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N deposition, N transformation and N leaching in acid forest soils

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Abstract. Nitrogen deposition, mineralisation, uptake and leaching were measured on a monthly basis in the field during 2 years in six forested stands on acidic soils under mountainous climate. Studies were conducted in three Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] plantations (D20: 20 year; D40: 40 yr; D60: 60 yr) on abandoned croplands in the Beaujolais Mounts; and two spruce (*Picea abies* Karst.) plantations (S45: 45 yr; S90: 90 yr) and an old beech (*Fagus sylvatica* L.) stand (B150: 150 yr) on ancient forest soils in a small catchment in the Vosges Mountains. N deposition in throughfall varied between 7–8 kg ha^{-1} year^{-1} (D20, B150, S45) and 15–21 kg ha^{-1} yr^{-1} (S90, D40, D60). N in annual litterfall varied between 20–29 kg ha^{-1} (D40, D60, S90), and 36–43 kg ha^{-1} (D20, S45, B150). N leaching below root depth varied among stands within a much larger range, between 1–9 kg ha^{-1} yr^{-1} (B150, S45, D60) and 28–66 kg ha^{-1} yr^{-1} (D40, S90, D20), with no simple relationship with N deposition, or N deposition minus N storage in stand biomass. N mineralisation was between 57–121 kg ha^{-1} yr^{-1} (S45, D40, S90) and between 176–209 kg ha^{-1} yr^{-1} in (B150, D60 and D20). The amounts of nitrogen annually mineralised and nitrified were positively related. Neither general soil parameters, such as pH, soil type, base saturation and C:N ratio, nor deposition in throughfall or litterfall were simply related to the intensity of mineralisation and/or nitrification. When root uptake was not allowed, nitrate leaching increased by 11 kg ha^{-1} yr^{-1} at S45, 36 kg ha^{-1} yr^{-1} at S90 and between 69 and 91 kg ha^{-1} yr^{-1} at D20, D40, B150 and D60, in relation to the nitrification rates of each plot. From this data set and recent data from the literature, we suggest that: high nitrification and nitrate leaching in Douglas-fir soils was likely related to the former agricultural land use. High nitrification rate but very low nitrate leaching in the old beech soil was related to intense recycling of mineralised N by beech roots. Medium nitrification and nitrate leaching in the old spruce stand was related to the average level of N deposition and to the deposition and declining health of the stand. Very low nitrification and N leaching in the young spruce stand were considered representative of fast growing spruce plantations receiving low N deposition on acidic soils of ancient coniferous forests. Consequently, we suggest that past land use and fine root cycling (which is dependent on to tree species and health) should be taken into account to explain the variability in the relation between N deposition and leaching in forests.

Abbreviations: CEC – cation exchange capacity; IER – ion exchange resin; L, F and H – organic sublayers; N – nitrogen

Introduction

Nitrogen plays a major role in the diversity and the stability of ecosystems (Tamm 1986; Bobbink and Roelofs 1995; Hornung and Reynolds 1995), and in the nutrition and productivity of forest stands (Nadelhoffer et al. 1985). In areas with low anthropogenic N inputs under cold or temperate climate, nitrogen nutrition of forest stands is usually a limiting factor (Keeney 1980; Nadelhoffer et al. 1992). Instead, in polluted areas, atmospheric deposition of nitrogen compounds often exceeds stand requirements (Aber et al. 1989; Cole 1992; Gundersen 1992). Over a wide range of sites and deposition values, there is a general correlation between N deposition, N nutrition and N leaching (Gundersen et al. 1998a).

However, especially for intermediate values of deposition (10–20 kg ha^{-1} yr^{-1}), there is no simple correlation between N deposition, N availability and N leaching. In fact, the fate of nitrogen inputs depends on the interactions between each flux of the nitrogen cycle. Among these fluxes, the assessment of nitrification is of critical importance because the leaching of N is in the form of nitrate. In acidic soils, nitrification is favoured when soil pH increases and C:N decreases (Gundersen et al. 1998b; Persson et al. 2000a). However, apart from extreme conditions, net nitrification in the mineral soil cannot be easily predicted from its chemical composition (Persson et al. 2000a).

Our study was designed to measure and compare the major N fluxes in various forest ecosystems which are representative of very large forested areas on acid soils in the mountainous climate range of France. The aim was to discuss the relationships between ecosystem characteristics, N deposition, N mineralisation and nitrification. Moreover, past land use was considered because most forest soils in France, especially in the plantations, have been used for agriculture in the past (Cinotti 1996). Various effects of previous agricultural land use on forest soil properties have been described (Glatzel 1991; Hüttl and Schaaf 1995; Koerner et al. 1997), and a few studies describe a long term effect on nitrification activity (Compton and Boone 2000; Jussy et al. 2002) and on nitrate leaching (Feger 1992).

Material and methods

Stand characteristics

Six experimental plots were selected in two long-term experimental sites: the Strengbach catchment at Aubure (Probst et al. 1990), and the Aiguillettes forest at Vauxrenard (Ranger et al. 1995). Climate at the two sites is mountainous with an oceanic influence. At Vauxrenard, the elevation is lower (750 m v.s. 1050 m), temperature is higher (7 °C v.s. 5.4) and precipitation is lower (1000 mm v.s. 1300 mm) than at Aubure. Precipitation is evenly distributed throughout the year, part of it falling as snow from November to April.

Two spruce (*Picea abies* Karst.) plantations, one 90-years old (S90) and one 45-years old (S45), and a 150-year-old beech (*Fagus sylvatica* L.) stand (B150), were studied at Aubure (Vosges Mountains, France). The two adjacent spruce stands were facing south, whereas the beech stand was oriented toward the north and received higher precipitation (200 mm more, on average). Slopes were <20%. At Vauxrenard (north-east Massif Central, France), three adjacent Douglas-fir [*Pseudotsuga menziesii*

(Mirb.) Franco] plantations, aged 20-years (D20), 40-years (D40) and 60-years (D60) were studied. Slopes were gentle, always <5%. General stand characteristics are shown in Table 1. Stands S45 and S90 were Mg deficient and S90 was strongly defoliated. No understorey vegetation was present under the younger stands at each site (D20 and S45) because of their high density. The other stands of the Strengbach catchment had sparse understorey vegetation with patches of *Deschampsia flexuosa* and *Dryopteris filix-mas* at S90, and patches of *Dryopteris dilatata* and *Athyrium filix-femina* at B150. *Rubus fructicosus* formed patches in stands D40 and D60 at Vauxrenard. The LF sublayer was always thin (Table 1), between 1 and 3 cm. The C:N ratio of the FH sublayer increased from 17 to 24 with the age of the stand at Vauxrenard. At Aubure, it was lower in the beech stand (21) compared to the spruce stands (25–26).

At Aubure, soils developed from Brézouard granite, which is very poor in calcium and magnesium. At Vauxrenard, the bedrock is a tuff from the Upper Visean (Carboniferous), relatively rich in calcium and magnesium (Ezzaïm 1997). However, the fast specific weathering process of the amorphous phase of this bedrock leads to fine earth very poor in base cations. All soils were formed of weathering-resistant minerals, and were acidic with relatively low clay content, low pH and base saturation (Table 2). As the climate is more humid and cold, and the bedrock is poorer in base cations at Aubure, soils are more acid with higher C:N and podzolisation is more developed.

Stand histories

The three Douglas-fir stands comprised first rotations of this species. D20 and D40 were reforested after spruce plantations (from 1930 to 1975 for D20 and from 1870 to 1955 for D40). Prior to the spruce plantation, D20 was abandoned cropland and D40 was fallow land. D60 was afforested directly from abandoned (Table 1).

The history of B150 is known as far back as 1750, when it was forested with beech and fir (Archives Départementales du Haut Rhin C 1157 No. 14 1752). It was intensively managed as a coppice stand until 1874 and may have been grazed. Eleven thousand beech were planted in the area in 1846 but it is uncertain whether this planting involved the study plot. The two spruce stands are plantations following mixed fir and beech forest. The planting dates were around 1890 for S90 and 1950 for S45. The previous old forest at stand S90, close to the hill crest, was widely opened and probably grazed during the 19th century (Jussy et al. 2001).

N input–output fluxes

Biomass of foliage, branches, bole, stump and root (>2 mm diameter), as well as associated mineral content were measured in the different stands (Dambrine et al. 1991; Le Goaster et al. 1991; Ranger et al. 1995; Marques and Ranger 1997; Marques et al. 1997). Growth of branches, bole and stump were calculated from mathematical models integrating biomass and nutrient content. At B150 and S90,

Table 1. Stand characteristics at Aubure (S45, S90 and B150) and Vauxrenard (D20, D40 and D60).

Stand	S45[1]	S90[1]	B150[1]	D20[2]	D40[2]	D60[2]
Species	Spruce	Spruce	Beech	Douglas-fir	Douglas-fir	Douglas-fir
Age (years)	45	90	150	20	40	60
Tree density (trees ha^{-1})	2200	568	352	922	490	312
Mean circumference at 1.3 m (cm)	49	128	110	57	105	164
Mean tree height (m)	13	28	22	14	28	36
Basal area ($m^2 ha^{-1}$)	42	72	43	24	47	65
Stand health	Mg deficient 15% needle loss	Mg deficient 30% needle loss	Good	Good	Good	Good
Stand history	Beech and fir forest	Grazed forest	Grazed coppice	Second generation after crop	Second generation after fallow	First generation after crop
Ground vegetation	None	Grass, ferns (patches)	Ferns (sparse)	None	*Rubus fructicosus* (patches)	*R. fructicosus* (patches)
Soil type[3]	Dystric cambisol	Dystric cambisol	Haplic podzol	Dystric cambisol	Dystric cambisol	Dystric cambisol
Organic layer (L + F) thickness (cm)	3	1	2	2–3	1	1–2
Organic layer (F + H) C:N	25	26	21	17	20	24

[1] Le Goaster et al. (1991), Persson et al. (2000b).
[2] Ranger et al. (1997).
[3] FAO-UNESCO (1975).

Table 2. Physico-chemical characteristics of upper mineral soil (data from Poswa 1996 for S45 and S90; from Lefèvre, personal communication for B150; and from Marques 1996 for D20, D40 and D60).

Stand	Depth (cm)	pH_{H_2O}	OM[1] (%)	C:N	Ca[2]	K[2]	Mg[2]	Al[2]	BS[3] (%)	δ ^{15}N (‰)	Clay (%)	Silt (%)
S45	0–8	3.5	8.4	16.6	0.2	0.3	0.1	8.0	6	1.57 ± 0.12	14	20
S90	0–10	3.5	7.1	15.5	0.3	0.5	0.2	8.9	8	0.36 ± 0.34	20	23
B150	0–6	3.7	8.3	18.5	0.8	0.3	0.3	5.4	15	-0.36 ± 0.13	11	22
D20	0–12	4.2	8.5	12.4	0.8	0.3	0.2	7.2	15	3.32 ± 0.02	19	52
D40	0–15	4.4	5.7	12.3	0.4	0.2	0.1	6.6	9	2.66 ± 0.20	20	44
D60	0–10	4.3	8.2	12.8	0.6	0.3	0.2	5.8	15	3.32 ± 0.28	22	40

[1] OM: organic matter.
[2] meq $100\,g^{-1}$.
[3] BS: base saturation.

fine root biomass (<2 mm) and root nutrient pools were determined on soil cores collected from 15 randomly located points (Scarascia-Mugnozza et al. 2000), five times a year. Dry weight of live fine roots was measured after sieving and separating live from dead roots. Root growth and root turnover measurements were made using root window observations and sequential soil coring (Stober et al. 2000). Above-ground understorey biomass was determined at D60 in 1998 by destructive sampling of vegetation on 19-1 m^2 plots.

N deposition to the soil was collected in each stand by a set of 2–3 throughfall collectors, each composed by double gutters (2.17 m × 0.12 m each). At Vauxrenard during winter they were replaced by plastic bags placed in buckets (0.39 m diameter) 1.3 m above the soil level. In addition, simple gutters (2.0 m × 0.2 m) with a heating system to melt snow were used in D40 and S95. Seepage water was collected in 2–8 zero-tension lysimeters per stand, which were placed at 10 or 15 cm depth and 60 cm depth (see Probst et al. 1990; Marques et al. 1997). Samples were protected from light and temperature variation. Sampling occurred once or twice a month depending on the season. After filtering the samples (0.45 μm porosity), NH_4^+-N and NO_3^--N concentrations were measured colorimetrically (autoanalyser II, Technicon, Dublin), or by ionic chromatography (DX-300, Dionex, California, USA). Inputs and leachings of mineral N were calculated as the product of the water flux (throughfall and soil leaching respectively) and NO_3^--N and NH_4^+-N concentrations in the solutions. Drainage was calculated with a water model using the climatic data of the sites, stand structure and soil water retention curves (Granier et al. 1999). Potential evapotranspiration was computed from climatic parameters continuously recorded at the sites.

N mineralisation, nitrification and uptake: in situ *incubation*

The *in situ* incubation experiment took place from October 1994 to October 1996. Cores of undisturbed soil were incubated in nine stainless steel cylinders (7.6 cm inner diameter, 15 cm long) in each stand (Lemée 1967, Raison et al. 1987). Cylinders were placed in lines (about 40 cm between two cylinders) and two lines of successive incubations were separated by approximately 30 cm. Root uptake was suppressed in the cylinders and mineral N contents consequently were different inside and outside the cylinders after incubation. Incubated cores were sampled every 4 weeks at Vauxrenard year-round, and at Aubure from mid-October to mid-March; cores were sampled every 2 weeks from mid-March to mid-October at Aubure. At each sampling date, nine non-incubated soil cores also were sampled between each incubated cylinder, to assess the mineral N content of the soil outside the cylinders at the start of the incubation period, which also corresponded to the content at the end of the previous incubation period.

Nitrate leaching in the cylinders (without root uptake) was quantified using an anion exchange resin (Powers 1990, Hübner et al. 1991). The last centimeter of soil in the bottom of each cylinder was removed and replaced by a Nylon bag containing 40 g of resin (DOWEX 21K, 20–50 mesh). Before incubation, resin was saturated with Cl^- by a slow percolation of demineralised water followed by 1 M NaCl (1 L: 100 g of resin). In the Nylon bag, resin was mixed with 40 g of glass beads to increase the volume of the bags. In addition, beginning October 1995 at Aubure or April 1996 at Vauxrenard, ammonium leaching in the cylinders also was quantified, using cation exchange resin (IRN 77, 16–40 mesh). Before utilisation, cation resin was saturated with Na^+ by a slow percolation of demineralised water followed by 1 M HCl (1 L: 100 g of resin) and 1 M NaOH (1 L: 100 g of resin) with a final pH between 6 and 7. Six cylinders containing Nylon bags filled with a mixture of 40 g of cation exchange resin and 40 g of glass beads were used in addition to six cylinders containing an anion exchange resin (rather than nine used in the former period).

In the field, after removing the LF sublayer (between 1 and 3 cm thick), soil samples (nine in the first period, 12 in the second) were combined into three samples per time period, sieved <4 mm, and put in flasks containing 1 M KCl (40 g moist soil: 200 mL solution). Soil samples and resin bags then were transferred to the laboratory in a cool box. The samples were stored at +1 °C for 24 h. Sample moisture was determined on a subsample dried at 105 °C. Mineral N of soil samples in KCl was extracted by mechanical shaking (1 h), centrifugation of the supernatant and filtration.

Resin bags were rinsed with demineralised water to remove soil particles and adhering organic residues (Giblin et al. 1994). Rinsing with water had no effect on N desorption for anionic resins but desorbed 2% of NH_4-N, independently of the fixed amount of NH_4-N. The percentage of NH_4-N desorbed by rinsage was taken into account in the final calculation. Bags were opened, air-dried and sieved to separate resin and glass beads. Nitrate and ammonium were extracted by 1 M NaCl (4 g: 40 mL dwt:v) after manual shaking, batch contact (1 h) and filtration. Background levels of nitrogen (Kjønaas 1999a) were absent on both resin types before incubation, as determined by non-incubated control resin bags prepared at the same time as the incubated bags, stored in the lab at +1 °C during field incubation, air-dried and analysed with the incubated resin bags. Contrary to Kjønaas (1999a), we found that drying the cation resins sometimes caused an adsorption of atmospheric NH_4^+, which was accounted for by subtracting the NH_4^+ content of the controls.

Mineral nitrogen contents in KCl and NaCl extracts were measured by colorimetry (autoanalyser II, Technicon, Dublin).

As the amount of NH_4^+-N extracted from the soil varied with the amount of time the sample was in contact with KCl solution, we made a set of comparative measurements (1 h v.s. 24 or 48 h) in the laboratory. As a consequence, amounts of NH_4^+-N extracted from soil were divided by 1.5 (24 h) or 2.38 (48 h) depending on the duration of contact between soil and KCl.

Resin fixing efficiency was determined in the laboratory by slowly percolating similar volumes of different solutions through glass columns (2 cm diameter) containing 4 g of resin. Concentrations ranged from 3 to 60 mg N L^{-1} of KNO_3 (anionic resins) and from 0.5 to 20 mg N L^{-1} of NH_4Cl (cationic resins). Resin fixing efficiency was calculated by analysing the remaining amounts of inorganic nitrogen in the solutions collected after percolation. Anionic resin fixing efficiency was independent of the amount of nitrate percolated and was 94.3%. Cationic resin fixing efficiency was dependent on the amount of ammonium percolated. We found an empirical relationship between N input (I) and N adsorbed on the resin (A):

$$A = 0.947I - 3.252 \ \left(n = 13, r = 0.998, \text{units are } \mu\text{g g}^{-1}\right)$$

The desorption efficiency of NH_4 and NO_3 from resins was checked in the lab. Empirical relationships between desorbed nitrogen (D) and adsorbed nitrogen (A) were, for anionic resins: $A = 2.363D^{0.945}$ ($n = 30$, $r = 0.976$); and for cationic resin: $A = 1.887D - 2.141$ ($n = 13$, $r = 0.997$). In rare cases, when $D < 2.414$, A was calculated to be < to D, which is impossible; in this case, we set $A = D$).

Soil densities

Fluxes were calculated by a set of equations based on mineral nitrogen budgets outside and inside the cylinders corresponding to situations with and without root uptake. Soil densities used for hectare-based calculations were estimated at Aubure by taking the mean of the densities of non-incubated soil samples (0–15 cm layer) over 2 years of observation (183 replicates per stand). Mean densities were 0.69 kg dm^{-3} for S90 soil, to 0.58 kg dm^{-3} for S45 soil and B150 soil. At Vaux-renard, soil densities were estimated using the densities of the 0–15 cm layer of two pits in each stand (Marques 1996). Mean densities were 0.75 kg dm^{-3} for D20 soil, 0.71 for D40 soil and 0.53 for D60 soil.

Conceptual equations

A set of equations modified from Raison et al. (1987) were used to calculate mineralisation, nitrification and root uptake fluxes, taking into account deposition and losses by leaching.

T_{0i} = initial NO_3^--N (or NH_4^+-N) content at the beginning of the incubation period.
T_{0f} = final NO_3^--N (or NH_4^+-N) content of the soil outside the cylinders at the end of the incubation period.
$T_{0f\ NO_3} = T_{0i\ NO_3}$ + inputs of NO_3 + gross nitrification − root uptake of NO_3 − microbial immobilisation of NO_3 − leaching of NO_3 outside the cylinders.
$T_{0f\ NH_4} = T_{0i\ NH_4}$ + inputs of NH_4 + gross mineralisation − root uptake of NH_4 − microbial immobilisation of NH_4 − gross nitrification − leaching of NH_4 outside the cylinders.
T_1 = final NO_3^--N (or NH_4^+-N) content of the soil inside the cylinders at the end of the incubation period.
$T_{1\ NO_3} = T_{0i\ NO_3}$ + inputs of NO_3 + gross nitrification − microbial immobilisation of NO_3 − leaching of NO_3 inside the cylinders.
$T_{1\ NH_4} = T_{0i\ NH_4}$ + inputs of NH_4 + gross mineralisation − microbial NH_4 immobilisation − gross nitrification − leaching of NH_4 inside the cylinders[1]

Calculations

Net nitrification = $T_{1\ NO_3} - T_{0i\ NO_3}$ − inputs of NO_3 + leaching of NO_3 inside the cylinders.
Net ammonification = gross mineralisation − microbial NH_4 immobilisation − gross nitrification = $T_{1\ NH_4} - T_{0i\ NH_4}$ − inputs of NH_4 + leaching of NH_4 inside the cylinders.
Root uptake = $T_1 - T_{0f}$ − leaching outside the cylinders + leaching inside the cylinders.
Net mineralisation = net nitrification + net ammonification.
Microbial immobilisation was not quantified because it was assumed to be similar inside and outside the cylinders.

Soil ^{15}N analyses

The ^{15}N in the first layer of mineral soil was collected at five representative points within each of the experimental plots. Prior to analysis, soil samples were dried at 65 °C, and pulverised with a ball mill to pass a 40-mesh screen. ^{15}N:^{14}N ratios were measured using an elemental analyser (Carlo Erba NA 1500) coupled to a mass spectrometer (Finnigan Delta S) at the Service Central d'Analyse of Centre National de la Recherche Scientifique (Vernaison, France). Results are expressed in ‰ deviations from the international standard atmospheric N_2: $\delta^{15}N = [(R_{sample}/R_{standard})$ - $1] \times 1000$, where $R = {}^{15}N$:^{14}N (Mariotti 1983).

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[1] As ammonium leaching was not measured in 1995, values of 1996 were used to compute annual fluxes for the year 1995.

Table 3. Water content ($g\,g^{-1}$) in the upper soil layer (0–15 cm) inside and outside the cylinders at the six stands. Standard deviation in brackets.

Stand	Dormant season (mid-October to mid-April)		Growing season (mid-April to mid-October)	
	Inside	Outside	Inside	Outside
S45	0.52 (0.24)	0.43 (0.19)	0.44 (0.13)	0.35 (0.11)
S90	0.45 (0.11)	0.38 (0.07)	0.43 (0.11)	0.38 (0.13)
B150	0.85 (0.3)	0.75 (0.19)	0.84 (0.17)	0.71 (0.14)
D20	0.59 (0.12)	0.50 (0.12)	0.53 (0.11)	0.42 (0.11)
D40	0.53 (0.06)	0.46 (0.07)	0.49 (0.13)	0.43 (0.12)
D60	0.53 (0.07)	0.46 (0.06)	0.51 (0.08)	0.41 (0.08)

Results

Mean soil water content was the highest at B150 during the entire study and the lowest in the two spruce stands (Table 3). Soil water content was intermediate at Vauxrenard and there were no significant differences among the three stands. Soil water content was higher during the "dormant" season (October–April) than during the 'growing' season (April–October) and inside the cylinders compared to outside (Table 3).

The average mineral nitrogen concentration of the 0–15 cm horizon was lower at Aubure than at Vauxrenard. Ammonium was the main form of mineral N in the soil at S45, where nitrate concentration was close to zero. Nitrate-N represented about 30% of mineral N at B150 and S90, and 65–75% of mineral N in the soil at Vauxrenard. Mean mineral N contents followed approximately the nitrate-N contents: about 9 $kg\,ha^{-1}$ at S45 and S90; between 13 and 15 $kg\,ha^{-1}$ at B150, D20 and D40; and, 22 $kg\,ha^{-1}$ at D60. In all soils, mean contents fluctuated strongly according to an annual cycle. Contents and variability generally increased during the summer months.

Depending on the year, the amount of mineral N in throughfall was 7–8 $kg\,ha^{-1}\,yr^{-1}$ at S45, B150 and D20; and between 15 and 20 $kg\,ha^{-1}\,yr^{-1}$ at S90, D40 and D60 (Table 4). N deposition was roughly equal in 1995 and in 1996. Nitrate was the main form of throughfall N deposited on the soil (60–65%).

Leaching of mineral N at 15 cm depth with and without root uptake occurred mainly in the form of nitrate, except at S45 where about 40% was in the form of ammonium (Table 4). In all stands, N leaching from within the soil cores (without root uptake) was much higher than from outside the cores. At S45, almost no N was leached from the soil in the presence of roots, and suppression of root uptake increased N leaching by only 10 $kg\,ha^{-1}\,yr^{-1}$. At B150 also, almost no nitrogen was leached from the soil in the presence of roots, however, root uptake suppression increased N leaching by 80 $kg\,ha^{-1}\,yr^{-1}$ on average. N leaching was higher at S90 (20–25 $kg\,ha^{-1}\,yr^{-1}$) and D40 (11–17 $kg\,ha^{-1}\,yr^{-1}$), and root uptake suppression strongly increased leaching of N an average of +36 and +77 $kg\,ha^{-1}\,yr^{-1}$, respectively. N leaching was very high at D20 (117 and 45 $kg\,ha^{-1}\,yr^{-1}$ in 1995 and 1996) and D60 (88 and 35 $kg\,ha^{-1}\,yr^{-1}$ in 1995 and 1996), and increased by 70 and

Table 4. N fluxes at Aubure (S45, S90 and B150) and at Vauxrenard (D20, D40 and D60) from mid-October 1994 to mid-October 1996: N deposition in throughfall, N leaching at 15 cm depth (with and without root uptake) and at 60 cm depth, N mineralisation and root uptake, N in annual litterfall, annual immobilisation of N in bole and branches and in large roots[1]. All data in kg N ha^{-1} year^{-1}.

Stand	Throughfall	Leaching				Net mineralisation		Uptake	Litterfall	Immobilisation
		With root uptake[2]			Without root uptake[4] (At 15 cm depth)	NO_3^--N	NH_4^+-N			
		NO_3^--N at 15 cm depth	NH_4^+-N at 15 cm depth	At 60 cm depth[3]						
S45	7.1	1.4	1.0	4.4	13.2	7.7	49.4	63.3	38	17
S90	16.0	20.6	2.4	43.6	59.0	77.6	43.8	101.5	29	6
B150	7.6	3.7	1.2	0.9	84.3	126.3	50.2	183.1	43	6
D20	7.6	78.7	3.0	65.9	100.6	176.3	33.2	136.7	36	13
D40	18.8	10.8	3.1	28.2	91.1	100.5	12.5	119.6	20	13
D60	19.9	59.6	1.6	9.2	152.0	184.9	17.9	160.2	24	13

[1] From Dambrine et al. (1991) and Marques (1996) for above-ground biomass; Large root biomass measured at S45 and S90 (Le Goaster et al. 1991) and estimated according to Van Praag and Weissen (1991) at B150 and from Le Goaster et al. (1991) at Vauxrenard.

[2] Outside the cylinders.

[3] From mid-October 1994 to mid-October 1995.

[4] Inside the cylinders.

$91\,\mathrm{kg\,ha^{-1}\,yr^{-1}}$, on average when roots were cut. From 1995 to 1996, N leaching from the soil decreased at all plots, except those for which N leaching was already small (S45 and B150). In contrast, the variation was the opposite inside the cylinders, except at stand D40.

There was a significant correlation between the cumulative amount of NO_3^--N leaching from the soil, with and without roots, during the three winter months ($y = 11.55\ \log(x) + 10.08$; $r^2 = 0.58$; $P < 0.01$), as already mentioned by Kjønaas (1999b). No such correlation was found for NH_4^+–N.

Nitrate leaching at 60 cm depth in 1995 (data are not available for 1996, but results were similar for several former years, see Dambrine et al. 2000) was very low when nitrate leaching at 15 cm depth was already low, as was the case at S45 and B150. At the other plots, nitrate leaching occurred and either increased or decreased with depth (Table 4).

Net N mineralisation and net nitrification fluxes in the upper 15 cm of mineral soil were the lowest in the young spruce soil (S45) during the 2 years of study (Table 4): 40–74 $\mathrm{kg\,ha^{-1}\,yr^{-1}}$, of which only 10–20% was nitrified. In the other plots, annual net mineralisation varied from 121.4 to 209.5 $\mathrm{kg\,ha^{-1}\,year^{-1}}$. Annual net nitrification was between 62 and 73% of the mineralisation at S90 and B150, and between 83 and 96% of the mineralisation at Vauxrenard. The annual N mineralisation was the highest in B150, D20 and D60, and the lowest at S45. The inter annual variation was high with an increase of net mineralisation and net nitrification from 1995 to 1996 at S90, D20 and D60, and a decrease at B150, D40 and S45 (values not given). At S45 and B150, the annual flux of N mineralisation was taken up by roots. In contrast, annual N mineralisation always exceeded annual root uptake at S90, D20 and D60. At D40, root uptake was lower than mineralisation the first year, but higher the second year.

Annual N in litterfall was between 20 $\mathrm{kg\,ha^{-1}\,yr^{-1}}$ at D20 and 43 $\mathrm{kg\,ha^{-1}\,yr^{-1}}$ at B150 (Table 4). In total, annual N incorporation in the above-ground biomass and in large roots was always much lower than the calculated root uptake, except at S45 in 1996.

Soil δ^{15}N values were higher at Vauxrenard than at Aubure (Table 2). The former fallow at Vauxrenard which was afforested longer ago (D40) exhibited lower δ^{15}N values (−0.7‰) than the two former croplands afforested later (D60 and D20). At Aubure, the δ^{15}N values decreased from S45 to B150. The relation between soil δ^{15}N and nitrification was positive at Vauxrenard and negative at Aubure.

Discussion

Critique of the in situ *incubation method*

The possible bias of the *in situ* incubation method has been discussed many times (Raison et al. 1987, Adams et al. 1989, Sierra 1997). Uncertainties may exist in the assumption that mineralisation and nitrification rates neither are modified on the short term by severed root activity (Adams et al. 1989), nor are influenced by living root activity. Severed roots within the cylinders still may act as N sinks via uptake as long as roots are living (Raison et al. 1987); if so, production and uptake rates would be underestimated (see equations). On the other hand, the mineralisation of dead roots may lead to an overestimation of T_1, and consequently of uptake, mineralisation and nitrification (Hatch et al. 1990). The combination of both effects led Arnold et al. (1994) to conclude that cut roots had a minor effect. A direct influence of root activity on mineralisation rates has been suggested (Reydellet et al. 1997), but a field demonstration allowing quantification of such a process is presently lacking.

Uncertainty exists also in the assumption that physical and chemical conditions inside and outside the cylinders are similar. Soil compaction was limited in this experiment by the use of cylinders with a large inner diameter (7.6 cm). Soil moisture within the cylinders was usually greater (Table 3), which may have led to an overestimation of production and uptake rates (Grundmann et al. 1995). As conditions (soil moisture and severed roots) were different inside and outside the cylinders, microbial immobilisation was probably different inside and outside the cylinders. For example, enhanced microbial immobilisation in the cylinders would have led to a decrease of T_1, and consequently of uptake and mineralisation.

A 2- or 4-week period between sampling dates was chosen because the period between two sampling must be short enough to limit moisture buildup and decay of severed roots. It must also be long enough to measure differences in nitrogen concentrations inside and outside the cylinders (Raison et al. 1987), and produce substantial N amounts in the solution collectors. These periods were more convenient, given the distance between the sites and the laboratory.

The absolute values of the reported fluxes are subject to the above-mentioned potential bias, as well as the high spatial variability of N concentrations in soil, and the use of empirical relationships to correct for extraction procedures. However, as the method was applied identically at all sites, and soil physical and chemical properties are similar among all sites, therefore these problems should not bias inter-site comparisons.

Mineralisation and root uptake in beech and spruce

The N mineralisation rate calculated in the beech stand (176 kg ha^{-1} yr^{-1}) was higher than previously published values for beech or deciduous stands determined field incubation methods. Runge (1974) measured 112 kg ha^{-1} yr^{-1}, of which 50–60% was nitrified in a 125-years old beech stand; Van Praag and Weissen (1976) measured 55 and 110 kg ha^{-1} yr^{-1} in two beech stands in Belgium; and Reich et al. (1997) calculated 79 kg ha^{-1} yr^{-1}, on average, in a record 34 *in situ* incubations. The mineralisation rate calculated for the old spruce stand (121 kg ha^{-1} yr^{-1}) was also higher than the mean values recorded by Reich et al. (1997) for coniferous forests (58 kg ha^{-1} yr^{-1}); but Strader et al. (1989) recorded mineralisation rates, using *in situ* incubations, from 26 to 180 kg ha^{-1} yr^{-1} (97 kg ha^{-1} yr^{-1} on average) in 19 coniferous forests.

B150 differed from the two spruce stands in having higher rates of mineralisation and nitrification, in spite of a more podzolised soil. Part of this effect might be attributed to the higher soil moisture (Table 3) in the beech stand. However, higher mineralisation rates in soil from deciduous stands, compared to coniferous stands, were found in laboratory incubations (Mardulyn et al. 1993, Persson et al. 2000a), and *in situ* incubations (Son and Lee 1997). Gower and Son (1992) put forth the lower lignin to N ratio of litterfall to explain the higher mineralisation rates in deciduous stands.

Calculated uptake rates for S45, S90 and B150 were higher than the yearly mean uptake rates recorded by Cole (1981) for temperate forests: 47 kg N ha^{-1} for evergreen, and 75 for deciduous forests. N uptake at B150 was closer to values (up to 146 kg ha^{-1} yr^{-1}) calculated by Melillo (1981) for three temperate deciduous forests. By definition, the yearly flux of N uptake should be equal to the accumulation of N in woody biomass (bole, branches and large roots) plus the flux of N associated with the annual litterfall and fine root turnover. Root uptake of N at S90 and B150 was 67 and 134 kg ha^{-1} yr^{-1} higher, respectively, than the annual incorporation of N in the above-ground and large roots biomass. Fine root investigations at S90 and B150 showed that fine root biomass was extremely low compared to other European sites (800 kg ha^{-1} at S90 and 1500 kg ha^{-1} at B150 v.s. 1200–5500 kg ha^{-1} for spruce sites and 2600–3800 kg ha^{-1} for beech sites; Scarascia-Mugnozza et al. 2000). Growth in length and net primary production of roots were also lower at S90 compared to four other European sites (Stober et al. 2000). N concentration at B150 and S90 was 1.75 and 1.61% (Bauer et al. 2000), which corresponds to a N storage in fine root biomass of 26 and 13 kg ha^{-1}, respectively. It implies a fine root turnover time of 2–3 months at these stands. This time is 2–3 fold shorter than that determined by sequential coring at these stands, and 5–10 fold shorter than that obtained at these stands by root window observations (Stober et al. 2000). The higher fine root turnover obtained by the N budgeting method, compared to sequential coring at nitrifying sites, has been observed previously by Aber et al. (1985). This discrepancy probably results from the bias between the two methods: sequential coring should be done very frequently in order to measure short term variations in the root biomass. Incubations may lead to overestimated values if nitrification is controlled in the short term by root activity as suggested by Reydellet et al. (1997) and Olsson and Falkengren-Grerup (2000). Leaf biomass was higher at S45 and, although root biomass was not measured, comparative sap flow measurements (Biron 1994) showed that transpiration was 50% higher in S45 than in S90, thereby indicating a higher fine root biomass. Hence, root turnover time should be longer at S45. No data on fine root biomass and dynamics were available at Vauxrenard. However, the high calculated value of annual root uptake of N suggest that a rapid root turnover occurred.

Mineralisation, nitrification and $\delta^{15}N$ *in relation to past land use*

The rates of mineralisation and nitrification in the field were especially high at the Vauxrenard plots, which formerly were cultivated. Recently, higher net nitrification rates were measured also in new forests planted on formerly cultivated sites compared to ancient forests in New England (Compton and Boone 2000) and in the Vosges Mountains (Jussy et al. 2002). Högberg (1991) found a positive relationship between soil δ^{15}N and nitrification rate in a comparison of non-fertilised and nitrogen fertilised stands in experimental trials. Riga et al. (1971), Mariotti (1982), and Koerner et al. (1999) have shown that organic manure inputs increased soil δ^{15}N, but this effect may depend on the type of organic residues (Compton and Boone 2000). Nitrification at Vauxrenard was positively related to soil δ^{15}N and former manure inputs as noted by Jussy et al. (2002) in the Vosges Mountains. Improved nitrification probably has been triggered by deforestation, tillage (Lossaint and Rapp 1960), and manure input. High nitrification may have persisted because of improved soil fertility, a different microbial population dynamic oriented by the former manure inputs, and the cycling of higher amounts of nitrogen by litterfall, but no demonstration has been provided up to now.

By comparing adjacent stands of natural forest along an elevation gradient, Garten and Van Miegroet (1994) found a negative relationship between soil nitrification rate and δ^{15}N. This is similar to our findings at Aubure sites, which were never cultivated, but a detailed explanation for this pattern is lacking.

Controls on N leaching

Throughfall fluxes were within the range of European data (Gundersen 1992). Deposition of mineral nitrogen increased with stand age, and was higher in evergreen than in deciduous stands, as already noted by other authors (Van Praag and Weissen 1984, Emmett et al. 1993, Marques et al. 1997, Rothe et al. 2002). Throughfall deposition of N was close to N immobilisation in bole and branches at D20: about 5 kg N $\mathrm{ha^{-1}\,yr^{-1}}$ lower at S45, and about 5–10 kg higher in the other stands. It should be kept in mind that canopy uptake of N has not been measured and, therefore, total N deposition was probably higher (Marques et al. 1997; Harrison et al. 2000; Ignatova and Dambrine 2000). For the six stands, there was no apparent relationship between N leaching (15 cm depth or 60 cm depth) and N deposition, or deposition minus N immobilisation in aerial woody biomass. This especially was the case in stands D20 and D60, where leaching was high and deposition was lower than immobilisation (Figure 1). We did not find any significant relationship between N leaching and N flux in litterfall, or N deposition + N flux in litterfall (Figure 2). Gundersen et al. (1998b) found an increase of N leaching in relation to N deposition, and in a comparable manner at their previously ploughed Aber site in Wales, N leaching was higher than N in throughfall.

Although net nitrification was lower, deep leaching of nitrate was much higher at S90 than at B150. Higher nitrate leaching below conifers, in comparison to broadleaf trees, was observed by Gundersen et al. (1998a) and Rothe (2000). This may be related to higher N deposition on conifer foliage, and to higher use of nitrate by beech compared to spruce (Schulze et al. 2000). Lower values of nitrate assimilation in red spruce (*Picea rubens*) stands than in American beech (*Fagus*

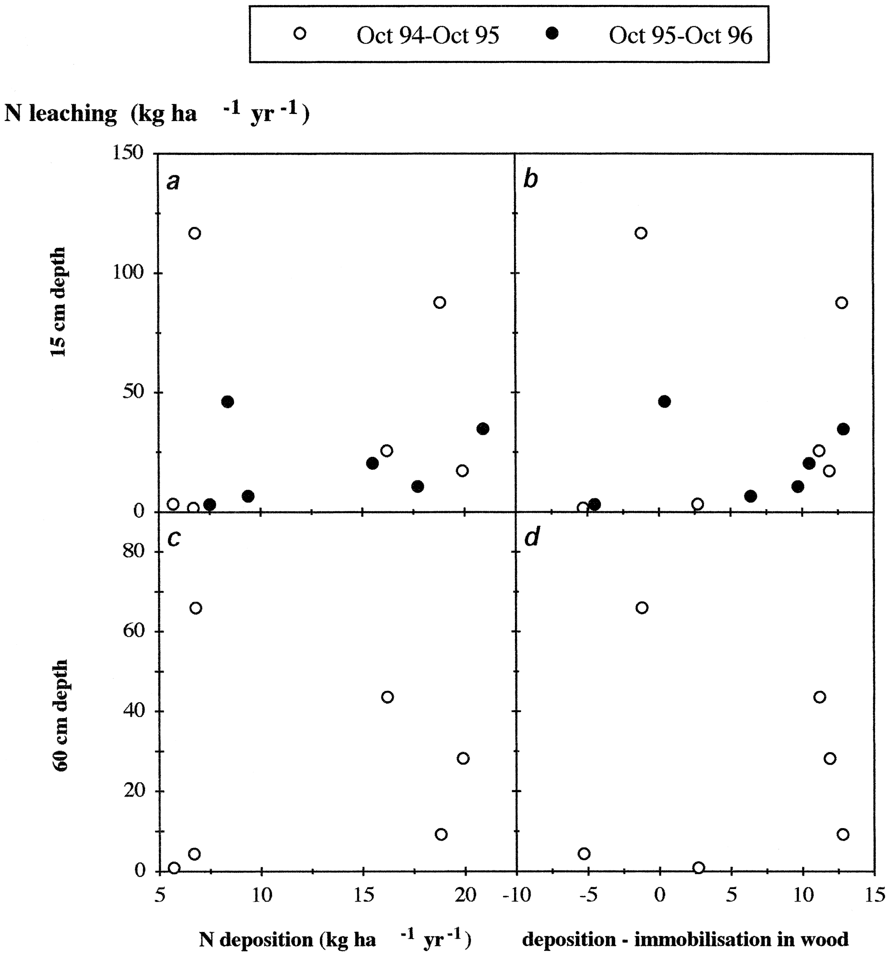

Figure 1. Relationship between N leaching at 15 cm (a, b) or at 60 cm depth (c, d) and N deposition (a, c) or N deposition minus immobilisation in bole and branches (wood) (b, d).

grandifolia) stands also were observed by Nadelhoffer et al. (1995). Nitrate leaching at declining spruce stands, such as S90, has also been observed (Paces 1985, Becquer et al. 1990, Feger 1992, Ranger et al. 1993). No simple cause was found to explain the poor nitrification at S45. We believe that it is representative of young stands (Gundersen et al. 1998a) planted on poor and acid soils of ancient forests, when deposition is low compared to growth requirements. As almost no nitrification occurs, and if nitrate deposition is low, nitrate cannot be leached. Emmett et al. (1993) and Harrison et al. (1995) measured an increase in nitrate leaching with stand age, probably related to increased N deposition and reduced N requirements. However, the trend with age was the opposite at Vauxrenard, suggesting the effect of past land use and time since afforestation might be more

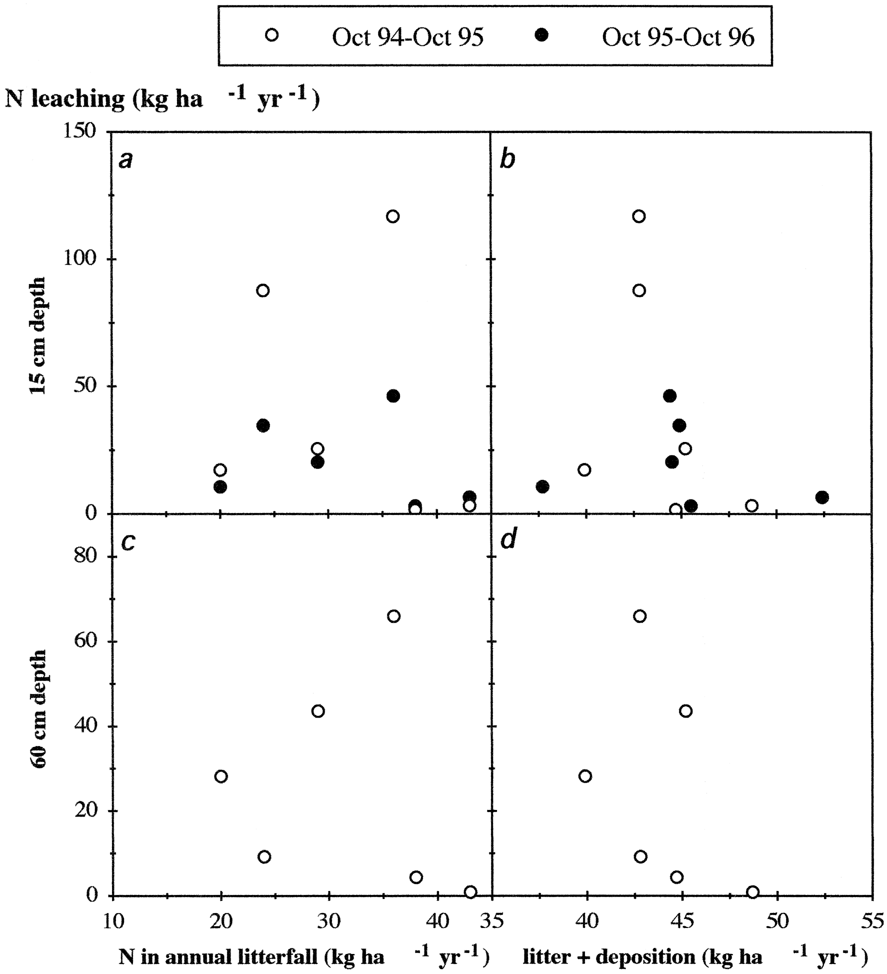

Figure 2. Relationship between N leaching at 15 cm (a, b) or at 60 cm depth (c, d) and N in annual litterfall (a, c) or N deposition plus N in annual litterfall (b, d).

important at that site. Compared to adjacent ancient forests, higher nitrate leaching was found also in a forest previously grazed by pigs (Norhstedt et al. 1996), and in a conifer plantation on former agricultural land (Magill et al. 1997).

Suppression of root uptake in the cylinders strongly increased N leaching, mainly in the form of nitrate, and especially in the beech and the Douglas fir-stands where the nitrification rates were the highest (but also in S45 where it was the lowest). B150 and, to a lesser extent D40, are strongly nitrifying stands. All the available N (deposited and mineralised) was taken up, consequently, there was little nitrate leaching. When root uptake was suppressed in these two stands, nitrate leaching was high (73–108 kg NO_3^-N ha^{-1} yr^{-1}). This indicates that nitrate leaching was not

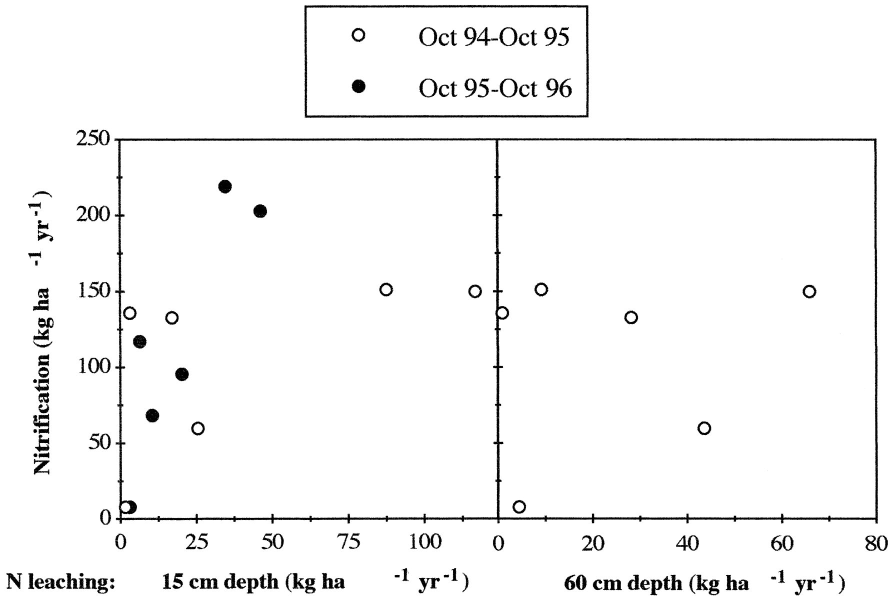

Figure 3. Relationship between nitrification and N leaching at 15 and 60 cm depth.

simply related to nitrate production rate (Figure 3). At D20 and D60, root uptake was high, albeit lower than mineral N production, and consequently, losses by leaching were very high and increased further when roots were cut. This indicates that, except at non-nitrifying plots (i.e., S45), nitrate leaching is controlled by root uptake. Hence, impairment of root function (by drought, acidification, decline...) will increase nitrate leaching (S90). Past land use also seems to strongly influence nitrate leaching (Feger 1992). As a result, taking into account the diversity of European forest ecosystems, nitrate leaching may not be related simply to N deposition or to the sum of N deposition and N in litterfall (Gundersen et al. 1998b).

One may question the role of understorey vegetation. In fact, Gebauer et al. (1998) found nitrate reductase activity per unit of biomass was 6-fold higher in the leaves of *Oxalis acetosella* than in the roots of *P. abies* in an 80-year-old Norway spruce stand in Germany. Cole (1981), in a 80-year-old spruce stand, and Van Praag and Weissen (1991), in a 90-year-old beech stand, indicated a N uptake by understorey of 10 and 14 kg ha^{-1} yr^{-1}, respectively. In 40-year-old aspen and pine stands in Minnesota, Perala and Alban (1982) found N contents in understorey biomass ranging from 11 to 36 kg ha^{-1}. N storage in above-ground understorey biomass reached 59 kg ha^{-1} at D60, but the storage was certainly lower at other plots, and close to zero at S45 and D20. However, even at D60, nitrate leaching was high. Hence, the sink function of the understorey vegetation does not seem to control nitrate leaching at these plots.

Conclusion

Six forest stands, typical of large areas of public and private forests in the mid-elevation range of France, were studied for N fluxes. The stands, all with acidic and sandy soils, included two Mg-deficient spruce stands and one beech stand on ancient forest soils that formerly were partly grazed, and three Douglas-fir plantations on former agricultural soils. All the sites received moderate amounts of N deposition but exhibited a large range of nitrate leaching. Among the sites, mineral nitrogen production varied considerably and was not related to N leaching. Compared to spruce, the lower leaching of nitrate measured in the beech stand seems related to a lower deposition on deciduous foliage, and also to a higher nitrate use efficiency. Nitrogen leaching increased at all sites in response to suppression of root uptake, which shows that N leaching was strongly controlled by root activity. However, nitrate leaching was high at formerly cultivated plots, regardless of the level of deposition and nitrogen uptake. Nitrate leaching at formerly cultivated plots probably results from the high mineralisation and nitrification rates of a labile pool of organic matter accumulated during the cultivation period (Magill et al. 1997; Aggangan et al. 1998; Compton and Boone 2000; Jussy et al. 2002), which surpasses the present forest stand requirement, especially during winter. High soil δ^{15}N appears as a good indicator of former agricultural use. This long term effect of former cultivation on soil nitrification and nitrate leaching may last for centuries until a new equilibrium between soil organic matter and annual organic matter input from the forest is reached. This time lag may be influenced strongly by the present level of N deposition. Further investigations are needed to describe and model the dynamic of organic matter from former agricultural periods and the incorporation of forest carbon in the soil with time. Because a large proportion of present forests are growing on former cultivated lands, N saturation in forests may be much more common than formerly thought, even at low levels of N deposition.

Consequently, we suggest that past land use and root activity, which is related to tree species and health, should be taken into account to explain the variability in the relationship between N deposition and leaching in forests receiving low to moderate amounts of N deposition.

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