Effects of acidification, liming and fertilization on the undergrowth of a pine forest stand in central Sweden

H.F. van Dobben

G.M. Dirkse

C.J.F. ter Braak

C.O. Tamm

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Contents

1 Abstract

The effects of 18 years of artificial acidification, liming and fertilization with N, P, K, Mg, S and micronutrients on the undergrowth of a pine stand on a nutrient poor soil in central Sweden are described. The effect of nitrogen on the composition of the vegetation is far stronger than the effect of the other treatments, causing a shift in dominance from cryptogams and Ericaceae towards *Deschampsia flexuosa* and ruderal species. Comparable changes observed in forest undergrowth in industrialized areas in northwestern Europe must be ascribed to atmospheric deposition of nitrogen rather than to deposition of acidity. The effects of P, K, Mg, S and micronutrients are to a certain degree similar to those of N, although far weaker. Effects of pairwise interactions of nutrients commonly occur.

2 Introduction

In recent years atmospheric deposition of acidity and nitrogen has been a matter of concern to both foresters and ecologists. In various countries it has been proposed or attempted to counteract possible negative effects on tree vitality by the addition of nutrients or lime to the forest soil (for a review, see Van Breemen 1990). On the other hand, nitrogen fertilizer is sometimes applied to forest in poor sites to increase productivity.

Both atmospheric deposition and addition of nutrients influence the composition of forest undergrowth. Atmospheric deposition may cause vegetation changes that are unwanted from a nature conservancy point of view, but measures intended to counteract atmospheric deposition may equally well have unwanted side-effects. Therefore, it seems appropriate to examine the ecological effects of nutrient addition to forests more closely before measures against atmospheric acidification or eutrophication are undertaken on a large scale.

Fortunately a number of factorial experiments exist that facilitate the study of such effects. Although the aim of these experiments was in the first place to study the effect of nutrient addition on the tree stand, their design makes them equally well suited for the study of vegetation. The present study focuses on an experiment located in central Sweden, where the effects of addition of (1) acid and lime and (2) N, P, K, Mg, S and micronutrients, applied singly and in a number of combinations at regular intervals over a period of c. 20 years, could be studied in an area with a low background deposition of nitrogen and acidity.

The aims are (a) to assess whether the increase in *Deschampsia flexuosa* and ruderal species at the expense of cryptogamic species (e.g. *Cladonia* and *Dicranum* spp.) reported from forests in areas with a high background deposition like Germany or The Netherlands (Wittig et al. 1985, Van Breemen 1990) can be ascribed to soil acidification or nitrogen enrichment; and (b) to investigate the effects on the undergrowth of addition of extra nutrients (P, K, Mg, S, micronutrients) to nitrogen enriched forest soil. It was also expected that the experiments would yield ecologically interesting information on limiting nutrients for species occurring in forest undergrowth.

3 Material and methods

3.1 Site description

The 'optimum nutrition experiment Lisselbo' is situated at 60°28'N / 16°57'E, c. 100 km NNW of Uppsala, at c. 80 m altitude. The soil is glaciofluvial sand, to some extent redeposited during the postglacial land upheaval above sea level. It is well drained, and the texture varies from fine sandy to gravelly and locally rather stony. The annual mean temperature is 3.1°C, mean annual precipitation is 593 mm. The stand age was 32 years at the time of data collection. The vegetation type of the stand can be classified as '*Vaccinium myrtillus* type' according to Lundmark (1974) (see column 1 of Table 2 for the cover of the most abundant species in the untreated plots).

The experiment was started in 1969; its set-up is described in detail by Tamm et al. (1974). It was designed to gain insight into the relation between tree growth and nutrient content of the needles. Therefore nutrients were applied at regular intervals, starting with high dosages that gradually decreased to attain nutrient levels in the needles that were as constant as possible. Nitrogen was applied yearly, the other nutrients less frequently. All nutrients were spread by hand. The nutrient regimes are summarized in Table 1. The stand was fenced in to avoid browsing by moose (*Alces alces*) but the fence proved to be ineffective on several occasions and was removed in 1985 (at that time most of the trees had attained a height where moose browsing was no longer harmful). The experiment consisted of three different sub-experiments, with a total of 72 plots measuring 30*30 m^2 each. The sub-experiments were treated separately in our analysis.

Table 1: Overview of the treatments. Amounts are in kg element $ha^{-1}.y^{-1}$, except acid which is in kg H_2SO_4 $ha^{-1}.y^{-1}$; periods are calendar years - 1900.

Experiment	Treatment	source	amount	period
E40	N1	NH_4NO_3	60	69, 70
			40	71 - 74 yearly
			30	75, 76
			20	77 - 87 yearly
E40, E41[1]), E42	N2	NH_4NO_3	120	69, 70
			80	71 - 74 yearly
			60	75, 76
			40	77 - 87 yearly[2])
E40	N3	NH_4NO_3	180	69, 70
			120	71 - 74 yearly
			90	75, 76
			60	77 - 87 yearly
E40, E41, E42	P	[3])	20	72
			40	69, 75, 77, 80, 83, 86
E40, E42	K	Supra PK	38	72
			76	69
			78	75, 77, 80, 83, 86[2])
E41	K	KCl	40	72
			80	69, 75, 77, 80, 83
E41	Mg	$MgCO_3$	50	69, 73, 77, 80, 83
E41	S	Na_2SO_4	40	69, 73, 77, 80, 83
E41	Micronutrients[4])			70, 73, 77
E42	ACID1	H_2SO_4	50	70 - 76 yearly
E42	ACID2	H_2SO_4	100	69, 75, 76
			50	70
			50 (twice)	71, 72, 73, 74
E42	LIME	ground limestone	2000	69

1) in E41 the N2 treatment was applied to all plots.
2) in 1986 and 1987 these treatments were only applied in E40.
3) in E40 and E42 as Supra PK, a commercial fertilizer containing (by weight) 6.8% P, 13.3% K, 16.0% Ca, and 13.0% Cl; in E41 as triple superphosphate.
4) composition of the micronutrient mixture: Cu, 12 $kg.ha^{-1}$; Zn, 12 $kg.ha^{-1}$; Mn, 12 $kg.ha^{-1}$; B, 5 $kg.ha^{-1}$; Mo, 1 $kg.ha^{-1}$. B was omitted in 1977. In E40, 2.5 $kg.ha^{-1}$ B was applied in 1977 and 1986.

E40 (32 plots, 4 blocks) is a 4*2 experiment with in each block three N levels (supplied as ammonium nitrate) plus a blank, with and without P and K (supplied as compound PK fertilizer).

E41 (20 plots, 4 blocks) has a 2^4 factorial design to test the effects of phosphorus (as triple superphosphate), potassium (as KCl), magnesium (as $MgCO_3$), and sulphur (as Na_2SO_4). The two-factor interactions of magnesium and sulphur and two three-factor interactions are confounded with the blocks. Each of the blocks contains one additional plot which received one of the treatments given in the block together with a mixture of micronutrients containing Cu, Zn, Mn, B and Mo. All plots were fertilized with ammonium nitrate at level N2 (Table 1).

E42 (20 plots, 2 blocks) has a 5*2 design in which the effects of acid, lime and irrigation were tested in combination with nitrogen, phosphorus and potassium. The factor with five levels consisted of sulphuric acid at two levels, lime at one level, irrigation (with water from a nearby oligotrophic lake), and a blank. Irrigation was however stopped in 1976 (11 years before the present data were collected) and was therefore not included in the present analysis; the irrigated plots were treated as extra blanks. The factor with two levels was no addition, or addition of nitrogen (as ammonium nitrate at level N2), phosphorus and potassium (as compound PK fertilizer).

3.2 Field methods

Fieldwork was carried out in August and September 1987. A five-meter wide buffer zone was excluded from the edges of the plots. In the remaining plot area cover percentages of phanerogams (including tree saplings), mosses and lichens were estimated and scored on a ten-point scale. All cryptogams were collected and the field identifications were checked. Nomenclature follows Lid (1987), Nyholm (1954-1969) and Wirth (1980) for phanerogams, bryophytes, and lichens, respectively.

3.3 Statistical methods

Before analysis, the ten-point scale of cover was transformed to ln(1 + mid cover percentage). Detrended correspondence analysis showed short gradients (<3 SD) and therefore linear ordination methods were used in subsequent analyses (Ter Braak & Prentice 1988). The effect of the treatments on the species was described by redundancy analysis, alias reduced rank regression (Davies & Tso 1982) by using the program CANOCO 3.1 (Ter Braak 1988). This technique is a form of principal component analysis in which axes are restricted by a multiple regression model. It is therefore also a restricted form of multivariate multiple regression. For designed experiments the regression model reduces to the model of an analysis of variance; the technique is then a form of multivariate analysis of variance (MANOVA). Blocks were used as covariables so as to eliminate their effects from the ordination.

The results of the ordinations are presented in the form of biplots (Ter Braak 1990; Jongman et al. 1987). In the usual biplot, species and samples are indicated by points (center of abbreviated name). In the biplot of an experiment, treatment combinations take the role of samples. A treatment combination is

displayed at the centroid of the samples that received it. The rules for interpretation are as follows (Jongman et al. 1987: pp 127-129): for a particular species, a notional arrow can be drawn from the origin to the species' point. The relative abundance of the species increases in the direction of the arrow; its length indicates the rate of increase. The mean abundance of the species in the treatments can therefore be derived from the biplot by projecting the treatment combinations on its arrow and by ordering the projection points. In this order, the origin indicates the overall mean.

The biplots are in (Euclidean) distance scaling so as to optimally represent the dissimilarity among treatment combinations. After analysis, the lengths of the notional species arrows are adjusted so that the biplot represents species abundance values that are standardized to unit variance (CANOCO scaling 1). Species with arrows pointing in about the same direction show a similar response to the treatments. To avoid overcrowding of the biplots, only those species are displayed that occur in more than half the number of plots of the experiment under consideration.

The biplots display the treatment means with some error. The goodness-of-fit is expressed by the sum of squares that the biplot displays, expressed as the percentage of the total regression sum of squares across the species. This measure can be interpreted as the percentage variance in the fitted abundance values explained by the biplot. The importance of the axes of a biplot is expressed by their eigenvalues. The eigenvalues are given as fractions of the total variance in the species data.

Forward selection was used to compare the relative importance of treatments and their combinations. For each dummy variable representing a treatment (Jongman et al 1987, p. 58) the 'extra fit' was calculated, i.e. the increase in regression sum of squares over all species with this variable as extra explanatory variable. At each step of the selection the variable with the largest extra fit was included in the regression model. Note that the extra fit only compares a given treatment with the treatments not yet included in the model.

Before including a term in the forward selection its statistical significance was tested by means of a Monte Carlo permutation test (also implemented in CANOCO). This test permutes residuals instead of the original data, which allows the effect of any single variable to be tested after correction for the effect of other (co)variables (Ter Braak 1992). The additions are not reported if the fraction of permutations yielding a better fit than the observed extra fit exceeded 0.1 for all the remaining terms. Permutations were always carried out within blocks. The procedure of selecting and testing variables was also applied to single species, and in that case the permutation test has the advantage over the usual t or F tests that no assumptions on normality need to be made.

In the forward selection, the dummy variables representing one- and two-factor combinations were treated equally, i.e. each particular two-factor combination (for example N2.P) was allowed to enter the model even if the corresponding single factor terms (N2 and P in the example) were not yet included. If interactions are important, this procedure highlights the factor combinations with extreme mean species abundances and can thus yield a more parsimonious summary of the data than the classical technique of selecting interactions after main effects.

4 Results

Table 2 gives the mean cover percentage of the most common species in some of the treatments. A more detailed analysis of the separate experiments is given below.

Table 2: Mean cover percentage (untransformed) in selected treatments of the species that occur in more than half of the plots of any experiment. abbr = abbreviated name (used in the biplots); control = mean of all untreated plots; +N = mean of all plots treated with only N (irrespective of dosage); +PK = mean of plots treated with only P and K; +NPK = mean of plots treated with only N, P and K (irrespective of dosage); +ACID = mean of acidified plots (irrespective of dosage) without N; +LIME = mean of limed plots without N; plots = number of plots on which mean is based.

abbr	control	+N	+PK	+NPK	+ACID	+LIME	full name
plots	8	13	4	15	4	2	
AGRc	0.01	0.02	0.00	0.06	0.00	0.00	Agrostis capillaris L.
ARCu	0.04	0.01	0.18	0.02	0.20	0.30	Arctostaphylos uva-ursi (L.)Sprengel
BEpe	0.06	0.10	0.13	0.03	0.03	0.00	Betula pendula Roth
BEpu	0.08	0.12	0.08	0.09	0.03	0.00	Betula pubescens Ehrhart
BRoe	0.00	0.89	0.03	2.19	0.03	0.00	Brachythecium oedipodium (Mitt.)Jaeg.
BRre	0.00	0.05	0.00	0.07	0.00	0.05	Brachythecium reflexum (Starke)Schimp.
CALa	0.00	0.02	0.05	0.06	0.00	0.00	Calamagrostis arundinacea (L.)Roth
CAvu	9.56	0.65	11.13	0.15	18.00	35.00	Calluna vulgaris (L.)Hull
CETi	8.95	0.47	2.38	0.24	4.50	7.00	Cetraria islandica (L.)Ach.
CHan	0.08	0.08	0.10	0.74	0.08	0.05	Chamerion angustifolium (L.)Holub
Carb	4.59	0.14	0.68	0.17	1.63	4.50	Cladonia arbuscula (Wallr.)Hale&Culb.
Ccen	0.09	0.04	0.08	0.01	0.10	0.10	Cladonia cenotea (Ach.)Schaer.
Cchl	0.06	0.07	0.05	0.03	0.08	0.10	Cladonia chlorophaea (Flörke ex Sommerf.)Sprengel s.l.
Ccoc	0.04	0.01	0.03	0.00	0.08	0.05	Cladonia coccifera (L.)Willd.
Ccor	0.15	0.05	0.20	0.07	0.30	0.30	Cladonia cornuta (L.)Hoffm.
Ccri	0.09	0.04	0.10	0.03	0.10	0.05	Cladonia crispata (Ach.)Flotow
Cphy	0.09	0.06	0.10	0.05	0.10	0.10	Cladonia phyllophora Ehrh. ex Hoffm.
Cran	5.84	0.18	1.15	0.13	3.25	7.00	Cladonia rangiferina (L.)Nyl.
Cste	0.14	0.00	0.03	0.01	0.08	0.10	Cladonia stellaris (Opiz)Brodo
Csul	0.30	0.07	0.10	0.05	0.88	0.30	Cladonia sulphurina (Michaux)Fr.
DEfl	0.62	63.23	4.40	69.00	0.10	0.10	Deschampsia flexuosa (L.)Trinius
DIpo	11.50	1.25	2.00	0.41	4.03	0.50	Dicranum polysetum Swartz
DIsc	0.21	0.75	0.38	0.25	0.08	0.30	Dicranum scoparium Hedw.
DIsp	0.06	0.03	0.08	0.03	0.30	0.30	Dicranum spurium Hedw.
DRYc	0.00	0.08	0.00	0.10	0.00	0.00	Dryopteris carthusiana (Villars)H.P.Fuchs
EMPn	0.19	0.08	0.55	0.02	0.30	3.75	Empetrum nigrum L.
HYLs	0.28	0.03	0.05	0.02	0.08	0.00	Hylocomium splendens (Hedw.)Schimp.
LOPh	0.00	0.03	0.00	0.05	0.00	0.00	Lophocolea heterophylla (Schrad.)Dum.
LUZp	0.04	0.12	0.10	0.09	0.00	0.00	Luzula pilosa (L.)Willdenow
MELp	1.85	0.12	0.18	0.05	0.05	0.05	Melampyrum pratense L.
PICa	0.30	0.87	0.88	0.64	0.20	0.10	Picea abies (L.)Karsten
PIsy	0.25	0.03	0.05	0.04	0.30	0.10	Pinus sylvestris L.
PLAd	0.00	0.03	0.00	0.17	0.00	0.00	Plagiothecium denticulatum (Hedw.)Schimp.
PLAl	0.00	0.12	0.03	0.15	0.00	0.00	Plagiothecium laetum Schimp.
PLEs	44.38	20.04	47.50	14.87	0.68	47.50	Pleurozium schreberi (Brid.)Mitt.
POHn	0.50	0.32	0.77	0.45	7.38	0.30	Pohlia nutans (Hedw.)Lindb.
POju	0.09	0.15	0.08	0.07	0.08	0.10	Polytrichum juniperinum Hedw.
PTIp	0.05	0.04	0.10	0.06	0.00	0.00	Ptilidium pulcherrimum (G.Web.)Vainio
RUBi	0.00	0.28	0.00	0.97	0.00	0.00	Rubus idaeus L.
RUMa	0.00	0.02	0.03	0.08	0.03	0.00	Rumex acetosella L.
SORa	0.03	0.15	0.08	0.11	0.00	0.00	Sorbus aucuparia L.
TRIe	0.01	0.03	0.00	0.18	0.00	0.00	Trientalis europaea L.
VAmy	18.88	11.42	9.75	1.23	4.50	7.00	Vaccinium myrtillus L.
VAvi	3.50	0.34	1.15	0.15	6.13	2.00	Vaccinium vitis-idaea L.

4.1 E40

The biplot (Figure 1) shows the centroids of the sample scores per treatment combination and a selection of the species scores. The biplot indicates a strong non-linear effect of N, and a lesser effect of P + K. At all N levels the effects of N and P + K were substitutable to a certain extent, i.e. extra P + K had the same effect as a little extra N (each arrow in Figure 1 points in the direction of the arrow representing the next higher N dosage). The size and significance of the observed effects are summarized in Table 3 under the heading 'all species'. Nitrogen addition was by far the most important, the difference between no N and N at any level accounted for 44% of the total variance. P + K and the difference between N1 and the higher N levels had small but significant contributions to the total of 63% variance accounted for. The difference between the treatments N2 and N3 was not significant at $p < 0.1$and neither was the interaction between N and P + K.

The position of the species scores in Figure 1 shows that Ericaceae, lichens, and bryophytes like *Pleurozium schreberi* and *Hylocomium splendens* were strongly disfavoured by N at any level, and, to a lesser extent, by P + K. *Deschampsia flexuosa* was strongly favoured by N at a low dosage (N1), and at that dosage also by P, but no extra effect was found of higher N dosages or the addition of P + K at these dosages. Ruderals like *Chamerion angustifolium* and *Rubus idaeus* showed a strong increase at higher N dosages, and were then additionally stimulated by P. The litter-inhabiting mosses *Brachythecium oedipodium* and *Plagiothecium laetum* show the same behaviour. Also the rejuvenation of trees was influenced by the treatments: at no N most tree saplings were *Pinus sylvestris*, at low dosages *Picea abies* and at high dosages *Betula* spp.

The relative importance of the treatment levels or of treatment combinations for individual species can approximately be derived from their positions in Figuur1. More quantitatively, the size and statistical significance of the effects on some selected species are summarized in Table 3. The species are selected to illustrate possible effects. The percentage variance accounted for by the full model exceeds 20% for all species occurring in more than half of the plots, with the exception of *Luzula pilosa*, and even for this species the effect of N was close to significance (Table 3). Table 3 shows that by far the strongest effect was found for *Deschampsia flexuosa*, which increased a 100-fold in cover in reaction to N (Table 2).

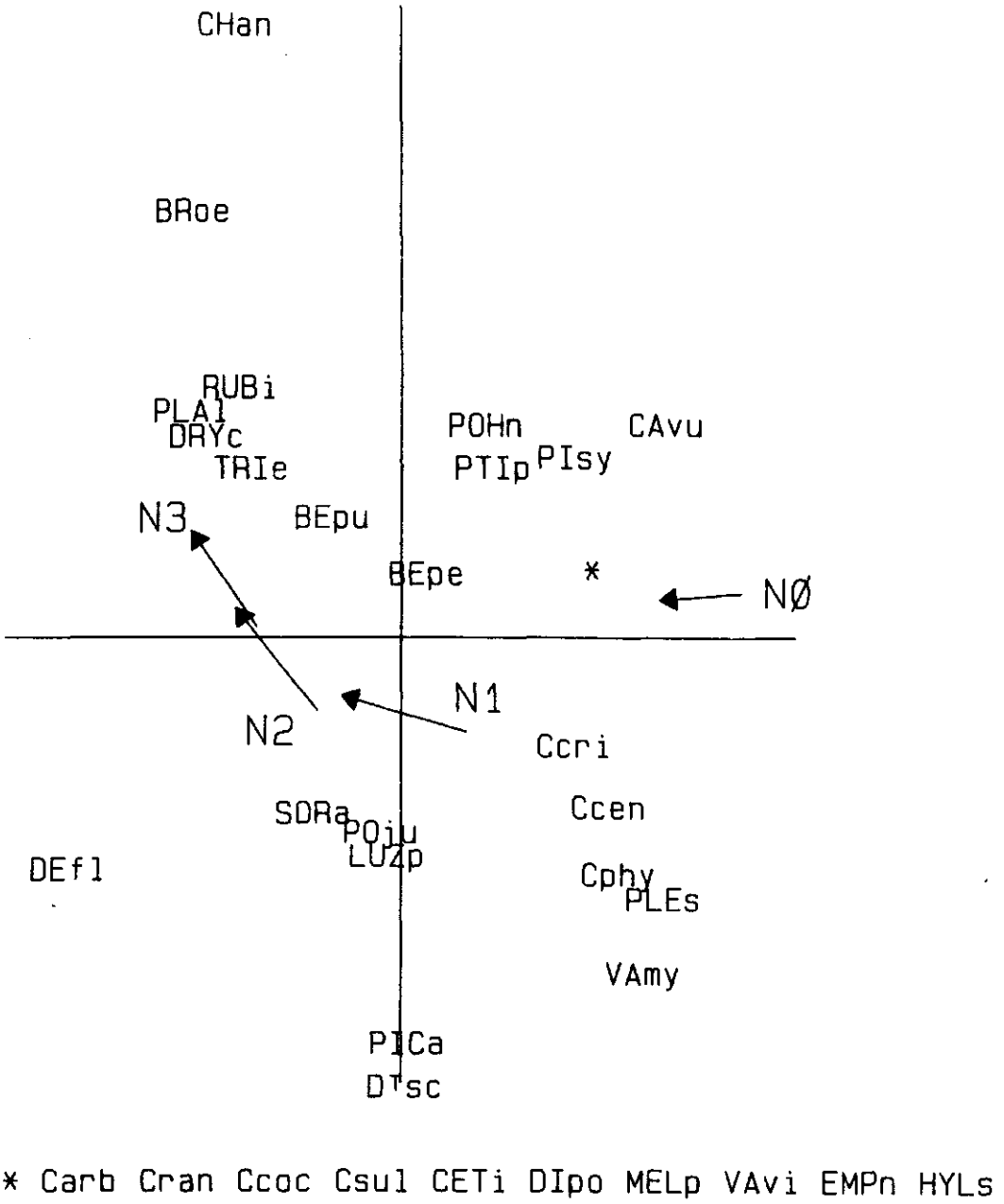


*Figure 1: Distance biplot of sample scores and species scores in E40, based on reduced rank regression with model N*P and covariable block. Sample scores are given as centroids per treatment combination, the arrows connecting the -P centroid (base) with the +P centroid (head) at each N level (the centroid for the main effect of a given treatment can be inferred as centroid of the combinations containing that treatment). Species scores (given for all species occurring in more than half of the plots) are located in the center of the abbreviated names. The biplot explains 92% of the variance in the fitted abundance values of the full model (eigenvalues of the first two axes are 0.52 and 0.06). See text for further interpretation of biplots and Table 2 for an explanation of the abbreviations.*

Table 3: Significance of treatment effects in E40 for the complete vegetation and some selected species. Model tested: N*P. The model given was derived by stepwise addition of the most significant terms to the model (forward selection); the table gives the order of addition. Sign indicates whether (under a model that includes all terms given in the table) species cover in the given treatment (after correction for the other terms) is higher (+) or lower (-) than mean cover. Differences in the cumulative fit and the sum of the extra fit and the cumulative fit in the preceding row are due to rounding errors. Significance: *** = $p \leq 0.001$; ** = $0.001 < p \leq 0.01$;* = $0.01 < p \leq 0.05$;? = $0.05 < p \leq 0.1$,ns = $p > 0.1$ ($n = 32$).

treatment	extra fit	cumulative fit	sign	p
all species				
-N	.44	.44		***
+N1	.08	.52		**
+P	.05	.58		**
full model		.63		
Betula pubescens				
+N3-P	.22	.22	+	**
full model		.25		
Brachythecium oedipodium				
+N3	.39	.39	+	***
+N2+P	.08	.47	+	*
full model		.51		
Calluna vulgaris				
-N	.56	.56	+	***
+N1-P	.03	.59	+	?
full model		.59		
Chamerion angustifolium				
+N3+P	.58	.58	+	***
+N2+P	.16	.75	+	***
full model		.75		
Cladonia rangiferina				
-N	.35	.35	+	**
-N+P	.04	.39	+	?
full model		.43		
Deschampsia flexuosa				
-N	.83	.83	-	***
N1-P	.04	.87	-	*
full model		.88		
Luzula pilosa				
+N2	.08	.08	+	?
full model		.11		
Picea abies				
+N3	.13	.13	-	*
-N-P	.08	.20	-	?
full model		.24		
Pinus sylvestris				
-N-P	.21	.21	+	*
full model		.32		
Pleurozium schreberi				
-N	.34	.34	+	**
+N1	.25	.59	-	***
+N3+P	.05	.64	-	?
full model		.64		
Vaccinium myrtillus				
+N3	.23	.23	-	**
+N2+P	.22	.46	-	**
+N1+P	.11	.56	-	**
full model		.61		

4.2 E41

Figure 2a shows the biplot of the centroids of the sample scores for all two-factor combinations, and Figure 2b the biplot of selected species scores. Table 4 summarizes the significance of some of the observed effects. In contrast to the experiments with nitrogen addition, there was no strongly dominating effect of a single nutrient. All nutrients in this experiment had roughly the same effect, viz. a displacement of the sample scores towards lower values on the first axis. The location of the convex hull of the centroids belonging to a given treatment in Figure 2a with respect to the origin gives an idea of its main effect; the size gives an idea of the importance of the other nutrients. The figure shows that K has a small main effect (its centroid is close to the origin), but acts as a modifier of the effects of other nutrients, as can be seen for example from the distance of the centroids for +P+K and +P-K.

The second axis divides the nutrients into two groups: (a) P and Mg, with a positive score, and (b) S and micronutrients, with a negative score. The convex hull of the micronutrient centroids is small and distant from the origin, yet few significant effects of micronutrients were found, which is probably due to the small number of plots with this treatment.

The position of the species scores in Figure 2b shows that addition of any of the tested nutrients caused a general shift from species that are usually associated with 'poor' sites (like lichens, Ericaceae and *Dicranum* spp.) towards species associated with 'rich' sites (like grasses and litter-inhabiting mosses). Within these groups species may react differently, being favoured (or disfavoured) either by P and Mg or by S and micronutrients, as indicated by the position of their scores on the second axis. Examples of species favoured by P and Mg are *Brachythecium oedipodium*, *Deschampsia flexuosa* and *Rubus idaeus*, while *Calamagrostis arundinacea* and *Cladonia cenotea* were favoured and *Pleurozium schreberi* was disfavoured by S and micronutrients. In fact the cover of each species seems to be determined by a unique combination of nutrients (Table 4).

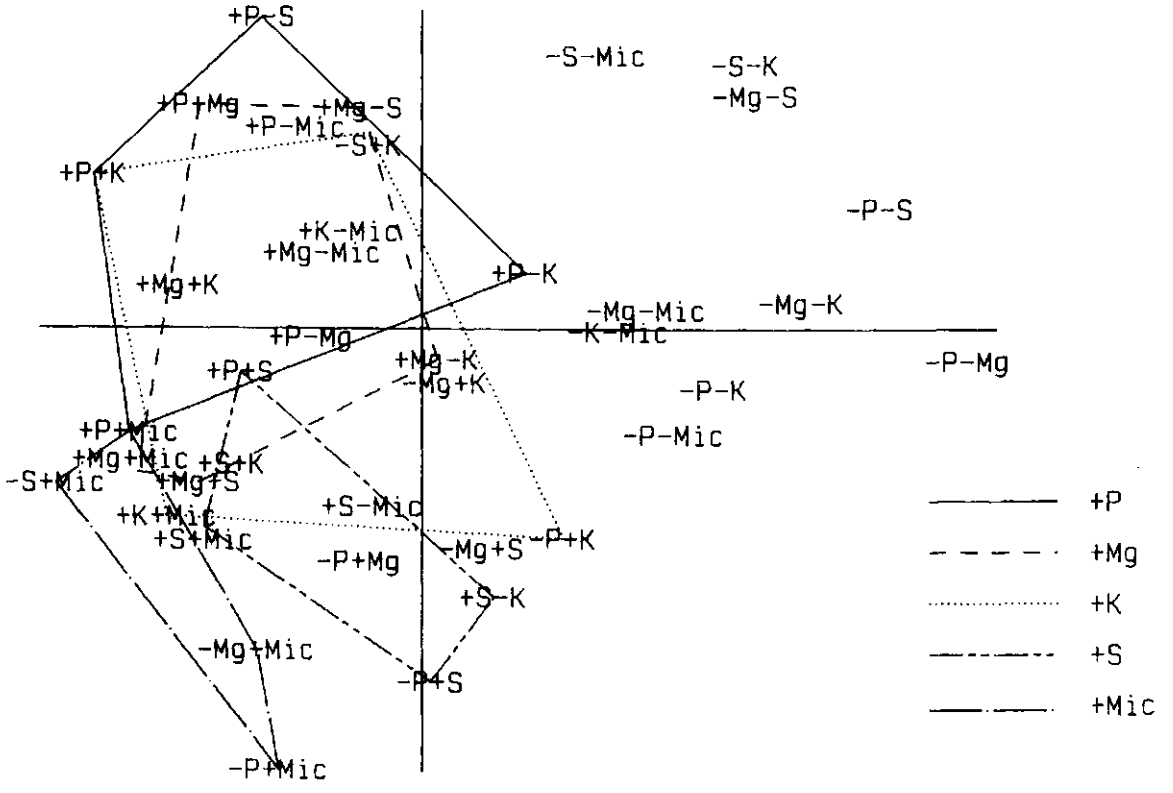
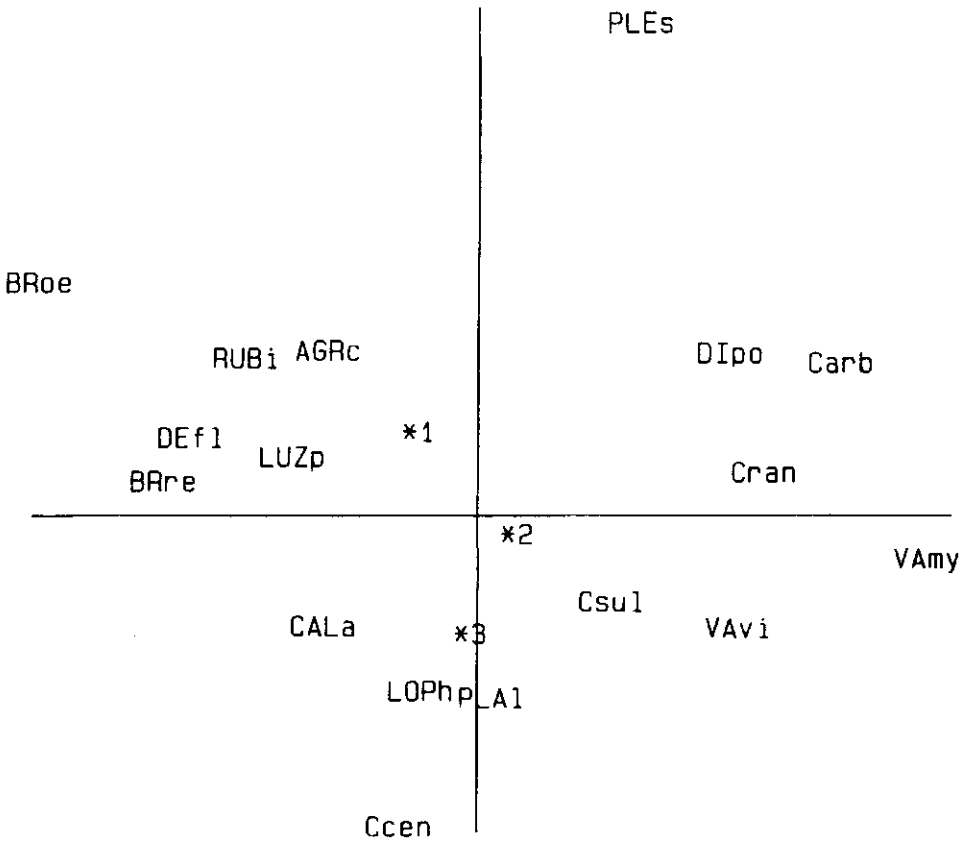


*Figure 2: Distance biplot of sample scores (2a) and species scores (2b) in E41 based on reduced rank regression with model P*K*Mg*S*Mic and covariable block, limited to main effects and two-factor interactions. Sample scores are given as centroids of two-factor combinations. The centroid for a main effect can be inferred as the weighted centroid of all interactions containing that treatment. For each treatment the convex hull is drawn around the centroids. The biplot explains 77% of the variance in the fitted abundance values (eigenvalues of the first two axes are 0.30 and 0.26).*



*1 SORa TRIe Ccor PTIp RUMa *2 POju CHan DIsc Cphy PICa DRYc BEpu
*3 PIsy POHn PLAd CAvu

Figure 2 b

Table 4: Significance of treatment effects in E41. Model tested: P*K*Mg*S*Mic, limited to main effects and two-factor interactions. Further explanation see Table 3 (n = 20).

treatment	extra fit	cumulative fit	sign	p
all species				
+P+K	.20	.20		**
-S-Mic	.18	.38		***
-P-Mg	.11	.49		**
+P+Mg	.04	.53		?
+Mic	.04	.57		?
+P+S	.04	.61		?
full model		.73		
all species with main effects + pure interactions model				
+P	.14	.14		*
+S	.14	.28		**
+Mg	.08	.36		*
full model		.73		
Betula pubescens				
+K-Mic	.20	.20	+	*
full model		.49		
Brachythecium oedipodium				
+P+K	.62	.62	+	***
-Mg+K	.09	.71	-	*
full model		.80		
Brachythecium reflexum				
+Mg	.25	.25	+	*
+P+K	.11	.36	+	?
-Mg+K	.05	.41	-	ns
-P+S	.07	.49	+	?
+S+Mic	.07	.56	-	?
-Mg+Mic	.06	.61	+	*
-P+Mic	.09	.70	+	*
full model		.72		
Calamagrostis arundinacea				
+Mg-K	.18	.18	+	*
-P+S	.15	.33	+	*
+P+K	.08	.41	+	ns
+S+K	.15	.57	-	*
full model		.64		
Cladonia cenotea				
-P+S	.28	.28	+	*
+S+Mic	.19	.47	+	*
full model		.61		
Cladonia rangiferina				
-P-Mic	.27	.27	+	**
+S+K	.18	.45	-	**
full model		.53		
Deschampsia flexuosa				
-P-Mg	.34	.34	-	***
-Mg+Mic	.11	.45	-	***
full model		.61		
Picea abies				
-S+Mic	.48	.48	+	***
full model		.71		
Pinus sylvestris				
-S+Mic	.19	.19	+	***
+P-Mg	.13	.32	-	*
-Mg+Mic	.06	.39	+	?
full model		.45		

treatment	extra fit	cumulative fit	sign	p
Pleurozium schreberi				
-S-Mic	.46	.46	+	**
-P+Mg	.12	.58	-	*
+Mg+S	.06	.64	+	*
full model		.71		
Vaccinium myrtillus				
-P-Mg	.55	.55	+	***
+K-Mic	.11	.65	-	*
+S-Mic	.05	.71	-	?
-Mg-K	.04	.75	+	?
+P-S	.03	.78	-	?
full model		.82		

An interesting phenomenon is that nearly all significant terms in Table 4 represent particular factor combinations, while significant main effects are rare. The standard approach for a factorial experiment of including interactions after main effects yielded few significant terms ($p < 0.1$). The significant main effects and 'pure' interactions explained only 36% of the variance in the 'all species' case, whereas the particular significant treatment combinations explained 61% (Table 4). Apparently, particular treatment combinations stand out, so the main effects model is ineffective.

Table 2 gives an indication of the effect of the combination of P and K on species cover, which was rather small for all species. For the other nutrients no mean cover values are given, but for these the effects were even smaller. On the other hand, the percentage variance accounted for by the full model was generally high (>50% for most species).

4.3 E42

The biplot with selected species scores and centroids of the sample scores for treatment combinations is found in Figure 3, significance levels are given in Table 5. Fertilization with NPK had the most important effect, but there was also a significant effect of acidification and liming. The difference between the two acidity levels was not significant at $p < 0.1$. The biplot shows that (unlike N and PK in E40) fertilization and manipulation of acidity caused a displacement of the sample scores in different (almost perpendicular) directions, which means that both influenced species composition in a different way. There was also a nearly significant ($p \simeq 0.06$) interaction effect between fertilization and manipulation of acidity. The nature of this interaction becomes apparent from Figure 3: the effect of acidification was less when plots were fertilized, while the effect of fertilization was less in limed plots. The interaction between NPK and lime should, however, be interpreted with care because the NPK+lime plots were more open due to tree damage caused by boron deficiency.

On the level of the individual species the effects of nitrogen were comparable to those found in E40. The reactions to manipulation of acidity differed among the species, irrespective of taxonomic position. Two species strongly reacted to acidity and only weakly to N: the bryophytes *Pohlia nutans* (strongly favoured by acidification) and *Pleurozium schreberi* (strongly disfavoured by acidification). Some species were only weakly influenced by acidity but strongly by nitrogen, like *Chamerion angustifolium* and *Deschampsia flexuosa*. Other species strongly reacted to both, e.g. *Calluna vulgaris* which was favoured by liming and disfavoured by fertilization. Among the *Cladonia* species some were favoured by acidification (*C. cenotea*, *C. sulphurina*), while others were disfavoured by acidification (*C. rangiferina*) or favoured by liming (*C. arbuscula*). The *Betula* species showed opposite reactions to acidity: *B. pendula* was favoured and *B. pubescens* disfavoured by acidification. Of the other tree species *Picea abies* did not show any significant reaction, while *Pinus sylvestris* seemed to prefer the unfertilized plots irrespective of acidity, but also those where both nitrogen and lime had been applied. The reactions of the *Pinus* saplings were consistent with findings of Tamm & Popovic (1989) who reported a significant negative effect of the interaction between N fertilization and acidification on the basal area increment of the dominant *Pinus* in the same experiment.

Table 5: significance of treatment effect in E42. Model tested: N*(ACID + LIME). Further explanation see Table 3 (n = 20).

treatment	extra fit	cumulative fit	sign	p
all species				
+N	.45	.45		***
+LIME	.09	.54		**
-ACID	.13	.67		***
+N-ACID	.03	.71		?
full model		.76		
Betula pendula				
-ACID	.34	.34	+	**
+ACID1	.30	.64	-	**
full model		.69		
Betula pubescens				
+N+ACID2	.47	.47	+	***
full model		.56		
Brachythecium oedipodium				
+N-ACID	.39	.39	+	*
full model		.52		
Calluna vulgaris				
+N	.67	.67	-	***
+LIME	.16	.84	+	***
full model		.86		
Chamerion angustifolium				
+N	.97	.97	+	***
-N+ACID2	.01	.97	+	**
full model		.97		
Cladonia arbuscula				
-N-ACID	.55	.55	+	***
+LIME	.10	.66	+	*
+N+ACID2	.05	.71	-	?
full model		.75		
Cladonia cenotea				
+N-ACID	.35	.35	-	**
+N+LIME	.15	.50	-	*
full model		.51		
Cladonia rangiferina				
+N	.69	.69	-	***
-N-ACID	.13	.82	+	**
+ACID2	.06	.87	-	**
full model		.91		
Deschampsia flexuosa				
+N	.89	.89	+	***
+N+LIME	.06	.95	-	***
full model		.95		
Pinus sylvestris				
-N-ACID	.28	.28	+	*
-N+ACID1	.28	.57	+	**
+N+LIME	.12	.69	+	*
full model		.72		
Pleurozium schreberi				
+ACID2	.29	.29	-	**
+ACID1	.48	.77	-	***
full model		.78		
Pohlia nutans				
-N+ACID2	.42	.42	+	**
+ACID1	.08	.50	+	?
+ACID2	.09	.59	+	*
full model		.61		

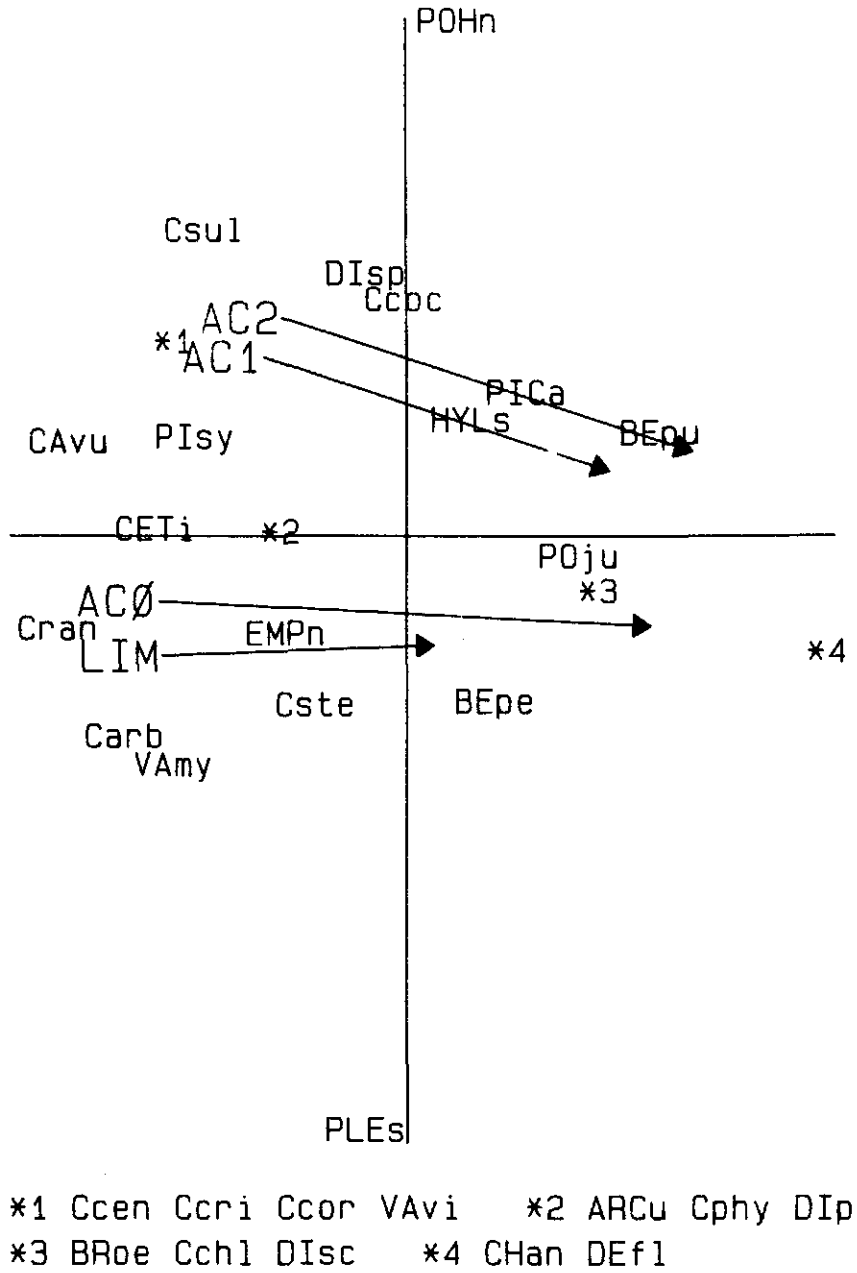


Figure 3: Distance biplot of sample scores and species scores in E42, based on reduced rank regression with model N(ACID + LIME) and covariable block. Sample scores are given as centroids per treatment combination, the arrows connecting the -N centroid (base) with the +N centroid (head) at each acid/lime level. The centroid for the main effect of a given treatment can be inferred as centroid of the combinations containing that treatment. The biplot explains 89% of the variance in the fitted abundance values (eigenvalues of the first two axes are 0.50 and 0.18).*

Like in E40 and E41, significant effects of the treatments can be found for most species; of the species that occur in more than half of the plots only a few (*Picea abies*, *Cladonia coccifera*, *C. stellaris* and *Hylocomium splendens*) have less than 30% of the variance accounted for by the full model and no significant effect of any of the terms. The effects of liming and acidification on mean cover were generally small (Table 2). The most conspicuous changes were found for the mosses *Pleurozium schreberi* (almost disappearing on acidification), *Pohlia nutans* (c. tenfold increase on acidification) and for *Calluna vulgaris* (c. threefold increase on liming).

5 Discussion

Of all treatments nitrogen fertilization had by far the most important effect. Addition of c. 60 kg N $ha^{-1}.y^{-1}$ caused a shift from a fine-grained vegetation dominated by Ericaceae, acrocarpous mosses and lichens, to a dense mat of *Deschampsia flexuosa* with pleurocarpous mosses growing on its litter and scattered individuals of ruderal species like *Chamerion angustifolium* and *Rubus idaeus*. If natural succession were allowed to proceed, a different forest type would eventually arise, with a dominance of *Betula* spp. or *Picea abies*.

The effect of phosphate was similar to the effect of N but far weaker. The occurrence of *Chamerion angustifolium* was extra favoured by P in the presence of N. The effects of acidification and liming were also small in comparison to those of N fertilization. In the fertilized plots there was little effect of acidification, in the unfertilized plots the effect was less weak but the vegetation change did not entail a shift towards a different taxonomical or ecological group. Opposite reactions to acidification or liming occurred within groups of closely related species such as *Cladonia* spp., *Vaccinium* spp. and *Betula* spp.

The effect of the treatments on the tree layer was small at the time of data collection, with the exception of the NPK + lime treatment, which caused severe boron deficiency. Therefore most of the observed effects are more likely due to differences in nutrient availability rather than to differences in light climate. However, in the N treated plots closure of the tree layer took place at an earlier stage than in the untreated plots (Tamm & Popovic 1989). Therefore larger differences in light climate may have existed in the past (before c. 1985). The possibility that the effect of such differences still persists cannot be completely ruled out.

Although the strongest effects were found for N, the nutrients appeared to be substitutable to a certain degree, with the exception of liming and acidification. Manipulation of soil pH on the one hand, and N addition on the other hand caused vegetation changes that were unrelated. Species favoured by N may be either favoured or disfavoured by liming, and vice versa. Probably Ca was not a limiting nutrient in our experiments. Since the acid was applied as sulphuric acid some of the apparent reactions to acidity might, however, be caused by sulphate. This could be the case with *Pleurozium schreberi* and *Cladonia cenotea* whose reaction to acidification in experiment E42 was similar to the reaction to S in experiment E41.

The effects of Mg and K, and, to a lesser extent, of S and micronutrients, were similar to those of P, and therefore also similar to those of N. It may be surprising to find significant effects of S and micronutrients which are generally considered to be no limiting factors for vegetation. However, for some species our observations of the effects of S and micronutrients are in agreement with those noted by others. This is e.g. the case for *Pohlia nutans*, which was stimulated by S and micronutrients (Figure 2) and also by acidity (Figure 3), and for *Pleurozium schreberi* which was disfavoured by S, micronutrients and acidity. In several studies on the effect of mine or smelter pollution on vegetation, *Pohlia*

nutans proved to be very resistant to sulphate, heavy metals and acidity, whereas *Pleurozium schreberi* was sensitive (review by Tyler 1990).

The results of our experiments indicate that the vegetation changes in forest undergrowth observed in industrialized areas are due to nitrogen deposition rather than to acidification. The N dosage applied in the experiments was in the same order of magnitude as the atmospheric N deposition in areas like The Netherlands, Belgium or northern Germany (c. 60 $kg.ha^{-1}.y^{-1}$; Asman & Van Jaarsveld 1990). The resulting increase in *Deschampsia flexuosa* and ruderal species was very similar to the observed vegetation changes (Wittig et al. 1985, Dirkse 1987, Van Breemen 1990). The acid dosages applied in our experiments were low (c. 0.5 and c. 1 kMol H $ha^{-1}.y^{-1}$) compared to the atmospheric acid deposition in industrial areas (c. 5 kMol H $ha^{-1}.y^{-1}$; Anonymus 1990) and the application of acid was stopped long before the present data were collected. However, many species significantly reacted to the acid treatments, but the resulting vegetation changes did not show any similarity to the vegetation changes observed in industrialized areas. Therefore, soil acidification seems less likely as a cause for large-scale vegetation changes, contrary to views held by Wittig et al. (1985) for Westphalian forests.

Our experiments showed that addition of other nutrients to balance the excess N will further stimulate the vegetation changes caused by N. Only liming seemed to mitigate the effects of N. However, other liming experiments showed that the effect of liming strongly depends upon the store of N present in the soil (Van Dobben et al. in prep.). An important part of the added N is stored in soil organic matter through microbial processes (Overrein 1967). The release of N from this organic matter depends upon the equilibrium between fixation and mineralization which in turn is pH-dependent (Haynes 1986). The present experiments were carried out on a N deficient soil, and liming has probably shifted this equilibrium towards a higher level of fixation, thereby decreasing the N pool available to the vegetation. The same effect was also described by Popovic & Andersson (1984). On soils that are less N deficient different effects of liming may be expected.

The results of E41 are generally consistent with Tilman's (1988) 'resource-ratio' hypothesis in that each species seemed to have its own limiting nutrients. Also micronutrients appeared to be limiting for certain species, and their importance may even be underestimated because of the small number of micronutrient-treated plots. As the limitation was generally not by a single nutrient but by a combination of nutrients, the number of niches that exist in a vegetation of species competing for nutrients is even larger than in the case of each nutrient being 'fully essential' in the sense of Tilman (1988). This might be an additional explanation for the species richness of vegetation on nutrient-poor soils.

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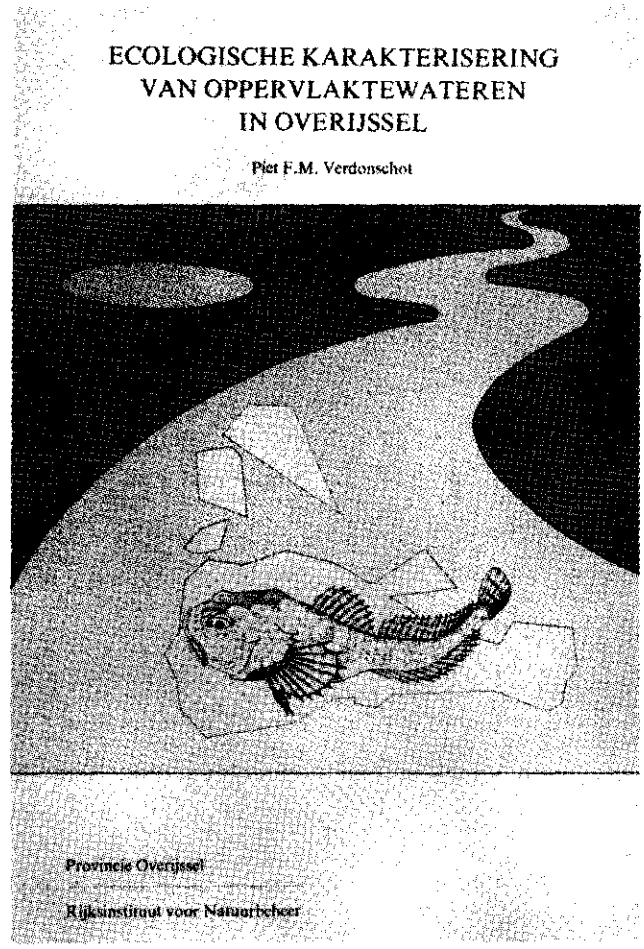

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