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Long-term vegetation changes in an *Abies alba* forest: natural development compared with response to fertilization

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Abstract. A fertilization experiment was set up in 1969 in a mature fir forest (*Abies alba* Mill.) in the Vosges Mountains in France, at an elevation of 800 m, on poor granites. It consists of 65 plots (250 m^2), divided into 8 treatments: control, N, P, Ca, N+P, N+Ca, P+Ca, N+P+Ca. The quantities of fertilizers were: 200 kg.ha^{-1} N, 150 kg.ha^{-1} P_2O_5, 1500 kg.ha^{-1} CaO. The humus type and the ground vegetation were described in 1969, and descriptions were repeated in 1989. Statistical analyses show that: 1. Liming, and liming only, has led to considerable alterations of the flora; the control plots are now dominated by *Vaccinium myrtillus*, a very acidophilous species, while the limed plots are dominated by *Festuca altissima* and numerous nitrophilous species. 2. Similarly, the humus layer of limed plots has changed from a mor or moder type to an acid mull type. That process might reflect an improvement of the biological activity and of the mineral nutrient cycle. 3. During the past 20 years, the unfertilized ground vegetation has changed, almost as expected from a moderate liming. Two possible causes of such a phenomenon are suggested: (a) a change in the light and temperature microclimate at the ground level, as a consequence of needle losses during the recent 'forest decline', which in turn could have improved organic matter mineralization; and/or (b) the chronic nitrogen deposition.

Keywords: *Abies alba*; Atmospheric deposition; Fertilization; Forest decline; France; Humus; Liming; Vegetation change.

Nomenclature: Tutin et al. (1964-1980) for vascular plants; Augier (1966) for mosses.

Introduction

Vegetation responds to the numerous changes that are constantly occurring within ecosystems. Consequently, the total species composition as well as individual species abundances may be used as biological indicators. Changes in forest vegetation may express the normal dynamics of the ecosystem (Rameau 1987), or represent long-term changes, for instance following slow variations in macroclimate (Neilson 1987), or may be caused by human activities (Blair & Brunett 1976). Silvicultural practice aims to alter competition, soil and/or microclimatic conditions in favour of specified tree species, but also affects the ground vegetation. Sometimes, the vigour of the vegetation response may even compromise the success of some silvicultural operations (Le Tacon et al. 1976).

Mineral fertilization may cause long-term effects on site properties. Though this practice occurs, e.g. in the 'ligniculture' of *Pinus pinaster* in the Landes region (southwestern France), it is rare in the usual silviculture of mature stands. Besides the immediate effects on wood productivity, fertilization may lead to more long-lasting beneficial changes, such as an improvement of soil biological activity and an alteration of the humus type (Toutain et al. 1987). Ground vegetation too may react strongly (Frochot, Picard & Dreyfus 1986).

Forest ecosystems also react to man-made atmospheric deposition and to the macroclimatic alterations induced by changes in the atmospheric composition of gases ('the greenhouse effect'). Both chemical and climatic factors appear now to be largely responsible for the forest declines that have occurred in various regions in Europe and North-America (Cramer & Cramer-Middendorf 1984; Auclair 1987; Kandler 1988; Becker 1989a; Landmann 1991). However, few studies have been dedicated to the consequences of atmospheric deposition on the natural vegetation (Pieri 1989). This is partly for methodological reasons, i.e. the difficulties in separating the various possible causes of the vegetation changes, partly due to practical problems, i.e. a lack of long-term studies with permanent plots. Most of the long-term studies emphasize the role of atmospheric nitrogen deposition for eutrophication of various site types and the spread of nitrophilous plants (Burger 1987; Falkengren-Grerup 1986; Kuhn et al. 1987; Rost-Siebert & Jahn 1988; Skeffington & Wilson 1988). The specific consequences of the acidification [as separated from deposition of nitrogen (Bonneau 1989)], are more unclear (Wittig, Ballach & Jeffrey Brandt 1985; Kuhn, Amiet & Hufschmid 1987; Falkengren-Grerup 1990; Falkengren-Grerup & Eriksson 1990).

We took advantage of a fertilization experiment, which was set up by two of the authors more than 20 years ago in the Vosges Mountains of northeastern France, in a region which is now much affected by forest decline. Initially, the aim of the experiment was to improve the productivity of silver fir (*Abies alba*) on very poor soil, potentially particularly sensitive to any increase in the supply of mineral elements, both intentional (fertilization), and unintentional (atmospheric deposition). The mineral elements initially supplied were nitrogen, phosphorus and/or calcium. Some preliminary soil analyses had shown that potassium might not be a limiting factor for *Abies* growth. The preparation of the experiment had been based upon an ecological and dendrometrical study of the site. Therefore, it was possible to compare the initial ecological data with new observations made 20 yr later at exactly the same place ('diachronic study'). Changes in the floristic composition might be due to fertilization or external factors in operation during 1969-1989. In addition, the various treatments, the control included, could be analysed and compared amongst themselves at the present time ('synchronic study').

Materials and Methods

General features of the site

The experimental site is the forest of Hospices de Nancy, Vosges Mountains, eastern France, between the Bonhomme and Louchbach passes (48° 09' N; 7° 06' E). Mean elevation is 800 m a.s.l., mean annual temperature is 7.0 °C, and annual precipitation is 1600 mm. The bedrock is Valtin granite, a rough Hercynian granite, poor in minerals. The soils are ochreous brown soils, with a moder humus type, or podzolic soils, with a moder or mor humus type. The slope is 20 % on average ($n = 40$; S.d = 3.5) and the aspect about North-West.

The experiment was set up in a pure and fairly even-aged *Abies alba* stand. In 1989, the average age was 115 yr (n = 493; S.d = 13). The ground vegetation was characterized by *Vaccinium myrtillus* and *Deschampsia flexuosa*, with also *Luzula sylvatica* and *L. luzuloides*.

Experimental scheme

A 40 m × 40 m square grid was used to define 65 plot centres, and the fertilizers were spread within a radius of 14 m around each centre. The 65 plots are contiguous. 40 of these plots, chosen because the stand proved to be more homogeneous after a preliminary dendrometrical study, were used for the 'fertilization experiment' strictly speaking. A completely randomized factorial design was used, with 8 treatments and 5 replicates. The treatments were as follows:

1 - T: control, no fertilizer;
2 - N: nitrogen;
3 - P: phosphorus;
4 - Ca: calcium;
5 - NP: nitrogen + phosphorus;
6 - NCa: nitrogen + calcium;
7 - PCa: phosphorus + calcium;
8 - NPCa: nitrogen + phosphorus + calcium.

Doses:

N: 200 kg/ha, i.e. 12.3 kg per plot, in the form of ammonium nitrate;

P: 150 kg/ha P2O5, i.e. 9.2 kg per plot, in the form of 'triple superphosphate';

Ca: 1500 kg/ha CaO, i.e. 92 kg per plot, in the form of slaked lime.

Phosphorus and calcium were supplied in the autumn of 1969, nitrogen in the spring of 1970, to avoid leaching during the winter. The N levels were below the threshold for burning plants.

Vegetation and soil survey

During the autumn of 1969, the soil was described in the centre of each of the 65 plots, and the humus type was identified as either mull, moder, mor, or intermediate types. The ground vegetation was described, within a radius of 9 m (254 m2), according to the Braun-Blanquet method, with 'total estimates' of the cover and density together of every plant. However, these inventories were not exhaustive, and involved only the 12 most common species at the site (see Tables 7 and 8).

During the autumn of 1989, similar observations were done in the same plots, but now with a complete vegetation analysis. Humus types were identified by the same person in 1969 and 1989. In order to increase the number of control samples, an 'adjacent' sample was analysed for each of the 40 fertilized plots. These samples were located in the buffer zone, always in the same direction and at the same distance (28 m).

Statistical analyses

Correspondence analysis (CA) (= reciprocal averaging) (Fisher 1940, Benzécri 1969) was used to extract the gradient structure of the data. In all calculations, Braun-Blanquet cover-abundance values were used as input data, with '+' converted into 1 , '1' into 2, etc. CA axes were scaled from 0 to 100. For the synchronic study, 80 samples from 1989 were analysed, i.e. the 40 samples located within the treated plots and the 40 'adjacent' ones, this in order to find possible changes in the floristic composition due to fertilization.

In order to test possible changes in the absence of fertilization, the diachronic study dealt with all of the 65 plots described in 1969 and 1989, i.e. 130 analyses, but only involving the 12 species identified in 1969.

Indicator values (IV) were used for interpretation of the possible biological meaning of the CA axes and for identification of the underlying factors responsible for the vegetation changes. Landolt's values (1977) were preferred to those of Ellenberg (1979), as they concern nearby Switzerland. R (reaction) and N (nitrogen) values (ranging from 1-5) proved to be the most efficient, i.e. respectively the reaction value, characterizing the content of free H-ions in the soil, and the nutrient value, which defines the nutrient contents (especially nitrogen) in the soil. In order to compare floristic samples, and thus their corresponding site characteristics, the mean IV for all species present in each sample (not weighted by abundance) was calculated.

Standard variance analysis was performed to check the overall significance of several treatments and *t*-tests to examine the difference between two means (Schwartz 1963). When analysing the increase or decrease of individual species, absences in both compared sets were included in the *t*-tests. When comparing two sets of homologous data, for instance characteristics recorded in the same plots but at two different times, or at the same time but in the 'normal' plots and in their 'adjacent' samples, 'paired comparison' (Kendall & Buckland 1971) was preferred to the usual *t*-test. In this case, a null hypothesis for the mean of differences between the elements of each pair is tested (Schwartz 1963).

Results

Synchronic study

The eigenvalues of the first four CA axes were: 0.246, 0.127, 0.099, 0.089. Only the first axis was biologically interpretable. Species at the one end of this axis include *Geranium robertianum* (R = 3, N = 4), *Galium odoratum* (3, 3), *Sambucus racemosa* (3, 4), *Silene dioica* (3, 4) and *Senecio fuchsii* (3, 4), which are reaction-neutral and slightly nitrogen-demanding. Species at the other end include *Leucobryum glaucum* (1,1), *Dryopteris carthusiana* (2,2), *Vaccinium myrtillus* (1,2) and *Deschampsia flexuosa* (2, 2), which are acidophilous and not nitrogen demanding. The following statistical tests were based on sample coordinates on axis 1.

Some interference might be assumed between the plots, as the distance between the periphery of a given sample and the nearest other treated area was rather small, i.e. 17 m for the 'normal' samples and 5 m for the 'adjacent' ones. That is why an initial analysis of variance dealt with the coordinates of the unfertilized plots only (Table 1a). *F* was not significant at $p = 0.05$.

Table 1. Analysis of variance on the coordinates of the plots on CA axis 1 (vegetation analyses from 1989). a. Unfertilized plots only; brackets relate to the 'adjacent' samples. b. All plots. Differences between the coordinate of a given 'normal' sample and the coordinate of its corresponding 'adjacent' sample. Means with same letter are not significantly different at $p = 0.05$. S. d. = Standard deviation.

a			b		
Treatment	Mean	S. d.	Treatment	Mean	S.d.
T	72.6 ^{a}	15.1	T	3.2^{ab}	10.3
(T)	75.8 ^{a}	19.5			
(N)	70.9 ^{a}	8.8	N	2.1^{ab}	3.7
(P)	80.1 ^{a}	14.8	P	7.5^{ab}	7.6
(Ca)	63.9 ^{a}	21.5	Ca	23.6^{cd}	12.3
(NP)	65.9 ^{a}	22.9	NP	– 6.7 ^{a}	13.2
(NCa)	57.8 ^{a}	31.2	NCa	14.8^{bc}	17.1
(PCa)	66.5 ^{a}	15.1	PCa	35.6 ^{d}	12.6
(NPCa)	66.6 ^{a}	6.7	NPCa	35.7 ^{d}	8.3
Degrees of freedom					
of treatments	8			7	
of error	32			28	
F treatment =	0.96 ns			9.53**	

A second analysis of variance dealt with the differences between the coordinates of the 'normal' samples and those of the 'adjacent' ones (Table 1b). *F* was found to be significant at $p = 0.01$, and this analysis resulted in a clear separation of the Ca treatments, whatever other fertilizer(s) were supplied, from the treatments without Ca, the control included. The movement of the limed plots from their adjacent samples, in direction of the neutro-nitrophilous end, was very pronounced (Fig. 1). Exceptions were two plots, whose adjacent samples were already close to the neutrophilous end. All of the plots supplied with Ca, with another element or not, were situated close to the neutrophilous end, except plots 20 (Ca) and 30 (NCa), whose adjacent samples were the most acidophilous ones. Conversely, the movements of the unlimed plots from their adjacent samples were much smaller and showed no preferential direction (Fig. 2; Table 1b). Thus, they might have reflected the natural local variability of the site characteristics mainly.

Table 2 shows the floristic composition of unlimed and limed plots. The mean R and N values of these 40 plots (and Standard deviations) were as follows:

	Mean R value (S.d)		Mean N value (S.d)	
Unlimed plots	2.216	(0.093)	2.613	(0.109)
Limed plots	2.461	(0.086)	2.928	(0.125)
t-test	8.38	***	8.28	***

Both were significantly different at $p < 0.001$. *Festuca altissima* (R = 3, N = 3) had an explosive increase in density and cover. Its abundance increased in practically all of the limed plots, and it often formed dense stands. Also increasing were *Senecio fuchsii* (3,4),

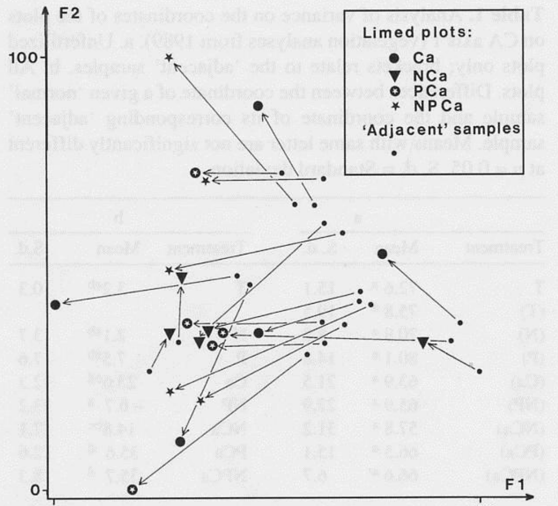

Fig. 1. Relative positions of the plots limed in 1969 and of their 'adjacent' control samples (analyses from 1989) in the CA ordination, axes 1 and 2.

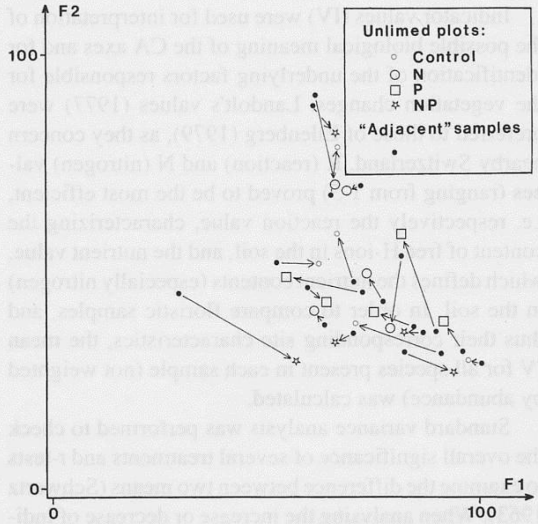

Fig. 2. Relative positions of the plots unlimed in 1969 and of their 'adjacent' control samples (analyses from 1989) in the CA ordination, axes 1 and 2. Same scale as in Fig. 1.

Athyrium filix-femina (3,3) and *Digitalis purpurea* (2, 4). The *t*-tests (Table 2) identified the species whose frequency and/or cover had increased significantly, e.g. *Sambucus racemosa* (3,4), *Urtica dioica* (3,5), *Silene dioica* (3,4), *Prenanthes purpurea* (3,3) and *Solidago virgaurea* (3,3). All of these are more or less neutro-nitrophilous species. The change in floristic composition at the acidophilous end was less spectacular. However, a significant decrease in abundance of *Deschampsia flexuosa* (2,2), *Sorbus aucuparia* (2,2), *Polytrichum formosum* (2,2) and *Vaccinium myrtillus* (1,2) was observed in the limed plots, together with a clear decrease in frequency of *Sorbus mougeotii* (2,2), *Dicranum scoparium* (2,2) and *Hypnum cupressiforme* (2,2).

Diachronic study

Vegetation data

As in the synchronic study, only the first axis of this second CA analysis was interpretable. It still appeared to express a nutrition gradient, in particular with *Vaccinium myrtillus* (1,2) and *Deschampsia flexuosa* (2, 2) at the one end, and *Festuca altissima* (3,3), *Oxalis acetosella* (3, 3) and *Rubus idaeus* (3, 4) at the other end.

Despite the low number of species, the result of the synchronic study was reproduced well in the analysis of the 1989 data: the limed plots were clearly separated from the unlimed plots (Fig. 3) with the exception of plots 20 and 30, already mentioned in the synchronic study. This was confirmed by a variance analysis of the coordinates of the CA (axis 1) of all samples (Table 3). Fig. 3 also reveals that almost all the 1969 samples are positioned towards the acidophilous end, whereas the control and unlimed 1989 samples occupy an intermediate position. This result was statistically confirmed both by the previous variance analysis (Table 3) and by paired comparisons of the 1969 and 1989 samples (Table 4).

The behaviour of each species was investigated by means of *t*-tests (Tables 5, 6). The increase of *Festuca altissima*, accompanied by *Oxalis acetosella*, *Rubus idaeus* and *R. fruticosus*, was confirmed in the limed plots (Table 5). Most species increased in frequency and density since 1969 (Table 6), except *Vaccinium myrtillus*, which is a very acidophilous species (R = 1). The spread of *Deschampsia flexuosa*, which is a less acidophilous species (R = 2), was only moderate. Spread appeared to be dramatic for the other species, especially for *Polytrichum formosum*, a slightly acidophilous species ($R = 2$), and *Oxalis acetosella*, *Rubus idaeus* and *Rubus fruticosus*, which are wide-ranging neutrophilous species.

Humus type

No clear trend appeared in the unlimed plots between 1969 and 1989 (Table 6), which was confirmed by a statistical paired comparison, by attributing a value

Table 2. Floristic composition in 1989 of the plots limed/unlimed in 1969 (Braun-Blanquet symbols; $p = +$). For each subset, species and samples arranged according to position on axis 1 of the first CA analysis. Results of the *t*-test at $p = 0.05$, added to the species name: $^{+}$ significantly more, $^{-}$ less frequent and/or abundant in the limed plots than in the unlimed ones.

	Limed plots	Unlimed plots
	13332323132432331123 61786684859097329700	12001200020001112120 11373219236485404255
Eurhynchium striatum	1 p	
Geranium robertianum	p	
Galium odoratum	p	
Galeopsis tetrahit	p	
Sambucus racemosa $^{+}$	p p pp p p pp	
Mnium punctatum	1 p1 p	p
Galium rotundifolium $^{+}$	1 1 1 1	
Urtica dioica $^{+}$	p p 1 p	
Mnium affine	pp	
Moehringia trinervia	p	
Epilobium montanum	p p	p
Silene dioica $^{+}$	p p p1 ppp	
Cardamine amara	p p p	
Stellaria nemorum $^{+}$	1pp 1 1	
Mycelis muralis	1	
Senecio fuchsii $^{+}$	23p1 11112p111pp1p	
Agrostis stolonifera	1	
Thuidium tamariscinum	p	p
Festuca altissima $^{+}$	54 1453351441424 4pp	p1 11
Taraxacum officinale	p	
Lonicera nigra	1	
Corylus avellana	p p	p
Athyrium filix-femina $^{+}$	1p1pp 111p pp 11ppp	p p
Dicranella heteromalla	1 1 p	p
Acer pseudoplatanus $^{+}$	p 1 p p	
Plagiochila asplenioides	1 p p	
Digitalis purpurea $^{+}$	111p11p pp11 p	1ppp p1
Dryopteris filix-mas	p1 1	
Polygonatum verticillatum	1 1 1 1	1 +
Prenanthes purpurea $^{+}$	1 112 1 1p1p111p1 1p	ppp1p 1 p1 p
Solidago virgaurea $^{+}$	11 pp pp p 1 1	p p p
Oxalis acetosella $^{+}$	322323332221323221	1111222221111 1
Rubus idaeus $^{+}$	4212444332122322211+	22122 p11p2 1 11p1
Luzula sylvatica	1121p 1p 41 3111511p	pp 5531 3 p1p
Rubus spec.	211122222222111 21++	1121112214211++111
Luzula luzuloides	1111122p 11 211 1p	34222 22 2211111
Fagus sylvatica	1 p 1 1 p p p1	pp11p1pp 1
Dryopteris dilatata	33232323232423232211	33433232332322133121
Galium saxatile	p 1	1 p p1
Abies alba	1421221132241114251	13131344325231132311
Sorbus aucuparia $^{-}$	p1 pp p1 ppp p1ppppp	11111pppp111111ppp1p
Deschampsia flexuosa $^{-}$	ppp111221122 1122p22	2 223212311331532311
Polytrichum formosum $^{-}$	1p112122 1112p21232	21222112231222123123
Sorbus mougeotii $^{-}$	p	p p p p 1
Vaccinium myrtillus $^{-}$	11121122312212231235	42224212321435233255
Rhytidiadelphus loreus	11 1112 112 1 32	1 1111p1 pp p 2p3
Picea abies $^{-}$	1p 1p pppp ppp1p1	p1 pp121 p1p pp11111
Epilobium angustifolium		p
Dicranum scoparium $^{-}$	p p 1 p p 112	pp 12p 11p1111p1p13
Carex pilulifera	p	p p p
Hypnum cupressiforme $^{-}$	p p 2	1 1 1 p1pp11
Ilex aquifolium	p pp 22	p p p 11 221
Hieracium spec.		p
Dryopteris carthusiana	p	pp 11
Leucobryum glaucum		p

ranging from 1 - 5 to each humus type. The resulting $t = 0.40$, not significant at $p = 0.05$. The small changes observed may be due to the fact that the soil was not observed at exactly the same places in 1969 and in 1989.

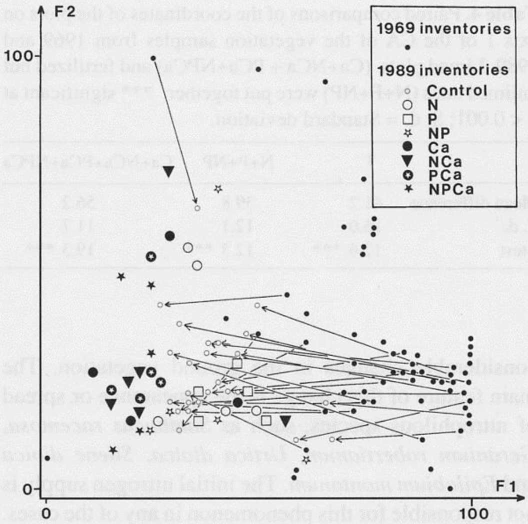

Fig. 3. Relative positions of the partial analyses (focused on 12 species) from 1969 and 1989 within the 65 plots of the experiment. A thin line joins the samples collected in 1969 and in 1989 in the non-fertilized plots.

Table 3. Analysis of variance on the coordinates of the plots on axis 1 of the CA on the partial vegetation samples of 1969 and 1989. Limed plots (Ca+NCa+PCa+NPCa) and fertilized but unlimed ones (N+P+NP) were put together. Means with same letter are not significantly different at $p = 0.05$.

Treatment	Mean	S. d.	
T(69)	18.1 ^{a}	18.7	Degrees of freedom
N+P+NP(69)	19.6 ^{a}	14.2	of treatments: 5
Ca+NCa+PCa+NPCa(69)	19.0 ^{a}	12.2	of error: 110
T(89)	59.3 ^{b}	10.5	
N+P+NP(89)	59.4 ^{b}	9.8	*F* treatment= 67.5 **
Ca+NCa+PCa+NPCa(69)	75.0 ^{a}	10.2	

On the other hand, in the plots that were limed in 1969 (Table 5), an almost systematic change was observed towards less acid humus types, significant at $p < 0.01$ ($t = 4.61$). With the exception of plot no. 30, already mentioned in the vegetation analysis, the humus types in the limed plots were acid mull or mull-moder in 1989.

Discussion and Conclusions

The fertilization carried out 20 yr ago at a site that was initially characterized by strongly acid soils and an almost pure layer of *Vaccinium myrtillus*, has resulted in

Table 4. Paired comparisons of the coordinates of the plots on axis 1 of the CA of the vegetation samples from 1969 and 1989. Limed plots (Ca+NCa + PCa+NPCa) and fertilized but unlimed ones (N+P+NP) were put together. *** significant at $p < 0.001$; S. d. = Standard deviation.

	T	N+P+NP	Ca+NCa+PCa+NPCa
Mean difference	41.2	39.8	56.2
S. d.	16.0	12.1	11.7
t-test	12.6 ***	12.3 ***	19.3 ***

considerable changes in the ground vegetation. The main feature of this change is the appearance or spread of nitrophilous species, such as *Sambucus racemosa*, *Geranium robertianum*, *Urtica dioica*, *Silene dioica* and *Epilobium montanum*. The initial nitrogen supply is not responsible for this phenomenon in any of the cases. The direct effect of such a supply in the form of ammonium nitrate, which is very soluble, is always transient. If the nitrogen compound is not absorbed by the vegetation immediately, it is rapidly removed from the soil through leaching, and is lost from the ecosystem (Bonneau & Souchier 1979).

On the contrary, the observed vegetational changes can be attributed to effects of calcium supply, but these effects must be indirect rather than direct, through an alteration of the ecosystem function. This is reflected in an improved biological activity of the humus, which may develop from an originally moder or mor type towards an acid mull type. This improved biological activity produces an improved and steady availability of inorganic nitrogen. Moreover, nitrogen is not the only element whose availability is improved in this way. Other major minerals are likely involved too, as is indicated by the spread of neutrophilous species such as *Senecio fuchsii*, *Festuca altissima*, *Digitalis purpurea* and *Oxalis acetosella*. Such profound changes as a result of liming is reported from beech forests by Toutain, Diagne & Le Tacon (1987), who found a significant increase in productivity as well. A dendro-ecological study is in progress at the present experimental site to answer the productivity question.

It appears that the floristic composition is little changed at the acidophilous end of the gradient, whatever the treatment. Thus, the corresponding species ought to be considered acido-tolerant rather than acidophilous in the strict sense of the word. Only the higher competitiveness of certain neutrophilous species, such as *Festuca altissima*, seems to be able to make these 'acidophilous' plants regress.

The changes observed in the present study will not be entirely advantageous for silviculture. The stand is now mature for cropping, and natural regeneration can begin. However, this is very difficult in pure *Abies alba* stands on soils characterized by an acid mull type, because of auto-intoxication processes (Becker & Drapier 1984). Problems are increased by the abundance of

Table 5. Partial floristic composition (Braun-Blanquet symbols; p = +) and humus type in 1969 and 1989, in the plots limed in the autumn of 1969. Results of the *t*-test at $p = 0.05$, added to the species name: $^+$ significantly more, $^-$ less frequent and/or abundant in 1989 than in 1969.

	1969	1989
	3353243333333221212	3213333342321233231
	1083004827596989766	0092387507498896616
Festuca altissima $^+$	p p	pp 421 144345315445
Oxalis acetosella $^+$	p	2233221232233323
Rubus idaeus $^+$	p	p122221223313424424
Prenanthes purpurea $^+$	ppp	p11p111pp1 1111 2 1
Rubus sp. $^+$		pp2 111221222212212
Luzula luzuloides $^+$	p p p p ppp	p 1111 1221p2 111
Polytrichum formosum $^+$		2312p1p 1221211211
Sorbus aucuparia $^+$		pppp1p ppp1p p p1p
Luzula sylvatica $^+$	p112pp 1p	p1511124 1p1 13 p11
Deschampsia flexuosa	pp1125111p422 1	222211p1212212 11pp
Ilex aquifolium	2 p	22 p p p
Vaccinium myrtillus	p4p35323533424342p	5313221122223211111
Humus type		
Acid mull	1 1 11	11 1111 1 1111111
Mull-moder	1 1 1 1 1 1	1 1 1 1
Moder	11 1 1 1	
Mor-moder		
Mor	1 1 1 1	1

Table 6. Partial floristic composition (Braun-Blanquet symbols; p = +) and humus type in 1969 and 1989, in the plots without addition of fertilizer. Results of the *t*-test at $p = 0.05$, added to the species name: $^+$ significantly more, $^-$ less frequent and/or abundant in 1989 than in 1969.

	1969	1989
	4455506665660054554444640	0556655565604406444404546
	9875352340013226142371541	5353407102226711193834425
Festuca altissima $^+$		p p p 1111
Oxalis acetosella $^+$	1 p1	1 1 2212222212221 1223
Rubus idaeus $^+$	p p	1 p11111p112p112212 p21
Prenanthes purpurea $^+$		p p 1pp p1p
Rubus spec. $^+$	p	p1p1p21111221212222122
Luzula luzuloides $^+$	pp 1	p pp1 1111222 1312122141
Polytrichum formosum $^+$	p 2	3132223322223213222223122
Sorbus aucuparia $^+$	p	p1p11pp1ppppp1pp1p2111p11
Luzula sylvatica $^+$	p 1 3	p 211 p1111pp51p 2 1p4
Deschampsia flexuosa $^+$	pppp22p4342p113p1 p	1113331243333414224222232
Ilex aquifolium $^+$	p 1 p	111 1 ppp1 p
Vaccinium myrtillus	pp5455455534p553351p113p	555343443323331 323223232
Humus type		
Acid mull	1 1	1
Mull-moder	1 1 1	1 11
Moder	1 1 11 1 1 1 11 1 1	11 1 1 1 1 111 1
Mor-moder		1 1 1
Mor	11111 111 1	111 11 11 1

Festuca altissima, which also has allelopathic properties and a high competition potential towards *Abies alba* seedlings (Becker & Bennett 1980).

More surprisingly, the long-term changes observed in the floristic composition without any deliberate fertilization are similar to the changes that a moderate lime supply could have induced. However, a comparable change in the humus morphology can not yet be noticed. Hence, the ground vegetation appears to react more rapidly than the humus.

The causes of changes in the ground layer are not obvious. Various, not mutually exclusive, hypotheses may be put forward:

1. The ageing of the ecosystem itself. Between 110 and 130 yr old, the stand studied is in a period of relative stability. Only dead or overtopped trees have been removed. The volume of the standing crop and, thus, the quantities of mineral elements stored in the wood, have been increasing for 20 yr. This should lead to soil acidification and a more acidophilous vegetation. This hypothesis is thus not no in accordance with the observations.

2.A result of the depression of growth that occurred in the 1970s and early 1980s ('forest decline'), and that have been proved to be induced to a large extent by climatic factors (Becker 1989a). The forest studied was particularly affected, through large needle losses and death of branches. Despite the present recovery, it is likely that the leaf area index is still lower than in 1969, and, due to the age of the stand, it will probably remain lower until its final felling. Needle losses have resulted in more organic matter and mineral elements returning to the soil, and, on the other hand, in more light energy reaching the ground level. These changes, favourable to the ground vegetation, may lead to an increase in humus biological activity and to an improvement of organic matter mineralization (Kenk & Fischer 1988).

3. Atmospheric deposits. Several impacts are possible:

a. Nitrogen compounds, continuously deposited in the form of nitrate or ammonium. They may have a significant effect on the forest ground vegetation, unlike the large but single nitrogen supply at the time of the fertilization in 1969. At present, nitrogen deposition amounts to about 17 kg $ha^{-1}yr^{-1}$ in the Central Vosges (Probst et al. 1990), which is still far from the levels that are becoming critical in other regions, such as the French Ardennes (Nys 1989), Belgium, and particularly the Netherlands (van Breemen & van Dijk 1988), where they exceed 50 kg ha^{-1} yr^{-1} and are inducing a serious disturbance in the mineral nutrition.

b. Input of major nutrient cations (K^+, Ca^{2+}, Mg^{2+}). This hypothesis seems less plausible, as there are no evident sources of an important increase in those elements during recent decades. On the contrary, a comparison of soil analyses made in 9 plots both in 1969 and in 1986 indicates a noticeable decrease in calcium (Landmann 1989).

c. Acid deposition. This may lead to increased weathering of the parent rock and release of exchangeable basic cations that may have been beneficial to the vegetation. Given the strong desaturation of the soils and the initial poorness of the parent rock, this hypothesis is not very convincing. There would even be a high risk of Al^{3+} release at toxic concentrations (Bonneau 1989).

All in all, it seems to us that the most plausible hypothesis may be the alteration of the light and temperature microclimate at ground level, and the sudden increase in mineralized organic matter due to the decline that started after the 1976 drought (Kenk & Fischer 1988). If this hypothesis is correct, the trends in vegetational change should reverse as the forest canopy closes again. The role of the atmospheric nitrogen deposits cannot be ruled out totally, but these deposits are rather low and have not increased much during the past few years (Probst et al. 1990). Nevertheless, if this second hypothesis is correct, the phenomenon ought to persist and even become more marked if the nitrous deposits increase. We must point out that both hypotheses are consistent with the 'explosion' of radial growth of *Abies alba* observed in the Vosges Mountains since the beginning of the 1980s, particularly on the poorest soils (Becker 1989b). This 'explosion' has still not been fully and convincingly explained.

Whatever the reasons for the changes documented, the phemomena involved require continued monitoring over the coming years.

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