



# sommerfeltia

21

K. Rydgren

Low-alpine vegetation in Gutulia National Park,  
Engerdal, Hedmark, Norway,  
and its relation to the environment

1994



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A reference site for vegetational and ecological monitoring of low-alpine vegetation has been established in Gutulia National Park, Engerdal, Hedmark, Norway. Fifty vegetation plots, each 1 m<sup>2</sup>, were distributed randomly along four open transects. Species abundance was recorded as frequency in 16 subplots. Each plot was supplied with measurements of 26 environmental variables. The first axes of DCA and LNMDS ordinations were closely similar. The first DCA axis was interpreted as a complex snow cover gradient. Several environmental variables varied along this gradient, among them unevenness, soil moisture and soil nutrient status. The cover of the bottom layer varied along the complex-gradient. DCA axis 2 was interpreted as a microclimatic gradient. Partitioning of the environmental and spatial variation in species composition showed that the spatial variation in the data set was rather low. Monitoring alpine vegetation is considered important since alpine ecosystems may be particularly vulnerable to airborne pollution.

Keywords: CCA, Environmental gradients, DCA, LNMDS, Low-alpine vegetation, Monitoring, Norway, Ordination, Permanent plots, TWINSpan, Vegetation.

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## INTRODUCTION

During the last decades, dramatic effects of long-distance airborne pollution have been demonstrated on Norwegian aquatic systems (e.g., SFT 1986, Henriksen et al. 1987). Several studies from Sweden (Falkengren-Grerup et al. 1987, Falkengren-Grerup & Eriksson 1990, Falkengren-Grerup & Tyler 1991a) and Norway (Dahl 1988, Bjørnstad 1991, Steinnes et al. 1993) have indicated a decrease in soil pH and exchangeable cations during the last decades. Forest decline and other vegetational changes that are likely to owe their origins to the effects of air-borne pollution, have been documented from C Europe (e.g., Wittig et al. 1985, Kubiková 1991, Farmer et al. 1992) and Sweden (e.g., Falkengren-Grerup 1986, 1990, Falkengren-Grerup & Eriksson 1990, Falkengren-Grerup & Tyler 1991b), while some indications for Norway are given by Dahl (1988) and Bjørnstad (1991). Bjørnstad (1991) observed increased amounts of some field layer species, e.g. *Deschampsia flexuosa*, in oak forests in Søgne, S Norway, while decline was observed for other species. The cover of the bottom layer decreased in most plots. In contrast, Dahl (1988) was unable to detect significant changes in alpine vegetation in Rondane during 40 years.

Lack of tradition with permanent marking of vegetation plots (Sunding 1985, R. Økland 1990), combined with no focus on vegetational changes until recently (see Løbersli 1989, T. Økland 1989, 1990, 1993, Brattbakk 1991, Fremstad 1991, Brattbakk et al. 1992, Wegener et al. 1992, Aamlid & Venn 1993, R. Økland & Eilertsen 1993) are the main reasons why the extent of pollution effects on Norwegian terrestrial vegetation is not known.

Early identification of vegetation changes puts considerable demands on the methodology; demands that are neither met by previous nor by all current studies (cf. R. Økland 1990, T. Økland 1990, R. Økland & Eilertsen 1993). For instance, cover estimation has been used for estimating species abundances despite frequency in subplots is recommended for monitoring purposes (T. Økland 1988). The importance of measuring environmental variables in connection with every vegetation sample plot is also stressed (T. Økland 1990). Such measurements are necessary to understand the causes of future vegetational changes.

Fennoscandian alpine vegetation has been intensively studied for most of this century (see R. Økland & Bendiksen 1985, Haapasaari 1988 and references quoted therein). Two complex-gradients have been considered the most important for local vegetational differentiation (R. Økland & Bendiksen 1985): a complex-gradient in nutrient status, and a topographic moisture-snow cover complex-gradient. Two other gradients may also be locally important (cf. R. Økland & Bendiksen 1985); a soil drainage gradient (cf. Gjærevoll 1956, Dahl 1957, 1975) and a soil stability gradient (Dahl 1957, Svalheim & Wegener 1990). Inference about gradient relationships of Norwegian alpine vegetation has mostly been by subjective judgment; most studies are based on selective sampling (exceptions are provided by Brattbakk (1991) and Hansen (in prep.)), and measurements of environmental variables in connection with each sample plot are mostly lacking (exceptions: Svalheim & Wegener (1990) and Hansen (in prep.)). Thus we still await valid confirmations of the gradient relationships inferred for alpine vegetation. Furthermore, the relative importance of the different complex-gradients in different regions is not known.

The present study was initiated by the Norwegian Institute of Land Inventory (NIJOS) to establish a reference site for vegetational and ecological monitoring of low-alpine vegetation



in Gutulia National Park, as a parallel to a spruce forest reference site in the project "Vegetational and ecological monitoring of boreal forests in Norway" (T. Økland 1990, 1993). The aim of this paper is to describe the poor, low-alpine vegetation of the reference site, to identify the most important vegetation gradients, and to explain their ecological basis.

## THE INVESTIGATION AREA

### GEOGRAPHICAL SITUATION AND GENERAL INFORMATION

The investigation area is situated within Gutulia National Park, Engerdal municipality, Hedmark county, Norway (Fig. 1). Gutulia National Park was protected by law in 1969 and comprises an area of 19 km<sup>2</sup> (Kielland-Lund 1972).

Gutulivola, 948 m a.s.l. and the highest point in the national park, is situated in the low-alpine belt. The lowest point of the park is situated approximately 620 m a.s.l. The upper forest limit varies between ca. 820 and 880 m, depending on topography. Most of the protected area is covered by forests and mires (cf. Wold 1989).

### GEOLOGY

The bedrock in Gutulia consists of quartz schist and meta-arkose (Sigmond et al. 1984); resistant to weathering and poor in plant nutrients. Bedrock richer in nutrients can be found locally (Nystuen & Trømborg 1972).

The morainic deposits, which are dominated by unsorted bottom moraine, are of greatest thickness in the lower part of the national park (Nystuen & Trømborg 1972). Glacifluvial deposits have also been recorded (Nystuen & Trømborg 1972).

### CLIMATE

The mean annual temperature (Tab. 1) for the normal period 1961-90 at the nearest meteorological station providing temperature data (Drevsjø, 672 m a.s.l., situated approxima-

Tab. 1. Normals and means for temperature and precipitation measured at stations close to the investigation area.

Parameter	Station	Period	Month												Year
			1	2	3	4	5	6	7	8	9	10	11	12	
Temp.	Drevsjø	1961-1990	-11.5	-10.2	-6.3	-1.1	5.5	10.5	11.9	10.6	5.9	1.6	-5.1	-9.6	0.2
Prec.	Valdalen	1968-1990	43	35	41	39	51	81	99	85	87	67	56	56	740

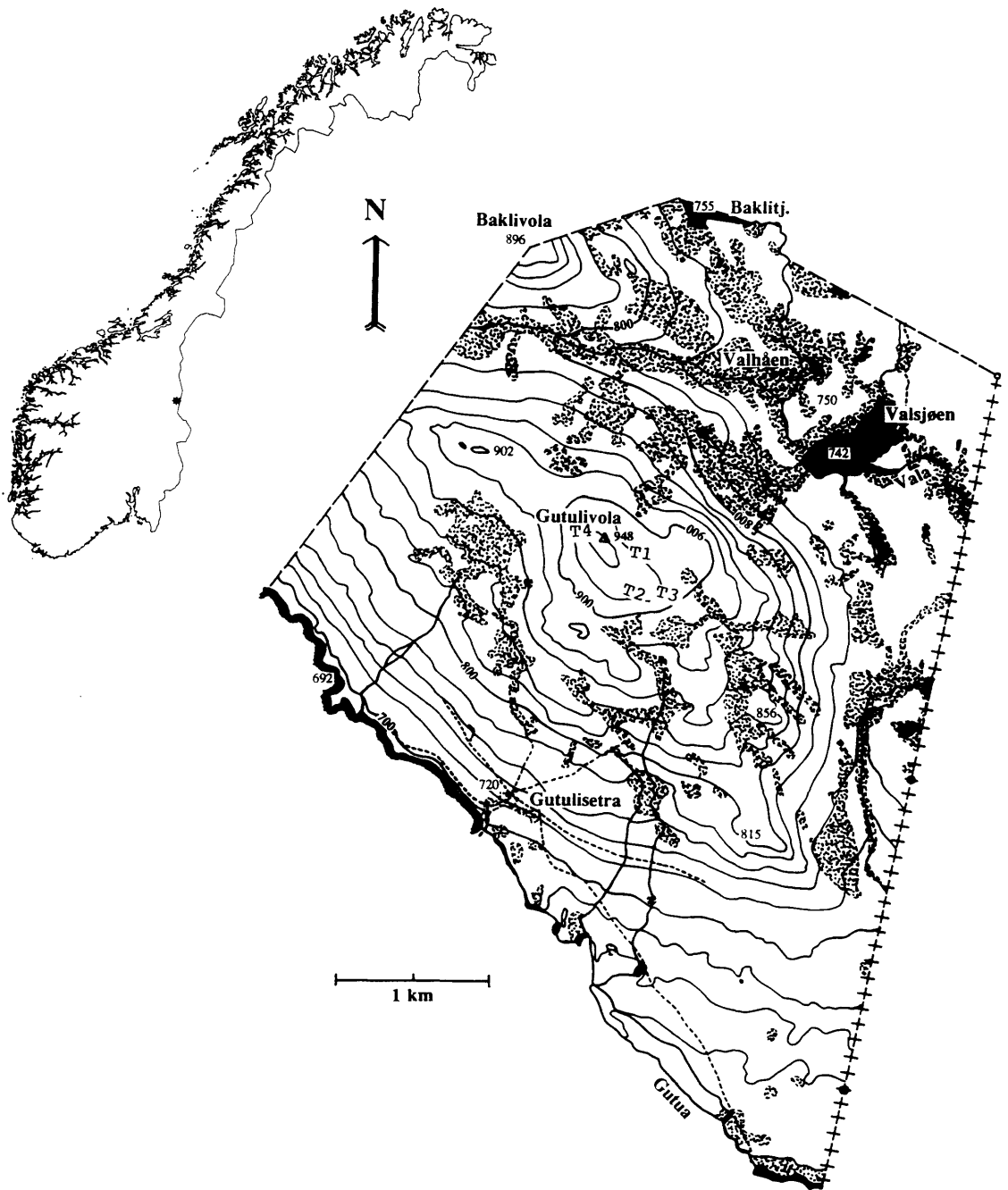


Fig. 1. Maps showing the geographical situation of Gutulia National Park in Norway and the situation of the four transects (T1-T4) at Gutulivola.

tely 15 km southwest of Gutulivola) is 0.2° C (Aune 1993). January is the coldest (-11.5 °C), July the warmest month (11.9 °C). Valdalen, 794 m a.s.l., situated 4 km north of Gutulivola, is the nearest meteorological station provided with precipitation data. The mean annual precipitation for the normal period 1968-90 at Valdalen is 740 mm (Norwegian meteorological Institute, unpubl.), with maximum precipitation from June to September (Tab. 1).

NNW is the prevailing wind direction throughout the year (measurements at Drevsjø, Norwegian meteorological Institute, unpubl.). SSE is the secondmost frequent wind direction from November to May. Drevsjø has a permanent snow cover lasting approximately from December to April (Norwegian meteorological Institute, unpubl.). However, the snow conditions at Gutulivola differ considerably from measurements at Drevsjø, due to the low-alpine situation and the strong gradients in local climatic conditions in the area.

## MANAGEMENT AND HUMAN INFLUENCE ON THE VEGETATION

The domesticated reindeer herds in Elgå reindeer grazing district, the southernmost grazing district in Norway (Severinsen 1987) of which the investigation area is a part, contains approximately 3000 deer (H. Hansen, pers. comm.). The Lapps have had a resort in the region for centuries. The intensity of reindeer grazing in the studied area is locally and temporally variable, but in general high in winter (Tømmervik & Johansen 1992). Tømmervik & Johansen (1992) consider the area Gutulivola - Drevsjø in general to be in good grazing condition; the grazing intensity balancing the carrying capacity.

Mountain dairy farming took place in Gutulia from ca. 1750 to 1949 (Kielland-Lund 1972). Except for the impact of reindeer grazing, few signs of past human activities are now left except close to Gutulisetra. Tourists visit Gutulisetra in increasing numbers; 2000 per year was estimated for the mid-eighties according to Evensen (1987).

## MATERIALS AND METHODS

The field work was carried out in 1992. Vegetation analyses and measurements of environmental variables were performed between 10th and 23rd of August.

### THE SAMPLING SCHEME AND RECORDING OF VEGETATION

Snow-bed vegetation (in the sense of R. Økland & Bendiksen 1985) was not analyzed; all available resources were instead concentrated on obtaining a satisfactory representation of the remaining variation in low-alpine vegetation.

A systematic sampling procedure (cf. R. Økland 1990) with four open transects was used. The transects were placed close to the peak Gutulivola (Fig. 1) and selected so as to include a maximum of local environmental variation, subjectively judged. The length of transects T1-T4 were 150 m, 225 m, 125 m and 175 m, respectively. Poor representation of site-types with low areal importance was avoided by mapping the distribution of three subjectively delimited vegetation series (xeric, subxeric, submesic; terminology in accordance with R. Økland & Bendiksen (1985)) along each transect. Field criteria used to delimit the series were as follows (cf. R. Økland & Bendiksen 1985): Dominance of *Cetraria nivalis* and occurrence of *Alectoria nigricans*, *A. ochroleuca* and *Cetraria cucullata* separated the xeric from the subxeric series. Shift in dominance from *Calluna vulgaris* to *Vaccinium myrtillus* separated the subxeric from the submesic series. Potential positions for sample plots, each 1 m<sup>2</sup>, were drawn at random, with the constraints that (1) neighbouring sample plots should be at least 1 m apart, and (2) stones and/or rock should not cover more than 50 % of the sample plot surface area. Fifty sample plots were distributed onto the four transects according to transect length. Within each transect, equal numbers of plots were drawn from each series, by using the first n accepted positions. The corners of the sample plots were permanently marked with subterranean eloxed aluminium tubes as well as with small wooden sticks.

For analysis of the vegetation, each 1 m<sup>2</sup> plot was divided into 16 0.0625 m<sup>2</sup> subplots. Presence/absence of each species was recorded in each subplot (vascular plants were considered present if they covered a subplot). Frequency in subplots, as recommended when reanalysis of sample plots is intended (cf. T. Økland 1988, 1990, R. Økland & Eilertsen 1993), was used for quantification of species abundances. Supplementary information collected for later use, but not further treated in the present study, included: rooting of vascular plants, presence of bryophyte sporophytes, cover of cryptogamic species in subplots on a 4-point scale, and percentage cover of each species in the 1 m<sup>2</sup> sample plot. The total cover of each of the field and bottom layers was also recorded. The latter was divided into cover of bryophytes and cover of lichens and used as biotic explanatory variables B1 (Cbry) and B2 (Clic), respectively.

## RECORDING OF ENVIRONMENTAL VARIABLES

Environmental variables were primarily recorded to aid in the interpretation of variation in vegetation. Measurements for all 26 variables recorded were made at or close to the 1 m<sup>2</sup> sample plots, by methods used in the NIJOS forest vegetation monitoring study (T. Økland 1990, 1993) and by R. Økland & Eilertsen (1993). A summary of the variables, including statistical properties and transformations applied, is given in Tab. 2.

*Aspect* and *slope* were measured at a representative position within each sample plot. Aspect, measured in the field on a 0-399° scale, was converted to a 0.00-2.00 scale using the following formula (cf. Beers et al. 1966):

$$\text{Aspect} = \cos (A_{\text{max}} - A) + 1$$

Tab. 2. Environmental variables 1-26 and biotic variables B1-B2; number, abbreviation, unit of measurement, range of scale, frequency distribution, and transformation applied.

No	Abbr.	Variable	Unit	Range	Distribution	Transform.
01	Slo	Slope	°	0-100	± Lognormal	ln (1+x)
02	HI	Heat index		-∞-+∞	± Normal	no
03	Asp	Aspect favourability		0-2	± Normal	no
04	Mois	Soil moisture	vol %	0-100	Lognormal	ln (1+x)
05	Sme	Soil depth, median	cm	0-∞	Normal	no
06	Sma	Soil depth, maximum	cm	0-∞	Normal	no
07	Smi	Soil depth, minimum	cm	0-∞	Lognormal	ln (1+x)
08	Une	Unevenness		0-∞	Lognormal	ln (1+x)
09	Con	Convexity		-∞-+∞	Normal	no
10	LI	Loss on ignition	%	0-100	Normal	no
11	pH <sub>H2O</sub>	pH, aqueous solution		0-14	± Lognormal	ln (1+x)
12	pH <sub>CaCl2</sub>	pH, measured in CaCl <sub>2</sub>		0-14	± Lognormal	ln (1+x)
13	K	Extractable K	ppm/LI	0-∞	Normal	no
14	Mg	Extractable Mg	ppm/LI	0-∞	Normal	no
15	Ca	Extractable Ca	ppm/LI	0-∞	Normal	no
16	Na	Extractable Na	ppm/LI	0-∞	Lognormal	ln (1+x)
17	H	Extractable H	ppm/LI	0-∞	Lognormal	ln (1+x)
18	Al	Extractable Al	ppm/LI	0-∞	Lognormal	ln (1+x)
19	Fe	Extractable Fe	ppm/LI	0-∞	Lognormal	ln (1+x)
20	Mn	Extractable Mn	ppm/LI	0-∞	Lognormal	ln (1+x)
21	Zn	Extractable Zn	ppm/LI	0-∞	Lognormal	ln (1+x)
22	P	Extractable P (with NH <sub>4</sub> NO <sub>3</sub> )	ppm/LI	0-∞	± Normal	no
23	S	Extractable S	ppm/LI	0-∞	Lognormal	ln (1+x)
24	P-Al	Extractable P (with AL)	ppm/LI	0-∞	± Lognormal	ln (1+x)
25	N	Total N	weight %/LI	0-100	Normal	no
26	Cstro	Cover of stones and rock		0-100	Lognormal	ln (1+x)
B1	Cbry	Cover of bryophytes		0-100	± Lognormal	ln (1+x)
B2	Clic	Cover of lichens		0-100	Normal	no

where  $A_{\max}$  was set to  $225^\circ$ , and  $A$  was the measured aspect.

*Heat index.* A heat index (Parker 1988, Heikkinen 1991) was calculated as

$$\text{Heat index} = \cos \alpha_1 \cdot \tan \alpha_2,$$

where  $\alpha_1$  is the deviation of aspect from  $225^\circ$  and  $\alpha_2$  is the slope. When slope was  $< 3^\circ$ , Heat index was set to be 0 (cf. Heikkinen 1991).

*Soil depth* was measured at 8 fixed points along the perimeter of the sample plot. The median ( $S_{me}$ ), maximum ( $S_{ma}$ ) and minimum ( $S_{mi}$ ) values were used for further analyses.

*Unevenness* was calculated from microtopographic measurements performed in every sample plot according to R. Økland & Eilertsen (1993), with the difference that 25 distances were recorded between the soil surface and the levelled frame: The distances were recalculated to heights above the lowest measured point in the sample plot,  $z_i$ ,  $i = 1, \dots, 25$ . The  $z_i$  values can be considered as a function of  $x$ , position in sample plot from left to right (0,1,2,3,4) and  $y$ , position from bottom to top (0,1,2,3,4);  $z_i = f(x_i, y_i)$ . The plane of best fit to the observations was estimated by regression:

$$z_i' = a_1 x_i + a_2 y_i + a_0.$$

The difference between observed values and fitted values from the regression model was

$$k_i = z_i' - z_i.$$

The following equation was used for calculation of unevenness,  $u$ :

$$u = (\sum_{i,j} |k_i - k_j|) / 40$$

where the sum is over all 40 pairs of adjacent subplots. Unevenness increases with increasing  $u$ .

*Convexity* was calculated from the  $z_i$  values (see above) according to R. Økland & Eilertsen (1993). A convex sample plot will have the largest  $k_i$ -values, a concave sample plot the lowest, near the plot centre. The average  $k_i$  for the 9 points closest to the plot centre was calculated and referred to as  $k_0$ . The mean deviation of  $k_i$  from  $k_0$  for the remaining 16 subplots was used as an index of the convexity of the sample plot:

$$c = (\sum_i k_0 - k_i) / 16,$$

where  $i = 1-6, 10, 11, 15, 16, 20-25$ .

A positive  $c$  value indicated a convex plot, a negative value indicated a concave plot, while values close to zero indicated plane, uneven or saddle-shaped plots (cf. R. Økland & Eilertsen 1993).

*Soil moisture.* Volumetric soil samples for determination of volumetric soil moisture were collected from the upper 5 cm of the humus layer (or the entire humus layer was sampled, if depth was less than 5 cm), just outside the vegetation plots. The samples were taken on August 22th, 1992, after 1.5 days without precipitation following a period with daily rain showers. The samples were stored in paper bags surrounded by plastic bags to prevent evaporation. The weight of the soil samples was determined immediately after returning to the

laboratory and again after drying at 105 °C to constant weight.

*Soil chemistry and loss on ignition.* A second set of soil samples was collected on the same day as the samples used for soil moisture determination. Each sample consisted of 3-4 subsamples. The samples were air dried, and later used for chemical analysis and determination of *loss on ignition* (indicating the organic matter content) at the Norwegian Agricultural Service Laboratory, Ås (procedures according to A.R. Selmer-Olsen, pers. comm.). The following chemical analyses were performed: *pH measured in aqueous solution*; *pH measured in CaCl<sub>2</sub>*; *total N* measured by the Kjeldahl method; *P-Al* (easily soluble P extracted with ammonium lactate, and measured with ICP); exchangeable cations (*K, Mg, Ca, Na, H, AL, Fe, Mn, Zn*) and anions (*P, S*), extracted in NH<sub>4</sub>NO<sub>3</sub> - their concentrations measured by ICP with a Thermo Jarrell Ash 1100 instrument. Concentrations of exchangeable ions were expressed as fractions of loss on ignition as recommended by T. Økland (1988). Total N was expressed as percentage of loss on ignition.

*Total cover of stone and rock* (in %) was also included as an environmental variable.

## GRADIENT ANALYSES

Ordination, or indirect gradient analysis techniques (ter Braak & Prentice 1988), were used to extract the major coenoclines (vegetational gradients) in the data set. Prior to ordination, species with frequency less than the median frequency were downweighted in proportion to their frequency (Eilertsen & Pedersen 1990, Eilertsen et al. 1990) using Biological Data Program/PC version 1.10 (Pedersen 1988).

### *DCA ordination*

Detrended correspondence analysis (DCA; Hill 1979a, Hill & Gauch 1980) was performed using the CANOCO-PC program, version 3.12 (ter Braak 1987, 1990). DCA was used with detrending by segments and non-linear rescaling as recommended by Knox (1989), R. Økland (1990) and Eilertsen (1991).

DCA ordination was performed on all 50 sample plots (the G50 data set). One sample plot, No. 12, acted as an outlier (Gauch 1982). DCA ordination was therefore also performed on the G49 data set, obtained by deletion of plot No. 12.

### *LNMDs ordination*

Local non-metric multidimensional scaling (LNMDs; Kruskal 1964a, 1964b, Sibson 1972) was performed on G50 and G49, using the KYST program (Kruskal et al. unpubl.) as implemented in DECODA, version 2.01 (Minchin 1986, 1990). The Bray-Curtis coefficient (percent dissimilarity), standardized by division with species maxima as recommended by Faith et al. (1987) and R. Økland (1990), was used. At least 20 different starting configurations were used for each data set, one of which was the DCA configuration, the remaining were random. Only two dimensional LNMDs solutions were taken into consideration. No solution was accepted



unless reached from at least two starting configurations, to avoid trapping in local minima (cf. Minchin 1987). To facilitate visual comparison between DCA and LNMDS configurations, the LNMDS axes were linearly rescaled in S.D. units by hybrid DCCA, using the LNMDS axis as the only constraining variable (R. Økland 1990, Eilertsen et al. 1990, R. Økland & Eilertsen 1993).

#### *Comparison of DCA and LNMDS configurations*

Corresponding axes of DCA and LNMDS ordinations were compared by calculation of Kendall's rank correlation coefficients,  $\tau$  (cf. Sokal & Rohlf 1981), between corresponding sample plot scores.

Procrustes analysis (Schönemann & Carroll 1970, Fasham 1977, Digby & Kempton 1987, Minchin 1987), performed using DECODA, version 2.01, was used to compare 2-dimensional DCA and LNMDS configurations. Procrustes analysis fits one configuration to another using a combination of origin translation, rigid rotation and reflection of reference axes, and uniform central dilation or contraction of scaling (Minchin 1987). The combination of transformations is found analytically, so as to minimize the sum of squared distances between each point in the fitted configuration and its corresponding point in the target configuration (Minchin 1987). The average of the sum-of-squared distances (RMS residuals) was used as a measure of the discrepancy between the configurations (cf. Minchin 1987). The bigger the RMS residuals, the more different were the configurations.

#### *Variation partitioning by (partial) constrained ordination*

The variation in the G49 species-sample plot matrix was partitioned into environmental and spatial variation by use of (partial) constrained canonical analysis (CCA; ter Braak 1986) as implemented in CANOCO, according to the procedure described by Borcard et al. (1992). The set {E} of environmental variables consisted of the 26 variables in Tab. 2. A set {S} of 9 spatial variables included the two-dimensional geographical co-ordinates, x and y, and combinations of these of power less than or equal to 3 (cf. Borcard et al. 1992). Distances between sample plots in the same transects are accurate to the nearest m, distances between the four transects accurate to  $\pm 10$  m. Each of {E} and {S} were subjected to CCA using forward selection of variables. The variables from {E} ( $\{E'\}$ ) and from {S} ( $\{S'\}$ ), contributing significantly ( $P \leq 0.01$ ) to the regression models, were used for further analyses. Four CCA analyses were performed (cf. Borcard et al. 1992): (1) CCA of the species-sample plot matrix, constrained by the significant environmental variables  $\{E'\}$ ; (2) CCA of the species-sample plot matrix, constrained by the significant spatial variables  $\{S'\}$ ; (3) CCA of the species-sample plot matrix, constrained by the significant environmental variables after removing the effect of the significant spatial variables (by using them as covariables); (4) CCA of the species-sample plot matrix, constrained by the significant spatial variables, after removing the effect of the significant environmental variables (by using them as covariables). The total variation in the species-sample plot matrix was given by the total inertia (TI). The variation explained by  $\{E'\}$ , E, was given by (1); the variation explained by  $\{S'\}$ , S, was given by (2); the variation explained by  $\{E'\}$ , not shared by  $\{S'\}$ ,  $E | S$ , was given by (3), and the variation explained by  $\{S'\}$ , not shared by  $\{E'\}$ ,  $S | E$ , was given by (4). The amount of

variation included in both  $\{E'\}$  and  $\{S'\}$ ,  $E \cap S$ , was calculated as  $E - E | S = S - S | E$ . The total variation explained by spatial and environmental variables, TVE or  $E \cup S$ , was calculated as  $E + S | E = S + E | S$ . Fractions of variation explained were obtained by division with TI.

## METHODS FOR ANALYSIS OF ENVIRONMENTAL DATA AND INTERPRETATION OF ORDINATION RESULTS

### *PCA ordination of environmental variables*

Principal component analysis (PCA; e.g., ter Braak & Prentice 1988), using CANOCO-PC version 3.12, was applied to the set of 26 environmental variables (transformed according to Tab. 2). PCA was run on a correlation matrix (after centering and standardization by division with standard deviation), and with Correlation biplot scaling of axes.

### *Correlation analyses*

Kendall's rank correlation coefficients (cf. Sokal & Rohlf 1981) were calculated between environmental (and biotic) variables, and between environmental (and biotic) variables and ordination axes.

### *Other techniques used for interpretation of ordination results*

The following additional techniques were used for interpretation of ordination results (cf. R. Økland 1990):

(1) *Isolines for environmental variables*. In order to illustrate the relationship between coenoclines (ordination axes) and environmental variables, isoline diagrams for environmental variables were constructed by the (third order polynomial) multiple regression model

$$Z = a_1x + a_2y + a_3x^2 + a_4xy + a_5y^2 + a_6x^3 + a_7x^2y + a_8xy^2 + a_9y^3 + a_0$$

where  $Z$  is the environmental (dependent) variable, while  $x$  (DCA 1 sample score),  $y$  (DCA 2 sample score) and combinations thereof are independent variables, and  $a_j$  are regression coefficients. Isolines were hand-fitted on plots of predicted (fitted) values for  $Z$  (backtransformed for transformed variables), and transferred to plots of the original (backtransformed) values. Kendall's rank correlation coefficients between the original and the expected values were calculated as a measure of the overall fit of the isoline diagram.

(2) *Isolines for biotic variables*, as above.

*Variation in species abundances along the ordination axes*

Ordination diagrams with each sample plot represented by a ring, the size of which proportional with the subplot frequency of a species, were prepared for all species occurring in at least 5 sample plots in the G49 data set.

## NUMERICAL CLASSIFICATION OF VEGETATION

Prior to numerical classification, species with frequency less than the median frequency were downweighted in proportion to their frequency (Eilertsen & Pedersen 1990, Eilertsen et al. 1990) using Biological Data Program/PC version 1.10 (Pedersen 1988).

TWINSPAN (Hill 1979b) was applied to the G49 data set in order to delimit vegetation types in an objective manner. Pseudospecies cut levels 0, 5, 10 and 15 were used. The resulting typification intended to serve a practical, and local descriptive purpose only.

## NOMENCLATURE

The nomenclature of vascular plants, mosses, hepatics and lichens follow Lid (1985), Corley et al. (1981), Grolle (1983) and Krog et al. (1980), respectively.

*Dicranum elongatum* was included in *D. fuscescens* agg., *Plagiothecium curvifolium* was included in *P. laetum* agg., *Polytrichum strictum* was included in *Polytrichum juniperinum* agg., *Barbilophozia hatcheri* was included in *B. lycopodioides* agg., *Lophozia longiflora* was included in *L. ventricosa* agg. *Cetraria ericetorum* was included in *C. islandica* agg., *Cladonia pleurota* was included in *C. coccifera* agg., both *C. chlorophaea* and *C. grayi* were included in *C. pyxidata* agg., both *C. crispata* and *C. subfurcata* were included in *C. squamosa* agg., *C. amaurocraea* was included in *Cladonia uncialis* agg. and *C. cervicornis* was included in *C. verticillata* agg.

Some atypical *Sphagnum russowii* may have been included in *S. capillifolium*. *Cladonia mitis* probably does not contain any *C. arbuscula*.

## RESULTS

### RELATIONSHIPS BETWEEN ENVIRONMENTAL AND BIOTIC VARIABLES

Positions of environmental variables relative to the first two PCA ordination axes are shown in Fig. 2. The Kendall rank correlations between the environmental variables and their significance probabilities are shown in Tab. 3.

P-Al, Mg, unevenness, loss on ignition, S and Na made up a group of six strongly positively correlated variables: the more uneven the plot, the larger the soil organic content and the higher extractable amounts of elements. Most members of this group were negatively correlated with H, Mn, Al and with the cover of stones and rock, and most were also strongly positively correlated with Na, Zn and moisture: increased soil moisture was followed by increasing organic content, increased Mg, Zn and S. pH was negatively related to Mg, Zn and P-Al. Significant correlations were also observed between slope and unevenness.

The biotic variable Bryophyte cover was positively correlated with the variables of the six-variable group. Lichen cover was negatively correlated with Bryophyte cover and most of the variables of the group.

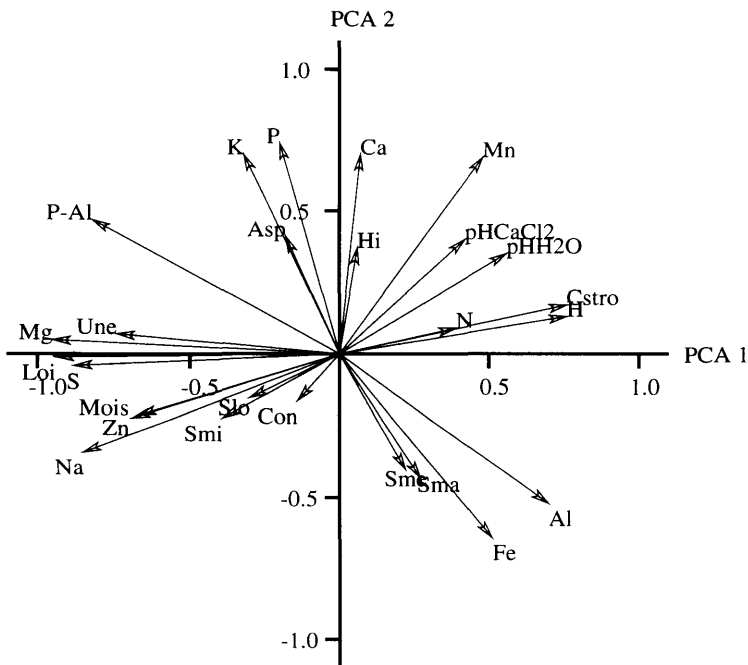
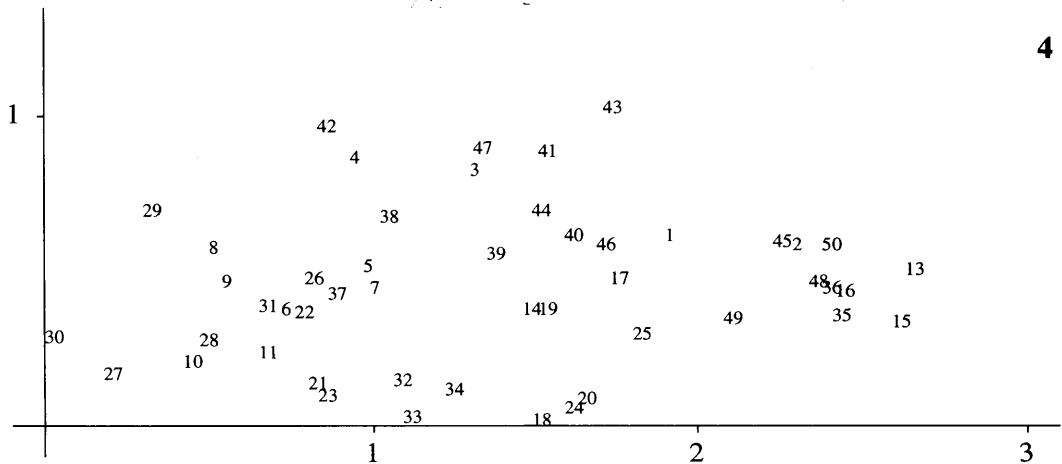
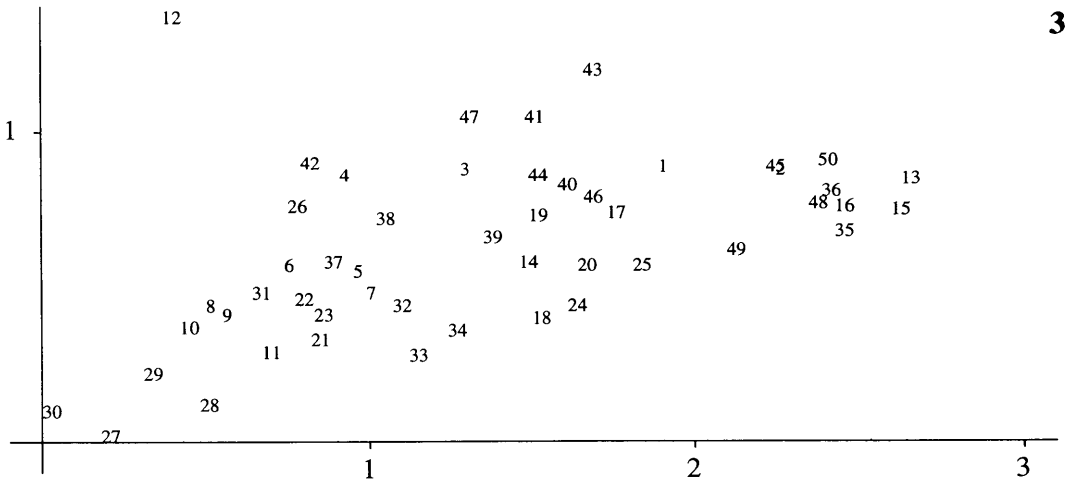


Fig. 2. PCA ordination of 28 environmental variables from the G49 data set, axes 1 and 2. Abbreviations for variable names in accordance with Tab. 2.

Tab. 3. Kendall rank correlations ( $\tau$ ) between 26 environmental variables and 2 biotic variables in the G49 data set (49 sample plots; lower triangle), with significance probabilities (upper triangle). \*\*\* -  $P \leq 0.001$ , \*\* -  $0.001 < P \leq 0.01$ , \*  $0.01 < P \leq 0.05$ . Correlations significant at level  $P \leq 0.001$  in bold face. Numbers and abbreviations for names of variables in accordance with Tab. 2.

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	B1	B2	
01 Slo	.	*	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.	
02 HI	-0.255	.	***	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.	n.s.	n.s.	n.s.	n.s.	n.s.
03 Asp	-0.148	<b>0.649</b>	.	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.	n.s.	n.s.	n.s.	n.s.
04 Mois	0.073	0.080	0.139	.	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 Sme	-0.125	0.057	0.002	-0.004	.	***	**	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.	
06 Sma	0.092	-0.181	-0.228	-0.089	<b>0.362</b>	.	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.	
07 Smi	0.039	0.018	-0.028	0.179	0.304	0.077	.	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 Une	<b>0.343</b>	-0.150	-0.029	0.293	-0.106	-0.154	0.135	.	n.s.	***	n.s.	n.s.	*	***	n.s.	***	***	**	**	*	*	n.s.	***	***	n.s.	***	***	***	
09 Con	0.011	0.067	0.081	0.176	0.085	-0.134	0.177	0.119	.	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.	
10 LI	0.164	0.069	0.127	<b>0.499</b>	-0.120	-0.108	0.280	<b>0.371</b>	0.066	.	***	***	n.s.	***	n.s.	***	***	**	***	***	***	n.s.	***	***	*	***	***	n.s.	
11 pH <sub>H2O</sub>	-0.114	0.016	-0.085	-0.208	-0.028	0.024	-0.111	-0.182	-0.113	<b>-0.426</b>	.	***	n.s.	***	n.s.	***	*	***	n.s.	***	***	n.s.	**	***	**	**	**	n.s.	
12 pH <sub>CaCl2</sub>	-0.062	0.030	-0.033	-0.147	-0.075	-0.011	-0.196	-0.142	-0.096	<b>-0.375</b>	<b>0.785</b>	.	n.s.	***	n.s.	**	n.s.	***	n.s.	**	***	*	*	***	*	**	n.s.		
13 K	0.058	0.135	0.120	0.099	-0.233	-0.168	0.033	0.216	-0.005	0.192	0.042	0.012	.	n.s.	**	n.s.	n.s.	*	***	n.s.	n.s.	***	n.s.	**	n.s.	n.s.	n.s.		
14 Mg	0.167	0.027	0.081	<b>0.443</b>	-0.118	-0.104	-0.239	<b>0.403</b>	0.119	<b>0.750</b>	<b>-0.422</b>	<b>-0.377</b>	0.153	.	n.s.	***	***	***	***	***	***	n.s.	***	***	*	***	***		
15 Ca	-0.106	0.178	0.192	-0.058	-0.161	-0.072	-0.007	-0.111	-0.106	-0.005	0.164	0.074	0.303	-0.058	.	**	n.s.	*	*	n.s.	**	**	n.s.	n.s.	n.s.	n.s.	n.s.		
16 Na	0.232	-0.088	-0.053	<b>0.470</b>	-0.032	-0.056	0.278	<b>0.447</b>	0.104	<b>0.638</b>	<b>-0.378</b>	-0.285	0.000	<b>0.616</b>	-0.272	.	***	**	n.s.	***	***	n.s.	***	***	n.s.	***	***	*	
17 H	-0.211	0.145	0.115	<b>-0.346</b>	0.107	0.080	-0.211	<b>-0.551</b>	-0.087	<b>-0.456</b>	0.238	0.144	-0.077	<b>-0.532</b>	0.192	<b>-0.702</b>	.	**	**	**	**	n.s.	***	***	n.s.	***	***	***	
18 Al	-0.047	-0.075	-0.098	-0.193	0.101	0.122	-0.153	-0.318	-0.055	<b>-0.471</b>	<b>0.367</b>	<b>0.369</b>	-0.225	<b>-0.565</b>	-0.201	-0.265	0.318	.	***	n.s.	**	***	***	***	*	***	*	n.s.	
19 Fe	-0.063	-0.035	-0.091	-0.128	0.173	0.249	-0.133	-0.291	-0.124	-0.315	0.101	0.078	<b>-0.374</b>	<b>-0.391</b>	-0.235	-0.146	0.257	<b>0.531</b>	.	n.s.	n.s.	***	**	***	**	*	n.s.		
20 Mn	-0.094	0.035	0.000	<b>-0.448</b>	0.001	0.022	-0.166	-0.223	-0.080	<b>-0.413</b>	<b>0.417</b>	0.353	0.133	<b>-0.337</b>	0.177	<b>-0.514</b>	0.338	0.048	-0.095	.	***	*	***	n.s.	*	**	n.s.		
21 Zn	0.152	-0.023	0.065	<b>0.348</b>	-0.049	-0.013	0.105	0.236	0.146	<b>0.560</b>	<b>-0.479</b>	<b>-0.419</b>	0.024	<b>0.541</b>	-0.269	<b>0.435</b>	-0.260	-0.293	-0.133	<b>-0.354</b>	.	n.s.	***	***	***	***	n.s.		
22 P	-0.023	0.075	0.110	-0.060	-0.051	-0.161	0.042	0.015	-0.010	0.104	-0.323	-0.237	<b>0.347</b>	0.163	0.296	-0.163	0.107	<b>-0.473</b>	<b>-0.371</b>	0.218	0.143	.	n.s.	***	n.s.	n.s.	n.s.		
23 S	0.223	-0.092	-0.077	<b>0.433</b>	-0.111	-0.072	0.259	<b>0.527</b>	0.048	<b>0.612</b>	-0.170	-0.227	0.165	<b>0.628</b>	-0.148	<b>0.753</b>	<b>-0.806</b>	<b>-0.383</b>	-0.291	<b>-0.369</b>	<b>0.393</b>	0.002	.	***	n.s.	***	***		
24 P-Al	0.143	0.049	0.103	0.288	-0.156	-0.172	0.189	<b>0.408</b>	0.114	<b>0.612</b>	<b>-0.443</b>	<b>-0.401</b>	0.267	<b>0.716</b>	0.097	<b>0.410</b>	<b>-0.442</b>	<b>-0.777</b>	<b>-0.536</b>	-0.172	<b>0.430</b>	<b>0.400</b>	<b>0.531</b>	.	*	***	***	*	
25 N	-0.112	-0.001	-0.132	-0.189	0.142	0.135	0.053	-0.121	-0.089	-0.213	0.312	0.263	-0.058	-0.235	-0.102	-0.157	0.141	0.242	0.269	0.242	-0.126	-0.082	-0.151	-0.226	.	n.s.	n.s.		
26 Cstro	-0.234	0.025	0.000	<b>-0.373</b>	-0.066	0.002	<b>-0.492</b>	-0.288	-0.190	<b>-0.564</b>	<b>0.395</b>	0.373	-0.162	<b>-0.535</b>	0.115	<b>-0.467</b>	<b>0.355</b>	<b>0.351</b>	0.238	0.305	<b>-0.420</b>	-0.168	<b>-0.456</b>	<b>-0.495</b>	0.198	.	***	n.s.	
B1 Cbry	0.308	-0.250	-0.165	0.265	-0.094	0.008	0.247	0.471	0.092	<b>0.427</b>	-0.184	-0.159	0.115	<b>0.419</b>	-0.154	<b>0.446</b>	<b>-0.412</b>	-0.262	-0.133	-0.127	0.304	0.074	<b>0.480</b>	<b>0.389</b>	0.025	<b>-0.482</b>	.	**	
B2 Clic	-0.069	0.010	0.044	-0.138	0.102	0.139	-0.084	<b>-0.348</b>	-0.096	-0.156	-0.057	-0.124	-0.158	-0.179	0.004	-0.244	<b>0.346</b>	0.167	0.044	0.010	0.029	0.046	-0.288	-0.199	-0.172	0.076	-0.315	.	



Figs 3-4. DCA ordinations, axes 1 and 2. Sample plot numbers plotted onto the sample plot positions. Axes scaled in S.D. units. Fig. 3. The G50 data set. Fig. 4. The G49 data set.

#### ORDINATION: THE G50 DATA SET

The DCA ordination of the G50 data set is shown in Fig. 3. Eigenvalues of DCA axes and the fraction of variation explained by them, are shown in Tab. 4. Sample plot No. 12 acted as a moderate outlier and was removed prior to further analysis. The LNMDS ordination (not shown) gave the same picture, also with sample plot No. 12 as an outlier.

The mean RMS residual obtained by comparing DCA and LNMDS by Procrustes analysis, was 0.178.

Tab. 4. DCA ordinations: total inertia (TI), eigenvalue (e.v.), fraction of variation explained (v.e.) by each axis (eigenvalue/total inertia) and gradient length (g.l.) in S.D. units.

Data set	TI	Axis	e.v.	v.e.	g.l.
G50	1.097	1	0.336	0.306	2.63
		2	0.085	0.077	1.35
		3	0.037	0.034	0.98
		4	0.029	0.026	0.93
G49	1.039	1	0.331	0.319	2.63
		2	0.066	0.064	1.01
		3	0.038	0.038	1.00
		4	0.023	0.023	0.78

#### ORDINATION: THE G49 DATA SET

##### *Characteristics of the ordinations*

The DCA ordination of the G49 data set is shown in Fig. 4, while eigenvalues of DCA axes and the fraction of variation explained by them, are shown in Tab. 4. DCA axes 2, 3 and 4 had low eigenvalues and gradient lengths. Only axes 1 and 2 were subjected to further interpretation.

The corresponding LNMDS ordination is shown in Fig. 5.

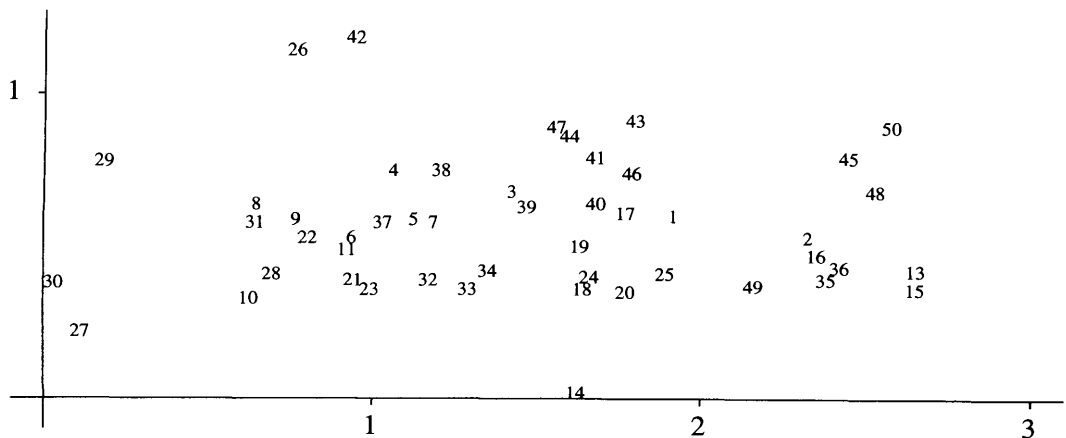


Fig. 5. LNMDS ordination of the G49 data set, axes 1 and 2. Sample plot numbers plotted onto the sample plot positions. Axes linearly rescaled in S.D. units.

Tab. 5. Kendall rank correlations ( $\tau$ ) between sample plot positions relative to ordination axes (DCA 1-4 and LNMDS 1-2, ordinations of the G49 data set), and environmental and biotic variables. \*\*\* -  $P \leq 0.001$ , \*\* -  $0.001 < P \leq 0.01$ , \*  $0.01 < P \leq 0.05$ . Correlations significant at level  $P \leq 0.001$  in bold face.

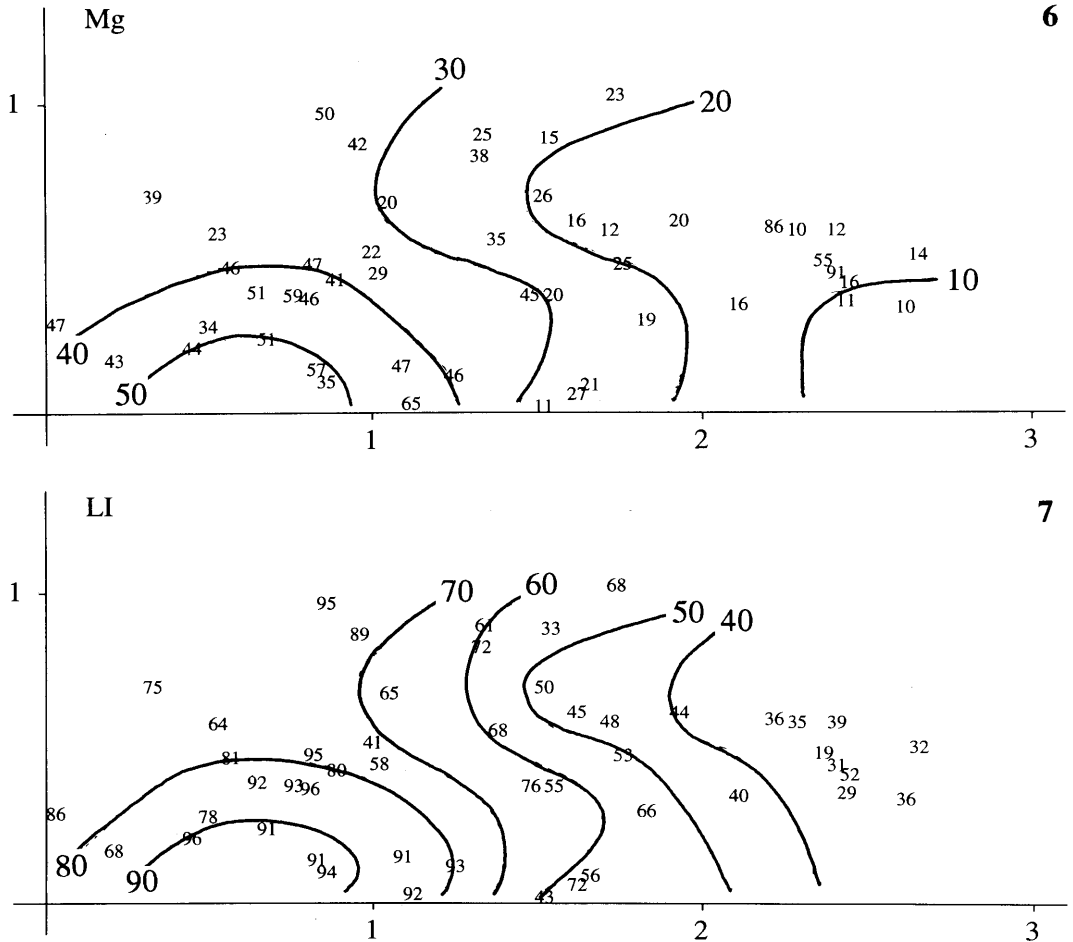
Variable	DCA 1		DCA 2		DCA 3		DCA 4		LNMDS 1		LNMDS 2	
	$\tau$	P	$\tau$	P	$\tau$	P	$\tau$	P	$\tau$	P	$\tau$	P
01 Slo	<b>-0.342</b>	***	-0.071	n.s.	0.071	n.s.	0.007	n.s.	-0.319	**	-0.047	n.s.
02 HI	0.042	n.s.	-0.316	**	0.107	n.s.	0.066	n.s.	0.013	n.s.	-0.272	**
03 Asp	-0.031	n.s.	<b>-0.428</b>	***	0.072	n.s.	0.041	n.s.	-0.062	n.s.	<b>-0.368</b>	***
04 Mois	<b>-0.342</b>	***	-0.172	n.s.	0.312	**	0.058	n.s.	<b>-0.360</b>	***	0.000	n.s.
05 Sme	0.178	n.s.	0.022	n.s.	0.032	n.s.	0.061	n.s.	0.180	n.s.	-0.018	n.s.
06 Sma	0.147	n.s.	0.216	*	-0.089	n.s.	0.051	n.s.	0.142	n.s.	0.180	n.s.
07 Smi	-0.198	n.s.	-0.068	n.s.	0.001	n.s.	0.276	**	-0.192	n.s.	-0.049	n.s.
08 Une	<b>-0.563</b>	***	-0.105	n.s.	0.208	*	-0.039	n.s.	<b>-0.560</b>	***	-0.012	n.s.
09 Con	-0.145	n.s.	-0.129	n.s.	0.083	n.s.	-0.026	n.s.	-0.165	n.s.	-0.092	n.s.
10 LI	<b>-0.566</b>	***	-0.194	*	0.140	n.s.	0.056	n.s.	<b>-0.590</b>	***	-0.080	n.s.
11 pH <sub>H2O</sub>	0.287	**	0.249	*	-0.013	n.s.	0.180	n.s.	0.304	**	0.207	*
12 pH <sub>CaCl2</sub>	0.221	*	0.183	n.s.	0.064	n.s.	0.104	n.s.	0.249	*	0.162	n.s.
13 K	-0.255	**	-0.077	n.s.	0.111	n.s.	0.099	n.s.	-0.262	**	0.017	n.s.
14 Mg	<b>-0.582</b>	***	-0.168	n.s.	0.077	n.s.	0.024	n.s.	<b>-0.616</b>	***	-0.075	n.s.
15 Ca	0.140	n.s.	-0.039	n.s.	-0.134	n.s.	0.048	n.s.	0.122	n.s.	-0.031	n.s.
16 Na	<b>-0.503</b>	***	-0.060	n.s.	0.250	*	0.014	n.s.	<b>-0.493</b>	***	0.068	n.s.
17 H	<b>0.471</b>	***	-0.010	n.s.	-0.191	n.s.	0.012	n.s.	<b>0.468</b>	***	-0.094	n.s.
18 Al	<b>0.381</b>	***	0.134	n.s.	0.104	n.s.	0.020	n.s.	<b>0.418</b>	***	0.112	n.s.
19 Fe	0.299	**	0.134	n.s.	0.012	n.s.	0.031	n.s.	0.320	**	0.129	n.s.
20 Mn	0.238	*	0.134	n.s.	-0.287	**	0.007	n.s.	0.235	*	-0.014	n.s.
21 Zn	<b>-0.429</b>	***	-0.121	n.s.	0.107	n.s.	-0.051	n.s.	<b>-0.435</b>	***	-0.085	n.s.
22 P	-0.122	n.s.	-0.066	n.s.	-0.223	*	0.024	n.s.	-0.133	n.s.	-0.105	n.s.
23 S	<b>-0.566</b>	***	0.014	n.s.	0.187	n.s.	-0.015	n.s.	<b>-0.570</b>	***	0.107	n.s.
24 P-Al	<b>-0.556</b>	***	-0.153	n.s.	-0.034	n.s.	-0.005	n.s.	<b>-0.590</b>	***	-0.100	n.s.
25 N	0.085	n.s.	0.192	n.s.	-0.107	n.s.	0.048	n.s.	0.119	n.s.	0.102	n.s.
26 Cstro	0.307	**	-0.044	n.s.	-0.032	n.s.	-0.174	n.s.	0.293	**	-0.065	n.s.
B1 Cbry	<b>-0.623</b>	***	0.110	n.s.	-0.090	n.s.	0.053	n.s.	<b>-0.609</b>	***	0.156	n.s.
B2 Clic	<b>0.564</b>	***	0.121	n.s.	-0.036	n.s.	-0.159	n.s.	<b>0.564</b>	***	0.045	n.s.

### Comparison of DCA and LNMDS configurations

The first axes in the two ordinations were closely similar and obviously represented the same major coenocline (cf. Figs 4 and 5), as evident from the high Kendall rank correlation between corresponding DCA 1 and LNMDS 1 sample plot scores ( $\tau = 0.935$ ,  $P < 0.001$ ). Sample plot positions along the second axes differed somewhat, but was still highly significant ( $\tau = 0.699$ ,  $P < 0.001$ ).

Removing the outlier (sample plot No. 12) did not improve the overall similarity of the DCA and LNMDS configurations (in two dimensions); the mean RMS residual was 0.198 for the G49 data set.

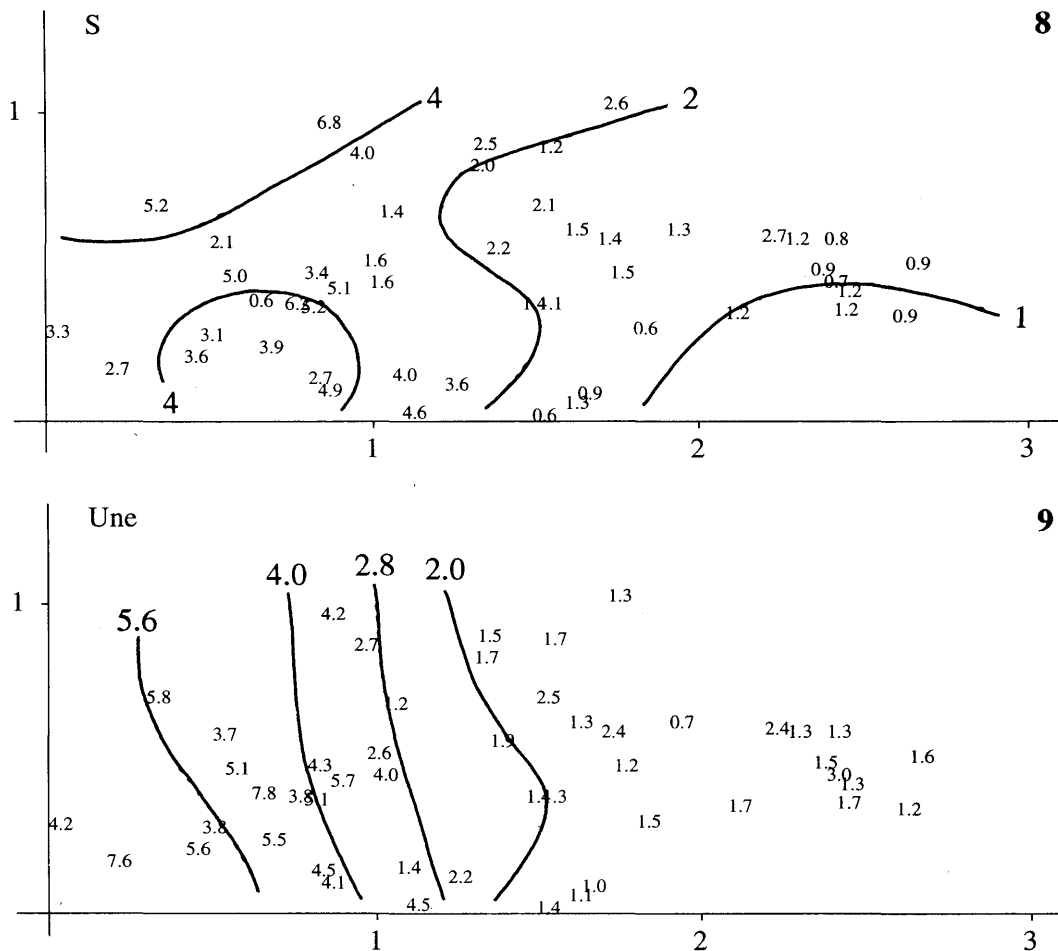




Figs 6-7. Values for environmental variables plotted onto the sample plot positions in the DCA ordination of the G49 data set, axes 1 and 2. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures. Fig. 6. Mg. The correlation between the original and expected values is  $\tau = 0.662$  ( $P < 0.001$ ). Fig. 7. Loss on ignition. The correlation between the original and expected values is  $\tau = 0.694$  ( $P < 0.001$ ).

#### *Environmental interpretation*

Kendall rank correlations between environmental variables and ordination axes are displayed in Tab. 5. Figs 6-12 show values and isolines for some of the environmental variables best correlated with DCA 1 and DCA 2. DCA 1 scores were most strongly correlated with Mg ( $\tau = -0.582$ ), loss on ignition ( $\tau = -0.566$ ), S ( $\tau = -0.566$ ), cover of stones and rock ( $\tau = 0.564$ ), unevenness ( $\tau = -0.563$ ) and P-Al ( $\tau = -0.556$ ). These variables were also most strongly correlated with LNMDS 1 (Tab. 5), but the order of decrease in  $\tau$  was different. The sample

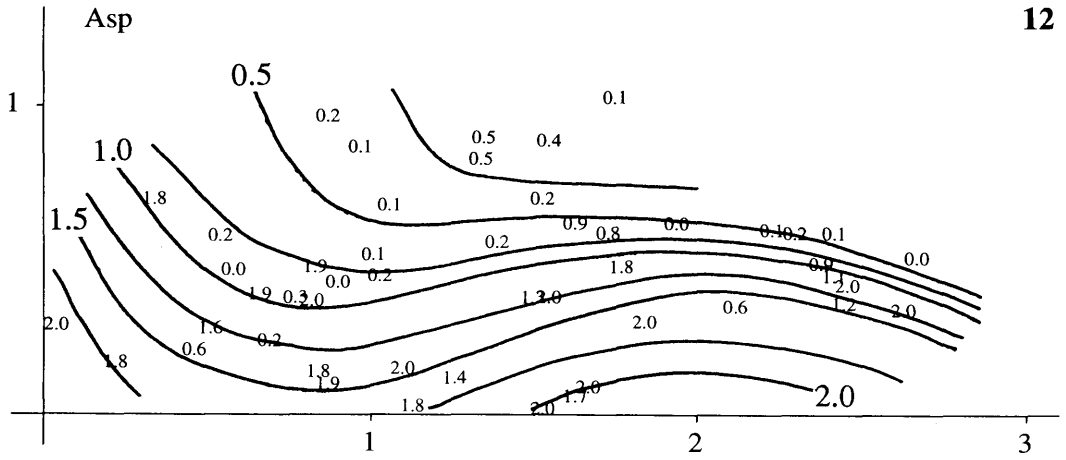


Figs 8-9. Values for environmental variables plotted onto the sample plot positions in the DCA ordination of the G49 data set, axes 1 and 2. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures. Fig. 8. S. The correlation between the original (ln-transformed) and expected values is  $\tau = 0.636$  ( $P < 0.001$ ). Fig. 9. Unevenness. The correlation between the original (ln-transformed) and expected values is  $\tau = 0.595$  ( $P < 0.001$ ).

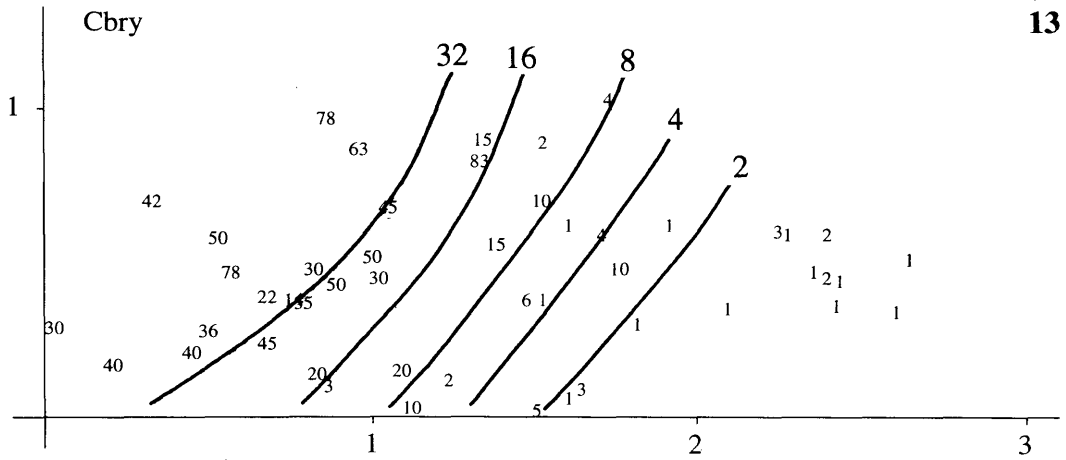
plots with the highest values for Mg (Fig. 6), loss on ignition (Fig. 7), S (Fig. 8), unevenness (Fig. 9) and P-Al (Fig. 10) were situated on the left side of the ordination diagram, while the sample plots with the highest cover of stones and rock (Fig. 11) were situated on the right hand side of the ordination diagram. Soil moisture was also significantly correlated with DCA 1 ( $\tau = -0.342$ ). The driest sample plots were situated to the right in the ordination diagram.

Only one variable, Aspect ( $\tau = -0.428$ ), had a correlation with DCA 2 significant at the highest level ( $P < 0.001$ ). The heat index ( $\tau = -0.316$ ) was the only other variable significantly





12



13

Figs 12-13. Values for environmental and biotic variables plotted onto the sample plot positions in the DCA ordination of the G49 data set, axes 1 and 2. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures. Fig. 12. Aspect. The correlation between the original and expected values is  $\tau = 0.512$  ( $P < 0.001$ ). Fig. 13. Cover of bryophytes. The correlation between the original (ln-transformed) and expected values is  $\tau = 0.687$  ( $P < 0.001$ ).

*Interpretation by means of biotic variables*

Correlations between ordination axes and the biotic variables are given in Tab. 5. Bryophyte cover decreased along DCA and LNMSD 1; the correlation coefficient between Cbry and DCA 1 ( $\tau = -0.623$ ) was more strongly significant than correlations between DCA 1 and any of the environmental variables. The cover of lichens increased along the first axes. Isolines for Cbry in the DCA ordination diagram are shown in Fig. 13.

*Variation in species abundances along the ordination axes*

Variation in frequency in subplots for the 49 species occurring in 5 or more sample plots in the G49 data set is shown in Figs 14-62. Five species occurred in all sample plots. Two of these were vascular plants, i.e. *Empetrum hermaphroditum* (Fig. 17) and *Vaccinium vitis-idaea* (Fig. 22), and three were lichens, i.e. *Cladonia coccifera* agg. (Fig. 47), *C. mitis* (Fig. 52) and *C. squamosa* agg. (Fig. 56). Many species occurred in most of the sample plots. Some of these increased with increasing DCA 1 scores, e.g., the lichens *Cetraria islandica* agg. (Fig. 44) and *Cladonia gracilis* (Fig. 50). Opposite trends were noted for *Cladonia bellidiflora* (Fig. 46) and *C. rangiferina* (Fig. 55), while *C. stellaris* (Fig. 57) was absent from sample plots at both ends along DCA 1. Some common species (e.g. *Pohlia nutans* (Fig. 29) and *Cladonia pyxidata* agg. (Fig. 54)) showed no trends, neither along DCA 1 nor along DCA 2.

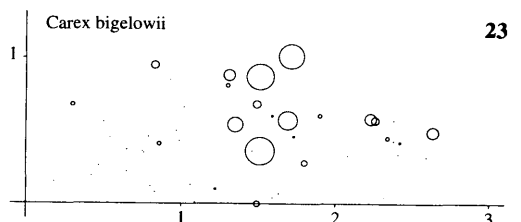
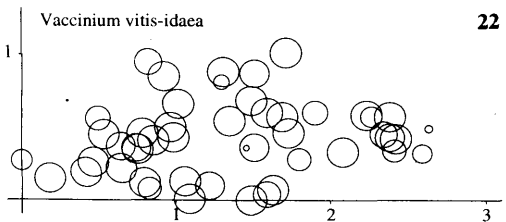
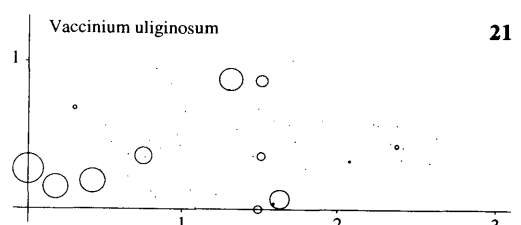
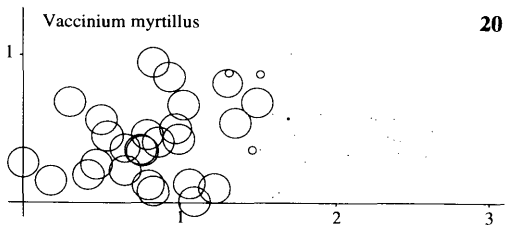
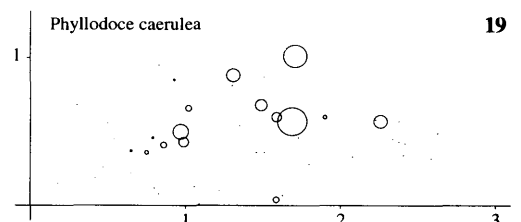
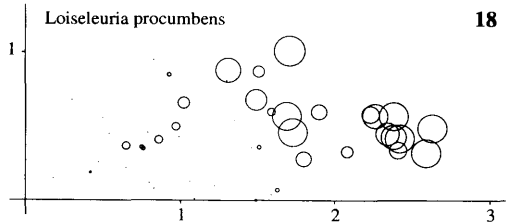
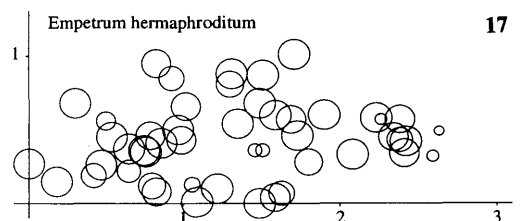
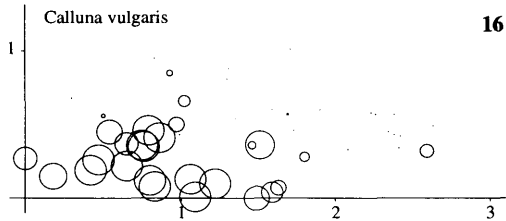
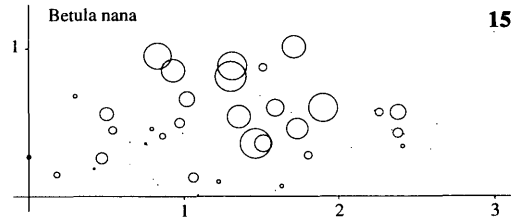
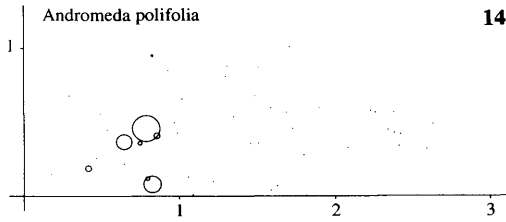
Many vascular plant and bryophyte species were restricted to the left hand side of the ordination diagram, e.g., *Vaccinium myrtillus* (Fig. 20) and *Deschampsia flexuosa* (Fig. 24) both absent for DCA 1 > 2.0 S.D. Even more strongly restricted distributions in the ordination diagram were noted for many bryophyte species, e.g., *Dicranum scoparium* (Fig. 27), *Pleurozium schreberi* (Fig. 28), *Barbilophozia floerkei* (Fig. 35) and *B. lycopodioides* agg. (Fig. 36). *Cladonia ecmocyna* (Fig. 49) was the species most strongly restricted to sample plots with low DCA 1 scores.

One example among several species restricted to the right hand side of the ordination diagram, was *Cladonia uncialis* agg. (Fig. 59), lacking in the two sample plots with lowest values along DCA 1 but having low quantities in sample plots with DCA 1 < 1.0. Among species restricted to plots with high DCA 1 scores, *Loiseleuria procumbens* (Fig. 18), *Cetraria cucullata* (Fig. 43), *C. nivalis* (Fig. 45) and *Cladonia macrophylla* (Fig. 51) could be mentioned. *Alectoria nigricans* (Fig. 41), *A. ochroleuca* (Fig. 42), *Cornicularia aculeata* (Fig. 61) and *Thamnolia vermicularis* (Fig. 62) were the species most strongly restricted to plots with high DCA 1 scores.

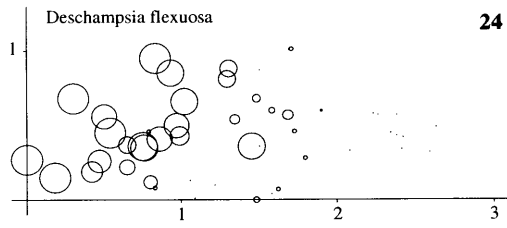
Some species showed differentiation along DCA 2, e.g., *Betula nana* (Fig. 15), *Phyllodoce caerulea* (Fig. 19), *Polytrichum juniperinum* agg. (Fig. 31), *Anastrophyllum minutum* (Fig. 33) and *Ptilidium ciliare* (Fig. 39). These species were most common in the uppermost part of the ordination diagram, as opposed to *Calluna vulgaris* (Fig. 16), which was most common in the lowermost part of the diagram.

## PARTITIONING THE VARIATION IN THE G49 SPECIES-SAMPLE PLOT MATRIX

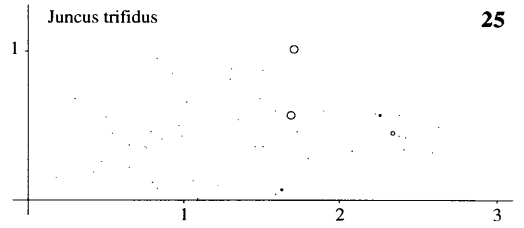
The total inertia of the G49 species-sample plot data matrix was 1.039. Five environmental variables, Asp, Une, LI, Ca and Mn, and two spatial variables ( $x$ ,  $y^3$ ) were retained by the forward selection procedure. The fractions of variation explained by sets and combinations of sets of explanatory variables were (Fig. 63): E (environmental variation) = 39.5%, of which E | S (non-spatial environmental variation) = 29.3%, S (spatial variation) = 15.2%, of which S | E (non-environmental spatial variation) = 5.1%, E|S (spatial and environmental variation) = 10.2%, and TVE = EUS = 44.5%. The unexplained variation was 55.5%.



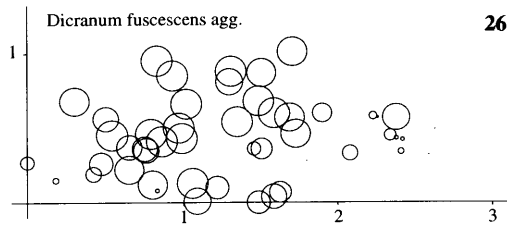
Figs 14-23. DCA of the G49 data set, axes 1 and 2 (scaled in S.D. units). Frequency in subplots for each species is plotted on the sample plot positions. The size of the circles is proportional to the frequency (0-16) in subplots. Fig. 14. *Andromeda polifolia*. Fig. 15. *Betula nana*. Fig. 16. *Calluna vulgaris*. Fig. 17. *Empetrum hermaphroditum*. Fig. 18. *Loiseleuria procumbens*. Fig. 19. *Phyllodoce caerulea*. Fig. 20. *Vaccinium myrtillus*. Fig. 21. *Vaccinium uliginosum*. Fig. 22. *Vaccinium vitis-idaea*. Fig. 23. *Carex bigelowii*.



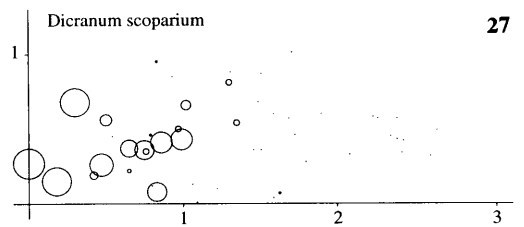
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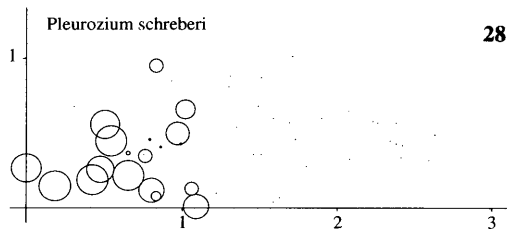
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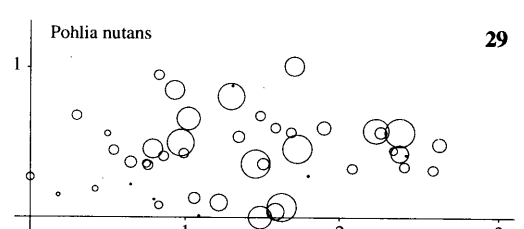
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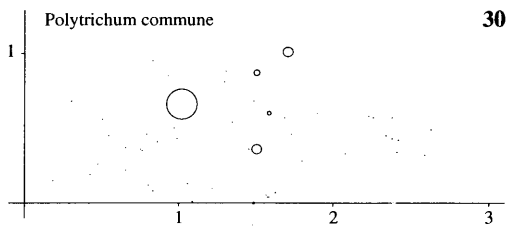
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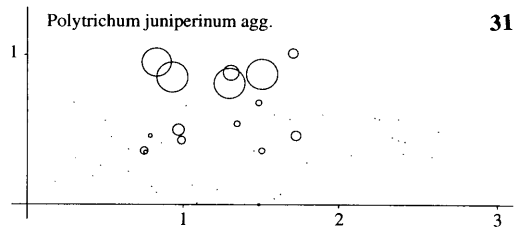
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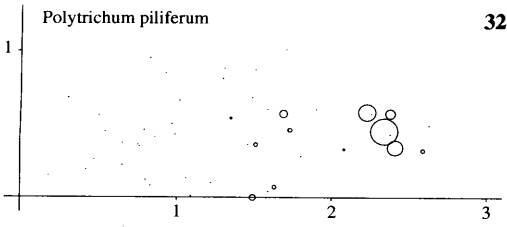
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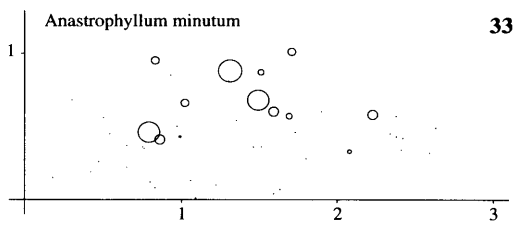
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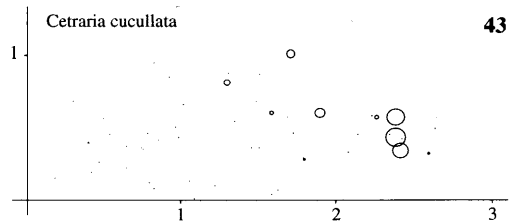
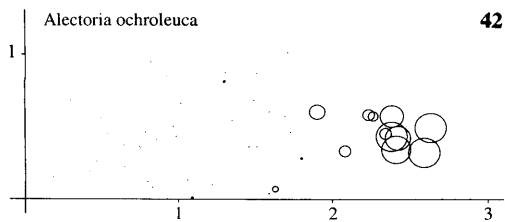
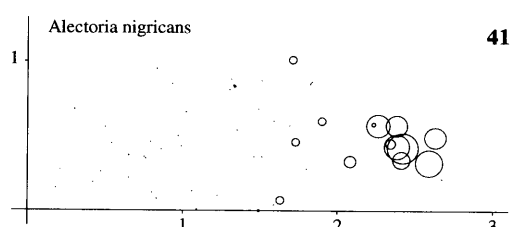
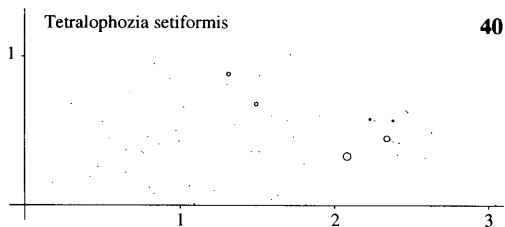
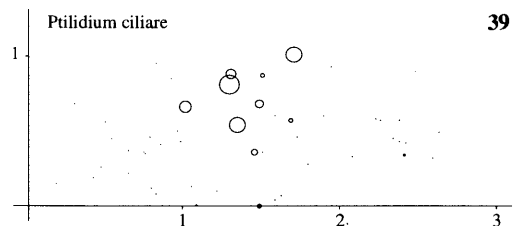
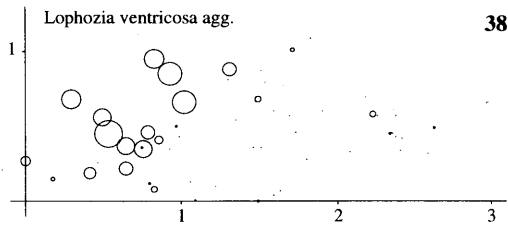
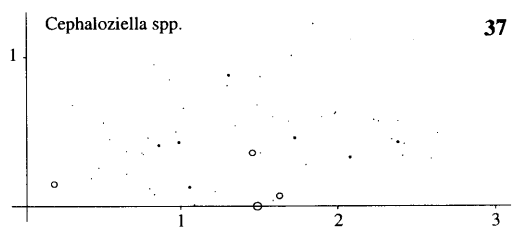
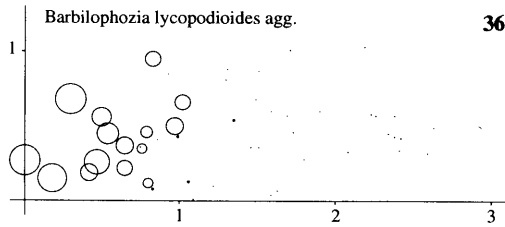
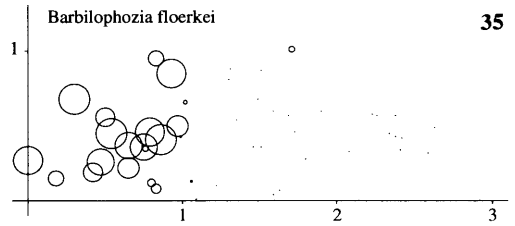
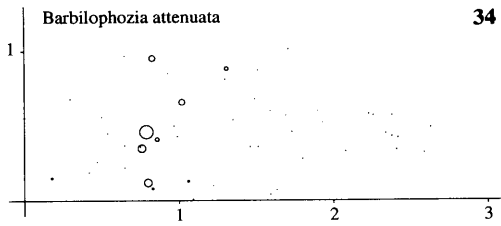


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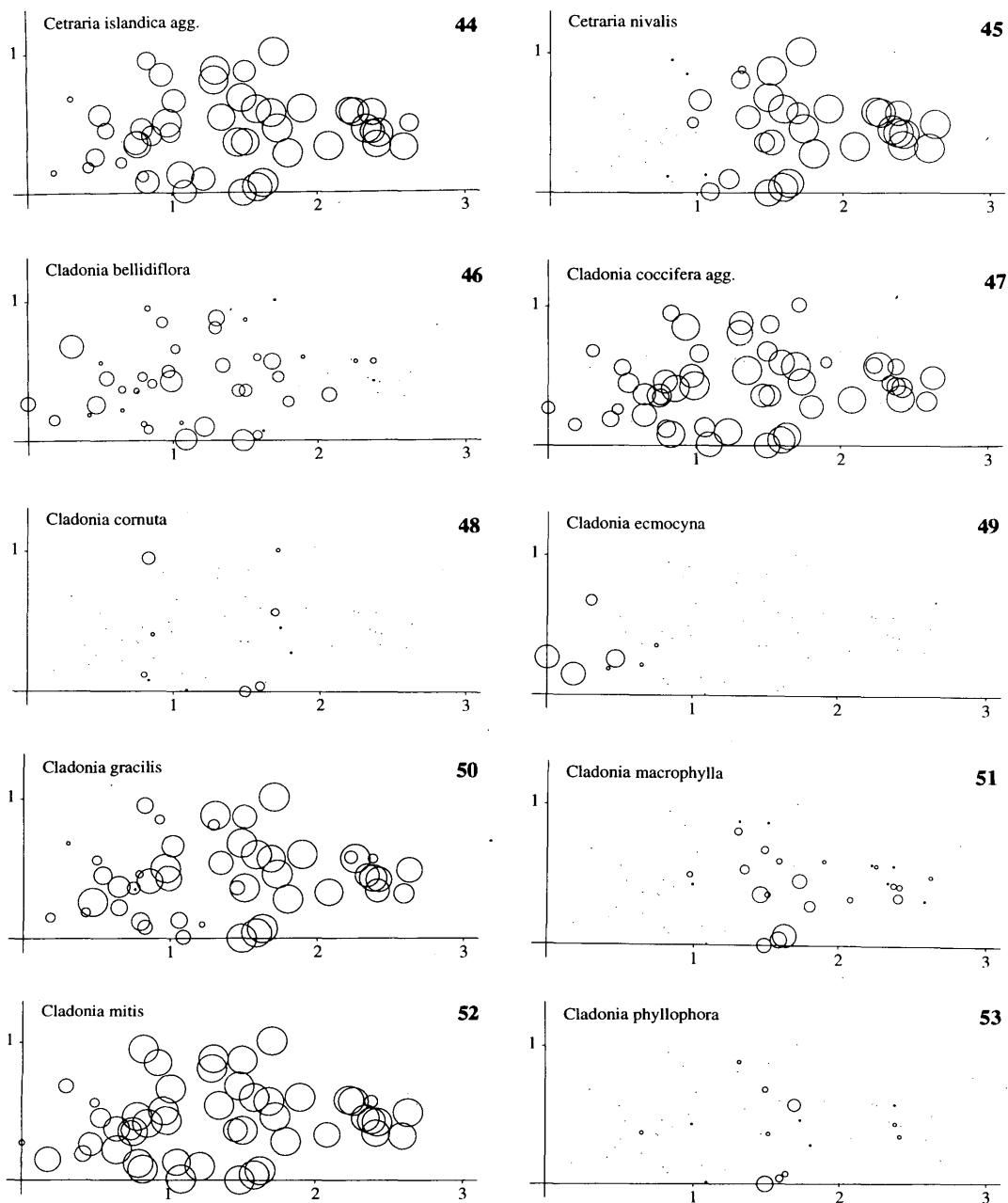
33

Figs 24-33. DCA of the G49 data set, axes 1 and 2 (scaled in S.D. units). Frequency in subplots for each species is plotted onto the sample plot positions. The size of the circles is proportional to the frequency (0-16) in subplots. Fig. 24. *Deschampsia flexuosa*. Fig. 25. *Juncus trifidus*. Fig. 26. *Dicranum fuscescens* agg. Fig. 27. *Dicranum scoparium*. Fig. 28. *Pleurozium schreberi*. Fig. 29. *Pohlia nutans*. Fig. 30. *Polytrichum commune*. Fig. 31. *Polytrichum juniperinum* agg. Fig. 32. *Polytrichum piliferum*. Fig. 33. *Anastrophyllum minutum*.

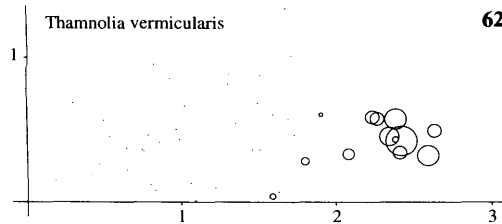
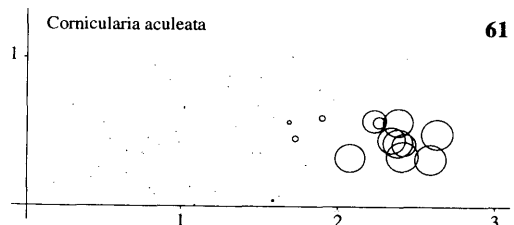
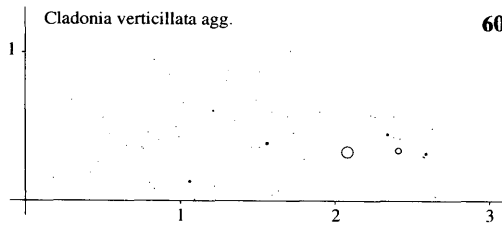
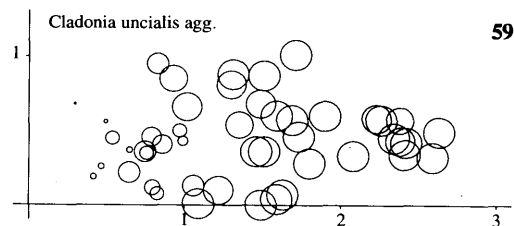
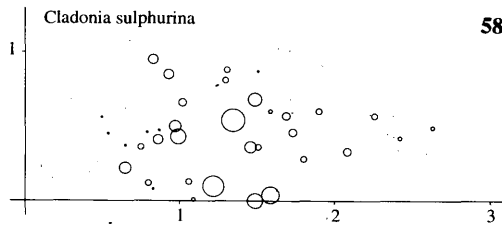
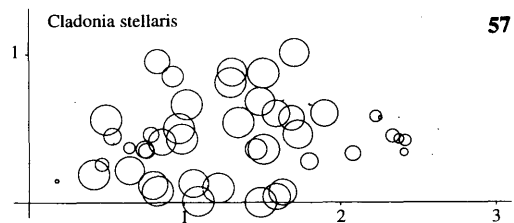
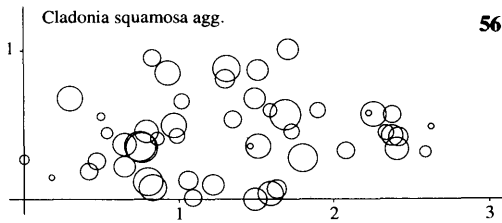
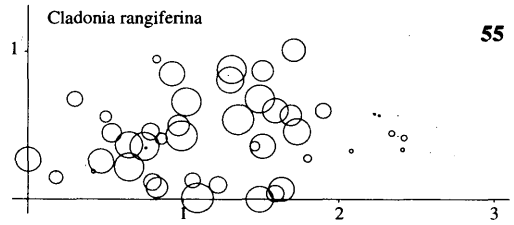
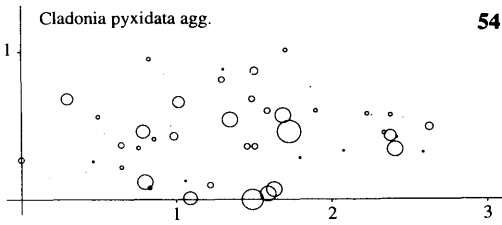


Figs 34-43. DCA of the G49 data set, axes 1 and 2 (scaled in S.D. units). Frequency in subplots for each species is plotted onto the sample plot positions. The size of the circles is proportional to the frequency (0-16) in subplots. Fig. 34. *Barbilophozia attenuata*. Fig. 35. *Barbilophozia floerkei*. Fig. 36. *Barbilophozia lycopodioides* agg. Fig. 37. *Cephaloziella* spp. Fig. 38. *Lophozia ventricosa* agg. Fig. 39. *Ptilidium ciliare*. Fig. 40. *Tetralophozia setiformis*. Fig. 41. *Alectoria nigricans*. Fig. 42. *Alectoria ochroleuca*. Fig. 43. *Cetraria cucullata*.





Figs 44-53. DCA of the G49 data set, axes 1 and 2 (scaled in S.D. units). Frequency in subplots for each species is plotted onto the sample plot positions. The size of the circles is proportional to the frequency (0-16) in subplots. Fig. 44. *Cetraria islandica* agg. Fig. 45. *Cetraria nivalis*. Fig. 46. *Cladonia bellidiflora*. Fig. 47. *Cladonia coccifera* agg. Fig. 48. *Cladonia cornuta*. Fig. 49. *Cladonia ecmocyna*. Fig. 50. *Cladonia gracilis*. Fig. 51. *Cladonia macrophylla*. Fig. 52. *Cladonia mitis*. Fig. 53. *Cladonia phyllophora*.



Figs 54-62. DCA of the G49 data set, axes 1 and 2 (scaled in S.D. units). Frequency in subplots for each species is plotted onto the sample plot positions. The size of the circles is proportional to the frequency (0-16) in subplots. Fig. 54. *Cladonia pyxidata* agg. Fig. 55. *Cladonia rangiferina*. Fig. 56. *Cladonia squamosa* agg. Fig. 57. *Cladonia stellaris*. Fig. 58. *Cladonia sulphurina*. Fig. 59. *Cladonia uncialis* agg. Fig. 60. *Cladonia verticillata* agg. Fig. 61. *Cornicularia aculeata*. Fig. 62. *Thamnolia vermicularis*.

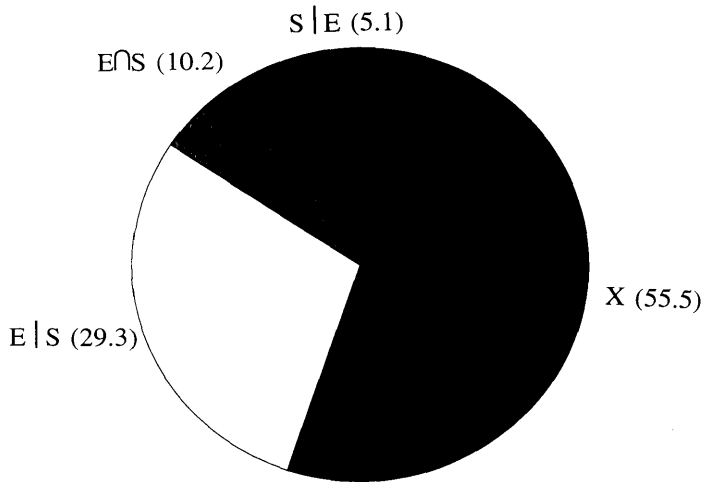


Fig. 63. Variation partitioning of the G49 species-sample plot matrix. E|S - nonspatial environmental variation; E∩S - spatially structured environmental variation; S|E - spatial variation that is not shared by the environmental variables; X - unexplained variation.

NUMERICAL CLASSIFICATION

The affinities of the most abundant species to the four TWINSPAN types are shown in Tab. 6. The four TWINSPAN types were distributed along DCA 1 without overlap (Fig. 64).

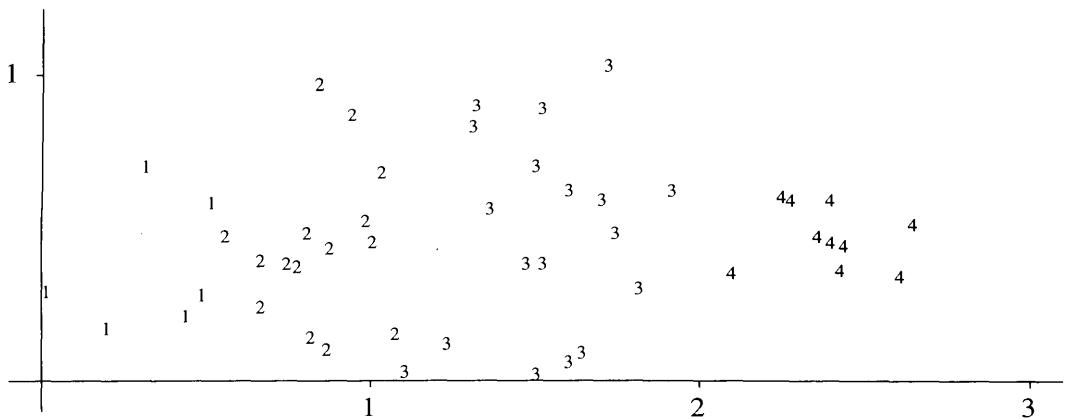


Fig. 64. TWINSPAN classification of the G49 data set (4-cluster level) plotted onto sample plot positions in the DCA ordination. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures.

Tab. 6. Survey table for the TWINSPAN numerical classification of the G49 data set into four vegetation types, N1-N4. Constancy percentage (C) and mean frequency in subplots (MFS) is tabulated for species with  $C \geq 50$  in at least one type.

Type	N1		N2		N3		N4	
	6		15		18		10	
Number of sample plots	C	MFS	C	MFS	C	MFS	C	MFS
<i>Empetrum hermaphroditum</i>	100	14.5	100	14.5	100	14.5	100	12.3
<i>Vaccinium vitis-idaea</i>	100	12.2	100	15.5	100	14.2	100	13.0
<i>Dicranum fuscescens</i> agg.	100	9.7	100	14.3	94	13.4	80	5.0
<i>Pohlia nutans</i>	83	3.4	100	6.2	94	8.0	100	7.0
<i>Cetraria islandica</i> agg.	83	6.8	93	11.6	100	15.3	100	14.7
<i>Cladonia coccifera</i> agg.	100	7.5	100	12.3	100	13.0	100	11.8
<i>Cladonia gracilis</i>	83	6.6	100	9.3	100	13.4	100	12.3
<i>Cladonia mitis</i>	100	8.7	100	15.1	100	15.8	100	14.5
<i>Cladonia pyxidata</i> agg.	67	3.0	73	3.6	100	5.0	90	3.0
<i>Cladonia rangiferina</i>	100	8.2	100	10.5	100	11.8	60	2.0
<i>Cladonia squamosa</i> agg.	100	7.2	100	11.3	100	10.6	100	8.4
<i>Cladonia stellaris</i>	67	10.3	100	12.5	100	14.5	70	5.4
<i>Cladonia uncialis</i> agg.	67	2.3	100	9.1	100	15.7	100	15.6
<i>Betula nana</i>	100	3.5	60	6.0	72	9.8	40	4.8
<i>Calluna vulgaris</i>	83	12.0	87	13.1	50	9.9	10	7.0
<i>Vaccinium myrtillus</i>	100	16.0	100	15.9	50	10.2	.	.
<i>Deschampsia flexuosa</i>	100	14.0	93	10.9	72	4.7	.	.
<i>Cladonia bellidiflora</i>	100	6.8	100	4.7	94	6.4	40	3.5
<i>Dicranum scoparium</i>	100	11.3	73	6.0	17	2.3	.	.
<i>Pleurozium schreberi</i>	83	15.2	87	7.5	6	13.0	.	.
<i>Barbilophozia floerkei</i>	100	12.2	100	9.1	6	3.0	.	.
<i>Barbilophozia lycopodioides</i> agg.	100	13.2	80	6.0	6	1.0	.	.
<i>Lophozia ventricosa</i> agg.	83	6.4	87	6.9	22	3.3	30	1.7
<i>Vaccinium uliginosum</i>	67	11.0	7	9.0	33	6.2	20	1.5
<i>Cladonia ecmocyna</i>	83	8.8	13	2.0	.	.	.	.
<i>Cladonia sulphurina</i>	17	1.0	93	3.7	89	5.1	40	2.8
<i>Phyllodoce caerulea</i>	.	.	53	3.0	39	7.1	10	7.0
<i>Barbilophozia attenuata</i>	17	1.0	53	3.1	6	2.0	.	.
<i>Loiseleuria procumbens</i>	17	1.0	47	3.4	67	8.4	100	12.2
<i>Carex bigelowii</i>	17	2.0	13	3.0	78	5.9	50	3.8
<i>Cetraria nivalis</i>	.	.	40	3.7	100	13.6	100	15.8
<i>Cladonia macrophylla</i>	.	.	13	2.0	78	5.4	100	2.2
<i>Polytrichum juniperinum</i> agg.	.	.	47	7.0	50	6.7	.	.
<i>Ptilidium ciliare</i>	.	.	7	6.0	50	4.9	10	1.0
<i>Cladonia phyllophora</i>	.	.	13	1.5	56	3.3	30	1.7
<i>Polytrichum piliferum</i>	.	.	.	.	33	2.3	60	6.5
<i>Alectoria nigricans</i>	.	.	.	.	28	3.4	100	9.9
<i>Alectoria ochroleuca</i>	.	.	.	.	28	2.8	100	11.1
<i>Cetraria cucullata</i>	.	.	.	.	28	3.0	50	6.0
<i>Comicularia aculeata</i>	.	.	.	.	22	2.3	100	13.7
<i>Thamnodia vermicularis</i>	.	.	.	.	17	3.0	100	8.5

Additional species (C < 50 in any vegetation type; vegetation type (C: MFS)):

*Betula pubescens* N3 (6: 1.0), *Pinus sylvestris* N3 (6: 4.0), *Andromeda polifolia* N1 (17: 3.0), N2 (47: 5.6), *Arctostaphylos alpinus* N1 (17: 1.0), N3 (17: 3.0), *Huperzia selago* N2 (7: 2.0), N3 (6: 3.0), *Trientalis europaea* N1 (17: 1.0), *Carex vaginata* N2 (7: 2.0), *Juncus trifidus* N3 (17: 3.0), N4 (20: 1.5), *Brachythecium reflexum* N2 (7: 1.0), *Dicranum affine* N2 (20: 1.7), *Plagiothecium laetum* agg. N1(17: 1.0), N2 (7: 1.0), *Polytrichum commune* N2 (7: 16.0), N3 (28: 3.2), *Racomitrium canescens* N4 (20: 3.0), *Sphagnum capillifolium* N2 (13: 5.0), *Anastrophyllum minutum* N2 (33: 5.0), N3 (33: 6.3), N4 (20: 3.5), *Barbilophozia binsteadii* N2 (20: 1.7), *Barbilophozia kunzeana* N1 (17: 1.0), *Calypogeia neesiana* N2 (27: 2.5), *Calypogeia sphagnicola* N2(13: 1.5), *Cephalozia lunulifolia* N2(20: 1.3), *Cephaloziella* spp. N1 (17: 3.0), N2 (20: 1.0), N3 (28: 2.4), N4 (20: 1.0), *Gymnocolea inflata* N4 (10: 3.0), *Gymnomitrium concinnatum* N4 (10: 2.0), *Lophozia bicrenata* N3(11: 1.0), N4 (10: 1.0), *Lophozia longidens* N3 (6: 7.0), N4 (10: 1.0), 46 *Marsupella* cf. *sphacelata* N4 (20: 5.5), *Mylia anomala* N2 (13: 2.0), *Tetralophozia setiformis* N3 (11: 2.0), N4 (40: 2.3), *Cladonia botrytes* N3 (6: 1.0), N4 (10: 1.0), *Cladonia comuta* N2(27: 3.3), N3 (39: 2.9), *Cladonia verticillata* agg. N2 (7: 1.0), N4 (40: 2.8), *Sphaerophorus globosus* N4 (20: 3.0), *Sphaerophorus fragilis* N4 (20: 1.5), *Sterocaulon* cf. *alpinum* N4 (20: 3.5).

Several species were absent from some types (Tab. 6). For example, *Vaccinium myrtillus* had its centre of gravity in types 1 and 2 and was absent from type 4. *Pleurozium schreberi*, *Barbilophozia lycopodioides* agg. and *Cladonia ecmocyna* were even more strongly restricted to types 1 and 2. *Cetraria nivalis* and *Cladonia macrophylla* were common in types 3 and 4, more rare in type 2, and absent from type 1. *Alectoria nigricans*, *Alectoria ochroleuca*, *Cornicularia aculeata* and *Thamnomia vermicularis* were common in type 4 while absent from types 1 and 2. *Phyllodoce caerulea*, *Polytrichum juniperinum* agg. and *Cladonia sulphurina* were examples of species with their centre of gravity in types 2 and 3.

## DISCUSSION

### ENVIRONMENTAL INTERPRETATION OF GRADIENTS IN VEGETATION

#### *The snow cover gradient*

The snow cover complex-gradient consists of many single environmental variables, e.g. topographic position, wind exposure, several temperature-based variables including length of the growing season, soil moisture and, to a lesser extent, soil nutrient status (e.g., Tengwall 1925, Dahl 1957, 1975, R. Økland & Bendiksen 1985, Svalheim & Wegener 1990). The snow cover complex-gradient is considered one of the most important gradients for alpine vegetation (see e.g. Vestergren 1902, Nordhagen 1943, Gjærevoll 1956, Dahl 1957, Bliss 1971, Sjørs 1971, R. Økland & Bendiksen 1985).

Evidence for interpretation of the main coenocline as a response to snow cover

Despite the lack of snow cover measurements in this study, the first DCA (and LNMDS) axes (representing the most important coenocline) are interpreted as a response to a snow cover complex-gradient. This interpretation is based upon:

(1) *Correlation of the first ordination axes with environmental variables that are expected to be correlated with snow cover.* Unevenness is one of the variables best correlated with DCA 1. The terrain on the exposed ridges with low and instable snow cover in winter is more even than further down the complex-gradient. This is probably due to the way the quaternary deposits are deposited at Gutulivola; larger stones and boulders are more abundant at protected places than on exposed slopes and ridges. Only weak correlations between ordination axes and unevenness are found in other studies from alpine areas (e.g., Svalheim & Wegener 1990). However, R. Økland & Eilertsen (1993) find increasing fine-scale unevenness (measured as in the present study) from the xeric to the submesic series (correspondence between series in the alpine and boreal zones is discussed by R. Økland & Bendiksen (1985)) in a S Norwegian coniferous forest. Some forest studies (e.g. Beatty 1984) indicate importance of microtopography also on coarser scales.

The strong correlation of cover of stones and rock with this coenocline reflects the increasing environmental harshness towards the ridges, e.g., increasing frost action (cf. Baadsvik 1974), resulting in slow development of vegetation and high risk of retrogressive development by wind erosion. Similar relationships are also indicated by R. Økland & Bendiksen (1985) and Svalheim & Wegener (1990). In the investigation area, these effects are likely to be strongly accentuated by the impact of reindeer herds. Contrary to the conclusions reached by Tømmervik & Johansen (1992), that the area Gutulivola - Drevsjø is in a good grazing condition, own field observations indicates that the vegetation is strongly influenced by reindeer grazing and trampling, particularly at the ridges, where poorly developed lichen specimens and signs of erosion are frequent. Strong winds redistribute the loose organic and inorganic material (cf. Baadsvik 1974); the less exposed sites acting as traps where organic debris accumulates (cf. Sheard & Geale 1983). The variation in loss on ignition along this coenocline may partly be due to this effect, but may also be due to properties of the soil of

the lichen-dominated ridges (Hinneri et al. 1975). The very thin humus layer of the ridges makes inclusion of mineral soil in soil samples hard to avoid (cf. similar observations in pine forests by Malmström (1949) and R. Økland & Eilertsen (1993)).

Soil moisture varies along this coenocline, as also observed by Tengwall (1925) and Jonasson (1981), among others. Variation in soil moisture is influenced by snow depth, duration, time of melting and the spatial distribution of snow in the terrain (cf. Dahl 1957). For instance, meltwater is a source of moisture for areas downslope (Dahl 1957, Billings & Bliss 1959, Isard 1986). Webber (1978) reports soil moisture to be the environmental variable most strongly correlated with the first coenocline in an ordination of Alaskan arctic vegetation. Other studies emphasizing the soil moisture gradient as an important gradient in Antarctic, Arctic or alpine vegetation are Billings & Mooney (1968), Dahl (1975), Whittaker (1987), Daniëls (1988) and Kappen et al. (1990). Williams et al. (1978) point out that soil moisture is one of the most prominent factors related to lichen distribution in the Arctic (also see Kappen et al. (1990)). The positive correlations between soil moisture, bryophyte cover, and humus organic matter content are likely to be due to a set of interacting factors: the denser the bottom layer and the higher the organic matter content, the less easily will the lee sides of ridges dry out. Furthermore, lee sides are better protected from desiccating winds than ridges (cf. Warren Wilson 1959). Such winds are especially important at the beginning of the growing season when the snow has disappeared (cf. Carlsson & Callaghan 1991). The correlation between soil moisture and DCA 1 might have been stronger if the soil samples used for moisture determination had been collected after a longer dry period and thus better represented soil moisture deficiency (cf. R. Økland & Eilertsen 1993).

A complex-gradient in nutrient availability is usually considered one of the most important gradients determining the variation in alpine vegetation (R. Økland & Bendiksen 1985). R. Økland & Bendiksen (1985) consider the snow cover and nutrient complex-gradients as independent. In pine forests on resistant bedrock, there are usually no significant variation in soil nutrient concentrations (R. Økland & Eilertsen 1993 and references quoted therein). However, in the middle and upper boreal spruce forests in Gutulia, a complex-gradient in nutrient status is the most important for differentiation of the vegetation (T. Økland 1993). Nutrient-based coenoclines in the alpine zones are documented by, e.g., Nordhagen (1928, 1943), Gjærevoll (1956), Dahl (1957, 1975, 1988), Sjørs (1971) and Svalheim & Wegener (1990). In this study, no obvious effects of nutrient variation are observed; total N and Ca do not show significant correlations neither with DCA 1 nor with DCA 2.  $\text{pH}_{\text{H}_2\text{O}}$  and  $\text{pH}_{\text{CaCl}_2}$  are significantly correlated with DCA 1, but not strongly so. Mg and S are the elements most strongly correlated with DCA 1. However, these elements are seldom considered as occurring in such small quantities that they limit plant growth (Sjørs 1971, Binkley & Vitousek 1989). The significance of these correlations, and the correlations between Na, Al and Zn and the major coenocline is not known. In tundra ecosystems, both Arctic and alpine, N and P are considered to be the most important nutrients limiting plant growth (e.g. Hinneri et al. 1975, Ulrich & Gersper 1978, Bowman et al. 1993). As with P, most of the N in the soil is organic and thus inaccessible to plants (Etherington 1982). From a theoretical point of view, the rates of N and P mineralization are likely to be better measures of the soil's ability to supply these nutrients than the total amounts (cf. Hesse 1971, Etherington 1982, Binkley & Vitousek 1989), but there are also difficulties connected with the use of mineralization rates as direct measures of availability (Binkley & Vitousek 1989).

(2) *Variation in biotic variables.* The main coenocline is associated with a shift from dominance by bryophytes to dominance by lichens. This shift is typically observed in almost

all alpine snow cover zonations published (e.g., Nordhagen 1928, 1943, Dahl 1957, R. Økland & Bendiksen 1985).

(3) *Variation in species abundances along the coenocline.* The distribution of species abundances supports the interpretation of the coenocline as a response to variation in snow cover. The chionophobic lichens (see Dahl 1957) are concentrated to the right hand side of the ordination diagram, while species known to demand a stable snow cover in winter are restricted to the left side of the diagram, e.g. *Vaccinium myrtillus* (Fig. 20) and *Cladonia cernocyna* (Fig. 49).

#### Effects of snow cover and associated environmental variables on vegetation

The main coenocline, from lichen-dominance to dominance by *Vaccinium myrtillus* and bryophytes, may be caused by the action of several among the correlated variables. R. Økland & Eilertsen (1993) interpreted a corresponding coenocline from xeric to submesic forests as primarily caused by tolerance to extreme drought (the soil moisture deficiency hypothesis). Increasing importance of shelter and variables associated with duration and stability of the snow cover towards alpine zones is stressed by Nordhagen (1928, 1943) and R. Økland & Bendiksen (1985). In the mountains, the snow is distributed in largely the same manner year after year, depending on topography and the fact that the prevailing winds during the winter are much the same over the years (e.g. Nordhagen 1943, Dahl 1957, Gjærevoll & Bringer 1965). The strong winds redistribute the snow from exposed slopes and ridges to protected depressions, resulting in a pronouncedly uneven distribution of the snow cover within short distances. Late-lying snowbeds and windswept dry ridges constitute the two extremes along the snow cover gradient (cf. Billings & Mooney 1968, R. Økland & Bendiksen 1985).

Increasing duration of snow cover implies protection of the plants from low temperatures, severe frost, desiccation, wind-induced erosion etc. (Dahl 1957, Longton 1988). Many species avoid the ridges, where a permanent snow cover is lacking even in the winter. Under the extreme conditions of ridges, the lichens make up the most abundant element (cf. Tab. 6). Many lichens, e.g. *Alectoria* species, are adapted to withstand mechanical stress and they are also able to photosynthesize under extreme conditions (Kappen 1973, Daniëls 1988, Kappen et al. 1990). A factor favouring lichens on dry ridges is their capability to use atmospheric moisture directly for photosynthesis (Williams et al. 1978). Lichens are generally considered more drought-tolerant than bryophytes (Kappen 1973). With very long duration of snow cover, the growing season is strongly reduced (Nordhagen 1943, R. Økland & Bendiksen 1985). Species of snow-beds (not included in this study) are characterized by several traits enabling them to utilize the short growing season (e.g., Resvoll 1917, Sveinbjörnsson & Oechel 1992).

#### *The microclimatic gradient*

Interpretation of the second ordination axes as a response to a complex-gradient associated with microclimate is based upon the strong correlations with aspect and the heat index; very few significant correlations exist with other variables. Sample plots with the most favourable aspect (S-facing slopes; sample plots from transects 2 and 3) have low DCA 2 scores. The two strongly correlated variables aspect and heat index are likely to express similar facets of microclimatic variation.



Microclimate as an important determinant of variation in vegetation is demonstrated for other ecosystems by, e.g., Dargie (1984), Rajakorpi (1987), Tong (1989), Heikkinen (1991) and Rydgren (1993).

According to Skartveit et al. (1975), the varying amounts to, and exchange properties of, radiant energy input to the surface are the main factors governing the microclimate during the snow-free period. Temperature is recognized as one of the most important factors limiting productivity in tundra ecosystems (e.g. Scott & Billings 1964, Billings & Mooney 1968). The average temperatures during day and night may differ considerably between south- and north-facing slopes; the south-facing slopes much warmer (cf. Baadsvik 1971). The importance of the microclimate in alpine areas is discussed by for instance, Baadsvik (1974), who shows restriction of some plant communities to south-facing slopes in a C Norwegian area (cf. also Nordhagen 1928, 1943, Dahl 1957).

#### SOURCES OF VARIATION IN SPECIES ABUNDANCES

The figures given for the fractions of variation in species abundances possible to explain by different sets of explanatory variables, are not strongly different from corresponding figures for a boreal S Norwegian pine forest (R. Økland & Eilertsen 1994). They found a TVE of 44.6% (44.5% here), of which 55% (66% here) was due to environmental factors alone, 17% (23% here) was shared environmental and spatial variation, and 28% (11% here) was strictly spatial. The general significance of these figures and the differences between them cannot be evaluated before more studies applying the variation partitioning approach to comparable vegetation are available for comparison.

The low fraction of purely spatial variation in the data set, and the relatively high fraction of variation explained by environmental variables, may indicate that all the important complex-gradients have been adequately represented among the environmental variables (Borchard et al. 1992, R. Økland & Eilertsen 1994). Unexplained variation constitutes about half the total variation (55%). Although appearing high, even larger fractions of unexplained variation was observed in spruce forest by R. Økland & Eilertsen (1994). It might well turn out that the figure of 44.5% found for TVE in this study is high relative to other studies, indicating that the structuring effect of the snow-cover complex-gradient on vegetation is among the stronger exhibited in boreal and alpine systems. Unexplained variation may be due to stochastic variation, unmeasured environmental variables or more complex spatial structures not explicable by the set of spatial variables (cf. Borchard et al. 1992).

#### CONSIDERATIONS FOR MONITORING: CHOICE OF VEGETATION TO BE MONITORED

The homeostatic power of the ecosystems of the world's cold region is generally considered to be lower than for most other ecosystems (Crawford 1989). The effects of pollutants on plants are considered to be more serious in these areas, where the metabolic activity is at a

minimum. Furthermore, alpine vegetation may possibly be a more easily read indicator of changes caused by pollutants than forest vegetation (cf. Bråkenhielm 1988).

Careful considerations are necessary before choosing what kind of alpine vegetation to include in vegetational and environmental monitoring, as alpine vegetation varies considerably over short distances due to fast changing environmental conditions (see e.g. Dahl 1957). In monitoring, as well as in general-purpose ecological analysis, inclusion of variation along gradients is strongly recommended (T. Økland 1990, R. Økland & Eilertsen 1993). Data sets with moderate to high  $\beta$  diversity are greatly preferred, as ordination techniques based on the correspondence analysis concept perform best under such conditions (ter Braak & Looman 1986, R. Økland 1990).

Possible effects of airborne pollutants are likely to be overridden in those alpine vegetation types experiencing strong environmental stress. Such vegetation types are likely to be poorly suited for monitoring purposes, at least until knowledge about their natural dynamics is available. Examples may be vegetation influenced by solifluction and snow-beds. Solifluction exerts a pronounced effect on alpine vegetation, increasing its importance with altitude (cf. Sjørs 1967). In the high-alpine belt all soils are influenced by solifluction (Dahl 1957). Solifluction is likely to be associated with an unstable and rapidly changing vegetation. Snow-bed vegetation displays a very complex pattern of variation (cf. Nordhagen 1943, Gjærevoll 1949, 1956, Dahl 1957, R. Økland & Bendiksen 1985, Svalheim & Wegener 1990), frequently with dominance of one or a few species, but also often with abundance of densely interwoven mats of small species, e.g. hepatics, that are almost impossible to record nondestructively in the field.

Gutulia is suited for monitoring purposes as the bedrock is poor and snow-beds are almost nearly lacking (cf. Wold 1989). An argument against the use of the alpine areas in Gutulia for monitoring purposes is the grazing by domesticated reindeer herds. Future vegetation changes due to alterations of the grazing pressure may interfere with, and be hard to separate from, the effects of airborne pollutants. Comparisons with the ongoing NIJOS monitoring of spruce forest in Gutulia (T. Økland 1993) may possibly aid such a separation.

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