sommerfeltia

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T. Økland

Vegetational and ecological monitoring of boreal forests in Norway. I. Rausjømarka in Akershus county, SE Norway.

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Vegetational and ecological monitoring of boreal forests in Norway was initiated in 1988, as a part of the programme "Countrywide monitoring of forest health" at Norwegian Institute of Land Invetory (NIJOS). Ten reference areas for monitoring will be established and analysed within five years; two new areas each year. Each of the monitoring areas is planned to be reanalysed every fifth year. In each monitoring area 10 macro sample plots, 50 m^2 each, are selected. Within each macro sample plot 5 meso sample plots, 1 m^2 each, are randomly placed and the vegetation is analysed by using frequency in subplots as measure of species abundance. Within each meso sample plot one micro sample plot (two in the first established monitoring area), 0.0625 m^2 each, is analysed by the same method. In connection with each meso sample plot several environmental variables are recorded. In each ma cro sample plot several tree variables and variables describing the terrain are recorded. The variables are used for environmental interpretation as well as for monitoring, since known relations between vegetation and environmental gradients form the basis of vegetational and ecological monitoring. Any future changes in vegetation, soil and the health of trees have to be interpreted in relation to the analysis of vegetation-environment relationships in order to identify changes due to air pollution or climatic changes.

The data from the first established monitoring area, Rausjømarka in Akershus county, are subjected to analysis in this paper. The most important vegetational and environmental gradients in the area are discussed, as well as the field methodology and the methods for data analysis to be used in integrated monitoring. The advantages of integrated monitoring of vegetation, soil and trees on the same sample plots are emphasized, including advantages for surveying and monitoring of species (bioindicators).

Keywords: Boreal forests, DCA, Monitoring, Norway, Norway spruce, Ordination, Permanent plots, Vegetation ecology.

Tonje Økland, Norwegian Institute of Land Inventory, Box 115, N-1430 Ås.

CONTENTS

INTRODUCTION

Forest damage related to air pollution has been a controversial issue since the end of the 1970s, as exemplified by the reports of so-called "new forest damages" (cf. Schütt & Cowling 1985, Krausse et al. 1986). The report from Czechoslovakia of 15000 km^2 of forest damaged mainly because of polluted air (Kubikova 1989) is among the most alarming.

From several countries, among them Norway and Sweden, acidification of soils during the last fifty years has been reported (Hallbäcken & Tamm 1986, Dahl 1988, Falkengren-Grerup et al. 1988). The general acidification of soils has apparently been caused by long distance airborne pollution (Dahl 1988, Battarbee et al. 1989). However, the degree to which damage to forests in Norway has been caused by deposition of airborne pollutants, and the extent of soil acidification, is still disputed. Our knowledge about the influence of air pollutants on the ground vegetation in Norwegian forests is insufficient. However, from Central Europe, considerable damage and vegetational changes have been reported (e.g. Kubikova 1989). In Czechoslovakian lowlands, *Vaccinium myrtillus* and *V. vitis-idaea* have disappeared, while *Calamagrostis villosa*, *C. arundinacea*, *Pteridium aquilinum* and *Rubus idaeus* have increased (Kubikova 1989). In the mountains species like *Trientalis europaea* and *Blechnum spicant* have declined. Remarkable changes have also been reported from West Germany (Wittig et al. 1985, Wittig & Neite 1985) and changes in vegetation, though not so dramatic, have also been reported from S Sweden (Falkengren-Grerup 1986).

The ground vegetation is an important part of the forest ecosystem and experience from Europe emphasizes the importance of monitoring changes in forest vegetation. Early stages of damage to the forest ecosystem, caused by air pollution and/or climatic changes, are likely to be reflected in the ground vegetation. Monitoring of the environmental variables on which the vegetation is dependent is necessary in order to interpret vegetational changes. Simultaneous monitoring of vegetation, environmental and tree variables may provide a basis for understanding complex vertical relations. Moreover, such integrated monitoring of vegetation and environmental variables is an important and necessary basis for other kinds of research, e.g. identification of possible bioindicators and monitoring of the population dynamics of single species.

The project for vegetational and ecological monitoring of boreal forests in Norway is a part of the programme "Countrywide monitoring of forest health" at Norwegian Institute of Land Inventory (NIJOS), and was initiated in 1988. Possible damage or changes caused by airborne pollutants or climatic changes are likely to vary on a regional scale. Thus, to span the regional variation, a sufficient number of monitoring areas should be established, though each area must have comparable vegetation and environmental conditions. Ten such monitoring areas will be established by NIJOS. Since 1988 two new monitoring areas have been established and analysed each year. Poor and medium-rich blueberry-dominated spruce forest was chosen for the investigation, since these are the most important forest types in Norway, quantitatively as well as from an economic point. The plan is to reanalyze each monitoring area every fifth year.

The most important purposes of the project are: (1) To make records of the present status of the ground vegetation, environmental conditions and the health of trees in representative reference areas in boreal coniferous forests. (2) To monitor possible quantitative or qualitative changes and correlations between changes in vegetation, in the abundance of species, in environmental conditions and in the health of trees in the same areas. (3) To identify possible bioindicators which could be subjected to monitoring on a greater scale, primarily within NIJOS's nation-wide grid of monitoring plots. (4) To get

increased knowledge about relations between vegetation and environment and about the ecology of single species, locally and regionally.

This paper is based on the report "Program "Overvåking av skogens sunnhetstilstand": Vegetasjonsøkologisk overvåking av boreal barskog i Norge" (T. Økland 1989), in turn based on data from the first established area, Rausjømarka in Akershus county, SE Norway. The specific purposes of this paper are: (1) To introduce the project and the monitoring methods, and evaluate and discuss the methodology. (2) To present and discuss the results from one of the reference areas; Rausjømarka in Akershus county, SE Norway.

THE INVESTIGATION AREA

GEOGRAPHICAL LOCATION AND GENERAL INFORMATION

The investigation area is situated in the southern part of Rausjømarka forest reserve in Enebakk municipality, Akershus county (UTM ca. PM 145 342, 240-285 m above sea level).

The area is owned by Oslo municipality and protected administratively by Oslo municipality. A more extensive area than presently protected is planned to be protected by law (jf. Krohn & Hardeng 1981). The area is managed by the Oslo municipality Forest Service.

GEOLOGY

The area belongs to the southeast Norwegian Precambrian and the bedrock consists of gneisses (Oftedahl 1980, Krohn & Hardeng 1981). The area is situated above the upper coastal line.

CLIMATE

A comprehensive account of the climate was given by Krohn & Hardeng (1981), using material from three different meteorological stations (Østmarka, Sørmarka and Enebakk). They reported estimates for the annual mean temperature to be 4.3° (for the normal period 1931-1960), the annual precipitation to be 780-900 mm and the annual number of days with precipitation $\geq$ 0.1 mm to be 148. The area belongs to the southern boreal zone (R. Økland, pers. comm., cf. Ahti et al. 1968, Abrahamsen et al. 1984).

MATERIALS AND METHODS

PLACEMENT AND PERMANENT MARKING OF SAMPLE PLOTS

A restricted random sampling procedure was used. Ten macro sample plots, each 5 x 10 m, were placed in order to represent the variation along presumably important ecological gradients; aspect, nutrient conditions, light conditions, topography, soil moisture conditions etc. (Figs 1-2).

Five meso sample plots, each 1 m^2, were randomly placed within each of the macro sample plots (Fig. 2). The positions of the meso sample plots were found by means of random numbers (Owen 1962). A meso sample plot was rejected if a tree > 2 m was rooted in it or if more than 20 % of the sample plot was covered by stones. In case of rejection a new position for the sample plot was found by testing potential meso plots for acceptability in a fixed order of priority to avoid subjectivity. All corners of the meso and macro sample plots were permanently marked with subterranean eloxed aluminium rods. Within each meso sample plot 2 micro sample plots, each 0.0625 m^2, were marked in the same way (Fig. 3). The macro and meso sample plots were also marked visibly with above ground markers. The sampling scheme was chosen as a supposedly optimal compromise between objectivity and time consumption (cf. R. Økland 1990).

ANALYSIS OF SAMPLE PLOTS

Each of the 50 meso sample plots were divided into 16 meso subplots, 0.0625 m^2 each (Figs 2-3). Presence/absence of all species was recorded for each of the meso subplots and frequency in subplots was calculated for each species (cf. T. Økland 1988). For vascular plants both presence by cover and presence by rooting were recorded in each subplot. The micro sample plots were analysed in the same way as the meso sample plots.

MEASUREMENTS OF ENVIRONMENTAL AND TREE VARIABLES

Measurements of environmental and tree variables are made for the following purposes: (1) Environmental interpretation of the vegetational patterns as reproduced by the ordinations. Variables used directly for environmental interpretation or for calculating variables used for this purpose are marked (E) below. (2) Monitoring of changes in soil and/or the health of the trees, which may in turn be correlated with changes in the vegetation. Most of the variables used for environmental interpretation are used for monitoring as well. (3) Background information (e.g. cover of each layer, cover of naked rock and stones, stumps etc., sketch map of the meso and micro sample plots, description of the terrain, vegetation type etc.). Terrain variables and tree variables, i.e. macro sample plot variables, are mostly those measured in NIJOS's net of countrywide monitoring plots (Rørå et al. 1988).

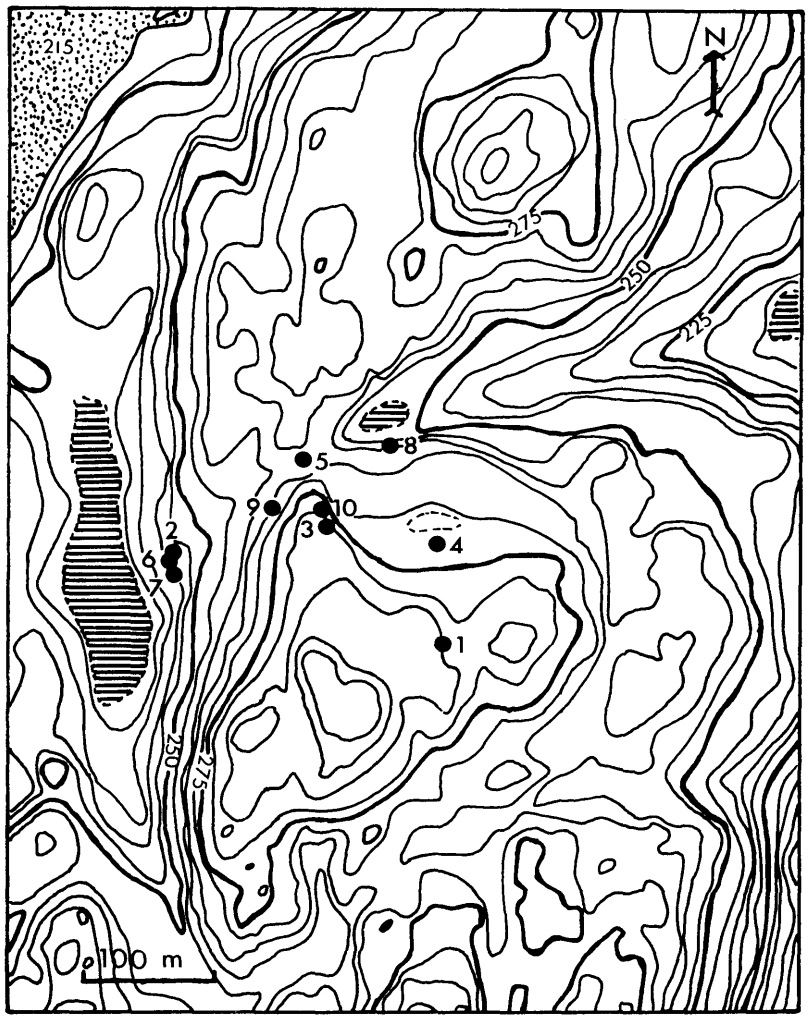


Fig. 1. Placement of macro sample plots in the investigated area. Macro sample plot 1 comprises meso sample plots 1 - 5, macro sample plot 2 comprises meso sample plots 6-10, etc. UTM grid reference of investigation area is PM 145-147, 341-343, 240-285 m.a.s.l.

Macro sample plot variables

Macro sample plot aspect (E) was measured by means of a compass (100^g), in a way to ensure representativeness for the macro sample plot. The measured values were recalculated to a scale expressing deviation from SSW (225°), considered to be the most favourable aspect (Dargie 1984) due to the favourable combination of high incoming radiation at times of the day with highest temperatures. An nine-point scale was used: 0 - SSW, 1 - S/SW, 2 - SSE/WSW, 3 - SE/W, 4 - ESE/WNW, 5 - E/NE, 6 - ENE/NNW, 7 - NE/N and 8 -

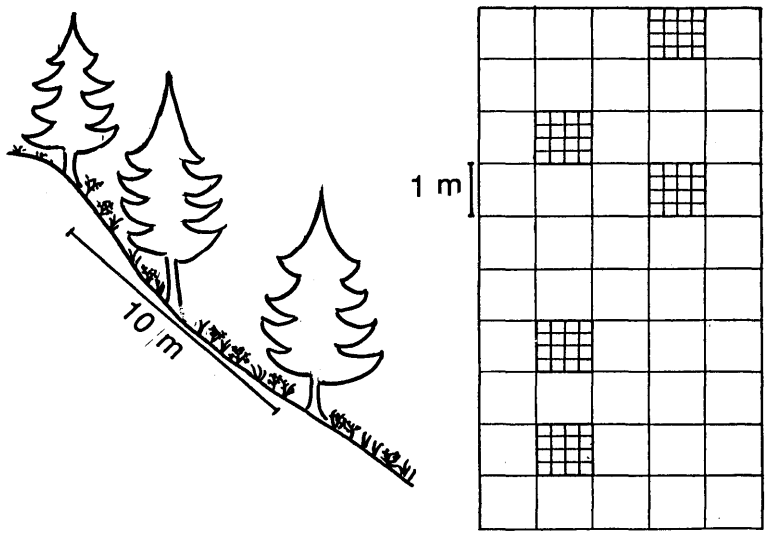


Fig. 2. An example of placement of macro sample plots in the terrain (to the left) and an example of placement of meso sample plots, each divided into 16 subplots, within the macro sample plot (to the right).

NNE.

Macro sample plot inclination (E) was measured by means of a clinometer (400^g), in a way to ensure representativeness for the macro sample plot.

Terrain shape was estimated subjectively (level, convex valley/hillside, concave valley/hillside, straight valley/hillside, valley bottom, depression, ridge, peak).

Macro sample plot surface roughness (E) was recorded on a 1-4 scale: 1 - even, quite regular terrain, i.e. < 100 roughnesses per decare, 2 - irregular terrain with large stones, i.e. ≥ 100 roughnesses per decare, 3 - boulder and scree and 4 - cliffs and crevices. Only roughnesses deviating at least 35 cm from the surrounding terrain surface were counted.

Macro sample plot soil depth (E) was estimated subjectively and recorded on a scale from 1 to 4 (1 - < 25 cm, 2 - 25-50 cm, 3 - 51-100 cm and 4 - > 100 cm).

Macro sample plot basal area (E) (measured at breast height) was determined by a relascope (Fitje & Strand 1973). Basal area expresses the tree density and thus the supply of light to the sample plots. Basal area was measured from the four corners of each macro sample plot and the average was calculated. Relascope factor 1 was used.

Macro sample plot light index (E) was calculated by use of the area and cover of crowns for all trees in each macro sample plot. The following formula was used (R.H. Økland, pers. comm.):

$$L = (\Sigma_i a_i b_i)/50$$

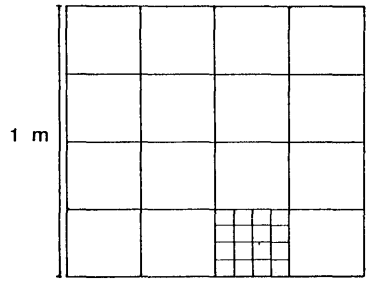


Fig. 3. Division of a meso sample plot into 16 meso subplots, and division of a micro sample plot (= meso subplot) into 16 micro subplots.

where a_i is the crown area and b_i is the crown cover (the vertical projection of living phytomass) of tree i.

Site quality expresses the ability of the ground to produce wood (Tveite & Braastad 1981). Site quality was based on of core samples taken at breast height from 2-3 trees close to the macro sample plot. H_{40} (site quality at 40 years age at breast height) was determined by means of graphs expressing the relations between site quality, age at breast height and dominant height of the stand (Tveite & Braastad 1981). The core samples were preferently taken from trees representative of the vegetation type dominating the macro sample plot.

Stand age was estimated from the age of the trees from which the core samples were taken.

Felling class, i.e. the stage of forest development (cf. Institutt for skogtaksasjon & Institutt for skogøkonomi 1987), was estimated for each macro sample plot.

Tree variables

Measurements were made according to Rørå (1988) when nothing else is mentioned.

Diameter at breast height (1.3 m) was calculated from the stem circumference in cm at breast height.

Tree height was measured in dm from normal stump height to the treetop.

Crown height was measured as the difference between total tree height and the distance from the ground to the point of the stem where the lowest green branch whorl grew, i.e. the lowest branch whorl not separated from the rest of the crown by more than one dry branch whorl (A. Rørå, pers. comm.).

Crown area (E), i.e. the area of the macro sample plot covered by the projection of the trees (the sum of areas within crown perimeters), was estimated from a sketch map of each macro sample plot with positions of meso sample plots, canopy perimeters and tree stems drawn in.

Social status of the trees, i.e. their competitive ability relative to the other trees in the stand (Skinnemoen 1969), was recorded by classification into one of six groups: suppressed trees, dominated trees, codominators, dominators, standards and free-standing trees. Dominators, standards and free-standing trees are more exposed to wind, sun and air pollution (Rørå et al. 1988).

Relative crown density, which is a measure of the health of the tree (Rørå et al. 1988), was estimated by binoculars as percentage of the presumed normal crown density for each tree.

Actual crown density (E) was defined as the crown density as it emerges estimated from beside the trees and relative to openings in the tree canopy, but independent of the normal crown density for the tree (A. Rørå, pers. comm.). The measurements were made by use of binoculars and recorded as a percentage.

Crown cover (E) was estimated as the percentage of the crown area covered by living phytomass of each tree.

Crown colouration, another measure of tree health (Rørå et al. 1988), was estimated on a 1-4 scale: 1 - normal green, 2 - somewhat discoloured, 3 - moderately discoloured and 4 - strongly discoloured.

Defoliation type, i.e. classification of various distribution types of damage symptoms in the tree crown (Rørå 1988, Rørå et al. 1988), was noted on a scale from 1 to 6 for spruce and 1 to 3 for pine.

Amount of cones was recorded on an eight-point scale, 4 for present year's cones and 4 for last year's cones (used only if no present-year cones were observed).

Mechanical and biotic damage was classified into 6 types: 0 - no damage, 1 - broken top, 2 - broken top; new top developed, 3 - dry top, 4 - dry top; new top developed, 5 - damage caused by insects and 6 - physical damage.

Meso sample plot variables

Inclination was measured at five fixed points in each meso sample plot and sample plot means were calculated.

Meso sample plot aspect was measured at the same five fixed points in each meso sample plot and the median value was calculated. This value was recalculated in the same way as for macro plot aspect.

Microtopography, expressed as indexes for *meso sample plot surface roughness* and *meso sample plot convexity* (R.H. Økland, pers. comm., R. Økland & Eilertsen in prep.) was calculated from measurements of vertical distance from the centre of each meso subplot to a levelled analyzing frame Thus 16 observations were made in each meso sample plot.

Meso sample plot soil depth was measured at six fixed points just outside the border of the meso sample plot. The minimum value, the maximum value and the median value were determined for each meso sample plot.

Litter index based on crown cover was calculated by means of the following equations (R. Økland, pers. comm., R. Økland & Eilertsen in prep.):

$$L_i = \sum_i (d_{ri}/d_i)\, b_i\, c_i\, (h_{ti} - h_{ki})$$ for trees with stem rooted within the crown perimeter

and

$$L_i = \sum_i b_i\, c_i\, (h_{ti} - h_{ki})$$ for trees with stem not rooted within the crown perimeter

where b_i is the cover of the crown of tree i, h_{ti} is the height of tree i, h_{ki} is the crown height of tree i, d_i is the distance from the centre of the stem to the crown periphery of tree i, measured through the centre of the meso sample plot (Fig. 4), d_{ri} is the distance from

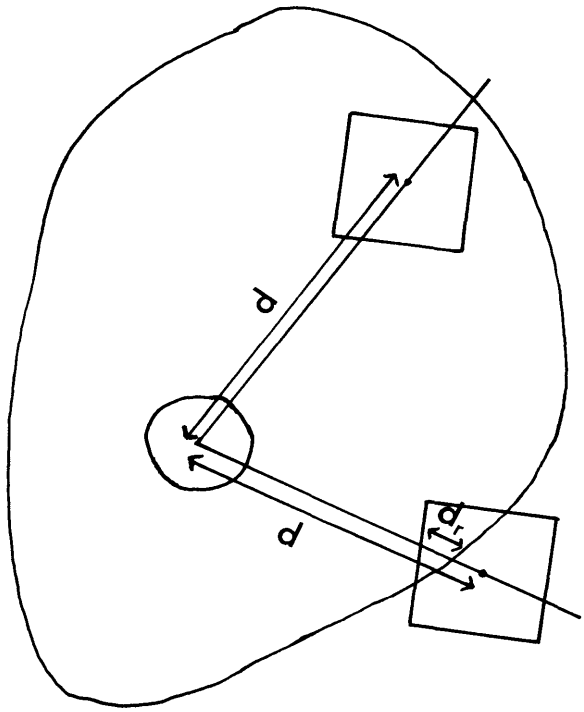


Fig. 4. The parameters d_i and d_{ri} used for calculation of the litter indexes. d_i - distance from centre of stem to the crown periphery, d_{ri} - distance from crown periphery to the border of the meso sample plot.

the crown periphery to the meso sample plot border along the line through the centre of the meso sample plot and the centre of stem of tree i (Fig. 4) and c_i is the fraction of the meso sample plot area situated under the crown of tree i.

Litter index based on actual crown density was calculated correspondingly, but b_i was replaced with e_i, actual crown density.

Soil moisture was determined by collecting volumetric soil samples from the upper 5 cm of the humus layer. The samples were collected about 10 cm from the border of each meso sample plot, whenever possible below the sample plot. All the soil samples were

collected on the same day, stored in paper bags surrounded by double plastic bags and kept frozen until they were weighed in the laboratory. After drying at 110°C to constant weight, the samples were weighed again and the percentage moisture was calculated.

Samples from the upper 5 cm of the humus layer of the soil for chemical analyses and loss on ignition were collected on the same day for all the meso sample plots and kept frozen until analysis. Several subsamples were collected outside the border of each meso sample plot and the subsamples were mixed, in order to counteract fine-scale spatial variation in physical and chemical properties of the humus. To avoid impact on the drainage regime, soil samples were never collected above the sample plot. The following analyses were performed by "Landbrukets analysesenter", Ås: loss on ignition, pH measured in aqueous solution, pH measured in $CaCl_2$, total N according to the Kjeldahl method and P-Al (standard method among others described by Baadsvik 1974). All exchangeable cations; Ca, Mg, K, Na, H, Al, Fe, Mn, Zn; and the anions P and S were extracted in NH_4NO_3 and their quantities determined by means of ICP (Inductive Coupled Plasma Emission Spectroscopy) with the Jarrel Ash model 1100 instrument. Concentrations were expressed as fractions of loss on ignition as recommended by T. Økland (1988).

THE DATA MATRICES AND DATA EDITING

Both the vegetation data matrices (species abundances in sample plots) and the ecological data matrix (values for environmental variables in sample plots) were entered on the computer by means of Biological Data Program/PC Version 1.01 (Pedersen 1988). Data editing was partly made by means of BDP/PC, partly by means of LOTUS 1-2-3 (Lotus Development Corporation 1989). Ecological variables with a lognormal or approximately lognormal distribution (Tab. 1) were converted to approximately normally distributed variables by use of the transformation ln (1 + x).

ORDINATION

Ordination methods are multivariate numerical methods used in vegetation ecology for the purpose of extracting the main structure in a data set; i.e. to arrange sample plots and/or species along the most important vegetational gradients in an ordination diagram. As vegetation is a function of environmental variables (Whittaker 1967), the variation along the ordination axes should be subjected to environmental interpretation.

Different ordination methods are based upon different mathematical/statistical models (cf. R. Økland 1990). Detrended correspondence analysis (DCA; Hill 1979, Hill & Gauch 1980) is based on a realistic model of moderate detail resulting in ordination axes that are mostly interpretable in environmental terms. The axes are rescaled into standard deviation units (S.D. units) reflecting degree of compositional turnover along the gradients (Hill 1979). An S.D. unit is defined as equal to the mean standard deviation of species distributions along the coenoclines, provided the distributions are Gaussian. A species normally appears, reaches its optimum and disappears within the span of 4 S.D. units. DCA simultaneously ordinates samples and species.

Detrended correspondence analysis (DCA; Hill 1979, Hill & Gauch 1980) was

Tab. 1. Characterization of environmental variables.

No.	Name	Unit	Range	Statistical distribution	Transformation
01	Macro inclination	g	0-100	uniform	no
02	Macro aspect	g, conv.	0-8	uniform	no
03	Macro surface roughness		1-4	uniform	no
04	Macro soil depth		1-4	uniform	no
05	Macro basal area			0-∞	uniformno
06	Macro light index			0-∞	uniformno
07	Meso inclination	g	0-100	normal-uniform	no
08	Meso aspect	g, recalc.	0-8	uniform	no
09	Meso surface unevenness		0-∞	lognormal	ln (1+x)
10	Meso convexity			-∞-+∞	normalno
11	Meso soil depth minimum	cm	0-∞	lognormal	ln (1+x)
12	Meso soil depth median	cm	0-∞	lognormal	ln (1+x)
13	Meso soil depth maximum	cm	0-∞	lognormal	ln (1+x)
14	Litter index based on crown cover		0-∞	lognormal	ln (1+x)
15	Litter index based on actual crown density		0-∞	lognormal	ln (1+x)
16	Soil moisture	vol. %	0-100	normal	no
17	Loss on ignition	%	0-100	bimodal	no
18	pH_{water}		0-14	normal	no
19	pH_{CaCl2}		0-14	normal	no
20	Ca	ppm/LI	0-∞	lognormal	ln (1+x)
21	Mg	ppm/LI	0-∞	lognormal	ln (1+x)
22	K	ppm/LI	0-∞	lognormal	ln (1+x)
23	Na	ppm/LI	0-∞	lognormal	ln (1+x)
24	H^+	ppm/LI	0-∞	± lognormal	ln (1+x)
25	Al	ppm/LI	0-∞	lognormal	ln (1+x)
26	Fe	ppm/LI	0-∞	lognormal	ln (1+x)
27	Mn	ppm/LI	0-∞	lognormal	ln (1+x)
28	Zn	ppm/LI	0-∞	± lognormal	ln (1+x)
29	Total N	weight %/LI	0-100	± lognormal	ln (1+x)
30	P-Al	ppm/LI	0-∞	lognormal	ln (1+x)
31	P	ppm/LI	0-∞	lognormal	ln (1+x)
32	S	ppm/LI	0-∞	± lognormal	ln (1+x)

performed by means of CANOCO (ter Braak 1987a) with the following options: detrending by segments, non-linear rescaling, no centring/standardization, as no omission of rare species and downweighting of species with frequency lower than the median frequency (as recommended by Eilertsen & Pedersen (1989) and Eilertsen et al. (1990)).

DCA was used for ordination of frequency in subplots data for 50 meso sample plots. Three sample plots with very low numbers of species were, however, deleted before all further analyses, as these appeared poorly characterized and thus acted as outliers (cf. T. Økland 1988). After the deletion, the frequency in subplots data for the 88 species in the remaining 47 meso sample plots were subjected to DCA ordination. The 47 meso sample plots were also subjected to DCA ordination with the micro sample plots as passive samples (i.e. the micro sample plots were placed in the ordination diagram of the meso sample

plots, without influencing the ordination structure).

METHODS FOR ANALYSIS OF ENVIRONMENTAL DATA AND INTERPRETATION OF ORDINATION RESULTS

Thirty-two of the recorded variables were used for the further analyses (Tab. 1). The remainder, i.e. the tree variables recorded only for monitoring purposes, will be subjected to analysis and related to vegetational data after the first reanalysis of sample plots, planned for 1993.

All meso sample plots within the same macro sample plot were given the same value for macro sample plot variables. Statistical analyses (analysis of correlations and regressions), were performed by means of LOTUS 1-2-3.

Ordination of environmental data by means of PCA

Principal component analysis (PCA, Pearson 1901) is based on a linear statistical model, i.e. requiring linear relations between the variables (the environmental variables) and the underlying environmental complex-gradients (ter Braak & Prentice 1988). Normally distributed environmental variables are generally in accordance with such a model. Variables with a relatively similar pattern of variation in a data set are placed near each other in a PCA ordination diagram.

PCA (centred and standardized by division with standard deviation) of 32 environmental variables recorded in 47 meso sample plots was performed by means of CANOCO.

Correlation analyses

Analyses of linear correlations between environmental variables and between environmental variables and DCA axes were performed by calculating Pearson's product moment correlation coefficients (Sokal & Rohlf 1981) by means of LOTUS 1-2-3.

Isoline diagrams

Values for environmental variables were plotted on the meso sample plot positions in the DCA ordination diagram in order to illustrate the relations between vegetation and environmental conditions. The values were smoothened by fitting a third order polynomial by means of LOTUS 1-2-3. Fitted (smoothened) values were used for drawing isolines on to the ordination diagram.

Vector fitting

Weighted correlations between environmental variables and DCA axes were calculated by means of CANOCO. Vectors of steepest descent (pointing in the direction of strongest

change) of environmental variables were fitted to the 32 environmental variables in the ordination of the 47 meso sample plots (cf. ter Braak 1987a, 1987b, R. Økland 1990), and indicated in the ordination diagram. The length of the vectors indicate the degree of correlation with the ordination axes.

Presentation of distributions of species abundances in the DCA ordination

For species occurring in five or more out of the 47 meso sample plots, frequency in subplots was plotted on to the meso sample plot positions in the DCA ordination diagram. When the distributions of species abundances are considered in relation to the interpreted meso sample plot ordination diagram, i.e. related to environmental gradients, valuable information about the autecology of the species is obtained.

NOMENCLATURE

The nomenclature of vascular plants follows Flora Europaea (cf. Moore 1982), of mosses follows Corley et al. (1981), except for *Rhytidiadelphus squarrosus* which was included in *R. subpinnatus*, of hepatics follows Grolle (1983), and of lichens follows Krog et al. (1980).

RESULTS

PCA ORDINATION OF ENVIRONMENTAL VARIABLES

Positions of the 32 environmental variables along the two first PCA axes are shown in Fig. 5. A group of variables with high loadings on PCA 1, i.e. strongly positively correlated variables, is made up by pH_{water}, pH_{CaCl2}, macro sample plot basal area, macro sample plot light index, Mn, Ca, Mg and both litter indexes (based on crown cover and based on actual crown density). H^+ was the variable with the lowest loading on PCA 1, i.e. the variable most strongly negatively correlated with the group mentioned above. Thus the first PCA axis was interpreted as a complex-gradient consisting of single gradients in cation concentrations, light, and litter conditions; increasing amounts of cations were correlated with increasing tree density and thus with decreasing light and increasing litter fall.

Macro sample plot aspect, meso sample plot aspect and loss on ignition were the variables with the highest loadings on PCA 2; thus the less favourable the aspect, the greater the loss on ignition, i.e. the greater amounts of organic matter in the soil. The variables macro and meso sample plot roughness also had high loadings on PCA 2. Among others, the variables Fe, Al, median soil depth and maximum soil depth had low loadings on PCA 2.

CORRELATIONS BETWEEN ENVIRONMENTAL VARIABLES

Correlations between the 32 environmental variables (based on values for the 47 meso sample plots) and their significance probabilities are shown in Tab. 2. The plexus diagram in Fig. 6 illustrates the strongest correlations in Tab. 2.

pH and the cations Ca, Mg and Mn were pairwise positively correlated; all of them important single gradients in a complex-gradient in nutrient conditions (PCA 1). The macro sample plot crown cover index was positively correlated with Ca, Mg, Mn and Zn; the more favourable the nutrient conditions, the more dense the forest and thus lower the light influx. Basal area, which was positively correlated with pH and the crown cover index, also expressed similar relationships. The litter indexes were positively correlated with Ca, Mn and the crown cover index, i.e. the amount of litter increased with increasing crown cover and more favourable nutrient conditions.

Meso sample plot and macro sample plot aspect were both negatively correlated with basal area; the more favourable the aspect, the greater the tree density. Meso sample plot aspect and macro sample plot aspect were strongly positively correlated, indicating that the within macro sample plot variation in aspect was small.

Loss on ignition was negatively correlated with pH, Mn and N. Thus the amount of organic matter decreased when nutrient conditions became more favourable and the amount of N increased. The amount of N was also positively correlated with pH and Mn. Loss on ignition was positively correlated with meso and macro sample plot aspect, i.e. the amount of organic matter in the soil increased when the aspect became less favourable. Loss on ignition was also strongly positively correlated with P.

The cations Al and Fe were strongly positively correlated, and both were negatively

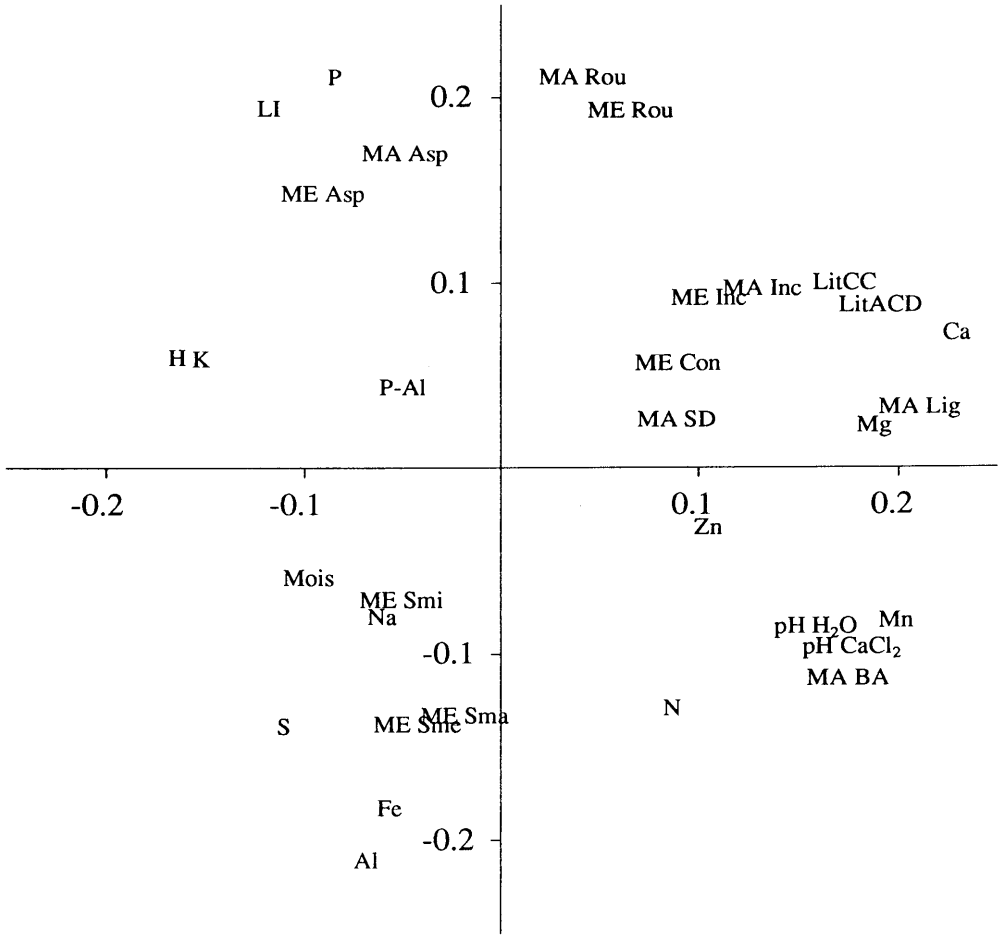


Fig. 5. PCA ordination of 32 environmental variables from 47 meso sample plots. MA Inc - Macro inclination. MA Asp - Macro aspect. MA Rou - Macro surface roughness. MA SD - Macro soil depth. MA BA - Macro basal area. MA Lig - Macro light index. ME Inc - Meso inclination. ME Asp - Meso aspect. ME Rou - Meso surface roughness. ME Con - Meso convexity. ME Smi - Meso soil depth minimum. ME Sme - Meso soil depth median. ME Sma - Meso soil depth maximum. LitCC - Litter index based on crown cover. LitACD - Litter index based on actual crown density. Mois - Soil moisture. LI - Loss on ignition.

correlated with the litter indexes and loss on ignition, i.e. the amounts of Al and Fe increased when the amount of litter and amount of organic matter in soil decreased. Al and Fe were also negatively correlated with macro sample plot surface roughness, in turn positively correlated with meso sample plot surface roughness and with macro sample plot inclination.

Tab. 2. Correlation coefficients between environmental variables (lower triangle), and their significance probabilities (upper triangle). 47 meso sample plots. Correlation coefficients r > 0.45 in bold face. *** - P < 0.01, ** - 0.01 < P < 0.05, * - P < 0.1, n.s. - P > 0.1 (two-sided tests). MA Inc - Macro inclination. MA Asp - Macro aspect. MA Rou - Macro surface roughness. MA SD - Macro soil depth. MA BA - Macro basal area. MA Lig - Macro light index. ME Inc - Meso inclination. ME Asp - Meso aspect. ME Rou - Meso surface roughness. ME Con - Meso convexity. ME Smi - Meso soil depth minimum. ME Sme - Meso soil depth median. ME Sma - Meso soil depth maximum. LitCC - Litter index based on crown cover. LitACD - Litter index based on actual crown density. Mois - Soil moisture. LI - Loss on ignition.

Variable	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
01 MA Inc	.	n.s.	***	***	n.s.	n.s.	***	n.s.	*	n.s.	*	*	*	n.s.	n.s.	n.s.	n.s.	**	**	***	***	**	*	n.s.	*	**	n.s.	n.s.	n.s.	n.s.	n.s.	***
02 MA Asp	0.137	.	***	**	***	n.s.	n.s.	***	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*	***	n.s.	n.s.	n.s.	n.s.	**	n.s.	**	*	**	**	n.s.	***	**	***	n.s.
03 MA Rou	**0.558**	**0.498**	.	n.s.	**	*	n.s.	**	***	n.s.	n.s.	**	*	n.s.	n.s.	n.s.	***	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	***	***	**	n.s.	*	n.s.	***	***
04 MA SD	0.396	-0.361	0.049	.	n.s.	n.s.	**	**	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**	*	n.s.	n.s.	n.s.	n.s.	n.s.	***	n.s.	**
05 MA BA	-0.066	**-0.691**	-0.303	0.133	.	***	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	***	***	***	**	*	***	n.s.	***	n.s.	n.s.	***	*	n.s.	**	***	n.s.
06 MA Lig	0.226	-0.151	0.275	0.232	**0.462**	.	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	***	***	**	n.s.	*	***	***	***	***	**	***	**	n.s.	***	*	n.s.	n.s.	n.s.	**
07 ME Inc	**0.491**	0.081	0.220	0.356	0.034	0.160	.	n.s.	***	*	**	***	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**	*	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	***
08 ME Asp	0.095	**0.767**	0.294	-0.325	**-0.662**	-0.395	0.052	.	**	n.s.	***	n.s.	n.s.	n.s.	n.s.	n.s.	***	n.s.	**	n.s.	*	*	n.s.	***	n.s.	n.s.	***	**	***	*	***	n.s.
09 ME Rou	0.264	0.353	**0.501**	0.106	-0.182	0.230	**0.525**	0.301	.	**	**	***	***	**	**	n.s.	***	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	***	***	n.s.	n.s.	n.s.	n.s.	***	**
10 ME Con	0.022	0.028	-0.031	0.071	0.059	0.135	0.283	0.090	0.289	.	n.s.	n.s.	n.s.	*	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	***	*	n.s.	n.s.	n.s.	n.s.	n.s.
11 ME Smi	-0.274	-0.115	-0.052	-0.092	0.192	-0.047	-0.352	**-0.789**	0.301	-0.120	.	***	***	**	*	n.s.	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
12 ME Sme	-0.278	-0.153	-0.313	-0.186	0.016	-0.153	**-0.510**	-0.065	**-0.502**	-0.033	**-0.534**	.	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**	**	n.s.	n.s.	n.s.**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**
13 ME Sma	-0.274	-0.025	-0.270	-0.306	0.049	-0.105	**-0.503**	-0.008	-0.434	-0.203	0.410	**0.846**	.	n.s.	n.s.	n.s.	n.s.	**	*	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.	**	*
14 LitCC	0.064	0.078	0.183	-0.016	0.164	**0.464**	-0.003	-0.021	0.325	0.259	-0.331	-0.150	-0.070	.	***	***	n.s.	n.s.	n.s.	**	***	*	*	*	***	***	***	*	n.s.	n.s.	n.s.	**
15 LitACD	0.081	0.033	0.178	0.013	0.233	**0.507**	0.000	-0.043	0.296	0.268	-0.298	-0.113	-0.023	**-0.988**	.	***	n.s.	n.s.	**	**	**	**	*	**	***	***	***	**	n.s.	n.s.	n.s.	**
16 Mois	-0.002	-0.262	0.023	-0.002	0.187	-0.308	0.037	-0.104	-0.091	-0.226	0.032	0.168	0.038	**-0.499**	**-0.491**	.	n.s.	n.s.	*	***	***	n.s.	***	*	**	n.s.	***	*	n.s.	n.s.	n.s.	n.s.
17 LI	-0.172	0.368	**0.462**	0.033	-0.386	-0.199	-0.098	0.369	0.395	0.030	0.055	-0.160	-0.215	0.062	0.019	0.010	.	***	***	**	***	***	n.s.	**	***	***	***	*	***	n.s.	***	n.s.
18 pH_{aq}	0.307	-0.195	0.230	-0.010	0.426	0.244	0.090	-0.229	-0.140	0.195	-0.213	0.206	0.324	0.178	0.243	-0.097	**-0.655**	.	***	**	**	***	n.s.	**	*	n.s.	***	n.s.	***	*	***	n.s.
19 pH_{ocm}	0.326	-0.185	-0.152	-0.018	**0.560**	0.423	0.121	-0.357	-0.137	0.140	-0.131	0.097	0.261	0.309	0.381	-0.272	**-0.716**	**0.891**	.	***	***	***	n.s.	***	n.s.	n.s.	***	n.s.	***	*	***	n.s.
20 Ca	0.438	-0.025	0.264	0.056	0.365	**0.658**	0.307	-0.191	0.253	0.217	-0.276	-0.329	-0.237	**0.562**	**0.597**	**-0.456**	-0.347	0.322	**0.541**	.	***	***	n.s.	***	***	***	***	***	n.s.	n.s.	n.s.	***
21 Mg	0.426	-0.007	0.165	0.128	0.265	0.420	0.243	-0.272	0.096	0.034	-0.206	-0.317	-0.162	0.256	0.303	-0.373	**-0.451**	0.290	**0.522**	**0.778**	.	n.s.	n.s.	***	*	n.s.	***	***	n.s.	*	n.s.	**
22 K	-0.340	0.325	0.041	-0.209	**-0.585**	**-0.530**	-0.307	0.265	-0.051	-0.225	0.059	-0.001	0.030	-0.256	-0.290	-0.036	0.424	**-0.542**	**-0.525**	-0.382	-0.059	.	n.s.	***	n.s.	n.s.	**	n.s.	**	***	***	***
23 Na	-0.253	-0.189	-0.178	-0.338	-0.013	-0.311	-0.013	-0.060	-0.158	0.009	-0.073	0.048	-0.001	-0.267	-0.260	**0.512**	0.163	0.034	-0.091	-0.241	-0.192	0.008	.	*	**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**
24 H	-0.190	0.356	0.110	-0.262	**-0.528**	**-0.463**	-0.109	**0.544**	0.168	-0.024	0.077	0.091	0.043	-0.321	-0.364	0.286	0.340	-0.352	**-0.522**	-0.405	-0.425	0.387	0.245	.	n.s.	n.s.	***	*	n.s.	*	**	n.s.
25 Al	-0.287	-0.274	**-0.655**	-0.007	0.113	-0.334	-0.119	-0.167	**-0.482**	-0.234	0.155	0.297	0.310	**-0.546**	**-0.530**	0.338	**-0.524**	0.274	0.160	**-0.543**	-0.281	-0.102	0.300	0.054	.	***	n.s.	n.s.	*	n.s.	***	***
26 Fe	-0.319	-0.298	**-0.615**	-0.027	0.064	-0.239	-0.171	-0.210	**-0.453**	**-0.463**	0.140	0.136	0.203	**-0.456**	**-0.556**	0.128	**-0.507**	0.002	0.000	-0.371	-0.046	0.121	0.123	0.012	**0.800**	.	n.s.	n.s.	*	n.s.	***	***
27 Mn	-0.020	-0.362	-0.324	-0.054	**0.529**	**0.452**	0.033	-0.412	-0.104	0.249	-0.048	0.003	0.074	0.440	**0.490**	-0.395	**-0.632**	0.439	**0.653**	**0.700**	**0.614**	-0.312	0.039	-0.382	-0.057	0.023	.	***	***	n.s.	***	n.s.
28 Zn	-0.234	-0.170	-0.161	-0.169	0.265	0.247	-0.081	-0.308	-0.029	-0.033	0.043	-0.090	0.076	0.256	0.301	-0.266	-0.244	-0.190	0.224	**0.465**	**0.614**	0.170	-0.052	-0.254	-0.168	0.149	**0.636**	.	n.s.	n.s.	n.s.	n.s.
29 N	0.149	-0.425	-0.255	0.022	0.205	0.183	0.068	-0.368	-0.117	-0.068	-0.100	0.139	0.154	0.017	0.010	0.215	**-0.649**	0.431	0.410	0.153	0.218	-0.317	0.188	-0.099	0.256	0.272	0.369	0.098	.	n.s.	**	n.s.
30 P-Al	-0.138	0.347	0.120	-0.371	-0.318	-0.189	-0.137	0.278	-0.042	-0.010	0.050	-0.027	-0.008	-0.105	-0.019	0.030	-0.026	-0.273	-0.251	0.042	0.268	0.441	0.172	0.260	-0.162	0.003	0.039	0.245	-0.015	.	**	*
31 P	-0.126	0.401	**0.476**	-0.088	-0.369	-0.100	0.015	0.409	**0.450**	-0.020	0.031	-0.293	-0.316	0.116	0.071	-0.082	**0.817**	**-0.727**	-0.726	-0.038	-0.132	**0.468**	-0.146	0.359	**-0.673**	-0.445	-0.368	0.098	**-0.494**	0.312	.	n.s.
32 S	**-0.705**	-0.189	**-0.581**	-0.375	-0.040	-0.342	0.449	-0.184	-0.350	0.038	0.231	0.355	0.275	-0.291	-0.304	0.134	-0.112	-0.052	-0.151	**-0.475**	-0.319	0.375	0.355	0.168	0.409	0.397	-0.002	0.060	0.126	0.253	-0.170	.

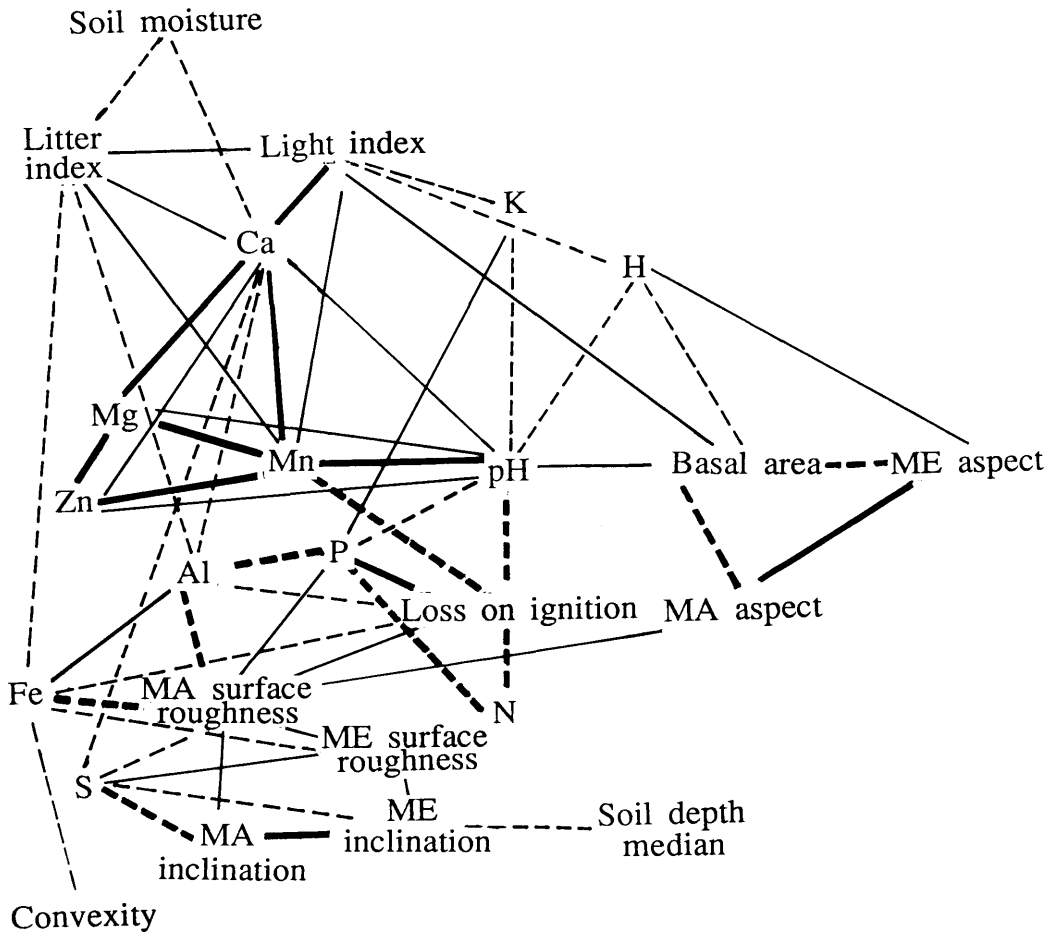


Fig. 6. Correlations between environmental variables (Tab. 2) displayed by means of a plexus diagram. Thick unbroken lines - positive correlations, $r > 0.6$; thick broken lines - negative correlations, $|r| > 0.6$; thin unbroken lines - positive correlations, $0.6 > r > 0.45$; thin broken lines - negative correlations, $0.6 > |r| > 0.45$. The displayed correlations were all significant at the highest level, $P < 0.01$.

Macro sample plot inclination was positively correlated with meso sample plot inclination, indicating that the within macro sample plot variation in inclination was small. Meso sample plot inclination was also negatively correlated with median meso sample plot soil depth, i.e. the greater the inclination, the more shallow the soil.

Soil moisture was positively correlated with Na and negatively correlated with Ca, Mg, Mn and the litter indexes. This means that the soil moisture increased when the amount of litter and the amounts of cations in the soil decreased. Soil moisture was not strongly correlated with any other variables.

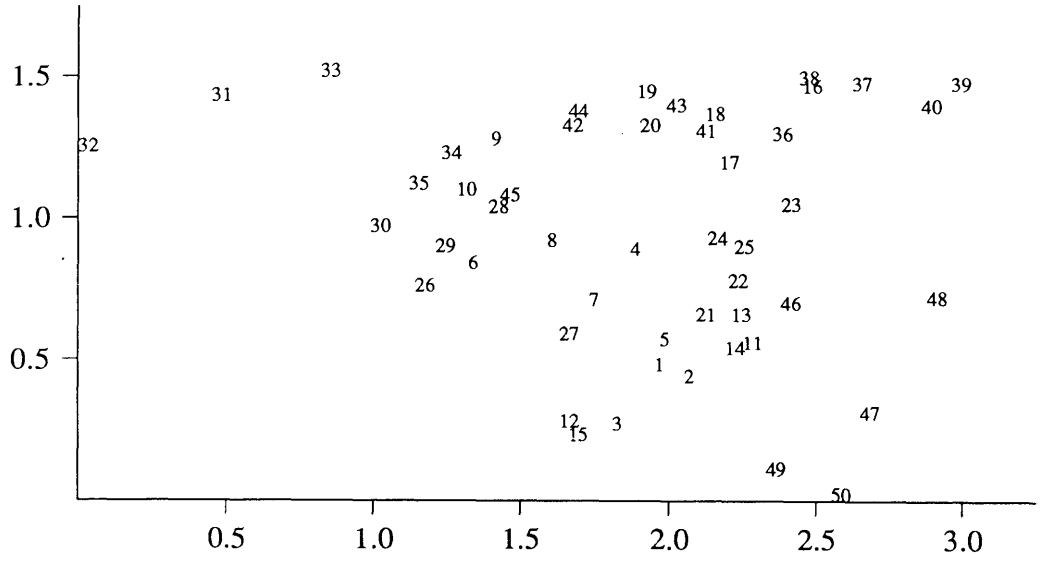


Fig. 7. DCA ordination of 50 meso sample plots, DCA 1 (horizontal) and DCA 2 (vertical). Scaling of axes in S.D. units. Sample plot numbers are indicated.

DCA ORDINATION OF MESO SAMPLE PLOTS

DCA ordination of all 50 meso sample plots is shown in Fig. 7. Meso sample plots 31, 32 and 33 were outliers and removed prior to further analysis.

The eigenvalues and gradient lengths of the first four DCA axes in the ordination of the 47 meso sample plots are shown in Tab. 3. DCA axes 3 and 4 were not further considered (low eigenvalues; low interpretability). The meso sample plot positions along DCA 1 and DCA 2 are shown in Fig. 8.

Fig. 9 shows the ordination diagram for 47 meso sample plots with the 94 micro sample plots as passive objects. Mean deviation of micro sample plots from the corresponding meso sample plot positions was 0.20 S.D. units along DCA 1, and 0.19 S.D. units along DCA 2. Mean distance from a meso sample plot to a corresponding micro sample plot was 0.30 S.D. units. The deviation between meso and micro sample plot positions indicated the existence of considerable variation within each meso sample plot.

CORRELATIONS BETWEEN ENVIRONMENTAL VARIABLES AND DCA AXES

Correlations between each of the 32 environmental variables and meso sample plot positions along DCA axes for the ordination of 47 meso sample plots are displayed in Tab. 4. Ordination diagrams with isolines for the variables most strongly correlated with the DCA

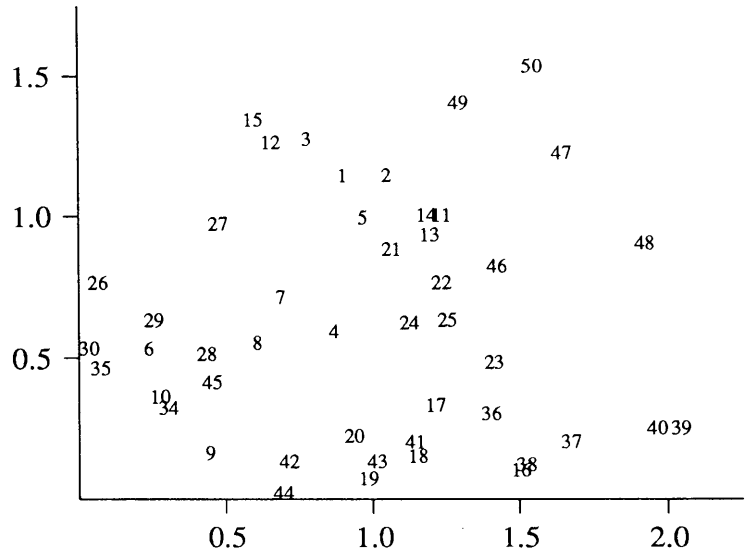


Fig. 8. DCA ordination of 47 meso sample plots, DCA 1 (horizontal) and DCA 2 (vertical). Scaling of axes in S.D. units. Sample plot numbers are indicated.

axes; i.e. the variables which were most important for differentiation of the vegetation are shown in Figs 10-22. Most strongly correlated with DCA 1 were macro sample plot crown cover index (Fig. 10), macro sample plot basal area (Fig. 11), pH_{CaCl2} (Fig. 12) and the cations Ca (Fig. 13), Mg (Fig. 14), Mn (Fig. 15) and Zn (Fig. 16); all of them except Zn had negative correlations with $|r| > 0.6$ and all of them were significant at the highest level. All of them were also negatively correlated with DCA 2 except Ca and Zn, which did not have significant correlations with other DCA axes. H^+ (Fig. 17) was positively correlated with DCA 1 (cf. pH). Thus the meso sample plots with high content of nutrients and low light influx (owing to greater tree density and crown cover) were placed at low S.D. values along DCA 1 and at relatively low S.D. values along DCA 2, i.e. in the lower left part of the ordination diagram. Accordingly, the meso sample plots at high S.D. values along both axes, i.e. the meso sample plots in the upper right part of the ordination

Tab. 3. Eigenvalues and gradient lengths for DCA axes in ordination of 47 meso sample plots.

	DCA 1	DCA 2	DCA 3	DCA 4
Eigenvalue	0.244	0.135	0.094	0.061
Gradient length (S.D. units)	2.008	1.515	1.673	1.442

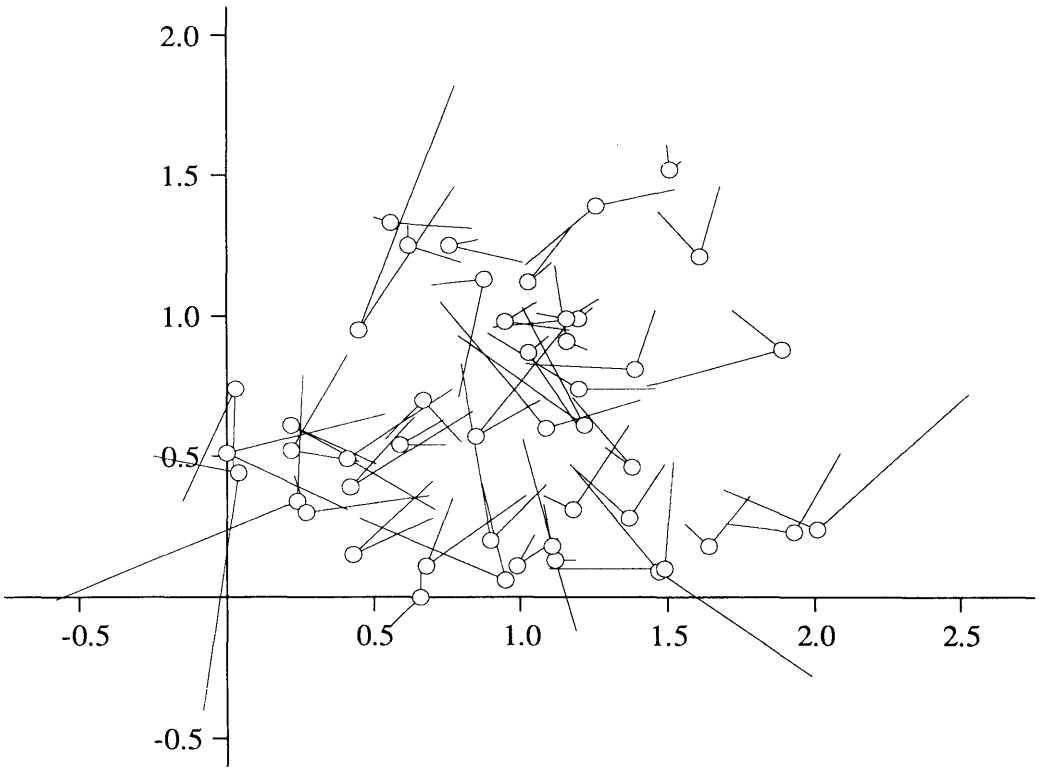


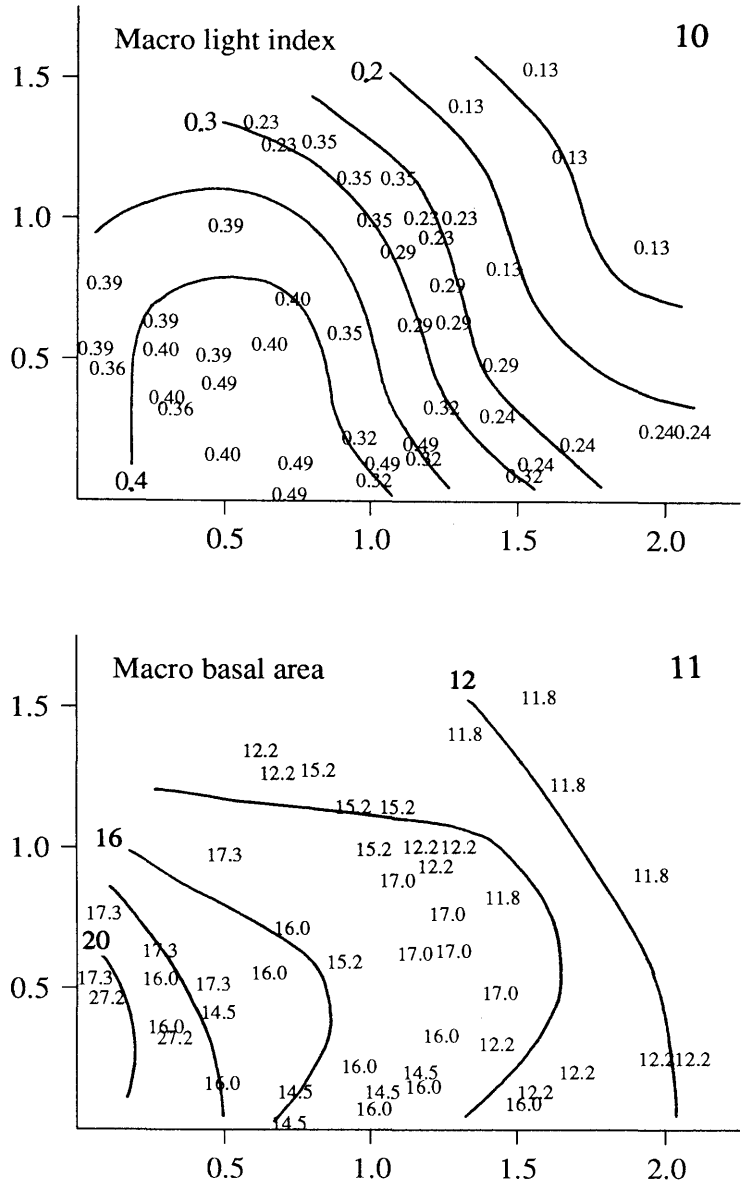
Fig. 9. DCA ordination of 47 meso sample plots (circles), DCA 1 (horizontal) and DCA 2 (vertical), with 94 micro sample plots as passive objects (ends of bars). Scaling of axes in S.D. units.

diagram, had a low content of nutrients and a high light influx. Meso sample plot aspect (Fig. 18), positively correlated with both axes, also had a relatively high correlation with DCA 1. Thus the meso sample plots in the lower left part of the ordination diagram, which were the sample plots with the highest content of nutrients, also had the most favourable aspects.

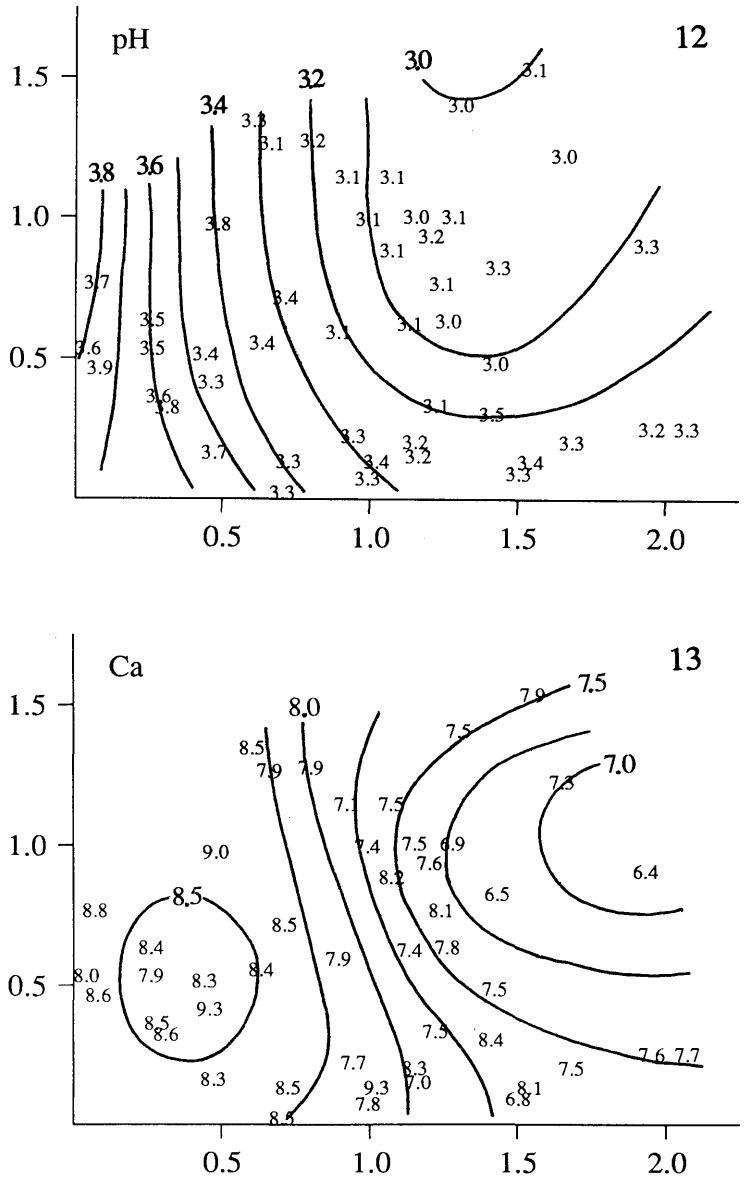
The litter indexes, exemplified by litter index based on actual crown density (Fig. 19), were both negatively correlated with DCA 1. Thus the amounts of litter were greatest for meso sample plots in the farthest left part of the ordination diagram, indicating a corresponding pattern of variation as nutrient and light conditions.

Total N (Fig. 20) had a strong negative correlation with DCA 2; i.e. the meso sample plots with low S.D. values along DCA 2 had the greatest content of N. K (Fig. 21) was strongly positively correlated with DCA 2.

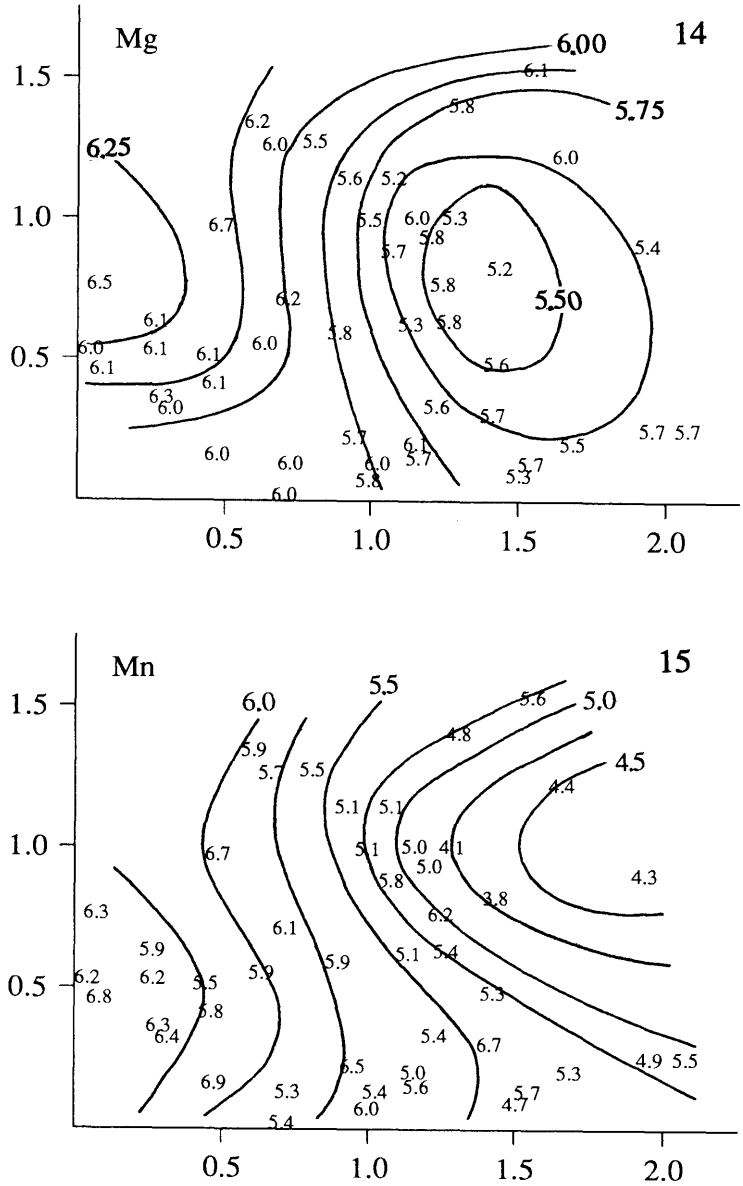
Soil moisture (Fig. 22) was the only variable which had a significantly strong positive correlation with DCA 1 and at the same time a negative correlation with DCA 2. Thus most of the moist sample plots were placed at high S.D. values along DCA 1 and low S.D. values along DCA 2; i.e. in the lower and far right part of the ordination diagram. The main direction of variation of the most important of the environmental variables in the



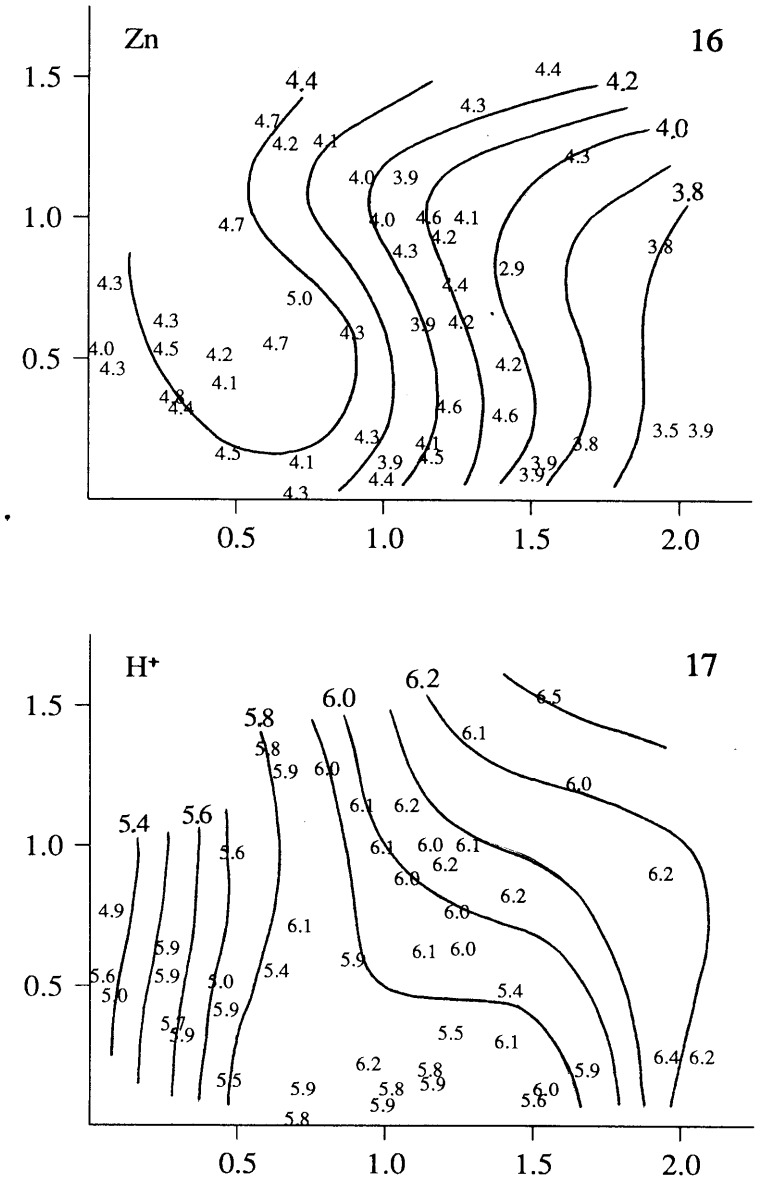
Figs 10-11. Isolines for environmental variables in the DCA ordination of 47 meso sample plots (Fig. 8.), DCA 1 (horizontal) and DCA 2 (vertical). Values for the environmental variables are plotted on to the meso sample plots' positions. Correlations between the original values and smoothened values as interpolated from the isolines, r, are shown. Scaling of axes in S.D. units. Fig. 10. Macro sample plot light index, r = 0.833. Fig. 11. Macro sample plot basal area, r = 0.721.



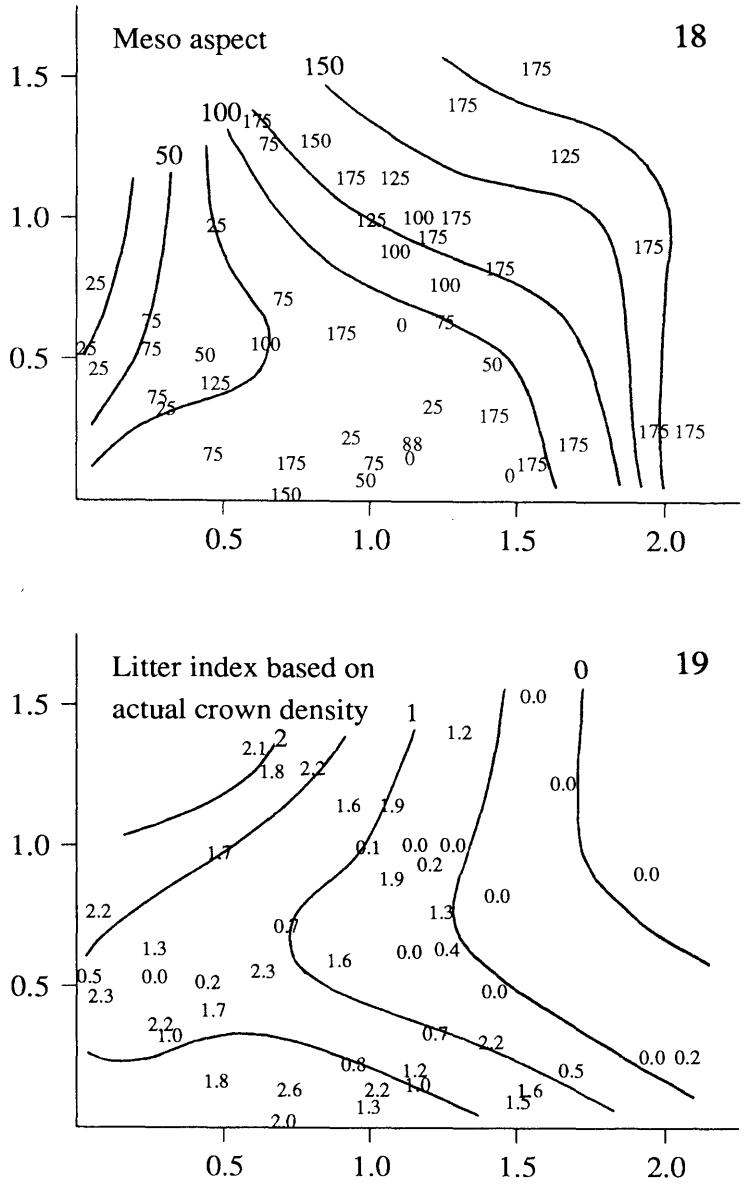
Figs 12-13. Isolines for environmental variables in the DCA ordination of 47 meso sample plots (Fig. 8), DCA 1 (horizontal) and DCA 2 (vertical). Values for the environmental variables are plotted on to the meso sample plots' positions. Correlations between the original values and smoothened values as interpolated from the isolines, r, are shown. Scaling of axes in S.D. units. Fig. 12. pH_{CaCl_2}, r = 0.833. Fig. 13. Ca as fraction of loss on ignition, ln-transformed values, r = 0.721.



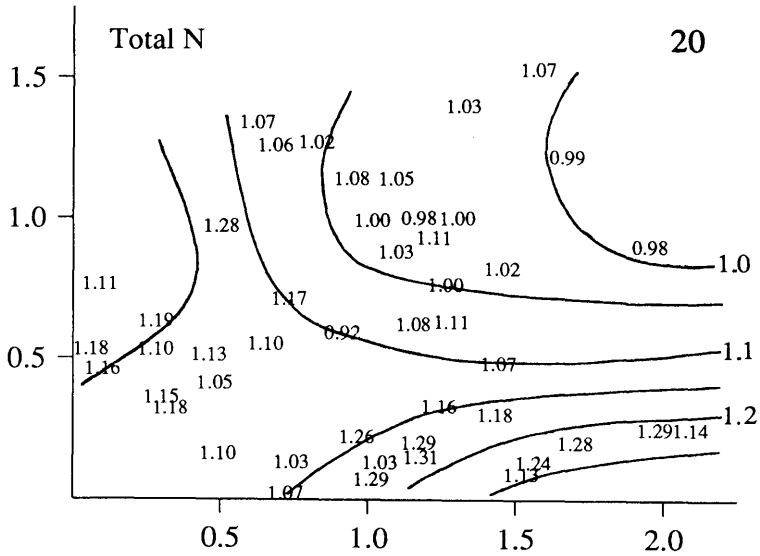
Figs 14-15. Isolines for environmental variables in the DCA ordination of 47 meso sample plots (Fig. 8), DCA 1 (horizontal) and DCA 2 (vertical). Values for the environmental variables are plotted on to the meso sample plots' positions. Correlations between the original values and smoothened values as interpolated from the isolines, r, are shown. Scaling of axes in S.D. units. Fig. 14. Mg as fraction of loss on ignition, ln-transformed values, r = 0.783. Fig. 15. Mn as fraction of loss on ignition, ln-transformed values, r = 0.753.

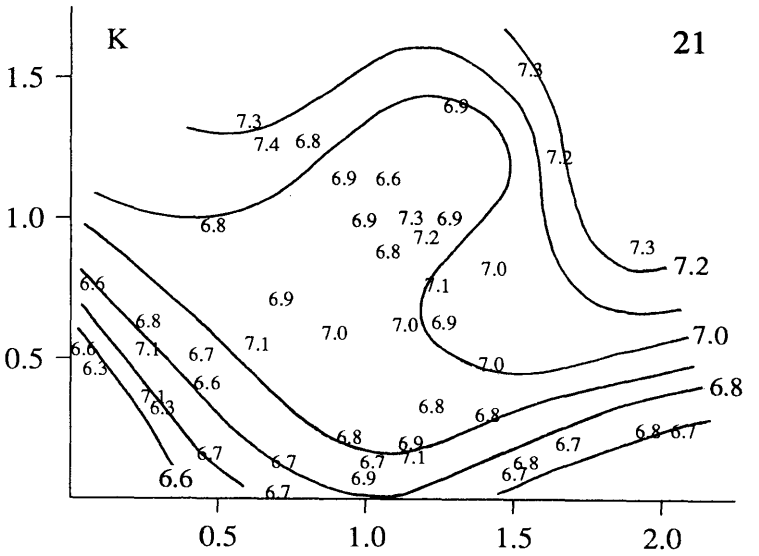


Figs 16-17. Isolines for environmental variables in the DCA ordination of 47 meso sample plots (Fig. 8), DCA 1 (horizontal) and DCA 2 (vertical). Values for the environmental variables are plotted on to the meso sample plots' positions. Correlations between the original values and smoothened values as interpolated from the isolines, r, are shown. Scaling of axes in S.D. units. Fig. 16. Zn as fraction of loss on ignition, ln-transformed values, r = 0.591. Fig. 17. H^+ as fraction of loss on ignition, ln-transformed values, r = 0.724.

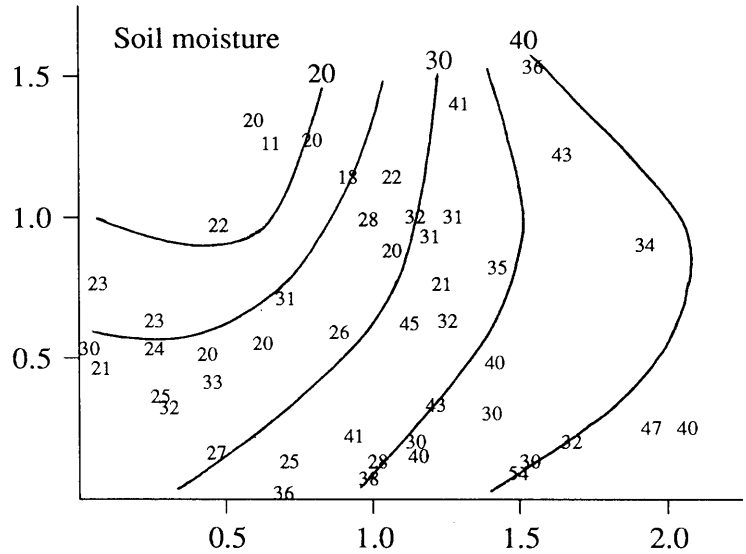


Figs 18-19. Isolines for environmental variables in the DCA ordination of 47 meso sample plots (Fig. 8), DCA 1 (horizontal) and DCA 2 (vertical). Values for the environmental variables are plotted on to the meso sample plots' positions. Correlations between the original values and smoothened values as interpolated from the isolines, r, are shown. Scaling of axes in S.D. units. Fig. 18. Meso sample plot light aspect, r = 0.666. Fig. 19. Litter index based on actual crown density, r = 0.681.





Figs 20-21. Isolines for environmental variables in the DCA ordination of 47 meso sample plots (Fig. 8), DCA 1 (horizontal) and DCA 2 (vertical). Values for the environmental variables are plotted on to the meso sample plots' positions. Correlations between the original values and smoothened values as interpolated from the isolines, r, are shown. Scaling of axes in S.D. units. Fig. 20. N in % of loss on ignition, ln-transformed values, r = 0.717. Fig. 21. K as fraction of loss on ignition, ln-transformed values, r = 0.729.



Figs 22. Isolines for soil moisture in the DCA ordination of 47 meso sample plots (Fig. 8), DCA 1 (horizontal) and DCA 2 (vertical). Values for the environmental variables are plotted on to the meso sample plots' positions. The correlation between the original values and smoothened values as interpolated from the isolines, r = 0.745. Scaling of axes in S.D. units.

DCA ordination of 47 meso sample plots is displayed in Fig. 23. The most important single gradients as well as the major complex-gradients are expressed by this figure; a diagonal complex gradient in nutrient conditions, light conditions and litter conditions ran from the lower left to the upper right in the ordination diagram, and a diagonal gradient in moisture conditions ran from the upper left to the lower right in the ordination diagram.

THE DISTRIBUTION OF SPECIES ABUNDANCE IN THE DCA ORDINATION

The distribution of species abundance in the DCA ordination of 47 meso sample plots is displayed in Figs 24-71 for the 48 species which occurred in at least 5 meso sample plots (i.e. 47 of total 88 species). Examples of different distributions of abundance in the ordination diagram are given below.

Vaccinium myrtillus (Fig. 28) had a high frequency in subplots in most of the meso sample plots; i.e. a typical example of a species with wide ecological amplitude. Other examples were *Deschampsia flexuosa* (Fig. 41), *Maianthemum bifolium* (Fig. 34), *Pleurozium schreberi* (Fig. 51), *Dicranum majus* (Fig. 45) and *Hylocomium splendens* (Fig. 47), i.e. common species in poor bilberry-dominated spruce forest.

Species with more narrow ecological amplitudes were restricted to parts of the ordination diagram. Examples of species restricted to the meso sample plots with high

Tab. 4. Correlations (Pearson's product-moment correlation coefficients, r) between environmental variables and DCA axes. *** - P < 0.01, ** - 0.01 < P < 0.05, * - P < 0.1, n.s. - P > 0.1 (two-sided tests).

No.	Name	DCA 1 r	p	DCA 2 r	p	DCA 3 r	p	DCA 4 r	p
01	Macro inclination	0.098	n.s.	-0.209	n.s.	0.358	n.s.	0.213	n.s.
02	Macro aspect	0.136	n.s.	0.399	***	0.137	**	0.233	n.s.
03	Macro surface roughness	0.017	n.s.	0.093	n.s.	0.285	*	0.107	n.s.
04	Macro soil depth	-0.211	n.s.	0.093	n.s.	0.440	***	0.107	n.s.
05	Macro basal area	-0.601	***	-0.260	*	-0.127	n.s.	0.331	**
06	Macro light index	-0.657	***	-0.505	***	0.272	*	0.291	**
07	Meso inclination	-0.174	n.s.	0.102	n.s.	0.168	n.s.	-0.082	n.s.
08	Meso aspect	0.467	***	0.314	**	0.058	n.s.	0.186	n.s.
09	Meso surface unevenness	-0.014	n.s.	0.103	n.s.	0.204	n.s.	-0.188	n.s.
10	Meso convexity	-0.208	n.s.	0.031	n.s.	0.127	n.s.	-0.188	n.s.
11	Meso soil depth minimum	-0.047	n.s.	-0.110	n.s.	-0.084	n.s.	-0.048	n.s.
12	Meso soil depth median	0.154	n.s.	-0.297	**	-0.060	n.s.	-0.133	n.s.
13	Meso soil depth maximum	0.032	n.s.	-0.198	n.s.	-0.189	n.s.	-0.071	n.s.
14	Litter index based on crown cover	-0.401	***	-0.133	n.s.	0.179	n.s.	0.125	n.s.
15	Litter index based on actual crown density	-0.467	***	-0.160	n.s.	0.190	n.s.	0.124	n.s.
16	Soil moisture	0.580	***	-0.329	**	-0.339	**	-0.041	n.s.
17	Loss on ignition	0.361	**	0.399	***	0.199	n.s.	0.231	n.s.
18	pH_{water}	-0.345	**	-0.352	***	-0.136	n.s.	-0.273	*
19	pH_{CaCl2}	-0.618	***	-0.370	**	-0.070	n.s.	-0.193	n.s.
20	Ca	-0.624	***	-0.226	n.s.	0.212	n.s.	0.216	n.s.
21	Mg	-0.615	***	-0.008	n.s.	0.087	n.s.	0.192	n.s.
22	K	0.344	**	0.506	***	-0.062	n.s.	0.190	n.s.
23	Na	0.345	**	-0.098	n.s.	-0.482	***	-0.152	n.s.
24	H^+	0.587	***	0.262	*	-0.075	n.s.	0.022	n.s.
25	Al	0.123	n.s.	-0.015	n.s.	-0.406	***	-0.306	**
26	Fe	0.042	n.s.	0.050	n.s.	-0.237	n.s.	-0.154	n.s.
27	Mn	-0.624	***	-0.267	*	-0.086	n.s.	-0.154	n.s.
28	Zn	-0.454	***	0.062	n.s.	-0.217	n.s.	0.094	n.s.
29	Total N	-0.044	n.s.	-0.529	***	-0.148	n.s.	-0.298	*
30	P-Al	0.087	n.s.	0.185	n.s.	-0.123	n.s.	0.058	n.s.
31	P	0.294	*	0.374	***	0.200	n.s.	0.274	*
32	S	0.206	n.s.	0.065	n.s.	0.367	**	-0.356	**

nutrient contents were *Carex digitata* (Fig. 40); a typical species for spruce forest dominated by low herbs, and *Convallaria majalis* (Fig. 31).

Species with the highest frequency in subplots in the meso plots with high nutrient content and in the moist meso sample plots with moderately high nutrient content were, among others, *Anemone nemorosa* (Fig. 30), *Oxalis acetosella* (Fig. 37, *Dryopteris expansa*

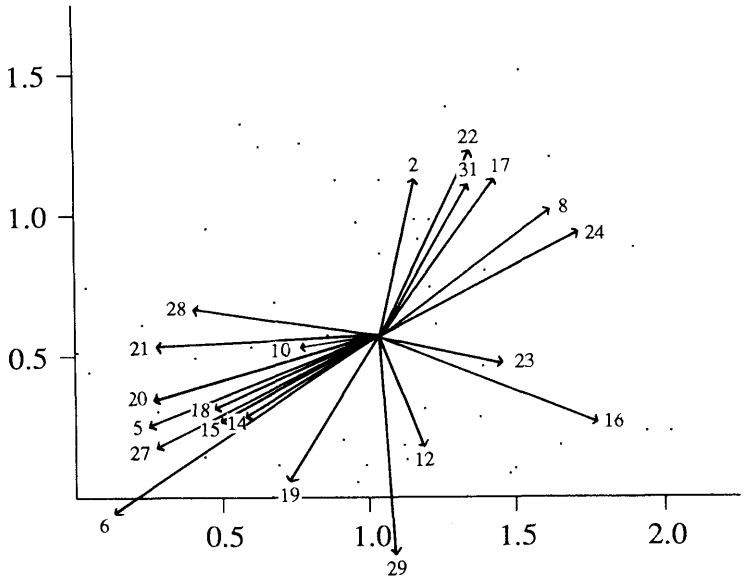


Fig. 23. Main directions of variation of some important environmental variables drawn on to the DCA ordination of 47 meso sample plots, DCA 1 (horizontal) and DCA 2 (vertical). Numbers of the variables refer to Tab. 1. Scaling of axes in S.D. units.

agg. (Fig. 32) and *Calamagrostis arundinacea* (Fig. 39), i.e. typical species of the so-called small fern spruce forest.

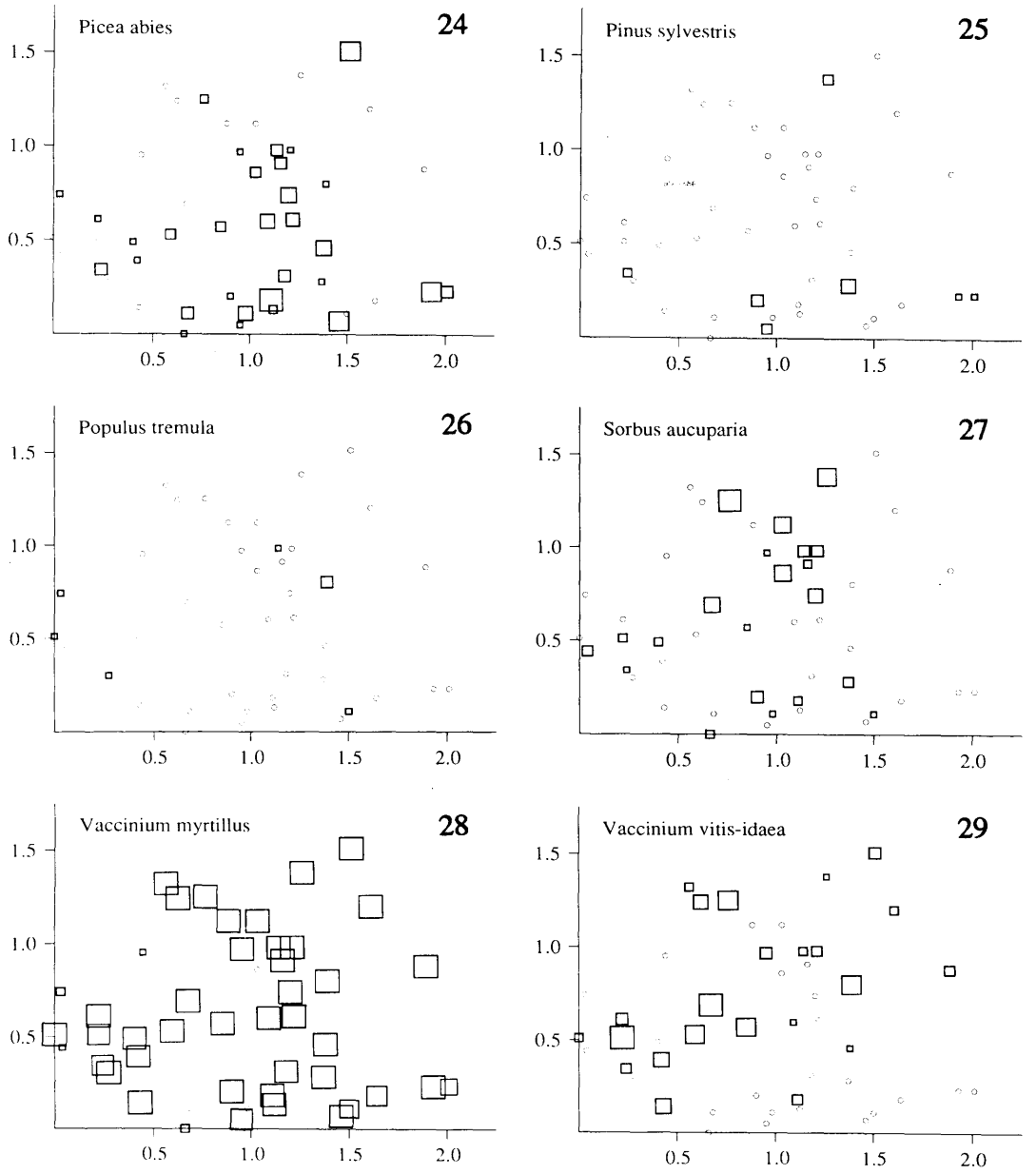
Examples of species with the highest frequency in subplots in moist meso sample plots with low to moderately high content of nutrients were *Hylocomium umbratum* (Fig. 48), *Sphagnum girgensohnii* (Fig. 56), *Sphagnum quinquefarium* (Fig. 57) and *Rhytidiadelphus subpinnatus* (Fig. 54).

An example of a species with highest frequency in subplots in the most dry meso sample plots was *Dicranum fuscescens* (Fig. 44).

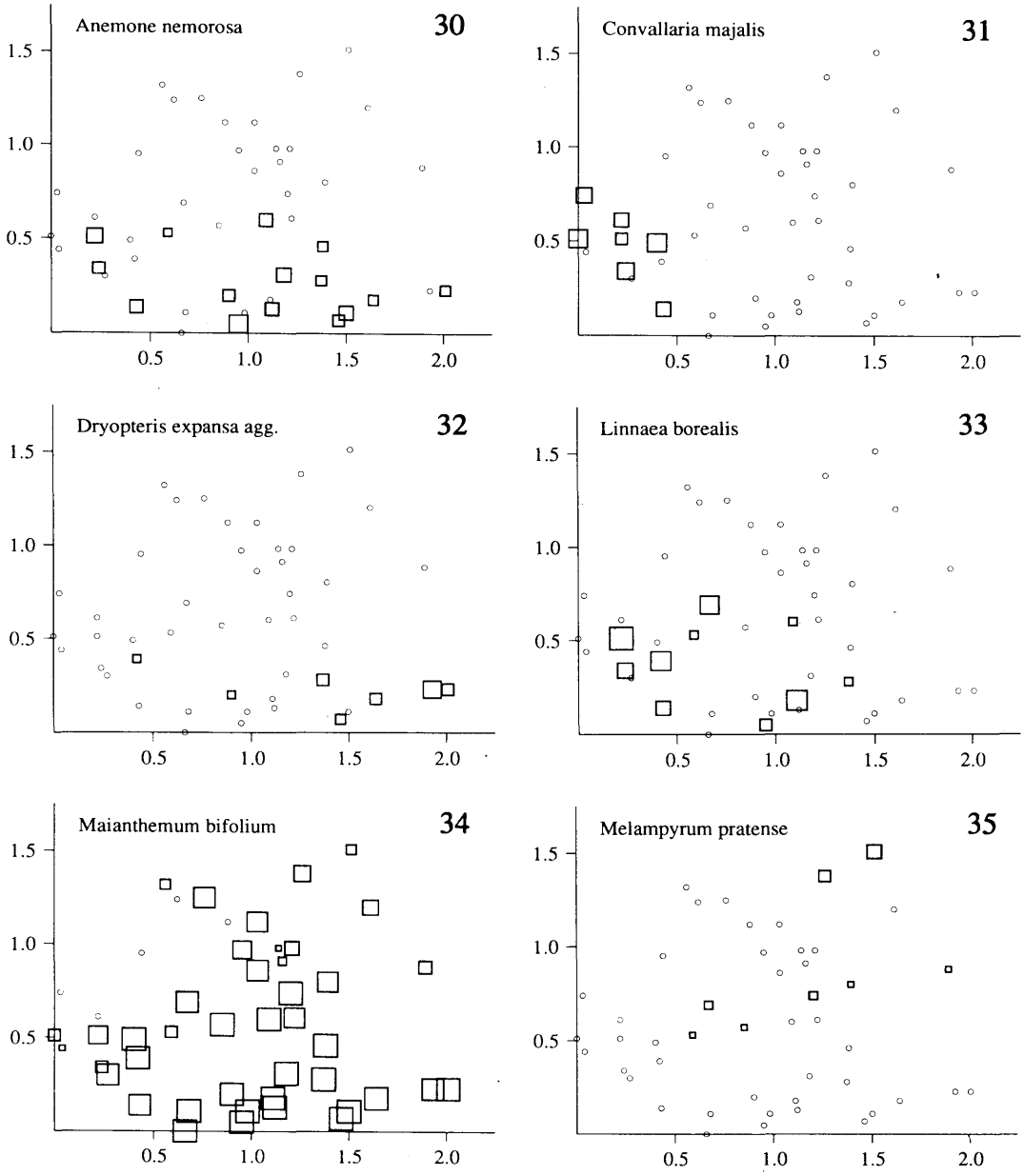
Some species had scattered occurences in different parts of the ordination diagram, apparently not related to the DCA axes in a simple way. Most likely, the occurrences were dependent on the realization of their special niches, combined with their competitive ability at that place. Examples of such species were hepatics and other small bryophytes ("pocket species"), like *Cephalozia bicuspidata* (Fig. 64), *Cephalozia lunulifolia* (Fig. 65), *Lepidozia reptans* (Fig. 66) and *Tetraphis pellucida* (Fig. 55).

MACRO SAMPLE PLOT SITE QUALITY

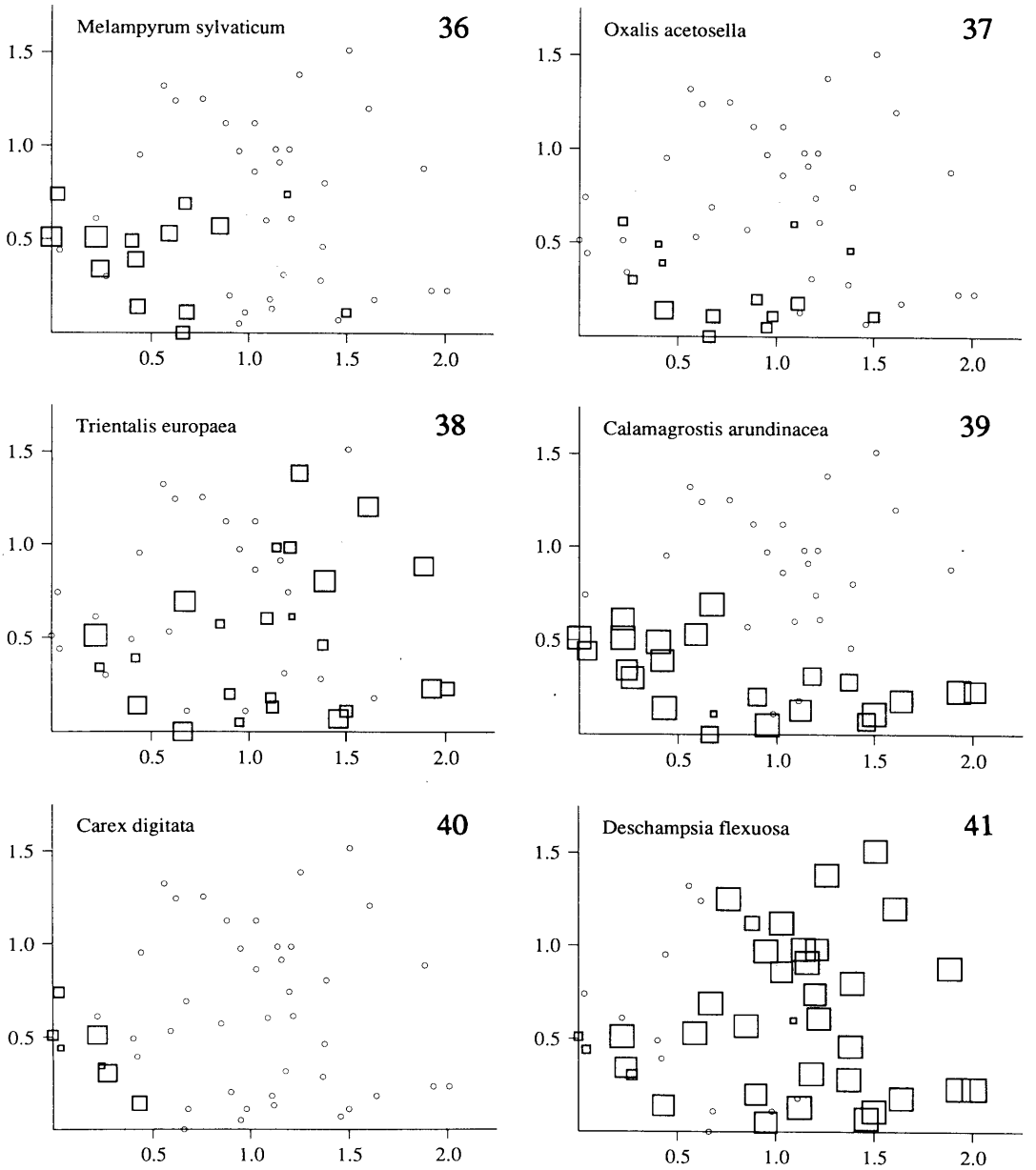
Site quality, H_{40}, had relatively small variation between macro sample plots. In Fig. 72 site quality is plotted on to the meso sample plot positions in the ordination diagram of 47 meso sample plots. Meso sample plots from the same macro sample plot were given the



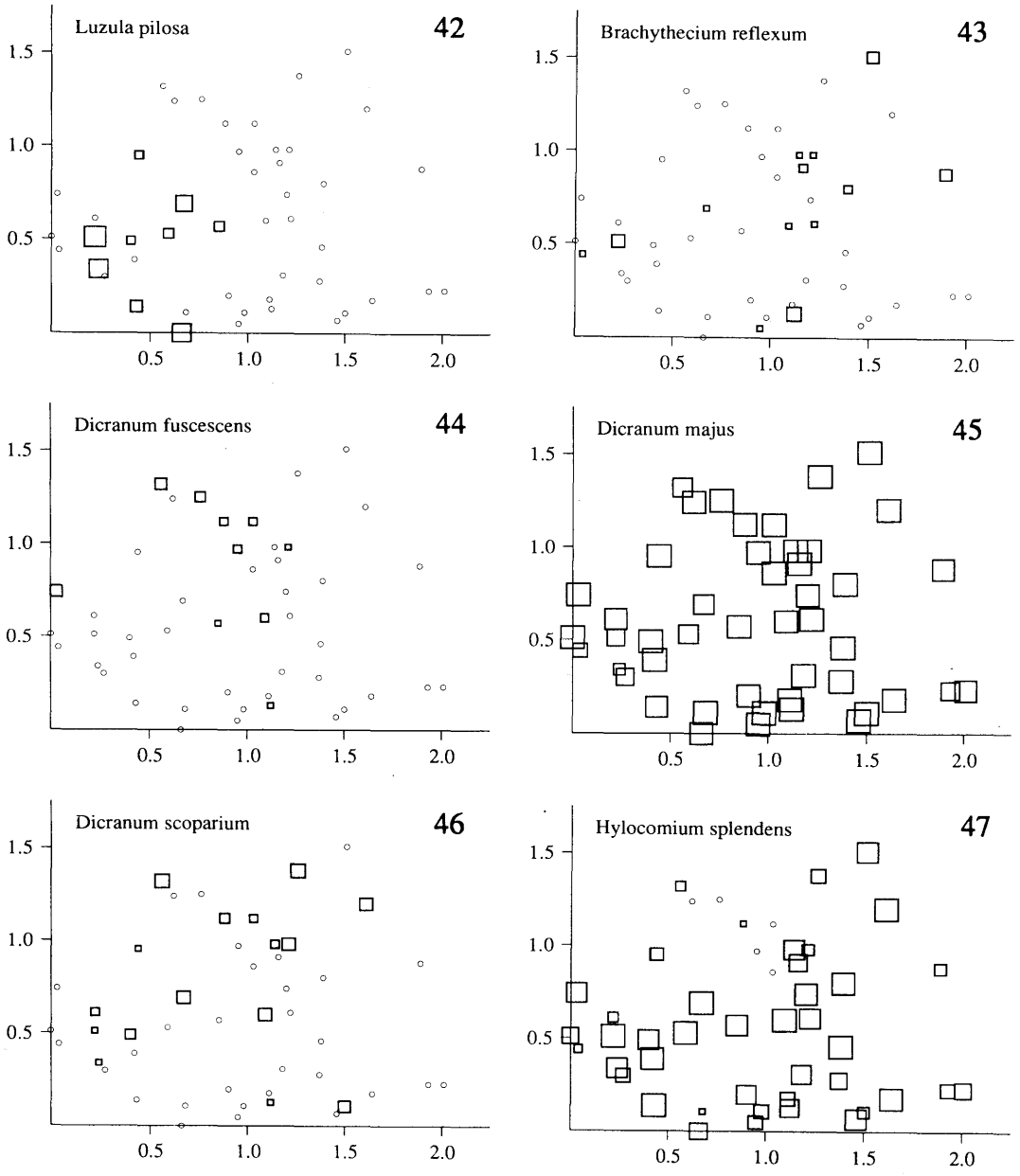
Figs 24-29. Distributions of species abundances. Frequency in subplots for each species in each meso sample plot indicated by squares are plotted on to the meso sample plots' positions in the DCA ordination of 47 meso sample plots, DCA 1 (horizontal) and DCA 2 (vertical). Scaling of axes in S.D. units. Size of squares is proportional to frequency in subplots. ◦ - species absent, ▫ - frequency in subplots = 1 (minimum), □ - frequency in subplots = 16 (maximum). Fig. 24. *Picea abies*. Fig. 25. *Pinus sylvestris*. Fig. 26. *Populus tremula*. Fig. 27. *Sorbus aucuparia*. Fig. 28. *Vaccinium myrtillus*. Fig. 29. *Vaccinium vitis-idaea*.



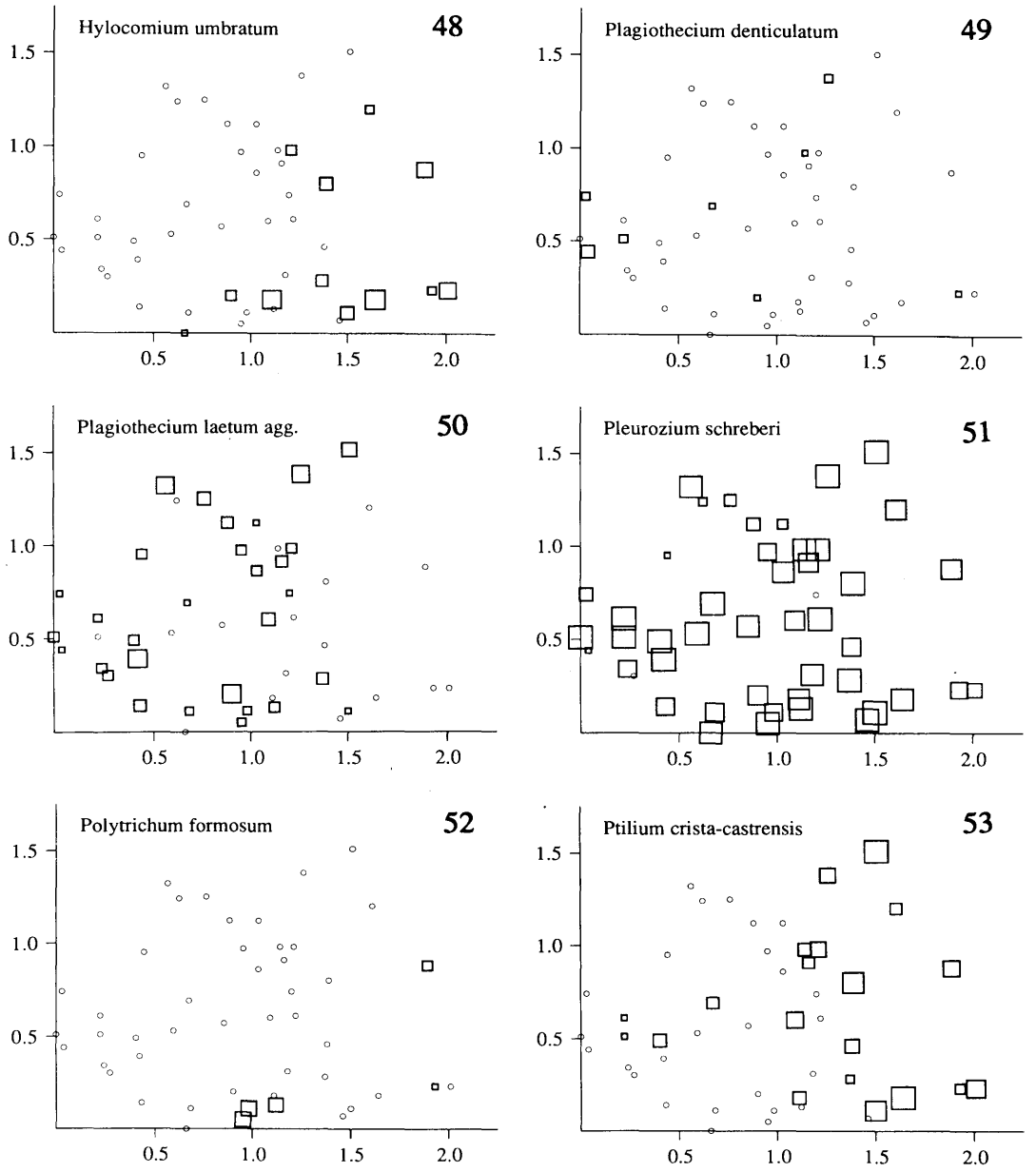
Figs 30-35. Distributions of species abundances. Frequency in subplots for each species in each meso sample plot indicated by squares are plotted on to the meso sample plot positions in the DCA ordination of 47 meso sample plots, DCA 1 (horizontal) and DCA 2 (vertical). Scaling of axes in S.D. units. Size of squares is proportional to frequency in subplots. ∘ - species absent, ▫ - frequency in subplots = 1 (minimum), □ - frequency in subplots = 16 (maximum). Fig. 30. *Anemone nemorosa*. Fig. 31. *Convallaria majalis*. Fig. 32. *Dryopteris expansa* agg. Fig. 33. *Linnaea borealis*. Fig. 34. *Maianthemum bifolium*. Fig. 35. *Melampyrum pratense*.



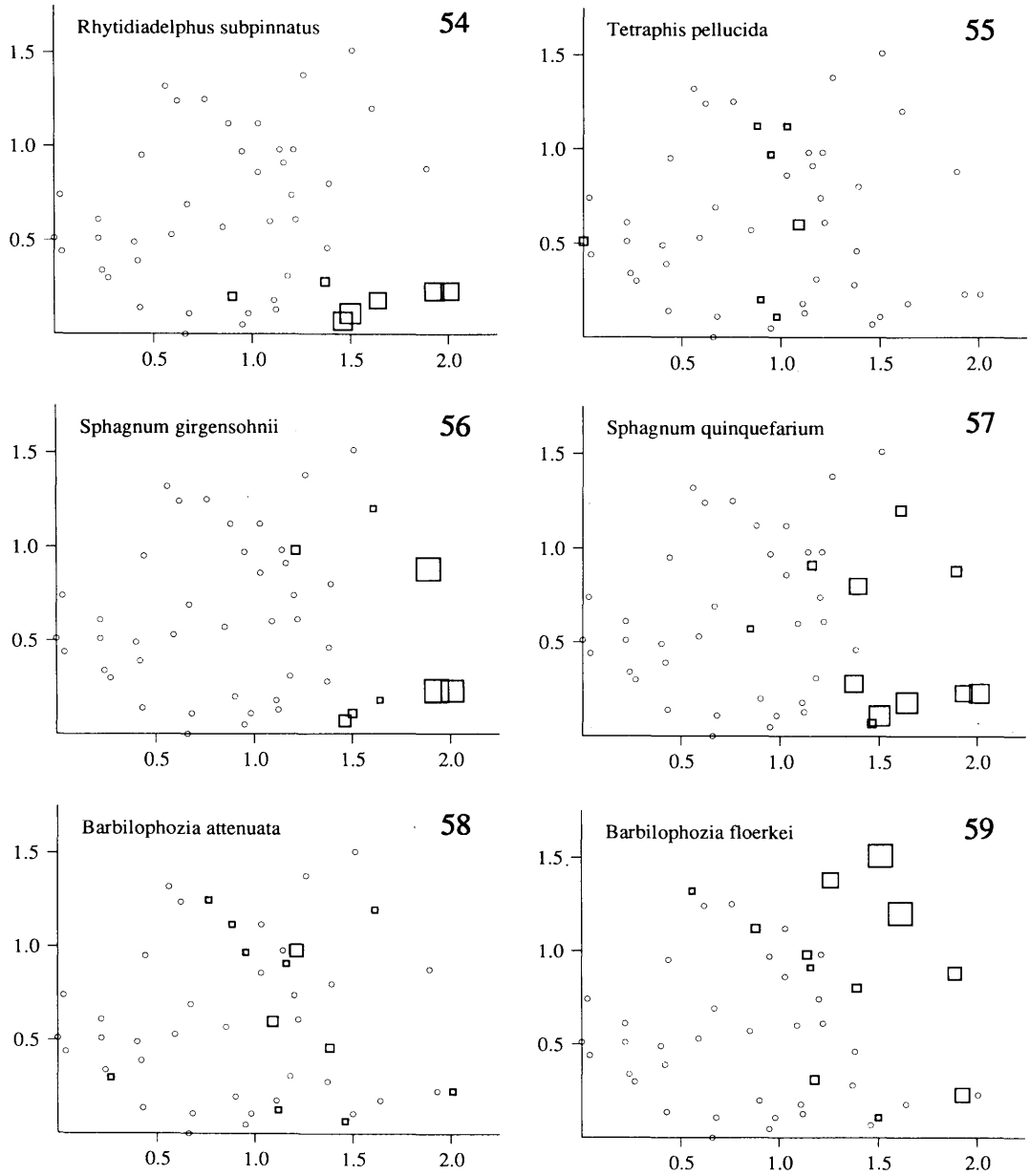
Figs 36-41. Distributions of species abundances. Frequency in subplots for each species in each meso sample plot indicated by squares are plotted on to the meso sample plot positions in the DCA ordination of 47 meso sample plots, DCA 1 (horizontal) and DCA 2 (vertical). Scaling of axes in S.D. units. Size of squares is proportional to frequency in subplots. ◦ - species absent, ▫ - frequency in subplots = 1 (minimum), □ - frequency in subplots = 16 (maximum). Fig. 36. *Melampyrum sylvaticum*. Fig. 37. *Oxalis acetosella*. Fig. 38. *Trientalis europaea*. Fig. 39. *Calamagrostis arundinacea*. Fig. 40. *Carex digitata*. Fig. 41. *Deschampsia flexuosa*.



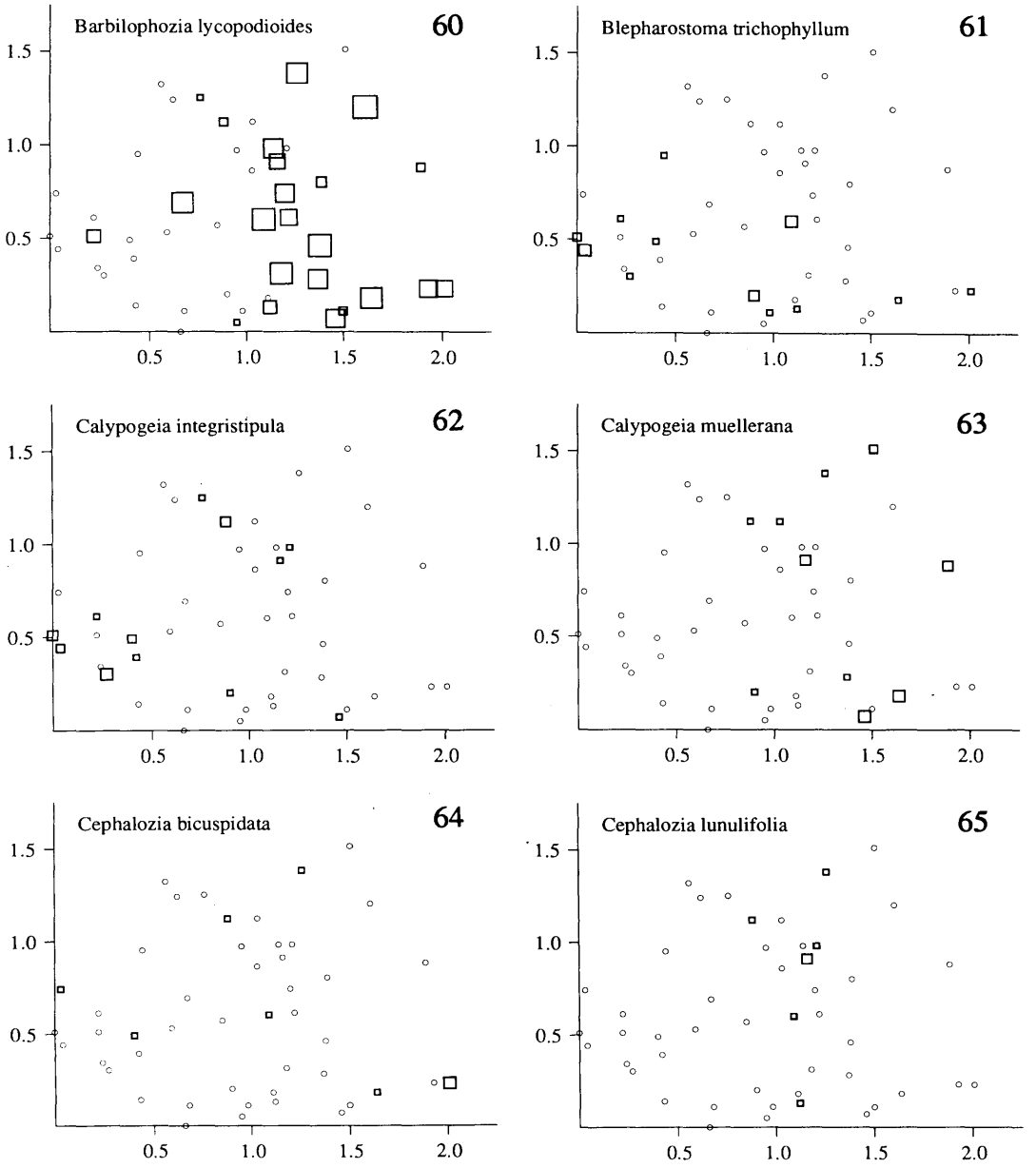
Figs 42-47. Distributions of species abundances. Frequency in subplots for each species in each meso sample plot indicated by squares are plotted on to the meso sample plot positions in the DCA ordination of 47 meso sample plots, DCA 1 (horizontal) and DCA 2 (vertical). Scaling of axes in S.D. units. Size of squares is proportional to frequency in subplots. ◦ - species absent, ▫ - frequency in subplots = 1 (minimum), □ - frequency in subplots = 16 (maximum). Fig. 42. *Luzula pilosa*. Fig. 43. *Brachythecium reflexum*. Fig. 44. *Dicranum fuscescens*. Fig. 45. *Dicranum majus*. Fig. 46. *Dicranum scoparium*. Fig. 47. *Hylocomium splendens*.



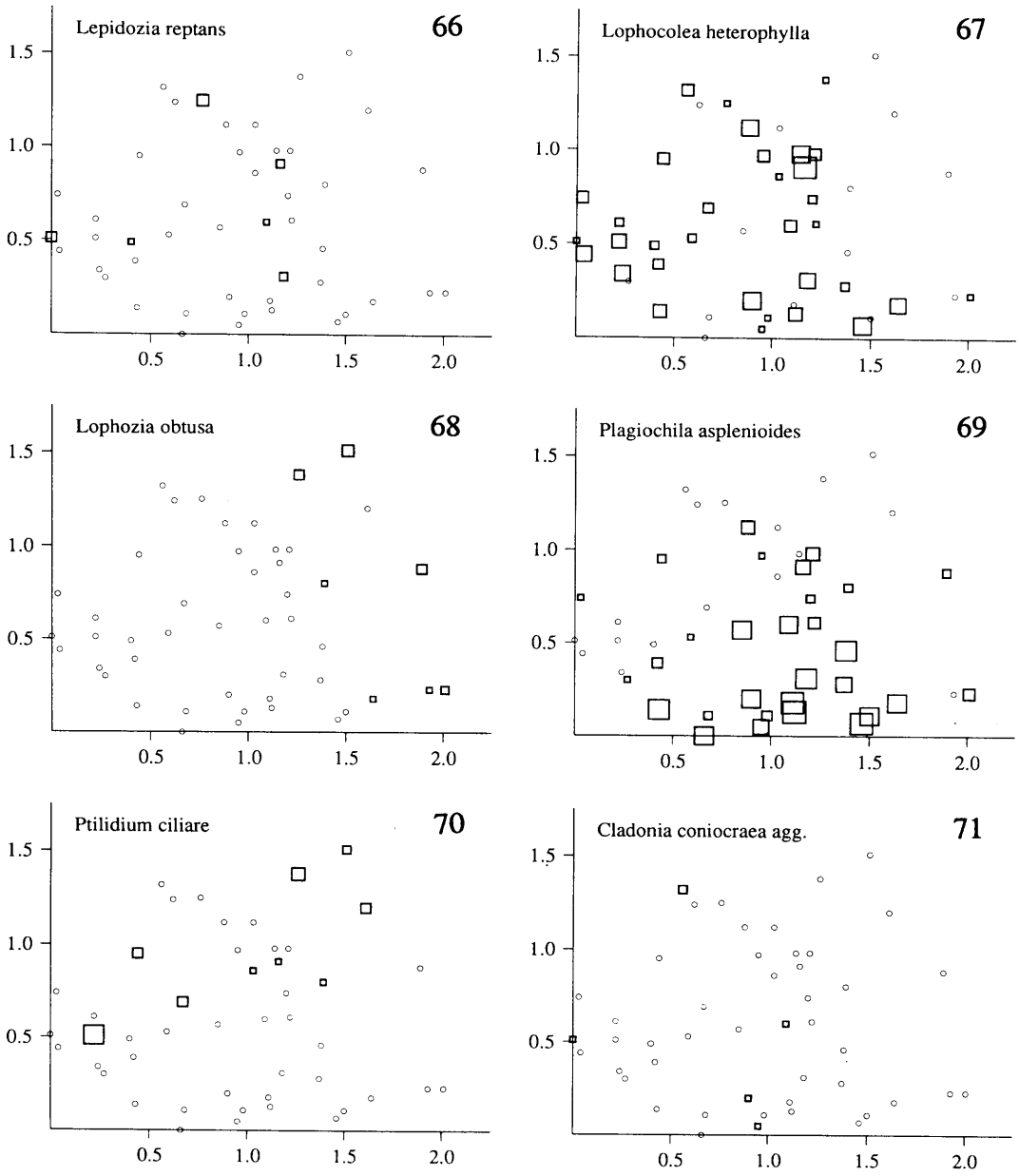
Figs 48-53. Distributions of species abundances. Frequency in subplots for each species in each meso sample plot indicated by squares are plotted on to the meso sample plot positions in the DCA ordination of 47 meso sample plots, DCA 1 (horizontal) and DCA 2 (vertical). Scaling of axes in S.D. units. Size of squares is proportional to frequency in subplots. ◦ - species absent, ▫ - frequency in subplots = 1 (minimum), □ - frequency in subplots = 16 (maximum). Fig. 48. *Hylocomium umbratum*. Fig. 49. *Plagiothecium denticulatum*. Fig. 50. *Plagiothecium laetum* agg. Fig. 51. *Pleurozium schreberi*. Fig. 52. *Polytrichum formosum*. Fig. 53. *Ptilium crista-castrensis*.



Figs 54-59. Distributions of species abundances. Frequency in subplots for each species in each meso sample plot indicated by squares are plotted on to the meso sample plot positions in the DCA ordination of 47 meso sample plots, DCA 1 (horizontal) and DCA 2 (vertical). Scaling of axes in S.D. units. Size of squares is proportional to frequency in subplots. ◦ - species absent, ▫ - frequency in subplots = 1 (minimum), □ - frequency in subplots = 16 (maximum). Fig. 54. *Rhytidiadelphus subpinnatus*. Fig. 55. *Tetraphis pellucida*. Fig. 56. *Sphagnum girgensohnii*. Fig. 57. *Sphagnum quinquefarium*. Fig. 58. *Barbilophozia attenuata*. Fig. 59. *Barbilophozia floerkei*.



Figs 60-65. Distributions of species abundances. Frequency in subplots for each species in each meso sample plot indicated by squares are plotted on to the meso sample plot positions in the DCA ordination of 47 meso sample plots, DCA 1 (horizontal) and DCA 2 (vertical). Scaling of axes in S.D. units. Size of squares is proportional to frequency in subplots. ○ - species absent, ▫ - frequency in subplots = 1 (minimum), □ - frequency in subplots = 16 (maximum). Fig. 60. *Barbilophozia lycopodioides*. Fig. 61. *Blepharostoma trichophyllum*. Fig. 62. *Calypogeia integristipula*. Fig. 63. *Calypogeia muellerana*. Fig. 64. *Cephalozia bicuspidata*. Fig. 65. *Cephalozia lunulifolia*.



Figs 66-71. Distributions of species abundances. Frequency in subplots for each species in each meso sample plot indicated by squares are plotted on to the meso sample plot positions in the DCA ordination of 47 meso sample plots, DCA 1 (horizontal) and DCA 2 (vertical). Scaling of axes in S.D. units. Size of squares is proportional to frequency in subplots. ◦ - species absent, ▫ - frequency in subplots = 1 (minimum), □ - frequency in subplots = 16 (maximum). Fig. 66. *Lepidozia reptans*. Fig. 67. *Lophocolea heterophylla*. Fig. 68. *Lophozia obtusa*. Fig. 69. *Plagiochila asplenioides*. Fig. 70. *Ptilidium ciliare*. Fig. 71. *Cladonia coniocraea* agg.

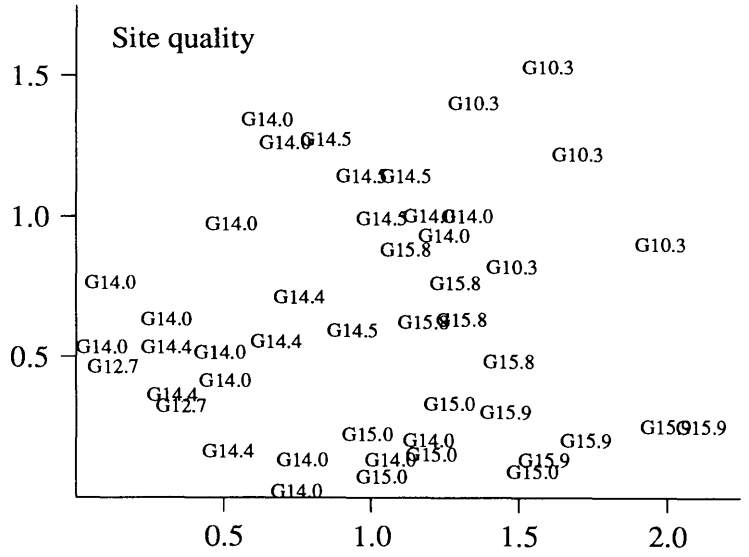


Fig. 72. Site quality for macro sample plots plotted on to the DCA ordination of 47 meso sample plots (Fig. 8), DCA 1 (horizontal) and DCA 2 (vertical). Scaling of axes in S.D. units.

same value for site quality. Meso sample plots positioned in the upper right part of the ordination diagram (macro sample plot 10; meso sample plots 45-50), i.e. the meso sample plots with lowest nutrient content, had the lowest site quality, G10.3. Meso sample plots in the lower right part of the ordination diagram (macro sample plot 8; meso sample plots 36-40), i.e. meso sample plots with highest soil moisture, had the highest site quality, which was G15.9. No clear relationship between site quality and tree density (basal area) emerged, as the meso sample plots in the macro sample plots with greatest tree density (in the lower left part of the diagram) had intermediate site quality; G14.

DISCUSSION

ENVIRONMENTAL GRADIENTS

The nutrient gradient

Relations between vegetation and environmental variables should be interpreted with reference to the fact that environmental variables vary together, forming complex-gradients (Whittaker 1967, R. Økland & Bendiksen 1985). The vegetation may thus be related to a few main complex-gradients.

The nutrient gradient has very often been considered one of the most important complex-gradients in forest ecosystems (see, for instance Arnborg 1964, Dahl et al. 1967, Fremstad 1979, Carleton & Maycock 1980, Bergeron & Bouchard 1983, R. Økland & Bendiksen 1985, T. Økland 1988, Rydgren 1989, Tong 1989). Very often the nutrient gradient is correlated with other important gradients, for instance a gradient in moisture conditions (cf. Fremstad 1979, Carleton & Maycock 1980, T. Økland 1988, Rydgren 1989). In the present paper the nutrient gradient is correlated, among others, with gradients in light and litter conditions. Vegetation with species like *Carex digitata* and *Convallaria majalis* is restricted to sites with favourable aspect, high pH and high content of cations like Ca, Mg, Mn and Zn, promoting high tree production and thus high tree density, low light to the field layer and relatively great litter fall. To the contrary, vegetation with common and abundant species with wide ecological amplitudes, like *Deschampsia flexuosa*, *Maianthemum bifolium*, *Vaccinium myrtillus*, *Dicranum majus*, *Pleurozium schreberi* and *Hylocomium splendens*, occur on soils poor in nutrients, with lower production and more favourable light and litter conditions. Species on soils poor in nutrients are also common on soils rich in nutrients, and no species is restricted to habitats poor in nutrients.

Litter fall is partly correlated with the nutrient gradient, but additional variation exists on a finer scale, as the supply of litter necessarily is greater below trees than between trees. The result of this is most often a much lower number of species below trees than between trees. The effect of trees on ground vegetation in boreal forests has usually not been emphasized; an exception is Lahti & Väisänen (1987) who stress the influence of tree crowns. Indirectly, through the control of light and litter conditions, the tree crown is an important environmental factor to the vegetation.

Loss on ignition is negatively correlated with the nutrient gradient in the present paper. Thus in soils rich in nutrients the content of organic matter in the humus layer is less than in soils poor in nutrients (cf. Dahl et al. 1967, Fremstad 1979, T. Økland 1988). This may be explained by more rapid litter decomposition due to more favourable aspect, and in turn more favourable conditions for bacteria and earthworms (cf. Lindgren 1975, Fremstad 1979, T. Økland 1988). According to Staaf (1980), the cations Ca and Mg are dependent on organic matter as carrier substance, and thus the rate of decomposition is crucial for the availability of these important components of the nutrient gradient. Thus litter fall from trees is an important source of soil nutrients (Buldgen et al. 1983, T. Økland 1988).

Dahl et al. (1967) noted a significant correlation between total nitrogen content, expressed as percentage of loss on ignition, and base saturation. Dahl et al. (1967) emphasize the distinction between primary or original environmental factors, i.e. factors not dependent on processes in the forest ecosystem, and secondary environmental factors. The

content of nitrogen in the soil is considered as a secondary environmental factor dependent on a primary environmental factor. Bivalent cations, especially Ca, which do not directly restrict the growth of plants, are the most important contributor to base saturation and, according to Dahl et al. (1967), the primary environmental factor which through its contribution to the base saturation influences the nitrogen turnover in the soil. According to Dahl et al. (1967) the high productivity in eutrophic and calcium-rich forests may be partly due to this effect. In the present paper the content of nitrogen in soil is partly correlated with the nutrient gradient through correlations with pH and Mn, but no significant correlations between nitrogen and Ca exist (cf. T. Økland 1988).

The distinction between primary and secondary environmental factors is not always sharp (Dahl et al. 1967). Since Ca is dependent on organic matter as carrier substance, Ca may be considered as a secondary environmental factor as well. In the present paper the nitrogen content (given as percentage of loss on ignition) is negatively correlated with loss on ignition. This correlation may be due to the fact that nitrogen is rapidly released when the turnover of organic mattter is high and thus the loss on ignition is small.

The gradient in soil moisture

According to Lahti & Väisänen (1987) the soil moisture gradient was one of the main gradients in an investigation of south boreal coniferous forests in southern Finland. A corresponding soil moisture gradient was found by Rydgren (1989) in the investigation of herb-rich spruce forests in Nordland, N Norway. R. Økland & Bendiksen (1985) describe a soil moisture gradient in vegetation, without confirming this by means of measurements of soil moisture, in the investigation of boreal coniferous forests in Grunningsdalen, Telemark, SE Norway. R. Økland & Bendiksen (1985) give a survey of investigations classifying or typifying boreal coniferous forests according to moisture and nutrient conditions. An example of such an investigation is Arnborg (1964) who classifies vegetation and soils according to nutrient and moisture conditions in "The North Swedish forest site type classification". As mentioned above, the soil moisture gradient has often been considered to be correlated with the nutrient gradient in earlier investigations of forest vegetation. In the present paper the variation due to soil moisture is related to the nutrient gradient only to a small extent, as the gradient in soil moisture appears as an approximately diagonal gradient in the ordination, almost perpendicular to the complex main gradient; from dry, medium-rich soil with a relatively low number of species, to moist and relatively nutrient-poor to somewhat more rich soils, with species like *Anemone nemorosa*, *Calamagrostis arundinacea*, *Dryopteris expansa* agg, *Oxalis acetosella*, *Rhytidiadelphus subpinnatus*, *Sphagnum quinquefarium* and *S. girgensohnii*. *Anemone nemorosa*, *Calamagrostis arundinacea*, *Dryopteris expansa* agg. and *Oxalis acetosella* are not resticted to the meso sample plots with the highest soil moisture content, but also occur in the rich but moderately dry meso sample plots (spruce forest dominated by low herbs).

Anemone nemorosa, *Dryopteris expansa* agg. and *Oxalis acetosella* are customarily considered as typical species of so-called "small-fern spruce forest". In the present investigation these species occur when either the soil is sufficiently rich in nutrients, or the soil is sufficiently moist. Thus one might ask whether the "small-fern spruce forest" vegetation type has any ecologically meaningful foundation.

The gradient in soil moisture may be partly explained by topography on a scale between the microtopographical and the macrotopographical, i.e. by means of a topographical scale not considered in this investigation. *Sphagnum* spp. respond to this topographical scale by occurring in small depressions often considered seasonally

hygrophilous. Although samples for measuring soil moisture were not collected during a period rich in precipitation, the meso sample plots with *Sphagnum* spp. are still considerably more moist than the others. According to this investigation, there is thus no reason to use the term seasonally hygrophilous about such depressions. Rather they appear on the whole to be more moist than the surrounding terrain.

The soil moisture gradient is also partly correlated with the gradient in litter conditions; the greater the litter fall, the less the moisture in the soil. This may partly be due to lower crown throughfall when the canopy is more dense (and thus the litter fall is greater), partly due to the failure of coniferous litter to retain moisture, and partly due to the fact that the extent of water uptake in tree roots per unit area increases with increasing tree density (Schaetzl et al. 1989).

Investigations of the different aspects of the soil moisture gradient in boreal forests are still urgently needed. This is also the case for investigations of different methods of measuring soil moisture (cf. Rydgren 1989).

EVALUATION OF METHODS FOR MONITORING VEGETATION AND ENVIRONMENTAL CONDITIONS OF BOREAL CONIFEROUS FORESTS

Field methodology

Using methods for relating vegetation to the environmental variables on which vegetation is dependent should be considered an important part of all vegetation monitoring programmes. This is necessary in order to distinguish between changes caused by man, natural variation in vegetation and changes due to factors intrinsic to the ecosystems. Thus integrated vegetational and environmental monitoring is preferable both to monitoring of the vegetation and of the environmental variables alone. One example illustrating this point is the following: By monitoring the soil nutrient content, one may find that the amount of nutrients decreases during a period of time. However, such a change cannot in itself add much to the knowledge about the the forest ecosystem and its status, as one cannot know to what degree such changes affect the vegetation. Since the trees are important in the forest ecosystem, also as environmental factors influencing the vegetation of the field and bottom layers, monitoring of the trees on the same sample plots as the vegetation is very important. By monitoring vegetation of the field and bottom layers, trees and environmental variables on the same sample plots, changes in one or more variables may be discovered and interpreted. Possible parallel changes in the vegetation, soil and the health of trees may also be found.

Integrated vegetational and environmental monitoring is also a necessary basis for monitoring of possible bioindicators and for population biological monitoring, as variables of populations as well as variables of individuals have to be related to the species response to environmental gradients. This is necessary to obtain knowledge of local variation and to make a meaningful regional comparison. However, a regional comparison always has to be based on locally corresponding vegetation, e.g. bilberry-dominated forests (cf. R. Økland & Bendiksen 1985) as in the present monitoring project.

From what is mentioned above, methods for recording three types of variables are needed; vegetational variables, environmental variables and tree variables. The methods for recording vegetational variables which are used in this investigation are chosen partly by virtue of earlier experience with these methods (T. Økland 1988), but mainly to fit general

demands for monitoring of vegetation and environmental variables. A brief summary of such demands is given below.

The number of sample plots within the investigated area has to be high enough to: (1) include sample plots which represent the vegetational and environmental variation within the area, except variation not within the scope of the investigation, (2) be suitable for application of the relevant methods for data analyses; i.e. to be interpretable by means of multivariate numerical and statistical analyses, and (3) give knowledge about the environmental demands of the species. Experience from this investigation and earlier experience indicates a minimum number of 50 sample plots within an investigation area.

Placement of sample plots must be considered in relation to size and number of sample plots and the other demands mentioned above, besides statistical significance; the more objective the method for placement of sample plots, the higher the statistical significance, but the higher the number of sample plots are required (R. Økland 1990). A restricted random method for placement of sample plots (cf. T. Økland 1988) is considered to be most suitable for monitoring purposes on the basis of a compromise between objectivity, representativeness, statistical significance, number of sample plots and time needed for field analysis.

The size of sample plots has to be sufficient to ensure that in all sample plots the underlying environmental conditions can be safely represented from the total species composition (representativeness). On the other hand, the size of sample plots ought to be small enough to ensure a high resolving power; a sample plot cannot reflect the variation on scales finer than the sample plot size. Rydgren (1989) discusses this problem in an investigation of herb-rich spruce forests, and concludes that the sample plot size used in his investigation (25 m^2) is too large relative to the scale of variation of the most important environmental gradients (cf. also T. Økland 1988, in which the same sample plot size is used). The size of sample plots also has to be small enough to ensure that relatively small changes in the vegetation during time may be found.

Methods for recording species abundance must be considered in relation to the purpose of monitoring; repeated analysis of permanent sample plots is required. Thus reproducibility is very important, which also implies objectivity, exactness, independence of the observer and independence of time of the year the plots are analysed. Frequency methods satisfy these demands much better than cover estimations (T. Økland 1988) which have traditionally been used in vegetation ecology. The advantages of frequency methods compensate for the disadvantage of higher time consumption on field work (T. Økland 1988). Support for this view is provided by Kennedy & Addison (1987) who found that the sampling error in cover estimation is about 20 %. Frequency in subplots is chosen above point frequency, among other reasons because of the risk of missing many of the occurring species by using point frequency.

The suitability of each of the individual environmental variables and tree variables will not be evaluated in this paper. However, which of the environmental variables that are important for the interpretation of the relations between vegetation and environment or in particular for the interpretation of changes during time, cannot be known in advance. Thus, as many variables as possible should be recorded by the best methods available. In this investigation both standard methods and methods especially accommodated to the purposes of the investigation have been used.

Further development of field methodology is still needed, i.e. investigations and evaluation of methods for measuring soil moisture and improvements of methods for measuring other environmental variables etc.

Methods for data analyses

Since 1990 DCA has been a most popular method for ordination of vegetational data. The advantages of this method in preference to for instance RA (reciprocal averaging) and PCA, seem obvious (Gauch 1982a, Minchin 1987). However, there is no agreement on the evaluation of DCA relative to LNMDS (local nonmetric multidimensional scaling). DCA has been claimed to be close to the theoretical optimum of ordination methods (Gauch 1982b). Some authors consider DCA to be more suitable than LNMDS (Gauch et al. 1981, Oksanen 1983), while others hold the opposite opinion (cf. Beals 1984, Kenkel & Orlóci 1986, Minchin 1987, Wartenberg et al. 1987). Minchin (1987) tests DCA and LNMDS on the same simulated data sets, and finds that LNMDS generally shows better gradient recovery than DCA. However, the properties of simulated data sets are often unrealistic in comparison to field data sets (Eilertsen et al. 1990, R. Økland 1990) and this may influence the result of the testing of ordination methods. What is likely to be true is that for some data sets DCA is the best method, for others LNMDS is the best (Økland 1990). Rydgren (1989) uses both methods on a field data set and finds DCA more useful with regard to ecological interpretability, but does not give any general recommendations as to the choice of ordination method. However, DCA also has some advantages as compared with LNMDS; DCA provides a scaling of gradients in beta diversity (reflecting compositional turnover), DCA is part of an integrated concept for gradient analysis, containing regression, calibration, ordination and constrained ordination, and DCA requires less computer time.

DCA and LNMDS are based on fundamentally different methodological concepts. Congruent results with both methods when applied to the same data set, provide a very strong indication that the main structure of the data set has been extracted (R. Økland 1990). Until further testing on data sets with realistic data properties is done, DCA will be used for the data analyses of the vegetation data set for monitoring of boreal forests, but LNMDS may be used in addition in order possibly to extract further information.

The methods for analysing environmental data and interpretation of ordination diagrams have to be subjected to repeated evaluation. Little attention has been paid to this subject, as compared to the evaluation and development of ordination methods.

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