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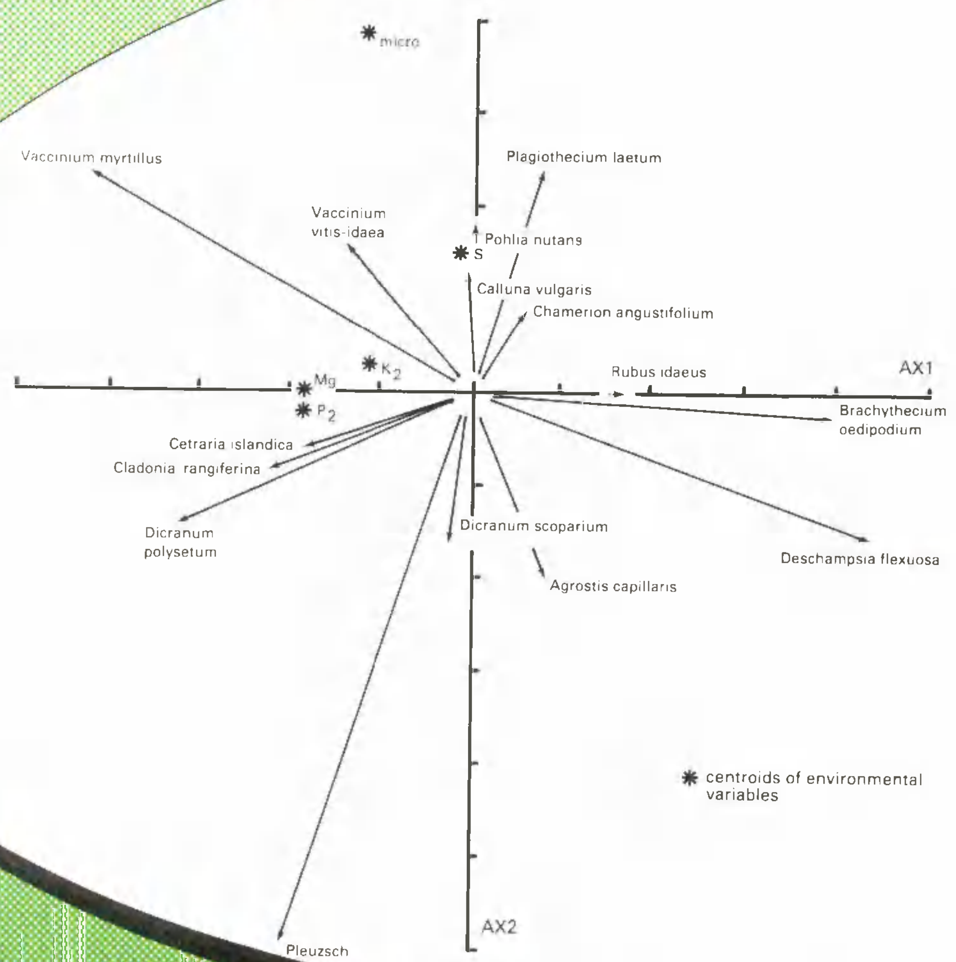

RIJKSINSTITUUT VOOR NATUURBEHEER
Arnhem, Leersum en Texel

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PREFACE

In 1987, the Research Institute for Nature Management (RIN, Leersum, The Netherlands) started a project to study the effects of forest fertilization and liming on groundlayer vegetation in scots pine forests on poor sandy soils. Consequently, the Institute got interested in forest fertilization experiments in other parts of Europe.

In Sweden five experiments were started about twenty years ago. They were performed by the Swedish University of Agricultural Sciences (Uppsala) and proved to be useful in the RIN project, mostly because they had been maintained very well for quite a long time and because they were situated in rather unpolluted areas. Atmospheric N deposition at Lisselbo for example, averages 10 kg/ha/yr, whereas in The Netherlands the average is about four times as high.

This project was carried out in close cooperation with the Department of Ecology and Environmental Research, Swedish University of Agricultural Sciences in Uppsala.

The report deals with the effects of experimental fertilization on the vegetation of herb and moss layers in a scots pine forest near Lisselbo (Sweden).

SAMENVATTING

In het kader van project 291 (Effecten van bemesting en bekalking op de ondergroei van dennenbossen op voedselarme, droge zandgrond) werden bosbemestingsproeven in dennenbossen in Midden-Zweden (Lisselbo) bestudeerd. Aanleiding tot het onderzoek was het vermoeden dat de ondergroei van de Nederlandse dennenbossen is veranderd ten gevolge van een verhoogde beschikbaarheid van nutriënten, in het bijzonder van stikstof (N). De bedoelde verandering uit zich in het verdwijnen van korstmossen (Cladonia spp.) en Ericaceae en het verschijnen van grassen als *Deschampsia flexuosa* en *Agrostis capillaris*.

Het gehucht Lisselbo ligt ca. 100 km ten noorden van Uppsala, te midden van uitgestrekte dennenbossen (*Pinus sylvestris*) die de zuidelijke uitlopers vormen van een noordelijk type naaldbos waarin weinig loofhout voorkomt. De ondergroei bestaat hoofdzakelijk uit *Calluna vulgaris*, *Vaccinium vitis-idaea*, *V. myrtillus*, 10-20 soorten Cladonia, acrocarpe mossen (voornamelijk Dicranum spp.) en pleurocarpe mossen als *Pleurozium schreberi* en *Hylocomium splendens*.

Het bos waarin de bemestingsexperimenten (E40, E41 en E42) worden uitgevoerd, is ca. 30 jaar oud en bestaat uit dennen van de tweede generatie. Het proefgebied ligt op een helling die onderaan fijnzandiger is dan bovenaan. Bovenaan is de helling steniger. De proefvelden werden in 1968 uitgezet en de eerste behandelingen vonden in 1969 plaats.

In augustus-september 1987 werd de vegetatie van de netto proefveldjes beschreven: per veldje een soortenlijst van korstmossen, mossen en hogere planten voorzien van hun geschatte bedekking. De verwerking van de gegevens vond plaats met behulp van de programma's TWINSPAN, DECORANA, CANOCO en GENSTAT. In deze samenvatting worden alleen de resultaten van een CANOCO-analyse (partiële redundantieanalyse; RDA) besproken.

E40 is een stikstoftrappenproef, en bestaat uit 32 veldjes. De stikstof (ammoniumnitraat) wordt jaarlijks in het voorjaar met de hand uitgestrooid. Er zijn vier bemestingsniveaus: N0, N1, N2 en N3. Sinds 1977 komen deze overeen met resp. 0, 20, 40 en 60 kg N/ha/jr. De helft van de proefveldjes krijgt bovendien een PK-mengmeststof. De proef is in viervoud uitgevoerd. De eerste as van de RDA-biplot is sterk gecorreleerd met de stikstofgift. Soorten waarvan de bedekking duidelijk wordt verhoogd door stikstofgift,

zijn *Deschampsia flexuosa, Dryopteris carthusiana, Rubus idaeus* en *Brachythecium oedipodium*. Soorten waarvan de bedekking afneemt door het toedienen van ammoniumnitraat zijn *Calluna vulgaris, Vaccinium myrtillus, Melampyrum pratense, Dicranum polysetum, Pleurozium schreberi, Cetraria islandica* en Cladonia spp. Een gecombineerde toediening van P2K2 en ammoniumnitraat leidt tot een toename van *Chamerion angustifolium, Trientalis europaea* en *Stellaria graminea*.

E41 is een factoriële proef en bestaat uit 20 veldjes. Nagegaan wordt wat het effect is van fosfor, kalium, magnesium, micronutriënten of sulfaat bij een stikstofbemesting van 40 kg N/ha/jr. Stikstof werd jaarlijks met de hand toegediend, de andere mineralen eens per drie jaar (voor het laatst in 1985). De behandelingen verklaren samen slechts 20% van de variantie in de soortabundanties. Slechts 63% daarvan wordt verklaard door de eerste twee ordinatieassen. Daarom moet aan de resultaten van de analyse van deze proef niet teveel gewicht worden toegekend. De RDA-biplot suggereert een positief effect van micronutriënten op de bedekking van *Vaccinium myrtillus* en *V. vitis-idaea*. *Pohlia nutans* en *Plagiothecium laetum* lijken positief te reageren op toediening van sulfaat.

E42 is een ingewikkeld experiment en bestaat ook uit 20 veldjes. Het werd opgezet om de effecten van zure regen na te bootsen. Het belangrijkste onderdeel ervan wordt gevormd door de veldjes waar men heeft geprobeerd de pH van de bodem te verlagen of te verhogen. Verlaging werd bereikt met verdund zwavelzuur (twee niveaus) en verhoging met kalk. De pH-manipulatie vond plaats bij twee bemestingsniveaus (NPK-mengmeststof: N0 en N2). De proef is in tweevoud uitgevoerd. De eerste RDA-as verdeelt de proefveldjes in bemest (N2) en onbemest (N0). Bemesting blijkt dus de belangrijkste verklarende variabele te zijn. Soorten die hierop positief reageren, zijn *Deschampsia flexuosa, Chamerion angustifolium* en *Brachythecium oedipodium*. Negatief door bemesting beïnvloed worden onder andere *Calluna vulgaris, Cetraria islandica* en *Vaccinium vitis-idaea*. Deze resultaten zijn vrijwel hetzelfde als in proef E40. De tweede RDA-as verdeelt de veldjes in verzuurde en bekalkte. Sterk positief op verzuring reageert *Pohlia nutans*. Bekalking zonder bemesting bevordert het optreden van *Vaccinium myrtillus* en *Calluna vulgaris*. Bekalking in combinatie met bemesting bevordert het optreden van *Rubus idaeus, Dryopteris carthusiana* en *Dicranum scoparium*.

1. INTRODUCTION

The effects of air pollution have become a severe problem in The Netherlands, especially atmospheric N deposition which averages about 40 kg/ha/yr. Not only epiphytic lichens or mosses are threatened (De Wit 1976), also heathlands, which tend to change into grass-dominated communities (Berdowski 1987). The herb layer vegetation of Dutch forests has probably changed dramatically during the last thirty years (De Vries 1982, Jansen & Van Dobben 1987). *Deschampsia flexuosa* and *Urtica dioica* now play a major role in most forests (Dirkse 1987). Recently it became clear that atmospheric NH_4^+ from livestock farming causes strong soil acidification (Van Breemen et al. 1982) and raised levels of plant-available soil N, presumably leading to considerable changes in species composition of the forest herb layer.

Many effects of experimental forest fertilization have been described (Van den Burg 1986). Despite these investigations, relatively little is known about the effects on other components of the forest ecosystem than trees. Some studies of fertilizer effects on forest undergrowth have been published (Persson 1981 & Gerhardt & Kellner 1986). However, most of the important Swedish optimal nutrition experiments have never been evaluated floristically.

Nitrogen fertilizers are used in Swedish forestry because they increase stem wood production with 40-50% during the first five years after application (Rosvall 1979). Use of forest fertilizers in Sweden started in 1960. In the beginning only one fertilization took place, about five years before final cutting. Later systems for regular rotation of fertilizer additions have been worked out by some of the large forest-owning organizations with, i.a., fertilization at seven-year intervals starting after the first commercial thinning. According to Hansson (1984) approximately 8% of the Swedish forest area have been fertilized with nitrogen. The average supply is 145-150 kg N/ha.

In 1987 we got the opportunity by the courtesy of Dr. A. Aronsson (Swedish University of Agricultural Sciences, Uppsala) to study the Lisselbo experiment with regard to phanerogams, bryophytes, and lichens.

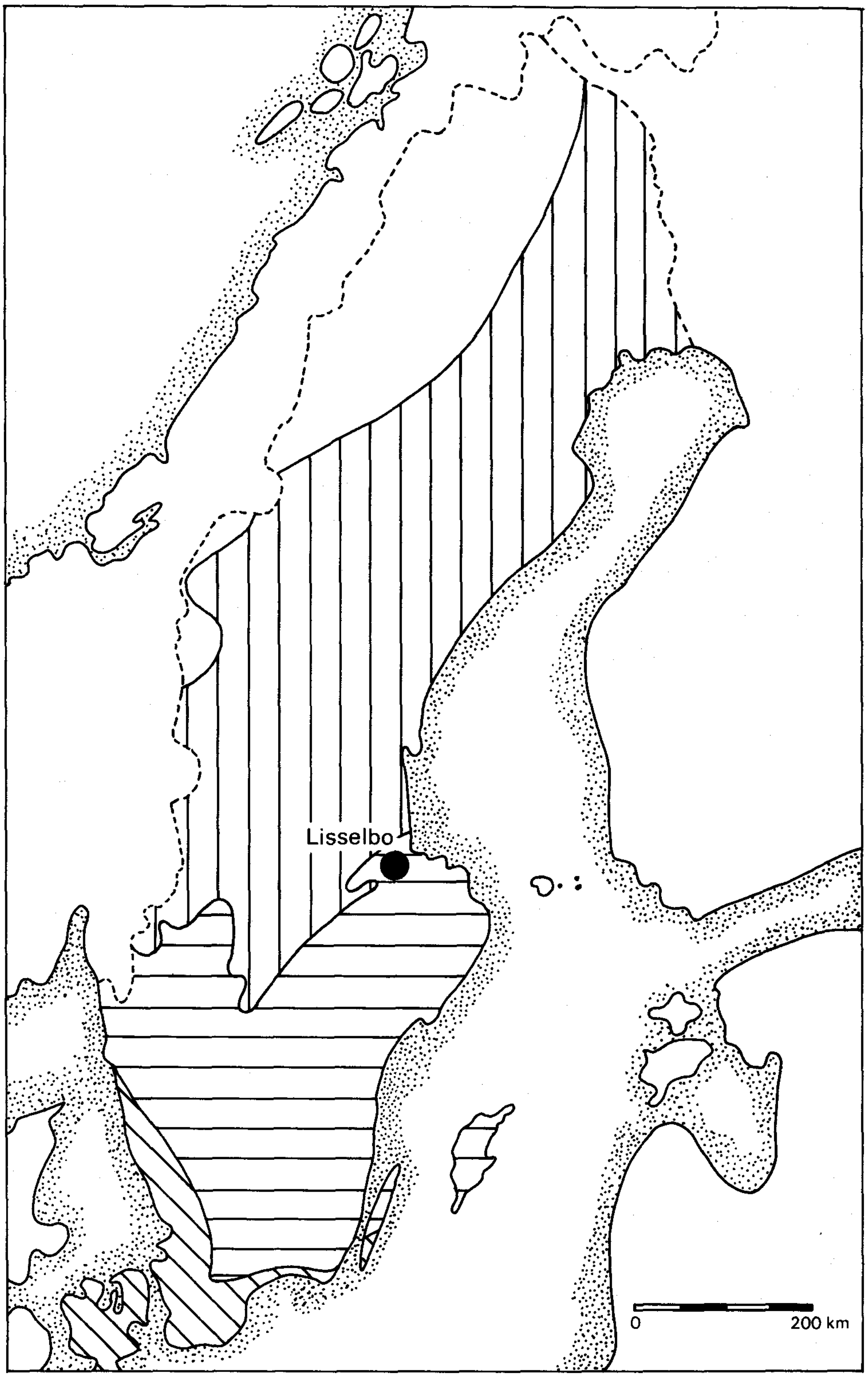

Figure 1. Geographical location of the Lisselbo forest optimal nutrition experiments in Sweden. Indicated are Swedish forest regions according to Sjörs (1965): without bars: alpine and birchwood region; vertical bars: northern coniferous region; horizontal bars: southern coniferous region; diagonal bars: southern deciduous region.

2. MATERIAL AND METHODS

2.1 Site description

Lisselbo forms a part of the parish of Hedesunda in the province of Gästrikland in the lowland of Central Sweden. It is situated along the N 254, about 100 km NNW of Uppsala (figs. 1, 3). Mean annual precipitation totals about 600 mm. Some other meteorological data are provided in figure 2.

The Lisselbo region is slightly undulated, with shallow depressions and low sandy ridges (esker remnants), showing the topography and sediment distribution of an ancient archipelago (Sjörs 1965). The altitude differences are mostly less than 100 m. Eskers are among the characteristic features of the eastern Swedish lowlands. These are vermicular landforms, formed by sedimentation of coarse grained glacifluvial drift in ice tunnels or between ice walls. They may reach a height of more than 10 m and a length of many kilometers. Just after the retreat of the ice after the last glaciation the experimental area was below sea level, as was much of the Swedish lowland. Due to wave action during the isostatic recovery of the land the eskers eroded. Top material was washed away and redeposited on the lower parts.

The optimal nutrition experiment is performed in a stand of Scots pine (*Pinus sylvestris*). It was designed by the Swedish University of Agricultural Sciences (Uppsala) at the request of the owner of the forest. The reason for this was the very low production of the stand.

The term optimal nutrition experiment indicates a 'type of experiment in which a wide range of combinations of nutrient applications is tested and in which foliage samples are collected and analysed in order to follow and to a certain degree control the changes in internal nutrient level in the test plants' (Tamm et al. 1974). Five optimal nutrition experiments have been performed in Sweden (fig. 1), some of them as part of the Swedish IBP program (Vik 1975).

The research site is situated on the western slope of an eroded esker which emerges 5-10 m above the surroundings. The soil is sandy, and well to excessively well drained. The texture of the sand varies from gravelly to

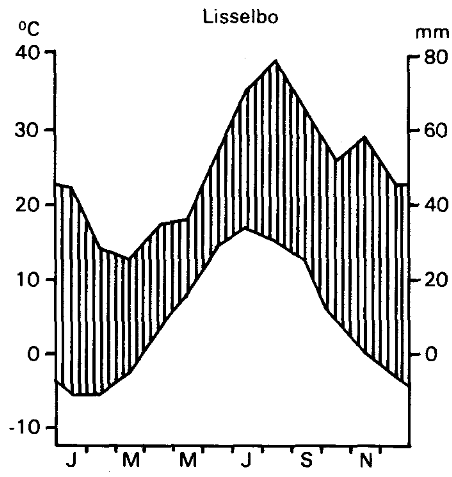

Figure 2. Climate diagram of the forest optimal nutrition experiment at Lisselbo. Lower curve: mean monthly temperatures. Upper curve: mean monthly precipitation. Averages are for the period 1931-1960 (from Tamm et al. 1974).

fine sandy. Particularly along the crest of the esker there is a high frequency of stones (Tamm et al. 1974).

In this part of Sweden most of the eskers are covered with scots pine forest (*Pinus sylvestris*) with an admixture of spruce (*Picea abies*) and oak (*Quercus robur* and *Q. petraea*) (Tamm et al. 1974). These forests represent a northern coniferous type at the edge of its southern limits. This means that conifers are dominant but that most of the broad-leaved trees (i.a. *Quercus robur, Acer platanoides*) may also be present (Sjörs 1965).

The experimental stand consists of about 30-year old scots pine and some young spruce. The undergrowth is mainly formed by ericaceous species (*Calluna vulgaris, Vaccinum myrtillus, V. vitis-idaea,* and *Arctostaphylos uva-ursi*), bryophytes (*Dicranum scoparium, D. polysetum, D. fuscescens, D. drummondii,* and *Pleurozium schreberi*) and lichens (Cladina spp. and Cladonia spp.). In 1954, an exceptionally heavy storm blew down most of the former stand, destroying about one third of the standing volume in the parish of Hedesunda, where Lisselbo is situated. The remaining trees were also removed and in the spring of 1955 the site was scarified and sown. In 1965 a number of trees were removed in order to regulate the spacing of the young stand, consisting of both naturally regenerated and sown pines (Tamm et al. 1974).

2.2 Experiment description

The Lisselbo experiment was briefly described by Tamm et al. (1974) from which most of the following has been taken. The experiment consists of 72 plots which were laid out in 1968. The plots (fig. 3) measure 30 x 30 m^2. Destructive activities (i.a. soil and biomass sampling) are restricted to the outer margins (5 m) of the plots. Hence the net plots measure 20 x 20 m^2. The plots are neatly marked in the field and serve three different experiments (E 40, E 41, and E 42). There are 66 treated plots and 6 blanks. The treatments started in the spring of 1969, except for the irrigation which could not start until the summer of 1970. All nutrients were spread by hand. The main treatments (i.e. N supplies) were repeated yearly in spring, according to the schemes in tables 1-3.

To avoid disturbance of the experiment by browsing moose (*Alces alces*), the area was fenced in. However, moose passed the fence on several occasions. The fence was removed in 1985.

E40 (32 plots) is mainly a dosage experiment, with three dosages and four replicates. The nitrogen levels are applied with or without a PK treatment. The last treatment before the vegetation study took place in 1987. We added plot 26 as a blank to the data submitted to TWINSPAN. This plot had been laid out in 1968 but was not included into the experimental design. As a consequence it did not receive any treatment nor was it included into former statistical analyses.

E 41 (20 plots) is a factorial experiment with balanced blocks to test the effect of addition of P, K, Mg, and S in the presence of a nitrogen containing nutrient. Each of the blocks contains one additional plot which receives a mixture of micronutrients, in addition to one of the treatments in the block. The last treatment took place in 1985. We added plot 74 as a blank to the data submitted to TWINSPAN. Although it had been laid out at the start of the experiment, it was not included into the experimental design, nor experimentally treated or included into former statistical analyses.

E42 (20 plots) is a complicated experiment in which the effect of soil pH

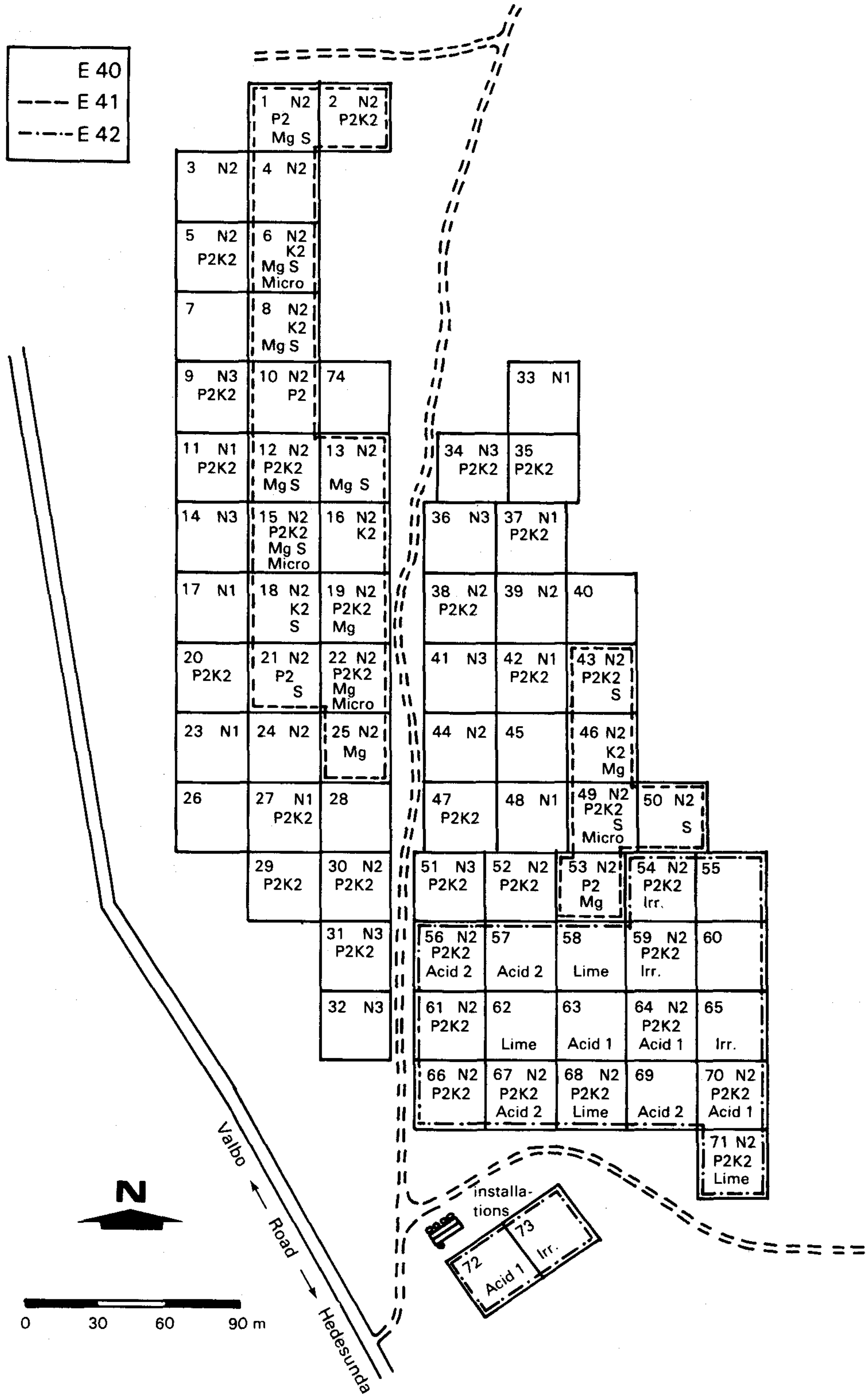

Figure 3. Lay-out of the Lisselbo experimental area. The experiments E41 and E42 were abandoned in 1986. As a consequence, the fence and the installations were removed (from Tamm et al. 1974).

Table 1. Fertilizer regimes of experiment E40. Amounts are in kg/ha. N=Ammonium nitrate. P and K are given as a compound PK fertilizer. B=Borium.

Year	N1	N2	N3	P2	K2	B
1969	60	120	180	40	76	-
1970	60	120	180	-	-	-
1971	40	80	120	-	-	-
1972	40	80	120	20	38	-
1973	40	80	120	-	-	-
1974	40	80	120	-	-	-
1975	30	60	90	40	78	-
1976	30	60	90	-	-	-
1977	20	40	60	40	78	2.5
1978	20	40	60	-	-	-
1979	20	40	60	-	-	-
1980	20	40	60	40	78	-
1981	20	40	60	-	-	-
1982	20	40	60	-	-	-
1983	20	40	60	40	78	-
1984	20	40	60	-	-	-
1985	20	40	60	-	-	-
1986	20	40	60	40	78	2.5
1987	20	40	60	-	-	-

manipulations is tested at two nutrient levels: without fertilization and with an addition of a NPK fertilizer. Acidification was achieved by application of dilute sulphuric acid in two dosages. The diluted acid was poured out from a can. pH increases were achieved by application of lime. E42 also contains a qualitative irrigation experiment, to test whether an improvement in water regime affects tree growth. The irrigation water was taken from a small, oligotrophic lake in the neighbourhood. The last irrigation and acid application took place in 1976. The nitrogen treatment stopped in 1985.

2.3 Field work

The field work took place from August till November 1987. Species composition (phanerogams, bryophytes, and lichens) and abundance were recorded in all net-plots. From every plot modest quantities of all

Table 2. Fertilizer regimes of experiment E41, abandoned in 1985. Amounts are in kg/ha. N=Ammonium nitrate; P=Triple super phosphate; K=Potassium chloride; Mg=Magnesium carbonate; S=Sodium sulphate.

Year	N2	P2	K2	Mg	S	Cu	Zn	Mn	B	Mo
1969	120	40	80	50	40	-	-	-	-	-
1970	120	-	-	-	-	12	12	12	5	1
1971	80	-	-	-	-	-	-	-	-	-
1972	80	20	40	-	-	-	-	-	-	-
1973	80	-	-	50	40	12	12	12	5	1
1974	80	-	-	-	-	-	-	-	-	-
1975	60	40	80	-	-	-	-	-	-	-
1976	60	-	-	-	-	-	-	-	-	-
1977	40	40	80	50	40	12	12	12	-	1
1978	40	-	-	-	-	-	-	-	-	-
1979	40	-	-	-	-	-	-	-	-	-
1980	40	40	80	50	40	-	-	-	-	-
1981	40	-	-	-	-	-	-	-	-	-
1982	40	-	-	-	-	-	-	-	-	-
1983	40	40	80	50	40	-	-	-	-	-
1984	40	-	-	-	-	-	-	-	-	-
1985	40	-	-	-	-	-	-	-	-	-

Table 3. Fertilizer regimes of experiment E42. The acidification stopped in 1976. The whole experiment was abandoned in 1985. N=Ammonium nitrate. P and K form a compound PK fertilizer. Ca=ground limestone. A=acid (diluted H_2SO_4). Irr=irrigation. Amounts are in kg/ha, except for irrigation which is in mm.

Year	N2	P2	K2	Ca	A1	A2	Irr.
1969	120	40	76	2000	-	100	-
1970	120	-	-	-	50	50	92
1971	80	-	-	-	50	50+50	70
1972	80	20	38	-	50	50+50	47
1973	80	-	-	-	50	50+50	36
1974	80	-	-	-	50	50+50	113
1975	60	40	78	-	50	100	50
1976	60	-	-		50	100	12
1977	40	40	78	-	-	-	-
1978	40	-	-	-	-	-	-
1979	40	-	-	-	-	-	-
1980	40	40	78	-	-	-	-
1981	40	-	-	-	-	-	-
1982	40	-	-	-	-	-	-
1983	40	40	78	-	-	-	-
1984	40	-	-	-	-	-	-
1985	40	-	-	-	-	-	-

cryptogams were collected to assure reliable identification.

Identification

In most cases the Svensk Flora (Krok & Almquist 1984) allowed proper identification of phanerogams and pteridophytes. However, as usual in field work, some difficulties have to be acknowledged.

1. *Dryopteris expansa* is closely allied to D. carthusiana. It proved to be very difficult to make a clear distinction between them in the field. As the benefit of the doubt was given to the latter, this name was probably used too often at the expense of the former. However, both species probably behaved equally in the experiments.

2. Identification of species of the genus Hieracium proved to be almost impossible. In this case we therefore refer to groups of species.

3. *Salix caprea* is another case. Willows occur rarely in the plots. They invariably consist of no more than a few short twigs, with or without leaves, which makes proper identification unsatisfactory. The name *Salix caprea* was applied to all these specimens, because this is the most common willow in the Lisselbo area. However, some might have belonged to other species.

Special attention was paid to proper identification of the bryophytes and lichens. Bryophytes were identified according to Nyholm (1954-1969). Within the hepatic genus Cephaloziella no further distinction was made between species.

Lichens were identified according to Poelt & Vezda (1977), Dahl & Krog (1973), and Wirth (1980). *Cladonia chlorophaea* has to be taken in a broad sense, because the chemical species within this complex were not distinguished separately. In *Placynthiella uliginosa*, *P. icmalea* is included. *Cladonia crispata* and *C. squamosa* were difficult to distinguish. As much specimens of intermediate morphology occurred and *C. squamosa* could not definitely be recognized, it was decided to include possible occurrences of *C. squamosa* into the name *C. crispata*.

Abundance

Abundance was estimated as cover percentage in a nine-point scale:

Cover percentage	code
>0 - 0,1%	1
>0,1 - 1%	2
>1 - 5%	3
>5 - 10%	4
>10 - 25%	5
>25 - 50%	6
>50 - 75%	7
>75 - 90%	8
>90 -100%	9

2.4 Data analysis

The records were thoroughly checked and copied onto computer files. All computer processing was done with a Microvax computer. After conversion into a condensed format (Hill 1979a) the files were submitted to the programs TWINSPAN (Hill 1979a), DECORANA (Hill 1979b), and CANOCO (Ter Braak 1988; Jongman et al. 1987). Additionally the statistical package program GENSTAT (Alvey et al. 1982) was used.

TWINSPAN is a polythetic divisive method of classification for species as well as samples. The result is a two-way tabular matrix arrangement of samples and species. The program also identifies one to several species which are particularly diagnostic of each division in the classification (indicator species). The basics of TWINSPAN are as follows (after Hill 1979a):

1. Identify a main direction of variation in the data by the method of reciprocal averaging (Hill 1973).
2. Divide the ordination at its middle to get a crude dichotomy.
3. Identify differential species that are preferential to one side or the other of the crude dichotomy.
4. Construct a refined ordination, using the differential species as a basis.
5. Divide the refined ordination at an appropriate point.
6. Construct a simplified ordination, based on a few highly preferential

species (indicator species). See whether the dichotomy suggested by the refined ordination can be reproduced by a division of the indicator ordination and indicate the differences as misclassifications.

7. Print out the resulting ordered two-way table.

The CANOCO program (Ter Braak 1988) is an extension of DECORANA (Hill 1979b); it provides several multivariate methods including correspondence analysis (CA), principal components analysis (PCA), and their canonical variants Canonical Correspondence Analysis (CCA) and Redundancy Analysis (RDA). The word canonical means that species abundance data and environmental data are mutually analysed. In canonical techniques regression and ordination have been integrated into a multivariate direct gradient analysis, which allows the detection of relationships between species and environmental variables (Ter Braak 1988). CANOCO also performs analyses in which the effects of particular environmental variables (covariables) are eliminated from the ordination. This is called a partial analysis (see Ter Braak 1987). The results are usually displayed in a biplot. The biplot is an ordination diagram in which species and sites or environmental variables are jointly displayed. Classes of nominal variables are displayed in the ordination diagrams as centroids of the sites belonging to the classes. Nominal variables in this context are variables which consist of classes.

3. RESULTS

3.1 Approximative exploration

As a first approximation the plots of all experiments, irrespective of their treatment were submitted to TWINSPAN. The program was run with default options and four cut levels: 1, 2, 3, and 4. These cut levels crudely divide the nine-point cover scale as follows: 1 (0-3), 2 (4-5), 3 (6), 4 (7-9). For more technical information about cut levels one is referred to Hill (1979a).

The TWINSPAN result is shown in table 4. The first two lines indicate sample names that coincide with plot numbers (read vertically). The last six lines must also be read vertically and indicate vegetational clusters in a binary way. The major clusters are separated by vertical lines.

Many species are almost restricted to the clusters on the left-hand side (main cluster 0, 50 plots) in table 4, such as *Rubus idaeus*, *Brachythecium oedipodium*, and *Plagiothecium laetum*. *Deschampsia flexuosa* is far more abundant (> 50% cover) on the left-hand side than on the right-hand side, where it covers less than 25%. These four species have been called indicator species by TWINSPAN, which means that they suffice in describing the main vegetation variation, without loosing much information. The following species play a less distinctive role, but nevertheless occur twice as often on the lefthand-side as on the other side (preferential species): *Agrostis capillaris*, *Sorbus aucuparia*, *Calamagrostis arundinacea*, *Rumex acetosella*, *Trientalis europaea*, *Polytrichum longisetum*, *Brachythecium salebrosum*, *Dryopteris carthusiana*, *Lophocolea heterophylla*, *Brachythecium reflexum*, *Carex pilulifera*, and *Plagiothecium denticulatum*.

This cluster has subsequently been divided into two subclusters (00 and 01) of which 01 is characterized by lichen species as indicators: *Cladonia anomaea* and *Cladina rangiferina*. In addition this subcluster has the following preferentials *Cetraria islandica*, *Cladonia sulphurina*, *Cladonia corniculata*, *Cladonia chlorophaea*, *Calluna vulgaris*, *Dicranum spurium*, *Ptilium crista-castrensis*, *Betula pendula*, *Empetrum nigrum*, *Cladonia cenotaea*, *Cladonia coccifera*, *Hylocomium splendens*, *Dicranum fuscescens*, *Cladonia crispata*, *Cephaloziella* spec., *Vaccinium myrtillus* (10-25% cover), and *Pleurozium schreberi* (> 50% cover).

Table 4. TWINSPAN table of field and bottom layer vegetation of the Lisselbo experimental plots, containing all recorded species.

Plot number	123 22235 114 11 1	335 11455 134445567336652344212	6756567676	3344 22745662
Species	3044512581918112984	1626353392602690640291640748773	7188732239	43557768405059
Taraxacum spec.	-------------------	1-1--1-1-----1---------1-------	-1--------	--------------
Acer platanoides	-------------------	----1--------------------------	----------	--------------
Calliergon stramineum	-------------------	----1--------------------------	----------	--------------
Anthoxanthum odoratum	-------------------	-----1-----1-------------------	----------	--------------
Senecio sylvaticus	-------------------	1----------------------1-------	----------	--------------
Lepidozia reptans	-------------------	-1-----------------------------	----------	--------------
Splachnum ovatum	-------------------	--------------1----------------	----------	--------------
Galium album	-------------------	--1----------------------------	----------	--------------
Mycelis muralis	-------------------	-----------------------1-------	----------	--------------
Ribes nigrum	-------------------	--------1----------------------	----------	--------------
Ptilidium ciliare	-------------------	-----1--------------11---1-----	----------	--------------
Placyntiella uliginosa	-------------------	---------------1---------------	----------	--------------
Brachythecium salebrosum	---1--1---------111	---1--1-11-1111-1-----1--------	----------	--------------
Sphagnum capillaceum	-------------1-----	-------------11--------------1-	----------	--------------
Drepanocladus uncinatus	--------1----------	-------11-------------1--------	----------	--------------
Cladonia digitata	-----------1-----11	---------1---1--------------111	----------	--------------
Maianthemum bifolium	---1---------------	-----------------------------11	----------	--------------
Carex canescens	-------------------	------------------------------1	----------	--------------
Lycopodium complanatum	-------------------	------------------------------1	----------	--------------
Plagiothecium laetum	-111111111111111-11	1111111-111111111111-1111111111	----------	-1------------
Carex ovalis	1-----1-11--1-----1	----1---------------------1----	----------	--------------
Tayloria tenuis	----------1----1---	-------------------------------	----------	--------------
Achillea millefolium	---------------1---	-------------------------------	----------	--------------
Poa pratensis	----1-1------------	-------1-----------------------	----------	--------------
Cirsium palustre	----1--------------	-------------------------------	----------	--------------
Brachythecium velutinum	----1--------------	-------------------------------	----------	--------------
Lophocolea bidentata	----------1--------	-------------------------------	----------	--------------
Dryopteris expansa	--11---------------	-------------------------------	----------	--------------
Leptobryum pyriforme	--1----------------	-------------------------------	----------	--------------
Prunus padus	---1---------------	-------------------------------	----------	--------------
Trientalis europaea	11111-111111---1---	11111111111------------1-1--1-1	----------	-----1--1-----
Lophocolea heterophylla	11-1-11-1-1-11-1--1	111-1-111---1111---------1-----	-1--------	--------------
Brachythecium reflexum	-111-111111----1111	-11111111---11111------1-111--1	1------1--	--------------
Brachythecium starkei	-----1----1-11-1--1	-1-11-1------------------------	----------	--------------
Galeopsis tetrahit	-----1---11-1------	1----1-----1-------------------	----------	--------------
Cladonia bacillaris	------------------1	----1--------------------------	----------	--------------
Festuca ovina	--------------1----	------------------------------1	----------	--------------
Rubus idaeus	2112211111221111111	11111111111---1-11111111---1-11	-1--------	--------------
Brachythecium oedipodium	1111122122311212322	2122222212111222111111-11111111	1--------1	1-------------
Polytrichum longisetum	---11-1-1111-1---11	-1111--1111----1--1111-----1--1	----------	--------------
Dryopteris carthusiana	11111111111111-1111	111111111-11-111--111111-------	-1--------	--------------
Tetraphis pellucida	--1-1------111-1---	----1-------------------11-1---	----------	--------------
Plagiothecium denticulatum	-111-1-1--211--11-1	-11-11-----1-111-1----1-------1	----------	--------------
Stellaria graminea	------1-11----1111-	--1--------1-------------------	-1--------	--------------
Carex nigra	1-1--11------------	-------------1----------------1	1---------	--------------
Linnaea borealis	--1-11-----11------	-----------------1------1----11	----------	-----1-----1--
Rumex acetosella	---1111--1--1-111--	1-11-1-11-11-------11111-------	----1-----	----1---------

Polytrichum formosum	-------------1-1---	-1---------------------1-------	1---------	--------------
Calamagrostis arundinacea	-1--1-1--1----11111	----21-11------1-1---111111----	-1--------	-------------1
Carex pilulifera	--1------1--1----11	------------11---1--1--1-----1-	1---------	--------------
Deschampsia flexuosa	444444444444444444	444444444444444444444443443444	4412111111	42211222111111
Agrostis capillaris	----1--11-111-1111-	1---1111-11--1--1-11-11--1-1-1-	-1--------	------1---1---
Sorbus aucuparia	111111111111111111	11111111111-11-1-1111111-1-1-	11-1------	111-11--11----
Polytrichum commune	1-----------------	1-----------1-----1-----------	----------	-----1--------
Aulacomnium palustre	1-----------------	------------1---------1-------1	----------	-----1--------
Luzula pilosa	11111111--111111111	---1-1-1-111111----1----1111111	----------	111111111----1
Dicranum montanum	1--1---------1-1-11	----1--11---1------11-------1--	---------1	-1-------1-1-1
Hieracium tridentata s.l.	---1---11----------	--1--1-----1-------------------	----------	-------1-----1
Betula pubescens	111111111111111111	111111-11111-1111111111-111-111	11----1-1-	111111-111--1-
Dicranum scoparium	11111111-1111111111	121-11111111111111212111-111122	111111-1-1	111-111-111111
Ptilidium pulcherrimum	-1--1-11--11-1-11-1	11-11-111--111-1-1---1-111-11--	---1------	-111111-11--11
Chamerion angustifolium	-112111112111-11-1-	211-111111121111111111111111111	11111-1--1	1111111111-111
Salix caprea	111-1-------1--1---	---------11-111--111---1-11--11	--------11	--1--11-1--1-1
Picea abies	212111211112111111	111111111112111111111112212112	1111111111	11111121111111
Hieracium vulgatiforme s.l.	-----------1-------	-----------------------1------1	---1------	--------------
Frangula alnus	-----------1-------	-----------------------1-------	-1--------	--------------
Ptilium crista-castrensis	1---------------1--	----11111--------1-----1-------	11-------1	--------------
Betula pendula	---1-1------------1	111---11-----111-111-1111--1---	-----1----	1----111--111-
Veronica officinalis	----------1--------	1---1--------------------------	-1--------	--------------
Cephaloziella spec.	-------------1-1---	11---1-11---111------------1---	-------1--	-1-11---------
Polytrichum juniperinum	1----1--11-11111111	111111111-11111111111111111-11	111111-111	11-11111111-11
Pohlia nutans	111111111111111111	111111111111-111221111111111111	2112312112	11111111111112
Pinus sylvestris	1--1--1---11--11-1-	---111-1-111-111-11---11---1---	1111111111	111111-1-1111-
Cladonia sulphurina	-----------1-1----	111-111--111111111111111-11-11	1111112111	11111111111111
Cladonia cornuta	-----------1--111--	1111111-11111111111111-11-111-	-111111111	11111111111111
Cladonia chlorophaea	-----------1--11--1	1--1111-1-1--1111111111-111-11	11111111--	1111-1--11-111
Cladonia anomaea	------------------	1--11111-1111111-11111111111111	-111111111	11111111111-11
Hylocomium splendens	-------1-----------	--1111111-1---1-111-1-1-1--1111	1---11--11	---111111-11--
Vaccinium myrtillus	221111111111211111111	121211112122112212224121223322 2	1122321221	24323333344422
Pleurozium schreberi	2212221221141222322	222122234233321112134444433442 4	2444112441	44444444444444
Vaccinium vitis-idaea	11111-1111111111111	111111111111111111111111111111	1222123232	12222221112111
Melampyrum pratense	1-1-1111-1-1--1--11	-----1---1--11--------1-1-11111	-111-11---	-11112221111--
Dicranum polysetum	11-111-111111111111	1211111111111-111111112222111 1	1211113111	22222433324122
Populus tremula	11---------1----111	----1-1---------------1----1111	11-----11-	------1-1-11-1
Dicranum fuscescens	-1-1---1-----------	---1---1--1-11-1-1-----111-1---	-----1--11	-111111-11111-
Cladonia deformis	------------------	--------------------------1----	----------	1-------------
Solidago virgaurea	------------------	------------------------------1-	----------	-------------1
Cladonia mitis	------------------	1------------------------------	----------	-------------1
Deschampsia cespitosa	------------------	--------------------------1----	----------	------------1-
Cladonia coniocraea	------------------	-----1-11----------------------	-111-----1	-----------1--
Vaccinium uliginosum	------------------	----1---------------1-1-------	1------1--	----------1---
Cladonia macilenta	------------------	------------------------------1	---------1	--------------
Placyntiella oligotropha	------------------	--------------1----------------	-1--------	--------------
Cladonia carneola	------------------	----------------11-------------	--1--1----	--------------
Cladina stellaris	------------------	---------1-----1--1--1-1-------	-1111111--	--11-----11---
Dicranum spurium	-1-----------------	--1---1-11--11-11111-111--1----	1-11111111	11111-----1111
Ceratodon purpureus	------------------	-------1---------------1-------	-------1-1	----1---------
Cladina arbuscula	-----------111111--	11111-1111111111-1211111111111	1222221222	11112111123321
Cetraria islandica	--------------1----	11111-1-11-111-112222122-1111--	2221222232	11221121122432
Cladina rangiferina	------------------	-11-11111111111111211111111-1--1	1221222222	11211111123322
Cladonia cenotaea	------------1-----1	---1111------111111-1-1-1---111	111-111111	-111-11-111111

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Cladonia coccifera          ------------------- -1-11---1----11--11------------ 1-1-1-1--1 ---------111-1
Lycopodium annotinum        ------------------- -------------1----------------- -1-------- ------1-------
Calluna vulgaris            -1-1--------1-1111- 11111111111111111111111111111-- 1342233434 12422112133232
Empetrum nigrum             ------------------- 11-------------11-1-111---11--- 1121111111 11111-11111112
Cladonia crispata           ------------------- -1---------111-1---111--11--111 1---111111 --1111111-1111
Trapeliopsis granulosa      ------------------1 ---------------1--1---1-----1-- 11-111--1- -11---------1-
Cladonia botrytis           ------------------- --1--------------------1------- ---------- -1-----------1
Cladonia gracilis           ------------------- --------------1---------------- ---------- ---------1----
Cynodontium strumiferum     ------------------- ------------1------------------ ---------- ---------1----
Arctostaphylos uva-ursi     ------------------- 1---------------1----11-------- 11111111-1 -11111111----1
Buxbaumia aphylla           ------------------- ------------------------------- ---------1 --1---1-------
Cladonia furcata            ------------------- ------------------------------- 111------- --------------
Peltigera aphtosa           ------------------- ------------------------------- ---1------ --------------
Peltigera spuria            ------------------- ------------------------------- -1-------- --------------
Dianthus deltoides          ------------------- ------------------------------- -1-------- --------------
Arabis arenosa              ------------------- ------------------------------- -1-------- --------------
Juniperus communis          ---------------1--- ----------1-------------------- ---------- -11--1--1--1--
Dicranum drummondii         ------------------- ------------------------------- ---------- ---------1-1--
Cephalozia connivens        ------------------- ------------------------------- ---------- ---1----------
Dicranum flagellare         ------------------- ------------------------------- ---------- ----------1---

                            0000000000000000000 0000000000000000000000000000000 1111111111 11111111111111
                            0000000000000000000 1111111111111111111111111111111 0000000000 11111111111111
                            0000000000011111111 0000000000000000000000001111111 0011111111 00000000011111
                            0001111111101111111 0000000000000001111111111000011   00111111 00000111100001
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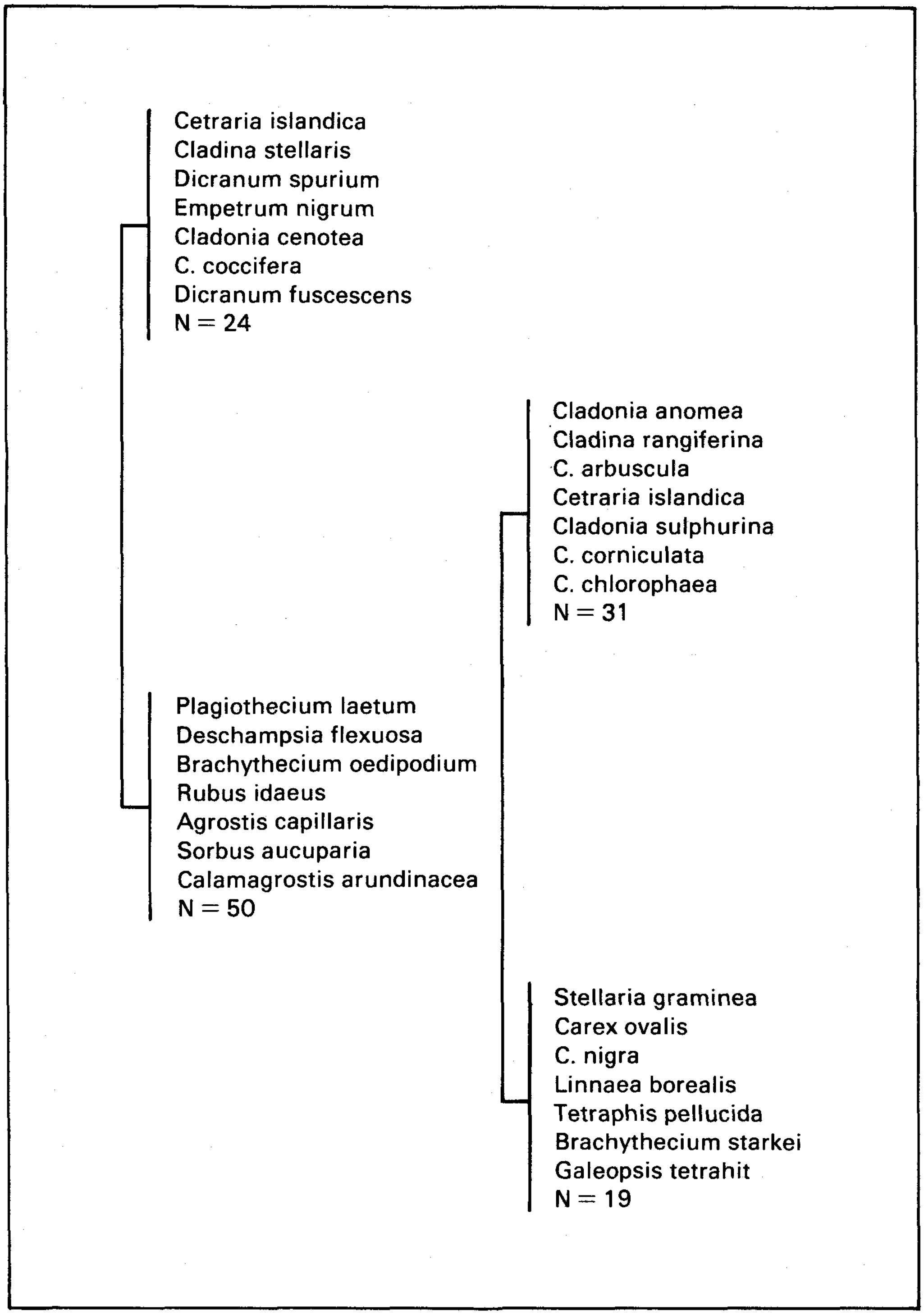

Figure 4. Summary of the main TWINSPAN divisions of the Lisselbo data. Indicated are the number of plots (N) involved in each division and the indicator species and preferentials. The first division has an eigenvalue of 0.271.

The other subcluster (00) has no indicators but is charactrerized by the following preferentials *Stellaria graminea*, *Carex ovalis*, *C. nigra*, *Linnaea borealis*, *Tetraphis pellucida*, *Brachythecium starkei*, *Galeopsis tetrahit*, and *Rubus idaeus*.

The right-hand side cluster (1, 24 plots) has no indicator species but only preferentials. These are *Cetraria islandica*, *Cladina stellaris*, *Dicranum spurium*, *Empetrum nigrum*, *Cladonia cenotea*, *C. coccifera*, *Dicranum fuscescens*, *Cladonia crispata*, *Arctostaphylos uva-ursi*, *Juniperus communis*, *Lecidea granulosa*, *Cladonia coniocrea*, *Cladina arbuscula*, *Calluna vulgaris* (50-75% cover), *Vaccinium vitis-idaea* (10-25% cover), *Dicranum polysetum* (10-50% cover), *Pohlia nutans* (10-25% cover), *Cladina rangiferina*, *Vaccinium myrtillus* (50-75% cover), and *Pleurozium schreberi* (> 50% cover).
The subdivision of this cluster is very uneven, resulting in one cluster consisting of only two plots, and another of 21 plots, and probably meaningless. Therefore, this subdivision is discarded.

The TWINSPAN clusters are summarized up to two levels in figure 4, in which indicator species and main preferentials are shown in order of decreasing importance. Summarizing table 4, three vegetation types can be distinguished:

00. A Deschampsia-Stellaria type with a high cover of *Deschampsia flexuosa*, *Rubus idaeus*, *Plagiothecium laetum*, *Brachythecium oedipodium*, *Stellaria graminea*, *Carex ovalis*, and *C. nigra*, but without lichens;

01. A Deschampsia-Cladonia type with high cover of *Deschampsia flexuosa*, *Rubus idaeus*, *Plagiothecium laetum*, *Brachythecium oedipodium*, and some lichens (esp. Cladonia spp.), but without *Stellaria graminea*, *Carex ovalis*, and *C. nigra*;

1. A Cetraria-Cladina type with lichens with *Cetraria islandica*, *Cladina stellaris*, *Dicranum spurium*, and *Empetrum nigrum*, and a very low cover of *Deschampsia flexuosa* (< 5%).

The distribution of vegetation types over the plots (fig. 5) allows some preliminary inferences on the effects of the treatments.
The Deschampsia-Stellaria type (00) occurs in plots with a moderate (N2) or high (N3) N supply. Species composition of the field layer vegetation in these plots closely resembles actual Dutch pine forests (Dirkse 1987).

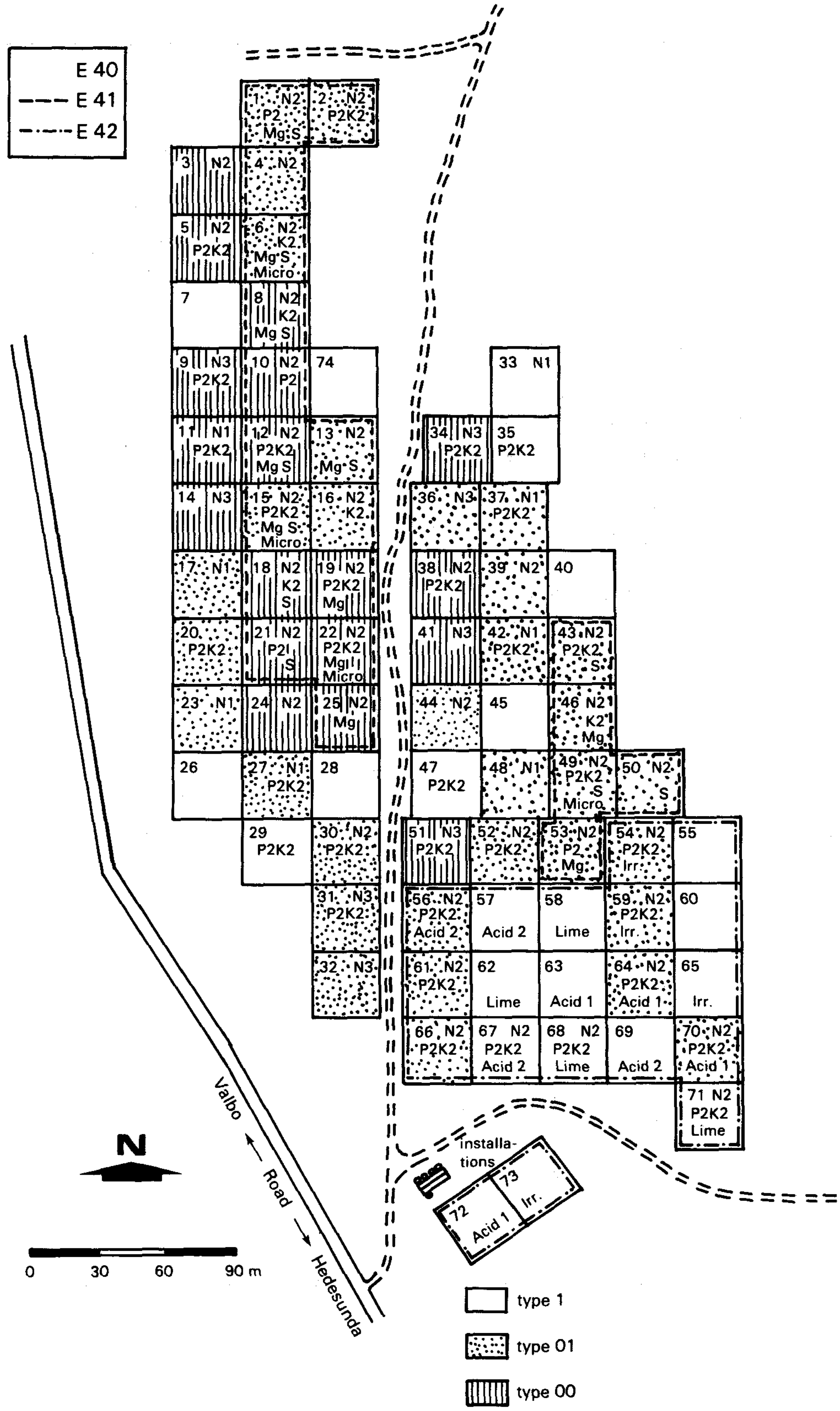

Figure 5. The three main types of field and moss layer vegetation assigned to the plots. Legend: Type 00; Type 01; Type 1. For explanation see text.

The Deschampsia-Cladonia type (01) occurs in all but one low (N1) and many moderately (N2) N treated plots, irrespective of additional supplies.
The Cetraria-Cladina type (1) occurs in untreated plots and in P2K2 treated plots. Moreover, most of the plots of experiment E42 belong to this type except for the plots with an N2 supply, which mainly belong to the Deschampsia-Cladonia type.

3.2 Detailed analysis

Choice of ordination methods

Response of the species to the treatments in the three experiments (E40, E41, and E42) was further analysed with the program CANOCO (Ter Braak 1987). The CANOCO program allows a performance of a canonical form of principal components analysis, called Redundancy Analysis (RDA), and canonical correspondence analysis (CCA). The choice between these techniques depends on the underlying structure of the data, especially on the species response curves. CCA is a more general technique than RDA because it assumes unimodal species-response curves, whereas RDA assumes monotonic response curves. RDA attempts to fit a straight line to the data of each species by selecting the linear combination of environmental variables that gives the smallest sum of squares (see Ter Braak 1987). CCA is a weighted average technique 'that selects the linear combination of environmental variables that maximizes the dispersion of the species scores' (Ter Braak 1987). Whether the data are unimodal or linear may be revealed by plotting the abundance curves of the most important species against N supply. This is done for *Deschampsia flexuosa* (fig. 6), which strongly reacts to the treatments and as a consequence plays a major role in the variation among the plots. The response curve of *D. flexuosa* is not unimodal but more or less linear, which seem to hold for most species in table 4.

Linear regression of *D. flexuosa* cover on N supply accounts for 74% of the variance. The linear regression gives too high an estimate of cover for both lowest and highest N supplies. Regression of cover on the square root of N supply fits the data better, it accounts for 82% of the variance. In statistical analysis of the response of individual species it therefore seems worthwhile to transform the N supply to its square root, to linearize

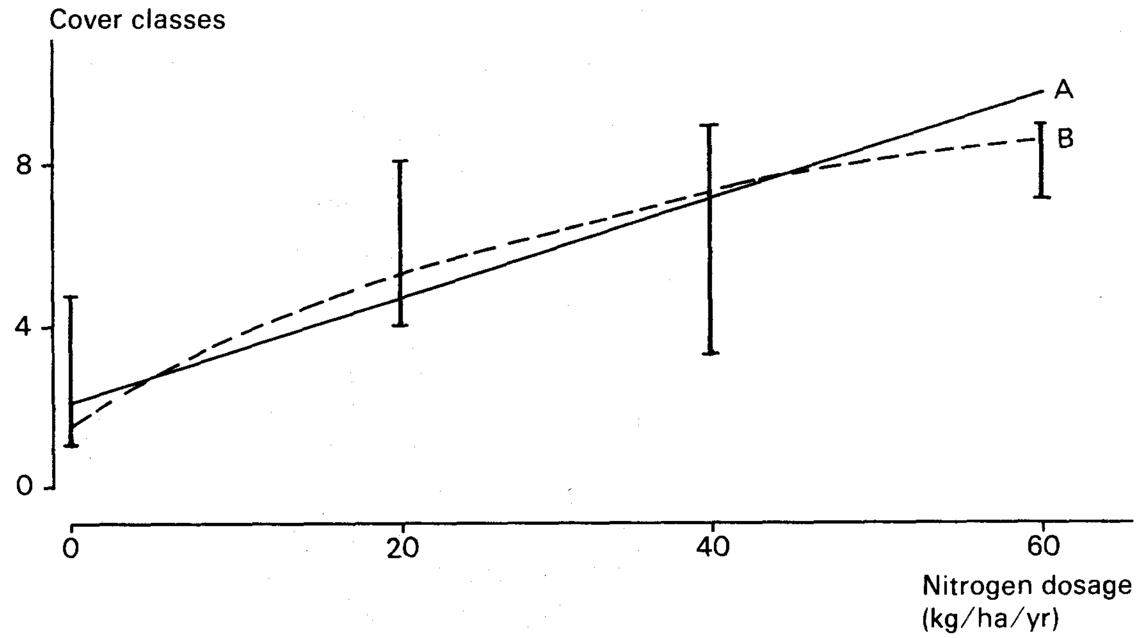

Figure 6. Cover class of *Deschampsia flexuosa* (C) versus nitrogen supply in kg/ha/yr (N). Linear regression resulted in the following relationship: C=0.11762(N)+2.391. Regression of C on the square root of N (SQRT(N)) resulted in: C=0.8613(SQRT(N))+1.889. The latter equation has a better fit.

the data. However, we used the variable N untransformed.

An exploratory application of DCA (Detrended Correspondence Analysis; Hill 1979b) to the floristic data resulted in a gradient length of 2.1 standard deviations (SD). The total bell-shaped response curve of a particular species extends over 4 SD (Hill 1979b). So in our data probably only a part of the response curve is realised. This does neither point at clear unimodal response curves. Therefore, linear methods (PCA and RDA) were considered more appropriate to analyse the Lisselbo data than unimodal methods (CCA) do.

3.3 Experiment E40

The nitrogen dosage experiment E40 consists of 32 plots. Both nitrogen supply and P2K2 addition were treated as nominal variables.
As plots on top of the esker have a better drained soil than plots on the lower part, a possible effect of these differences had to be removed. Therefore the position of the plots relative to the slope of the esker has been taken into account as a covariable; technically this turns the RDA into

a partial RDA (see Ter Braak 1987).

Species and sample scores have been combined into a biplot (fig. 7) in which both N supply and P2K2 are indicated by an asterisk. The species are represented by arrows. The sample scores (plots) are represented by four signatures: open circles, closed circles, open squares, and closed squares, indicating the four levels of N application (N0, N1, N2, N3), respectively. The biplot can be interpreted by the rules of a Euclidean distance PCA biplot. The length of an arrow indicates the rate of change. The angle between arrows roughly reflects correlation between species. Species with perpendicular arrows show no correlation, whereas arrows pointing in the same direction indicate highly correlated species. Only species with long arrows are represented in the biplot (fig. 7).

Almost all information is extracted by the first RDA axis with an eigenvalue of 0.367, accounting for 40% explained variance in species abundances. It is correlated with N addition, describing a gradient from unfertilized plots to N3 treated plots. A Monte Carlo test, using the sum of all eigenvalues (TRACE) as a test statistic (see Ter Braak 1988) showed the N effect to be highly significant ($p < 0.01$). The second axis contributes negligibly (eigenvalue 0.045) to the information. All higher axes have eigenvalues of less than 0.020 and have therefore been discarded. *Deschampsia flexuosa*, *Brachythecium oedipodium*, *Plagiothecium laetum*, *Dryopteris carthusiana*, and *Rubus idaeus* show the highest negative scores on the first axis, indicating a strong effect of high N dosages, which clearly benefit these species. Moreover, all species on the left-hand part of the diagram are more or less positively influenced by N supply. *Calluna vulgaris*, Cladonia spp., Cladina spp., *Vaccinium myrtillus*, *Melampyrum pratense*, *Dicranum polysetum*, and *Pleurozium schreberi* behave in the opposite way. These species decrease with increasing N supply. *Vaccinium myrtillus*, *Dicranum scoparium*, *Populus tremula*, and *Linnaea borealis* tend to be favoured by a low N gift (N1), but disfavoured by larger gifts. *Chamerion angustifolium*, *Rumex acetosella*, and *Hieracium tridentata* s.l. seem to react positively on a P2K2 addition.

The effect of P2K2 addition alone may be highlighted by treating N as a covariable, thus removing all possible N effects from the species abundance data. P2K2 had little effect upon the species composition, slightly

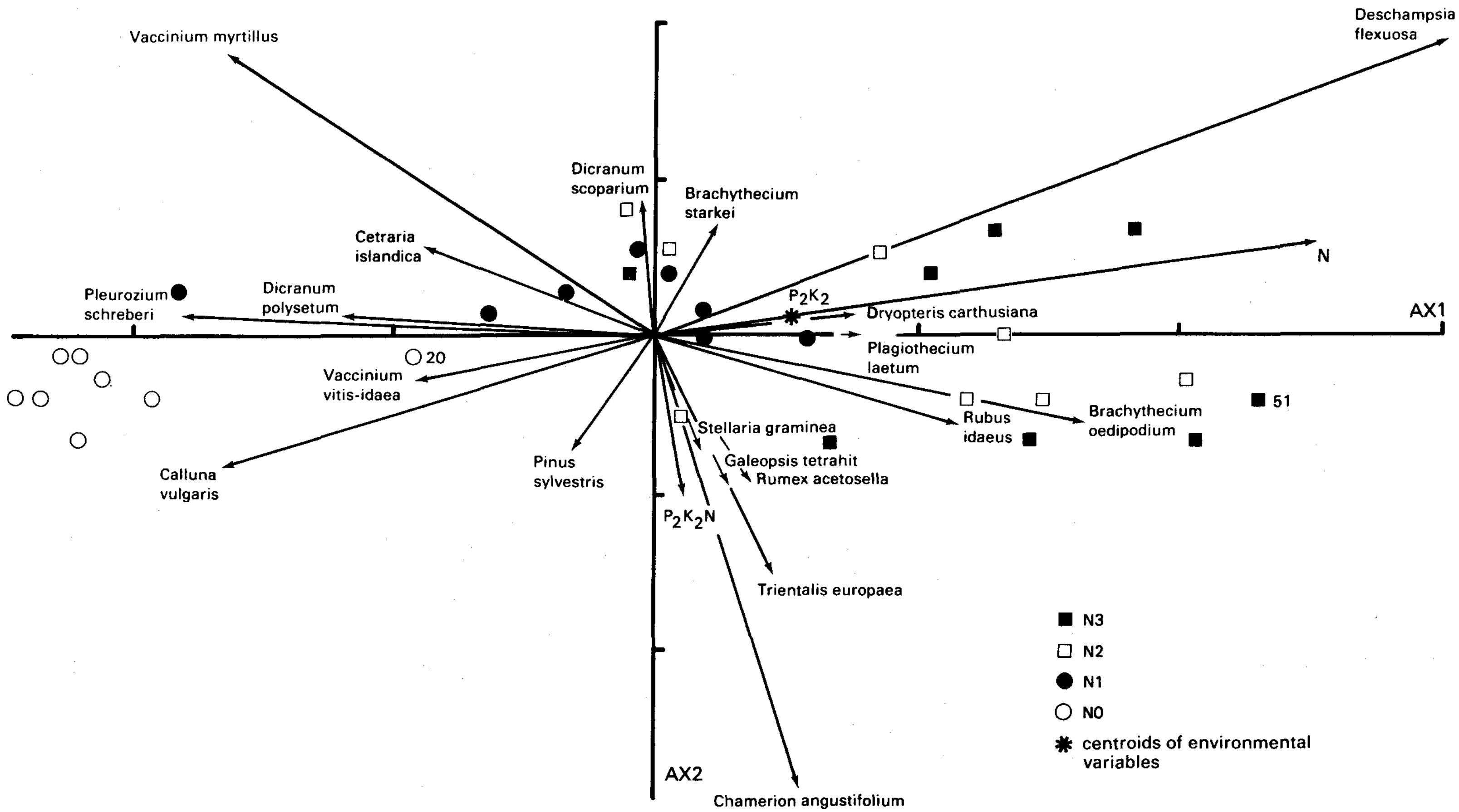

Figure 7. RDA ordination diagram (Euclidean distance biplot) of the Lisselbo E40 data with species and N supply represented by arrows.

favouring only *Deschampsia flexuosa* and *Calamagrostis arundinacea* (fig. 8). A Monte Carlo test of significance of the first canonical ordination axis showed the P2K2 effect to be just significant at the 5% level.

In addition, the combined effect of N and P2K2 was taken into account by incorporating the cross product of these treatments into the RDA analysis as an extra environmental variable. Both nitrogen supply and P2K2 were now treated as covariables. Only the first two axes are shown, respectively having eigenvalues of 0.047 and 0.020. Evidently, an additional gift of P2K2 to N favours strongly *Chamerion angustifolium*, *Trientalis europaeus*, *Rubus idaeus*, and *Rumex acetosella*. *Galeopsis tetrahit* and *Stellaria graminea* are less favoured, as may be inferred from the biplot (fig. 8). From the same plot it may be seen that *Vaccinium myrtillus*, *Melampyrum pratense*, *Dicranum polysetum* and to a lesser extent *Cladina stellaris* and *Cetraria islandica* respond negatively to additional supply of P2K2. Again, Deschampsia flexuosa is slightly favoured by a P2K2 gift without N.

3.4 Experiment E41

All plots of factorial experiment E41 were given a nitrogen dosage (40 kg/ha/yr). The factors P2, K2, Mg, S, and micronutrients (Cu, Zn, Mn, B, and Mo) were tested in a factorial design in four blocks. The experiment consists of 21 plots, but plot 74 has been added to the blanks, so 22 plots have been analysed. Five treatments (P2, K2, Mg, S, micro) have been taken into consideration as nominal environmental variables. Position on the esker again was used as covariable.

From the RDA biplot (fig. 9) the following can be concluded:
The main treatment effects explained 20% of the variance in species abundances, of which 63% is extracted in the first two axes of RDA, the eigenvalues of these being 0.075 and 0.049, respectively. So the effects are minor and the biplot should be interpreted with caution.

Axis 1 shows a negative correlation with P2 and Mg (viz. -0.6551, -0.5837). These additions seem to have a negative influence on *Brachythecium oedipodium*, *B. reflexum*, *Rubus idaeus*, *Stellaria graminea*, and *Calamagrostis arundinacea*. Moreover, the diagram suggests that grasses (i.a. *Deschampsia flexuosa* and *Agrostis capillaris*) are disfavoured by P2 and Mg supplies.

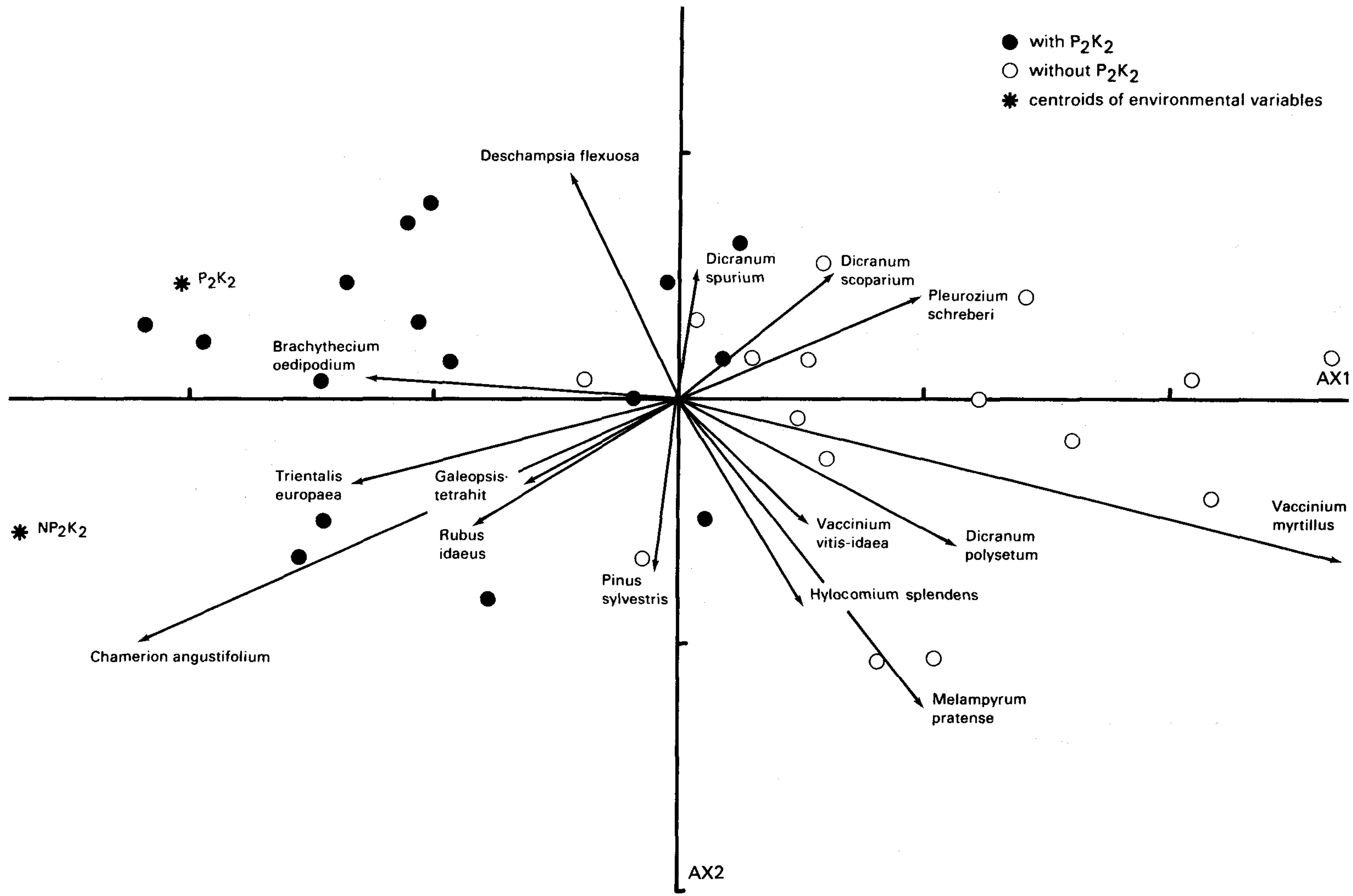

Figure 8. RDA ordination diagram (Euclidean distance biplot) of the Lisselbo E40 data with the N effect removed, highlighting the joint effect of P2K2 and N treatment.

Vaccinium vitis-idaea and *V. myrtillus* on the contrary are positively influenced by these supplies, and seem to be favoured by additions of micro nutrients. *Plagiothecium laetum* and *Pohlia nutans* seem to be strongly favoured by addition of sulphate.

3.5 Experiment E42

E42 is a complex experiment, in which artificial pH manipulation (lime, S1 and S2) was tested against N supply (N2). An irrigation experiment has also been included, but was discarded because the treatments were stopped more than ten years ago. These plots have been considered as blanks. In the analysis the following treatments have been taken into consideration as nominal environmental variables: lime, S1, S2, N2.

In the RDA biplot (fig. 10) the experimental plots have been indicated by four signatures: open circles, closed circles, open squares, and closed squares. Representing four treatment classes: not acidified and not fertilized, only acidified, only fertilized, and both acidified and fertilized plots, respectively. Hence circles indicate unfertilized plots and squares indicate fertilized plots.

From the RDA biplot the following can be concluded:
The first RDA axis (eigenvalue 0.33) is strongly correlated with NPK, indicating that N treatments dominate pH manipulation. In fact, the first axis divides the set into fertilized and unfertilized plots. Species reacting positively on NPK supply are on the right-hand side of the biplot: i.a. *Deschampsia flexuosa*, *Chamerion angustifolium*, *Rubus idaeus*, *Dryopteris carthusiana*, and *Brachythecium oedipodium*. Species negatively influenced by NPK supply are on the left-hand side: i.a. *Calluna vulgaris*, *Cetraria islandica*, and *Vaccinium vitis-idaea*. The second axis is correlated to pH. *Pohlia nutans* seems confined to strongly acidified plots. *Cladonia cenotea* and *Dicranum spurium* show the same reaction, but to a lesser degree. *Pleurozium schreberi* behaves in the opposite way, avoiding acidified plots. Intermediate, but nevertheless favoured by liming, are *Calluna vulgaris*, *Empetrum nigrum*, and Cladonia spp. Strongly favoured by liming are *Melampyrum pratense*, *Dicranum polysetum*, and *Vaccinium myrtillus*.
It may seem strange that Ericaceae are favoured by liming. However, as is

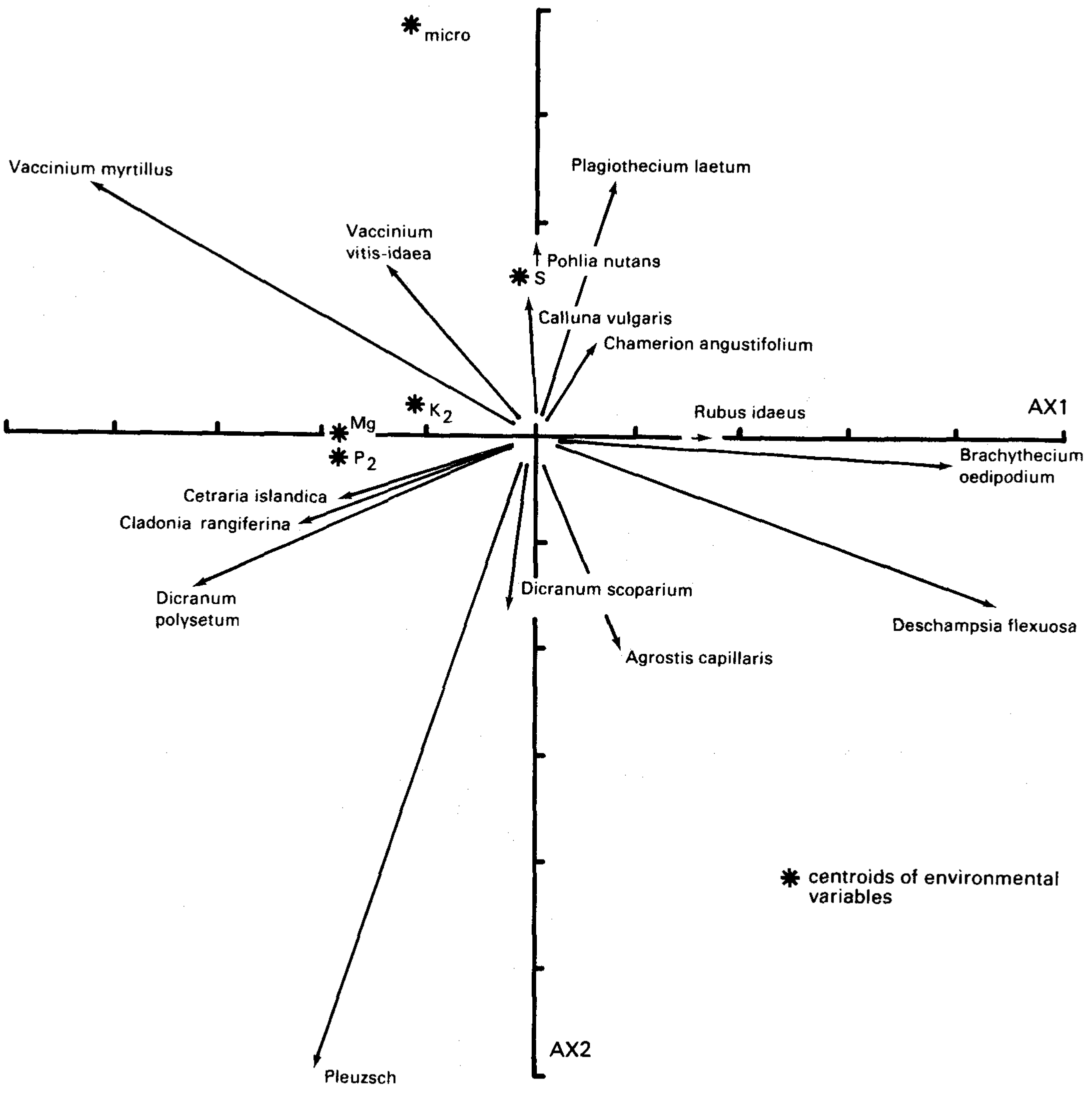

Figure 9. RDA ordination diagram (Euclidean distance biplot) of the Lisselbo E41 data with species represented by arrows and treatments by their centroids.

known from several cases (see Van den Burg 1986, Haynes 1986), liming may raise microbial N demand which decreases the amount of plant-available N, and therefore favours Ericaceae.

Finally, in an attempt to summarize the results of the three experiments, all plots have been submitted to CANOCO (partial RDA) taking into consideration only N supply, because this factor has turned out to overrule all other ones. Prior to the analysis the data were made uncorrelated with all other treatments, position on the slope, and whether the treatments had been stopped or not. The four levels of N supply have been treated as nominal variables. In the biplot (fig 11) they are represented by asterisks (N0, N1, N2, N3). The biplot explains 90% of the variation in the data. A Monte Carlo test revealed (see Ter Braak 1988) the first RDA axis to have a significance of 0.01. So the effect of N supply (corrected for all other effects) is statistically significant. All species negatively influenced by any fertilization are on the lower left-hand side of the diagram. As a consequence, *Vaccinium vitis-idaea*, *Calluna vulgaris* and *Cetraria islandica* are almost confined to unfertilized plots.

Among the species favoured by considerable N supply (N2, N3) are *Deschampsia flexuosa*, *Rubus idaeus*, *Dryopteris carthusiana*, *Chamerion angustifolium*, and the mosses *Plagiothecium laetum*, *P. denticulatum*, and *Brachythecium oedipodium*. The latter are litter inhabiting pleurocarpous moss species (Nyholm 1954-1969).

Several species take an intermediate position, being favoured by a low level of N supply (N1) but disfavoured by larger levels. Among these are *Melampyrum pratense*, *Vaccinium myrtillus*, and the mosses *Dicranum scoparium* and *Pleurozium schreberi*.

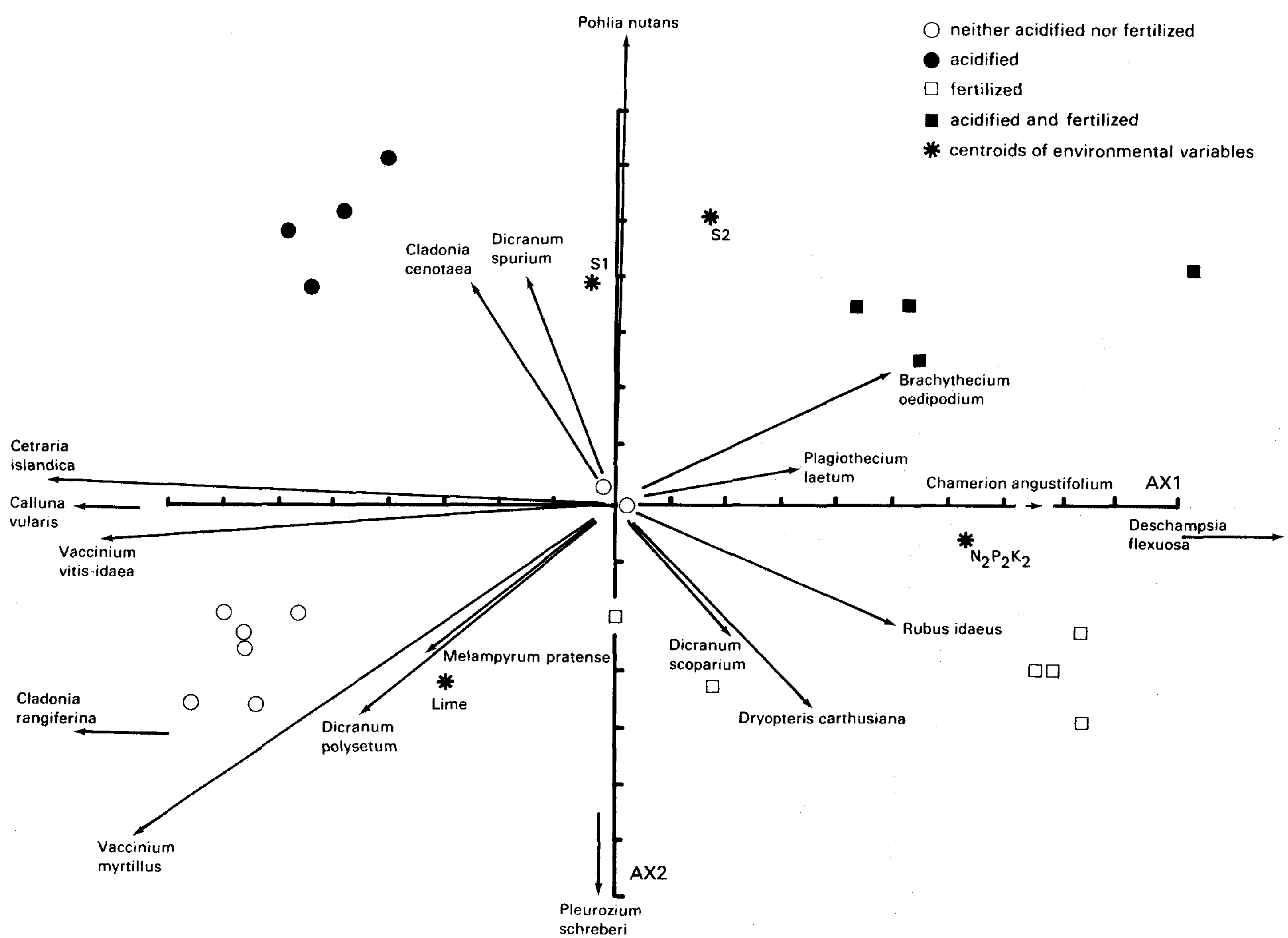

Figure 10. RDA ordination diagram (Euclidean distance biplot) of the Lisselbo E42 data with species represented by arrows and treatments by their centroids.

4. DISCUSSION

The effects of experimental forest fertilization on species composition of moss and herb layers of a pine forest are obvious. The rather rough nine-point scale (in data analysis even transformed to a four-point scale) used to estimate species cover, did not blur the effects. This crude cover estimate was chosen to get an overview of the effects. Yet, a more detailed estimation of cover or abundance might have been desirable, especially in the light of further statistical analysis of the response to the treatments of individual species.

The results of a multivariate analysis of the floristic data leave hardly any doubt about inorganic N as a factor dominating all other factors considered in this study (P included).

Disfavoured by any N addition are *Vaccinium vitis-idaea*, *Calluna vulgaris*, *Cetraria islandica*, and *Dicranum polysetum*.

Favoured by some addition (N1: 20 kg N/ha/yr) but disfavoured by more are *Vaccinium myrtillus*, *Pleurozium schreberi*, and *Dicranum scoparium*.

Favoured by considerable N additon (N2-N3: 40-60 kg N/ha/yr) are *Rubus idaeus*, *Dryopteris carthusiana*, *Chamerion angustifolium*, *Deschampsia flexuosa*, *Brachythecium oedipodium*, and *Plagiothecium laetum*.

According to Burgtorf (1981), Holmen et al. (1976), and Tamm (1974) the same holds for the N effects on growth of Scots pine and spruce. Tamm and Holmen et al. were able to attribute a slight increase of tree growth to P application in addition to N. Application of P alone may only have any effect on extremely poor sites where P is growth restricting, or on sites extremely rich in nitrogen, where P is again the limiting factor in plant growth. Van den Burg (1986) has reviewed the European literature on forest liming. Most of the experiments were intended to investigate whether wood production could be raised and therefore little is reported on the effects of liming on field and bottom layer vegetation. In addition, in most experiments it is not clear whether liming was preceded by ploughing or not. Moreover, most reports concerning effects on field and bottom-layer species are based upon floristic data that are far from exhaustive. Nevertheless, some traits in effects on species composition may be recognized. Apart from extremely poor soils, liming usually leads to a higher abundance of i.a. *Chamerion angustifolium* and *Rubus idaeus*. Under spruce it may even lead to

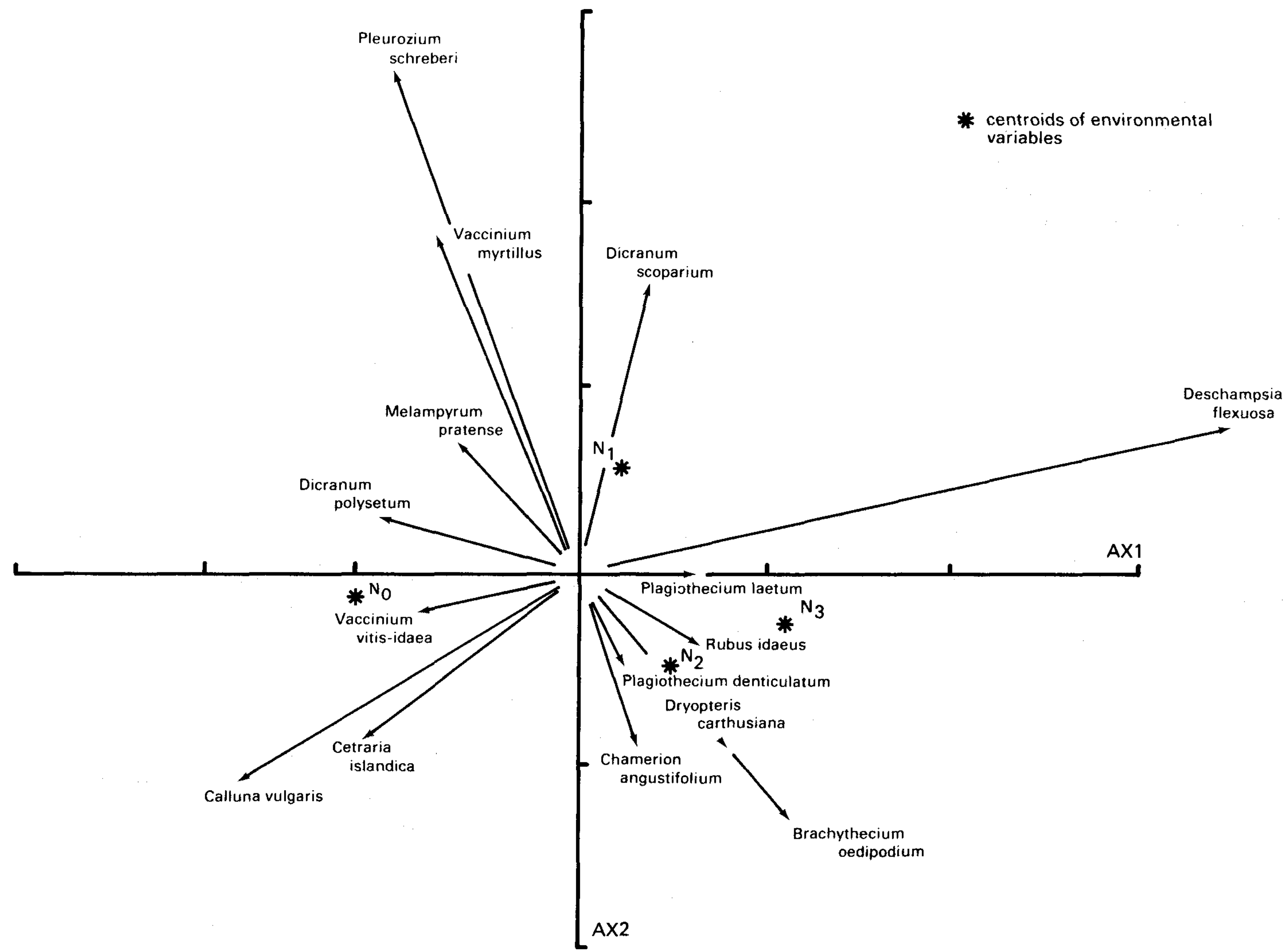

Figure 11. RDA ordination diagram (Euclidean distance biplot) of all Lisselbo data with the effect of all treatments removed, except for N. Three classes of species can be recognized. 1. species disfavoured by any N addition; 2. species favoured by some N addition, but disfavoured by more; 3. species favoured by considerable N addition.

the appearance of *Stellaria media*, *Sambucus racemosa*, *S. nigra*, and *Urtica dioica*. To a certain degree these effects simulate those of nitrogen fertilization. They reflect the 'priming effect' of liming upon the net mineralization of soil organic N (Singh et al. 1969). It is known that Al or Fe salts may even stronger stimulate mineralization of N (Singh et al. 1969). The mechanisms of this stimulation are not fully known (Haynes 1986).

The effects of N fertilizers on the undergrowth vegetation have particularly been studied by a.o. Persson (1981) and Gerhardt & Kellner (1986). Persson studied the effect of ammonium nitrate on species composition in permanent plots (1973-1980) in a young stand of scots pine at Ivantjärnsheden, situated ca. 60 km N of Lisselbo. Annually repeated fertilization strongly benefitted *Chamerion angustifolium* and *Rubus idaeus* whereas lichens (Cladonia spp.) disappeared. Gerhardt & Kellner (1986) made a comparitive study of species composition in plots with different fertilizer treatments and non-fertilized plots in stands of scots pine and spruce at four Swedish localities. Repeated fertilization caused negative responses of *Cladina rangiferina*, *Pleurozium schreberi*, and *Hylocomium splendens*. The grass *Deschampsia flexuosa* increased significantly in the plots with high nitrogen (as urea or ammonium nitrate) supplies. Mosses growing on litter (i.a. Brachythecium spp. and Plagiothecium spp.) had increased in the fertilized plots. To a large extent, these results agree well with the results of the Lisselbo experiments, stressing the major importance of mineral soil nitrogen as a factor for plant growth and species composition.

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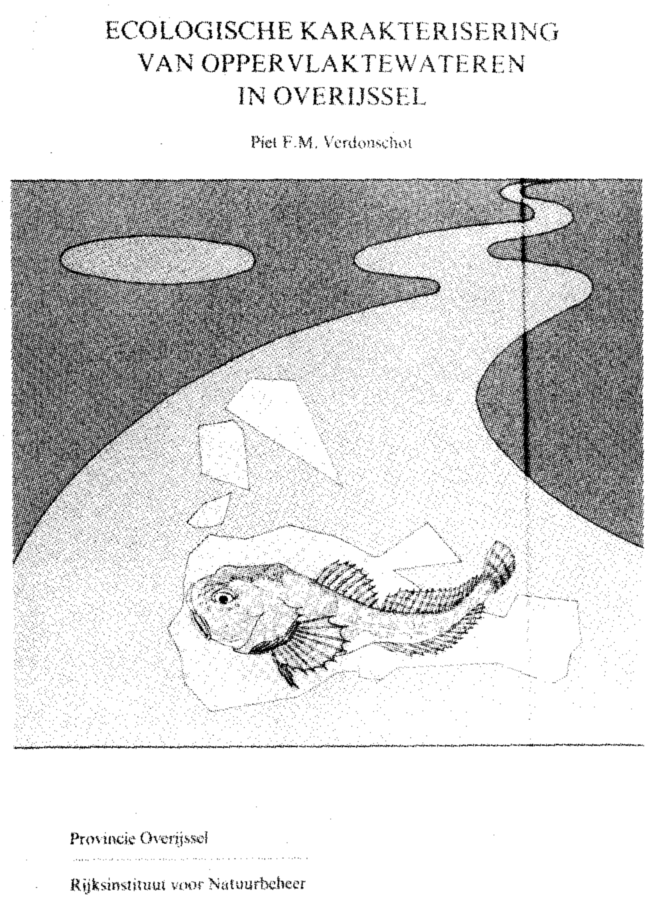

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