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Nitrogen cycling in an acid forest ecosystem in the Netherlands under increased atmospheric nitrogen input

The nitrogen budget and the effect of nitrogen transformations on the proton budget

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Abstract. Within a long-term research project studying the biogeochemical budget of an oak-beech forest ecosystem in the eastern part of the Netherlands, the nitrogen transformations and solute fluxes were determined in order to trace the fate of atmospherically deposited NH_4^+ and to determine the contribution of nitrogen transformations to soil acidification.

The oak-beech forest studied received an annual input of nitrogen via throughfall and stemflow of 45 kg N ha^{-1} yr^{-1}, mainly as NH_4^+, whereas 8 kg N ha^{-1} yr^{-1} was taken up by the canopy. Due to the specific hydrological regime resulting in periodically occurring high groundwater levels, denitrification was found to be the dominant output flux (35 kg N ha^{-1} yr^{-1}). N_2O emmission rate measurements indicated that 57% of this gaseous nitrogen loss (20 kg N ha^{-1} yr^{-1}) was as N_2O. The forest lost an annual amount of 11 kg N ha^{-1} yr^{-1} via streamwater output, mainly as NO_3^-.

Despite the acid conditions, high nitrification rates were measured. Nitrification occurred mainly in the litter layer and in the organic rich part of the mineral soil and was found to be closely correlated with soil temperature. The large amount of NH_4^+ deposited on the forest floor via atmospheric deposition and produced by mineralization was to a large extent nitrified in the litter layer. Almost no NH_4^+ reached the subsurface soil horizons. The NO_3^- was retained, taken up or transformed mainly in the mineral soil. A small amount of NO_3^- (9 kg N ha^{-1} yr^{-1}) was removed from the system in streamwater output. A relatively small amount of nitrogen was measured in the soil water as Dissolved Organic Nitrogen.

On the basis of these data the proton budget of the system was calculated using two different approaches. In both cases net proton production rates were high in the vegetation and in the litter layer of the forest ecosystem. Nitrogen transformations induced a net proton production rate of 2.4 kmol ha^{-1} yr^{-1} in the soil compartment.

Introduction

In the Netherlands, the atmospheric deposition of ammonium is believed to be an important factor responsible for soil acidification (Van Breemen et al. 1987). The ammonia originates from volatilization from manure, produced by the bio-industry. The manure is stored in large amounts and excessively used as fertilizer on arable land and pastures in large parts of the Netherlands. The ammonia reacts with sulphur dioxide forming ammonium sulphate aerosols, which are intercepted by forest canopies. The ammonium deposited on the forest floor by throughfall and stemflow can act as an acidifying nutrient in the soil, depending on the transformations in the soil after deposition. A maximal acidifying effect of deposited ammonium is reached after complete nitrification, followed by leaching of the highly mobile nitrate out of the soil system (Van Breemen et al. 1986).

In order to determine the contribution of atmospheric deposition to soil acidification, a long-term research project was initiated to study the biogeochemical budget of an oak-beech forest in the eastern part of the Netherlands. Because of the importance of the deposition of ammonium, attention was focused on the nitrogen cycle of the forest. The effect of the deposition of inorganic nitrogen species on the proton cycle can be evaluated by quantifying the nitrogen transformations relevant to soil acidification.

In this paper, data on nitrogen storage, fluxes and biogeochemical nitrogen transformations are presented. Finally these results are integrated into an overall nitrogen budget, which forms the basis for quantification of the role of nitrogen on soil acidification.

Experimental conditions

Site description

The forest studied, called the Tenkink forest, is located in the eastern part of the Netherlands (52 °N, 6°40′E), near the town of Winterswijk. At the meteorological station of Winterswijk, mean monthly temperatures vary from 1 °C in January to 19 °C in July. Average annual precipitation is 805 mm, which results in 592 mm of throughfall under the oak-beech canopy and 20 mm of stemflow (1979—1987).

The dominating tree species is oak (*Quercus robur L.*) with a second tree layer of beech (*Fagus sylvatica L.*), spruce (*Picea abies (L.) Karsten*), pine (*Pinus sylvestris L.*) or hornbeam (*Carpinus betulus L.*). The fieldlayer consists of a scarce undergrowth of wood anemone (*Anemona nemorosa L.*), may lily (*Maianthenum bifolium (L.) F.W. Schmidt*) and wood sorrel (*Oxalis acetosella L.*). The experimental plot was situated in the sites dominated by oak and beech trees, with some scattered hornbeam trees.

The age of the oak and beech trees varies between 90—110 and 50—55 years respectively. The area has been forested for about 300 years.

The soils (Dystric planosols FAO 1974; Aeric Albaqualfs USDA 1975) have developed in sandy loam textured boulder clay deposits, covered by a sandy layer of about 30—40 cm in thickness, which is a weathering residue of the boulder clay. The boulder clay is underlain by a completely water impermeable Jurassic clay. The sandy layer and the top of the boulder clay are distinctly acid ($pH_{(CaC12)}$ 2.9—3.8) with pH values increasing further down in the profile. On top of the profile a well developed litter layer can be identified, consisting of a L(itter)- and a F(ermentation)-layer. The water table fluctuates from 15—45 cm below ground level between January and May, to 100—300 cm in the rest of the year. Streamflow is mainly generated by lateral flow through the sandy topsoil (Duijsings et al. 1983). Runoff ceases as soon as the watertable falls below 30—45 cm in accordance with the mean depth of the boulder clay.

More information about the Tenkink forest, concerning runoff sources, precipitation chemistry, spatial variability of nutrient depositions under the canopy, forest hydrology and proton budget has been presented by Duijsings et al. (1983), Duijsings et al. (1986a), Duijsings et al. (1986b), Bouten (1987) and Verstraten et al. (1990), respectively.

Experimental design

The overall objective of the project was to determine the contribution of atmospheric deposition to total soil acidification by means of a catchment approach. In order to be able to integrate soil chemical, -physical and — biological measurements, two representative experimental oak-beech plots of about 20*20 m. were chosen within a catchment of about 3 ha. The choice was made using vegetation- and soil parameters as criteria, aiming at the establishment of representative plots for the total catchment. All results mentioned in this paper were obtained from these plots. Not all measurements were carried out on both plots simultaneously.

The longterm research project lasted from 1979 until 1987. More specific data on nitrogen cycling presented in this paper were collected in 1986, 1986 and 1987.

Methods

Accumulation in the vegetation

In the autumn of 1984, measurements of the Diameter at Breast Height

(DBH) were performed in 6 plots of 25*25 m. within the oak-beech vegetation of the Tenkink forest. In 3 plots tree heights were determined as well. Three oak- and 6 beech-trees of average size were felled during the winter of 1984 and the biomass of their above ground components was determined. Total above ground biomass was calculated on the basis of these average trees.

To determine the storage of nitrogen in the trunk, the relation between nitrogen concentration and height of the trunk was calculated using linear regression. By imagining the trunk as a cone, the nitrogen storage was calculated per volume of 1 m length and integrated for the whole trunk. The storage in branches and twigs was calculated using the measured dry mass and nitrogen content of these parts. All root (coarse and fine roots) data were obtained from the literature.

The total nitrogen concentration in the organic samples was determined by means of a salicylic acid-thiosulphate modification of the regular Kjehldahl procedure (Bremner & Mulvaney 1982).

Accumulation in the soil

To gain information about the biomass of the forest floor, the L(itter)- and F(ermentation)-layer were frequently sampled (weekly, 4 replicates) during the period from august 1986 until November 1987. For each sample, dry mass was determined after drying at 70 °C until constant mass. Total nitrogen concentration was determined from a random selection of these samples.

The concentration of NH_4^+, NO_3^-, NO_2^- and Dissolved Organic Nitrogen (DON) in the LFH-layer and in the Ah1 (top 7 cm) were determined at intervals of 4 weeks during a 2 year period. These concentrations were used to estimate the storage of these nitrogen species. The total nitrogen concentration in these layers was determined in a bulked sample of 12 soil samples. In addition, the bulk density and nitrogen concentration of the Ah2 and the E horizon were determined.

The total nitrogen concentration in the organic and mineral samples was determined by means of a Kjehldahl procedure as described above. The inorganic nitrogen, absorbed plus water soluble NH_4^+ and water soluble NO_3^- and NO_2^- contents were determined colorimetrically after an extraction in 1 M. KC1 solution (ratio soil/solution = 1:20). The DON content of the extract was determined after reduction of the organic nitrogen compounds in the extract to NH_4^+ in a K_2SO_4/H_2SO_4 environment.

Atmospheric deposition, throughfall and stemflow

In this study, the total atmospheric input of nitrogen was calculated as the sum of the canopy uptake of nitrogen and the input of nitrogen by throughfall and stemflow.

Throughfall was sampled by 2 bulk collectors under the oak-beech forest canopy. The collectors consisted of a high pressure polyethylene funnel with an orifice of 400 cm^2 and a 5L polyethylene bottle. The dark coloured bottles were exchanged every 2 weeks. Coarse polyethylene filters ($d = 2$ mm) were used in the funnels to prevent contamination by fallen leaves and insects as much as possible.

The nutrient depositions on a ha and two-weekly basis were corrected in accordance with a comparison of the results of these collectors with the nutrient depositions measured by 11 collectors in the same vegetation in the period from September 1979 until January 1982 (Duijsings et al. 1986b).

The deposition of nitrogen by stemflow was calculated on the basis of earlier simultaneous measurements of throughfall and stemflow (Duijsings et al. 1986a).

The electrical conductivity, pH and alkalinity of all water samples were determined in the field immediately after replacing the collection bottles. In the laboratory all water samples were filtered (0.20 μm) and analyzed colorimetrically for NH_4^+, NO_3^- + NO_2^-, NO_2^-, SO_4^{2-}, ortho P, $C1^-$ and Dissolved Organic Carbon (DOC), using a continuous flow autoanalyzer and for K, Na, Ca, Mg, Fe, Mn, and Al using an atomic absorption spectrophotometer. The DON concentration was determined after destruction (K_2SO_4/H_2SO_4) of the sample and a subsequent analysis of the total NH_4^+ concentration and correction of the initial NH_4^+ concentration.

Canopy uptake

The canopy uptake of nitrogen by the vegetation was calculated from a comparison of precipitation- and throughfall chemistry of the periods in leaf and leafless periods. It was assumed that the amount of manganese and potassium that was leached out of the canopy, was counteracted by an uptake of NH_4^+.

Below-ground uptake

The total annual uptake was quantified as the sum of the annual increment in standing crop and litter production. Stemwood increments were estimated by counting the number of growth rings in the outer cm of wood cores taken at breast height from all sample trees. The accumulation of biomass in the other woody components (including coarse roots) was assumed to be proportional to trunk accumulation. To determine the annual accumulation of nitrogen in the vegetation, the nitrogen concentrations at the height of the highest stemdiscs (20 and 13 m for oak and beech, respectively) were used. For the branches and twigs, measured nitrogen concentrations were used. Fine root production and relevant nitrogen concentrations were derived from the literature.

Litter production

The litter production of the oak-beech vegetation of the Tenkink forest was determined by means of litter traps of 0.96 m^2. Three of these traps were placed per plot. The litter was collected at intervals varying from 2 weeks in autumn, up to 12 weeks in winter, spring and summer. The annual litter production of coarse (woody) roots was assumed to be proportional to the litterfall of branches and twigs. An estimate of the fine root turnover rate and relevant nitrogen concentrations were derived from the literature.

Net nitrogen mineralization and nitrification

During a 2 year period (April 1985—April 1987) incubations in the field were performed to estimate *in situ* net nitrogen mineralization and nitrification rates (Tietema et al. 1990).

Intact soil cores were taken by means of PVC tubes (d = 7.5 cm), closed at the top and bottom to prevent input and output of nitrogen solutes and incubated in the field for 4 weeks. Two holes in the top of the tube assured a sufficient aeration. After incubation the soil cores were divided into litter (L– + F– layer) and top 7 cm (Ah1) of the mineral soil. The concentrations of NH_4^+, NO_3^- and NO_2^-, determined after an extraction of the freeze-dried material in 1M KCl, were compared with the concentrations in reference samples, taken at the same date close (within 10 cm) to the incubated sample.

The differences in NO_3^- concentration between the incubation samples and the related reference samples were considered to be caused by nitrification during the incubation period. The changes in total mineral nitrogen during incubation were used to estimate net nitrogen mineralization. In order to calculated rates on an areal basis, the mean mass of all collected samples per layer was used.

A similar incubation experiment of 4 weeks was caried out in September/October 1987, which considered not only the LF-layer and the top 7 cm of Ah, but also the folowing 2 layers of 7 cm. These second and third layers of 7 cm of the mineral soil consisted of the Ah2 and part of the E horizon. Annual nitrogen transformation rates in these layers were calculated as a percentage of the rates in the top 7 cm of the mineral soil.

The annual rates in these layers were obtained by extrapolation of this percentage to the annual rates found in the top 7 cm. It was assumed that the occurrence of nitrification in those layers was limited to periods with low groundwater tables, while net nitrogen mineralization could occur throughout the year.

Denitrification

Denitrification rates were determined using the closed chamber method to measure N_2O emissions (Hutchinson & Mosier 1981). The closed chamber method entails the measurement of the accumulation of N_2O within a chamber placed on the topsoil. Vacuumized 5 ml tubes (Venoject) were used to sample the air from the inside of the chamber at several time intervals. The air samples were analyzed for N_2O within one day after collection, using a gas chromatograph, equipped with a 2m*1/8″ stainless steel Poropak Q column (80/100 mesh) and a ^{63}Ni electron capture detector (ECD). Helium was used as a carriergas at a constant flow rate of 15 ml min^{-1}. The temperature of column and detector were 50 and 200 °C, respectively. For analyses, 250 μl of the air samples, was injected into the sampling port by means of a syringe.

In parallel with the N_2O flux measurements, CO_2 flux measurements were also performed, using the same closed chamber method. These results were compared with CO_2 flux measurements using the ventilated chamber method carried out simultaneously. Freijer & Bouten (1991) showed that the closed cover method underestimated the CO_2 efflux due to the changed concentration gradient in the soil profile which resulted in a decreased efflux during the measurement. The mathematical solution presented by Hutchinson & Mosier (1981) corrected for the altered concentration gradient, but did not incorporate the effect of increasing storage of CO_2 in the soil profile. From a comparison of both methods it was concluded that the CO_2 fluxes measured during 1987 by means of the ventilated chamber method were 1.69 times higher than the results obtained with the closed chamber method (Freijer & Bouten 1991). Because of the strong similarities between the N_2O and CO_2 molecules (mass, diffusion constant), the results from the N_2O flux measurements were corrected by the same factor.

The closed chamber method was used on a weekly basis during the period from February 1987 to December 1987. Two chambers were inserted in the topsoil. Air samples were taken at intervals of 0, 2, 4, 8, 16, 32, 48, 64, 96, 128 and 192 minutes after the start.

Nitrogen flux by soil water

To determine the nitrogen flux in infiltrating soil water, different types of soil water sampling devices were used to sample soil water at several depths in the soil.

In May 1986 suction lysimeters were installed. Frequently these lysimeters had to be re-installed, because of leakage caused by soil faunal consumption activity on the Versapore membranes. As a consequence, a varying number of samples were taken during the period from May 1986 until December 1987. Two different types of suction lysimeters were employed. To sample the soil water on the border between litter layer and mineral soil, the suction was maintained by means of an electrical pump. The suction was predetermined and constant during the fortnightly period of sampling. The soil water underneath the Ah1 horizon was sampled by means of lysimeters with a suction determined by the groundwater table. This was done using a siphon, where the suction in mbar was equal to the depth of the groundwater table in cm. This relation was found to be realistic by a comparison of pressure heads and groundwater table measurements.

Ceramic cups were used to sample soil water in and underneath the Ah2 horizon from January 1986 until December 1987. These cups were emptied and vacuumized again on a two week basis. The nitrogen fluxes between the soil horizons studied were calculated by multiplying the concentrations with the water fluxes, calculated by the simulation model FORHYD (Bouten 1987) as a function of the throughfall water flux (Table 1). For the horizons underneath the Ah, however, lateral transport made it impossible for FORHYD to calculate the vertical fluxes. For these horizons the mean annual element-chloride ratios were used, assuming chloride to behave as a conservative parameter in the soil.

The calculations for each year were performed from May 15 to May 15

Table 1. Water fluxes in the soil system expressed as a fraction of the throughfall flux.

	Growing season	Non growing season
Months:	M, J, J, A, S	O, N, D, J, F, M, A
Throughfall	1.00	1.00
LF-water flux	0.80	0.95
Ah1-water flux	0.60	0.95

of the next year. This made it possible to compare more years with each other, because measurements in 1985 started in May.

Streamwater output

In order to determine the discharge from the catchment, a 30° V-notch weir was installed in the catchment outlet and the water level was recorded automatically. Water samples from the streamwater were taken fortnightly to determine the relation between discharge and element concentration. The output was calculated with help of a rating curve method.

Nitrogen budget

The nitrogen budget of the whole ecosystem as well as for the different soil horizons was established by use of the measured nitrogen storage, transformations and fluxes. The distribution of NH_4^+ uptake in the soil profile was calculated by assuming a constant storage of NH_4^+ within the soil horizons. The total uptake of NO_3^- was determined by the difference between total below-ground nitrogen uptake and total below-ground NH_4^+ uptake. The NO_3^- balance was then completed by calculating the NO_3^- loss by denitrification assuming a constant storage of NO_3^-. The contribution of uptake and denitrification to the disappearance of NO_3^- within each soil horizon was estimated assuming a dominance of denitrification in the organic rich part of the mineral soil (Ah1), compared to a dominance of NO_3^- uptake in the Ah2. The translocation rate of organic nitrogen from the litter layer to the mineral soil was estimated using a mean residence time in the litter layer of 6½ years and the extrapolated measured relation between incubation time and absolute amount of nitrogen in decomposing litter (unpub. results).

Results

Accumulation in the vegetation

The number of beech trees per hectare showed a very high standard deviation (Table 2). This resulted in a relatively high degree of uncertainty concerning the estimation of standing crop and nitrogen storage. No dead trees nor living beech trees with a diameter of less than 7 cm were felled. Nevertheless, in order to estimate total forest biomass and nitrogen storage some assumptions were made. The specific mass of dead standing

Table 2. Tree density, forest biomass and nitrogen storage in the Tenkink forest.

	n (ha^{-1})		Biomass (ton ha^{-1})	Nitrogen (kg N ha^{-1})
Oak	360 (20)	trunk	218 (35)	417
		branches	25 (3)	112 (62)
		twigs	5 (1)	33 (9)
		coarse roots	32	189
		fine roots	6	64
		total	286	815
Beech (>7cm)	611 (195)	trunk	36 (18)	82
		branches	10 (5)	49 (37)
		twigs	3 (2)	31 (21)
		coarse roots	7	38
		fine roots	4	42
		total	60	242
Beech (<7cm)	95 (15)	total	2	9
Standing dead		total	45	225
Total biomass			393	1291

Figures between brackets indicate standard deviation based on 3 oak and 6 beech trees sampled.

crop was assumed to be half the value of living trees, while for the small beech trees it was assumed to be equal to the older trees. The average nitrogen concentration in dead standing crop and in the small beech trees was assumed to be 5 mg N kg^{-1}.

An estimation of the coarse root biomass was carried out by assuming that below-ground (woody) biomass equalled 13% of the above-ground biomass (Duvignead & Denaeyer-Desmet 1970). The nitrogen concentration in these woody roots was derived from the same authors. The fine roots biomass estimate was taken from the dataset of a mixed deciduous forest in the UK (Cole & Rap 1981), while the nitrogen concentration in these roots was assumed to be 1.06% (Van Praag et al. 1988).

Accumulation in the soil

A total of 6438 kg N ha^{-1} stored nitrogen was measured in the forest floor (LF) and in the top 26 cm (Ah1, Ah2 and E horizon) of the soil profile (Table 3), of which inorganic nitrogen accounted for only 0.5%.

The largest quantity of nitrogen was stored in the organic rich part of the mineral soil. This Ah1 layer with a mean depth of 7 cm contained about 50% of total soil nitrogen. Within the fraction of mobile nitrogen species, nearly 60% of the total storage was in the form of Dissolved Organic Nitrogen. This relative importance of DON in an acid forest soil was earlier emphasized by Stevens & Wannop (1987). No quantitatively significant amounts of NO_2^- in the soil were estimated.

Within the soil samples taken to determine the nitrogen storage, no distinction was made between minerals, soil organic matter and small roots. As a consequence, results obtained by estimating the belowground nitrogen storage and the nitrogen stored in the soil organic matter will contain some overlap, caused by the release of nitrogen from roots during analyses.

Atmospheric deposition, throughfall and stemflow

The variation between the years with respect to the deposition of various nitrogen species in throughfall and stemflow is rather small (Table 4). Further, no tendency towards increasing or decreasing depositions for nitrogen is evident during the studied period. By averaging 8 years of measurements, a mean input by throughfall and stemflow of 34, 8 and 3 kg N ha^{-1} yr^{-1} was found for NH_4^+, NO_3^- and DON, respectively.

Table 3. Dry mass and the concentration and storage of total nitrogen, NH_4^+, NO_3^- and DON in the LF, Ah1, Ah2 and E horizon.

	LF (7 cm)	Ah1 (7 cm)	Ah2 (7 cm)	E (12 cm)
Biomass (t. ha^{-2})	29.8	569	863	1980
Total N (%)	1.97	0.53	0.17	0.07
N/NH_4^+ (mg kg^{-1})	120	10	2	1
N/NO_3^+ (mg kg^{-1})	22	5	5	4
N/DON (mg kg^{-1})	140	29	10	7
Tot. N (kg ha^{-1})	587	3016	1467	1368
N/NH_4^+ (kg ha^{-1})	4	6	2	2
N/NO_3^+ (kg ha^{-1})	1	3	4	9
N/DON (kg ha^{-1})	4	17	9	14

The thickness of the soil horizons is indicated between brackets.

Table 4. Nitrogen (kg N ha^{-1} yr^{-1}) and water fluxes (mm H_2O yr^{-1}) in throughfall and stemflow.

Species	79/80	80/81	81/82	82/83	83/84	84/85	85/86	86/87	79–85 avg	std
N/NH_4^+	27	24	34	41	39	35	36	36	34	6
N/NO_3^-	7	7	8	7	9	10	8	9	8	1
N/org. N	nd	nd	nd	nd	nd	nd	3	3	3	0
mm H_2O	496	640	678	584	637	598	613	648	612	55

nd = not determined

Plant uptake (canopy)

A canopy uptake rate of 8 kg N/NH_4^+ ha^{-1} yr^{-1} was calculated for the Tenkink forest. The estimation of this rate is important because it comprises, together with the input of nitrogen by throughfall and stemflow, the total deposition of nitrogen on the system studied.

Plant uptake (below-ground)

The results for the annual increment in standing crop are summarized in Table 5. The estimate of net primary production in the fine roots was based on a literature survey by Vogt (pers. comm.). She found that fine root net primary production decreased with an increasing amount of nitrogen in above-ground litterfall. As the amount of nitrogen in the above-ground litterfall (94 kg N ha^{-1} yr^{-1}) in the Tenkink forest is higher than the highest value (62 kg N ha^{-1} yr^{-1}) she reported, we assumed the fine roots net primary production to equal that particular highest value found in an oak forest in Belgium (1100 kg ha^{-1} yr^{-1}).

Total plant nitrogen uptake, calculated as the sum of annual increment in standing crop (27 kg N ha^{-1} yr^{-1}) and total litter production (113 kg N ha^{-1} yr^{-1}), amounted to 140 kg N ha^{-1} yr^{-1}. As canopy uptake was estimated to be 8 kg N ha^{-1} yr^{-1}, below-ground uptake amounted to 132 kg N ha^{-1} yr^{-1}.

Litter production

The above-ground litter production in the Tenkink forest ranged from 64 to 125 kg N ha^{-1} yr^{-1}, with a mean value of 94 kg N ha^{-1} yr^{-1} (Table 6).

Table 5. Yearly increment of biomass and storage of nitrogen in the oak-beech vegetation in the Tenkink forest.

		Biomass (kg ha^{-1} yr^{-1})	Nitrogen (kg N ha^{-1} yr^{-1})
Oak	trunk	2100	5.47
	branches	250	1.11
	twigs	30	0.30
	coarse roots	310	1.71
	fine roots	600	6.36
	total oak	3290	14.95
Beech	trunk	1220	3.21
	branches	350	1.68
	twigs	110	1.02
	coarse roots	220	1.20
	fine roots	500	5.30
	total beech	2400	12.41
Oak and beech		5690	27.36

Table 6. Measured above-ground litter production (dry matter and nitrogen in kg (N) ha^{-1} yr^{-1}): average values and standard deviations of 3 litter traps. In addition the estimated root turnover rate in the Tenkink forest is given.

Year	82	83	84	85	86	87	82–87 avg	82–87 stdv
	Above-ground litter production							
Dry mass:	6110	8120	6130	4440	7980	6420	6590	1970
Nitrogen:	92	125	102	64	73	93	94	28

	Below-ground litter production		
	coarse roots	fine roots	total
Dry mass:	1210	1100	2310
Nitrogen:	7	12	19

The quality and quantity of the litter production varied largely between the studied years. This was partly the result of plant phenology (e.g. the irregular seed production of beech) or environmental factors (e.g. the increased deposition of branches and twigs in 1983 due to strong winds).

In the literature survey of Vogt (pers. comm.) the fine root turnover rate of only one deciduous forest was reported. In coniferous forests, fine root turnover rates in general were of the same order as fine root net primary production. For the Tenkink forest we assumed that fine root turnover equalled the net primary production (1100 kg ha^{-1} yr^{-1}).

Net mineralization and nitrification

Net mineralization and nitrification rates in both litter layer and top of the mineral layer clearly showed a seasonal pattern, closely positively correlated with temperature (Fig. 1A and B). The highest coefficients of correlation between the transformation rates and temperature (Table 7) were obtained by eliminating datapoints with a gravimetric water content lower than 200% and 50% for the LF and the Ah layer respectively, indicating the threshold values at which the water content is no longer a limiting factor for nitrogen transformations in this litter.

Net nitrogen mineralization in the litter layer (Table 8), on a mass basis as well as on an areal basis, was found to be higher than in the top of the mineral soil. The nitrification rate in the litter layer on a mass basis was

Table 7. Regression equations from field incubation experiments with intact cores.

Layer	Process	Equation	R^2
LF	nitrification	$NI = 7.34*e^{0.19T}$	0.78
	net mineralization	$NM = 21.71*e^{0.15T}$	0.82
Ah	nitrification	$NI = 0.52*e^{0.22T}$	0.72
	net mineralization	$NM = 1.47*e^{0.13T}$	0.49

Table 8. Net mineralization and nitrification rates in kg N ha^{-1} yr^{-1}.

	Net mineralization			Nitrification		
	85/86	86/87	avg	85/86	86/87	avg
LFH	89	38	62	38	22	30
Ah1 (0– 7 cm)	50	27	41	42	30	35
Ah2 (7–14 cm)			10			4
Ah2/E (14–21 cm)			2			1
Total			115			69

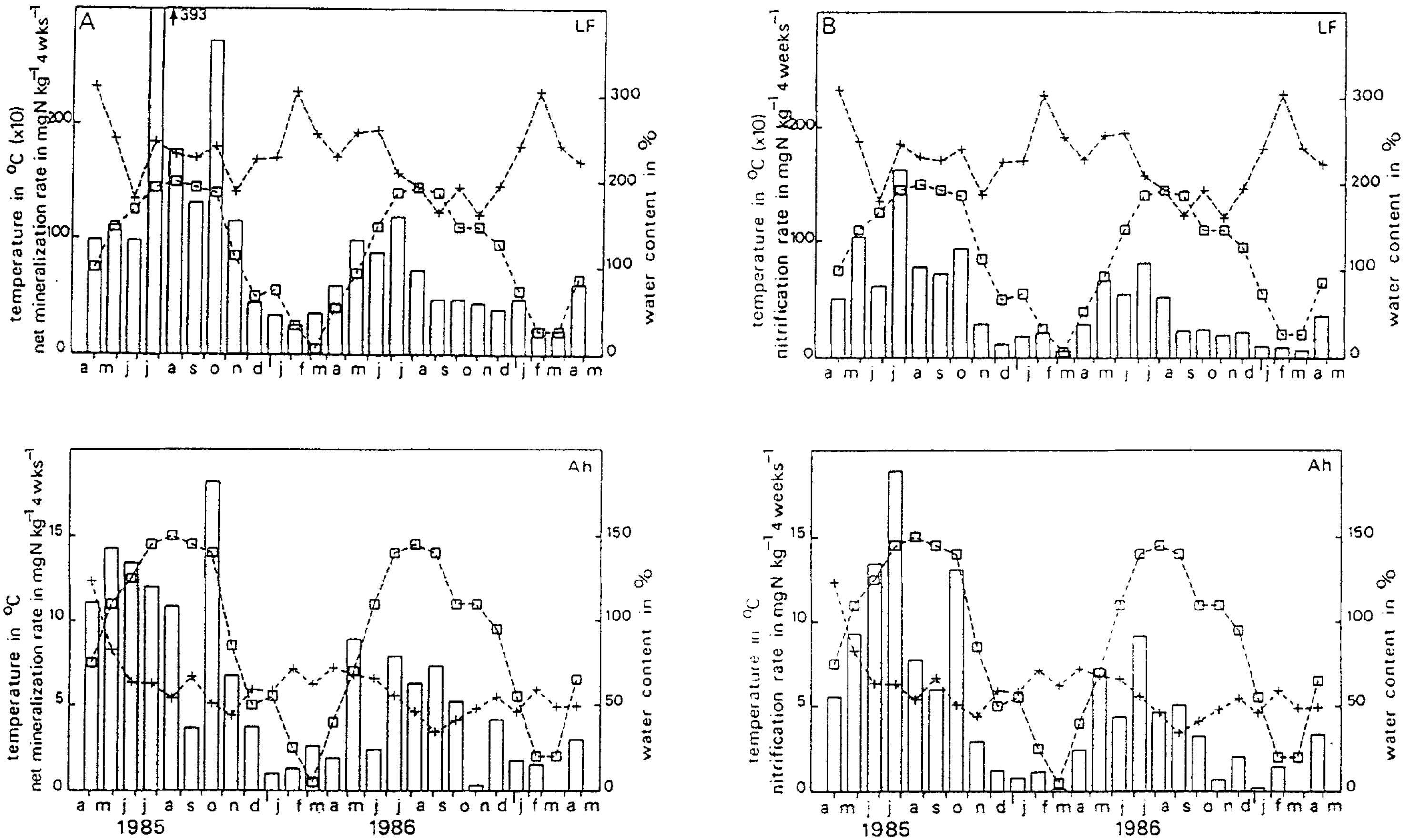

Fig. 1. Net nitrogen mineralization (*A*) and nitrification rates (*B*) in mg N kg^{-1} dry soil per 4 weeks, in the litter layer (LF) and in the top 7 cm of the mineral soil (Ah).

found to be higher than in the top 7 cm of the Ah. On an areal basis however, the nitrification rates in both layers were about equal, due to differences in bulk density of both layers.

Denitrification

The weekly measured N_2O fluxes revealed high temporal variability (Tietema et al. 1991). The fluxes ranged from non detectable values (<0.1 mg N m^{-1} day^{-1}) to a maximum value of 41 mg N m^{-2} day^{-1}. The 2 highest fluxes comprised 60% of the extrapolated annual N_2O loss, which amounted to 20 kg N/N_2O ha^{-1} yr^{-1}. This high temporal variability made the extrapolation of weekly measured rates to annual nitrogen losses very questionable.

Unpublished results obtained by laboratory measurements with intact soil cores (methodology described by Kroeze et al. (1989)) from the Tenkink forest indicated that despite the high acidity (pH 3.0—3.5) in the top soil, the further reduction of N_2O to N_2 seemed to be a quantitatively important process. This implies that the measured N_2O flux did not represent the total gaseous nitrogen loss of the system. It should, thus, only be seen as an indication of a minimal nitrogen loss by denitrification.

Nitrogen flux by soil water

The element-chloride ratios (Fig. 2) gave relative measures of fluxes. In combination with the measured fluxes (Table 9), the absolute value of the unknown fluxes can be calculated using this element-chloride ratio. The two methods combined gave us the nitrogen fluxes in the soil water (Fig. 3). In order to simplify the system, the soil system was divided into 4 layers: LFH, Ah1, Ah2 and other horizons.

In contrast to ammonium, the nitrate flux in LF- water was much

Table 9. Fluxes of NH_4^-, NO_3^- and DON in throughfall and in soil water.

Year: 86/87	NH_4^-	NO_3^-	org. N
Throughfall	36	9	3
LF (0 cm)	15	60	8
Ah1 (−7 cm)	1	42	6

The fluxes are mean values in kg N ha^{-1} yr^{-1}.

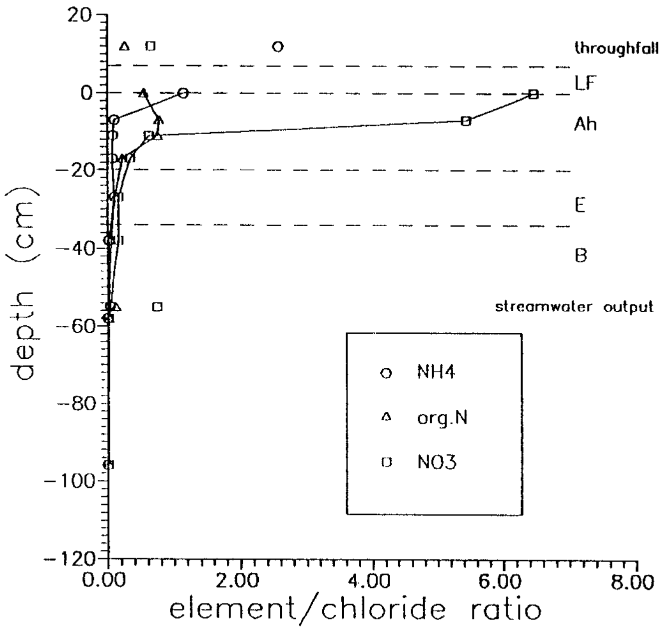

Fig. 2. Mean nutrient-chloride ratios (ammonium, nitrate and organic nitrogen) in throughfall, soil water and streamwater output. The values are the mean measurements (throughfall and streamwater output) for 2 years (85/86 and 86/87) or the value for 1 year (86/87).

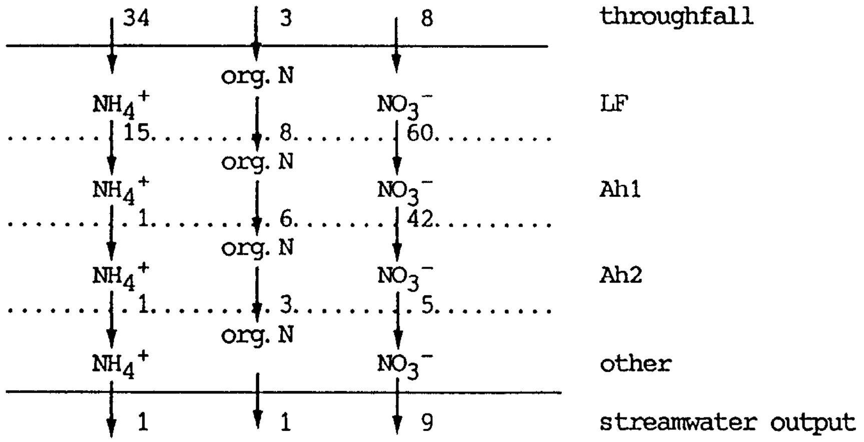

Fig. 3. Nitrogen fluxes (kg N ha^{-1} yr^{-1}) in throughfall, soil solution and streamwater output.

higher than in throughfall (Fig. 3). The large difference between the ammonium and nitrate flux in throughfall was nearly equalized by the transformations in the litter layer. Nearly all NH_4^+ disappeared within the Ah1 horizon, while a large part of the amount of the NO_3^- was removed from the Ah2. DON was produced in the LF layer and taken up again in the subsoil. The nitrogen flux in streamwater output was found to be somewhat higher in soil water from tha Ah2 to the E horizon. This is not very surprising because the occurrence of streamwater was strongly related to the groundwater table. Streamwater occurred when the groundwater table fluctuated between 15 and 45 cm below the ground surface in the period from December until May. As a consequence, this water originated from the Ah2 and/or E-layer and might have had higher concentrations.

Streamwater output

Only a very small amount fo nitrogen, mainly NO_3^-, is exported from this forested catchment by streamwater (Table 10).

Tietema et al. (1991) measured occasional high N_2O concentrations in the soil atmosphere near the groundwater table. Calculations according to Moraghan & Buresh (1977) using Henry's law indicated that these peak values of up to 100 ppm N_2O would lead to a maximum output of 0.3 kg N ha^{-1} yr^{-1} of dissolved N_2O by streamwater, which is a negligible amount compared to the output of the other nitrogen species.

Table 10. Nitrogen and water fluxes (kg N ha^{-1} yr^{-1}) by streamwater output.

Species	79/80	80/81	81/82	82/83	83/84	84/85	79–85	
							avg	sd
N/NH_4^+	1	nd	1	1	1	1	1	0
N/NO_3^-	11	nd	9	6	9	10	9	2
N/org. N	nd	nd	nd	nd	nd	nd	nd	nd
mm H_2O	244	358	215	142	188	216	227	73

nd = not determined

Nitrogen budget

By integrating the data on nitrogen storage and nitrogen transformations and -fluxes, a nitrogen budget of the system was calculated (Fig. 4). After combining the measured nitrogen fluxes in and out of the litter layer with the net mineralization and nitrification rates, a discrepancy was revealed. The NO_3^- flux in soil water from the litter layer (60 kg N ha^{-1} yr^{-1}) could

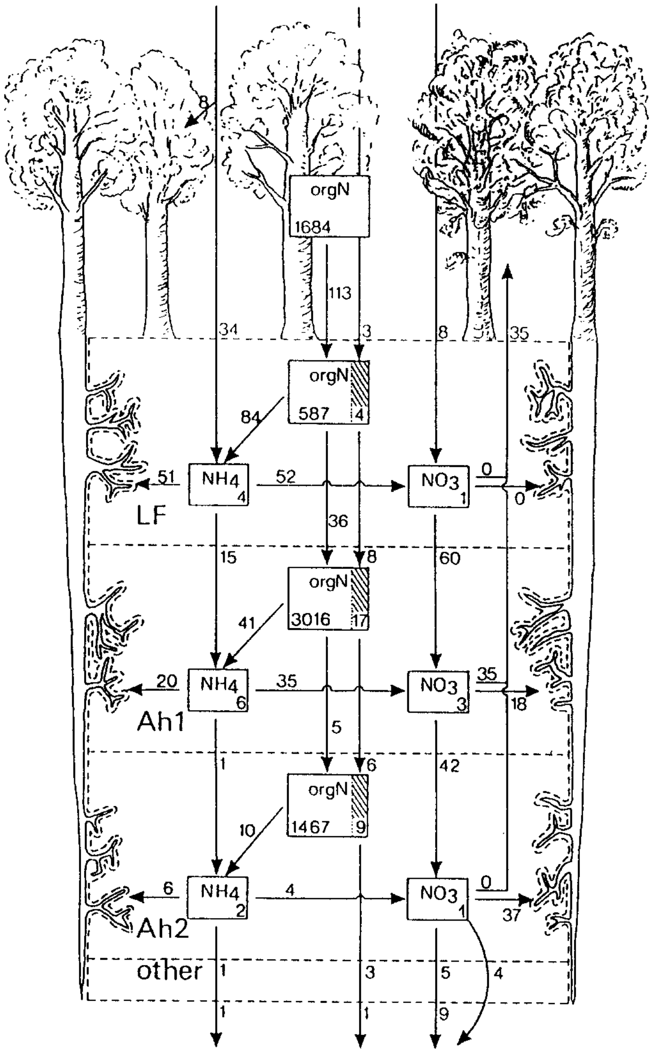

Fig. 4. The nitrogen budget as it is used for analyzing the effects of the nitrogen transformations on the proton budgets of the different compartments of the ecosystem. The shaded part of the organic nitrogen boxes indicates the amount of Dissolved Organic Nitrogen. All numbers in kg N ha^{-1} yr^{-1}.

not be explained by the measured NO_3^- production and input rate of 30 and 8 kg, respectively. In the following analysis, it is assumed that the data for the nitrogen fluxes in soil water were more reliable than the mineralization and nitrification data, due to the possible effects of the manipulation and isolation of the soil during the field incubation experiment. The gap between leached NO_3^- and produced and deposited NO_3^- would mean a minimum correction of these rates of 22 kg N ha^{-1} yr^{-1}, which would lead to rates of 52 and 84 kg N ha^{-1} yr^{-1}, respectively, as shown in Fig. 4. The translocation rate of organic nitrogen from the litter layer to the mineral soil was calculated to be 36 kg N ha^{-1} yr^{-1}. The translocation rate to the Ah2 and other horizons were assumed to be 5 and 0 kg N ha^{-1} yr^{-1}, respectively.

The nitrogen budget (Fig. 4) implied a total annual gaseous nitrogen loss by denitrification of 35 kg N ha^{-1} in contrast with the measured minimum N/N_2O flux rate of 20 kg N ha^{-1} yr^{-1}. Total nitrogen belowground uptake by the vegetation amounted to a total uptake of NH_4^+ and NO_3^- of 77 and 55 kg N ha^{-1} yr^{-1}, respectively.

The results indicated that the soil horizons underneath the Ah2 horizon were of minor importance with respect to the nitrogen budget. The increase of 4 kg N ha^{-1} yr^{-1} between the border of the Ah2 and the E horizon, and the nitrogen output in streamwater originated from a direct flux of NO_3^- from the Ah2 to the streamwater during extremely high groundwater tables.

The other nitrogen budget showed that total nitrogen accumulation in the vegetation amounted to 27 kg N ha^{-1} yr^{-1}. It should be noted, however, that during determination of the growth of the vegetation, the growth rings of the preceding 10 years (± 1973—1984) were considered, while the most important soil measurements in this context were done during the timespan of 1985—1987.

The total ecosystem accumulated nitrogen at a rate of about 7 kg N ha^{-1} yr^{-1}, indicating an aggrading system.

Discussion

Nitrogen cycling

The atmospheric input of inorganic nitrogen species measured in the Tenkink forests falls within the range of throughfall data collected in a large number of forest in the Netherlands (Schneider & Bresser 1988). The input data of respectively 34 and 9 kg N ha^{-1} yr^{-1} for NH_4^+ and NO_3^- are representative for areas with an average agricultural activity in the central, eastern and southern part of the Netherlands, whereas higher NH_4^+ depositions (values up to 100 kg ha^{-1} yr^{-1}) are measured in areas with very intensive stock breeding like 'De Peel' (Roelofs et al. 1985), and in forest edges close to an emission source (Draaijers et al. 1988). Differences in nitrogen inputs have led to a broad range in nitrogen status in the Netherlands (Van Breemen & Verstraten 1990). In an oak forest in the central part of the Netherlands a relatively low nitrogen input of 27 kg ha^{-1} yr^{-1} by throughfall was measured (Tietema, in prep.), while almost no inorganic nitrogen could be detected in the soil solution. On the other hand, Van Dijk et al. (1991) studied a Scots pine forest in De Peel in which decades of excessive nitrogen inputs have led to decreased vitality of the vegetation accompanied by elevated concentrations of NH_4^+ and NO_3^- in the soil solution and increased NO_3^- leaching. The Tenkink forest can be characterized as being intermediate in this range from nitrogen limited to nitrogen saturated forest ecosystems. Relatively high production data in the Tenkink forest coincide with increased inorganic nitrogen concentrations in the soil. Probably, the ecosystem has been pushed beyond nitrogen limitation by the increased nitrogen inputs.

The actual effect of the increased nitrogen input on the forest nitrogen cycle can only be evaluated by comparing the data from this study with standard concepts and data from comparable forests, as no measurements from this forest before the increase of the nitrogen inputs are available. As mentioned earlier, annual growth rate of the vegetation, as well as the annual litter (organic matter and nitrogen) production rate were somewhat higher compared to other Dutch forest ecosystems (Van Breemen et al. 1988) and high compared to other deciduous forest ecosystems from the temperate climatic zone (Staaf & Berg 1981).

The mean net mineralization rate of 115 kg N ha^{-1} y^{-1} measured in the Tenkink forest fitted well within the rates obtained from a literature study by Melillo (1981), who calculated an average net mineralization rate of 110 kg N ha^{-1} yr^{-1} for zonal deciduous forests of Central Europe.

Despite the acid conditions, the occurrence of nitrification in acid forest soils has frequently been reported (Klein et al. 1983; Stevens & Wannop 1987; Vonk 1987; Van Breemen et al. 1987). In the Tenkink forest, both LF-layer and top of the mineral soil contributed about equally to the total nitrification rate in the system, due to the relatively high organic matter content in this mineral surface layer. This is in contrast with other studies where a large part of added $^{15}NH_4^+$ was nitrified in the forest floor (Stams et al. 1991) or nitrification occurred mainly in the upper mineral horizons (Federer 1983). Stams et al. (1990) concluded that the nitrification measured in an acid forest soil in the Netherlands was largely autotrophic, whereas De Boer et al. (1991) described an acid-sensitive and an acid-tolerant type of chemo-lithotrophic nitrification in acid coniferous forest litter. In other studies, the measured nitrification was mainly attributed to heterotrophic organisms (Kilham 1987; Lang 1986).

Despite the high nitrifying potential of the soil and the subsequent increased NO_3^- concentrations in the soil solution, a high denitrification rate prevented the occurrence of a significant output of NO_3^- to the surface water. The specific hydrological regime in the Tenkink forest resulted in a measured loss of NO_3^- by denitrification of at least 20 kg N/N_2O ha^{-1} yr^{-1} and an estimated total nitrogen loss of 35 kg N ha^{-1} yr^{-1}. A relatively small amount of 9 kg N/NO_3^- was removed by streamwater. This relative importance of denitrification in removing NO_3^- prevented NO_3^- leaching and subsequent soil acidification, however, the production of N_2O is also considered to be a potential environmental hazard, as N_2O is an important trace gas affecting the global climate (Crutzen & Ehalt 1977). The estimated gaseous nitrogen loss in the Tenkink forest of 35 kg N ha^{-1} yr^{-1} is high compared to the typical range of gaseous nitrogen emissions in undisturbed forest ecosystems of <1 to perhaps 10 or 20 kg N ha^{-1} yr^{-1} (Bowden 1986). The high denitrification rate in this forest may have been the result of the combination of increased NO_3^- availability (Bowden 1986; Klemedtsson & Svensson 1988) and the occasional high groundwater table in the Tenkink forest.

Proton budget

The net proton production in a strictly defined system related to the nitrogen transformations can be quantified by the sum of net NH_4^+ input and net NO_3^- output (Van Breemen et al. 1982), assuming a negligible change in storage of NH_4^+ and NO_3^- in that system (see Eq. 1).

Net proton production:

$$(NH^+_{4\,(in)} - NH^+_{4\,(out)}) - (NO^-_{3\,(in)} - NO^-_{3\,(out)}) \qquad (1)$$

Van Breemen et al. (1987) calculated the proton budget from the nitrogen transformations of the upper 90 cm of the soil of 4 neighbouring woodland sites. They used throughfall and leaching data for their analyses, implying a system definition of the studied soil compartment including the living roots. In this approach (method I) there is no need to take the uptake of NH_4^+ and NO_3^- into account. In this study, also the proton budget of strictly the soil compartments, excluding the roots, was determined. In this case (method II) it is necessary to estimate the uptake of inorganic nitrogen, which is a transfer of loaded nitrogen ions over the border of the defined compartment. The soil atmosphere is considered to be a part of the soil system. This implies that the transformation of NO_3^- to N_2O and N_2 occurs within the soil system, while the unloaded gaseous nitrogen forms actually leave the system. As a consequence, the denitrification fluxes are not used in Eq. (1). It should be stressed, however, that denitrification prevents NO_3^- from leaching out of the system and thus influences the proton budget.

The results of both approaches are compared in Table 11. Assuming the system definition of method II to be more realistic, it can be concluded than nitrogen transformations cause high net proton production rates in the vegetation and in the litter layer of the forest ecosystem. In the vegetation this is caused by the predominance of NH_4^+ uptake over NO_3^- uptake, while the relatively high proton production in the LFH layer is due to the combination of a high NH_4^+ input via atmospheric deposition and a fast leaching of NO_3^-, balanced by a large uptake of NH_4^+.

As might have been expected, both methods lead to different absolute values of net proton production rates in the various compartments. This is caused by the different uptake rate of NH_4^+ and NO_3^- in the soil horizons. However, from both methods it can be concluded that the nitrogen transformations cause net proton production in the litter layer, while protons are consumed in the organic rich part of the mineral soil. This is in accordance with the results obtained by Van Breemen et al. (1988) in the acid Hackfort sites.

Finally it should be mentioned that the overall net proton production rate in the soil, including the effect of all element transformations is 4.5 kmol H^+ ha^{-1} yr^{-1} in the Tenkink forest (Verstraten et al. 1990). Due to system definition this overall value has to be compared with the value of 2.4 kmol H^+ ha^{-1} yr^{-1} of the soil compartment obtained by method I (Table 11). These results indicate a contribution of 53% by nitrogen transformations to the overall proton production rate in the soil. The value measured in this forest fits well within the range of values measured by Van Breemen et al. (1988) in the three comparable Hackfort sites in the vicinity of the Tenkink forest (61, 66 and 55% of sites A, B and C, respectively). As in the Tenkink forest, denitrification is expected to play a

Table 11. Net proton production rates due to nitrogen transformations.

	net H^+ production ($kmol\ ha^{-1}\ yr^{-1}$)	
method:	I	II
ecosystem	3.0	3.0
vegetation	0.6	2.1
soil (total)	2.4	0.9
LF	5.1	1.4
Ah1	−0.3	−0.4
Ah2	−2.4	−0.1
other horizons	0.0	0.0

quantitatively important role in nitrogen cycling in the Hackfort forest sites, due to relatively wet soil conditions. This is in contrast with the dry sandy soils in other parts of the Netherlands, where a majority of the Dutch forests are located. It is suggested that in these dry sandy forest soils the contribution of nitrogen cycling in soil acidification exceeds the values measured in the Tenkink and the Hackfort forest sites, due to the minor importance of denitrification as a proton consuming process.

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