release of ^{15}N by mineralization from labeled litter might slow with time, and that ^{15}N stabilizes in increasingly recalcitrant forms, which are much less available for micro-organisms.

Plants were, in general, a much weaker sink for the nitrogen deposition than the soil. Our recovery rates of 14% of ^{15}N-ammonium and 26% of ^{15}N-nitrate label match well with the range of rates reported in other tracer studies (Nômmik 1966; Mead & Pritchett 1975a,b; Nambiar & Bowen 1986; Preston & Mead 1990; Emmett & Quarmby 1991; Mead & Preston 1994; Nadelhoffer et al. 1995). The unexpected low amount of ^{15}N retained by *P.abies* indicates the high nitrogen competition between the dominant tree and the understory species. Differences among life forms become obvious when comparing the grass *D.flexuosa* with the ericaceous shrubs *C.vulgaris* or *V.myrtillus*. Although *D.flexuosa* showed highest ^{15}N concentrations within the understory, the grass retained less ^{15}N per square meter due to lower biomass. Different rooting patterns and sink strengths of the understory species might be responsible for these observations. Differences in N uptake might explain results from Petersen (1988), who showed that pine trees growing in monocultures produced 4-5 times more biomass than trees growing together with the grass *Calamagrostis rubescens*. However, the competition of different members within a plant community, as reflected in 2-3 times higher tracer retention in the understory vegetation (9 to 16% in the understory) than in the dominant spruce (3 to 7%), might also pose nutritional problems to individual species (Buchmann et al. 1995a). However, the long-term community structure will be influenced not only by access to nutrient resources but also by the trees' ability to compete for light by increased shading of the lower vegetation and by the establishment of a closed canopy.

The increased ^{15}N recovery rates in spruce tissues during the 15 months after tracer application suggest a constantly increasing supply from soil ^{15}N pools, even compensating for the increase in biomass. However, understory vegetation does not seem to access the same N pools as spruce because recovery rates in understory plants decreased over time. This observation may be evaluated in context of the "vernal dam" hypothesis, originally proposed by Muller & Bormann in 1976. Spring ephemeral plants and soil microbial communities act as a buffer reducing N loss with snow melt due to early spring N uptake and short-term N immobilization. In our tracer study, total ^{15}N recovery rates stayed very high throughout the experimental period, indicating high overall N retention within the system (Fig. 5). Furthermore, the seasonal course of ^{15}N uptake from ammonium and nitrate in the soil solution by *P.abies* showed a very sharp increase right after tracer application (Buchmann et al. 1995b), followed by a relatively flat but steadily increasing seasonal course. This was attributed to either successful competition for nutri-

ents by micro-organisms (Schimel & Firestone 1989; Davidson et al. 1990; 1992; Jamieson & Killham 1994; Nadelhoffer et al. 1995) or to a secondary slow release of immobilized tracers from microbial and understory biomass. Although the original hypothesis was proposed for short-term immobilization in spring with a subsequent slow release, this finding might be more general (see Zak et al. 1990).

Another aspect of N competition is added to this system by the presence of fungi. While Gebauer & Dietrich (1993) measured natural $\delta^{15}N$ values between −3.5 and +2.3‰ for different fungi species in the same study area, our $\delta^{15}N$ values of fruit bodies collected in the reference plots were highly enriched (+7 to +63‰). This might be due to a widespread mycelium and ^{15}N transport across the 3 m-buffer zone among plots. Sink strength of fungi seems to be high as indicated by their high N concentrations (3 mmol N/g_{dw}). However, the nitrogen isotopic composition of reference plants was not elevated, suggesting that ^{15}N tracer sequestered by fungi was not transferred to the plants. A re-sampling after several years may give more information about this phenomenon.

All ^{15}N-tracer studies known to us demonstrated the importance of soil and soil micro-organisms in the retention of ammonium and nitrate-N deposition on very different spatial scales (soil core, pot, plot, watershed) and temporal levels (days, weeks, months, years) as well as with different levels of disturbance (Matson et al. 1987). While most of these studies focused on either one form of N or one ecosystem compartment, we tried to integrate all these factors. In this ^{15}N tracer study, the organic soil horizon was identified as the major N sink for ammonium and nitrate deposition in a *P.abies* plantation, reflecting a high immobilization capacity of soil microorganisms. The observed temporal movement of ^{15}N tracer through the soil profile corresponded well with a decrease in the second year's recovery rate as well as with estimates of the leaching rates of deposited nitrate (Durka et al. 1994). The higher ^{15}N retention of the understory vegetation compared to Norway spruce during the first 8 months after labeling, indicated the strong competition for N between understory and dominant tree species and the influence of community structure on the internal N cycling of an ecosystem. Furthermore, the high enrichment of fungi growing in reference plots raised questions about long-term transfer among different organisms within an ecosystem. ^{15}N tracer studies can be used to increase our knowledge about N resource use of organisms, such as understory vegetation or fungi, and contribute to our understanding of ecosystem N budgets and changes in internal N dynamics.

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Appendix 1. Regression analyses for different biomass compartments of *P.abies* (biomass in g_{dw}/tree).

Dependent Variable	Equation*	r^2 adjusted
Stem (wood & bark)	$y = 10^{(2.43-0.0032*x1+0.063*x2)}$	.956
Branches (1- to 6-yr-old, wood & bark)	$y = -92.145 + 97.31 * x2$	.889
Total wood & bark	$y = 839.705 + 401.513 * x2 - 817.634 * x3$	.986
Needles (1 to 6-yr-old)	$y = -33.390 + 119.063 * x2$	.930
Needles (1-yr-old)	$y = 201.788 + 3.837 * x1$	.930
(2-yr-old)	$y = 10.295 + 32.633 * x2$	.900
(3-yr-old)	$y = -655.850 + 340.613 * x4$	.920

with

x1 = absolute height [m] * crown area^2 [m^2],
x2 = absolute height [m] * crown area [m^2],
x3 = crown area [m^2]
x4 = absolute height [m]

* Stepwise regression. The independent variables x1 to x4 were calculated using data collected in April 1991. The biomass of the stem bark was estimated by using bark density (0.29 g/cm^3) and bark volume. The difference between the total biomass of the stem and the stem bark resulted in the biomass of stem wood.