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A correlative evaluation of nitrogen cycling in the forest ecosystems of the EC projects NITREX and EXMAN

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Abstract

Results from two EC ecosystem manipulation projects (NITREX and EXMAN) were integrated by a correlation analysis. The analysis focused on ambient nitrogen input and output and on the nitrogen concentrations in various compartments of the ecosystems. The dataset included 12 sites (11 coniferous forests and one alpine vegetation) covering a range of atmospheric nitrogen inputs from 3 to 60 kg N ha⁻¹ year⁻¹. Nitrogen input by precipitation and by throughfall were highly positively correlated, although the regressions differed for sites at which NO₃⁻ deposition dominates compared with sites at which NH₄⁺ dominates. In general, nitrogen concentrations in needles, in needle litterfall and in the organic layer, as well as in drainage, were more closely correlated to nitrogen input in precipitation than throughfall. Variations in nitrogen concentrations in needles, in needle litterfall and in the organic layer explained 96% of the variation in nitrogen output.

Keywords: Nitrogen cycling; Forest ecosystem; NITREX project; EXMAN project

1. Introduction

Acid rain caused by increased air pollution is a large-scale environmental problem threatening natural and semi-natural ecosystems. The effects of acid rain are dramatically visible in many forested areas in northern and central Europe. In an increasing number of countries the role of nitrogen in acid rain with respect to soil acidification and forest dieback has been recognised.

Nitrogen is unique among nutrients in many respects. Nitrogen comes mainly from the atmosphere and is intimately tied to organic matter, whereas other major nutrients come primar-

ily from soil minerals and can accumulate to a substantial degree on soil exchange complexes. Accumulation of nitrogen on soil exchange complexes is minor owing to the high biological demand relative to exchange capacity (Johnson, 1992). The annual input of nitrogen is generally small compared with the organic pool of nitrogen in the ecosystem. Chronically high nitrogen inputs (either anthropogenic or natural) may cause 'nitrogen saturation', when the availability of inorganic nitrogen is in excess of total plant and microbial nutritional demand (Aber et al., 1989). The first signs of nitrogen saturation are often the appearance of NO₃⁻ in drainage water or the onset of significant amounts of denitrification; both symptoms signal an opening of the

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normally closed biogeochemical nitrogen cycle within the ecosystem (Dise and Wright, 1992).

Long-term ecosystem manipulation experiments on a catchment or plot scale provide a valuable tool to assess the effects of atmospheric nitrogen deposition on ecosystem functioning. Two forest ecosystem manipulation projects are underway in Europe within the framework of the EC Research Programmes STEP and ENVIRONMENT. These two projects, Experimental Manipulation of Forest Ecosystems in Europe (EXMAN) (Rasmussen et al., 1990) and Nitrogen Saturation Experiments (NITREX) (Dise and Wright, 1992), address the biogeochemical cycling of elements in coniferous forest ecosystems and in particular the role of atmospheric nitrogen deposition. The general methodology of both projects is comparable; plots or catchments are manipulated in order to study the ecosystem response and obtain more insight in ecosystem functioning in relation to atmospheric deposition. The manipulations involve irrigation, fertiligation, liming, acidification, removal of water and atmospheric deposition by roof constructions, and increased nitrogen inputs.

Here we describe and integrate results from both projects and examine relationships between inputs, pools and fluxes of nitrogen in these ecosystems. The integration focuses on site properties (fluxes and concentrations in compartments) characteristic for nitrogen cycling. As the results on the effects of the different manipulations are not yet available from all sites involved, only data from the control plots are considered. The data were obtained from the participating researchers and derived from Beier and Rasmussen (1993) and Dise and Wright (1992).

2. Material and methods

A total of 12 sites in northwest and central Europe are included in EXMAN (six) and NITREX (eight), with two sites (Klosterhede and Solling) in common (Fig. 1) (Table 1). The sites are in coniferous forests, except for Sogndal, Norway, which has alpine vegetation. Norway



Fig. 1. Location of the NITREX and EXMAN sites in Europe.

spruce (*Picea abies* L.) dominates at most sites, except for Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco) and Scots pine (*Pinus sylvestris* L.) at the Dutch sites and Sitka spruce (*Picea sitchensis* [Bond] Carr.) at the UK site. The sites cover a wide range of atmospheric nitrogen (and sulphur) inputs (Table 2), from heavily polluted sites in central Europe with over 60 kg N ha⁻¹ year⁻¹ to relatively unpolluted sites in Ireland and western Norway with less than 10 kg N ha⁻¹ year⁻¹.

The dataset comprises inorganic nitrogen fluxes in input (bulk precipitation and throughfall) and output (drainage), the age of the trees and various parameters characterising the internal nitrogen cycling in the system (Table 2). In general, the fluxes are average values of 2–3 years. The nitrogen flux in drainage is catchment output in Sogndal and Gårdsjön, and leaching of nitrogen below the rooting zone in the other sites. The nitrogen output fluxes were calculated by multiplying inorganic nitrogen concentrations in soil or drainage water with water fluxes. For three sites (Solling, Ballyhooley and Höglwald) nitrogen fluxes were calculated from soil water concentrations under the assumption that chloride flux out equals chloride flux in throughfall. The

Table 1

Sites (abbreviations) and characteristics. Data from Beier and Rasmussen (1993) and Dise and Wright (1992)

Site	Project	Dominant tree species	Soil classification ^a
Sogndal (Sg)	NITREX	Alpine vegetation	Lithic Haplumbrept
Klosterhede (Kl)	EXMAN/NITREX	<i>Picea abies</i> (Norway spruce)	Typic Haplorthod
Gårdsjön (Ga)	NITREX	<i>Picea abies</i> (Norway spruce)	Ortic Humic Podzol
Höglwald (Ho)	EXMAN	<i>Picea abies</i> (Norway spruce)	Typic Hapludult
Ballyhooly (Ba)	EXMAN	<i>Picea abies</i> (Norway spruce)	Typic Haplorthod
Aber (Ab)	NITREX	<i>Picea sitchensis</i> (Sitka spruce)	Ferric Stagnopodzol
Solling (Sl)	EXMAN/NITREX	<i>Picea abies</i> (Norway spruce)	Aquic Dystrochrept
Alptal (Al)	NITREX	<i>Picea abies</i> (Norway spruce)	Umbric Gleysol
Harderwijk (Ha)	EXMAN	<i>Pinus sylvestris</i> (Scots pine)	Typic Udipsamment
Kootwijk (Ko)	EXMAN	<i>Pseudotsuga menziesii</i> (Douglas fir)	Plaggic Dystrochrept
Speuld (Sp)	NITREX	<i>Pseudotsuga menziesii</i> (Douglas fir)	Ortic Podzol
Ysselsteyn (Ys)	NITREX	<i>Pinus sylvestris</i> (Scots pine)	Humic Haplorthod

^aAccording to Soil Survey Staff (1990) or FAO (1988) classification systems.

internal nitrogen parameters include the nitrogen concentrations in needles (current and first-year), in litter production (needle and total), in the ectorganic layer (L+F+H), and the total amount of nitrogen in litterfall.

Correlation analysis between all variables and information on interdependencies between variables were used to limit the number of variables in the regression analysis and to identify hypotheses for testing by multiple regression analysis. Regression analysis focused on four questions: (1) Are the nitrogen fluxes in precipitation and throughfall related? (2) Are the nitrogen concentrations in ecosystem compartments such as foliage and organic layer related to the input of nitrogen by precipitation and throughfall? (3) Is it possible to predict the nitrogen output in drainage by the nitrogen input by precipitation and throughfall? (4) Is it possible to predict the nitrogen output in drainage by the nitrogen concentration in one or more compartments in the ecosystem?

3. Results and discussion

The flux of NH_4^+ was positively correlated with the flux of NO_3^- in precipitation ($R^2=0.62$, $P<0.002$, $n=12$). Total nitrogen output by drainage was mainly NO_3^- (Table 2). Consequently, the number of parameters used in the

regression analysis was limited by selecting total inorganic nitrogen ($\text{NH}_4^+ + \text{NO}_3^-$) fluxes for precipitation and drainage, rather than separate fluxes for NH_4^+ and NO_3^- . Next, the nitrogen concentration in current-year and first-year needles were highly correlated ($R^2=0.96$, $P<0.001$, $n=11$), as well as the nitrogen concentration in total and needle litterfall ($R^2=0.86$, $P<0.002$, $n=11$). As a result the nitrogen concentration in current-year needles and in needle litterfall were used in the regression analysis as characteristics of foliage and litterfall, respectively.

Total nitrogen flux in litterfall was not significantly correlated with any of the other variables. Other factors such as dominant tree species, developmental stage and tree density probably regulate the total nitrogen flux in litterfall. The age of the trees was negatively correlated only with the nitrogen concentration in the needles ($R^2=0.53$, $P=0.032$, $n=11$, for current-year needles).

3.1. Nitrogen fluxes in precipitation vs. throughfall

The NH_4^+ flux in throughfall and the total inorganic nitrogen flux in precipitation were highly correlated ($R^2=0.72$, $P<0.001$, $n=11$) (Fig. 2). The sites fall into two distinct groups. The first group includes eight sites and linear regression

Table 2
Data used in the correlation analysis. All nitrogen fluxes are in $\text{kg N ha}^{-1} \text{ year}^{-1}$; all nitrogen concentrations ($[\text{N}]$) in percentage of dry matter; tree age in years

	Sogndal	Kloster- hede	Gård- sjön	Högl- wald	Bally- hooly	Aber	Solling	Aptal	Harder- wijk	Koot- wijk	Speuld	Yssel- steyn
NH_4^+ flux in bulk precipitation (pnh4)	1.4	3.3	4.6	6.0	3.4	4.6	7.2	6.6	10.3	11.1	15.0	21.0
NO_3^- flux in bulk precipitation (pno3)	1.3	4.4	5.6	4.6	1.4	6.3	6.1	8.3	4.6	5.6	8.0	11.0
Total N flux in precipitation (ptotn)	2.7	7.7	10.2	10.6	4.8	10.9	13.3	14.9	14.9	16.7	23.0	33.0
NH_4^+ flux in throughfall (tnh4)		16.5	4.3	20.8	6.3	7.0	20.2	7.9	31.1	29.6	38.0	47.0
NO_3^- flux in throughfall (tno3)		10.8	8.0	9.5	2.6	8.2	19.3	12.8	11.5	11.8	17.0	14.0
Total N flux in throughfall (ttotn)		27.3	12.3	30.3	8.9	15.2	39.5	20.7	42.6	41.4	55.0	61.0
NH_4^+ flux in drainage (dnh4)	0.1	0.1	0.0	0.2	0.8	1.7	0.5		0.1	0.0	2.0	3.0
NO_3^- flux in drainage (dno3)	0.1	0.0	0.1	44.2	5.3	6.0	22.3		6.0	16.8	27.0	40.0
Total N flux in drainage (dtotn)	0.1	0.1	0.1	44.4	6.1	7.7	22.8		6.1	16.8	29.0	43.0
N flux in litterfall (ltotn)		40			56	52	35		43	36	33	56
tree age (age)		72	84	39	52	33	58	185	80	39	31	45
$[\text{N}]$ current-year needles (cyn)		1.21	1.34		1.60	1.57	1.53	0.90	1.60	1.90	2.09	2.21
$[\text{N}]$ first-year needles (fyn)		1.17	1.31				1.50	0.85	1.88	1.98	2.31	2.33
$[\text{N}]$ litterfall (lf)		0.98	1.14		1.05	1.00			0.93	0.95	1.45	1.54
$[\text{N}]$ needle litterfall (nlf)		1.10	1.07		1.10	1.10	1.43		1.00	1.20	1.67	2.10
$[\text{N}]$ in ectorganic layer (ect)		1.00	1.78		1.50	1.50	1.59		1.60	1.60	2.08	2.44

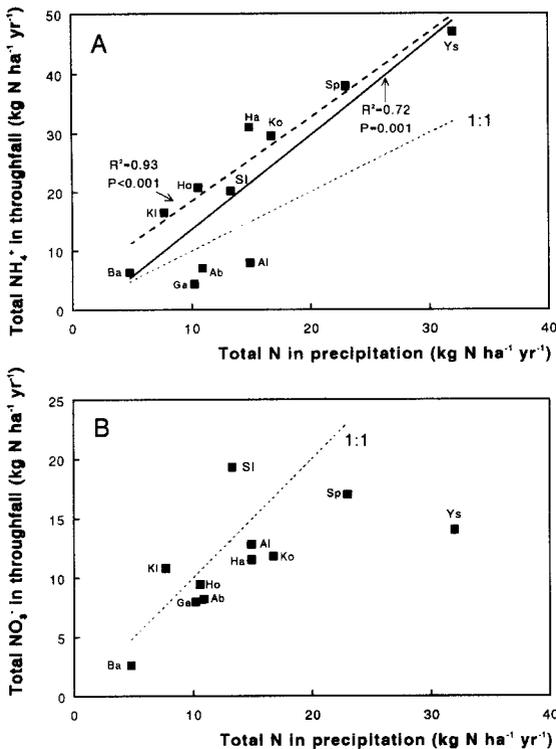


Fig. 2. Relationship between the total N flux in precipitation and (A) NH_4^+ and (B) NO_3^- fluxes in throughfall. The solid line corresponds to the regression line calculated with all data. The dashed line denotes the regression lines calculated with a subgroup of the sites. The dotted line is the 1:1 line.

gave a high regression coefficient ($R^2=0.93$, $P<0.001$), where the three sites in the second group lie close together (Fig. 2). The two groups differ in the amount and form of nitrogen input: the first group has generally higher nitrogen inputs with more than 50% NH_4^+ , whereas the second group has lower inputs with less than 50% NH_4^+ (Fig. 3). Although the two ranges of nitrogen inputs overlap, the sites within this overlap clearly fit in one or the other group. Dry deposition of NH_4^+ accounts for much of the difference. In the first group (Ys, Ha, Ko, Sp, Ho, Ba, Kl, SI) nitrogen input is mainly by dry deposition of NH_4^+ ; these sites are all located in areas of moderate to intensive agricultural activity. At sites of the second group (Ab, Al, Ga), atmospheric nitrogen input primarily occurs as NO_3^- ; these sites are located in unpolluted areas.

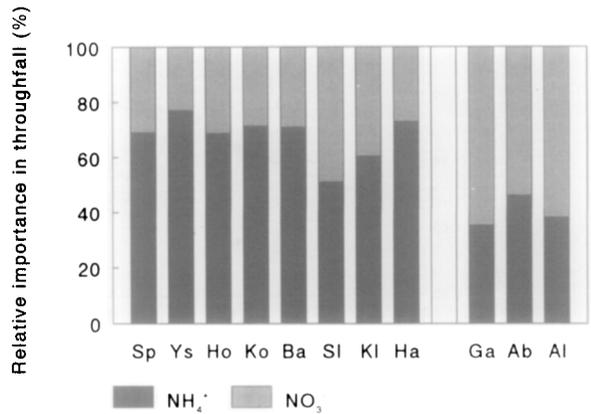


Fig. 3. Relative importance of NH_4^+ and NO_3^- in the total inorganic N flux in throughfall.

3.2. Nitrogen input vs. system nitrogen concentrations

No significant correlations were found between the NO_3^- flux in throughfall and the system nitrogen concentrations. Regression coefficients of total inorganic or NH_4^+ flux in throughfall on system nitrogen concentrations were about equal. System nitrogen concentrations were correlated with nitrogen inputs via precipitation and throughfall. At the sites dominated by NH_4^+ deposition the correlations with the current-year needles and the ectorganic layer were higher and the regression lines steeper relative to linear regression with data from all ten sites (Fig. 4) (Table 3). Increased nitrogen concentrations in the various ecosystem compartments is apparently caused by increased nitrogen inputs (McNulty et al., 1991; Heinsdorf, 1993; Tietema, 1993). The large range of NH_4^+ fluxes in throughfall may mask a relationship between NO_3^- in throughfall and system nitrogen concentrations. Manipulation experiments with nitrogen deposition show that in systems leaking NO_3^- , the flux of N out is more closely related to flux of NO_3^- rather than NH_4^+ in throughfall (Gundersen and Rasmussen, 1995; Emmett et al., 1995). This implies that NH_4^+ inputs have a larger relative contribution to internal ecosystem changes than NO_3^- inputs.

The relationships between nitrogen input by throughfall and nitrogen concentrations in eco-

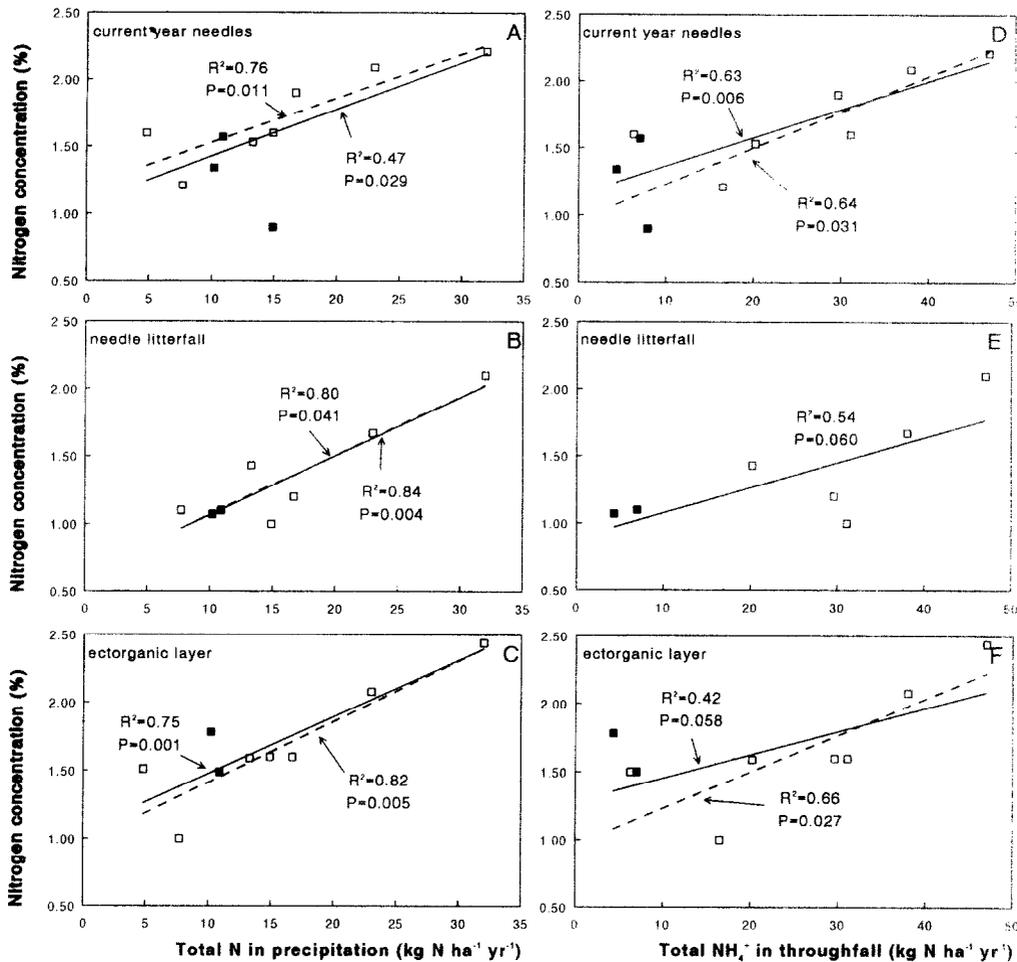


Fig. 4. Relationship between the total N input in precipitation (A–C) and NH_4^+ input in throughfall (E–F), with the N concentrations in current-year needles (A+D), in needle litterfall (B+E) and in the ectorganic layer (C+F). The open symbols represent the sites at which ammonium deposition dominates; the closed symbols represent the sites at which nitrate deposition dominates. The solid lines correspond to the regression lines calculated with all data. The dashed lines denote the regression lines for only the sites at which ammonium deposition dominates.

system compartments are not linear. At sites with low N input (and NO_3^- dominated), N concentrations in ecosystem compartments might reflect some minimum level. Also canopy uptake of NH_4^+ may contribute additional input that influences these relationships. The relative position of the NO_3^- -dominated sites compared with the NH_4^+ -dominated sites in the throughfall relations (Figs. 4(D)–4(F)), however, indicates that the NO_3^- -dominated sites have higher nitrogen concentrations than NH_4^+ -dominated

sites with the same nitrogen input by throughfall. This implies that the canopy uptake of NH_4^+ is higher in the NO_3^- -dominated sites (with generally low nitrogen input), compared with NH_4^+ -dominated sites (with generally high nitrogen inputs) (Hauhs et al., 1989). The NO_3^- -dominated sites in this study are few and span a narrow range in nitrogen input. The passage of nitrogen through the canopy and the subsequent transformation by canopy processes appears responsible for the difference between precipitation and throughfall.

Table 3

Regression coefficients (R^2), number of sites (n), significance levels (*** P <0.001; ** P <0.01; * P <0.1; NS, not significant), intercepts (I) and slopes (S) of regression lines. Numbers in parentheses indicate standard errors. The abbreviations of sites and variables are listed in Tables 1 and 2

Independent variable(s)	Dependent variable	Sites	R^2	n	P	I	S
ptotn	tnh4	All except Sg	0.72	11	***	-2.33 (5.33)	1.60 (0.33)
		Ys, Ha, Ko, Sp, Ho, Kl, So, Ba,	0.94	8	***	4.27 (2.72)	1.42 (0.16)
ptotn	cyn	All except Sg and Ho	0.47	10	*	1.08 (0.22)	0.035 (0.013)
		Ys, Ha, Ko, Sp, Kl, So, Ba,	0.76	7	**	1.20 (0.15)	0.033 (0.008)
	nlf	All except Sg, Ho, Ba and Al	0.84	8	**	0.55 (0.17)	0.047 (0.008)
		Ys, Ha, Ko, Sp, Kl, So	0.80	6	*	0.48 (0.21)	0.050 (0.011)
ect	All except Sg, Ho and Al	0.75	9	**	1.06 (0.15)	0.042 (0.009)	
	Ys, Ha, Ko, Sp, Kl, So, Ba,	0.82	7	**	0.96 (0.17)	0.045 (0.009)	
tnh4	cyn	All except Sg and Ho	0.63	10	**	1.16 (0.14)	0.021 (0.006)
		Ys, Ha, Ko, Sp, Kl, So, Ba,	0.64	7	*	1.19 (0.20)	0.020 (0.006)
	nlf	All except Sg, Ho, Ba and Al	0.54	8	*	0.90 (0.22)	0.019 (0.008)
		Ys, Ha, Ko, Sp, Kl, So	0.50	6	NS	NS	NS
ect	All except Sg, Ho and Al	0.42	9	*	1.29 (0.20)	0.017 (0.008)	
	Ys, Ha, Ko, Sp, Kl, So, Ba,	0.66	7	*	0.96 (0.26)	0.027 (0.009)	
ptotn	dtotn	All except Al	0.47	11	*	-2.24 (7.52)	1.366 (0.483)
		All except Al and Ho	0.83	10	***	-7.37 (3.06)	1.507 (0.242)
tnh4	All except Sg and Al	0.43	10	*	0.80 (8.06)	0.761 (0.311)	
	All except Sg, Al and Ho	0.66	9	**	-2.76 (5.57)	0.782 (0.211)	
tno3	All except Sg and Al	0.20	10	NS	NS	NS	
	All except Sg, Al and Ho	0.41	9	*	-6.76 (10.48)	1.864 (0.845)	
cyn nlf ect cyn + nlf + ect	dtotn	All except Sg, Al, Ho and Ba	0.79	8	**	-48.5 (7.6)	38.17 (8.08)
			0.91	8	***	-35.1 (4.8)	38.08 (4.79)
			0.66	8	*	-33.6 (9.6)	29.04 (8.56)
			0.96	8	**	-45.2 (7.4)	17.52 ^a (8.33)
						29.02 ^b (7.34)	
						-4.30 ^c (7.19)	

^a Coefficient for cyn.

^b Coefficient for nlf.

^c Coefficient for ect.

3.3. Nitrogen fluxes in input vs. output

Only a very weak correlation was found between nitrogen input and output using the data from all 11 sites (Fig. 5). If the Höglwald site is excluded as an outlier, the correlation was highly significant ($R^2=0.83$, $P<0.001$, $n=10$). The Höglwald site has a relatively low nitrogen input via precipitation ($11 \text{ kg N ha}^{-1} \text{ year}^{-1}$) and throughfall ($30 \text{ kg N ha}^{-1} \text{ year}^{-1}$), but a very high nitrogen output ($44 \text{ kg N ha}^{-1} \text{ year}^{-1}$). Unless nitrogen inputs from dry deposition or fog are greatly underestimated, the data suggest that this forest is undergoing a net loss of nitrogen. Höglwald was a beech stand before the spruce

trees were planted. The higher nitrogen transformations in the organic matter originating from this old deciduous litter compared with the coniferous spruce litter might possibly cause this high net output. Also, the estimated output by drainage might be overestimated as it was calculated from the mean annual NH_4^+ and NO_3^- concentrations in the soil solution using chloride as a conservative ion.

In a survey of 65 forested European plots and catchments, Dise and Wright (1995) found that below a deposition threshold of about $10 \text{ kg N ha}^{-1} \text{ year}^{-1}$, no significant nitrogen leaching occurred. Such a threshold is also apparent within this NITREX-EXMAN dataset (Fig. 5).

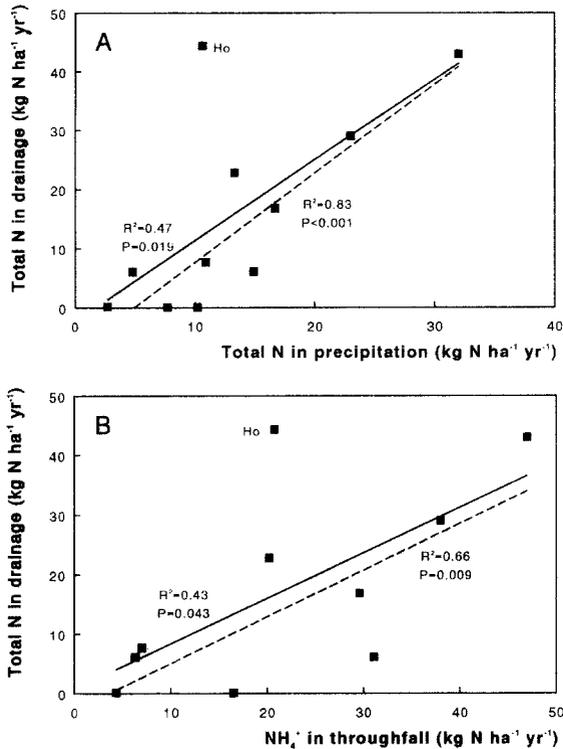


Fig. 5. Relationship between the total N output in drainage and (A) the total N input in precipitation and (B) NH_4^+ input in throughfall. The solid lines correspond to the regression line calculated with all data. The dashed lines denote the regression lines calculated excluding the outlier Hoglwald (Ho) site.

3.4. System nitrogen concentrations and age vs. nitrogen output

The nitrogen concentration in needle litterfall was the best single predictor of nitrogen output by drainage (Fig. 6). Multiple regression using nitrogen concentrations in current-year needles, in needle litterfall and in the ectorganic layer as independent variables explained 96% of the variation in nitrogen output in drainage (Table 3). The degree of nitrogen saturation is apparently strongly correlated with these nitrogen concentrations. As nitrogen saturation is defined as the state of the system at which the availability of inorganic nitrogen exceeds plant and microbial demand (Aber et al., 1989), this implies that the nitrogen concentrations in these compartments provide a useful measure of nitrogen ex-

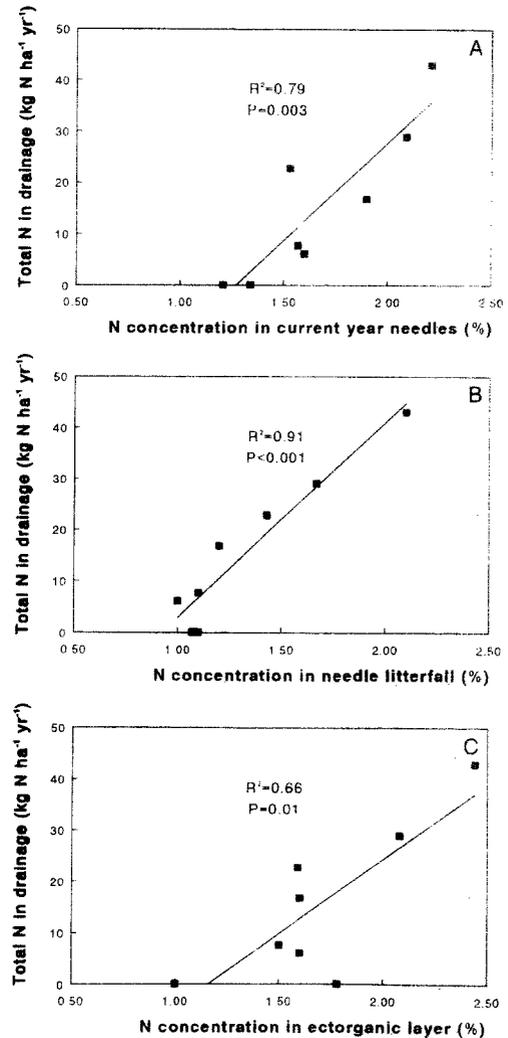


Fig. 6. Relationships between the total N output in drainage and the N concentrations in (A) current-year needles, (B) needle litterfall, and (C) the ectorganic layer.

cess and thus of nitrogen demand (Vitousek et al., 1982). These relatively easy-to-measure system characteristics might offer a useful tool to predict regional patterns of nitrogen saturation.

4. Concluding remarks

Generalisations based on these data from only 12 sites should be tested with larger datasets.

These sites are in forests with different tree species, soils and history of land use. The dataset is too small to take into account these different characteristics.

The data do, however, clearly demonstrate the links between the nitrogen input to forested ecosystems, the nitrogen concentrations in the different compartments in the system and the nitrogen output. A chronically high input of nitrogen will in the long run increase the concentrations and the output. At these sites the effect of nitrogen inputs on nitrogen status appears to dominate the internal site characteristics. The role

- 2, Commission of the European Communities, Brussels, 101 pp.
- Dise, N.B. and Wright, R.F., 1995. Nitrogen leaching from European forests in relation to nitrogen deposition. *For. Ecol. Manage.*, 71: 153–161.
- Emmett, B.A., Brittain, A., Hughes, S., Gorres, J., Kennedy, V., Norris, D., Rafarel, R., Reynolds, B. and Stevens, P.A., 1995. Nitrogen additions (NaNO_3 and NH_4NO_3) at Aber forest, Wales: I. Response of throughfall and soil water chemistry. *For. Ecol. Manage.*, 71: 45–59.
- Food and Agriculture Organization, 1988. *FAO/UNESCO Soil Map of the World. Revised legend.* FAO, Rome.
- Gundersen, P. and Rasmussen, L., 1995. Nitrogen mobility in a nitrogen limited forest soil at Klosterhede, Denmark, examined by NH_4NO_3 addition. *For. Ecol. Manage.*, 71: