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O. Eilertsen

Vegetation patterns and structuring processes in coastal shell-beds at Akerøya, Hvaler, SE Norway.

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The vegetation of shell-beds is studied in an island on the coast of Skagerak, SE Norway. Within this restricted area 125 sample plots, 1 m^2 each, were distributed by a restricted random procedure. Frequency in subplots and percentage cover were used for estimation of species abundance. A set of 33 environmental variables was obtained from each sample plot. Ecological gradients corresponding to the main vegetational gradients are identified by means of DCA ordination results correlated with environmental data. DCA ordination results are further interpreted by the use of an earlier classification of the vegetation and by application of Grime's strategy concept. The following complex gradients were recognized: (1) the primary successional gradient, influenced by variables dependent on site age, e.g. elevation, distance from the sea, and rate of decomposition of mollusc shells, (2) the secondary successional gradient, from open meadow vegetation via open shrub vegetation to dense shrub vegetation, highly correlated with variables independent of site age, e.g intensity of grazing, (3) the nutrient availability gradient, and (4) the soil moisture gradient. Interpretation of relations between coenoclines and environmental variables was performed by Kendall rank correlation and relationships among ecological variables analysed by PCA ordination. Direct gradient analysis by *rh*-DCCA is used as a supplement to DCA. The ratio between the *rh*-DCCA eigenvalue of the first ordination axis and the corresponding eigenvalue of the first residual (unconstrained) axis is used to quantify the importance of each environmental variable. The performed multivariate analyses show that the successional pathways on shell-bed shores are dependent on the grazing pressure. The relative importance of the following structuring processes is discussed: (1) interspecific interaction (competition, coexistence and facilitation), (2) destabilizing factors (disturbance and fluctuations), (3) stress, and (4) chance. Ordination and association analyses shows that *Juniperus communis* is the most important structuring species in the material. Grazing is necessary to reduce overgrowth by junipers and to maintain a high species diversity.

The field data are used for inspection of the performance of different rescaling and detrending options, available with DCA ordination. Non-linear rescaling appears to be less influenced by deviant sample plots as compared to linear rescaling, and the S.D. units of the axes produced by non-linear rescaling are considered better interpretable in terms of a unimodal model of species responses to ecological gradients. Available options for detrending by polynomials are shown to be inferior to the detrending by segments option, as polynomial detrending may impose a polynomial distortion on the point configuration in the ordination space.

Keywords: Association analyses, DCA, Detrending, Environmental gradients, Evolutionary strategies, Hybrid-CCA, Non-linear rescaling, Ordination, Patch dynamics, Succession.

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CONTENTS

INTRODUCTION

The flora on shell deposits in the Oslofjord area and along the west coast of Sweden has been studied by e.g. Størmer (1936), Nilsson (1934, 1945), Hauge (1948) and Ryvarden (1972). The vegetation on shell deposits in the same area has been studied by Breien (1933), Hallberg (1959, 1965, 1971), Hallberg & Ivarson (1965) and Halvorsen (1980). Numerical classification of shell-bed vegetation at Akerøya was accomplished by Halvorsen (1980) who interpreted the results of numerical classification and ordination in terms of succession from naked shell-beds to species-rich pastures and dense shrubs. The effect of grazing on coastal grassland areas has not been much addressed by Norwegian ecologists, but several Swedish studies emphasize changes in vegetational composition and standing crop in relation to grazing by cattle and sheep on limestone grasslands, e.g. Sjögren (1971), Rosén & Sjögren (1973, 1974), Rosén (1982).

The use of multivariate techniques has increased steadily since their introduction to ecologists in the 1950s and early 1960s (Kent & Ballard 1988). In the last decade DCA and MDS have become established as the prevailing ordination concepts in studies by Fennoscandian ecologists. Studies by Oksanen (1983, 1984), Verwijst & Cramer (1986), Cramer & Hytteborn (1987), Lahti & Väisänen (1987), T. Økland (1988, 1990), R.Økland (1989, 1990a), Tonteri et al. (1990a, 1990b), can be mentioned. Recent theoretical vegetation science is characterized by an overall emphasis on vegetation theory, from which both dynamic phenomena and appropriate choice of numerical methods are approached (van der Maarel 1989).

Multivariate methods have proved to be important tools in studies of the vegetation dynamics. For instance, many papers show how careful description of patterns can elucidate the probable underlying processes, e.g. the proceedings of the late 1980's IAVS symposia (Prentice & van der Maarel 1987, Miles et al. 1988). The use of multivariate methods have consolidated earlier vegetational knowledge, and brought it to a level where the theoretical framework can be more easily explained, generalized, tested and integrated with data of e.g. the environment, ecophysiology and population dynamics.

Vegetation ecologists have devoted much attention to multivariate methods in the 1980's. For instance, the ordination methods have been evaluated with respect to applicability, interpretability, instability etc., both in real and simulated data-sets (cf. Minchin 1987, Oksanen 1988, R. Økland 1990c). The increase in the use of these methods has given valuable experience that is necessary for a further methodological development. A prerequisite for application of ordination methods is that they perform satisfactorily when subjected to thorough tests on simulated data-sets. Further use of different ordination methods with different methodological options and data manipulations will continue to give information relevant to improvement of models.

The aims of this investigation are: (1) to identify the main vegetational gradients in the shell-beds of Akerøya, and the corresponding environmental complex-gradients, (2) to discuss the main structuring processes in this vegetation, (3) to assess effects and give recommendations on different management regimes, and (4) to evaluate different methodological options available in DCA ordination.

THE INVESTIGATION AREA

GEOGRAPHICAL SITUATION

Akerøya is an island in the Hvaler archipelago, Østfold county. The estimated size of the island is 1.6 km^2 (Ryvarden 1972). Akerøya is freely exposed to Skagerak, situated on the east side of the Oslofjord (Fig. 1).

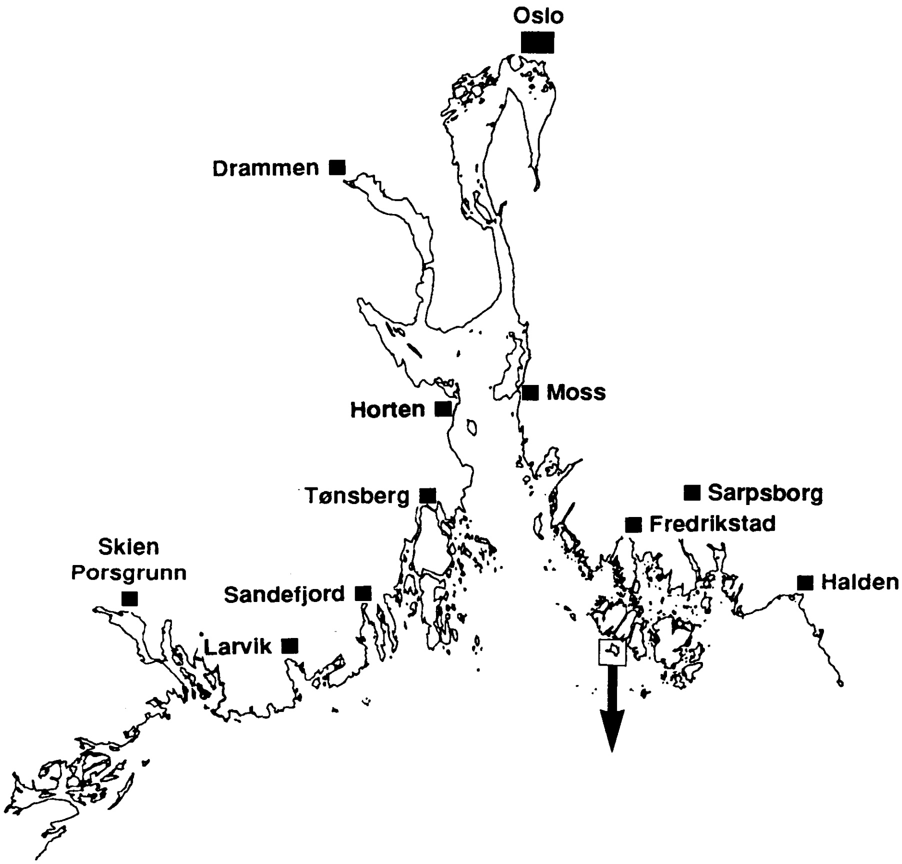


Fig. 1. The position of Akerøya relative to the Oslofjord.

BEDROCK AND SHELL DEPOSITS

The Precambrian bedrock mainly consists of granites. Barth (1960) estimated the contents of SiO_2 at 75%. The highest point of Akerøya, Reduten, is situated 32 m above sea level (Fig. 2). According to the investigation of shore-line displacement in southern Østfold by Danielsen (1970), Akerøya first became dry land towards the end of the Atlantic period, about 6000 B.P. The highest situated shell deposits occur at 16 m above sea level, and were deposited in the Subboreal period, ca 4000 B.P. A brief survey of mollusc composition in the shell-beds is given by Halvorsen (1980). Strongly decomposed gastropod shells dominate the upper shell-beds; in the lower shell-beds less decomposed pelecypod shells mostly. The depth of the shell deposits varied from zero where bordering on rock outcrops, to more than 1 m in depressions. The altitude of the shell-beds, *SB 1-22*, is shown in Fig. 2.

TOPOGRAPHY AND HYDROLOGY

The western part of Akerøya is relatively plane, situated below 3 m above sea level (Fig. 2). The shell-beds occupy slightly convex to slightly concave areas, and include slopes and depressions. Shell-beds bordering on elevated rock outcrops often receive seepage water from above.

The higher central part of the island is situated from 5 to 16 m above sea level. Shell-beds vary with respect to aspect. The influence of seepage water is limited; however one of the shell-beds, a partly excavated sand-pit, *SB 8*, is strongly concave, and in spring mostly containing standing water.

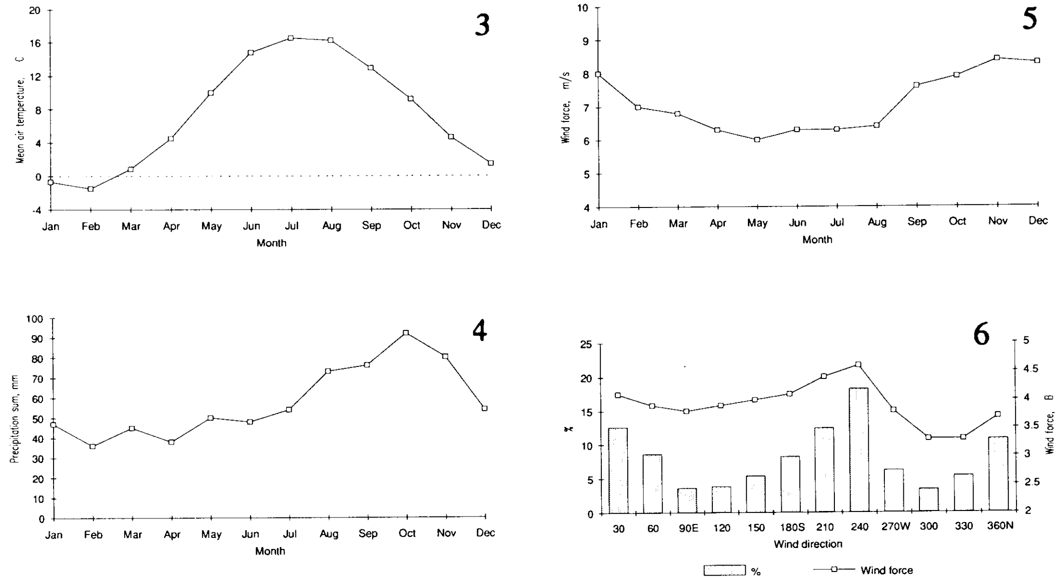
The southern part of the area varies with respect to both aspect and inclination. The sites are situated up to 10 m above sea level. Most of the sites are plane to convex. Apart from a few concave fissures of restricted areal extension and hence at least seasonally abundant water supply, most sites are convex and well drained.

All epilittoral sites were at more than 1.0 m above the water level, while the littoral sites were situated in a zone 0.30 m to 0.90 m above the water level. The altitude of each site is given with respect to the reference level for the ebb tide at vernal equinox. Data of the water levels in outer Oslofjord, taken from the nearest station Helgeroa, is given by the Norwegian Hydrographic Service. Measurements are given for 1990, but the data shows insignificant annual deviation. The altitude for mean low tide is 0.14 m, mean water level is 0.25 m, mean flood tide is 0.39 m, and flood tide at autumnal equinox is 0.50 m. The highest observed water level is 1.44 m.

CLIMATE

The coastal areas of the outer Oslofjord are situated within the Boreonemoral zone (Dahl et al. 1986). The climate is relatively humid, suboceanic. Climatic data, Figs 3-6, are given by

Fig. 2. Map of Akerøya, showing the delimitation of the 22 shell-beds, *SB 1-22*, in the investigation area. The number of the sample plots within each shell-bed is specified. Contour interval: 5 m.



Figs 3-6. Meteorological data from Færder Fyr, for the normal period 1961-1990. - Fig. 3. Monthly mean air temperature. - Fig. 4. Monthly mean precipitation. - Fig. 5. Monthly mean wind force. Data from Ferder Fyr, for the normal periode 1961-1990. - Fig. 6. Percentage distribution of different wind directions and wind forces during the year.

the Norwegian Meteorological Institute, Climate Department. Measurements from the nearest meteorological station, Færder (17 km west of Akerøya), are given for the normal period 1961-1990. Annual mean temperature is 7.4 °C. Fig. 3 shows the monthly mean temperatures during the year. Mean annual precipitation is 693 mm. Fig. 4 gives the distribution of the monthly mean precipitation during the year. Fig. 5 gives a survey of the mean wind force through the year. The prevailing seasonal wind direction is N in winter and SW during the rest of the year. Fig. 6 shows the frequency distribution of the different wind directions during the year.

MANAGEMENT AND HUMAN INFLUENCE ON THE VEGETATION

The start of agriculture in southern Østfold is estimated to be the transition between the Atlantic and Subboreal periods, 5000 years B.P. (Danielsen 1970). According to Halvorsen (1980), Akerøya has probably been influenced by man since the first establishment of stable vegetation. Ryvarden (1972) and Halvorsen (1980) give brief accounts of human activities up to 1979. From 1980 the grazing intensity on the island has been regulated to 120 sheep. The grazing starts in May and lasts until November.

Akerøya is an important area for outdoor recreation, due to its central position in the fairway to Sweden. The central part of the island is used for recreation, and includes a harbour, a camp with a water post and a restored fortification from 1660. Almost all human activity is canalized in this area.

The western and the southern parts of Akerøya were protected as a nature reserve in 1978, and restrictions were imposed upon human entry to it in the bird breeding season, from April 15 to July 15.

MATERIALS AND METHODS

The field work was carried out during the summers of 1982 and 1983.

THE SAMPLING METHODOLOGY

The positions of the 22 shell-beds studied, *S1* - *S22*, are shown in Fig. 2. From the epilittoral, 15 large shell-beds, selected from the 32 shell-beds studied by Halvorsen (1980), make up Subset *A*. The remaining 7 shell-beds situated in the littoral zone constitute Subset *B*.

The entire dataset, *AB*, consists of 125 sample plots, each 1 m^2, placed according to a restricted random procedure. The number of sample plots per shell-bed was proportional to the shell-bed area, although with a minimum of 2 sample plots per shell-bed, to avoid a poor representation of shell-beds in the geolitteral zone. The sampling procedure did not impose any restrictions upon statistical treatments for Subset *A*, as each point has the same probability of being chosen (cf. Greig-Smith 1964). Sample plots in Subset *B* are, however, slightly overrepresented in the entire dataset.

The sample plots were analysed twice, in April-May and in June-July. This enhanced inclusion of the full species composition, and facilitated determination to species of even heavily grazed specimens. Each sample plot was divided into 16 subplots, each of 0.0625 m^2 (25 cm x 25 cm). Presence/absence of all species was recorded for each subplot, and frequency in subplots was used for estimation of species abundance. As a supplement, percentage cover was recorded; the total cover of the shrub, field and bottom layers, bare patches and rocks, and the total cover of each species.

ENVIRONMENTAL MEASUREMENTS

Measurements of abiotic and biotic environmental variables were made for interpretation of vegetational patterns as summarized by the ordinations.

External environmental variables

A set of variables was used to describe the position of the site in relation to different external environmental factors.

Elevation was measured with a standard optical levelling instrument at the centre of each sample plot. The horizontal control point at Reduten, 31.56 m above the sea level (according to the Norwegian Hydrographic Service), was taken as basis for levelling. The sample plot altitude was used for ranking of sample plots according to site age.

Distance from the sea was measured in the centre of each sample plot with a standard tachymetrical instrument. The value was used as an indication of the impact of sea spray, physical forces and salinity.

Aspect was measured as degrees and converted to a linear five-point scale along a gradient from NNE (25^{o}) to SSW (225^{o}), in accordance with Dargie (1984). SSW (225^{o}) is considered to be the most favourable aspect due to the high incoming radiation at times of the day with highest temperatures, thus $225^{o} \pm 40^{o}$ is given the highest value.

Inclination was measured with a clinometer.

Exposition to wind was measured with a standard wind gauge 5 times during fieldwork, in each sample plot. The mean value was calculated and transformed to a linear five value scale.

Effects of grazing and trampling were subjectively judged from observations in the field combined with information of topography, passability, disturbance etc. for each sample plot and scored on a five point-scale.

Soil variables

Volumetric soil samples were taken from the upper 5 cm of the shell/humus layer at 4 fixed points around each sample plot. The subsamples were mixed in order to counteract the spatial variation in physical and chemical properties of the soil, as recommended by e.g. Zhang (1983). All soil samples were brought to the laboratory and frozen the same day they were collected.

Soil moisture was determined gravimetrically (cf. Andersson & Ericson 1963) as the ratio between the weight of soil dried at 105^{o}C (until constant weight) and the weight of fresh soil.

Loss on ignition was determined according to a standard procedure (Andersson 1970). To calculate the variance, 5 parallels from each of 5 selected soil samples were run. The variance within each set of parallels was small as compared to the variance of the sample plot means for the entire dataset.

Mechanical composition of the soil was determined after dry sieving, with mesh widths of 2 mm, 0.63 mm, 0.2 mm, and 0.063 mm (the standard logarithmical scale used by the Norwegian Geotechnical Institute). The cylinder of sieves was put to horizontal shaking, 300 min^{-1}, for 10 minutes. The percentage of the soil sample in each of the following soil-fractions was calculated; (1) coarse fraction > 2 mm, (2) coarse fraction > 0.63 mm, (3) fine fraction < 0.2 mm and (4) fine fraction < 0.063 mm.

Soil samples were analysed chemically. Five parallels from each of 5 selected soil samples were run. The intra-plot variation was small relative to inter-group variation.

Ph was measured electrometrically by a standard Ph-meter (Radiometer PHM 83 Autocal) in a sedimented water suspension (Baadsvik 1974).

Extraction of exchangeable cations was performed according to recommendations from the Norwegian Agricultural Service Laboratory (A.R. Selmer-Olsen, pers. comm.); 100 ml neutralized 1M NH_4Ac solution was added to 20 g of the soil fraction, < 2 mm, shaken and left overnight. The solution was then filtered into a 250 ml volumetric flask. The soil was repeatedly washed out with 1M NH_4Ac to make a total leachate of 250 ml.

Sodium and potassium were determined in the extract, diluted in a cesium chloride solution (Schollenberger & Simon 1945), by atomic absorption spectrophotometry (Varia-tectron AA-5). [Na^+] and [K^+] are given as m.e./100 g fine soil and in percent of CEC.

Calcium and magnesium were determined in the extract, diluted in a strontium chloride solution, by atomic absorption spectrophotometry. $[Ca^{2+}]$ and $[Mg^{2+}]$ are given as m.e./100 g and in percent of CEC.

Exchangeable hydrogen (exchangeable acidity of the soil) was determined by titration of the extract with 0.05M NaOH solution until Ph = 7 (Radiometer PHM 80). $[H_3O^+]$ is given as m.e./100 g.

Exchangeable cations, CEC, was calculated as the sum of $[Na^+]$, $[K^+]$, $[Ca^{2+}]$, $[Mg^{2+}]$, and $[H_3O^+]$, and given as m.e./100 g.

Total amount of nitrogen was determined according to the Kjeldahl method. Fine soil was treated with concentrated H_2SO_4 by means of Tecator Digestion System 6 and transferred to a Tecator Kjeltec System 1002 Distilling Unit, and the ammonium was measured by a standard colorimetric method. Total N was given as percent of soil weight and as percent of organic content.

Phosphorus was determined by means of AL-extraction (Egener et al. 1960). Colorimetric analysis (Harwood et al. 1969) was performed by the Norwegian Agricultural Service Laboratory. Concentrations were given as mg/100 g fine soil and in percent of organic content.

Chloride was determined by $Ca(NO_3)_2$ extraction (Bolton 1971). Colorimetric analysis was performed by Norwegian Agricultural Service Laboratory. $[Cl^-]$ was given in mg/100 g fine soil.

DATA EDITING

Editing of vegetation data was performed by BDP (Rustan 1984, Rustan & Pedersen 1988, Pedersen 1988). The entire vegetation dataset, *AB*, was edited into a 231x125 matrix, treating each species as one row and each sample as one column. The main matrix was separated into Subset *A*, epilittoral sites, and *B*, littoral sites, to remove the most obvious floristic heterogeneity. Subset *A* made up a 221x111 matrix.

Downweighting of rare species was performed according to the standard option in CANOCO version 2.1 (ter Braak 1987b). The use of median frequency as basis for downweighting as proposed by Eilertsen & Pedersen (1988) gives no essential improvement on this dataset, in contrast with datasets containing one or more highly frequent species, and having a large share of rare species (Eilertsen et al. 1990). All species with frequency below 20% of the frequency of the most common species were downweighted in proportion to their frequency (Hill 1979).

Weighting of matrix elements was performed by the power function (van der Maarel 1979, Clymo 1980);

$$y_{ij} = f(x_{ij}) = a \cdot x_{ij}^{w},$$

where x_{ij} is the original and y_{ij} the weighted value of species *i* in sample plot *j*, a is a ranging scalar, and w the weighting parameter. Unweighted values of frequency in subplots, w = 1, gives a scale range of 16 (R. Økland 1986a). To promote comparability between the two abundance scales (Eilertsen et al. 1990), the range of the percentage cover scale was transformed to 16, which gives;

$$w = \ln 16 / \ln 100 = 0.6$$

This corresponds to an intermediate range of the scale, as recommended by Jensén (1978), van der Maarel (1979), Gauch (1982a) and R. Økland (1986a).

By using the presence/absence data of the 16 subplots in all 125 sample plots, a 231x2000 matrix was created. This binary scale addresses qualitative variation only (Smartt et al. 1974a, 1974b, Jensén 1978, R. Økland 1986a, Eilertsen et al. 1990).

CLASSIFICATION

Classification of vegetation data

The sample plots were subjectively classified by means of their floristic content, using the classification of shell-bed vegetation by Halvorsen (1980). Halvorsen numbered the blocks from I to VII, to reflect the main hypothetical successional pathways. Accordingly, the sample plots from the geolitteral zone (Subset *B*), not included in Halvorsen (1980), were considered a block on their own and termed Block 0.

Classification by means of the C-S-R model

Grime (1974) proposed a classification of plant species according to evolutionary strategy. The three viable combinations of high and low stress with high and low disturbance have been associated with following primary strategies of the established phase (Grime 1977): (1) competitors, C, (2) stress-tolerators, S, and (3) ruderals, R. A number of 86 species (all species in the *AB* dataset, included in the survey by Grime et al 1988) were given partial C, S and R values, according to indications of their established strategy given by Grime et al. The sum of partial C, S and R value was constrained to be 12 for each species. For all sample plots, the prominence of each strategy was calculated by addition of the species values, divided by the sum of all three partial species values.

ORDINATION AND ECOLOGICAL ANALYSES

Ordination analyses were performed by the CANOCO program (ter Braak 1987b) on the VAX-cluster at USE, University of Oslo. Statistical analysis was processed by SPSS/PC+ (Norušis 1983) on a personal computer and $SPSS^X$ (Norušis 1987) on VAX.

DCA ordination

Detrended Correspondence Analysis (DCA; Hill 1979, Hill & Gauch 1980, Ter Braak 1987b) was used for indirect gradient analysis (ordination). As the vegetation is a function of environmental factors (Whittaker 1956, 1967), the DCA axes are coenoclines interpretable in ecological terms. DCA was performed with (1) the entire *AB* dataset, using either frequency in subplots or percentage cover transformed to r = 16, as abundance scale, (2) Similarly, with Subset *A*, and (3) the *AB* dataset of 2000 subplots. Heterogeneity within the sample plots was assessed by visual inspection of the ordination subplot score dispersion. Ordination stability was assessed by studying the conformity between the different DCA ordinations.

Methodological options in correspondence analysis

Nonlinear rescaling of ordination axis was performed in order to provide reliable gradient length estimates, in S.D. units (Hill 1979, Knox 1989). To evaluate relative performance of nonlinear rescaling, all ordinations were performed with linear rescaling as well. As an index of sample-plot distribution along DCA axis c, the following was used

$$l_c = g_{90} / g_{100},$$

where g_{90} is the shortest segment of the axis comprising 90% of the sample plots and g_{100} is the gradient length.

Detrending was performed to remove the arch effect. Four detrending methods were compared; detrending by segments and detrending by 2nd, 3rd and 4th order polynomials. The first two axes of the DCA ordinations were considered.

rh-DCCA ordination

Detrended canonical correspondence analysis (DCCA; ter Braak 1987a, 1987b) was used for direct gradient analysis. The analysis was used to extract one "canonical" axis, i.e. an axis constrained by a supplied environmental variable. A (rescaled) hybrid analysis, rh-DCCA, was performed, in order to estimate the residual variation after extracting the constrained axis. An expression of the importance of an environmental variable within a dataset was given by the ratio

$$r = e_{C1}/e_{R1}$$

where e_{C1} is the eigenvalue of the canonical axis and e_{R1} is the eigenvalue of the first unconstrained residual axis. The ratios for Dataset *AB* and Subset *A* are denoted r_{AB} and r_A, respectively. To compare the contribution of the environmental parameter in relation to the total floristic variation an importance ratio *i* was expressed as;

$$i = e_{C1} / e_{DCA1}$$

To evaluate the effects of removing Subset *B* from Dataset *AB*, the ratio $\delta_{A,AB}$ was defined as

$$\delta_{A,AB} = i_A / i_{AB}.$$

If $\delta_{A,AB} > 1$, the importance of the investigated environmental variable has increased, and if $\delta_{A,AB} < 1$, it has decreased.

PCA ordination of environmental parameters

Principal component analysis, PCA, was performed by CANOCO (ter Braak 1987b). PCA ordination requires linear relationships between the environmental variables and the underlying environmental complex-gradients (ter Braak & Prentice 1988). In general, environmental variables satisfy this criterion. The ordination of environmental parameters was performed on a secondary ecological variable/sample plot matrix, formed by centring and division by standard deviation of variables in order to make the environmental variables comparable and with equal weight.

Nonparametric correlation analysis between environmental parameters

Correlation analysis was performed by procedure NONPAR CORR in SPSS^X based on Kendall's τ (Conover 1980). A.R.E., asymptotic relative efficiency, for this test is given by Stuart (1956). Fenstad et al. (1977) emphasize Kendall's τ in preference to Spearman's σ when compared by stochastic simulation under normal and heavy tailed distribution of errors. The correlation coefficient was used as a test statistic to test for independence between two random variables, X and Y;

$$\tau = \frac{N_c - N_d}{n(n-1) / 2}$$

where N_c denotes the number of concordant and N_d the number of discordant pairs of observations (Conover 1980), and n is the number of observations.
In the two-tailed test the null hypotheses are;

H_0: X_i and Y_i are mutually independent.

The alternative hypothesis, H_1, is the conveniently negations. For each pair of variables correlation coefficients and significance probabilities are given.

ANALYSIS OF INTERSPECIFIC ASSOCIATIONS

Association analysis was performed by chi-square test for independence (Conover 1980). The data were arranged into 2x2 contingency tables, in which the rows, R_i, represent the number of subplots in which species *i* is present and absent, respectively, and the columns, C_j, the corresponding data of species *j*. Then H_0 is

$$H_0\colon\ P(R_i,C_j) = P(R_i) \cdot P(C_j),$$

while H_1 is the conveniently negation. The test statistic is given by

$$\chi^2 = \sum_{i=1}^{2}\sum_{j=1}^{2} \frac{(n_{ij} - E_{ij})^2}{E_{ij}}$$

where n_{ij} is the observed number of sample plots categorized in the *i*th row of the *j*th column, and E_{ij} is the expected number of sample plots in the *i*th row of the *j*th column given H_0 is true.

Associations between pairs of species were evaluated in separate blocks of the data set; an early successional phase (Blocks I-II), an intermediate successional phase (Blocks III-IV) and an established phase (Blocks V-VII). Thus, the number of negative associations due to niche separation along major environmental gradients is reduced.

Associations between pairs of species were considered positive when two species co-occurred more often than expected and negative when two species co-occurred less often than expected, at the 5% probability level. The associations were nonsignificant when the observed proportion of joint occurrences did not depart significantly from the expected value. Symbols were given to quantify the degree of significant association ($\chi^2 > 3.84$);

Interspecific association;	Positive	Negative
$\chi^2 < 6.25$	+	-
$\chi^2 \in [6.25\ ,\ 12.5>$	++	--
$\chi^2 \in [12.5\ ,\ 25>$	+++	---
$\chi^2 \in [25\ ,\ 50>$	++++	----
$\chi^2 \in [50\ ,\ 100>$	+++++	-----
$\chi^2 \in [100\ ,\ 200>$	++++++	------
$\chi^2 > 200$	+++++++	-------

Associations were calculated between each species *i* that occurred in more than 30% of the subplots and all other species occurring in more than 10% of the subplots in the blocks in question. The sum of χ^2 values between species *i* and all other species *j* was calculated for all *i*.

NOMENCLATURE

The nomenclature of vascular plants follows Flora Europaea (cf. Moore 1982). Mosses follow Corley et al. (1981) and hepatics follow Grolle (1976). Lichens follow Krog et al. (1980).

RESULTS

CLASSIFICATION OF VEGETATION

A survey of the 231 species registered in this study, and their abbreviations, is given in Tab. 1.

Classification of species by means of the C-S-R model

Tab. 1 shows the classification of 86 species according to plant strategy. The distribution of primary C, S and R strategies were 3, 12, and 7 respectively. The secondary strategies showed the following distribution; CS 3, CR 4, SR 9 and CSR 15. The sum of partial values for all 86 species were; C 231, S 423 and R 378 (competitors 22%, stress-tolerators 41%, and ruderals 37%).

Classification of sites

The vegetation of shell-beds at Akerøya was classified into 8 blocks. Some sites differed from the rest and did not fit into the classification. Because of the low number of plots, they were not considered to constitute new blocks, but instead described as "lost units". Tab. 2 gives a survey of the most important species in each block.

Below, the exclusive species (characterized only by occurrence in one block), and the constants (occurrence in more than 75% of the sample plots) are listed.

Block 0 consisted of 14 sample plots, all in the littoral zone, directly exposed to sea spray. Exclusive species in this vegetation type were *Glaux maritima, Sagina maritima, Spergularia marina, Juncus gerardi, Puccinellia maritima* and *Desmatodon heimii*. Constants were *Agrostis stolonifera* and *Plantago maritima*.

Block I occurred in a narrow zone of shallow soil, 1-2 m above sea level. The 15 sample plots were only directly exposed to sea spray when there were strong winds and rough sea. The only exclusive species was *Urtica dioica*. Constants were *Amblystegium serpens, Arenaria serpyllifolia, Bryum spp., Festuca rubra, Sedum acre* and *Taraxacum spp.*

Block II consisted of 13 sample plots, confined to a narrow zone just above Block I, never directly exposed to sea spray. The most conspicuous difference from Block I was the occurrence of *Festuca ovina*. Other constants were *Achillea millefolium, Arenaria serpyllifolia, Bryum spp., Cerastium fontanum, Cladonia furcata, Galium verum, Hypnum cupressiforme, Sedum acre* and *Taraxacum spp.*

Block III consisted of 10 sample plots, located slightly above Block II. The sample plots were partly situated on rocks with a thin layer of soil, partly on soil heavily exposed to erosion. The only exclusive species in this block was *Anagallis arvensis*. Due to the high areal importance of bare patches, many of the pioneer species of blocks I and II occurred. However, the importance of grassland species increased gradually with the distance from the sea. Constant species were *Acinos arvensis, Arenaria serpyllifolia, Bryum spp., Cladonia furcata,*

Tab. 1. Survey table. All species registered and their abbreviations are tabulated. C, S and R strategy partial values are given for 86 species of vascular plants.

			CSR-strategy	C	S	R
Arct	uva	Arctostaphylos uva-ursi				
Call	vul	Calluna vulgaris	CS	6	6	0
Empe	nig	Empetrum nigrum	CS	6	6	0
Juni	com	Juniperus communis				
Prun	spi	Prunus spinosa				
Ribe	spi	Ribes spicatum				
Rosa	spp	Rosa spp.				
Sali	rep	Salix repens	C	12	0	0
Achi	mil	Achillea millefolium	CR-CSR	5	2	5
Acin	arv	Acinos arvensis				
Agri	eup	Agrimonia eupatoria				
Alli	spp	Allium spp.	CR-CSR	5	2	5
Anag	arv	Anagallis arvensis	R-SR	0	3	9
Ante	dio	Antennaria dioica				
Anth	vul	Anthyllis vulneraria				
Arab	tha	Arabidopsis thaliana	SR	0	6	6
Arab	hir	Arabis hirsuta	S-SR	0	9	3
Aren	ser	Arenaria serpyllifolia	SR	0	6	6
Arme	mar	Armeria maritima				
Aspl	tri	Asplenium trichomanes	S	0	12	0
Aste	tri	Aster tripolium				
Atri	has	Atriplex hastata				
Bide	tri	Bidens tripartita				
Botr	lun	Botrychium lunaria				
Caki	mar	Cakile maritima				
Camp	rot	Campanula rotundifolia	S	0	12	0
Caps	bur	Capsella bursa-pastoris	R	0	0	12
Card	hir	Cardamine hirsuta	SR	0	6	6
Carl	vul	Carlina vulgaris	SR	0	6	6
Cent	jac	Centaurea jacea				
Cent	lit	Centaurium littorale				
Cent	pul	Centaurium pulchellum				
Cera	fon	Cerastium fontanum	R-CSR	2	2	8
Cera	sem	Cerastium semidecandrum				
Cirs	vul	Cirsium vulgare	CR	6	0	6
Clin	vul	Clinopodium vulgare				
Coch	dan	Cochlearia danica				
Coch	off	Cochlearia officinalis				
Cory	pum	Corydalis pumila				
Erig	ace	Erigeron acer	SR	0	6	6
Erop	ver	Erophila verna				
Euph	mic	Euphrasia micrantha				
Frag	ves	Fragaria vesca	CSR	4	4	4
Gale	tet	Galeopsis tetrahit	R-CR	3	0	9
Gali	apa	Galium aparine	CR	6	0	6
Gali	bor	Galium boreale				
Gali	ver	Galium verum	CS-CSR	5	5	2
Gent	ama	Gentianella amarella				
Gent	uli	Gentianella uliginosa				
Gera	rob	Geranium robertianum	R-CSR	2	2	8
Gera	san	Geranium sanguineum				
Geum	riv	Geum rivale				
Glau	mar	Glaux maritima				
Glec	hed	Glechoma hederacea	CSR	4	4	4

Tab. 1 (continued).

			CSR-STRATEGY	C	S	R
Hepa	nob	Hepatica nobilis				
Hern	gla	Herniaria glabra				
Hier	aur	Hieracium aurantiacum agg.				
Hier	pil	Hieracium pilosella agg.	S-CSR	2	8	2
Hier	spp	Hieracium spp.	S-CSR	2	8	2
Horn	pet	Hornungia petraea				
Hypo	mac	Hypochoeris maculata				
Lath	pra	Lathyrus pratensis	CSR	4	4	4
Leuc	vul	Leucanthemum vulgare	CR-CSR	5	2	5
Lina	vul	Linaria vulgaris	CR	6	0	6
Linu	cat	Linum catharticum	SR	0	6	6
Lotu	cor	Lotus corniculatus	S-CSR	2	8	2
Matr	mar	Matricaria maritima	R	0	0	12
Medi	lup	Medicago lupulina	R-SR	0	3	9
Moeh	tri	Moehringia trinervia	SR	0	6	6
Myce	mur	Mycelis muralis	CSR	4	4	4
Orch	mas	Orchis mascula				
Pimp	sax	Pimpinella saxifraga	S	0	12	0
Plan	lan	Plantago lanceolata	CSR	4	4	4
Plan	maj	Plantago major	R-CSR	2	2	8
Plan	mar	Plantago maritima				
Plan	med	Plantago media				
Pgal	vul	Polygala vulgaris	S	0	12	0
Poly	odo	Polygonatum odoratum				
Poly	avi	Polygonum aviculare	R	0	0	12
Poly	per	Polygonum persicaria	R	0	0	12
Ppod	vul	Polypodium vulgare				
Pote	ans	Potentilla anserina				
Pote	arg	Potentilla argentea				
Pote	ere	Potentilla erecta	S-CSR	2	8	2
Prim	ver	Primula veris	S	0	12	0
Prun	vul	Prunella vulgaris	CSR	4	4	4
Ranu	acr	Ranunculus acris	CSR	4	4	4
Ranu	bul	Ranunculus bulbosus	SR-CSR	2	5	5
Rubu	ida	Rubus idaeus				
Rubu	sax	Rubus saxatilis				
Rume	ace	Rumex acetosella	CSR	4	4	4
Rume	cri	Rumex crispus	R-CR	3	0	9
Sagi	mar	Sagina maritima				
Sagi	nod	Sagina nodosa				
Sagi	pro	Sagina procumbens	R-CSR	2	2	8
Saxi	gra	Saxifraga granulata				
Saxi	tri	Saxifraga tridactylites	SR	0	6	6
Scle	per	Scleranthus perennis				
Sedu	acr	Sedum acre	S	0	12	0
Sedu	alb	Sedum album				
Sedu	tel	Sedum telephium				
Sene	jac	Senecio jacobaea	R-CR	3	0	9
Sile	nut	Silene nutans				
Sile	vul	Silene vulgaris ssp. maritima				
Sola	nig	Solanum nigrum				
Soli	vir	Solidago virgaurea	S	0	12	0
Sper	mar	Spergularia marina				
Sper	rub	Spergularia rubra				
Stel	gra	Stellaria graminea				
Stel	med	Stellaria media	R	0	0	12
Tara	spp	Taraxacum spp.	R-CSR	2	2	8

Tab. 1 (continued).

			CSR-STRATEGY	C	S	R
Thal	min	Thalictrum minus				
Thym	pul	Thymus pulegioides				
Trif	arv	Trifolium arvense				
Trif	aur	Trifolium aureum				
Trif	fra	Trifolium fragiferum				
Trif	pra	Trifolium pratense	CSR	4	4	4
Trif	rep	Trifolium repens	CR-CSR	5	2	5
Urti	dio	Urtica dioica	C	12	0	0
Urti	ure	Urtica urens	R-CR	3	0	9
Vale	off	Valeriana officinalis	CSR	4	4	4
Verb	tha	Verbascum thapsus				
Vero	arv	Veronica arvensis	SR	0	6	6
Vero	cha	Veronica chamaedrys	S-CSR	2	8	2
Vero	off	Veronica officinalis				
Vero	ser	Veronica serpyllifolia				
Vici	cra	Vicia cracca	C-CSR	8	2	2
Vici	lat	Vicia lathyroides				
Viol	arv	Viola arvensis				
Viol	can	Viola canina				
Viol	rup	Viola rupestris				
Viol	tri	Viola tricolor				
Agro	can	Agrostis canina	CSR	4	4	4
Agro	cap	Agrostis capillaris	CSR	4	4	4
Agro	sto	Agrostis stolonifera	CR	6	0	6
Anth	odo	Anthoxanthum odoratum	SR-CSR	2	5	5
Arrh	ela	Arrhenatherum elatius	C	12	0	0
Aven	pra	Avenula pratensis	S-CS	3	9	0
Aven	pub	Avenula pubescens	S-CSR	2	8	2
Briz	med	Briza media	S	0	12	0
Brom	hor	Bromus hordeaceus	R	0	0	12
Cala	epi	Calamagrostis epigejos				
Care	car	Carex caryophyllea	S	0	12	0
Care	dig	Carex digitata				
Care	dis	Carex distans				
Care	ech	Carex echinata				
Care	eri	Carex ericetorum				
Care	fla	Carex flacca	S	0	12	0
Care	hir	Carex hirta				
Care	nig	Carex nigra	S-CS	3	9	0
Care	pan	Carex panicea	S	0	12	0
Dant	dec	Danthonia decumbens	S	0	12	0
Desc	fle	Deschampsia flexuosa	S-CS	3	9	0
Equi	arv	Equisetum arvense	CR	6	0	6
Fest	ovi	Festuca ovina	S	0	12	0
Fest	pra	Festuca pratensis	CSR	4	4	4
Fest	rub	Festuca rubra	CSR	4	4	4
Hier	odo	Hierochloë odorata				
Junc	ger	Juncus gerardi				
Loli	per	Lolium perenne	CR-CSR	5	2	5
Luzu	cam	Luzula campestris	S-CSR	2	8	2
Meli	nut	Melica nutans				
Moli	cae	Molinia caerulea	CS	6	6	0
Poa	ann	Poa annua	12	0	0	12
Poa	com	Poa compressa				
Poa	pra	Poa pratensis agg.	CSR	4	4	4
Poa	sub	Poa subcaerulea				
Pucc	mar	Puccinellia maritima				

Tab. 1 (continued).

Ambl	ser	Amblystegium serpens	Cetr	eri	Cetraria ericetorum
Barb	spp	Barbula spp.	Cetr	isl	Cetraria islandica
Brac	alb	Brachythecium albicans	Clad	arb	Cladonia arbuscula
Bryu	arg	Bryum argenteum	Clad	bac	Cladonia bacillaris
Bryu	spp	Bryum spp.	Clad	chl	Cladonia chlorophaea
Camp	chr	Campylium chrysophyllum	Clad	fim	Cladonia fimbriata
Cera	pur	Ceratodon purpureus	Clad	fol	Cladonia foliacea
Clim	den	Climacium dendroides	Clad	fur	Cladonia furcata
Desm	hei	Desmatodon heimii	Clad	sub	Cladonia cf. furcata ssp. subrangiformis
Dicr	sco	Dicranum scoparium	Clad	gra	Cladonia gracilis
Dist	cap	Distichium capillaceum	Clad	poc	Cladonia pocillum
Ditr	fle	Ditrichum flexicaule	Clad	por	Cladonia portentosa
Enca	str	Encalypta streptocarpa	Clad	pyx	Cladonia pyxidata
Fiss	cri	Fissidens cristatus	Clad	rfe	Cladonia rangiferina
Homa	lut	Homalothecium lutescens	Clad	rfo	Cladonia rangiformis
Homa	ser	Homalothecium sericeum	Clad	sym	Cladonia symphycarpa
Hypn	cup	Hypnum cupressiforme	Corn	acu	Cornicularia aculeata
Isot	alo	Isothecium alopecuroides	Parm	con	Parmelia conspersa
Myur	jul	Myurella julacea	Parm	sax	Parmelia saxatilis
Neck	com	Neckera complanata	Pelt	can	Peltigera canina
Plag	cus	Plagiomnium cuspidatum	Pelt	leu	Peltigera leucophlebia
Poly	jun	Polytrichum juniperinum	Pelt	nec	Peltigera neckeri
Rhod	ros	Rhodobryum roseum	Pelt	ruf	Peltigera rufescens
Rhyt	rug	Rhytidium rugosum	Pseu	fur	Pseudevernia furfuracea
Scle	pur	Scleropodium purum	Rama	pol	Ramalina polymorpha
Thui	abi	Thuidium abietinum	Rama	sub	Ramalina subfarinacea
Tort	fla	Tortella flavovirens	Xant	par	Xanthoria parietina
Tort	fra	Tortella fragilis			
Tort	tor	Tortella tortuosa			
Tort	rur	Tortula ruralis			
Weis	con	Weissia controversa			
Ceph	spp	Cephaloziella spp.			
Marc	pol	Marchantia polymorpha			
Metz	fur	Metzgeria furcata			
Ptil	cil	Ptilidium ciliare			
Radu	com	Radula complanata			

Cerastium fontanum, Ditrichum flexicaule, Festuca ovina, F. rubra, Galium verum, Hornungia petraea, Hypnum cupressiforme, Sedum acre, S. album and *Taraxacum spp.*

Block IV occurred in the transition between the xeric pioneer sites and the established sites. The most conspicuous difference between these 10 sites and the Block III sites were the disappearance of *Cochlearia officinalis* and the reduced occurrence of pioneer species of the shore, e.g. *Festuca rubra, Sedum acre* and *S. album.* In addition to the constants of Block III, *Achillea millefolium, Campanula rotundifolia, Linum catharticum* and *Sagina nodosa* were constants in Block IV.

Block V consisted of 21 typical mesic grassland sites, and was most typically developed far from the sea, in the central parts of the island. Most of the species that were found in Block IV reappeared in Block V. Although, in addition, a number of typical grassland species increased, e.g. *Achillea millefolium, Avenula pratensis, Carex caryophyllea, Euphrasia micrantha, Galium verum, Lotus corniculatus* and *Luzula campestris.*

Block VI, consisting of 12 sample plots, was characterized by high occurrence of *Juniperus communis.* Thus, a number of species increased their abundance in these grassland

Tab. 2. Synopsis of the species composition of classified blocks and lost units (L.U.). For each species, values of within-block constancy and mean frequency in subplots are given.

	Block 0	Block I	Block II	Block III	L.U. I	Block IV	Block V	Block VI	L.U. II	Block VII
Glau mar	57 - 77									
Sagi mar	36 - 59									
Sper mar	57 - 66									
Junc ger	100 - 89									
Pucc mar	57 - 76									
Desm hei	36 - 55									
Caps bur	21 - 17	7 - 13								
Coch dan	29 - 33	33 - 28								
Poly per	21 - 13	13 - 28								
Sagi pro	21 - 67	13 - 88								
Rume cri	29 - 20	60 - 15								
Urti dio		27 - 44								
Atri has	64 - 24	20 - 21	8 - 25							
Brac alb		54 - 45	23 - 15							
Plan maj	36 - 50		8 -100	50 - 45						
Poa ann	7 -100			20 - 9						
Clad gra		7 -100	15 - 56	30 - 31						
Anag arv				20 - 59						
Coch off	21 - 52	47 - 54	46 - 16	40 - 20	33 - 38					
Pote ans	36 - 83	13 - 28			67 - 72					
Ambl ser	43 - 64	80 - 46	15 - 34		33 - 75					
Agri eup		6 - 6	54 - 52		33 - 13					
Geum riv			8 - 6		67 - 56					
Trif rep	14 - 38	7 - 38	15 - 9	20 - 13		20 - 28				
Arme mar		67 - 46	46 - 29			10 - 13				
Gale tet	21 - 31	13 - 16				10 - 6	5 - 6			
Agro sto	100 - 77	27 - 41	23 - 44	10 - 31	67 - 34	10 - 13	9 - 28			
Pote arg		7 - 19	15 - 25	20 - 16		30 - 19	5 - 13			
Rume ace		13 - 59	46 - 20	10 - 50		20 - 13	5 - 44			
Cera sem		40 - 60	62 - 53	60 - 28	33 - 6	30 - 27	5 - 25			
Clad rfo		20 - 35	23 - 38	40 - 33		20 - 19	32 - 19			
Plan mar	79 - 45		8 - 69					33 - 11		
Sagi nod	50 - 74	27 - 45	23 - 48	30 - 42	33 - 13	70 - 36	23 - 18	33 - 23		
Scle per	7 - 63	20 - 46				10 - 13	5 - 13	8 - 19		
Poa sub	7 -100	13 - 47	54 - 58	50 - 41		40 - 41	41 - 41	8 - 43		
Erop ver		13 - 19		20 - 22			5 - 56	8 - 13		
Saxi tri		13 - 34	38 - 69	60 - 31		50 - 32	32 - 17	8 - 13		
Sedu alb		27 - 48	54 - 24	70 - 56		20 - 28	4 - 25	8 - 13		
Brom hor		13 - 47	46 - 50	40 - 25		40 - 41		8 - 6		
Cera pur		47 - 38	54 - 45	20 - 41		10 - 38	27 - 31	8 - 50		
Clad fol		13 - 56	54 - 51	40 - 48			27 - 23	8 - 6		
Clad fur		60 - 62	92 - 74	90 - 49	33 - 75	50 - 43	86 - 33	17 - 19		
Corn acu		7 - 6	23 - 29	40 - 16		30 - 10	45 - 16	8 - 6		
Anth vul		6 - 6				30 - 15	5 - 6		33 - 13	
Vero arv		13 - 22	15 - 63						33 - 13	
Cent lit	29 - 83			10 - 25			5 - 19	8 - 44		4 - 13
Cera fon	14 - 19	60 - 51	92 - 57	80 - 41	67 - 25	90 - 43	64 - 34	58 - 25	33 - 13	57 - 26
Cirs vul	7 - 6	33 - 10	15 - 13	10 - 6	33 - 13	20 - 9	14 - 15	17 - 9		9 - 13
Linu cat	7 - 88		8 - 88	60 - 53	33 - 44	80 - 82	100 - 74	83 - 55	33 - 6	35 - 45
Medi lup	21 - 58	13 - 78	54 - 43	40 - 14	67 - 41	50 - 48	23 - 28	25 - 25		9 - 38
Stel med	71 - 39	20 - 29			33 - 19			8 - 31		4 - 19
Tara spp	14 - 41	80 - 39	77 - 36	90 - 33	100 - 15	80 - 39	68 - 22	42 - 15		17 - 25
Fest rub	64 - 88	100 - 94	100 - 98	100 - 46	100 - 83	70 - 57	27 - 17	50 - 43	33 - 31	61 - 64
Bryu spp	29 - 66	80 - 60	92 - 61	100 - 68	100 - 19	100 - 56	77 - 54	92 - 34	33 - 6	9 - 16
Juni com		13 - 6	46 - 11	70 - 56	100 - 71	70 - 38	50 - 24	92 - 91	67 - 72	100 -100
Rosa spp		6 - 6		10 - 6		20 - 6	5 - 6	25 - 17	33 - 31	22 - 9
Achi mil		20 - 63	77 - 79	70 - 61	67 - 34	90 - 61	86 - 77	42 - 28	67 - 44	26 - 26
Aren ser		87 - 81	92 - 90	100 - 63	33 - 6	100 - 63	77 - 37	83 - 19		4 - 25
Camp rot		7 - 7	8 - 6	50 - 26	67 - 22	80 - 38	100 - 60	83 - 39	67 - 47	70 - 30
Gali ver		33 - 70	85 - 75	80 - 38	100 - 54	80 - 59	91 - 78	42 - 70	100 - 88	74 - 38
Gera rob		13 - 31	15 - 31	40 - 27		30 - 6	5 - 13	17 - 13		35 - 30
Hier pil		7 - 13				40 - 52	68 - 35	33 - 17		4 - 19
Horn pet		7 - 19	46 - 65	80 - 56		70 - 63	45 - 46	83 - 29		13 - 38
Lotu cor		27 - 36	46 - 46	70 - 21	67 - 50	50 - 13	82 - 35	42 - 18	67 - 38	13 - 15
Pimp sax		7 - 38	15 - 16	30 - 13	67 - 56	50 - 16	46 - 24	58 - 23	67 - 22	78 - 30
Plan lan		40 - 61	54 - 65	50 - 49	33 - 25	50 - 45	32 - 25	8 - 38		13 - 15
Sedu acr		100 - 83	77 - 71	90 - 51	33 - 13	50 - 44	18 - 22	33 - 20		9 - 9
Thym pul		7 - 38	15 - 31	30 - 50		40 - 30	64 - 50	50 - 63	33 - 25	30 - 34
Vici cra		13 - 31	8 - 19		67 - 38	20 - 28	14 - 15	8 - 13	67 - 34	26 - 18
Viol tri		27 - 35	54 - 39	60 - 38	67 - 6	20 - 13	14 - 13	8 - 6		4 - 19
Barb spp		7 - 56	38 - 31	50 - 78		80 - 38	68 - 46	83 - 19		13 - 17
Bryu arg		33 - 14		10 - 19		40 - 13	14 - 23	25 - 15	33 - 6	4 - 6
Camp chr		7 - 13			67 - 38	50 - 38	50 - 51	92 - 42	33 - 6	44 - 32
Ditr fle		7 - 13	46 - 54	90 - 64	33 - 13	80 - 48	45 - 56	75 - 30		13 - 21
Homa lut		7 - 31	31 - 36	80 - 43		80 - 72	82 - 66	42 - 53		35 - 25
Hypn cup		53 - 59	100 - 91	100 - 65	33 - 44	90 - 71	86 - 77	67 - 45		61 - 54
Plag cus		7 - 25	23 - 54	20 - 28		60 - 16	27 - 25	25 - 31		30 - 36
Tort tor		13 - 13	15 - 47	10 - 69		50 - 36	23 - 45	58 - 29	33 - 7	26 - 20

Tab. 2 (continued).

	Block 0	Block I	Block II	Block III	L.U. I	Block IV	Block V	Block VI	L.U. II	Block VII
Tort rur		60 - 42	54 - 40	30 - 29		10 - 38		8 - 25		4 - 19
Clad pyx		13 - 13	31 - 38	40 - 47		40 - 39	64 - 35	42 - 26		30 - 19
Pelt can		40 - 16	62 - 48	30 - 27		20 - 9	14 - 15			4 - 13
Clad sym			8 - 25	30 - 48		30 - 39	9 - 53			
Euph mic			15 - 34	20 - 19		30 - 50	77 - 49	25 - 15		
Enca str			8 - 56	30 - 29		10 - 44	14 - 42	42 - 29		
Ante dio			8 - 25	60 - 16		60 - 46	73 - 70	67 - 36	67 - 19	13 - 29
Arab hir			8 - 19	20 - 19	33 - 13	40 - 16	23 - 23	25 - 15		4 - 25
Botr lun			38 - 23	70 - 24		40 - 39	27 - 28	17 - 9		9 - 6
Card hir			8 - 75							22 - 35
Cent jac			8 - 19	20 - 41	67 - 88	40 - 45	45 - 28	58 - 38		9 - 22
Glec hed			8 - 13	30 - 19	67 - 44	10 - 13	5 - 6	17 - 9		65 - 42
Soli vir			15 - 75			40 - 20	18 - 11	25 - 19	33 - 38	17 - 20
Agro cap			8 - 6	30 - 19		30 - 54	59 - 63	75 - 35		4 -100
Care car			8 - 13	20 - 41		40 - 48	82 - 84	17 - 34	100 - 29	4 - 25
Fest ovi			46 - 51	90 - 89	67 - 59	90 - 97	100 - 99	100 - 80	100 - 79	83 - 40
Luzu cam			8 - 6			30 - 17	55 - 38			13 - 18
Dicr sco			23 - 38	40 - 36		30 - 19	45 - 54	25 - 35	33 - 44	17 - 13
Tort fla			23 - 75	20 - 34		30 - 44	23 - 34	8 - 50		9 - 22
Cetr isl			46 - 11	50 - 20	33 - 19	30 - 19	36 - 14	33 - 13		4 - 6
Ranu bul				10 - 13		20 - 22	14 - 54			
Pseu fur				20 - 13			14 - 13			
Hier aur				10 -100		20 - 9	9 - 19	17 - 34		
Dant dec				10 - 6	33 - 94	10 - 13	14 - 42	42 - 35		
Thui abi				40 - 38		40 - 16	32 - 33	42 - 30		
Tort fra				20 - 75		10 - 50	5 -100	33 - 27		
Acin arv				80 - 74		80 - 62	59 - 47	92 - 22		22 - 20
Erig ace				20 - 25			14 - 23	8 - 19		13 - 13
Thal min				30 - 10	33 - 38	50 - 34	68 - 22	58 - 38	67 - 47	65 - 37
Agro can				10 - 31		20 - 72	23 - 35	8 - 31		17 - 17
Anth odo				20 - 22	33 - 13	20 - 41	23 - 49		33 - 13	13 - 40
Aven pra				40 - 31	33 - 25	50 - 51	86 - 23	42 - 34	100 - 65	30 - 34
Care dig				10 - 6		30 - 8	5 - 6	50 - 26		57 - 49
Care fla				10 - 13	67 -100	50 - 28	45 - 56	75 - 65	100 - 75	39 - 48
Desc fle				10 - 31		10 - 13	9 - 25	17 - 16		22 - 26
Poa pra				10 - 38	33 - 38	20 - 38	14 - 17	25 - 35		61 - 49
Dist cap				20 - 31	33 - 19	10 - 31	9 - 13	17 - 13	33 - 6	13 - 8
Homa ser				10 - 13		30 - 15	5 - 13			9 - 19
Clad arb				10 - 13		20 - 6	18 - 13	8 - 38		4 - 6
Care nig					67 - 53			8 - 31		
Frag ves					33 - 75			42 - 36		26 - 44
Pote ere					33 - 81		5 - 13	42 - 20	67 - 59	26 - 28
Prun vul					33 - 69		5 - 6	8 - 25		13 - 38
Rubu ida					33 - 6			8 - 25		13 - 31
Trif pra					33 - 19					17 - 27
Briz med					33 -100	20 - 25	73 - 61	83 - 73	100 - 69	39 - 40
Fiss cri					67 - 44	60 - 52	86 - 66	100 - 57	33 - 6	48 - 45
Alli spp						20 - 69	14 - 17			
Gent ama						20 - 31	5 - 19			
Saxi gra						20 - 16	9 - 13			
Arab tha						20 - 9	9 - 19	8 - 6		
Cala epi						20 - 31	5 - 19	8 -100		
Care eri						20 - 44	59 - 55	25 - 31	33 - 19	
Viol rup						10 - 13	5 - 19	8 - 6	67 - 44	
Aspl tri						20 - 6				4 - 6
Gera san						10 - 19	14 - 19	33 - 27	67 - 22	17 - 30
Hypo mac						10 - 6	36 - 16			4 - 31
Plan med						20 - 25	45 - 18		33 - 63	9 - 16
Rubu sax						10 - 6	18 - 22	17 - 9	67 - 44	48 - 24
Aven pub						20 - 25	23 - 23	8 - 50		13 - 48
Hier odo						20 - 31				4 - 13
Ryth rug						30 - 31	55 - 44	25 - 27		9 - 6
Radu com						10 - 44		25 - 29		39 - 36
Arct uva							9 - 9		100 -100	
Vici lat							5 - 6	8 - 6	33 - 6	
Cory pum							5 - 6	8 - 13		39 - 58
Poly odo							5 - 56	8 - 13	33 - 13	17 - 22
Ppod vul							9 - 16	33 - 22	33 - 69	43 - 26
Sile nut							9 - 16	8 - 13		35 - 24
Meli nut							9 - 13	50 - 52		17 - 64
Gali bor								8 - 6		26 - 14
Hepa nob								42 - 21	33 -13	26 - 47
Prim ver								8 - 25		22 - 16
Vero off								8 - 31		30 - 41
Metz fur								17 - 19		61 - 49
Pgal vul									33 - 69	4 - 13
Moeh tri										48 - 31
Vero cha										22 - 40

Tab. 2 (continued).

Species with within-block constancy < 20%;

Call vul (V;5-19), Empe nig (VII;4-13), Prun spi (VII;13-23), Ribe spi (VII;4-44), Sali rep (VI;8-56),

Aste tri (0;14-22), Bide tri (0;7-6), Caki mar (0;7-6, I;7-13), Carl vul (VI;17-9), Cent pul (0;7-13, 8-31), Clin vul (VII;17-17), Gali apa (I;13-50), Gent uli (III;10-44), Hern gla (V;5-13), Hier spp (II;8-6, IV;10-13, V;5-25, VII;13-13), Lath pra (I;7-50), Leuc vul (III;10-6), Lina vul (II;8-6, VI;8-63, VII; 13-31), Matr mar (0;7-13, I;7-25), Myce mur (VII;4-6), Orch mas (VII;4-25), Poly avi (0;7-6, I;7-13), Ranu acr (III;10-44, VI;8-13, VII;4-6), Sedu tel (I;7-6, VII;4-6), Sene jac (III;10-6), Sile vul (I;7-13), Sola nig (0;7-13), Sper rub (II;15-16), Stel gra (I;7-19, III; 10-6, VII;17-33), Trif arv (IV;10-19), Trif aur (V;4-6), Trif fra (0;7-13, I;7-19), Urti ure (0;14-6, I;13-19), Vale off (VII;9-34), Verb tha (VII;4-19), Vero ser (VII;4-13), Viol arv (I;7-6, IV;10-6), Viol can (17-19),

Arrh ela (VII;9-39), Care dis (0;14-13), Care ech (IV;10-6), Care hir (VI;8-63), Care pan (VI;8.31), Equi arv (VII;4-50), Fest pra (IV;10-13, V;5-13, VII;9-47), Loli per (IV;10-38), Moli cae (V;5-19, VI;17.22), Poa com (III;10-6, 17-25, VII;13-77),

Clim den (II;8-38, IV;10-25, VI;8-13), Isot alo (VI;8-50, VII;4-19), Myur jul (V;5-31), Neck com (VI;17-16, VII;9-28), Poly jun (V;5-25), Rhod ros (V;5-13), Scle pur (IV;10-13), Weis con (IV;10-25),

Ceph spp (I;13-16, II;8-6, V;5-19), Marc pol (IV;10-56, VI;8-25), Ptil cil (III;10-38, V;5-56),

Cetr eri (II;8-13, VI;8-6), Clad bac (IV;10-13), Clad chl (V;5-13), Clad fim (IV;10-6), Clad sub (I;13-56), Clad poc (III;10-13), Clad por (V;5-19), Clad rfe (III;10-13, IV;10-13, V;14-17), Parm com (I;7-6), Parm sax (III;10-13), Pelt leu (V;5-19), Pelt nec (I;7-63, II;8-25), Pelt ruf (I;7-6, II;8-50, V;5-56), Rama pol (II;8-13, IV;10-19), Rama sub (VI; 8-6), Xant par (I;13-9, III;10-13)

sites with scattered, dispersed or open juniper shrubs, e.g. *Melica nutans* and *Polypodium vulgare*. In Block VI junipers became an important structuring species, although junipers were also encountered in blocks III and IV with lower occurrence. *Galium boreale, Hepatica nobilis, Primula veris, Veronica officinalis* and *Metzgeria furcata* have found their niches among this shrub vegetation. Constants were *Acinos arvensis, Agrostis capillaris, Arenaria serpyllifolia, Barbula spp, Bryum spp, Campanula rotundifolia, Campylium chrysophyllum, Carex flacca, Ditrichum flexicaule, Festuca ovina, Hornungia petraea, Linum catharticum.*

Block VII was made up by 23 sample plots of dense or closed juniper shrubs. Exclusive species in this sites were *Moehringia trinervia* and *Veronica chamaedrys.* Apart from *Hepatica nobilis* and *Melica nutans*, the species which first appeared in Block VI increased the performance from Block VI to Block VII. In addition, some of the species that increased from Block V to Block VI showed further increase on to Block VII. Besides juniper, the only constant in this block was *Festuca ovina.*

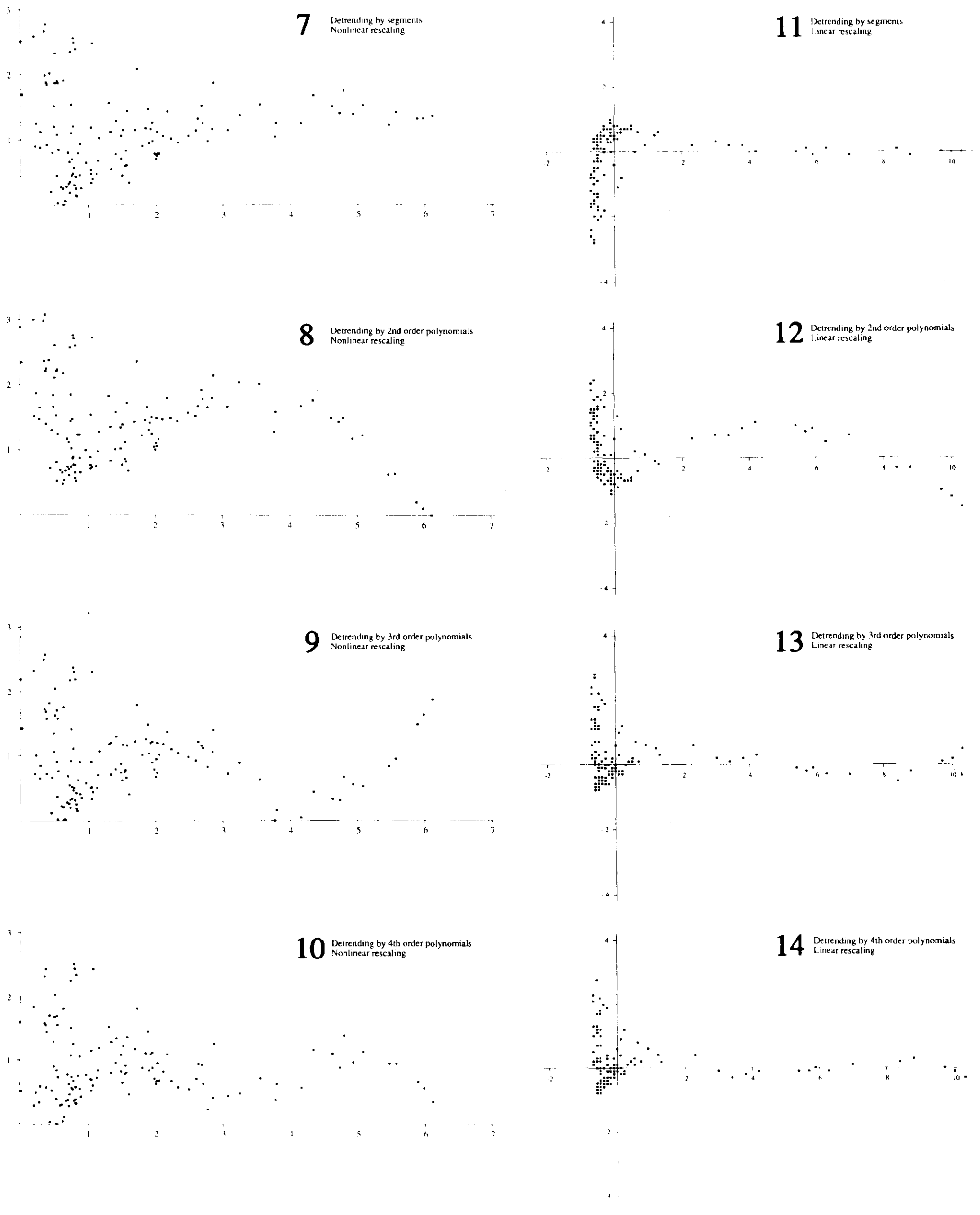
Lost Units I included 3 sample plots with occurrence of both juniper shrubs and pioneer species of the primary blocks.

Lost Units II showed high similarity to the blocks VI and VII, although each subplot of the 3 sample plots in question were dominated by *Arctostaphylos uva-ursi.* Because of its openness, low growth form and extensive lateral spread, many of the Block V grassland species occurred in the sites.

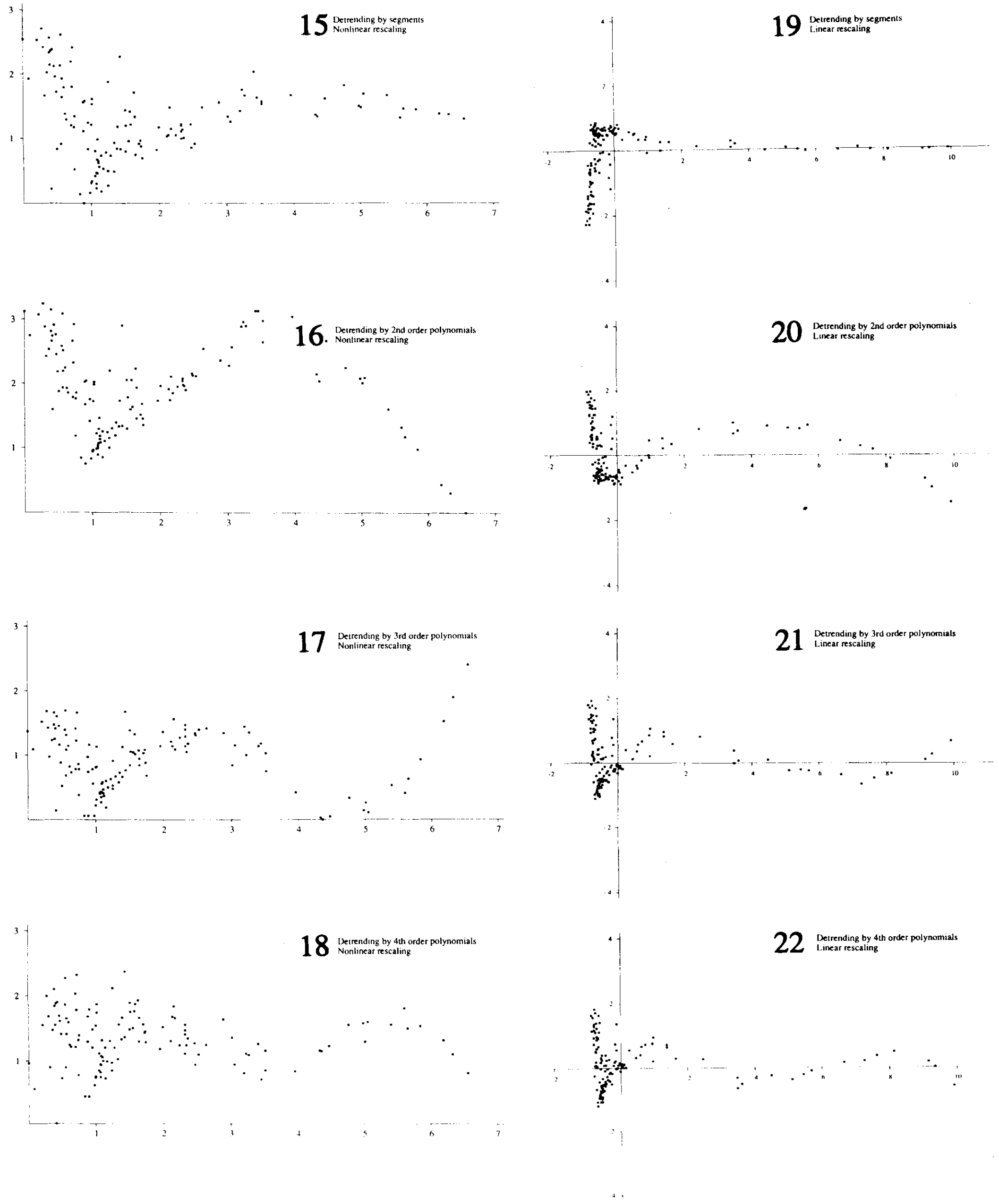
PERFORMANCE OF DETRENDING AND RESCALING OPTIONS IN DCA ORDINATION

Detrending

Figs 7-10 show DCA ordination axes 1 and 2 in the ordinations of the entire *AB* dataset, using



Figs 7-14. DCA ordinations of unweighted frequency in subplots data (r = 16). Dataset *AB* sample plot configuration, using nonlinear (Figs 7-10) and linear (Figs 11-14) rescaling options, DCA 1 (horizontal axes) and DCA 2 (vertical axes). - Figs 7 and 11. Detrending by segments. - Figs 8 and 12. Detrending by 2nd order polynomials. - Figs 9 and 13. Detrending by 3rd order polynomials. - Figs 10 and 14. Detrending by 4th order polynomials.



Figs 15-22. DCA ordinations of percentage cover data weighted with w = 0.6 (r = 16). Dataset *AB* sample plot configuration, using nonlinear (Figs 15-18) and linear (Figs 19-22) rescaling options, DCA 1 (horizontal axes) and DCA 2 (vertical axes). - Figs 15 and 19. Detrending by segments. - Fig. 16 and 20. Detrending by 2nd order polynomials. - Fig 17 and 21. Detrending by 3rd order polynomials. - Fig 18 and 22. Detrending by 4th order polynomials.

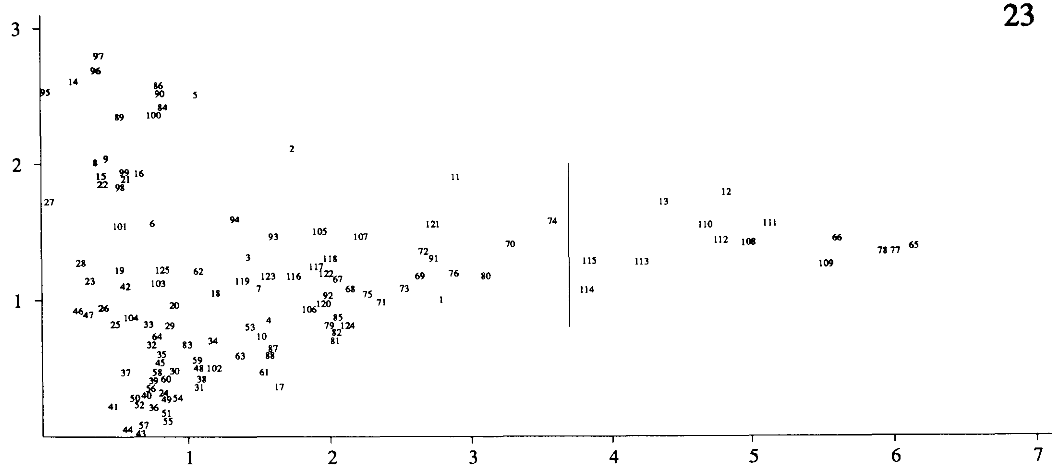
the 4 options for detrending. Detrending by segments, Fig. 7, shows a distinct tongue effect. Thus, the dispersion of sample plots along DCA 2 decreases gradually for increasing values along DCA 1. Detrending by polynomials, in addition, produced different polynomial distortions. Detrending by 2nd order polynomials distorted the first axis into an arc along the second DCA axis (Fig. 8). Correspondingly, detrending by 3rd order polynomials produced a 3rd order polynomial distortion (Fig. 9) and detrending by 4th order polynomials produced 4th order polynomial distortions (Fig. 10).

Figs 11-14 show similar sample plot configurations, based upon percentage cover as measure of species amounts in the *AB* dataset. Axes are further extended as compared with Figs 7-10.

Tab. 3. Comparison of DCA using different detrending options, with nonlinear and linear rescaling. g_{100} - gradient length, g_{90} - length of gradient core (the shortest segment including 90% of the sample plots), $l_c = g_{90}/g_{100}$. Dataset *AB* and Subset *A* values are shown for both frequency in subplots, f, and percentage cover, p.

Data set	Axis	Non-linear rescaling			Linear rescaling		
		g_{100}	g_{90}	l_c	g_{100}	g_{90}	l_c
*AB*f	1	6.11	3.79	0.62	11.00	4.10	0.37
	2_{Seg}	2.78	2.02	0.73	3.80	2.50	0.66
	2_{2nd}	3.08	2.09	0.68	3.90	2.60	0.67
	2_{3rd}	2.58	1.79	0.69	3.60	2.10	0.58
	2_{4th}	2.52	1.61	0.63	3.60	2.10	0.58
*AB*p	1	6.56	4.36	0.66	10.80	4.36	0.40
	2_{Seg}	2.71	2.05	0.76	3.14	2.47	0.78
	2_{2nd}	3.24	2.15	0.66	3.44	2.35	0.68
	2_{3rd}	2.40	1.44	0.60	3.04	2.35	0.77
	2_{4th}	2.37	1.23	0.52	3.04	2.27	0.75
*A*f	1	3.82	2.87	0.75	4.09	3.09	0.76
	2_{Seg}	2.71	1.60	0.59	3.80	1.72	0.45
	2_{2nd}	2.67	1.65	0.62	3.21	1.96	0.61
	2_{3rd}	2.46	1.45	0.58	2.78	1.55	0.55
	2_{4th}	2.44	1.47	0.60	2.82	1.54	0.55
*A*p	1	4.04	3.09	0.76	4.32	3.30	0.76
	2_{Seg}	2.23	1.33	0.60	2.45	1.46	0.60
	2_{2nd}	2.82	1.29	0.46	3.54	1.58	0.45
	2_{3rd}	1.80	1.22	0.67	1.87	1.28	0.68
	2_{4th}	1.75	1.23	0.70	1.85	1.29	0.70

23



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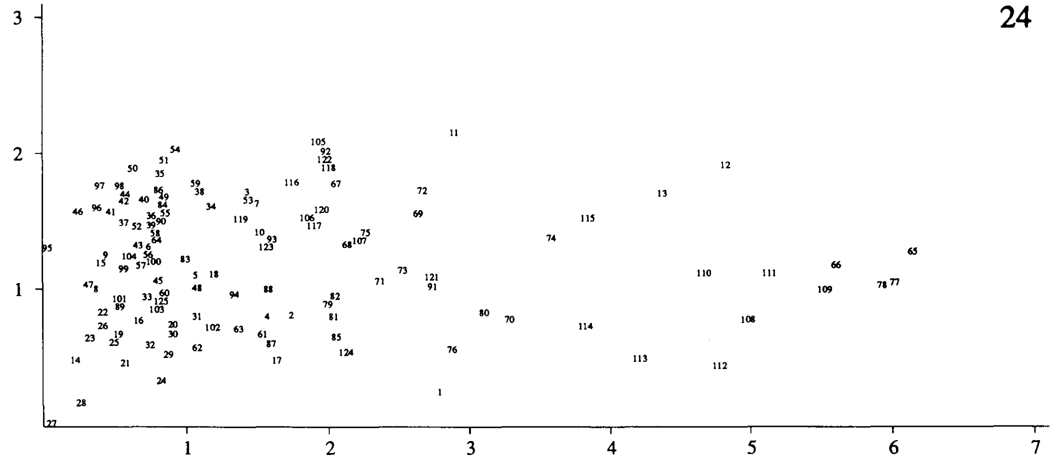
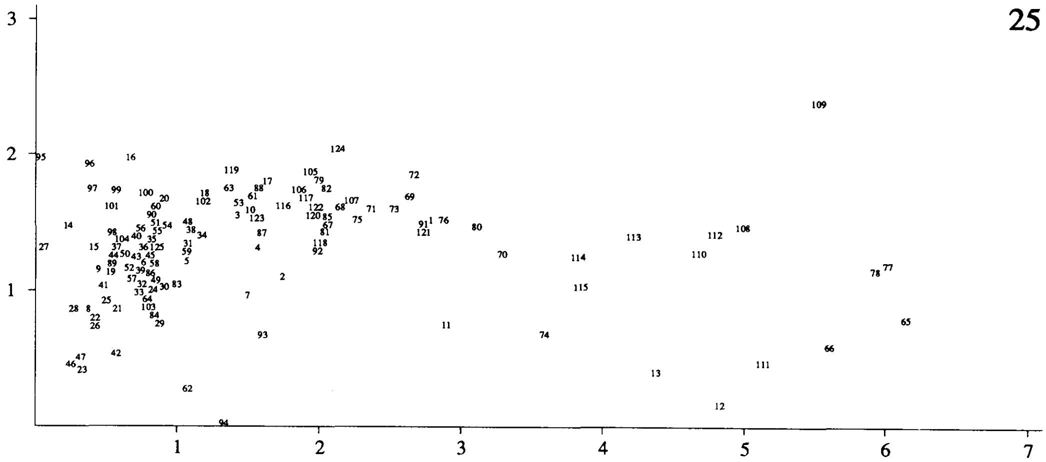


Figs 23-24. DCA ordinations of unweighted frequency in subplots data, with site number plotted onto the sample plot positions. - Fig. 23. DCA 1 (horizontal axis) and DCA 2 (vertical axis) of Dataset *AB*. - Fig. 24. DCA 1 (horizontal axis) and DCA 3 (vertical axis) of Dataset *AB*.

Rescaling

A comparison of DCA ordinations with nonlinear rescaling and the corresponding DCA ordinations with linear rescaling (Figs 15-22), demonstrated the following trends, independent of the detrending option: (1) the sample plots were to a great extent concentrated around the centroid when linear rescaling option was used, (2) sample plot separation increased gradually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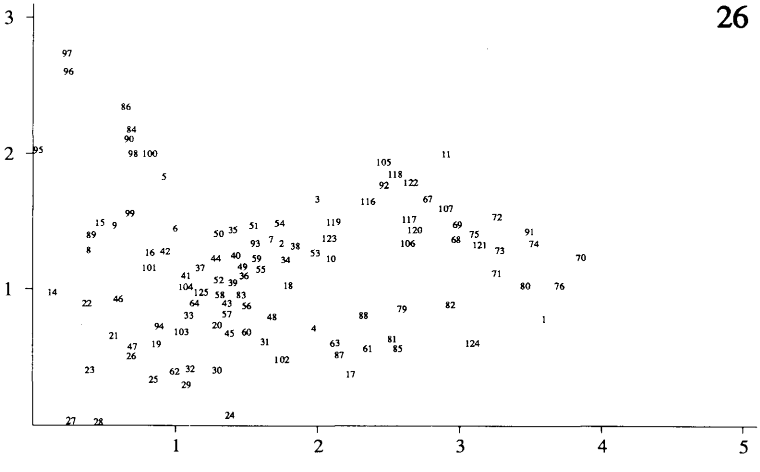
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Figs 25-26. DCA ordinations of unweighted frequency in subplots data, with site number plotted onto the sample plot positions. - Fig. 25. DCA 1 (horizontal axis) and DCA 4 (vertical axis) of Dataset *AB*. - Fig. 26. DCA 1 (horizontal) and DCA 2 (vertical) of Subset *A*.

towards the gradient end-points when linear rescaling was used, while sample plots appeared more evenly distributed with non-linear rescaling, and (3) the DCA axes were longer when linear rescaling option was used, measured in S.D. units.

A quantitative expression of points (1) and (2) is apparent from Tab. 3, showing that the length of thecore of the first axes, independent of abundance scale, is far higher when non-linear rescaling option is used. No trends in difference in core length were observed for the

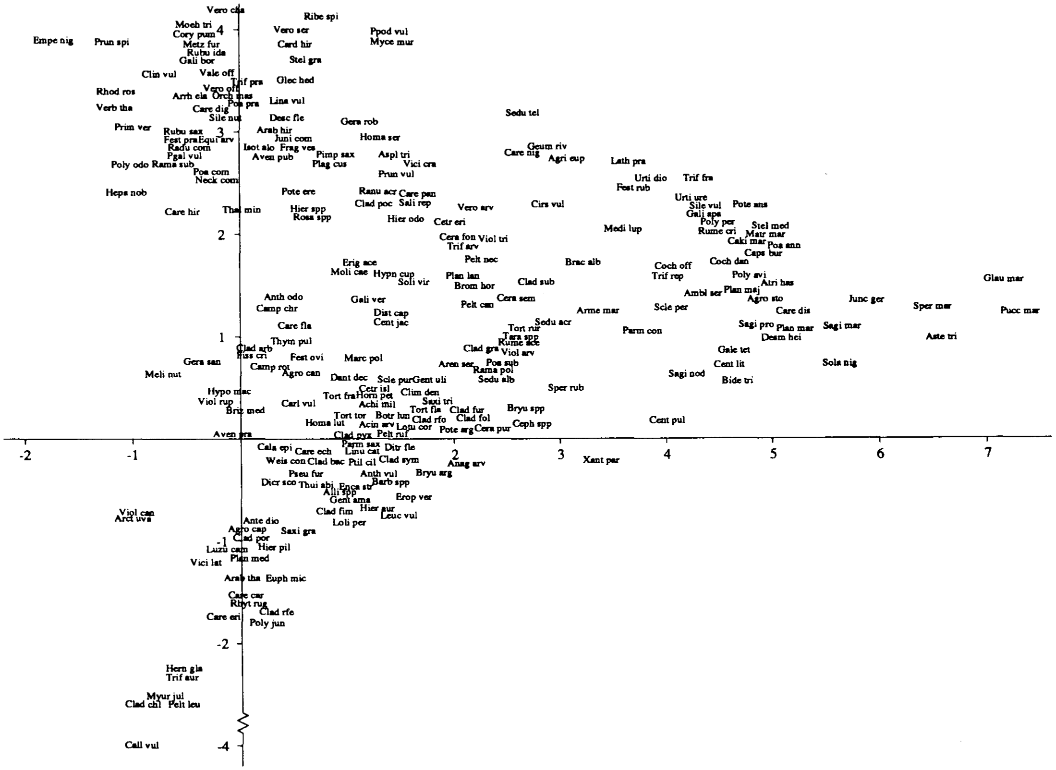


Fig. 27. DCA ordination of unweighted frequency in subplots data, with species name plotted onto the species optima. DCA 1 (horizontal axis) and DCA 2 (vertical axis) of Dataset *AB*.

second axes.

Assessment

On account of the results above, frequency in subplots was used for estimation of species abundance, and detrending by segments and nonlinear rescaling were chosen for DCA ordinations.

INDIRECT GRADIENT ANALYSES AND INTERPRETATION BY CLASSIFICATION

DCA ordination of sample plots

Axes 1 and 2 of the DCA ordination of Dataset *AB* is shown in Fig. 23. The division into

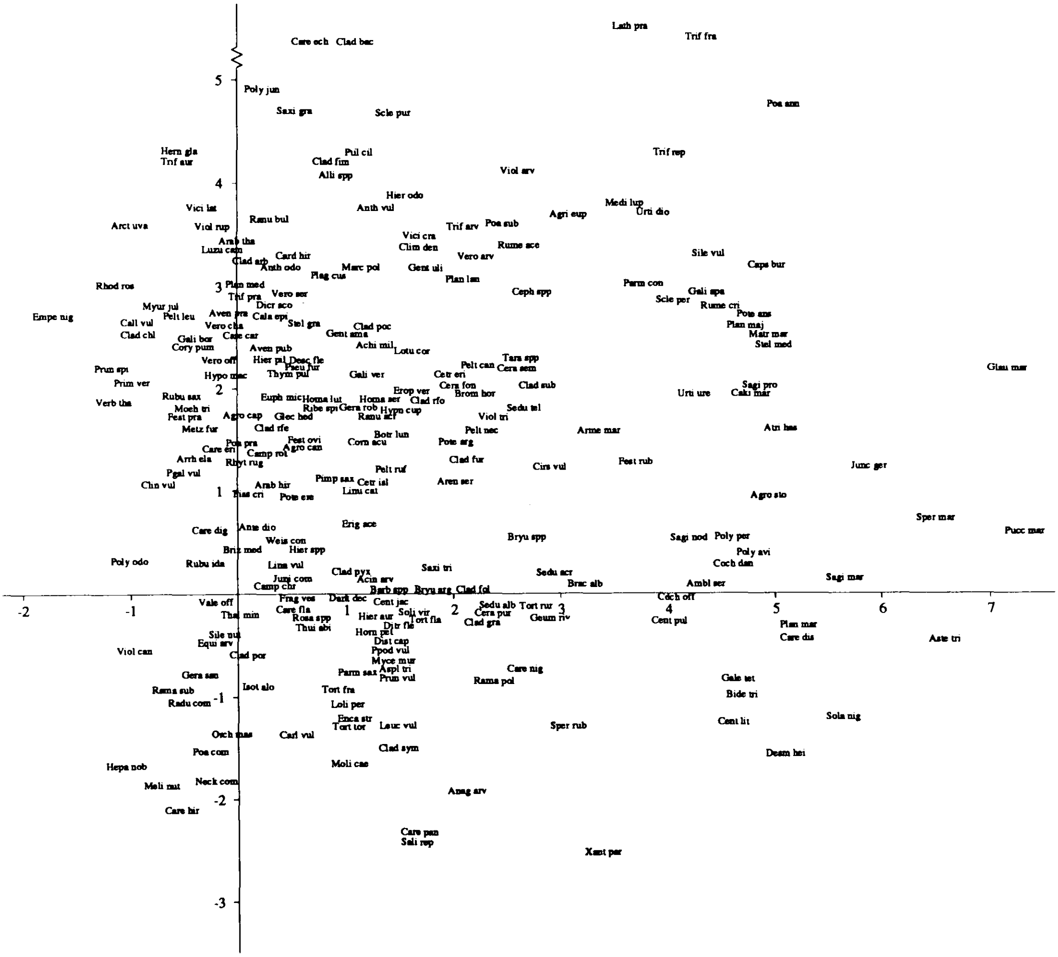


Fig. 28. DCA ordination of unweighted frequency in subplots data, with species name plotted onto the species optima. DCA 1 (horizontal axis) and DCA 3 (vertical axis) of Dataset *AB*.

Subsets *A* and *B* is indicated by an broken line. The ordination shows one major gradient in the species composition along the first axis (eigenvalue 0.69). Subsequent eigenvalues were considerably lower (0.30, 0.16 and 0.13). DCA 1 versus DCA 3 and DCA 4, respectively, are shown in Figs 24-25. Axes 1 and 2 of the DCA ordination of Subset *A* is given in Fig 26. By exclusion of Subset *B*, the sample plots of the littoral zone, the main axis is shortened from 6.11 S.D. units to 3.82 S.D. units, and the triangular configuration of Fig. 23 is changed to a more rectangular configuration. The reduction of species turnover along the first DCA axis is evident from the reduction of the eigenvalue (0.434). The subsequent axes also shows eigenvalue reduction, but to a smaller extent (0.20, 0.13 and 0.10).

The corresponding species ordination of the *AB* dataset is given in Fig. 27, showing the

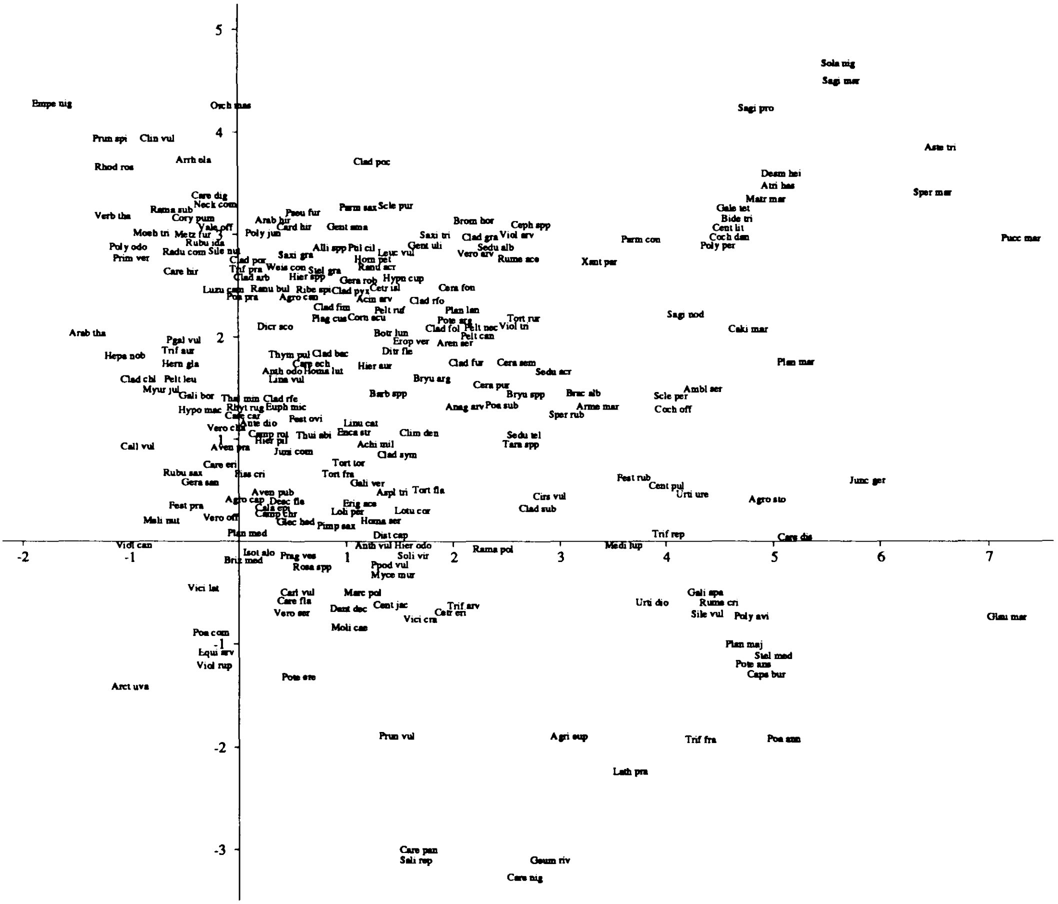
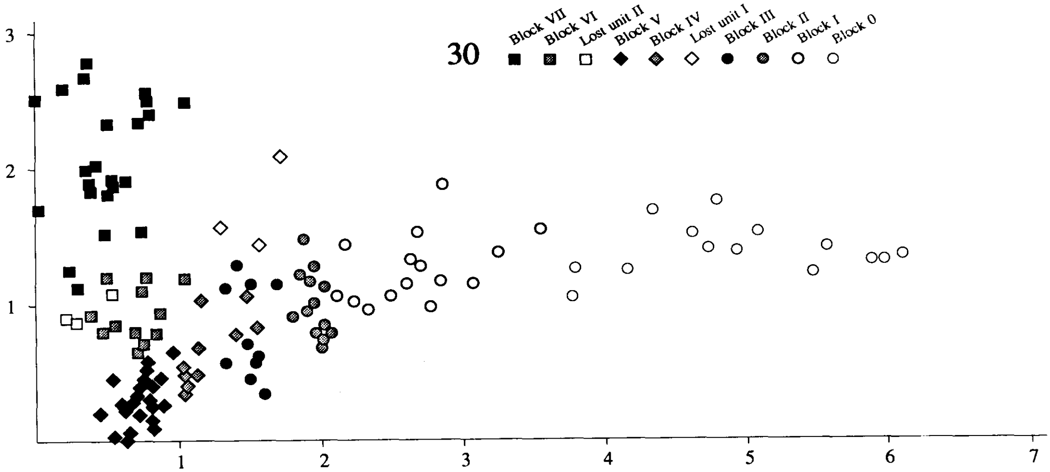
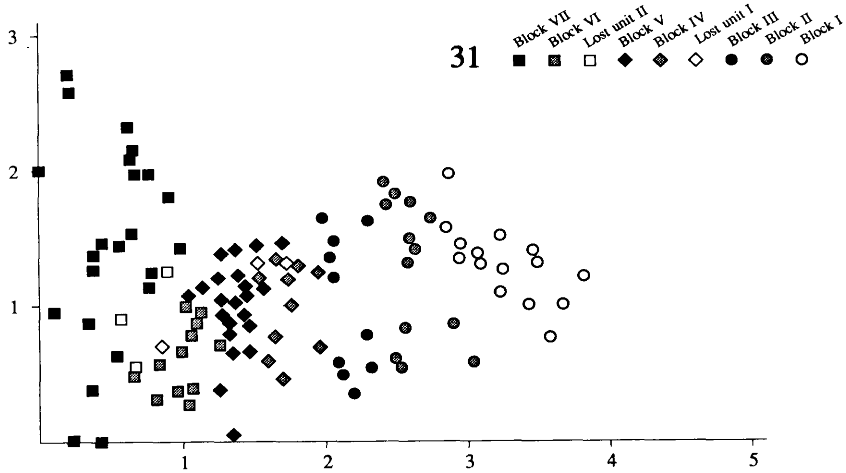


Fig. 29. DCA ordination of unweighted frequency in subplots data, with species name plotted onto the species optima. DCA 1 (horizontal axis) and DCA 4 (vertical axis) of Dataset *AB*.

spatial distribution of all 231 species. The distribution of species shows the same triangular configuration as for the sample plots. The extremes along axis 1 are occupied by, among others, herbs like *Glaux maritima* and *Spergularia marina* and graminids like *Juncus gerardi* and *Puccinellia maritima*. Frequent species occurring at the lower part of axis 2 are, e.g., herbs like *Antennaria dioica* and *Euphrasia micrantha*, graminids like *Carex ericetorum, C.* caryophyllea and *Luzula campestris*, and cryptogams like *Rhytidium rugosum*. Species at the upper part of axis 2 are, e.g., shrubs like *Juniperus communis* and *Rosa spp*., herbs like *Corydalis pumila, Moehringia trinervia, Polypodium vulgare, Primula veris, Veronica chamaedrys* and *V. officinalis*, and cryptogams like *Metzgeria furcata* and *Radula complanata*. Corresponding plots of DCA 1 versus DCA 3 and DCA 4 are shown in Figs. 28-29.

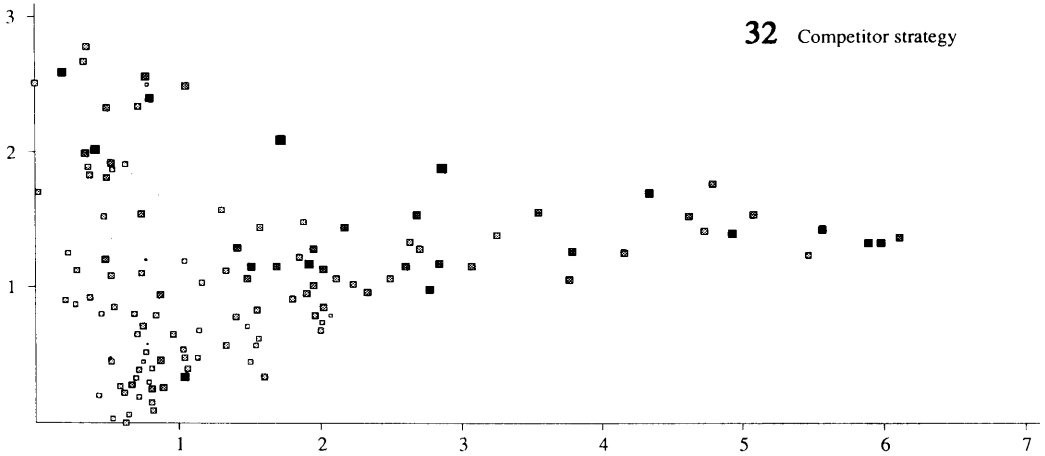




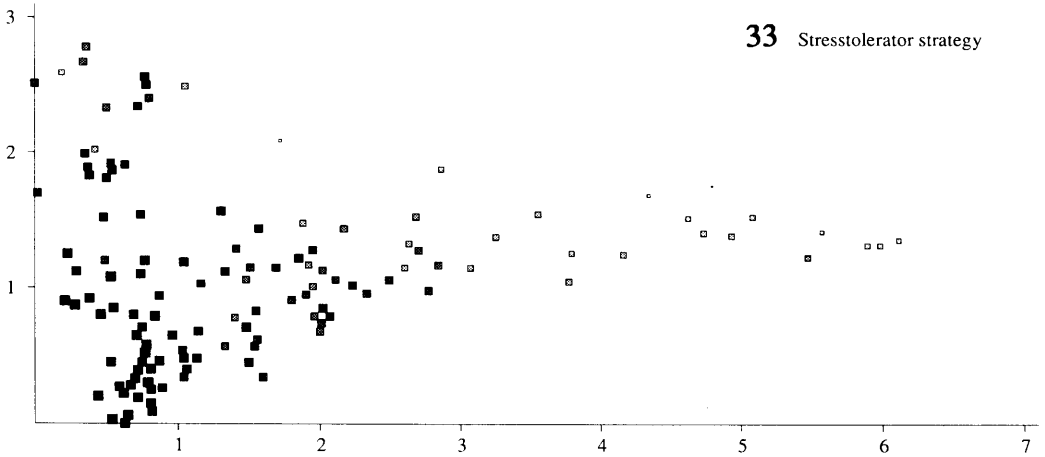
Figs 30-31. Classification of sample plots into blocks. DCA 1 (horizontal axis) and DCA 2 (vertical axis). - Fig. 30. Dataset *AB*. - Fig. 31. Subset *A*.

Interpretation of DCA ordination by classification

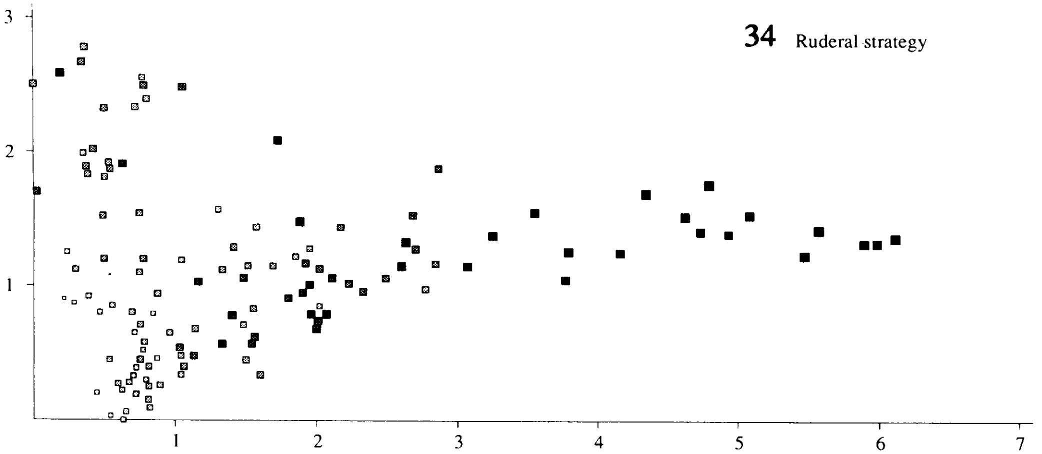
Fig. 30 shows the classification into blocks plotted on to the sample plot positions of the first and second DCA axes of Dataset *AB*. The first ordination axis showed (from the right) a sequence of sample plots from the geolittoral sites of Block 0 and the epilittoral pioneer vegetation of Blocks I and II, via the intermediate Blocks III and IV, to the grassland sites of Block V, VI and VII. The last 3 blocks were separated along DCA 2, Block VII including a



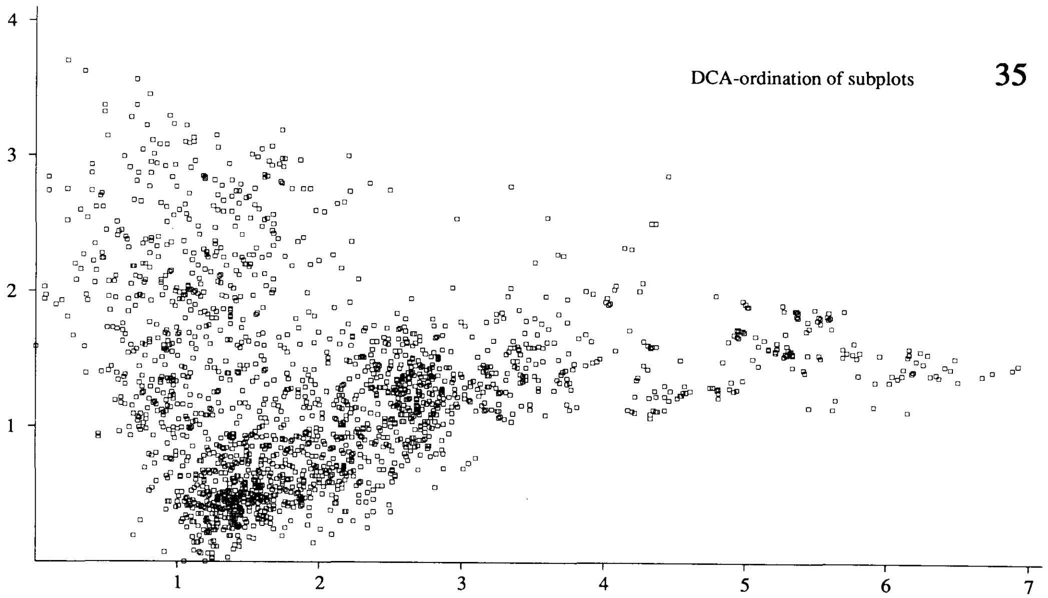
32 Competitor strategy



33 Stresstolerator strategy



34 Ruderal strategy



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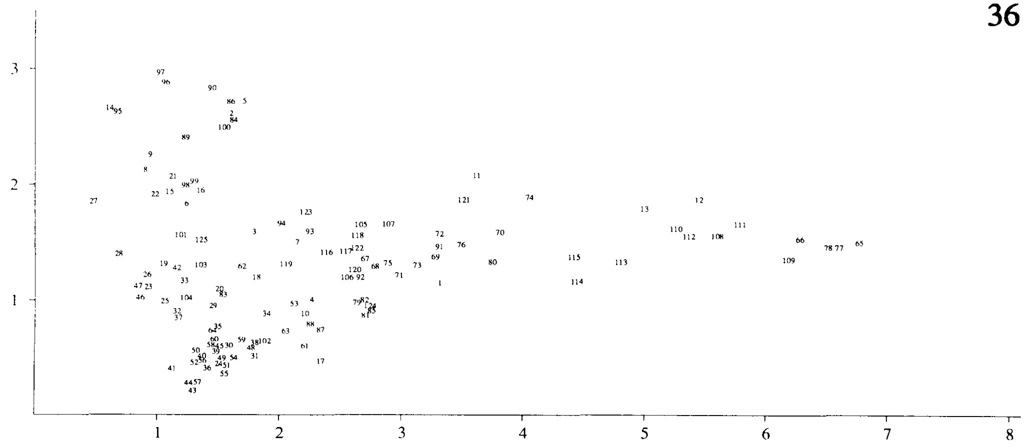


Figs 35-36. DCA ordination of presence/absence data of 2000 subplots of Dataset *AB*. Fig. 35. DCA 1 (horizontal axis) and DCA 2 (vertical axis). Fig. 36. The centroids of the scores for the 16 subplot constituting each sample plot. The sample plot numbers are placed at centroids.

Figs 32-34 (left). C, S and R strategy values plotted onto the positions in the DCA ordination. DCA 1 (horizontal axis) and DCA 2 (vertical axis) of the *AB* dataset. Low strategy values are indicated by small square size and light shades of grey, progressively higher strategy values are indicated by larger size and darker shades of grey. - Fig. 32. Competitor strategy. - Fig 33. Stress-tolerator strategy. - Fig 34. Ruderal strategy.

segment of DCA 2 larger than the two other blocks taken together. Lost Unit I aligned with Block III along DCA1, but was separated from this along DCA 2. Lost Unit II occupied a position between blocks VI and VII along DCA 2. The within-block dispersion of sample plot scores differed strongly; Blocks 0 and I each occupied more than 1.5 S.D. along DCA 1, while Block 2 showed a dispersion of 0.25 S.D. Blocks 0, I, V and VI showed low dispersion along DCA 2, while Block VII showed a dispersion of more than 1.5 S.D., thus spanning more than 60 % of the axis!

Fig. 31 shows the classification plotted on to the sample plot position in the DCA ordination of Subset *A*. The first axis of the ordination showed the same sequence of sample plots, although the gradient length is shortened more than 2 S.D. The first axis showed a linear sequence from Block I to Block VII. The sample plots showed better dispersion along DCA 2. Lost Unit I was projected on to different blocks, while Lost Unit II remained in the transition between blocks VI and VII, closest to Block VII.

Interpretation of DCA ordination by means of the C-S-R model

Figs 32-34 shows C, S and R partial values for the sample plots, plotted on to the positions in the DCA ordination. The three ordination plots showed distinct distributional patterns for the strategies distribution of strategies.

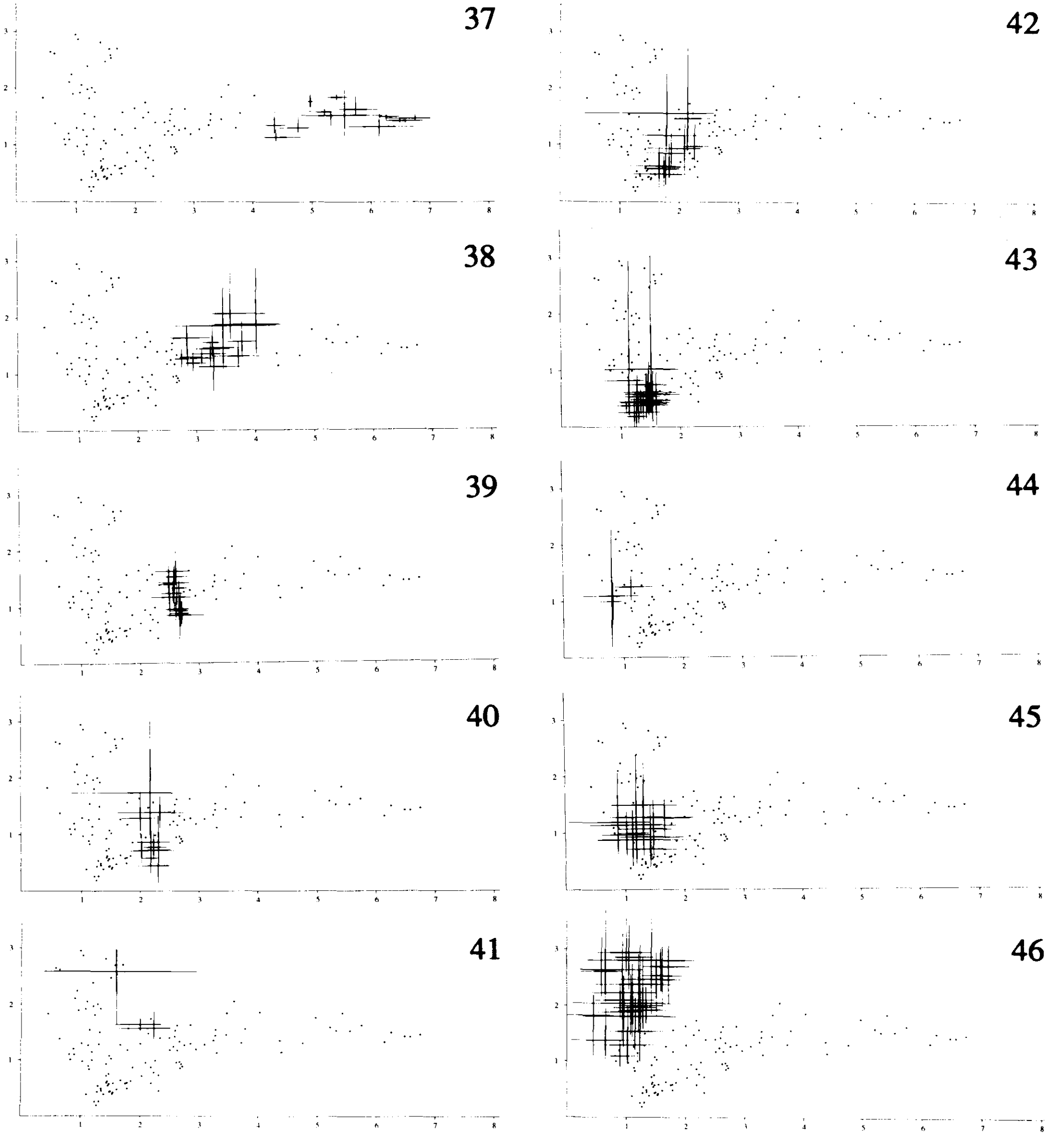
Competitor strategists (Fig. 32) showed a tendency to concentration in the upper and right part of the ordination plot, i.e. blocks 0, I, II, and VII. For Block III, this tendency is conspicuous; the upper part showed higher competitor values than the lower.

Stress-tolerator strategists (Fig. 33) were most dominant in the left part of the ordination plot, and higher for low than for high DCA 2 scores. Blocks III, IV and VII showed intermediate stress-tolerator values, while Blocks V and VI showed higher values. The greatest contribution of stress-tolerators was found in the three sample plots of Lost Unit II.

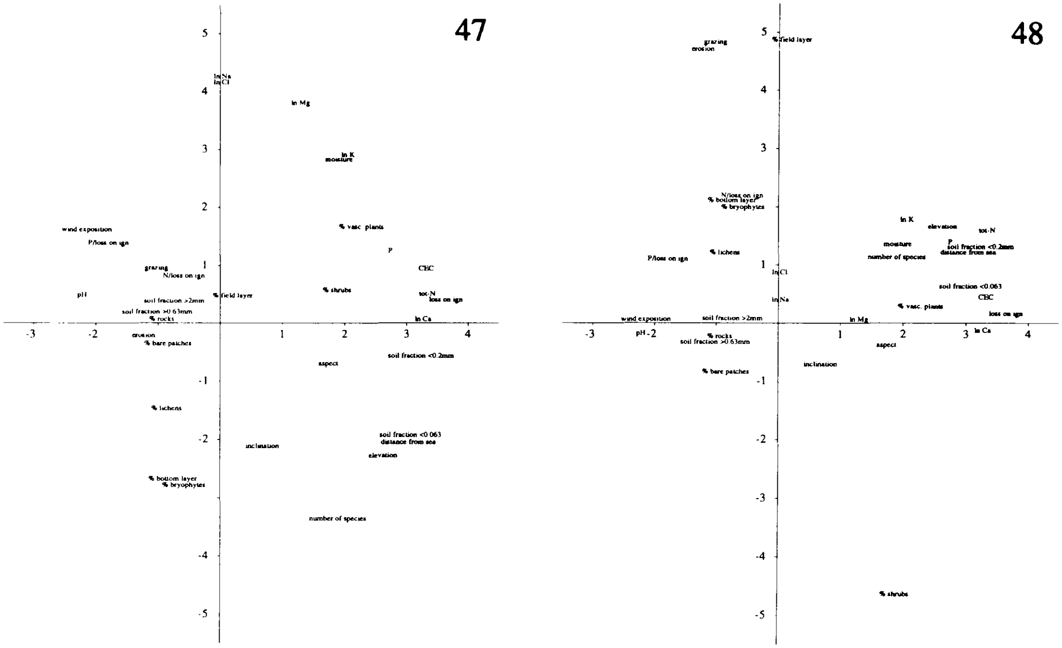
Ruderal strategists (Fig. 34) showed a gradual increase towards higher sample plot scores along DCA 1; blocks II, I and 0. Along DCA 2, a slight, but significant, increase was observed for increasing sample plot scores.

DCA ordination of subplots

Axes 1 and 2 of the DCA ordination of binary data from the 2000 subplots is given in Fig. 35. The eigenvalues of the first four axes, 0.71, 0.30, 0.20, and 0.15, were slightly larger than the correspondent eigenvalue of the sample plot ordination (0.69, 0.30, 0.16, and 0.13). In addition to the increase in eigenvalues, the estimates of β-diversity increased, thus the gradient length of axis 1 was 6.92. However, visually inspected, the conformity between the DCA ordination of the 125 sample plots and the 2000 subplots was very high. Thus, subplot ordination scores were used to evaluate the homogeneity of each sample plot. Fig. 36 shows the centroid of subplot scores for each sample plot with respect to axes 1 and 2 of the DCA ordination of 2000 subplots. Figs 37-46 show the within sample plot dispersion of subplots scores for each of the blocks and lost units. The tendency for high within sample plot dispersion was most pronounced in Blocks IV and VI. Block IV showed high internal heterogeneity, situated in the transition between the xeric Block III vegetation and the more established vegetation of Blocks V-VII. Block VI occurred in the transition from open



Figs 37-46. Dispersion of sample plots in DCA ordination of subplots; DCA 1 (horizontal axis) and DCA 2 (vertical axis). Narrow lines indicate the maximum and minimum subplot position, bold lines indicate the standard deviation of the 16 subplots constituting each sample plot. - Fig. 37. Block 0. - Fig. 38. Block I. - Fig. 39. Block II. - Fig. 40. Block III. - Fig. 41. Block IV. - Fig. 42. Lost unit I. - Fig. 43. Block V. - Fig. 44. Block VI. - Fig. 45. Lost unit II. - Fig. 46. Block VII.



Figs 47-48. PCA ordination of 33 environmental variables in 125 sample plots in Dataset *AB*. - Fig. 47. PCA 1 (horizontal axis) and PCA 2 (vertical axis). - Fig. 48. PCA 1 (horizontal axis) and 3 (vertical axis).

grassland (Block V) to juniper-dominated shrub vegetation (Block VII) and also included small juniper thickets expanding in typical Block V vegetation. The "Lost Units" also showed high within sample plot dispersion of subplot scores. Lost Unit I, intermediate between Blocks II and VII, showed a greater dispersion along DCA 1 than along DCA 2. Lost Unit II, between Block VI and Block VII, on the contrary showed greater dispersion along DCA 2. Block III showed considerable variation in within sample plot dispersion; low for low DCA 2 scores, higher for high DCA 2 scores (> 1 S.D.).

ENVIRONMENTAL ANALYSES

PCA ordination of environmental variables

Figs 47-48 show the results of the PCA ordination of environmental variables in Dataset *AB*. The eigenvalues, 0.27 for PCA 1, 0.16 for PCA 2, and 0.13 for PCA 3, respectively, indicated the percentage variance accounted for by different axes. The variables were not strongly clustered in the ordination space, but rather evenly distributed. Anyway, some weak groupings could be imagined, according to the spatial relationships of the variables.

Group I showed high loadings on PCA 1, and slightly positive loadings on PCA 2. It was made up by loss on ignition, total N and P, negatively correlated with erosion and percentage cover of bare patches.

Group II showed high loadings on PCA 1, and slightly negative loadings on PCA 2. It was made up by fine soil fractions, distance from sea and elevation, negatively correlated with the coarse soil fractions and pH.

Group III was made up by $[Cl^-]$ and the cation concentrations ($[Na^+]$, $[Mg^{2+}]$ and $[K^+]$). This group showed the highest loadings on PCA 2. Percentage cover of bryophytes, and thus the percentage cover of the bottom layer, correspondingly showed the highest negative correlations.

Group IV consisted of moisture, highly negatively correlated to percentage cover of lichens. These variables showed intermediate positions in the ordination plot, with equal preference for both axes.

Group V showed low loadings on both PCA axes. Examination of PCA 3, meanwhile, showed highest loadings for just these variables; percentage cover of the field layer, grazing and erosion (by trampling), and correspondingly negative correlation with percentage cover of the shrub layer (Fig. 48).

Direct gradient analysis

Tab. 4 shows the results of the rescaled constrained hybrid ordination, *rh*-DCCA, performed with one axis constrained to be a linear combination of each of the 33 environmental variables.

For the *AB* dataset, the highest ratios of importance, i_{AB}, were observed for the environmental variables most strongly correlated with DCA 1, e.g. elevation, $[Cl^-]$, $[Na^+]$ and total number of species (all $i > 0.7$). Other variables with high importance ratios were grazing intensity ($i_{AB} = 0.66$) and percentage cover of shrubs ($i_{AB} = 0.47$).

The highest importance ratios for Subset *A*, i_A, were obtained among the most important variables in the *AB* dataset, i.e. percentage cover of shrubs ($i_A = 0.86$), elevation ($i_A = 0.57$) and grazing ($i_A = 0.52$). In addition, variables related to disturbance, e.g. erosion ($i = 0.62$), coarse and fine soil fraction (all $i > 0.4$), loss on ignition ($i = 0.52$), CEC ($i = 0.58$) and nutrients as tot-N, Ca^{2-} (both $i > 0.5$) are important. Tab. 4 shows the effect of deletion of Subset *B* on the relative importance of environmental variables. Only 5 among the 33 variables showed $\delta_{A_{AB}} < 1$, indicating that removal of plots from the geolitteral zone strongly enhanced interpretability of epilittoral vegetational trends in terms of environmental gradients, and further indicated that vegetation of Block 0 might depend on another set of environmental variables than the epilittoral vegetation.

Tab. 4. Eigenvalues of *rh*-DCCA ordinations of each of the 33 environmental variables, for Dataset *AB* and Subset *A*. e_{CI} - eigenvalue of the constrained axis, e_{RI} - eigenvalue of the first recidual axis, $r = e_{cI}/e_{RI}$, $i = e_{cI}/e_{DCAI}$ (where e_{DCAI} is the eigenvalue of the first axis of the corresponding DCA ordination), and $\delta_{A,AB} = i_A/i_{AB}$.

	ABe_{CI}	ABe_{RI}	r_{AB}	Ae_{CI}	Ae_{RI}	r_A	r_A	i_{AB}	$i_A\delta_{A,AB}$
elevation	0.251	0.352	0.711	0.192	0.339	0.566	0.363	0.443	1.220
distance	0.238	0.529	0.450	0.183	0.330	0.557	0.345	0.423	1.223
> 2 mm	0.165	0.677	0.244	0.175	0.354	0.495	0.239	0.403	1.684
> 0.63 mm	0.160	0.676	0.236	0.170	0.373	0.456	0.231	0.392	1.694
< 0.2 mm	0.183	0.659	0.278	0.166	0.382	0.436	0.266	0.383	1.442
< 0.063 mm	0.254	0.554	0.458	0.193	0.378	0.512	0.367	0.446	1.213
soil moisture	0.188	0.546	0.345	0.152	0.314	0.484	0.273	0.351	1.284
loss on ign	0.196	0.617	0.318	0.172	0.329	0.523	0.284	0.396	1.394
tot-N	0.182	0.659	0.276	0.169	0.320	0.529	0.263	0.390	1.482
N/loss on ign	0.055	0.550	0.101	0.034	0.425	0.080	0.080	0.079	0.978
P	0.131	0.667	0.196	0.134	0.376	0.358	0.189	0.310	1.633
P/loss on ign	0.207	0.509	0.407	0.109	0.339	0.323	0.300	0.252	0.840
ln Cl	0.329	0.404	0.816	0.091	0.373	0.245	0.477	0.211	0.442
ln Na	0.337	0.406	0.831	0.122	0.393	0.310	0.488	0.281	0.575
ln K	0.116	0.630	0.185	0.105	0.380	0.276	0.169	0.241	1.428
ln Mg	0.190	0.566	0.335	0.125	0.399	0.315	0.275	0.289	1.052
ln Ca	0.236	0.632	0.373	0.202	0.320	0.630	0.341	0.465	1.363
pH	0.197	0.541	0.364	0.160	0.347	0.461	0.285	0.369	1.293
CEC	0.196	0.657	0.298	0.186	0.319	0.583	0.283	0.429	1.512
aspect	0.098	0.641	0.153	0.082	0.382	0.215	0.142	0.189	1.330
inclinat	0.069	0.639	0.108	0.038	0.421	0.092	0.100	0.089	0.893
wind exposition	0.215	0.625	0.344	0.175	0.347	0.505	0.311	0.404	1.295
erosion	0.263	0.575	0.458	0.241	0.388	0.622	0.381	0.556	1.458
grazing	0.260	0.392	0.662	0.206	0.392	0.524	0.376	0.474	1.259
% bare patches	0.099	0.676	0.147	0.103	0.407	0.252	0.143	0.237	1.648
% rocks	0.060	0.646	0.093	0.047	0.385	0.124	0.087	0.110	1.262
% shrubs	0.315	0.669	0.471	0.303	0.354	0.856	0.456	0.698	1.529
% field layer	0.152	0.676	0.224	0.148	0.410	0.362	0.220	0.342	1.555
% bottom layer	0.182	0.620	0.293	0.168	0.360	0.468	0.263	0.388	1.474
% vasc. plants	0.153	0.658	0.232	0.159	0.322	0.495	0.221	0.367	1.657
% bryophytes	0.146	0.619	0.235	0.129	0.381	0.340	0.211	0.298	1.413
% lichens	0.140	0.678	0.206	0.140	0.346	0.404	0.203	0.322	1.588
number of species	0.319	0.389	0.820	0.188	0.380	0.495	0.462	0.433	0.935

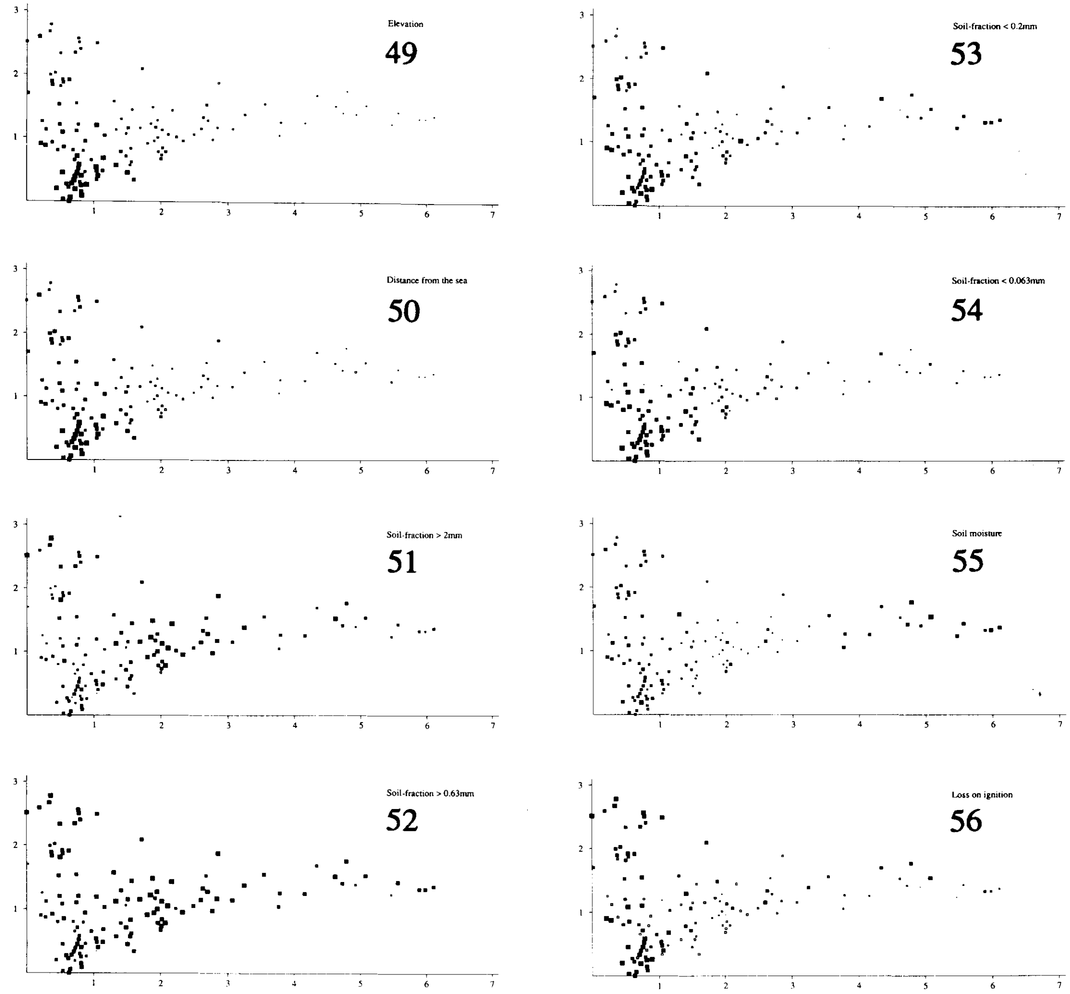
INTERPRETATION OF DCA ORDINATION BY ENVIRONMENTAL VARIABLES

Correlations between DCA axes and environmental variables

Kendall rank correlations between sample plot positions along DCA axes and each of the 33 environmental variables are displayed in Tab. 5.

Tab. 5. Kendall rank correlations between ecological variables and DCA axes of Dataset *AB* and Subset *A*. Correlation coefficients (upper values) and their significance probabilities (lower values) are specified.

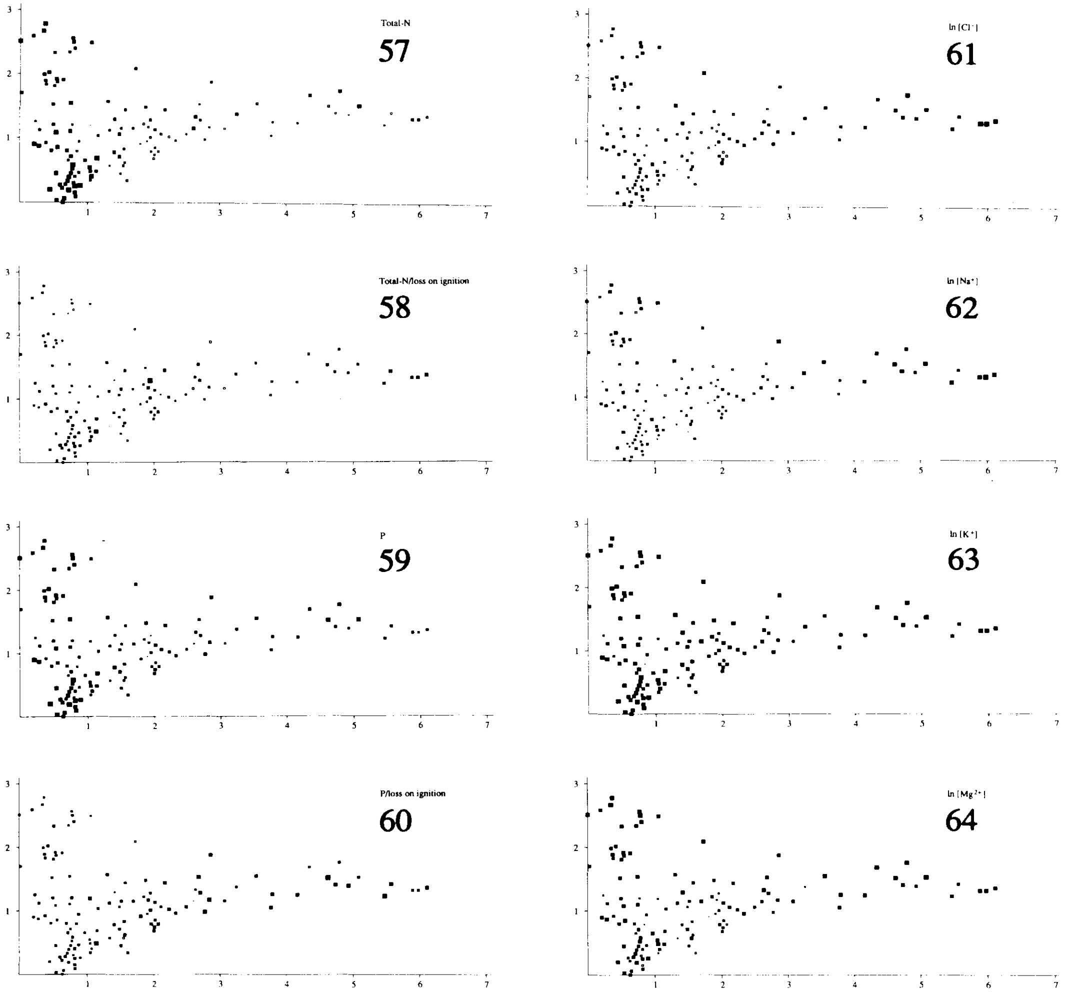
	Dataset *AB*				Subset *A*			
	DCA 1	DCA 2	DCA 3	DCA 4	DCA 1	DCA 2	DCA 3	DCA 4
elevation	-0.5078 0	-0.3767 0	0.0233 0.701	-0.0360 0.553	-0.2637 0	-0.2042 0.002	0.0108 0.866	-0.2471 0
distance	-0.5051 0	-0.3149 0	0.0220 0.717	-0.1039 0.088	-0.3225 0	-0.1691 0.009	-0.0395 0.541	-0.1575 0.015
> 2 mm	0.1881 0.002	0.0948 0.118	0.1795 0.003	0.2943 0	0.3047 0	0.2994 0	0.0431 0.504	0.0411 0.524
> 0.63 mm	0.2051 0.001	0.1640 0.007	0.0947 0.119	0.2929 0	0.2767 0	0.2359 0	0.1072 0.097	0.1181 0.067
< 0.2 mm	-0.3255 0	-0.2713 0	0.0547 0.368	-0.2437 0	-0.2638 0	-0.1765 0.006	-0.1146 0.076	-0.2156 0.001
< 0.063 mm	-0.4284 0	-0.3462 0	0.0611 0.316	-0.1106 0.070	-0.2457 0	-0.1891 0.003	-0.0319 0.623	-0.2646 0
soil moisture	-0.217 0	0.0723 0.234	0.0472 0.437	-0.2977 0	-0.4704 0	-0.0146 0.821	-0.0991 0.125	0.0341 0.598
loss on ign	-0.4111 0	-0.0524 0.387	0.2673 0	-0.1072 0.078	-0.3558 0	0.1725 0.008	-0.0798 0.216	-0.0772 0.231
tot-N	-0.3738 0	-0.0649 0.287	0.303 0	-0.173 0.005	-0.3254 0	0.1331 0.040	-0.1653 0.011	-0.1200 0.064
N/loss on ign	0.1782 0.003	-0.0849 0.161	0.0321 0.597	-0.1081 0.075	0.1183 0.066	-0.0511 0.428	-0.2130 0.001	-0.0778 0.116
P	-0.2425 0	0.0322 0.598	0.2814 0	-0.1003 0.101	-0.2385 0	0.2276 0	-0.0779 0.230	-0.0778 0.230
P/loss on ign	0.3545 0	0.0714 0.239	-0.1303 0.032	0.0839 0.167	0.291 0	-0.0333 0.605	0.0072 0.911	0.0376 0.559
ln Cl	0.1974 0.001	0.2981 0	0.0715 0.240	-0.1355 0.026	-0.0513 0.428	0.2464 0	-0.1092 0.092	0.1729 0.008
ln Na	0.1407 0.021	0.3556 0	0.0517 0.397	-0.0898 0.141	-0.0954 0.141	0.2383 0	-0.0008 0.990	0.2261 0
ln K	-0.0253 0.679	0.1101 0.071	0.3458 0	-0.1376 0.024	-0.1414 0.029	0.3183 0	-0.1876 0.004	-0.0379 0.559
ln Mg	0.0220 0.717	0.3186 0	0.172 0.005	-0.0849 0.163	-0.1960 0.002	0.3225 0	-0.0036 0.955	0.1371 0.034
ln Ca	-0.4803 0	-0.0555 0.363	0.1283 0.036	-0.1030 0.092	-0.4554 0	0.0278 0.668	0.0379 0.559	-0.0245 0.706
pH	0.4617 0	0.0566 0.356	-0.3331 0	-0.0096 0.876	0.3508 0	-0.2614 0	0.0653 0.317	0.1139 0.081
CEC	-0.3930 0	0.0062 0.918	0.1661 0.006	-0.1324 0.029	-0.4408 0	0.0795 0.217	0.0051 0.937	-0.0141 0.827
aspect	-0.2851 0	-0.1098 0.079	0.0852 0.173	0.0070 0.911	-0.2273 0.001	0.0041 0.951	0.0046 0.945	-0.0604 0.361
inclination	-0.1596 0.012	-0.1930 0.002	-0.0202 0.750	0.0663 0.296	0.0324 0.630	-0.0851 0.205	0.0622 0.354	-0.1357 0.043
wind exposition	0.4718 0	0.2412 0	-0.0996 0.149	0.1591 0.021	0.3370 0	0.0947 0.195	0.0845 0.248	0.1627 0.026
erosion	0.4331 0	-0.3390 0	0.0538 0.423	0.0501 0.456	0.4443 0	-0.1579 0.028	-0.1413 0.049	-0.3402 0
grazing	0.4656 0	-0.2414 0	0.2029 0.002	0.0407 0.542	0.4262 0	0.0504 0.483	-0.2770 0	-0.3870 0
% bare patches	0.2107 0.002	-0.1337 0.052	-0.3033 0	0.1137 0.098	0.2379 0.001	-0.2798 0	0.1108 0.130	0.0870 0.234
% rocks	0.3296 0	-0.0006 0.994	-0.0150 0.829	0.1514 0.029	0.3098 0	-0.0169 0.820	-0.0110 0.882	-0.0123 0.869
% shrubs	-0.5609 0	0.2618 0	-0.1305 0.045	-0.1898 0.004	-0.6340 0	-0.0246 0.719	0.1455 0.033	0.3092 0
% field layer	0.1946 0.002	-0.2608 0	0.2658 0	-0.0395 0.525	0.2083 0.002	0.0522 0.429	-0.2757 0	-0.3064 0
% bottom layer	0.0813 0.190	-0.3983 0	0.0138 0.824	0.3589 0	0.3892 0	-0.0577 0.381	0.1284 0.051	-0.3721 0



Figs 49-56. Quantitative distribution of environmental variables along DCA 1 (horizontal axis) and DCA 2 (vertical axis). Low values are indicated by small square size and light shades of grey, progressively higher values are indicated by larger size and darker shades of grey. - Fig. 49. Elevation. -Fig. 50. Distance from the sea. - Fig. 51. Soil fraction > 2 mm. - Fig. 52. Soil fraction > 0.63 mm. - Fig. 53. Soil fraction < 0.2 mm. - Fig. 54. Soil fraction < 0.063 mm. - Fig. 55. Soil moisture. - Fig. 56. Loss on ignition.

Dataset *AB* correlations

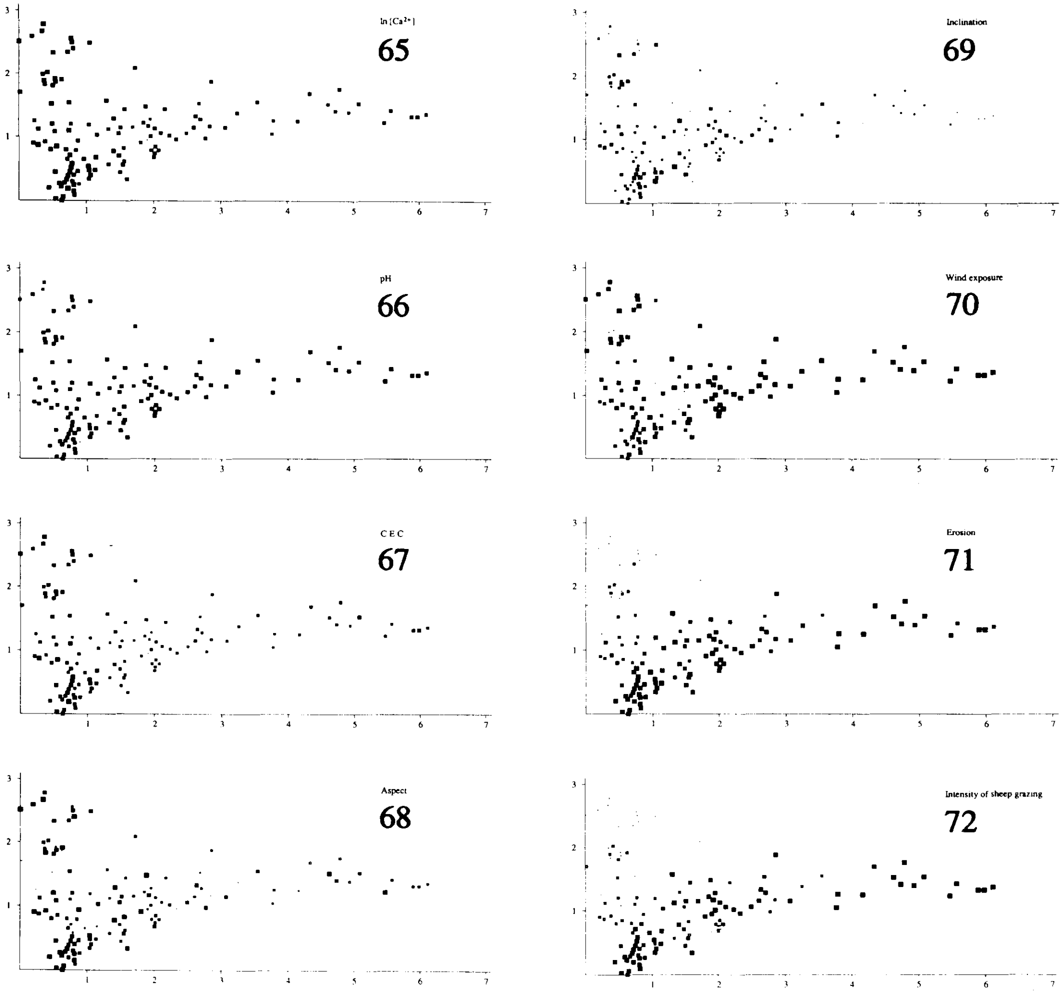
The left part of Tab. 5 lists the Kendall rank correlation coefficients and their significance probabilities, for comparisons of the environmental parameters and the four DCA axes in Dataset *AB*.



Figs 57-64. Quantitative distribution of environmental variables along DCA 1 (horizontal axis) and DCA 2 (vertical axis). Low values are indicated by small square size and light shades of grey, progressively higher values are indicated by larger size and darker shades of grey. - Fig. 57. Total-N. - Fig. 58. Total-N/loss on ignition. - Fig. 59. P. - Fig. 60. P/loss on ignition. - 61. ln [Cl^-]. - Fig. 62. ln [Na^+]. - Fig. 63. ln [K^+]. - Fig. 64. ln [Mg^{2+}]

The first DCA axis was highly correlated with the percentage cover of shrubs ($\tau=-0.5609$), elevation ($\tau=-0.5078$) and distance from sea ($\tau=-0.5051$). Ca^{2+} ($\tau=-0.4803$), the fine-soil fraction (<0.063mm; $\tau=-0.4284$) and loss on ignition ($\tau=-0.4111$) were also highly correlated with DCA 1. Another, highly correlated variable was grazing intensity ($\tau=0.4656$).

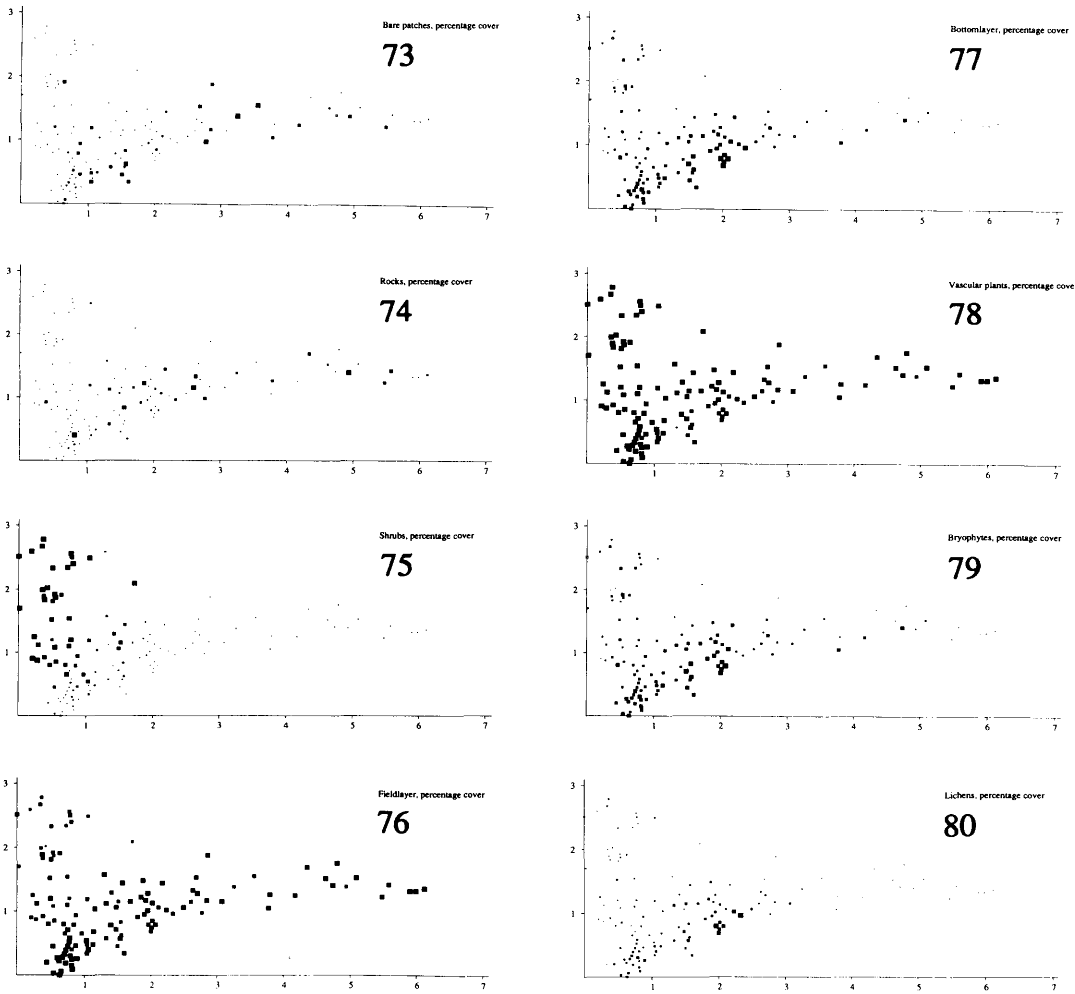
The second DCA axis was highly negatively correlated with percentage cover of the bottom and field layers ($\tau=-0.3983$, respectively -0.2608) and positively correlated with



Figs 65-72. Quantitative distribution of environmental variables along DCA 1 (horizontal axis) and DCA 2 (vertical axis). Low values are indicated by small square size and light shades of grey, progressively higher values are indicated by larger size and darker shades of grey. - Fig. 65. ln [Ca^{2+}]. - Fig. 66. pH. - Fig. 67. C E C. - Fig. 68. Aspect. - Fig. 69. Inclination. - Fig. 70. Wind exposure. - Fig. 71. Erosion. - Fig. 72. Intensity of sheep grazing.

percentage cover of shrubs (τ=0.2618). The elevation and fine-soil fraction were highly negatively correlated (τ=-0.3767 and -0.3462).

The third DCA axis was highly positively correlated with [K^+], total nitrogen, and phosphorus content (τ, respectively, 0.3458, 0.3030 and 0.3186). The negative correlation with the percentage cover of bare patches (τ=-0.3033) and positive correlation with loss on ignition (τ=0.2673) were in accordance with significant correlations of percentage cover of the field



Figs 73-80. Quantitative distribution of environmental variables along DCA 1 (horizontal axis) and DCA 2 (vertical axis). Low values are indicated by small square size and light shades of grey, progressively higher values are indicated by larger size and darker shades of grey. - Fig. 73. Bare patches, percentage cover. - Fig. 74. Rocks, percentage cover. - Fig. 75 Shrubs, percentage cover. - Fig. 76. Field layer, percentage cover. - Fig. 77. Bottom layer, percentage cover. - Fig. 78. Vascular plants, percentage cover. - Fig. 79. Bryophytes, percentage cover. - Fig. 80. Lichens, percentage cover.

layer (τ= 0.2658) and strong indications of grazing (τ=0.2029). pH showed a high negative correlation (τ=-0.3331).

The fourth DCA axis was negatively correlated with moisture and the fine soil fraction (τ=-0.2977, respectively -0.2437), while the coarse fractions were positively correlated

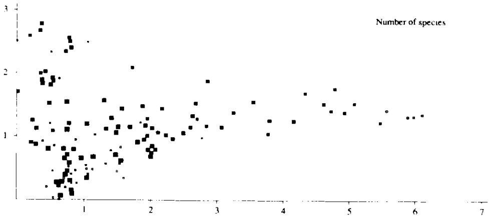


Fig. 81. Quantitative distribution of number of species along DCA 1 (horizontal axis) and DCA 2 (vertical axis). Low values are indicated by small square size and light shades of grey, progressively higher values are indicated by larger size and darker shades of grey.

(>2mm; τ=0.2943 and >0.63mm; τ=0.2929). The axis was highly correlated with percentage cover of the bottom layer (τ=0.3589).

Subset *A* correlations

The right part of Tab. 5 shows the correlation coefficients and their significance probabilities between the environmental parameters and the four DCA axes of Subset *A*;

The first DCA axis showed higher correlation with the percentage cover of shrubs (τ=-0.6340) than in the case of dataset AB. The correlation coefficient of moisture was also higher than along DCA 1 of the Dataset *AB* ordination (τ=-0.4704).

The second DCA axis was negatively correlated with elevation (τ=-0.2042), while the content of Mg^{2+}, K^+ and Na^+ (τ=0.3225, 0.3183 and 0.2383) and Cl^- (τ=0.2464) were significantly positively correlated. The coarse soil fraction also show a positive correlation (>2mm; τ=0.2994 and >0.63mm; τ=0.2359).

The third DCA axis was highly negatively correlated with percentage cover in the field layer (τ=-0.2757). Grazing (τ=-0.2770) and nitrogen in percent of loss on ignition (τ=-0.2130) showed negative correlations.

The fourth DCA axis showed high negative correlations with the intensity of grazing (τ=-0.3870) and erosion (by trampling) (τ=-0.3402). The cover of shrubs was positively correlated (τ=0.3092) with DCA 4, while the bottom and field layers were negatively correlated (τ=-0.3721 and -0.3064).

Quantitative distribution of environmental variables along DCA 1 and 2

Figs 49-81 show each of the 33 environmental variables, expressed by quantitative symbols, plotted on to the sample plot scores of DCA 1 and 2. A number of variables showed quantitative optimum within a limited segment of the ordination plot.

For some variables, the highest quantitative scores occurred near the end-point of one of the ordination axes, with a gradual decline towards the opposite end. The high correlation coefficient between the variable and the DCA axis indicated an adequate spatial pattern of structural importance. Examples are shown by e.g. *elevation* (Fig. 49) and *loss on ignition* (Fig. 56). For a number of variables, significant trends along one axis also influences the correlation with the other axes. Fig. 50 shows how the contribution of the sample plot values

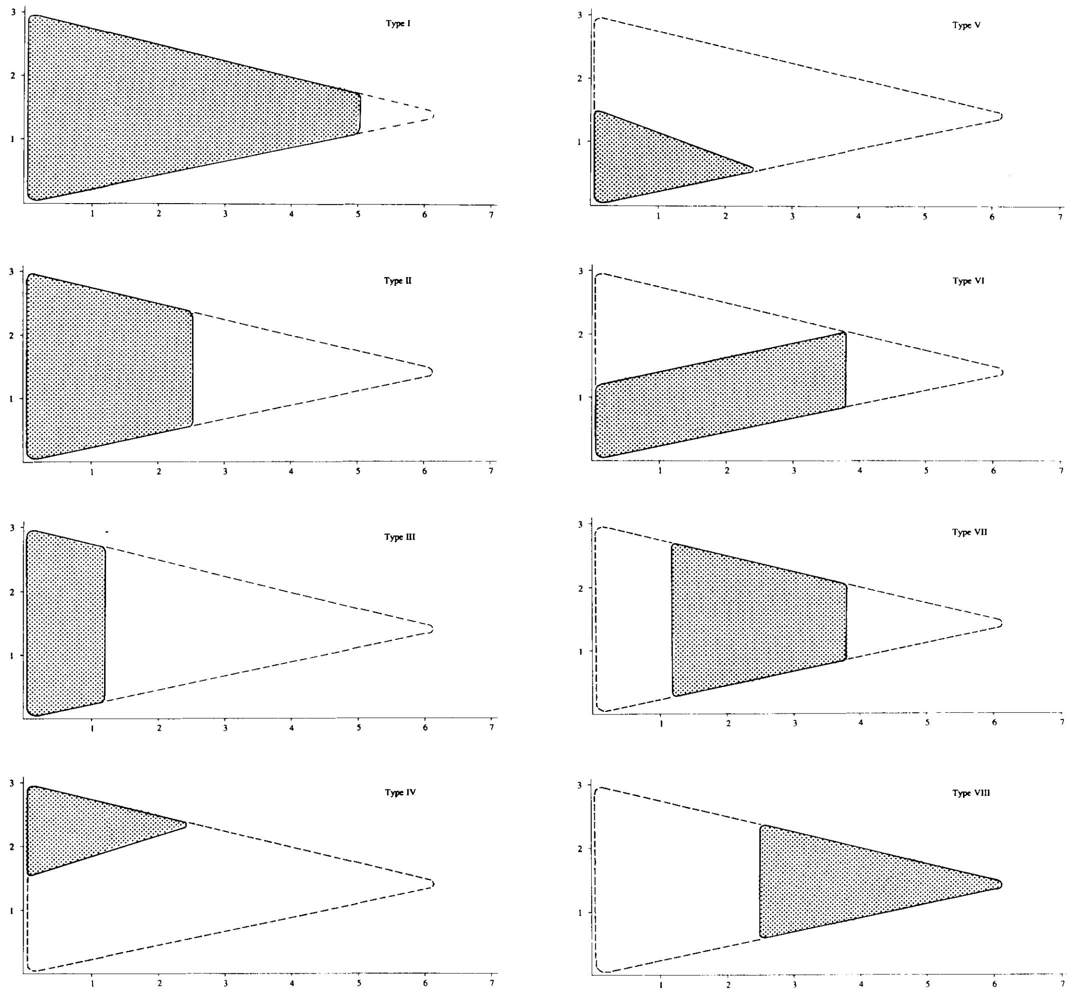
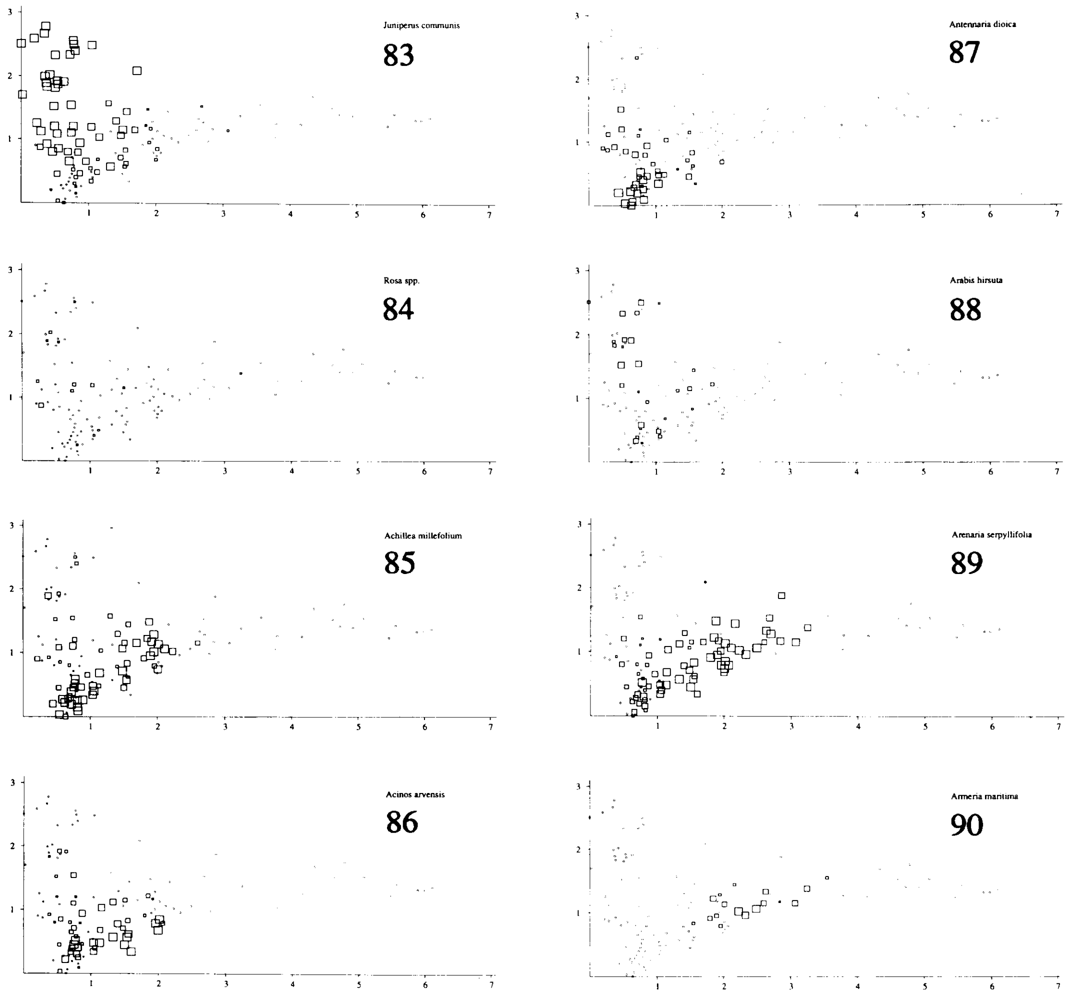


Fig. 82. Model of the main different species distributional patterns, conventionalized in DCA ordination plot of Dataset *AB*. DCA 1 (horizontal axis) DCA 2 (vertical axis).

from the left 4 S.D. segment of DCA 1 will increase the negative correlation between *distance to sea* and DCA 2.

Low correlation coefficients between an environmental variable and the ordination axes do not necessarily imply that the variable in question does not have an important structuring effect on the vegetation. One example is shown in Fig. 51, where the coarse soil fraction (> 2 mm) has highest values in the middle of the ordination plot, and thus low correlation coefficients with both ordination axes.

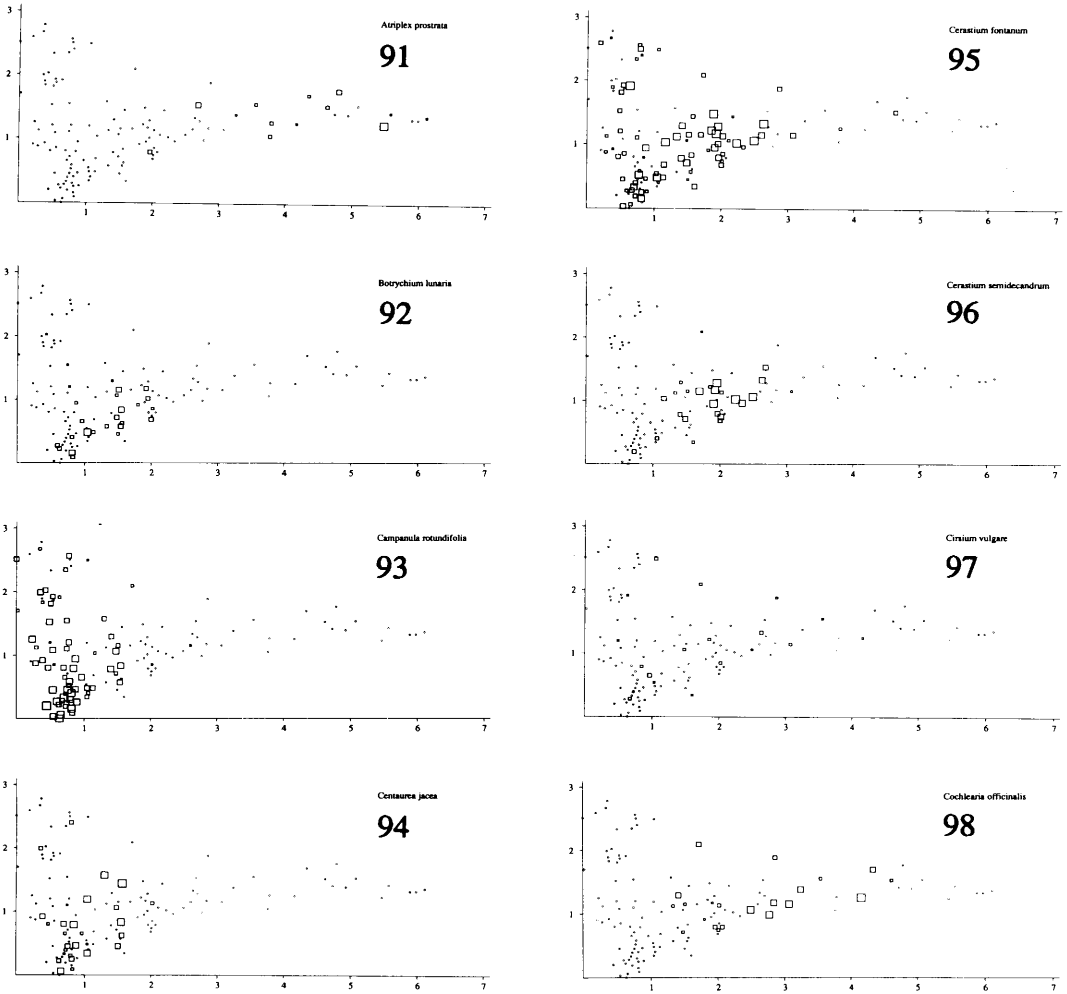


Figs 83-90. Distribution of species abundances. Frequency in subplots for each species is plotted onto the sample plot positions in the DCA ordination of Dataset *AB*; DCA 1 (horizontal axis) and DCA 2 (vertical axis). Small circles indicate absence. Squares indicate where the species is present. Low frequency in subplots is indicated by small square size, progressively higher frequency is indicated by larger size. - Fig. 83. *Juniperus communis*. - Fig. 84. *Rosa spp*. - Fig. 85. *Achillea millefolium*. - Fig. 86. *Acinos arvensis*. - Fig. 87. *Antennaria dioica*. - Fig. 88. *Arabis hirsuta*. - Fig 89. *Arenaria serpyllifolia*. - Fig. 90. *Armeria maritima*.

SPECIES DISTRIBUTIONAL PATTERNS

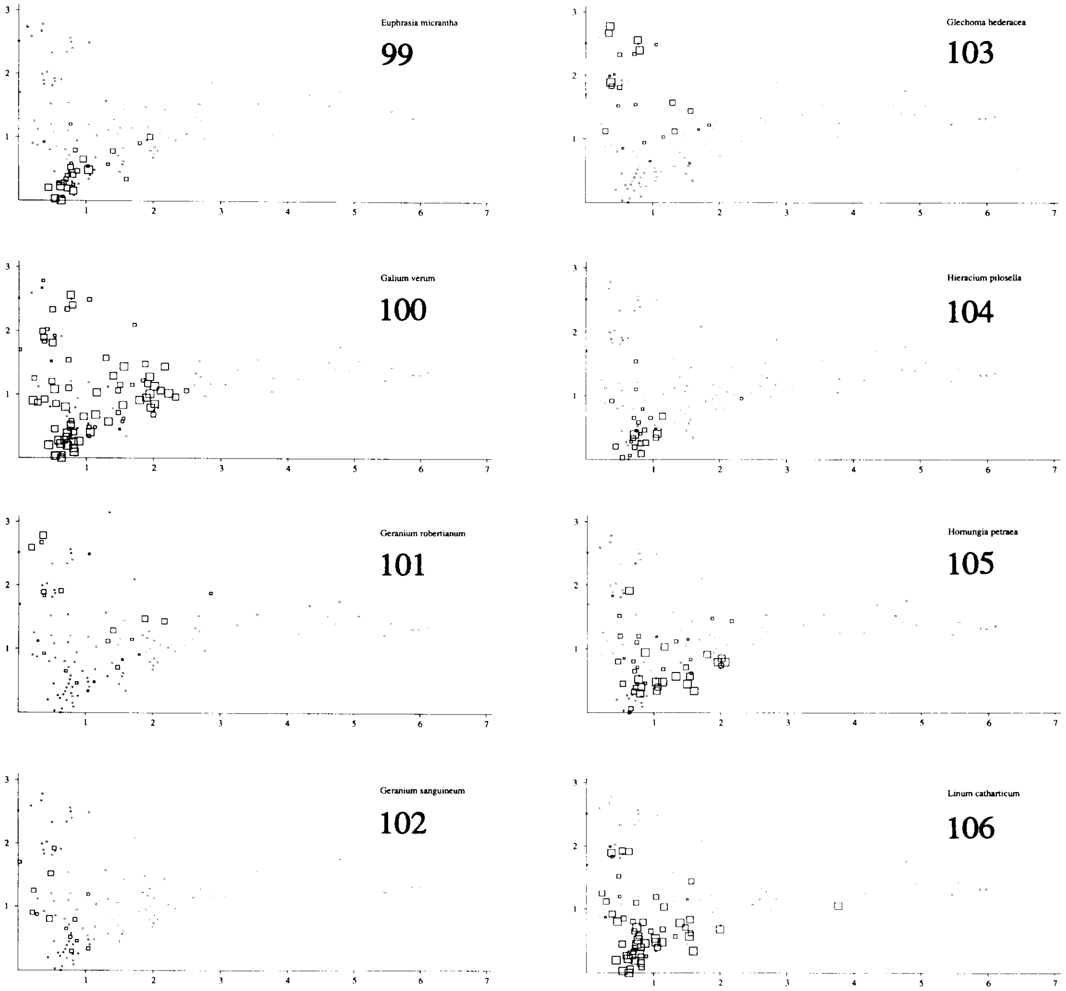
Distribution of species abundance in DCA ordination space

A number of different distribution patterns resulted from combinations of different variables,



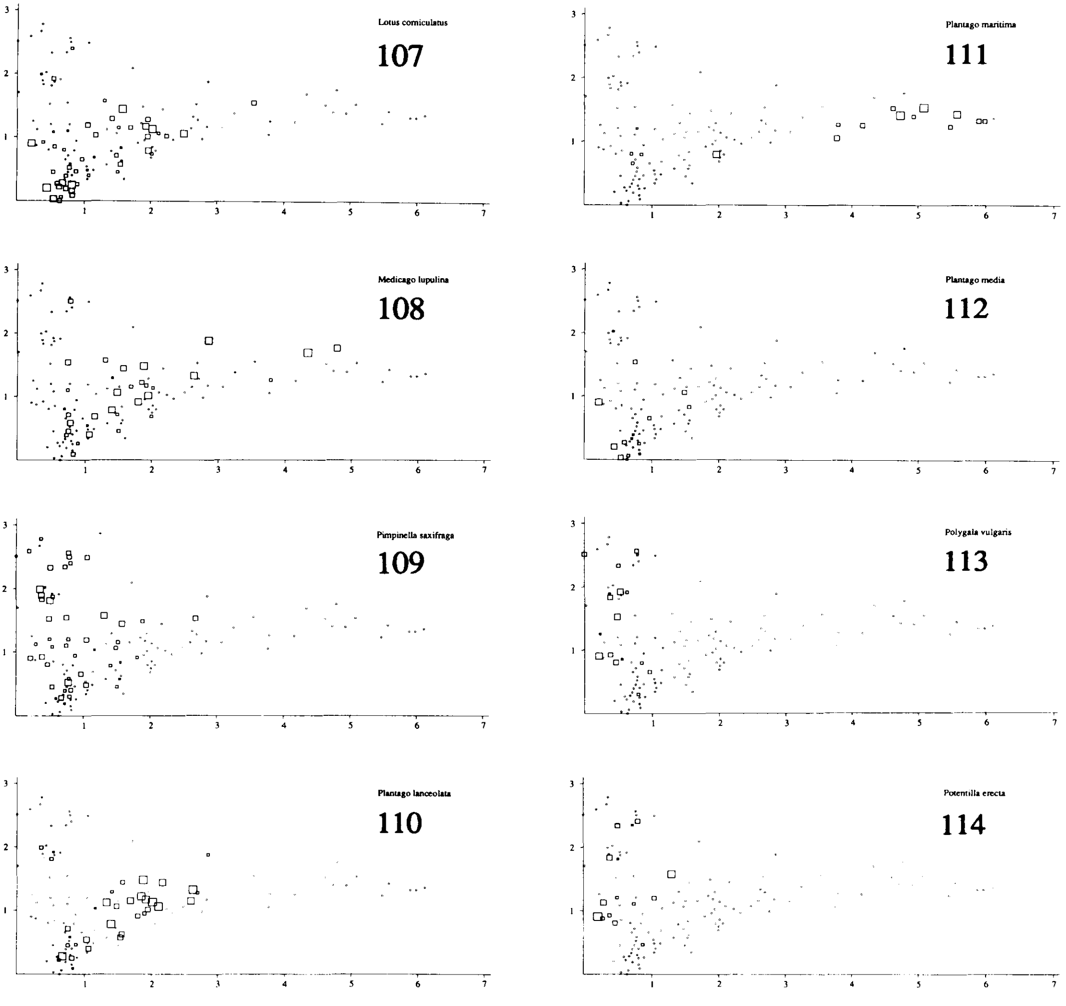
Figs 91-98. Distribution of species abundances. Frequency in subplots for each species is plotted onto the sample plot positions in the DCA ordination of Dataset *AB*; DCA 1 (horizontal axis) and DCA 2 (vertical axis). Small circles indicate absence. Squares indicate where the species is present. Low frequency in subplots is indicated by small square size, progressively higher frequency is indicated by larger size. - Fig. 91. ***Atriplex prostrata***. - Fig. 92. ***Botrychium lunaria***. - Fig. 93. ***Campanula rotundifolia***. - Fig. 94. ***Centaurea jacea***. - Fig. 95. ***Cerastium fontanum***. - Fig. 96. ***Cerastium semidecandrum***. - Fig. 97. ***Cirsium vulgre***. - Fig. 98. ***Cochlearia officinalis***.

e.g. placement of mode and habitat niche breadth. Fig. 82 show conventionalized models of the main different patterns; types I - VIII. Important quantitative variables, such as constancy within the niche and frequency in subplots, increased the variation within species additionally.



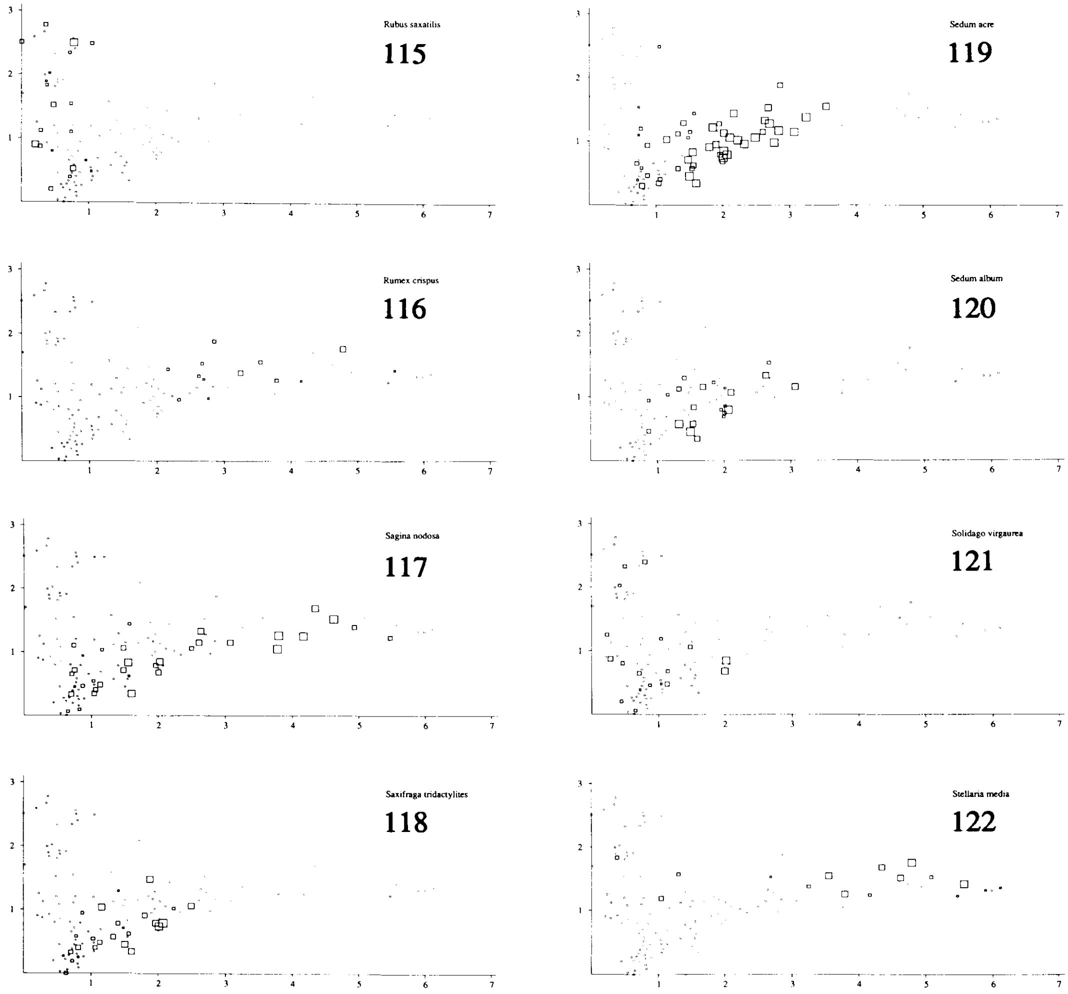
Figs 99-106. Distribution of species abundances. Frequency in subplots for each species is plotted onto the sample plot positions in the DCA ordination of Dataset *AB*; DCA 1 (horizontal axis) and DCA 2 (vertical axis). Small circles indicate absence. Squares indicate where the species is present. Low frequency in subplots is indicated by small square size, progressively higher frequency is indicated by larger size. - Fig. 99. *Euphrasia micrantha.* - Fig. 100. *Galium verum.* - Fig. 101. *Geranium robertianum.* - Fig. 102. *Geranium sanguineum.* - Fig. 103. *Glechoma hederacea.* - Fig. 104. *Hieracium pilosella.* - Fig. 105. *Hornungia petraea.* - Fig. 106. *Linum catharticum.*

Figs 83-171 show the distribution of species abundance (frequency in subplots) for 89 species, with occurrence in more than 10% of the 125 sample plots in the DCA ordination of Dataset *AB*. The different distributional patterns were exemplified by a selection of species:



Figs 107-114. Distribution of species abundances. Frequency in subplots for each species is plotted onto the sample plot positions in the DCA ordination of Dataset *AB*; DCA 1 (horizontal axis) and DCA 2 (vertical axis). Small circles indicate absence. Squares indicate where the species is present. Low frequency in subplots is indicated by small square size, progressively higher frequency is indicated by larger size. - Fig. 107. *Lotus corniculatus*. - Fig. 108. *Medicago lupulina*. - Fig. 109. *Pimpinella saxifraga*. - Fig. 110. *Plantago lanceolata*. - Fig. 111. *Plantago maritima*. - Fig. 112. *Plantago media*. - Fig. 113. *Polygala vulgaris*. - Fig. 114. *Potentilla erecta*.

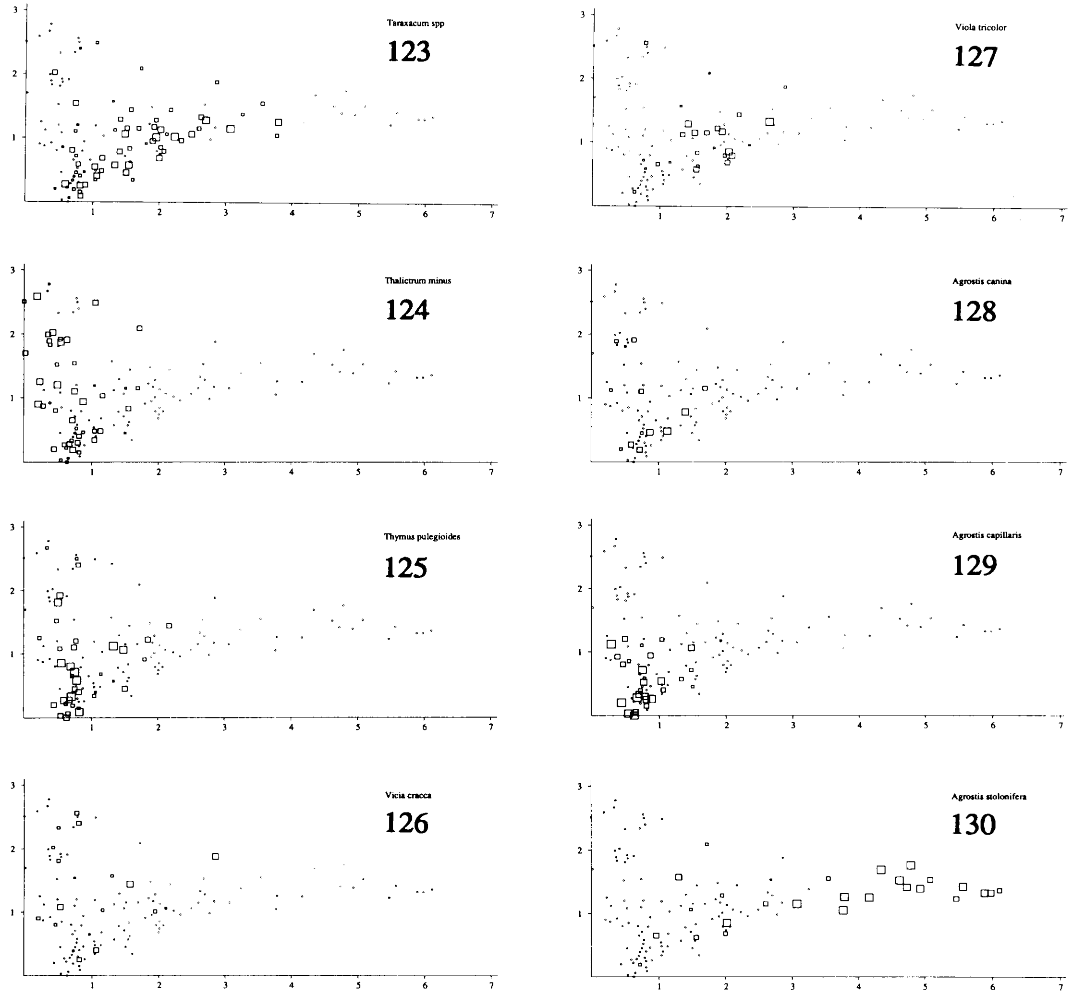
Type I was characterized by very wide niche breadth. The species were evenly distributed along DCA 2, and within a segment of 4-5 S.D. along DCA 1, i.e. only with lack of occurrence near the gradient end-points. Examples of herbs and graminids were *Cerastium*



Figs 115-122. Distribution of species abundances. Frequency in subplots for each species is plotted onto the sample plot positions in the DCA ordination of Dataset *AB*; DCA 1 (horizontal axis) and DCA 2 (vertical axis). Small circles indicate absence. Squares indicate where the species is present. Low frequency in subplots is indicated by small square size, progressively higher frequency is indicated by larger size. - Fig. 115. ***Rubus saxatilis***. - Fig. 116. ***Rumex crispus***. - Fig. 117. ***Sagina nodosa***. - Fig. 118. ***Saxifraga tridactylites***. - Fig. 119. ***Sedum acre***. - Fig. 120. ***Sedum album***. - Fig. 121. ***Soliodago virgaurea***. - Fig. 122. ***Stellaria media***.

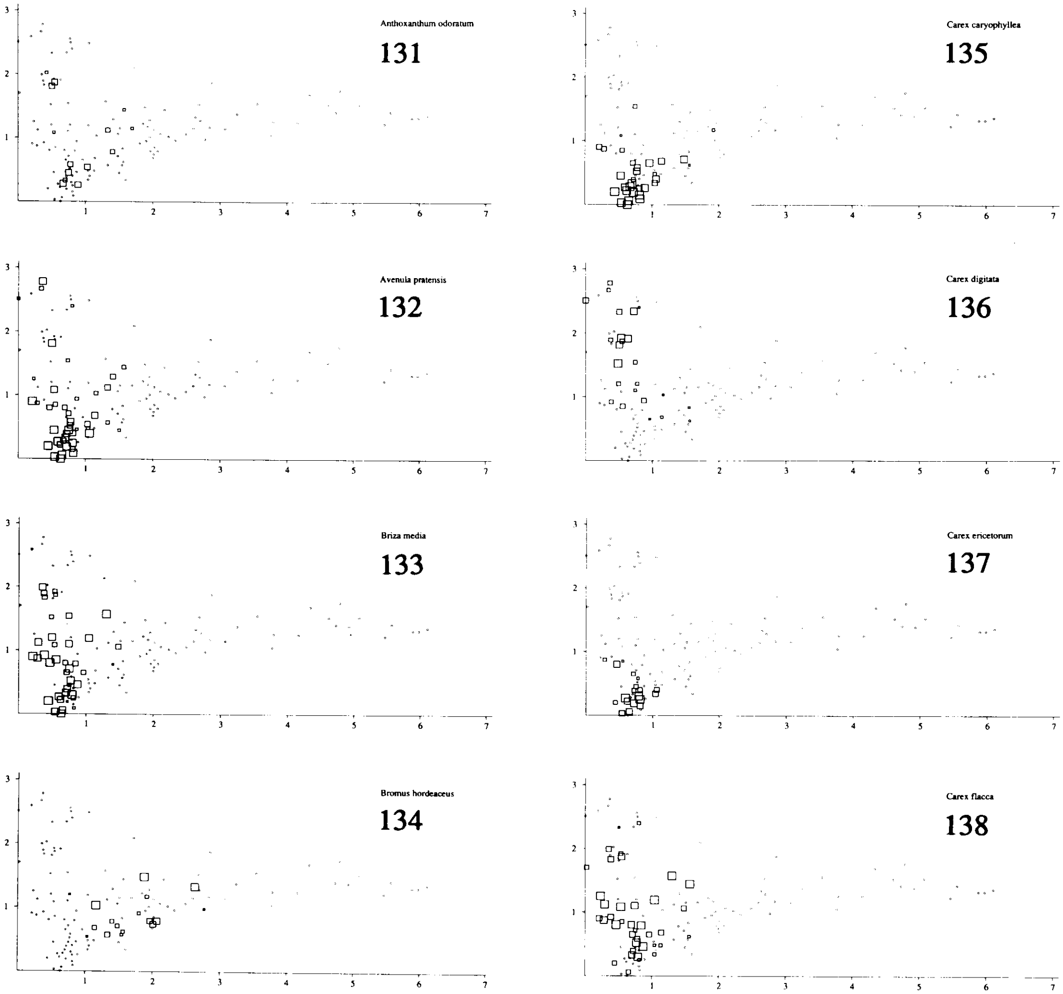
fontanum (Fig. 95) and *Festuca rubra* (Fig. 140). *Cirsium vulgare* (Fig. 97) showed a more scattered distribution.

Type II showed wide niche breadth. The species were evenly distributed along DCA 2,



Figs 123-130. Distribution of species abundances. Frequency in subplots for each species is plotted onto the sample plot positions in the DCA ordination of Dataset *AB*; DCA 1 (horizontal axis) and DCA 2 (vertical axis). Small circles indicate absence. Squares indicate where the species is present. Low frequency in subplots is indicated by small square size, progressively higher frequency is indicated by larger size. - Fig. 123. *Taraxacum spp*. - Fig. 124. *Thalictrum minus* - Fig. 125. *Thymus pulegioides*. - Fig. 126. *Vicia cracca*. - Fig. 127. *Viola tricolor*. - Fig. 128. *Agrostis canina*. - Fig. 129. *Agrostis capillaris*. Fig. 130. *Agrostis stolonifera*.

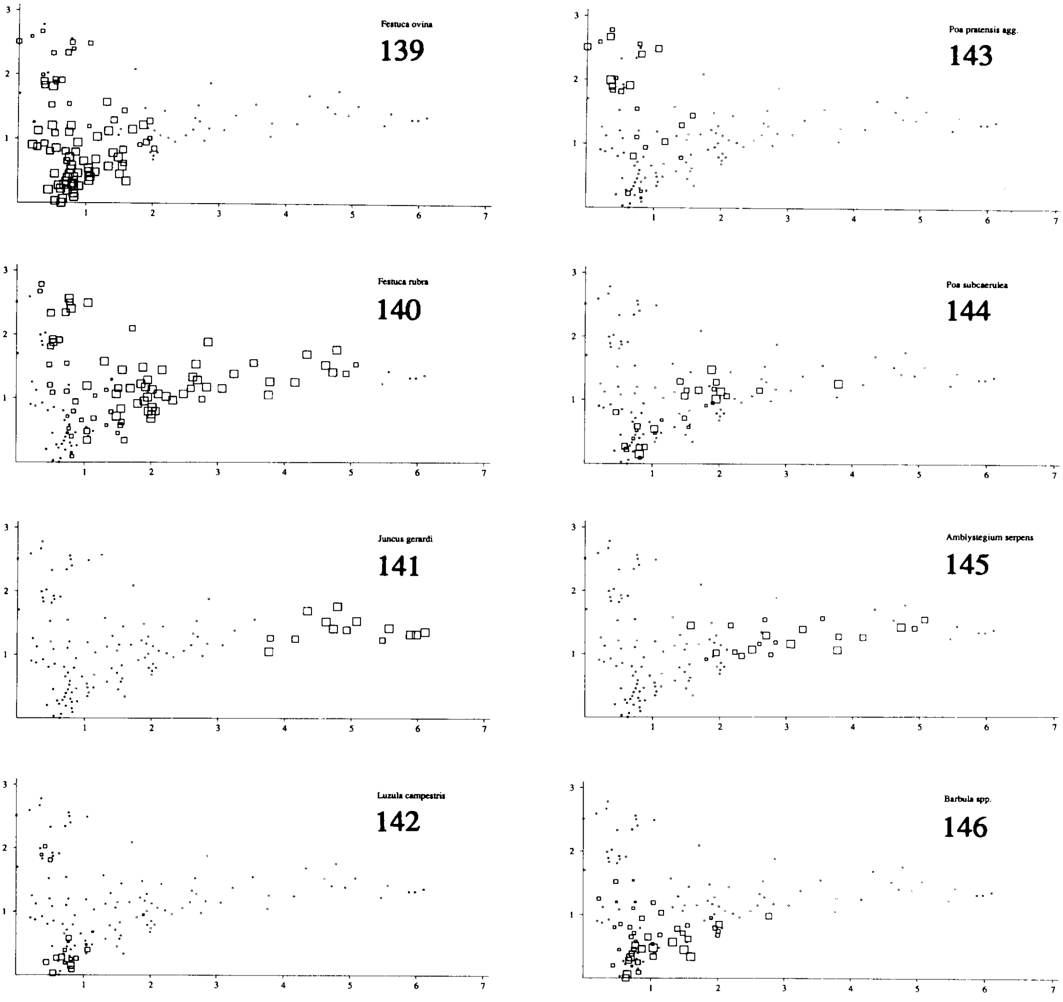
and within a segment of 2-3 S.D. along DCA 1, from the left side (low DCA 1 values). Examples of herbs and graminids were *Galium verum* (Fig. 100) and *Festuca ovina* (Fig. 139). The only cryptogam species with this distribution pattern was *Hypnum cupressiforme* (Fig.



Figs 131-138. Distribution of species abundances. Frequency in subplots for each species is plotted onto the sample plot positions in the DCA ordination of Dataset *AB*; DCA 1 (horizontal axis) and DCA 2 (vertical axis). Small circles indicate absence. Squares indicate where the species is present. Low frequency in subplots is indicated by small square size, progressively higher frequency is indicated by larger size. - Fig. 131. *Anthoxanthum odoratum*. - Fig. 132. *Avenula pratensis*. - Fig. 133. *Briza media*. - Fig. 134. *Bromus hordeaceus*. Fig. 135. *Carex caryophyllea*. - Fig. 136. *Carex digitata*. - Fig. 137. *Carex ericetorum*. - Fig. 138. *Carex flacca*.

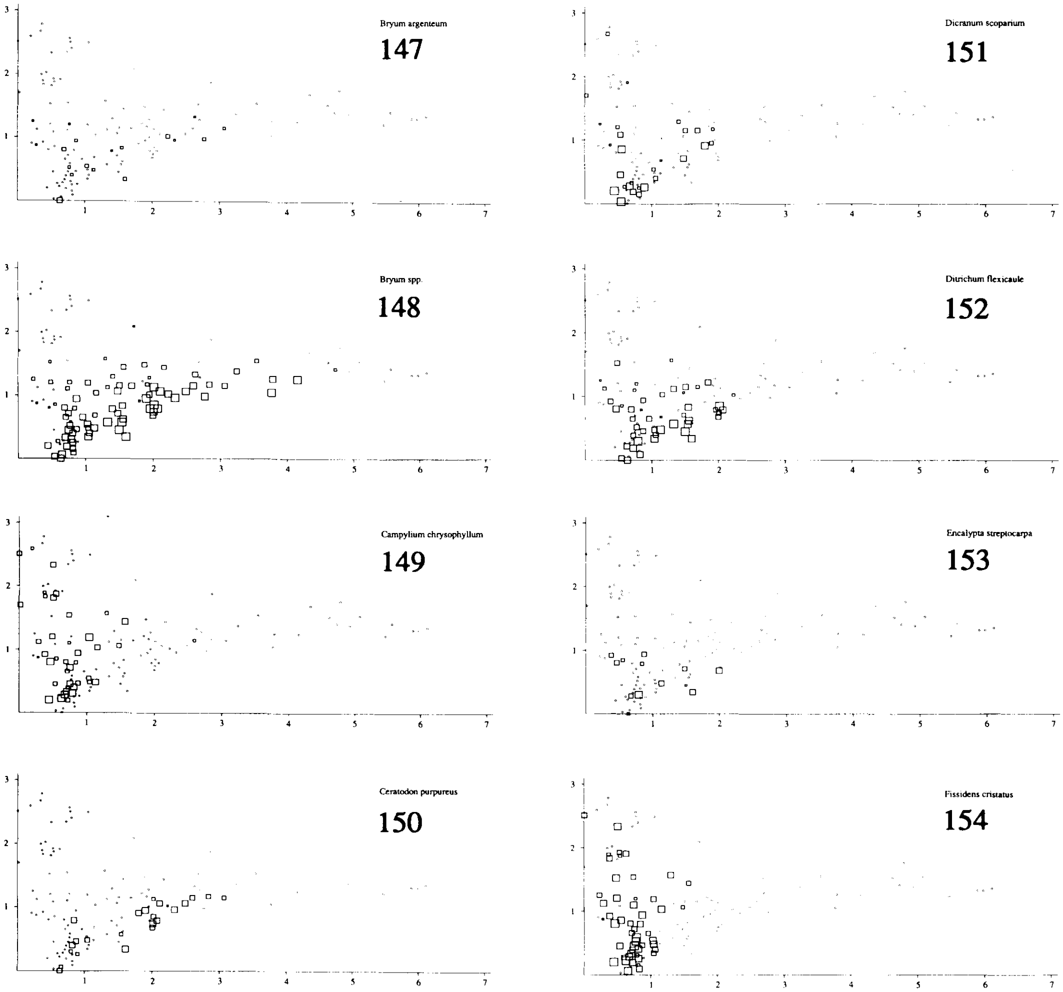
156), although *Campylium chrysopyllum* (Fig. 149) show similar occurrences, but with slightly narrower niche breadth.

Type III showed shorter niche breadth than type II. The species were evenly distributed



Figs 139-146. Distribution of species abundances. Frequency in subplots for each species is plotted onto the sample plot positions in the DCA ordination of Dataset *AB*; DCA 1 (horizontal axis) and DCA 2 (vertical axis). Small circles indicate absence. Squares indicate where the species is present. Low frequency in subplots is indicated by small square size, progressively higher frequency is indicated by larger size. - Fig. 139. *Festuca ovina*. - Fig. 140. *Festuca rubra*. - Fig. 141. *Juncus gerardi*. - Fig. 142. *Luzula campestris*. - Fig. 143. *Poa pratensis* agg. - Fig. 144. *Poa subcaerulea*. - Fig. 145. *Amblystegium serpens*. - Fig. 146. *Barbula* spp.

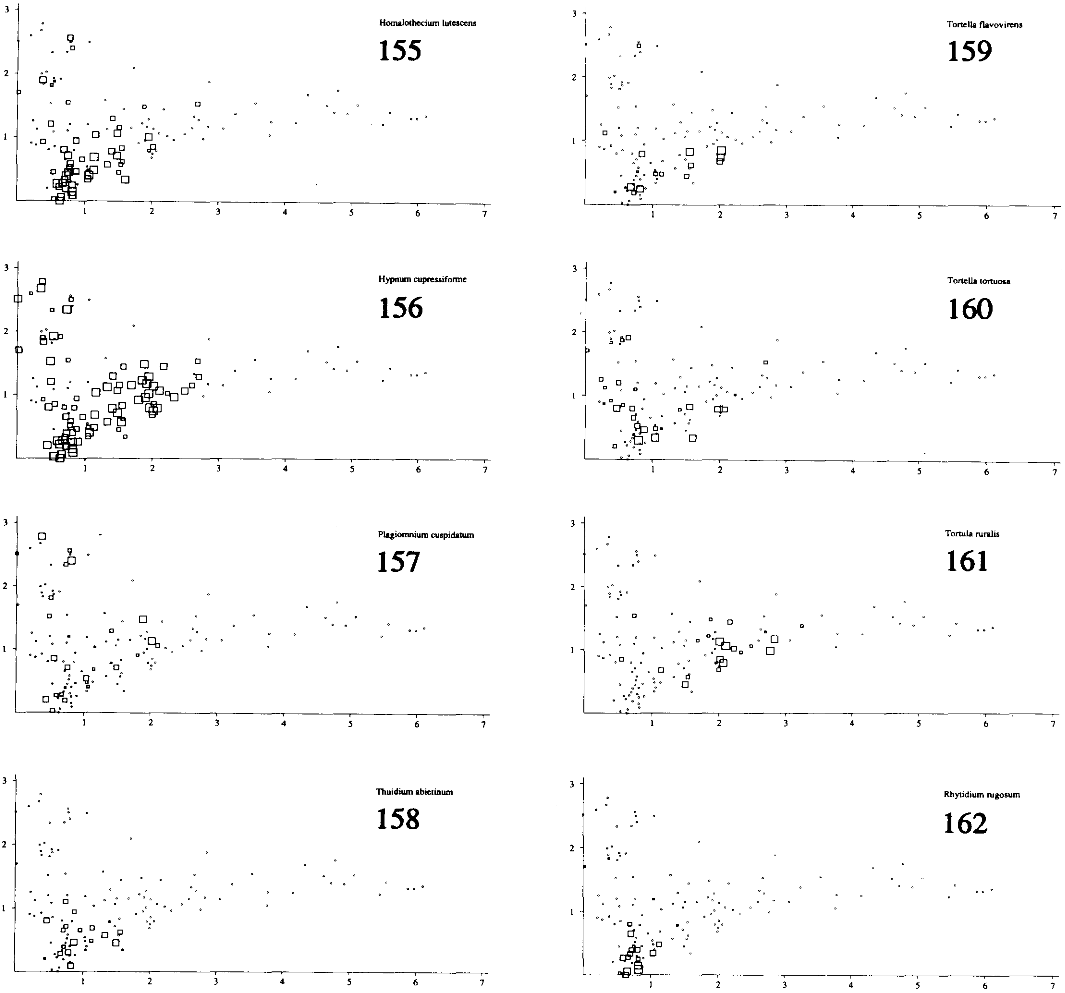
along DCA 2, but only within a segment of 1-2 S.D. along the left part of DCA 1. Examples of herbs were *Rubus saxatilis* (Fig. 115) and *Thalictrum minus* (Fig. 124). Among the graminids *Carex flacca* (Fig. 138), and among the bryophytes *Fissidens cristatus* (Fig. 154),



Figs 147-154. Distribution of species abundances. Frequency in subplots for each species is plotted onto the sample plot positions in the DCA ordination of Dataset *AB*; DCA 1 (horizontal axis) and DCA 2 (vertical axis). Small circles indicate absence. Squares indicate where the species is present. Low frequency in subplots is indicated by small square size, progressively higher frequency is indicated by larger size. - Fig. 147. ***Bryum argenteum***. - Fig. 148. ***Bryum*** spp. - Fig. 149. ***Campylium chrysophyllum***. - Fig. 150. ***Ceratodon purpureus***. - Fig. 151. ***Dicranum scoparium***. - Fig. 152. ***Ditrichum flexicaule***. - Fig. 153. ***Encalypta streptocarpa***. - Fig. 154. ***Fissidens cristatus***.

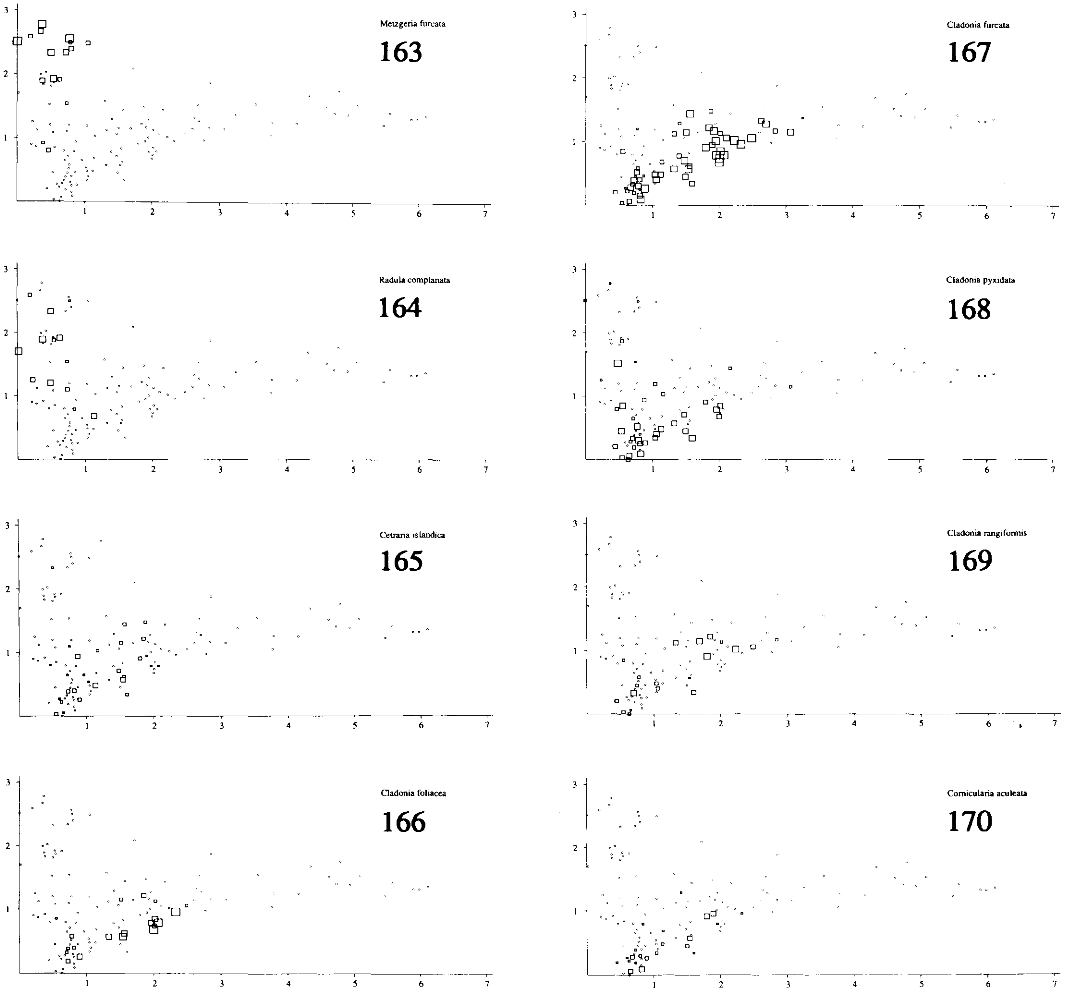
showed this distributional pattern.

Type IV accorded with the distribution of shrubs, with modes in the upper left part of the ordination plot. *Juniperus communis* (Fig. 83) showed high constancy within its niche and



Figs 155-162. Distribution of species abundances. Frequency in subplots for each species is plotted onto the sample plot positions in the DCA ordination of Dataset *AB*; DCA 1 (horizontal axis) and DCA 2 (vertical axis). Small circles indicate absence. Squares indicate where the species is present. Low frequency in subplots is indicated by small square size, progressively higher frequency is indicated by larger size. - Fig. 155. ***Homalothecium lutescens.*** - Fig. 156. ***Hypnum cupressiforme.*** - Fig. 157. ***Plagiomnium cuspidatum.*** - Fig. 158. ***Rhytidium rugosum.*** - Fig. 159. ***Thuidium abietinum.*** - Fig. 160. ***Tortella flavovirens.*** - Fig. 161. ***Tortella tortuosa.*** - Fig. 162. ***Tortula ruralis.***

high frequency in subplots, while *Rosa spp.* (Fig. 84), showed scattered occurrences. Examples of this distribution for herbs and graminids are shown for *Glechoma hederacea* (Fig. 103) and *Carex digitata* (Fig. 136). Except for the hepatics *Metzgeria furcata* (Fig. 163) and *Radula*



Figs 163-170. Distribution of species abundances. Frequency in subplots for each species is plotted onto the sample plot positions in the DCA ordination of Dataset *AB*; DCA 1 (horizontal axis) and DCA 2 (vertical axis). Small circles indicate absence. Squares indicate where the species is present. Low frequency in subplots is indicated by small square size, progressively higher frequency is indicated by larger size. - Fig. 163. *Metzgeria furcata*. - Fig. 164. *Radula complanata*. - Fig. 165. *Cetraria islandica*. - Fig. 166. *Cladonia foliacea*. - Fig. 167. *Cladonia furcata*. - Fig. 168. *Cladonia pyxidata*. - Fig. 169. *Cladonia rangiformis*. - Fig. 170. *Cornicularia aculeata*.

complanata (Fig. 164), no cryptogams showed this distribution pattern.

Type V comprised the exclusive grassland species, with modes in the lower left part of the ordination plot. Examples of herbs were *Euphrasia micrantha* (Fig. 99), *Hieracium*

Tab. 6. Interspecific associations within blocks I-II between highly frequent species (occurrence in more than 30% of the sample plots) and frequent species (occurrence in more than 10% of the sample plots). $\Sigma\chi^2$ - the sum of χ^2-values between the highly frequent species and the set of frequent species. $n^{-1}\ \Sigma\chi^2$ - the mean χ^2-value between the highly frequent species and the set of frequent species. Symbols, see p. 18.

	Achi mil	Hypn cup	Clad fur	Gali ver	Cera fon	Sedu acr	Aren ser	Fest rub
Achi mil		++++++	0	+++++	+++++	----	0	+
Acin arv	--	0	++++	+++	0	0	++	0
Aren ser	0	++++	+++++	+	++	+++		++++
Arme mar	0	0	0	0	+++	+++	+++	+
Cera fon	+++++	++	+	+++		---	++	+++
Cera sem	++++	+++	++	+++	+++++	0	0	0
Coch off	----	++++	0	----	0	+++	0	0
Gali ver	+++++	+++++	+++		+++	---	+	+++
Horn pet	0	++++	++++	++	--	0	+++	0
Lotu cor	++++	+++	+	++++	+++	-	0	0
Medi lup	++	0	0	0	+++	----	+	+
Plan lan	+++++	++++	--	++	++++	---	++	++
Rume ace	++	0	0	0	++++	0	0	0
Sagi nod	--	---	0	0	++	0	+	0
Sagi pro	0	---	--	---	++++	0	0	0
Saxi tri	0	++++	++++	0	0	0	+++	0
Sedu acr	----	---	+	---	---		+++	0
Sedu alb	--	0	+++	---	0	---	++	0
Soli vir	---	0	+++	+	0	0	0	0
Tara spp	0	0	+++	+	+++	0	+	++
Urti dio	---	----	----	---	--	---	-	0
Vero arv	0	+++	0	++	0	--	++	0
Viol tri	-	0	++	0	+	0	++	0
Agro sto	--	---	0	0	0	0	0	0
Brom hor	0	++	+	-	++	--	+++	0
Fest ovi	++++	++++	0	+++	+++	0	0	0
Fest rub	+	++	++	+++	+++	0	++++	
Poa sub	++++++	+++++	-	+++++	+++	-----	0	+
Ambl ser	---	0	0	-	0	++	0	+
Barb spp	0	-	0	0	-	0	0	0
Brac alb	0	0	0	0	---	+++	++	0
Bryu spp	+	++	++++	++	0	+++	+++	0
Cera pur	0	++	+++	0	0	+++	+++	0
Ditr fle	0	+	++++	0	0	+	++	0
Homa lut	0	+++	0	+	0	--	0	0
Hypn cup	++++++		++++	+++++	++	---	++++	++
Plag cus	++++	+++	-	+++	+	---	++	0
Tort fla	0	0	++++	0	-	++	++	0
Tort rur	0	0	0	+	---	++++	0	--
Clad fol	---	+++	+++++	0	0	0	+++	0
Clad fur	0	++++		+++	0	+	+++++	++
Clad sub	0	+++	0	++	0	0	--	0
Clad gra	---	+++	++++	0	--	+++	++	0
Clad pyx	--	0	+++	+	0	0	++	0
Clad rfo	0	0	++++	+++	+	+++	++	0
Pelt can	++++	+++	++	++++	0	0	++	0
$\Sigma\chi^2$	853.52	830.09	705.25	651.07	543.39	479.43	440.30	176.79
$n^{-1}\ \Sigma\chi^2$	18.97	18.45	15.67	14.47	12.08	10.65	9.78	3.93

pilosella (Fig. 104) and *Linum catharticum* (Fig. 106). Typical graminids were *Agrostis capillaris* (Fig. 129), *Carex caryophyllea* (Fig. 135) and *C. ericetorum* (Fig. 137). Examples of bryophytes were *Barbula spp.* (Fig. 146) and *Rhytidium rugosum* (Fig. 158).

Type VI occurred in a segment of 3-4 S.D. along DCA 1, with complementary distributional patterns to type IV. Examples of herbs and graminids were *Arenaria serpyllifolia* (Fig. 89) and *Poa subcaerulea* (Fig. 144). Examples of bryophytes were *Bryum spp.* (Fig. 148)

Tab. 7. Interspecific associations within blocks III-IV between highly frequent species (occurrence in more than 30% of the sample plots) and frequent species (occurrence in more than 10% of the sample plots). $\Sigma\chi^2$ - the sum of χ^2-values between the highly frequent species and the set of frequent species. n^{-1} $\Sigma\chi^2$ - the mean χ^2-value between the highly frequent species and the set of frequent species. Symbols, see p. 18.

	Acin arv	Horn pet	Ditr fle	Aren ser	Linu cat	Hypn cup	Achi mil	Fest ovi
Juni com	--	0	0	0	---	0	0	----
Achi mil	0	0	0	+	0	+++		0
Acin arv		+++++	+++++	++++	+++	0	0	++++
Alli spp	0	--	--	0	+++	++	0	+
Anag arv	++	0	+	0	0	----	--	-
Ante dio	+	++	++	0	0	---	0	0
Aren ser	++++	+++++	++++		0	++	+	++++
Botr lun	++	0	+	0	+	0	++	0
Camp rot	--	--	0	0	+	+++	0	0
Cent jac	0	0	++	0	0	--	++	-
Cera fon	0	0	0	++	0	+++	0	++
Cera sem	-	0	--	++	0	+++	++	+
Euph mic	+++	++	0	0	++++	--	0	++
Gali ver	--	0	0	0	0	+++	+++	0
Gera rob	--	-	0	0	--	+	0	0
Hier aur	++	+++	0	0	+++	--	--	+
Hier pil	0	0	0	0	0	0	++++	+
Horn pet	+++++		+++++	+++++	++	0	0	++++
Linu cat	+++	++	0	0		0	0	++++
Lotu cor	0	0	0	0	0	++	+++	0
Medi lup	---	---	----	-	0	+++	+++	0
Pimp sax	0	0	0	0	0	0	0	0
Plan lan	-	----	--	0	0	+++	0	0
Sagi nod	0	0	+	0	++	0	0	0
Saxi tri	++++	++++	++	+++	+	0	--	++
Sedu acr	++	+++	+++	+++	0	0	0	0
Sedu alb	++	+++	+++	+++	-	0	0	+
Tara spp	0	0	0	0	0	++	+	0
Thal min	0	+	0	0	0	0	0	+
Thym pul	0	-	0	0	----	0	0	--
Viol tri	-	--	0	0	-	+++	+	0
Agro can	+	0	0	0	+++	0	--	-
Agro cap	---	-	-	--	0	0	0	0
Anth odo	--	---	--	-	0	0	---	+
Aven pra	--	0	0	0	0	0	0	0
Brom hor	0	+	0	0	+	++	0	+
Care car	0	0	-	0	0	++	++++	++
Care fla	0	0	0	0	0	0	+++	-
Fest ovi	++++	++++	+	++++	++++	++	0	
Fest rub	0	--	0	0	-	0	++++	--
Poa pra	0	0	--	0	0	0	--	0
Poa sub	----	----	---	--	--	0	+++	-
Barb spp	+++++	+++++	++++	+++	+	----	--	+++
Bryu spp	++++	+++	++++	+	0	0	0	0
Camp chr	0	+	0	0	+++	0	0	0
Cera pur	+++	+++	+	0	+++	--	0	+
Dicr sco	--	--	-	0	-	+	+++	0
Ditr fle	+++++	+++++		++++	0	0	0	+
Enca str	++	++	+++	0	+++	0	0	+
Fiss cri	0	0	0	0	+++	-	0	+
Homa lut	+	+	0	++	+	+++	++	0
Hypn cup	0	0	0	++	0		+++	++
Plag cus	-	-	--	0	0	0	0	+
Thui abi	++	+++	+++	++	0	--	0	0
Tort fla	0	0	+++	0	++	0	0	0
Tort fra	+++	0	+++	0	+	-	0	0
Tort tor	0	+	++	0	++	+++	0	+
Tort rur	+	0	0	++	0	0	+	+
Cetr isl	++	+	++	0	++	0	0	0
Clad fol	+++	0	++++	0	0	0	0	0
Clad fur	++++	+++	+++	++	+	0	0	0
Clad pyx	+++	++++	+++	++	0	0	0	++
Clad rfo	0	0	0	0	0	0	0	+
Clad sym	+	0	+++	++	++	-	0	0
$\Sigma\chi^2$	764.41	753.47	675.77	428.23	416.74	403.08	374.76	368.01
n^{-1} $\Sigma\chi^2$	12.13	11.96	10.73	6.80	6.61	6.40	5.95	5.84

Tab. 7 (continued).

	Sedu acr	Homa lut	Gali ver	Clad fur	Fest rub	Juni com	Cera fon
Juni com	0	0	+++	0	+		0
Achi mil	0	++	+++	0	++++	0	0
Acin arv	++	+	--	++++	0	--	0
Alli spp	0	++	0	0	--	--	0
Anag arv	+	0	--	0	0	0	--
Ante dio	0	0	0	0	0	0	0
Aren ser	+++	++	0	++	0	0	++
Botr lun	0	0	0	++	+	0	0
Camp rot	0	++	0	0	0	0	0
Cent jac	+++	0	0	-	+++	0	--
Cera fon	0	0	0	0	0	0	
Cera sem	0	0	0	0	+	0	+++
Euph mic	-	0	-	0	0	--	++
Gali ver	0	+++		0	0	+++	0
Gera rob	+	0	0	0	0	0	0
Hier aur	++	++	-	0	0	--	0
Hier pil	+	++++	+++	0	0	-	-
Horn pet	+++	+	0	+++	--	0	0
Linu cat	0	+	0	+	-	---	0
Lotu cor	0	0	0	+	0	+	+
Medi lup	--	+++	++	0	0	--	0
Pimp sax	0	0	0	0	0	0	0
Plan lan	--	--	--	0	0	--	0
Sagi nod	+++	+++	++	0	+++	0	0
Saxi tri	+++	0	0	0	--	0	0
Sedu acr		0	0	0	+	0	0
Sedu alb	++++	-	0	0	0	0	0
Tara spp	0	+	+	0	-	0	--
Thal min	0	0	++	0	0	0	0
Thym pul	0	0	--	0	0	0	0
Viol tri	0	0	0	0	0	+	++
Agro can	---	0	--	0	0	0	0
Agro cap	0	0	0	0	0	0	0
Anth odo	--	--	---	--	--	--	0
Aven pra	--	0	+++	0	---	0	0
Brom hor	0	0	+++	0	0	++	++
Care car	0	++++	+++	0	+	---	0
Care fla	0	++	+	0	++	0	0
Fest ovi	0	0	0	0	--	----	++
Fest rub	+	0	0	0		+	0
Poa pra	0	0	++	--	0	+++	++
Poa sub	-	0	0	0	+	0	0
Barb spp	+++	0	0	0	0	-	0
Bryu spp	++	0	0	0	0	0	---
Camp chr	0	0	0	0	0	+	++
Cera pur	0	0	--	0	0	--	0
Dicr sco	0	0	0	++	++	0	++
Ditr fle	+++	0	0	+++	0	0	0
Enca str	+	+++	0	0	0	0	0
Fiss cri	0	0	0	-	-	0	0
Homa lut	0	+++	0	0	0	0	
Hypn cup	0	+++	+++	0	0	0	+++
Plag cus	0	0	0	0	0	0	++
Thui abi	0	0	0	+	--	0	0
Tort fla	++	0	0	0	+	-	0
Tort fra	0	0	-	+	0	0	--
Tort tor	+++	0	0	-	--	0	0
Tort rur	++	0	0	0	0	-	-
Cetr isl	0	0	-	+++	0	0	0
Clad fol	0	0	0	++++	0	0	--
Clad fur	0	0	0		0	0	0
Clad pyx	++	++++	0	++	-	0	-
Clad rfo	0	-	-	0	0	0	0
Clad sym	0	-	0	+	+	0	-
$\Sigma\chi^2$	340.21	339.41	322.38	271.17	262.96	255.38	231.67
$n^{-1}\ \Sigma\chi^2$	5.40	5.39	5.12	4.30	4.17	4.05	3.68

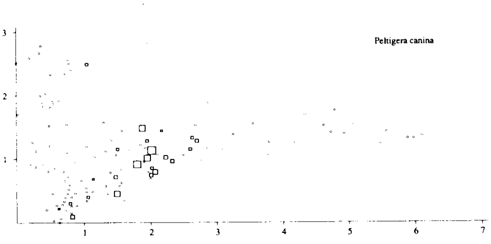


Fig. 171. Distribution of species abundances. Frequency in subplots for *Peltigera canina* is plotted onto the sample plot positions in the DCA ordination of Dataset *AB*; DCA 1 (horizontal axis) and DCA 2 (vertical axis). Small circles indicate absence. Squares indicate where the species is present. Low frequency in subplots is indicated by small square size, progressively higher frequency is indicated by larger size.

and *Ceratodon purpureus* (Fig. 150). A number of lichens species showed distributional patterns of Type VI. A typical species is *Cladonia furcata* (Fig. 167).

Type VII showed modes in the central part of the ordination plot, and lack of occurrence both in the left and the right part along DCA 1. Examples of herbs were *Armeria maritima* (Fig. 90), with very narrow ecological amplitude, and *Sagina nodosa* (Fig. 117). Among graminids *Bromus hordeaceus* (Fig. 134) showed this type of distribution.

Type VIII showed distribution patterns almost complementary to Type III. Examples of graminids were *Agrostis stolonifera* (Fig. 130) and *Juncus gerardi* (Fig. 141).

Some species departed from the typification, either by showing intermediate patterns or by showing scattered occurrences in different parts of the ordination plot. One example of intermediate distribution between two types is shown for *Amblystegium serpens* (Fig. 145), showing a transition between types VII and VIII. Examples of scattered occurrences were herbs like *Plantago maritima* (Fig. 111), and graminids like *Anthoxanthum odoratum* (Fig. 131), and *Luzula campestris* (Fig. 142).

Interspecific association analysis

The results of the association analyses are shown in Tabs. 6-8. Species *i* occurring in more than 30% of the sample plots make up the columns, and species *j* with occurrence more than 10% make up the rows. The χ^2 association between species *i* and *j*, and the χ^2 sum between species *i* and all species in the *j*-th row is shown at the bottom of the tables.

Tab. 6 shows the χ^2 associations between the most frequent species of blocks I-II. The results showed dominance of highly positive values, which indicated insignificant competition between pairs of plants species for space or resources. *Achillea millefolium*, with the highest χ^2 sum (853.52), showed equal numbers of positive and negative associations, although the positive were considerable higher. In the bryophyte *Hypnum cupressiforme*, with the second highest χ^2 sum (830.09), positive associations were four times as many as the negative. The results showed that high frequency of *Hypnum* did not inhibit other species considerably. *Festuca rubra*, differed from all of the other species, showing appreciably lower χ^2 sum (176.79), as a result of high frequency in all of the sample plots (Fig. 140).

Tab. 8. Interspecific associations within blocks V-VII between highly frequent species (occurrence in more than 30% of the sample plots) and frequent species (occurrence in more than 10% of the sample plots). $\Sigma\chi^2$ - the sum of χ^2-values between the highly frequent species and the set of frequent species. $n^{-1}\ \Sigma\chi^2$ - the mean χ^2-value between the highly frequent species and the set of frequent species. Symbols, see p. 18.

	Juni com	Fest ovi	Achi mil	Linu cat	Aven pra	Gali ver	Hypn cup	Briz med	Fiss cri	Camp rot
Juni com		-------	-------	-------	-------	------	-----	----	----	-----
Achi mil	-------	++++++		+++++	++++++	++++++	+++++	+	+++	++++
Acin arv	-----	++++	+++	+++++	+++	0	0	++	++++	++
Ante dio	------	++++++	+++++	++++++	+++++	+++++	+++++	+++++	+++++	+++++
Arab hir	++	0	0	--	---	---	0	-	+++	0
Aren ser	-----	+++++	+++	++++	+	++	+++	+++	++++	+++
Camp rot	-----	+++++	++++	++++	++++	+++	++	0	+++	
Cent jac	--	++	0	+++	0	0	0	++++	+++	0
Cera fon	-	+++	++	++	0	0	+++	0	0	0
Cory pum	+++++	----	---	----	0	---	0	----	----	---
Euph mic	------	+++++	++++++	++++++	+++++	++++++	+++++	+++	0	++++
Frag ves	++	0	---	0	---	--	---	++	0	---
Gali ver	------	+++++	++++++	+++	+++++		++++	0	0	+++
Glec hed	+++++	-----	---	----	-	0	--	---	----	----
Hepa nob	++++	-----	---	--	---	--	--	0	-	-
Hier pil	------	+++++	++++++	+++	++++	++++	+++	++	++	+++
Horn pet	--	++++	-	++++	0	--	-	0	+++	++
Linu cat	-------	++++++	+++++		+++++	+++	++++	+++++	+++++	++++
Lotu cor	-----	++++	++++++	+++++	+++++	+++++	+++++	+++	+++	+++
Moeh tri	++++	-----	---	----	0	---	0	----	----	--
Pimp sax	+++	0	0	-	--	0	--	0	0	0
Poly vul	++++	--	---	0	--	--	+	0	++	-
Rubu sax	++	0	0	-	0	0	0	0	0	-
Tara spp	----	++	++++	0	+++	++++	+++	0	0	+
Thal min	+++	--	0	0	--	-	0	0	0	0
Thym pul	-----	+++++	+++	++++	+++++	++++	+	++	+++	++
Vero off	+++	-	---	---	0	0	--	--	-	--
Agro cap	------	+++++	+++	+++++	++++	+++	+++	++++++	+++	++
Anth odo	---	++	++	0	+++	0	0	--	0	0
Aven pra	-------	+++++	++++++	+++++		+++++	++++	++	++++	++++
Aven pub	-	0	0	0	0	++	0	0	-	0
Briz med	----	++++	+	+++++	++	0	0		++++	0
Care car	-------	++++++	+++++++	++++++	+++++++	++++++	++++++	+++	++++	+++++
Care dig	+++++	---	----	----	---	----	+	--	0	--
Care eri	------	+++++	+++++	+++++	+++++	++++	+++++	+++	+++	+++
Care fla	0	+	-	++++	--	---	----	++++++	+++	0
Dant dec	0	++	0	+++	0	0	0	++++	++	++
Fest ovi	-------		++++++	++++++	+++++	+++++	++++	++++	+++++	+++++
Fest rub	+++++	-----	----	----	----	-	---	----	++	----
Luzu cam	-----	++++	++++++	++	+++++	+++++	++++	0	0	+++
Meli nut	+++++	----	----	0	----	--	-	++	++	0
Poa pra	+++++	----	---	----	--	0	--	---	----	---
Poa sub	-----	++++	++++++	+++	+++	++++	++++	0	0	+++
Barb spp	-----	+++++	++	+++++	++++	++	++	++	++++	+++
Bryu spp	------	+++++	+++	+++++	+++++	++	++	++++	++++	++++
Camp chr	-	++	0	+++	0	0	0	++++	+++++	0
Dicr sco	-----	++++	+++++	++++	+++++	+++++	++++	0	0	+++
Ditr fle	----	+++++	+++	+++++	+	++	+++	++++	++	++
Fiss cri	----	+++++	+++	+++++	++++	0	++	++++		+++
Homa lut	-------	++++++	++++++	+++++	+++++	+++++	+++++	++	+++	+++
Hypn cup	-----	++++	+++++	++++	++++	++++		0	++	++
Plag cus	0	0	0	0	++	++	0	0	-	0
Rhyt rug	-----	++++	++++	++	+++++	++++	+++++	0	0	++++
Thui abi	---	+++	+++	++++	0	0	0	++	0	0
Tort tor	0	+++	0	++++	--	--	0	++++	+++	0
Metz fur	+++++	-----	----	----	---	---	0	----	---	----
Radu com	++++	----	--	--	----	0	0	--	0	---
Clad fur	------	+++++	+++++	+++	+++	++++	++++	0	0	+
Clad pyx	----	+++	+	+++	+++	++	+++	+	++++	0
$\Sigma\chi^2$	4396.23	2904.28	2781.61	2351.01	2142.62	1618.18	1325.09	1050.66	1015.17	957.90
$n^{-1}\ \Sigma\chi^2$	73.27	48.40	46.36	39.18	35.71	26.97	22.08	17.51	16.92	15.97

Tab. 7 shows the χ^2 associations between the most frequent species of blocks III-IV. The majority of associations were positive, indicating lack of interspecific competition also in blocks III-IV. Bryophytes showed particularly high positive χ^2 values. Within these blocks three species showed higher χ^2 sums, *Acinos arvensis* (764.41), *Hornungia petraea* (753.47) and *Ditrichum flexicaule* (675.77).

Tab. 8 shows the χ^2 associations between the most frequent species of blocks V, VI and VII. In contrast to the above-mentioned, the results for these blocks showed considerably higher χ^2 sums. The χ^2 sum for *Juniperus communis* was 4396.23, and all of the frequent species showed large values; e.g. *Festuca ovina* (2904.28), *Achillea millefolium* (2781.61), *Linum catharticum* (2351.01) and *Avenula pratensis* (2142.62). The strong competitive ability of juniper was indicated by the strongly negative χ^2 associations to a number of other species. Tab. 8 shows almost complementary patterns between juniper and all the other highly frequent species, indicating the important structuring feature of juniper.

DISCUSSION

INTERPRETATION OF VEGETATION - ENVIRONMENT RELATIONSHIPS

The ordination analyses of Dataset *AB* and Subset *A* reveal the existence of four main coenoclines, or vegetation gradients, in the shell-bed vegetation of Akerøya. The gradual change in the species composition, or compositional turnover, along the first four DCA axes, each expresses unique vegetational variability. The coenoclines are, however, generally not independent of each other, but rather partly correlated. This is clear from the effect of removing Subset *B* from Dataset *AB*, upon which the reduced first coenocline is combined with the second coenocline to form the first DCA axis of the Subset *A* ordination. The purpose of separate ordination of a subset, derived from the original dataset by deletion of samples from a limited ordination segment, is to show that environmental gradients relevant in one part of the ordination are not necessarily relevant in another part (Peet 1980). This partial correlation between coenoclines does not, however, preclude a separate discussion of four coenoclines. The coenoclines are strongly correlated with the environmental variables, and all four are interpretable as responses to environmental complex-gradients.

The primary successional gradient: dependent on site age

Primary successional series have often been inferred from the study of spatial sequences or zonations in vegetation, on the assumption that they reflect different stages in temporal sequences (Odum 1969, Mueller-Dombois & Ellenberg 1974, Whittaker 1975, Miles 1979). This concept has been used widely for shore vegetation (Cowles 1899, Westhoff 1947, Olson 1958, Pierce & Kershaw 1976, Verwijst & Cramer 1986). A number of ecologists have suggested that the classical succession paradigm needs to be reexamined, e.g. Drury & Nisbet (1973), Horn (1974), Egler (1976), Pickett (1976), Connell & Slayter (1977) and Peet & Christensen (1980). Simultaneously with indicating the importance of successional complexity, alternative approaches and formulations are proposed. The zonational approaches are all reductionist, emphasizing life-histories and competitive relations of component species rather than the emergent properties of communities (Peet & Christensen 1980). Succession should be considered as a gradient in time.

Considering the succession sequences as gradients, the vegetation development of coastal shell-beds is characterized by a primary, site age-dependent, successional gradient, from young recently emerged sites to the older, higher situated ones. In the present study, PCA ordination of environmental variables uncovered five groups of more or less independent variables. The coherence of PCA group *II* and the two neighbouring groups *I* and *III* indicates that the successional sequence is correlated with a number of environmental variables. Elevation, distance from the sea, fine soil fraction and loss on ignition, and [Ca^{2+}] all show high correlation with DCA 1. These variables also have high eigenvalues, e_{Cl}, and importance values, i_A, in *rh*-DCCA ordinations.

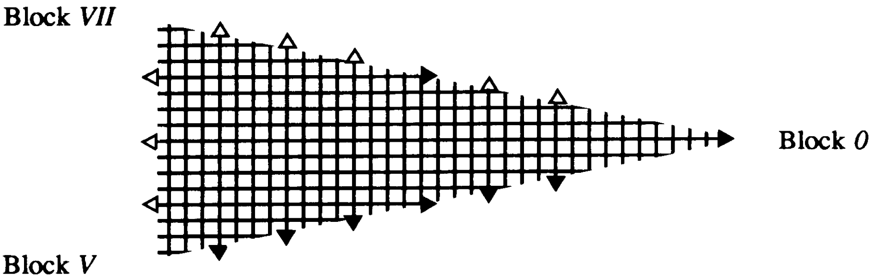
Over temporal scales of thousands of years, the succession is accompanied by the gradual change in soil conditions and vegetational structure. The humification, measured by loss on ignition and total N and P and the long-term decomposition of the pelecypod and gastropod deposits, is highly correlated with elevation and distance from the sea. A salinity gradient is also highly correlated with this successional trend. Although the saline conditions influence all sites, the sites in the primary phases, located near the shoreline, receive much higher amounts of [Na^+] and [Cl^-]. A gradual decline in salinity occurs until it stabilizes in the established sites. Despite the fact that ion concentrations are ln-transformed, a most pronounced decline is seen in the transition from the littoral to the epilittoral sites. [Ca^{2+}] and CEC increases towards the established phase. This is in accordance with the gradually increasing amounts of decomposed fine-fractioned shellsand. At first sight it may be surprising that pH decreases while [Ca^{2+}] and CEC increases. This is, however, due to the accompanying increase in humification, highly correlated with loss on ignition, causing pH to decrease while [Ca^{2+}] increases due to shell decomposition. pH never descends below 7, not even in the topsoil under a juniper canopy which is constantly acidified by needle litter.

Fig. 30 and Tab. 2 express the gradual change of performance for all 231 species, reflecting the trend along the primary successional gradient. At the end of the sequence, interference with a site-age-independent secondary successional gradient occurs. This complicates the straightforward interpretation of the successional trend. According to Austin (1977) the interpretation of existing spatial variation representing different stages of a temporal sequence may lead to erroneous conclusions. Verwijst & Cramer (1986) emphasize three obstacles to such interpretation: (1) environmental gradients can interfere with the successional trend, e.g. edaphic and topographic heterogeneity (Olson 1958) or salt spray gradients (Oosting 1954), (2) the directions of transitions between stages are hypothetical (Walker 1970) and successional trends should therefore be sustained by quantitative data on site age and population structure (Lawrence et al. 1967, Peet & Christensen 1980), and (3) human activities may disturb the sequence (Screiber 1980). All these obstacles occur in this material, and thus complicate the uncovering of the main complex gradients.

A method simplifying the interpretation is to remove a set of sample plots with well known characteristics (Peet 1980). Such a procedure is frequently used with success, e.g., T. Økland (1988), Rydgren (1989), R. Økland (1990a), and Svalheim & Wegener (1990). The removal of Subset *B* uncovers a more linear successional sequence, from Block I to Block VII. This is shown in the DCA ordination of Subset *A*, which accords with successional pathways in shell-beds described by Halvorsen (1980). The change in spatial distribution of samples in the Subset *A* ordination may be expressed by the reduced influence of the Lost Unit I and particularly the interactions between the early successional sites and sparsely to more dense sites of juniper shrubs.

The secondary successional gradient: dependent on herbivore impact

The secondary, site age independent, successional gradient is caused by different impacts of grazing and trampling. The productive pastures of Block V, most attractive for grazing, occur at the highest situated shell-beds, far from the establishing sites by the shore, while the typical shrub dominated sites of Block VII show optimal performance at intermediate altitudes. Thus the two successional gradients are not spatially coincident, but nevertheless show considerable interactions. The secondary successional gradient is highly correlated with impact of herbivores. *rh*-DCCA ordinations show high eigenvalues and thus high importance values for these variables when taken as constraining variables; grazing (e_{Cl} = 0.26 and i_A = 0.38), erosion (by trampling) (e_{CI} = 0.26 and i_A = 0.38) and percentage cover of shrubs (e_{CI} = 0.32 and i_A = 0.45). Thus, the straightforward vegetational series from Block I to Block VII expresses an oversimplification of the actual number of successional pathways. A more adequate successional pattern is showed by the following combination of successional routes between blocks:



This model must be regarded as dynamic, thus both successional gradients (◁— - primary, ⇧ - secondary) are highly influenced by disturbance, and reversals (—▶ , ↓) continuously occur. The view of succession as a replacement sequence driven by autogenic environmental modification has been rejected by e.g. Egler (1954, 1976), Niering & Egler (1955), Drury & Nisbet (1973), and Connell & Slayter (1977). They emphasize the importance of differential longevity, life history and competitive relations of component species rather than the emergent properties of communities. The structuring processes underlying these vegetational patterns are discussed later.

The triangular configuration of the Dataset *AB* ordination indicates (from right to left) the underlying site-age-dependent gradient from the primary sites to the established sites, combined with the progressively more important underlying site-age-independent successional gradient. This variability also accords well with the species abundance pattern of *Juniperus communis*, showing gradually increase from Block I to Block VI and from Block V to Block VII. This is the single most strongly structuring species along DCA 2, and also by far the most strongly associated species, positively and negatively, with other species in blocks V-VII. Almost no species is indifferent to juniper cover.

Grazing affects vegetation very strongly, as evident from ordinations and analyses of interspecific association patterns in block V-VII. In the ordination of environmental variables grazing (group V) spanned PCA 3. Grazing provides an important selection pressure, e.g. by affecting species relative abundances or plant growth habits (Grime 1973a, Whittaker 1977a, Naveh & Whittaker 1980). According to Rosén (1982) grazing was found to suppress juniper, dwarf shrubs, and some graminids. At Akerøya stress-tolerators such as *Briza media, Carex caryophyllea, C. ericetorun, C. flacca* and above all *Festuca ovina* are well adapted to these conditions. The same was observed for more or less prostrate herbs and acrocarpous mosses. This accords well with grassland studies by Sjögren (1971) and Rosén (1982). Species seemingly having high tolerances to grazing are *Achillea millefolium, Anthyllis vulneraria, Campanula rotundifolia, Galium verum, Pimpinella saxifraga* and *Solidago virgaurea*. Among bryophytes, *Homalothecium lutescens, Ditrichum flexicaule, Fissidens cristatus* and *Rhytidium rugosum* seem to withstand grazing well.

Ammar (1978) shows that cessation of grazing may lead to successional changes. To retain the vegetational structure of shell-beds with regard to expansion and overgrowing of junipers, a balanced herbivore activity is required. Implications for management and conservation are discussed later (pp. 78-79).

The nutrient availability gradient

In contrast to the traditional generalizations, successional changes in biomass, primary production and species diversity cannot be assumed to be consistently upward (Loucks 1970, Auclair & Goff 1971, Whittaker 1972, 1977b, Peet 1978); maximum values of these parameters are often found in the central part of successional sequences.

The soil's content of nitrogen and phosphorus is positively correlated with the primary successional gradient, although the nutrients show pronounced variability within the blocks, independent of successional phases. An indication of the importance of these nutrients is the high correlations with DCA 3. Sites, both in the littoral and in the epilittoral zones, have a relatively large amount of nitrophilous and phosphorophilous species. Their distributions accords well with ratios of total N and P as percentage of organic content (loss on ignition); apparently good estimates for the availability of these nutrients.

In the littoral zone, ordinations show clear separation of drift-influenced sites and other early phase sites, poor in nutrients. Nitrophilous and phosphorophilous species, e.g. *Atriplex hastata, Cakile maritima, Potentilla anserina, Galium aparine, Matricaria maritima , Urtica dioica and U. urens*, occur in a limited segment in the coenoplane spanned by DCA 1-2. In addition to their ability to sustain high rates of uptake of water and mineral nutrients and thus to maintain dry-matter production under stress, these species can overgrow and exclude other species by more efficient ability to utilize the favourable nutrient supply. The continuous supply of nutrients to driftshores and driftlines provided by decomposing algae makes such sites have a stable high level of available nitrogen and phosphorus.

In the epilittoral zone, the supply of drift material gradually declines in proportion to distance from the sea, and manuring becomes the most important source of nitrogen and phosphorus. Plants' access to these nutrients is more occasional in the epilittoral zone than on the driftshores, thus nitrophilous and phosphorophilous species do not show any pronounced separation from the other species in the ordination. However, DCA 3 is also highly correlated with nutrients other than nitrogen and phosphorus. K^+, Mg^{2+}, pH and CEC are all significantly correlated with DCA 3.

A general problem when studying effects of manuring is to find an adequate measure of the nutrient availability, both spatially and temporally, and to connect the measure to the vegetation study (performed at one point of time). Experiments with NPK fertilizer in grassland vegetation indicate some corresponding trends (Rosén 1982), resulting in significantly higher production and causing the importance of graminids and herbs to increase, *Festuca ovina* the most.

The soil moisture gradient

Soil moisture shows higher correlations with DCA 4 than with the other axes in the *AB* dataset ordination. However, as regards the quantitative distribution of soil moisture, highest performance is found near both ends of DCA 1. When removing Subset *B*, the soil moisture gradually increases from Block I to Block VII. This is shown by the pronounced increase in correlation coefficient between soil moisture and DCA 1 for Subset *A*. Another expression of the importance of soil moisture is shown by the high values of i_{AB}, i_A and $\delta_{A,AB}$ from the *rh*-DCCA ordinations. The *AB* dataset correlations between soil moisture and the four DCA axes, indicate variability of soil moisture conditions on different scales: (1) large-scale variability, reflecting the gradual humification along the primary successional gradient, highly correlated with DCA 1, and (2) fine-scale variability, reflecting differences in macro- and microtopography within one square m or less, correlated with DCA 4.

Performance of *Carex nigra, C. panicea, Geum rivale* and *Salix repens* at the negative end, and *Clinopodium vulgare, Empetrum nigrum* and *Prunus spinosa* at the positive end of DCA 4, accords well with the axis as negatively correlated with moisture. Concave terrain and small depressions receive more run-off water than the plane and convex surfaces. The distribution of species along DCA 4 does not express any clear replacement series from mesic to xeric species. The xeric end is represented by a number of more or less ruderal species, such as winter annuals, that are early flowering. This must be considered as an adaptation to the xeric conditions in the summer and autumn. Typical examples of such stress-tolerant ruderals (Grime 1979) located at the xeric part of DCA 4 are *Arenaria serpyllifolia, Hornungia petraea, Linum catharticum* and *Saxifraga tridactylites*. Temporal variation in moisture conditions plays an important role in the patch dynamics of shell-bed vegetation. Seasonal conditions are often highly correlated with the surface concavity of the sample plots, although this generalization implies a simplification. The most pronounced exception to this is found in the higher situated areas of naked granite bedrocks, at sites overlaid by a shallow layer of deposited shells. Such sites, also the plane and convex areas, receive large amounts of water from snowmelt and rainfall in the spring. The contrast between these spring conditions with waterlogging and the extreme drought occurring in summer is notable. The evaporation in summer is strengthened due to heating of the adjacent naked rock and shallow top-soil.

STRUCTURING PROCESSES

The ordinations and the other analyses of coastal shell-bed vegetation at Akerøya show a triangular structure, reflecting different successional pathways from open sea-shore vegetation of low α-diversity to different types of more or less established vegetation of distinctly higher diversity, combined with different intensity of herbivore activity. In addition, different availabilities of water and nutrients influence the vegetational patterns. Two types of processes are considered to be the most important ones in generating these patterns and influencing the vegetation dynamics; competition between individuals, inter- or intraspecific, and different destabilizing factors causing fine-scale environmental disasters (sensu Harper 1977: 877).

Interspecific interactions: competition, coexistence and facilitation

Competition

Different kinds of competition are usually supposed to be the most important interactions between species, affecting the involved species in a negative way. Plants with high competitive ability are termed competitors (Grime 1974, 1979). At present much interest centres upon the mechanisms involved in competition, and the determinants of relationships between plant morphology and competitive ability (cf. Grace 1990). Two apparently contrasting views are held by Grime (1979) and Tilman (1982, 1988).

According to Grime (1979), competitors exploit conditions of low stress and low disturbance (phenomena which restrict photosynthetic production, and cause partial or total destruction of plant biomass, respectively). Grime (1973c) defines competition as the tendency of neighbouring plants to utilize the same resources. Thus, success in competition reflects the plants' capacities for resource capture. Grime emphasizes the positive correlation between the plants' competitive ability and their maximum relative growth rate (RGR_{max}).

Tilman (1982) also proposes a resource-based, quantitative and mechanistic theory of plant competition. Further developments of this model, more realistic for higher plants, are referred to as ALLOCATE (Tilman 1988). This model for size-structured populations describes plants in terms of their allocation to roots, stems, leaves and seeds. The key feature in this model is that the species with lowest minimum resource requirements, R^*, is the species expected to be the superior competitor. Both Grime's and Tilman's approaches to competition can be applied to the study of structure in shell-beds at Akerøya.

Competitive exclusion frequently occurs in the dense shrubs, where there is low density-independent mortality (cf. Silvertown & Law 1987). The competitive exclusion of a large number of grassland species is the predicted outcome of long-lasting competition with *Juniperus communis* in a stable environment; almost no species is indifferent to juniper cover. Grime (1973b) has classified herbaceous plants according to the extent to which certain competitive attributes are evident in the genotype. Four features of competitors are appropriate to junipers in this study: (1) tall stature, (2) a growth form which allows extensive and intensive exploit of the environment above and below ground, (3) a high RGR_{max}, and (4) a tendency to deposit a dense layer of litter on the ground surface.

Three types of competition are recognizable (cf. Chesson & Case 1986):

Competition between plants for space occurs in the shell-bed vegetation, as neighbour interactions in sense of Turkington et al. (1977) and Turkington & Harper (1979). The association analyses uncover a gradual increase in χ^2-values along the primary successional gradient from early sites (in blocks I-II), via intermediate sites (in blocks III-IV) to established sites (in blocks V-VII). However, apart from juniper, positive associations contribute much more strongly than negative. Most of the negative associations are interpretable from the ordination results as a result of niche-differentiation. The association analyses give no evidence for interactions between layers in the early and intermediate successional phases. However, in the established phase, evidence from ordinations and association analyses emphasizes the dependence of the field and bottom layers on structural properties of the shrub layer, by the prominence of inverse relationships.

Competition for resources, especially resources in short supply, in natural vegetation is hard to assess. According to R. Økland (1990b, 1990c), a species may be absent from a site within its fundamental niche because it is an inferior competitor for resources, but may more often be absent from marginal sites for other reasons, e.g. low density of propagules, low tolerance for diffuse competition (cf. Wilson & Keddy 1986), etc. However, several laboratory experiments, e.g. with diatoms (Tilman 1982), have demonstrated the importance of competition for resources in short supply. Another, and more clearly visible, type of competition for resources is expressed by the ability to utilize the supply of resources. In the drift-influenced shores with ample nutrient supply, and in highly productive manured pastures, a number of species show high resource utilization abilities.

This study was not designed for testing of Tilman's or Grime's approaches to resource competition. However, the results of ordination analyses, the correlation between DCA 1 coenocline and the gradual increase of humification, and DCA 3 coenocline and the gradual increase of nutrients, lend some support to Grime's approach.

According to During & van Tooren (1990), a number of descriptive studies show that resource competition among bryophytes and from bryophytes plays a less decisive role. For instance studies of Marion et al. (1982) in an arctic tussock tundra show that with respect to nitrogen capture the competitive ability was lower for bryophytes than for vascular plants, thus the vascular plants were clearly nitrogen-limited while the bryophytes were not.

Pre-emptive competition seems to have little significance in this vegetation. Species with high performance in the early successional phases gradually decline towards the established phase. Species like *Achillea millefolium, Arabis hirsuta, Arenaria serpyllifolia, Botrychium lunaria, Cerastium fontanum, Festuca rubra, Glechoma hederacea, Solidago virgaurea* and *Taraxacum spp.* all increase from the early phase to the intermediate phase, and then decline in the established phase. A number of stress-tolerant ruderals thus do not appear able to utilize this advantage over plants arriving later. However, a group of species, such as *Agrostis capillaris, Antennaria dioica, Campanula rotundifolia, Carex caryophyllea, Centaurea jacea, Festuca ovina, Galium verum, Linum catharticum, Lotus corniculatus*, and *Thymus pulegioides*, show a gradual increase from their first appearance in the early successional phase to the established phase. There is however, no evidence in favour of interpreting this pattern as pre-emptive competition; a common feature of this group is the high ability to resist grazing. This accords well with the evolutionary strategy of these species; all are more or less stress-tolerators.

Cryptogams are often considered as important colonizers of bare ground, acting as pioneer plants in an early successional phase and as regenerators in patches exposed to disturbance. According to R. Økland (1990c), pre-emptive competition is likely to be widespread among bryophytes and lichens, as establishment is easier on naked soil patches than in dense moss cushions (cf. Schuster 1966). This accords well with Rydin (1986), who considers pre-emptive competition as more important than interactive competition in bogs. In coastal shell-bed vegetation, on the other hand, no evidence is given for the prominence of cryptogams in utilization of this advantage over seed plants or other cryptogams. High frequency of cryptogams in the established phase is not likely to be due to rapid colonization, but to the ability to resist grazing.

Coexistence and facilitation

The association analyses show a high number of coexisting species in all successional phases. Besides being the most important structuring species with regard to competition, *Juniperus communis* is also the most important species influencing coexistence. Thus a large number of species find protection against desiccation and grazing under the cover of *Juniperus*.

The ability of species to coexist on a fine scale seems to contradict the importance of competition. This apparent contradiction may be explained by non-equilibrium theories (Chesson & Case 1986), emphasizing dynamics in fluctuating environments, or by avoidance of competition through niche differentiation. Apart from *Juniperus communis*, associations between pairs of species are mainly positive.

Bryophytes and lichens with almost the same preferences for light, nutrient supply and soil water availability show highly positive associations and apparently no competition in block III-IV patches. However, this generalization is certainly not valid when bryophytes are sufficiently abundant. The bryophyte with the highest χ^2-sum, *Ditrichum flexicaule*, shows no significant association with the other two most frequent mosses, *Hypnum cupressiforme* and *Homalothecium lutescens*.

The large number of significantly positive associations between vascular plants and cryptogams indicates coexistence, and may even indicate facilitation. Frequent species like *Acinos arvensis, Arenaria serpyllifolia, Hornungia petraea* and *Linum catharticum* show unequivocally positive associations with the most common bryophytes and lichens. The population dynamics and performance of many vascular plant species may be locally affected by the density of the bryophyte layer. During & van Tooren (1990) state that "bryophytes do not live their life in splendid isolation, but are involved in complex webs of interactions with many other plants in the ecosystem". Van Tooren (1988) shows that seed predation was higher on bare surfaces than in sites covered by bryophytes. Rabotnov (1969) and Keizer et al. (1985) showed more successful germination in grassland sites with bryophyte colonies. However, contrasting evidence is given by Johnson & Thomas (1978) showing significantly higher mortality of juvenile plants and significantly higher mortality in moss patches than on bare soil.

Ryser (1990) distinguished three major patterns of seedling establishment in relation to the influence of neighbouring plants. These are relevant to interpretation of results from Akerøya, emphasizing the relationships between patterns of species occurrence and establishment.

Low mortality in all microsites. Species such as *Plantago lanceolata* and *Medicago lupulina* with large seeds (weight approximately 2 mg) are able to expand their roots and leaves quickly. Thus, mortality due to desiccation of the topsoil and the shading in the closing vegetation is reduced. The high χ^2-association with *Hypnum cupressiforme* may indicate a facilitation in open sites with bryophyte cover.

Low mortality in gaps, reduced survival under vegetation cover. Species producing large seed banks of small seeds show low establishment rates in dense vegetation. Stress-tolerant ruderals (Grime 1979), with large numbers of seedlings, but high mortality, show different patterns with regard to establishment in open as contrasted with denser sites. In general, the χ^2-tests show positive associations between cryptogams and SR-strategists, but species like e.g. *Erophila verna, Hornungia petraea,* and *Saxifraga tridactylites* show preference for open blocks III-IV sites over Block V sites with a more densely stocked field layer. *Linum catharticum*, on the other hand, shows the best performance in Block V. This is in accordance with Ryser (1990), suggesting a better establishment of *Linum* in the gaps of intermediate size rather than in sparse vegetation (cf. also Hillier 1984, Schenkeveld & Verkaar 1984 and Kelly 1989).

High mortality in open microsites, improved establishment in closed vegetation. Seedlings of species such as *Corydalis pumila, Polygala vulgaris, Polygonatum odoratum, Primula veris,* and *Silene nutans* were not observed in the open Block III-IV sites, and only exceptionally in Block V. However, it is likely that other factors than sheep grazing cause this absence from open sites and the preference for dense Block VII sites. Species with low or intermediate seed weight and small seed banks show high mortality due to desiccation of the top soil. This is partly in accordance with studies of *Arabis hirsuta* and *Primula veris* by Ryser (1990), although *Arabis* at Akerøya occurs abundantly in open habitats as well.

Destabilizing factors: disturbance and fluctuations

In classical vegetation theory, interspecific competition was claimed to be the major determinant of population dynamics. In a number of non-equilibrium sites, however, this structuring factor is obviously of less importance. Disturbance is probably the overall most important factor at the non-equilibrium sites at Akerøya, and is one of the main structuring factors at all. The impact of disturbance can be so strong that it often prevents equilibrium (Huston 1979). The mechanisms causing vegetational changes after disturbance have long been debated (e.g., Egler 1954, Drury & Nisbet 1973, Horn 1975, Pickett 1976, Connell & Slatyer 1977, McIntosh 1980, Finegan 1984, Tilman 1985). It is generally accepted that sites with recurrent disturbances, severe enough to kill individuals of species, will be revegetated by a set of species that is qualitatively or quantitatively different from the original set (Belsky 1986). In other words, disturbance increases the spatial heterogeneity of the vegetation by creating patches suitable for colonization by assemblages of species that may differ from the rest of the vegetation. At Akerøya disturbance is mainly caused by erosion from sheep trampling, followed by a synergistic effect of drought and wind-exposure, as suggested by Halvorsen (1980). This impact often results in radical changes within the sample plots in short time spans. The effect of erosion is at times pronounced, especially in the earlier successional sites, where only a thin humus-layer covers the shell-sand.

Species diversity

Disturbance acts both as a destructive force and as a prerequisite for rapid plant establishment. This causes a "shifting mosaic" (Bormann & Likens 1979, Heinselman 1981). Besides the spatial heterogeneity, the temporal dynamics of the system may also be considerable. Disturbance affects the intensity of competition by increasing the density-independent mortality (Peet et al. 1983). By temporarily reducing the competitive pressure, disturbance allows species to expand their realized niches. Thus, disturbance should have the complementary effects of increasing α-diversity while decreasing β-diversity. In the shell-bed vegetation of Akerøya, disturbance creates niches for a number of opportunists. Dicot ruderals such as *Capsella bursa-pastoris, Polygonum aviculare, P. persicaria, Stellaria media* and monocot ruderals such as *Bromus hordeaceus* and *Poa annua* are favoured by disturbance. The most pronounced structural change in vegetational composition caused by disturbance is the strong element of stress-tolerant ruderals in unstable and shallowly humus-covered Block III-IV sites. Plants, adapted by evolution to persist through severe disturbance, show several common features, such as short life-cycle (annuals or short-lived perennials), exploiting of environments intermittently favourable for rapid plant growth, and high rates of dry matter production to facilitate rapid completion of life-cycles and maximize seed production (Baker 1965, Grime & Hunt 1975, Grime 1979). The high mortality caused by desiccation favours stress-tolerant ruderals. An adaptation to the xeric conditions is the early flowering of winter-annuals, such as *Anagallis arvensis, Arenaria serpyllifolia, Cerastium fontanum, C. semidecandrum, Erophila verna, Linum catharticum, Medicago lupulina, Sagina nodosa, S. procumbens, Stellaria media* and *Veronica arvensis.*

A number of xerophilous cryptogams show a similar, high abundance in eroded patches. Grassland bryophytes form an often neglected part of the vegetation (van Tooren et al. 1987), and little is known about population dynamics and evolutionary adaptations. During (1979), Slack (1977, 1982), Grime (1979), Grime et al. (1990), Watson (1980a, 1980b, 1981), and others have considered bryophyte strategies. Slack (1977) maintains that bryophytes may often act like opportunistic fugitive species. During (1979) refers to such species as shuttle species, while Grime (1979), Grime et al. (1990) classifies them as stress-tolerators or ruderals. Within the xeric open patches caused by disturbance, bryophytes, especially acrocarps of the Pottiales, appear to be favoured by non-equilibrium conditions. The majority of shell-bed bryophytes show stress-tolerator and ruderal features, although *Fissidens cristatus* and hepatics such as *Metzgeria furcata* and *Radula complanata*, are somewhat deviant in this respect. They are slow-growing and assume higher abundance slowly through the capacity to retain and protect captured resources in conditions where stronger competitors, according to Grime et al. (1990), suffer greater losses through higher rates of tissue turnover and ineffective defenses against herbivory.

Grime (1979) classifies lichens as stress-tolerators, due to features which are expressed in a most extreme form; slow growth-rate, longevity, opportunism and physiological acclimatization. Using a Tilman (1988) approach to competition, it is more reasonable to classify the majority of lichens as stress-tolerant competitors. This is in accordance with Rogers (1990), who links asexual reproduction of lichens with strategies in such a way that sorediate species tend to be stress-tolerators, isidiate species competitors, and species with no specialized mode of vegetative reproduction are either ruderals or competitors. *Cladonia* species, in which fragments of thallus rather than a special organ are apparently used as reproductive structures, should thus be classified as competitors. This is important, since *Cladonia* constitute more than 50% of the lichen species in this material.

Nutrient cycling and ecosystem energetics

To understand the relationships among disturbance and patch dynamics, it is necessary to take the nutrient dynamics into account. Disturbance disrupts the nutrient cycling both by a decline in plant uptake and by a general increase of decomposition and mineralization (Vitousek 1985). The time required for nutrient uptake in plants to return to predisturbance levels depends on vegetation structure and disturbance intensity. In grazed shell-bed vegetation, the disturbance regime is to a great extent predictable due to relatively stable fluctuations caused by constant impact by herbivores, desiccation and wind erosion. In the Blocks III-IV sites, total nitrogen and phosphorus contents were expected to be at levels intermediate to those of the primary successional phase and the established phase. Measurements do, however, show significantly lower values. This indicates that the plant nutrient uptake never reaches the predisturbed level but settles on a lower level. Thus, the nitrogen and phosphorus content in the disturbed sites and the early successional sites show similar levels, while the species diversity is different. This is caused by drift-influence and interference with changes in a number of other environmental variables, but also different nutrient availability per se. According to Melillo et al. (1982), nutrient availability in the early successional phase shows high levels because the litter of pioneer species may decompose more rapidly. This is in accordance with Vitousek (1983) who suggests a particularly high nutrient release during decomposition when pioneer plants grow under high nutrient conditions. Bryophytes, however, show rates of decomposition different from that of phanerogams. According to Longton (1984), decomposition rates of bryophyte material are generally low. In spite of relatively low net primary productivity and low decomposition rates, the contribution of nutrients from bryophyte decomposition is probably underestimated. In contrast to vascular plants, their main growing period is in spring and autumn. This is most favourable in areas like Akerøya, as grazing by herbivores does not occur from November to May.

Stress

In contrast to most other ecosystems, production in these manured coastal shell-beds is normally not restricted by nutrient supplies (e.g. calcium, nitrogen or phosphorus). Restriction may, however, occur as a result of environmental stress (e.g. sheep trampling followed by drought). The generally most important factor causing stress is the herbivore activity, adversely affecting establishment, production and mortality. A number of stress-tolerators are comparatively long-lived and exhibit adaptations for endurance of conditions of limited productivity, e.g. leaf form often small, leathery or needle-like, evergreenness, opportunistic photosynthesis, slow growth and low production devoted to reproduction (Grime 1979).

Stress-tolerators are of quantitative importance in Block V, although factors restricting production are important in all blocks; salt-stress in blocks 0-II, desiccation and nutrient stress in blocks I-IV, shortage of light in blocks VI-VII etc. Herbivore activity has been considered as an important disturbance factor. As described above (pp. 75-77), this is the major structural process in blocks III-IV. In Block V, on the other hand, the stress component plays a more prominent part than the disturbance component; plants adapted to desiccation and nutrient stress also are the best tolerators of high grazing intensity.

The sites in the littoral zone and the lower part of epilittoral zone are exposed to fluctuations in sea spray intensity and desiccation. A set of physiological and morphological traits functions as adaptation to such stress. A number of persistent species are salt-tolerant, spending energy on maintenance of osmotic balance or salt extrusion. In the primary phase of shell-bed vegetational succession, the abundance of succulents is high, i.e. *Cochlearia danica, C. officinalis, Glaux maritima, Sedum acre* and *S. album*. As in the disturbed sites of Block III-IV, early successional sites (blocks I-II) include a high fraction of ruderal stress-tolerators, adapted to suboptimal environmental conditions by different evolutionary tradeoffs. Species reduce the ability to compete for all resources by diverting energy away from adaptations contributing to resource capture. This accords with the Grime (1979) approach, while Tilman (1982) has focused on tradeoffs that are compromises between abilities to compete for different resources.

Chance

Although the main variation in species abundances is normally accounted for as responses to gradients (R. Økland 1990c), the importance of chance, or random processes, is probably strongly underestimated in most vegetation ecological studies. Randomness may be caused by, e.g., intraspecific genetic variability and differences in life history parameters. Given its strategic, southern position, Akerøya is very attractive as a feeding habitat for migrating birds. Dispersal of diaspores, for instance by migrating birds, is thus likely to be taken as an important source of apparent randomness.

MANAGEMENT AND CONSERVATION

The impact of domestic animals

The grazing intensity at Akerøya has varied throughout this century. A small farm in the central eastern part of the island was abandoned in the late 1940s. Until then, the island was used for grazing by sheep and cattle. The number of cattle was gradually reduced until ceasing in the early 1950s. Grazing by sheep has proceeded continually during this century. As many as 200 sheep have been grazing at Akerøya simultaneously, but in the late 1970s the number was reduced to 40. According to Rosén's investigations at Öland (Rosén 1982), a recommended stocking rate when grazing is maintained for an uninterrupted period is 0.7 sheep equivalents per hectare. A direct application to Akerøya indicates a recommendation of 112 sheep equivalents, but the vegetation of limestone grasslands at Öland differs from the studied shell-bed vegetation. When taking the proportion of unproductive bare bedrocks into account, the grazing intensity on the island, regulated to 120 sheep, may be sufficient to prevent overgrowth. If grazing intensity increases, there is a risk that taxa with low grazing tolerance may decline. According to Rosén (1982), a decrease in grazing intensity, either with scattered or sporadic grazing or with a reduced permanent grazing pressure, will result in overgrowth of the present vegetation.

Grazing by domestic animals is selective. Sheep and cattle select leaf in preference to stems, and green material in preference to dry (Arnold 1964). Leaves and green material contain more nitrogen, soluble carbohydrates and phosphate than stems and old material (Rosén 1982).

A characteristic feature of Akerøya today is the number of diverse ecological niches. Management is necessary to maintain this variation. The importance of management and conservation is treated by van der Maarel (1971) and Grubb (1976), among others. Maintenance of chalk grasslands in general, and shell-bed vegetation in particular, is dependent on a careful balance; sufficient grazing intensity is needed to prevent an expansion of shrub vegetation and a decrease in species diversity, while overgrazing reduces the diversity of the ecosystem as well.

The many ecological niches in the heterogeneous shell-bed landscape result in a high diversity of invertebrate species. Studies of insect fauna in the coastal areas of the Oslo-fjord, e.g. Andersen & Fjeldså (1984), Midtgaard & Aarvik (1984) and Andersen & Søli (1988), stress the importance of a responsible management programme. Among the different habitats, the dry meadows have the highest numbers of rare species. To prevent the open grasslands from being invaded by shrubs and trees, clearing is suggested in many areas. However, Ehnström & Waldén (1986) consider that clearing also destroys valuable habitats and impoverishes the fauna.

Bird inventories at the Ornithological Station of Akerøya (J.I. Iversen, pers. comm.), support the importance of maintenance of the open vegetation. Common snipe, lapwing, meadow pipit and skylark all depend on open grasslands for successful breeding. These species are found in various numbers at Akerøya, and will experience breeding difficulties if grasslands are replaced by shrubs. Common eider and other ducks, however, breed on rather shallow soils in this windswept landscape, and the overgrowth will probably not be so extensive as to influence the breeding habitats of these species significantly. Given its strategic, southern position, Akerøya is very attractive as feeding habitat for migrating birds. The rich fauna of invertebrates, in turn dependent on the vegetational composition, enhances the value of this island as a foodstore for birds.

Recommendations of management regimes

If the grazing of domestic animals ceases, the island will eventually offer fewer niches, which consequently will result in lower biological diversity. To prevent a decrease in diversity, a stabilized grazing pressure is necessary. Grazing intensities exceeding 1 sheep equivalent per hectare are not recommended, as overgrazing is likely to result. On the other hand, a level below 0.7 sheep equivalents will lead to an even more serious threat by overgrowth. The recommended grazing pressure is continuous impact of 130-150 sheep.

Recommendations of clearing of shrubs and trees are not given unambiguous support. When it comes to open juniper thickets, several more or less rare plant species find satisfactory nutrient, light and moisture conditions in these habitats. In the open vegetation grazing animals cause a unique selective impact by trampling and manuring. The impact of clearings cannot be compared with the impact of domestic animals; a reduction in the disturbance regime will inevitably decrease species diversity. However, a selective clearing of dense shrubs may be initiated if the grazing activity, for some reason, cannot be maintained.

EVALUATION OF THE DCA ORDINATION METHOD

Failures of DCA

The DCA method has steadily increased in popularity the last 10 years, to become the state-of-the-art method for ordination (Kent & Ballard 1988). Gauch (1982a, 1982b) stated that the method is not far from the theoretical optimum for ordination methods. More recently, the method has received much criticism for its heuristics. Especially the *a posteriori* corrections of the conspicuous faults of CA have been criticized (e.g. Pielou 1984, Kenkel & Orlóci 1986, Minchin 1987, Wartenberg et al. 1987). In addition to this criticism of the detrending and rescaling options, attention has also been given to the tongue effect and the instability problem (Minchin 1987, Oksanen 1988, R. Økland 1990a, 1990c).

The tongue effect may have several origins (R. Økland 1990a, 1990c). Some tongues reflect "true" structure, while others are artifactual. Ordination of the *AB* dataset shows a distinct tongue structure. The ecological interpretation in this paper gives clear indications of an adequate extended triangular structure of this dataset. This tongue *shape* reflects the successional pathways from the early phase sites to the environmentally more diverse sites of the established phase. The configuration expresses that the number of important environmental parameters and the interactions between them increase from the pioneer sites in the littoral and low-lying epilittoral sites towards the established sites. The tongue structure also reflects that the diversity of structuring processes (interspecific interactions, disturbance, stress etc.) increase proportionally with the number of different habitats. The stability of the ordination structure is evident from a comparison of the standard ordination with the ordination using another abundance scale (percentage cover) and the corresponding subplot ordination. Congruence of patterns is a strong evidence for the adequacy of the tongue structure in this case.

Instability problems of DCA often occur in situations where two or more eigenvectors show nearly equal eigenvalues (Oksanen 1988, R. Økland 1990a, 1990c). Kenkel & Orlóci (1986) and Minchin (1987) claim poorer performance of DCA than local nonmetric multidimentional scaling, LNMDS, in tests with simulated data sets. R. Økland (1990c) shows that this does not hold true when the first ordination axis is long, and considerably longer than the second ordination axis. R. Økland compared DCA and LNMDS for three different simulated datasets, with coenoplanes of 6 x 1.5 S.D., 5 x 2 S.D. and 2.4 x 2 S.D. DCA recovered the two underlying gradients better than LNMDS for the 6 x 1.5 S.D.coenoplane, while DCA was inferior to LNMDS with regard to recovery of the underlying gradients of the 5 x 2 S.D. and the 2.4 x 2 S.D. coenoplanes. This is an indication that DCA is the adequate choice of ordination method for the present dataset, as the dimension of the coenoplane of the first two ordination axes was 6.11 x 2.78 S.D. for *AB* sample plot ordination and 6.92 x 3.70 S.D. for the corresponding *AB* subplot ordination.

In addition to reproducing "true" patterns of species distribution, the ordination method should give a reliable estimate of compositional turnover (R. Økland 1990c). Much attention is given to species distributions along environmental gradients (Whittaker 1967, Gauch 1982a, Austin 1985, 1987, R. Økland 1986b, 1986c, Minchin 1987, Palmer & Dixon 1990). In DCA ordination estimates of β-diversity, or the rate of change in species composition along an environmental gradient, are measured in units of standard deviations of species turnover, S.D. units (Gauch & Whittaker 1972, Hill & Gauch 1980). Advantages of the S.D. unit are the simple interpretation and the relative robustness (R. Økland 1986a, 1990a, 1990c). However, lower reliability is reported when β-diversity is low (Oksanen 1983), and the deviations from the unimodal response model are significant. A number of options, concerning sampling design, recordings of species abundance, and data manipulations, influence the β-diversity estimate (Eilertsen & Pedersen 1988, Eilertsen et. al 1990, R. Økland 1990c, R. Økland et al. 1990, Palmer & Dixon 1990). The difference in β-diversity estimates (S.D. units) between the *AB* sample plot ordination and the *AB* subplot ordination is probably not caused by instability, but by dependence on sample plot size. A decrease in sample plot size causes reduction of species occurrences within each sample plot, leading to a decrease in within-sample plot heterogeneity, and a decrease of species niche breadths (R. Økland 1986c, Palmer & Dixon 1990), thus the standard deviation of species response curves decreases. As β-diversity is inversely related to niche breadth (R. Økland et al. 1990), the predicted outcome of a decrease in sample plot size is an increase in β-diversity. This accords well with the result from earlier studies of the same material (Eilertsen & Pedersen 1988), where a slightly significant increase in gradient length was seen when sample plot size was reduced in the series 1 - 1/4 - 1/9 - 1/16 m^2. However this cannot fully explain the pronounced difference in gradient length between the *AB* sample plot ordination and the *AB* subplot ordination; in addition the increase in number of samples from 125 to 2000 must be taken into account.

Detrending

The option for detrending by polynomials available in CANOCO (ter Braak 1987b) is inferior to detrending by segments, as also shown by Knox (1989). Instead of correcting supposed faults of the method, polynomial detrending introduces distortions as the sample plots may be regressed on to a polynomial function. This study supports the advice of Knox (1989) against the use of detrending by polynomials, in contrast to recommendations by ter Braak (1987b), ter Braak & Prentice (1988) and Peet et al. (1988).

Poor performance of DCA relative to MDS was suggested by Pielou (1984), Kenkel & Orlóci (1986), Minchin (1987) and Wartenberg et al. (1987) to be caused by inappropriateness of either or both the non-linear rescaling and the detrending by segments options. It remains to be seen whether the theoretical advantages of detrending by polynomials (claimed by Hill & Gauch 1980, Kenkel & Orlóci 1986, Minchin 1987, Ter Braak & Prentice 1988) will result in an improved, workable algorithm.

Rescaling

The method of non-linear rescaling in DCA gives a scaling of axes in units of mean standard deviation of species turnover (S.D. units; cf. Hill 1979, Hill & Gauch 1980), interpretable in terms of parameters of the unimodal model of species response to ecological gradients (cf. Gauch 1982a).

Arguments in favour of scaling gradients in units of compositional turnover or β-diversity units have repeatedly been suggested (Hill & Gauch 1980, Wilson & Mohler 1983, R. Økland 1986a, 1986c, 1990a 1990d, Peet et al. 1988, Eilertsen et al. 1990). R. Økland (1986b) showed that symmetry of species response curves along a gradient increased by nonlinear rescaling. Minchin et al. (unpubl., in Minchin 1989) state that this increase of curve symmetry "simply reflects this bias of DCA, rather than providing independent support for the Gaussian model." R. Økland (1990d) replies that "this increase in curve symmetry reflects no bias, but merely the fact that zones exist along gradients, with stronger or lesser change in compositional turnover than the average", and that this is "an important property of the relationships of plant species and environmental gradients."

This study shows that the non-linear rescaling procedure in DCA is superior to linear rescaling, both with respect to distribution of sample plots along an axis and with respect to vulnerability to outliers. Minchin (1987) opens for non-linear rescaling as a possible reason for occasional poor performance of DCA, but no material is cited in support of this suggestion. Ter Braak & Prentice (1988) "advice against the routine use of non-linear rescaling", claimed to "aggravate the problems of DCA, identified by Minchin (1987)". This study shows that linear rescaling, as suggested by ter Braak & Prentice (1988), causes concentration of the sample plot configuration on extended axes and increases the influence of outliers. This accords well with the observation of Oksanen (1988) that non-linear rescaling gives a more balanced configuration of sample plots in DCA ordination.

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