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Vegetation-environment relationships of boreal spruce forests in ten monitoring reference areas in Norway

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Vegetational and environmental monitoring of boreal spruce forest was initiated in 1988, as a part of the programme "Contrywide Monitoring of Forest Health" at the Norwegian Institute of Land Inventory (NIJOS). As a basis for monitoring, relationships between trees, understory vegetation and environmental conditions (vertical relationships) were analysed for each of ten reference areas. The reference areas were selected to span regional gradients, in climatic conditions and deposition of airborne pollutants, in old-growth, so-called "bilberry-dominated", "small-fern" and "low-herb", also paludified, spruce forests south of the Polar Circle. Fifty 1-m^2 meso sample plots, randomly chosen within ten 50-m^2 macro sample plots in each reference area, were subjected to vegetation analysis, using frequency in subplots as species abundance measure. Environmental (including soil chemical) and tree parameters were recorded for meso as well as macro sample plots.

The main vegetational gradients were found by parallel use of DCA and LNMDS ordination methods and subjected to environmental interpretation, mainly by means of non-parametric correlation analyses. DCA and LNMDS in most cases revealed the same main gradients in vegetation, but outliers were more frequent in LNMDS ordinations, due to higher vulnerability of this method to plots with deviating number of species. A complex-gradient in nutrient conditions, with pH and the concentration of nitrogen as the most constantly contributing variables, but with considerable between-area variation with respect to important cations, was evident in nine reference areas. Soil moisture varied along the second vegetational gradient in most areas. In the three most humid reference areas, the Ca concentration was related to variation in soil moisture and gradients from below to between trees, while unrelated or inversely related to the same vegetational gradient as pH. Species abundances were plotted on plot positions in DCA ordinations in order to summarize the species' responses to environmental variation in each area.

Variation in vegetation in the total data set (500 meso sample plots) was partitioned onto two sets of explantory variables (environmental and climatic/geographical) by use of CCA, in order to find the relative importance of environmental and climatic/geographical variation. The fraction of variation exclusively explained by environmental variables was about 17%, while only 5% of the variation was explained exclusively by climatic variables. The variation shared by both sets of variables was about 8%.

The main vegetational gradients and environmental/climatic/geographical complex-gradients in the total data set were found by DCA and subsequent interpretation of axes. The main complex-gradients found by separate analyses of data from each reference area, were reflected along the DCA axes in total ordinations, but differences between areas with respect to positions along both environmental and climatic/geographical gradients were also evident.

Meso plot occurrences of selected species were plotted in a DCA ordination of the total data set, with variation exclusively due to climatic/geographical variables removed, in order to express regional similarities and differences in the species' responses to the environment. The different patterns of species' distributions in the DCA ordination were discussed in the light of their use as indicators of specified environmental conditions.

Keywords: Boreal spruce forest, CCA, DCA, Ecology, Environment, Gradient, LNMDS, Monitoring, Norway, Ordination, Permanent plots, Vegetation.

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

CONTENTS

INTRODUCTION

Since the first reports of the so-called "new forest damages" (cf. Ulrich et al. 1979, Schütt & Cowling 1985, Krause et al. 1986), effects of airborne pollutants on forest ecosystems (e.g. trees, understory vegetation and soil conditions) have been important issues for research (e.g. Abrahamsen 1984, Falkengren-Grerup 1986, Falkengren-Grerup et al. 1987, Dahl 1988, Bjørnstad 1991, Nellemann & Frogner 1994, R. Økland 1995c). However, the lack of knowledge of the relationships between different components of forest ecosystems in their natural state soon became obvious, and the need for more knowledge, and monitoring, of the forest ecosystem became apparent (cf. T. Økland 1990, R. Økland & Eilertsen 1993).

The understory vegetation is expected to be particularly sensitive to airborne pollutants and/or climatic change (Frisvoll 1989, Flatberg & Frisvoll 1991, R. Økland & Eilertsen, in press). Increased knowledge of the complex relationships between understory vegetation, trees and environment is required to identify changes in the boreal forest ecosystem. Establishment of reference areas with permanent plots, which makes replicable, repeated registrations possible, is thus an important premise for monitoring. Reference areas with permanent plots for simultaneous monitoring of coniferous trees, understory vegetation and environmental parameters in boreal forests were, however, not established until efforts were made in the late 1980s (cf. R. Økland & Eilertsen 1993). Another important premise for monitoring and studies of vegetation-environment relationships is that the sampling methods allow statistical analysis; implying high degrees of objectivity in the sampling scheme and the measure for quantification of species abundances (cf. T. Økland 1988, 1990). The limit for significance of change in vegetation from one point of time to another is thereby considerably lowered (cf. T. Økland 1990, R. Økland & Eilertsen 1993).

In accordance with the requirements mentioned above, ten reference areas for monitoring were established from 1988 to 1992 as part of the programme "Countrywide Monitoring of Forest Health" at the Norwegian Institute of Land Inventory (NIJOS). Since changes in, and damages to, the forest ecosystem may vary regionally (cf. Tveite 1987, Nellemann & Frogner 1994), these reference areas were placed in different regions of Norway where boreal Norway spruce (*Picea abies*) forest occurs (cf. T. Økland 1993). Preliminary interpretations of vegetation-environment relationships in two of the reference areas were given by T. Økland (1989, 1990, 1993). Sampling methods were also discussed by T. Økland (1990).

Investigations of vegetation-environment relationships in Norwegian boreal forests have so far either been restricted to one study area (e.g. T. Økland 1990, Rydgren 1993, R. Økland & Eilertsen 1993) or been based upon more descriptive (and subjective) methods (e.g. Dahl et al. 1967, Kielland-Lund 1981). Statistical documentation of main vegetational gradients and their relationship with environmental parameters is sparse (see however T. Økland 1990, Rydgren 1993, R. Økland & Eilertsen 1993). Regional variation in vegetational response to the environment in Norwegian boreal forest, has not earlier been documented using numerical and statistical methods.

Few studies, if any, have examined the relationships between boreal spruce forest vegetation and environment in a superhumid climate (cf. R. Økland & Bendiksen 1985). Thus, our knowledge of local and regional variation in each species' response to the environment is also incomplete, notably with respect to humid forests. Our knowledge of local and regional variation in each species' response to the environment is also incomplete with respect to less humid forests in the central and northern parts of Norway.

An important question of boreal forest ecology is the relative importance of variation in vegetation due to local environmental conditions and due to regional (climatic) differences. Knowledge of these relationships is also needed for many applied purposes, e.g. classification and mapping of vegetation. Recently developed methods (Borcard et al. 1992, R. Økland & Eilertsen 1994, cf. also ter Braak 1986, 1987a) allow partitioning of the variation in a vegetational data set on different sets of explanatory variables.

The complexity of relationships in the boreal spruce forest calls for use of multivariate statistical methods in analyses of main gradients in vegetation and environmental interpretation of these gradients (cf. R. Økland 1990a). The performance of the ordination methods Detrended Correspondence Analysis (DCA, Hill 1979, Hill & Gauch 1980) and Local Non-metric Multidimensional Scaling (LNMDS, Kruskal 1964a, 1964b, Kruskal et al. 1973, Minchin 1987), has been discussed since 1980 (Gauch et al. 1981, Kenkel & Orlóci 1986, Minchin 1987, Wartenberg et al. 1987, Peet et al. 1988, R. Økland 1990, R. Økland & Eilertsen 1993). DCA has been a popular method since 1980 due to its easy availability and the documentation by Hill & Gauch (1980), Gauch et al. (1981) and Gauch (1982) of its superiority over Reciprocal Averaging (RA, or Correspondence Analysis, CA) and Principal Component Analysis (PCA). However, several authors point to distortions in DCA (Minchin 1987, Oksanen 1988, R. Økland 1990a, 1990b, R. Økland & Eilertsen 1993). Minchin (1987) concludes that LNMDS is superior to DCA in tests with simulated data sets, while practical usage on field data sets have demonstrated that both methods usually recover the main complex-gradients (cf. Rydgren 1993, R. Økland & Eilertsen 1993). Comparisons of LNMDS and DCA ordinations on the same data set have been performed by several authors (e.g. Oksanen 1983, R. Økland & Eilertsen 1993, Rydgren 1993, 1994). However, parallel use of DCA and LNMDS ordinations on several different but comparable field data sets have so far not been performed.

The most important purpose of this study is to provide a basis for vegetational and environmental monitoring of boreal spruce forest in reference areas representing different regions of Norway, implying: (1) to find the main relationships between trees, understory vegetation and environmental conditions in ten reference areas; i.e. (i) to identify main gradients in vegetation and environment in each area, as well as similarities and differences between these areas, (ii) to improve knowledge of the autecology of boreal forest species; (2) to analyse the total data set (the data from all reference areas in one set) in order to (i) find the relative importance of variation due to local environmental and regional climatic conditions (ii) to identify main complex-gradients in total data set and (iii) to improve knowledge of regional variation in the species' responses to environmental gradients; and (3) to evaluate DCA and LNMDS ordination methods by comparing interpreted ordination diagrams from the ten reference areas.

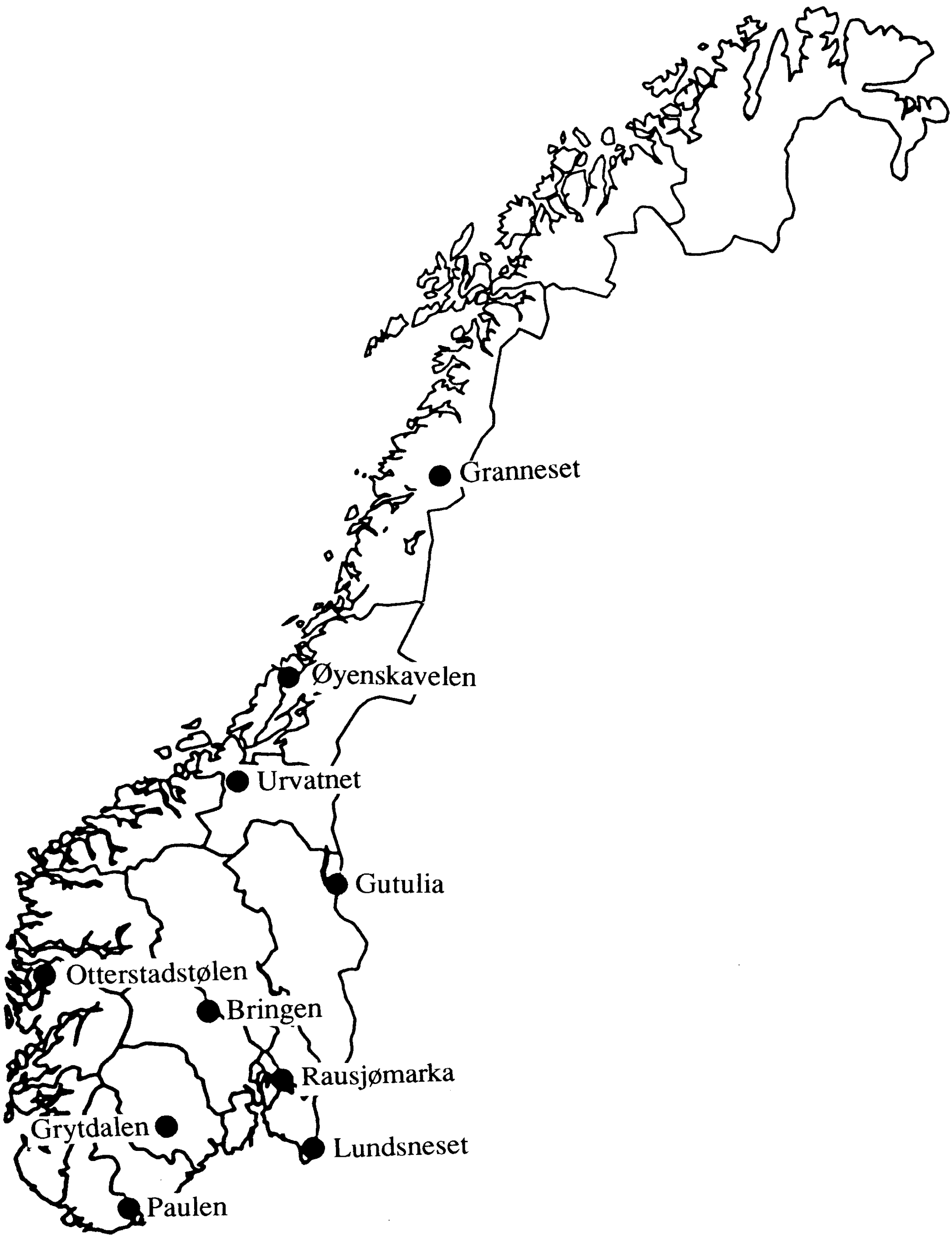

Fig. 1. Map of Norway showing the positions of the ten monitoring reference areas.

THE REFERENCE AREAS

The most important criteria for choice of reference areas were that they should: (1) contain old spruce forest, influenced by forestry and other external conditions as little as possible, (2) comprise a comparable range of variation in vegetation and environment (the so-called "blueberry-dominated", "smallfern and" and "low-herb" spruce forest types, with variation in sites with different nutrient and soil moisture conditions, aspects, etc.), (3) be protected or planned to be protected, and (4) be geographically representative for the variation in spruce

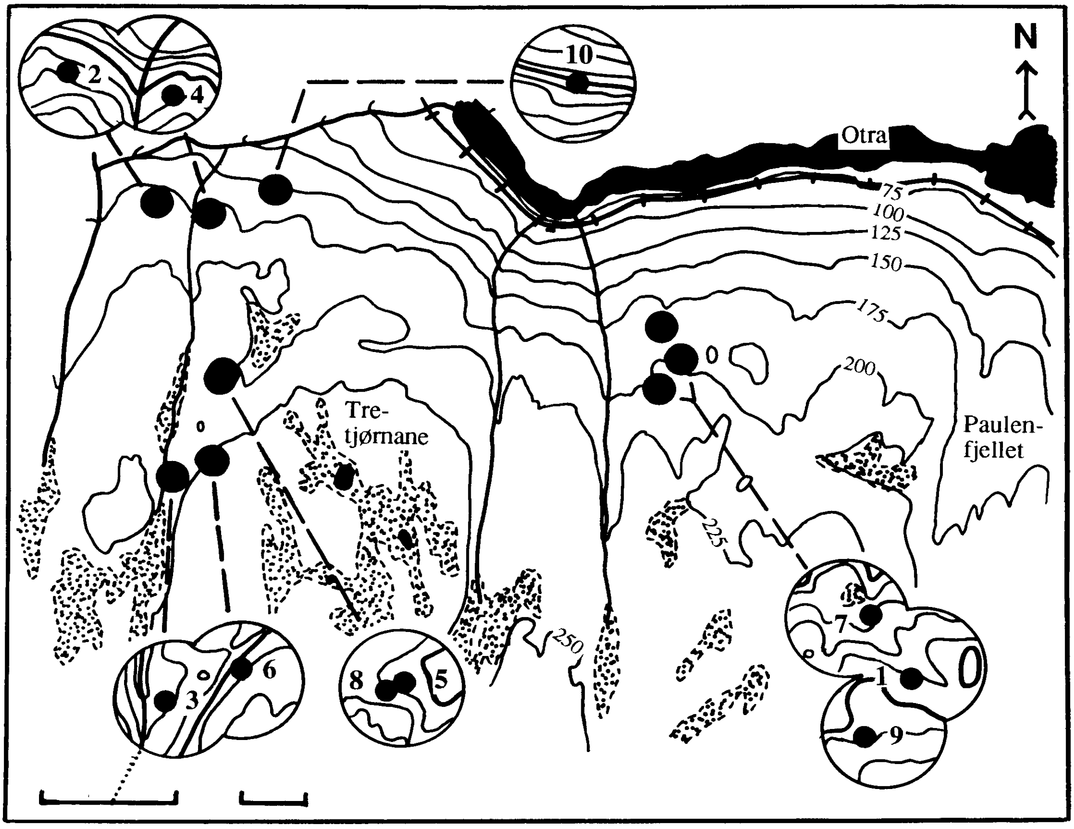

Fig. 2. Paulen: map of the reference area with positions of macro plots 1-10. Small dots surrounded by broken line: mire; filled area: tarn, lake, main river; double continuous line: road; broken line: path; continuous line with small transverse lines: railway; small rectangles: buildings (log cabins, etc.); broken lines alternating with crosses: national border. Altitudes in m. The immediate surroundings (radius ca. 50 m) of each macro plot is shown in insert maps. Rulers = 100 m for main and insert maps. Contour interval: 25 m in main map, 5 m in insert.

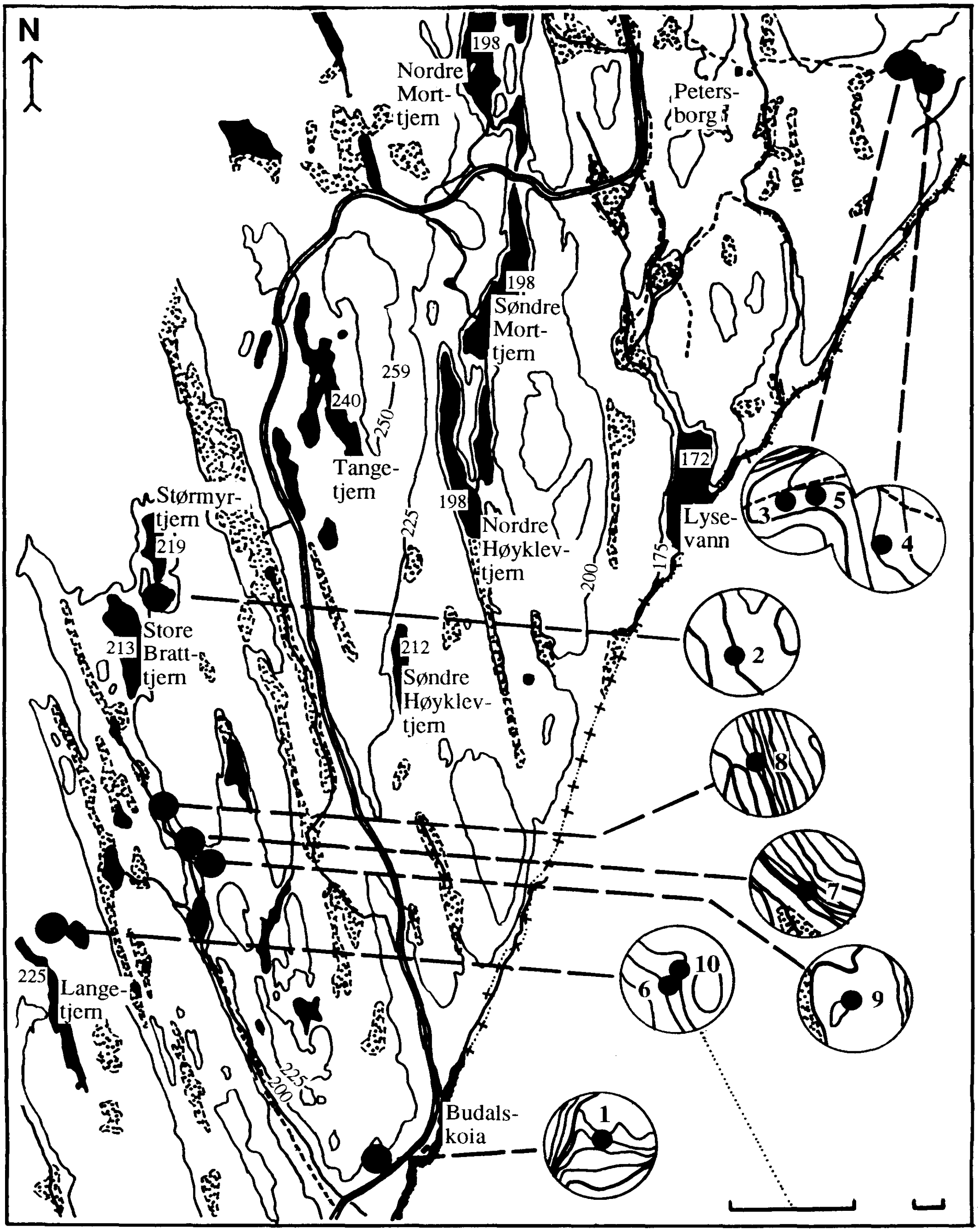

Fig. 3. Lundsneset: map of the reference area with positions of macro plots 1-10. Legend: see Fig. 2. The immediate surroundings (radius ca. 50 m) of each macro plot is shown in insert maps. Rulers = 100 m for main and insert maps. Contour interval: 25 m in main map, 5 m in insert.

Tab. 1. Monitoring areas: geographic position, climate and background information. UTM (Universal Transverse Mercator) grid reference is with respect to the World Geodetic System (WGS84). All reference areas belong to zone 32W, except for Gutulia and Granneset which belong to 33W. Vegetation zone according to Dahl et al. (1986) and R.H. Økland (pers. comm.), terminology according to Ahti et al. (1968). Vegetation section according to Moen & Odland (1993) and R.H. Økland (pers. comm.). Mean annual precipitation is estimated from 1961-90 normals (Førland 1993) for stations close to each study area, also taking topographic position and altitude (cf. Sjörs 1948, Førland 1979) into account. Temperature is based upon 1961-90 normals (Aune 1993) for stations close to each area, adjusted for altitude according to Laaksonen (1976).

Reference area	County	Munici-pality	Lat. (°N)	Long. (°E)	UTM grid reference	Vegetation zone	Vegetation section	Altitude (m)	Area (km^2)	Annual precipi-tation (mm)	Temperature (°C)			Year of ana-lysis
											Year	Jan.*	Jul.	
Paulen	Vest-Agder	Vennesla	58°18-19′	7°55-56′	MK 37-38,63-64	Boreo-Nemoral	Western (O2)	150-275	3	1600	5.6	-2.8	14.5	1990
Lundsneset	Østfold	Aremark	59°03-05′	11°42-45′	PL 55-58,49-52	Boreo-Nemoral (-Southern Boreal)	Western (O2) (-Slightly western, O1)	120-240	10	900	5.3	-4.2	15.4	1992
Grytdalen	Telemark	Drangedal	59°15′	8°37′	ML 78-79,68-69	Middle Boreal	Western (O2) - (-Slightly western, O1)	475-550	0.5	1100	3.7	-6.2	13.8	1988
Rausjømarka	Akershus	Enebakk	59°49′	11°02′	PM 14,33-34	Southern Boreal	Slightly western (O1)	220-300	0.2	850	3.8	-6.6	14.4	1988
Bringen	Buskerud	Flå	60°32-34′	9°23-24′	NN 21-22,12-14	Middle Boreal	Transitional (OC)	600-750	6	650	0.8	-9.8	12.6	1991
Otterstadstølen	Hordaland	Modalen	60°49′	5°45′	LN 23-24,46-47	Southern Boreal	Strongly western (O3)	220-350	2	3500	4.5	-3.3	12.8	1989
Gutulia	Hedmark	Engerdal	62°00-01′	12°09-13′	UJ 51-53,78-79	(Middle Boreal-) Northern Boreal	Transitional (OC)	700-850	4	700	-0.3	-12.0	11.4	1989
Urvatnet	Sør-Trøndelag	Meldal	63°06-07′	9°48-49′	NQ 40-41,98-99	Southern Boreal - Middle Boreal	Western (O2) (-Slightly western, O1)	300-400	3	900	3.0	-6.0	12.1	1992
Øyenskavelen	Nord-Trøndelag	Namdals-eid	64°17′	10°57-58′	NS 94-95,31	Southern Boreal - Middle Boreal	Strongly western (O3) (-Western, O2)	220-300	3	2000	2.4	-6.7	12.1	1991
Granneset	Nordland	Rana	66°30-31′	14°52-53′	VP 94-95,77	Middle Boreal	Transitional (OC)	225-325	0.5	1300	1.3	-9.1	12.1	1990

* - refers to month with lowest mean normal temperature 1961-90 (January in most cases, occasionally February)

forest in Norway, with respect to climate, deposition of airborne pollutants, etc. The ten reference areas are spread throughout Norway south of the Polar Circle (Fig. 1). Their county and municipality locations and the size of the studied areas are given in Tab. 1.

GEOLOGY

Seven of the reference areas belong to the southern, younger Precambrian province of Norway (Oftedahl 1980). *Paulen*, *Grytdalen* and *Bringen* belong to the central-southern Precambrian area (Oftedahl 1980), where the bedrock mainly consists of granitic gneisses (Barth 1960). *Lundsneset* and *Rausjømarka* belong to the southeastern Precambrian area (Oftedahl 1980), the grey gneiss zone (Barth 1960, Oftedahl 1980). The bedrock is strongly folded, without in-

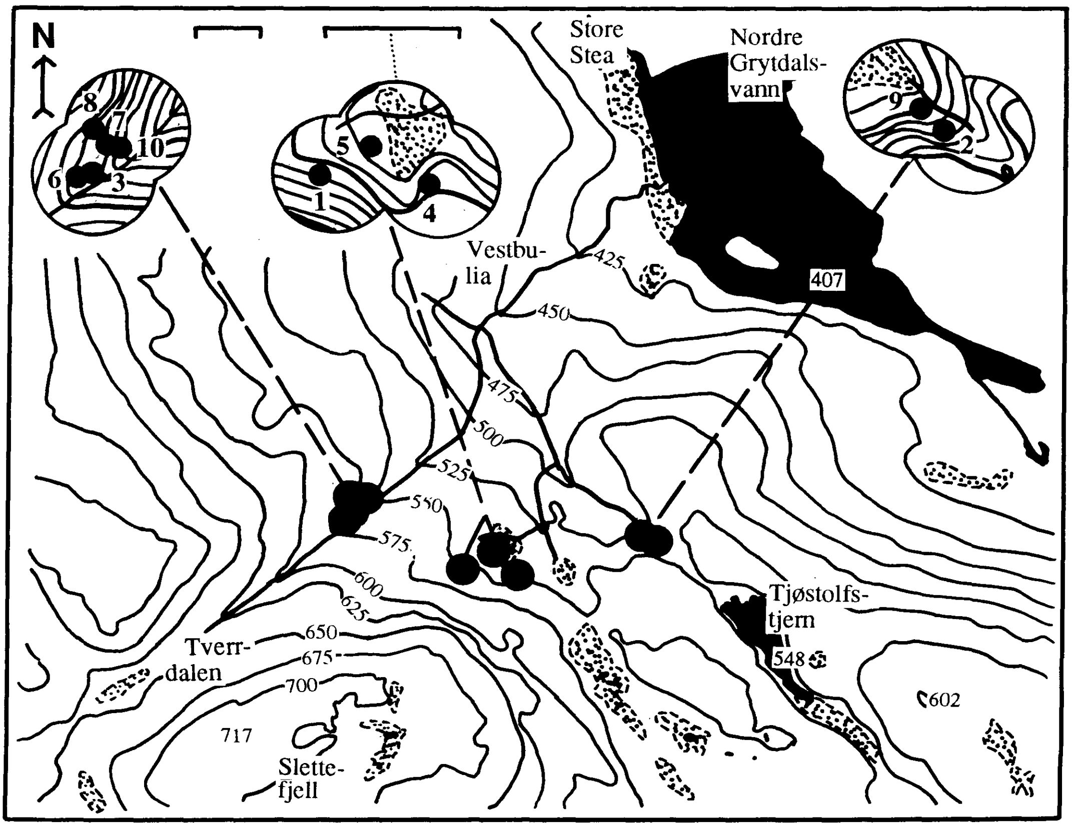

Fig. 4. Grytdalen: map of the reference area with positions of macro plots 1-10. Legend: see Fig. 2. The immediate surroundings (radius ca. 50 m) of each macro plot is shown in insert maps. Rulers = 100 m for main and insert maps. Contour interval: 25 m in main map, 5 m in insert.

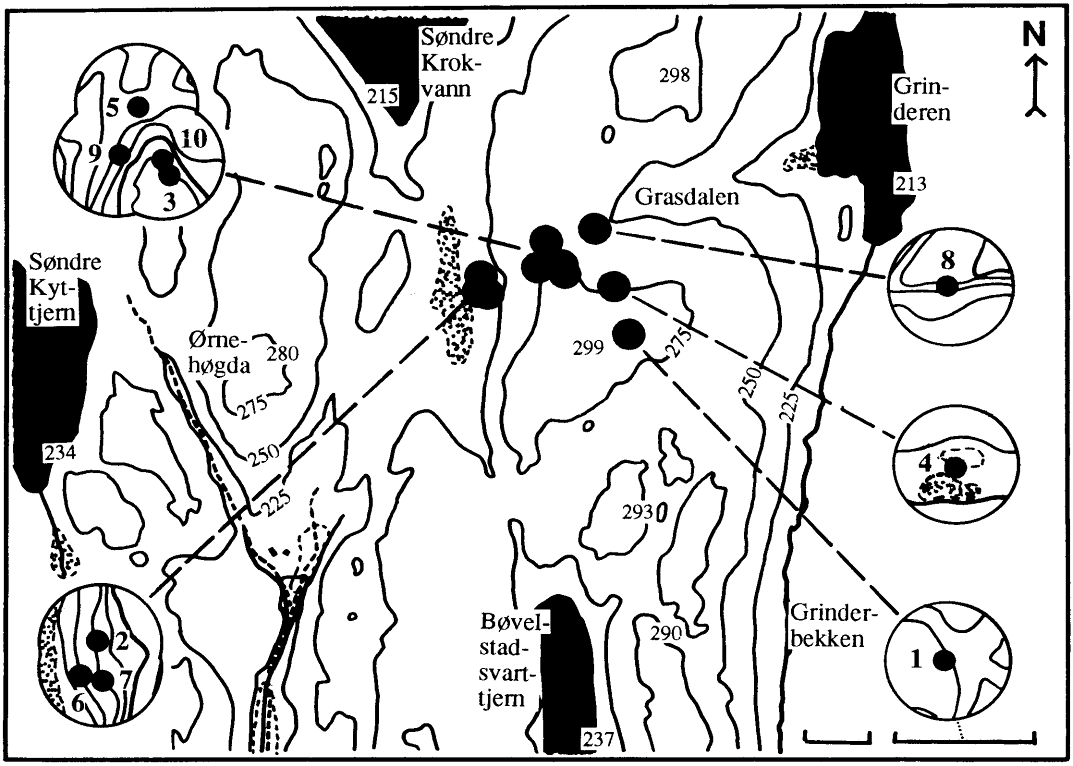

Fig. 5. Rausjømarka: map of the reference area with positions of macro plots 1-10. Legend: see Fig. 2. The immediate surroundings (radius ca. 50 m) of each macro plot is shown in insert maps. Rulers = 100 m for main and insert maps. Contour interval: 25 m in main map, 5 m in insert.

trusives (Oftedahl 1980). *Otterstadstølen* and *Øyenskavelen* belong to the Namsos-Bergen coastal gneiss area, and the bedrock is strongly folded (Oftedahl 1980).

Gutulia belongs to the late Precambrian rocks, the sparagmite region of southern Norway (Oftedahl 1980). The bedrock consists of quartz schist and meta-arcose (Sigmond et al. 1984), but mica schists also occur (Nystuen & Trømborg 1972).

Urvatnet and *Granneset* belong to the north-central Norwegian Caledonides (Oftedahl 1980). Urvatnet belongs to the Trondheim Nappe complex of the Trondheim Region (Oftedahl 1980), and the bedrock mainly consists of Greenstone with quartz keratophyre and gabbro (Oftedahl 1980). Granneset belongs to the Nordland region, and the bedrock is a fine-grained mixture of garnet-, quartz- and calcareous mica schist, marble, mica gneiss and quartzite (Gjelle 1978).

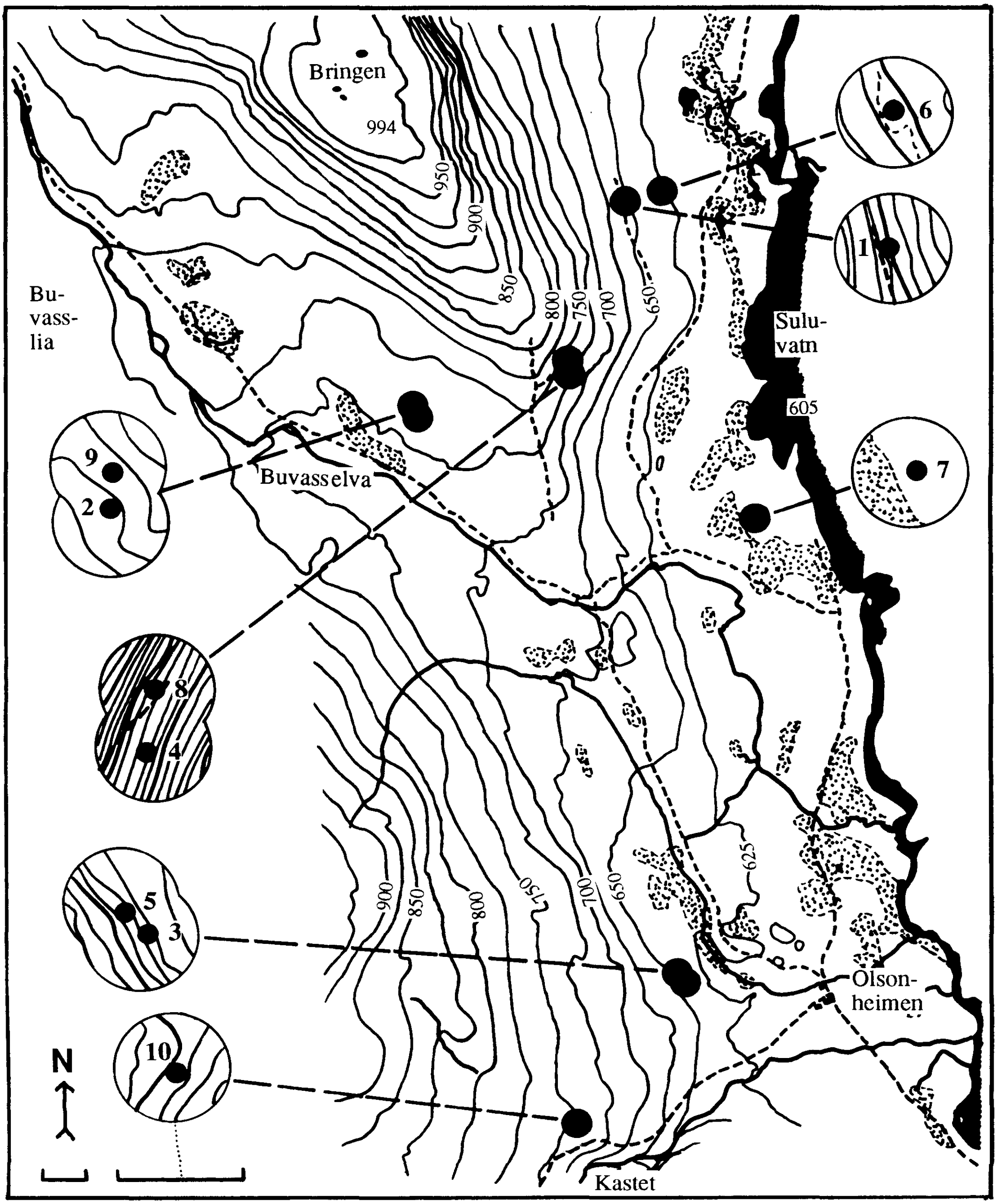

Fig. 6. Bringen: map of the reference area with positions of macro plots 1-10. Legend: see Fig. 2. The immediate surroundings (radius ca. 50 m) of each macro plot is shown in insert maps. Rulers = 100 m for main and insert maps. Contour interval: 25 m in main map, 5 m in insert.

TOPOGRAPHY AND QUATERNARY DEPOSITS

All reference areas are situated above the upper coastal line (cf. Holtedahl & Andersen 1960).

The topography in *Paulen* (Fig. 2) is characterized by steep, mostly north-facing hillsides and a fissure valley landscape, with relative heights 25-50 m, above ca. 200 m. *Lundsneset* (Fig. 3) belongs to a fissure valley landscape, with fissure valleys mainly in a NNW to SSE direction. In *Grytdalen* (Fig. 4) the main valley is U-shaped with steep, broken hillsides. The landscape is strongly undulating, with relative heights of main shapes of 300-600 m, and up to 50 m within single hillsides. The investigated area is situated in the upper part of the hillside southwest of the main valley. Also *Rausjømarka* (Fig. 5) belongs to a fissure valley landscape. In these four reference areas morainic deposits are very sparse or virtually absent.

In *Bringen* (Fig. 6) the main and secondary valleys are U-shaped. The landscape is strongly undulating with relative heights of 300-600 m and low fine-scale brokenness. The investigated area extends from the bottom of the main valley to upper parts of the steep talus slopes of adjacent hillsides. The bottom of the valley is covered by morainic deposits. Also in *Otterstadstølen* (Fig. 7) the main and secondary valleys are U-shaped with low fine-scale brokenness, and the investigated area extends from the bottom of the main valley to the upper

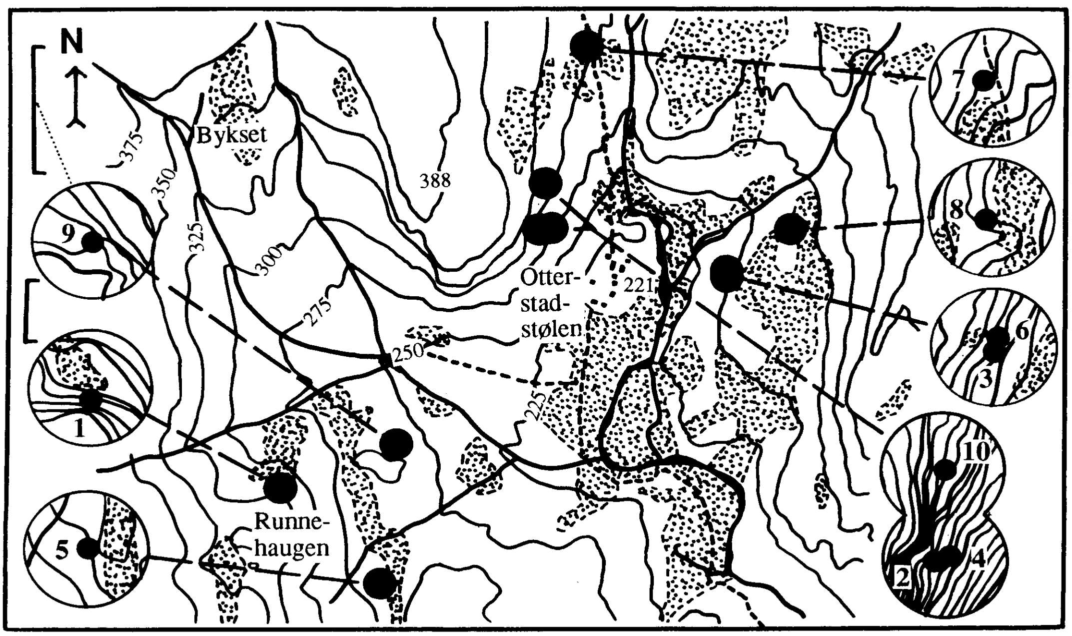

Fig. 7. Otterstadstølen: map of the reference area with positions of macro plots 1-10. Legend: see Fig. 2. The immediate surroundings (radius ca. 50 m) of each macro plot is shown in insert maps. Rulers = 100 m for main and insert maps. Contour interval: 25 m in main map, 5 m in insert.

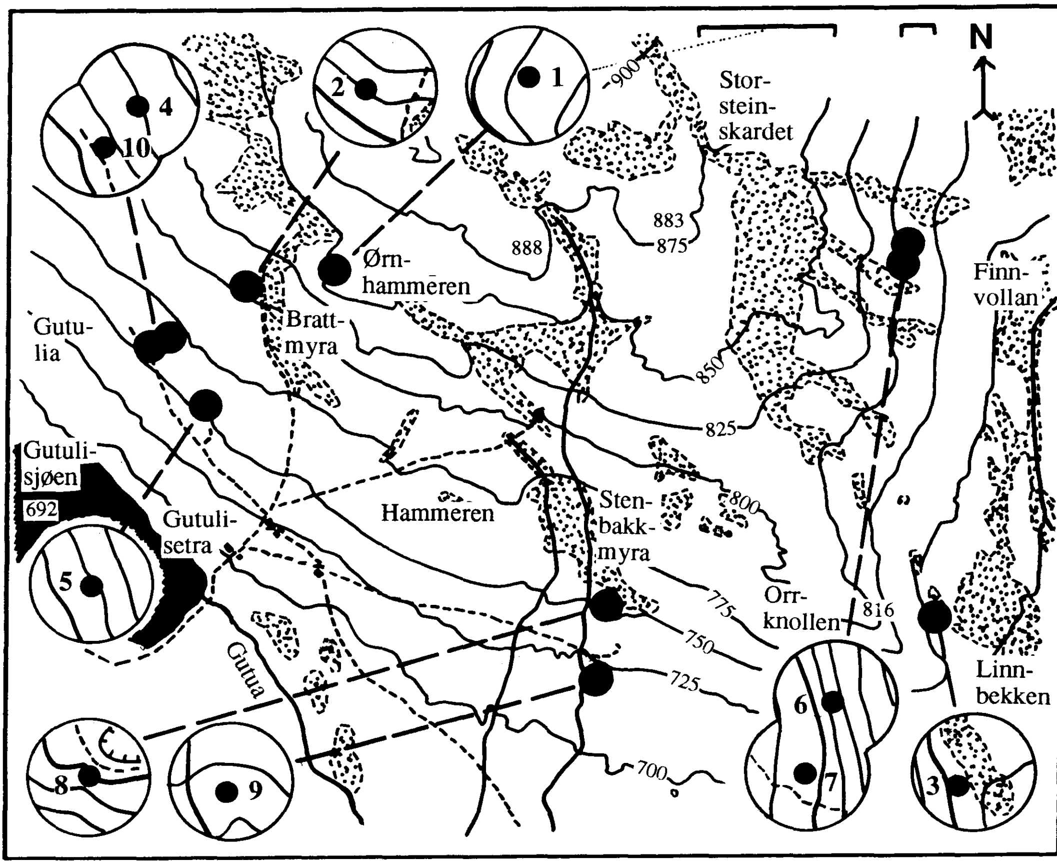

Fig. 8. Gutulia: map of the reference area with positions of macro plots 1-10. Legend: see Fig. 2. The immediate surroundings (radius ca. 50 m) of each macro plot is shown in insert maps. Rulers = 100 m for main and insert maps. Contour interval: 25 m in main map, 5 m in insert.

part of adjacent steep talus slopes. The landscape is a typical western Norwegian fjord landscape with relative heights up to 1000 m. Considerable morainic material is deposited in the hillside east of the Otterstadelva river.

Gutulia (Fig. 8) is characterized by a gently undulating landscape with relative heights of 150-300 m and coarse shapes. The bedrock is more or less covered with morainic deposits. The landscape surrounding *Urvatnet* (Fig. 9) is generally broken, with relative heights up to 150 m. The hillside southwest of Urvatnet is steep, otherwise steepness and terrain shapes are variable. The bedrock is covered with a discontinuous or thin layer of morainic deposits (Reite 1984). Exposed bedrock occurs southwest of Urvatnet. The dominating direction of the ice movement was towards the northwest (Reite 1984); thus the deposited material is mainly low-weathering (Reite 1984). In *Øyenskavelen* (Fig. 10) the landscape is gently undulating with moderately steep hillsides, with relative heights of 150-300 m and a sparsity of fine shapes.

Most of the investigated area, particularly the valley-bottom, is covered with morainic deposits. *Granneset* (Fig. 11) is part of a mountainous landscape, with relative heights of 700-1000 m. The investigated area is situated on a ridge with sides of increasing steepness towards the river Stormdalsåga, which surrounds the ridge on the northwest, north and east. A continuous cover of morainic deposits, locally with great thickness (variation from 0.5 to seve-

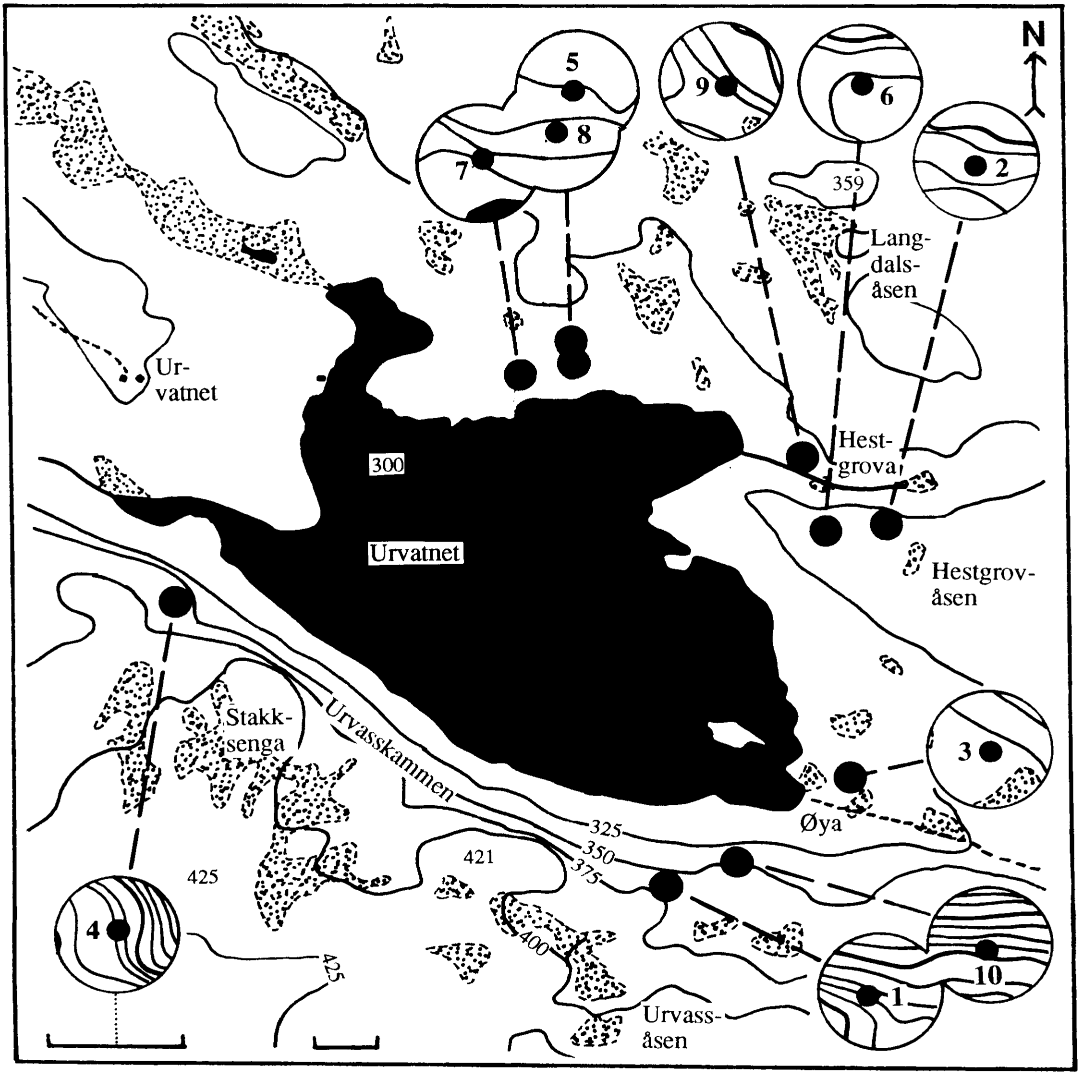

Fig. 9. Urvatnet: map of the reference area with positions of macro plots 1-10. Legend: see Fig. 2. The immediate surroundings (radius ca. 50 m) of each macro plot is shown in insert maps. Rulers = 100 m for main and insert maps. Contour interval: 25 m in main map, 5 m in insert.

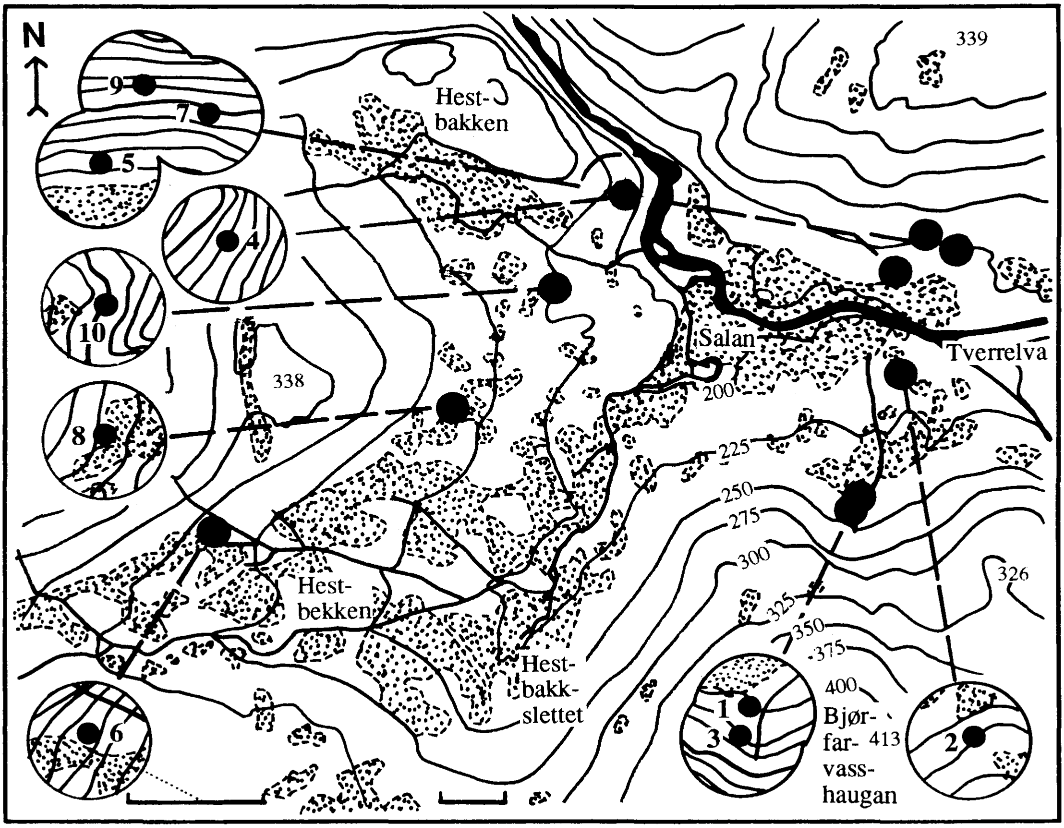

Fig. 10. Øyenskavelen: map of the reference area with positions of macro plots 1-10. Legend: see Fig. 2. The immediate surroundings (radius ca. 50 m) of each macro plot is shown in insert maps. Rulers = 100 m for main and insert maps. Contour interval: 25 m in main map, 5 m in insert.

ral meters, Sveian 1984), largely conceals the bedrock relief and gives rise to a terrain that is planar or gently undulating on a fine scale. The main direction of ice movement was from the east, where granite and granitic gneisses dominate the bedrock (Sveian 1984).

CLIMATE

The reference areas were selected to span main climatic gradients. Tab. 1 shows mean temperature for the year and for the coldest and warmest month estimated for each reference area. Temperatures generally decrease with increasing altitude, and from south to north.

Summer temperatures are high (> 13 °C) for the four southernmost areas: Paulen, Lundsneset, Grytdalen and Rausjømarka. Gutulia has the lowest summer temperature. Winter temperatures are highest (> -5°C) in Paulen, Lundsneset and Otterstadstølen, lowest in Bringen, Gutulia and Granneset.

Mean annual precipitation, estimated from 1961-90 normals for each reference area (Tab. 1), is particularly high in Otterstadstølen and Øyenskavelen. Bringen and Gutulia have the lowest mean annual precipitation.

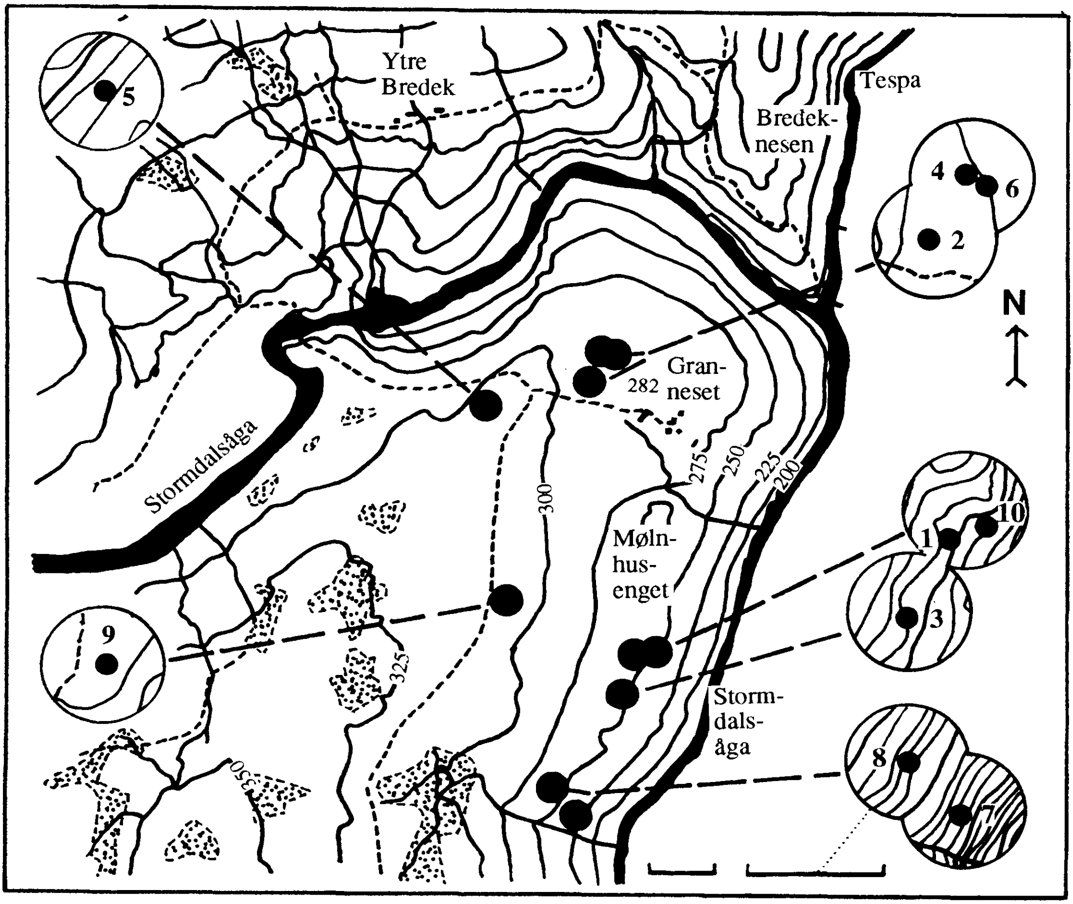

Fig. 11. Granneset: map of the reference area with positions of macro plots 1-10. Legend: see Fig. 2. The immediate surroundings (radius ca. 50 m) of each macro plot is shown in insert maps. Rulers = 100 m for main and insert maps. Contour interval: 25 m in main map, 5 m in insert.

VEGETATION ZONES AND SECTIONS

The reference areas span the Boreal zones (terminology according to Ahti et al. 1968) from the Boreo-Nemoral (Paulen and Lundsneset) to the Northern Boreal (Gutulia), with best representation of the Southern and Middle Boreal zones (Tab. 1). The areas also span vegetation sections (terminology according to Ahti et al. 1968, also see Moen & Odland 1993) from the strongly western section (Otterstadstølen and Øyenskavelen) to the transitional section (Bringen, Gutulia and Granneset, Tab. 1).

FOREST HISTORY, FOREST STRUCTURE AND EXTERNAL INFLUENCE

All monitoring reference areas are protected as Nature Reserves (Paulen, Grytdalen, Lundsneset, Rausjømarka, Urvatnet, and Øyenskavlen) or as National Parks (Gutulia and Granneset) or are planned to be protected (Otterstadstølen). Within each reference area, the parts most unaffected by forestry and other external impacts were preferentially chosen. The terminology of forest structre follows O. Børset (1985), who define four different phases in the last stage of forest development: (1) the optimal phase; great tree stocks and little or no regeneration; (2) the ageing phase; signs of weakness due to old age, such as fungal attacks, insect attacks and storm-felling increasingly frequent, and with smaller or greater gaps arising in the stands; (3) the decaying phase; larger areas attacked by fungi, insects and/or felled by storms, whereby creating opportunities for new forests to grow up, and (4) the regeneration phase; continued regeneration, often in groups, finally resulting in a multilayered forest.

Paulen

The investigated area is owned by the Norwegian state and is part of the Paulen Nature Reserve, protected by law since 1993. According to Moe (1994a), most of the forest in Paulen is in the optimal phase, but smaller stands in the ageing phase occur. Although pine is the dominating tree in the Nature Reserve, spruce is expanding in the area (Moe 1994a). Moe (1994a) suggests an age of about 90-110 years to be representative for the oldest spruce trees. Despite traces of old forestry, which probably was extensive in the late nineteenth century, the external impact on the forest is in many places small enough to give an impression of virginity (Moe 1994a). According to Moe (1994a), fire has been of little importance for forest structure.

Lundsneset

The investigated area is owned by the Norwegian state and is a part of the Lundsneset Nature Reserve, protected by law since 1993. According to Korsmo & Svalastog (1993a), most of the forest is in the late optimal phase, and only to a small degree influenced by modern forestry. A small area has previously been protected administratively (Brattetjønn Forest Reserve, cf.

Erikstad & Hardeng 1988) by Statsskog (formerly the Directorate of State Forests). In this part, no signs of forestry can be traced. Stumps and traces of forest fires are also absent from several other parts of the Nature Reserve (cf. Korsmo & Svalastog 1993a). A forest road runs through the area.

Grytdalen

The investigated area is privately owned and a part of the Grytdalen Nature Reserve, protected by law since 1993. An area of ca. 12 km^2 has been protected administratively since 1971. The first immigration of spruce to this region probably took place at the start of the 15th or 16th century (Hafsten 1985). According to Moe (1994b), the optimal and ageing phases dominate, and the forest least influenced by forestry occurs in the upper part of the hillsides. Extensive forestry was practiced in the main valley around 1910, and in 1950-52, while the investigated area most probably has not been influenced by forestry (Haugen 1991b, Moe 1994b). Traces of forest fires occur (cf. Moe 1994b).

Rausjømarka

The investigated area is owned by the Forest Service of Oslo municipality and is a part of the Østmarka Nature Reserve, protected by law since 1990. The area was previously protected administratively by the owner (Erikstad & Hardeng 1988). According to Korsmo & Svalastog (1993b), most of the forest is in the late optimal phase. The centre of Østmarka Nature Reserve has only been subjected to selection felling, and most recently about 60 years ago (B. Økland 1994). The investigated area is situated in the southern part of the Nature Reserve, which is regarded to be the part of the area least influenced by forestry (Korsmo & Svalastog 1993b). Krohn & Hardeng (1981) reported most of the forest to be from 80 to 160 years old, with high regeneration and without evidence of modern forestry practices.

Bringen

The investigated area is owned by the Norwegian State and is a part of Bringen Nature Reserve, protected by law since 1954 (revised in 1985). According to Svalastog & Korsmo (1995) a major part of the forest is influenced by selection felling, but the irregular composition of age classes of the forest is close to that of virgin forests. Near the main river the late optimal phase is common. The ageing phase occurs in Buvassdalen, and this part of the forest is least influenced by forestry, with a tree age of 195 to 295 years (Svalastog & Korsmo 1995).

Otterstadstølen

The investigated area is privately owned, and is a part of an area planned protected by law as a Nature Reserve (I. Dahl, pers. comm.). Otterstadstølen comprises the westernmost natural spruce forest in Norway (cf. Hafsten 1985). The forest has a considerable element of big and old trees, particularly in the hillside west of the huts (cf. H. Bergmann, unpubl.). The most dominating phases are optimal and ageing phases with some elements of the decaying phase, and the large variation in age classes, with regeneration in gaps, gives an impression of long continuity (H. Bergmann, unpubl.). Some trees in the western part of the area are determined by H. Bergmann (unpubl.) to be between 110 and 123 years, presumably representative for the dominant tree generation in the area. Pollen analyses show that the spruce immigrated to the area less than 400 years ago (Fægri 1949), but according to H. Bergmann (unpubl.) traces of human activity are older than that, and human aid in dispersal cannot be excluded.

Gutulia

The investigated area is owned by the Norwegian State and is protected as a part of Gutulia National Park since 1968. According to Korsmo & Larsen (1994) most of the forest is in the ageing phase, but some elements of the decaying and the late optimal phases also occur. The area around Gutulisetra comes closest to a virgin forest according to Korsmo & Larsen (1994). Mountain dairy farming was performed regularly until 1949 (Kielland-Lund 1972, Wold 1989). Later on, the pasture has been grazed again by cattle for some years. Domesticated reindeer still graze the pasture. The spruce forest is, however, not greatly influenced by grazing or previous forestry. According to Wold (1989) at least four forest fires have occurred in historical time. However, traces of forest fire are most abundant in pine forest in the area. According to Korsmo & Larsen (1994), Gutulia National Park is one of the boreal forest ecosystems in southern Norway which is closest to a virgin forest (cf. also Huse 1964).

Urvatnet

The investigated area is owned by the Norwegian State and is protected as a part of the Urvatnet Nature Reserve since 1992. The area has previously been protected administratively by Statsskog (cf. A. Børset 1979, Erikstad & Hardeng 1988). According to A. Børset (1979), Angell-Petersen (1988) and Haugen (1991a), the investigated area is relatively unaffected by previous selection felling, notably in the oldest forest south and southwest of Urvatnet, where tree ages up to 160 years have been recorded.

Øyenskavelen

The investigated area is owned by the Norwegian State, and is protected as a part of the Øyenskavelen Nature Reserve since 1992. According to H. Bergmann (unpubl.) and Haugen (1991a), the investigated area is moderately influenced by previous selection felling, with dominance of the ageing phase. Some measurements made by H. Bergmann (unpubl.) revealed ages of dominating trees from 90 to 165 years. Some mountain pastures occur within the Reserve but outside the investigated area. Sheep and cattle were still grazing in the investigated area at the time of analysis (1991), thus the vegetation is locally moderately influenced by grazing.

Granneset

The investigated area is owned by the Norwegian State and protected as a part of the Saltfjellet-Svartisen National Park since 1989. The area has previously been protected administratively by Statsskog (cf. A. Børset 1979, Erikstad & Hardeng 1988). Granneset represents the northernmost area of continuously distributed natural spruce forest in Norway (cf. Ryvarden et al. 1972, Lid et al. 1994). According to Korsmo et al. (1993), spruce is spreading in the area. The optimal and ageing phases mostly dominate, and the forest is influenced by forestry to a very small degree (Korsmo et al. 1993) although some stumps occur (A. Børset 1979).

MATERIAL AND METHODS

The field registrations were performed in the years 1988 - 1992 (Tab. 1).

PLACEMENT AND MARKING OF SAMPLE PLOTS

A restricted random sampling procedure was used. In each reference area (Figs 2-11) ten macro sample plots, each 5 × 10 m (Fig. 12) were placed subjectively in order to represent the variation along presumably important ecological gradients; in aspect, nutrient conditions, light supply, topograpic conditions, soil moisture, etc. Stands not visibly affected by forestry and other external impacts were preferentially chosen. Five meso sample plots, each 1 m^2, were randomly placed within each of the macro sample plots (Fig. 12). The positions of the meso plots were found by means of random numbers (Owen 1962). A meso plot was rejected if a tree taller than 2 m was rooted inside it or if more than 20% of the plot was covered by

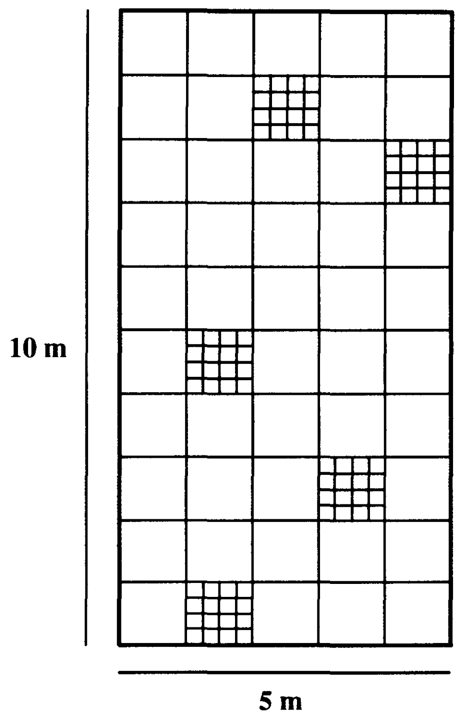

Fig. 12. Example of macro plot with five randomly placed meso plots (each divided into 16 subplots) drawn in. Ruler = 1 m.

stones. In case of rejection, a new position for the meso plot was selected from a predefinedpriority list to avoid subjectivity. All corners in the meso and macro plots were permanently marked with subterranean eloxed aluminium tubes. A micro plot of 0.0625 m^2 (Fig. 12) was marked within each meso plot, in a fixed position. The macro and meso plots were also marked visibly by use of above-ground markers. The described sampling scheme is regarded as an optimal compromise between objectivity and time consumption (cf. R. Økland 1990a).

RECORDING OF VEGETATION IN THE SAMPLE PLOTS

Each of the 500 meso plots (50 meso plots in each reference area) were divided into 16 meso subplots (Fig. 12), 0.0625 m^2 each. Presence/absence of all species was recorded for each of the meso subplots, and frequency in subplots was calculated for each species (cf. T. Økland 1988, 1990). A species was recorded as present when covering any part of the subplot. Each of 500 micro plots (one fixed subplot within each meso plot) were analyzed in the same way as the meso plots, but will not be further treated here (cf. T. Økland 1990).

RECORDING OF ENVIRONMENTAL AND TREE PARAMETERS

Environmental and tree parameters were measured for the following purposes: (1) Environmental interpretation of the vegetational patterns. Parameters used for local environmental interpretation (directly or calculated from measured parameters), are numbered consecutively (Tab. 2). (2) Forthcoming monitoring of changes in soil chemistry and/or the health of the trees, which may in turn be related to changes in the vegetation. Most of the variables used for environmental interpretation will be used for monitoring as well. (3) Background information (e.g. the cover of each vegetation layer, cover of naked rock, stones, stumps, sketch map of the meso and micro plots, terrain descriptions, etc.). Several of these parameters of this kind will not be described in detail here.

Tree parameters

All trees that were (i) rooted within the macro plot, (ii) rooted within a 2-m buffer zone bordering on the plot, or (iii) covering the plot, were marked with numbers. The *tree height* was measured in dm from normal stump height to the treetop. *Crown height* was measured as the difference between total tree height and the distance from the ground to the point of the stem where the lowest green branch whorl (i.e. the lowest green branch whorl which was separated from the rest of the crown by less than two dry branch whorls) emerged (A. Rørå, pers. comm.). *Crown area*, i.e. the area within the vertical projection of the crown perimeter, was estimated from a sketch map of each macro plot with positions of meso plots, canopy perimeters and tree stems drawn in. *Crown cover* was estimated as the percentage of the

Tab. 2. Environmental parameters; number, abbreviation, unit of measurement, range of scale, presumed statistical distribution, and transformation. ppm - parts per million, ddu - day-degree unit.

No	Abbrev.	Parameter	Unit	Pot. range	Distribution	Transformation
Environmental parameters						
01	MA Inc	Macro plot inclination	g	0-100	uniform	no
02	MA Asp	Macro plot aspect	g, recalc.	0-200	uniform	no
03	MA Hi	Macro plot heat index		-∞-+∞	± normal	no
04	MA BA	Macro plot basal area		0-∞	uniform	no
05	MA Lig	Macro plot light index	0-∞	uniform	no	
06	ME Inc	Meso plot inclination	g	0-100	uniform	no
07	ME Asp	Meso plot aspect	g, recalc.	0-200	uniform	no
08	ME Hi	Meso plot heat index	-∞-+∞	± normal	no	
09	ME Rou	Meso plot roughness		0-∞	lognormal	ln (1+x)
10	ME Con	Meso plot convexity		-∞-+∞	normal	no
11	ME Smi	Soil depth, minimum	cm	0-∞	lognormal	ln (1+x)
12	ME Sme	Soil depth, median	cm	0-∞	lognormal	ln (1+x)
13	ME Sma	Soil depth, maximum	cm	0-∞	lognormal	ln (1+x)
14	LitCC	Litter index, crown cover	0-∞	lognormal	ln (1+x)	
15	LitACD	Litter index, actual crown density		0-∞	lognormal	ln (1+x)
16	Mois	Soil moisture	vol. %	0-100	uniform	no
-	Ranked Mois	Ranked soil moisture		1-50	uniform	no
17	LI	Loss on ignition	%	0-100	bimodal	no
18	pH_{H20}	pH, aquous solution		0-14	normal	no
19	pH_{CaCl2}	pH, measured in $CaCl_2$		0-14	normal	no
20	Ca	Exchangeable Ca	100 ppm/LI	0-∞	± lognormal	ln (1+x)
21	Mg	Exchangeable Mg	100 ppm/LI	0-∞	± lognormal	ln (1+x)
22	K	Exchangeable K	100 ppm/LI	0-∞	± lognormal	ln (1+x)
23	Na	Exchangeable Na	100 ppm/LI	0-∞	± lognormal	ln (1+x)
24	H^+	Exchangeable acidity	100 ppm/LI	0-∞	± lognormal	ln (1+x)
25	Al	Exchangeable Al	100 ppm/LI	0-∞	± lognormal	ln (1+x)
26	Fe	Exchangeable Fe	100 ppm/LI	0-∞	± lognormal	ln (1+x)
27	Mn	Exchangeable Mn	100 ppm/LI	0-∞	± lognormal	ln (1+x)
28	Zn	Exchangeable Zn	100 ppm/LI	0-∞	± lognormal	ln (1+x)
29	Total N	Total nitrogen	weight %/LI	0-5	± lognormal	ln (1+x)
30	P-AL	AL-soluble phosphorus	100 ppm/LI	0-∞	± lognormal	ln (1+x)
31	P	Exchangeable P	100 ppm/LI	0-∞	± lognormal	ln (1+x)
32	S	Exchangeable S	100 ppm/LI	0-∞	± lognormal	ln (1+x)
Climatic/geographical parameters						
C1	Prec.	Annual precipitation	mm	0-∞	uniform	
C2	T	Mean annual temperaure	°C		uniform	
C3	ETS	Effective temperature sum	ddu	0-∞	uniform	
C4	Tamm's H	Tamm's humidity index	mm	0-∞	uniform	
C5	Lat.	Latitude	°		uniform	
C6	Long.	Longitude	°		uniform	
C7	Alt.	Altitude	m		uniform	

crown area covered by living phytomass of each tree. *Actual crown density* was defined as the crown density, i.e. a measure of the health of the tree (see below), as it appears from beside the trees, the relative amount of light openings in the tree canopy taken into account, but independent of the presumed normal crown density for the tree (A. Rørå, pers. comm.). The estimates were made by use of binoculars and recorded as percentages.

The following parameters were recorded exclusively for monitoring purposes or as background information, and were not used for further analysis in this study: *Relative crown density*, a measure of the health of the tree (Rørå 1988, Rørå et al. 1988, Venn et al. 1993); *crown colour* (Rørå et al. 1988, Kvamme 1992), another measure of tree health; *defoliation type*, i.e. a classification of various damage symptoms according to their distribution types in the tree crown (Rørå 1988, Rørå et al. 1988); *social status of the trees*, their competitive ability relative to the other trees in the stand (Skinnemoen 1969); *amount of cones; mechanical and biotic damages* (Rørå et al. 1988, Kvamme 1992); *diameter at breast height* (1.3 m), calculated from the stem circumference in cm at breast height; *site quality* (Tveite & Braastad 1981), based on core samples taken at breast height from 2-3 trees close to the macro plot (cf. T. Økland 1990); *stand age*, estimated from the age of the cored trees; and *felling class*, the stage of forest development (cf. Institutt for skogtaksasjon & Institutt for skogøkonomi 1987).

Macro sample plot parameters

(1) *Macro plot inclination* (α_1) was measured, representative for the macro plot, by means of a clinometer (400^g). (2) *Macro plot aspect unfavourability*, α_2, expressed as deviation from SSW (225^g, cf. T. Økland 1990, R. Økland & Eilertsen 1993, where the parameter is incorrectly termed aspect favourability), was calculated from clinometer measurements (400^g) representative for the macro plot. SSW is considered to be the most favourable aspect (Dargie 1984, Heikkinen 1991) due to high incoming radiation at times of day with high temperatures. (3) *Macro plot heat index*; Parker's index (Parker 1988), was calculated by the following formula:

$$\text{MA Hi} = \tan \alpha_1 \cdot \cos \alpha_2$$

where α_1 and α_2 are defined above. (4) *Macro plot basal area* measured at breast height was determined by a relascope (Fitje & Strand 1973). Basal area expresses the tree density and thus the supply of light to understory vegetation. Basal area was measured from the four corners of each macro plot and the average was calculated. Relascope factor 1 was used. (5) *Macro plot light index* was calculated by use of the crown area, a_i (see below), and crown cover, b_i (see below), for all trees $i = 1,...,n$ in each macro plot (cf. T. Økland 1990, R. Økland & Eilertsen 1993):

$$\text{MA Lig} = \Sigma_i\, a_i \cdot b_i /50$$

High values of the index indicate high tree cover, and thus low radiation to the understory vegetation.

Meso sample plot parameters

(6) *Meso plot inclination* was measured, representative for each meso plot, by a compass (0-100^g, α_3). (7) *Meso plot aspect unfavourability* was measured, representative for each meso plot, by a clinometer compass (0-400^g, recalculated to 0-200^g, α_4). This value was recalculated in the same way as for macro plot aspect unfavourability. (8) *Meso plot heat index* was calculated as for macro plot heat index:

$$\text{ME Hi} = \tan \alpha_3 \cdot \cos \alpha_4$$

Microtopographic indices were calculated from measurements of the vertical distance from the centre of each meso subplot to a levelled analyzing frame. For each meso plot, the 16 observations were used to calculate indices for (9) *meso plot surface roughness* and (10) *meso plot convexity*, see formula in R. Økland & Eilertsen (1993).

Meso plot soil depth was measured in eight fixed positions just outside the border of the meso plot. The (11) *minimum soil depth*, (12) *median soil depth* and (13) *maximum soil depth* were determined for each meso plot. (14) *Litter index based on crown cover* was calculated by means of the following equations (T. Økland 1990, R. Økland & Eilertsen 1993):

$$L_i = \Sigma_i \, (d_{ri} / d_i) \cdot b_i \cdot c_i \cdot (h_{ti} - h_{ki})$$

for all trees i = 1,...,n with stem rooted within the crown perimeter and

$$L_i = \Sigma_i \, b_i \cdot c_i \cdot (h_{ti} - h_{ki})$$

for all trees i = 1,...,n with stem not rooted within the crown perimeter, where: b_i is the cover of the crown of the tree i; h_{ti} is the height of the tree i; h_{ki} is the crown height of tree i; d_i is the distance from the centre of the stem to the crown periphery of tree i, measured through the centre of the meso plot; d_{ri} is the distance from the crown periphery to the proximal meso plot border (i.e. the side facing the stem of the tree) along the line through the centre of the meso plot and the centre of the stem of tree i; and c_i is the fraction of the meso plot area situated under the crown of tree i. (15) *Litter index based on actual crown density* was calculated correspondingly, but b_i was replaced with e_i; actual crown density. The litter idices thus express canopy influence the meso plots.

(16) *Soil moisture* was determined for volumetric soil samples, collected from the upper 5 cm of the humus layer. The samples were collected about 10 cm from the border of each meso plot, whenever possible below the plot. All samples from one reference area were collected on the same day, after a period of some days without rainfall, with the aim of representing median soil moisture conditions, i.e. the normal soil moisture at the site (cf. T. Økland 1990, R. Økland & Eilertsen 1993). The samples were stored in paper bags kept inside double plastic bags and kept frozen until they were weighed in the laboratory. After drying at 110 °C to constant weight, the samples were weighed again and percentage moisture was calculated.

In order to improve the comparability in analysis of the total data set, the soil moisture values were ranked for each reference area, and used as a new variable; *ranked moisture.*

A second set of soil samples were collected from the upper 5 cm of the humus layer for determining (17) *loss on ignition* and for chemical analyses (18-32). All samples from the meso plots in one reference area were collected on the same day and kept frozen until analysis. Several subsamples were collected outside the border of each meso plot and the subsamples were mixed in order to counteract fine-scale spatial variation in physical and chemical properties of the humus. To avoid impacting the drainage regime of the plot, soil samples were never collected above the plots. The following analyses were performed by Landbrukets analysesenter, Ås:

(17) *Loss on ignition*, (18) pH_{H2O}, pH measured in aquous solution, (19) pH_{CaCl2}, pH measured in $CaCl_2$, (29) *total N* and (30) *P-AL* (standard method among others described by Baadsvik 1974). Concentrations of the cations; (20) *Ca*, (21) *Mg*, (22) *K*, (23) *Na*, (24) *exchangeable acidity*, hereafter referred to as H^+ , (25) *Al*, (26) *Fe*, (27) *Mn*, (28) *Zn*; as well as the anions (31) *P* and (32) *S* were determined in NH_4NO_3-extract by means of ICP (Inductively-Coupled Plasma Emission Spectroscopy) with the Jarrell Ash model 1100 instrument. Concentrations were expressed as fractions of loss on ignition as recommended by T. Økland (1988).

The 32 parameters used for environmental interpretation variables will be referred to as environmental variables.

RECORDING OF CLIMATIC AND GEOGRAPHICAL PARAMETERS

Mean annual precipitation (normal period 1961-90; Førland 1993) was esimated for each reference area and mean annual temperature (Aune 1993, corrected for altitude according to Laaksonen 1976) was estimated for each macro plot (Tab. 2). Effective temperature sum according to Laaksonen (1979) and Tamm's index of humidity (Tamm 1959) was calculated for each macro plot. Latitude and longitude for each reference area, and altitude for each macro plot, were read from maps.

THE DATA MATRICES AND DATA EDITING

The vegetation data matrices were entered on the computer by means of Biological Data Program/PC, Versions 1.01 and 1.10 (Pedersen 1988). The environmental, climatic and geographical data matrices were entered on the computer by means of LOTUS 1-2-3, Version 3.0 (Lotus Development Corporation 1989). Data editing was partly made by means of BDP/PC, partly by means of LOTUS 1-2-3. Environmental parameters with lognormal or approximately lognormal distributions were converted to approximately normally distributed variables by use of the transformation ln (1 + x), see Tab. 2.

NUMERICAL AND STATISTICAL ANALYSES OF DATA SETS FROM EACH REFERENCE AREA

Ordination of vegetation data sets

Two ordination methods were used to extract the main gradients in the ten vegetation data sets:

Detrended Correspondence Analysis, DCA (Hill 1979, Hill & Gauch 1980), of frequency in subplot data sets from the 50 plots in each reference area, was performed by means of CANOCO, Version 3.12 (ter Braak 1987b, 1990). The following options were used: detrending by segments, non-linear rescaling and down-weighting of species with a frequency lower than the median frequency in proportion to their frequency as recommended by Eilertsen & Pedersen (1989) and Eilertsen et al. (1990).

For some reference areas (Paulen, Lundsneset, Rausjømarka and Urvatnet), plots appearing as strong outliers in the ordination were removed prior to all further analyses (cf. T. Økland 1988, 1990). The new, reduced data matrix was subjected to new DCA ordination. Fractions of the total variation in vegetation explained by the DCA axes were calculated by dividing eigenvalues with total inertia (cf. Greenacre 1984, Borcard et al. 1992).

Local Non-metric Multidimensional Scaling, LNMDS (Kruskal 1964a, 1964b, Kruskal et al. 1973, Minchin 1987) of frequency in subplots data sets from each reference area with outliers in the DCA ordinations of 50 plots removed, was carried out using DECODA, Version 2.01 (Minchin 1990). The following options were used: dimensionality = 2, dissimilarity measure = percentage dissimilarity (Bray-Curtis), standardized by division with species maxima (as recommended by Faith et al. 1987), at least 100 starting configurations, of which one was the DCA, maximum number of iterations = 1000, stress reduction ratio for stopping iteration procedure (stress is a measure of correspondence between floristic dissimilarities between plots and the distance between plots in the ordination diagram) = 0.99999. Solutions were not accepted unless reached from at least two different starting configurations. The LNMDS axes were linearly rescaled in S.D. units by means of DCCA (one LNMDS axis used as constraining variable) in CANOCO, in order to enhance comparability with the corresponding DCA axes (cf. R. Økland 1990a, R. Økland & Eilertsen 1993, T. Økland 1993).

Methods for analyses of environmental data sets and interpretation of ordination results

Thirty-two of the recorded/calculated parameters were used for further analyses (Tab. 2). All meso plots within a macro plot were given the same value for macro plot parameters. Analyses of correlations were performed by means of STATGRAPHICS, Version 6.0 (Manugistics Inc. 1992).

Ordination of environmental data by means of PCA

Principal Component Analysis (Pearson 1901), PCA, of 32 environmental variables recorded in the 50 meso plots in each reference area, was performed by means of CANOCO. Variables were centered and standarized by division with standard deviation prior to analyses. Correlation biplot scaling of axes was used in order to optimize the fit of angles between variables (vectors) to inter-variable correlations (ter Braak 1987c).

Correlation analyses

Correlations between environmental variables, between DCA and LNMDS axes and between environmental variables and DCA and LNMDS axes, were calculated as Kendall's non-parametric correlation coefficient τ (Kendall 1938). Kendall's τ were chosen because this coefficient only takes the ranks of variables into account.

Isoline diagrams

Values for environmental variables most strongly correlated with DCA axes 1 and 2 were plotted on meso plot positions in the DCA ordination diagram for each reference area in order to illustrate the relations between vegetation and environmental conditions. The values were smoothened by fitting a third order polynomial by means of LOTUS 1-2-3. Fitted (smoothened) values were used for drawing isolines into the ordination diagram. The multiple coefficient of determination, R^2, between original and predicted values was used as a measure of goodness-of-fit of the isolines. Plots were made only for variables with Kendall's correlation coefficient $\tau \geq 0.3$ with one of the DCA axes 1 or 2 and $R^2 \geq 0.4$, except for two cases: the variable MA Lig ($R^2 = 0.395$) in the data set from Gutulia and the variable LitACD ($R^2 = 0.379$) in the data set from Øyenskavelen.

Distributions of species abundances in the DCA ordination

For each reference area, subplot frequencies for species occurring in five or more meso plots were plotted at the meso plot positions in the DCA ordination diagram. By relating distribution of species abundances to an environmentally interpreted meso plot ordination diagram, valuable information about the autecology of the species was obtained.

NUMERICAL AND STATISTICAL ANALYSES OF THE TOTAL DATA SET

Variation partitioning

The relative importance of climatic/geographical (explanatory variable set {C}) versus environmental variables (explanatory variable set {E}) for variation in vegetation, was assessed by variation partitioning (Borcard et al. 1992, R. Økland & Eilertsen 1994), a three-step technique by which the total data set was subjected to Canonical Correspondence Analyses, CCA (ter Braak 1986, 1987a) on the total data set by means of CANOCO. The three steps were as follows:

(1) CCA with significant climatic/geographical variables, {C}, as explanatory variables. Forward selection of the seven variables was performed prior to CCA in order to find which of the climatic/geographical variables that contributed significantly at $P < 0.001$ (Monte Carlo tests, 999 permutations, cf. ter Braak 1990). The variation explained by these variables is the denoted C, which can be partitioned into $C|E$ (variation exclusively explained both by climatic/geographical variables and by environmental variables) and $C|E$ (variation which can only be explained by climatic/geographical variables).

(2) CCA with significant environmental variables, {E}, as explanatory variables. Forward selection of the thirty-two variables was performed prior to CCA. The variation explained by these variables is the denoted E, which can be partitioned into C∩E (see above) and E | C (variation exclusively explained by environmental variables).

(3) CCA with the significant climatic/geographical variables as covariables (the variation due to the covariables was partialled out) and the significant environmental variables as explanatory variables; giving the variation exclusively explained by environmental variables, E|C.

Explained variation was converted to fractions by division with total inertia.

DCA of the total data set

DCA was performed on the total data set consisting of 500 plots from the ten reference areas. The same options were used as in DCA of data from each reference area.

A second DCA ordination of the total data set was also performed, using 7 covariables for the climatic/geographical variation not shared with the environmental variables (C|E in the terminology used for variation partitioning). These covariables were found as follows:

A CCA, with the 32 environmental variables as covariables and the seven climatic/-geographical variables as explanatory variables, was performed on the total data set. The resulting (maximally constrained) seven CCA axes (with sample scores that are linear combinations of the environmental variables, cf. Palmer 1993) represent a linear combination of hypothetic variables corresponding to the variation exclusively attributable to the climatic/geographical variables ({C|E}).

Kendall's τ was calculated for correlations between DCA axes (both ordinations) and between DCA axes and environmental and climatic/geographical variables for total data sets.

The DCA ordination with covariables was used for studying regional variation in the response of vegetation to main complex-gradients. For selected species, occurrence was plotted at meso plot positions by use of different symbols for each reference area.

NOMENCLATURE

The nomenclature of vascular plants follows Lid et al. (1994). *Alchemilla* spp. may include all spp. except *A. alpina* L. *Dryopteris expansa* agg. may include *D. expansa* (C.Presl.) Fraser-Jenkins & Jermy, *D. dilatata* (Hoffm.) A. Gray, and *D. carthusiana* (Vill.) Fuchs. *Hieracium* is classified to section.

Bryophytes follow Frisvoll et al. (1995). *Dicranum fuscescens* agg. may include *D. flexicaule* Brid. and *D. fuscescens* Sm. *Hypnum cupressiforme* agg. may include *H. andoi* A.J.E.Sm., *H. cupressiforme* Hedw., *H. jutlandicum* Holmen & Warncke and *H. resupinatum* Spruce. *Plagiothecium laetum* includes var. *secundum* (Lindb.) Frisv. et al. (= *P. curvifolium* Limpr.). *P. nemorale* includes *P. succulentum* (Wils.) Lindb. The genus *Polytrichastrum* G.L.Sm. is not recognized as distinct from *Polytrichum* Hedw. *Racomitrium canescens* agg. may include *R. canescens* (Hedw.) Brid. and *R. ericoides* (Brid.) Brid. *R. heterostichum* agg. may include *R. heterostichum* (Hedw.) Brid. and *R. affine* (Web. & Mohr) Lindb.

Rhytidiadelphus squarrosus agg. includes *R. squarrosus* (Hedw.) Warnst. and *R. subpinnatus* (Lindb.) T.Kop. *Schistidium apocarpum* agg. is in accordance with Corley et al. (1981). *Cephalozia lacinulata* Jack ex Spruce is reported as new to Norway. *Chiloscyphus coadunatus* refers to var. *rivularis* (Raddi) Frisvoll et al. (= *Lophocolea bidentata* (L.) Dum.). *Lophozia ventricosa* agg. includes *L. silvicola* Buch and *L. ventricosa* (Dicks.) Dum. and may also include *L. longiflora* (Nees) Schiffn.

Lichens follow Krog et al. (1994). *Cladonia arbuscula* agg. may include *C. arbuscula* (Wallr.) Flot. and *C. mitis* Sandst. *Cladonia chlorophaea* agg. may include *C. chlorophaea* (Flörke ex Sommerf.) Spreng., *C. cryptochlorophaea* Asah., *C. grayi* Merr. ex Sandst. *C. fimbriata* (L.) Fr., *C. merochlorophaea* Asah., and *C. pyxidata* (L.) Hoffm. *Cladonia coccifera* agg. may include *C. borealis* S.Stenroos, *C. coccifera* (L.) Willd. and *C. pleurota* (Flörke) Schaer. *Cladonia coniocraea* agg. may include *C. coniocraea* (Flörke) Spreng. and *C. ochrochlora* Flörke.

RESULTS

For strongly correlated variables (e.g. the two pH measurements, macro and meso plot values for inclination, aspect unfavourability and the heat index, the litter indices and the soil depth variables), attention is often paid to the variable in each pair which was most strongly related to ordination axes and/or other variables. For example, pH actually refers to pH_{CaCl2} for all reference areas except Paulen. The variable most strongly correlated in each case is not always specified in the text, but is evident from correlation tables.

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Correlations between environmental variables

Concentrations of P and the cations Ca, Mg, Mn and Zn were pairwise more or less strongly positively correlated (most $\tau > 0.5$; see Tab. 3, Fig. 13). The concentration of K was positively correlated with the concentrations of Ca, Mg and P, while the H^+ concentration was negatively correlated with the concentrations of all elements in this subgroup of correlated variables. Soil moisture, pH and the concentrations of Al, S, pH and total N made up another subgroup of more or less strongly positively correlated variables ($\tau > 0.6$ for pH with total N). The concentrations of Al and K were negatively correlated. These two subgroups of variables made up one group of correlated variables, as variables in one group were negatively correlated, often strongly, with variables in the other (Fig. 13). The litter indices were positively correlated with the concentration of Ca.

This large group of correlated variables was connected to another group of pairwise correlated topographic variables via macro plot basal area, which was negatively correlated with soil moisture and the concentration of S in the first group and the heat indices in the other. The heat indices were negatively correlated with aspect unfavourability as well as with inclination.

PCA ordination of environmental variables

Eigenvalues of the first two PCA axes were 0.353 and 0.156, thus 50.9% of the variation in measured environmental variables was explained by the first two PCA axes.

pH, Al, H^+, total N, S and soil moisture, i.e. the variables in the second subgroup of the large group of correlated variables, obtained high loadings on PCA 1 (Fig. 14), while Ca, Mg, Zn, Mn, and P; i.e. cations of the first subgroup of correlated variables, obtained low loadings on this axis. Aspect unfavourability and inclination (the group of topographic variables), and macro plot basal area, which was connected to this group, obtained high loadings on PCA 2, while low loadings were obtained by the heat indices.

The results of the PCA ordination were consistent with the correlations between variables (Tab. 3, Fig. 13).

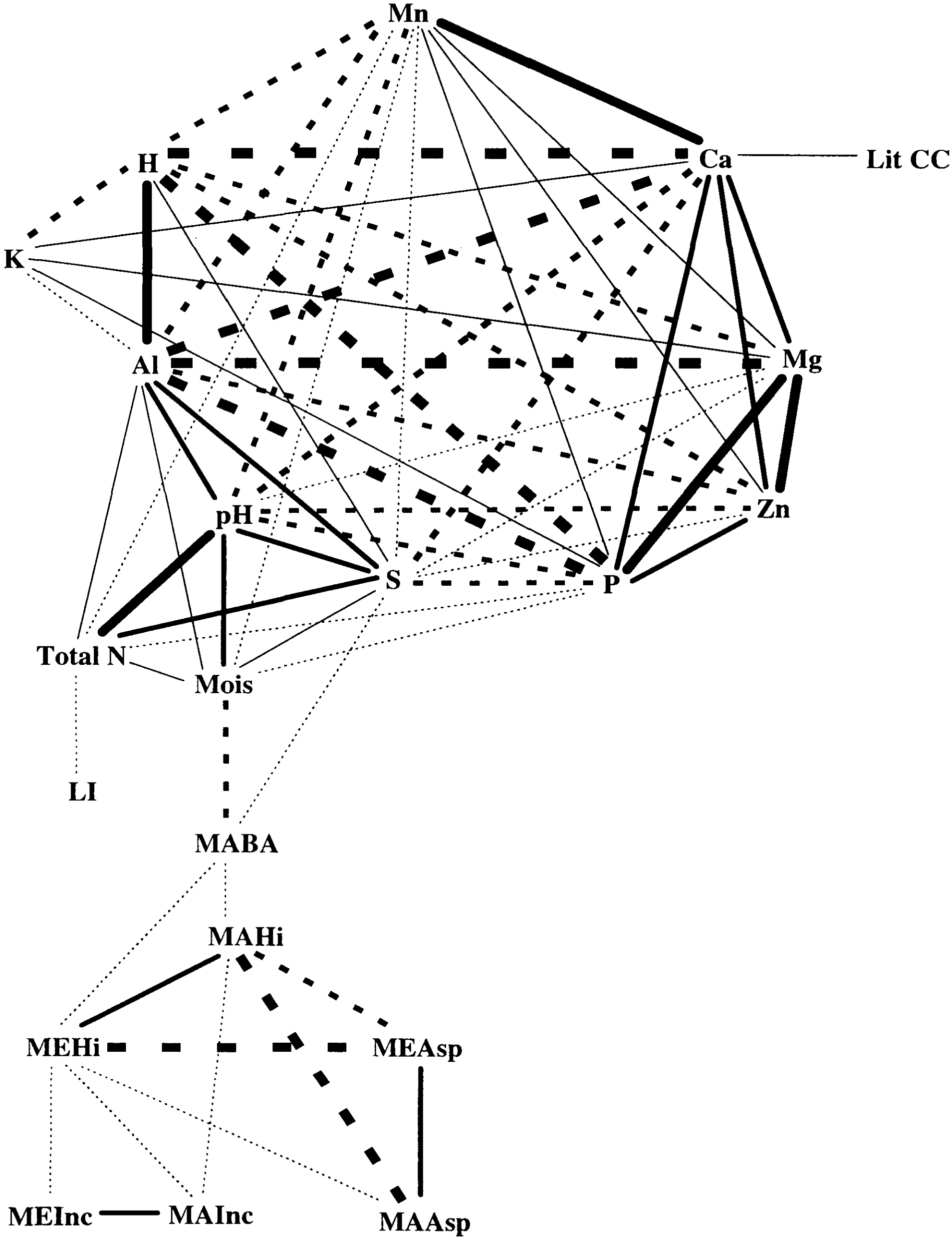


Fig. 13. Paulen: plexus diagram visualizing Kendall's τ between pairs of environmental variables. Significance probabilities for τ are indicated by lines with different thickness (in order of decreasing thickness): $|\tau| \geq 0.60$, $0.45 \leq |\tau| < 0.60$, $0.35 \leq |\tau| < 0.45$. Continuous lines refer to positive correlations, broken lines to negative.

Tab. 3. Paulen: Kendall's nonparametric correlation coefficient τ between 32 environmental variables in the 50 meso sample plots (lower triangle), with significance probabilities (upper triangle). Correlations significant at level P < 0.0001 in bold face. n.s. - significance probability > 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 2.

Variable	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
01 MA Inc	*	n.s.	**.0000**	n.s.	n.s.	**.0000**	.0370	.0006	n.s.	n.s.	n.s.	n.s.	.0490	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
02 MA Asp	.1379	*	**.0000**	n.s.	n.s.	n.s.	**.0000**	**.0000**	n.s.	n.s.	.0209	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0021	.0026	.0217	n.s.	.0113	.0010	n.s.	n.s.	.0089	n.s.	.0041	.0041	.0767
03 MA Hi	**-.4495**	**-.7047**	*	n.s.	n.s.	n.s.	**.0000**	**.0000**	n.s.	n.s.	.0321	n.s.	n.s.	n.s.	n.s.	.0009	n.s.	n.s.	n.s.	.0021	n.s.	.0173	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
04 MA BA	.1591	.1150	-.4045	*	n.s.	n.s.	.0023	.0005	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**.0000**	n.s.	.0021	.0023	n.s.	.0334	n.s.	n.s.	.0428	.0073	.0463	.0307	n.s.	.0027	.0108	.0053	.0001
05 MA Lig	-.0899	-.0682	-.0222	-.1348	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0593	.0034	.0018	n.s.	.0772	.0388	.0377	.0461	.0013	.0258	**.0000**	.0226	.0236	.0131	n.s.	.0426	.0137	.0006	.0028	n.s.
06 ME Inc	**.5333**	.0562	-.2589	.1305	.0200	*	n.s.	**.0000**	.0343	.0683	n.s.	.0351	.0350	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0900	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
07 ME Asp	.2141	**.4630**	**-.4937**	.3129	-.1474	.1605	*	**.0000**	n.s.	n.s.	.0515	n.s.	n.s.	n.s.	n.s.	.0041	n.s.	n.s.	n.s.	n.s.	n.s.	.0132	.0817	n.s.	n.s.	n.s.	n.s.	.0760	n.s.	n.s.	n.s.	n.s.
08 ME Hi	-.3500	**-.4300**	**.5618**	-.3552	.1083	**-.4280**	**-.7283**	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0026	n.s.	n.s.	n.s.	n.s.	n.s.	.0130	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
09 ME Rou	.1172	.0325	-.0669	-.0408	.0687	.2121	.0480	-.1029	*	n.s.	n.s.	n.s.	.0212	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0403	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
10 ME Con	-.1319	.1676	-.0403	-.0590	.1295	.,1825	.0984	.0313	-.0919	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
11 ME Smi	.1154	.2424	-.2213	.0819	-.0575	-.0137	.1949	-.1529	.0025	.1530	*	.0001	.0868	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0432	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0950	n.s.	n.s.	n.s.	n.s.
12 ME Sme	-.1255	.1243	-.0599	.0476	-.0702	-.2106	.0322	.0460	-.0942	.0487	.3984	*	**.0000**	n.s.	n.s.	.0706	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0238	n.s.	n.s.
13 ME Sma	-.2023	.0492	.0704	.0182	-.1923	-.2113	-.0240	.0708	-.2279	.0099	.1717	**.5942**	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0174	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
14 LitCC	-.0562	-.0787	.0564	-.0147	.2973	-.0126	-.0964	.1131	.1254	.0734	-.0260	-.0600	-.1064	*	**.0000**	.0669	.0364	.0331	n.s.	.0001	n.s.	.0139	.0019	.0016	.0071	n.s.	.0078	n.s.	.0047	.0464	.0437	n.s.
15 LitACD	-.0528	-.0998	-.0976	-.0563	.3167	-.0294	-.1139	.1502	.1132	.0892	-.0235	-.1203	-.1422	**.8729**	*	n.s.	n.s.	.0960	n.s.	.0008	n.s.	.0455	.0037	.0037	.0149	n.s.	.0473	n.s.	.0387	.0437	.0760	n.s.
16 Mois	-.1456	-.1133	.3358	**-.5972**	-.0256	-.1529	-.2818	.2942	.0872	-.0025	.0217	.0123	.0519	-.1794	-.1297	*	n.s.	**.0000**	**.0000**	.0027	.0078	n.s.	n.s.	.0013	.0002	n.s.	.0001	.0071	.0001	.0006	.0003	**.0000**
17 LI	-.0820	-.0909	-.0120	.1598	.1793	.0234	.0692	-.0893	.0322	.0313	.0996	.1776	.0148	.2052	.1472	-.1179	*	.0052	.0088	.0205	n.s.	.0694	.0315	.0084	.0007	.0118	.0645	n.s.	.0003	n.s.	.0027	.0006
18 pH_{H2O}	.0461	.1232	.0821	-.3312	-.2208	-.0930	-.0202	.0665	.0106	.0484	.1261	.0966	.1357	-.2201	.1722	**.4513**	-.2883	*	**.0000**	**.0000**	**.0000**	n.s.	.0383	.0007	**.0000**	n.s.	**.0000**	**.0000**	**.0000**	**.0000**	**.0000**	**.0000**
19 pH_{CaCl2}	.0139	.1602	.0687	-.3297	-.2225	-.1356	.0230	.0545	.0539	.0636	.1364	.1040	.1123	-.1575	-.1199	**.4363**	-.2710	**.8853**	*	.0001	**.0000**	n.s.	.0396	.0010	**.0000**	n.s.	**.0000**	**.0000**	**.0000**	**.0000**	**.0000**	**.0000**
20 Ca	-.0207	-.3163	.1593	.1378	.2019	.0468	-.0854	.0711	.1192	.0279	-.2012	-.1181	-.1168	.3815	.3273	-.2924	.2267	**-.4756**	-.4107	*	**.0000**	.0001	.0205	**.0000**	**.0000**	n.s.	**.0000**	**.0000**	.0009	**.0000**	**.0000**	**.0000**
21 Mg	.1464	-.3094	.0690	.2171	.3263	.1687	-.1561	.0842	-.0074	.0197	-.1227	-.1099	-.1102	.1408	.1386	-.2597	.1432	**-.4371**	**-.4949**	**.5657**	*	.0001	.0438	**.0000**	**.0000**	n.s.	.0001	**.0000**	.0009	**.0000**	**.0000**	**.0000**
22 K	-.1103	-.2362	.2411	-.0396	.2257	-.0885	-.2431	.2426	-.0123	.1397	-.0359	.0082	.0181	.2407	.1961	-.0735	.1776	-.1661	-.1281	.3894	.3731	*	n.s.	**.0000**	**.0000**	n.s.	.0006	.0025	.0290	.0002	**.0000**	n.s.
23 Na	-.0551	-.1386	.0809	-.0982	**.5017**	-.0635	-.1708	.1381	.2015	.0625	-.0676	-.0886	-.2337	.3045	.2847	-.0229	.2103	-.2133	-.2124	.2261	.1967	.1543	*	n.s.	.0864	.0358	n.s.	n.s.	.0224	n.s.	.0544	n.s.
24 H^+	.0293	.2606	-.1133	-.2068	-.2308	.0384	.1298	-.1430	.0271	-.1184	.1094	.0131	.0280	-.3095	-.2847	.3136	-.2578	.3497	.3387	**-.6555**	**-.5935**	**-.5380**	-.1167	*	**.0000**	n.s.	**.0000**	**.0000**	.0010	**.0000**	**.0000**	**.0000**
25 Al	-.0327	.3390	-.0911	-.2739	-.2291	.0418	.0904	-.0594	-.0436	-.0033	.1244	.0476	.0839	-.2636	-.2387	.3642	-.3314	**.5438**	**.5441**	**-.6996**	**-.6180**	**-.4024**	-.1673	**.7208**	*	.0695	**.0000**	**.0000**	.0001	**.0000**	**.0000**	**.0000**
26 Fe	-.0982	.0444	.0622	-.2033	.2513	.0334	-.0953	.0760	-.0189	.0362	-.1545	-.1492	-.1234	.0458	.0451	.0800	-.2463	-.1521	-.1597	-.0302	.0482	.0286	.2049	.1527	.1771	*	n.s.	n.s.	n.s.	n.s.	n.s.	.0895
27 Mn	-.0276	-.1176	-.0043	.2205	.0349	.0635	.1035	-.0874	.0913	.0296	-.1411	-.1115	-.1234	.2603	.1944	-.3708	.1809	**-.5211**	**-.4440**	**.6408**	.3829	.3339	.0857	**-.4857**	**-.5200**	.0482	*	**.0000**	.0001	.0002	**.0000**	**.0000**
28 Zn	-.0637	-.2693	.1627	.1275	.2053	.0150	-.1741	.1528	-.0831	.0510	-.1662	-.1296	-.0740	.1523	.1567	-.2630	.0499	**-.4861**	**-.4598**	**.5657**	**.6016**	.2947	.1053	**-.5216**	**-.5690**	.0351	**.4449**	*	.0171	**.0000**	**.0000**	.0002
29 Total N	-.0190	.1176	.0894	-.3067	-.2496	-.1119	-.0690	.0989	.0025	-.0279	.0643	.0131	.1020	-.2767	-.2026	.3855	-.3576	**.6225**	**.6083**	-.3241	-.3241	-.2131	-.2229	.3224	.3927	-.1167	-.3829	-.2327	*	.0012	**.0000**	**.0000**
30 P-AL	.0845	-.2957	.0639	.2604	.3487	.1521	-.0970	.0564	.0288	-.0082	-.1429	-.2216	-.1581	.1950	.1979	-.3367	.0876	**-.4489**	**-.4523**	**.5319**	**.7034**	.3652	.1544	**-.5531**	**-.6005**	.0760	.3685	**.5858**	-.3162	*	**.0000**	**.0000**
31 P	.0293	-.2855	.0588	.2844	.3025	.0944	-.1257	.0490	.0000	.0156	-.1554	.-.1206	-.1325	.1974	.1740	-.3505	.2931	**-.5379**	**-.5645**	**.5635**	**.6909**	**.4263**	.1878	**-.6648**	**-.7644**	-.0915	**.4165**	**.5733**	**-.3985**	**.6751**	*	**.0000**
32 S	-.0844	.1821	.0469	-.4118	-.0673	-.1620	-.1002	.1266	.0238	.0263	.0443	.0197	.0346	-.1506	-.1042	**.4296**	-.3347	**.5211**	**.5494**	**-.4661**	**-.4367**	-.1592	.0041	**.4416**	**.5673**	.1657	**-.4041**	-.3682	**.4759**	**-.4273**	**-.5178**	*

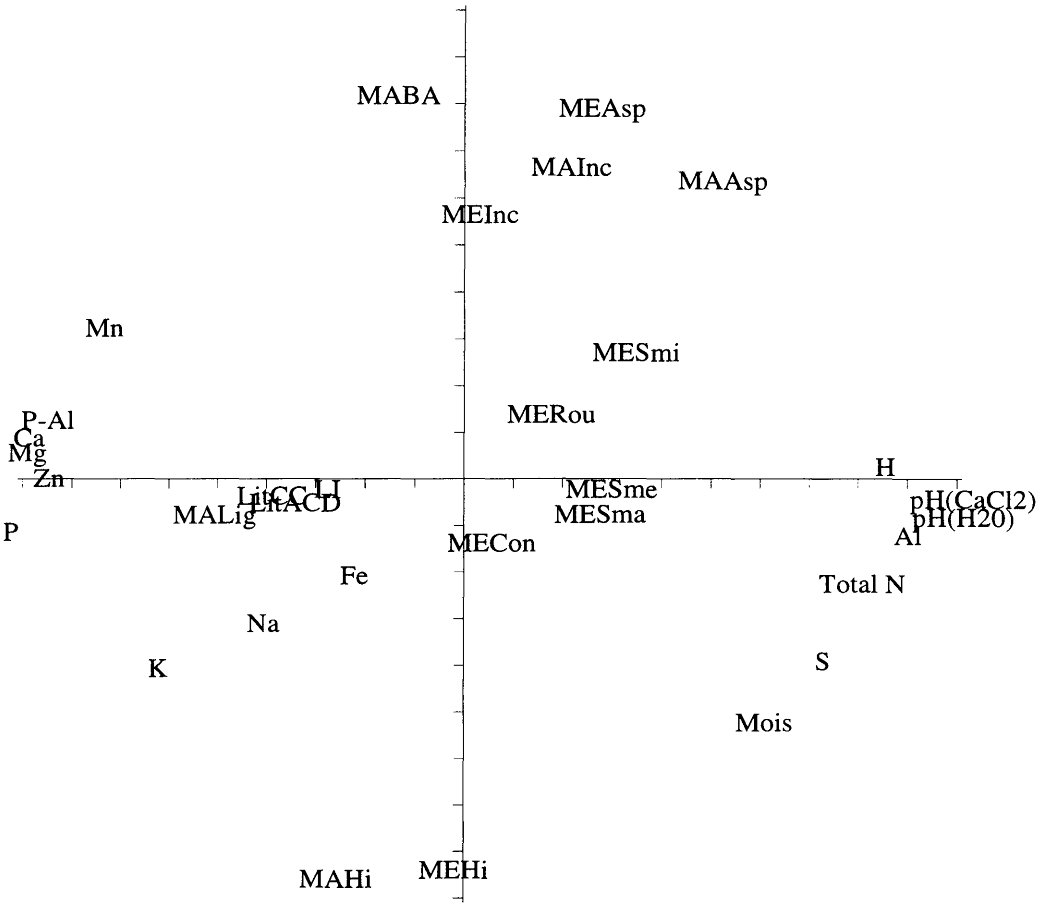


Fig. 14. Paulen: PCA ordination of 32 environmental variables (names abbreviated in accordance with Tab. 2), axes 1 (horizontal) and 2 (vertical). Positions of variables in the ordination give the head of variable vectors.

DCA and LNMDS ordination

Plot No. 8 was an outlier along DCA 1, separated from the other plots by ca. 0.9 S.D. units along the axis (Fig. 15). This plot, which contained 11 species (area average was 17.4), was removed prior to further analysis. The plots were relatively evenly distributed along the axes of both DCA (Fig. 16) and LNMDS (Fig. 17) ordinations of the 49 remaining meso plots, although with highest density of plots near the centroids. Gradient lengths for LNMDS 1 and DCA 1 were approximately the same, but LNMDS 2 was shorter than DCA 2 (2.0 and 2.7 S.D., respectively).

DCA 1 explained 15.1% of the variation in the vegetation. The fraction of variation explained by DCA 2 was ca. 52% of that for DCA 1 (Tab. 4), declining less strongly for subsequent axes. The eigenvalues of DCA 3 and DCA 4 were low (0.112 and 0.085, respectively), corresponding to explained fractions of variation below 5%.

Tab. 4. Paulen: Eigenvalues and the fraction of variation explained for DCA axes 1-4.

	DCA 1	DCA 2	DCA 3	DCA 4
Eigenvalues	0.337	0.177	0.112	0.085
Fraction of variation explained	0.151	0.079	0.050	0.038

Correlations between DCA and LNMDS ordination axes and between ordination axes and environmental variables

The correlations between DCA 1 and LNMDS 1 and between DCA 2 and LNMDS 2 were both strong (τ = 0.660 and τ = 0.543, respectively, Tab. 5). The variables correlated with DCA 1 and LNMDS 1 were mostly the same. Correlation coefficients for the most strongly correlated variables were generally slightly higher for LNMDS 1 than for DCA 1. Most of the variables correlated with DCA 2 were also correlated with LNMDS 2, but less strongly.

The variables most strongly correlated with DCA 1 were concentrations of Ca (Fig. 25), Mn (Fig. 30), Zn (Fig. 31) and P (Figs 33-34) with negative correlations, and pH (Fig. 24) and concentrations of H^+ (Fig. 28) and Al (Fig. 29), which were positively correlated. Other correlated variables were the litter index (Fig. 22) and concentrations of Mg (Fig. 26) and K (Fig. 27), negatively correlated with the axis, and soil moisture (Fig. 23), pH (Fig. 24) and

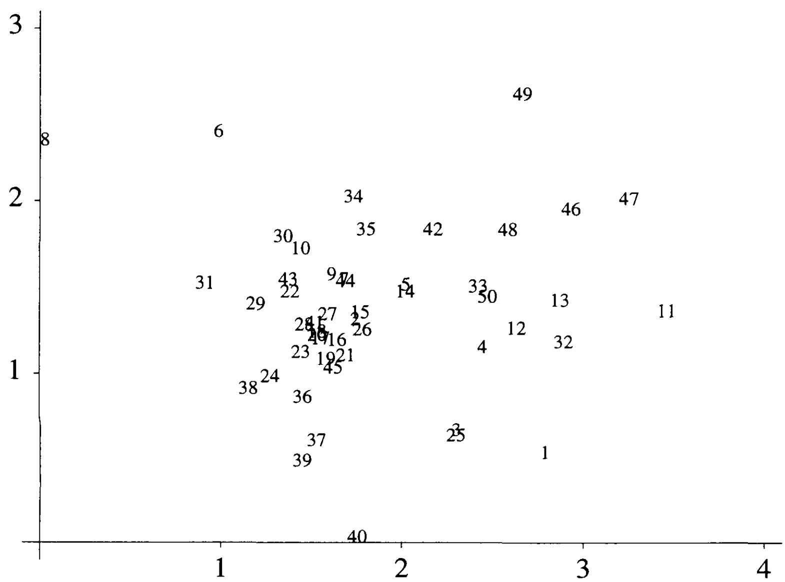
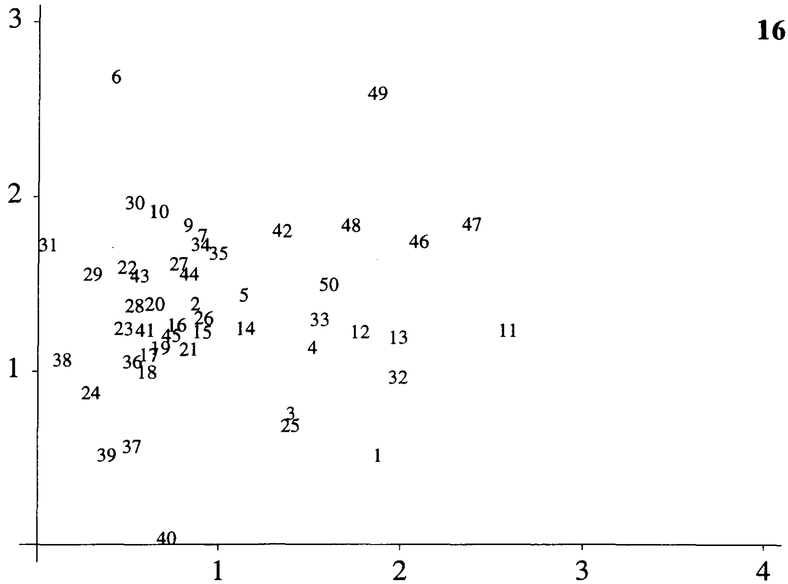
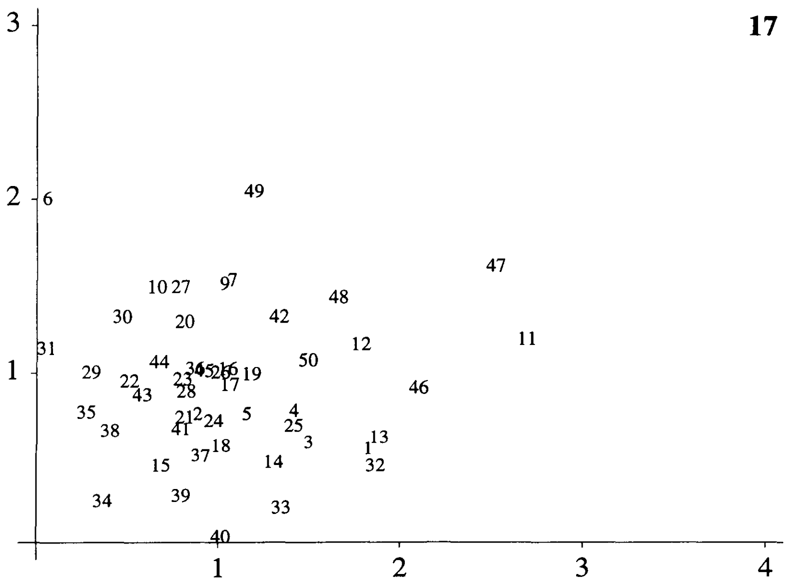


Fig. 15. Paulen: DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Meso plot numbers are plotted onto the sample plot positions. Scaling of axes in S.D. units.





Figs 16-17. Paulen: ordinations of 49 meso plots (plot No. 8 omitted), axes 1 (horizontal) and 2 (vertical). Meso plot numbers are plotted onto the sample plot positions. Fig. 16. DCA ordination. Scaling of axes in S.D. units. Fig. 17. LNMDS ordination. Axes linearly rescaled in S.D. units.

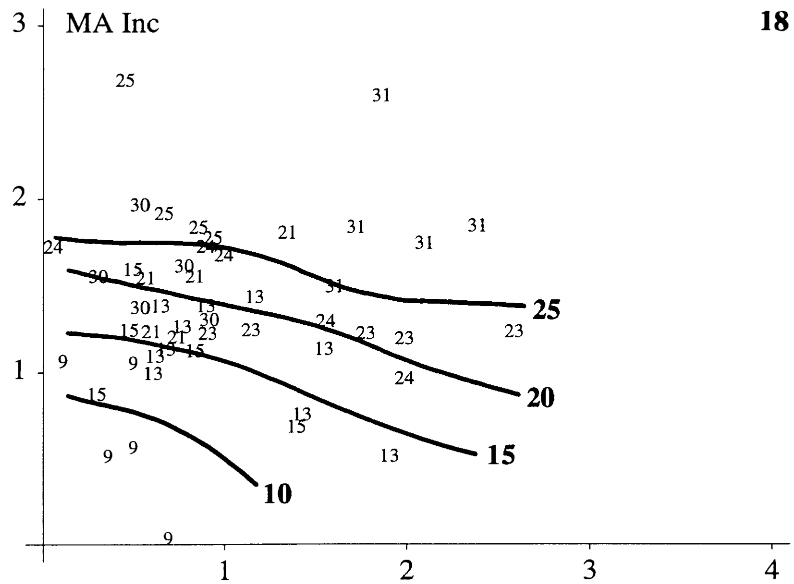
Tab. 5. Paulen: Kendall's nonparametric correlation coefficient τ between DCA and LNMDS axes, and between 32 environmental variables in the 49 meso sample plots and sample plot positions with respect to DCA and LNMDS axes, and their significance probabilities. Correlations significant at level P < 0.0001 in bold face. n.s. - significance probability > 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 2.

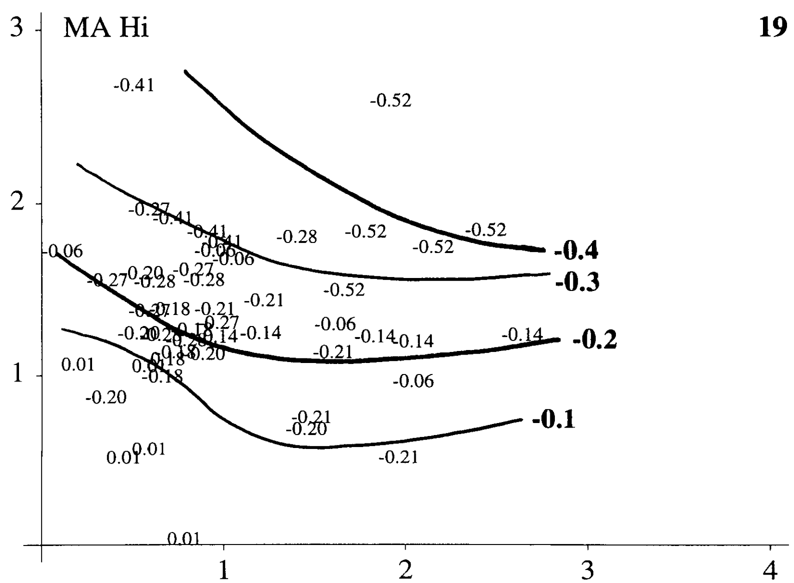
Variable	DCA 1		DCA 2		DCA 3		DCA 4		LNMDS 1		LNMDS 2	
	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P
LNMDS 1	**.6604**	**.0000**	-.1731	.0801	.1466	n.s.	.1256	n.s.				
LNMDS 2	.0315	n.s.	**.5433**	**.0000**	.2830	.0042	-.2862	.0039				
01 MA Inc	.2438	.0184	**.5754**	**.0000**	-.1089	n.s.	-.2030	n.s.	.0404	n.s.	.3564	.0006
02 MA Asp	.2425	.0198	.2600	.0126	.3190	.0022	-.0018	n.s.	.2728	.0086	.3308	.0015
03 MA Hi	-.1583	n.s.	**-.4566**	**.0000**	-.1708	.0959	.0615	n.s.	-.0834	n.s.	**-.4880**	**.0000**
04 MA BA	-.2042	.0482	.2071	.0453	.2403	.0201	.0235	n.s.	-.1787	.0834	.3421	.0009
05 MA Lig	-.1423	n.s.	.0578	n.s.	-.2349	.0220	-.3236	.0016	-.2697	.0084	-.0674	n.s.
06 ME Inc	.1501	n.s.	**.4839**	**.0000**	-.1563	n.s.	-.1085	n.s.	-.0810	n.s.	.2395	.0173
07 ME Asp	.0892	n.s.	.2249	.0238	.1999	.0444	.0843	n.s.	.1241	n.s.	.2884	.0037
08 ME Hi	-.1339	n.s.	-.3474	.0004	-.1229	n.s.	-.0009	n.s.	-.1157	n.s.	-.3404	.0006
09 ME Rou	.0240	n.s.	.1220	n.s.	-.2860	.0041	.0516	n.s.	-.1499	n.s.	-.1122	n.s.
10 ME Con	.0009	n.s.	-.0893	n.s.	.1039	n.s.	-.0086	n.s.	.0557	n.s.	-.0420	n.s.
11 ME Smi	.1681	.0952	.0636	n.s.	.2213	.0281	-.0183	n.s.	.2225	.0269	.2277	.0235
12 ME Sme	.0137	n.s.	-.0960	n.s.	.2441	.0140	.0000	n.s.	.1529	n.s.	.0743	n.s.
13 ME Sma	-.0524	n.s.	-.1427	n.s.	.1770	.0755	.0852	n.s.	.1165	n.s.	.0127	n.s.
14 LitCC	-.3043	.0021	.0479	n.s.	-.0060	n.s.	-.2108	.0338	-.3812	.0001	.0691	n.s.
15 LitACD	-.2424	.0146	.0343	n.s.	-.0206	n.s.	-.1949	.0501	-.3419	.0006	.0444	n.s.
16 Mois	.3332	.0007	-.3045	.0021	-.1995	.0436	.1153	.2443	.3503	.0004	-.3724	.0002
17 LI	-.1247	n.s.	-.0752	n.s.	.0231	n.s.	-.2791	.0049	-.1491	n.s.	.0605	n.s.
18 pH_{H2O}	**.4801**	**.0000**	-.1659	n.s.	.0565	n.s.	.1982	.0577	**.5372**	**.0000**	-.1264	n.s.
19 pH_{CaCl2}	.3810	.0003	-.1683	n.s.	.1042	n.s.	.1740	.0962	**.4841**	**.0000**	-.0775	n.s.
20 Ca	**-.5479**	**.0000**	.0571	n.s.	.0205	n.s.	-.1512	n.s.	**-.5918**	**.0000**	-.0527	n.s.
21 Mg	-.3690	.0002	.1458	n.s.	-.1125	n.s.	-.1051	n.s.	**-.4898**	**.0000**	-.0527	n.s.
22 K	-.3928	.0001	-.0537	n.s.	-.0085	n.s.	-.2264	.0223	-.3367	.0006	-.0595	n.s.
23 Na	-.1474	n.s.	-.0333	n.s.	-.3001	.0024	-.2760	.0053	-.2398	.0151	-.1224	n.s.
24 H^+	**.4764**	**.0000**	-.0299	n.s.	-.0546	n.s.	.1529	n.s.	**.4898**	**.0000**	.0017	n.s.
25 Al	**.5190**	**.0000**	-.0640	n.s.	.0341	n.s.	.1974	.0464	**.5544**	**.0000**	-.0119	n.s.
26 Fe	-.0605	n.s.	.0094	n.s.	-.1500	n.s.	.0812	n.s.	-.0867	n.s.	-.1667	.0911
27 Mn	**-.4985**	**.0000**	.0988	n.s.	.0801	n.s.	-.0931	n.s.	**-.4983**	**.0000**	.0204	n.s.
28 Zn	**-.4746**	**.0000**	.0162	n.s.	.0119	n.s.	-.1205	n.s.	**-.4762**	**.0000**	-.0289	n.s.
29 Total N	.3213	.0012	-.1254	n.s.	.1279	n.s.	.2144	.0304	.3656	.0002	-.1190	n.s.
30 P-AL	**-.4870**	**.0000**	.1340	n.s.	-.1007	n.s.	-.0778	n.s.	**-.5821**	**.0000**	.0000	n.s.
31 P	**-.4365**	**.0000**	.0802	n.s.	-.0810	n.s.	-.1470	n.s.	**-.5028**	**.0000**	-.0026	n.s.
32 S	.3059	.0020	-.1731	.0801	-.0818	n.s.	.0795	n.s.	**.4116**	**.0000**	-.1616	n.s.

concentrations of total N (Fig. 32) and S (Fig. 35), all positively correlated with DCA 1.

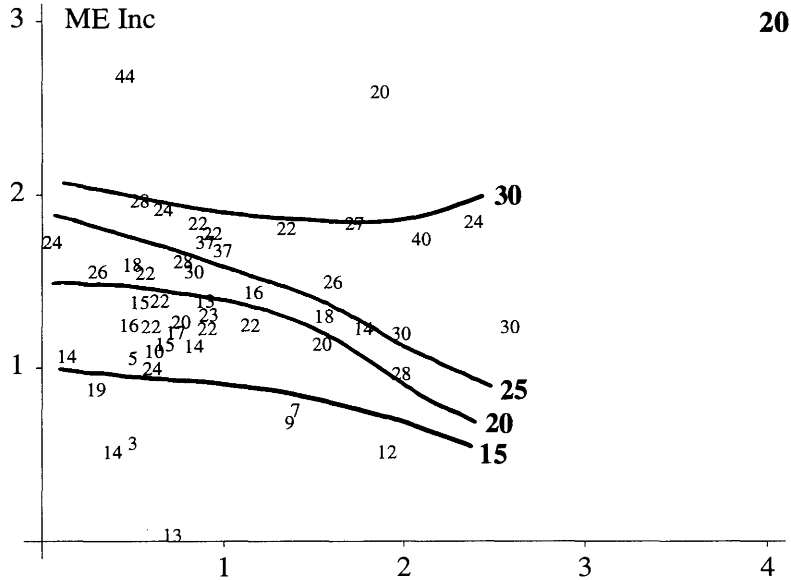
Inclination (Figs 18 and 20) was most strongly correlated with DCA 2 (positive correlations). Strong correlations were observed also for the heat indices (Figs 19 and 21, negative correlations). Soil moisture was also correlated with DCA 2 at P < 0.0025.

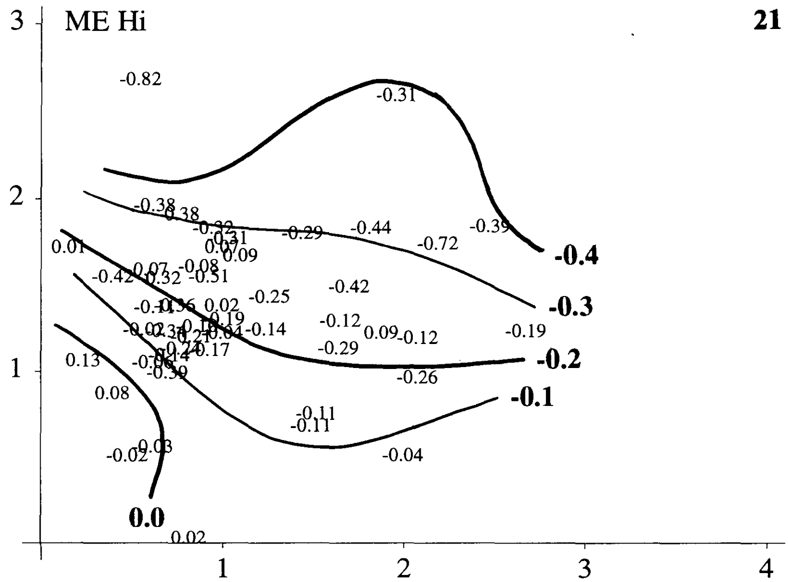
No variables were correlated with DCA 3 or DCA 4 at P < 0.001.



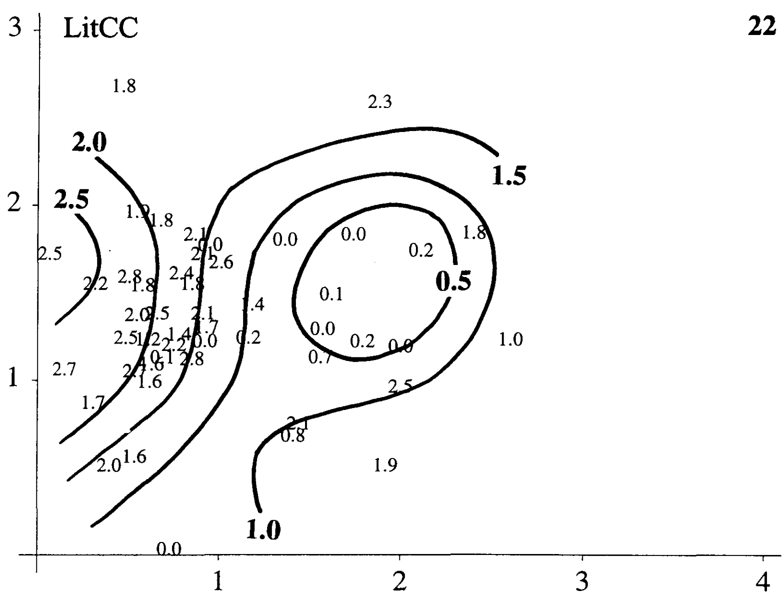


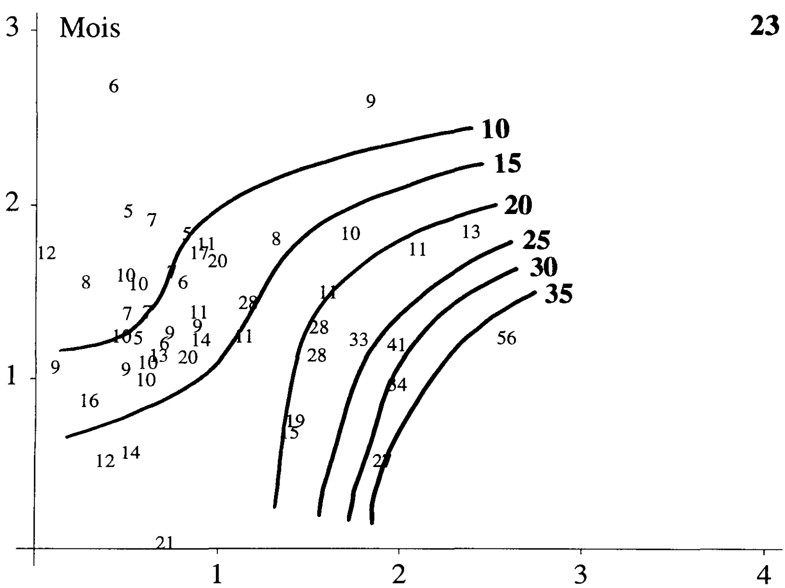
Figs 18-19. Paulen: isolines for environmental variables in the DCA ordination of 49 meso plots (plot No. 8 omitted), axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots' positions. Scaling of axes in S.D. units. Fig. 18. MA Inc (R^2 = 0.634). Fig. 19. MA Hi (R^2 = 0.572). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.



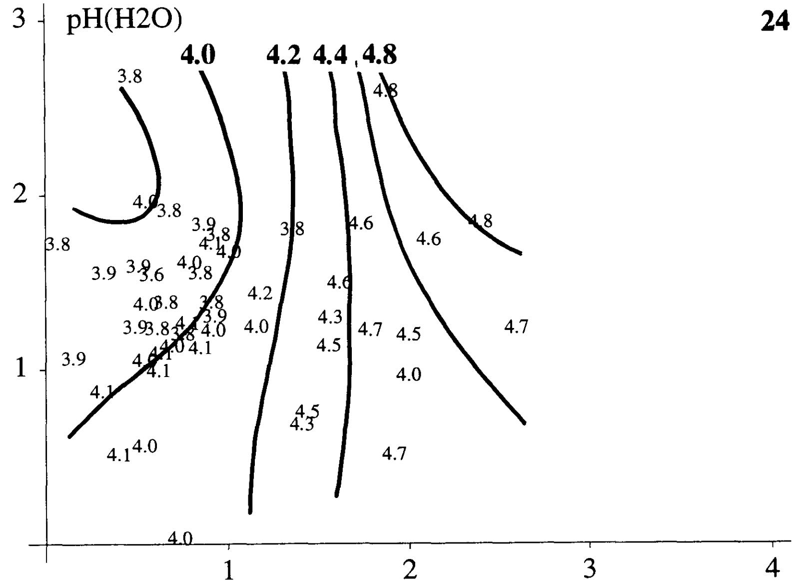


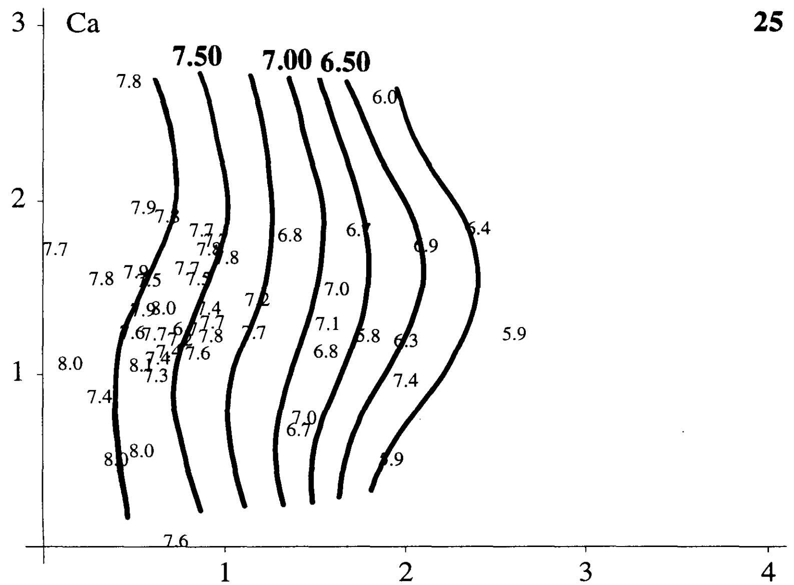
Figs 20-21. Paulen: isolines for environmental variables in the DCA ordination of 49 meso plots (plot No. 8 omitted), axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 20. ME Inc (R^2 = 0.630). Fig. 21. ME Hi (R^2 = 0.448). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.



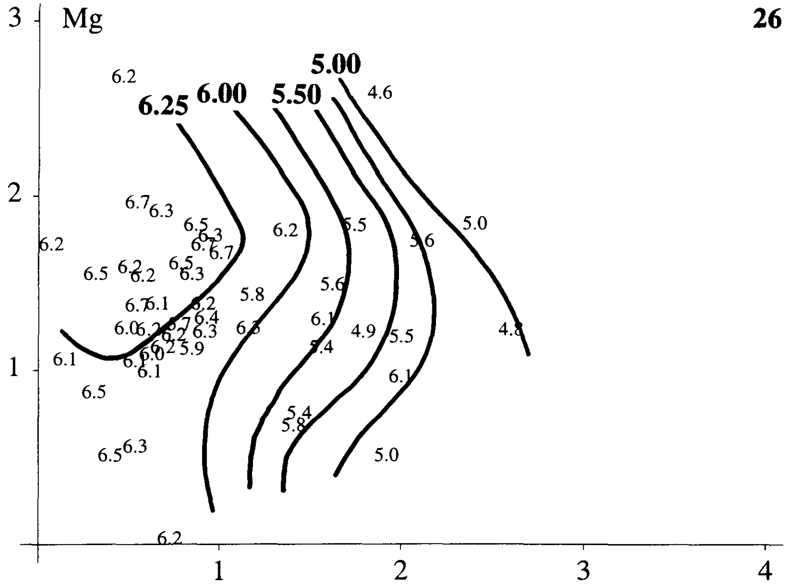


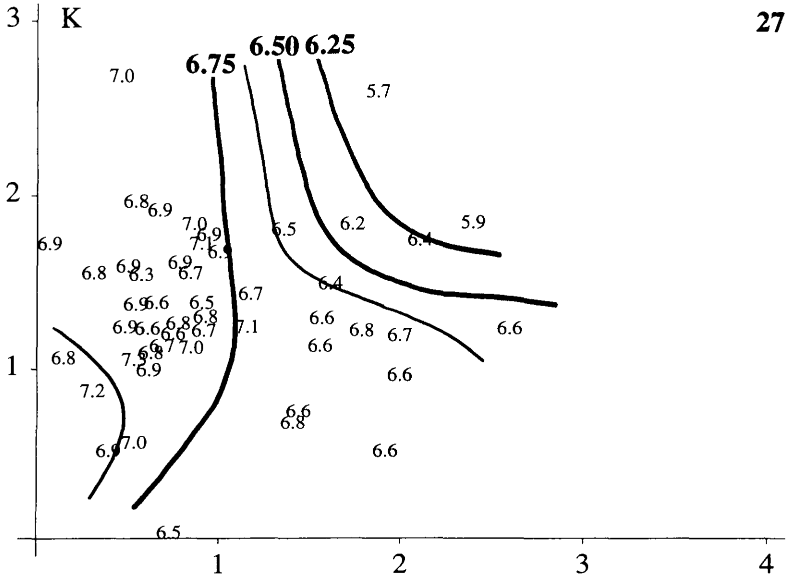
Figs 22-23. Paulen: isolines for environmental variables in the DCA ordination of 49 meso plots (plot No. 8 omitted), axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 22. Lit CC (R^2 = 0.480). Fig. 23. Mois (R^2 = 0.709). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.





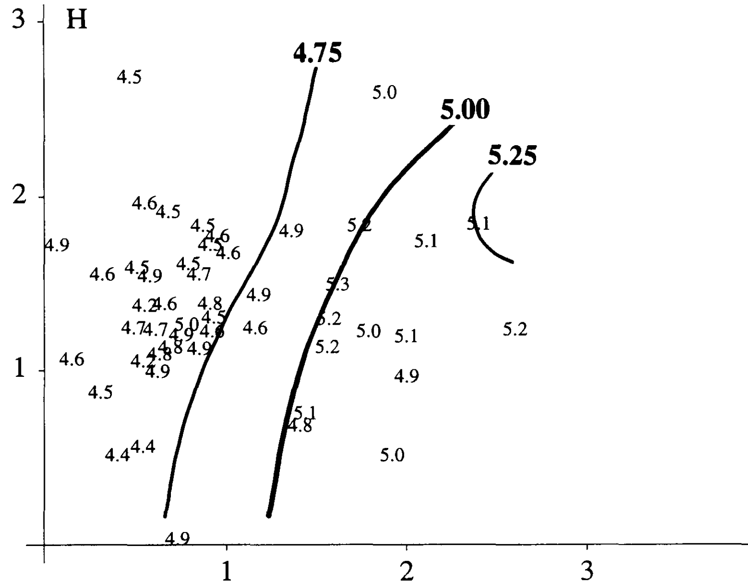
Figs 24-25. Paulen: isolines for environmental variables in the DCA ordination of 49 meso plots (plot No. 8 omitted), axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 24. pH_{H2O} (R^2 = 0.770). Fig. 25. Ca (R^2 = 0.738). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.



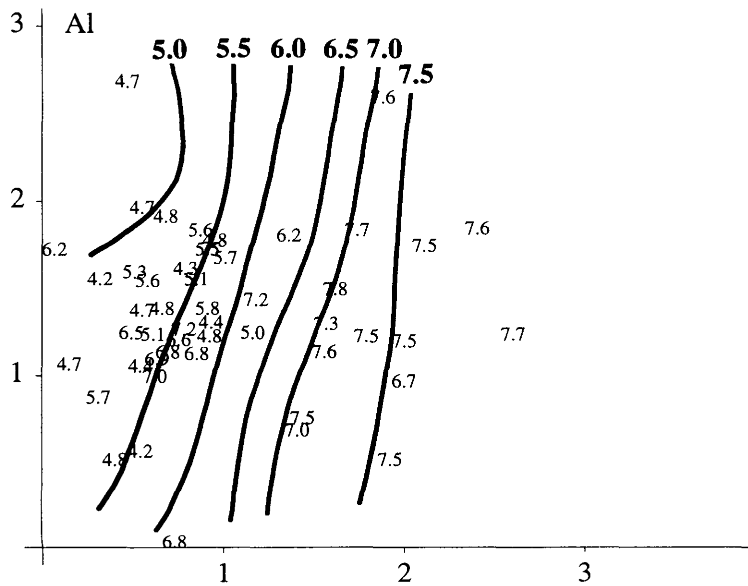


Figs 26-27. Paulen: isolines for environmental variables in the DCA ordination of 49 meso plots (plot No. 8 omitted), axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 26. Mg (R^2 = 0.742). Fig. 27. K (R^2 = 0.647). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.

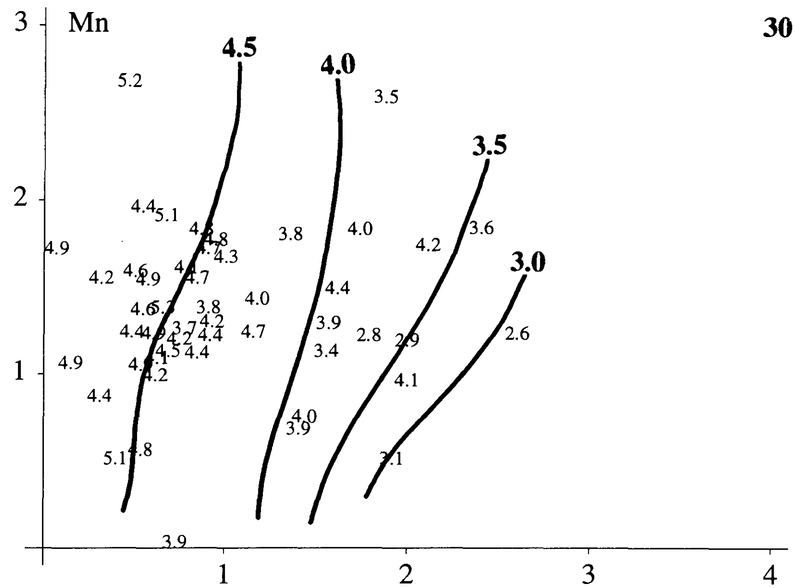
28

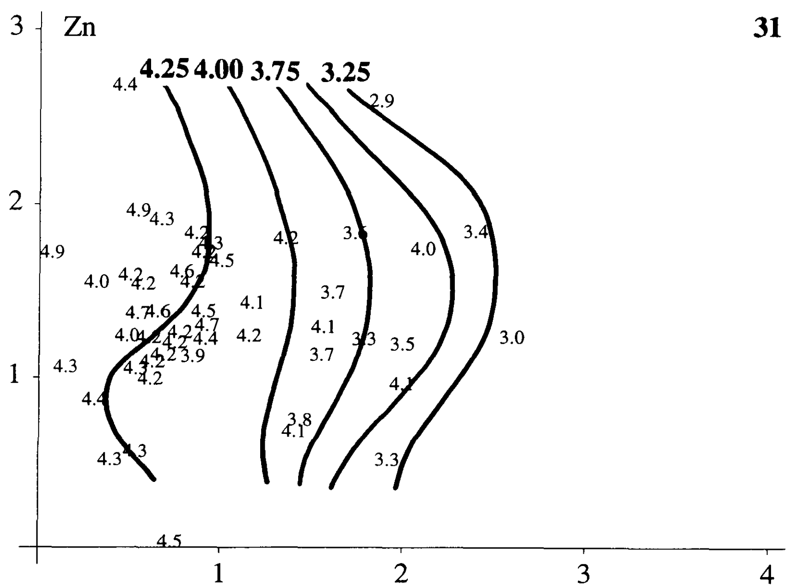


29



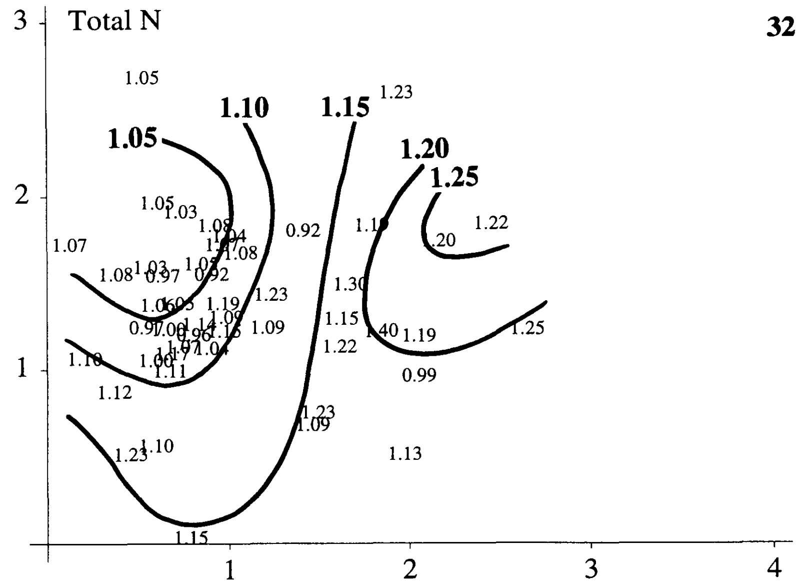
Figs 28-29. Paulen: isolines for environmental variables in the DCA ordination of 49 meso plots (plot No. 8 omitted), axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 28. (R^2 = 0.596). Fig. 29. Al (R^2 = 0.600). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.



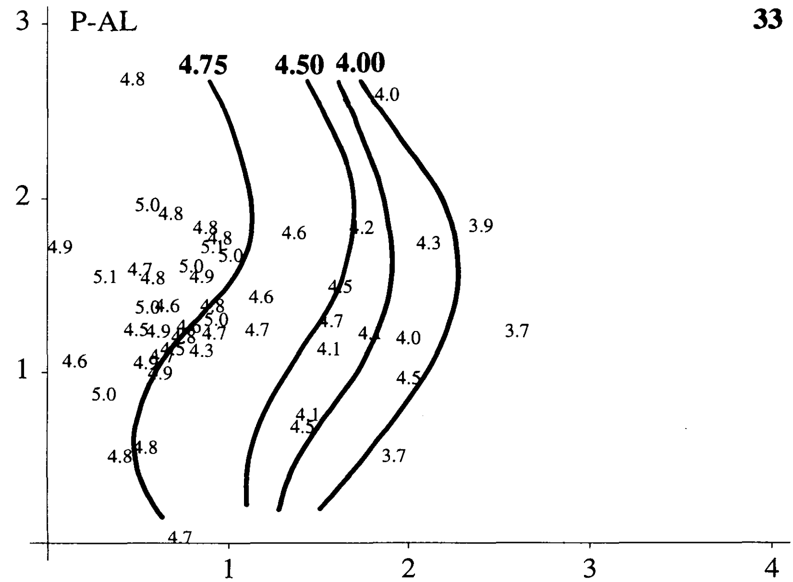


Figs 30-31. Paulen: isolines for environmental variables in the DCA ordination of 49 meso plots (plot No. 8 omitted), axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots' positions. Scaling of axes in S.D. units. Fig. 30. Mn (R^2 = 0.618). Fig. 31. (R^2 = 0.725). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.

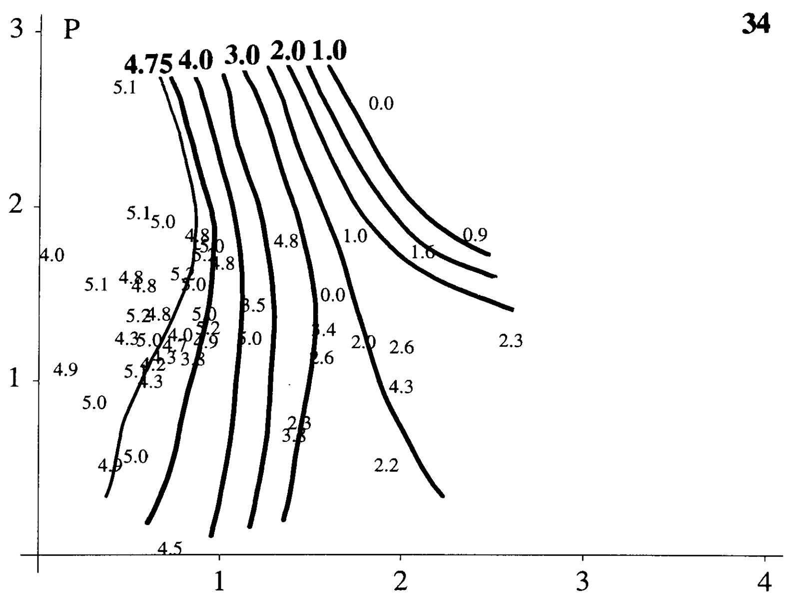
32

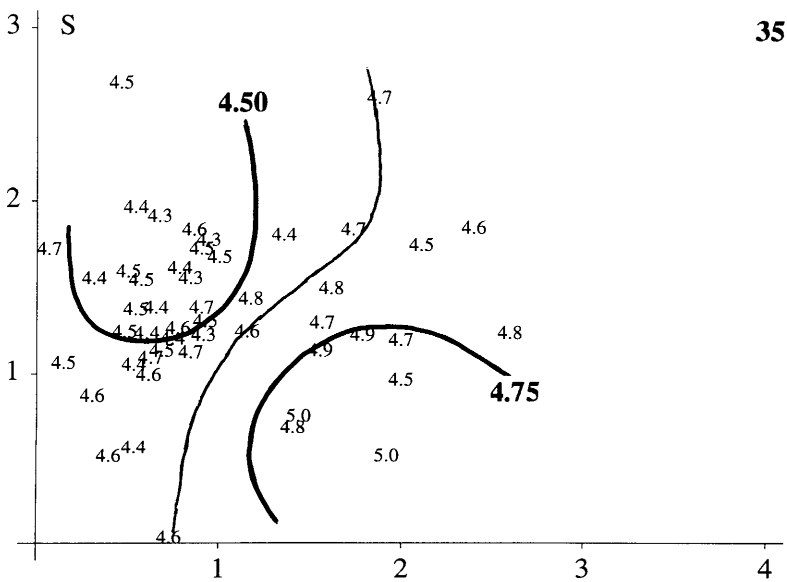


33

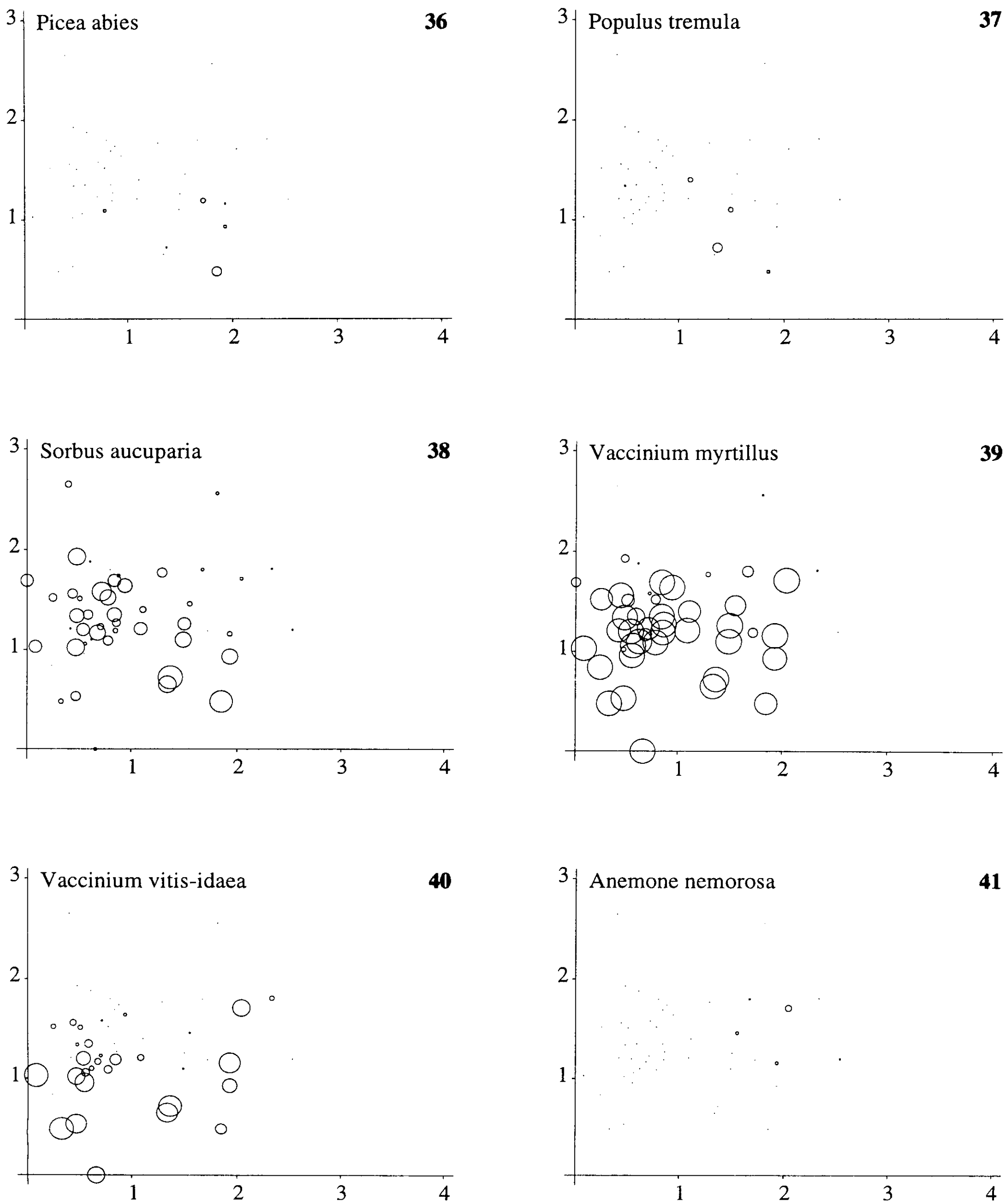


Figs 32-33. Paulen: isolines for environmental variables in the DCA ordination of 49 meso plots (plot No. 8 omitted), axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots' positions. Scaling of axes in S.D. units. Fig. 32. Total N (R^2 = 0.424). Fig. 33. P-AL (R^2 = 0.767). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.

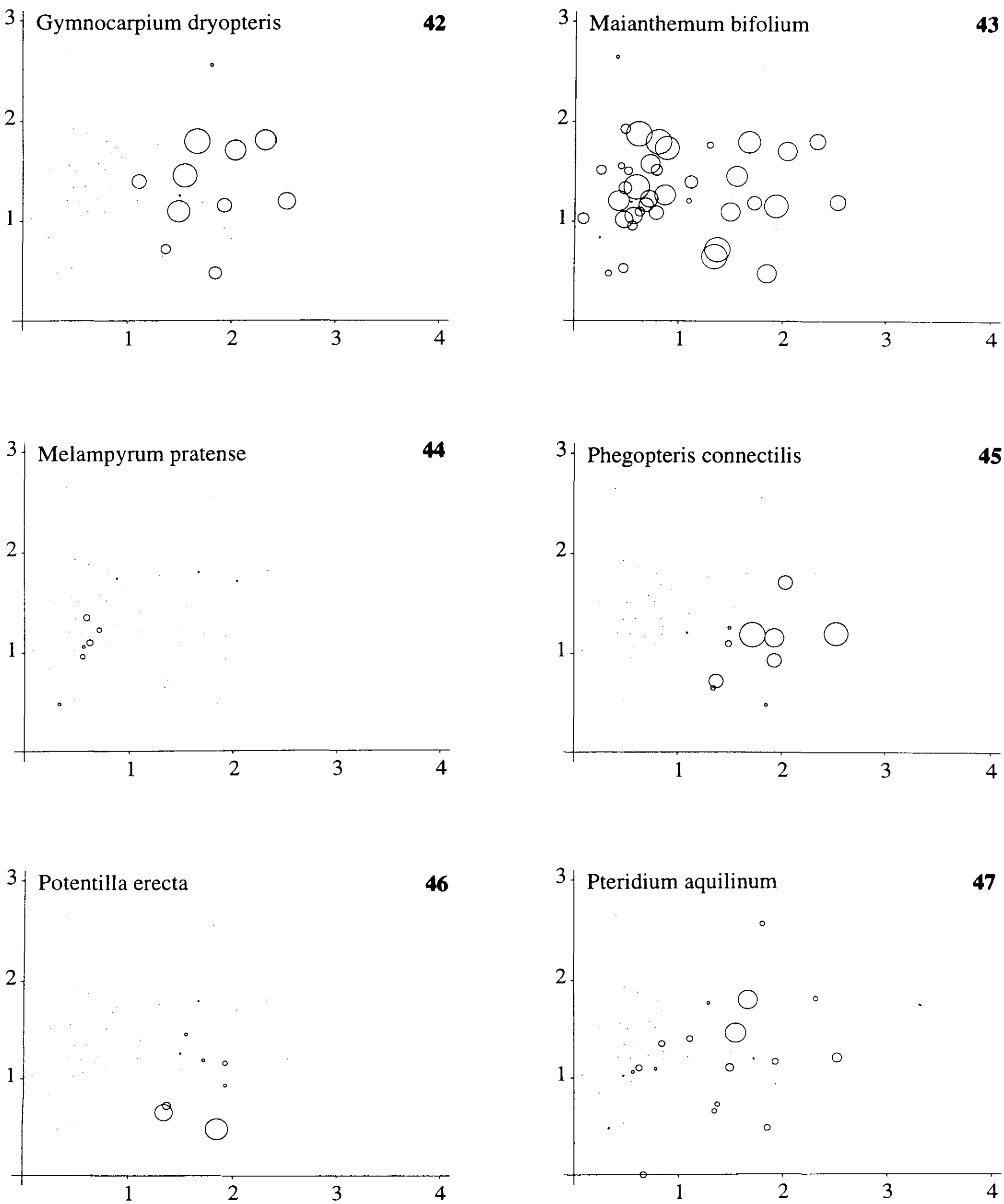




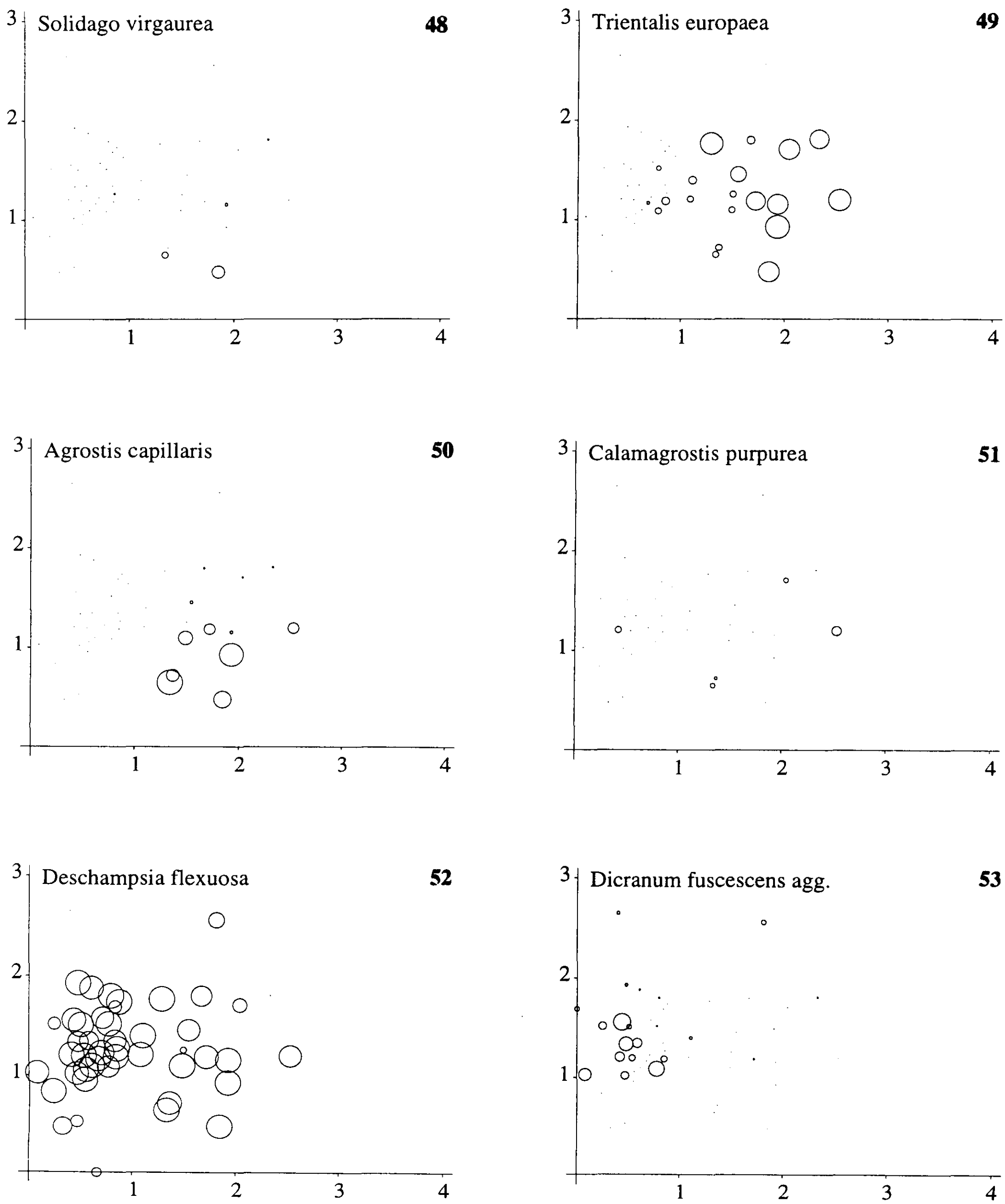
Figs 34-35. Paulen: isolines for environmental variables in the DCA ordination of 49 meso plots (plot No. 8 omitted), axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. P. (R^2 = 0.781). Fig. 35. (R^2 = 0.546). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.



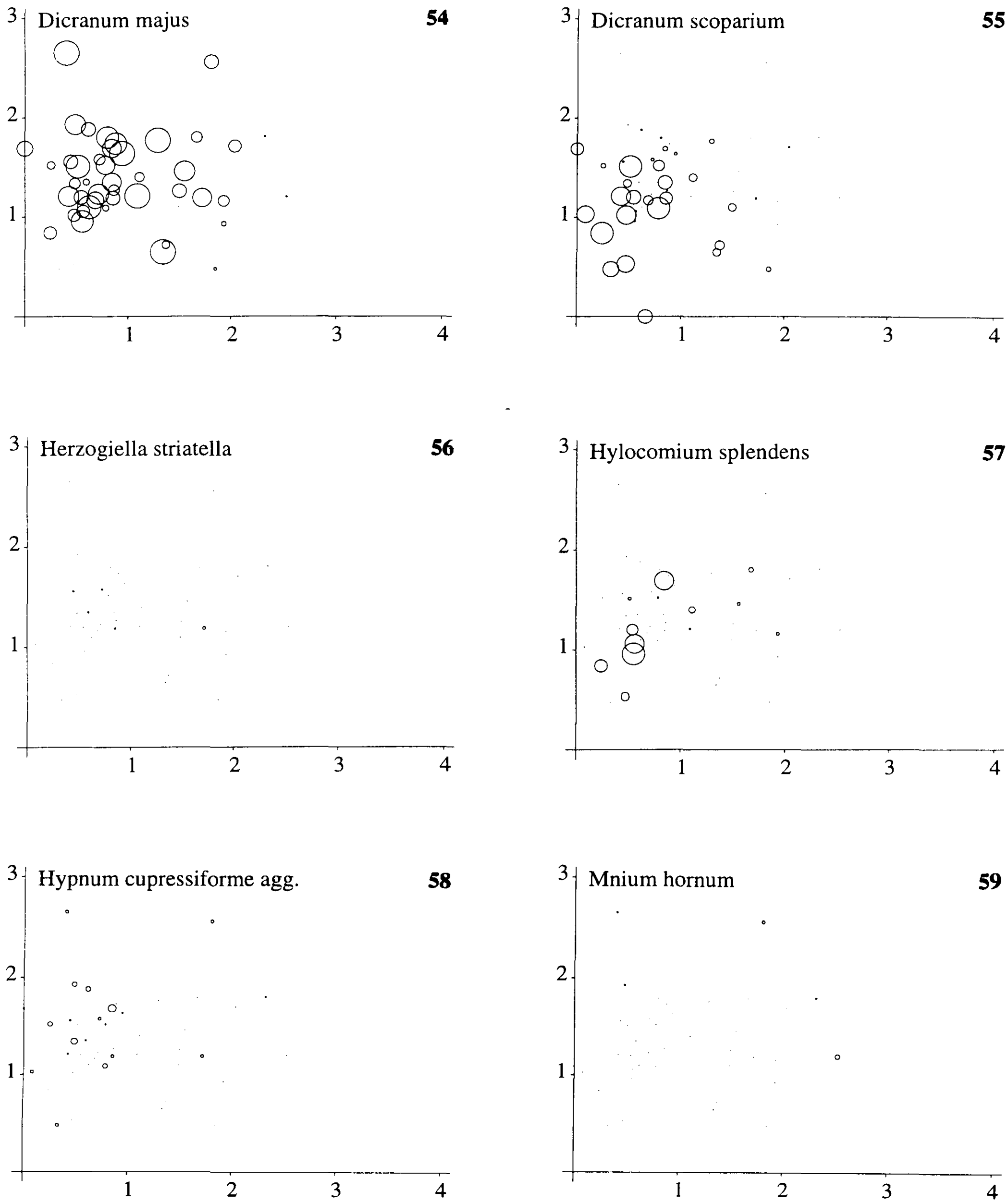
Figs 36-41. Paulen: distributions of species abundances in the DCA ordination of 49 meso plots (plot No. 8 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 36. *Picea abies*. Fig. 37. *Populus tremula*. Fig. 38. *Sorbus aucuparia*. Fig. 39. *Vaccinium myrtillus*. Fig. 40. *Vaccinium vitis-idaea*. Fig. 41. *Anemone nemorosa*.



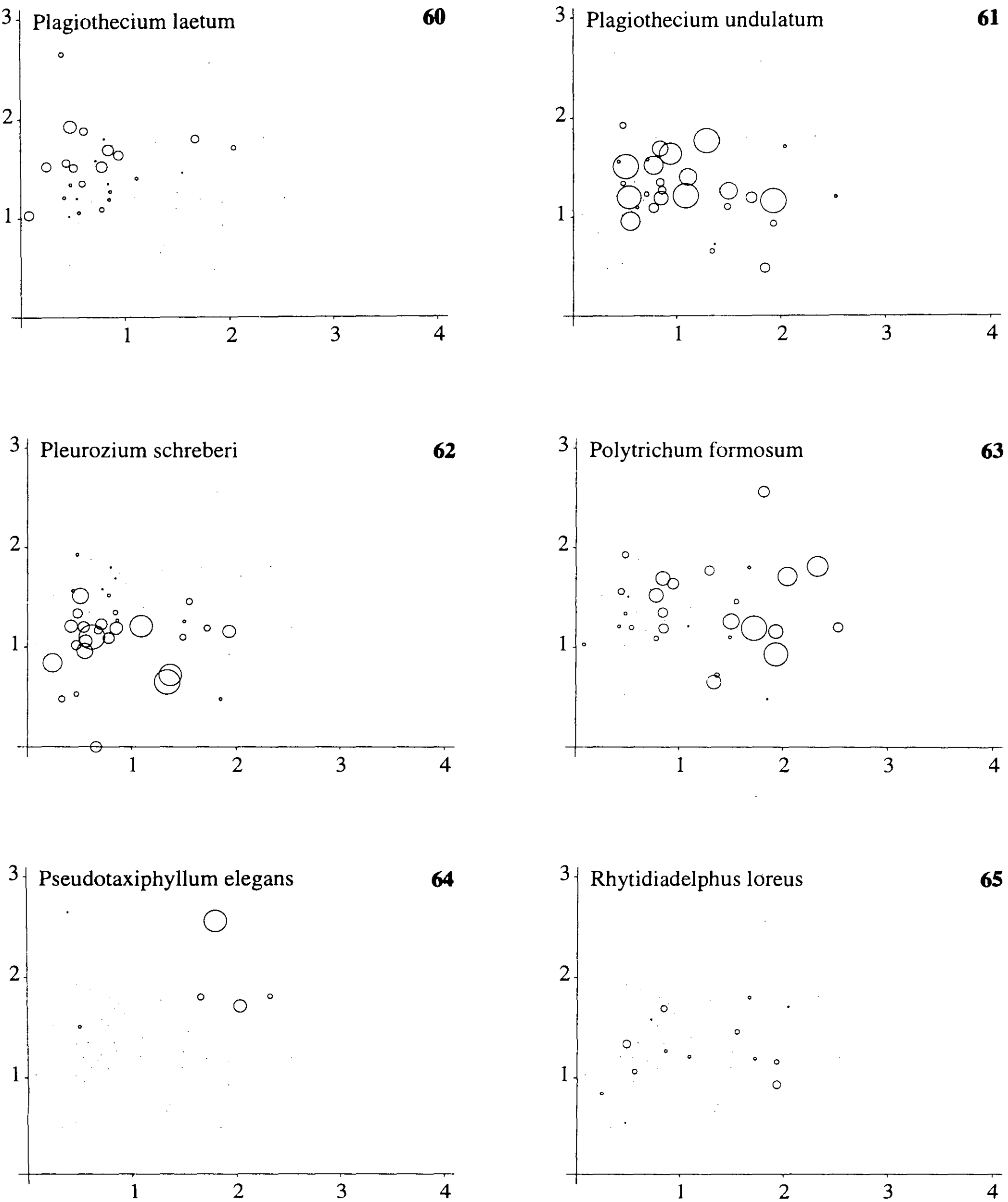
Figs 42-47. Paulen: distributions of species abundances in the DCA ordination of 49 meso plots (plot No. 8 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 42. *Gymnocarpium dryopteris*. Fig. 43. *Maianthemum bifolium*. Fig. 44. *Melampyrum pratense*. Fig. 45. *Phegopteris connectilis*. Fig. 46. *Potentilla erecta*. Fig. 47. *Pteridium aquilinum*.



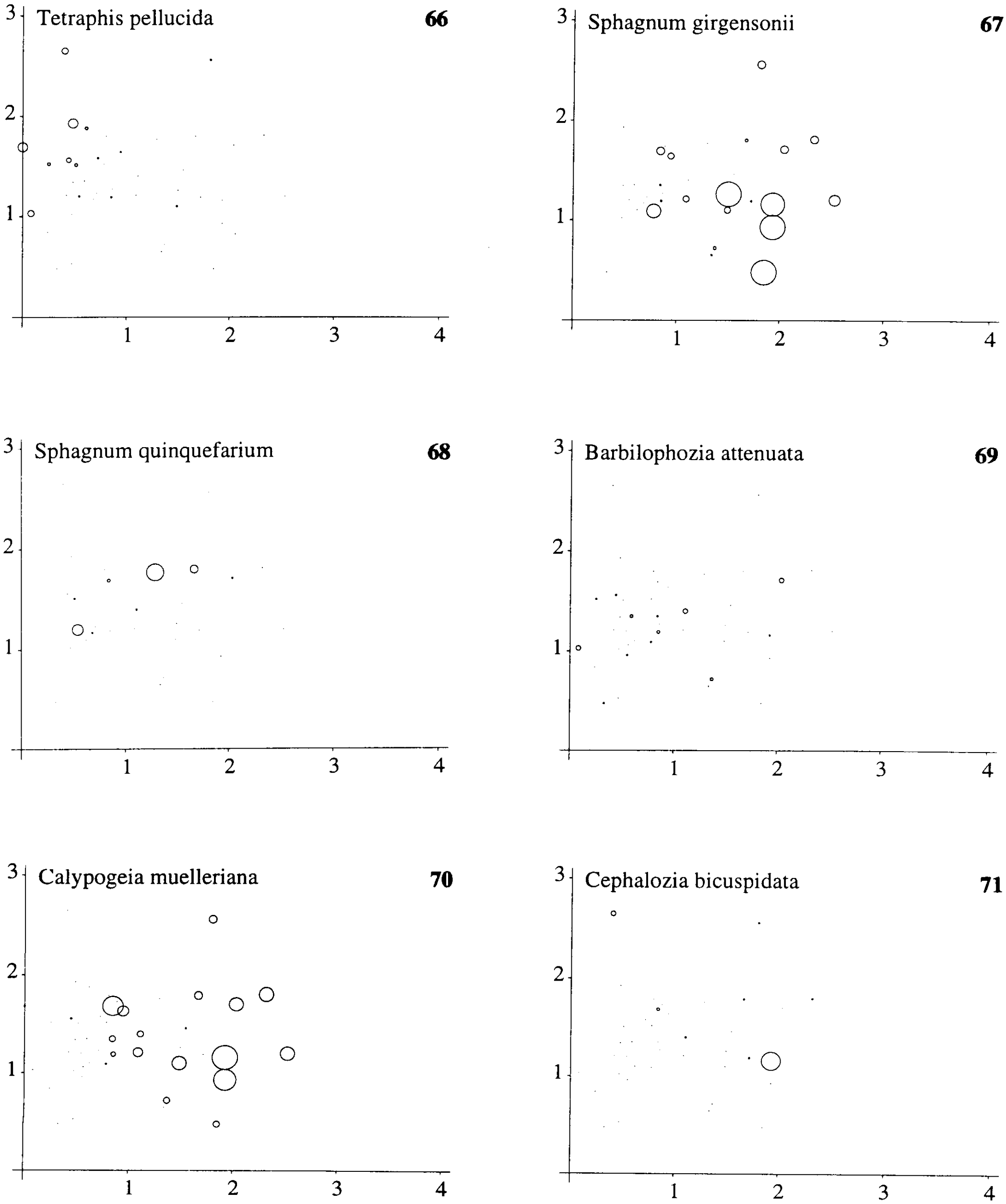
Figs 48-53. Paulen: distributions of species abundances in the DCA ordination of 49 meso plots (plot No. 8 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 48. *Solidago virgaurea*. Fig. 49. *Trientalis europaea*. Fig. 50. *Agrostis capillaris*. Fig. 51. *Calamagrostis purpurea*. Fig. 52. *Deschampsia flexuosa*. Fig. 53. *Dicranum fuscescens* agg.



Figs 54-59. Paulen: distributions of species abundances in the DCA ordination of 49 meso plots (plot No. 8 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 54. *Dicranum majus*. Fig. 55. *Dicranum scoparium*. Fig. 56. *Herzogiella striatella*. Fig. 57. *Hylocomium splendens*. Fig. 58. *Hypnum cupressiforme* agg. Fig. 59. *Mnium hornum*.



Figs 60-65. Paulen: distributions of species abundances in the DCA ordination of 49 meso plots (plot No. 8 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 60. *Plagiothecium laetum*. Fig. 61. *Plagiothecium undulatum*. Fig. 62. *Pleurozium schreberi*. Fig. 63. *Polytrichum formosum*. Fig. 64. *Pseudotaxiphyllum elegans*. Fig. 65. *Rhytidiadelphus loreus*.



Figs 66-71. Paulen: distributions of species abundances in the DCA ordination of 49 meso plots (plot No. 8 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 66. *Tetraphis pellucida*. Fig. 67. *Sphagnum girgensohnii*. Fig. 68. *Sphagnum quinquefarium*. Fig. 69. *Barbilophozia attenuata*. Fig. 70. *Calypogeia muelleriana*. Fig. 71. *Cephalozia bicuspidata*.

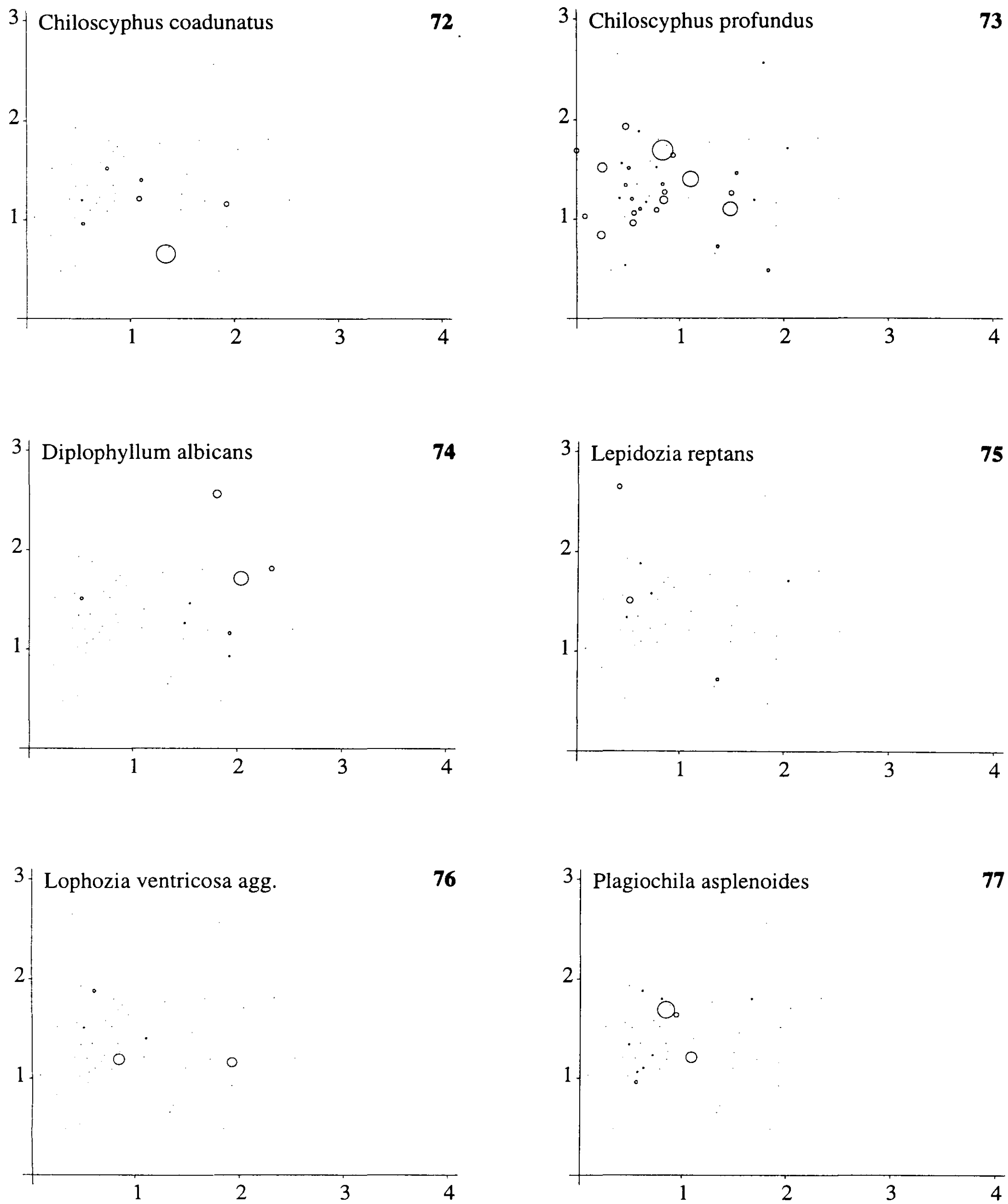


Fig. 72-77. Paulen: distributions of species abundances in the DCA ordination of 49 meso plots (plot No. 8 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 72. *Chiloscyphus coadunatus*. Fig. 73. *Chiloscyphus profundus*. Fig. 74. *Diplophyllum albicans*. Fig. 75. *Lepidozia reptans*. Fig. 76. *Lophozia ventricosa* agg. Fig. 77. *Plagiochila asplenioides*.

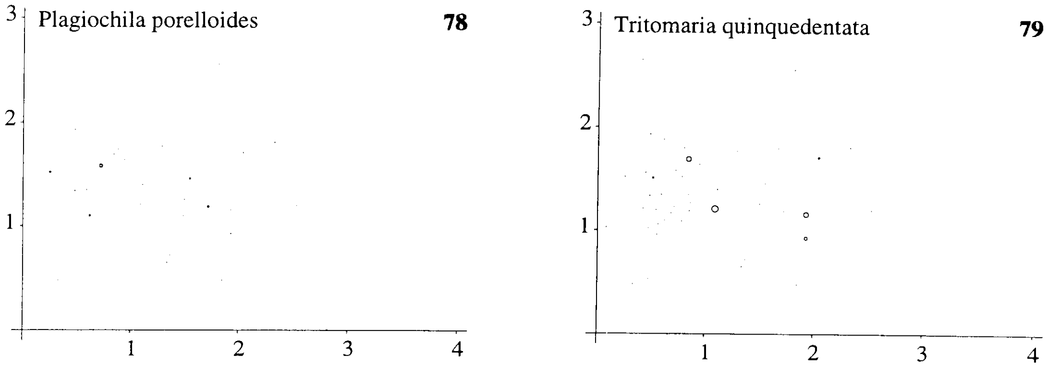


Fig. 78-79. Paulen: distributions of species abundances in the DCA ordination of 49 meso plots (plot No. 8 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 78. *Plagiochila porelloides*. Fig. 79. *Tritomaria quinquedentata*.

The distribution of species abundance in the DCA ordination

Forty-four of a total of 87 species occurred in 5 or more of the 49 meso plots (Figs 36-79).

Deschampsia flexuosa (Fig. 52) and *Maianthemum bifolium* (Fig. 43), typical examples of species with a wide ecological amplitude, were abundant in most meso plots.

Examples of species restricted to meso plots on sites with low pH, low total N and relatively low soil moisture, but with high content of cations like Ca and Mn (left part of the ordination), were *Melampyrum pratense* (Fig. 44), *Dicranum fuscescens* agg. (Fig. 53), *D. scoparium* (Fig. 55) and *Plagiothecium laetum* (Fig. 60). Several species were restricted to the right part of the ordination (higher pH and total N, low Ca and Mn content); *Agrostis capillaris* (Fig. 50) occurred in sites with relatively high soil moisture and low inclination (lower right in the ordination), while *Phegopteris connectilis* (Fig. 45) and *Gymnocarpium dryopteris* (Fig. 42) had wider amplitudes along DCA 2.

Species with preference for sloping sites (high DCA 2 scores) were *Pseudotaxiphyllum elegans* (Fig. 64) and *Tetraphis pellucida* (Fig. 66), while *Potentilla erecta* (Fig. 46) were restricted to less strongly sloping sites with higher soil moisture.

LUNDSNESET

Correlations between environmental variables

The heat indices, inclination and the macro plot light index (pairwise positively correlated) were negatively correlated with aspect unfavourability (Tab. 6, Fig. 80). Concentrations of the cations Ca and Mn were strongly positively correlated, and both were positively correlated with the heat indices. The heat indices and the concentration of Ca were also positively correlated with the light index. Together with concentrations of the cations Ca, Mn and Mg (positively correlated with the heat indices) and H^+ (negatively correlated with the latter), the terrain variables formed a group of correlated variables (cf. Fig. 80).

Several other variables were correlated with variables in this group. The concentration of Fe was strongly positively correlated with the concentration of Al, in turn positively correlated with the concentration of H^+. The concentration of Zn was positively correlated with concentrations of Mg, Ca and P-AL. The concentration of P-AL was also positively correlated with the concentration of Mn. Soil moisture and loss on ignition were negatively correlated with concentrations of Ca and Mn. Concentration of total N was positively correlated with pH, in turn negatively correlated with loss on ignition. Soil depth was negatively correlated with inclination.

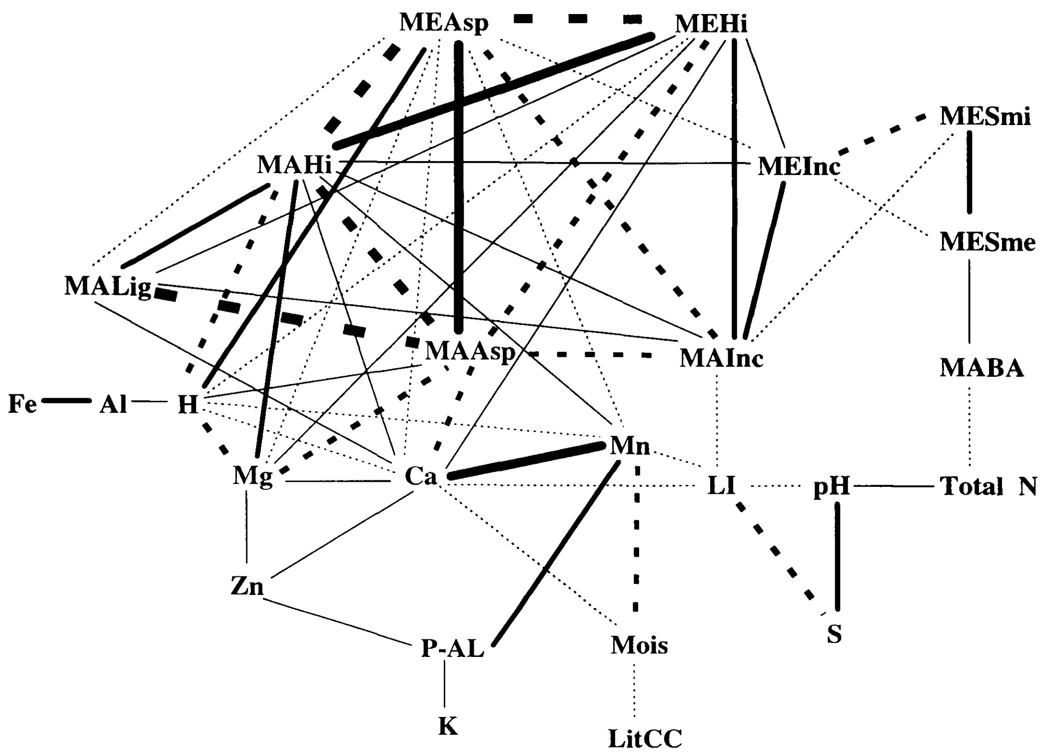


Fig. 80. Lundsneset: plexus diagram visualizing Kendall's τ between pairs of environmental variables. Significance probabilities for τ are indicated by lines with different thickness (in order of decreasing thickness): $|\tau| \geq 0.60$, $0.45 \leq |\tau| < 0.60$, $0.35 \leq |\tau| < 0.45$. Continuous lines refer to positive correlations, broken lines to negative.

Tab. 6. Lundsneset: Kendall's nonparametric correlation coefficient τ between 32 environmental variables in the 45 meso sample plots (lower triangle), with significance probabilities (upper triangle). Correlations significant at level P < 0.0001 in bold face. n.s. - significance probability > 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 2.

Variable	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
01 MA Inc	*	**.0000**	**.0000**	n.s.	.0001	**.0000**	**.0000**	**.0000**	n.s.	n.s.	.0006	.0192	n.s.	n.s.	n.s.	.0492	.0002	n.s.	.0381	.0031	.0062	n.s.	n.s.	.0059	n.s.	.0609	.0016	.0144	n.s.	n.s.	n.s.	n.s.
02 MA Asp	**-.5394**	*	**.0000**	n.s.	**.0000**	.0009	**.0000**	**.0000**	n.s.	n.s.	.0050	.0317	.0132	n.s.	n.s.	.0551	.0286	n.s.	.0682	**.0000**	**.0000**	n.s.	n.s.	**.0000**	n.s.	n.s.	.0021	.0108	.0319	n.s.	n.s.	n.s.
03 MA Hi	**.4495**	**-.7333**	*	n.s.	**.0000**	.0005	**.0000**	**.0000**	n.s.	n.s.	.0018	.0304	.0310	n.s.	n.s.	.0128	.0690	n.s.	n.s.	**.0000**	**.0000**	n.s.	n.s.	**.0000**	.0786	n.s.	.0004	.0704	n.s.	n.s.	n.s.	n.s.
04 MA BA	-.1163	.0920	.0000	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0001	.0023	n.s.	n.s.	n.s.	n.s.	.0091	.0134	n.s.	n.s.	.0772	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0007	n.s.	n.s.	n.s.
05 MA Lig	.4045	**-.6000**	**.5111**	.0000	*	.0103	.0002	.0001	.0626	n.s.	.0062	.0755	.0741	.0299	.0384	.0140	.0743	n.s.	n.s.	.0001	.0173	.0540	n.s.	.0236	.0098	n.s.	.0054	.0181	n.s.	n.s.	n.s.	n.s.
06 ME Inc	**.5919**	-.3436	.3594	-.0864	.2663	*	.0002	**.0000**	n.s.	n.s.	**.0000**	.0002	.0123	n.s.	n.s.	n.s.	.0074	n.s.	n.s.	.0198	.0157	n.s.	n.s.	.0499	n.s.	n.s.	.0150	n.s.	n.s.	n.s.	n.s.	n.s.
07 ME Asp	**-.4918**	**.6644**	**-.7126**	.1051	-.3873	-.3769	*	**.0000**	n.s.	.0665	.0177	.0231	.0985	n.s.	n.s.	.0079	.0253	n.s.	n.s.	.0001	**.0000**	n.s.	n.s.	**.0000**	n.s.	n.s.	.0003	.0204	n.s.	n.s.	n.s.	n.s.
08 ME Hi	**.5395**	**-.5991**	**.7423**	-.0071	.3860	**.4103**	**-.7921**	*	n.s.	n.s.	.0109	.0939	n.s.	n.s.	n.s.	.0076	.0314	n.s.	n.s.	.0003	**.0000**	n.s.	n.s.	**.0000**	n.s.	.0848	.0012	.0513	n.s.	n.s.	n.s.	n.s.
09 ME Rou	-.0341	.1459	-.1408	-.0009	-.1908	.0674	.1329	-.1267	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0653	n.s.	n.s.	n.s.	.0730	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
10 ME Con	.0486	-.1673	.1175	-.1030	.1089	.1018	-.1819	.1192	-.0083	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
11 ME Smi	-.3574	.2911	-.3244	.1525	-.2841	**-.4551**	.2394	-.2547	.0733	.0025	*	**.0000**	.0017	n.s.	n.s.	n.s.	.0031	n.s.	n.s.	.0170	.0805	n.s.	n.s.	n.s.	n.s.	n.s.	.0024	n.s.	n.s.	n.s.	n.s.	n.s.
12 ME Sme	-.2412	.2196	-.2213	.3993	-.1817	-.3780	.2259	-.1651	.0811	-.0083	**.5665**	*	**.0000**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0718	n.s.	.0472	n.s.	n.s.	n.s.
13 ME Sma	-.1562	.2537	-.2209	.3206	-.1829	-.2533	.1646	-.1381	.0863	-.0208	.3166	**.5750**	*		.0906	.0480	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0282	n.s.	n.s.	n.s.
14 LitCC	.0561	-.1075	.1075	-.1298	.2201	.0261	-.1297	.0802	-.1194	.0593	.0758	-.0636	-.1673	*	**.0000**	.0003	n.s.	n.s.	n.s.	.0747	n.s.	n.s.	n.s.	n.s.	.0682	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
15 LitACD	.0664	-.1126	.0717	-.1493	.2099	.0025	-.0851	.0393	-.1044	.0082	.0909	-.0802	-.1955	**.8649**	*	.0007	n.s.	n.s.	n.s.	.0993	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
16 Mois	-.2008	.1943	-.2522	.0309	-.2488	-.1533	.2616	-.2606	.0455	-.0008	.0883	.1164	.0720	-.3517	-.3321	*	.0371	n.s.	.0460	**.0000**	n.s.	n.s.	n.s.	.0192	.0020	n.s.	**.0000**	.0244	n.s.	.0021	.0007	.0943
17 LI	-.3808	.2230	-.1853	.0160	-.1819	-.2697	.2218	-.2114	-.0100	.0141	.2979	.1263	.0425	-.0461	-.0675	.2048	*	.0087	.0005	.0002	n.s.	n.s.	.0052	n.s.	.0115	.0017	.0002	.0095	n.s.	.0501	n.s.	**.0000**
18 pH_{H2O}	.1366	-.1207	.0364	-.2925	.0192	.0578	-.0603	-.0386	-.0372	-.0009	-.0813	-.1707	-.0725	-.0285	.0046	-.0588	-.2782	*	**.0000**	n.s.	n.s.	-.0343	.0230	n.s.	n.s.	n.s.	.0543	n.s.	**.0000**	.0343	n.s.	.0003
19 pH_{CaCl2}	.2292	-.2000	.1295	-.2780	.1467	.1045	-.1365	.0593	-.0740	.0138	-.1137	-.1679	-.0203	.1170	.1262	-.2109	-.3695	**.8220**	*	.0247	n.s.	n.s.	.0697	n.s.	n.s.	n.s.	.0024	n.s.	**.0000**	.0551	n.s.	**.0000**
20 Ca	.0031	**-.4540**	**.4438**	-.0053	.4012	.2333	-.3959	.3544	-.1821	.0263	-.2387	-.0965	.0281	.1742	.1611	**-.4410**	-.3601	.1074	.2373	*	.0003	n.s.	.0645	**.0000**	.0010	n.s.	**.0000**	.0001	n.s.	.0005	.0015	n.s.
21 Mg	.0062	**-.5460**	**.5665**	-.1040	.2411	.2417	**-.4487**	**.4279**	-.0927	.1315	-.1748	-.1196	-.1042	-.0433	-.0760	-.0833	-.0164	-.0303	-.0037	.3551	*	.0224	n.s.	**.0000**	.0105	n.s.	.0024	.0003	n.s.	.0149	.0864	n.s.
22 K	-.0379	.0264	.0179	-.1834	-.1951	.0345	-.0165	-.0523	-.0513	.1397	.0538	-.1081	-.0116	-.0875	-.1006	-.0833	.1266	.2230	.1552	.0547	.2229	*	n.s.	n.s.	n.s.	.0102	n.s.	n.s.	n.s.	.0002	.0010	n.s.
23 Na	.0207	.0060	.0929	.1023	-.0520	-.0008	-.0643	.1258	-.0149	-.0838	-.0067	.0371	-.0314	.0450	.0090	.1013	.2746	-.2396	-.1917	-.1804	.0890	-.0743	*	.0533	n.s.	n.s.	n.s.	.0229	.0776	.0007	n.s.	.0059
24 H^+	-.2808	**.4625**	**-.4830**	.0882	-.2291	-.1962	**.4652**	**-.4067**	.1771	.0608	.1277	.0899	.0496	-.1218	-.1071	.2287	.0510	-.0615	-.1460	**-.4351**	**-.4563**	-.0971	-.1886	*	.0001	.0438	.0001	.0762	n.s.	.0994	n.s.	n.s.
25 Al	-.0965	.1611	-.1781	-.1323	-.2616	-.1028	.1427	-.1234	.1184	.0896	-.0008	-0413	-0091	-.1783	-.1538	.3015	-.2484	.1598	.1160	-.3201	-.2499	-.1388	-.1029	.3757	*	**.0000**	.0523	.0960	.0380	n.s.	.0002	.0055
26 Fe	.1912	-.0366	.0809	-.1199	-.0434	.1154	-.1138	.1682	.0811	.1463	-.1445	-.0388	-.0678	-.0728	-.1071	.1274	-.3074	-.0395	-.0201	-.1118	-.0547	-.2506	.0269	.1967	**.5259**	*	n.s.	n.s.	n.s.	.0316	.0005	.0493
27 Mn	.3222	-.3109	.3586	-.1534	.2820	.2434	-.3563	.3152	-.1423	-.0148	-.3042	-.1774	-.0215	.1365	.1267	**-.4541**	-.3683	.2028	.3213	**.6245**	.2963	-.1429	-.1184	-.3763	-.1895	-.0563	*	.0013	n.s.	**.0000**	**.0000**	.0025
28 Zn	.2499	-.2582	.1832	-.1482	.2395	.1264	-.2286	.1904	.0058	.1291	-.1253	-.1486	-.0968	-.0065	-.0131	-.2198	-.2549	.0331	.0630	.3920	.3561	.1127	-.2221	-.1731	-.1626	.0065	.3136	*	n.s.	.0001	.0021	n.s.
29 Total N	.0965	-.2172	-.0077	-.3527	.0349	-.0295	-.0874	-.0180	-.0348	.0773	-.0420	-.1956	-.2166	.0417	.1120	.0637	-.1562	**.5259**	**.4490**	-.0237	-.0482	.0629	-.1722	.0139	.2025	.0596	-.0629	.0376	*	.0155	-.1167	.1918
30 P-AL	.1068	-.1133	.0417	-.1464	.0469	.1187	-.1039	.0245	.0480	.0493	-.0555	-.1130	-.0066	-.0090	.0008	-.3005	-.1924	.2230	.2026	.3404	.2376	.3649	-.3306	-.1608	-.1535	-.2098	**.4841**	.3757	.0155	*	**.0000**	.0014
31 P	.0724	-.0503	.0094	.0652	.0792	.0985	-.0643	.0163	-.0215	.0247	-.0420	-.0470	.0447	-.0303	-.0221	-.3299	-.0411	.0193	.0237	.3094	.1673	.3208	-.1559	-.1592	-.3642	-.3388	**.4008**	.3005	-.1167	**.6033**	*	n.s.
32 S	.1275	.0247	-.0451	-.1446	-.0128	.0884	-.0148	-.0098	.0099	.1019	-.1244	-.1081	.0397	.0253	.0253	-.1633	**-.4982**	.3846	**.4764**	.1216	-.0629	.1363	-.2686	.1429	.2711	.1918	.2947	.1307	.1918	.3110	.1363	*

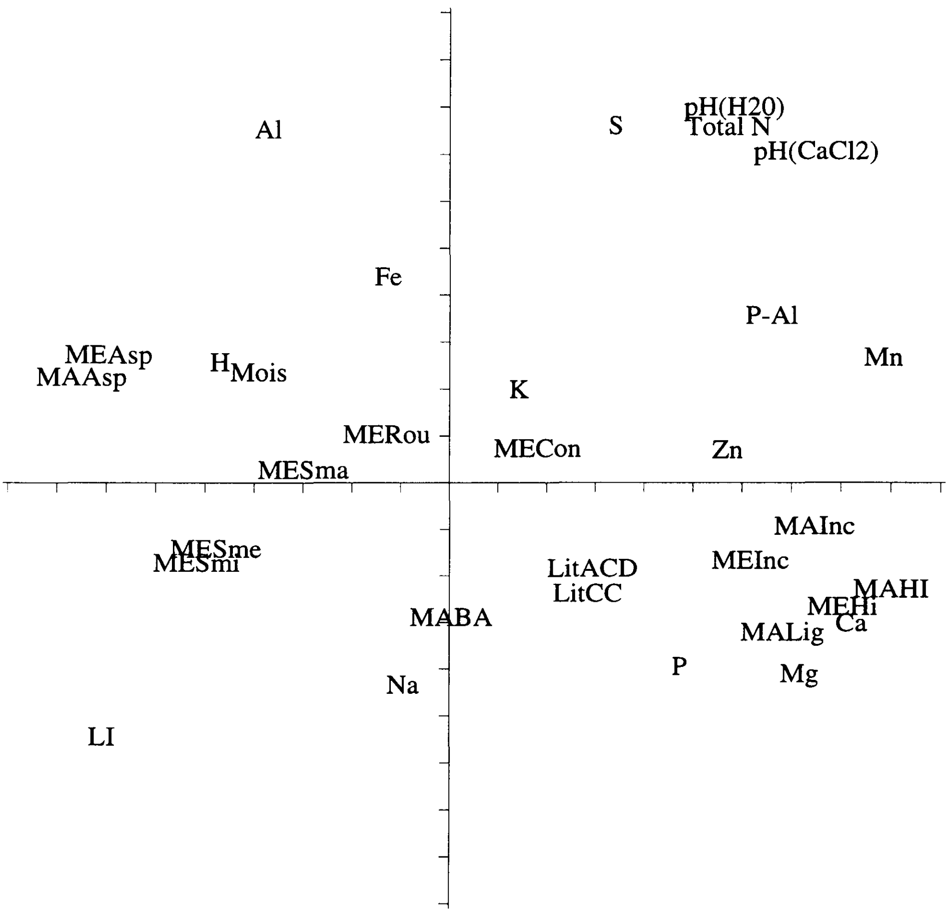


Fig. 81. Lundsneset: PCA ordination of 32 environmental variables (names abbreviated in accordance with Tab. 2), axes 1 (horizontal) and 2 (vertical). Positions of variables in the ordination give the head of variable vectors.

PCA ordination of environmental variables

Eigenvalues of the first two PCA axes were 0.295 and 0.152, thus 44.7% of the variation in measured environmental variables was explained by the first two PCA axes.

The strongly positively correlated variables of the group described above (Mn, Ca, Mg, the heat indices, inclination and the macro plot light index), as well as variables related to this group (P-Al, pH and Zn) obtained high loadings on PCA 1 (Fig. 81). Low loadings were obtained by variables negatively correlated with the group mentioned above; aspect unfavourability, loss on ignition, soil depth and, less strongly, H^+ and soil moisture.

Al, S, pH and total N obtained high loadings on PCA 2, while the lowest loading was obtained by loss on ignition.

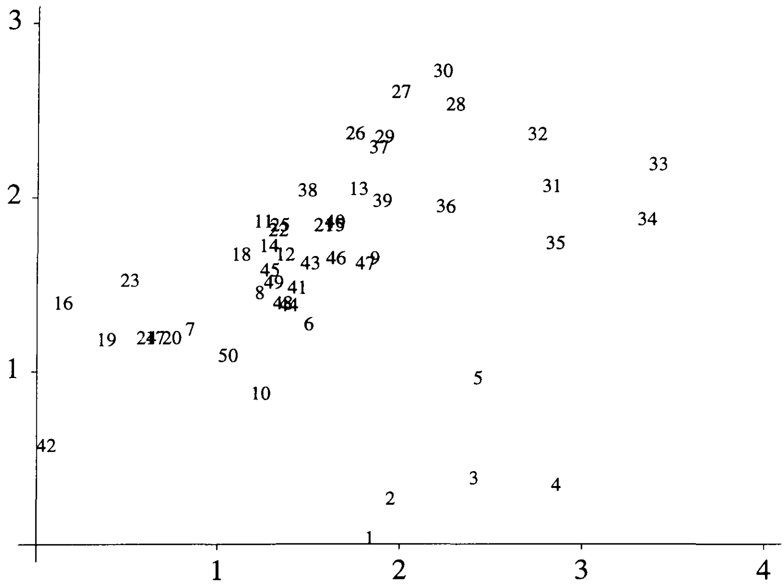


Fig. 82. Lundsneset: DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Meso plot numbers are plotted onto the sample plot positions. Scaling of axes in S.D. units.

The results of the PCA ordination were thus largely consistent with the correlations between variables (Tab. 6, Fig. 80).

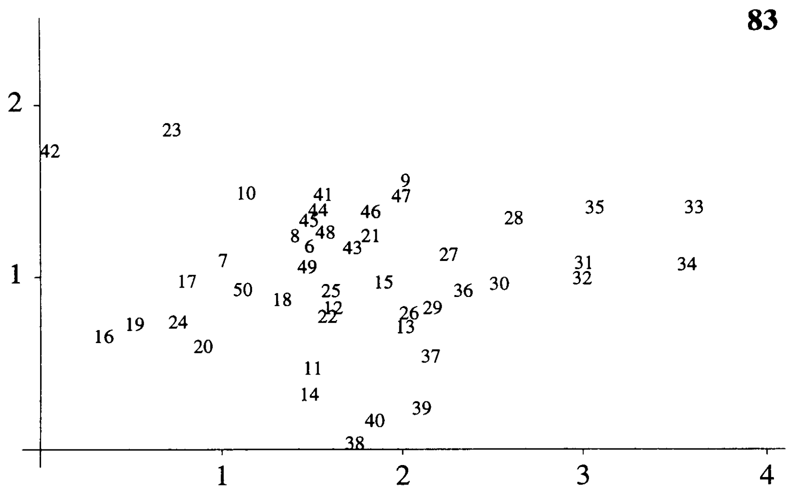
DCA and LNMDS ordination

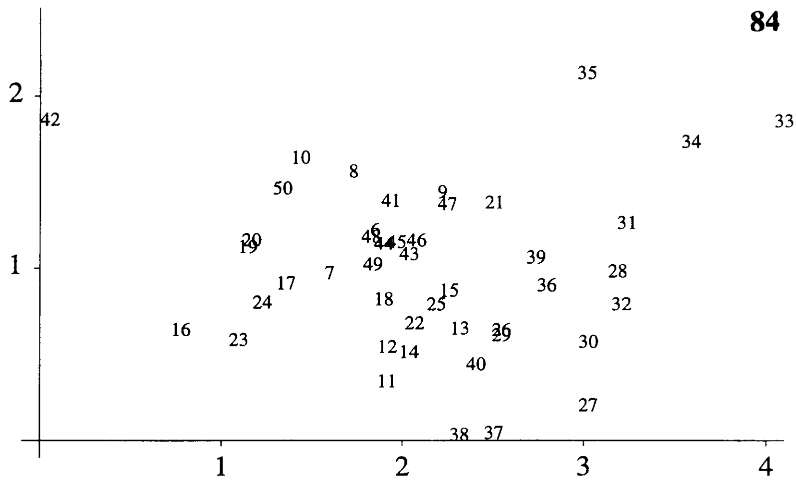
Plot Nos 1-5 made up a disjunct group in the DCA ordination (Fig. 82) and were removed prior to further analysis. These were species-rich plots (17-32 species, compared to the area average of 14.5).

Plots were relatively evenly distributed along the first two axes in the DCA ordination of the remaining 45 plots (Fig. 83). Plot No. 42 acted as an outlier along LNMDS 1 (Fig. 84), and made LNMDS 1 somewhat longer than DCA 1. The second axes were of approximately equal lengths, measured in S.D. units.

Tab. 7. Lundsneset: Eigenvalues and the fraction of variation explained for DCA axes 1-4.

	DCA 1	DCA 2	DCA 3	DCA 4
Eigenvalues	0.448	0.133	0.102	0.066
Fraction of variation explained	0.186	0.055	0.042	0.027





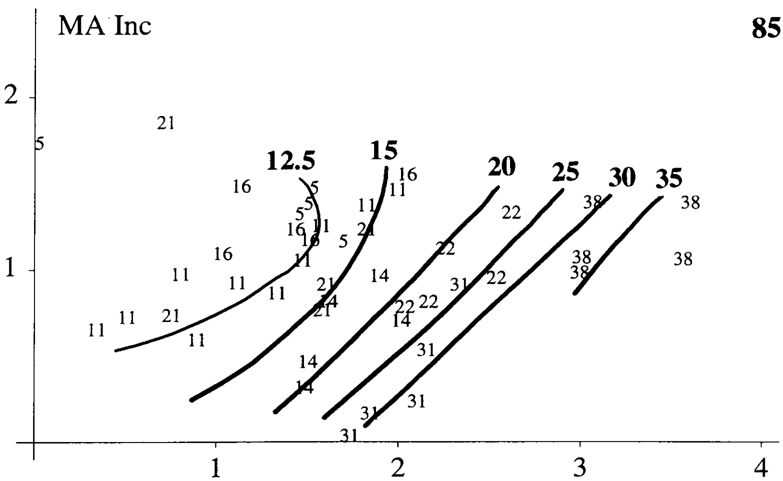
Figs 83-84. Lundsneset: ordinations of 45 meso plots (plot Nos 1-5 omitted), axes 1 (horizontal) and 2 (vertical). Meso plot numbers are plotted onto the sample plot positions. Fig. 83. DCA ordination. Scaling of axes in S.D. units. Fig. 84. LNMDS ordination. Axes linearly rescaled in S.D. units.

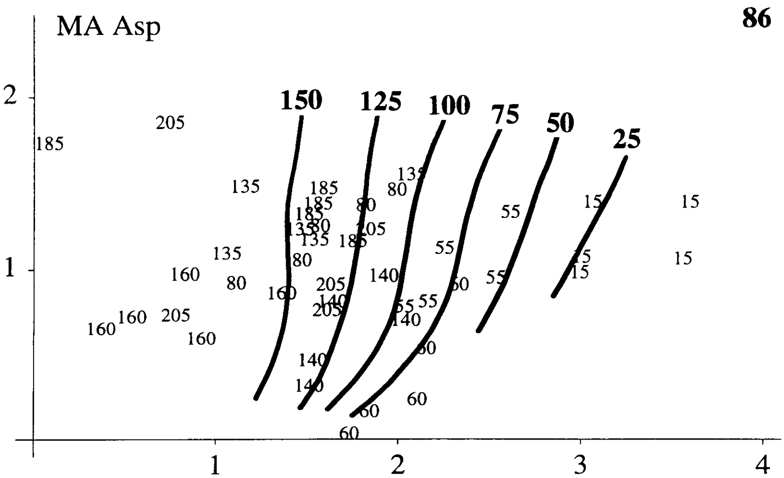
DCA 1 explained as much as 18.6% of the variation in the vegetation (Tab. 7). The explained fraction of variation declined strongly to DCA 2, being only 5.5% or ca. 30% of the fraction explained by DCA 1. The eigenvalues of DCA 3 and DCA 4 were low (0.102 and 0.066, respectively), corresponding to explained fractions of variation below 5%.

Correlations between DCA and LNMDS ordination axes and between ordination axes and environmental variables

The correlation between DCA 1 and LNMDS 1 ($\tau = 0.877$; Tab. 8) and between DCA 2 and LNMDS 2 ($\tau = 0.519$) were both strong.

The variables most strongly correlated with DCA 1 (which were also strongly correlated



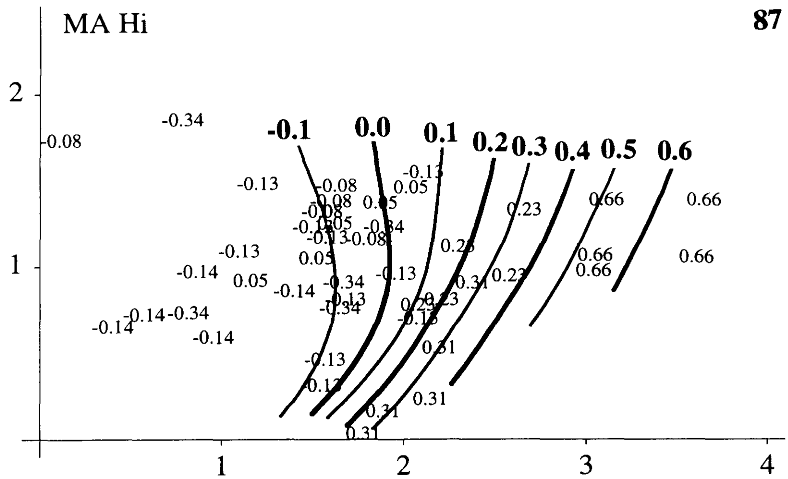


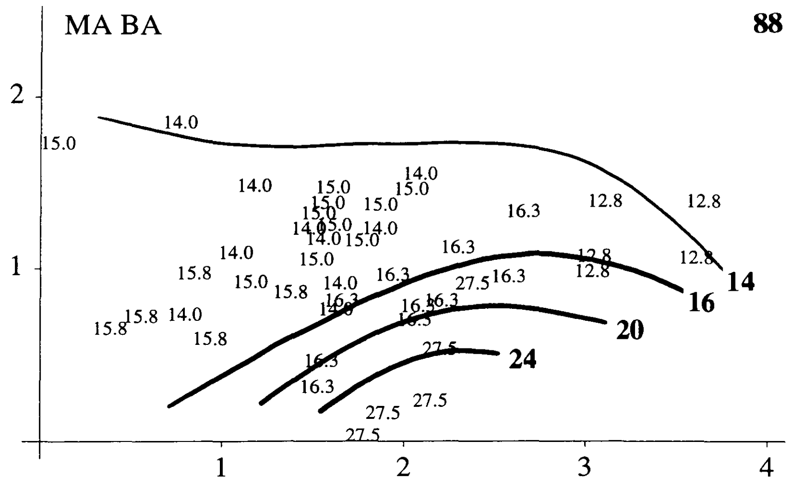
Figs 85-86. Lundsneset: isolines for environmental variables in the DCA ordination of 45 meso plots (plot Nos 1-5 omitted), axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 85. MA Inc (R^2 = 0.757). Fig. 86. MA Asp (R^2 = 0.684). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.

with LNMDS 1 with similar τ values) were inclination (Figs 85 and 90), the heat indices (Figs 87 and 92) and the macro plot light index (Fig. 89), all positively correlated, and aspect unfavourability (Figs 86 and 91) and concentration of H^+, with negative correlations. Other

Tab. 8. Lundsneset: Kendall's nonparametric correlation coefficients τ between DCA and LNMDS axes, and between 32 environmental variables in the 45 meso sample plots and sample plot positions with respect to DCA and LNMDS axes, and their significance probabilities. Correlations significant at level P < 0.0001 in bold face. n.s. - significance probability > 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 2.

Variable	DCA 1		DCA 2		DCA 3		DCA 4		LNMDS 1		LNMDS 2	
	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P
LNMDS 1	**.8768**	**.0000**	-.0061	n.s.	-.2141	.0381	-.0323	n.s.				
LNMDS 2	-.0121	n.s.	**.5192**	**.0000**	.2909	.0048	.3030	.0033				
01 MA Inc	**.5297**	**.0000**	-.1472	n.s.	**-.4717**	**.0000**	-.0505	n.s.	**.5512**	**.0000**	-.1601	n.s.
02 MA Asp	**-.5763**	**.0000**	.0318	n.s.	.0572	n.s.	-.0657	n.s.	**-.5361**	**.0000**	-.0148	n.s.
03 MA Hi	**.5869**	**.0000**	-.0085	n.s.	.0509	n.s.	.1398	n.s.	**.5636**	**.0000**	.0297	n.s.
04 MA BA	.0476	n.s.	**-.4503**	**.0000**	-.1250	n.s.	-.0852	n.s.	.0763	n.s.	**-.5212**	**.0000**
05 MA Lig	**.4661**	**.0000**	-.0742	n.s.	-.0403	n.s.	-.1631	n.s.	**.4428**	**.0000**	-.0233	n.s.
06 ME Inc	.3730	.0004	-.0608	n.s.	-.2976	.0051	.0314	n.s.	.3751	.0004	-.0524	n.s.
07 ME Asp	**-.5210**	**.0000**	.0225	n.s.	.0715	n.s.	-.1287	n.s.	**-.5026**	**.0000**	-.0449	n.s.
08 ME Hi	**.5508**	**.0000**	-.0616	n.s.	-.0899	n.s.	.0798	n.s.	**.5528**	**.0000**	-.0071	n.s.
09 ME Rou	-.0440	n.s.	.1627	n.s.	-.0685	n.s.	.2384	.0224	-.0522	n.s.	.2179	.0369
10 ME Con	.0387	n.s.	.0224	n.s.	-.0509	n.s.	.0488	n.s.	.0061	n.s.	.1587	n.s.
11 ME Smi	-.3076	.0037	.0636	n.s.	.1408	n.s.	.0240	n.s.	-.3389	.0014	.0594	n.s.
12 ME Sme	-.1366	n.s.	-.1284	n.s.	-.0265	n.s.	-.0020	n.s.	-.1203	n.s.	-.1305	n.s.
13 ME Sma	-.1400	n.s.	-.1748	.0939	-.0787	n.s.	-.0051	n.s.	-.1196	n.s.	-.1789	-.0865
14 LitCC	.2551	.0137	.0870	n.s.	.1235	n.s.	-.0668	n.s.	.2632	.0110	-.0040	n.s.
15 LitACD	.2256	.0291	.0759	n.s.	.1002	n.s.	-.0981	n.s.	.2377	.0215	.0172	n.s.
16 Mois	-.3131	.0024	.1172	n.s.	-.0101	n.s.	.0545	n.s.	-.2949	.0043	.0889	n.s.
17 LI	-.1783	.0866	.3311	.0015	.2782	.0075	.0968	n.s.	-.2292	.0276	.2802	.0071
18 pH_{H20}	-.1791	n.s.	-.0503	n.s.	-.0574	n.s.	-.0855	n.s.	-.1791	n.s.	-.1112	n.s.
19 pH_{CaCl2}	-.0128	n.s.	-.0849	n.s.	-.1361	n.s.	-.1361	n.s.	-.0035	n.s.	-.1849	n.s.
20 Ca	.4182	.0001	-.1980	.0552	-.0343	n.s.	-.1111	n.s.	.4162	.0001	-.1374	n.s.
21 Mg	.3111	.0026	-.0141	n.s.	-.0283	n.s.	.1737	.0925	.3333	.0012	.0828	n.s.
22 K	-.1616	n.s.	.0384	n.s.	.0404	n.s.	.0970	n.s.	-.1636	n.s.	.0990	n.s.
23 Na	.2707	.0088	.1636	n.s.	-.0323	n.s.	.0929	n.s.	.3051	.0031	.0061	n.s.
24 H^+	**-.4323**	**.0000**	-.0061	n.s.	.0040	n.s.	-.0040	n.s.	**-.4505**	**.0000**	.0586	n.s.
25 Al	-.2981	.0039	.0515	n.s.	-.0596	n.s.	.0879	n.s.	-.2638	.0107	.0758	n.s.
26 Fe	.0263	n.s.	.0525	n.s.	-.1636	n.s.	.0869	n.s.	.0485	n.s.	.0687	n.s.
27 Mn	.3030	.0033	-.2081	.0439	-.0889	n.s.	-.0404	n.s.	.3374	.0011	-.0788	n.s.
28 Zn	.1041	n.s.	-.1566	n.s.	-.1465	n.s.	-.0354	n.s.	.1344	n.s.	.0697	n.s.
29 Total N	-.0929	n.s.	.1192	n.s.	.0162	n.s.	-.0162	n.s.	-.1354	n.s.	-.0141	n.s.
30 P-AL	-.1111	n.s.	-.2061	.0460	-.0222	n.s.	.0424	n.s.	-.0970	n.s.	-.0162	n.s.
31 P	.0141	n.s.	-.2424	.0189	-.0101	n.s.	-.0384	n.s.	.0283	n.s.	-.0566	n.s.
32 S	-.1697	n.s.	-.2485	.0161	-.1576	n.s.	-.1576	n.s.	-.1394	n.s.	-.2283	.0270

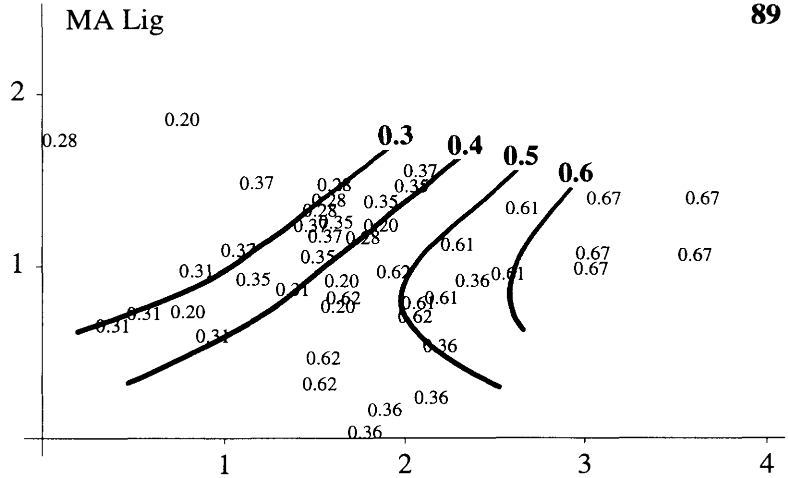


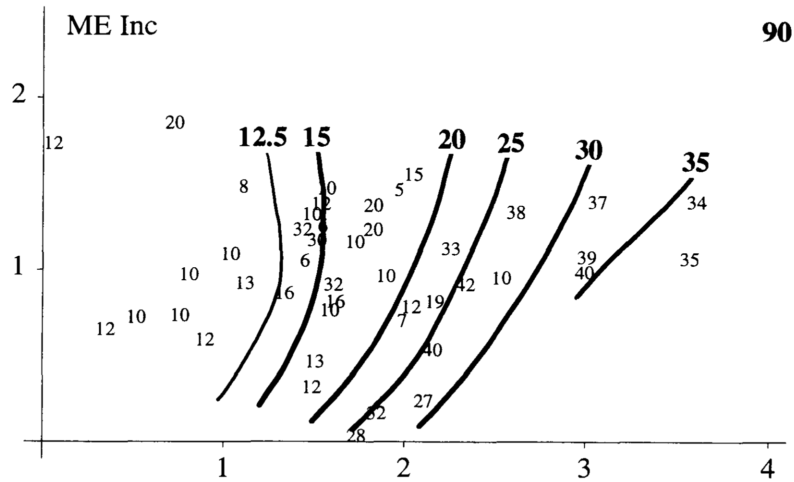


Figs 87-88. Lundsneset: isolines for environmental variables in the DCA ordination of 45 meso plots (plot Nos 1-5 omitted), axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots' positions. Scaling of axes in S.D. units. Fig. 87. MA Hi ($R^2 = 0.835$). Fig. 88. MA BA ($R^2 = 0.732$). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.

correlated variables were concentrations of Ca (Fig. 96), Mg (Fig. 97) and Mn (Fig. 98) with positive correlations, and minimum soil depth (Fig. 93) and soil moisture (Fig. 94) which were negatively correlated with DCA 1 and LNMDS 1.

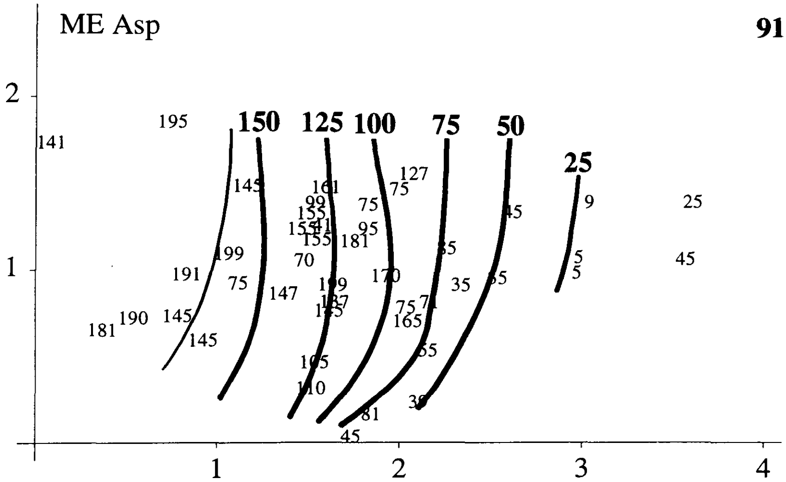
The only variable strongly correlated with DCA 2 and LNMDS 2 was macro plot basal area (Fig. 88), with a negative correlation. Loss on ignition (Fig. 95) was positively correlated

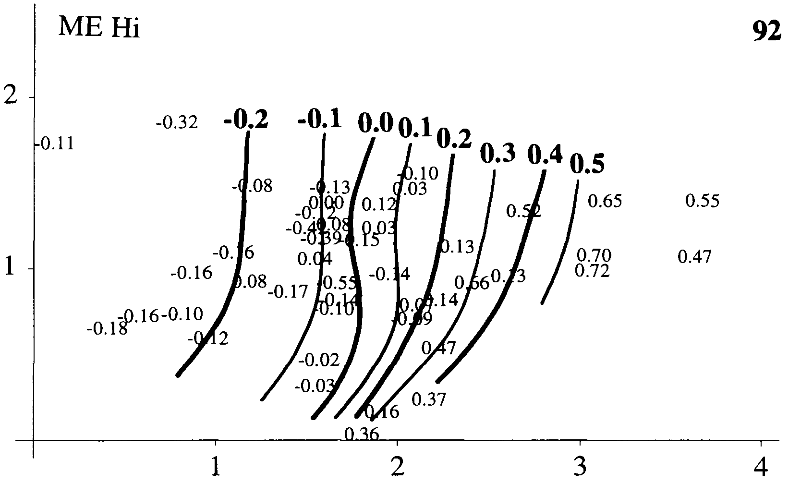




Figs 89-90. Lundsneset: isolines for environmental variables in the DCA ordination of 45 meso plots (plot Nos 1-5 omitted), axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots' positions. Scaling of axes in S.D. units. Fig. 89. MA Lig (R^2 = 0.617). Fig. 90. ME Inc (R^2 = 0.479). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.

with DCA 2. Macro plot inclination was strongly correlated with DCA 3, although less strongly than with DCA 1 and LNMDS 1.





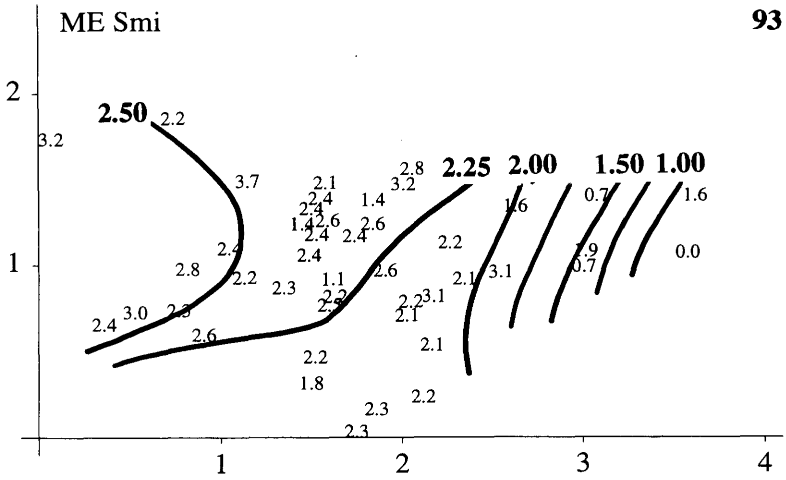
Figs 91-92. Lundsneset: isolines for environmental variables in the DCA ordination of 45 meso plots (plot Nos 1-5 omitted), axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots' positions. Scaling of axes in S.D. units. Fig. 91. ME Asp ($R^2 = 0.659$). Fig. 92. ME Hi ($R^2 = 0.433$). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.

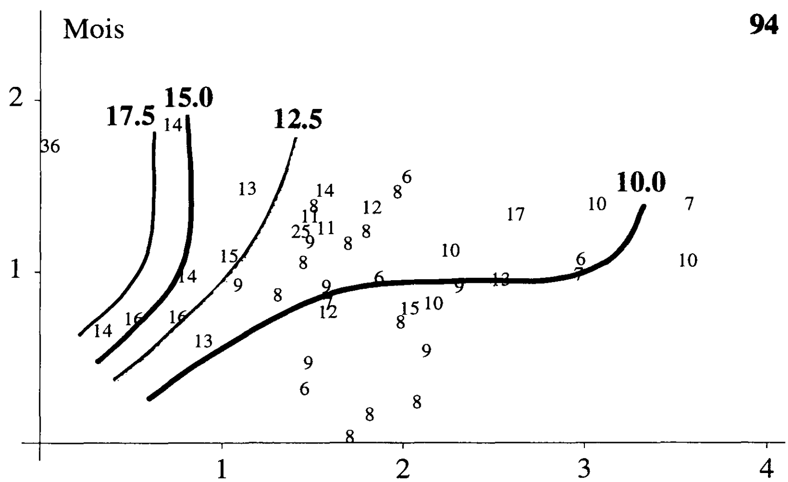
The distribution of species abundance in the DCA ordination

Thirty-four of a total of 86 species occurred in 5 or more of the 45 meso plots (Figs 99-132).

Pleurozium schreberi (Fig. 117) and *Dicranum majus* (Fig. 110), typical examples of species with wide ecological amplitude, were abundant in most plots.

Examples of species restricted to relatively moist sites with low inclination on unfavour-



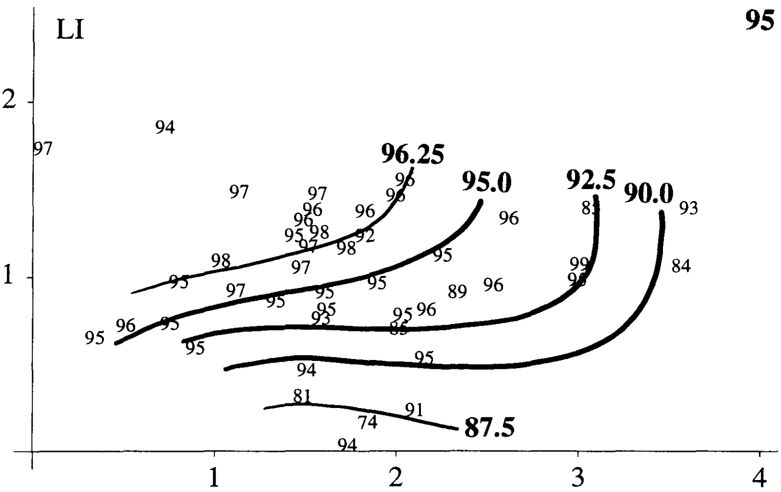


Figs 93-94. Lundsneset: isolines for environmental variables in the DCA ordination of 45 meso plots (plot Nos 1-5 omitted), axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots' positions. Scaling of axes in S.D. units. Fig. 93. ME Smi ($R^2 = 0.433$). Fig. 94. Mois ($R^2 = 0.665$). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.

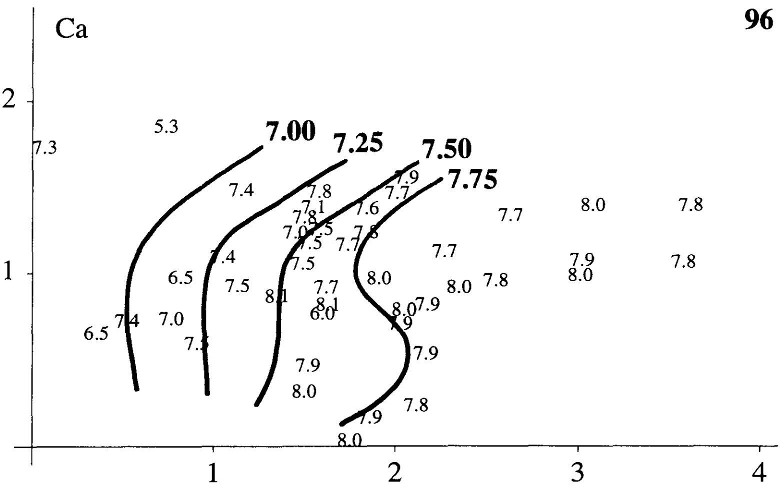
able aspects (the left part of the ordination diagram) were *Maianthemum bifolium* (Fig. 103), *Deschampsia flexuosa* (Fig. 107), *Trientalis europaea* (Fig. 105), *Sphagnum quinquefarium* (Fig. 123), *Sphagnum girgensohnii* (Fig. 122) and *Ptilidium ciliare* (Fig. 127).

Hypnum cupressiforme agg. (Fig. 114), *Pohlia nutans* (Fig. 118) and *Cladonia rangiferina* (Fig. 132) occurred in plots from topographically more favourable, but drier sites with higher inclination (to the right in the ordination).

95



96



Figs 95-96. Lundsneset: isolines for environmental variables in the DCA ordination of 45 meso plots (plot Nos 1-5 omitted), axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots' positions. Scaling of axes in S.D. units. Fig. 95. LI (R^2 = 0.407). Fig. 96. Ca (R^2 = 0.532). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.

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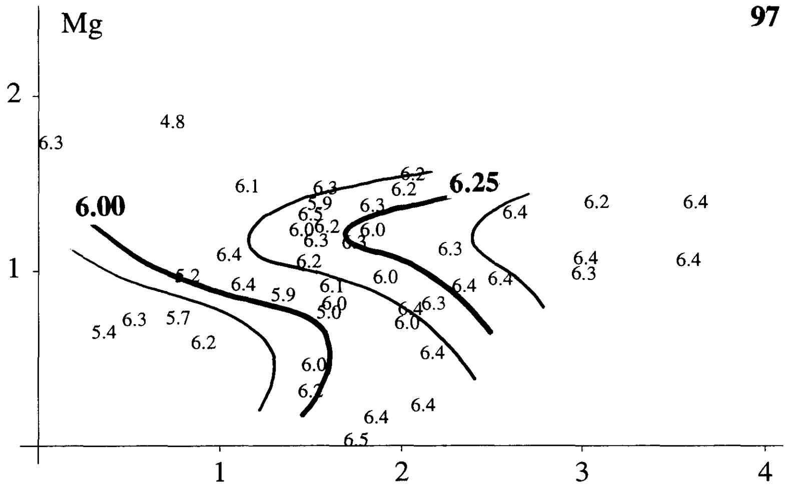
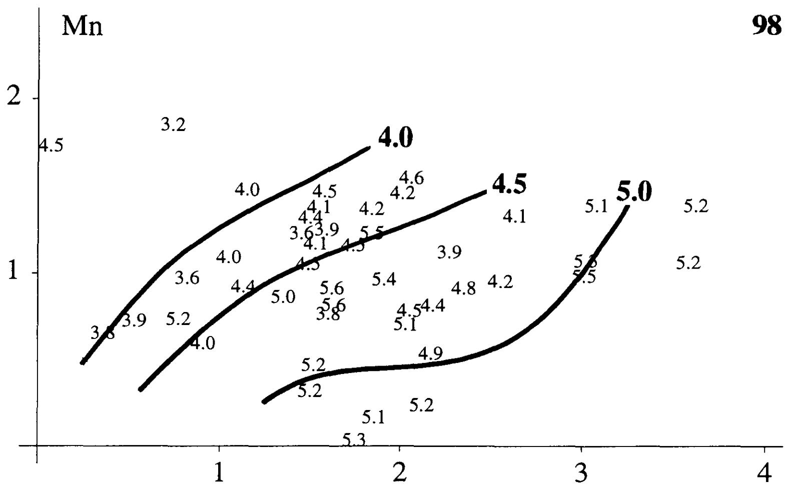
Correlations between environmental variables

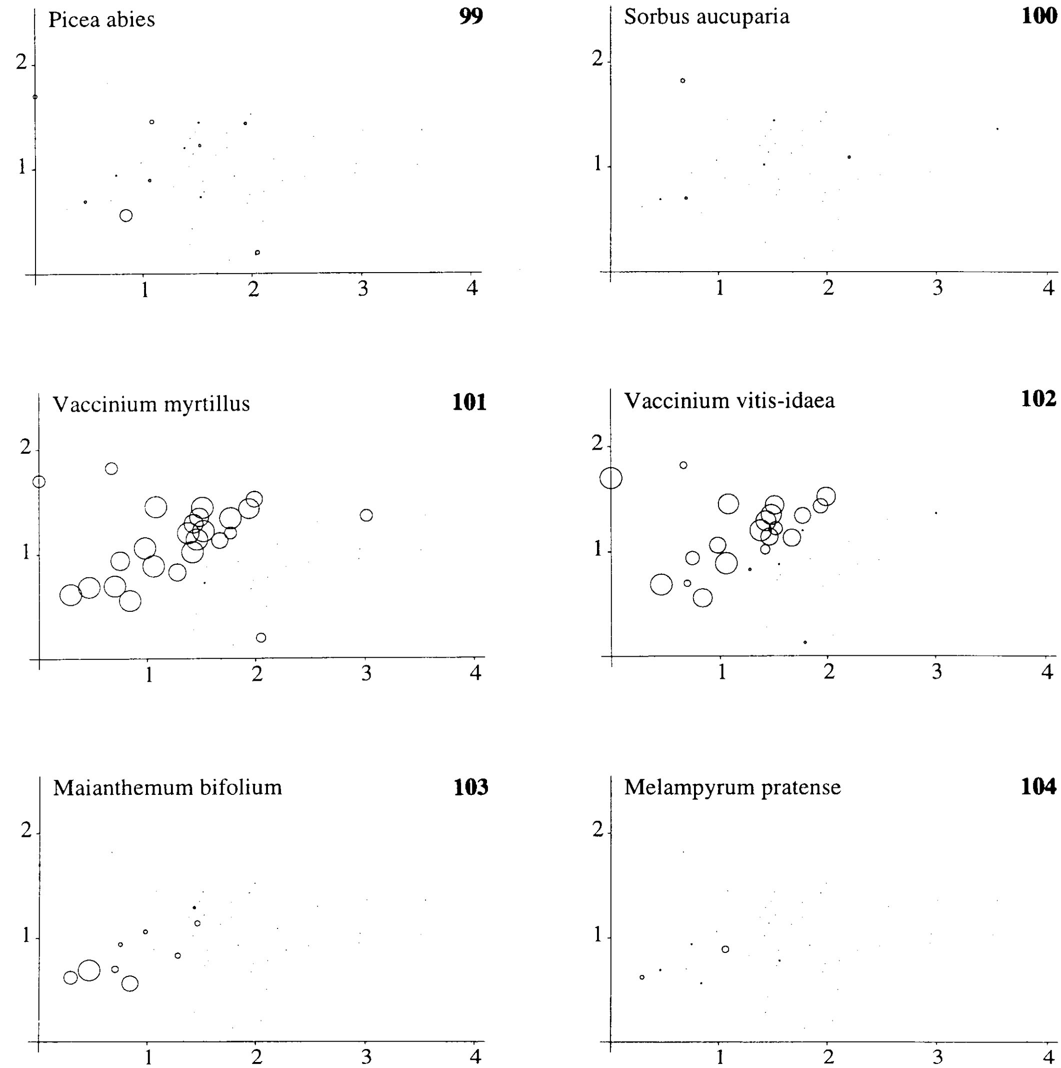
pH and the concentrations of most cations (Ca, Mn and Zn, positively correlated with pH, and





Figs 97-98. Lundsneset: isolines for environmental variables in the DCA ordination of 45 meso plots (plot Nos 1-5 omitted), axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 97. Mg (R^2 = 0.444). Fig. 98. Mn (R^2 = 0.452). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.

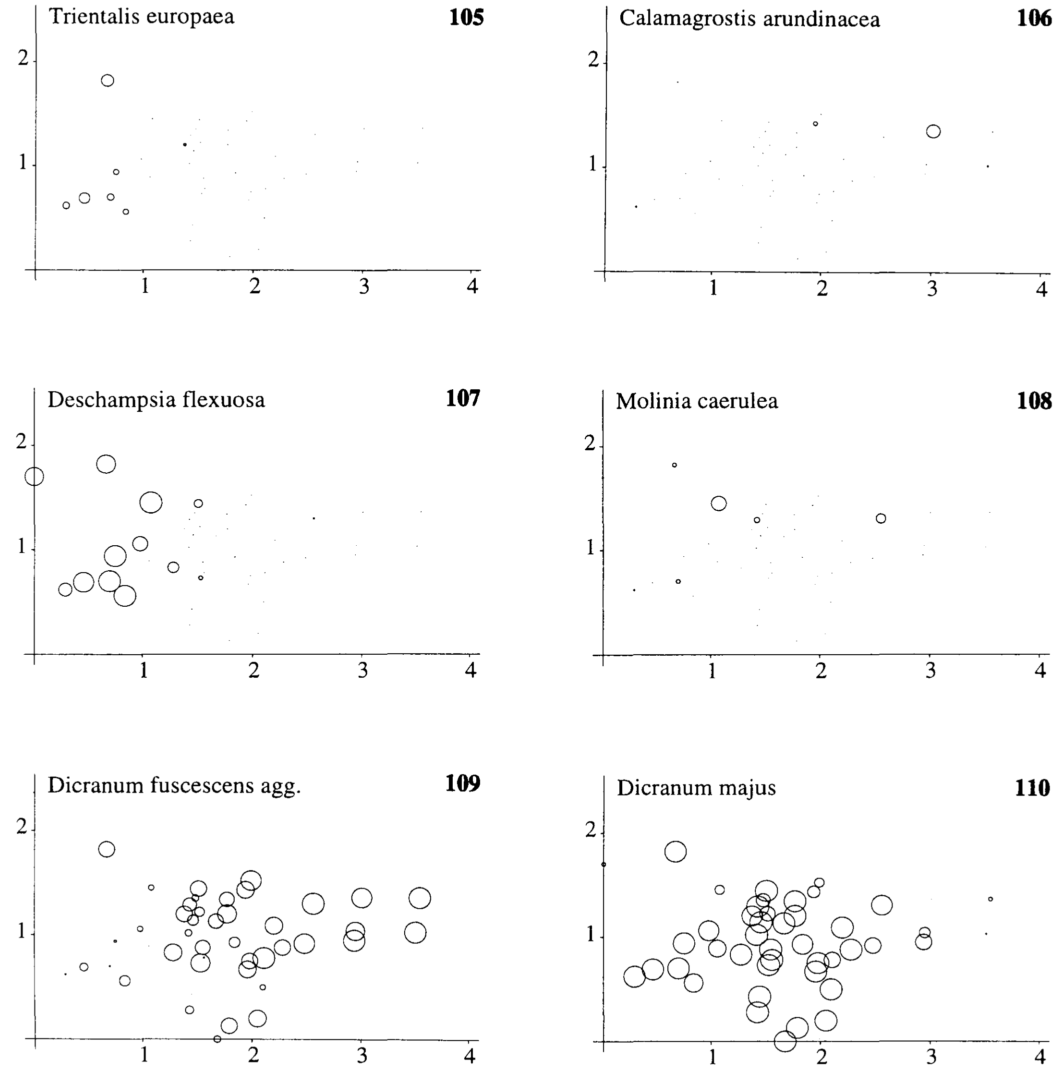
Na, Al and H^+, negatively correlated with pH) made up a group of variables with more or less strong pairwise correlations (Tab. 9, Fig. 133). Particularly strong correlations ($\tau > 0.6$) were found between pH and concentrations of Mn, Ca and Al. Among other variables connected to this group, the macro plot light index and the litter indices (positively correlated with concentrations of Zn and Ca, respectively) could be mentioned. Soil moisture was positively correlated with concentrations of Na and Al.



Figs 99-104. Lundsneset: distributions of species abundances in the DCA ordination of 45 meso plots (plot Nos 1-5 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 99. *Picea abies*. Fig. 100. *Sorbus aucuparia*. Fig. 101. *Vaccinium myrtillus*. Fig. 102. *Vaccinium vitis-idaea*. Fig. 103. *Maianthemum bifolium*. Fig. 104. *Melampyrum pratense*.

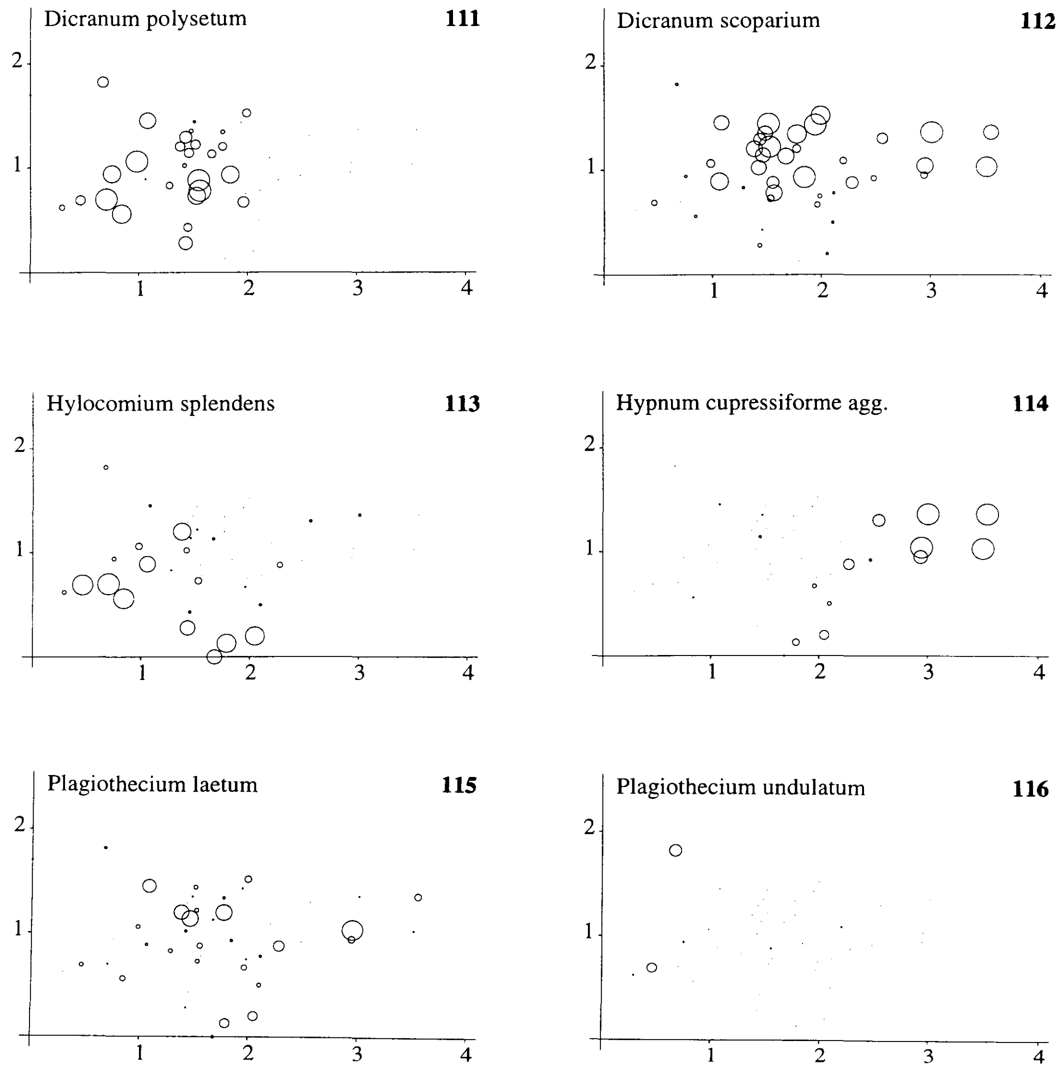
A second group of correlated variables consisted of the concentration of total N and the heat indices and aspect unfavourability. The heat indices were positively and aspect unfavourability was negatively correlated with total N. Meso plot aspect unfavourability was negatively correlated with inclination, in turn negatively correlated with macro plot basal area.

Connections between the two groups of correlated variables were provided by the strong



Figs 105-110. Lundsneset: distributions of species abundances in the DCA ordination of 45 meso plots (plot Nos 1-5 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 105. *Trientalis europaea*. Fig. 106. *Calamagrostis arundinacea*. Fig. 107. *Deschampsia flexuosa*. Fig. 108. *Molinia caerulea*. Fig. 109. *Dicranum fuscescens* agg. Fig. 110. *Dicranum majus*.

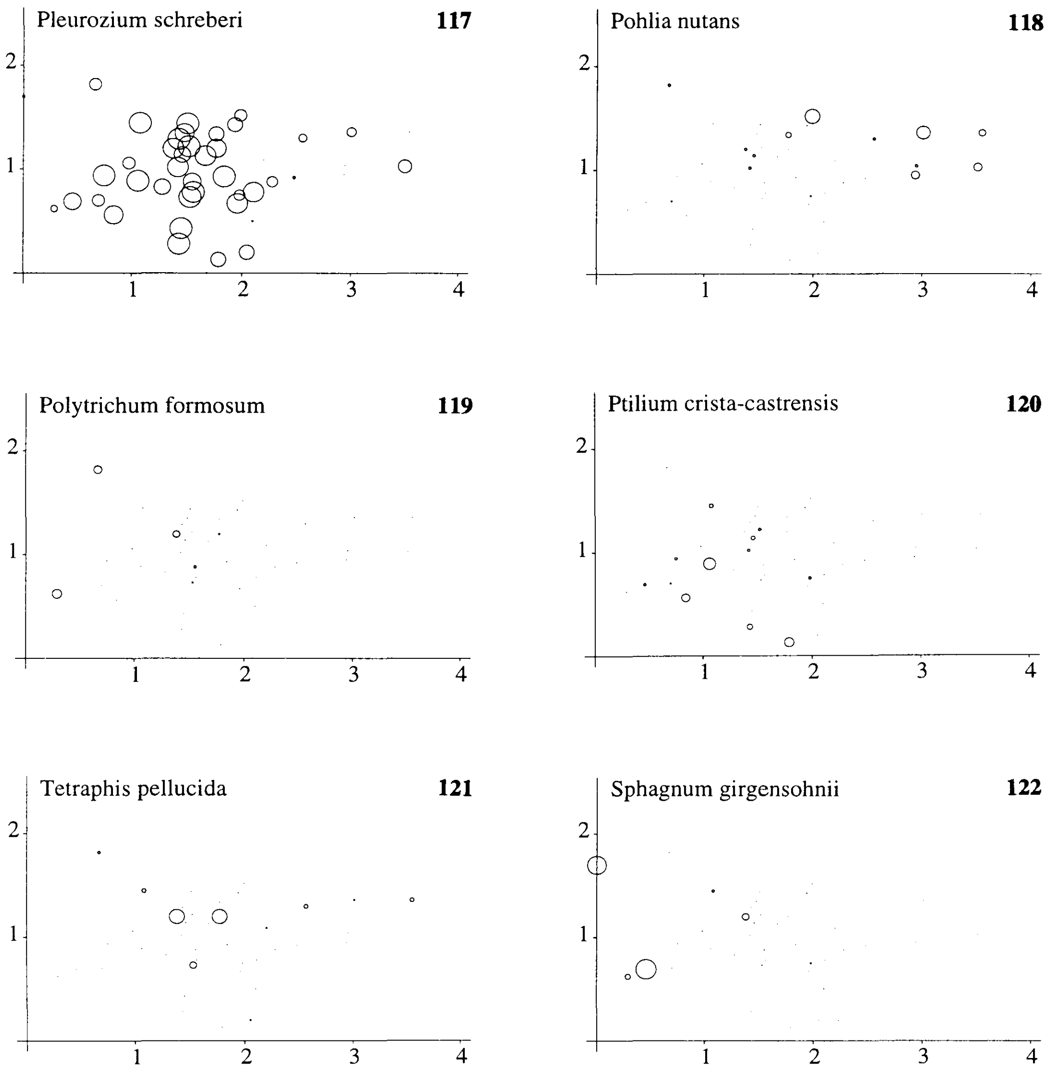
positive correlation between pH and the concentration of total N, the correlations between pH and most variables in the second group, and the correlations of several other variables with variables in both groups (e.g. soil depth, loss on ignition and concentration of P-AL).



Figs 111-116. Lundsneset: distributions of species abundances in the DCA ordination of 45 meso plots (plot Nos 1-5 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 111. Dicranum polysetum. Fig. 112. *Dicranum scoparium*. Fig. 113. *Hylocomium splendens*. Fig. 114. *Hypnum cupressiforme* agg. Fig. 115. *Plagiothecium laetum*. Fig. 116. *Plagiothecium undulatum*.

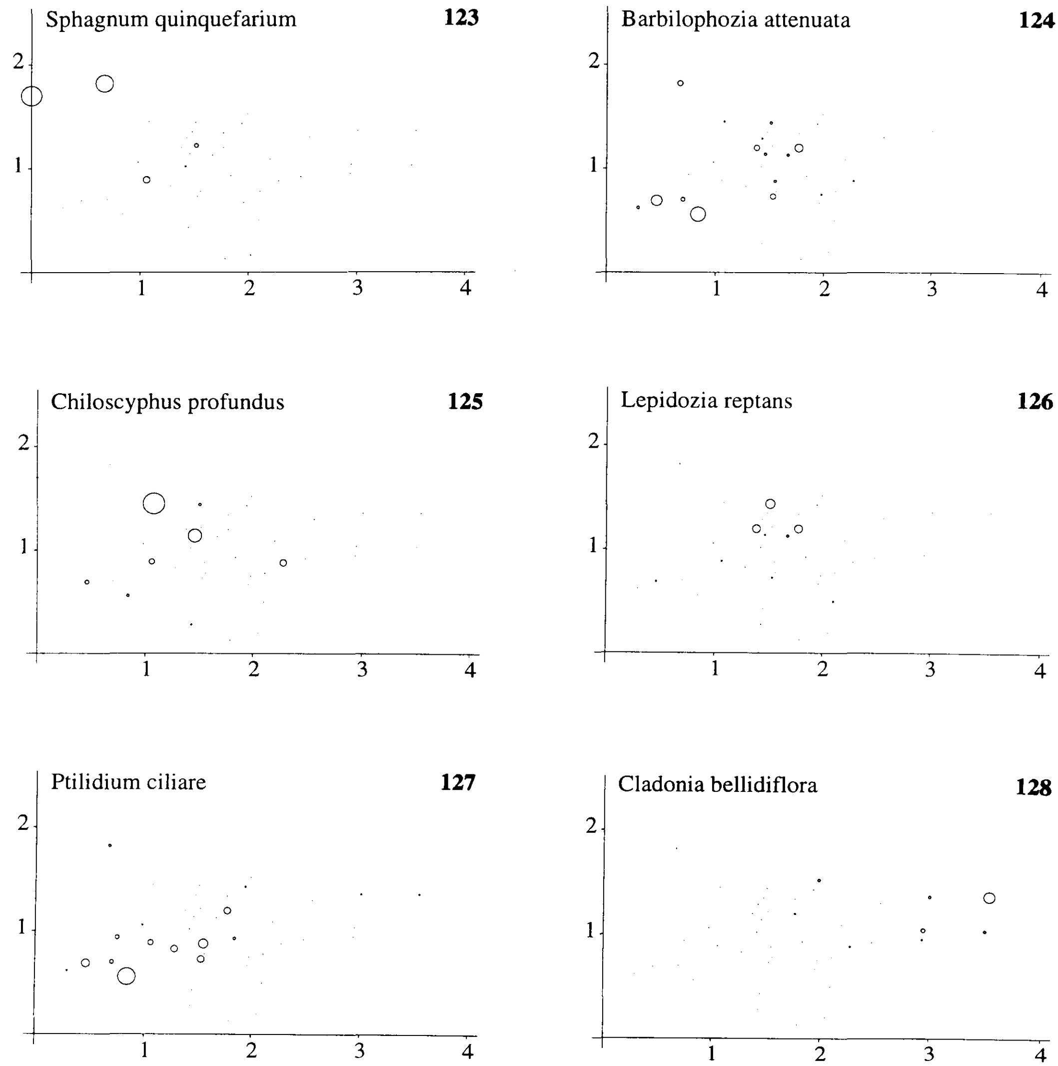
PCA ordination of environmental variables

Eigenvalues of the first two PCA axes were 0.316 and 0.123, thus 43.9% of the variation in measured environmental variables was explained by the first two PCA axes.



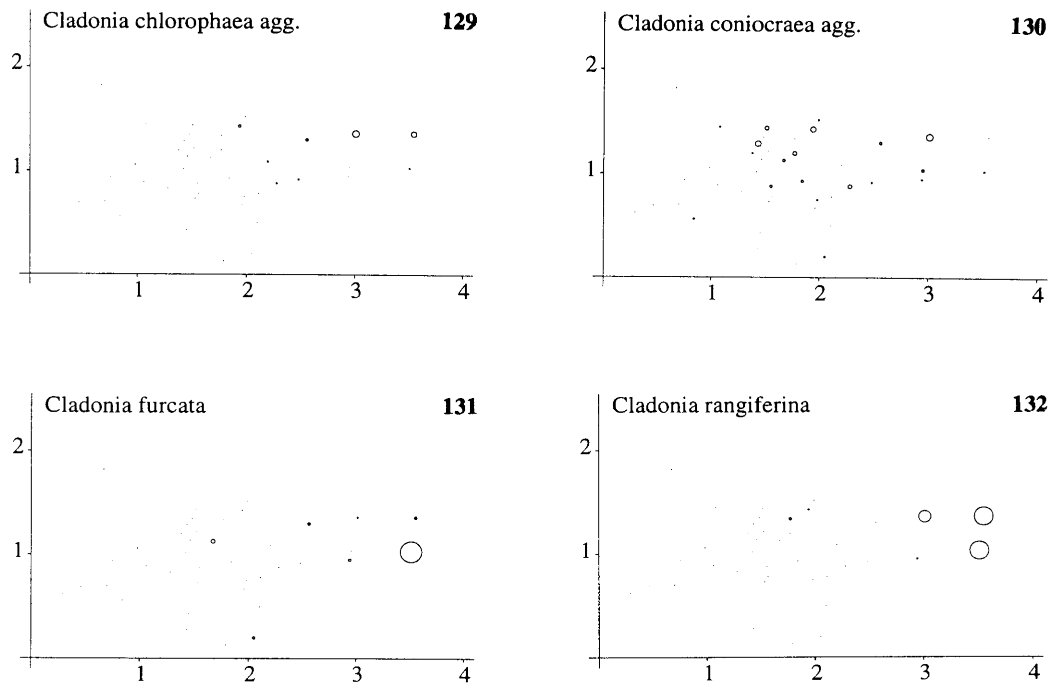
Figs 117-122. Lundsneset: distributions of species abundances in the DCA ordination of 45 meso plots (plot Nos 1-5 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 117. *Pleurozium schreberi*. Fig. 118. *Pohlia nutans*. Fig. 119. *Polytrichum formosum*. Fig. 120. *Ptilium crista-castrensis*. Fig. 121. *Tetraphis pellucida*. Fig. 122. *Sphagnum girgensohnii*.

pH and the cations strongly positively correlated with pH, total N and the macro plot heat index, obtained high loadings on PCA 1 (Fig. 134). Low loadings were obtained by those variables in the two groups of correlated variables which were negatively correlated with some of the above-mentioned variables. This is consistent with the correlations between variables (Tab. 9, Fig. 133).



Figs 123-128. Lundsneset: distributions of species abundances in the DCA ordination of 45 meso plots (plot Nos 1-5 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 123. *Sphagnum quinquefarium*. Fig. 124. *Barbilophozia attenuata*. Fig. 125. *Chiloscyphus profundus*. Fig. 126. *Lepidozia reptans*. Fig. 127. *Ptilidium ciliare*. Fig. 128. *Cladonia bellidiflora*.

The low eigenvalue of PCA 2 may explain why variables strongly separated along this axis were generally weakly negatively correlated or uncorrelated with each other (e.g. the heat indices and Al with K and Mg). Pairwise strongly negatively correlated variables within both of the above-mentioned groups separated slightly along this axis.



Figs 129-132. Lundsneset: distributions of species abundances in the DCA ordination of 45 meso plots (plot Nos 1-5 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 129. *Cladonia chlorophaea* agg. Fig. 130. *Cladonia coccifera* agg. Fig. 131. *Cladonia furcata*. Fig. 132. *Cladonia rangiferina*.

DCA and LNMDS ordination

The plots were relatively evenly distributed along the first two DCA axes (Fig. 135), while the LNMDS ordination was influenced by outliers (Fig. 136); plots 26 (with 13 species), 28 and 29 (with 29 and 30 species; area average was 20.5 species) were separated from the other plots by ca. 1.0 S.D. along LNMDS 1. Plots 16 and 22 were moderate outliers along LNMDS 2. Thus, 90% of the plots were concentrated between 0.1 and 1.8 S.D. along LNMDS 1 and between 0.4 and 1.6 S.D. along LNMDS 2. The gradient lengths were approximately equal for DCA 1 and LNMDS 1, and for DCA 2 and LNMDS 2.

The fraction of variation in vegetation explained by DCA 1 was 18.3%, while for DCA 2 this variation declined to 41.9% of the fraction explained by DCA 1 (Tab. 10). The eigenvalues of DCA 3 and DCA 4 were low (0.112 and 0.060, respectively), corresponding to explained fractions of variation below 5%.

Tab. 9. Grytdalen: Kendall's nonparametric correlation coefficient τ between 32 environmental variables in the 50 meso sample plots (lower triangle), with significance probabilities (upper triangle). Correlations significant at level P < 0.0001 in bold face. n.s. - significance probability > 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 2.

Variable	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
01 MA Inc	*	.0014	n.s.	.0003	n.s.	.0002	**.0000**	.0019	n.s.	n.s.	n.s.	.0492	.0966	n.s.	n.s.	n.s.	.0475	.0405	.0789	n.s.	n.s.	.0108	n.s.	.0208	n.s.	n.s.	n.s.	n.s.	.0447	n.s.	n.s.	.0283
02 MA Asp	-.3410	*	**.0000**	n.s.	n.s.	n.s.	**.0000**	**.0000**	n.s.	n.s.	.0471	.0367	n.s.	.0927	n.s.	n.s.	.0038	.0003	**.0000**	.0011	n.s.	.0654	.0003	.0046	.0080	n.s.	.0069	.0062	**.0000**	.0028	.0207	.0059
03 MA Hi	.1591	**-.8222**	*	.0569	n.s.	n.s.	**.0000**	**.0000**	n.s.	n.s.	.0046	.0036	.0324	.0995	n.s.	.0974	.0641	.0008	.0003	.0089	.0480	.0269	.0001	.0630	.0098	n.s.	.0056	.0033	**.0000**	.0031	.0014	.0031
04 MA BA	-.3865	-.0222	.2000	*	.0553	**.0000**	n.s.	n.s.	n.s.	n.s.	.0669	n.s.	.0285	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0293	n.s.
05 MA Lig	.0698	-.1591	.1591	-.2046	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0208	.0173	n.s.	n.s.	.0032	.0023	.0030	.0412	n.s.	.0033	.0952	.0466	n.s.	n.s.	**.0000**	.0056	n.s.	n.s.	n.s.
06 ME Inc	.3802	-.0739	-.0137	**-.4208**	.0571	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0799	n.s.	n.s.	.0746	.0104	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
07 ME Asp	**-.4354**	**.6240**	**-.5901**	-.0077	-.1463	-.0827	*	**.0000**	n.s.	n.s.	.002	.0007	.0138	n.s.	n.s.	n.s.	.0008	.0002	.0007	.0446	.0238	.0078	.0061	.0656	.0656	.0681	.0322	.0047	**.0000**	.0034	.0446	.0152
08 ME Hi	.3198	**-.6346**	**.6891**	.1508	.1176	-.0848	**-.7600**	*	n.s.	n.s.	.0141	.0204	.0301	n.s.	n.s.	n.s.	n.s.	.0036	.0067	n.s.	.0358	.0149	.0136	n.s.	n.s.	.0864	n.s.	.0266	.0001	.0388	.0598	.0093
09 ME Rou	.0141	-.0499	.0791	.0430	.0317	.0972	-.1268	.0033	*	n.s.	.0059	.0207	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0732	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0631	n.s.
10 ME Con	-.0876	.0265	-.0231	.0711	-.0780	-.0546	-.0083	.0345	-.0108	*	n.s.	n.s.	n.s.	.0746	.0774	.0126	n.s.	.0301	.0041	.0542	n.s.	n.s.	.0283	.0015	.0009	n.s.	.0052	.0522	n.s.	n.s.	n.s.	n.s.
11 ME Smi	-.1500	.2080	-.2969	-.1920	-.0564	-.0034	.3777	-.2479	-.2803	.1439	*	**.0000**	**.0000**	n.s.	n.s.	n.s.	.0005	**.0000**	.0017	n.s.	.0555	.0697	n.s.	.0328	.0289	n.s.	.0083	.0233	.0002	.0223	.0289	.0122
12 ME Sme	-.2043	.2135	-.2979	-.1343	-.0863	-.0283	.3351	-.2286	-.2299	.0614	**.6320**	*	**.0000**	.0337	.0284	n.s.	.0010	.0018	.0157	.0170	n.s.	.0022	n.s.	.0141	.0370	.0772	.0186	.0101	.0005	.0056	.0135	.0830
13 ME Sma	-.1725	.0929	-.2185	-.2237	.0422	.1737	.2437	-.2135	-.0699	.0688	**.4620**	**.6292**	*	n.s.	n.s.	n.s.	.0731	.0394	n.s.	n.s.	.0531	.0006	n.s.	n.s.	n.s.	n.s.	.0990	n.s.	.0129	.0065	.0048	n.s.
14 LitCC	.0246	-.1755	.1719	.0953	.2452	-.0138	-.0850	.0512	.0715	-.1802	-.1532	-.2157	-.0491	*	**.0000**	.0262	n.s.	.0244	.0018	.0003	n.s.	n.s.	.0997	.0229	.0006	n.s.	.0057	.0009	n.s.	n.s.	n.s.	n.s.
15 LitACD	.0173	-.1684	.1684	.0882	.2524	-.0052	-.0850	.0529	.0888	-.1785	-.1604	-.2226	-.0474	**.9696**	*	.0210	n.s.	.0234	.0016	.0002	n.s.	n.s.	.0962	.0240	.0008	n.s.	.0066	.0006	n.s.	n.s.	n.s.	n.s.
16 Mois	-.1037	.1269	-.1678	.0980	-.1211	-.1753	.1149	-.0482	-.0165	.2446	.0247	.0833	-.0223	-.2237	-.2322	*	n.s.	n.s.	.0254	.0056	n.s.	n.s.	**.0000**	.0124	.0003	.0066	.0006	.0014	n.s.	.0244	.0358	n.s.
17 LI	-.2043	.2936	-.1878	.1485	-.1677	-.2524	.3298	-.1587	-.0892	-.0008	.3508	.3258	.1768	-.0197	-.0214	.0245	*	-.3455	-.3330	-.1849	.0409	.1031	.1816	.3108	.1505	-.1881	-.2405	-.2323	-.3926	-.2323	-.0458	-.1636
18 pH_{H_2O}	.2210	-.3851	.3561	.1410	.3181	.0079	-.3779	.2980	.0236	-.2229	**-.4357**	-.3231	-.2126	-.2373	.2392	-.1455	-.3455	*	**.0000**	**.0000**	n.s.	n.s.	.0015	.0001	**.0000**	n.s.	**.0000**	.0001	**.0000**	.0075	n.s.	.0003
19 pH_{CaCl_2}	.1894	**-.4407**	.3793	.1228	.3280	.0166	-.3463	.2769	-.0105	-.2949	-.3314	-.2493	-.1171	.3285	.3322	-.2285	-.3330	**.8421**	*	**.0000**	n.s.	n.s.	**.0000**	**.0000**	**.0000**	n.s.	**.0000**	**.0000**	**.0000**	.0026	n.s.	.0003
20 Ca	.1002	-.3297	.2649	.1150	.3059	.0140	-.1970	.1249	.0494	-.1888	-.1474	-.2352	-.0289	.3654	.3705	-.2702	-.1849	**.4972**	**.6491**	*	.0066	n.s.	.0003	**.0000**	**.0000**	n.s.	**.0000**	**.0000**	.0046	.0011	n.s.	.0113
21 Mg	-.1333	.1014	-.2002	-.1423	.2100	.0733	.2216	-.2049	-.1203	.0246	.1934	.1048	.1904	-.0102	-.0051	-.0057	.0409	-.0589	.0069	.2653	*	.0014	n.s.	n.s.	n.s.	n.s.	n.s.	.0474	n.s.	n.s.	n.s.	n.s.
22 K	-.2633	.1866	-.2240	-.0639	.1455	.0370	.2610	-.2376	-.1764	-.0673	.1831	.3012	.3388	.1400	.1417	-.1037	.1031	.0191	.1004	.1118	.3110	*	n.s.	n.s.	.0576	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0895
23 Na	-.1089	.3654	-.3961	-.0043	-.3024	-.0881	.2692	-.2408	-.0775	.2150	.1508	.1493	.0734	-.1656	-.1673	**.4678**	.1816	-.3257	**-.4327**	-.3518	.0335	.0073	*	.0030	.0001	n.s.	**.0000**	**.00000**	.0016	.0039	.0721	n.s.
24 H^+	-.2379	.2871	-.1883	.0128	-.1717	-.1490	.1806	-.0367	-.0692	.3119	.2155	.2418	.0322	-.2288	-.2271	.2441	.3108	-.4036	**-.4690**	**-.5396**	-.1445	.0188	.2989	*	**.0000**	n.s.	**.0000**	.0001	.0102	.0030	n.s.	n.s.
25 Al	-.0863	.2683	-.2615	-.1627	-.2048	-.0239	.1806	-.1069	.0198	.3250	.2206	.2055	.0800	-.3466	-.3381	.3567	.1505	**-.5526**	**-.6664**	**-.6784**	-.1396	-.1853	.3763	**.5347**	*	n.s.	**.0000**	**.0000**	.0097	.0001	.0721	.0028
26 Fe	.1490	-.0946	.0128	-.0349	-.0200	-.0370	-.1789	.1673	.0775	.0148	-.1542	-.1741	-.0816	-.0581	-.0563	.2653	-.1881	.1299	.1073	.0433	-.0449	-.1559	.0727	-.0563	.0531	*	-.0171	-.0547	.1167	.0090	-.1004	.1396
27 Mn	.0967	-.2734	.2803	.1337	.1333	.0584	-.2101	.1429	.0429	-.2741	-.2666	-.2319	-.1624	.2783	.2732	-.3339	-.2405	**.4885**	**.6352**	**.6065**	-.0008	.0841	**-.4449**	**-.4106**	**-.6833**	-.0171	*	**.0000**	.0035	**.0000**	.0069	.0001
28 Zn	.1577	-.2768	.2973	-.0026	**.5847**	.0453	-.2774	.2163	.0527	-.1904	-.2291	-.2533	-.0981	.3347	.3432	-.3127	-.2323	.3933	**.4933**	**.5265**	.1935	.0792	**-.4694**	-.3861	**-.4727**	-.0547	**.3976**	*	.0002	.0136	n.s.	.0493
29 Total N	.2065	**-.4455**	**.4660**	.0639	.2850	.0173	**-.4102**	.3943	.0626	-.0213	-.3705	-.3424	-.2449	.0632	.0649	-.1282	-.3926	**.5665**	**.4881**	.2767	-.0759	-.1020	-.3078	-.2506	-.2522	.1167	.2849	.3616	*	.0002	.0621	.0002
30 P-AL	.1176	-.3024	.2990	.1252	-.0270	-.0173	-.2872	.2016	.0363	-.1067	-.2308	-.2731	-.2679	-.0273	-.0393	-.2196	-.2323	.2737	.3081	.3192	.0906	.0449	-.2816	-.2989	-.3861	.0090	**.4351**	.2408	.3600	*	**.0000**	.0025
31 P	.0235	-.2343	.3228	.2206	-.1298	-.0469	-.1970	.1837	.1830	-.1198	-.2206	-.2434	-.2778	.0461	.0341	-.2049	-.0458	.1022	.1263	.1543	-.0776	-.0906	-.1755	-.0857	-.1755	-.1004	.2637	.0824	.1820	**.5380**	*	.0255
32 S	.2257	-.2786	.2990	.0366	.1229	.1243	-.2380	.2539	.0066	-.0197	-.2530	-.1708	-.1509	.1178	.1229	-.1184	-.1636	.3707	.3669	.2473	-.0857	.1657	-.1086	-.0841	-.2914	.1396	.3927	.1918	.3600	.2947	.2180	*

Correlations between DCA and LNMDS ordination axes and between ordination axes and environmental variables

The correlation between DCA 1 and LNMDS 1 was very strong (τ = 0.798), while LNMDS 2 was correlated, but considerably less strongly so, with DCA 2 as well as with DCA 3 (τ = 0.345 and 0.327, respectively). The variables most strongly correlated with DCA 1 and LNMDS 1 were the same (Tab. 11), but correlations with DCA 1 were generally stronger.

Variables strongly positively correlated with DCA 1 (and LNMDS 1) were pH (Fig. 142), and concentrations of Ca (Fig. 143), Mn (Fig. 147), Zn (Fig. 148) and total N (Fig. 149), and the heat indices (Figs 138, 141), while concentations of Al (Fig. 146), Na (Fig. 144), H^+ (Fig. 145) and aspect unfavourability (Figs 137, 140) were negatively correlated with DCA 1. Other variables that were positively correlated with the first axes were P-AL (Fig. 150) and the macro plot light index (Fig. 139). Soil moisture was slightly negatively correlated with DCA 1.

No variable was strongly correlated with axes of order higher than 1 (τ < 0.3, P > 0.004).

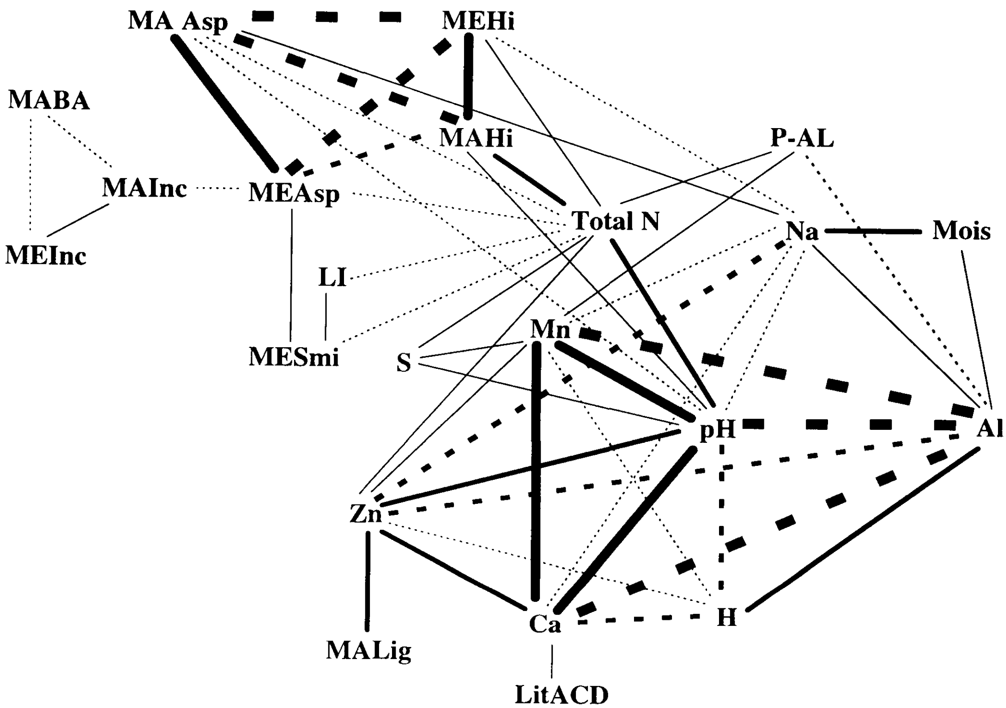


Fig. 133. Grytdalen: plexus diagram visualizing Kendall's τ between pairs of environmental variables. Significance probabilities for τ are indicated by lines with different thickness (in order of decreasing thickness): $|\tau| \geq 0.60$, $0.45 \leq |\tau| < 0.60$, $0.35 \leq |\tau| < 0.45$. Continuous lines refer to positive correlations, broken lines to negative.

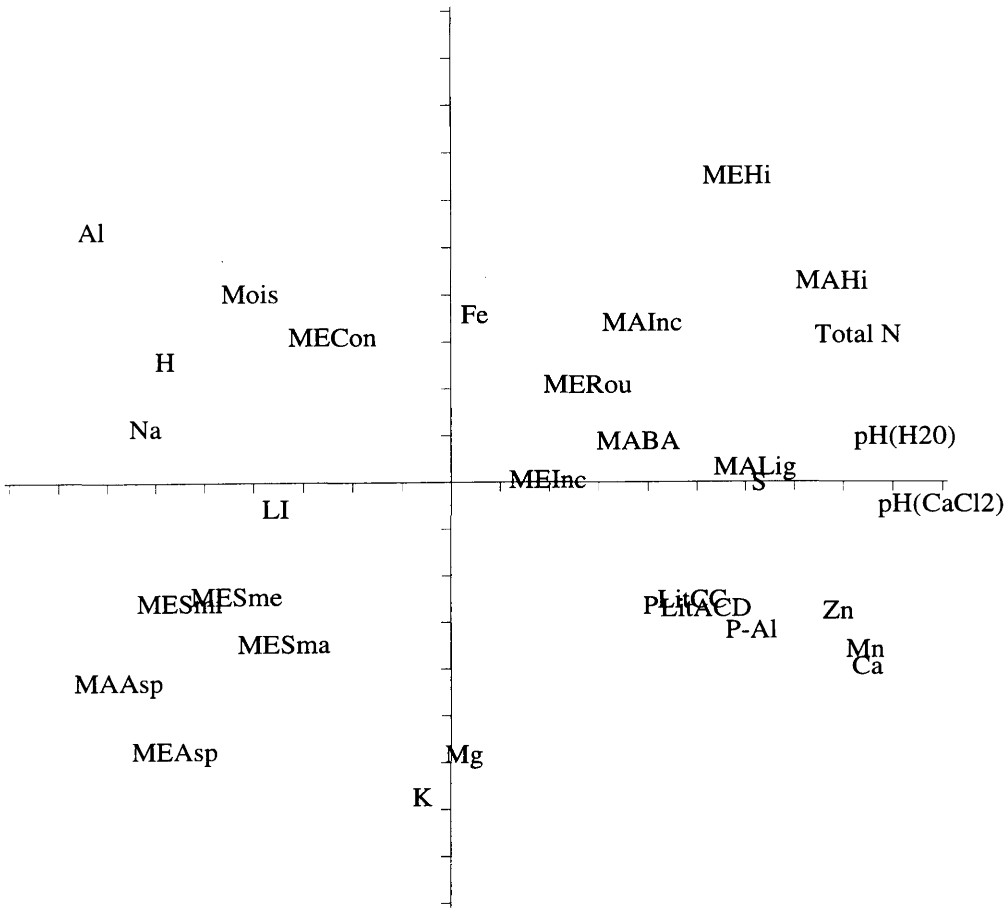
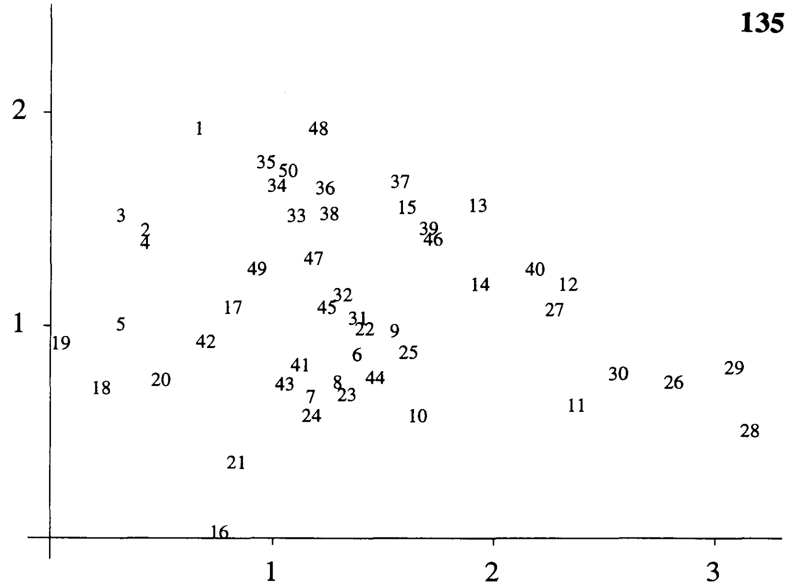
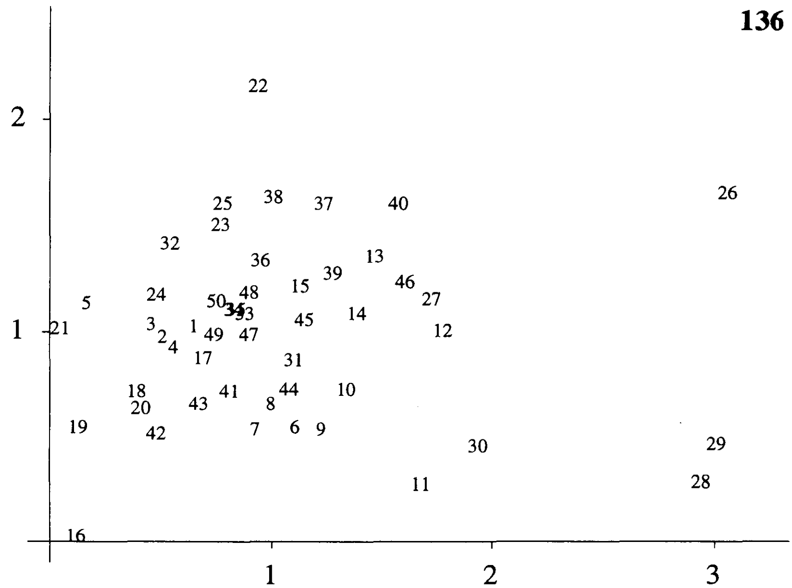


Fig. 134. Grytdalen: PCA ordination of 32 environmental variables (names abbreviated in accordance with Tab. 2), axes 1 (horizontal) and 2 (vertical). Positions of variables in the ordination give the head of variable vectors.

Tab. 10. Grytdalen: Eigenvalues and the fraction of variation explained for DCA axes 1-4.

	DCA 1	DCA 2	DCA 3	DCA 4
Eigenvalues	0.429	0.180	0.112	0.060
Fraction of variation explained	0.183	0.077	0.048	0.026

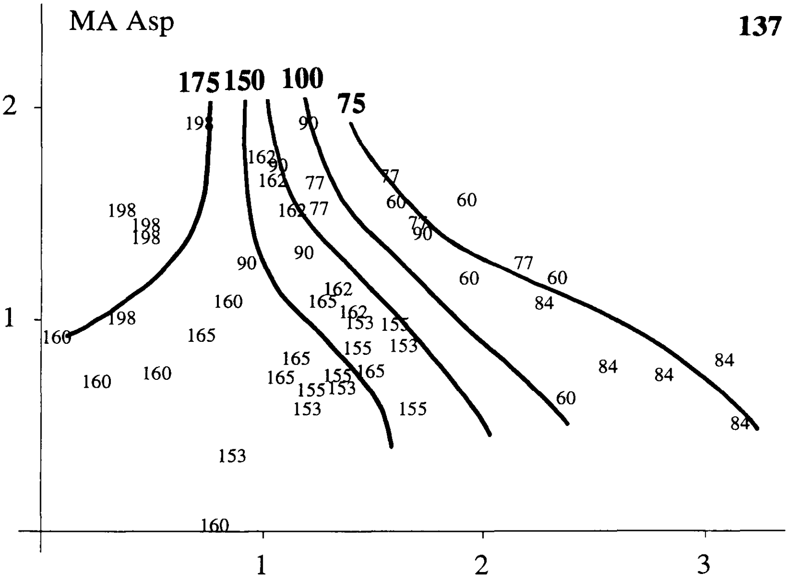


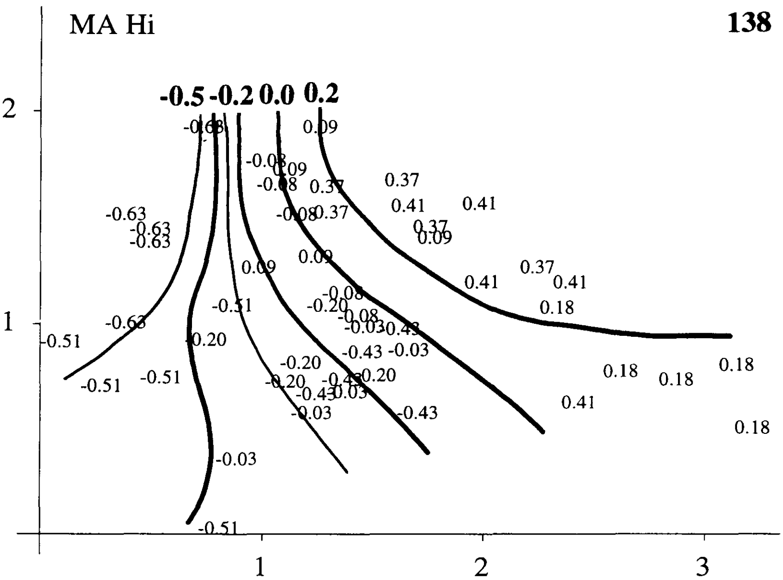


Figs 135-136. Grytdalen: ordinations of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Meso plot numbers are plotted onto the sample plot positions. Fig. 135. DCA ordination. Scaling of axes in S.D. units. Fig. 136. LNMDS ordination. Axes linearly rescaled in S.D. units.

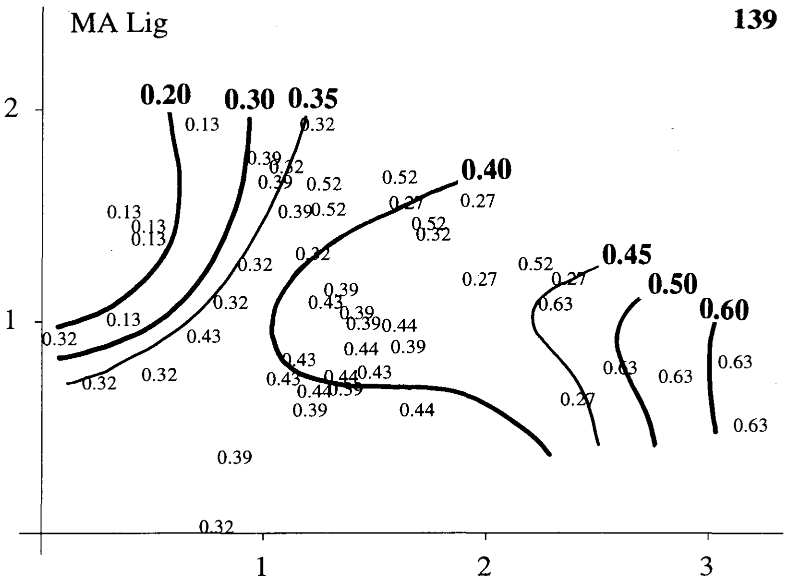
Tab. 11. Grytdalen: Kendall's nonparametric correlation coefficient τ between DCA and LNMDS axes, and between 32 environmental variables in the 50 meso sample plots and sample plot positions with respect to DCA and LNMDS axes, and their significance probabilities. Correlations significant at level P < 0.0001 in bold face. n.s. - significance probability > 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 2.

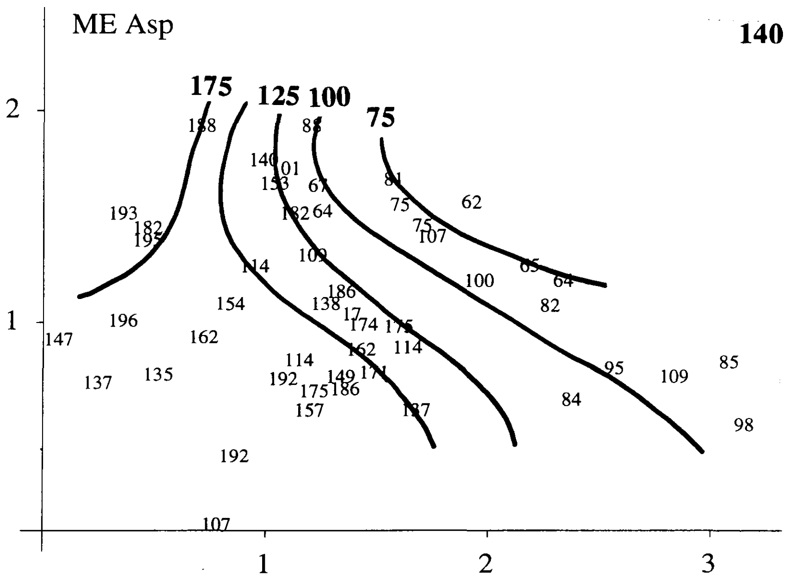
Variable	DCA 1		DCA 2		DCA 3		DCA 4		LNMDS 1		LNMDS 2	
	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P
LNMDS 1	**.7976**	**.0000**	.0351	n.s.	-.1363	n.s.	-.0563	n.s.				
LNMDS 2	.1380	n.s.	.3747	.0001	.3273	.0008	.2049	.0358				
01 MA Inc	.1978	.0545	.1403	n.s.	.0340	n.s.	-.0131	n.s.	.3041	.0031	-.0096	n.s.
02 MA Asp	**-.5324**	**.0000**	-.0332	n.s.	-.1235	n.s.	-.2411	.0173	**-.4557**	**.0000**	-.1814	.0731
03 MA Hi	**.5494**	**.0000**	.1423	n.s.	.1610	n.s.	.2070	.0409	**.4694**	**.0000**	.2905	.0041
04 MA BA	.1269	n.s.	-.0826	n.s.	.1031	n.s.	.1627	n.s.	-.0043	n.s.	.0656	n.s.
05 MA Lig	.4157	.0001	-.2065	.0447	-.1821	.0767	-.0601	n.s.	.3965	.0001	-.0200	n.s.
06 ME Inc	.0535	n.s.	.2198	.0254	-.0700	n.s.	-.2231	.0233	.1967	.0454	-.0617	n.s.
07 ME Asp	**-.4120**	**.0000**	-.1330	n.s.	-.0919	n.s.	-.1510	n.s.	**-.4251**	**.0000**	-.1231	n.s.
08 ME Hi	.3845	.0001	.1118	n.s.	.2473	.0113	.2065	.0343	.3192	.0011	.2702	.0056
09 ME Rou	.0181	n.s.	.1846	.0607	-.1599	n.s.	.2209	.0248	.0972	n.s.	.0676	n.s.
10 ME Con	-.2167	.0271	.0279	n.s.	.1067	n.s.	.0804	n.s.	-.2183	.0260	.0016	n.s.
11 ME Smi	-.2445	.0155	-.1031	n.s.	.2632	.0091	-.0911	n.s.	-.3331	.0010	.1883	.0623
12 ME Sme	-.2352	.0170	-.1526	n.s.	.1857	.0595	-.0388	n.s.	-.3441	.0005	.1262	n.s.
13 ME Sma	-.0899	n.s.	-.1789	.0692	.0882	n.s.	-.0585	n.s.	-.1756	.0745	.0420	n.s.
14 LitCC	.2612	.0094	-.0785	n.s.	-.2647	.0085	.0734	n.s.	.2681	.0077	.0461	n.s.
15 LitACD	.2561	.0109	-.0871	n.s.	-.2834	.0048	.0683	n.s.	.2630	.0089	.0341	n.s.
16 Mois	-.2686	.0059	-.0906	n.s.	.1265	n.s.	.0857	n.s.	-.2784	.0043	.0824	n.s.
17 LI	-.2585	.0082	-.0180	n.s.	.2421	.0133	.0622	n.s.	-.3305	.0007	.2618	.0074
18 pH_{H20}	**.5509**	**.0000**	-.2339	.0222	-.1680	n.s.	.0277	n.s.	**.5076**	**.0000**	-.1992	.0515
19 pH_{CaCl2}	**.6387**	**.0000**	-.2648	.0096	-.1540	n.s.	.0623	n.s.	**.5504**	**.0000**	-.1402	n.s.
20 Ca	**.5380**	**.0000**	-.2571	.0084	-.1282	n.s.	.0073	n.s.	**.4955**	**.0000**	-.0433	n.s.
21 Mg	-.0008	n.s.	-.2898	.0030	-.0204	n.s.	-.1363	n.s.	-.0106	n.s.	-.0955	n.s.
22 K	-.0498	n.s.	-.2147	.0278	-.0857	n.s.	-.1102	n.s.	-.0890	n.s.	-.0955	n.s.
23 Na	**-.4841**	**.0000**	-.0416	n.s.	.0971	n.s.	-.1004	n.s.	**-.4514**	**.0000**	-.1151	n.s.
24 H^+	**-.4204**	**.0000**	.1461	n.s.	.1673	.0864	.1494	n.s.	**-.4531**	**.0000**	.1608	.0994
25 Al	**-.5167**	**.0000**	.2294	.0187	.1624	n.s.	.0857	n.s.	**-.4873**	**.0000**	.0710	n.s.
26 Fe	.0318	n.s.	-.1135	n.s.	.0220	n.s.	.1543	n.s.	.0580	n.s.	-.1380	n.s.
27 Mn	**.5102**	**.0000**	-.0752	n.s.	-.1527	n.s.	-.0106	n.s.	**.5069**	**.0000**	-.0416	n.s.
28 Zn	**.5739**	**.0000**	-.1200	n.s.	-.2106	.0244	-.0253	n.s.	**.5543**	**.0000**	.0318	n.s.
29 Total N	**.4873**	**.0000**	-.0139	n.s.	-.0514	n.s.	.0808	n.s.	**.4645**	**.0000**	-.0514	n.s.
30 P-AL	.3143	.0013	.1298	n.s.	.0367	n.s.	.0612	n.s.	.3306	.0007	.0563	n.s.
31 P	.1690	.0834	.2392	.0142	.0939	n.s.	.1869	.0554	.1755	.0721	.2506	.0102
32 S	.2882	.0031	.0286	n.s.	-.0155	n.s.	.0808	n.s.	.3110	.0014	.0237	n.s.



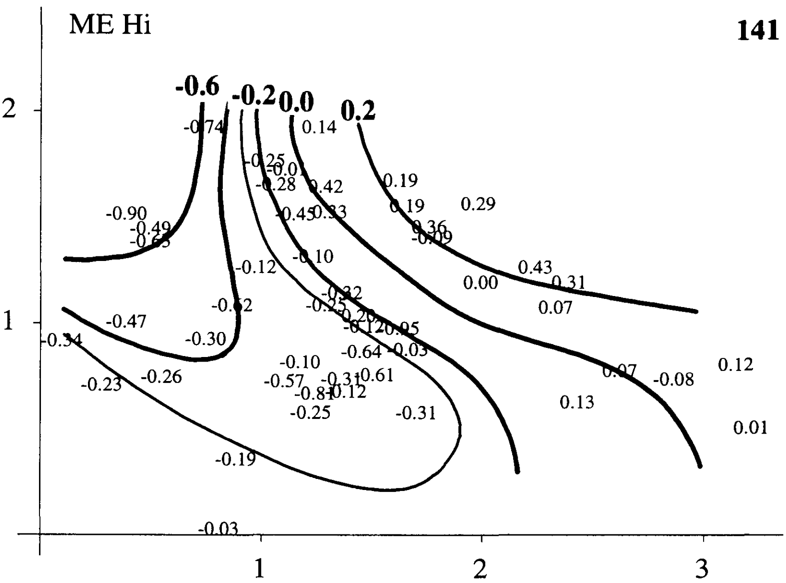


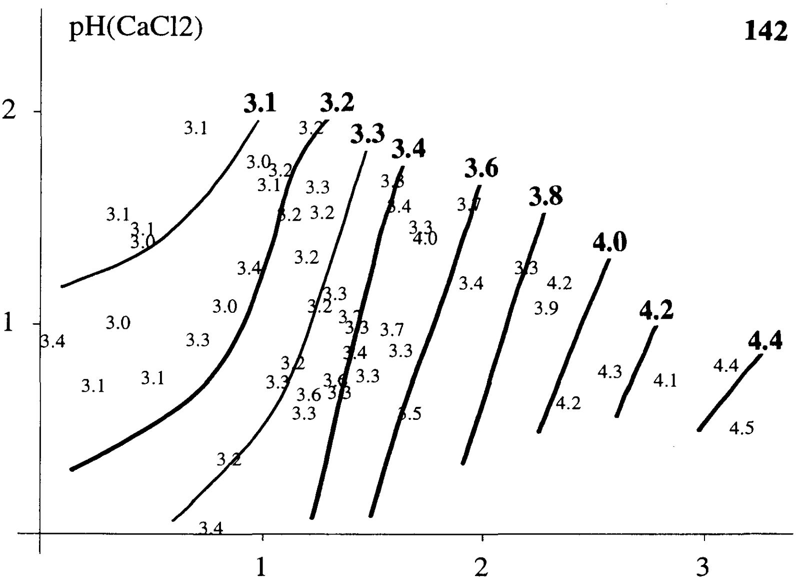
Figs 137-138. Grytdalen: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots' positions. Scaling of axes in S.D. units. Fig. 137. MA Asp (R^2 = 0.791). Fig. 138. MA Hi (R^2 = 0.774). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.



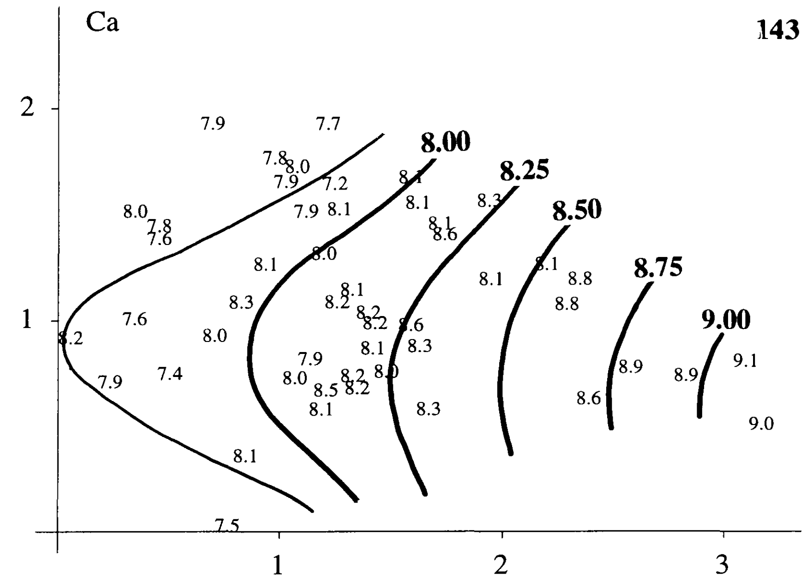


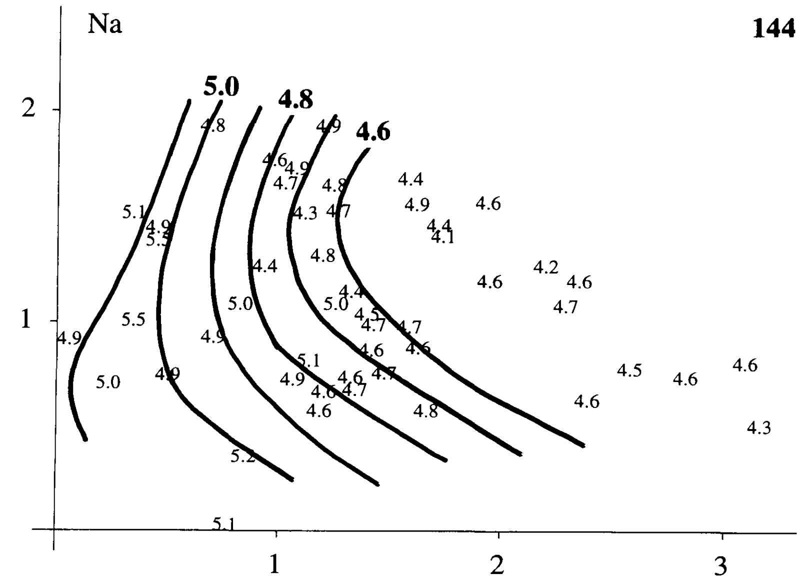
Figs 139-140. Grytdalen: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots' positions. Scaling of axes in S.D. units. Fig. 139. MA Lig (R^2 = 0.596). Fig. 140. ME Asp (R^2 = 0.609). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.



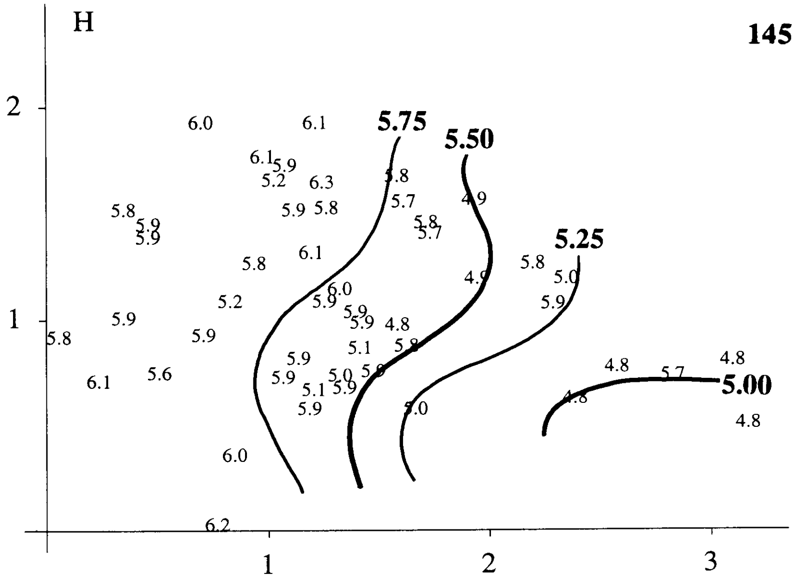


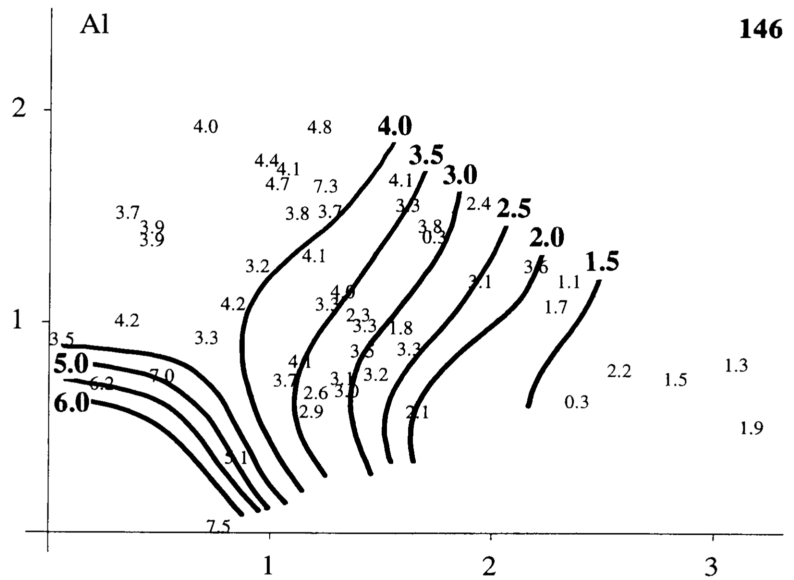
Figs 141-142. Grytdalen: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 141. ME Hi (R^2 = 0.609). Fig. 142. pH_{CaCl2} (R^2 = 0.809). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.



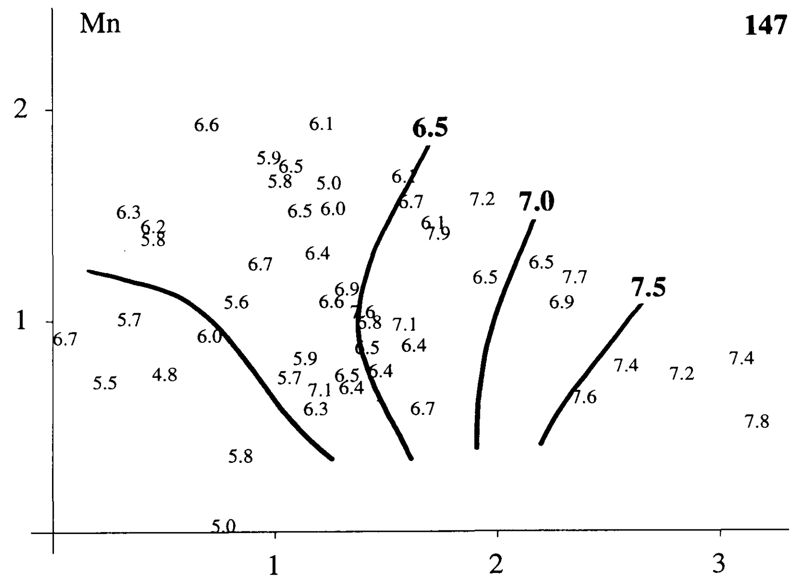


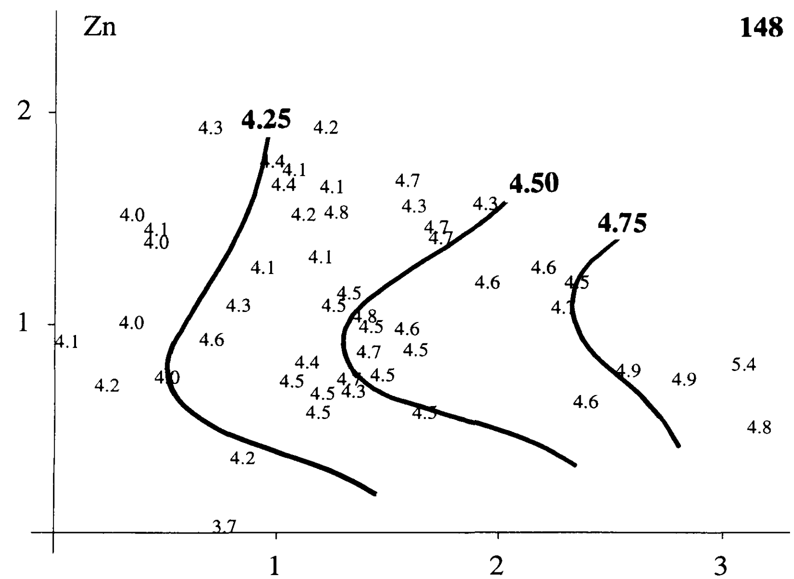
Figs 143-144. Grytdalen: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots' positions. Scaling of axes in S.D. units. Fig. 143. Ca ($R^2 = 0.709$). Fig. 144. Na ($R^2 = 0.515$). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.



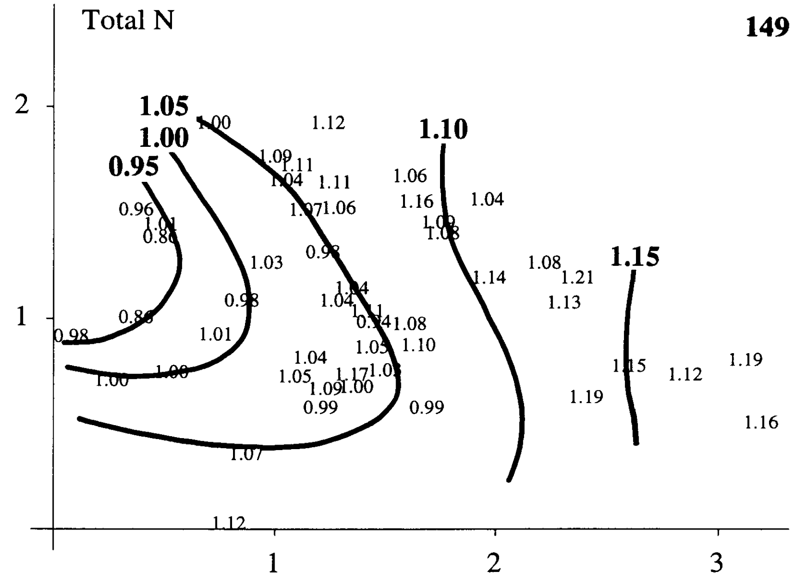


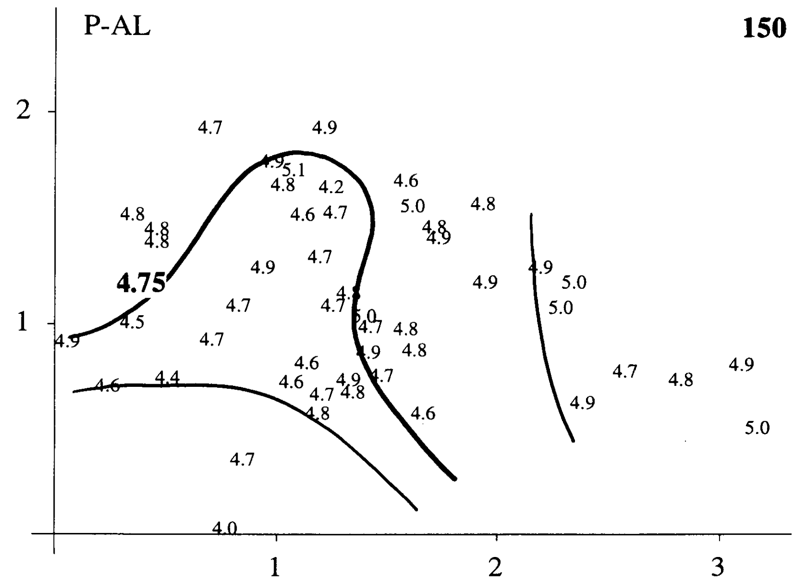
Figs 145-146. Grytdalen: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 145. H^+ ($R^2 = 0.441$). Fig. 146. Al ($R^2 = 0.685$). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.



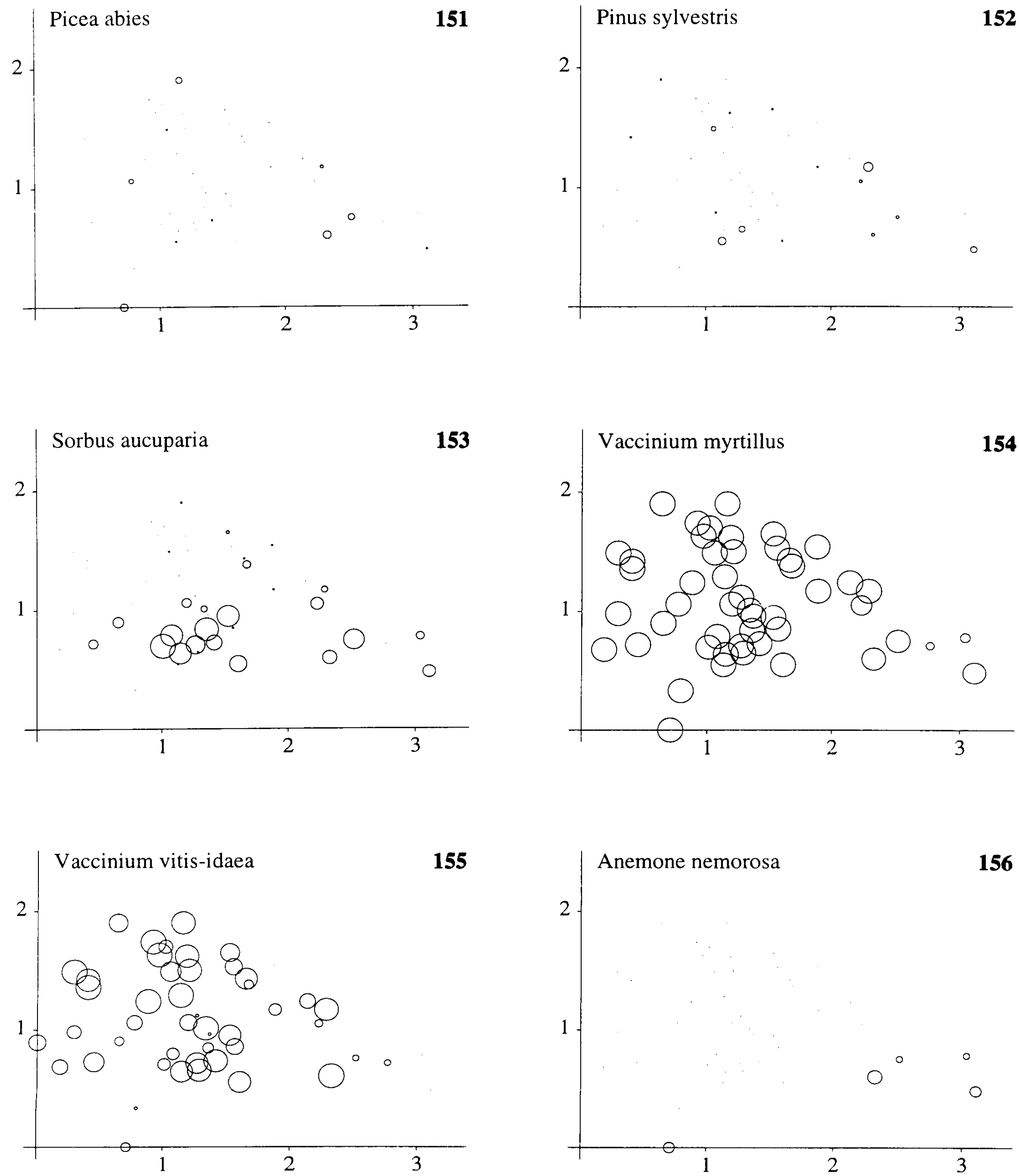


Figs 147-148. Grytdalen: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots' positions. Scaling of axes in S.D. units. Fig. 147. Mn (R^2 = 0.593). Fig. 148. Zn (R^2 = 0.729). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.

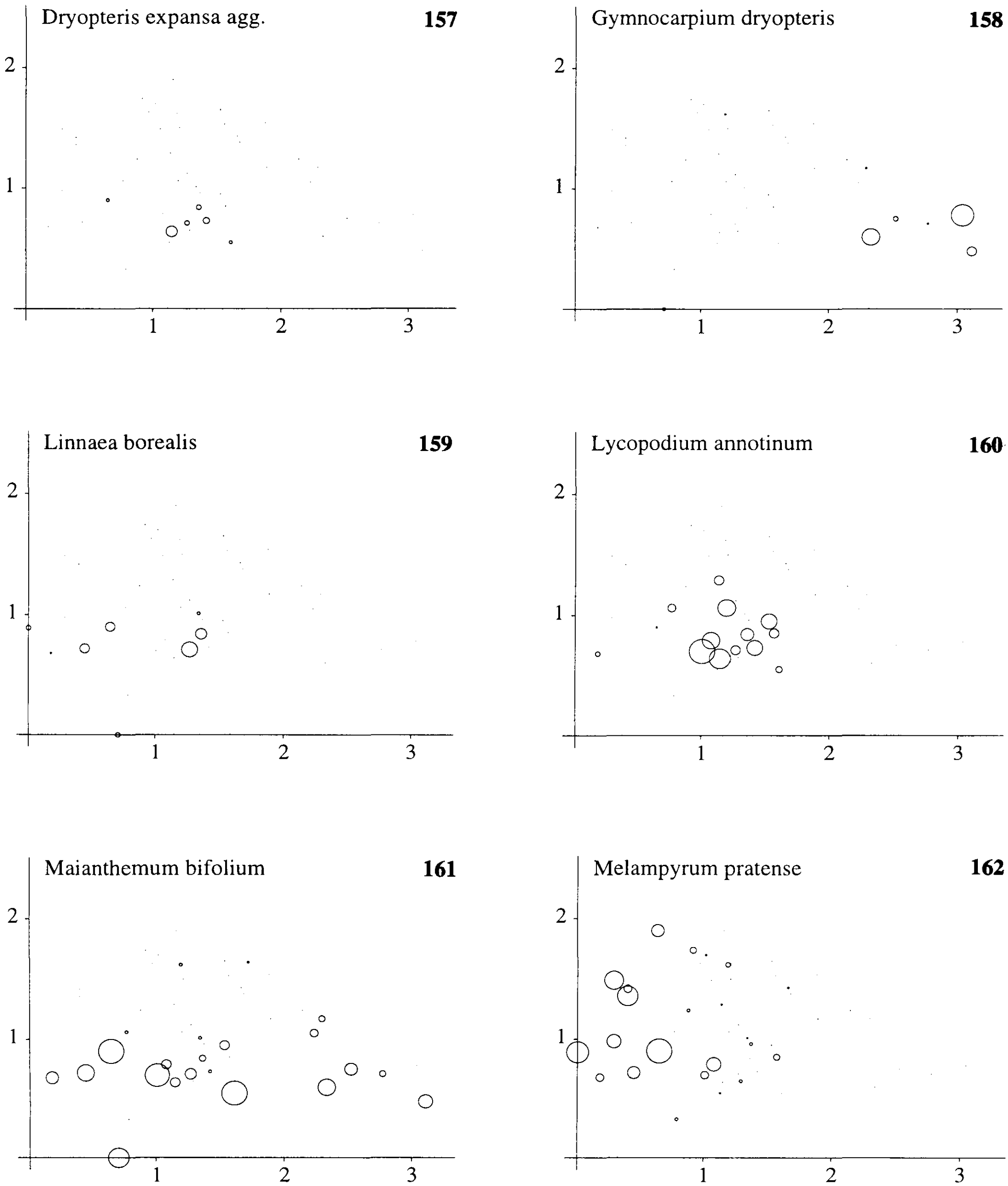




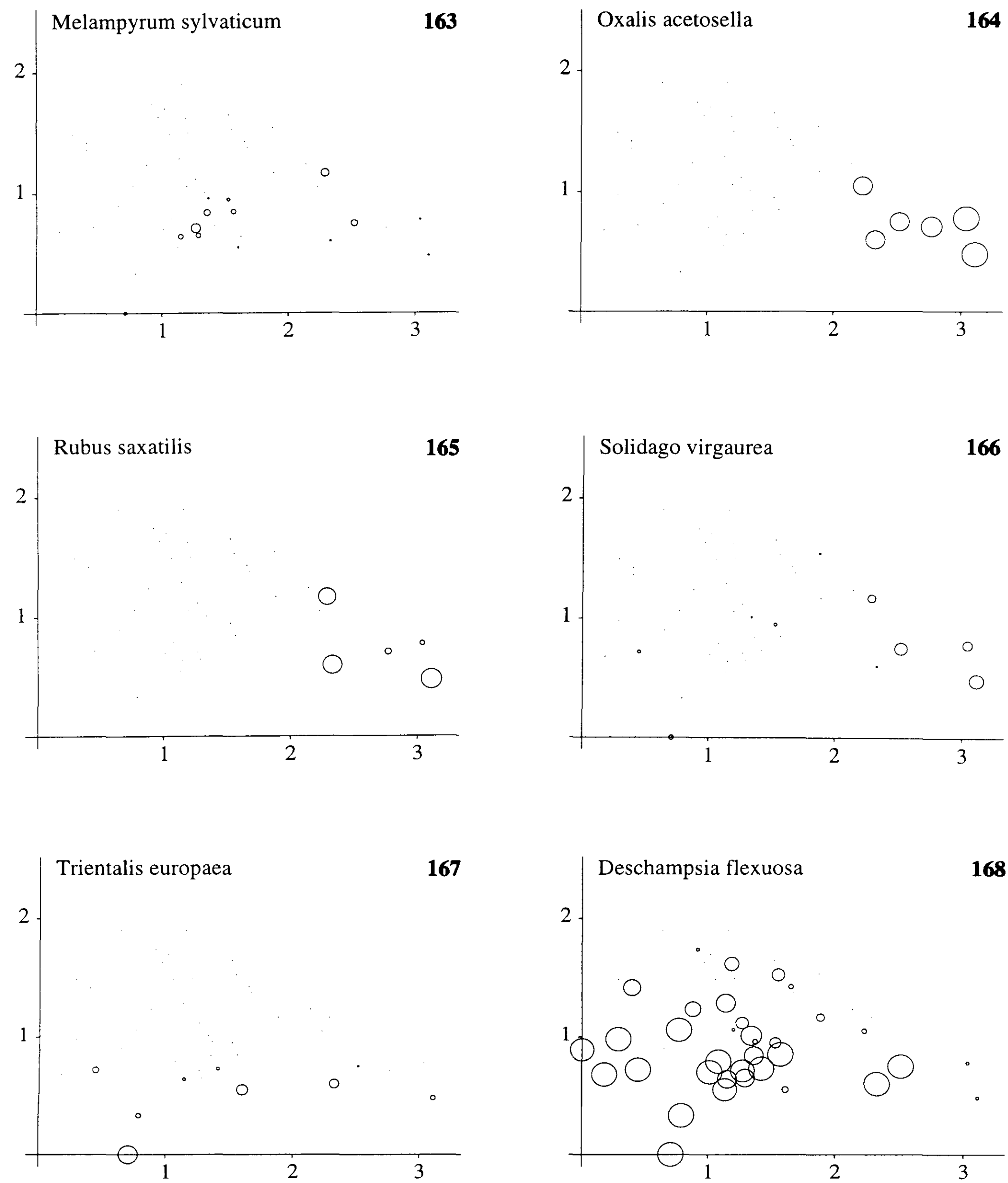
Figs 149-150. Grytdalen: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 149. Total N (R^2 = 0.641). Fig. 150. P-AL (R^2 = 0.459). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.



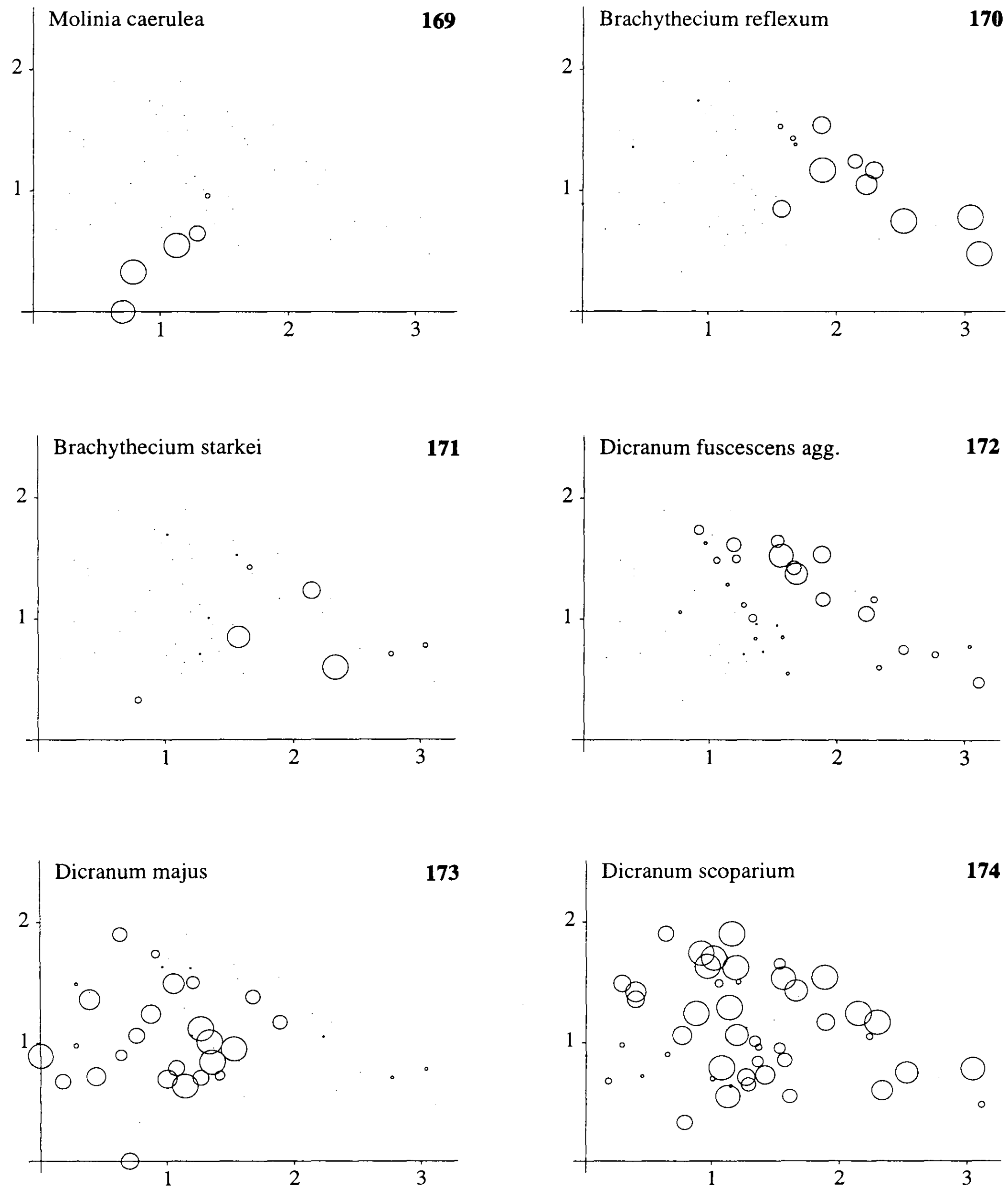
Figs 151-156. Grytdalen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 151. *Picea abies*. Fig. 152. *Pinus sylvestris*. Fig. 153. *Sorbus aucuparia*. Fig. 154. *Vaccinium myrtillus*. Fig. 155. *Vaccinium vitis-idaea*. Fig. 156. *Anemone nemorosa*.



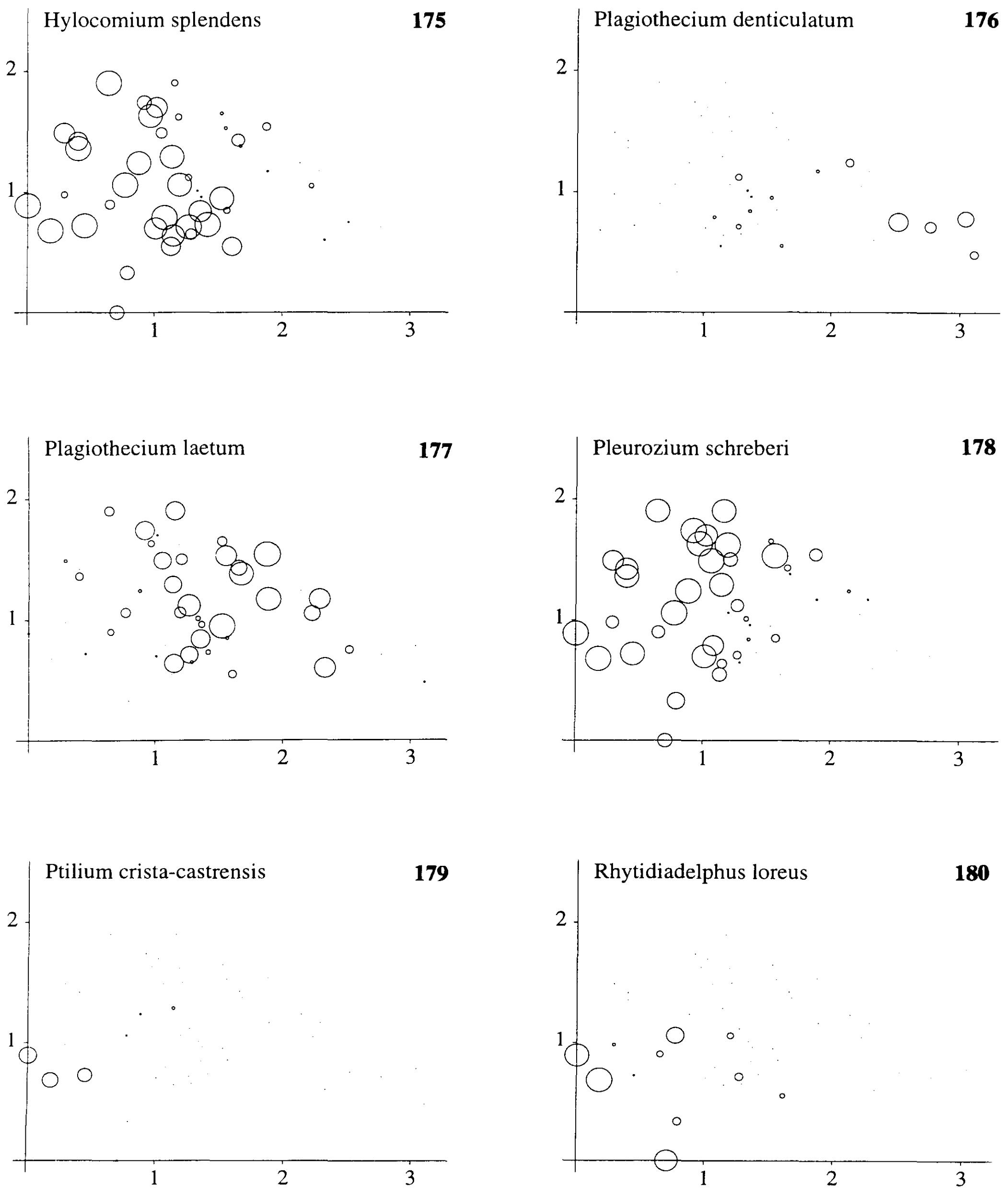
Figs 157-162. Grytdalen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 157. *Dryopteris expansa* agg. Fig. 158. *Gymnocarpium dryopteris*. Fig. 159. *Linnaea borealis*. Fig. 160. *Lycopodium annotinum*. Fig. 161. *Maianthemum bifolium*. Fig. 162. *Melampyrum pratense*.



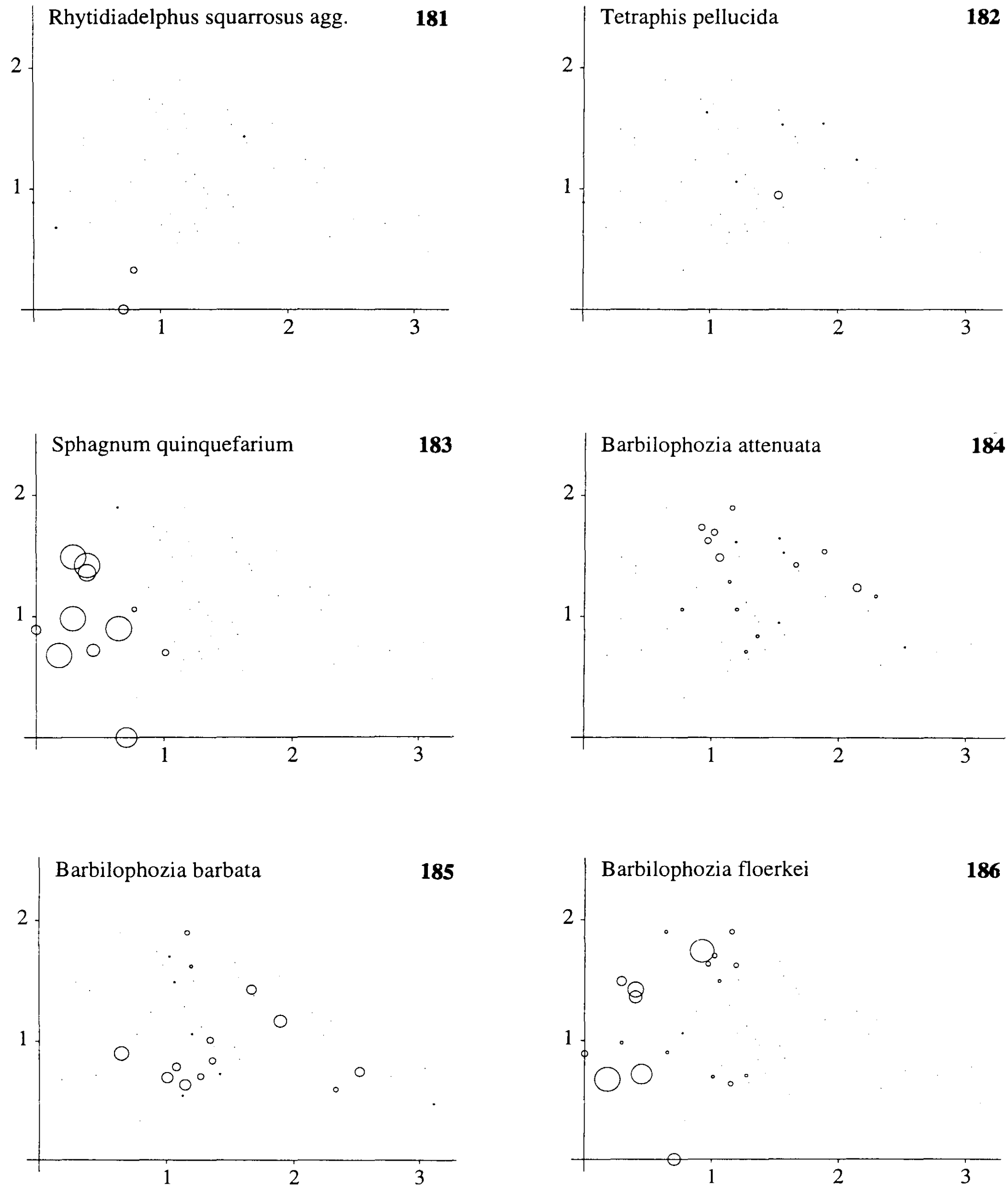
Figs 163-168. Grytdalen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 163. *Melampyrum sylvaticum*. Fig. 164. *Oxalis acetosella*. Fig. 165. *Rubus saxatilis*. Fig. 166. *Solidago virgaurea*. Fig. 167. *Trientalis europaea*. Fig. 168. *Deschampsia flexuosa*.



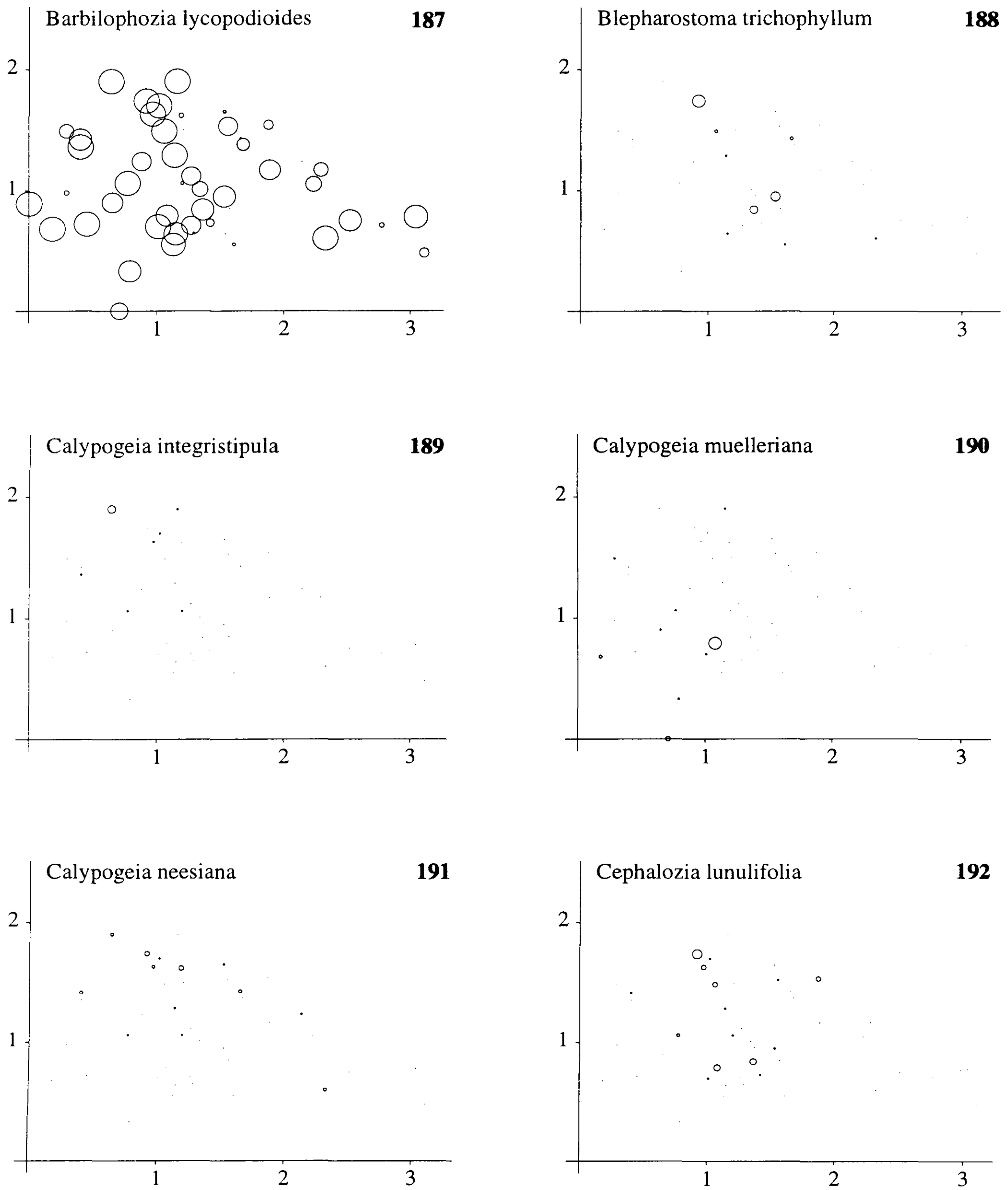
Figs 169-174. Grytdalen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 169. *Molinia caerulea.* Fig. 170. *Brachythecium reflexum.* Fig. 171. *Brachythecium starkei.* Fig. 172. *Dicranum fuscescens* agg. Fig. 173. *Dicranum majus.* Fig. 174. *Dicranum scoparium.*



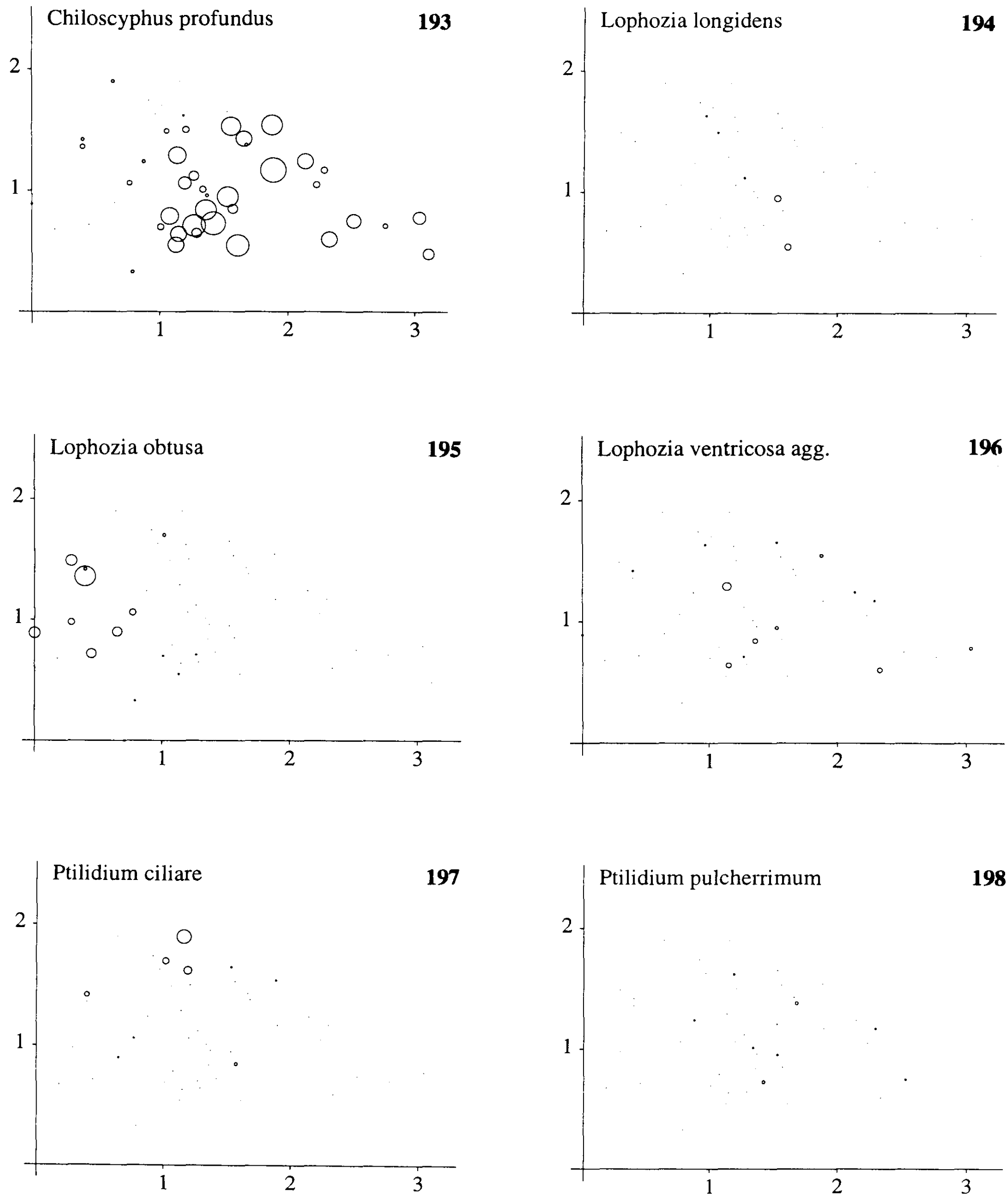
Figs 175-180. Grytdalen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 175. *Hylocomium splendens*. Fig. 176. *Plagiothecium denticulatum*. Fig. 177. *Plagiothecium laetum*. Fig. 178. *Pleurozium schreberi*. Fig. 179. *Ptilium crista-castrensis*. Fig. 180. *Rhytidiadelphus loreus*.



Figs 181-186. Grytdalen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 181. *Rhytidiadelphus squarrosus* agg. Fig. 182. *Tetraphis pellucida*. Fig. 183. *Sphagnum quinquefarium*. Fig. 184. *Barbilophozia attenuata*. Fig. 185. *Barbilophozia barbata*. Fig. 186. *Barbilophozia floerkei*.



Figs 187-192. Grytdalen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 187. *Barbilophozia lycopodioides*. Fig. 188. *Blepharostoma trichophyllum*. Fig. 189. *Calypogeia integristipula*. Fig. 190. *Calypogeia muelleriana*. Fig. 191. *Calypogeia neesiana*. Fig. 192. *Cephalozia lunulifolia*.



Figs 193-198. Grytdalen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 193. *Chiloscyphus profundus*. Fig. 194. *Lophozia longidens*. Fig. 195. *Lophozia obtusa*. Fig. 196. *Lophozia ventricosa* agg. Fig. 197. *Ptilidium ciliare*. Fig. 198. *Ptilidium pulcherrimum*.

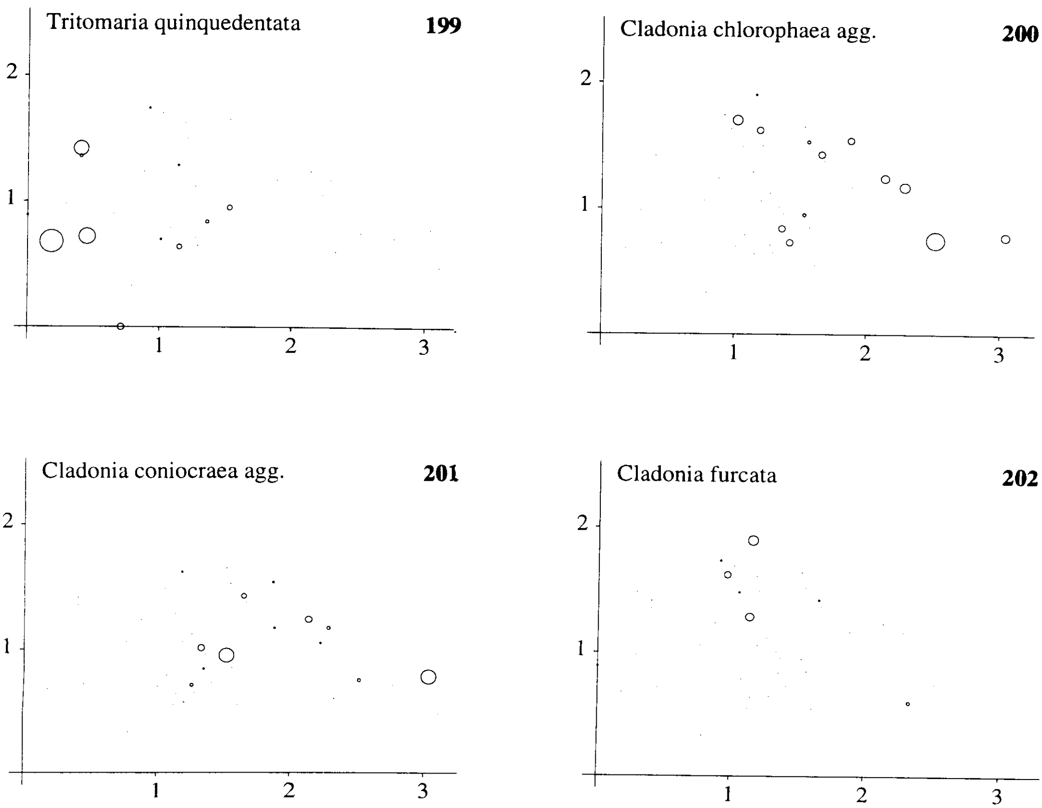
The distribution of species abundance in the DCA ordination

Fifty-two of a total of 102 species occurred in 5 or more of the 50 meso plots (Figs 151-202).

Vaccinium myrtillus (Fig. 154), a typical example of a species with wide ecological amplitude, was abundant in most of the meso plots. Other examples were *Deschampsia flexuosa* (Fig. 168), *Dicranum scoparium* (Fig. 174) and *Barbilophozia lycopodioides* (Fig. 187), all common species in poor, bilberry-dominated spruce forest.

Examples of species restricted to plots from sites with favourable aspect, high pH, high nutrient content and dense forest (high DCA 1 scores), were *Rubus saxatilis* (Fig. 165), *Oxalis acetosella* (Fig. 164), *Gymnocarpium dryopteris* (Fig. 158), *Anemone nemorosa* (Fig. 156), *Brachythecium reflexum* (Fig. 170), and *B. starkei* (Fig. 171).

Species typical of moist or humid bilberry-dominated spruce forests, poor in nutrients,



Figs 199-202. Grytdalen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 199. *Tritomaria quinquedentata*. Fig. 200. *Cladonia chlorophaea* agg. Fig. 201. *Cladonia coccifera* agg. Fig. 202. *Cladonia furcata*.

and restricted to plots with low DCA 1 scores (farthest left in the diagram), were *Rhytidiadelphus loreus* (Fig. 180), *Sphagnum girgensohnii* (Fig. 183), *Barbilophozia floerkei* (Fig. 186), *Lophozia obtusa* (Fig. 195) and *Tritomaria quinquedentata* (Fig. 199).

Lycopodium annotinum (Fig. 160) and *Barbilophozia attenuata* (Fig. 184) exemplified species restricted to plots with intermediate DCA 1 scores.

RAUSJØMARKA

Correlations between environmental variables

pH and concentrations of the cations Ca, Mg and Mn were pairwise positively correlated (Tab. 12, Fig. 203). The macro plot light index, macro plot basal area and the litter indices were also positively correlated. Via correlations between concentrations of Ca and Mn and the tree variables, all the mentioned variables made up one group of positively correlated variables.

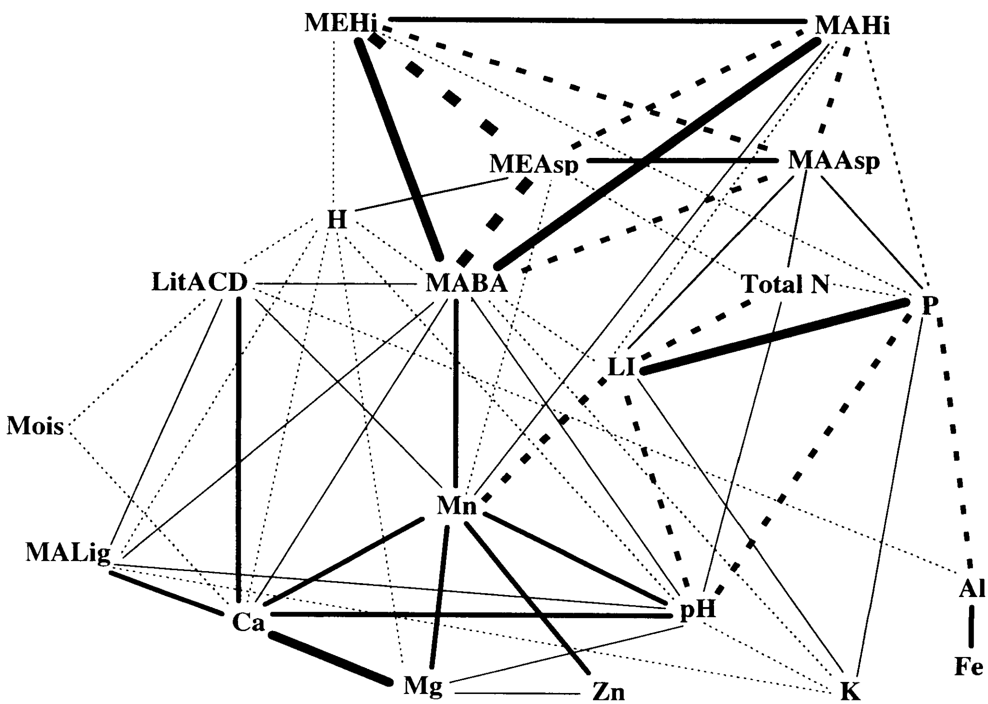


Fig. 203. Rausjømarka: plexus diagram visualizing Kendall's τ between pairs of environmental variables. Significance probabilities for τ are indicated by lines with different thickness (in order of decreasing thickness): $|\tau| \geq 0.60$, $0.45 \leq |\tau| < 0.60$, $0.35 \leq |\tau| < 0.45$. Continuous lines refer to positive correlations, broken lines to negative.

Tab. 12. Rausjømarka: Kendall's nonparametric correlation coefficient τ between 32 environmental variables in the 50 meso sample plots (lower triangle), with significance probabilities (upper triangle). Correlations significant at level P < 0.0001 in bold face. n.s. - significance probability > 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 2.

Variable	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
01 MA Inc	*	n.s.	n.s.	n.s.	n.s.	.0028	n.s.	n.s.	.0803	n.s.	.0446	.0297	.0211	n.s.	n.s.	n.s.	n.s.	n.s.	.0684	.0042	.0122	.0427	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**.0000**
02 MA Asp	.0899	*	**.0000**	**.0000**	n.s.	n.s.	**.0000**	**.0000**	.0097	n.s.	n.s.	.0661	n.s.	n.s.	n.s.	n.s.	.0001	.0081	.0028	n.s.	n.s.	.0108	.0663	.0087	n.s.	n.s.	.0016	.0955	.0001	.0299	.0002	n.s.
03 MA Hi	-.1348	**-.5111**	*	**.0000**	.0200	n.s.	**.0000**	**.0000**	.0142	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0002	.0193	.0344	n.s.	n.s.	.0305	n.s.	.0110	n.s.	.0319	.0002	.0716	-0027	.0067	.0002	n.s.
04 MA BA	.0000	**-.5229**	**.7502**	*	.0003	n.s.	**.0000**	**.0000**	.0949	n.s.	n.s.	n.s.	n.s.	n.s.	.0311	.0104	.0001	.0031	.0004	.0006	.0078	.0003	n.s.	**.0000**	n.s.	n.s.	**.0000**	.0086	.0014	.0022	.0009	n.s.
05 MA Lig	.0899	-.1111	.2444	.3865	*	n.s.	.0130	.0073	n.s.	n.s.	n.s.	n.s.	n.s.	.0007	.0001	.0358	.0110	.0356	.0007	**.0000**	.0025	.0003	.0889	.0001	n.s.	n.s.	.0020	n.s.	n.s.	n.s.	n.s.	.0922
06 ME Inc	.3093	.0942	-.0233	-.0124	.1322	*	n.s.	n.s.	.0001	n.s.	.0029	.0001	.0006	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0756	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0018
07 ME Asp	.0806	**.5999**	**-.5387**	**-.6734**	-.2680	.0676	*	**.0000**	.0279	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0020	.0373	.0071	.0446	.0096	.0142	n.s.	**.0000**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**.0000**
08 ME Hi	-.0138	**-.4772**	**.5779**	**.6060**	.2723	-.0357	**-.7906**	*	.0159	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0027	.0182	.0094	.0694	.0228	.0420	n.s.	.0002	n.s.	n.s.	.0016	.0955	.0001	.0299	.0002	n.s.
09 ME Rou	.1802	.2643	-.2506	-.1735	.0784	.3925	.2308	-.2381	*	n.s.	.0119	.0002	.0033	.0525	.0999	n.s.	.0109	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0027	.0341	n.s.	n.s.	n.s.	n.s.	.0011	.0275
10 ME Con	-.0199	-.0428	.1318	.1488	.0856	.0915	-.0446	.0271	.0274	*	n.s.	n.s.	n.s.	.0548	.0497	.0128	n.s.	.0186	.0735	.0512	n.s.	.0619	n.s.	n.s.	n.s.	.0350	.0088	n.s.	n.s.	n.s.	n.s.	n.s.
11 ME Smi	-.2106	-.1213	.0791	.1178	-.0387	-.3023	-.1393	.1165	-.2545	-.0034	*	**.0000**	.0005	.0442	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0411
12 ME Sme	-.2254	-.1890	.1127	.0515	-.1127	-.3835	-.1140	.1058	-.3738	.0726	**.4647**	*	**.0000**	n.s.	n.s.	n.s.	n.s.	.0410	n.s.	n.s.	.0689	n.s.	n.s.	n.s.	.0161	n.s.	n.s.	n.s.	n.s.	n.s.	.0140	.0085
13 ME Sma	-.2374	-.0378	-.0189	-.0369	-.0722	-.3410	.0117	.0091	-.2915	-.0505	.3503	**.6611**	*	n.s.	n.s.	n.s.	n.s.	.0494	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0170	n.s.	n.s.	n.s.	n.s.	n.s.	.0471	.0294
14 LitCC	.0000	-.0250	.0147	.1579	.3458	.0151	-.0648	-.0166	.1930	.1901	-.2038	-.1018	-.0834	*	**.0000**	**.0000**	n.s.	.0709	.0056	**.0000**	.0615	.0056	n.s.	.0009	.0002	.0008	.0008	.0984	n.s.	n.s.	n.s.	.0324
15 LitACD	.0148	-.0707	.0655	.2240	.3948	.0075	-.1232	.0356	.1637	.1942	-.1568	-.0606	-.0509	**.9092**	*	**.0000**	n.s.	.0230	.0010	**.0000**	.0137	.0018	n.s.	.0001	.0003	.0006	.0001	.0268	n.s.	n.s.	n.s.	.0235
16 Mois	.0630	-.0944	-.1688	-.2675	-.2156	.0294	.0226	-.0357	-.0235	-.2475	.0488	.0794	.0720	**-.4150**	**-.4190**	*	n.s.	n.s.	.0108	.0002	.0049	n.s.	.0013	.0089	.0106	n.s.	.0023	.0627	n.s.	n.s.	n.s.	n.s.
17 LI	-.1215	.3954	-.3750	-.3923	-.2574	-.0149	.3209	-.2938	.2509	-.0829	-.0101	-.1230	-.0767	-.0364	-.0835	.0523	*	**.0000**	**.0000**	.0015	.0006	.0002	.0402	.0196	.0031	.0032	**.0000**	.0200	**.0000**	n.s.	**.0000**	n.s.
18 pH_{H2O}	.1703	-.2815	.2489	.3194	.2236	.0079	-.2275	.2425	-.1578	.2422	-.0743	.2128	.2032	.1871	.2353	-.1657	**-.4929**	*	**.0000**	.0008	.0200	**.0000**	n.s.	.0406	.0398	n.s.	.0001	n.s.	.0001	.0016	**.0000**	n.s.
19 pH_{CaCl2}	.1955	-.3177	.2251	.3798	.3594	.0335	-.2944	.2667	-.1178	.1844	-.0431	.1257	.1387	.2871	.3407	-.2652	**-.5256**	**.8115**	*	**.0000**	.0001	**.0000**	n.s.	.0006	n.s.	n.s.	**.0000**	.0520	.0001	.0136	**.0000**	n.s.
20 Ca	.2922	-.1176	.1415	.3522	**.4704**	.1226	-.2089	.1776	.1073	.1911	-.1247	-.1355	-.1245	**.4482**	**.5066**	-.3644	-.3096	.3454	**.5134**	*	**.0000**	.0008	n.s.	.0001	.0006	.0483	**.0000**	.0004	.0437	n.s.	n.s.	.0018
21 Mg	.2563	-.0734	.1126	.2741	.3072	.1095	-.2697	.2229	.0256	.0871	-.1021	-.1806	-.1535	.1846	.2433	-.2792	-.3337	.2389	.3982	**.6151**	*	n.s.	n.s.	.0003	.0219	n.s.	**.0000**	**.0000**	.0308	n.s.	n.s.	.0454
22 K	-.2075	.2591	-.2197	-.3717	-.3668	-.1762	.2559	-.1995	.0000	-.1835	.0473	-.0225	.0538	-.2738	-.3093	.0974	.3664	**-.4301**	**-.4252**	-.3271	-.1149	*	n.s.	.0102	n.s.	n.s.	.0136	n.s.	.0053	.0002	.0003	.0067
23 Na	-.0696	-.1876	.0740	.0264	-.1739	.0084	-.0996	.0157	-.1150	.0489	.0034	.0285	.0108	-.1570	-.1528	.3210	-.2022	.0938	-.0044	-.0932	-.0578	-.0273	*	n.s.	.0170	n.s.	n.s.	n.s.	.0595	n.s.	n.s.	.0101
24 H^+	-.0940	.2661	-.2576	**-.4258**	-.4077	-.0282	**.4243**	-.3710	.0611	-.1092	.0253	.0624	.0668	-.3277	-.3797	.2592	.2281	-.2102	-.3544	-.3753	-.3504	.2518	.1478	*	.0224	.0633	.0021	.0308	n.s.	n.s.	n.s.	n.s.
25 Al	-.1293	-.1372	.1457	.0113	-.1457	-.0679	-.0729	.1334	-.2955	-.0894	.1247	.2386	.2350	-.3646	-.3604	.2531	-.2884	.2109	.1018	-.3358	-.2241	-.0385	.2352	.2232	*	**.0000**	n.s.	.0733	.0993	n.s.	**.0000**	.0152
26 Fe	-.1466	-.1492	.2174	.0480	-.0912	-.0091	-.0685	.0982	-.2089	-.2068	.0438	.0499	.0396	-.3300	-.3390	.1528	-.2877	-.0460	-.0418	-.1929	-.0336	.1361	.1222	.1816	**.5067**	*	n.s.	n.s.	.0847	n.s.	.0126	.0265
27 Mn	-.0129	-.3187	.3716	**.4934**	.3136	-.0480	-.3564	.2660	-.1255	.2568	.0573	.1039	.0519	.3307	.3893	-.3013	**-.4779**	.4148	**.5395**	**.5596**	**.4630**	-.2418	.0965	-.3001	-.0662	-.0131	*	**.0000**	.0007	n.s.	.0043	n.s.
28 Zn	-.1664	-.1696	.1833	.2717	.1645	-.1424	-.2538	.1481	-.1336	.1056	.0923	.0460	.1144	.1638	.2194	-.1852	-.2283	.0750	.2003	.3450	**.4334**	.1005	.0481	-.2121	-.1758	.0600	.4764	*	.0787	.0773	n.s.	n.s.
29 Total N	.0770	-.4070	.3044	.3289	.1590	.0499	-.3514	.2635	-.1443	.0387	-.0085	.1435	.0753	.0929	.1020	.0491	**-.4812**	.3961	.3981	.1975	.2117	-.2738	.1863	-.1403	.1615	.1689	.3320	.1731	*	n.s.	.0001	n.s.
30 P-AL	-.1045	.2203	-.2750	-.3162	-.0973	-.0689	.2351	-.2624	.0207	-.0658	.0034	-.0941	-.0281	-.1491	-.1582	.1397	.0589	-.3243	-.2537	-.0786	.1402	.3713	.0579	.1229	-.0884	.1024	-.0475	.1737	-.1183	*	.0008	.0802
31 P	-.0717	.3767	-.3750	-.3417	-.1512	.0697	.3377	-.3536	.3227	-.1176	-.0642	-.2442	-.1959	.0017	-.0323	-.0033	**.6069**	**-.6150**	**-.5487**	-.1040	-.0705	.3525	-.1332	.1598	**-.4758**	-.2442	-.2793	-.0033	-.3772	.3299	*	n.s.
32 S	**-.4843**	-.0891	.1199	.0035	-.1713	-.3106	-.0956	.0708	-.2183	.0553	.2058	.2625	.2155	-.2120	-.2244	.1060	-.0214	-.0375	-.1059	-.3055	-.1965	.2670	.2547	.0806	.2382	.2178	-.0312	.0611	.0659	.1720	-.0626	*

Soil moisture was negatively correlated with Ca and the litter indices.

Loss on ignition was strongly positively correlated with P while strongly negatively correlated with total N and pH. These variables made up a second group of correlated variables, connected to the first group by strong correlations between pH and the concentration of Mn (positive), and between pH and loss on ignition (negative). The concentration of Al, strongly positively correlated with the concentration of Fe, and the concentration of K were both correlated with variables in this second group.

A third group of pairwise strongly correlated variables that had connections to both of the other groups included the macro plot basal area, aspect unfavourability (negatively correlated with basal area) and the heat indices (see Fig. 203).

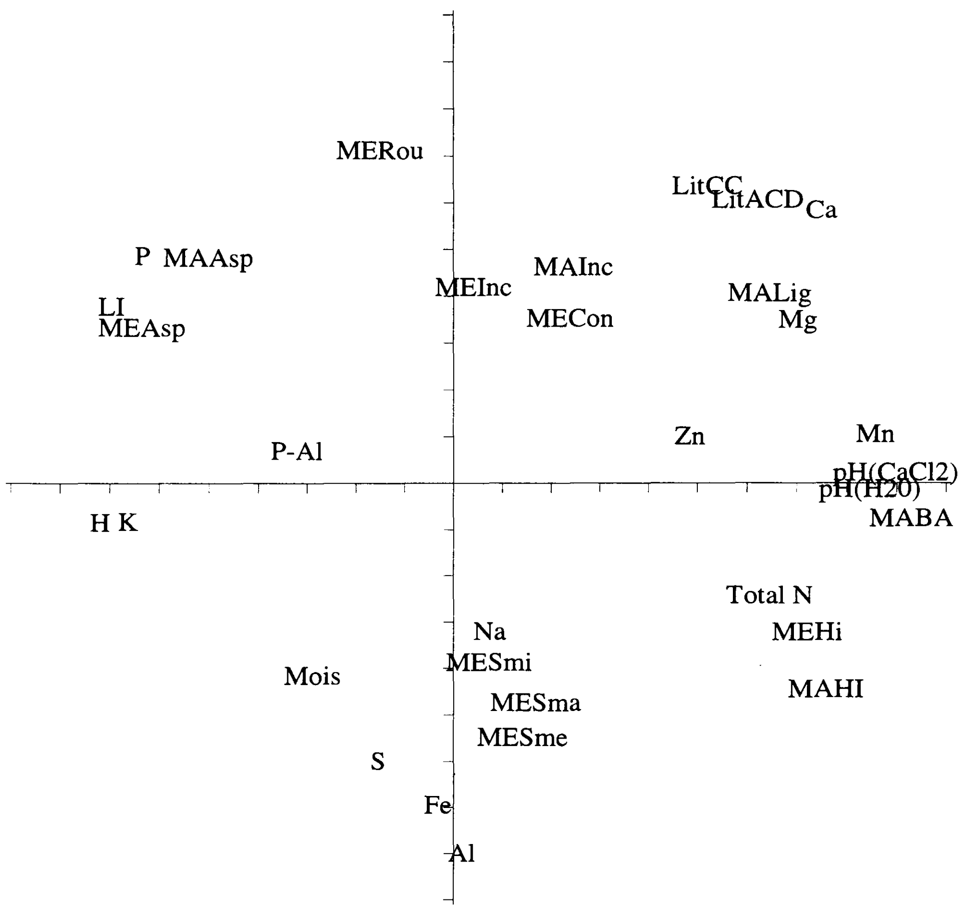


Fig. 204. Rausjømarka: PCA ordination of 32 environmental variables (names abbreviated in accordance with Tab. 2), axes 1 (horizontal) and 2 (vertical). Positions of variables in the ordination give the head of variable vectors.

PCA ordination of environmental variables

Eigenvalues of the first two PCA axes were 0.279 and 0.186, thus 46.5% of the variation in measured environmental variables was explained by the first two PCA axes.

Macro plot basal area, pH, Mn, Ca and variables that were more or less strongly positively correlated with these, such as Mg, the heat indices, the macro plot light index and litter indices, obtained high loadings on PCA 1 (Fig. 204). High loadings were also obtained by total N. Low loadings were obtained by H^+, K, P, loss on ignition and aspect unfavourability, variables strongly negatively correlated with one or more of pH, Mn and macro plot basal area.

Ca and the litter indices obtained high loadings on PCA 2, but the highest loading on this axis was obtained by the surface roughness index, with no strong correlations with other variables. Low loadings were obtained by Al and Fe with negative correlations with the litter indices ($0.0001 < P < 0.001$), S and soil depth with weak relationships with other variables, and soil moisture which was negatively correlated with Ca and the litter indices.

Tab. 13. Rausjømarka: Eigenvalues and the fraction of variation explained for DCA axes 1-4.

	DCA 1	DCA 2	DCA 3	DCA 4
Eigenvalues	0.245	0.142	0.092	0.069
Fraction of variation explained	0.138	0.080	0.052	0.039

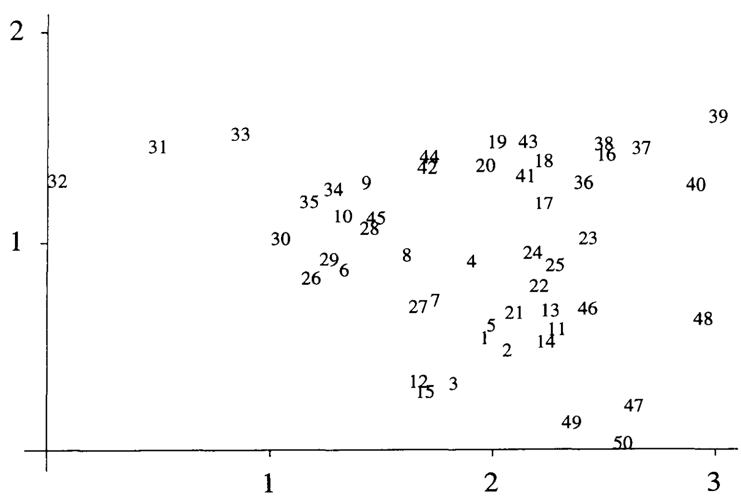
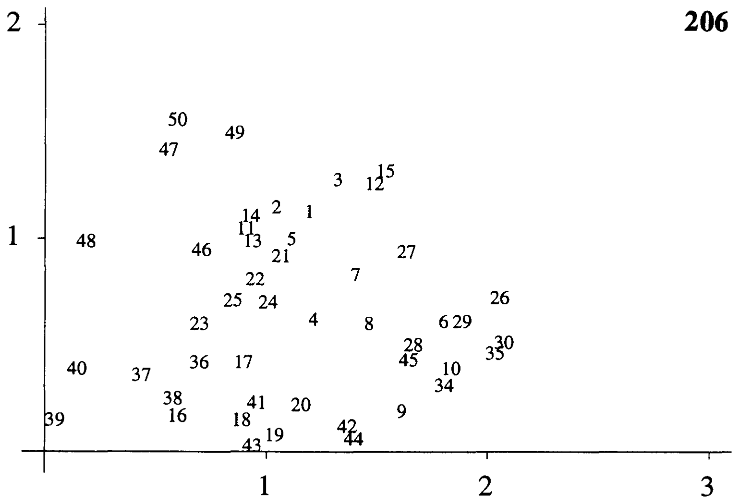
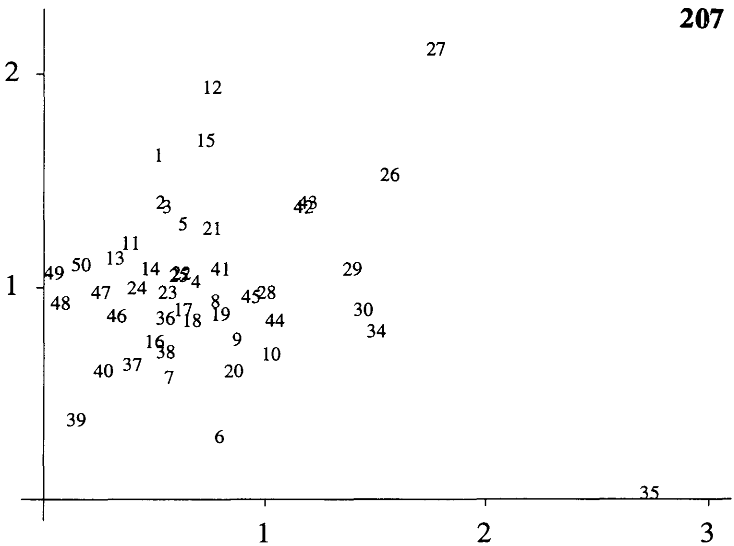


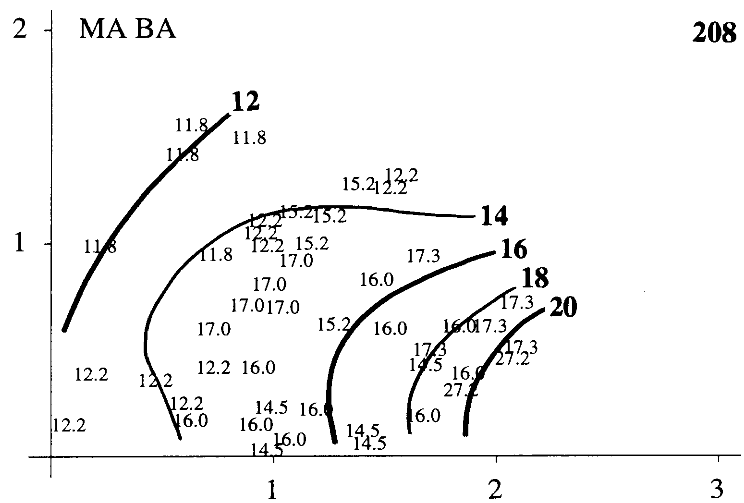
Fig. 205. Rausjømarka: DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Meso plot numbers are plotted onto the sample plot positions. Scaling of axes in S.D. units.

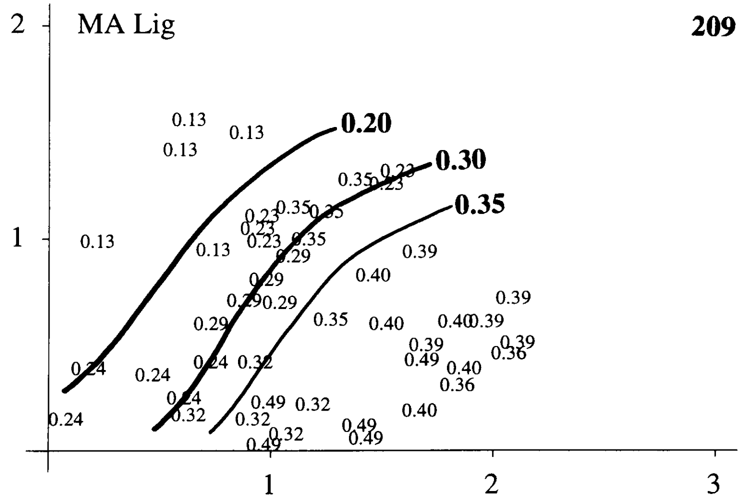




Figs 206-207. Rausjømarka: ordinations of 47 meso plots (plot Nos 31-33 omitted), axes 1 (horizontal) and 2 (vertical). Meso plot numbers are plotted onto the sample plot positions. Fig. 206. DCA ordination. Scaling of axes in S.D. units. Fig. 207. LNMDS ordination. Axes linearly rescaled in S.D. units.

The PCA ordination was mainly consistent with the correlations between variables (Tab. 12, Fig. 203), and emphasized the close connections between the three groups of correlated variables.

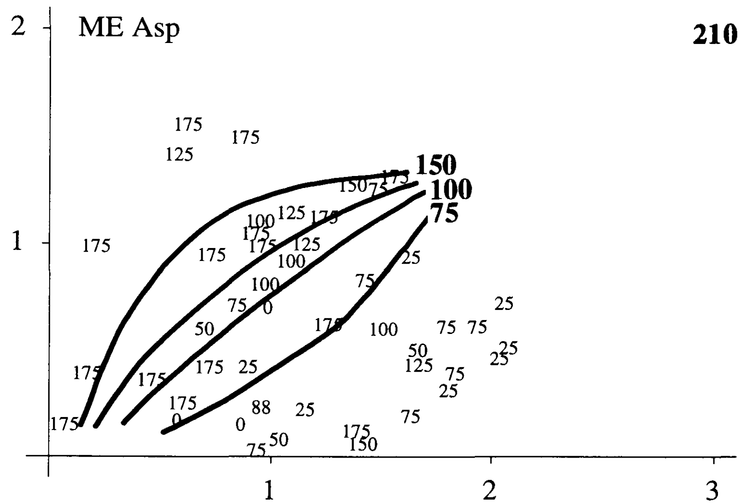


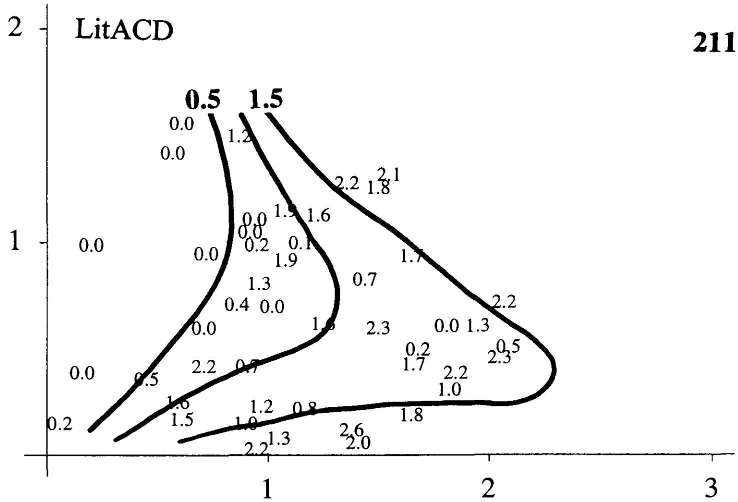


Figs 208-209. Rausjømarka: isolines for environmental variables in the DCA ordination of 47 meso plots (plot Nos 31-33 omitted), axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots' positions. Scaling of axes in S.D. units. Fig. 208. MA BA (R^2 = 0.526). Fig. 209. MA Lig (R^2 = 0.791). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.

DCA and LNMDS ordination

Meso plot Nos 31, 32 and 33 acted as outliers in the DCA ordination (Fig. 205) and were removed prior to further analysis. The number of species in these plots was 15, 8 and 8, re-

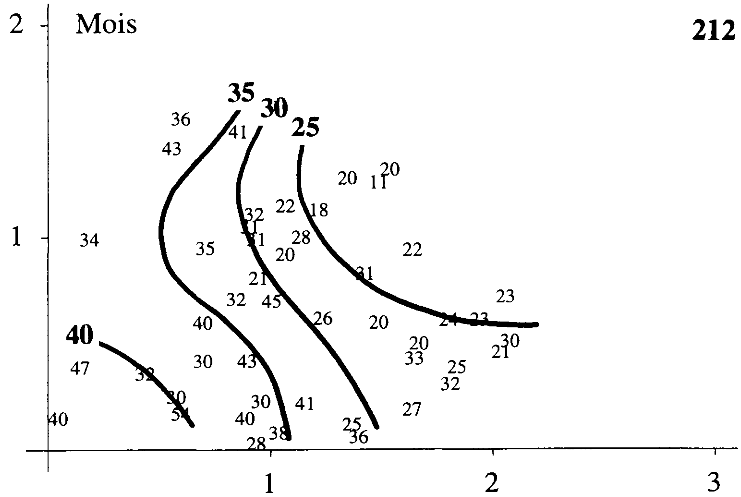


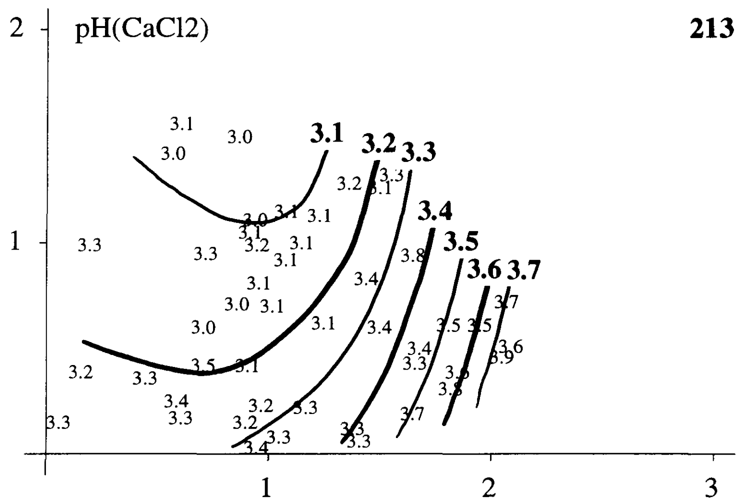


Figs 210-211. Rausjømarka: isolines for environmental variables in the DCA ordination of 47 meso plots (plot Nos 31-33 omitted), axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 210. MA Asp (R^2 = 0.449). Fig. 211. Lit ACD (R^2 = 0.462). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.

spectively (area average was 17.6 species).

The plots were relatively evenly distributed along the first two axes in the DCA ordination of the remaining 47 plots (Fig. 206). In LNMDS, plot No. 35 (with 19 species, mostly with low frequency in subplots) acted as a strong outlier along the first axis (Fig. 207).

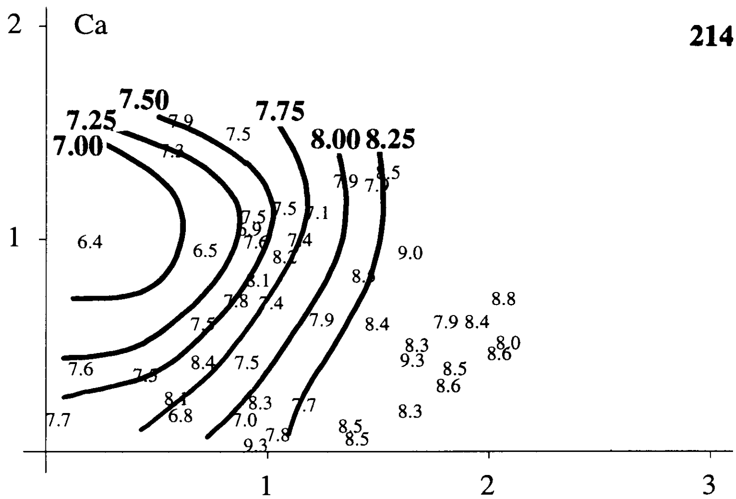


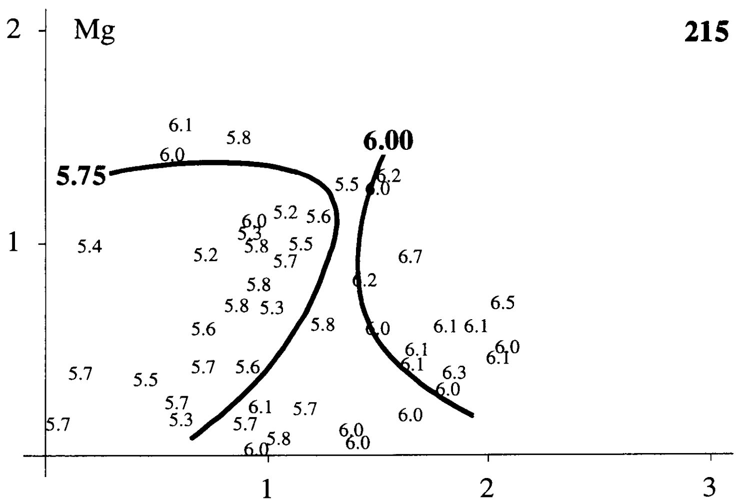


Figs 212-213. Rausjømarka: isolines for environmental variables in the DCA ordination of 47 meso plots (plot Nos 31-33 omitted), axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots' positions. Scaling of axes in S.D. units. Fig. 212. Mois (R^2 = 0.561). Fig. 213. pH_{CaCl2} (R^2 = 0.754). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.

Plots were less evenly distributed in the LNMDS than in the DCA ordination. Disregarding the outlier in LNMDS, gradient lengths were ca. 2 S.D. units for axes 1 and 2 of both ordinations.

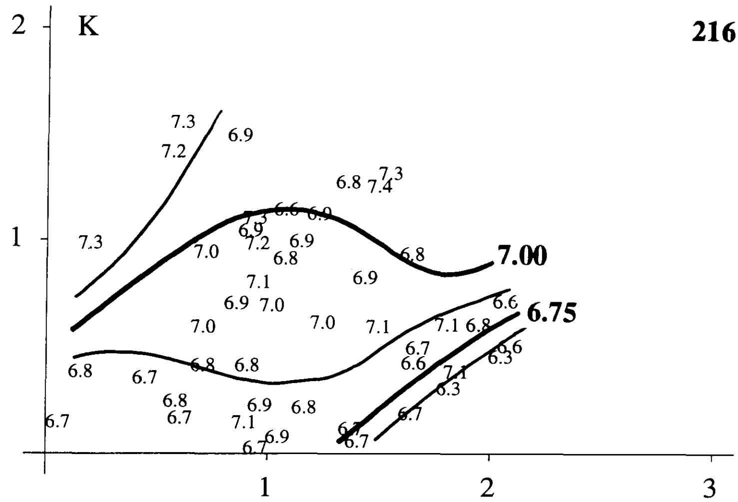
The fraction of variation in vegetation explained by DCA 1 was 13.8%, and decreased

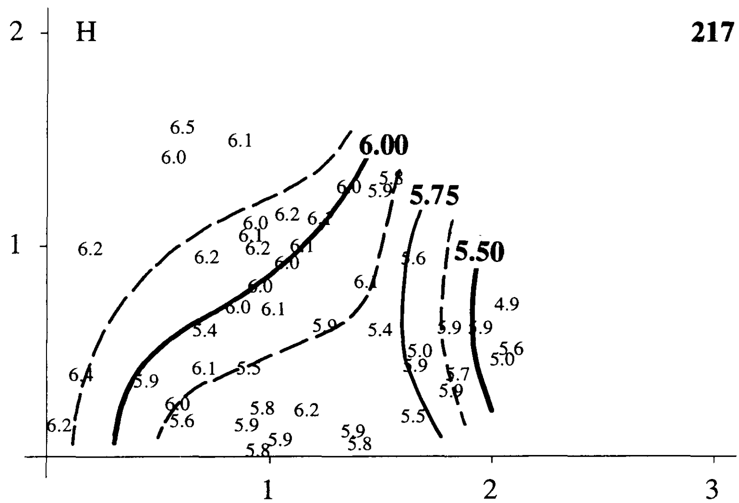




Figs 214-215. Rausjømarka: isolines for environmental variables in the DCA ordination of 47 meso plots (plot Nos 31-33 omitted), axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots' positions. Scaling of axes in S.D. units. Fig. 214. Ca (R^2 = 0.536). Fig. 215. Mg (R^2 = 0.626). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.

for subsequent axes (to 58-75% of the variation explained by the previous axis; Tab. 13). The eigenvalues of DCA 3 and DCA 4 were low (0.092 and 0.069, respectively), corresponding to explained fractions of variation below 6%.





Figs 216-217. Rausjømarka: isolines for environmental variables in the DCA ordination of 47 meso plots (plot Nos 31-33 omitted), axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 216. K (R^2 = 0.536). Fig. 217. H^+ (R^2 = 0.503). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.

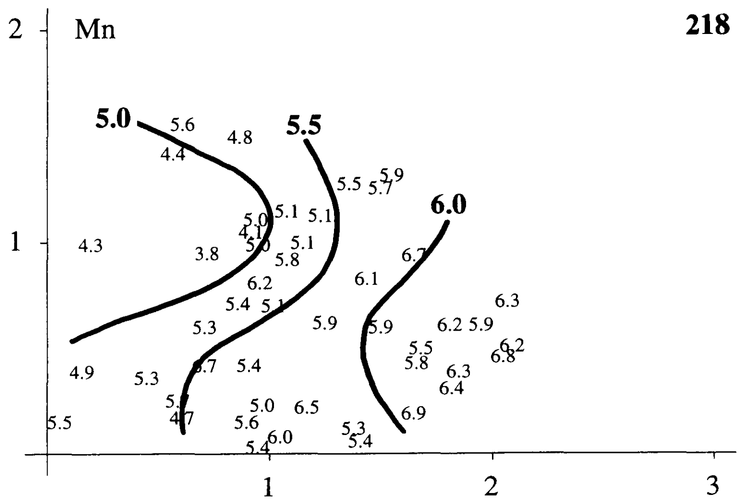
Correlations between DCA and LNMDS ordination axes and between ordination axes and environmental variables

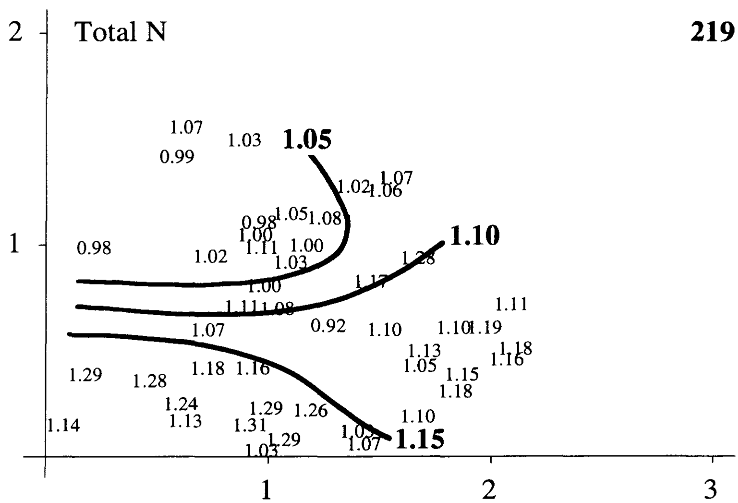
DCA 1 and LNMDS 1 were strongly correlated (τ = 0.645; Tab. 13), while LNMDS 2 was

Tab. 14. Rausjømarka: Kendall's nonparametric correlation coefficient τ between DCA and LNMDS axes, and between 32 environmental variables in the 50 meso sample plots and sample plot positions with respect to DCA and LNMDS axes, and their significance probabilities. Correlations significant at level P < 0.0001 in bold face. n.s. - significance probability > 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 2.

Variable	DCA 1		DCA 2		DCA 3		DCA 4		LNMDS 1		LNMDS 2	
	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P
LNMDS 1	**.6453**	**.0000**	-.2888	.0043	.2360	.0198	.2151	.0340				
LNMDS 2	.1346	n.s.	.4095	.0001	.3493	.0006	.2654	.0089				
01 MA Inc	-.0442	n.s.	-.1641	n.s.	.2084	.0494	-.0542	n.s.	.0871	n.s.	.0166	n.s.
02 MA Asp	-.0776	n.s.	.3454	.0010	.1582	n.s.	-.0973	n.s.	-.2610	.0127	.3287	.0017
03 MA Hi	.2678	.0108	-.0602	n.s.	-.0650	n.s.	.3405	.0012	.3209	.0022	-.0561	n.s.
04 MA BA	**.4560**	**.0000**	-.1822	.0886	.0299	n.s.	.3395	.0016	**.5297**	**.0000**	-.0436	n.s.
05 MA Lig	**.5123**	**.0000**	-.3765	.0003	.1757	.0947	-.0681	n.s.	**.5955**	**.0000**	-.0329	n.s.
06 ME Inc	.1092	n.s.	.0348	n.s.	.1036	n.s.	.1605	n.s.	.0854	n.s.	.1586	n.s.
07 ME Asp	-.3242	.0027	.2502	.0204	.0699	n.s.	-.2652	.0142	**-.4401**	**.0000**	.1130	n.s.
08 ME Hi	.2905	.0042	-.2141	.0348	.0065	n.s.	.2427	.0170	**.4117**	**.0000**	-.0816	n.s.
09 ME Rou	.0000	n.s.	.0525	n.s.	.0629	n.s.	-.0056	n.s.	-.0056	n.s.	.2597	.0107
10 ME Con	.2007	.0485	.0131	n.s.	.0738	n.s.	.2059	.0434	-.1990	.0496	.0911	n.s.
11 ME Smi	.0489	n.s.	-.0393	n.s.	.0192	n.s.	-.0202	n.s.	.0564	n.s.	-.1730	.0954
12 ME Sme	-.0671	n.s.	-.1606	n.s.	-.0350	n.s.	-.0152	n.s.	-.0094	n.s.	-.2278	.0262
13 ME Sma	-.0384	n.s.	-.1021	n.s.	-.1349	n.s.	-.1052	n.s.	-.0550	n.s.	-.2062	.0425
14 LitCC	.2759	.0070	-.1761	.0854	.1526	n.s.	.1124	n.s.	.3650	.0003	.1360	n.s.
15 LitACD	.3313	.0012	-.1920	.0606	.1686	.0996	.1189	n.s.	**.4201**	**.0000**	.1425	n.s.
16 Mois	**-.4297**	**.0000**	-.1898	.0646	-.3137	.0023	-.1676	n.s.	-.3265	.0014	-.3321	.0012
17 LI	-.1914	.0588	.2805	.0056	.1608	n.s.	-.0745	n.s.	-.2554	.0114	**.4165**	**.0000**
18 pH_{H20}	.2387	.0256	-.2636	.0137	-.0995	n.s.	.1167	n.s.	.3072	.0039	-.2755	.0097
19 pH_{CaCl2}	.4103	.0001	-.3245	.0024	.0200	n.s.	.0581	n.s.	**.4983**	**.0000**	-.2596	.0150
20 Ca	**.4645**	**.0000**	-.1988	.0496	.2110	.0373	.0466	n.s.	**.5646**	**.0000**	.0370	n.s.
21 Mg	**.4363**	**.0000**	-.0214	n.s.	.1042	n.s.	-.0084	n.s.	**.4458**	**.0000**	.0417	n.s.
22 K	-.2089	.0398	.3413	.0008	-.0588	n.s.	-.2216	.0296	-.3158	.0018	.1040	n.s.
23 Na	-.2347	.0217	-.0648	n.s.	-.3260	.0014	-.0358	n.s.	-.2311	.0233	-.3078	.0025
24 H^+	-.3942	.0001	.2566	.0113	-.1702	.0931	-.0876	n.s.	**-.5428**	**.0000**	-.0056	n.s.
25 Al	-.1059	n.s.	-.0669	n.s.	-.2463	.0150	-.0242	n.s.	-.1907	.0589	-.3683	.0003
26 Fe	-.0344	n.s.	-.0344	n.s.	-.1934	.0563	-.0326	n.s.	-.1194	n.s.	-.2583	.0105
27 Mn	**.4515**	**.0000**	-.1654	n.s.	.0121	n.s.	.1081	n.s.	**.5146**	**.0000**	-.1462	n.s.
28 Zn	.2923	.0041	.0551	n.s.	-.1439	n.s.	-.0421	n.s.	.2484	.0143	-.0512	n.s.
29 Total N	.0839	n.s.	-.3730	.0002	-.1968	.0528	.1337	n.s.	.1821	.0722	-.2898	.0042
30 P-AL	-.0168	n.s.	.0819	n.s.	-.1071	.2913	-.1755	.0844	-.0909	n.s.	-.0575	n.s.
31 P	-.1071	n.s.	.2683	.0082	.1826	.0721	-.1055	n.s.	-.1716	.0897	.3813	.0002
32 S	-.1252	n.s.	.0187	n.s.	-.3056	.0027	-.0206	n.s.	-.1731	.0879	-.1787	.0781

correlated with DCA 2 (τ = 0.410) as well as with DCA 3 (τ = 0.349). The same set of variables were correlated with DCA 1 and LNMDS 1. Correlations were higher with LNMDS 1 (with one exception, soil moisture, cf. Tab. 13). The concordance of LNMDS 2 and DCA

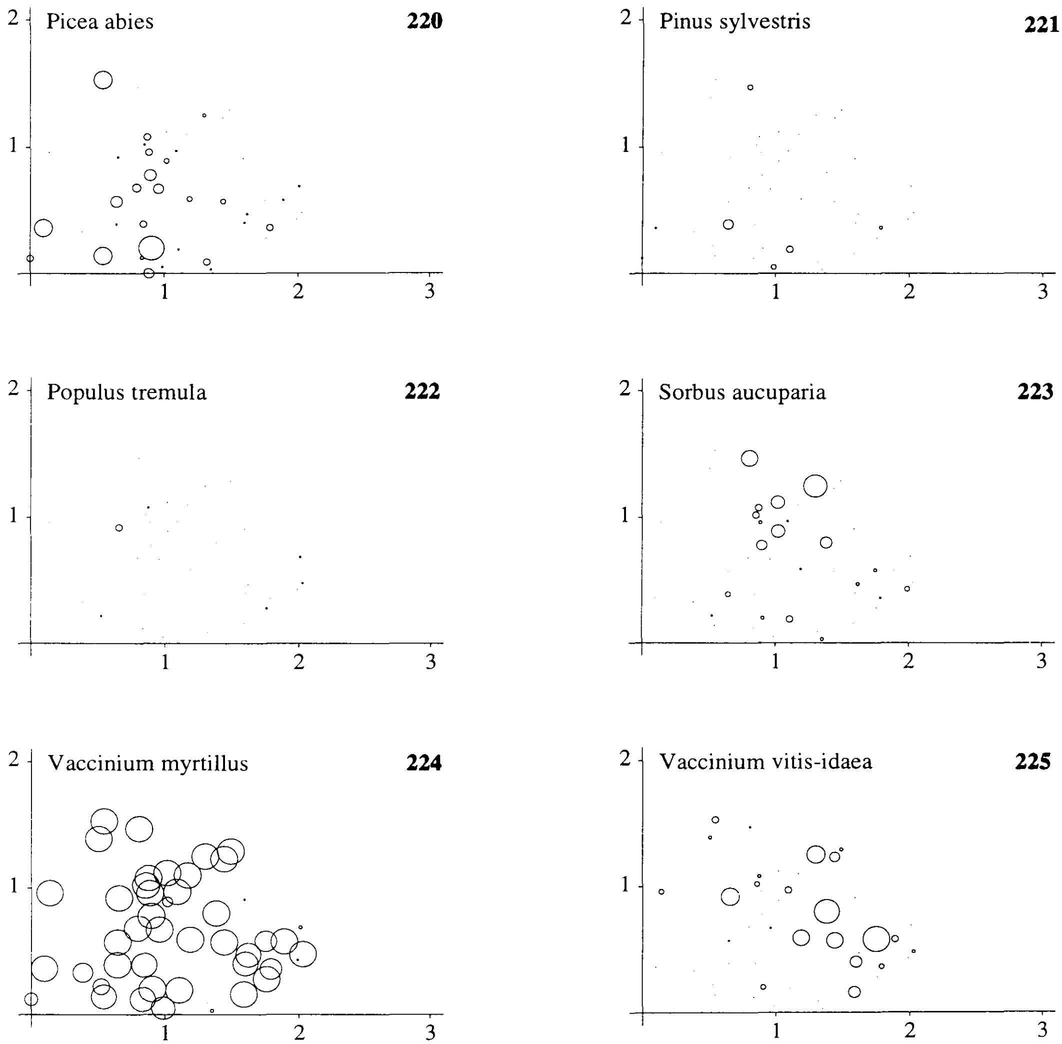




Figs 218-219. Rausjømarka: isolines for environmental variables in the DCA ordination of 47 meso plots (plot Nos 31-33 omitted), axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 218. Mn (R^2 = 0.573). Fig. 219. Total N (R^2 = 0.485). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.

2 with respect to correlated variables was lower (cf. Tab. 13).

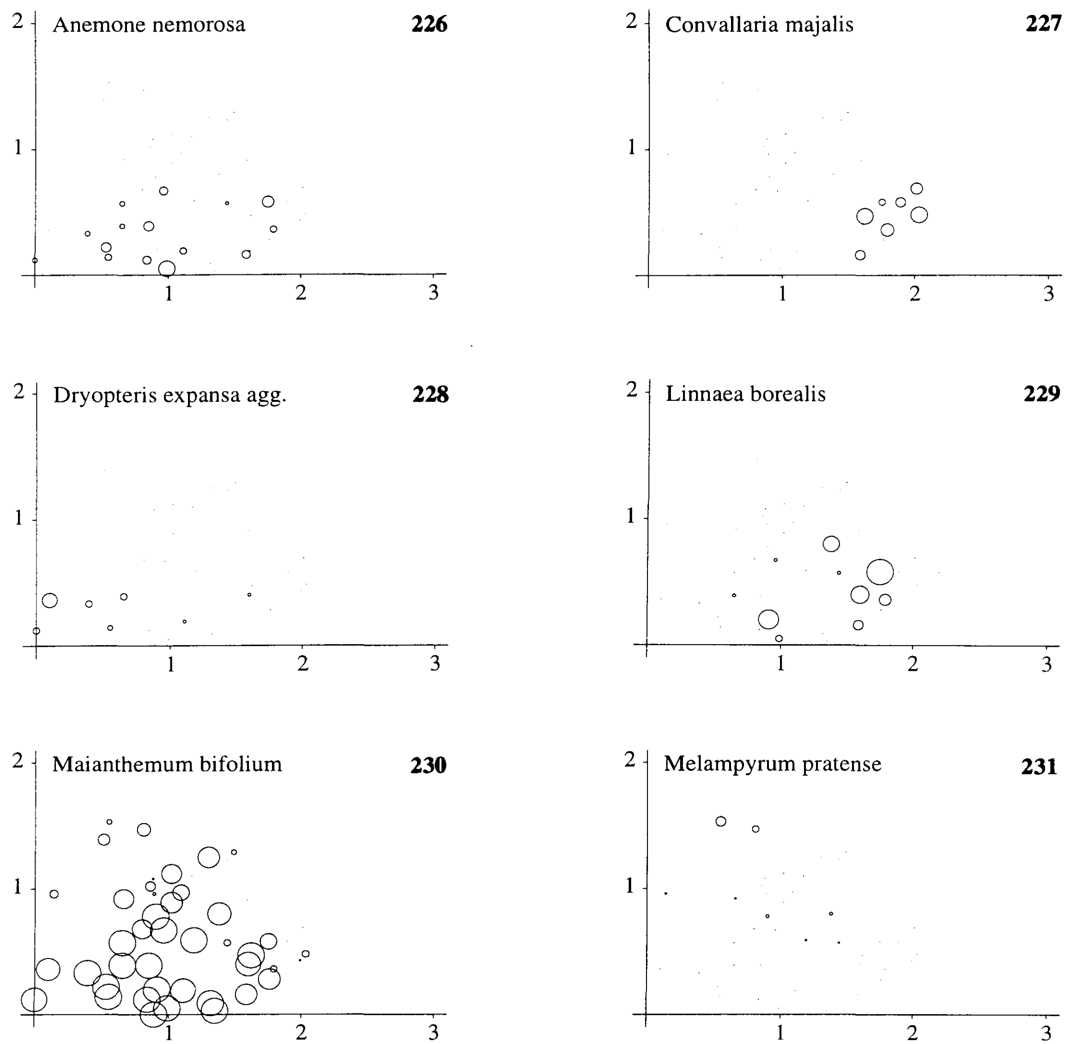
Variables strongly correlated with DCA 1 (and LNMDS 1) included the macro plot light index (Fig. 209) and macro plot basal area (Fig. 208), pH (Fig. 213) and the cations Ca (Fig. 214), Mg (Fig. 215) and Mn (Fig. 218), all with positive correlations. Other correlated varia-



Figs 220-225. Rausjømarka: distributions of species abundances in the DCA ordination of 47 meso plots (plot Nos 31-33 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 220. *Picea abies*. Fig. 221. *Pinus sylvestris*. Fig. 222. *Populus tremula*. Fig. 223. *Sorbus aucuparia*. Fig. 224. *Vaccinium myrtillus*. Fig. 225. *Vaccinium vitis-idaea*.

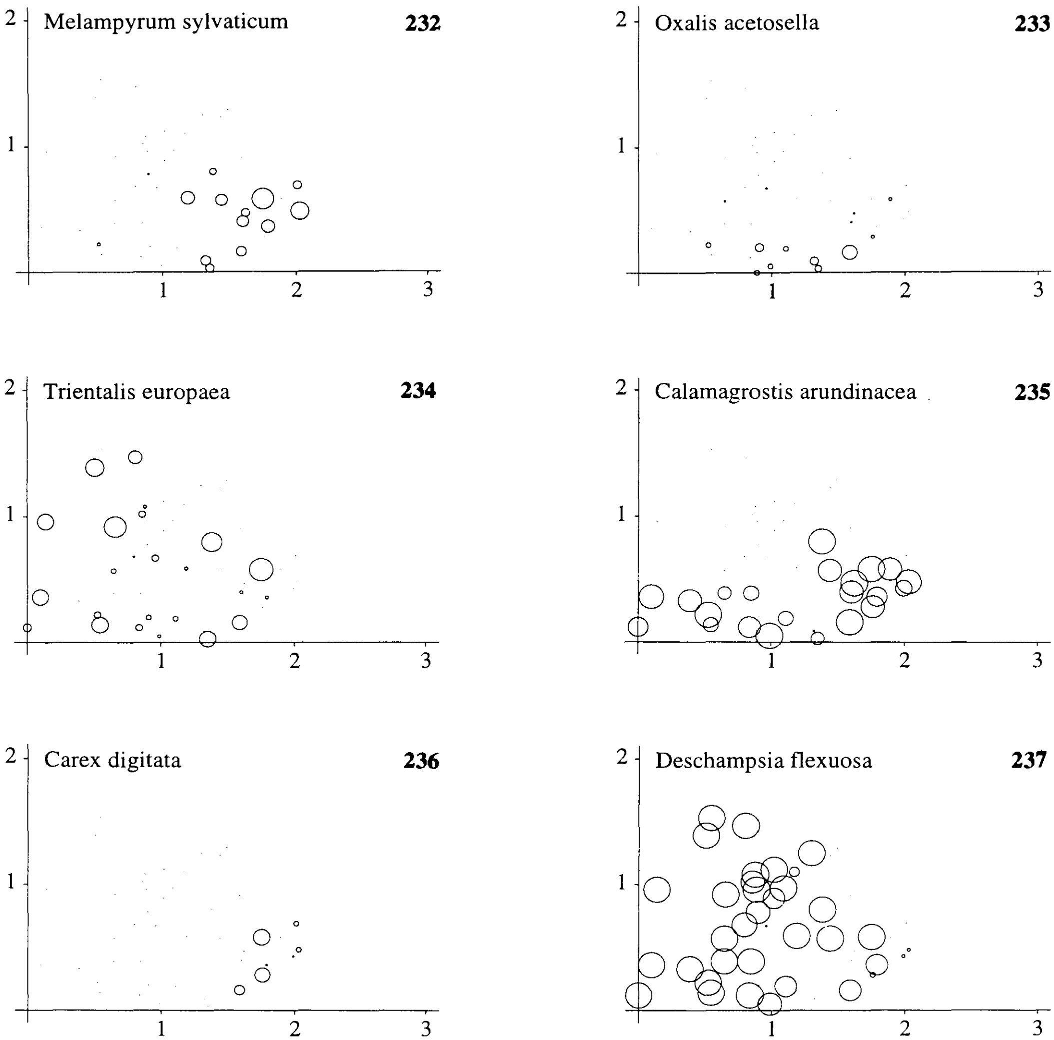
bles were the litter index (Fig. 211) which was positively correlated, and aspect unfavourability (Fig. 210), soil moisture (Fig. 212) and the concentration of H^+ (Fig. 217) with negative correlations.

No variables were correlated with DCA 2 (or DCA axes of higher order) at $P < 0.0001$. Variables correlated with DCA 2 at $P < 0.005$ were macro plot aspect unfavourability and the



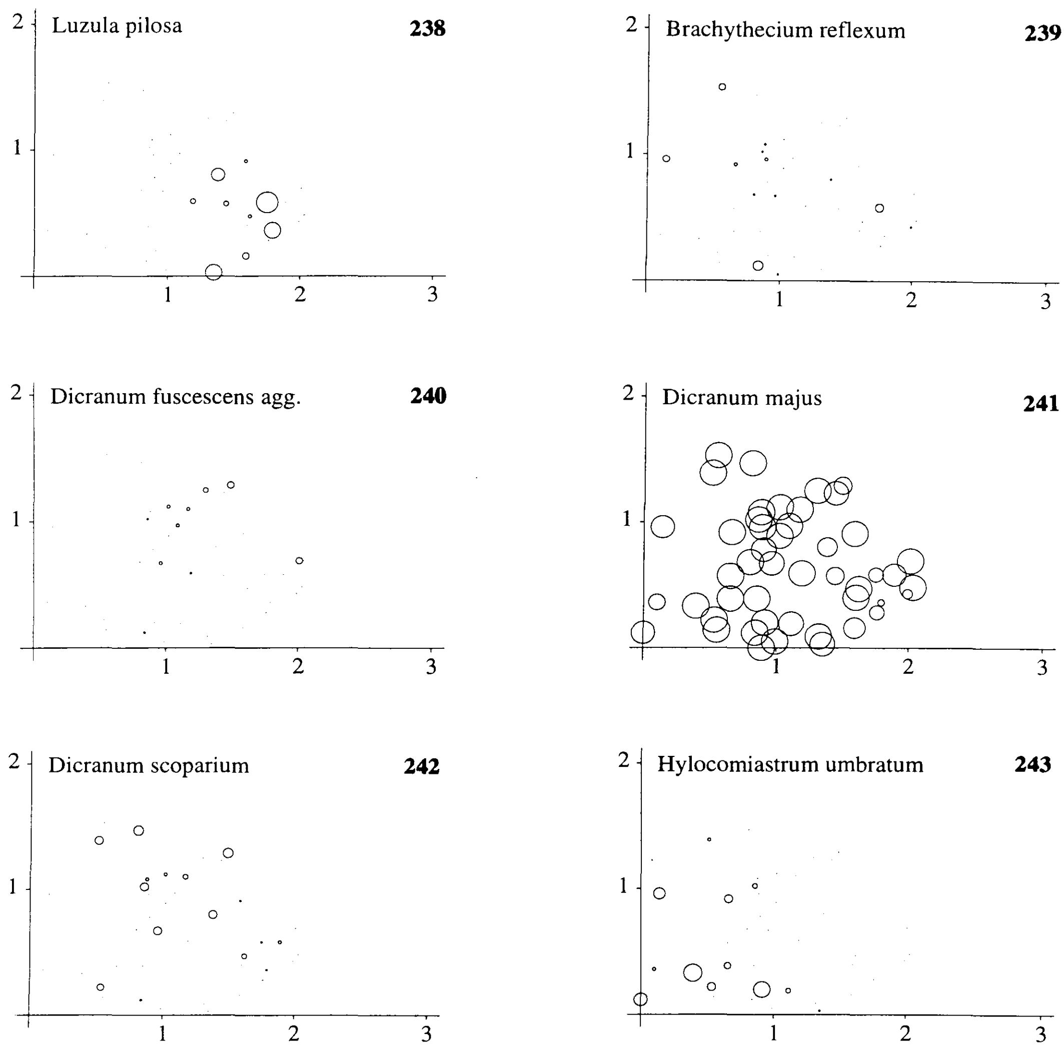
Figs 226-231. Rausjømarka: distributions of species abundances in the DCA ordination of 47 meso plots (plot Nos 31-33 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 226. *Anemone nemorosa*. Fig. 227. *Convallaria majalis*. Fig. 228. *Dryopteris expansa* agg. Fig. 229. *Linnaea borealis*. Fig. 230. *Maianthemum bifolium*. Fig. 231. *Melampyrum pratense*.

concentration of K (Fig. 216) with positive correlations, and the macro plot light index, pH and the concentration of total N (Fig. 219) with negative correlations. The light index and pH were thus correlated with both DCA 1 and DCA 2. Loss on ignition was strongly (positively) correlated with LNMDS 2.



Figs 232-237. Rausjømarka: distributions of species abundances in the DCA ordination of 47 meso plots (plot Nos 31-33 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 232. *Melampyrum sylvaticum*. Fig. 233. *Oxalis acetosella*. Fig. 234. *Trientalis europaea*. Fig. 235. *Calamagrostis arundinacea*. Fig. 236. *Carex digitata*. Fig. 237. *Deschampsia flexuosa*.

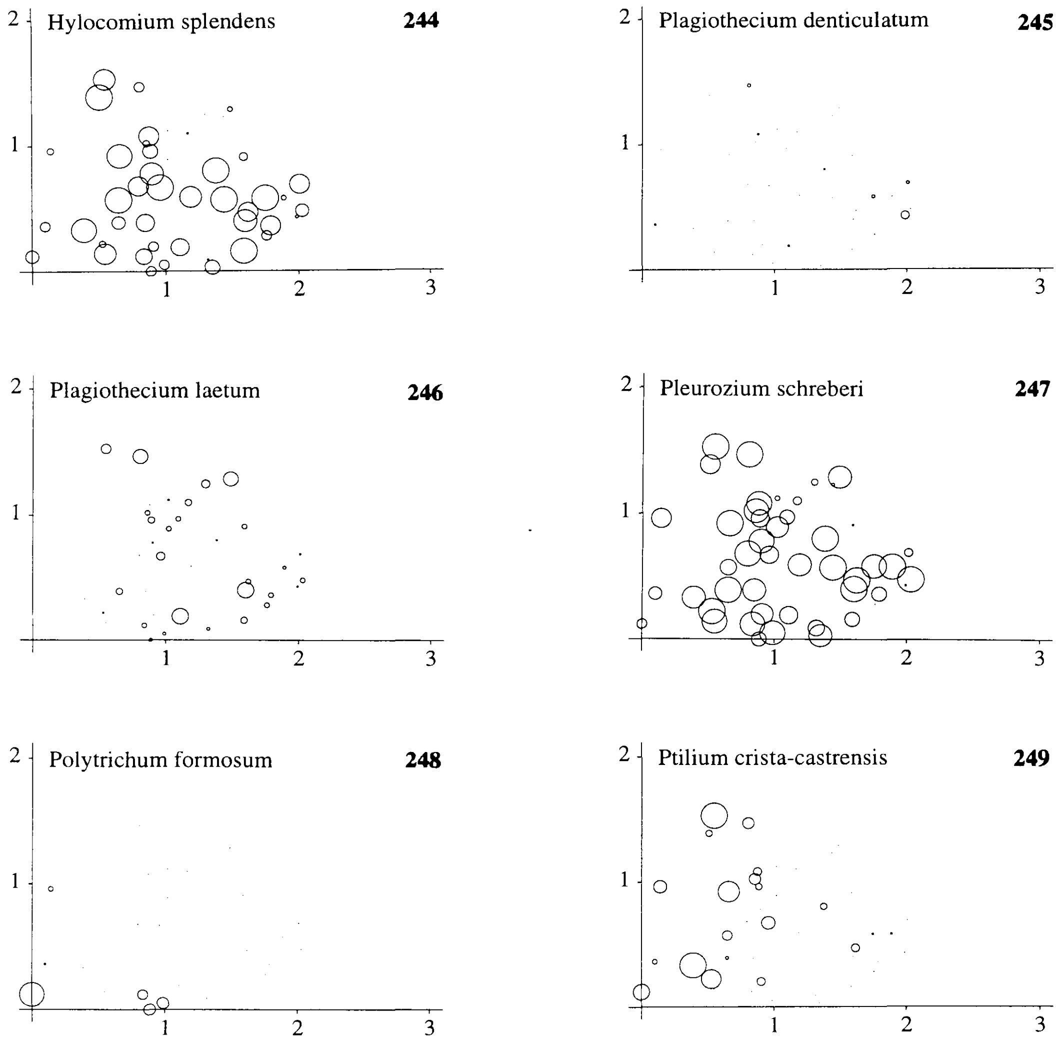
The variables most strongly correlated ($\tau > 0.3$) with DCA 3 were concentrations of Na and S. Macro plot heat index was the variable most strongly correlated with DCA 4.



Figs 238-243. Rausjømarka: distributions of species abundances in the DCA ordination of 47 meso plots (plot Nos 31-33 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 238. *Luzula pilosa*. Fig. 239. *Brachythecium reflexum*. Fig. 240. *Dicranum fuscescens* agg. Fig. 241. *Dicranum majus*. Fig. 242. *Dicranum scoparium*. Fig. 243. *Hylocomiastrum umbratum*.

The distribution of species abundance in the DCA ordination

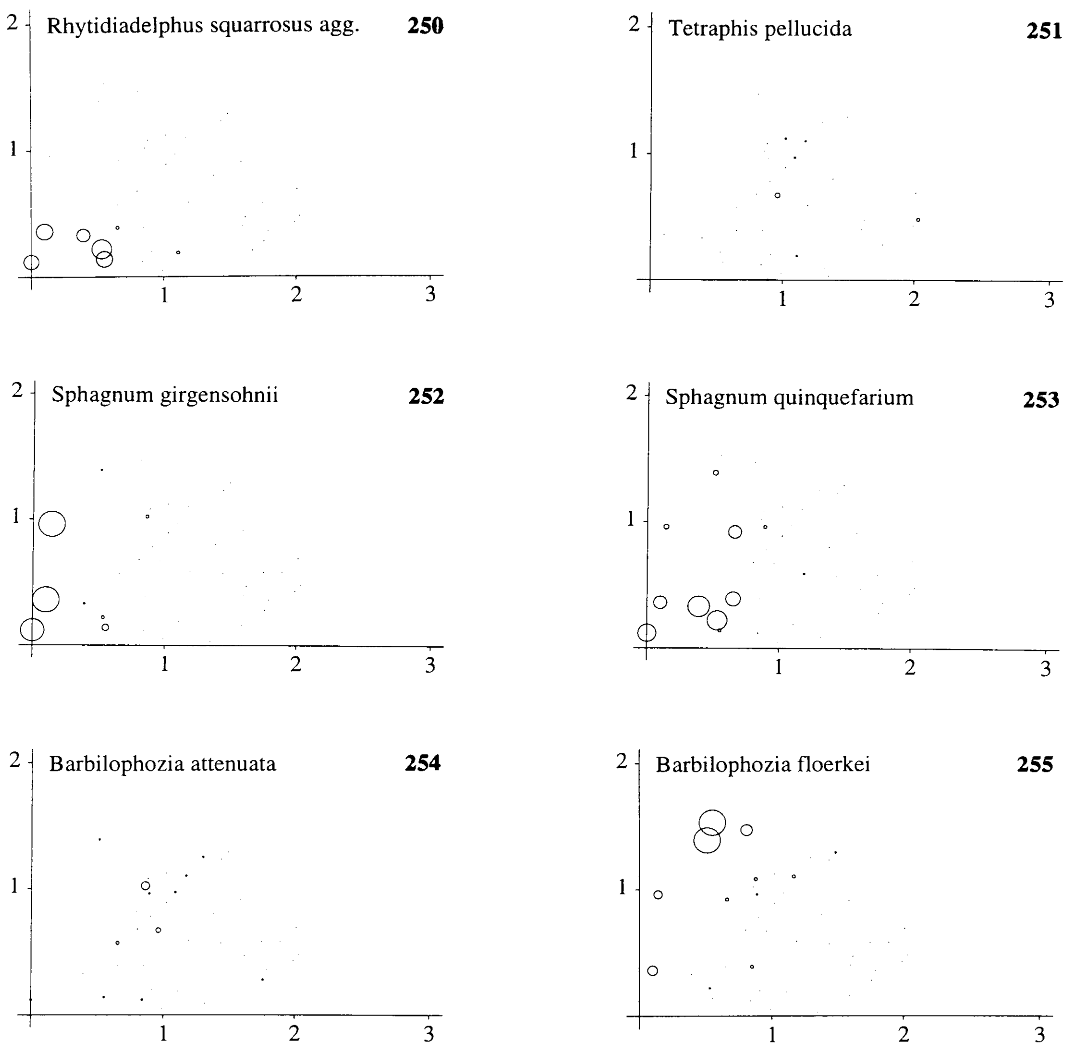
Forty-eight of a total of 88 species occurred in at least 5 of the 47 meso plots (Figs 220-267).
Vaccinium myrtillus (Fig. 224), a typical example of a species with wide ecological am-



Figs 244-249. Rausjømarka: distributions of species abundances in the DCA ordination of 47 meso plots (plot Nos 31-33 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 244. *Hylocomium splendens*. Fig. 245. *Plagiothecium denticulatum*. Fig. 246. *Plagiothecium laetum*. Fig. 247. *Pleurozium schreberi*. Fig. 248. *Polytrichum formosum*. Fig. 249. *Ptilium crista-castrensis*.

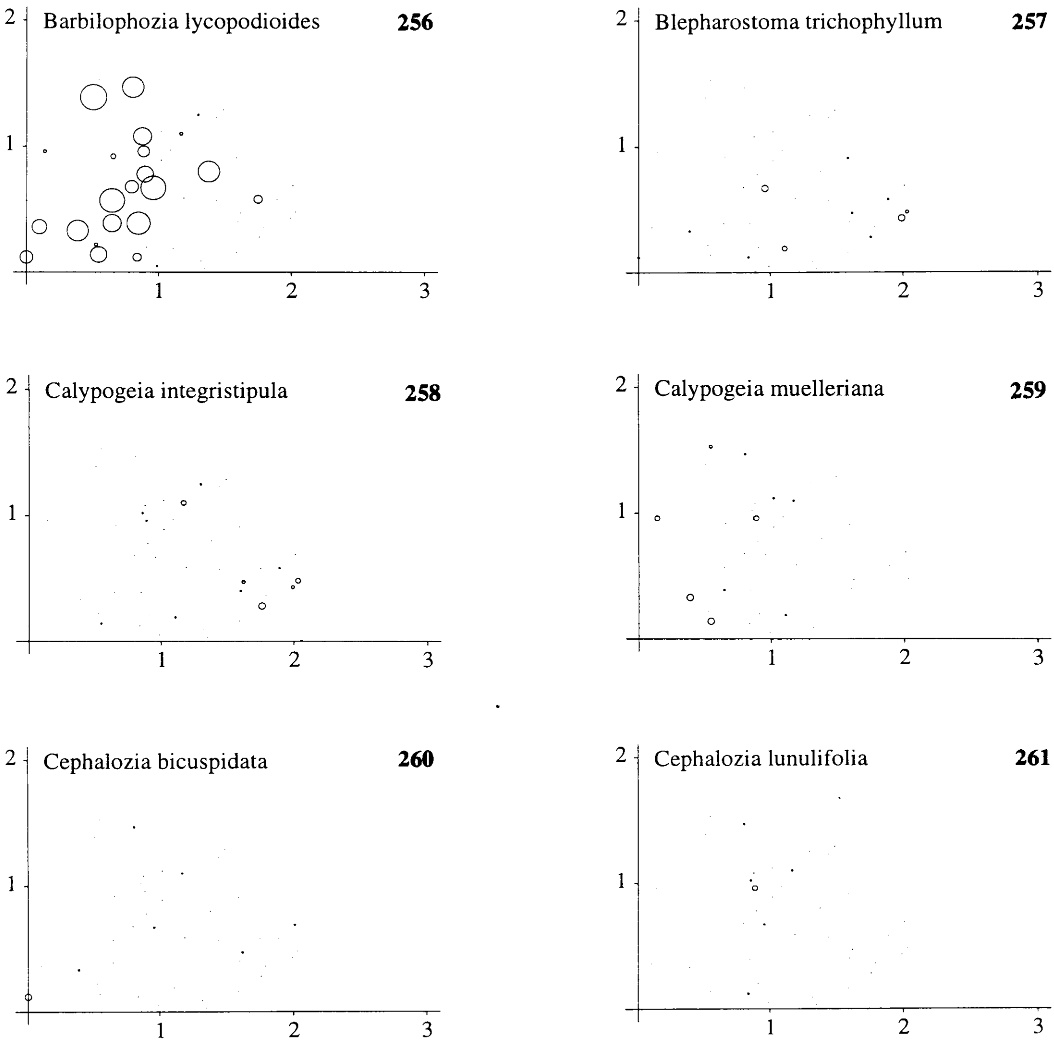
plitude, was abundant in most plots. Other examples were *Deschampsia flexuosa* (Fig. 238), *Pleurozium schreberi* (Fig. 247) and *Dicranum majus* (Fig. 241), common species in poor bilberry-dominated spruce forest.

Examples of species restricted to meso plots from moist sites, mostly relatively poor in



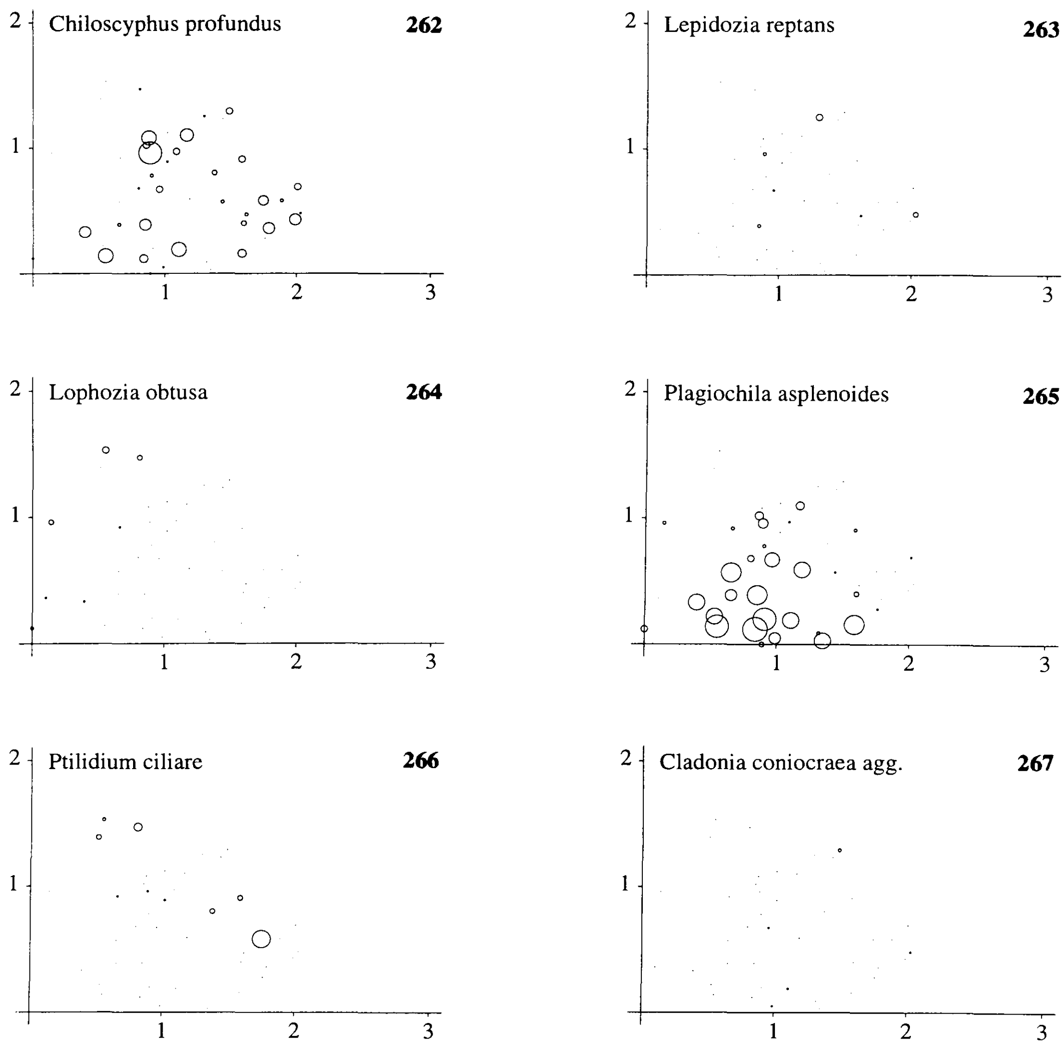
Figs 250-255. Rausjømarka: distributions of species abundances in the DCA ordination of 47 meso plots (plot Nos 31-33 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 250. *Rhytidiadelphus squarrosus* agg. Fig. 251. *Tetraphis pellucida*. Fig. 252. *Sphagnum girgensohnii*. Fig. 253. *Sphagnum quinquefarium*. Fig. 254. *Barbilophozia attenuata*. Fig. 255. *Barbilophozia floerkei*.

nutrients (lower left part of the DCA ordination), were *Sphagnum girgensohnii* (Fig. 252), *Sphagnum quinquefarium* (Fig. 253) and *Rhytidiadelphus squarrosus* agg. (Fig. 250). *Dicranum fuscescens* agg. (Fig. 240) was concentrated to plots on relatively dry sites (upper right in the ordination).



Figs 256-261. Rausjømarka: distributions of species abundances in the DCA ordination of 47 meso plots (plot Nos 31-33 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 256. *Barbilophozia lycopodioides*. Fig. 257. *Blepharostoma trichophyllum*. Fig. 258. *Calypogeia integristipula*. Fig. 259. *Calypogeia muelleriana*. Fig. 260. *Cephalozia bicuspidata*. Fig. 261. *Cephalozia lunulifolia*.

Examples of species restricted to plots with high pH and high concentrations of nutrients like Ca, Mg and Mn, mostly occuring in dense forests with favourable aspect and low soil moisture (lower right part of the DCA ordination diagram) were *Convallaria majalis* (Fig. 227), *Melampyrum sylvaticum* (Fig. 232) and *Carex digitata* (Fig. 236).



Figs 262-267. Rausjømarka: distributions of species abundances in the DCA ordination of 47 meso plots (plot Nos 31-33 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 262. *Chiloscyphus coadunatus*. Fig. 263. *Chiloscyphus profundus*. Fig. 264. *Lophozia obtusa*. Fig. 265. *Plagiochila asplenoides*. Fig. 266. *Ptilidium ciliare*. Fig. 267. *Cladonia coniocraea* agg.

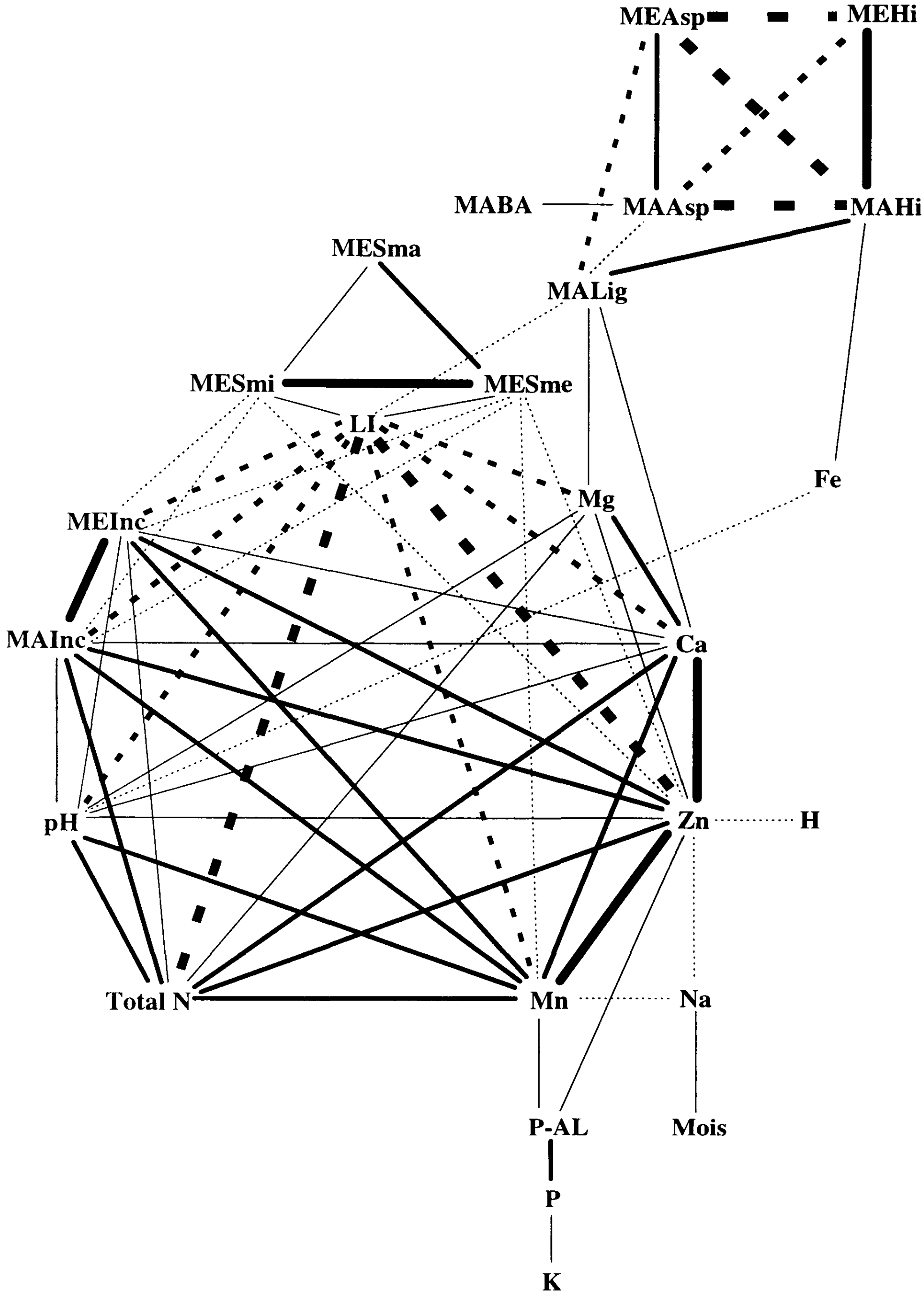


Fig. 268. Bringen: plexus diagram visualizing Kendall's τ between pairs of environmental variables. Significance probabilities for τ are indicated by lines with different thickness (in order of decreasing thickness): $|\tau| \geq 0.60$, $0.45 \leq |\tau| < 0.60$, $0.35 \leq |\tau| < 0.45$. Continuous lines refer to positive correlations, broken lines to negative.

Tab. 15. Bringen: Kendall's nonparametric correlation coefficient τ between 32 environmental variables in the 50 meso sample plots (lower triangle), with significance probabilities (upper triangle). Correlations significant at level P < 0.0001 in bold face. n.s. - significance probability > 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 2.

Variable	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
01 MA Inc	*	.0896	n.s.	n.s.	.0056	**.0000**	n.s.	.0095	n.s.	n.s.	.0002	.0001	.0306	n.s.	n.s.	n.s.	**.0000**	.0078	.0001	**.0000**	.0041	.0270	.0027	.0103	n.s.	n.s.	**.0000**	**.0000**	**.0000**	.0851	n.s.	n.s.
02 MA Asp	.1798	*	**.0000**	.0007	**.0000**	.0559	**.0000**	**.0000**	n.s.	n.s.	.0473	n.s.	n.s.	n.s.	n.s.	.0860	n.s.	.0023	.0114	n.s.	n.s.	.0269	n.s.	n.s.	n.s.	.0006	n.s.	n.s.	n.s.	n.s.	n.s.	.0630
03 MA Hi	-.1348	**-.7778**	*	.0030	**.0000**	n.s.	**.0000**	**.0000**	n.s.	n.s.	.0897	n.s.	n.s.	n.s.	.0971	n.s.	n.s.	.0674	n.s.	n.s.	n.s.	.0845	n.s.	.0028	n.s.	.0004	.0758	n.s.	n.s.	n.s.	n.s.	n.s.
04 MA BA	.1591	.3596	-.3146	*	n.s.	.0408	.0333	.0355	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0586	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0037	.0108	n.s.
05 MA Lig	.2955	**-.4495**	**.4944**	-.0227	*	.0018	**.0000**	.0010	n.s.	n.s.	.0712	.0026	n.s.	n.s.	.0878	.0472	.0002	n.s.	n.s.	**.0000**	.0002	n.s.	.0946	n.s.	n.s.	.0030	.0258	.0006	.0076	.0258	n.s.	n.s.
06 ME Inc	**.7364**	.1956	-.1560	.2109	.3224	*	n.s.	.0141	n.s.	.0347	.0002	.0001	.0029	n.s.	n.s.	n.s.	**.0000**	.0081	.0002	.0001	.0043	n.s.	.0056	.0041	n.s.	n.s.	**.0000**	**.0000**	**.0000**	.0186	n.s.	n.s.
07 ME Asp	.1544	**.5668**	**-.6456**	.2185	**-.4596**	.1039	*	**.0000**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0756	n.s.	n.s.	n.s.	n.s.	n.s.	.0473	.0195	n.s.	n.s.	.0574	.0021	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
08 ME Hi	-.2651	**-.4884**	**.6507**	-.2150	.3377	-.2426	**-.7751**	*	n.s.	n.s.	.0779	n.s.	.0511	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0533	n.s.	.0102	.0343	.0183	.0302	n.s.	n.s.	n.s.	n.s.	n.s.
09 ME Rou	-.0391	-.0892	.0206	-.1640	-.0382	-.1215	-.0513	-.0049	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0596
10 ME Con	.1325	.0582	-.0308	.0078	.0234	.2092	.0182	-.0740	-.0281	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0909	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
11 ME Smi	-.3840	-.2047	.1750	-.1356	-.1876	-.3740	-.1344	.1757	-.0673	.0201	*	**.0000**	**.0000**	n.s.	n.s.	n.s.	**.0000**	n.s.	.0789	.0018	.0234	n.s.	n.s.	.0515	.0130	n.s.	.0005	**.0000**	.0030	.0013	.096	n.s.
12 ME Sme	-.4072	-.0903	.0628	-.0487	-.3097	-.3945	-.0473	.1479	-.0257	-.0655	**.6751**	*	**.0000**	n.s.	n.s.	n.s.	**.0000**	n.s.	.0727	.0037	.0314	n.s.	.0314	.0861	.0436	n.s.	.0002	.0001	.0123	.0008	.099	n.s.
13 ME Sma	-.2218	-.0917	.1585	-.0485	-.0338	-.2949	-.0694	.1918	.0223	-.0495	**.4096**	**.4934**	*	n.s.	n.s.	n.s.	.0403	n.s.	n.s.	n.s.	n.s.	.0195	n.s.	.0118	n.s.	n.s.	.0092	.0046	n.s.	.0014	.0357	n.s.
14 LitCC	-.0313	-.1588	.1537	.0043	.1459	-.0599	-.1590	.0709	.1475	.0703	-.1068	-.1479	-.1572	*	**.0000**	.0079	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0152	n.s.	n.s.	.0491	n.s.	n.s.	n.s.	.0363	n.s.	n.s.
15 LitACD	-.0208	-.1656	.1690	.0165	.1752	-.0449	-.1754	.0972	.1358	.0603	-.1034	-.1577	-.1571	**.9147**	*	.0072	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0174	n.s.	n.s.	.0276	n.s.	n.s.	n.s.	.0445	n.s.	n.s.
16 Mois	-.1063	.1743	-.1213	-.0579	-.2030	-.1176	.1104	-.1018	.0214	.0453	.0812	.0463	.0412	-.2616	-.2646	*	.0789	.0469	n.s.	.0365	n.s.	.0284	**.0000**	n.s.	.0146	n.s.	.0049	.0067	n.s.	.0183	.0322	n.s.
17 LI	**-.5880**	-.0793	.0708	-.0931	-.3742	**-.5298**	-.0189	.1188	.0074	.0164	**.4327**	**.4018**	.2013	-.1482	-.1251	.1721	*	.0005	**.0000**	**.0000**	**.0000**	n.s.	.0021	.0554	n.s.	n.s.	**.0000**	**.0000**	**.0000**	.0017	n.s.	n.s.
18 pH_{H2O}	.2809	.3194	-.1917	-.0835	.0009	.2701	.0959	-.0878	-.1105	.0171	-.1156	-.1022	-.0487	-.1080	-.1379	.2013	-.3498	*	**.0000**	.0059	**.0000**	n.s.	n.s.	.0305	n.s.	.0006	.0013	.0172	**.0000**	n.s.	.0007	.0652
19 pH_{CaCl2}	.4190	.2647	-.1691	-.0358	.0842	.3802	.0871	-.1463	-.1060	.0102	-.1804	-.1825	-.0922	-.0342	-.0632	.0630	**-.4602**	**.8255**	*	.0001	**.0000**	n.s.	n.s.	.0044	n.s.	.0004	**.0000**	.0001	**.0000**	n.s.	.0121	.0241
20 Ca	**.4169**	-.1286	.0520	-.1034	**.4497**	.3956	-.1060	.0368	.1324	-.0213	-.3105	-.2861	-.1338	.1037	.0855	-.2047	**-.5711**	.2781	.4039	*	**.0000**	n.s.	.0039	.0025	n.s.	n.s.	**.0000**	**.0000**	**.0000**	n.s.	n.s.	n.s.
21 Mg	.2929	-.0571	.0929	-.1930	.3808	.2816	-.1947	.1219	.0321	-.0936	-.2253	-.2119	-.1240	.0197	.0164	.0540	**-.4992**	**.4634**	**.4429**	**.5543**	*	n.s.	n.s.	n.s.	n.s.	n.s.	.0043	**.0000**	**.0000**	n.s.	.0748	n.s.
22 K	-.2257	-.2240	.1746	.0362	.0861	-.1181	-.2293	.1890	-.1028	-.0952	.0284	-.0355	-.2291	.1596	.1463	-.2145	.1103	-.1437	-.1374	-.1151	-.0318	*	n.s.	n.s.	n.s.	.0565	n.s.	n.s.	n.s.	.0008	**.0000**	.0994
23 Na	-.3067	.0111	.0724	-.1585	-.1706	-.2733	-.0583	.1088	.0436	-.0476	.1435	.2119	.1404	-.2386	-.2335	**.4192**	.2998	.0094	-.1561	-.2816	-.0155	-.1037	*	.0010	.0004	.0544	**.0000**	**.0000**	.0028	.0011	.0598	n.s.
24 H^+	-.2619	-.1065	.3024	-.0982	-.0258	-.2833	-.1586	.2512	-.0387	.0246	.1936	.1690	.2471	.0346	.0378	.0196	.1871	-.2185	-.2868	-.2947	.1178	-.0090	.3208	*	.0076	.0682	.0011	.0003	.0438	.0164	n.s.	n.s.
25 Al	-.1430	-.0230	.1406	-.1223	-.0258	-.1412	-.1865	.2070	-.0633	.1658	.2470	.1987	.1256	.0642	.0789	.2391	.0711	.1386	.0288	-.1429	.1069	-.1020	.3453	.2604	*	.0133	.0080	.0421	n.s.	.0290	.0014	n.s.
26 Fe	-.1388	-.3477	.3562	-.0836	.3025	-.0991	-.3025	.2309	-.0181	-.0140	-.0676	-.1551	-.1446	.1934	.2163	.0238	.0163	-.3454	-.3556	-.0898	.0833	.1862	.1878	.1780	.2417	*	.0049	n.s.	n.s.	n.s.	.0200	n.s.
27 Mn	**.5289**	.1576	-.1797	.0965	.2274	**.5310**	.1126	-.2119	-.0617	.0492	-.3472	-.3636	-.2553	.0790	.0543	-.2751	**-.5743**	.3257	**.4938**	**.4792**	.2784	.0269	**-.4400**	-.3192	-.2588	-.2744	*	**.0000**	**.0000**	.0003	n.s.	.0513
28 Zn	**.4928**	.0349	-.0843	.1137	.3498	**.5194**	.0156	-.0957	.0074	-.0197	**-.4240**	-.3801	-.2783	.1004	.0871	-.2652	**-.6413**	.2406	.3835	**.6376**	**.4237**	.0122	**-.3959**	-.3535	-.1984	-.1029	**.6392**	*	**.0000**	.0002	n.s.	n.s.
29 Total N	**.5169**	.0673	-.0554	-.0224	.2722	**.4435**	.0600	-.1285	-.0288	.0689	-.2954	-.2465	-.0911	.0856	.0427	-.1212	**-.6479**	**.4107**	**.5226**	**.4906**	**.4367**	-.1380	-.2914	-.1967	-.0090	-.1486	**.4988**	**.5102**	*	.0196	n.s.	n.s.
30 P-AL	.1757	.0213	.0043	.2963	.2274	.2321	-.0551	-.0450	-.0666	-.0919	-.3188	-.3306	-.3128	.2057	.1973	-.2309	-.3064	-.0706	.0305	.1298	.1151	.3273	-.3192	-.2343	-.2131	.1339	.3502	.3584	.2278	*	**.0000**	n.s.
31 P	-.0379	-.1235	.1593	.2602	.1154	.0388	-.1274	.0597	.0255	-.0394	-.1652	-.1624	-.2061	.1382	.1430	-.2096	.0449	-.3410	-.2528	-.0710	-.1739	**.4008**	-.1837	.0122	-.3127	.2270	.0645	.0367	-.1200	**.4922**	*	.0547
32 S	.0190	.1883	-.1252	-.0017	-.1602	.0107	-.0074	.0008	-.1850	-.0771	-.0167	.0437	-.1043	.1185	.0822	-.0458	-.0776	.1862	.2274	-.0269	.0531	.1608	.0041	.0204	.0906	-.1323	.1902	.0808	.0939	.1445	.0547	*

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Correlations between environmental variables

Nine variables made up a group of pairwise more or less strongly correlated variables ($\tau > 0.35$, $P < 0.0003$ for all pairs): pH, and concentrations of total N, Mn, Ca, Mg, Zn, and the two inclination variables (all positively correlated) and loss on ignition (negatively correlated with all the others; Tab. 15, Fig. 268). The soil depth variables were pairwise strongly correlated, and associated with the large group via minimum and median soil depth; positively correlated with loss on ignition and negatively correlated with inclination. Other variables associated with the large group were concentrations of P (positive correlations), and concentra-

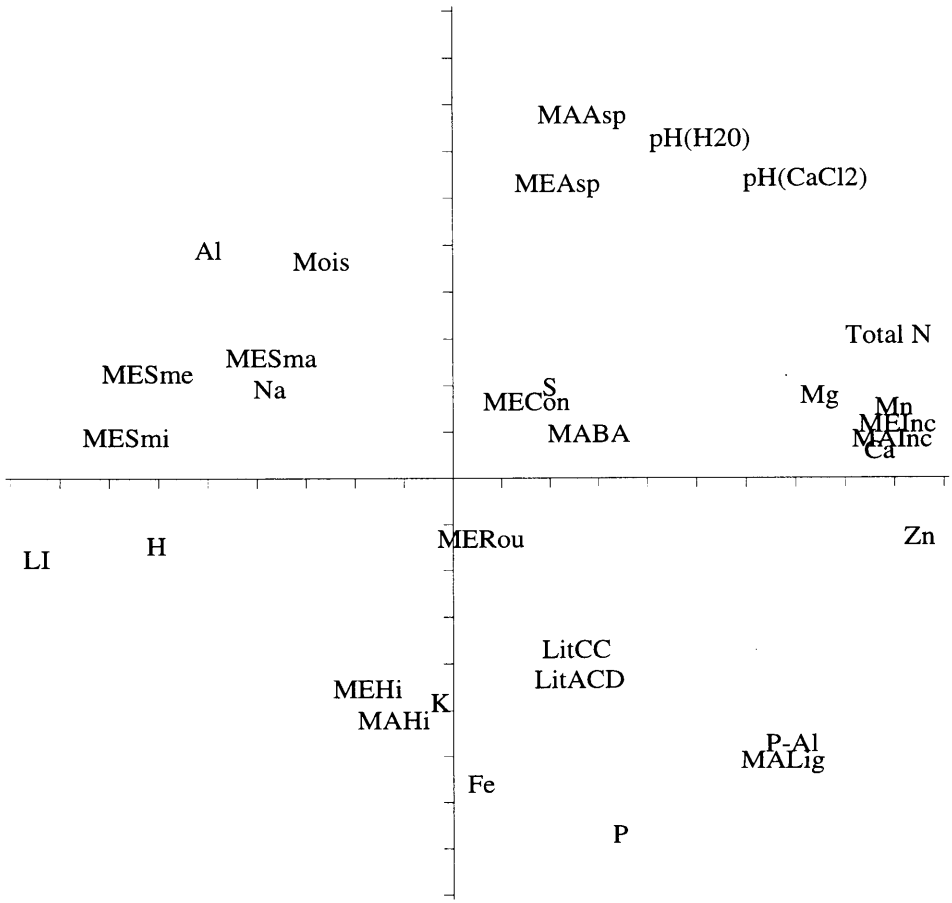


Fig. 269. Bringen: PCA ordination of 32 environmental variables (names abbreviated in accordance with Tab. 2), axes 1 (horizontal) and 2 (vertical). Positions of variables in the ordination give the head of variable vectors.

tions of Fe and Na (negative correlations). The concentration of Na was also positively correlated with soil moisture.

Aspect unfavourability was negatively correlated with the heat indices. These four topographic variables were correlated with the macro plot light index (the heat indices positively correlated), in turn connecting to the large group via the correlations with concentrations of Ca and Mg (both positive) and loss on ignition (negative). Macro plot basal area was correlated (positively) with macro plot aspect unfavourability.

PCA ordination of environmental variables

Eigenvalues of the first two PCA axes were 0.295 and 0.177, thus 47.2% of the variation in measured environmental variables was explained by the first two PCA axes.

The positively correlated variables of the nine-variable group obtained high loadings on PCA 1, while loss on ignition obtained the lowest loading (Fig. 269). Variables associated with this group obtained either relatively high (P-AL and the macro plot light index) or relatively low (minimum and medium soil depth and H) loadings.

Aspect unfavourability and pH obtained the highest loadings on PCA 2. Other variables with relatively high loadings on this axis were Al and soil moisture. Several variables obtained low loadings on PCA 2: P, Fe, K and the macro plot light index, the heat indices and the litter indices.

The first PCA axis was consistent with the correlations between variables (Tab. 15, Fig. 268), while the second axis indicated complex relationships between tree-related variables, topographic variables and soil acidity.

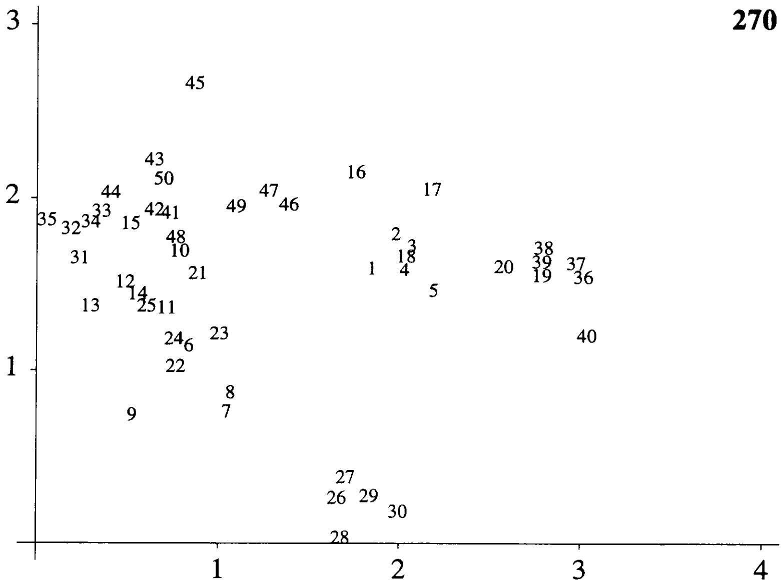
DCA and LNMDS ordination

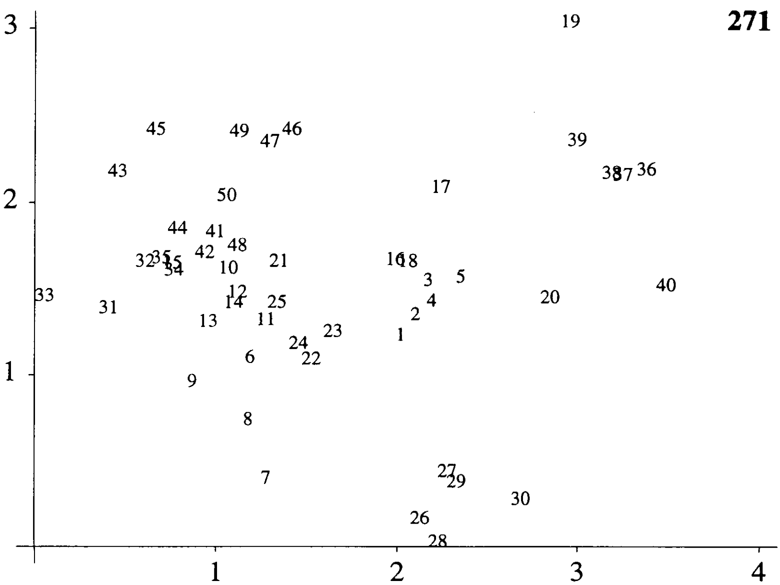
Plot Nos 26-30 made up a somewhat isolated group both in the DCA (Fig. 270) and LNMDS (Fig. 271) ordinations. The remaining plots were relatively evenly distributed along the first two axes of both ordinations. Gradients were slightly longer in LNMDS than in DCA ordination.

DCA 1 explained 18.5% of the variation in vegetation (Tab. 16). The fraction of variation explained by DCA 2 was ca. 48% of that explained by DCA 1, and decreasing to ca. 43% of DCA 2 for DCA 3. The eigenvalues of DCA 3 and DCA 4 were low (0.092 and 0.078, respectively), corresponding to less than 4% of the total variation explained.

Tab. 16. Bringen: Eigenvalues and the fraction of variation explained for DCA axes 1-4.

	DCA 1	DCA 2	DCA 3	DCA 4
Eigenvalues	0.457	0.218	0.092	0.078
Fraction of variation explained	0.185	0.088	0.038	0.032





Figs 270-271. Bringen: ordinations of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Meso plot numbers are plotted onto the sample plot positions. Fig. 270. DCA ordination. Scaling of axes in S.D. units. Fig. 271. LNMDS ordination. Axes linearly rescaled in S.D. units.

Tab. 17. Bringen: Kendall's nonparametric correlation coefficient τ between DCA and LNMDS axes, and between 32 environmental variables in the 50 meso sample plots and sample plot positions with respect to DCA and LNMDS axes, and their significance probabilities. Correlations significant at level P < 0.0001 in bold face. n.s. - significance probability > 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 2.

Variable	DCA 1		DCA 2		DCA 3		DCA 4		LNMDS 1		LNMDS 2	
	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P
LNMDS 1	**.7763**	**.0000**	-.2653	.0066	-.0612	n.s.	.2131	.0290				
LNMDS 2	.0727	n.s.	**.6473**	**.0000**	.0906	n.s.	.1135	n.s.				
01 MA Inc	.3584	.0004	.1085	n.s.	-.3515	.0006	.1792	.0791	.3894	.0001	.2826	.0056
02 MA Asp	.2087	.0393	**-.4217**	**.0000**	-.2666	.0084	.2939	.0037	.3723	.0002	-.3280	.0012
03 MA Hi	-.1082	n.s.	**.4506**	**.0000**	.4046	.0001	-.2820	.0054	-.2343	.0207	.3705	.0003
04 MA BA	-.0655	n.s.	.0465	n.s.	-.2016	.0482	.2602	.0108	-.0345	n.s.	-.0930	n.s.
05 MA Lig	.0879	n.s.	**.6168**	**.0000**	.0345	n.s.	-.0948	n.s.	-.0930	n.s.	**.6185**	**.0000**
06 ME Inc	.3212	.0011	.1809	.0666	-.3609	.0003	.1610	n.s.	.2948	.0028	.2717	.0059
07 ME Asp	.0633	n.s.	-.3772	.0001	-.3065	.0018	.3180	.0012	.2112	.0314	-.2736	.0053
08 ME Hi	-.1219	n.s.	.2823	.0039	.3592	.0002	-.3625	.0002	-.2201	.0244	.1727	.0775
09 ME Rou	-.0847	n.s.	.0107	n.s.	-.0518	n.s.	.0913	n.s.	-.0354	n.s.	.0617	n.s.
10 ME Con	.0640	n.s.	-.0197	n.s.	.0443	n.s.	.0837	n.s.	.0460	n.s.	.0312	n.s.
11 ME Smi	-.2621	.0084	-.1703	.0868	.3572	.0003	-.2771	.0053	-.2387	.0164	-.2771	.0053
12 ME Sme	-.1888	.0552	-.2284	.0204	.2762	.0050	-.1921	.0511	-.1344	n.s.	-.3240	.0010
13 ME Sma	-.1404	n.s.	-.0172	n.s.	.2225	.0233	-.1650	.0925	-.0649	n.s.	-.0829	n.s.
14 LitCC	-.0247	n.s.	.1711	.0815	.1037	n.s.	.1316	n.s.	-.0938	n.s.	.1925	.0500
15 LitACD	-.0395	n.s.	.1858	.0584	.1134	n.s.	.1167	n.s.	-.1118	n.s.	.2104	.0321
16 Mois	.2210	.0239	-.3766	.0001	.1670	.0878	.0688	n.s.	.2931	.0027	-.2914	.0029
17 LI	-.3930	.0001	-.2623	.0072	.2721	.0053	-.1446	n.s.	-.3554	.0003	-.3636	.0002
18 pH$_{H20}$	**.6471**	**.0000**	-.1998	.0479	.0366	n.s.	-.0400	n.s.	**.6063**	**.0000**	-.0893	n.s.
19 pH$_{CaCl2}$	**.6669**	**.0000**	-.0798	n.s.	-.0831	n.s.	.0170	n.s.	**.5956**	**.0000**	.0288	n.s.
20 Ca	.2914	.0028	.2849	.0035	-.2196	.0244	-.0106	n.s.	.2016	.0388	.3731	.0001
21 Mg	**.5020**	**.0000**	.1429	n.s.	-.0547	n.s.	-.0253	n.s.	.3927	.0001	.2082	.0329
22 K	-.2359	.0156	.2245	.0214	.0073	n.s.	-.1788	.0670	-.3616	.0002	-.0139	n.s.
23 Na	.0318	n.s.	-.1935	.0474	.2980	.0023	.0727	n.s.	.0694	n.s.	-.1445	n.s.
24 H$^+$	-.1673	.0864	.0939	n.s.	**.4155**	**.0000**	.0694	n.s.	-.1886	.0533	.1004	n.s.
25 Al	.1673	.0864	-.1363	n.s.	.3780	.0001	.0580	n.s.	.1755	.0721	-.0547	n.s.
26 Fe	-.0882	n.s.	.2303	.0183	.1878	.0544	.1062	n.s.	-.2074	.0336	.2662	.0064
27 Mn	.2604	.0076	.2278	.0196	-.3453	.0004	.0400	n.s.	.2261	.0205	.1984	.0421
28 Zn	.2457	.0118	.3078	.0016	**-.3959**	**.0000**	.0612	n.s.	.1886	.0533	.3176	.0011
29 Total N	**.4351**	**.0000**	.1543	n.s.	-.1771	.0695	.1102	n.s.	-3780	.0001	.2718	.0053
30 P-AL	-.0367	n.s.	.2735	.0051	-.2963	.0024	.0824	n.s.	-.0645	n.s.	.1657	.0895
31 P	-.2767	.0046	.2751	.0048	-.1118	n.s.	.0808	n.s.	-.3469	.0004	.1478	n.s.
32 S	.1102	n.s.	-.0792	n.s.	.0073	n.s.	-.0547	n.s.	.1314	n.s.	-.1053	n.s.

Correlations between DCA and LNMDS ordination axes and between ordination axes and environmental variables

The correlations between DCA 1 and LNMDS 1 and between DCA 2 and LNMDS 2 were strong (τ = 0.776 and τ = 0.647, respectively, Tab. 17). The variables most strongly correlated with each of DCA 1 and DCA 2 were also strongly correlated with LNMDS 1 and LNMDS 2, respectively. With few exceptions, the correlation coefficient τ of significantly correlated variables were lower for an LNMDS than the corresponding DCA axis.

The variables most strongly correlated with DCA 1 (and LNMDS 1) were, in order of decreasing τ: pH (τ = 0.67, Fig. 280), and concentrations of Mg (Fig. 281) and total N (Fig. 283), all positively correlated. Other correlated variables were inclination (Figs 272 and 276), positively correlated, and loss on ignition (Fig. 279), which was negatively correlated.

Variables strongly positively correlated with DCA 2 (and LNMDS 2) were the macro plot light index (τ = 0.617, Fig. 275) and the macro plot heat index (Fig. 274), while macro plot aspect unfavourability (Fig. 273) was strongly negatively correlated with DCA 2. Other correlated variables were meso plot aspect unfavourability (Fig. 277), soil moisture (Fig. 278) and the concentration of Zn (Fig. 282).

Ten variables were significantly correlated with DCA 3 at $P < 0.002$, H^+ and Zn strongly so ($P < 0.0001$). However, as DCA 3 only explained 3.8% of the variation in vegetation, no further interpretation of this axis was made.

The distribution of species abundance in the DCA ordination

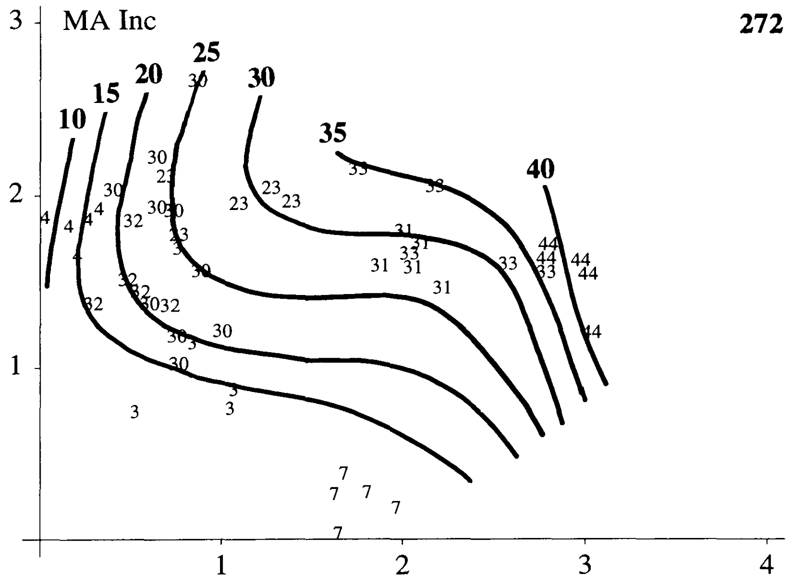
Seventy-two of a total of 115 species occurred in at least 5 of the 50 meso plots (Figs 284-355).

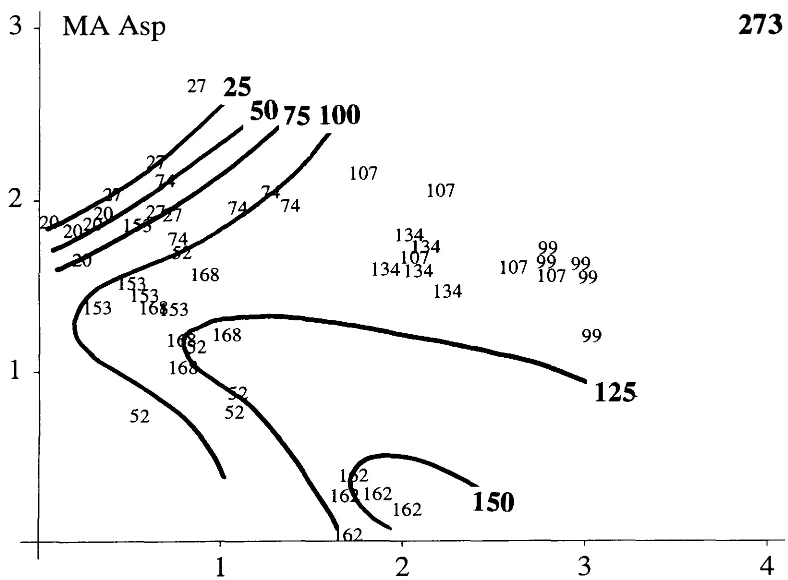
Vaccinium myrtillus (Fig. 287) and *Deschampsia flexuosa* (Fig. 310), typical examples of species with wide ecological amplitude, were abundant in most plots.

Examples of species restricted to meso plots on sites with low pH, low nutrient content and high content of organic matter in the soil (left-hand side of the DCA ordination) were *Lycopodium annotinum* (Fig. 297), *Ptilium crista-castrensis* (Fig. 327) and *Ptilidium ciliare* (Fig. 349). Examples of species restricted to sites with relatively high pH and high nutrient content (the right-hand side in the ordination) were *Geranium sylvaticum* (Fig. 291), *Fragaria vesca* (Fig. 290), *Brachythecium salebrosum* (Fig. 315) and *Mnium spinosum* (Fig. 321).

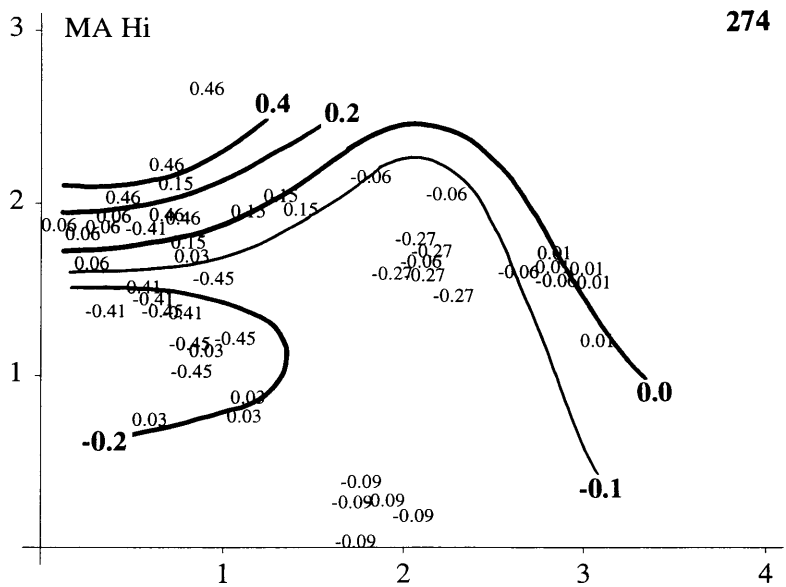
Examples of species restricted to plots from dry sites on favourable aspects with low light supply (dense forest), and that appear to be independent of pH or soil nutrient contents (high abundance in plots with high DCA 2 scores), were *Dicranum fuscescens* agg. (Fig. 317) and *Barbilophozia barbata* (Fig. 337). Other species restricted to relatively dry sites with moderate supply of light, but with high pH and high content of nutrients in the soil (upper right part of the ordination) were *Hieracium* Sect. *Sylvatica* (Fig. 293), *Carex digitata* (Fig. 309), *Melica nutans* (Fig. 312) and *Mnium stellare* (Fig. 322).

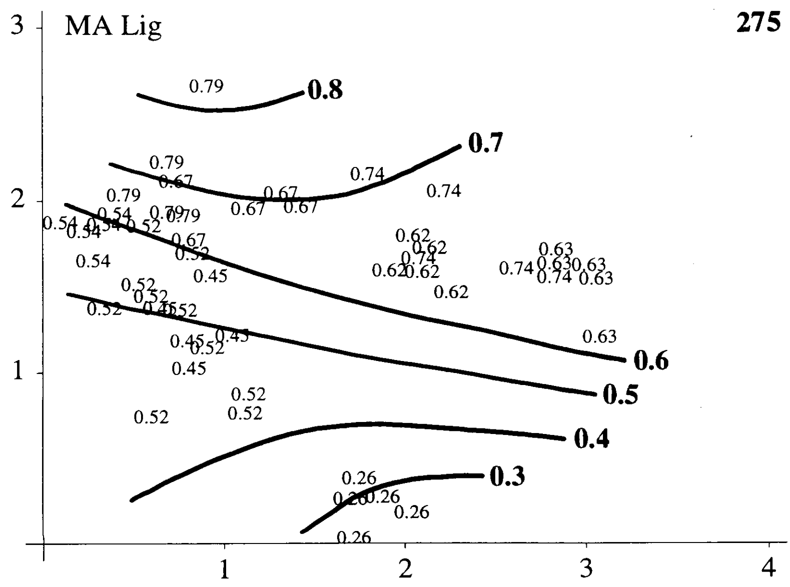
Phegopteris connectilis (Fig. 303) and *Sphagnum angustifolium* (Fig. 333) were mainly restricted to plots from moist sites with a high supply of light, on unfavourable aspects and with moderately high content of nutrients in the soil (intermediate DCA 1 scores, low DCA 2 scores). *Listera cordata* (Fig. 296) and *Sphagnum girgensohnii* (Fig. 334) were restricted to moist sites, low in pH and nutrients (lower left part of the ordination).



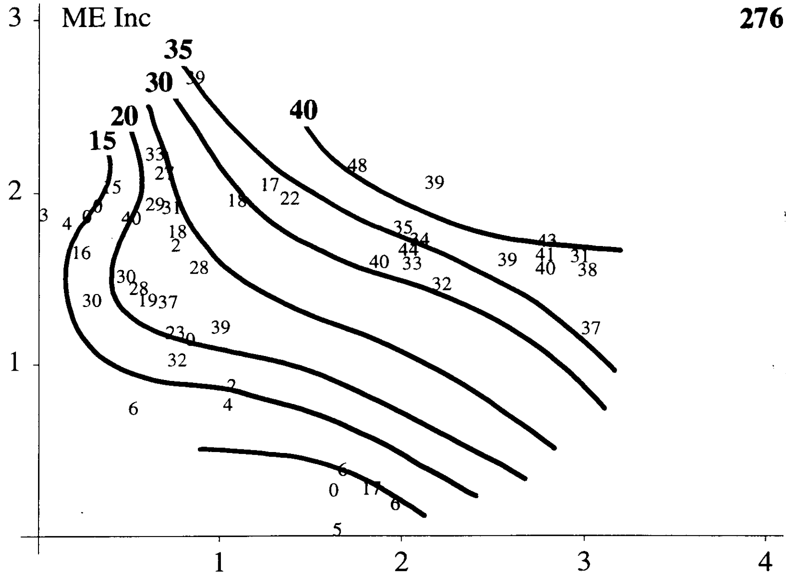


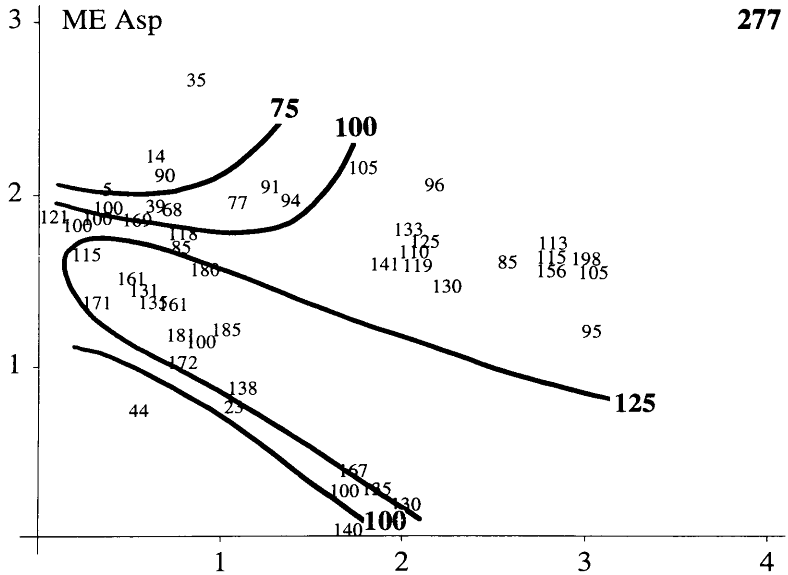
Figs 272-273. Bringen: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 272. MA Inc (R^2 = 0.619). Fig. 273. MA Asp (R^2 = 0.527). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.



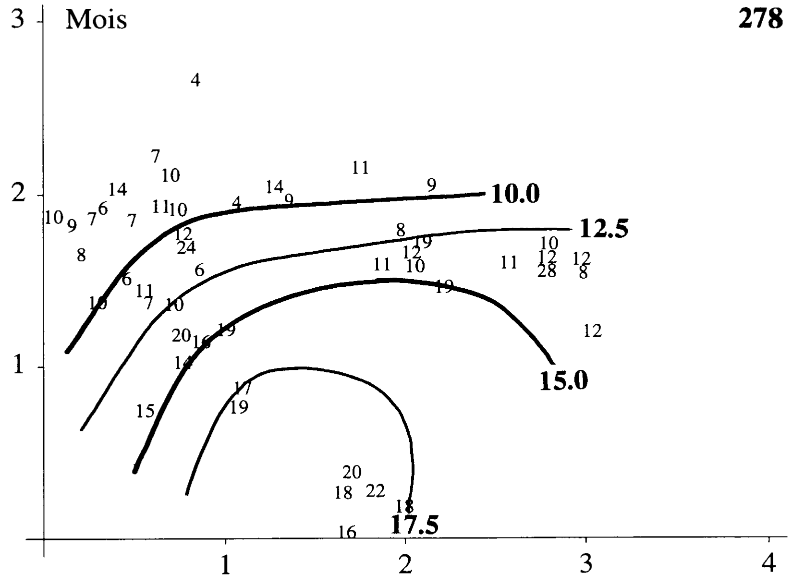


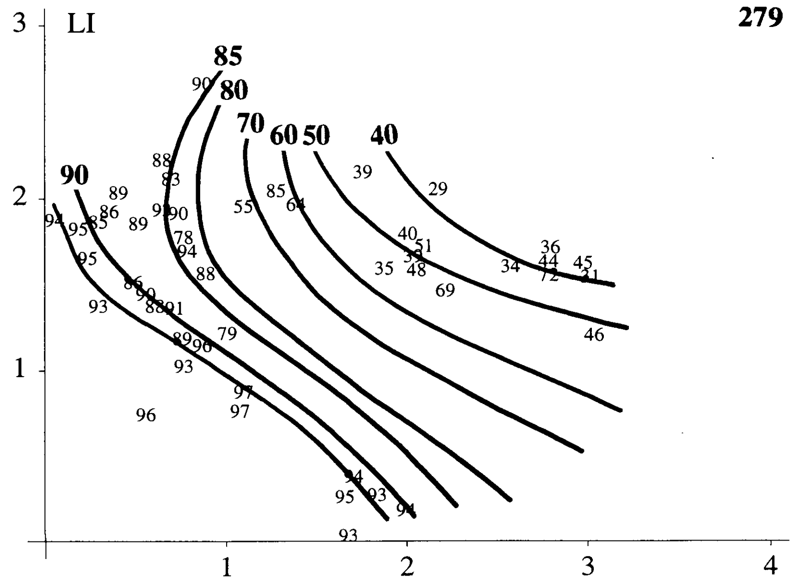
Figs 274-275. Bringen: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots' positions. Scaling of axes in S.D. units. Fig. 274. MA Hi (R^2 = 0.559). Fig. 275. MA Lig (R^2 = 0.838). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.



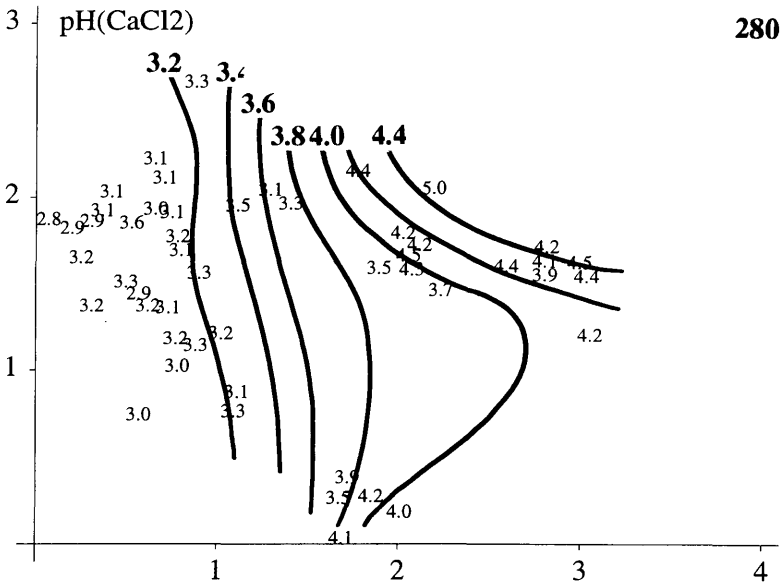


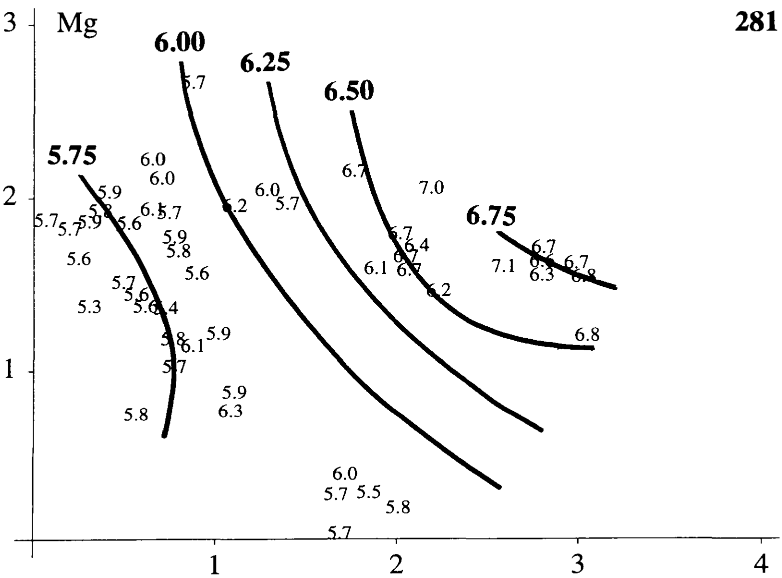
Figs 276-277. Bringen: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 276. ME Inc (R^2 = 0.566). Fig. 277. MA Asp (R^2 = 0.435). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.





Figs 278-279. Bringen: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots' positions. Scaling of axes in S.D. units. Fig. 278. Mois ($R^2 = 0.422$). Fig. 279. LI ($R^2 = 0.867$). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.





Figs 280-281. Bringen: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 280. pH_{CaCl2} (R^2 = 0.850). Fig. 281. Mg (R^2 = 0.759). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.

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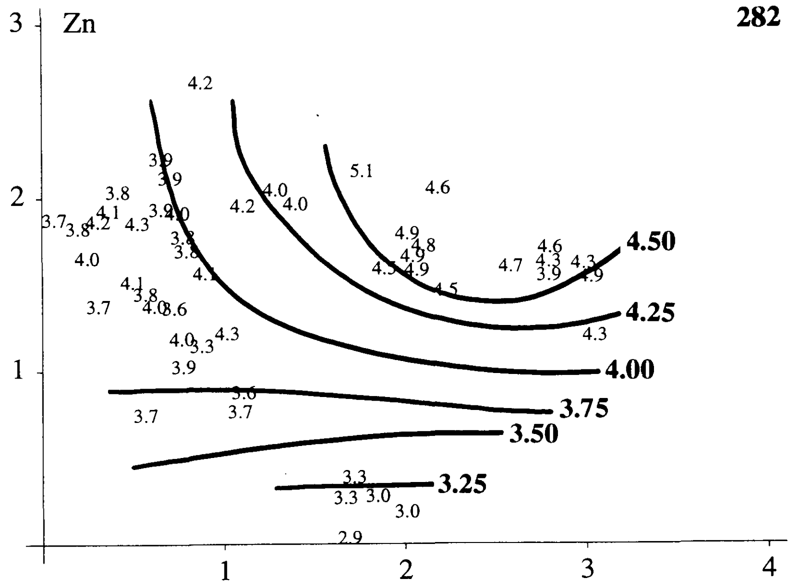
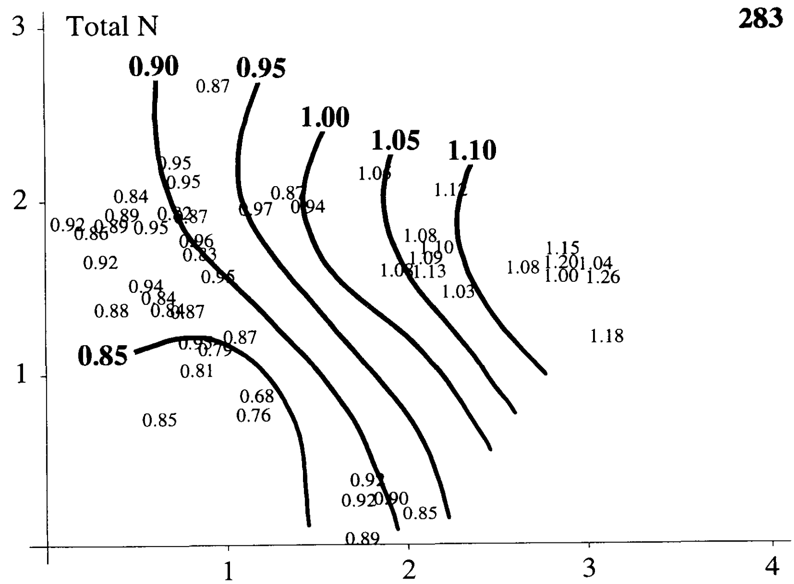
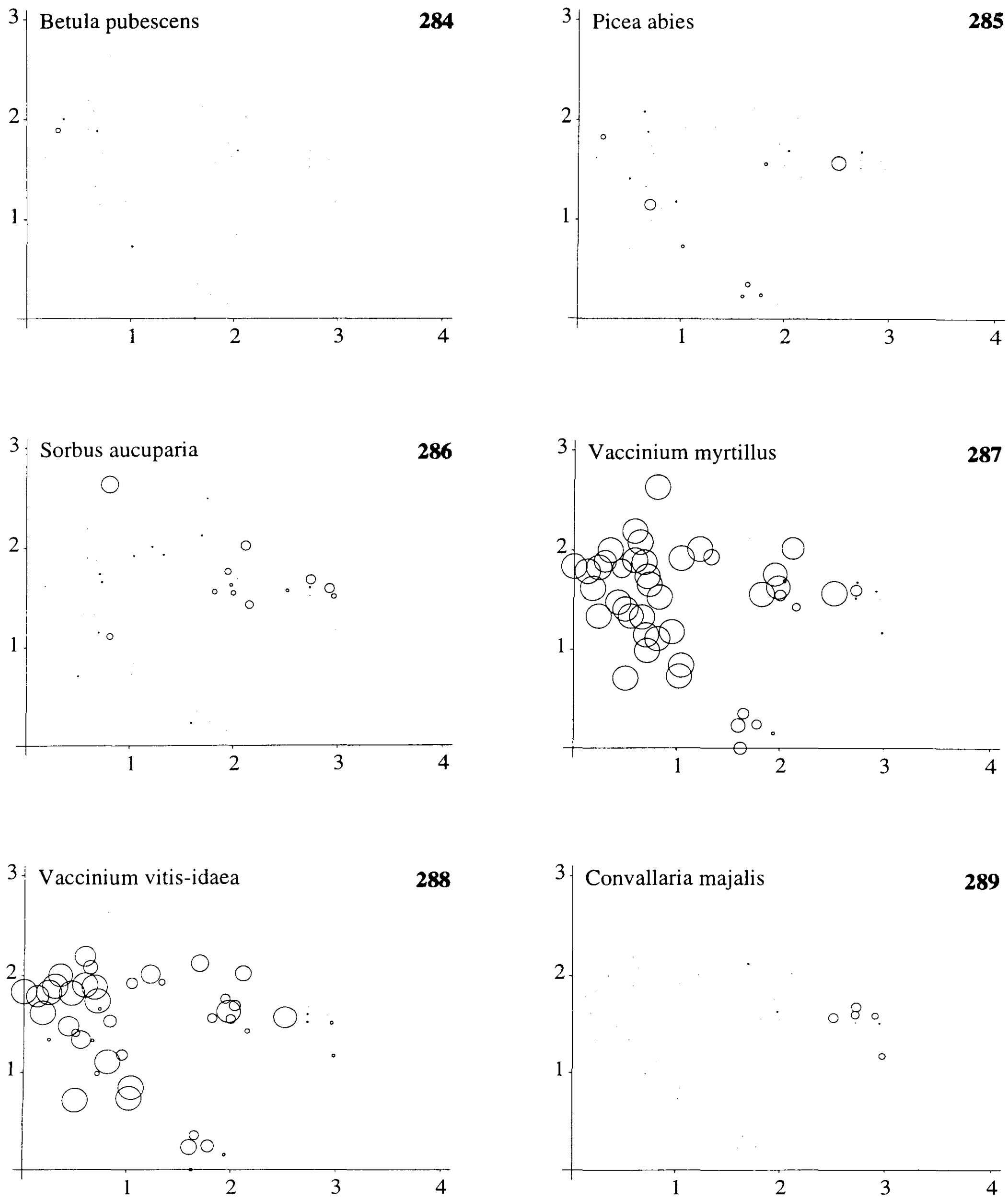


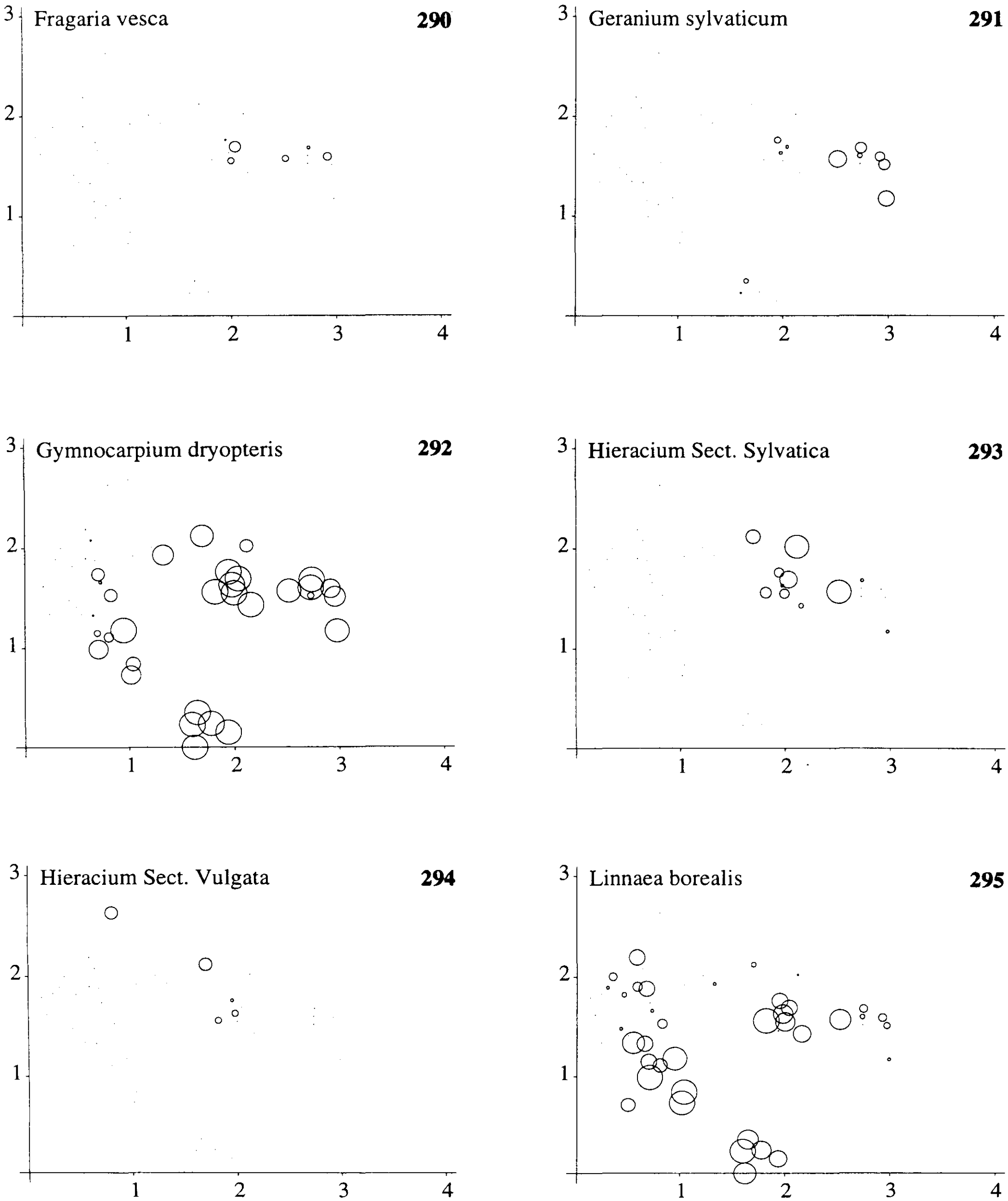
283



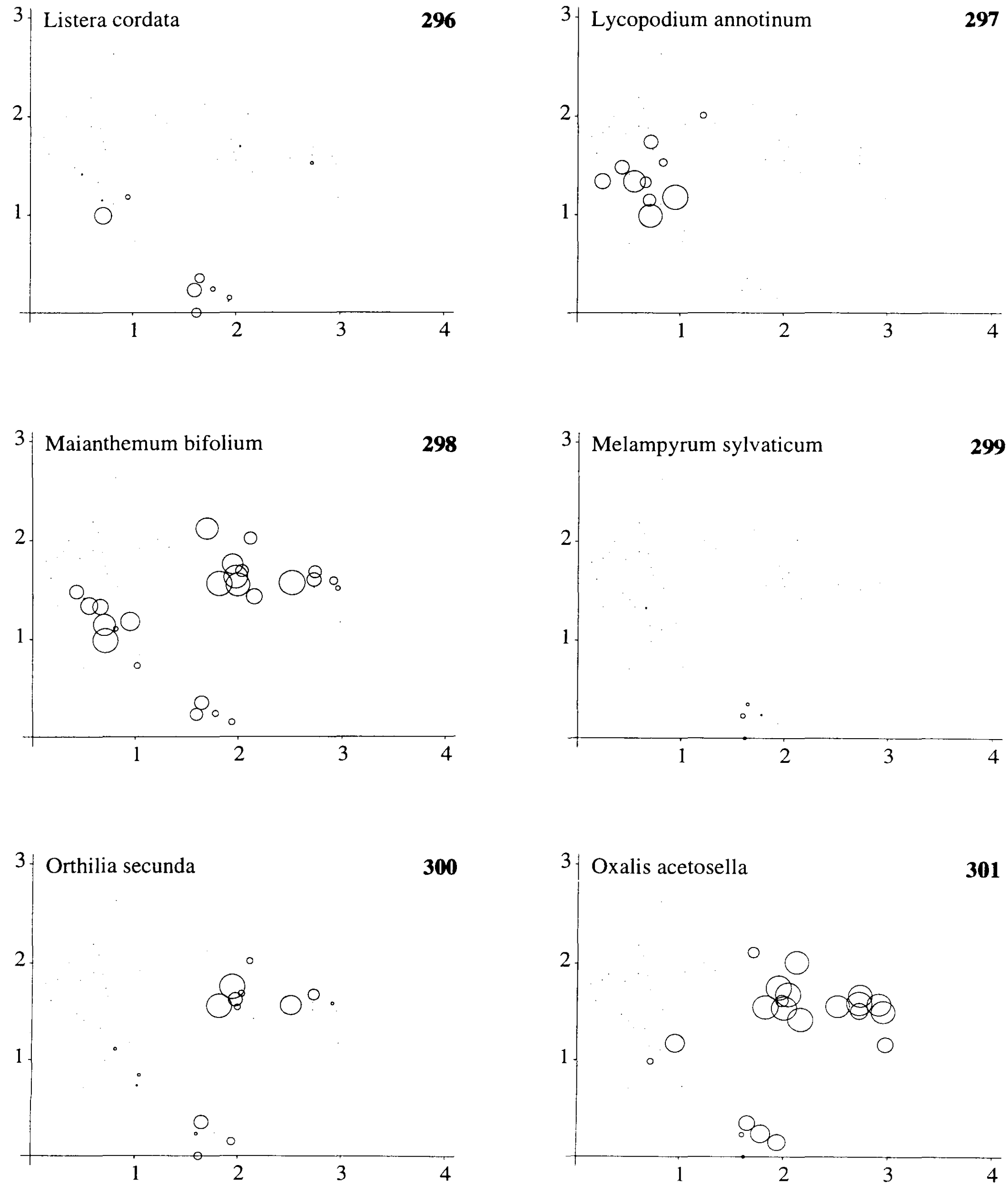
Figs 282-283. Bringen: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 282. Zn ($R^2 = 0.779$). Fig. 283. Total N ($R^2 = 0.776$). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.



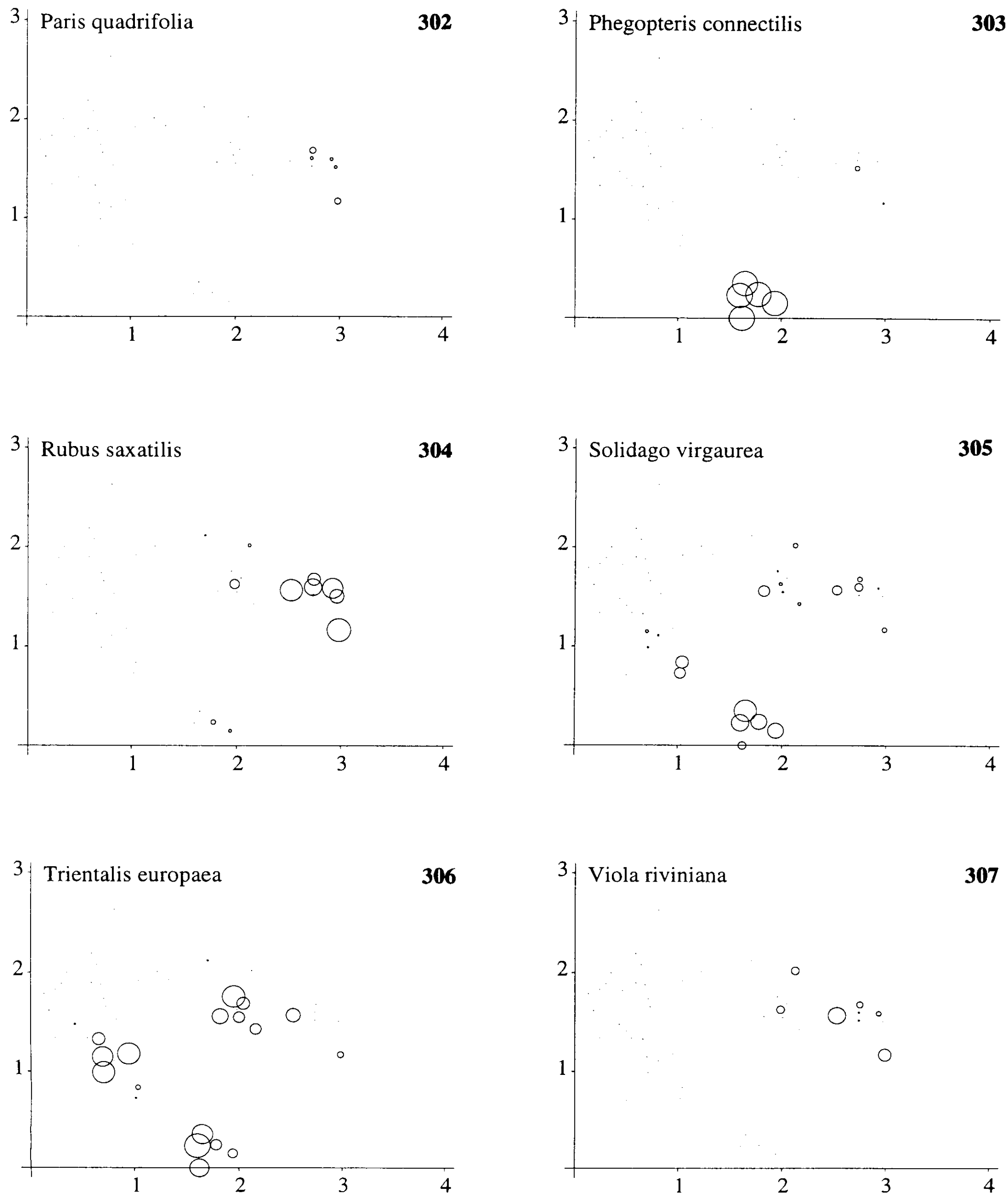
Figs 284-289. Bringen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 284. *Betula pubescens*. Fig. 285. *Picea abies*. Fig. 286. *Sorbus aucuparia*. Fig. 287. *Vaccinium myrtillus*. Fig. 288. *Vaccinium vitis-idaea*. Fig. 289. *Convallaria majalis*.



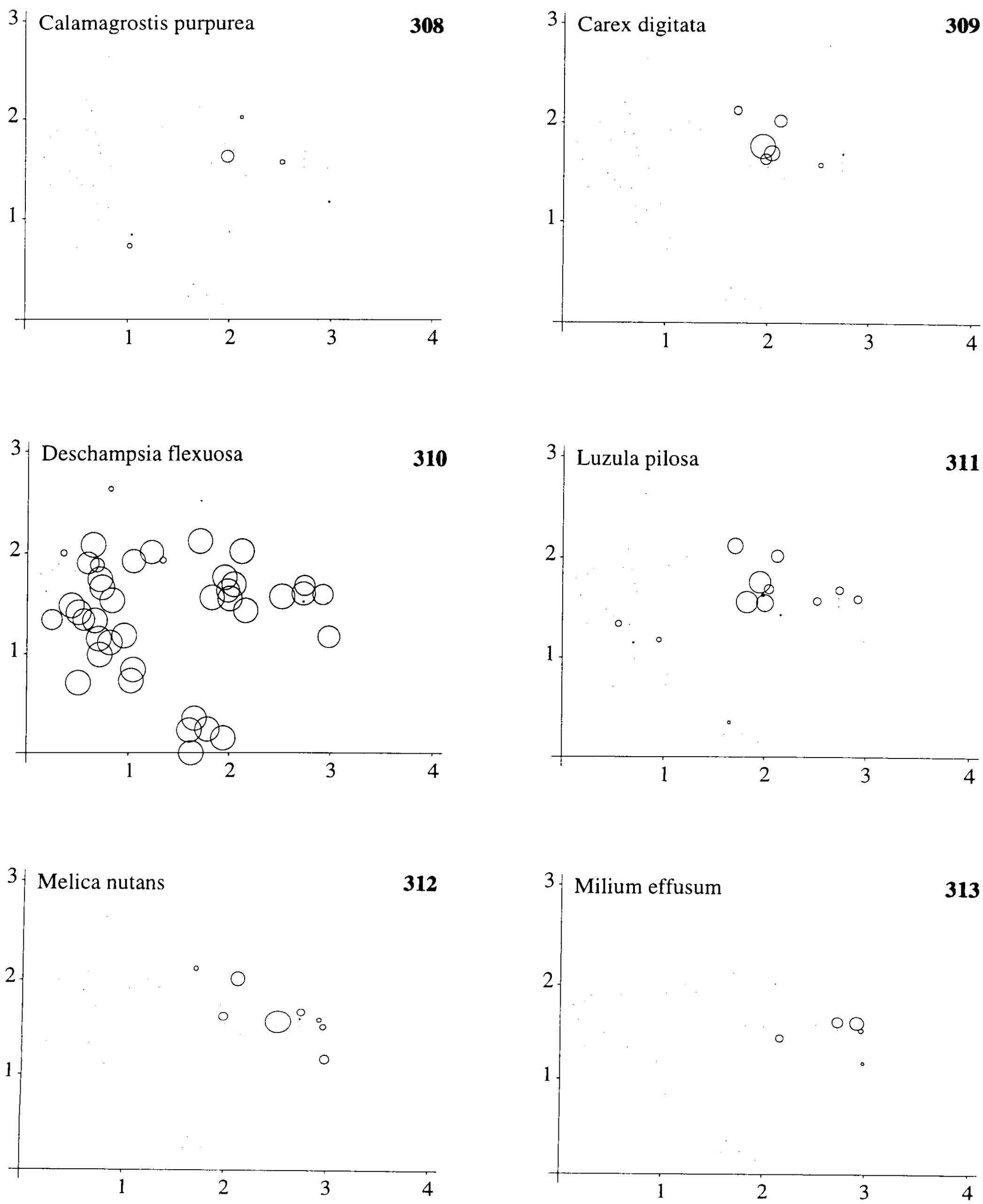
Figs 290-295. Bringen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 290. *Fragaria vesca*. Fig. 291. *Geranium sylvaticum*. Fig. 292. *Gymnocarpium dryopteris*. Fig. 293. *Hieracium Sect. Sylvatica*. Fig. 294. *Hieracium Sect. Vulgata*. Fig. 295. *Linnaea borealis*.



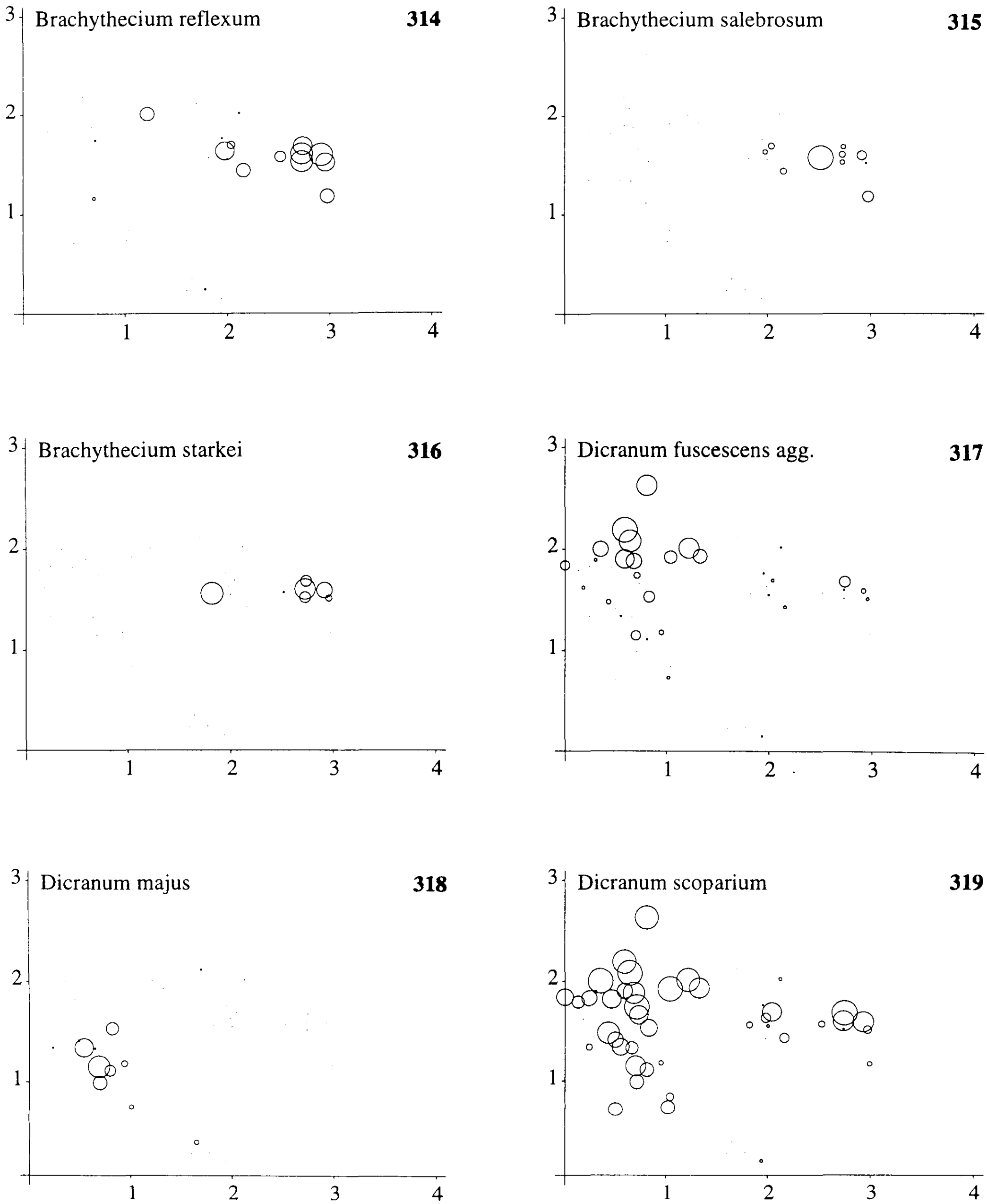
Figs 296-301. Bringen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 296. *Listera cordata*. Fig. 297. *Lycopodium annotinum*. Fig. 298. *Maianthemum bifolium*. Fig. 299. *Melampyrum sylvaticum*. Fig. 300. *Orthilia secunda*. Fig. 301. *Oxalis acetosella*.



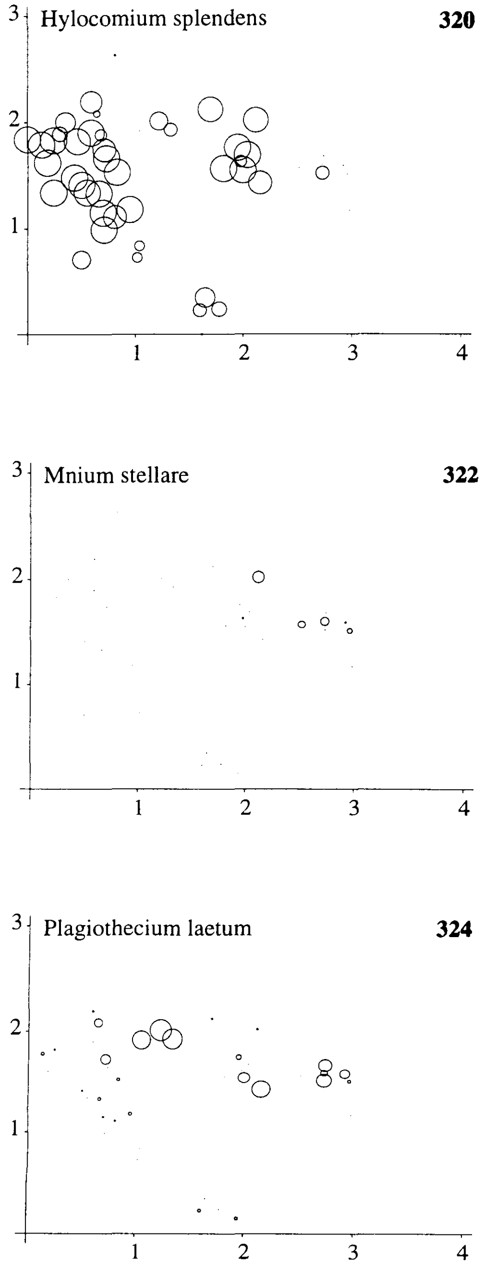
Figs 302-307. Bringen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 302. *Paris quadrifolia*. Fig. 303. *Phegopteris connectilis*. Fig. 304. *Rubus saxatilis*. Fig. 305. *Solidago virgaurea*. Fig. 306. *Trientalis europaea*. Fig. 307. *Viola riviniana*.



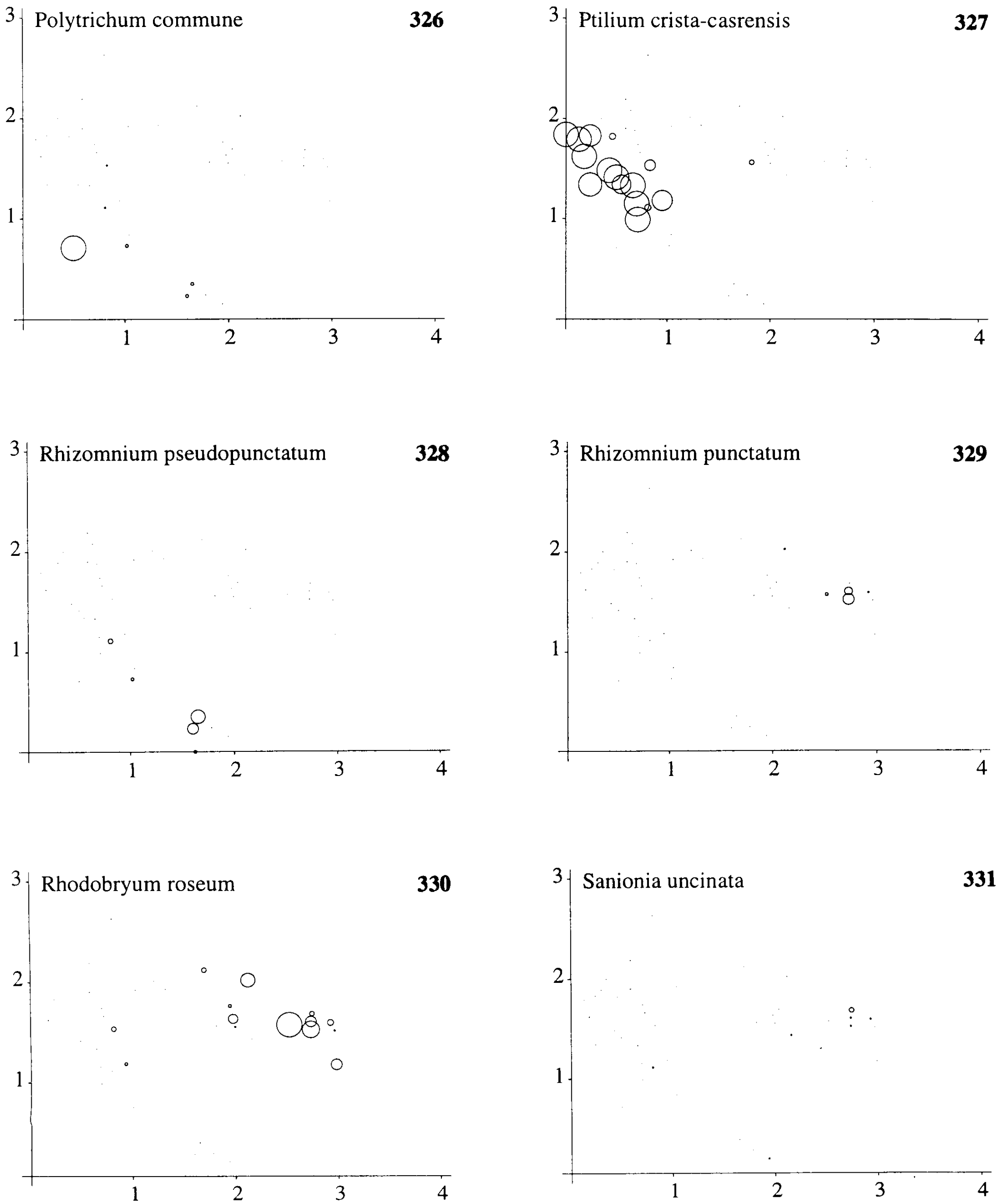
Figs 308-313. Bringen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 308. *Calamagrostis purpurea*. Fig. 309. *Carex digitata*. Fig. 310. *Deschampsia flexuosa*. Fig. 311. *Luzula pilosa*. Fig. 312. *Melica nutans*. Fig. 313. *Milium effusum*.



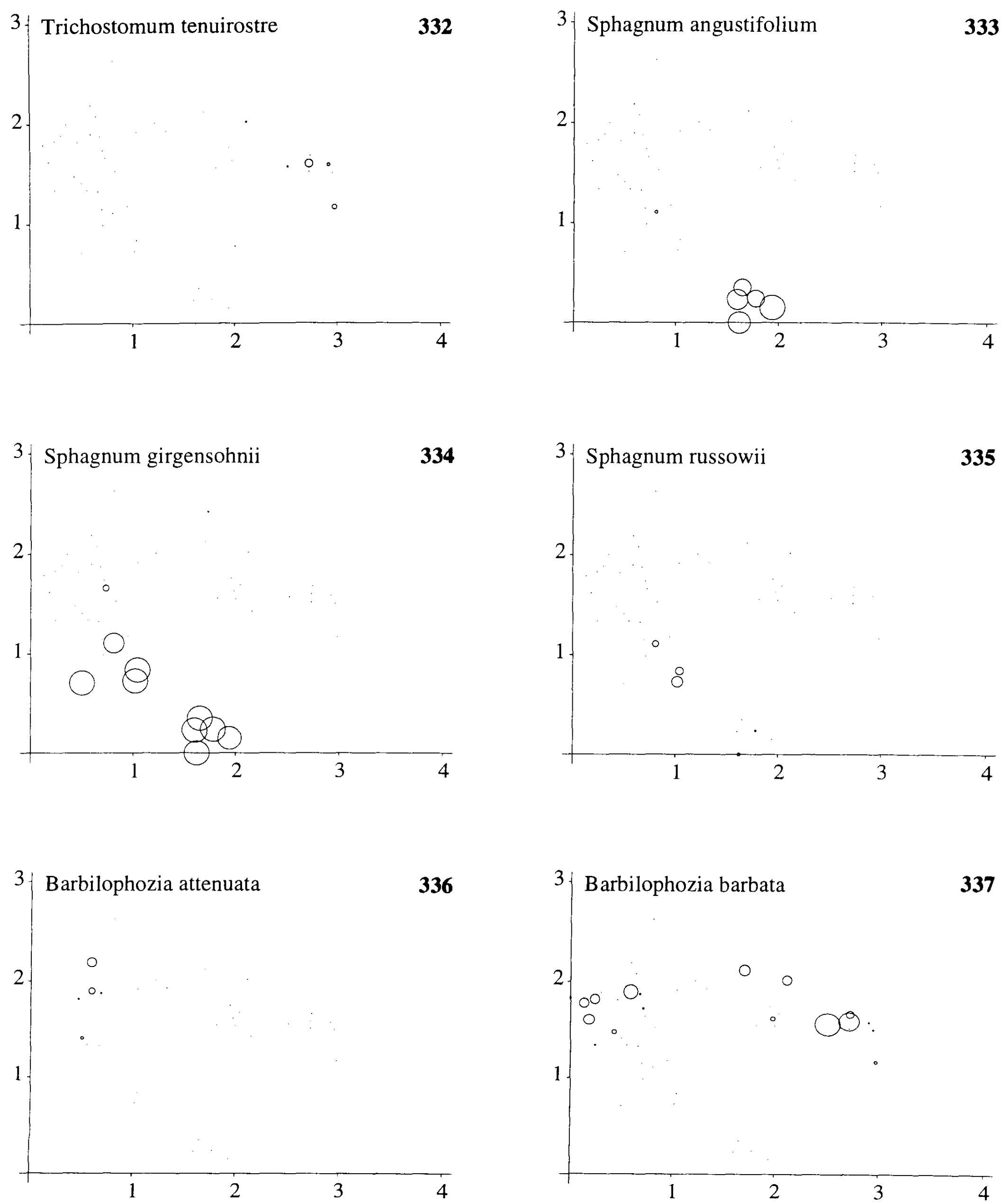
Figs 314-319. Bringen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 314. *Brachythecium reflexum*. Fig. 315. *Brachythecium salebrosum*. Fig. 316. *Brachythecium starkei*. Fig. 317. *Dicranum fuscescens* agg. Fig. 318. *Dicranum majus*. Fig. 319. *Dicranum scoparium*.



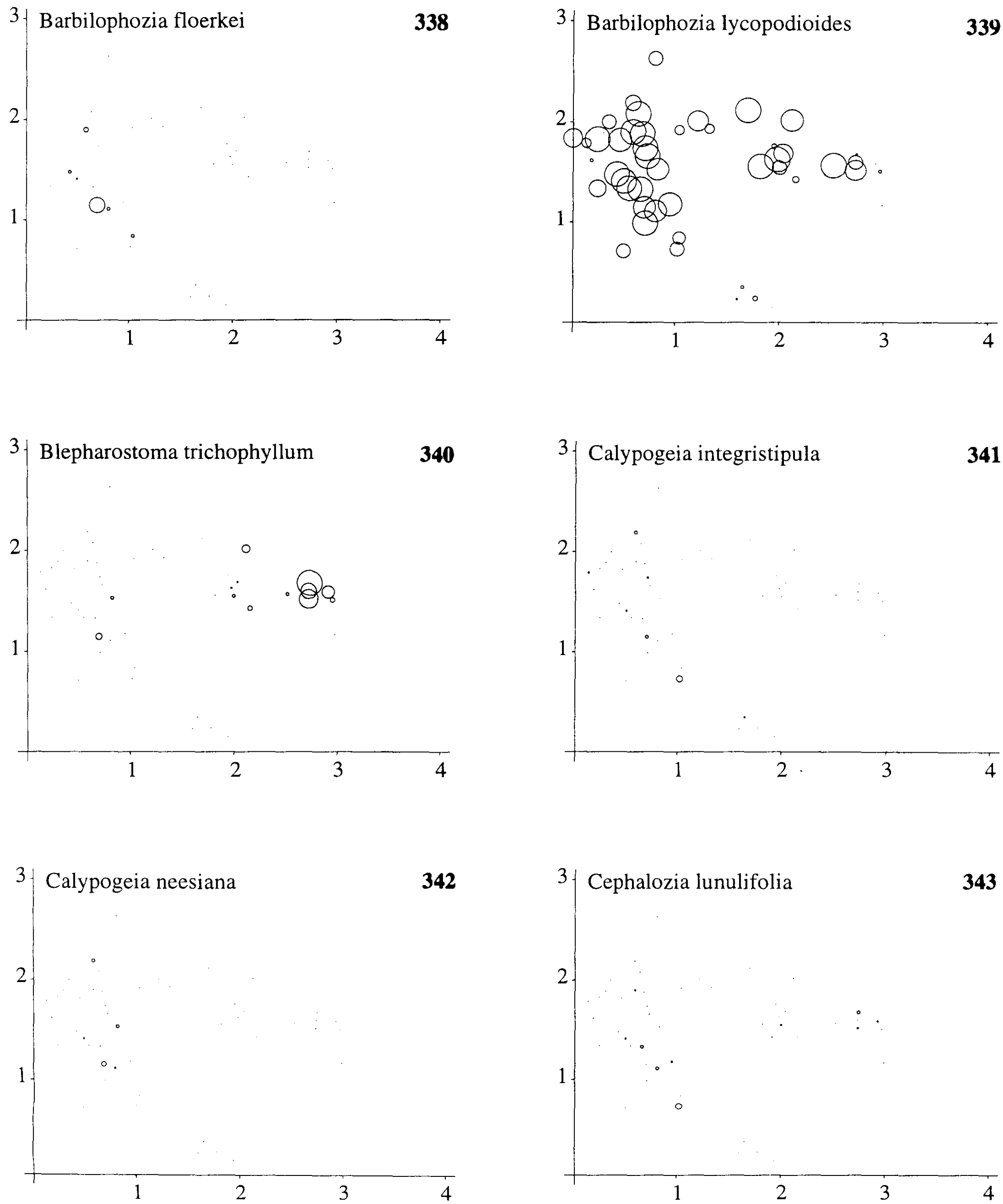
Figs 320-325. Bringen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 320. *Hylocomium splendens*. Fig. 321. *Mnium spinosum*. Fig. 322. *Mnium stellare*. Fig. 323. *Plagiothecium denticulatum*. Fig. 324. *Plagiothecium laetum*. Fig. 325. *Pleurozium schreberi*.



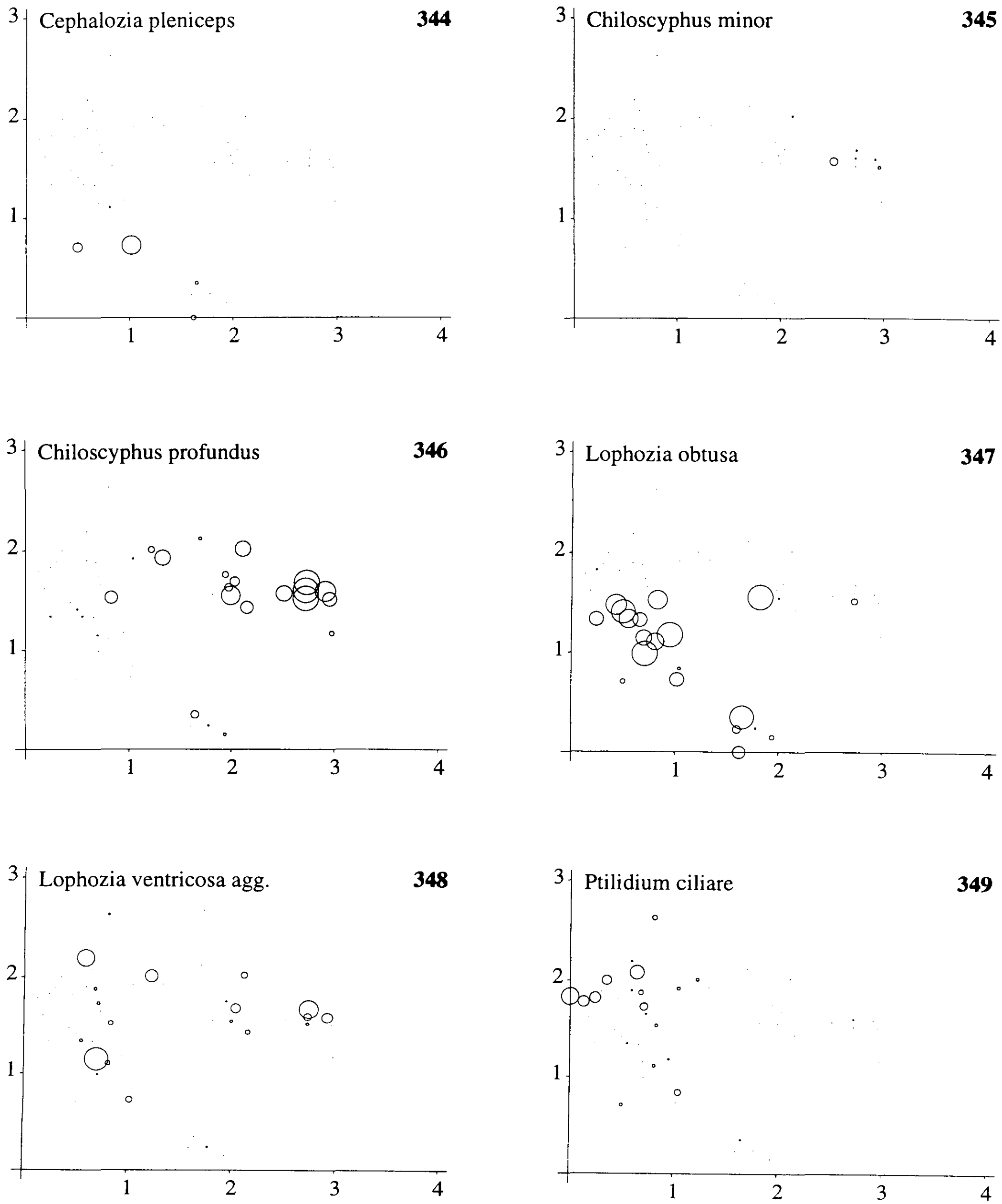
Figs 326-331. Bringen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 326. *Polytrichum commune*. Fig. 327. *Ptilium crista-castrensis*. Fig. 328. *Rhizomnium pseudopunctatum*. Fig. 329. *Rhizomnium punctatum*. Fig. 330. *Rhodobryum roseum*. Fig. 331. *Sanionia uncinata*.



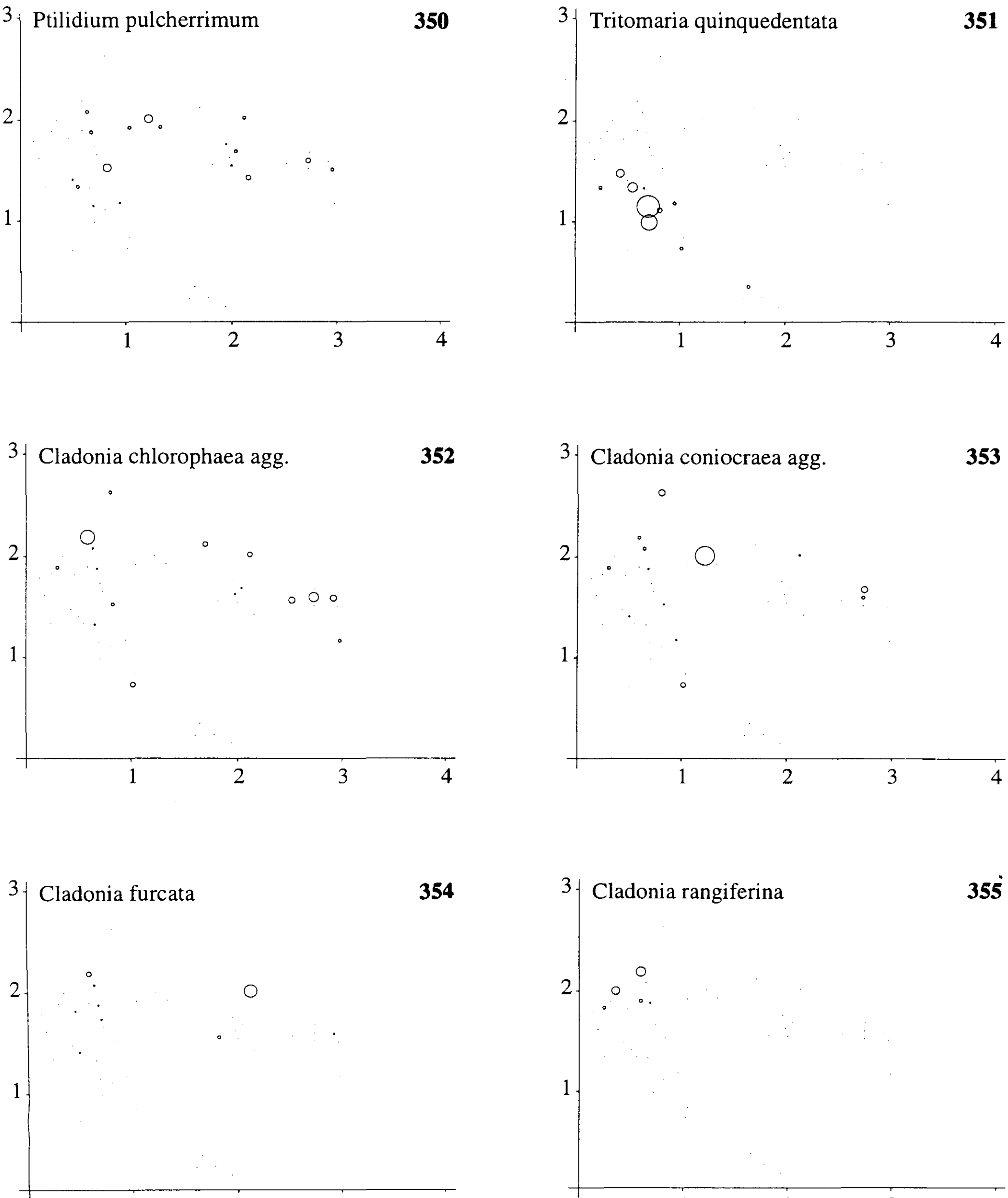
Figs 332-337. Bringen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 332. *Trichostomum tenuirostre*. Fig. 333. *Sphagnum angustifolium*. Fig. 334. *Sphagnum girgensohnii*. Fig. 335. *Sphagnum russowii*. Fig. 336. *Barbilophozia attenuata*. Fig. 337. *Barbilophozia barbata*.



Figs 338-343. Bringen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 338. *Barbilophozia floerkei*. Fig. 339. *Barbilophozia lycopodioides*. Fig. 340. *Blepharostoma trichophyllum*. Fig. 341. *Calypogeia integristipula*. Fig. 342. *Calypogeia neesiana*. Fig. 343. *Cephalozia lunulifolia*.



Figs 344-349. Bringen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 344. *Cephalozia pleniceps*. Fig. 345. *Chiloscyphus minor*. Fig. 346. *Chiloscyphus profundus*. Fig. 347. *Lophozia obtusa*. Fig. 348. *Lophozia ventricosa* agg. Fig. 349. *Ptilidium ciliare*.



Figs 350-355. Bringen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 350. *Ptilidium pulcherrimum*. Fig. 351. *Tritomaria quinquedentata*. Fig. 352. *Cladonia chlorophaea* agg. Fig. 353. *Cladonia coniocraea* agg. Fig. 354. *Cladonia furcata*. Fig. 355. *Cladonia rangiferina*.

OTTERSTADSTØLEN

Correlations between environmental variables

A group of correlated variables consisted of concentrations of Ca and Mn, and litter indices, which were pairwise positively correlated and negatively correlated with H^+ (Tab. 18, Fig. 356). Several variables were associated with this group: the macro plot light index by positive correlations with concentrations of Ca and Mn, soil moisture by negative correlation, and the concentration of S by negative correlation with the litter indices, and the concentration of Al by strong positive correlation with the concentration of H^+ and negative correlation with the

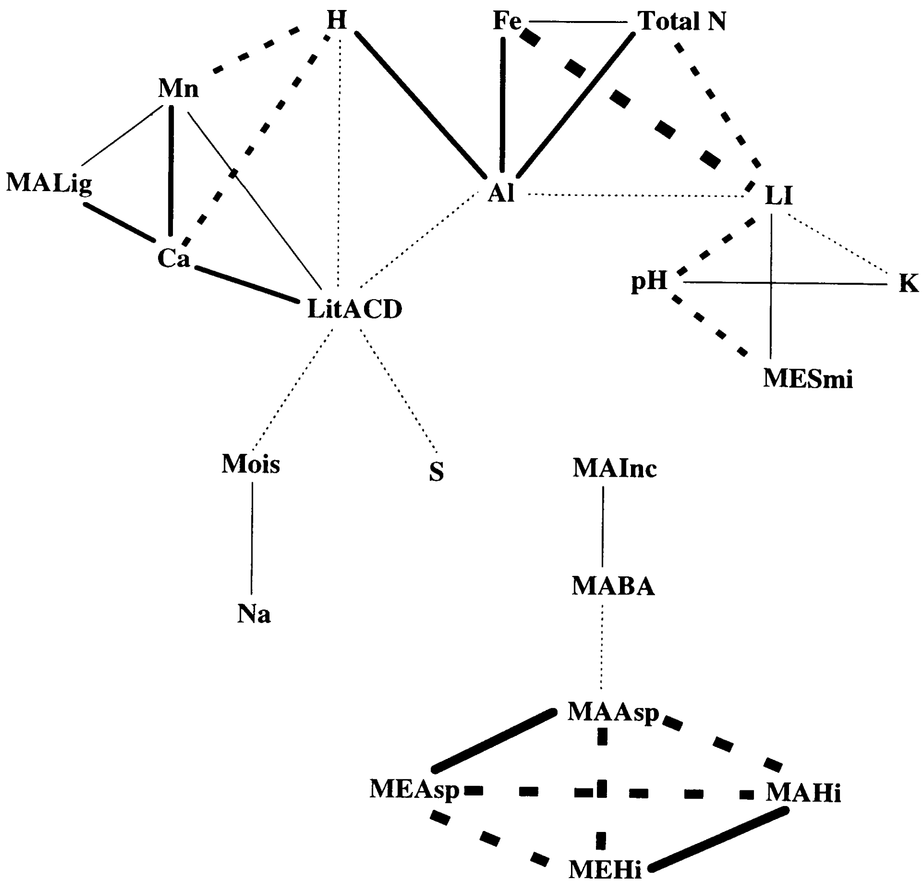


Fig. 356. Otterstadstølen: plexus diagram visualizing Kendall's τ between pairs of environmental variables. Significance probabilities for τ are indicated by lines with different thickness (in order of decreasing thickness): $|\tau| \geq 0.60$, $0.45 \leq |\tau| < 0.60$, $0.35 \leq |\tau| < 0.45$. Continuous lines refer to positive correlations, broken lines to negative.

Tab. 18. Otterstadstølen: Kendall's nonparametric correlation coefficient τ between 32 environmental variables in the 50 meso sample plots (lower triangle), with significance probabilities (upper triangle). Correlations significant at level P < 0.0001 in bold face. n.s. - significance probability > 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 2.

Variable	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16
01 MA Inc	*	n.s.	n.s.	**.0000**	.0538	.0168	n.s.	n.s.	n.s.	.0508	.0811	n.s.	n.s.	.0202	.0189	.0137
02 MA Asp	-.0714	*	**.0000**	**.0000**	.0192	n.s.	**.0000**	**.0000**	n.s.	n.s.	.0690	n.s.	.0326	n.s.	n.s.	n.s.
03 MA Hi	.0732	**-.8336**	*	.0002	.0181	.0778	**.0000**	**.0000**	n.s.	n.s.	n.s.	n.s.	.0657	n.s.	n.s.	n.s.
04 MA BA	**.4473**	**-.4368**	.4002	*	n.s.	n.s.	.0022	.0006	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
05 MA Lig	.2095	.2501	-.2561	-.1348	*	n.s.	.0257	.0499	n.s.	n.s.	.0137	n.s.	n.s.	.0070	.0135	n.s.
06 ME Inc	.2532	.1431	-.1863	.0585	.0363	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0490
07 ME Asp	.0027	**.6886**	**-.6872**	-.3139	.2272	.0225	*	**.0000**	n.s.	n.s.	n.s.	n.s.	.0045	n.s.	n.s.	n.s.
08 ME Hi	.0294	**-.6579**	**.7006**	.3480	-.1985	-.0703	**-.8176**	*	n.s.	n.s.	n.s.	n.s.	.0035	n.s.	n.s.	n.s.
09 ME Rou	.0607	.0227	.0679	-.0060	.0239	.0182	.0279	.0588	*	n.s.	.0022	n.s.	n.s.	n.s.	n.s.	n.s.
10 ME Con	.2053	-.0963	.0565	.1012	.0214	.0681	-.0264	.0049	-.1534	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
11 ME Smi	-.1864	-.1910	.1517	.0962	-.2547	-.1034	-.1464	.0936	-.3053	.0764	*	.0049	n.s.	n.s.	n.s.	.0536
12 ME Sme	-.1219	-.1050	.0278	.0009	.0145	-.0748	-.0396	.0656	-.0664	-.1269	.2813	*	.0004	n.s.	n.s.	n.s.
13 ME Sma	-.0343	-.2222	.1941	.1316	.1120	-.0469	-.2818	.2882	-.0710	-.0498	.1472	.3517	*	.0569	.0360	n.s.
14 LitCC	.2448	-.0527	.0414	.1329	.2750	.1151	-.0746	.0774	-.0338	.1481	-.0599	.0165	.1891	*	**.0000**	.0003
15 LitACD	.2476	-.0695	.0513	.1478	.2519	.1194	-.0871	.0931	-.0330	.1456	-.0692	.0174	.2083	**.9547**	*	.0002
16 Mois	-.2579	.0148	-.0616	-.0517	-.0946	-.1944	.0682	-.0988	-.0735	-.1214	.1923	.1132	-.0124	-.3524	-.3715	*
17 LI	-.2949	-.0838	.0894	-.0302	-.1603	-.2220	-.1102	.0932	-.2216	-.0911	.4043	.1511	.124	.0503	.0429	.0245
18 pH_{H_2O}	-.0380	.2392	-.3409	-.2227	.0544	.0616	.2492	-.2345	.2407	-.0157	-.3362	-.0811	-.0791	-.2006	-.1946	.1060
19 pH_{CaCl_2}	.0771	.2896	-.3122	-.2081	.3045	.0199	.2839	-.2740	.2750	.0045	**-.4506**	-.1461	-.0659	-.0369	-.0306	.0187
20 Ca	.2490	.0270	-.0098	.0965	**.5426**	.1150	.0222	-.0286	.0033	.1574	-.0953	-.0279	.2040	**.4891**	**.4868**	-.1804
21 Mg	.0152	.0497	-.0027	.1447	.2820	-.0885	.0551	-.0220	-.0392	.0279	.0368	.0131	.0751	-.0395	-.0519	.2702
22 K	.1348	.2832	-.2151	.0879	.3177	.0670	.2506	-.2016	.1045	.0394	-.3160	-.0886	-.0537	.0263	.0206	.0580
23 Na	-.2847	.0776	-.1187	.0017	-.2138	.0339	.0600	-.0824	-.1976	-.0689	.3010	.0558	.0206	-.2898	-.2875	.3698
24 H^+	.0098	-.1316	.0651	.0172	-.3348	.0273	-.0912	.1086	-.0114	-.0525	-.0251	-.0787	-.1511	**-.4298**	**-.4341**	.0808
25 Al	.0562	.0654	-.1223	-.0913	-1082	.0703	.0534	-.0286	.1421	-.0508	-.2441	-.1033	-.1528	-.3574	-.3517	.0678
26 Fe	.2454	-.0305	.0402	.0448	.0520	.1845	.0058	.0008	.1976	.0590	-.2809	-.0984	-.0702	-.1564	-.1475	-.0139
27 Mn	.1669	.1159	-.0509	-.0052	.3603	.0819	.0518	-.0743	.0898	.1050	-.2073	-.0361	.1313	**.4473**	**.4457**	-.2229
28 Zn	.1758	-.0514	.0598	.1034	.1780	.0753	-.0386	.0335	-.1748	.2083	.0819	.0246	-.0190	.3360	.3336	-.1347
29 Total N	.0455	-.0566	.0152	.0706	-.0639	.0058	-.0551	.1053	.1813	-.0033	-.2374	-.0525	-.0140	-.2997	-.2858	.1527
30 P-AL	.0170	-.1002	.1276	.1723	.2002	-.1001	-.0320	.0449	-.0147	.0164	.0167	.0656	.0388	-.0082	-.0140	.2980
31 P	-.0366	-.1124	.2044	.2188	.0963	-.1216	-.0616	.0857	-.0196	.0656	.1522	.0672	.0107	.0198	.0140	.2114
32 S	-.2490	-.0148	.0330	-.1017	-.2428	-.0256	-.0041	.0188	.0784	-.2116	-.0084	.1164	-.0537	-.3771	-.3649	.2229

Variable	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
01 MA Inc	.0049	n.s.	n.s.	.0174	n.s.	n.s.	.0065	n.s.	n.s.	.0191	n.s.	.0931	n.s.	n.s.	n.s.	.0174
02 MA Asp	n.s.	.0271	.0086	n.s.	n.s.	.0059	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
03 MA Hi	n.s.	.0019	.0053	n.s.	n.s.	.0393	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0502	n.s.
04 MA BA	n.s.	.0380	.0571	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0914	.0320	n.s.
05 MA Lig	n.s.	n.s.	.0050	**.0000**	.0054	.0017	.0347	.0009	n.s.	n.s.	.0004	.0787	n.s.	.0480	n.s.	.0165
06 ME Inc	.0248	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0618	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
07 ME Asp	n.s.	.0158	.0070	n.s.	n.s.	.0107	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
08 ME Hi	n.s.	.0223	.0088	n.s.	n.s.	.0388	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
09 ME Rou	.0234	.0191	.0086	n.s.	n.s.	n.s.	.0429	n.s.	n.s.	.0429	n.s.	.0734	.0633	n.s.	n.s.	n.s.
10 ME Con	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0335	n.s.	n.s.	n.s.	.0308
11 ME Smi	.0001	.0013	**.0000**	n.s.	n.s.	.0015	.0025	n.s.	.0143	.0048	.0374	n.s.	.0171	n.s.	n.s.	n.s.
12 ME Sme	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
13 ME Sma	n.s.	n.s.	n.s.	.0386	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
14 LitCC	n.s.	.0523	n.s.	**.0000**	n.s.	n.s.	.0032	**.0000**	.0003	n.s.	**.0000**	.0006	.0023	n.s.	n.s.	.0001
15 LitACD	n.s.	.0599	n.s.	**.0000**	n.s.	n.s.	.0035	**.0000**	.0003	n.s.	**.0000**	.0007	.0036	n.s.	n.s.	.0002
16 Mois	n.s.	n.s.	n.s.	.0645	.0056	n.s.	.0002	n.s.	n.s.	n.s.	.0224	n.s.	n.s.	.0023	.0303	.0224
17 LI	*	.0003	**.0000**	n.s.	n.s.	**.0000**	n.s.	n.s.	.0001	**.0000**	n.s.	n.s.	**.0000**	n.s.	n.s.	.0167
18 pH_{H_2O}	-.3679	*	**.0000**	n.s.	n.s.	.0874	n.s.	n.s.	.0001	.0022	n.s.	.0029	.0002	n.s.	.0148	.0972
19 pH_{CaCl_2}	**-.4727**	**.7264**	*	.0926	n.s.	.0003	n.s.	n.s.	.0032	.0024	.0308	.0640	.0024	n.s.	.0640	n.s.
20 Ca	-.0997	-.0452	.1758	*	n.s.	.0438	.0224	**.0000**	.0124	n.s.	**.0000**	.0023	.0721	.0456	n.s.	.0004
21 Mg	-.1063	-.1372	-.0455	.1118	*	.0006	.0093	.0834	n.s.	n.s.	n.s.	n.s.	.0156	**.0000**	**.0000**	n.s.
22 K	**-.4070**	.1755	.3811	.1967	.3339	*	n.s.	.0776	n.s.	.0039	.0316	n.s.	.0513	.0093	.0554	n.s.
23 Na	.0834	-.0261	-.1455	-.2229	.2539	.0253	*	.0895	n.s.	n.s.	.0048	n.s.	n.s.	n.s.	.0621	.0053
24 H^+	-.1406	.0834	-.0866	**-.4857**	-.1690	-.1722	.1657	*	**.0000**	.0059	**.0000**	.0084	.0009	.0171	.0102	.0149
25 Al	-.3841	.4100	.3079	-.2441	-.0612	.0073	.0678	**.5624**	*	**.0000**	.0149	.0005	**.0000**	n.s.	.0015	.0056
26 Fe	**-.6767**	.3144	.3168	.0465	.0465	.2816	.0286	.2686	**.4743**	*	n.s.	n.s.	**.0000**	n.s.	n.s.	.0027
27 Mn	.1259	.0122	.2258	**.5429**	.0204	.2098	-.2751	**-.4661**	-.2376	.0367	*	n.s.	.0576	n.s.	n.s.	.0016
28 Zn	.0343	-.3057	-.1937	.2980	.0890	.1053	-.1053	-.2571	-.3388	-.0090	.1478	*	.0124	.0027	.0009	n.s.
29 Total N	**-.4741**	.3787	.3168	-.1755	.2359	.1902	.0873	.3241	**.5461**	**.4122**	-.1853	-.2441	*	n.s.	n.s.	.0012
30 P-AL	-.0883	-.1494	-.0866	-1951	**.5771**	.2539	.1478	-.2327	-.1576	.0449	.0253	.2931	.1461	*	**.0000**	n.s.
31 P	.0180	-.2502	-.1937	.1543	**.4906**	.1869	.1820	-.2506	-.3094	-.0416	.0073	.3241	.0139	**.7273**	*	n.s.
32 S	-.2338	.1702	-1276	-.3437	.0678	.1527	.2718	.2376	.2702	.2931	-.3078	-.1020	.3159	.1249	.1265	*

litter indices.

Another group of pairwise more or less strongly correlated variables included the concentrations of Al, Fe and total N, pH and loss on ignition, the last mentioned negatively correlated with the others. The concentration of K and minimum soil depth were associated with this second group (Fig. 356). The two groups of variables were connected by the association of Al with both.

A third group of correlated variables, consisting mainly of terrain variables, had no connections with the other groups.

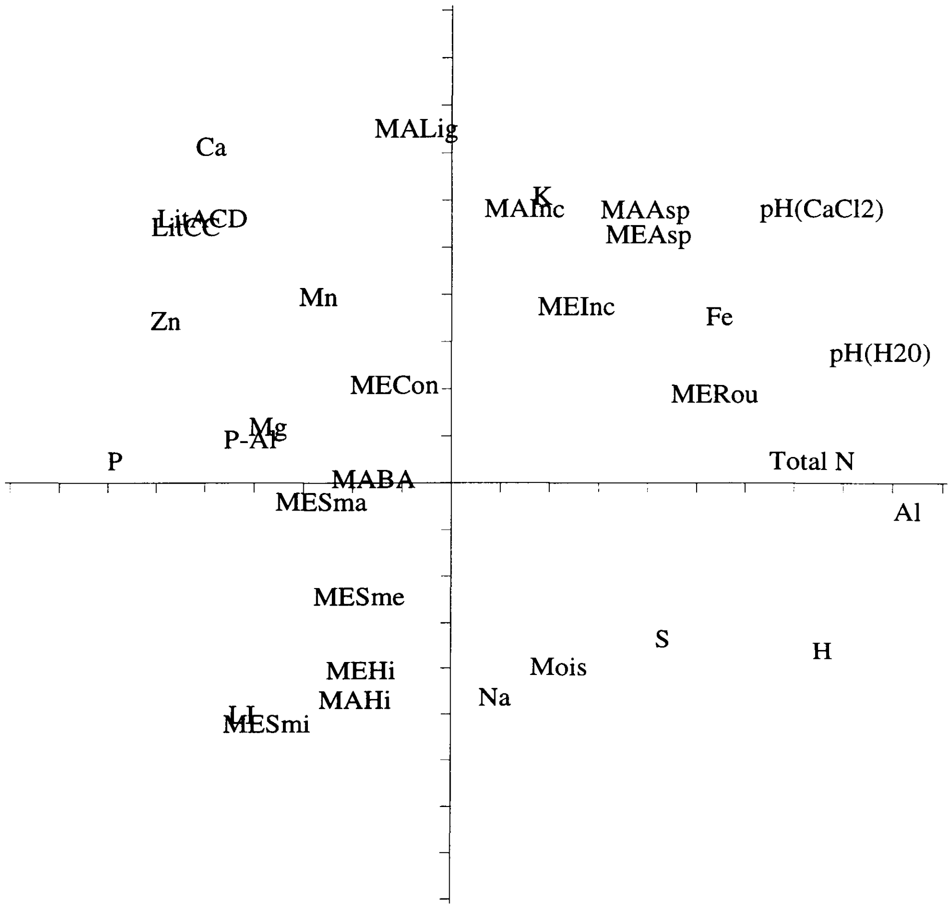


Fig. 357. Otterstadstølen: PCA ordination of 32 environmental variables (names abbreviated in accordance with Tab. 2), axes 1 (horizontal) and 2 (vertical). Positions of variables in the ordination give the head of variable vectors.

PCA ordination of environmental variables

Eigenvalues of the first two PCA axes were 0.216 and 0.173, thus 38.9% of the variation in measured environmental variables was explained by the first two PCA axes.

The positively correlated variables Al, pH, total N, and H^+ obtained high loadings on PCA 1 (Fig. 357). P, Zn, Mg and several other variables of both groups (litter indices, Ca, loss on ignition, minimum soil depth) that were negatively correlated with the variables above, obtained low loadings on PCA 1.

Variables associated with all three groups were separated along PCA 2. Ca and the macro plot light index obtained high loadings on this axis, while Na and soil moisture obtained low loadings. From the second group, pH and K obtained high, and minimum soil depth and loss on ignition obtained low loadings. Aspect unfavourability and the heat indices from the third group of correlated variables were also separated along PCA 2.

The PCA results indicated somewhat more complex relationships between variables than evident from the correlations (Tab. 18, Fig. 356).

DCA and LNMDS ordination

The plots were relatively evenly distributed along the first two axes of the DCA (Fig. 358) and LNMDS (Fig. 359) ordinations. Corresponding ordination axes had similar gradient lengths.

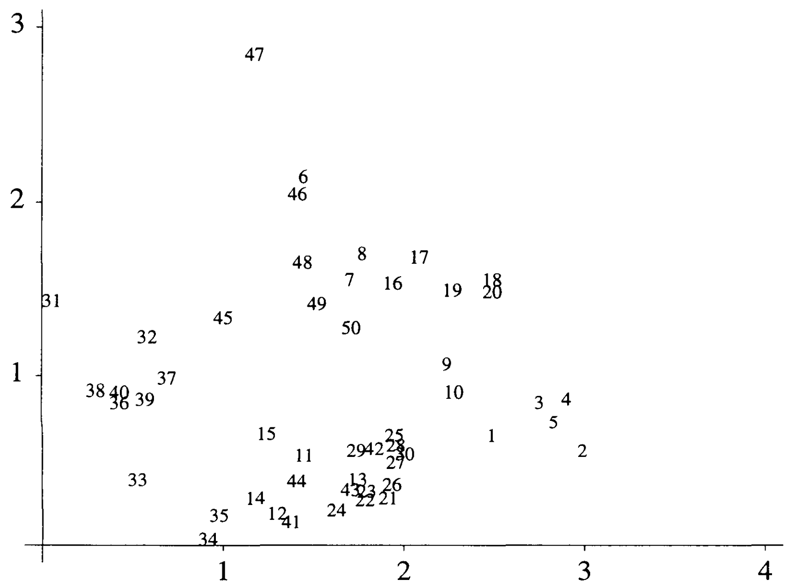


Fig. 358. Otterstadstølen: DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Meso plot numbers are plotted onto the sample plot positions. Scaling of axes in S.D. units.

Tab. 19. Otterstadstølen: Eigenvalues and the fraction of variation explained for DCA axes 1-4.

	DCA 1	DCA 2	DCA 3	DCA 4
Eigenvalues	0.327	0.227	0.107	0.067
Fraction of variation explained	0.140	0.097	0.046	0.029

DCA 1 and DCA 2 explained 14.0 and 9.7% of the variation in vegetation, respectively (Tab. 19). The strongest drop in explained fraction of variation, 47.2%, was observed between DCA 2 and DCA 3. The eigenvalues of DCA 3 and DCA 4 were low (0.107 and 0.067, respectively), corresponding to explained fractions of variation below 5%.

Correlations between DCA and LNMDS ordination axes and between ordination axes and environmental variables

Corresponding axes of DCA and LNMDS ordinations were strongly correlated ($\tau > 0.7$; Tab. 20). With few exceptions the corresponding DCA and LNMDS axes were correlated with the

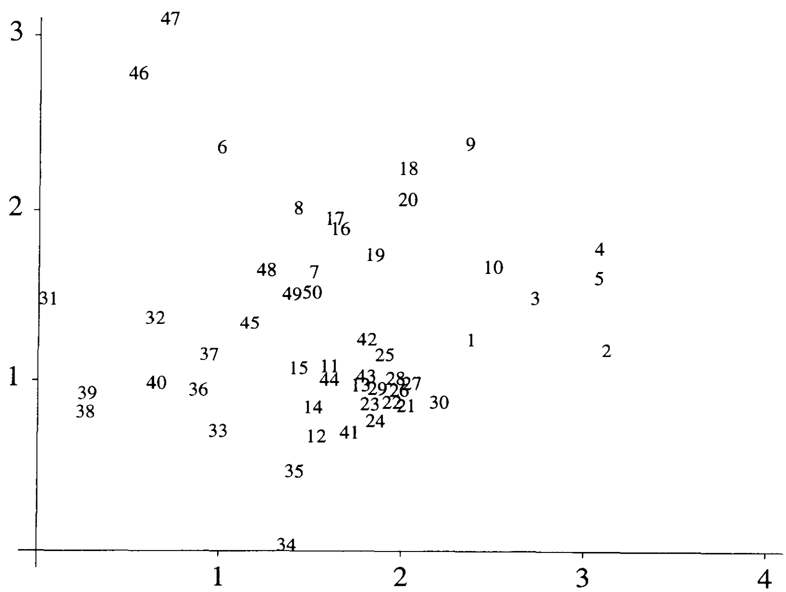


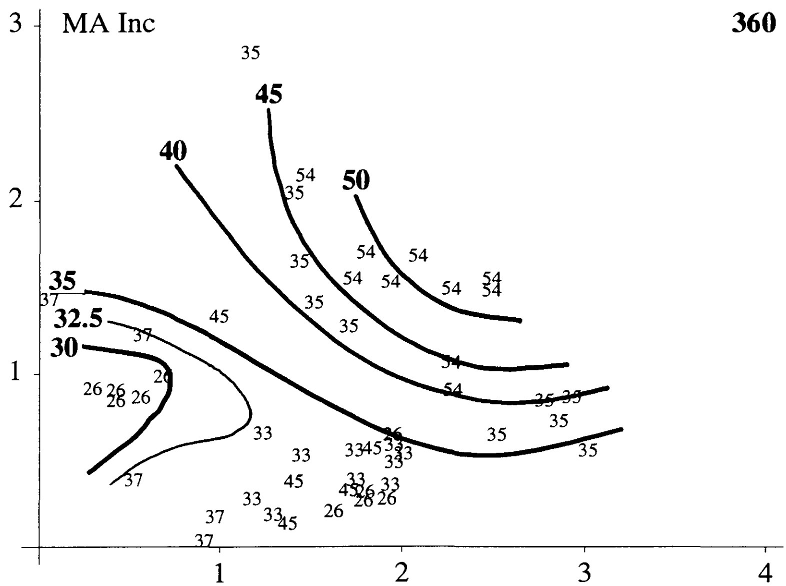
Fig. 359. Otterstadstølen: LNMDS ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Meso plot numbers are plotted onto the sample plot positions. Axes linearly rescaled in S.D. units.

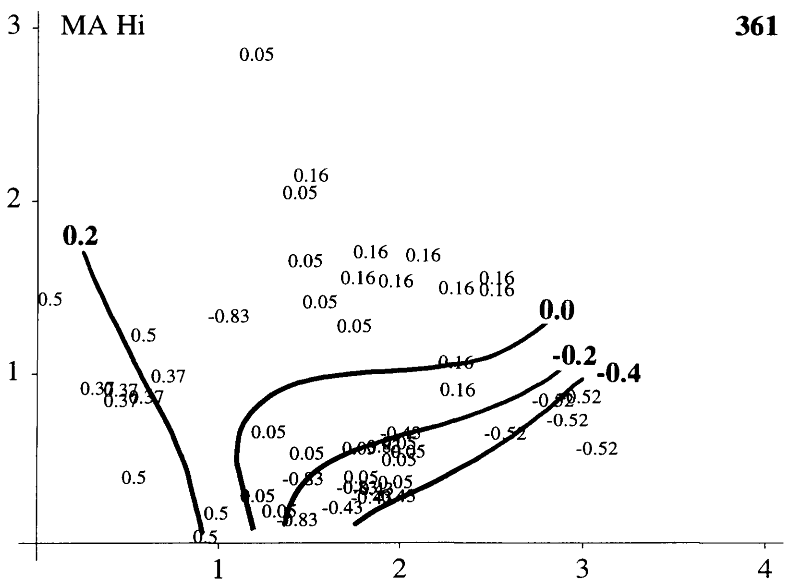
Tab. 20. Otterstadstølen: Kendall's nonparametric correlation coefficients τ between DCA and LNMDS axes, and between 32 environmental variables in the 50 meso sample plots and sample plot positions with respect to DCA and LNMDS axes, and their significance probabilities. Correlations significant at level P < 0.0001 in bold face. n.s. - significance probability > 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 2.

Variable	DCA 1		DCA 2		DCA 3		DCA 4		LNMDS 1		LNMDS 2	
	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P
LNMDS 1	**.7747**	**.0000**	-.1543	n.s.	-.0645	n.s.	.0008	n.s.				
LNMDS 2	.2620	.0073	**7110**	**.0000**	.1282	n.s.	-.1102	n.s.				
01 MA Inc	.1990	.0573	.3204	.0022	.3418	.0011	-.0830	n.s.	.0759	n.s.	**.4578**	**.0000**
02 MA Asp	.2797	.0066	-.2292	.0259	-.0322	n.s.	.2362	.0217	.3547	.0006	-.0532	n.s.
03 MA Hi	-.3007	.0040	.2133	.0410	-.0348	n.s.	-.2811	.0071	-.3900	.0002	-.0259	n.s.
04 MA BA	-.1396	n.s.	.2119	.0378	.2050	.0445	-.1309	n.s.	-.1999	.0502	.2567	.0119
05 MA Lig	.3092	.0023	.1712	.0908	.3194	.0016	.1985	.0499	.2138	.0347	.2751	.0066
06 ME Inc	.0653	n.s.	.1745	.0772	-.0571	n.s.	.1960	.0471	-.0058	n.s.	.2225	.0242
07 ME Asp	.2901	.0031	-.2424	.0135	.0370	n.s.	.2243	.0223	.3427	.0005	-.0698	n.s.
08 ME Hi	-.2539	.0093	.2441	.0124	-.0841	n.s.	-.2016	.0388	-.3127	.0014	.0890	n.s.
09 ME Rou	.2205	.0239	.1094	n.s.	-.1241	n.s.	-.0947	n.s.	.1682	.0848	.1274	n.s.
10 ME Con	.0115	n.s.	.1214	n.s.	.1476	n.s.	.0049	n.s.	-.0607	n.s.	.1017	n.s.
11 ME Smi	**-.4414**	**.0000**	-.1605	n.s.	.0585	n.s.	.0669	n.s.	-.3662	.0002	-.2876	.0039
12 ME Sme	-.1148	n.s.	-.0361	n.s.	.0722	n.s.	.0508	n.s.	-.0968	n.s.	-.1132	n.s.
13 ME Sma	-.0074	n.s.	.2882	.0035	.0768	n.s.	.0190	n.s.	-.1049	n.s.	.2155	.0288
14 LitCC	-.0296	n.s.	**.5813**	**.0000**	.2684	.0063	.1153	n.s.	-.2240	.0227	**.4891**	**.0000**
15 LitACD	-.0321	n.s.	**.5956**	**.0000**	.2496	.0111	.0947	n.s.	-.2298	.0194	**.5000**	**.0000**
16 Mois	.0188	n.s.	**-.4498**	**.0000**	-.0335	n.s.	.0286	n.s.	.1657	.0895	**-.4188**	**.0000**
17 LI	**-.5182**	**.0000**	-.0311	n.s.	.0670	n.s.	-.0376	n.s.	**-.4642**	**.0000**	-.1929	.0483
18 pH_{H20}	**.5264**	**.0000**	-.1164	n.s.	-.2241	.0290	-.0695	n.s.	**.5906**	**.0000**	.0434	n.s.
19 pH_{CaCl2}	**.5881**	**.0000**	.0134	n.s.	-.1169	n.s.	-.0509	n.s.	**.5524**	**.0000**	.1847	.0772
20 Ca	.1314	n.s.	**.4204**	**.0000**	.2359	.0156	.0563	n.s.	-.0351	n.s.	**.4547**	**.0000**
21 Mg	.0531	n.s.	-.1673	.0864	.1641	.0927	.2327	.0171	.0857	n.s.	-.1265	n.s.
22 K	.3567	.0003	-.0694	n.s.	.1020	n.s.	.1282	n.s.	.2980	,0023	.0890	n.s.
23 Na	-.1641	.0927	-.3649	.0002	-.1608	.0994	.1265	n.s.	-.0269	n.s.	-.3567	.0003
24 H^+	.0400	n.s.	-.2284	.0187	-.2016	.0388	-.1004	n.s.	.1445	n.s.	-.2114	.0303
25 Al	.3241	.0009	-.1314	n.s.	-.2931	.0027	-.0547	n.s.	**.4090**	**.0000**	-.0220	n.s.
26 Fe	.3731	.0001	.0253	n.s.	-.1494	n.s.	-.0155	n.s.	.3567	.0003	.1445	n.s.
27 Mn	.1510	n.s.	.3943	.0001	.2229	.0224	-.0873	n.s.	-.0122	n.s.	.3796	.0001
28 Zn	-.2082	.0329	.1624	.0960	.1771	.0695	.1151	n.s.	-.2898	.0030	.0890	n.s.
29 Total N	.3600	.0002	-.1086	n.s.	-.2278	.0196	-.1167	n.s.	**.4220**	**.0000**	-0090	n.s.
30 P-AL	-.0661	n.s.	-.1069	n.s.	.1527	n.s.	.0939	n.s.	-.0498	n.s.	-.1249	n.s.
31 P	-.1886	.0533	-.1053	n.s.	.1380	n.s.	.1053	n.s.	-.1690	.0834	-.1690	.0834
32 S	-.0465	n.s.	-.3486	.0004	-.3078	.0016	.0939	n.s.	.0841	n.s.	-.3567	.0003

same variables, at comparable significance levels. DCA 3 and DCA 4 were not correlated with any variables at the P < 0.001 level.

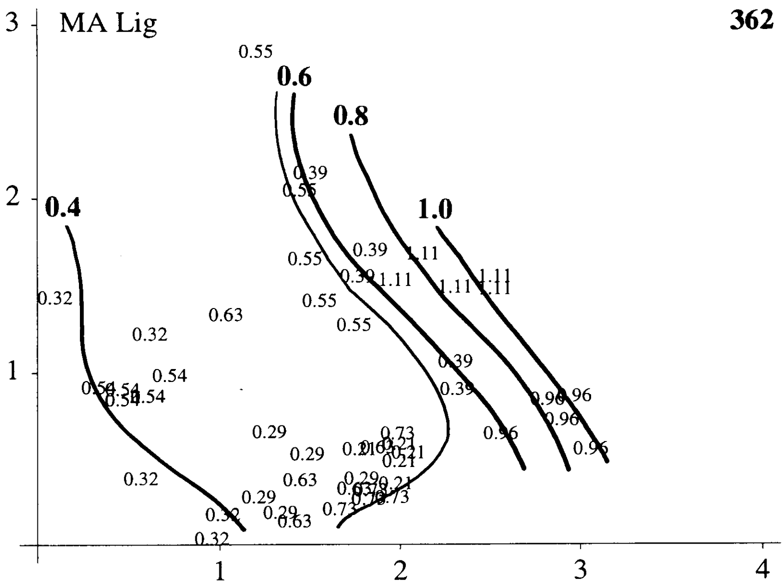
The variables most strongly correlated with DCA 1 were pH (positively correlated at





Figs 360-361. Otterstadstølen: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 360. MA Inc (R^2 = 0.609). Fig. 361. MA Hi (R^2 = 0.546). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.

362



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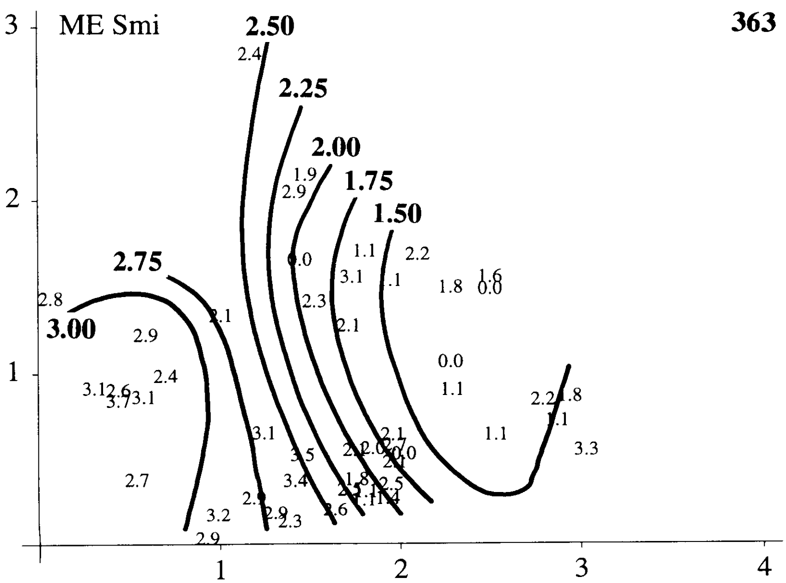
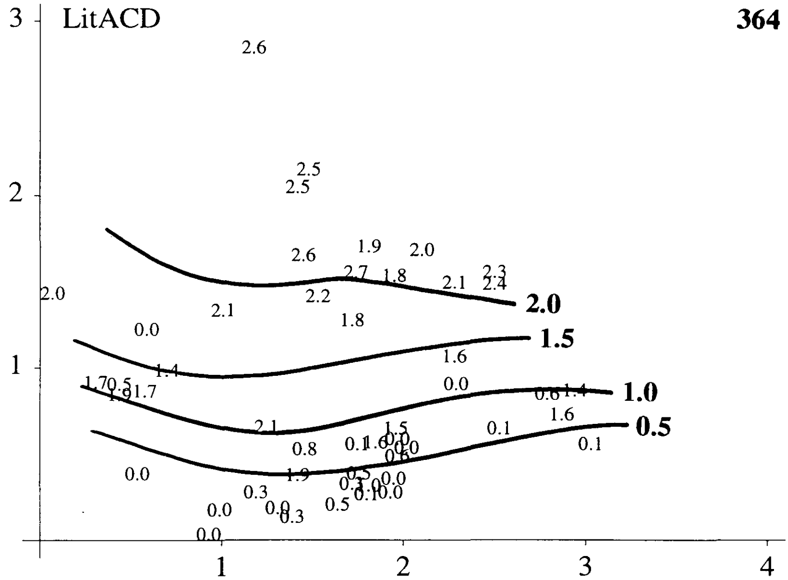
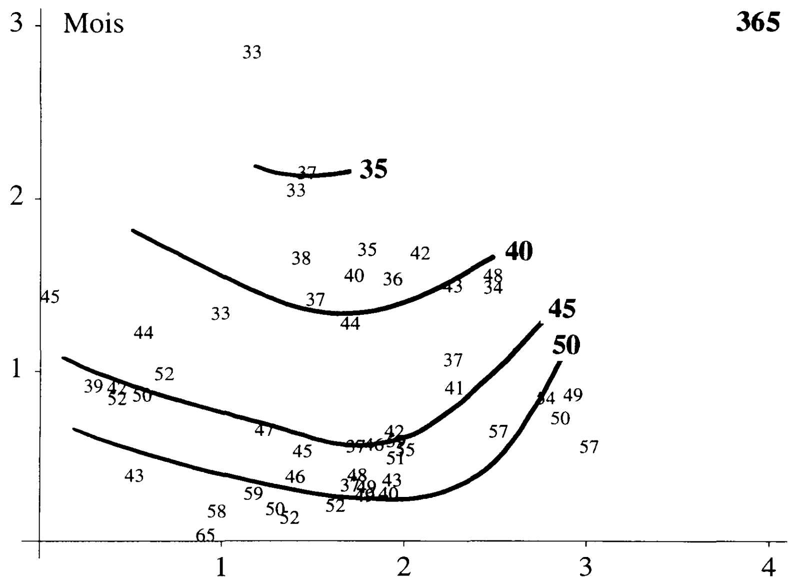
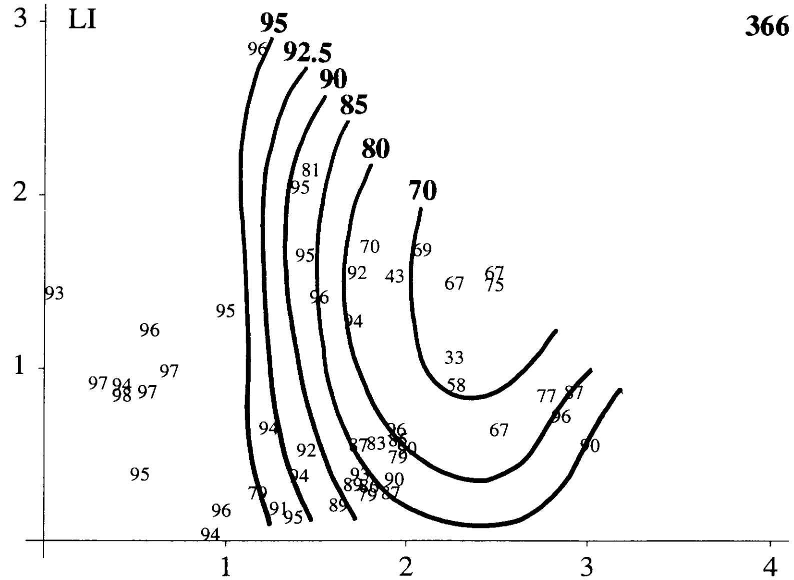


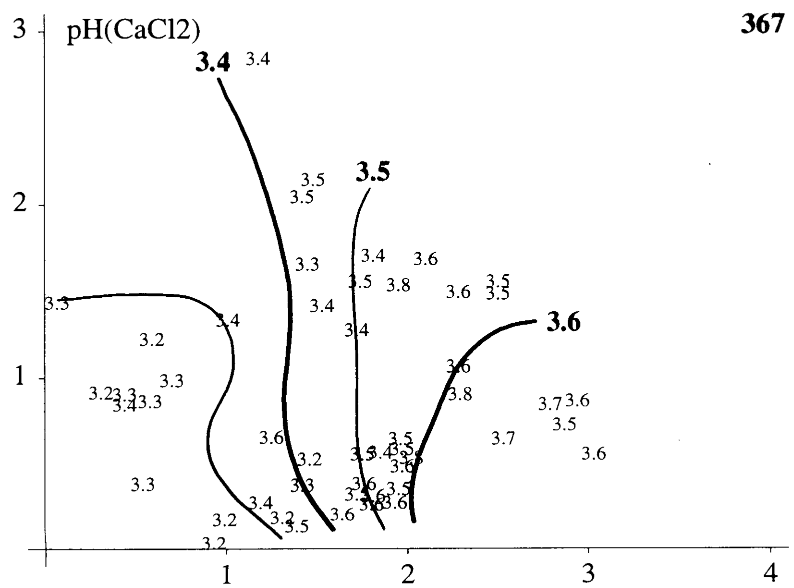
Figs 362-363. Otterstadstølen: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots' positions. Scaling of axes in S.D. units. Fig. 362. MA Lig (R^2 = 0.586). Fig. 363. ME Smi (R^2 = 0.438). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.



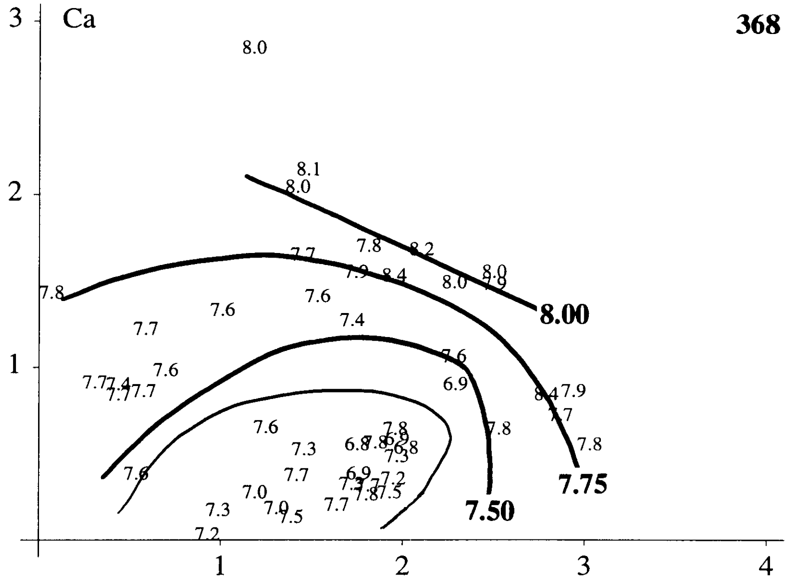


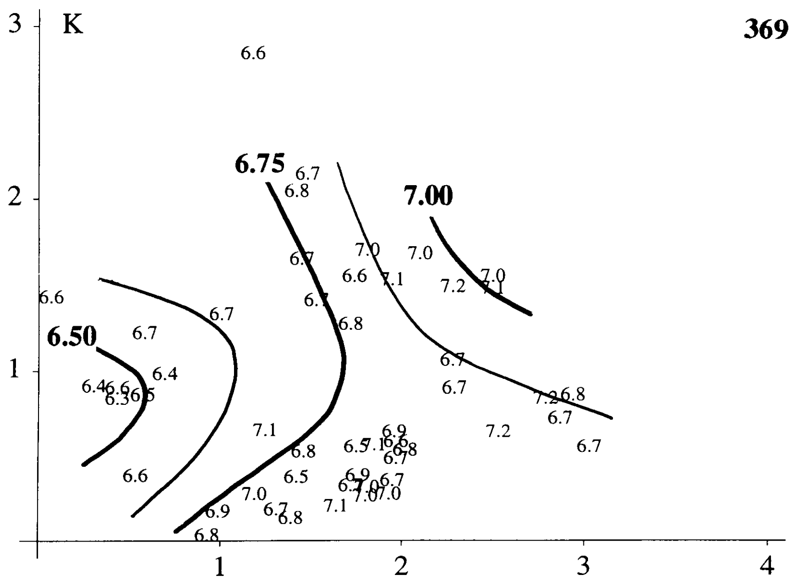
Figs 364-365. Otterstadstølen: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots' positions. Scaling of axes in S.D. units. Fig. 364. Lit ACD (R^2 = 0.691). Fig. 365. Mois (R^2 = 0.537). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.



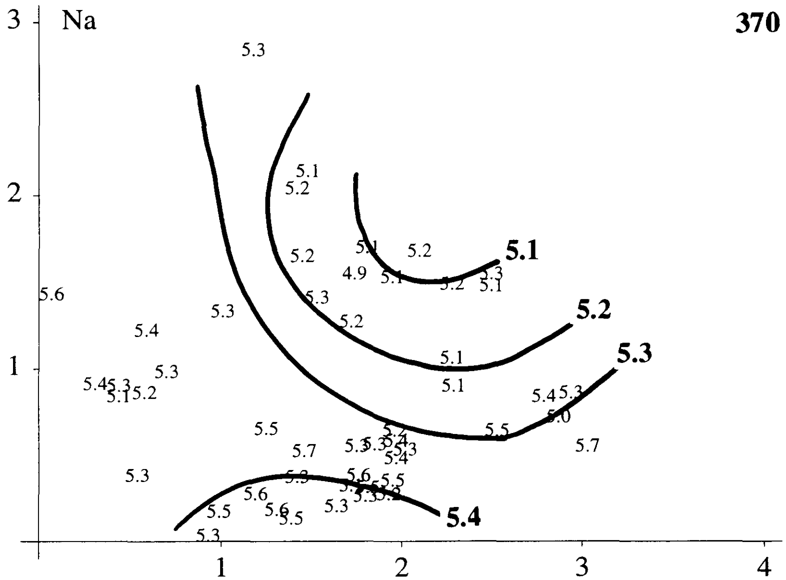


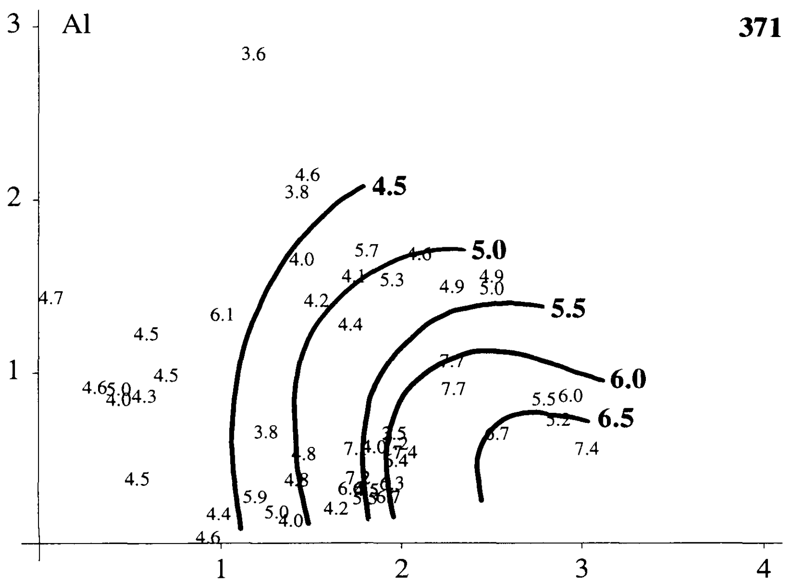
Figs 366-367. Otterstadstølen: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 366. LI ($R^2 = 0.546$). Fig. 367. pH_{CaCl2} ($R^2 = 0.626$). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.





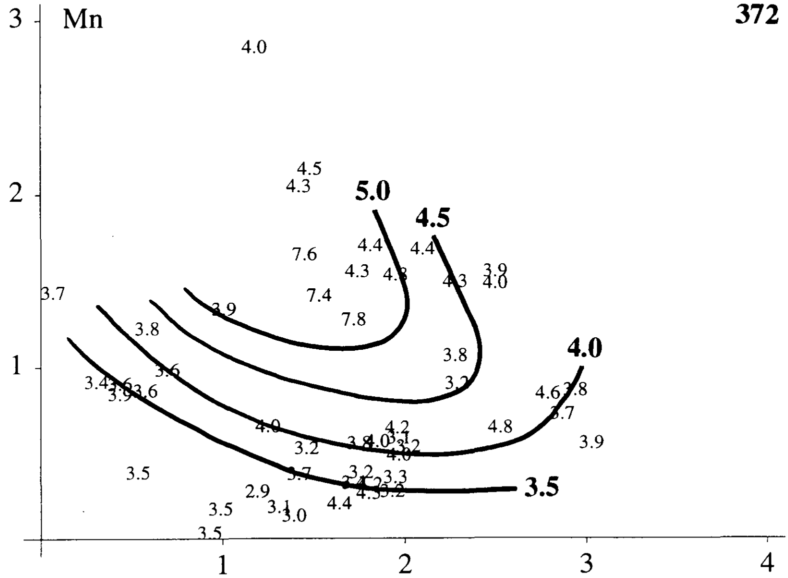
Figs 368-369. Otterstadstølen: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 368. Ca (R^2 = 0.516). Fig. 369. K (R^2 = 0.476). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.



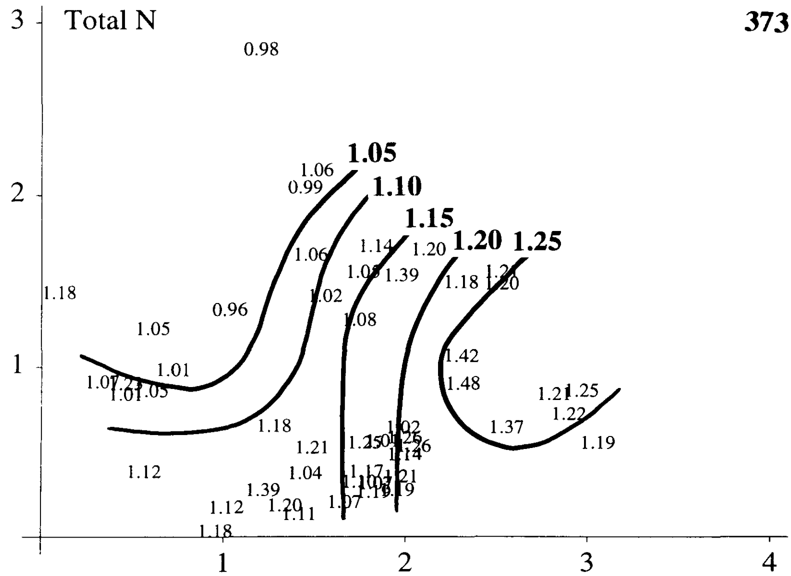


Figs 370-371. Otterstadstølen: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 370. Na (R^2 = 0.424). Fig. 371. Al (R^2 = 0.422). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.

372



373



Figs 372-373. Otterstadstølen: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 372. Mn (R^2 = 0.440). Fig. 373. Total N (R^2 = 0.441). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.

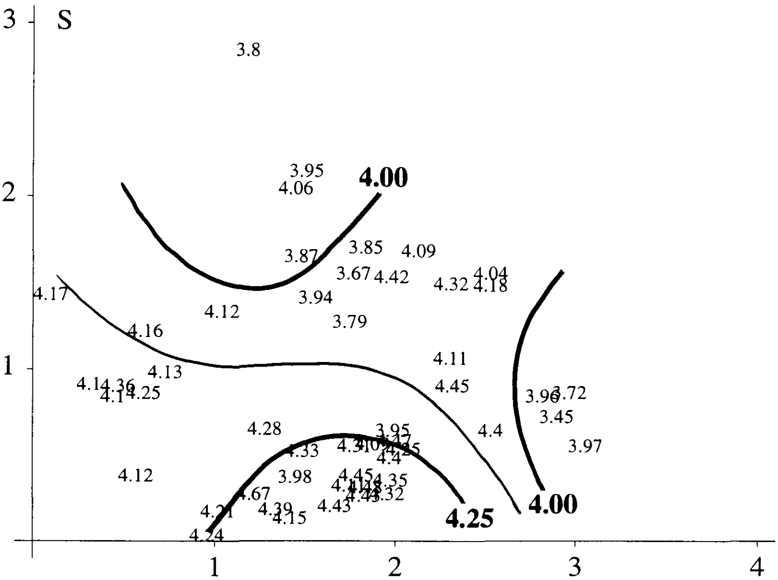


Fig 374. Otterstadstølen: isolines for S in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. R^2 (the coefficient of determination between original and smoothened values as interpolated from the isolines) = 0.464. Names of environmental variables in accordance with Tab. 2.

P < 0.0001; Tab. 20, Fig. 360), and loss on ignition (Fig. 366) and minimum soil depth (Fig. 363), both negatively correlated. Other correlated variables (with $\tau > 0.3$) were the macro plot light index (Fig. 362) and concentrations of K (Fig. 369), Al (Fig. 371), Fe and total N (Fig. 373), all positively correlated, and the macro plot heat index (Fig. 361), which was negatively correlated with DCA 1.

The variables most strongly correlated with DCA 2 were the litter indices (Fig. 364), soil moisture (negatively; Fig. 365) and concentration of Ca (Fig. 368), all with $\tau > 0.4$ and P < 0.0001. Other variables correlated with DCA 2 were macro plot inclination (Fig. 360) and the concentration of Mn (Fig. 372), with positive correlations, and concentrations of Na (Fig. 370) and S (Fig. 374), with negative correlations with the axis.

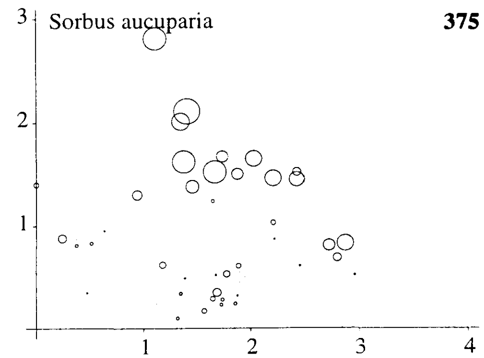
All variables correlated with DCA 3 ($\tau > 0.3$) had higher correlations with DCA 1 or DCA 2.

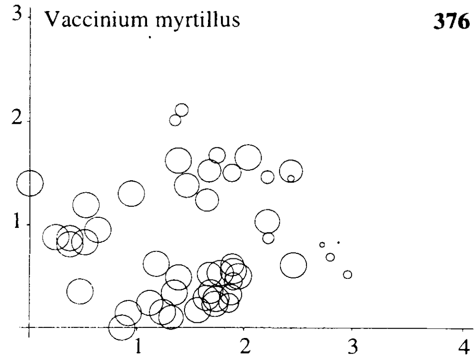
The distribution of species abundance in the DCA ordination

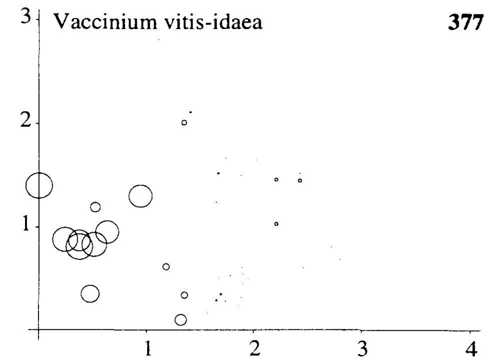
Seventy of a total of 123 species occurred in at least 5 of the 50 meso plots (Figs 375-444).

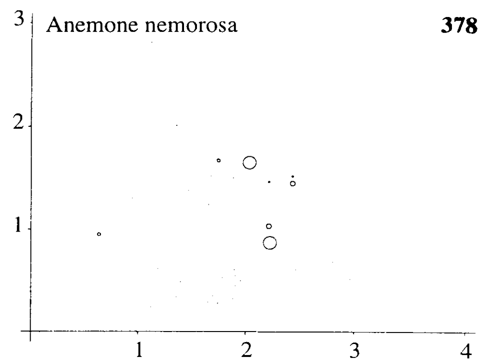
Vaccinium myrtillus (Fig. 376) and *Deschampsia flexuosa* (Fig. 394), typical examples of species with wide ecological amplitude, were abundant in most meso plots.

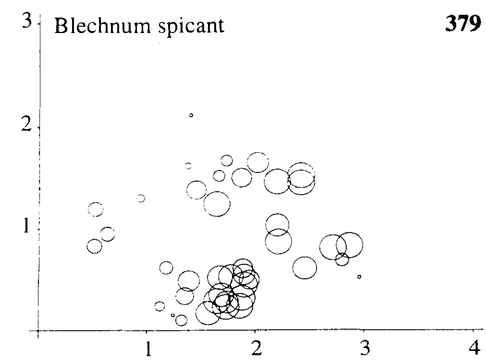
Examples of species confined to sites with low pH and low total N (left part of the ordi-

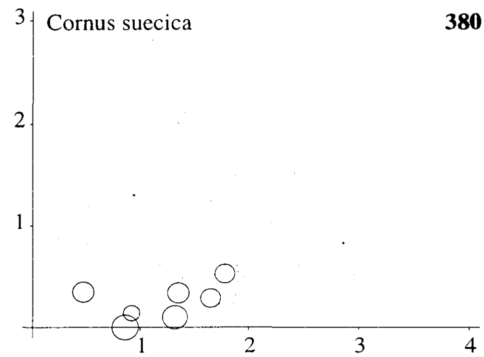




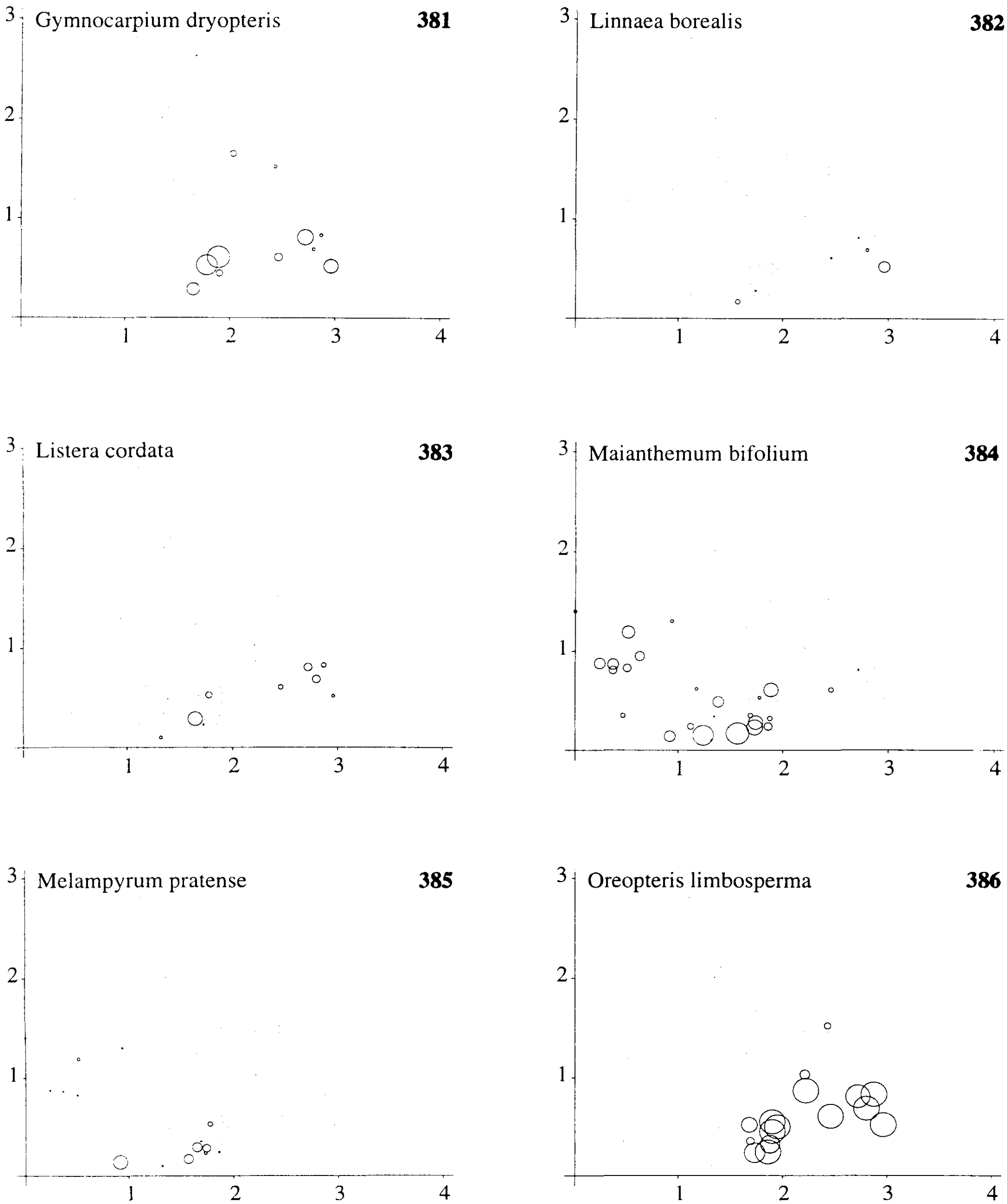




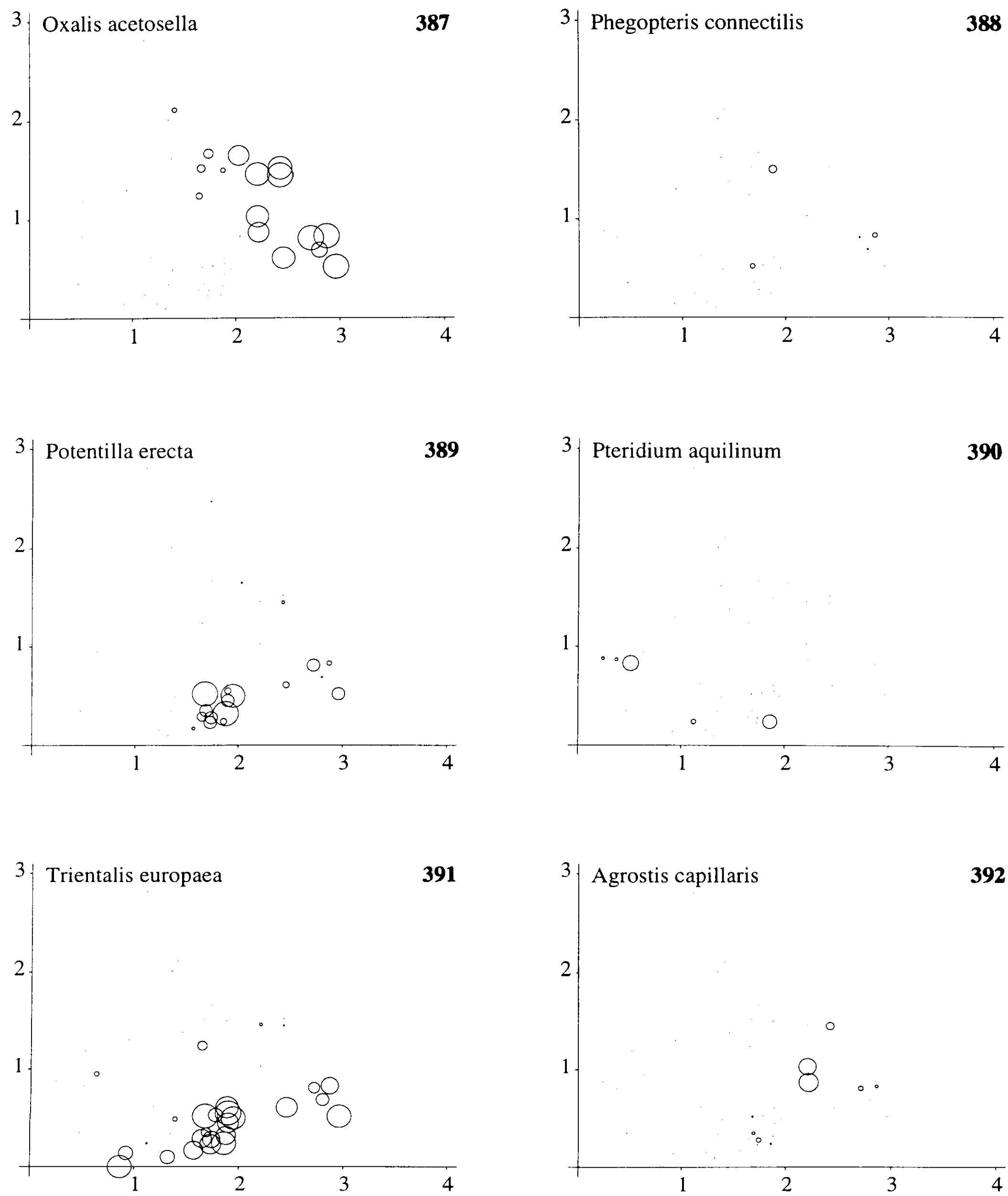




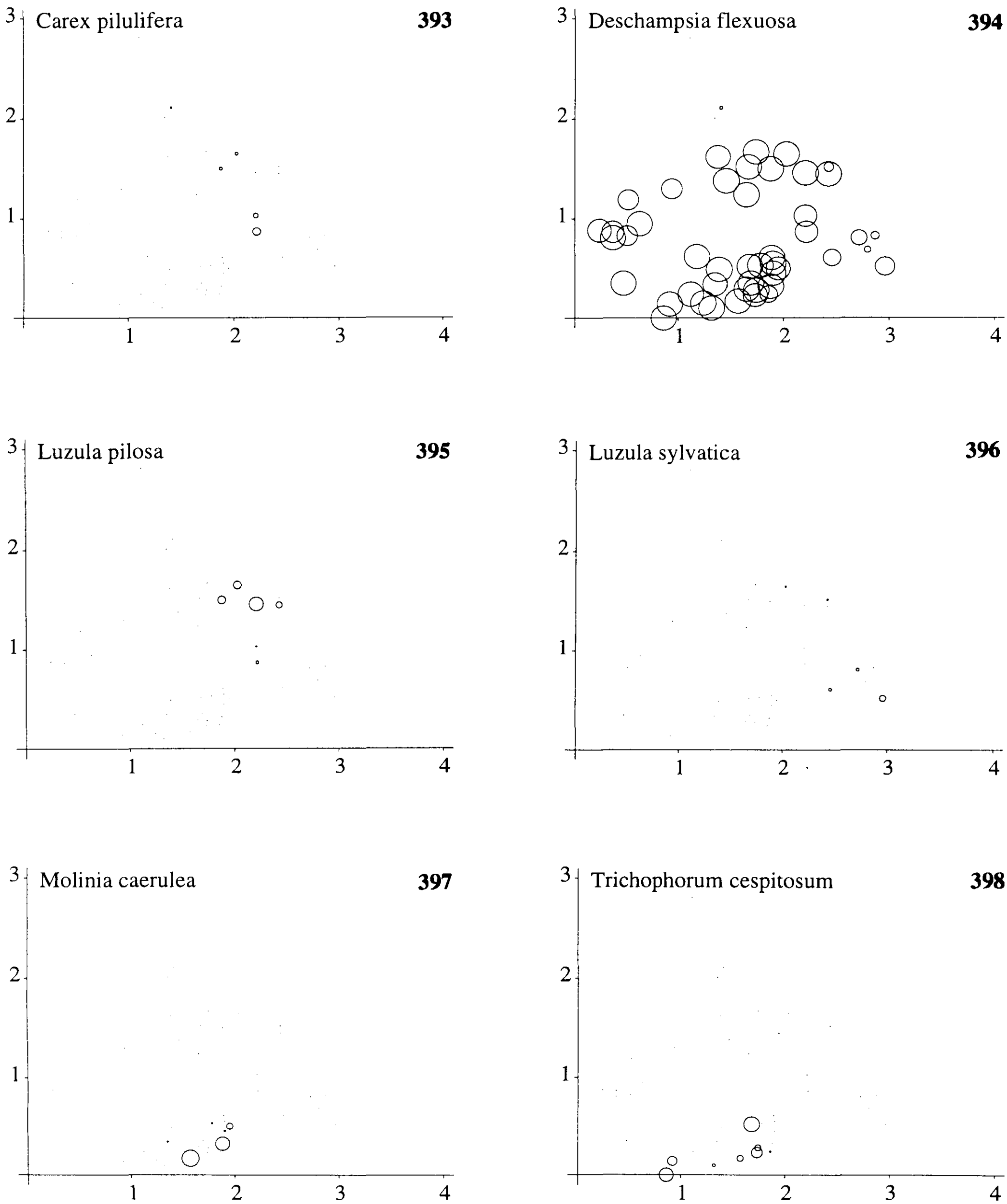
Figs 375-380. Otterstadstølen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 375. *Sorbus aucuparia*. Fig. 376. *Vaccinium myrtillus*. Fig. 377. *Vaccinium vitis-idaea*. Fig. 378. *Anemone nemorosa*. Fig. 379. *Blechnum spicant*. Fig. 380. *Cornus suecica*.



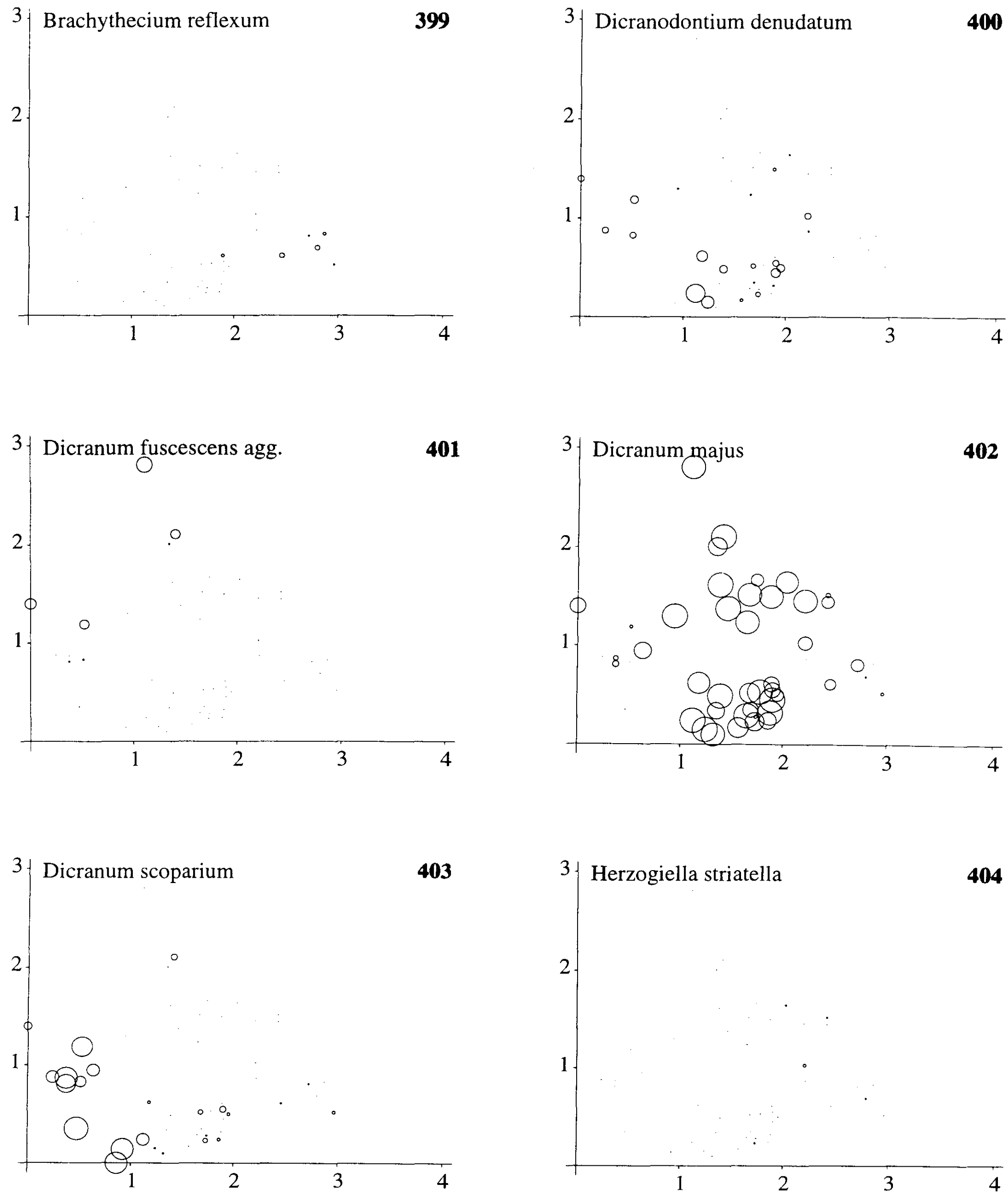
Figs 381-386. Otterstadstølen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 381. *Gymnocarpium dryopteris*. Fig. 382. *Linnaea borealis*. Fig. 383. *Listera cordata*. Fig. 384. *Maianthemum bifolium*. Fig. 385. *Melampyrum pratense*. Fig. 386. *Oreopteris limbosperma*.



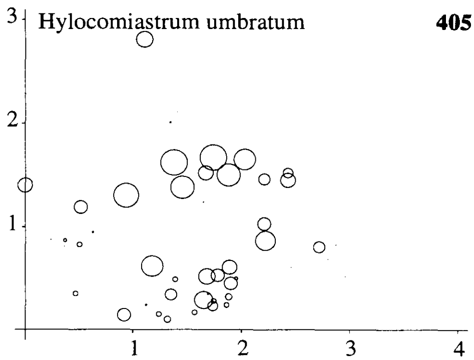
Figs 387-392. Otterstadstølen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 387. *Oxalis acetosella*. Fig. 388. *Phegopteris connectilis*. Fig. 389. *Potentilla erecta*. Fig. 390. *Pteridium aquilinum*. Fig. 391. *Trientalis europaea*. Fig. 392. *Agrostis capillaris*.

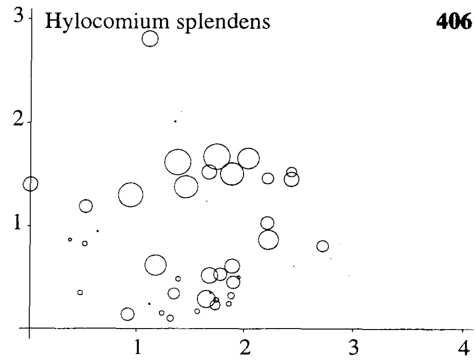


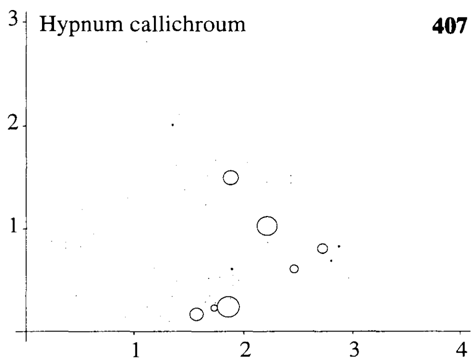
Figs 393-398. Otterstadstølen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 393. *Carex pilulifera*. Fig. 394. *Deschampsia flexuosa*. Fig. 395. *Luzula pilosa*. Fig. 396. *Luzula sylvatica*. Fig. 397. *Molinia caerulea*. Fig. 398. *Trichophorum cespitosum*.

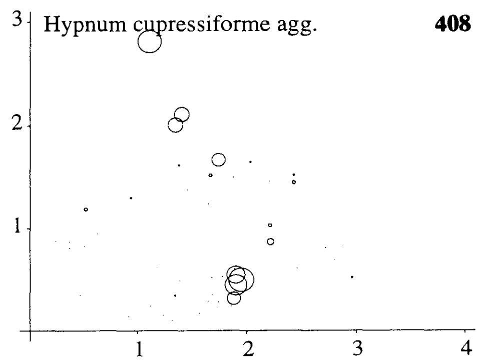


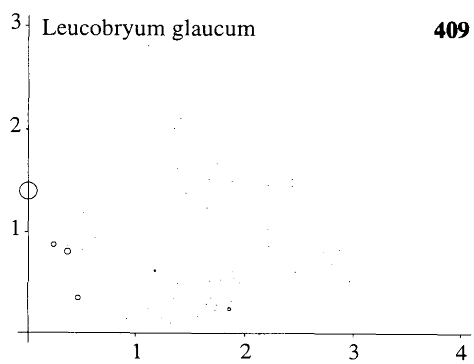
Figs 399-404. Otterstadstølen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 399. *Brachythecium reflexum*. Fig. 400. *Dicranodontium denudatum*. Fig. 401. *Dicranum fuscescens*. Fig. 402. *Dicranum majus* agg. Fig. 403. *Dicranum scoparium*. Fig. 404. *Herzogiella striatella*.

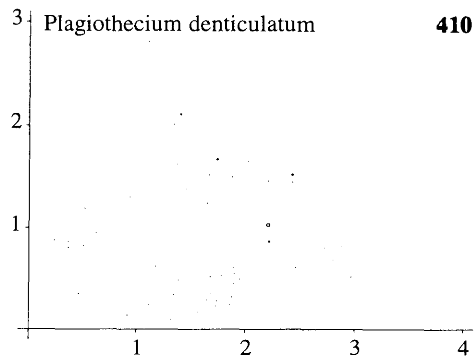




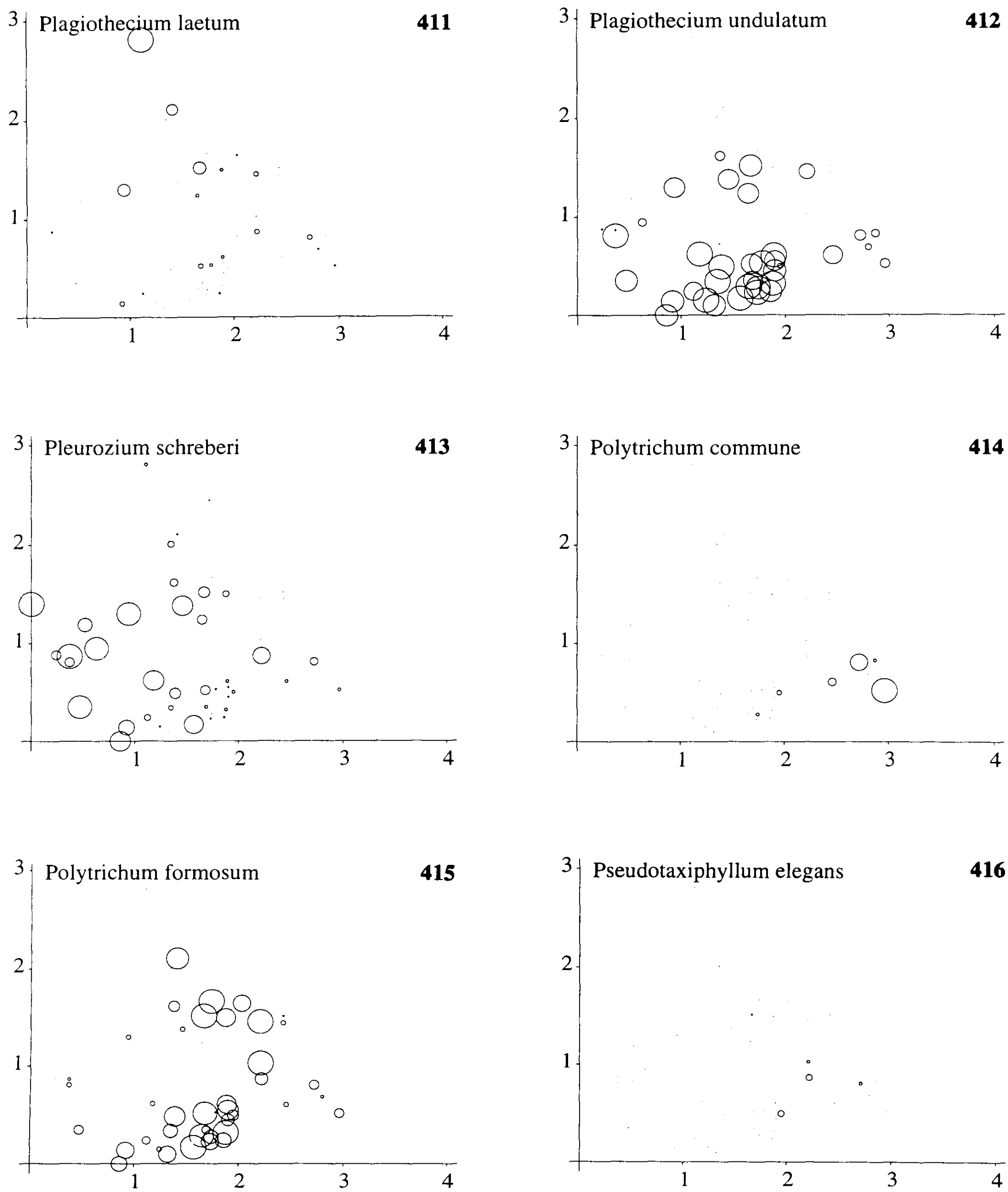




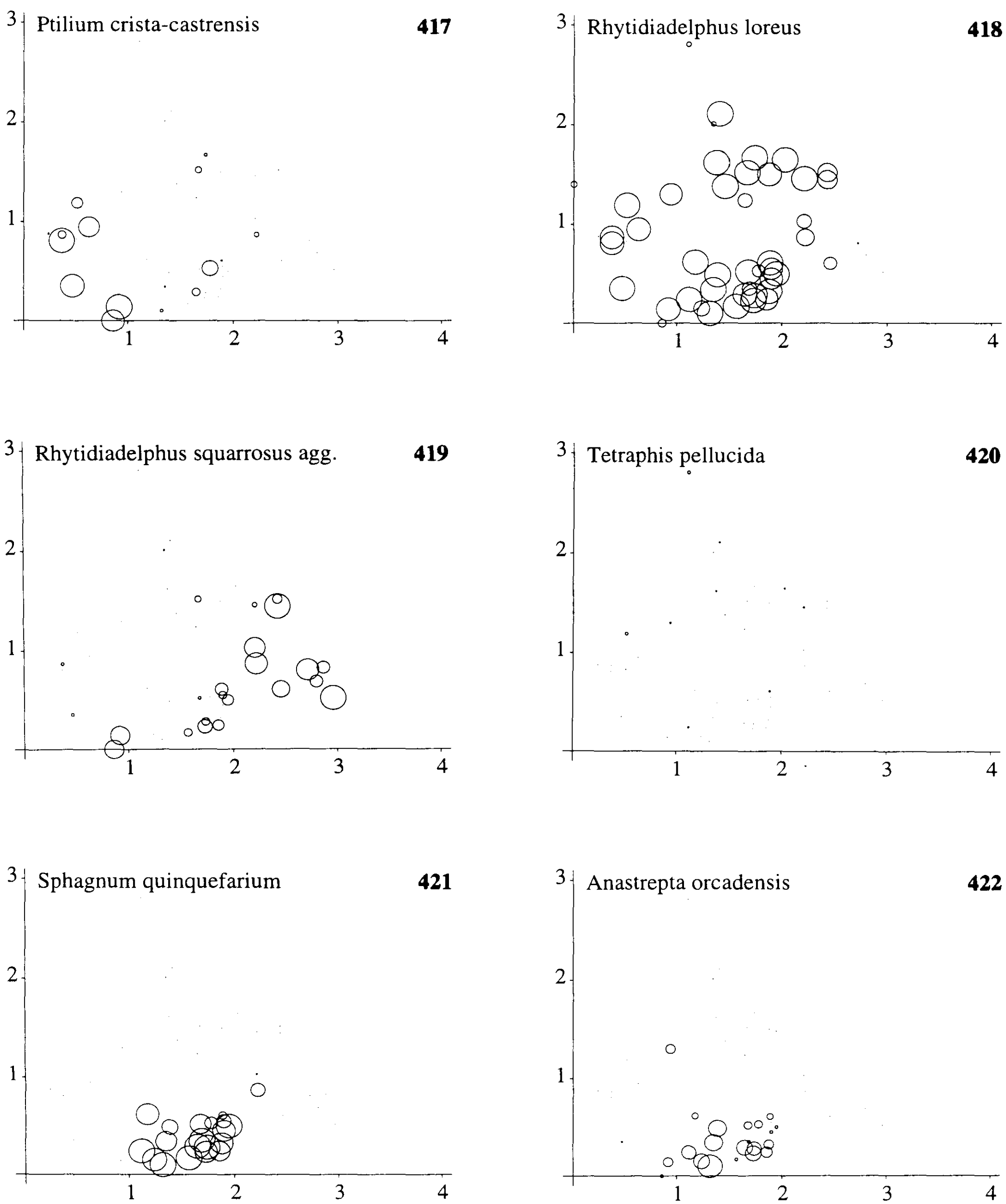




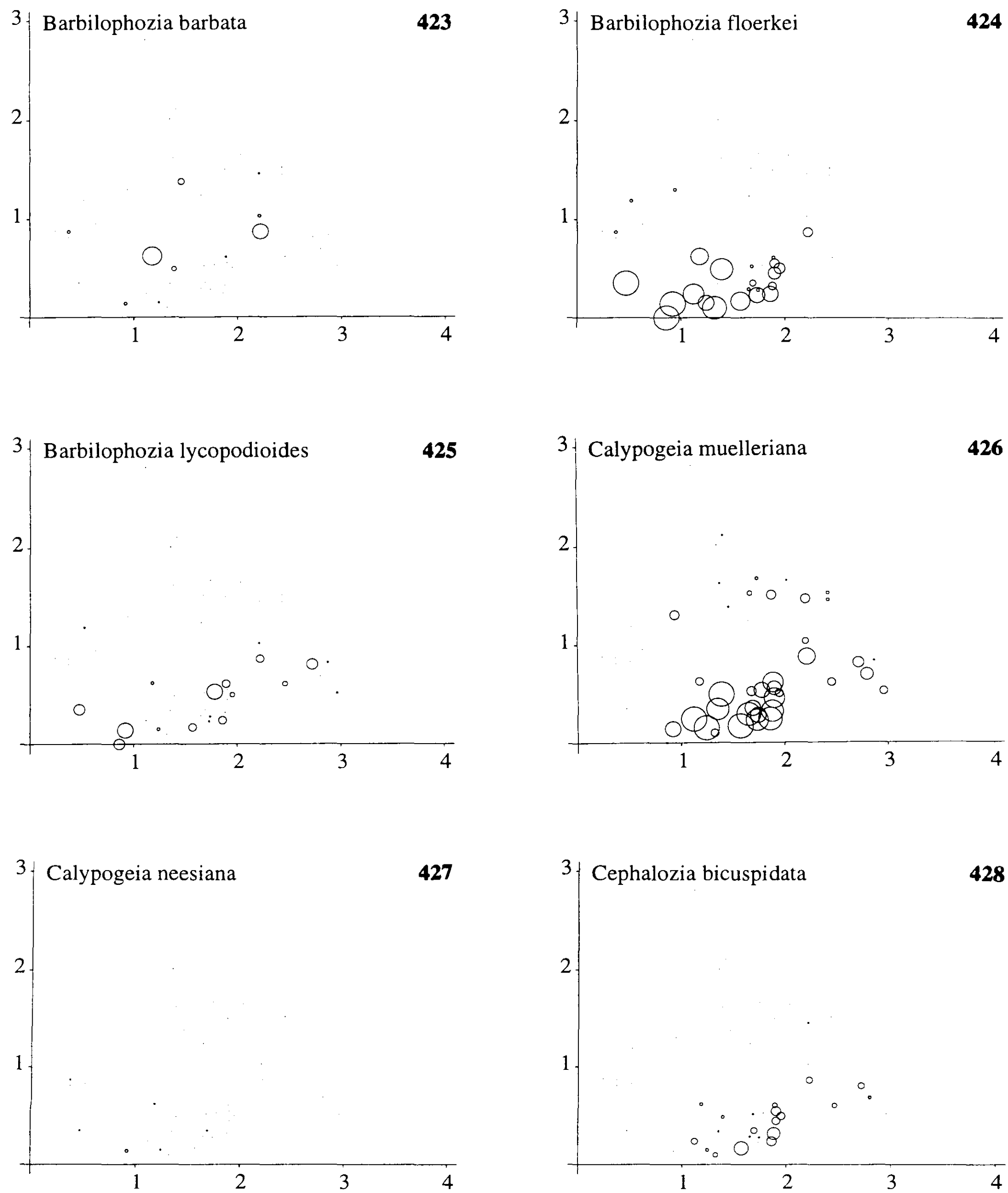
Figs 405-410. Otterstadstølen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 405. *Hylocomiastrum umbratum*. Fig. 406. *Hylocomium splendens*. Fig. 407. *Hypnum callichroum*. Fig. 408. *Hypnum cupressiforme* agg. Fig. 409. *Leucobryum glaucum*. Fig. 410. *Plagiothecium denticulatum*.



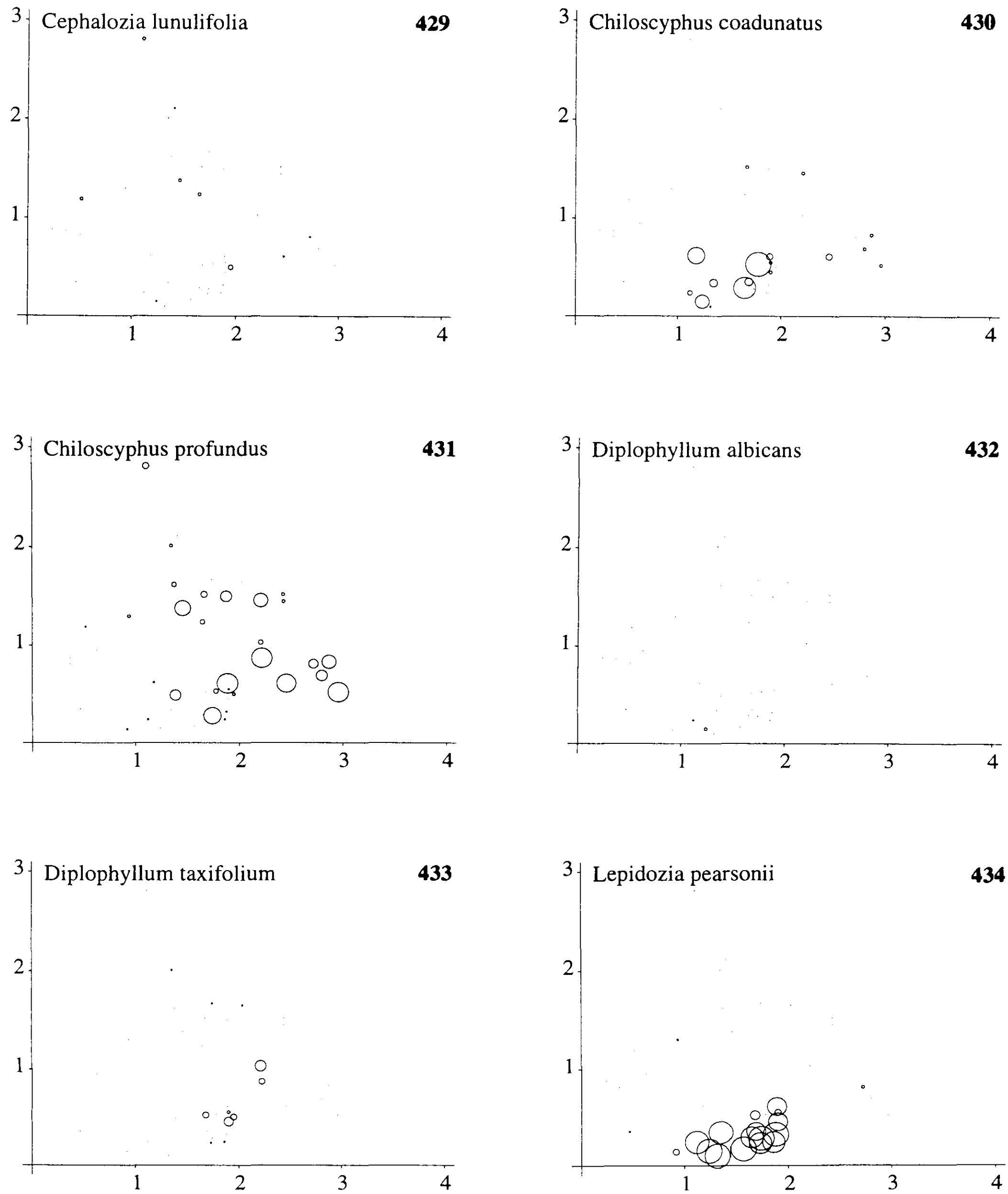
Figs 411-416. Otterstadstølen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 411. *Plagiothecium laetum*. Fig. 412. *Plagiothecium undulatum*. Fig. 413. *Pleurozium schreberi*. Fig. 414. *Polytrichum commune*. Fig. 415. *Polytrichum formosum*. Fig. 416. *Pseudotaxiphyllum elegans*.



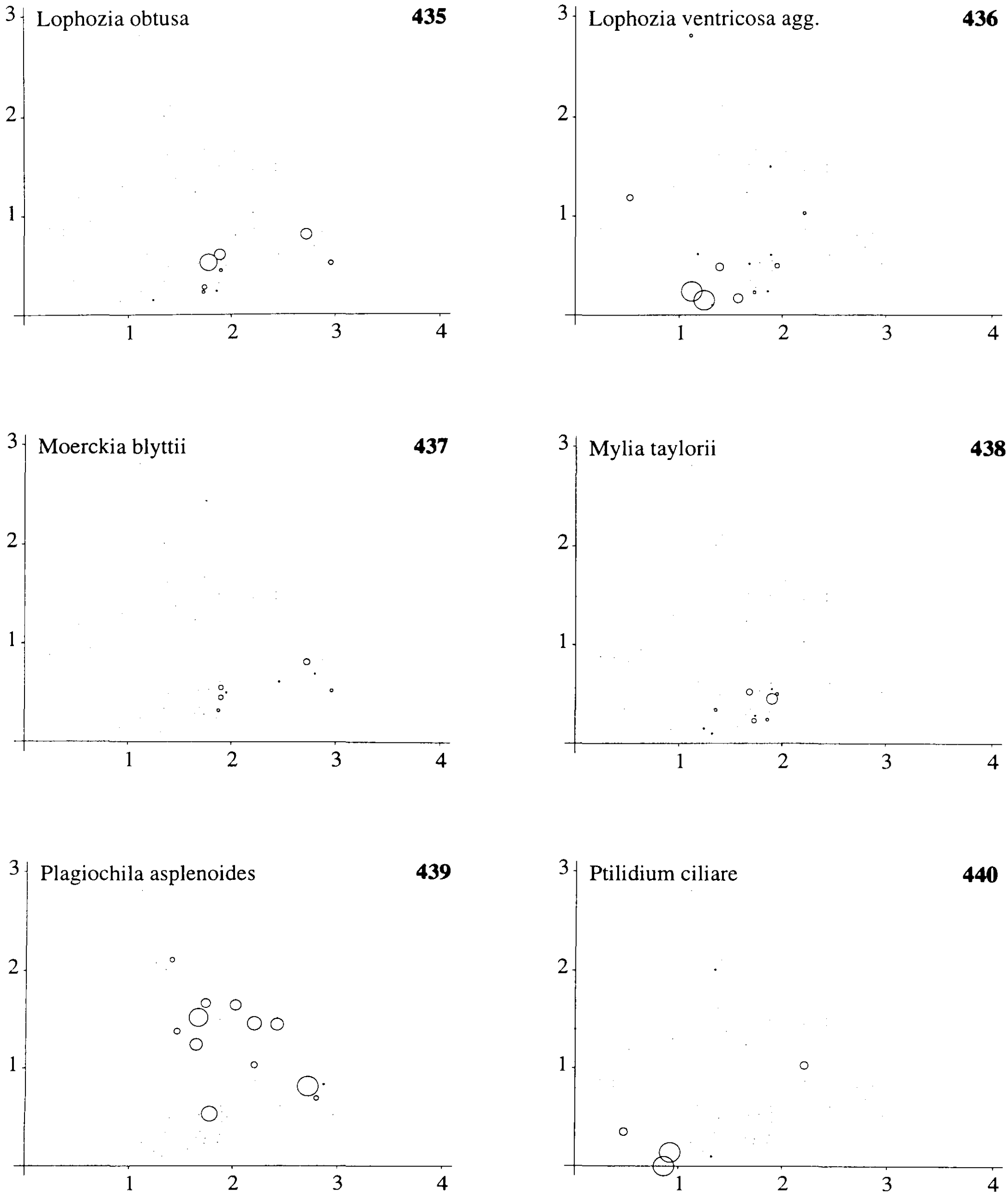
Figs 417-422. Otterstadstølen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 417. *Ptilium crista-castrensis*. Fig. 418. *Rhytidiadelphus loreus*. Fig. 419. *Rhytidiadelphus squarrosus* agg. Fig. 420. *Tetraphis pellucida*. Fig. 421. *Sphagnum quinquefarium*. Fig. 422. *Anastrepta orcadensis*.



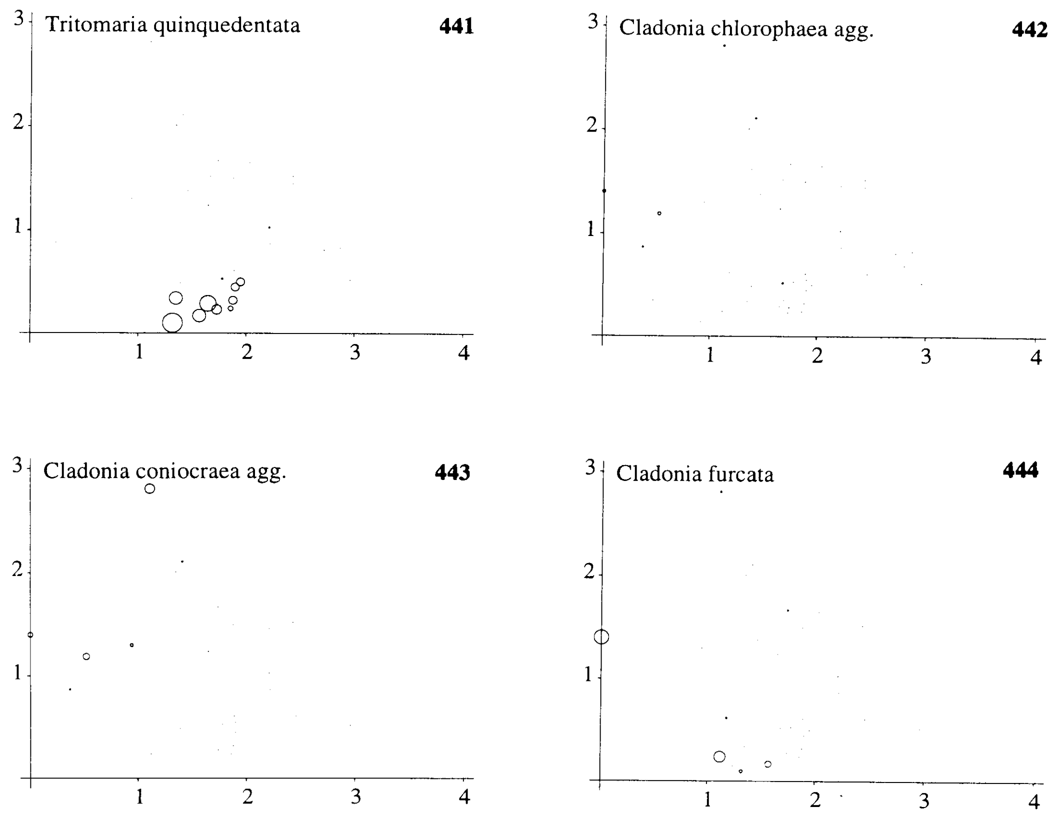
Figs 423-428. Otterstadstølen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 423. *Barbilophozia barbata*. Fig. 424. *Barbilophozia floerkei*. Fig. 425. *Barbilophozia lycopodioides*. Fig. 426. *Calypogeia muelleriana*. Fig. 427. *Calypogeia neesiana*. Fig. 428. *Cephalozia bicuspidata*.



Figs 429-434. Otterstadstølen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 429. *Cephalozia lunulifolia*. Fig. 430. *Chiloscyphus coadunatus*. Fig. 431. *Chiloscyphus profundus*. Fig. 432. *Diplophyllum albicans*. Fig. 433. *Diplophyllum taxifolium*. Fig. 434. *Lepidozia pearsonii*.



Figs 435-440. Otterstadstølen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 435. *Lophozia obtusa*. Fig. 436. *Lophozia ventricosa* agg. Fig. 437. *Moerchia blyttii*. Fig. 438. *Mylia taylorii*. Fig. 439. *Plagiochila asplenoides*. Fig. 440. *Ptilidium ciliare*.



Figs 441-444. Otterstadstølen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 441. *Tritomaria quinquedentata*. Fig. 442. *Cladonia chlorophaea* agg. Fig. 443. *Cladonia coniocraea* agg. Fig. 444. *Cladonia furcata*.

nation) were *Vaccinium vitis-idaea* (Fig. 377) without variation in abundance along DCA 2, and *Dicranum fuscescens* agg. (Fig. 401) with higher abundance in drier sites and beneath trees (upper left in the ordination).

Examples of species with concentration to sites with high pH and N content (the right part of the ordination) were *Anemone nemorosa* (Fig. 378), *Oxalis acetosella* (Fig. 387), *Hypnum callichroum* (Fig. 407) and *Luzula pilosa* (Fig. 395), restricted to drier sites (plots with high DCA 2 scores), and *Oreopteris limbosperma* (Fig. 386), *Potentilla erecta* (Fig. 389) and *Polytrichum commune* (Fig. 414), concentrated on sites with higher soil moisture (lower right in the ordination).

Several species were restricted to moist sites between trees or in open forests (lowermost part of the ordination): *Cornus suecica* (Fig. 380), *Trichophorum cespitosum* (Fig. 398), *Dicranodontium denudatum* (Fig. 400), *Sphagnum quinquefarium* (Fig. 421), *Anastrepta* *orcadensis* (Fig. 422), *Barbilophozia floerkei* (Fig. 424), *Lepidozia pearsonii* (Fig. 434), and *Mylia taylorii* (Fig. 438). Few species, e.g. *Dicranum fuscescens* agg. (Fig. 401) and *Hylocomium splendens* (Fig. 406) were characteristic for the dry sites beneath trees (the uppermost part of the ordination).

GUTULIA

Correlations between environmental variables

pH, loss on ignition and concentrations of Ca, Mn, total N, and H^+ made up a group of pairwise more or less strongly correlated variables (τ > 0.35, except for the correlation between total N and Ca, Fig. 445, Tab. 21). Loss on ignition and the concentration of H^+ were

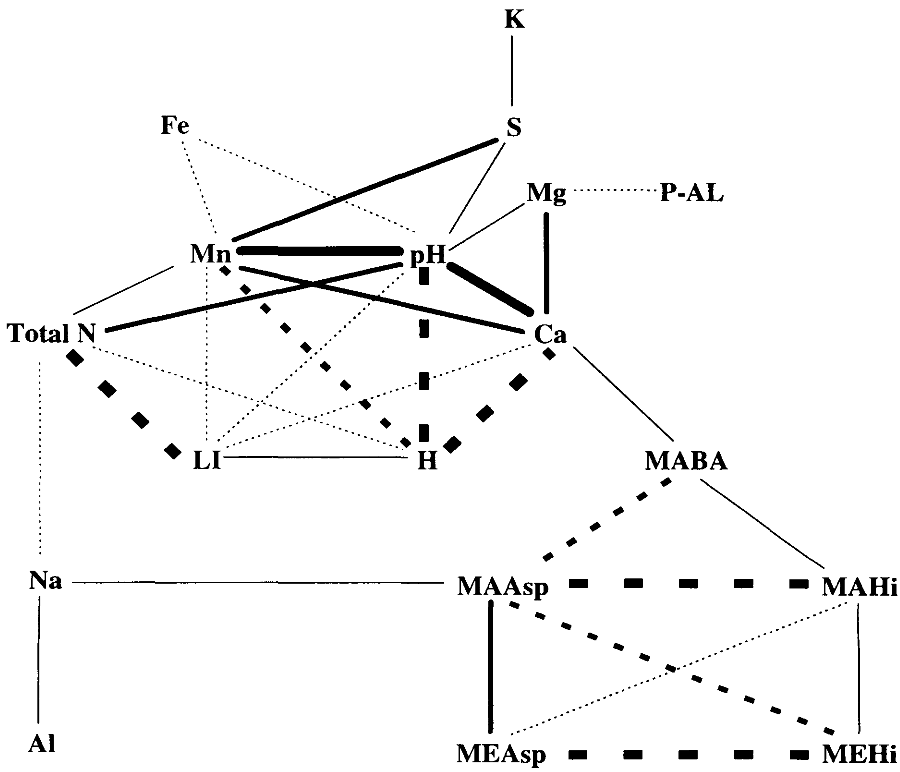


Fig. 445. Gutulia: plexus diagram visualizing Kendall's τ between pairs of environmental variables. Significance probabilities for τ are indicated by lines with different thickness (in order of decreasing thickness): $|\tau| \geq 0.60$, $0.45 \leq |\tau| < 0.60$, $0.35 \leq |\tau| < 0.45$. Continuous lines refer to positive correlations, broken lines to negative.

Tab. 21. Gutulia: Kendall's nonparametric correlation coefficient τ between 32 environmental variables in the 50 meso sample plots (lower triangle), with significance probabilities (upper triangle). Correlations significant at level P < 0.0001 in bold face. n.s. - significance probability > 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 2.

Variable	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
01 MA Inc	*	n.s.	.0569	n.s.	n.s.	**.0000**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0830	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0519
02 MA Asp	.0460	*	**.0000**	**.0000**	.0027	n.s.	**.0000**	**.0000**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0053	n.s.	n.s.	.0585	n.s.	n.s.	.0002	.0331	.0195	.0234	n.s.	n.s.	.0392	n.s.	n.s.	n.s.
03 MA Hi	.2000	**-.6901**	*	.0003	.0015	n.s.	.0001	**.0000**	n.s.	n.s.	n.s.	n.s.	n.s.	.0225	.0611	n.s.	.0924	n.s.	n.s.	n.s.	n.s.	n.s.	.0630	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
04 MA BA	-.0667	**-.5521**	.3778	*	.0200	n.s.	.0074	.0054	n.s.	n.s.	n.s.	n.s.	.0970	n.s.	n.s.	n.s.	.0369	n.s.	n.s.	.0004	.0293	n.s.	.0787	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0189	.0333	n.s.
05 MA Lig	.0222	.3220	-.3333	-.2444	*	n.s.	n.s.	n.s.	n.s.	.0772	n.s.	n.s.	n.s.	.0075	.0149	.0326	n.s.	n.s.	n.s.	n.s.	.0021	n.s.	.0362	n.s.	.0076	n.s.	n.s.	.0561	n.s.	n.s.	n.s.	.0630
06 ME Inc	**.5266**	-.0233	.1126	.1420	.0346	*	n.s.	n.s.	n.s.	n.s.	n.s.	.0306	.0146	n.s.	n.s.	n.s.	.0236	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
07 ME Asp	.1634	**.5174**	-.3941	-.2770	.1494	.0860	*	**.0000**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0545	n.s.	n.s.	.0899	n.s.	n.s.	.0278	.0244	n.s.	.0514	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
08 ME Hi	-.1474	**-.5363**	**.4321**	.2821	-.1133	-.0224	**-.7205**	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0343	n.s.	n.s.	n.s.	n.s.	n.s.	.0032	n.s.	.0350	.0587	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
09 ME Rou	.0060	-.0829	.0707	.0401	-.1304	-.0050	-.1030	.0776	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
10 ME Con	-.0444	.0389	-.0564	-.0034	-.1795	.0358	.0067	-.0328	-.1532	*	n.s.	.0989	n.s.	n.s.	n.s.	.0848	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0747	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
11 ME Smi	.0106	-.0220	.0974	.0620	-.0177	.1044	.0017	.0433	-.0195	-.0255	*	**.0000**	**.0000**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
12 ME Sme	.1507	.0544	.0232	.0422	.1283	.2164	-.0186	.0165	.0578	-.1631	**.6063**	*	**.0000**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0436	n.s.	n.s.
13 ME Sma	.1647	-.0580	.0922	.1698	-.0060	.2444	-.0915	.0835	-.0430	-.1567	**.4319**	**.6154**	*	n.s.	n.s.	n.s.	.0829	.0698	.0804	.0500	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0120	n.s.	n.s.
14 LitCC	.0035	.1576	-.2373	-.0301	.2780	.0155	-.0348	-.0042	-.0696	.0519	.0679	.0875	.0378	*	**.0000**	.0138	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0329	n.s.	n.s.	.0701	n.s.	n.s.	n.s.	n.s.
15 LitACD	-.0177	.1393	-.1948	.0018	.2532	.0173	-.0574	.0246	-.0509	.0468	.0732	.0703	.0498	**.9277**	*	.0174	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0812	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
16 Mois	.0187	.0609	.0818	-.0409	-.2165	-.0116	-.0226	.0057	.0711	.1688	-.0467	-.0759	-.0223	-.2470	-.2385	*	.0695	n.s.	n.s.	n.s.	n.s.	n.s.	.0012	n.s.	.0006	n.s.	n.s.	**.0000**	.0026	.0565	.0239	n.s.
17 LI	-.1757	.2887	-.1706	-.2115	-.0409	-.2244	.1920	-.2069	.0973	.0410	-.0306	-.1570	-.1712	-.0739	-.0654	.1774	*	.0003	**.0000**	.0001	n.s.	n.s.	.0006	**.0000**	.0250	.0565	**.0000**	n.s.	**.0000**	n.s.	n.s.	.0261
18 pH_{H2O}	.0699	-.0385	-.1053	.1195	-.0080	.1276	-.0426	.0322	-.0322	-.0323	-.0767	.1243	.1845	.1234	.0846	-.0560	-.3685	*	**.0000**	**.0000**	**.0000**	n.s.	n.s.	**.0000**	n.s.	.0003	**.0000**	n.s.	.0001	.0006	.0001	.0001
19 pH_{CaCl2}	.0429	-.1069	-.0604	.1689	-.0114	.0810	-.0740	.0512	-.0227	-.0564	-.1029	.1179	.1766	.1395	.1011	-.1267	**-.4191**	**.9020**	*	**.0000**	**.0000**	n.s.	n.s.	**.0000**	.0578	**.0000**	**.0000**	n.s.	**.0000**	.0080	.0012	**.0000**
20 Ca	.0417	-.1957	.0247	.3586	-.1388	.1486	-.1692	.0996	-.0245	.0123	-.0272	.1312	.1933	.1324	.0865	-.0866	-.3727	**.6929**	**.6929**	*	**.0000**	n.s.	n.s.	**.0000**	.0598	.0027	**.0000**	n.s.	.0010	.0004	.0021	.0039
21 Mg	-.0622	-.1005	-.0281	.2206	-.3109	.0274	-.1491	.1127	-.0670	.1171	.0424	.0718	.1272	-.0458	-.0815	.0833	-.1210	**.4656**	**.4245**	**.5102**	*	.0834	.0196	.0005	n.s.	.0214	.0006	n.s.	n.s.	.0001	.0005	.0048
22 K	.1065	.0159	-.0060	-.0264	-.1491	-.1369	.0234	-.0882	.0523	.0909	-.1341	-.1361	-.0859	-.0119	-.0204	.0376	-.0997	.1264	.1443	.0808	.1690	*	.0864	.0343	n.s.	.0438	.0035	n.s.	n.s.	.0234	n.s.	**.0000**
23 Na	.0400	.3827	-.1883	-.1780	-.2121	-.0158	.2194	-.2875	.0245	.1744	.0238	-.0487	-.0479	-.0645	-.0662	.3152	.3367	-.0636	-.1560	-.0727	.2278	.1673	*	n.s.	**.0000**	.0214	n.s.	n.s.	**.0000**	.0513	n.s.	n.s.
24 H^+	-.0639	.2204	-.0877	-.1423	.0690	-.0822	.2244	-.1470	.0049	-.0025	.1205	-.0602	-.0958	-.1256	-.0899	.1209	**.4463**	**-.6030**	**-.6493**	**-.6261**	-.3420	-.2065	.1559	*	.0015	.0010	**.0000**	.0303	**.0000**	n.s.	n.s.	.0008
25 Al	-.0792	.2416	-.0758	-.0826	-.2700	-.1469	.1558	-.2058	.0506	.0778	.0747	-.0256	-.0694	-.2138	-.1748	.3348	.2190	-.1331	-.1896	-.1837	.0873	-.0351	**.4318**	.3094	*	.0388	n.s.	.0043	.0124	.0224	.0016	n.s.
26 Fe	.0843	.2345	-.0826	-.1406	.1252	.1369	.1943	-.1846	-.0065	.0500	.1052	.0140	-.0760	-.0102	-.0051	.1535	.1864	-.3638	**-.4060**	-.2931	-.2245	-.1967	.2245	.3208	.2016	*	**.0000**	n.s.	.0171	n.s.	n.s.	.0024
27 Mn	.0894	-.1481	.0383	.1303	-.0366	.0008	-.0770	.0457	-.0376	-.0532	-.1459	.0322	.0562	.0713	.0356	-.1143	**-.4299**	**.6301**	**.6896**	**.4661**	.3355	.2849	-.1069	**-.5722**	-.0645	**-.4024**	*	.0939	**.0000**	n.s.	.0107	**.0000**
28 Zn	.0298	.0829	-.1099	-.0929	.1934	.0772	.0017	-.0539	-.0474	-.1450	.0153	.1031	.0264	.1816	.1358	**-.4181**	-.1422	.0416	.0889	.1412	-.0612	.0220	-.1118	-.2114	-.2784	-.0155	.0939	*	.0621	n.s.	.0043	n.s.
29 Total N	.0128	-.2134	.0128	.0741	.1184	.0689	-.1139	.1568	.0049	-.1089	-.0085	.1196	.0876	.0645	.0356	-.2940	**-.6081**	.3876	**.4530**	.3224	.0939	-.0122	**-.4367**	**-.3992**	-.2441	-.2327	**.3992**	.1820	*	n.s.	n.s.	.0329
30 P-AL	-.0094	-.0846	.1133	-.2377	.1610	-.1535	.0151	-.0294	.0180	-.0647	-.1324	-.1989	-.2478	-.1069	-.1052	-.1862	.0360	-.3435	-.2651	-.3453	-.3878	.2212	-.1902	.0661	-.2229	-.0090	-.1053	.1543	.0220	*	**.0000**	.0329
31 P	.0298	-.0494	.0911	-.2155	.1218	.0124	.0368	-.0425	.0310	-.0172	-.0238	-.1180	-.1190	-.0424	-.0645	-.2205	.0850	-.4011	-.3238	-.2996	-.3388	.1396	-.1445	.0922	-.3078	.0727	-.2490	.2784	-.0498	**.6604**	*	-.0743
32 S	.1968	.0000	-.0690	.0434	-.1883	.0357	.0921	-.1388	.0033	.0745	-.0781	.0008	.0430	.0322	-.0068	-.0751	-.2174	.3893	**.4262**	.2816	.2751	**.4792**	.0710	-.3257	.0122	-.2963	**.5053**	.0988	.2082	-.0024	-.0743	*

positively correlated. Both were negatively correlated with the other variables in the group, which were pairwise positively correlated. Several variables were connected to this group; e.g. the concentration of Mg (positively correlated with pH and the concentration of Ca), the concentration of Fe (negatively correlated with pH and the concentration of Mn) and the concentration of Na (negatively correlated with the concentration of total N).

The four variables expressing incoming radiation and aspect favourability made up a group of correlated variables that was connected to the first group via macro plot basal area and the concentration of Na, both correlated with variables in both groups. Soil moisture and concentrations of Na and Al were pairwise positively correlated ($\tau > 0.3$, $P < 0.002$).

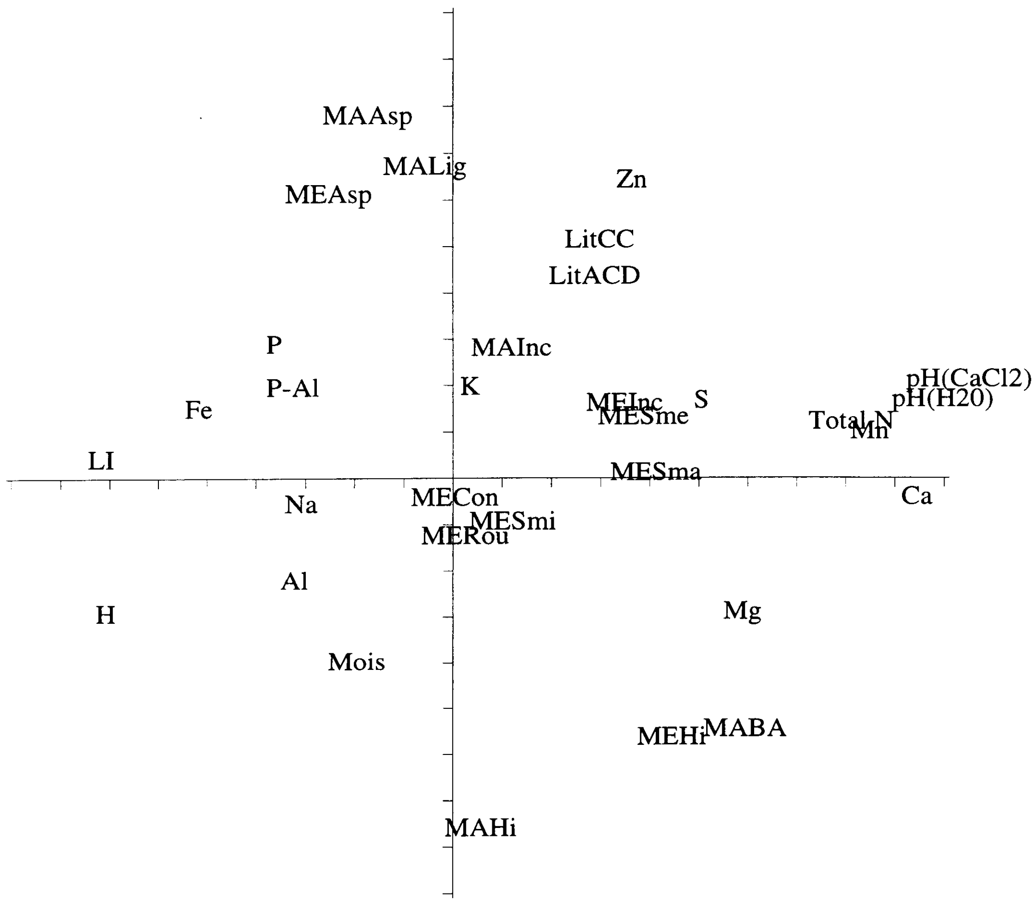


Fig. 446. Gutulia: PCA ordination of 32 environmental variables (names abbreviated in accordance with Tab. 2), axes 1 (horizontal) and 2 (vertical). Positions of variables in the ordination give the head of variable vectors.

PCA ordination of environmental variables

Eigenvalues of the first two PCA axes were 0.227 and 0.133, thus 36.0% of the variation in measured environmental variables was explained by the first two PCA axes.

High loadings on PCA 1 were obtained by positively correlated variables of the first of the groups above: pH, Ca, Mn and total N (Fig. 446). LI, Fe and H^+, all negatively correlated with the former, obtained low loadings on PCA 1.

Aspect unfavourability, the macro plot light index and Zn, partly also the litter indices, obtained high loadings on PCA 2 while low loadings were noted for the heat indices and macro plot basal area.

The two main groups of correlated variables (cf. Tab. 21) were thus reflected also in the PCA ordination (Fig. 446).

DCA and LNMDS ordination

Plot No. 12 (and, in the case of LNMDS also plot No. 6) occupied a somewhat isolated position with respect to the first two DCA (Fig. 447) and LNMDS (Fig. 448) axes. In both ordinations, plots showed some concentration around the centroid. DCA 1 and LNMDS 1 were of comparable gradient lengths, while LNMDS 2 was ca. 0.75 S.D. units longer than DCA 2.

DCA 1 and DCA 2 explained 13.8 and 8.6% of the variation in vegetation, respectively (Tab. 22). The explained fraction of variation decreased strongly from DCA 2 to DCA 3, to

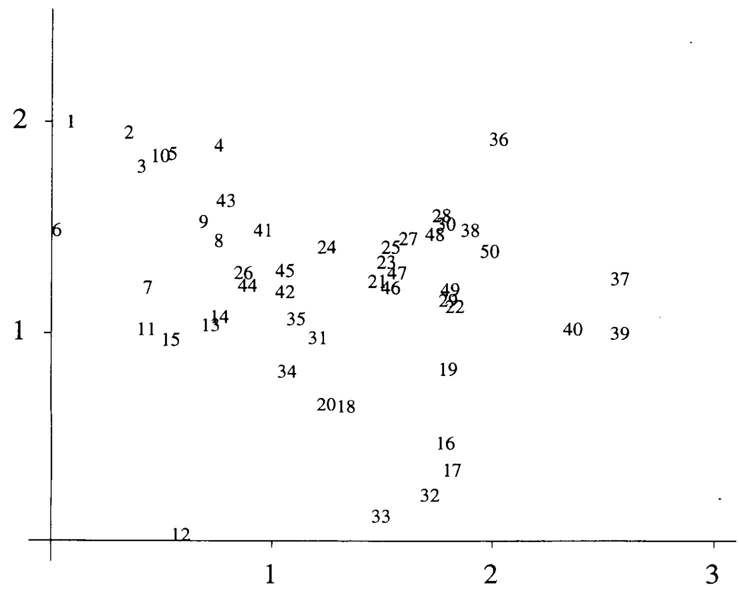


Fig. 447. Gutulia: DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Meso plot numbers are plotted onto the sample plot positions. Scaling of axes in S.D. units.

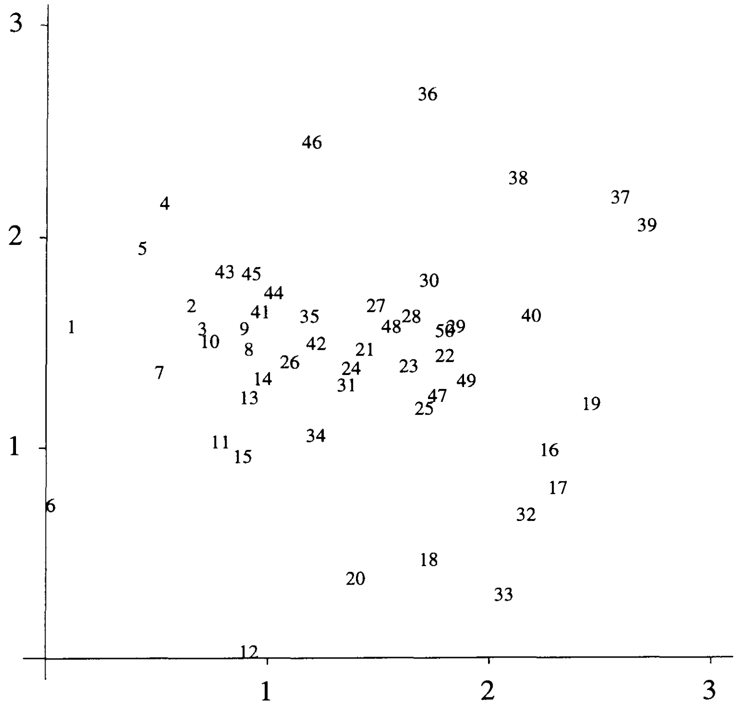


Fig. 448. Gutulia: LNMDS ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Meso plot numbers are plotted onto the sample plot positions. Axes linearly rescaled in S.D. units.

46.5% of the variation explained by the former. The eigenvalues of DCA 3 and DCA 4 were low (0.095 and 0.072, respectively), and the explained fraction of variation was below 4%.

Tab. 22. Gutulia: Eigenvalues and the fraction of variation explained for DCA axes 1-4.

	DCA 1	DCA 2	DCA 3	DCA 4
Eigenvalues	0.330	0.206	0.095	0.072
Fraction of variation explained	0.138	0.086	0.040	0.030

Tab. 23. Gutulia: Kendall's nonparametric correlation coefficient τ between DCA and LNMDS axes, and between 32 environmental variables in the 50 meso sample plots and sample plot positions with respect to DCA and LNMDS axes, and their significance probabilities. Correlations significant at level $P < 0.0001$ in bold face. n.s. - significance probability > 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 2.

Variable	DCA 1		DCA 2		DCA 3		DCA 4		LNMDS 1		LNMDS 2	
	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P
LNMDS 1	**.8034**	**.0000**	-.3127	.0014	-.0123	n.s.	.1148	n.s.				
LNMDS 2	.1155	n.s.	**.5027**	**.0000**	.3153	.0013	-.1542	n.s.				
01 MA Inc	-.0231	n.s.	-.1871	.0653	-.3060	.0026	-.0103	n.s.	-.0026	n.s.	-.2411	.0173
02 MA Asp	-.2141	.0391	-.1344	n.s.	.0115	n.s.	-.2037	.0499	-.1499	n.s.	-.1481	n.s.
03 MA Hi	.0350	n.s.	.0145	n.s.	-.1829	.0717	.2139	.0354	.0213	n.s.	-.0707	n.s.
04 MA BA	.2419	.0172	-.0726	n.s.	.1008	n.s.	.3833	.0002	.1848	.0679	.1474	n.s.
05 MA Lig	.1205	n.s.	.3340	.0010	-.0068	n.s.	-.2636	.0095	-.1934	.0561	.2360	.0198
06 ME Inc	-.0192	n.s.	.0166	n.s.	-.0708	n.s.	.0634	n.s.	-.0058	n.s.	.0423	n.s.
07 ME Asp	-.1496	n.s.	-.1571	n.s.	-.0689	n.s.	-.2078	.0380	-.1156	n.s.	-.1122	n.s.
08 ME Hi	.1376	n.s.	.2203	.0244	-.0082	n.s.	.1862	.0575	.1176	n.s.	.1372	n.s.
09 ME Rou	-.0262	n.s.	-.0287	n.s.	-.0557	n.s.	.2404	.0142	.0114	n.s.	-.1388	n.s.
10 ME Con	-.0567	n.s.	-.0493	n.s.	.0501	n.s.	-.0436	n.s.	-.0352	n.s.	-.0794	n.s.
11 ME Smi	-.0477	n.s.	-.0213	n.s.	.0970	n.s.	-.0878	n.s.	-.0815	n.s.	.1052	n.s.
12 ME Sme	.0637	n.s.	-.0579	n.s.	.0439	n.s.	-.0133	n.s.	.0536	n.s.	.0833	n.s.
13 ME Sma	.1359	n.s.	-.0953	n.s.	.0232	n.s.	.0614	n.s.	.1190	n.s.	.0545	n.s.
14 LitCC	.0085	n.s.	.1634	n.s.	.1873	.0625	-.1577	n.s.	-.0933	n.s.	.2613	.0091
15 LitACD	-.0289	n.s.	.1344	n.s.	.1651	n.s.	-.1321	n.s.	-.1324	n.s.	.2393	.0170
16 Mois	-.0541	n.s.	-.3350	.0006	-.0377	n.s.	.1354	n.s.	.0719	n.s.	**-.4900**	**.0000**
17 LI	**-.4592**	**.0000**	.0795	n.s.	.0558	n.s.	-.0189	n.s.	-.3776	.0001	-.1978	.0429
18 pH_{H_2O}	**.6841**	**.0000**	-.2424	.0164	.1098	n.s.	.0596	n.s.	**.6403**	**.0000**	.0416	n.s.
19 pH_{CaCl_2}	**.7297**	**.0000**	-.1632	n.s.	.0825	n.s.	.0329	n.s.	**.6409**	**.0000**	.1141	n.s.
20 Ca	**.5872**	**.0000**	-.1605	n.s.	.2727	.0053	.1804	.0656	**.5184**	**.0000**	.1265	n.s.
21 Mg	**.4234**	**.0000**	-.3176	.0012	.1384	n.s.	.0705	n.s.	**.4955**	**.0000**	-.0106	n.s.
22 K	.1122	n.s.	-.1621	n.s.	-.1876	.0553	-.0508	n.s.	-.1478	n.s.	-.2245	.0214
23 Na	-.1712	.0803	-.3324	.0007	.1073	n.s.	-.0197	n.s.	-.0580	n.s.	-.3584	.0002
24 H^+	**-.5004**	**.0000**	.0589	n.s.	-.1188	n.s.	-.0262	n.s.	**-.4612**	**.0000**	-.0727	n.s.
25 Al	-.0958	n.s.	-.3553	.0003	.0270	n.s.	.0902	n.s.	.0041	n.s.	-.2996	.0021
26 Fe	**-.4234**	**.0000**	.0950	n.s.	.0942	n.s.	-.0508	n.s.	-.3861	.0001	-.0694	n.s.
27 Mn	**.5954**	**.0000**	-.1588	n.s.	-.0958	n.s.	-.0180	n.s.	**.5429**	**.0000**	.0433	n.s.
28 Zn	.0057	n.s.	.3160	.0012	.0713	n.s.	-.1246	n.s.	-.0727	n.s.	.2963	.0024
29 Total N	**.4922**	**.0000**	.1670	n.s.	.0156	n.s.	-.0607	n.s.	.3829	.0001	.3502	.0003
30 P-AL	-.2809	.0041	.3324	.0007	-.1859	.0575	-.2460	.0121	-.3273	.0008	.0514	n.s.
31 P	-.3415	.0005	.3897	.0001	-.1351	n.s.	-.2345	.0167	**-.3959**	**.0000**	.1069	n.s.
32 S	**.3989**	**.0000**	-.1916	.0502	-.1564	n.s.	.0033	n.s.	.3747	.0001	-.0465	n.s.

Correlations between DCA and LNMDS ordination axes and between ordination axes and environmental variables

DCA 1 and LNMDS 1 were very strongly (τ = 0.803; Tab. 23) correlated. DCA 2 and LNMDS 2 were also strongly correlated (τ = 0.503). The variables most strongly correlated ($P < 0.0001$) with DCA 1 (and LNMDS, although mostly with lower correlation coefficient) were pH (with τ = 0.730, Fig. 452) and concentrations of Mn (Fig. 458), Ca (Fig. 453), total N (Fig. 460), Mg (Fig. 454), and S (Fig. 462), all positively correlated, and loss on ignition (Fig. 451), and concentrations of H^+ (Fig. 456), and Fe, all negatively correlated.

Concentrations of Mg (Fig. 454) and P (Fig. 461) were correlated with DCA 1, DCA 2 and LNMDS 1, but insignificantly correlated with LNMDS 2. The concentration of total N was correlated with DCA 1, LNMDS 1 and LNMDS 2, but insignificantly correlated with DCA 2.

Soil moisture was strongly negatively correlated with LNMDS 2 (τ = -0.490, $P < 0.0001$), while no variable was correlated with DCA 2 at this significance level. Concentrations of Na and total N were correlated with LNMDS 2 at $0.0001 < P < 0.002$, while eight variables were correlated with DCA 2 at this level: soil moisture (Fig. 450), macro plot light index (Fig. 449), and concentrations of P (Fig. 461), Al (Fig. 457), Na (Fig. 455), P-AL, Mg and Zn (Fig. 459); those with negative loadings on PCA 2 having negative correlations with DCA 2.

Only macro plot inclination was significantly correlated with DCA 3 at $P < 0.005$ and only macro plot basal area was correlated with DCA 4 at the same significance level.

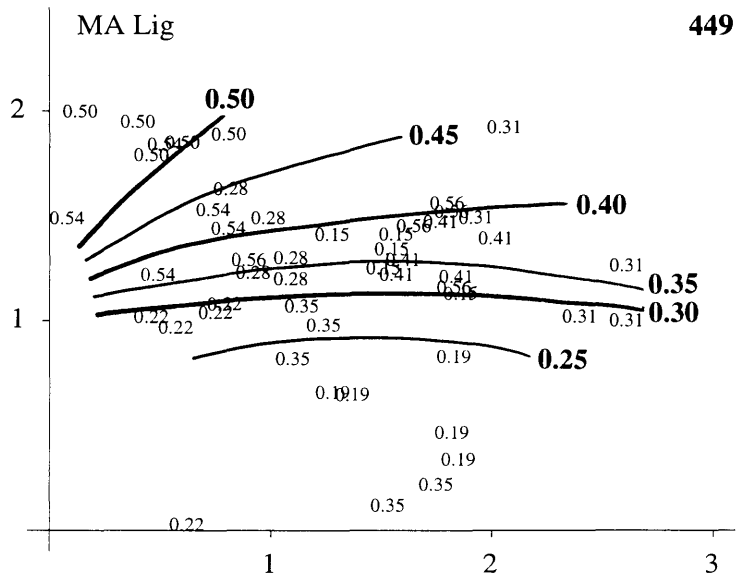
The distribution of species abundance in the DCA ordination

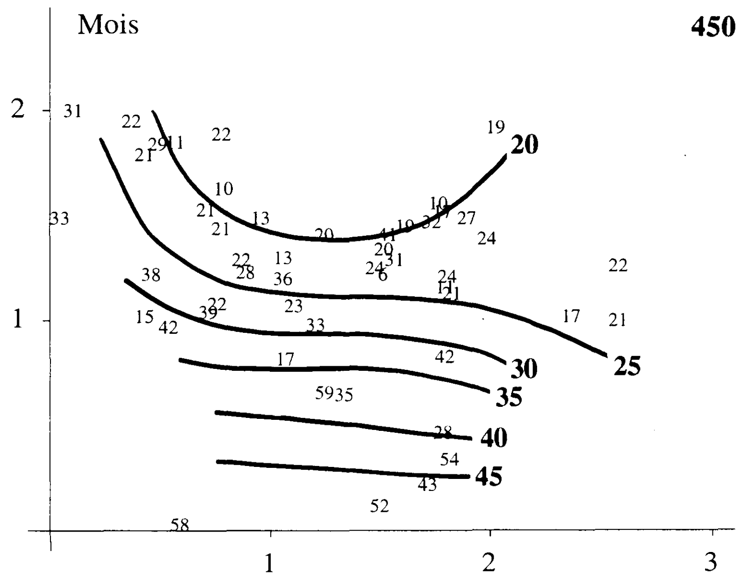
Sixty-two of a total of 126 species occurred in at least 5 of the 50 meso plots (Figs 463-524).

Vaccinium myrtillus (Fig. 465), a typical example of a species with wide ecological amplitude, was abundant in most meso plots. Other examples of abundant species that are common species in poor bilberry-dominated spruce forest were *Deschampsia flexuosa* (Fig. 485) and *Hylocomium splendens* (Fig. 492) and *Barbilophozia lycopodioides* (Fig. 510).

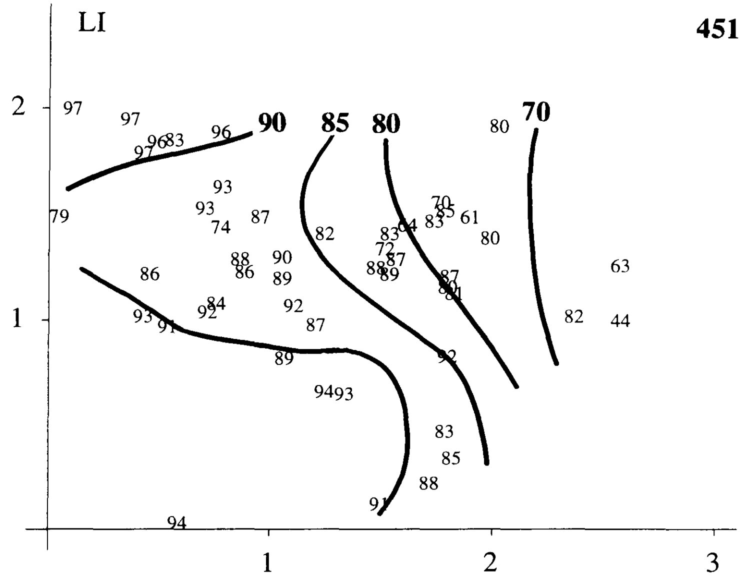
Several species were restricted to parts of the ordination diagram. *Dicranum fuscescens* agg. (Fig. 488) mainly occurred on dry sites with low content of nutrients (low DCA 1, high DCA 2 scores). Species with high abundance on sites with high nutrient contents made up a continuum from *Mnium spinosum* (Fig. 493) and *Rhodobryum roseum* (Fig. 500), with higher abundance at high DCA 2 scores (dry sites), to *Geranium sylvaticum* (Fig. 468) and *Rhytidiadelphus squarrosus* agg. (Fig. 501), with higher abundance in plots with intermediate DCA 2 values.

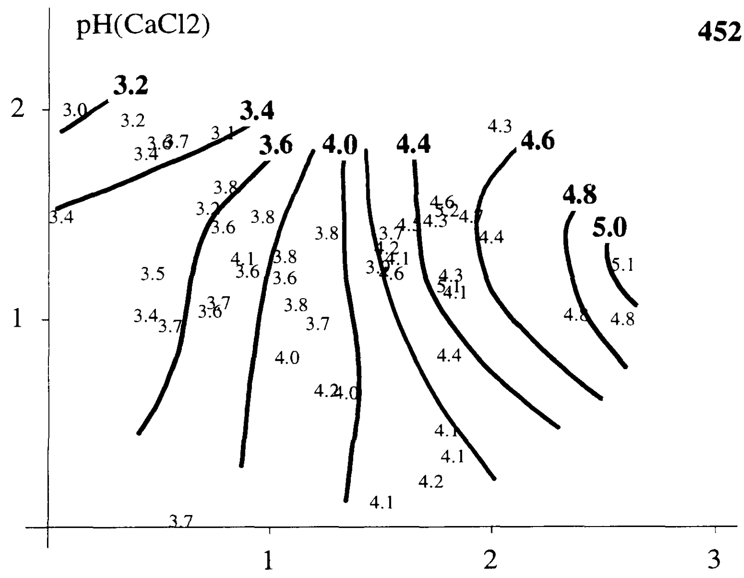
Straminergon stramineum (Fig. 503), *Sphagnum angustifolium* (Fig. 504) and *Sphagnum girgensohnii* (Fig. 505) are examples of species with low DCA 2 scores (preference for moist sites).



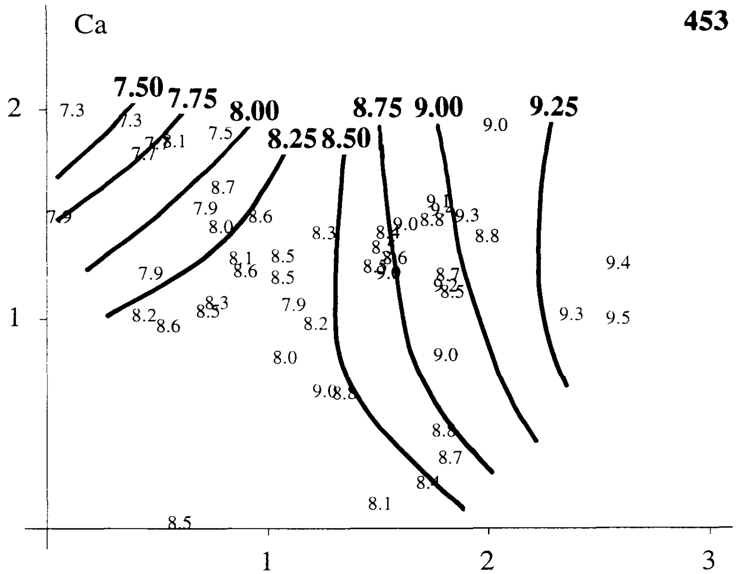


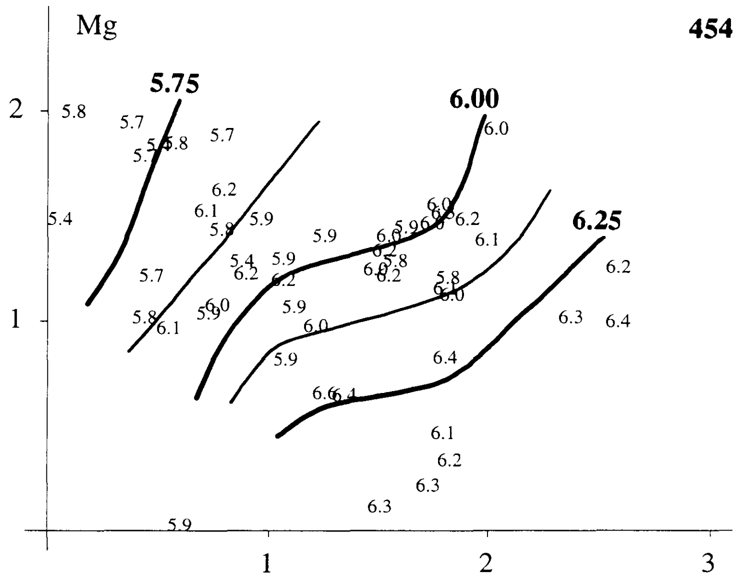
Figs 449-450. Gutulia: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots' positions. Scaling of axes in S.D. units. Fig. 449. MA Lig (R^2 = 0.395). Fig. 450. Mois (R^2 = 0.527). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.



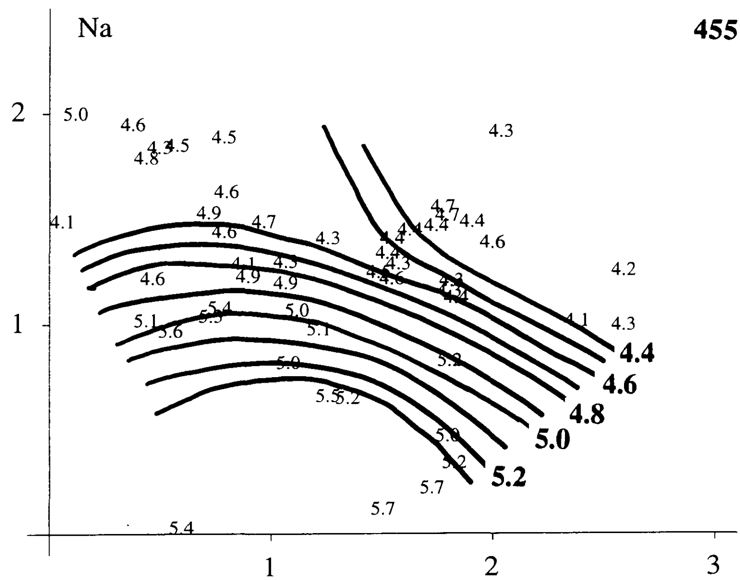


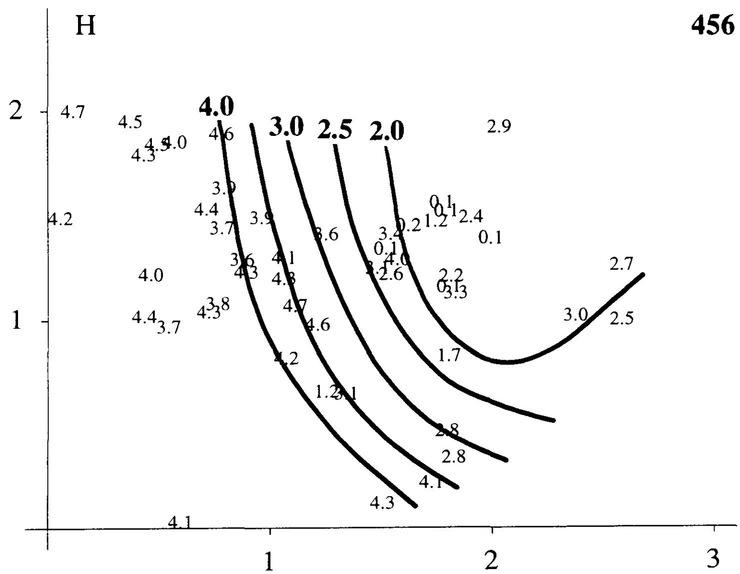
Figs 451-452. Gutulia: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots' positions. Scaling of axes in S.D. units. Fig. 451. LI (R^2 = 0.619). Fig. 452. pH_{CaCl2} (R^2 = 0.782). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.



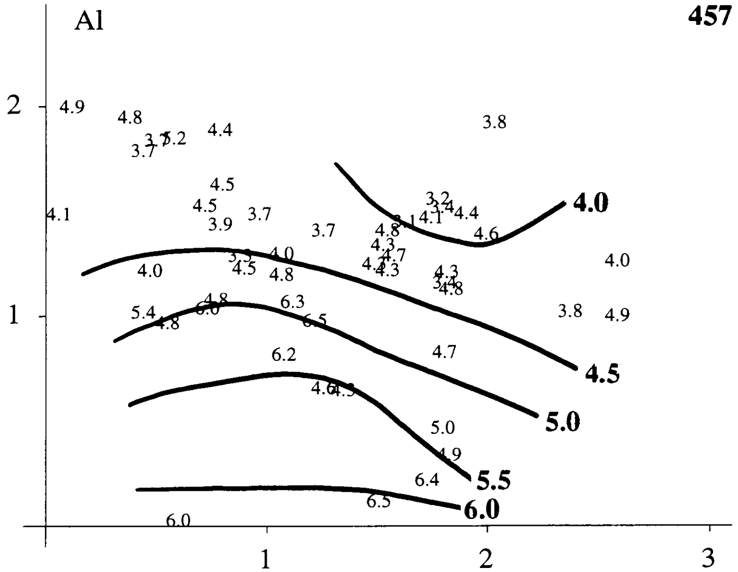


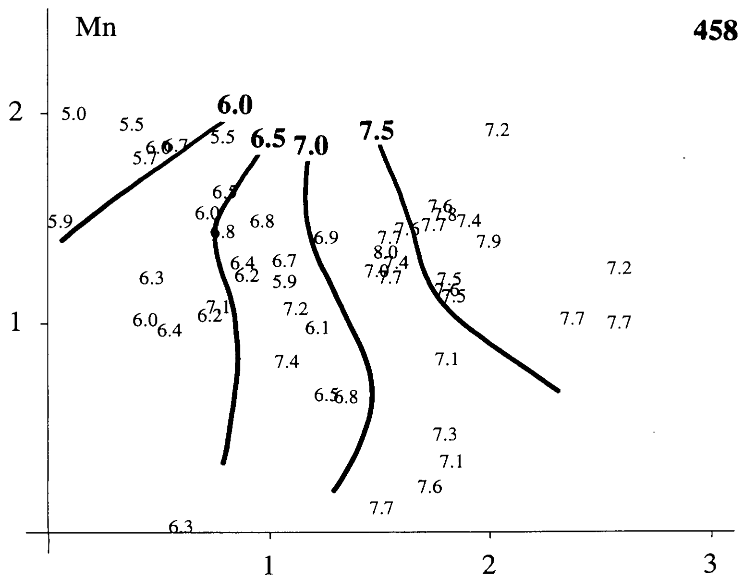
Figs 453-454. Gutulia: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 453. Ca (R^2 = 0.756). Fig. 454. Mg (R^2 = 0.529). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.



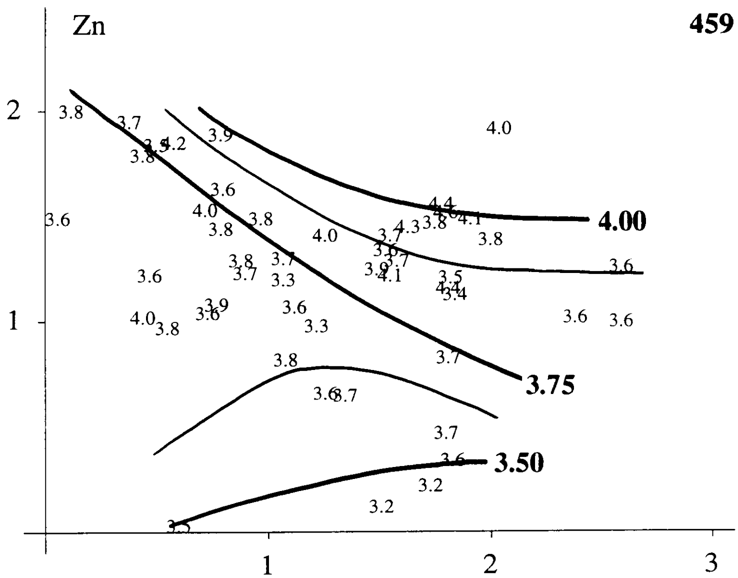


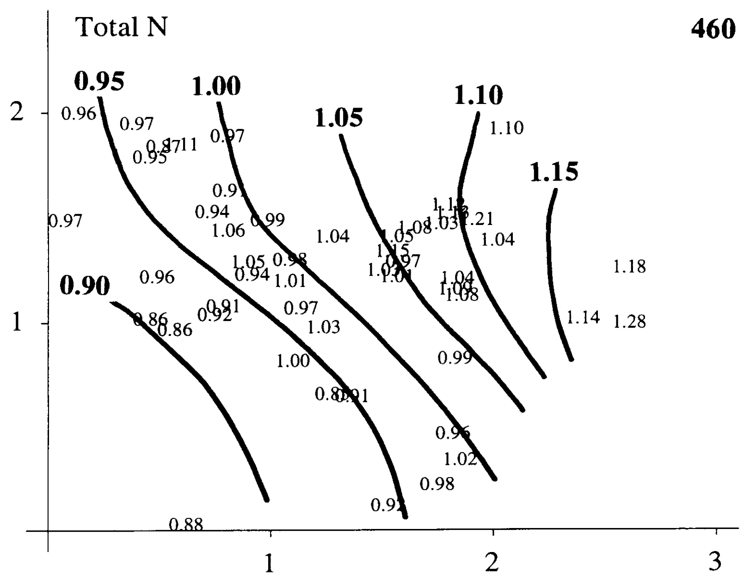
Figs 455-456. Gutulia: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots' positions. Scaling of axes in S.D. units. Fig. 455. Na (R^2 = 0.700). Fig. 456. H^+ (R^2 = 0.587). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.



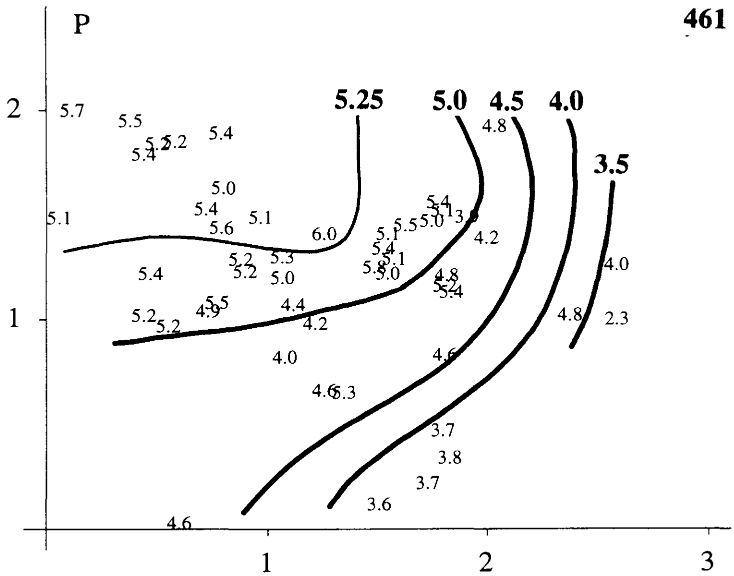


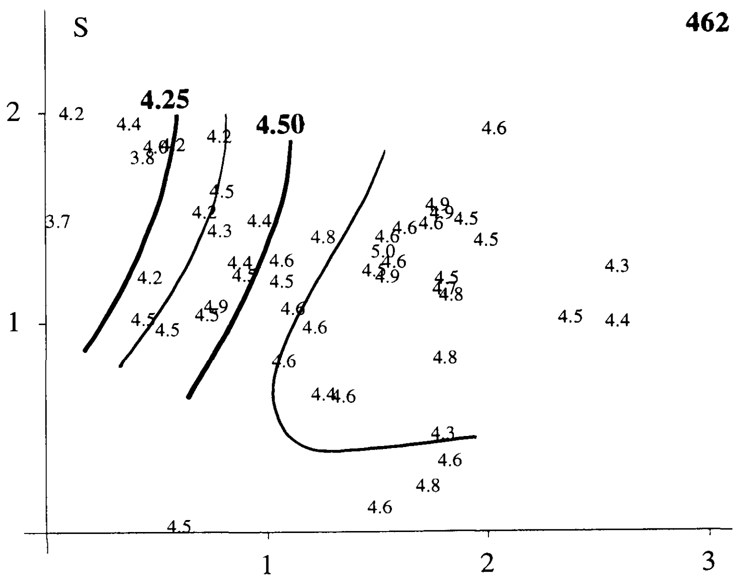
Figs 457-458. Gutulia: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 457. Al (R^2 = 0.475). Fig. 458. Mn (R^2 = 0.788). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.



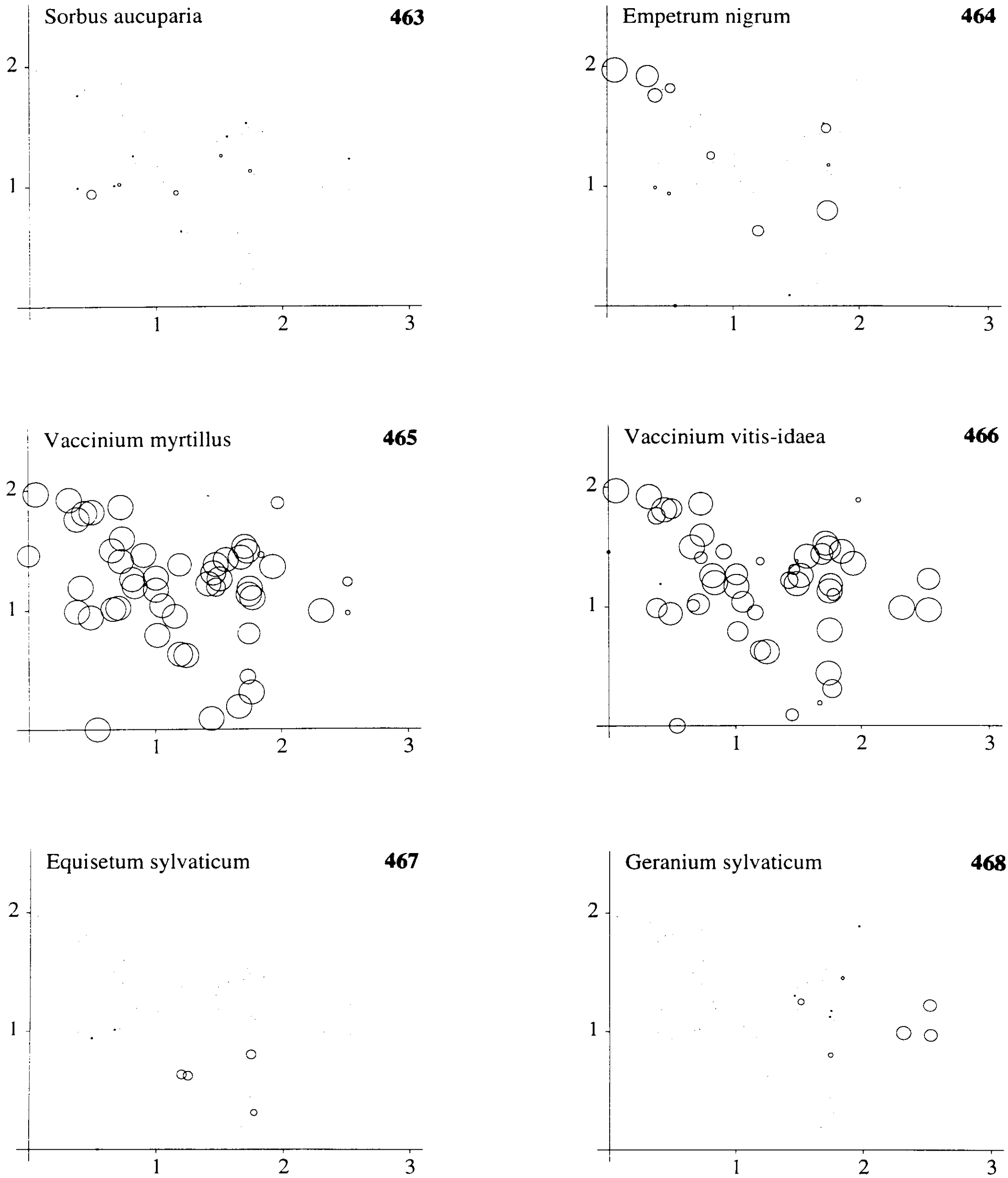


Figs 459-460. Gutulia: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 459. Zn (R^2 = 0.400). Fig. 460. Total N (R^2 = 0.719). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.

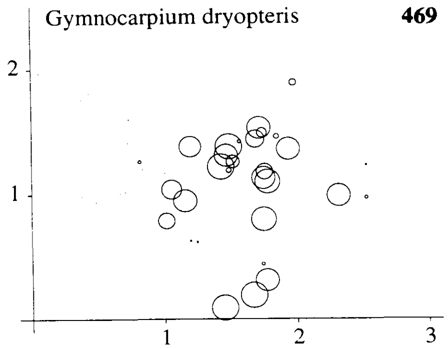


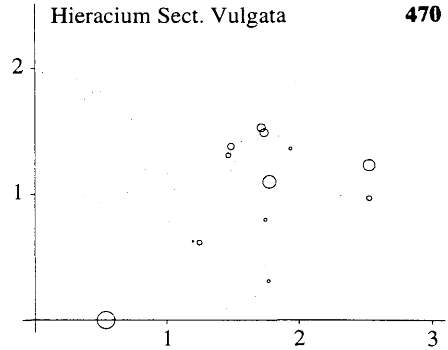


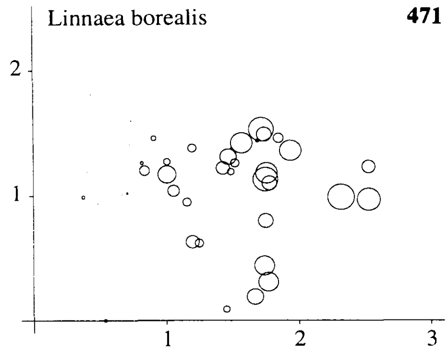
Figs 461-462. Gutulia: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 461. P (R^2 = 0.657). Fig. 462. S (R^2 = 0.607). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.

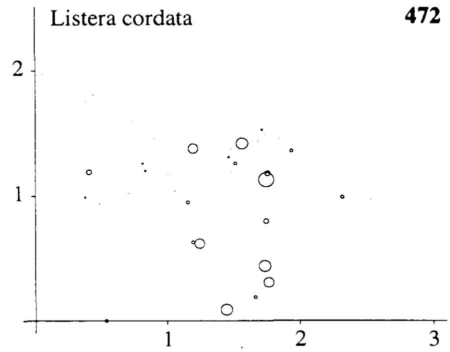


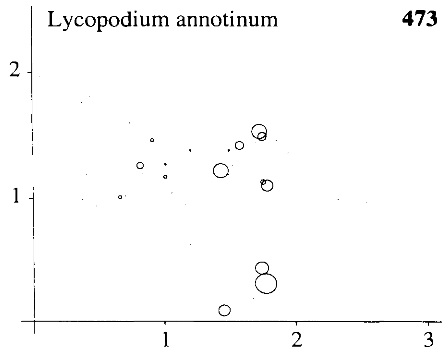
Figs 463-468. Gutulia: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 463. *Sorbus aucuparia*. Fig. 464. *Empetrum nigrum*. Fig. 465. *Vaccinium myrtillus*. Fig. 466. *Vaccinium vitis-idaea*. Fig. 467. *Equisetum sylvaticum*. Fig. 468. *Geranium sylvaticum*.

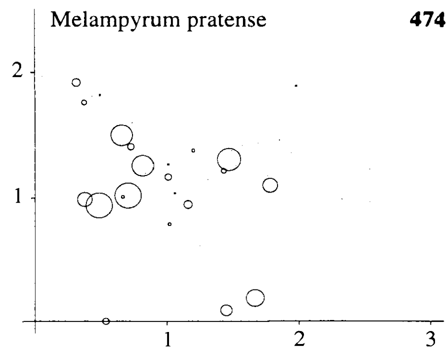




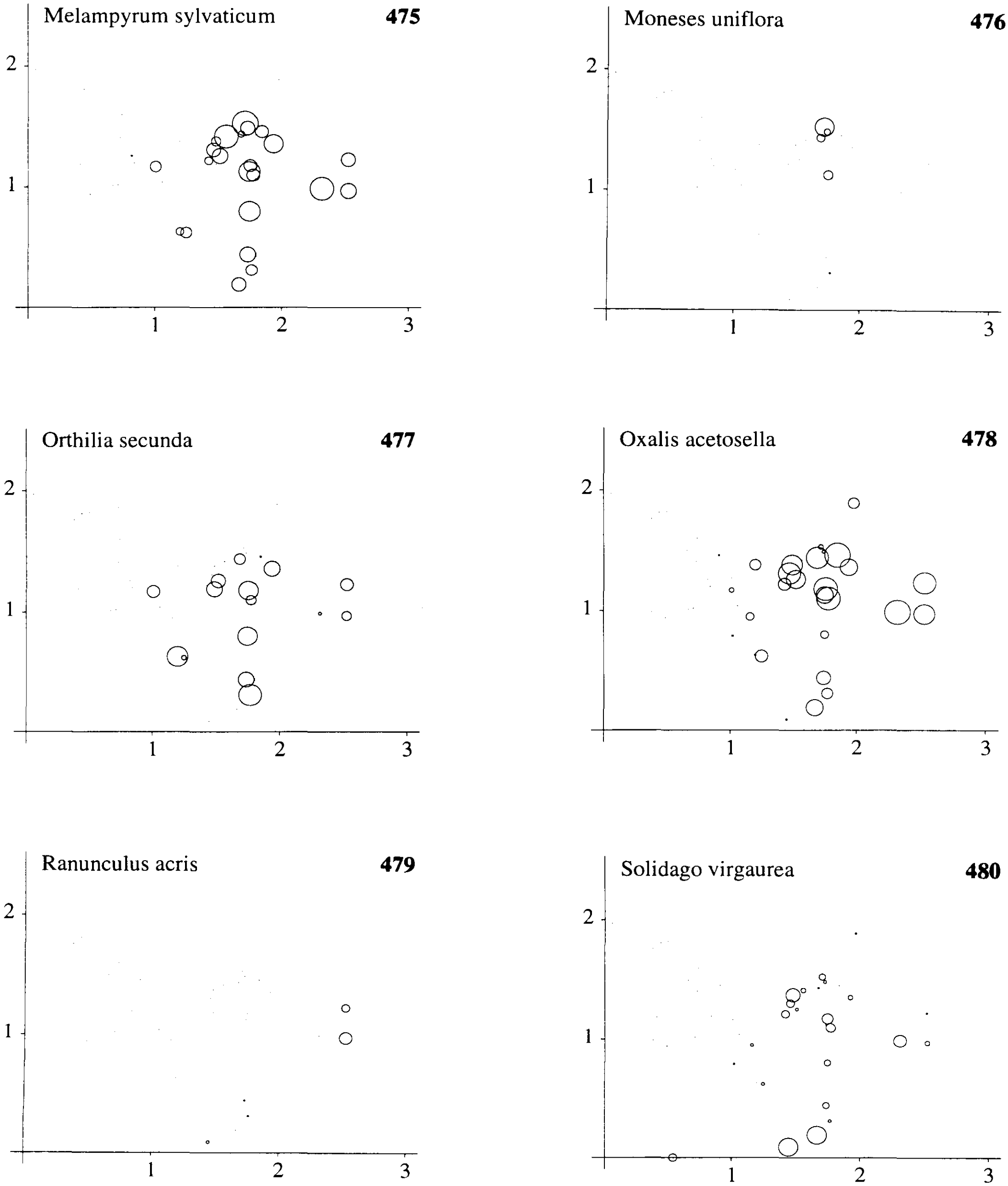




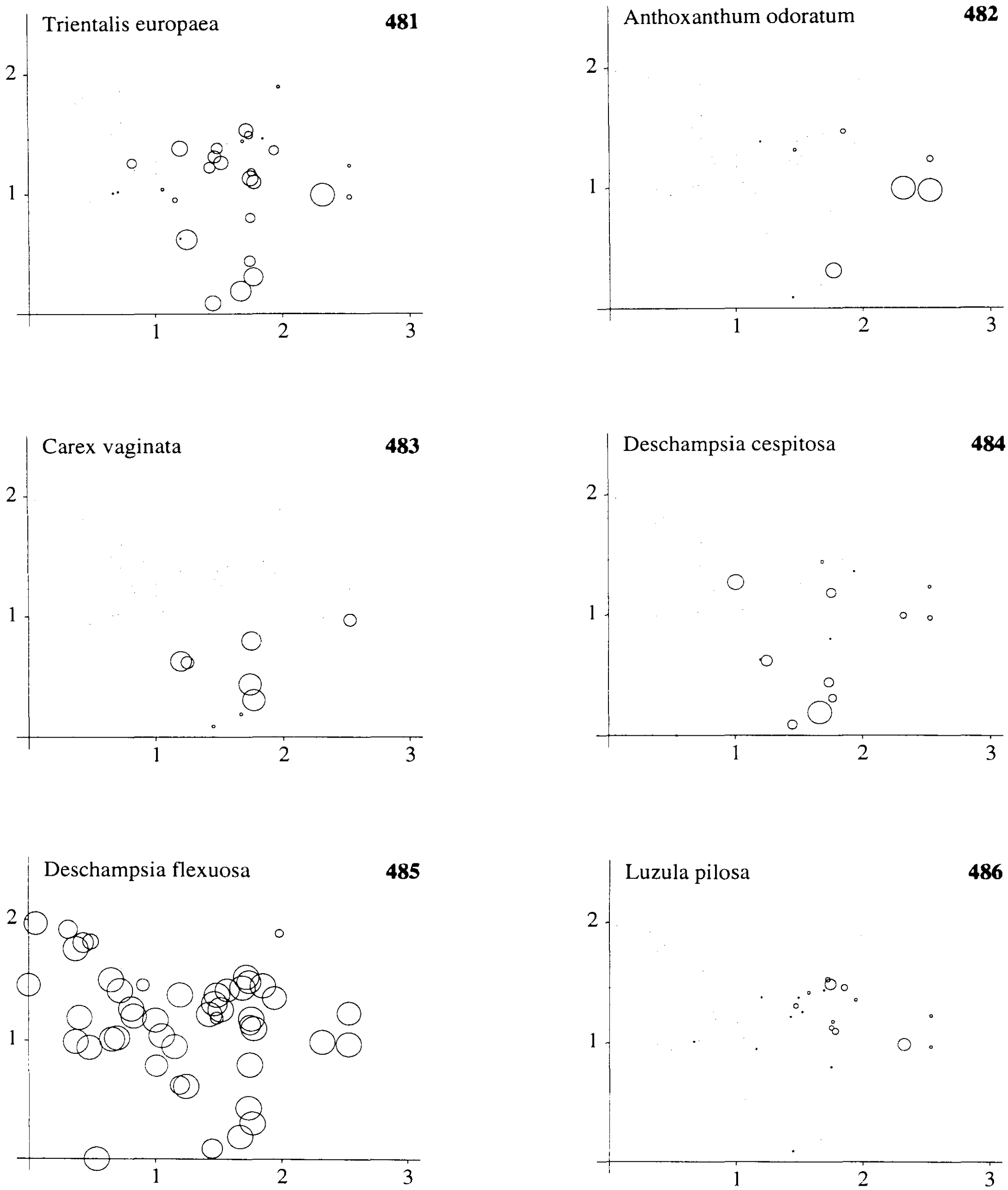




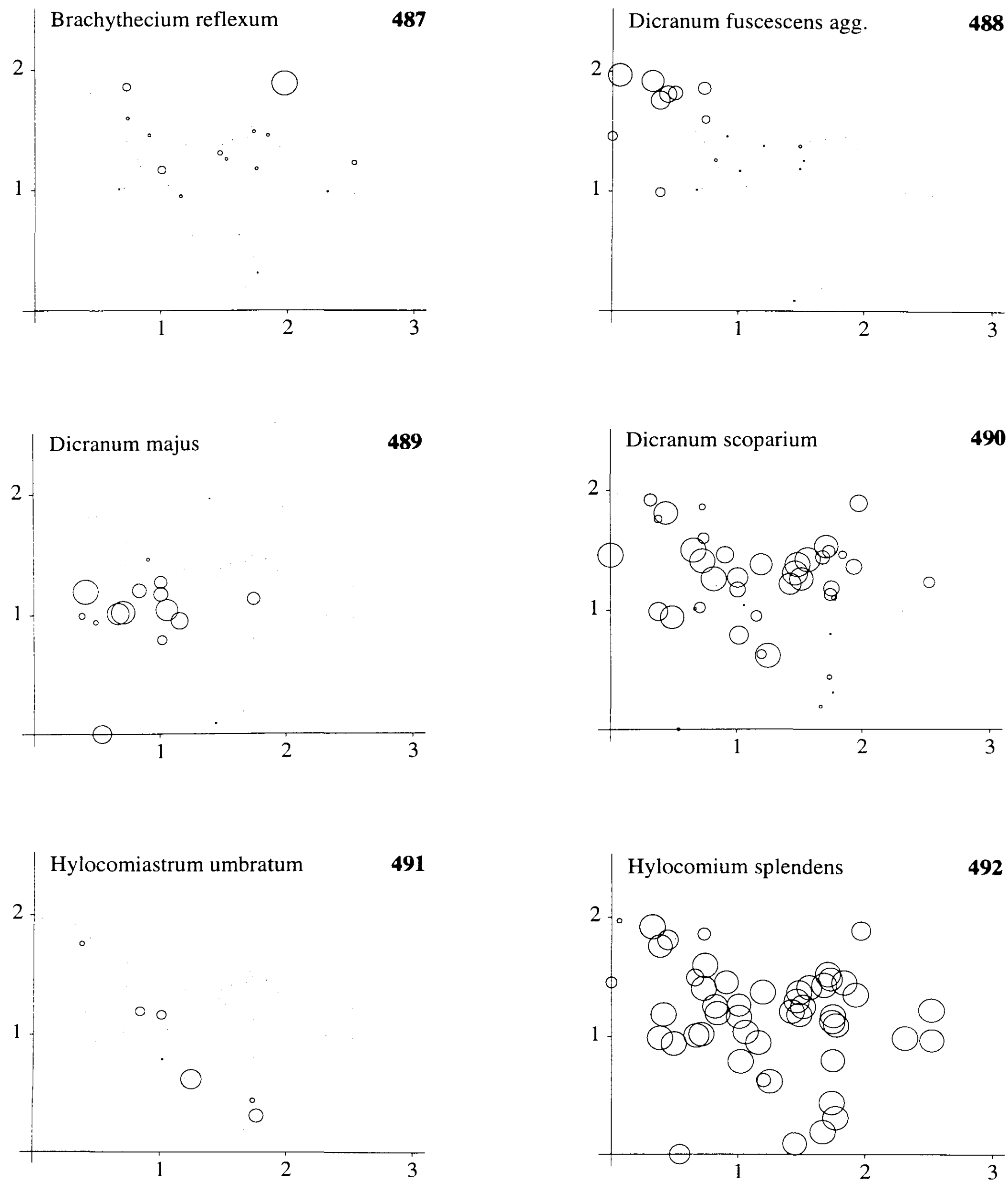
Figs 469-474. Gutulia: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 469. *Gymnocarpium dryopteris*. Fig. 470. *Hieracium Sect. Vulgata*. Fig. 471. *Linnaea borealis*. Fig. 472. *Listera cordata*. Fig. 473. *Lycopodium annotinum*. Fig. 474. *Melampyrum pratense*.



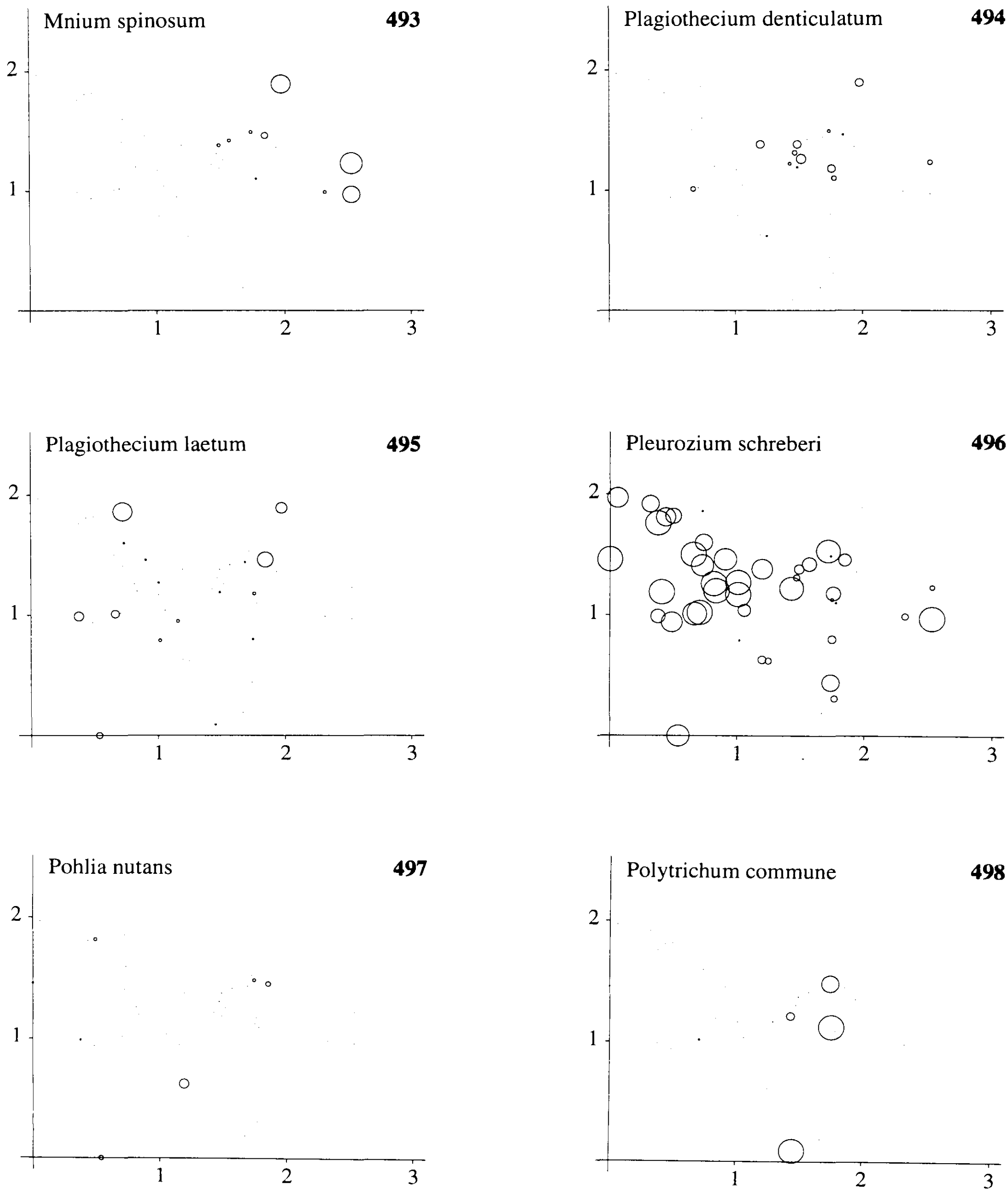
Figs 475-480. Gutulia: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 475. *Melampyrum sylvaticum*. Fig. 476. *Moneses uniflora*. Fig. 477. *Orthilia secunda*. Fig. 478. *Oxalis acetosella*. Fig. 479. *Ranunculus acris*. Fig. 480. *Solidago virgaurea*.



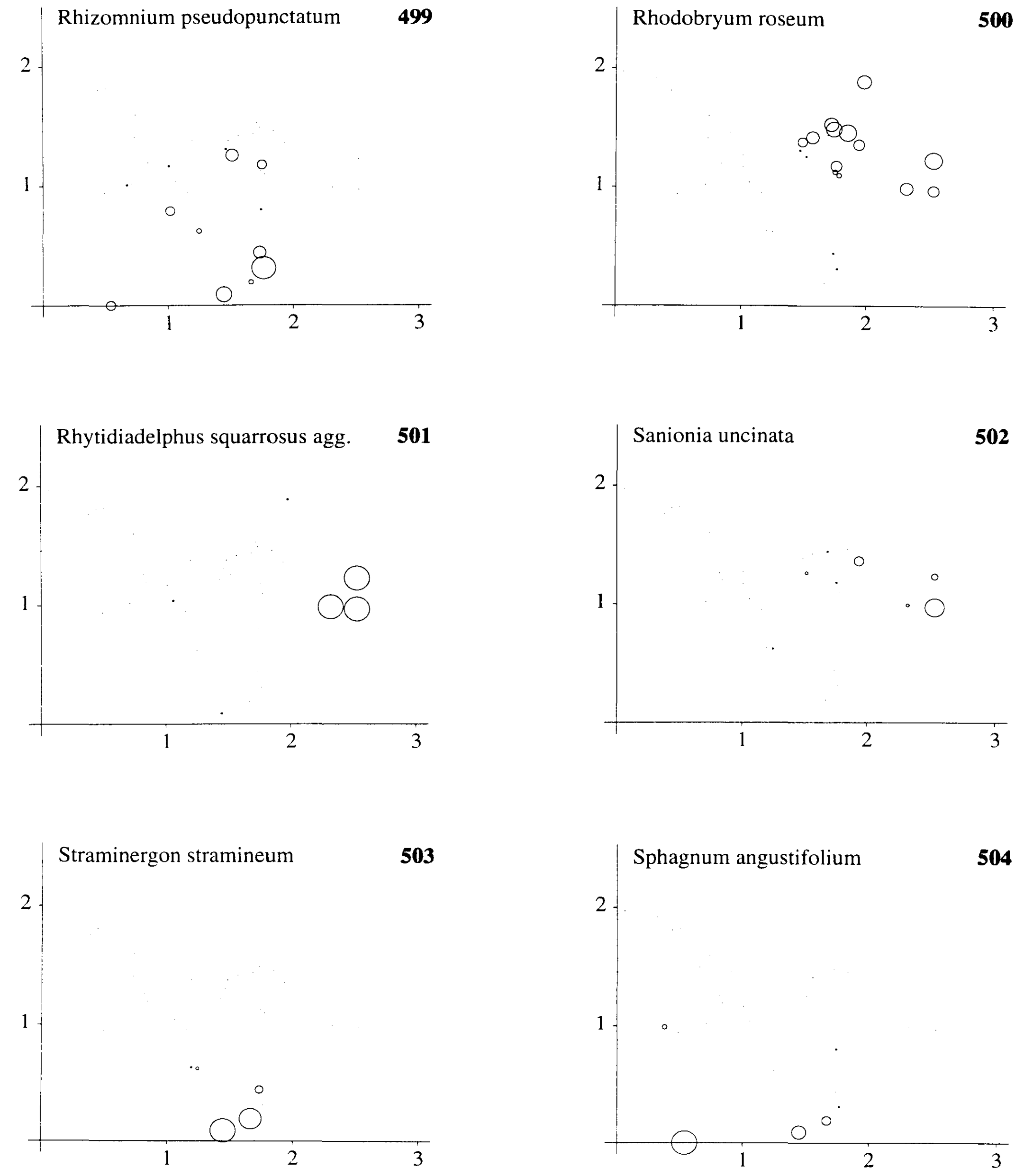
Figs 481-486. Gutulia: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 481. *Trientalis europaea*. Fig. 482. *Anthoxanthum odoratum*. Fig. 483. *Carex vaginata*. Fig. 484. *Deschampsia cespitosa*. Fig. 485. *Deschampsia flexuosa*. Fig. 486. *Luzula pilosa*.



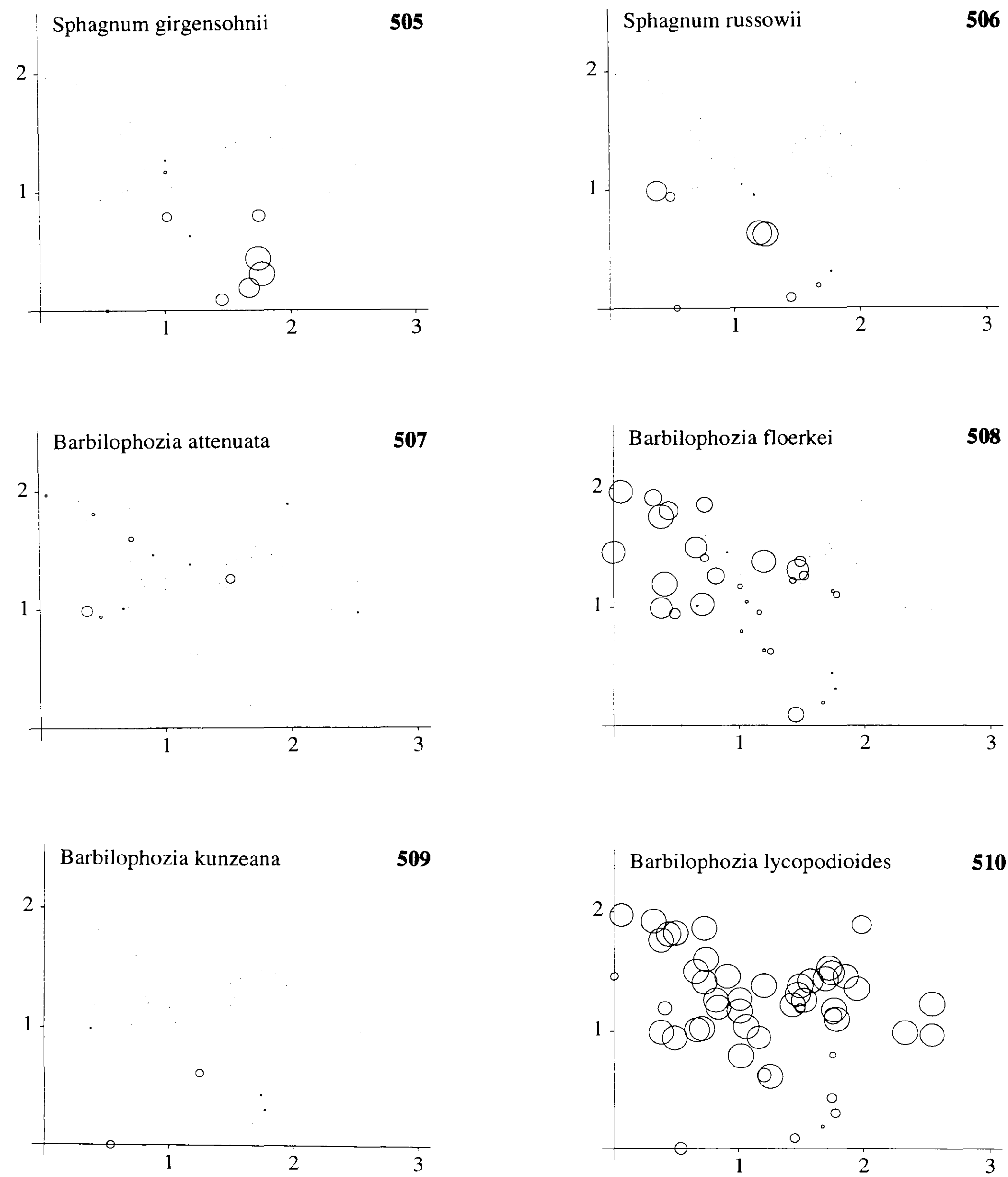
Figs 487-492. Gutulia: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 487. *Brachythecium reflexum*. Fig. 488. *Dicranum fuscescens* agg. Fig. 489. *Dicranum majus*. Fig. 490. *Dicranum scoparium*. Fig. 491. *Hylocomiastrum umbratum*. Fig. 492. *Hylocomium splendens*.



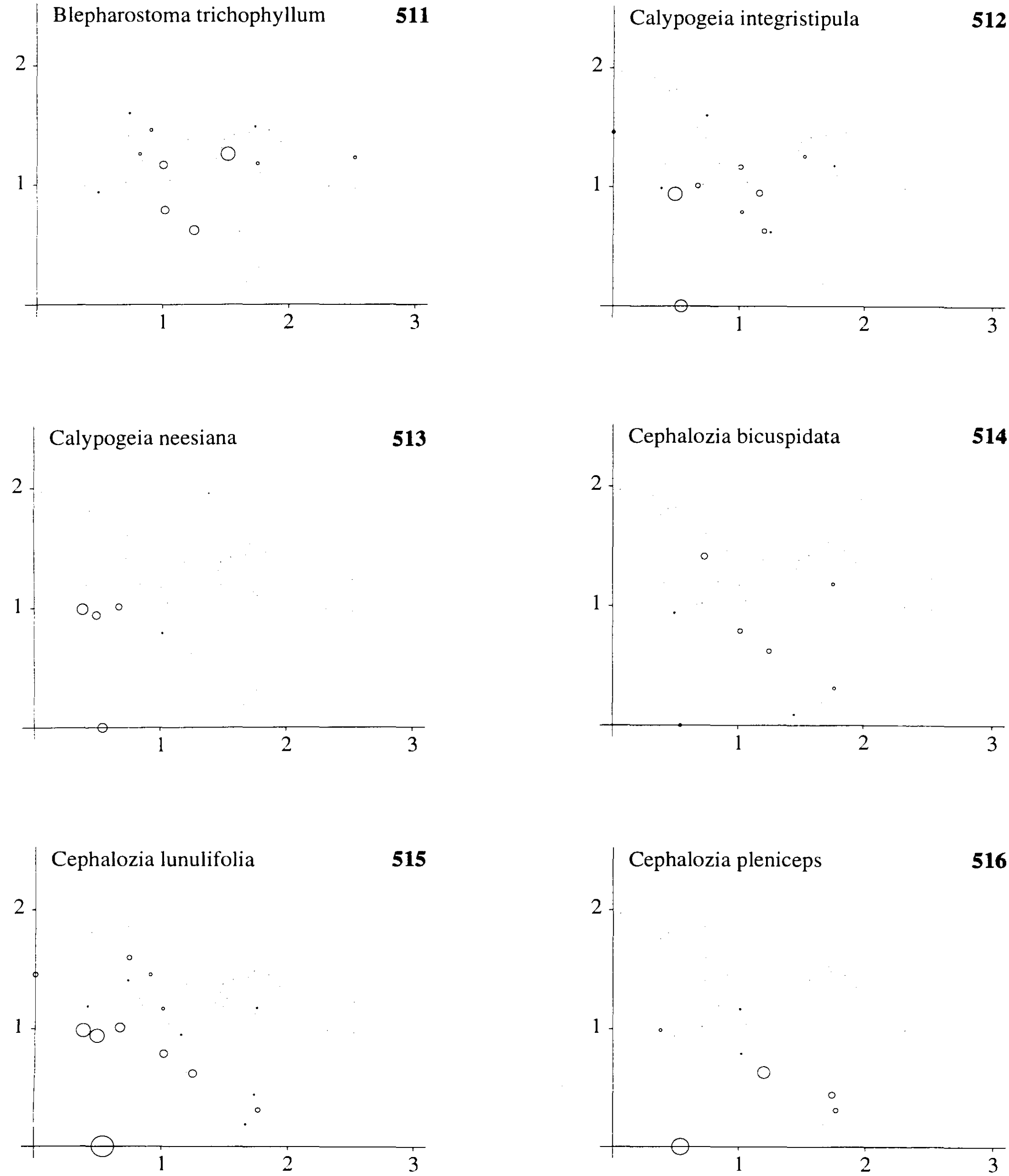
Figs 493-498. Gutulia: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 493. *Mnium spinosum*. Fig. 494. *Plagiothecium denticulatum*. Fig. 495. *Plagiothecium laetum*. Fig. 496. *Pleurozium schreberi*. Fig. 497. *Pohlia nutans*. Fig. 498. *Polytrichum commune*.



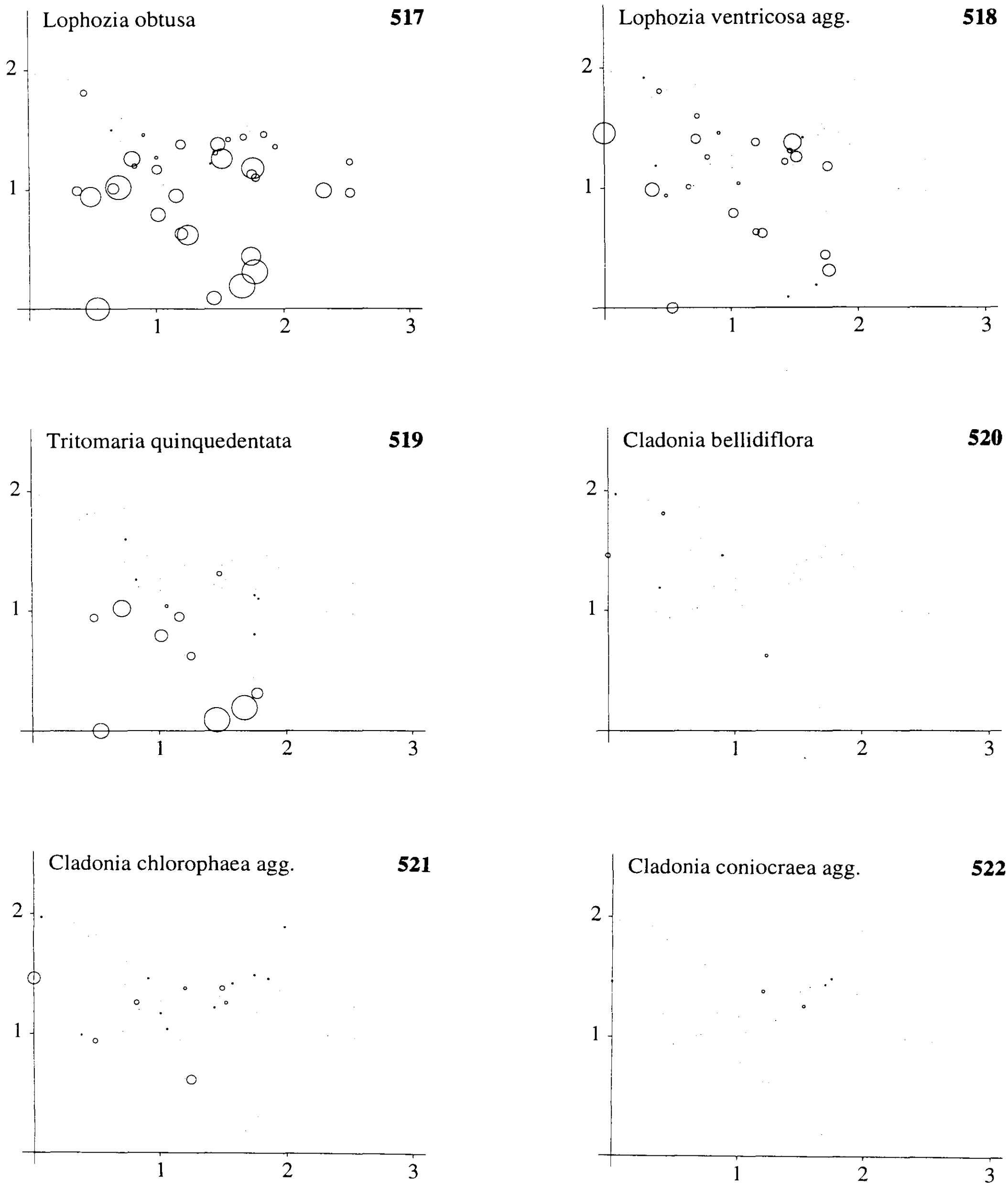
Figs 499-504. Gutulia: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 499. *Rhizomnium pseudopunctatum*. Fig. 500. *Rhodobryum roseum*. Fig. 501. *Rhytidiadelphus squarrosus* agg. Fig. 502. *Sanionia uncinata*. Fig. 503. *Straminergon stramineum*. Fig. 504. *Sphagnum angustifolium*.



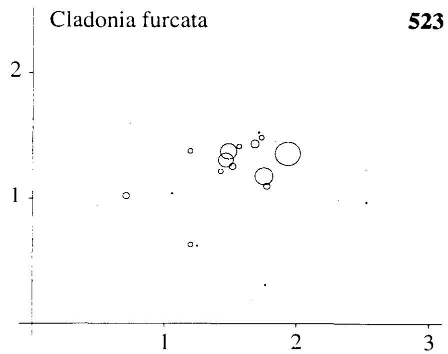
Figs 505-510. Gutulia: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 505. *Sphagnum girgensohnii*. Fig. 506. *Sphagnum russowii*. Fig. 507. *Barbilophozia attenuata*. Fig. 508. *Barbilophozia floerkei*. Fig. 509. *Barbilophozia kunzeana*. Fig. 510. *Barbilophozia lycopodioides*.

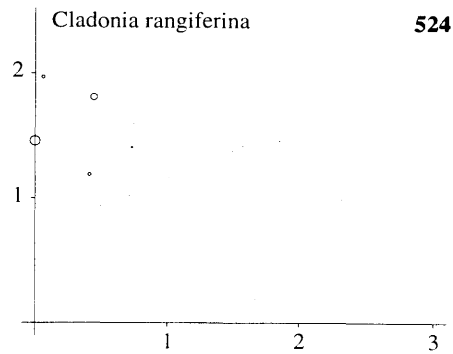


Figs 511-516. Gutulia: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 511. *Blepharostoma trichophyllum*. Fig. 512. *Calypogeia integristipula*. Fig. 513. *Calypogeia neesiana*. Fig. 514. *Cephalozia bicuspidata*. Fig. 515. *Cephalozia lunulifolia*. Fig. 516. *Cephalozia pleniceps*.



Figs 517-522. Gutulia: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 517. *Lophozia obtusa*. Fig. 518. *Lophozia ventricosa* agg. Fig. 519. *Tritomaria quinquedentata*. Fig. 520. *Cladonia bellidiflora*. Fig. 521. *Cladonia chlorophaea* agg. Fig. 522. *Cladonia coniocraea* agg.





Figs 523-524. Gutulia: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 523. *Cladonia furcata*. Fig. 524. *Cladonia rangiferina*.

URVATNET

Correlations between environmental variables

A group of pairwise strongly correlated variables ($\tau > 0.44$) was made up by pH, and concentrations of Ca, Mn, and H^+ and loss on ignition (Tab. 24, Fig. 525). The three first mentioned were pairwise positively correlated, while the concentration of H^+ and loss on ignition were positively correlated with each other, but negatively correlated with each of the other three variables. The concentration of total N was strongly positively correlated with pH and strongly negatively correlated with loss on ignition. The macro plot light index was positively correlated with pH and the concentration of Mn, and negatively correlated with the concentration of H^+ and loss on ignition. Several other variables (concentrations of Fe, Al, Mg, P, Zn, K, S) were associated with this group (see Fig. 525).

Another group of strongly correlated variables ($\tau > 0.55$) was made up by the heat indices which were negatively correlated with aspect unfavourability. This group had several connections with the first group; e.g. the positive correlations between the heat indices and each of pH, the light index and the concentration of Ca.

Macro plot inclination was negatively correlated with the heat index.

Macro plot basal area was associated with both groups; positively correlated with the light index and negatively correlated with macro plot aspect unfavourability.

Soil moisture was negatively correlated with both litter indices.

PCA ordination of environmental variables

Eigenvalues of the first two PCA axes were 0.277 and 0.153, thus 43.0% of the variation in measured environmental variables was explained by the first two PCA axes.

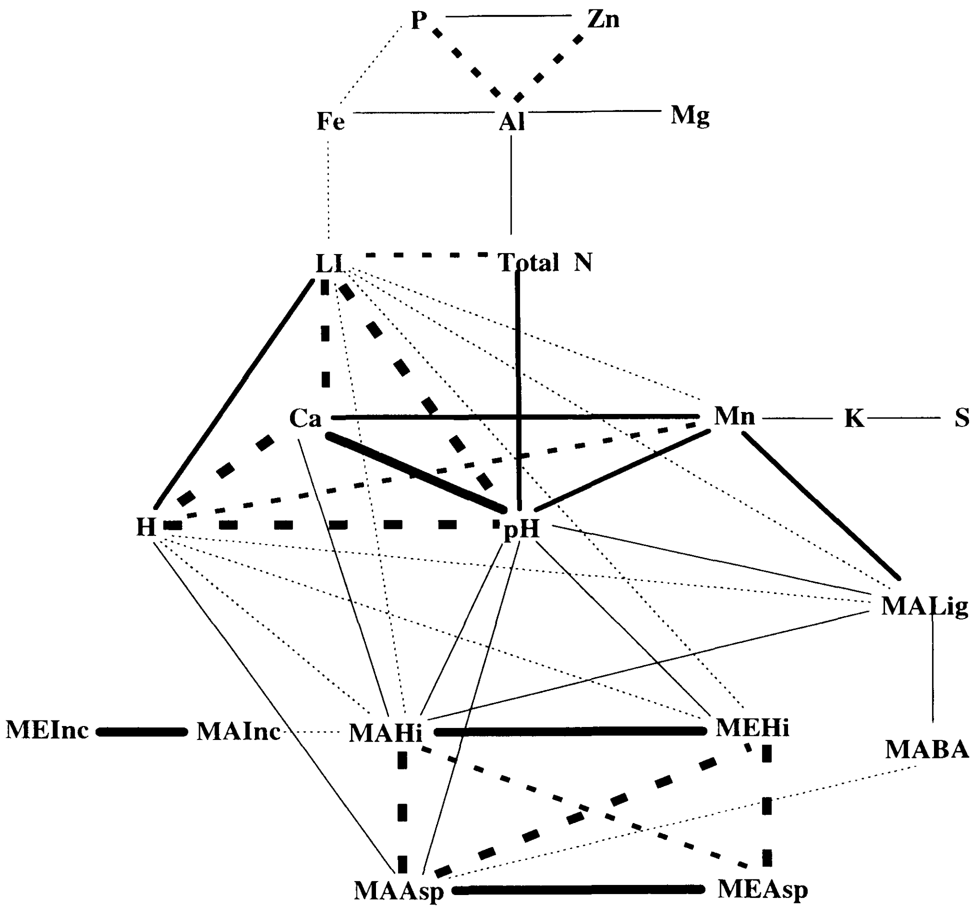


Fig. 525. Urvatnet: plexus diagram visualizing Kendall's τ between pairs of environmental variables. Significance probabilities for τ are indicated by lines with different thickness (in order of decreasing thickness): $|\tau| \geq 0.60$, $0.45 \leq |\tau| < 0.60$, $0.35 \leq |\tau| < 0.45$. Continuous lines refer to positive correlations, broken lines to negative.

Positively correlated variables within both major groups of correlated variables (pH, Ca, total N, the heat indices, Mn, and to a lesser extent also the macro plot light index) obtained high loadings on PCA 1 (Fig. 526), while variables of these groups with negative correlations with the variables mentioned above (loss on ignition, H^+, aspect unfavourability, P, to a lesser extent also P-AL, Zn and inclination) obtained low loadings on PCA 1 (Fig. 526). The two groups of correlated variables and the connections between them were thus reflected along PCA 1.

K, P-AL, Zn and P obtained the highest, while Al, soil depth and soil moisture obtained the lowest loadings on PCA 2.

Tab. 24. Urvatnet: Kendall's nonparametric correlation coefficient τ between 32 environmental variables in the 50 meso sample plots (lower triangle), with significance probabilities (upper triangle). Correlations significant at level P < 0.0001 in bold face. n.s. - significance probability > 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 2.

Variable	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
01 MA Inc	*	.0327	.0007	.2871	.0030	**.0000**	n.s.	.0247	n.s.	n.s.	n.s.	.0574	.0694	n.s.	n.s.	n.s.	.0067	.0617	.0032	.0137	n.s.	.0363	n.s.	.0125	n.s.	n.s.	.0103	n.s.	.0791	n.s.	n.s.	.0131
02 MA Asp	.2299	*	**.0000**	.0006	.0553	n.s.	**.0000**	**.0000**	n.s.	.0188	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0038	.0200	.0008	.0048	n.s.	n.s.	.0825	.0004	n.s.	n.s.	.0739	.0093	.0199	.0412	.0328	n.s.
03 MA Hi	-.3596	**-.8411**	*	.0109	.0003	.0185	**.0000**	**.0000**	n.s.	.0937	n.s.	.0298	n.s.	n.s.	n.s.	n.s.	.0001	.0174	**.0000**	.0005	n.s.	n.s.	.0293	**.0000**	n.s.	n.s.	.0041	n.s.	.0137	n.s.	.0830	.0974
04 MA BA	.1136	-.3678	.2697	*	.0007	.0475	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0802	.0241	.0307	.0093	n.s.	n.s.	.0039	n.s.	n.s.	.0181	n.s.	n.s.	.0035	.0419	n.s.
05 MA Lig	-.3146	-.2046	.3778	.3596	*	.0929	n.s.	.0281	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**.0000**	.0827	.0001	.0008	n.s.	.0031	.0039	**.0000**	n.s.	n.s.	**.0000**	n.s.	.0037	n.s.	.0460	.0461
06 ME Inc	**.6296**	.1259	-.2436	.2066	-.1738	*	.0807	.0016	n.s.	n.s.	n.s.	n.s.	.0671	n.s.	n.s.	n.s.	.0107	n.s.	.0098	.0267	n.s.	n.s.	n.s.	.0278	.0965	n.s.	.0578	n.s.	.0245	n.s.	n.s.	.0358
07 ME Asp	.0977	**.6125**	**-.5679**	-.1332	-.1249	.1748	*	**.0000**	n.s.	.0016	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0152	.0938	.0158	.0233	n.s.	n.s.	.0290	.0136	.0694	n.s.	.0894	.0056	n.s.	.0357	.0543	n.s.
08 ME Hi	-.2291	**-.6475**	**.7164**	.1241	.2223	-.3146	**-.6680**	*	n.s.	.0186	n.s.	.0492	.0877	n.s.	n.s.	n.s.	**.0000**	.0451	.0002	.0016	n.s.	n.s.	.0017	.0003	n.s.	n.s.	.0041	n.s.	.0102	n.s.	n.s.	n.s.
09 ME Rou	-.0269	.1107	-.0498	-.0972	-.0910	.0514	.1124	-.0378	*	.0005	.0783	.0875	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0877	n.s.	n.s.	n.s.	n.s.	n.s.	.0044	n.s.	.0542	.0802	n.s.
10 ME Con	.1132	-.2440	.1713	.0522	-.1335	-.0042	-.3124	.2319	-.3459	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0101	n.s.	n.s.	n.s.	n.s.	n.s.	.0490	n.s.	.0691	n.s.	.0288
11 ME Smi	.0061	.0600	-.1483	.0279	.0793	.0347	-.0224	-.1496	-.1749	.0560	*	**.0000**	**.0000**	n.s.	n.s.	n.s.	n.s.	.0296	n.s.	n.s.	n.s.	.0799	n.s.	n.s.	.0355	n.s.	n.s.	n.s.	n.s.	.0106	.0007	n.s.
12 ME Sme	.1951	.1070	-.2212	.0026	-.0206	.1019	.0223	-.1931	-.1689	.0673	**.5782**	*	**.0000**	.0726	.0602	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0195	n.s.	n.s.	.0532	n.s.	n.s.	.0233	n.s.	.0112	.0018	n.s.
13 ME Sma	.1864	.0105	-.0926	.1135	.0429	.1835	.0033	-.1676	-.0654	.0814	**.4466**	**.6515**	*	.0331	.0256	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0023	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0086	.0035	n.s.
14 LitCC	-.0026	.0123	-.0241	.1456	.1310	-.0042	.0365	-.0677	-.0350	-.0593	.1271	.1780	.2111	*	**.0000**	**.0000**	n.s.	n.s.	n.s.	.0841	n.s.	n.s.	n.s.	.0057	.0226	n.s.	.0048	.0376	n.s.	n.s.	n.s.	n.s.
15 LitACD	-.0035	-.0203	.0043	.1569	.0940	.0042	.0050	-.0562	-.0483	-.0192	.1422	.1863	.2211	**.8754**	*	.0004	n.s.	n.s.	n.s.	.0425	n.s.	n.s.	n.s.	.0085	.0236	n.s.	.0144	n.s.	n.s.	n.s.	n.s.	n.s.
16 Mois	-.0121	-.0357	.0196	-.1292	-.0792	-.0853	-.0844	.0008	-.0691	.0982	.0570	.0551	.0657	**-.4081**	-.3503	*	n.s.	n.s.	n.s.	n.s.	.0031	.0621	n.s.	n.s.	.0043	n.s.	.0554	.0066	.0576	.0513	.0365	n.s.
17 LI	.2776	.2991	-.4001	-.1288	**-.4561**	.2553	.2386	**-.4195**	.0306	.0671	-.0348	-.0016	.0140	-.0124	-.0207	-.0131	*	**.0000**	**.0000**	**.0000**	.0350	.0335	.0016	**.0000**	.0004	.0003	**.0000**	n.s.	**.0000**	.0296	.0080	.0061
18 pH_{H2O}	-.1966	-.2468	.2483	.1841	.1812	-.1380	-.1692	.2016	-.1076	-.0822	.2212	.1628	.0784	.1003	.1243	.0898	**-.4947**	*	**.0000**	**.0000**	.0417	n.s.	n.s.	**.0000**	n.s.	n.s.	.0002	.0800	.0004	.0007	**.0000**	.0095
19 pH_{CaCl2}	-.3093	-.3542	**.4438**	.2364	.3946	-.2541	-.2427	.3680	-.0654	-.0979	.1091	.0458	-.0068	.1457	.1577	.0008	**-.6602**	**.7628**	*	**.0000**	n.s.	.0144	.0270	**.0000**	n.s.	.0848	**.0000**	n.s.	**.0000**	.0190	.0020	n.s.
20 Ca	-.2515	-.2902	.3552	.2205	.3382	-.2209	-.2221	.3078	-.0329	-.0965	.1430	.0666	.0378	.1702	.1999	-.0514	**-.6325**	**.7114**	**.8228**	*	n.s.	.0316	.0776	**.0000**	n.s.	.0708	**.0000**	n.s.	.0005	.0059	.0007	n.s.
21 Mg	-.1223	.0061	-.0400	-.2653	-.0060	-.1205	.0680	-.0318	-.0362	-.0421	.0769	.1011	.0493	-.1355	-.1438	.2882	-.2065	.2050	.1120	.1053	*	n.s.	n.s.	n.s.	**.0000**	.0153	n.s.	.0028	.0012	n.s.	.0447	n.s.
22 K	-.2136	-.0131	.0946	.0224	.2990	-.1590	.0861	.0922	.1678	-.2533	-.1727	-.2293	-.2990	.2146	.0694	-.1820	-.2081	.1287	.2451	.2098	.0106	*	.0358	.0056	n.s.	n.s.	**.0000**	.0017	.0051	.0024	.0322	.0288
23 Na	-.0172	.1786	-.2206	-.0810	-.2922	.1540	.2139	-.3061	.0790	.0124	.0455	-.0173	.0394	-.0744	-.0430	.0824	.3097	-.0423	-.2215	-.1722	.1118	-.2049	*	.0224	n.s.	n.s.	.0010	n.s.	.0020	n.s.	n.s.	n.s.
24 H^+	.2550	.3669	**-.4455**	-.2946	**-.4319**	.2192	.2418	-.3551	.0642	.0899	-.0603	.0189	.0049	-.2726	-.2594	.1478	**.5129**	**-.5268**	**-.7217**	**-.6882**	.0302	-.2702	.2229	*	n.s.	n.s.	**.0000**	n.s.	.0023	n.s.	.0465	n.s.
25 Al	-.1602	-.1595	.1133	-.0879	.1542	-.1657	-.1779	.1576	-.1086	.0487	.2075	.1898	.1331	-.2247	-.2231	.2784	-.3458	.1118	.0918	.0367	**.4318**	-.1265	-.0841	.0335	*	**.0000**	n.s.	**.0000**	.0003	.0001	**.0000**	n.s.
26 Fe	.0543	-.0907	.1040	.0819	.1619	.0243	-.1246	.1290	-.0008	.0925	.0992	.1480	.1454	-.1066	-.0934	.1568	-.3557	.1534	.1727	.1764	.2368	-.0866	.0261	-.0670	**.4394**	*	n.s.	.0219	n.s.	.0002	.0003	n.s.
27 Mn	-.2619	-.1839	.2905	.2412	**.5631**	-.1891	-.1664	.2800	.0148	-.1526	.0984	-.0173	.0016	.2776	.2412	-.1869	**-.4457**	.3760	**.5449**	**.5282**	-.0792	**.4237**	-.3208	**-.5984**	-.0498	-.0082	*	.0088	.0171	n.s.	n.s.	.0007
28 Zn	-.0603	.2675	-.1457	-.0724	.0622	.0117	.2713	-.1184	.2797	-.1939	-.1496	-.2227	-.1495	.2049	.1603	-.2653	.1311	-.1762	-.0547	-.0335	-.2914	.3061	.0122	-.0465	**-.4678**	-.2238	.2555	*	.0033	**.0000**	.0001	n.s.
29 Total N	-.1792	-.2396	.2496	.0276	.2939	-.2242	-.1320	.2506	-.0724	-.0965	.0884	.0715	-.0542	-.1157	-.1206	.1853	**-.5277**	.3591	**.4556**	.3420	.3159	.2735	-.3012	-.2980	.3518	.1535	.2327	-.2865	*	n.s.	n.s.	.0008
30 P-AL	-.0138	.2100	-.1474	-.2981	-.0792	-.0368	.2057	-.0563	.1892	-.1791	-.2521	-.2490	-.2579	.0628	.0050	-.1902	.2130	-.3422	-.2350	-.2686	-.0857	.2963	-.1380	.1167	-.3731	-.3691	.0498	**.4090**	-.0188	*	**.0000**	n.s.
31 P	.1336	.2197	-.1755	-.2077	-.1994	.0996	.1886	-.0866	.1720	-.1090	-.3357	-.3058	-.2868	.0240	-.0058	-.2042	.2598	**-.4296**	-.3100	-.3299	-.1960	.2091	-.0784	.1944	**-.4753**	-.3521	-.1094	.3936	-.0931	**-.7432**	*	n.s.
32 S	-.2533	-.0863	.1678	-.0276	.2019	-.2092	-.0189	.1298	.1514	-.2154	.0041	-.1076	-.1413	-.0264	-.0264	.0188	-.2687	.2609	.3276	.2931	.1331	.3976	-.0367	-.2751	.0024	-.0278	.3306	.1053	.3273	.1184	.0278	*

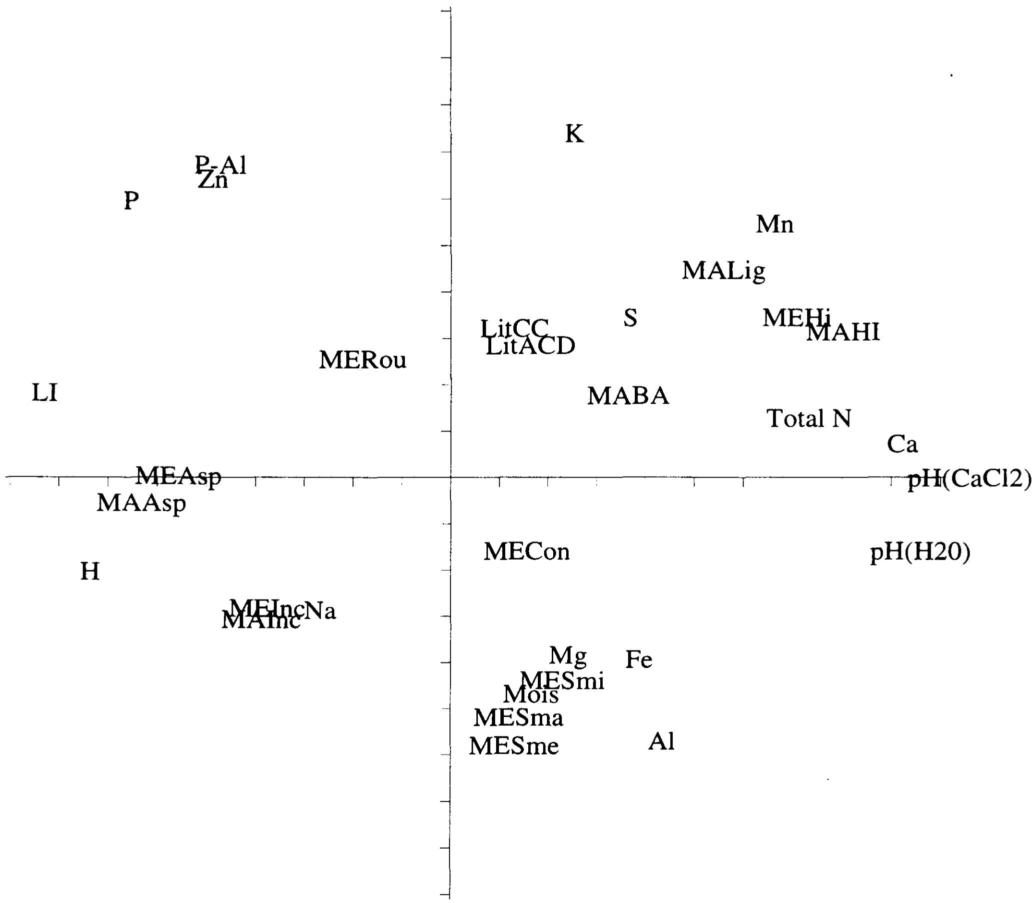


Fig. 526. Urvatnet: PCA ordination of 32 environmental variables (names abbreviated in accordance with Tab. 2), axes 1 (horizontal) and 2 (vertical). Positions of variables in the ordination give the head of variable vectors.

DCA and LNMDS ordination

Plot Nos 46, 47, 49 and 50 (with 16-26 species, area average 24.0 species) acted as moderate outliers in the DCA ordination (along DCA 2, see Fig. 527), and were removed prior to further analysis.

Both the DCA and LNMDS ordinations of the remaining 46 plots showed a gap along the first axes, slightly to the right of the centre, giving rise to two clusters (Figs 528-529). In DCA, the distribution of plots within each cluster was relatively even, while plots 27, 29 and 40 (with 12-14 species each, and mostly with few subplot occurrences) acted as outliers along LNMDS 2. The gradients were longer for LNMDS axes than for comparable DCA axes; for the second axis due to the outliers in the LNMDS ordination.

Tab. 25. Urvatnet: Eigenvalues and the fraction of variation explained for DCA axes 1-4.

	DCA 1	DCA 2	DCA 3	DCA 4
Eigenvalues	0.418	0.131	0.073	0.053
Fraction of variation explained	0.235	0.074	0.041	0.030

DCA 1 explained as much as 23.5% of the variation in vegetation (Tab. 25), while only 7.4%, 31.5% of the variation explained by DCA 1, was explained by DCA 2. The reduction in explained fraction of variation from DCA 2 to DCA 3 was 55.4% (4.1% was explained by DCA 3). The eigenvalues of DCA 3 and DCA 4 were low (0.073 and 0.053, respectively).

Correlations between DCA and LNMDS ordination axes and between ordination axes and environmental variables

The correlation between DCA 1 and LNMDS 1 was strong (τ = 0.650; Tab. 26). LNMDS 2 was strongly negatively correlated with DCA 4 (τ = -0.518), but only weakly correlated with DCA 2 and uncorrelated with DCA 3. The variables most strongly correlated with DCA 1 were strongly correlated also with LNMDS 1, but with lower correlation coefficients. Varia-

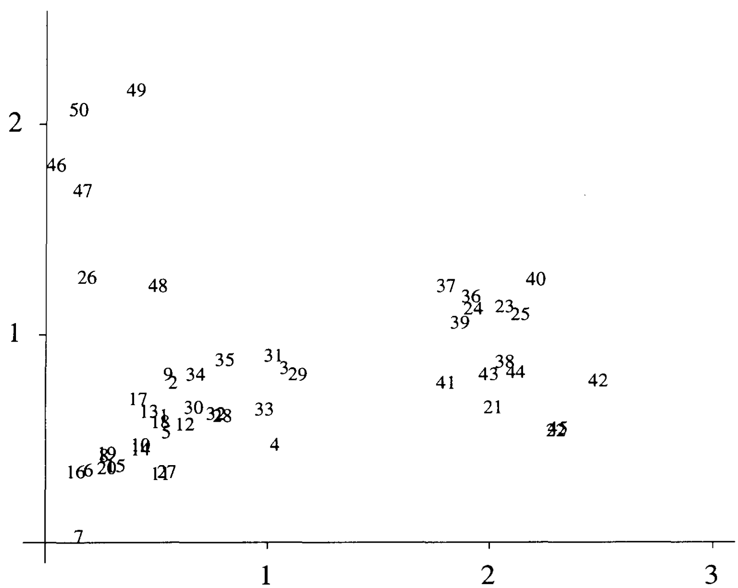
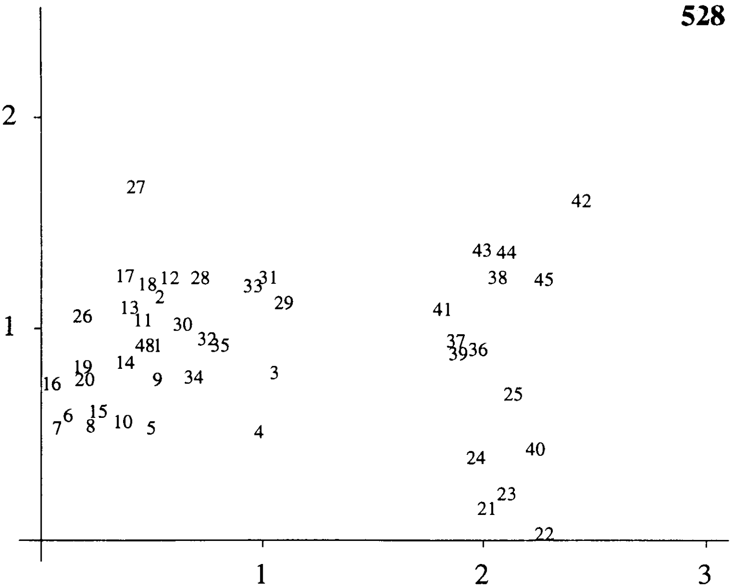
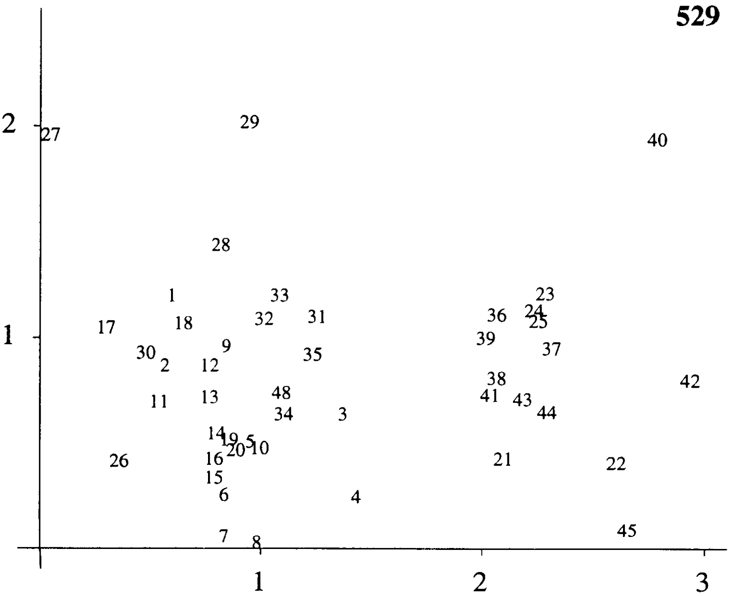


Fig. 527. Urvatnet: DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Meso plot numbers are plotted onto the sample plot positions. Scaling of axes in S.D. units.





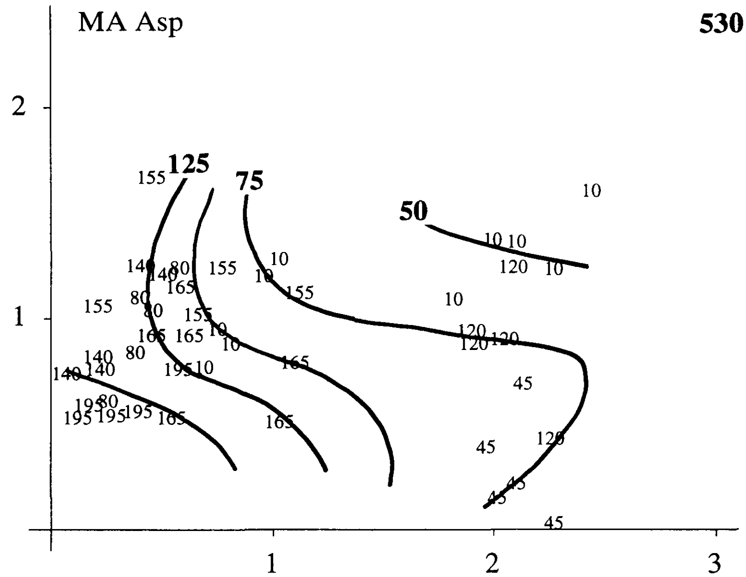
Figs 528-529. Urvatnet: ordinations of 46 meso plots (plot Nos 46, 47, 49 and 50 omitted), axes 1 (horizontal) and 2 (vertical). Meso plot numbers are plotted onto the sample plot positions. Fig. 528. DCA ordination. Scaling of axes in S.D. units. Fig. 529. LNMDS ordination. Axes linearly rescaled in S.D. units.

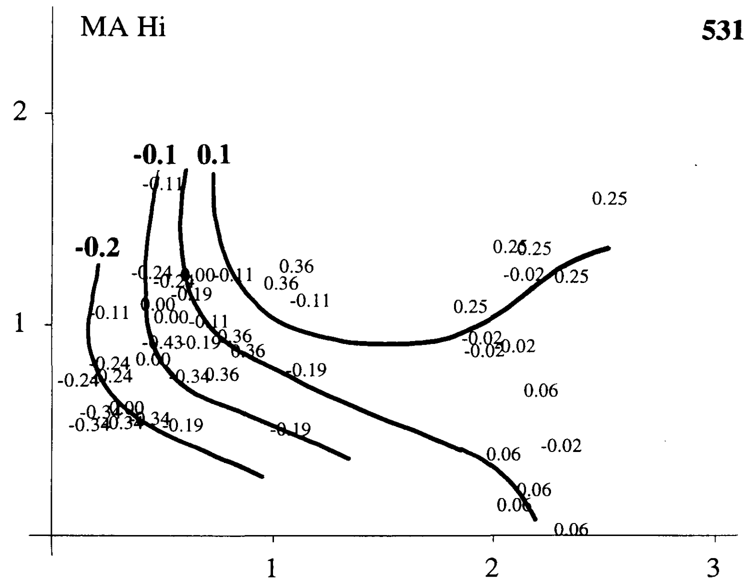
Tab. 26. Urvatnet: Kendall's nonparametric correlation coefficient τ between DCA and LNMDS axes, and between 32 environmental variables in the 46 meso sample plots and sample plot positions with respect to DCA and LNMDS axes, with significance probabilities. Correlations significant at level P < 0.0001 in bold face. n.s. - significance probability > 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 2.

Variable	DCA 1		DCA 2		DCA 3		DCA 4		LNMDS 1		LNMDS 2	
	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P
LNMDS 1	**.6502**	**.0000**	-.1691	.0975	.2928	.0041	.0570	n.s.				
LNMDS 2	.2649	.0095	.2649	.0095	.1005	n.s.	**-.5181**	**.0000**				
01 MA Inc	-.2398	.0251	.0984	n.s.	-.2521	.0185	.0225	n.s.	-.0820	n.s.	-.0851	n.s.
02 MA Asp	-.4162	.0001	-.1922	.0733	-.0545	n.s.	-.1367	n.s.	-.3278	.0022	-.1193	n.s.
03 MA Hi	**.4641**	**.0000**	.1628	n.s.	.0576	n.s.	.1082	n.s.	.2942	.0055	.1517	n.s.
04 MA BA	.3382	.0016	.3320	.0019	.0697	n.s.	-.1312	n.s.	.1783	.0958	.2799	.0090
05 MA Lig	.3873	.0003	.0859	n.s.	.1871	.0778	-.3488	.0010	.2700	.0109	.3703	.0005
06 ME Inc	-.1871	.0737	.1711	n.s.	-.0935	n.s.	.0816	n.s.	-.0836	n.s.	-.0109	n.s.
07 ME Asp	-.3133	.0022	-.0844	n.s.	.0087	n.s.	-.0941	n.s.	-.2609	.0108	-.1300	n.s.
08 ME Hi	.3643	.0004	.1169	n.s.	-.0087	n.s.	.0918	n.s.	.2850	.0052	.0889	n.s.
09 ME Rou	-.1801	.0796	.1315	n.s.	-.1918	.0619	-.0243	n.s.	-.2444	.0174	-.0214	n.s.
10 ME Con	.0430	n.s.	.0646	n.s.	.0411	n.s.	.1565	n.s.	.0763	n.s.	-.0205	n.s.
11 ME Smi	.2280	.0271	-.3317	.0013	.2123	.0396	-.1791	.0826	.2534	.0140	.1508	n.s.
12 ME Sme	.2113	.0397	-.2483	.0157	.2210	.0315	-.1860	.0703	.2814	.0062	.1091	n.s.
13 ME Sma	.1448	n.s.	-.1331	n.s.	.1020	n.s.	-.2051	.0456	.1876	.0675	.1945	.0581
14 LitCC	.1627	n.s.	.2548	.0135	.1980	.0551	**-.4273**	**.0000**	.0039	n.s.	**.5814**	**.0000**
15 LitACD	.1784	.0839	.2391	.0205	.2058	.0461	-.3959	.0001	.0314	n.s.	**.5540**	**.0000**
16 Mois	-.0918	n.s.	-.3623	.0004	-.0628	n.s.	.2348	.0214	.1150	n.s.	-.3886	.0001
17 LI	**-.6017**	**.0000**	-.0688	n.s.	.0533	n.s.	.1347	n.s.	**-.5436**	**.0000**	-.1493	n.s.
18 pH_{H2O}	**.6247**	**.0000**	-.0592	n.s.	.2116	.0443	-.0251	n.s.	**.6126**	**.0000**	.0803	n.s.
19 pH_{CaCl2}	**.7162**	**.0000**	.0436	n.s.	.1746	.0943	-.1051	n.s.	**.6011**	**.0000**	.1935	.0638
20 Ca	**.6676**	**.0000**	.0841	n.s.	.1633	n.s.	-.1420	n.s.	**.5652**	**.0000**	.2030	.0468
21 Mg	.0802	n.s.	-.2599	.0109	.1324	n.s.	.1594	n.s.	.2560	.0121	-.2610	.0106
22 K	.0280	n.s.	.1517	n.s.	.0609	n.s.	-.1594	n.s.	.0029	n.s.	.1508	n.s.
23 Na	-.1362	n.s.	-.1053	n.s.	.0937	n.s.	.2792	.0062	-.0802	n.s.	-.2513	.0138
24 H^+	**-.6155**	**.0000**	-.1865	.0676	-.1614	n.s.	.1362	n.s.	**-.4628**	**.0000**	-.3209	.0017
25 Al	.1865	.0686	-.2232	.0287	.1111	n.s.	.0531	n.s.	.3082	.0025	-.1837	.0720
26 Fe	.2146	.0356	-.0213	n.s.	.0019	n.s.	-.0077	n.s.	.2765	.0068	-.0938	n.s.
27 Mn	.3874	.0001	.1246	n.s.	.1652	n.s.	-.2986	.0034	.2850	.0052	**.4292**	**.0000**
28 Zn	-.2193	.0316	.1942	.0570	-.0396	n.s.	-.2483	.0112	-.3295	.0012	.2339	.0219
29 Total N	.3527	.0005	-.1923	.0595	-.0010	n.s.	-.0512	n.s.	.3894	.0001	-.0657	n.s.
30 P-AL	**-.4184**	**.0000**	.0106	n.s.	-.2155	.0347	-.0686	n.s.	**-.4164**	**.0000**	.0909	n.s.
31 P	**-.4273**	**.0000**	.1527	n.s.	-.2977	.0035	-.0097	n.s.	**-.4679**	**.0000**	.0242	n.s.
32 S	.2019	.0478	-.1034	n.s.	.0106	n.s.	-.0203	n.s.	.2155	.0347	.0232	n.s.

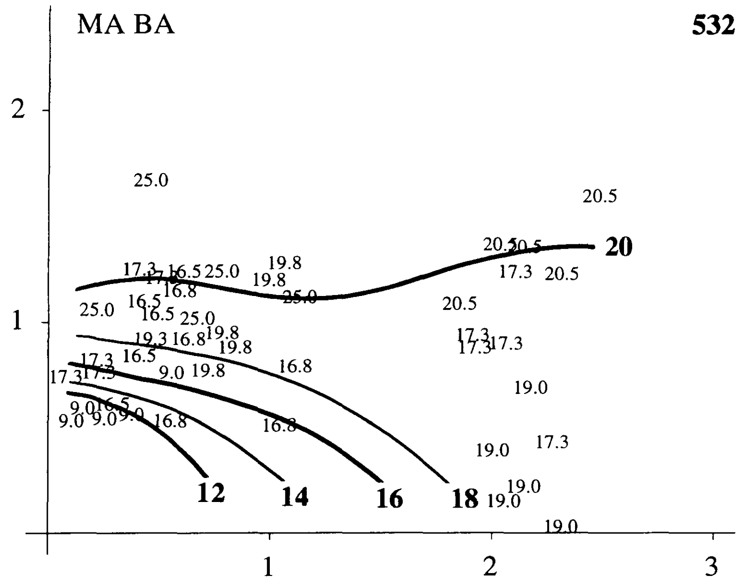
bles strongly correlated with LNMDS 2 were also correlated with DCA 4 (with opposite sign and lower τ), partly also with DCA 2.

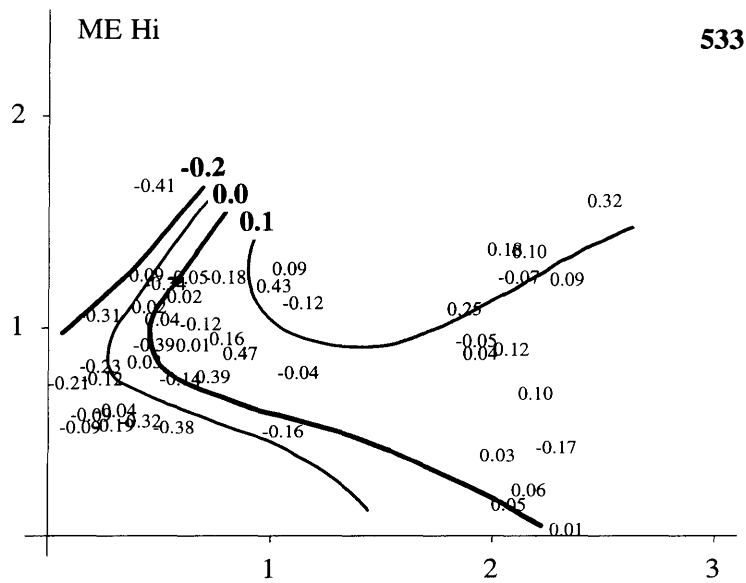
The variables most strongly correlated with DCA 1 were pH (τ = 0.716, Fig. 536) and the concentration of Ca (with τ = 0.668, Fig. 537), both positively correlated, and the concen-



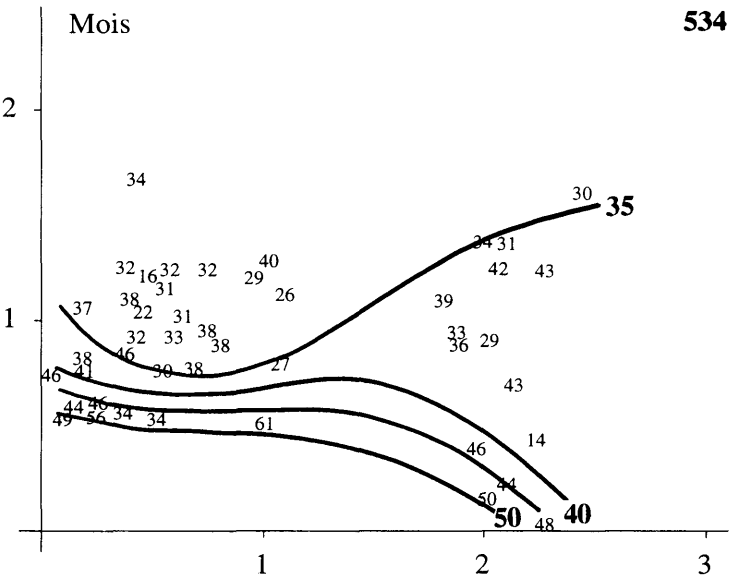


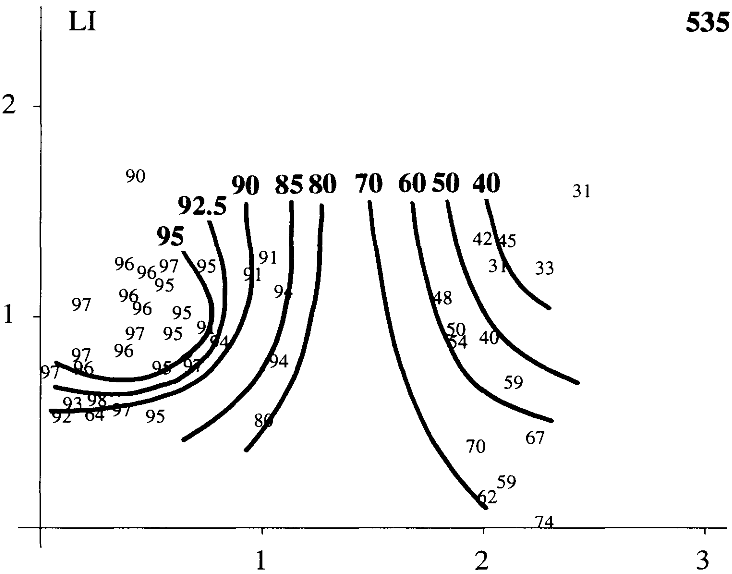
Figs 530-531. Urvatnet: isolines for environmental variables in the DCA ordination of 46 meso plots (plots 46, 47, 49 and 50 omitted), axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 530. MA Asp ($R^2 = 0.447$). Fig. 531. MA Hi ($R^2 = 0.476$). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.



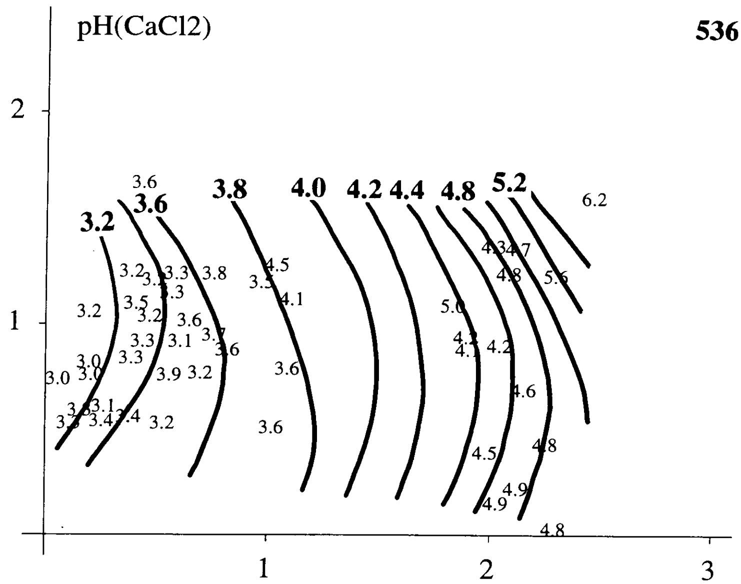


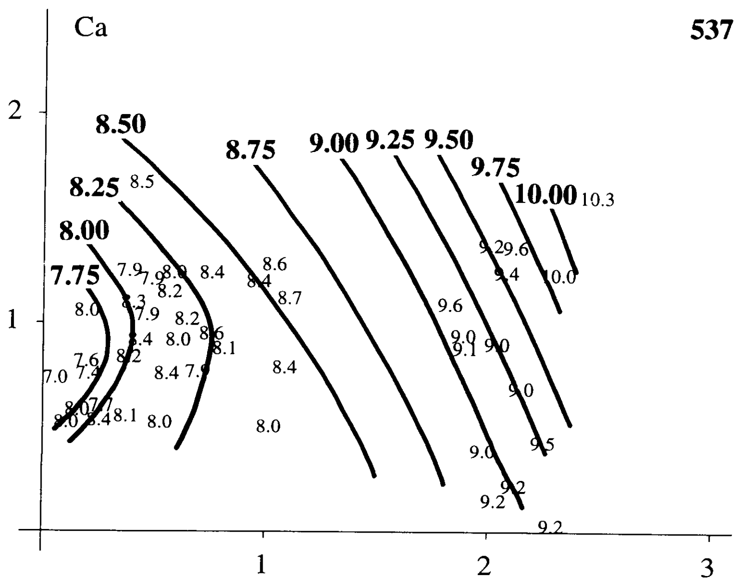
Figs 532-533. Urvatnet: isolines for environmental variables in the DCA ordination of 46 meso plots (plots 46, 47, 49 and 50 omitted), axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 532. MA BA (R^2 = 0.540). Fig. 533. ME Hi (R^2 = 0.414). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.





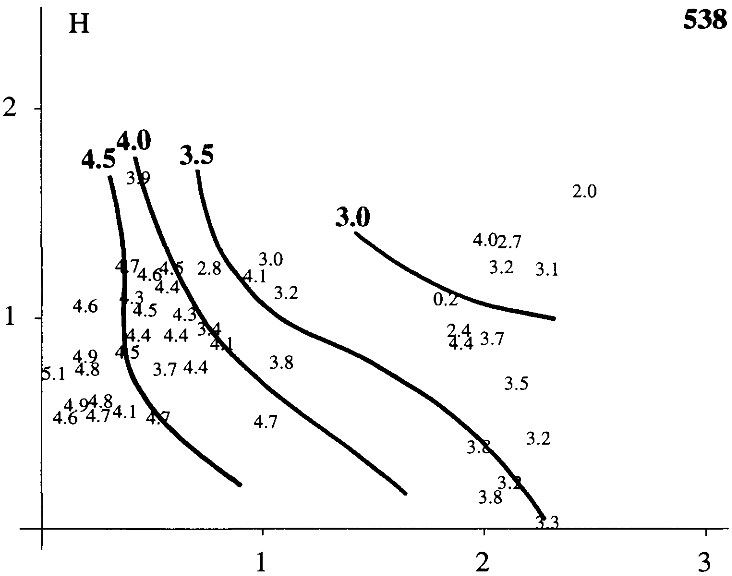
Figs 534-535. Urvatnet: isolines for environmental variables in the DCA ordination of 46 meso plots (plots 46, 47, 49 and 50 omitted), axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 534. Mois (R^2 = 0.499). Fig. 535. LI (R^2 = 0.936). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.





Figs 536-537. Urvatnet: isolines for environmental variables in the DCA ordination of 46 meso plots (plots 46, 47, 49 and 50 omitted), axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 536. pH_{CaCl2} (R^2 = 0.890). Fig. 537. Ca (R^2 = 0.882). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.

538



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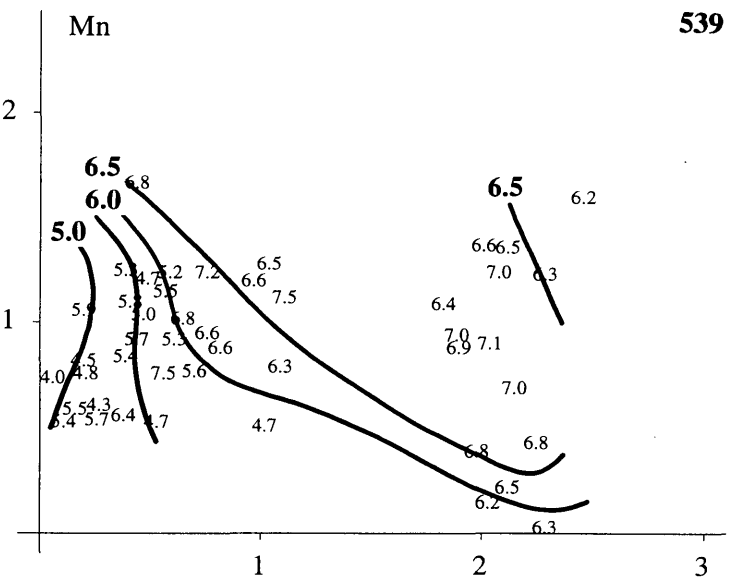
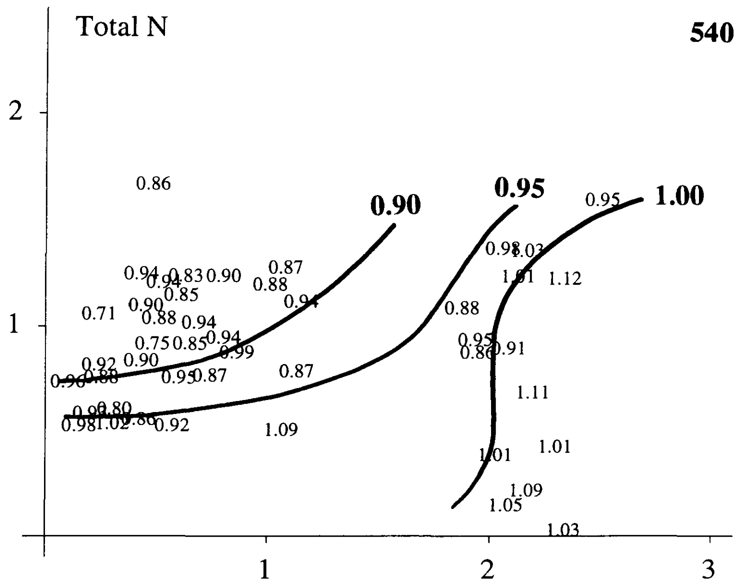
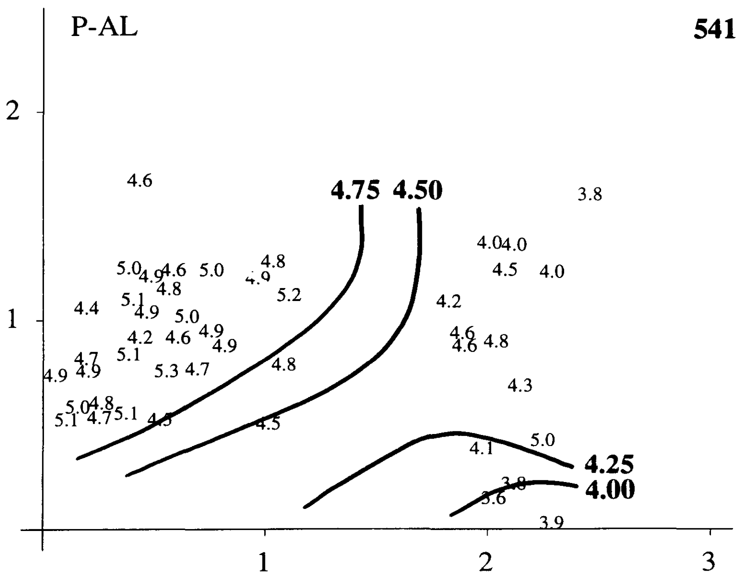


Figs 538-539. Urvatnet: isolines for environmental variables in the DCA ordination of 46 meso plots (plots 46, 47, 49 and 50 omitted), axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 538. H^+ (R^2 = 0.566). Fig. 539. Mn (R^2 = 0.596). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.





Figs 540-541. Urvatnet: isolines for environmental variables in the DCA ordination of 46 meso plots (plots 46, 47, 49 and 50 omitted), axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 540. Total N (R^2 = 0.476). Fig. 541. P-AL (R^2 = 0.739). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.

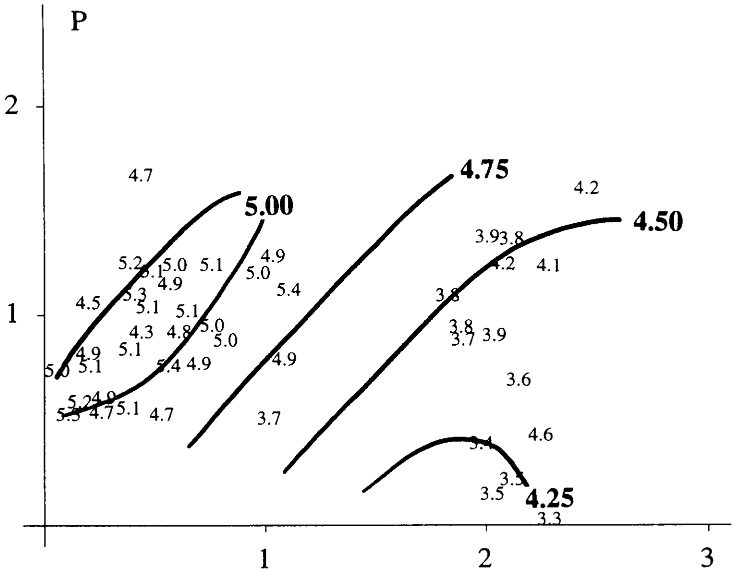


Fig. 542. Urvatnet: isolines for P in the DCA ordination of 46 meso plots (plots 46, 47, 49 and 50 omitted), axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. R^2 (the coefficient of determination between original and smoothened values as interpolated from the isolines) = 0.820. Names of environmental variables in accordance with Tab. 2.

tration of H^+ (τ = -0.616, Fig. 538) and loss on ignition (τ = -0.602, Fig. 537), both negatively correlated with DCA 1. Other more or less strongly positively correlated variables were the heat indices (Figs 531, 533), macro plot basal area, the macro plot light index, and concentrations of Mn (Fig. 539) and total N (Fig. 540). Aspect unfavourability (Fig. 530) and concentrations of P-AL (Fig. 541) and P (Fig. 542), were negatively correlated with DCA 1.

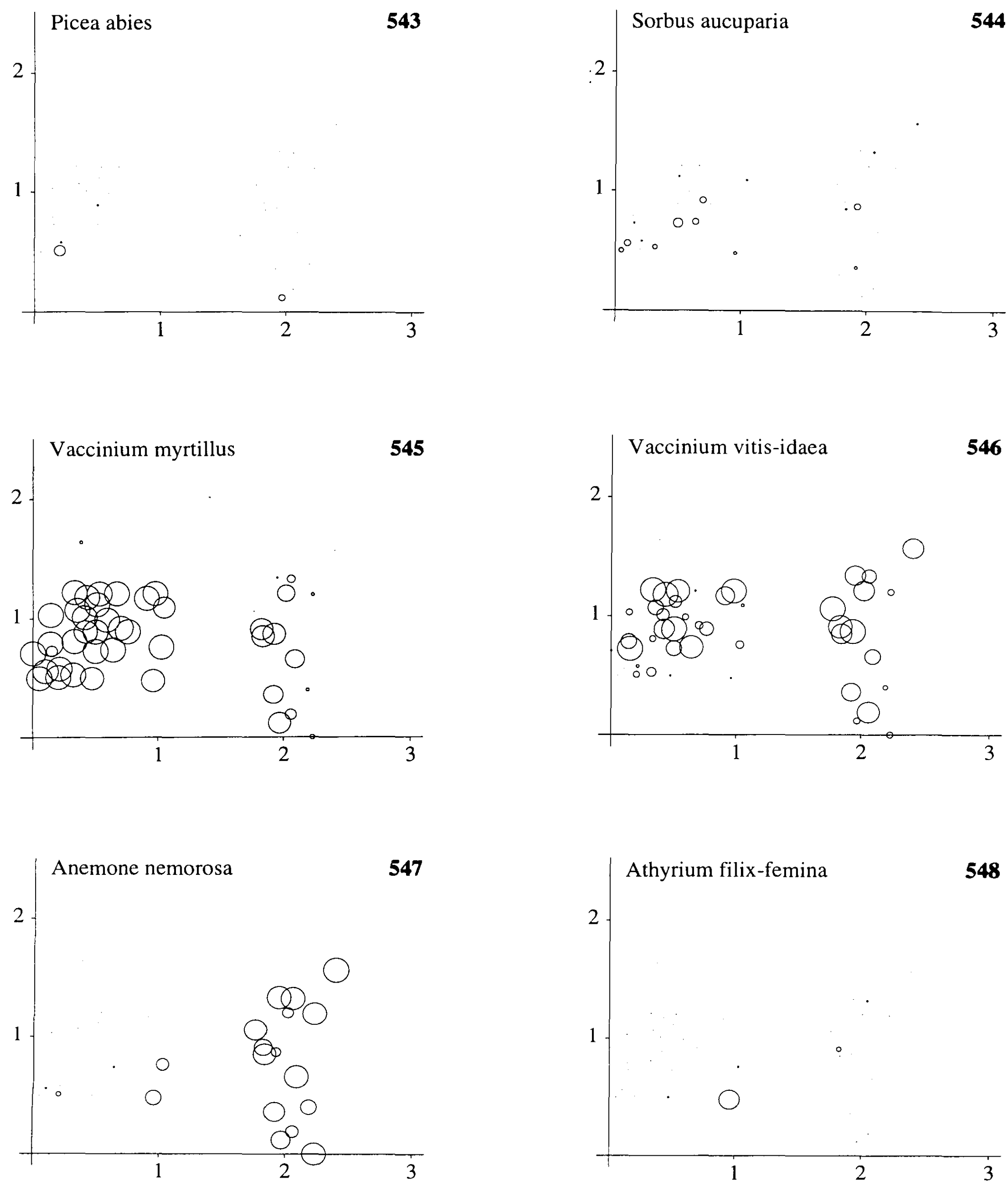
The variables most strongly correlated with DCA 2 were soil moisture (Fig. 534) and minimum soil depth, both with negative correlations, and macro plot basal area (Fig. 533) which was positively correlated with this axis.

The litter indices, the concentration of Mn and the macro plot light index were correlated with LNMDS 2 (strongly) and DCA 4 (less strongly).

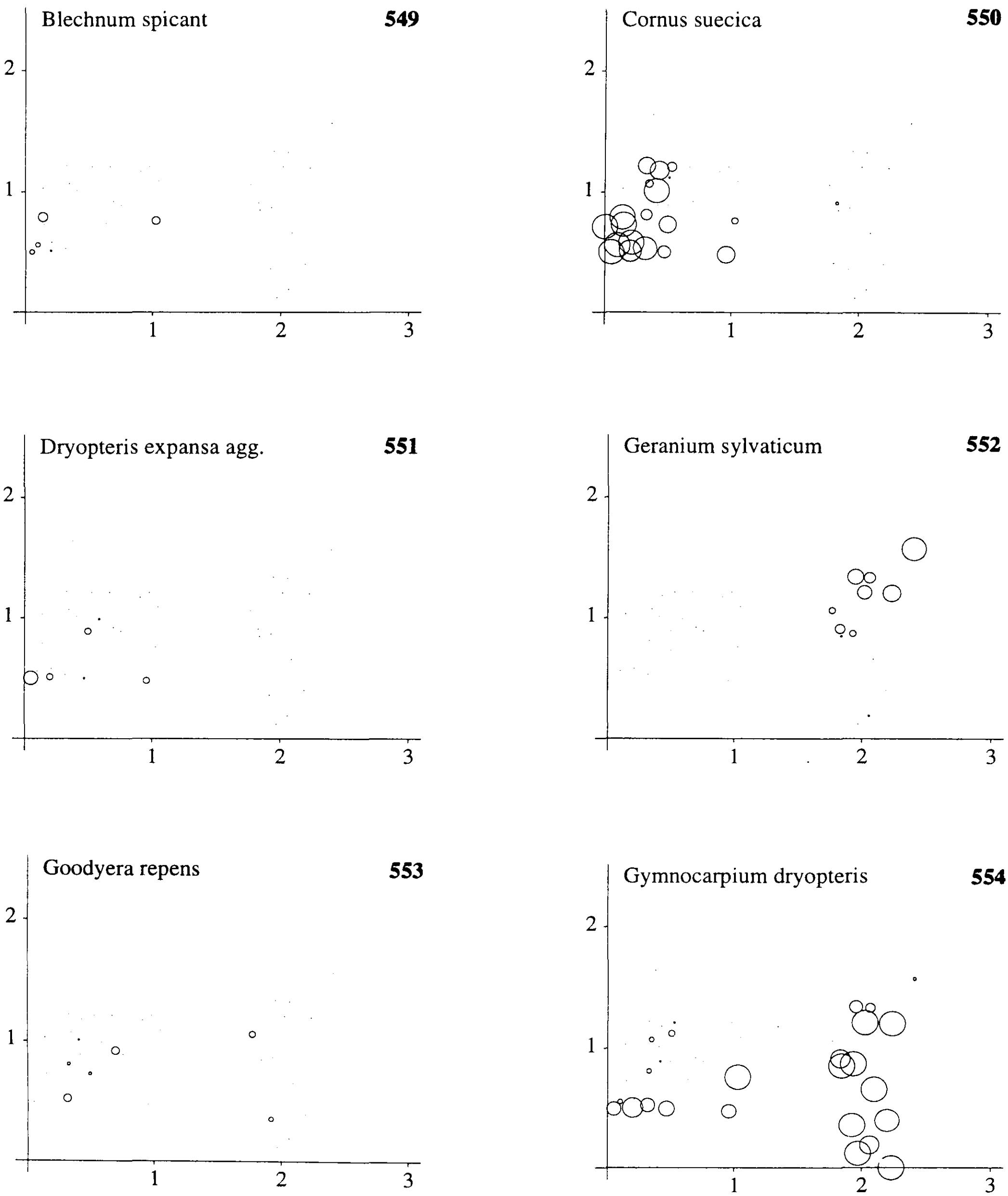
The distribution of species abundance in the DCA ordination

Sixty-two out of a total of 104 species occurred in 5 or more of the 46 meso plots (Figs 543-604).

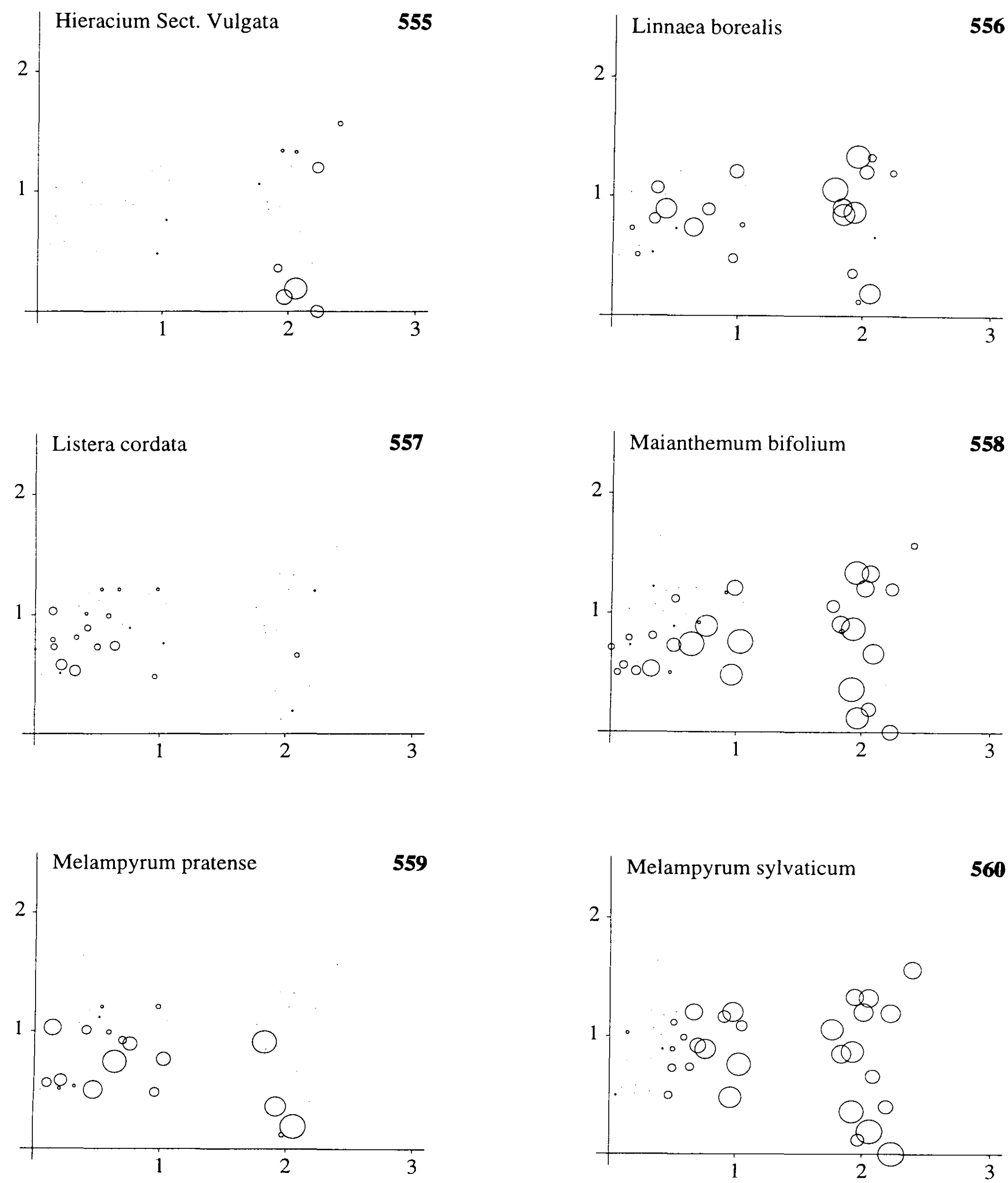
Vaccinium myrtillus (Fig. 545), *Deschampsia flexuosa* (Fig. 573) and *Hylocomium splendens* (Fig. 581), typical examples of species with wide ecological amplitude, were abundant in most meso plots.



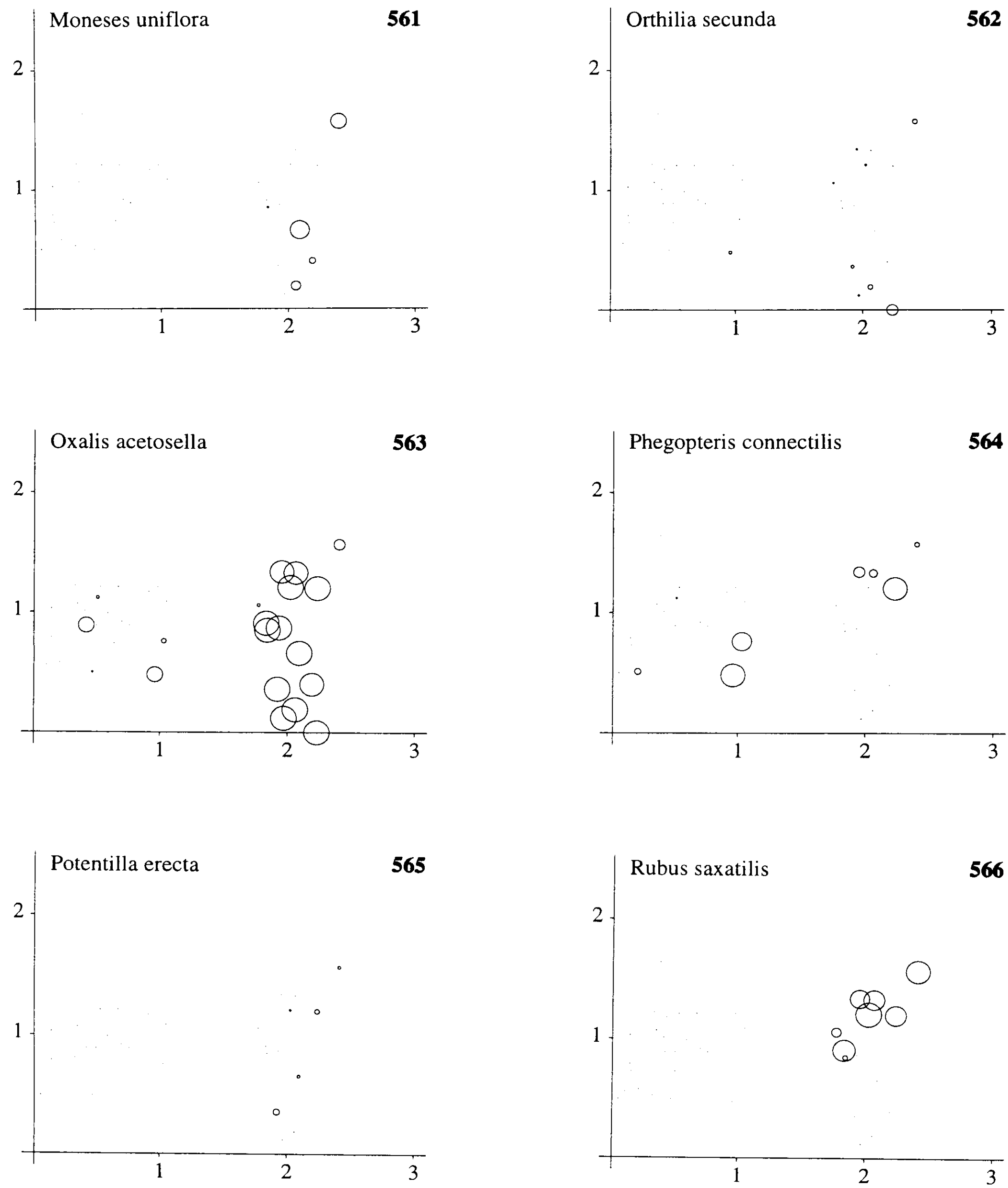
Figs 543-548. Urvatnet: distributions of species abundances in the DCA ordination of 46 meso plots (plot Nos 46, 47, 49 and 50 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 543. *Picea abies*. Fig. 544. *Sorbus aucuparia*. Fig. 545. *Vaccinium myrtillus*. Fig. 546. *Vaccinium vitis-idaea*. Fig. 547. *Anemone nemorosa*. Fig. 548. *Athyrium filix-femina*.



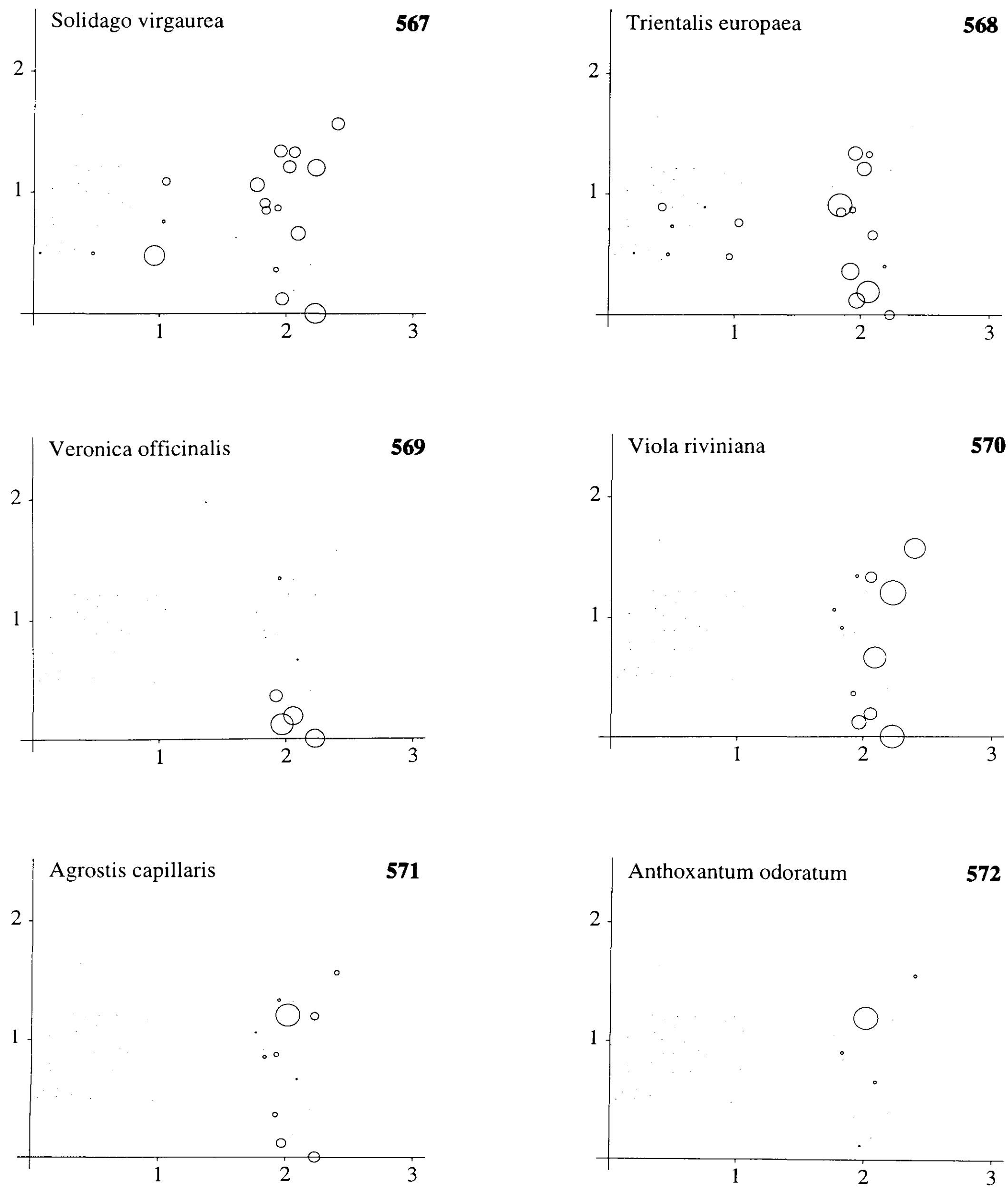
Figs 549-554. Urvatnet: distributions of species abundances in the DCA ordination of 46 meso plots (plot Nos 46, 47, 49 and 50 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 549. *Blechnum spicant*. Fig. 550. *Cornus suecica*. Fig. 551. *Dryopteris expansa* agg. Fig. 552. *Geranium sylvaticum*. Fig. 553. *Goodyera repens*. Fig. 554. *Gymnocarpium dryopteris*.



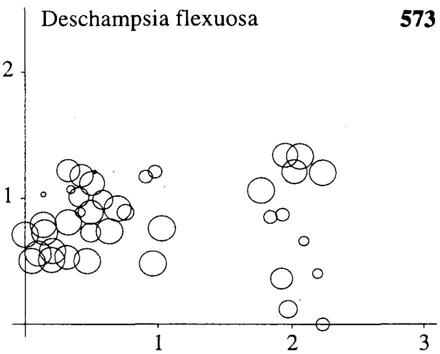
Figs 555-560. Urvatnet: distributions of species abundances in the DCA ordination of 46 meso plots (plot Nos 46, 47, 49 and 50 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 555. *Hieracium Sect. Vulgata*. Fig. 556. *Linnaea borealis*. Fig. 557. *Listera cordata*. Fig. 558. *Maianthemum bifolium*. Fig. 559. *Melampyrum pratense*. Fig. 560. *Melampyrum sylvaticum*.

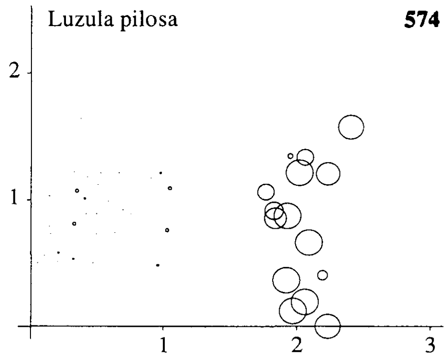


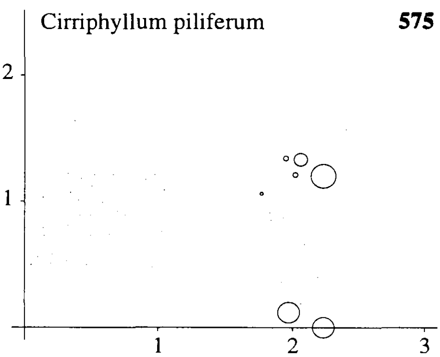
Figs 561-566. Urvatnet: distributions of species abundances in the DCA ordination of 46 meso plots (plot Nos 46, 47, 49 and 50 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 561. *Moneses uniflora*. Fig. 562. *Orthilia secunda*. Fig. 563. *Oxalis acetosella*. Fig. 564. *Phegopteris connectilis*. Fig. 565. *Potentilla erecta*. Fig. 566. *Rubus saxatilis*.

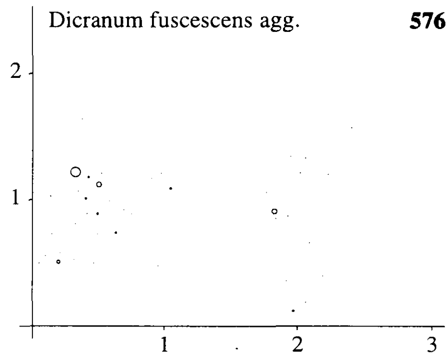


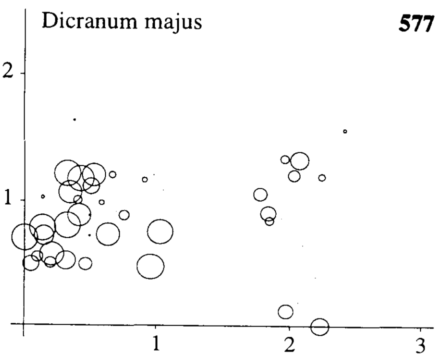
Figs 567-572. Urvatnet: distributions of species abundances in the DCA ordination of 46 meso plots (plot Nos 46, 47, 49 and 50 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 567. *Solidago virgaurea*. Fig. 568. *Trientalis europaea*. Fig. 569. *Veronica officinalis*. Fig. 570. *Viola riviniana*. Fig. 571. *Agrostis capillaris*. Fig. 572. *Anthoxanthum odoratum*.

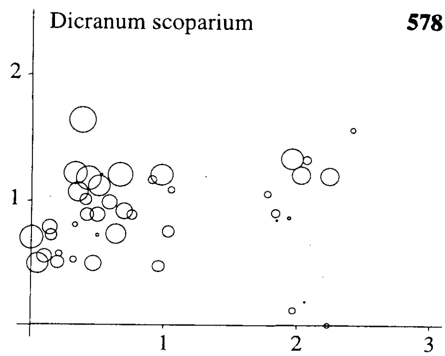




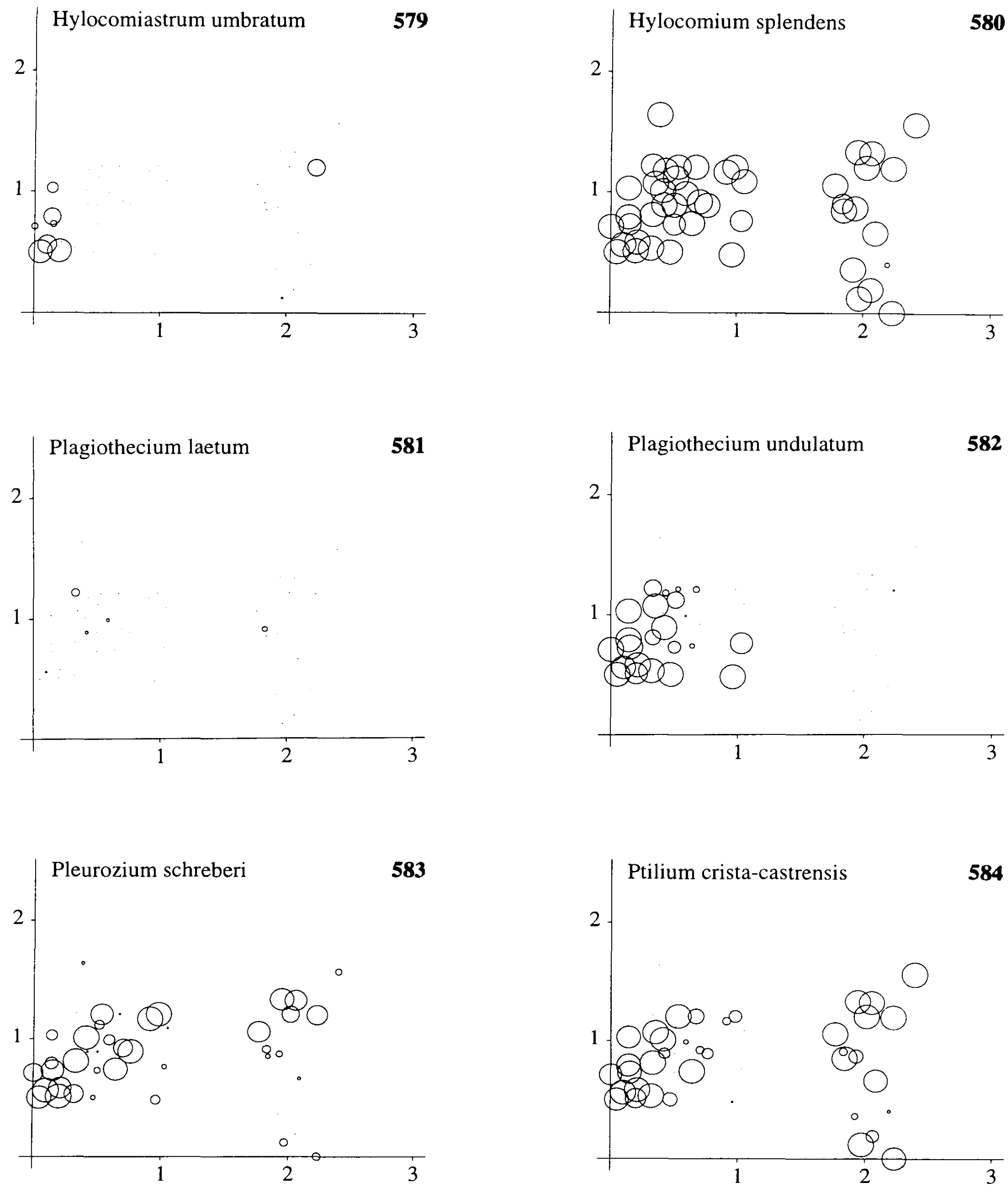




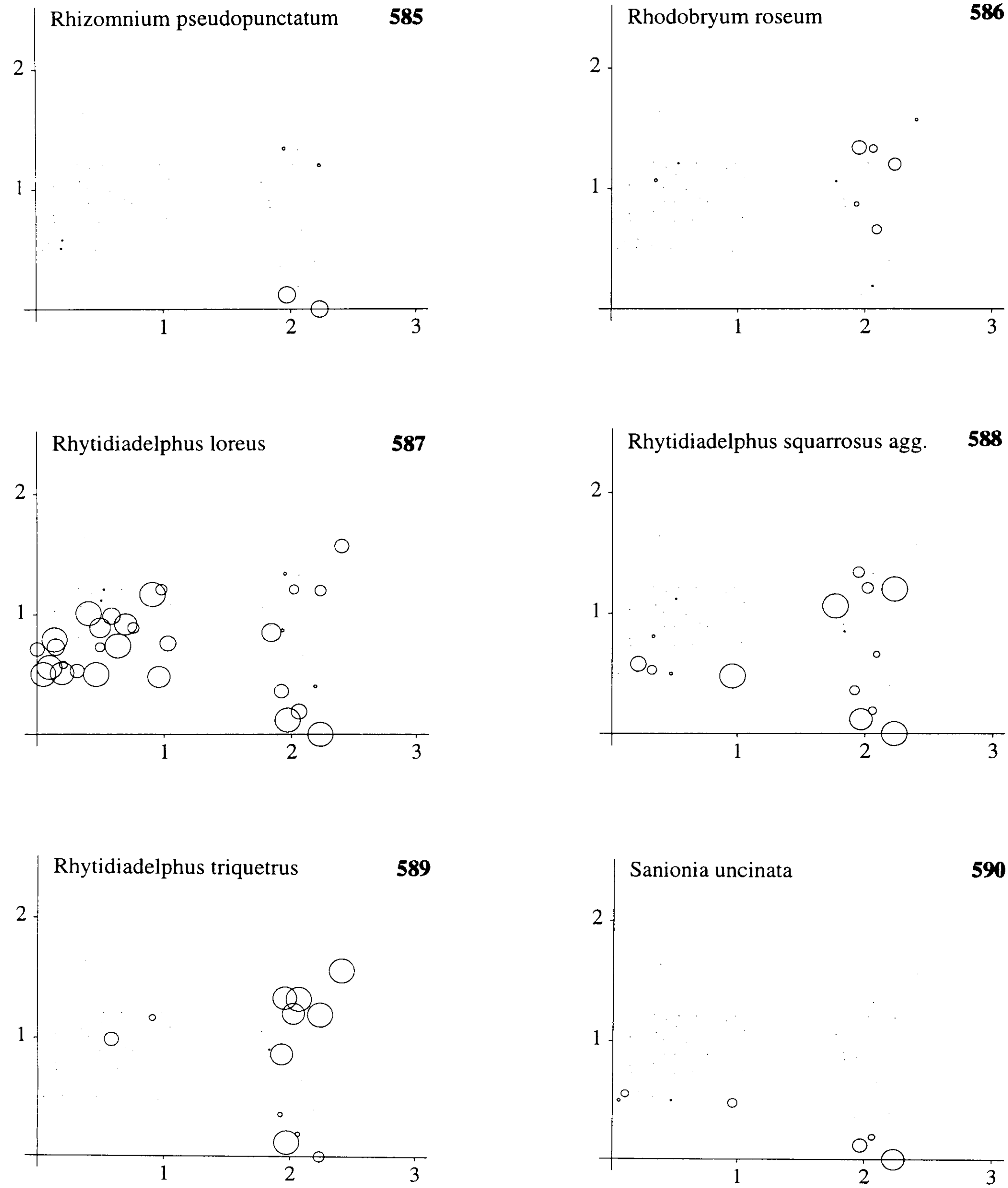




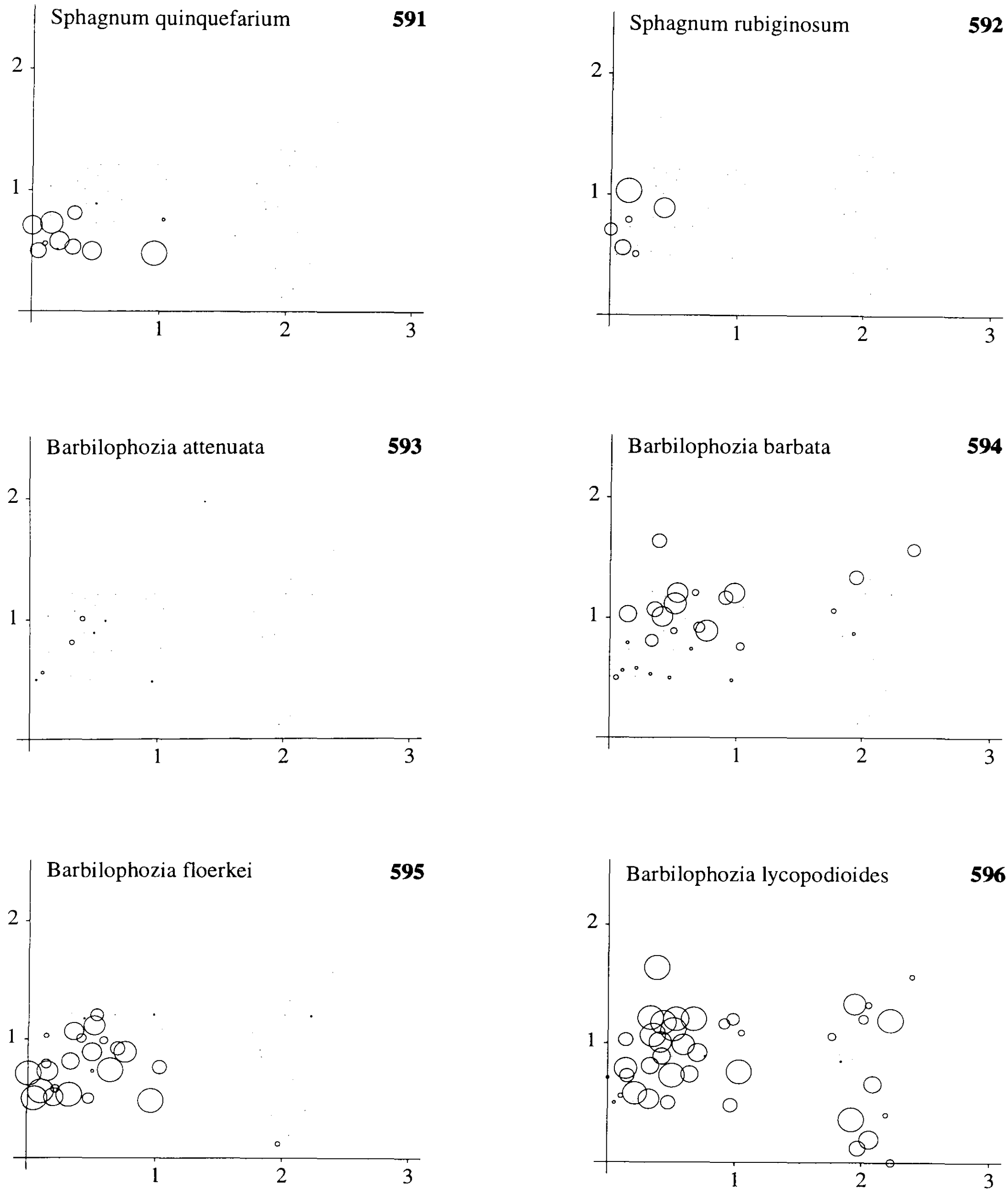
Figs 573-578. Urvatnet: distributions of species abundances in the DCA ordination of 46 meso plots (plot Nos 46, 47, 49 and 50 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 573. *Deschampsia flexuosa*. Fig. 574. *Luzula pilosa*. Fig. 575. *Cirriphyllum piliferum*. Fig. 576. *Dicranum fuscescens* agg. Fig. 577. *Dicranum majus*. Fig. 578. *Dicranum scoparium*.



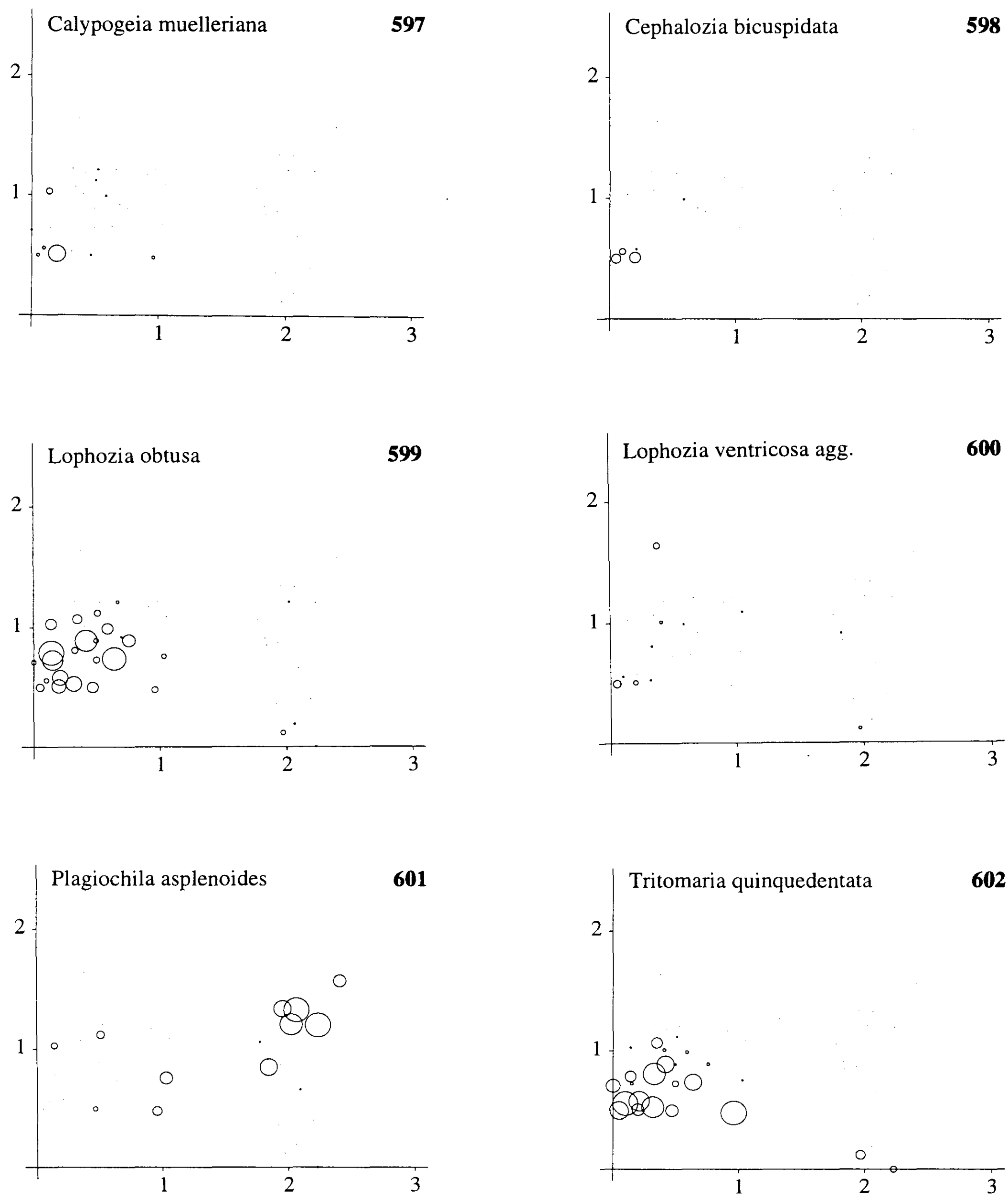
Figs 579-584. Urvatnet: distributions of species abundances in the DCA ordination of 46 meso plots (plot Nos 46, 47, 49 and 50 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 579. *Hylocomiastrum umbratum*. Fig. 580. *Hylocomium splendens*. Fig. 581. *Plagiothecium laetum*. Fig. 582. *Plagiothecium undulatum*. Fig. 583. *Pleurozium schreberi*. Fig. 584. *Ptilium crista-castrensis*.



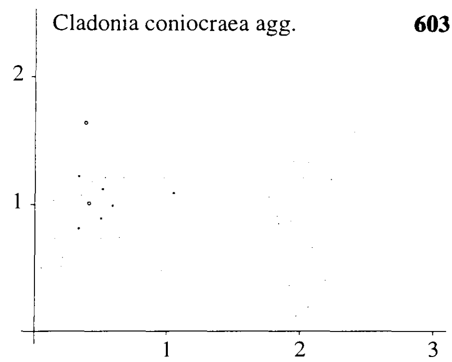
Figs 585-590. Urvatnet: distributions of species abundances in the DCA ordination of 46 meso plots (plot Nos 46, 47, 49 and 50 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 585. *Rhizomnium pseudopunctatum*. Fig. 586. *Rhodobryum roseum*. Fig. 587. *Rhytidiadelphus loreus*. Fig. 588. *Rhytidiadelphus squarrosus* agg. Fig. 589. *Rhytidiadelphus triquetrus*. Fig. 590. *Sanionia uncinata*.

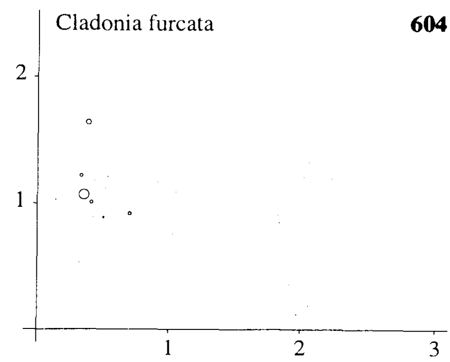


Figs 591-596. Urvatnet: distributions of species abundances in the DCA ordination of 46 meso plots (plot Nos 46, 47, 49 and 50 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 591. *Sphagnum quinquefarium*. Fig. 592. *Sphagnum rubiginosum*. Fig. 593. *Barbilophozia attenuata*. Fig. 594. *Barbilophozia barbata*. Fig. 595. *Barbilophozia floerkei*. Fig. 596. *Barbilophozia lycopodioides*.



Figs 597-602. Urvatnet: distributions of species abundances in the DCA ordination of 46 meso plots (plot Nos 46, 47, 49 and 50 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 597. *Calypogeia muelleriana*. Fig. 598. *Cephalozia bicuspidata*. Fig. 599. *Lophozia obtusa*. Fig. 600. *Lophozia ventricosa* agg. Fig. 601. *Plagiochila asplenoides*. Fig. 602. *Tritomaria quinquedentata*.





Figs 603-604. Urvatnet: distributions of species abundances in the DCA ordination of 46 meso plots (plot Nos 46, 47, 49 and 50 omitted), axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 603. *Cladonia coniocraea* agg. Fig. 604. *Cladonia furcata*.

Several species were restricted to one of the two clusters in the ordination. Examples of species restricted to the left-hand cluster (low DCA 1 scores) of plots, from more or less open sites, with unfavourable aspects, low pH and low nutrient content, were *Cornus suecica* (Fig. 550), *Plagiothecium undulatum* (Fig. 583), *Barbilophozia floerkei* (Fig. 595), *Lophozia obtusa* (Fig. 599) and *Tritomaria quinquedentata* (Fig. 602).

Sphagnum quinquefarium (Fig. 591) was restricted to the lower left part of the ordination, to sites with high soil moisture content. No species showed preference for dry sites with low pH and low nutrient content (the upper left in the ordination), but *Barbilophozia barbata* (Fig. 594) preferred dry plots (high DCA 2 scores), regardless of pH and nutrient content.

Examples of species with restriction to plots with high DCA 1 scores (more dense tree stands, on sites with favourable aspects, high pH and high content of nutrients) were *Moneses uniflora* (Fig. 561), *Viola riviniana* (Fig. 570), *Agrostis capillaris* (Fig. 571), *Cirriphyllum piliferum* (Fig. 575) and *Rhodobryum roseum* (Fig. 587). Moist sites (lower right part of the ordination diagram) were preferred by *Veronica officinalis* (Fig. 569); dry sites (upper right) by *Geranium sylvaticum* (Fig. 552) and *Rubus saxatilis* (Fig. 566).

ØYENSKAVELEN

Correlations between environmental variables

One group of correlated variables contained concentrations of Ca, Mg and P with pairwise positive correlations, and pH and concentrations of Al, Fe, S, H^+ and Mg, each negatively correlated at least with one of the concentrations of Ca, Mg and P (Tab. 27, Fig. 605). pH was negatively correlated with the concentration of Mg and P, and positively correlated with Al.

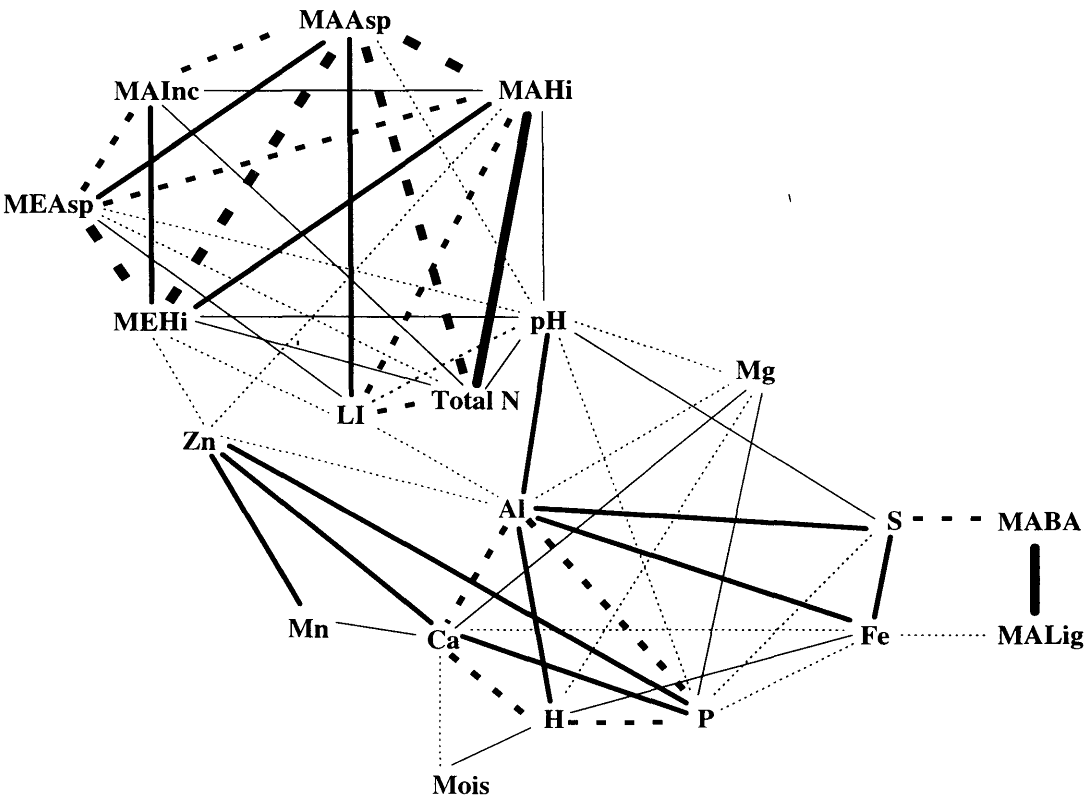


Fig. 605. Øyenskavelen: plexus diagram visualizing Kendall's τ between pairs of environmental variables. Significance probabilities for τ are indicated by lines with different thickness (in order of decreasing thickness): $|\tau| \geq 0.60$, $0.45 \leq |\tau| < 0.60$, $0.35 \leq |\tau| < 0.45$. Continuous lines refer to positive correlations, broken lines to negative.

No other strong correlations were found between pH and concentrations of other cations. Subgroups of strongly correlated variables were made up by (1) concentrations of Al, Ca, H^+ and P, and (2) concentrations of Al, Fe and S. The strongly correlated variables Mn and Zn were associated with the group via strongly positive pairwise correlations with the concentration of Ca and negative correlations with the concentration of Al. Soil moisture was negatively correlated with the concentration of Ca and positively correlated with the concentration of H^+. Macro plot basal area and the macro plot light index were strongly correlated, and connected to the group by negative correlations with S and Fe, respectively.

pH was also included in a second group of correlated variables. This group consisted of pH, the heat indices and inclination and concentration of total N, all positively correlated, and loss on ignition and aspect unfavourability which were negatively correlated with the other variables in the group. Strong pairwise correlations were found between variables in each of two subgroups: (1) inclination, aspect favourability and heat indices and (2) loss on ignition, the concentration of total N, the macro plot aspect unfavourability and macro plot heat index.

Tab. 27. Øyenskavelen: Kendall's nonparametric correlation coefficient τ between 32 environmental variables in the 50 meso sample plots in Øyenskavlen (lower triangle), with significance probabilities (upper triangle). Correlations significant at level P < 0.0001 in bold face. n.s. - significance probability > 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 2.

Variable	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
01 MA Inc	*	**.0000**	**.0000**	n.s.	n.s.	.0004	**.0000**	**.0000**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0674	.0897	.0009	n.s.	.0058	n.s.	n.s.	n.s.	.0463	n.s.	.0851	n.s.	n.s.	n.s.	.0002	.0048	n.s.	n.s.
02 MA Asp	**-.5843**	*	**.0000**	n.s.	.0569	.0841	**.0000**	**.0000**	n.s.	n.s.	.0283	n.s.	n.s.	.0806	.0194	n.s.	**.0000**	.0530	**.0000**	n.s.	.0098	n.s.	.0039	n.s.	.0080	n.s.	n.s.	.0008	**.0000**	.0150	n.s.	.0540
03 MA Hi	**.4495**	**-.8667**	*	n.s.	.0200	n.s.	**.0000**	**.0000**	n.s.	n.s.	n.s.	n.s.	n.s.	.0964	.0356	n.s.	**.0000**	.0190	.0007	n.s.	.0030	n.s.	.0125	.0974	.0037	n.s.	n.s.	**.0000**	**.0000**	.0606	.0974	.0941
04 MA BA	-.0966	.0239	.0716	*	**.0000**	.0947	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0617	n.s.	.0045	n.s.	n.s.	.0018	.0505	n.s.	.0069	.0065	n.s.	n.s.	n.s.	n.s.	.0362	**.0000**
05 MA Lig	.0899	-.2000	.2444	**.6922**	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0122	.0122	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0150	n.s.	n.s.	n.s.	.0003	.0207	.0037	.0654	n.s.	n.s.	.0028
06 ME Inc	.3693	-.1774	-0684	-.1785	-.1116	*	.0340	.0641	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0690	.0594	n.s.	n.s.
07 ME Asp	**-.4948**	**.5824**	**-.5158**	.1633	.0102	-.2103	*	**.0000**	n.s.	n.s.	n.s.	.0385	.0248	n.s.	n.s.	n.s.	.0002	.0598	.0004	n.s.	n.s.	n.s.	.0025	n.s.	.0007	n.s.	n.s.	.0010	.0003	.0003	.0149	.0343
08 ME Hi	**.4841**	**-.6040**	**.5511**	-.1217	.0383	.1833	**-.8339**	*	n.s.	n.s.	n.s.	.0418	.0427	n.s.	n.s.	n.s.	**.0000**	.0326	.0001	n.s.	.0927	n.s.	.0035	n.s.	.0004	n.s.	n.s.	.0002	**.0000**	.0005	.0156	.0056
09 ME Rou	-.0943	.0725	-.0587	-.0557	-.0760	-.0723	.0183	-.0414	*	n.s.	n.s.	.0441	n.s.	n.s.	n.s.	.0785	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0066	.0094	.0362	n.s.	n.s.	n.s.	n.s.	.0785	n.s.
10 ME Con	-.1491	.1329	-.0969	-.0083	-.0540	.0309	.0939	-.0624	-.1157	*	n.s.	n.s.	n.s.	n.s.	.0545	n.s.	n.s.	n.s.	n.s.	n.s.	.0115	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0706	n.s.	n.s.
11 ME Smi	-.1521	.2260	-.1565	.1205	.0191	.0652	.0535	-.0583	-.0566	.1081	*	**.0000**	.0078	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0305	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
12 ME Sme	.1325	-.0732	.1301	.0741	.0577	.1099	-.2045	.2007	-.2009	.0914	**.4307**	*	**.0000**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0013	n.s.	n.s.	n.s.	n.s.	.0101	.0956	n.s.	.0026	n.s.	n.s.
13 ME Sma	.0968	-.0483	.0948	.0287	-.0086	.1057	-.2220	.1990	-.0544	-.0707	.2673	**.6168**	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0334	n.s.	.0007	n.s.	n.s.	n.s.	n.s.	.0500	.0679	n.s.	.0001	.0094	n.s.
14 LitCC	.0962	-.1790	.1703	.1263	.2568	-.0783	-.0606	.0638	-.0647	-.1451	-.0786	-.0444	-.0461	*	**.0000**	.0086	n.s.	n.s.	.0285	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
15 LitACD	.1891	-.2398	.2156	.1153	.2571	.0067	-.1148	.0979	-.0521	-.1912	-.0491	-.0151	-.0084	**.8522**	*	.0097	n.s.	n.s.	.0213	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0932	n.s.	n.s.	n.s.
16 Mois	-.1733	.1398	-.0119	.0861	.0222	-.1037	.0205	-.0074	.1739	.0773	.0784	.0570	.1191	-.2596	-.2557	*	n.s.	.0575	n.s.	**.0000**	n.s.	.0005	n.s.	**.0000**	.0021	.0013	.0059	.0278	n.s.	n.s.	.0012	n.s.
17 LI	-.3400	**.4855**	**-.4787**	.1971	-.0145	-.1312	.3648	**-.4309**	-.0879	-.0280	.1602	.0786	.1440	-.0838	-.1363	.0679	*	n.s.	.0003	n.s.	.0290	.0721	.0024	.0833	.0001	n.s.	n.s.	.0302	**.0000**	n.s.	n.s.	.0013
18 pH_{H_2O}	.0597	-.2084	.2527	-.1595	.0148	-.1068	-.1958	.2218	.0502	-.0116	.0550	.1162	.1512	.1678	.1509	.1973	-.1655	*	**.0000**	.0175	.0011	.0418	n.s.	.0041	**.0000**	.0183	n.s.	.0013	.0312	.0132	**.0000**	.0003
19 pH_{CaCl_2}	.3017	**-.4425**	.3709	-.3216	-.0094	.0697	-.3699	.4249	.0201	-.0908	-.0884	.0420	.0749	.2326	.2448	-.0460	-.3777	**.6984**	*	n.s.	.0002	n.s.	.0489	n.s.	**.0000**	n.s.	n.s.	.0027	**.0000**	.0011	**.0000**	**.0000**
20 Ca	.1189	-.0111	-.0963	.0522	.0145	.0788	.0908	-.0857	-.1125	.0411	-.1116	-.0884	-.2098	.1284	.1178	**-.4175**	.0237	-.2466	-.1308	*	**.0000**	.0011	.0316	**.0000**	**.0000**	.0001	.0001	**.0000**	n.s.	.0056	**.0000**	.0033
21 Mg	-.0896	.2615	-.3007	.1327	.0009	.0456	.1448	-.1641	-.0811	.2481	.1150	.0751	-.0496	-.1334	-.1460	-.1054	.2134	-.3385	-.3870	**.3959**	*	.0804	.0014	**.0000**	**.0000**	.0329	n.s.	.0076	.0039	.0278	**.0000**	.0005
22 K	.0517	.0009	-.1116	-.3285	-.2462	.1202	.0679	-.0171	-.0149	.0427	-.2150	-.3179	-.3354	-.1069	-.1045	-.3423	-.1758	-.2112	.0622	.3176	.1706	*	n.s.	.0102	n.s.	n.s.	.0005	.0136	n.s.	.0113	n.s.	n.s.
23 Na	-.2033	.2922	-.2530	.2059	.0247	-.1020	.2954	-.2849	-.0414	.0296	.0916	.0157	.0083	.1334	.0796	-.0057	.2968	-.0504	-.2066	.2098	.3110	-.0841	*	.0776	.0020	n.s.	n.s.	.0533	.0004	n.s.	.0290	.0278
24 H^+	-.0534	-.0741	.1678	-.0522	-.0315	.0124	-.0794	.0808	.2681	-.0986	-.0183	-.0454	.0777	-.0704	-.0481	**.4436**	-.1693	.2979	.1507	**-.5086**	**-.4269**	-.2506	-.1722	*	**.0000**	**.0000**	.0513	.0005	n.s.	.0474	**.0000**	.0016
25 Al	.1757	-.2683	.2939	-.2846	-.1235	.0556	-.3314	.3437	.2565	-.0296	-.0433	.0157	.0892	-.0555	-.0265	.2998	-.3900	**.4322**	**.4808**	**-.4580**	**-.4220**	-.0922	-.3012	**.5184**	*	**.0000**	.0076	**.0000**	.0039	.0001	**.0000**	**.0000**
26 Fe	-.0465	-.0264	.1133	-.2864	-.3654	-.0174	-.0925	.1069	.2069	.0739	.0450	.0173	.1041	-.1583	-.1427	.3145	-.2428	.2448	.1543	-.3812	-.2082	-.0743	-.0188	**.4351**	**.5673**	*	n.s.	.0598	n.s.	n.s.	**.0000**	**.0000**
27 Mn	.0345	.0264	-.0860	-.1473	-.2343	.0124	.0745	-.1037	.0066	-.0460	-.1600	-.2535	-.1933	.1218	.1079	-.2688	.0237	-.1140	-.0207	.3910	.0057	.3388	-.0498	-.1902	-.2604	-.1445	*	**.0000**	n.s.	.0011	.0388	n.s.
28 Zn	-.1378	.3382	**-.4251**	-.0869	-.2939	-.0108	.3216	-.3616	-.0645	.0756	-.0467	-.1643	-.1801	-.0091	-.0348	-.2149	.2118	-.3332	-.3149	**.4727**	.2604	.2408	.1886	-.3404	**-.4433**	-.1837	**.4547**	*	.0004	.0010	.0001	.0187
29 Total N	.3825	**-.6874**	**.6312**	-.0448	.1866	.1800	-.3543	**.3992**	-.0033	-.0279	-.1450	.0206	.0033	.1152	.1659	-.0694	**-.4832**	.2236	**.4357**	-.0400	-.2816	.0612	-.3469	.1331	.2816	.0286	-.0286	-.3486	*	n.s.	n.s.	.0278
30 P-AL	-.2877	.2462	-.1900	.1400	-.0077	-.1866	.3543	-.3388	-.0513	.1774	-.1250	-.2965	-.3916	-.0820	-.1161	-.1136	.0384	-.2572	-.3419	.2702	.2147	.2473	.0939	-.1935	-.3845	-.1543	.3176	.3208	-.1363	*	**.0000**	.0316
31 P	-.1327	.1218	-.1678	.2205	.1371	-.0771	.2381	-.2359	-.1738	.0526	-.0667	-.1280	-.2561	.0340	.0166	-.3162	.1284	**-.4746**	**-.4393**	**.5135**	**.4514**	.1510	.2131	**-.4727**	**-.5951**	**-.4335**	.2016	.3910	-.1478	**.5314**	*	**-.3976**
32 S	.1516	-.1951	.1695	**-.4822**	-.3024	.1302	-.2070	.2702	.1440	-.0345	-.0833	-.0372	.0215	-.1516	-.1261	.1462	-.3148	.3792	**.4393**	-.2865	-.3388	.0988	-.2147	.3078	**.5771**	**.4612**	-.1510	-.2294	.2147	-.2098	**-.3976**	*

The two main groups intergraded extensively, e.g. pH belonged to both, the concentration of Al was correlated with loss on ignition and Zn was correlated with variables of both groups (see Fig. 605).

PCA ordination of environmental variables

Eigenvalues of the first two PCA axes were 0.296 and 0.141, thus 43.7% of the variation in measured environmental variables was explained by the first two PCA axes.

Variables of both groups mentioned above (pH, Al, S, H^+, total N and the heat indices) obtained high loadings on PCA (Fig. 606). Low loadings on PCA 1 were obtained by P, P-AL, Zn, Mg, Ca, aspect unfavourability and loss on ignition, all negatively correlated with pH

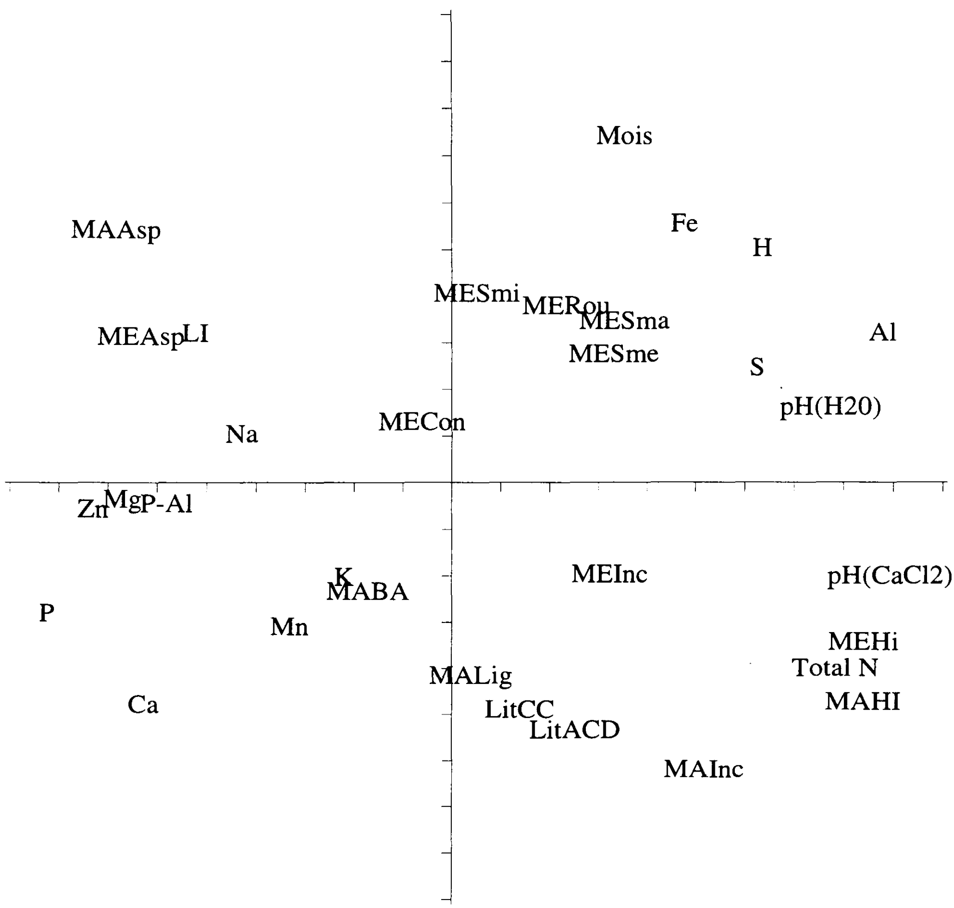
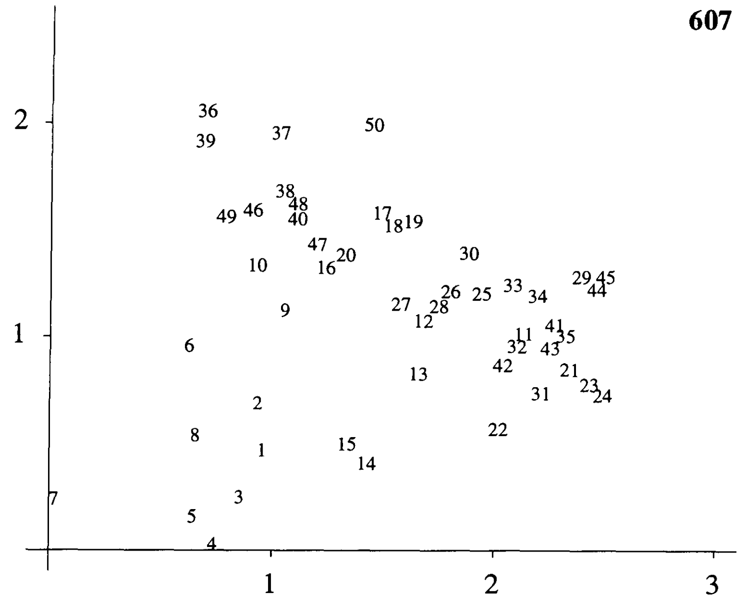


Fig. 606. Øyenskavelen: PCA ordination of 32 environmental variables (names abbreviated in accordance with Tab. 2), axes 1 (horizontal) and 2 (vertical). Positions of variables in the ordination give the head of variable vectors.



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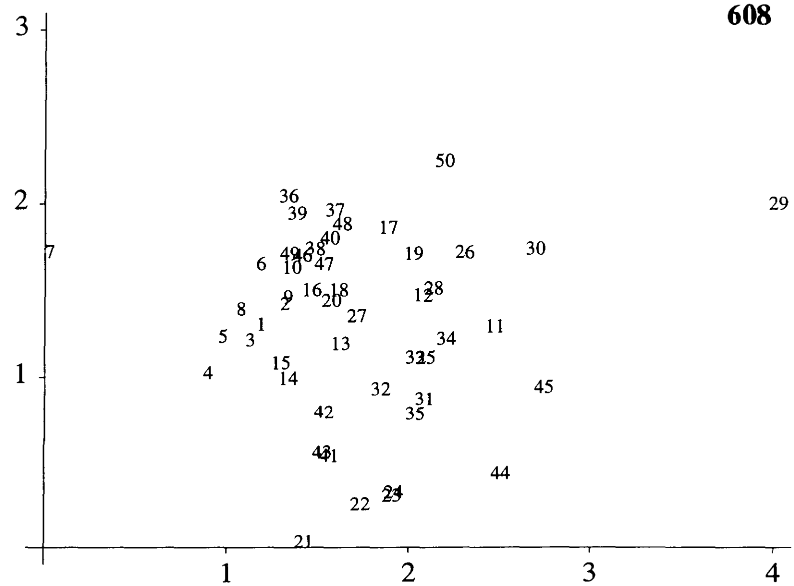

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Figs 607-608. Øyenskavelen: ordinations of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Meso plot numbers are plotted onto the sample plot positions. Fig. 607. DCA ordination. Scaling of axes in S.D. units. Fig. 608. LNMDS ordination. Axes linearly rescaled in S.D. units.

($|\tau|$ > 0.3, P < 0.005).

Soil moisture obtained the highest loading on PCA 2, while Ca (strongly negatively correlated with soil moisture), inclination, the heat indices and the litter indices obtained low loadings on PCA 2.

PCA results were thus consistent with the correlations between variables (Tab. 27, Fig. 605), emphasizing the central position of pH among the variables.

DCA and LNMDS ordination

Plot No. 7 (with 20 species, area average 33.8 species) was separated from the other plots by ca. 0.6 S.D. units along DCA 1. The other plots were relatively evenly distributed along the first two DCA axes (Fig. 607). Both plot No. 7, separated from the others by ca. 1.0 S.D. units along LNMDS 1, and plot No. 29 (with 13 species, and few subplot occurrences), separated from adjacent plots by ca. 1.3 S.D. units at the opposite end of LNMDS 1, acted as outliers in LNMDS ordination (Fig. 608). The plots were more evenly distributed along DCA than along LNMDS axes.

The fractions of variation explained (Tab. 28) by DCA 1 and DCA 2 were 15.8% and 10.3%, respectively. The fraction explained by DCA 3 was ca. 56% of that explained by DCA 2. The eigenvalues (Tab. 28) of DCA 3 and DCA 4 were low (0.108 and 0.068, respectively), corresponding to explained fractions of variation below 6%.

Correlations between DCA and LNMDS ordination axes and between ordination axes and environmental variables

Corresponding axes of the DCA and LNMDS ordinations were strongly correlated (τ > 0.5; Tab. 29). LNMDS 2 was, however, also correlated with DCA 1 (τ = -0.404), thus the variation expressed by DCA 1 was partly represented by LNMDS 1 and partly by LNMDS 2. Furthermore, LNMDS 1 was also partly correlated with DCA 3.

The variables most strongly correlated with LNMDS 1 and/or LNMDS 2 were, with the noteable exceptions of the litter indices, macro plot inclination (both correlated only with LNMDS 1) and the concentration of Zn (correlated with LNMDS 2), more strongly correlated with one or more of DCA axes 1-3.

The variables most strongly correlated with DCA 1 were macro plot aspect unfavourability (τ = -0.682, Fig. 610), and the concentration of total N (τ = 0.642, Fig. 620) and macro plot heat index (with τ = 0.613, Fig. 611). pH (Fig. 616), the meso plot heat index (Fig. 613),

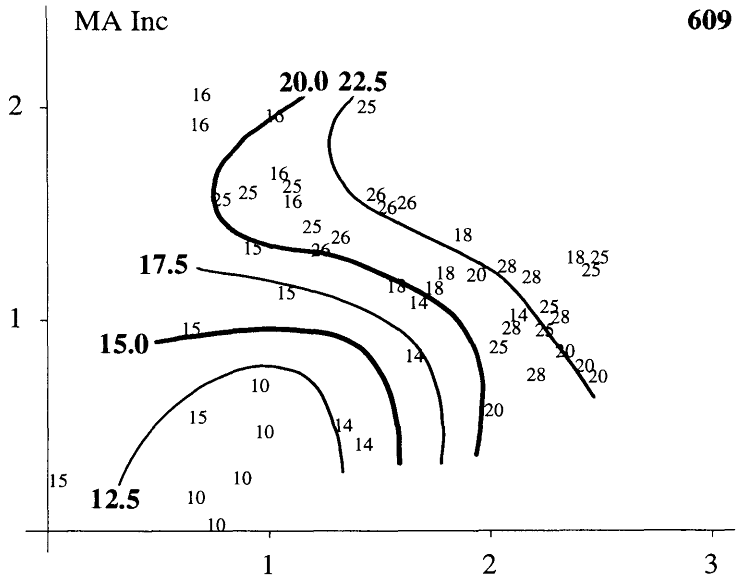
Tab. 28. Øyenskavelen: Eigenvalues and the fraction of variation explained for DCA axes 1-4.

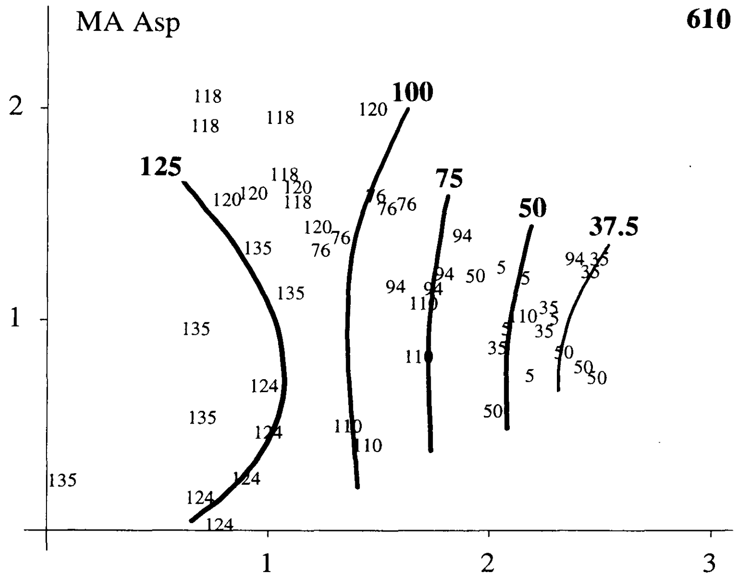
	DCA 1	DCA 2	DCA 3	DCA 4
Eigenvalues	0.295	0.193	0.108	0.068
Fraction of variation explained	0.158	0.103	0.058	0.036

Tab. 29. Øyenskavelen: Kendall's nonparametric correlation coefficient τ between DCA and LNMDS axes, and between 32 environmental variables in the 50 meso sample plots and sample plot positions with respect to DCA and LNMDS axes, and their significance probabilities. Correlations significant at level P < 0.0001 in bold face. n.s. - significance probability > 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 2.

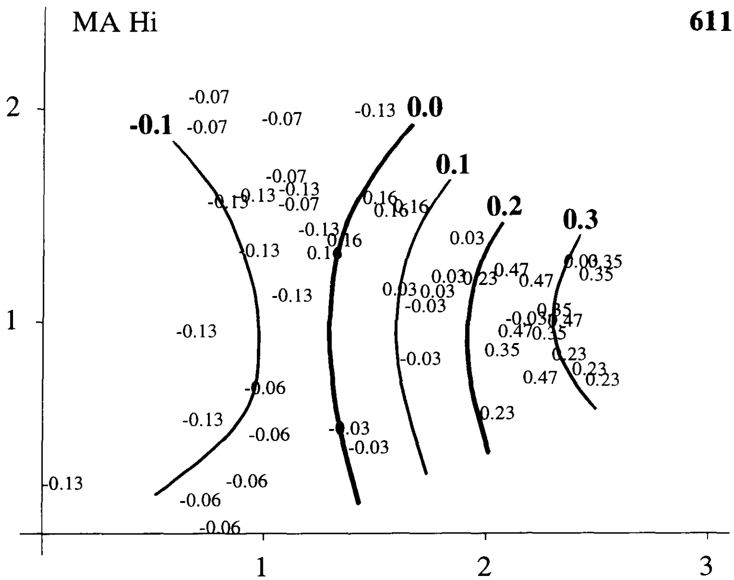
Variable	DCA 1		DCA 2		DCA 3		DCA 4		LNMDS 1		LNMDS 2	
	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P
LNMDS 1	**.5935**	**.0000**	.2392	.0142	-.3446	.0004	.0367	n.s.				
LNMDS 2	**-.4041**	**.0000**	**.5020**	**.0000**	-.1421	n.s.	-.0759	n.s.				
01 MA Inc	.3808	.0002	.2895	.0046	.0371	n.s.	.0345	n.s.	.3877	.0001	-.0448	n.s.
02 MA Asp	**-.6823**	**.0000**	.0060	n.s.	-.0460	n.s.	.0247	n.s.	**-.4779**	**.0000**	.3433	.0007
03 MA Hi	**.6125**	**.0000**	-.1337	n.s.	-.0307	n.s.	-.0775	n.s.	.3603	.0004	**-.4608**	**.0000**
04 MA BA	-.0540	n.s.	-.1583	n.s.	-.2526	.0165	-.1986	.0593	.0412	n.s.	.1125	n.s.
05 MA Lig	.2564	.0113	-.1218	n.s.	-.1704	.0924	-.2257	.0258	.2768	.0062	-.0946	n.s.
06 ME Inc	.1385	n.s.	.2231	.0242	.1842	.0629	.1186	n.s.	.1070	n.s.	.0240	n.s.
07 ME Asp	-.3609	.0002	-.0139	n.s.	-.1375	n.s.	.0679	n.s.	-.2447	.0124	.2889	.0031
08 ME Hi	**.4139**	**.0000**	-.0057	n.s.	.1454	n.s.	-.0841	n.s.	.2359	.0156	-.3176	.0011
09 ME Rou	-.1225	n.s.	-.0645	n.s.	.1134	n.s.	.1357	n.s.	-.1936	.0500	-.1125	n.s.
10 ME Con	-.1018	n.s.	-.0805	n.s.	.1635	.0958	-.0230	n.s.	-.1807	.0656	.0411	n.s.
11 ME Smi	-.2016	.0424	-.1000	n.s.	-.0325	n.s.	-.1550	.0537	-.1916	.0537	.0483	n.s.
12 ME Sme	.0553	n.s.	-.1181	n.s.	-.0644	n.s.	-.0917	n.s.	-.0322	n.s.	-.1181	n.s.
13 ME Sma	.0562	n.s.	-.1917	.0520	-.0636	n.s.	.1091	n.s.	-.0446	n.s.	-.2049	.0378
14 LitCC	.2776	.0049	.1085	n.s.	**-.4277**	**.0000**	-.0853	n.s.	**.5096**	**.0000**	.0373	n.s.
15 LitACD	.3053	.0020	.1211	n.s.	-.3776	.0001	-.1029	n.s.	**.5144**	**.0000**	.0017	n.s.
16 Mois	-.1675	.0864	**-.4747**	**.0000**	.2305	.0183	-.1413	n.s.	**-.4404**	**.0000**	-.2982	.0023
17 LI	**-.4080**	**.0000**	-.0728	n.s.	-.1309	n.s.	.1415	n.s.	-.2608	.0076	.2330	.0171
18 pH_{H2O}	.2572	.0132	-.3085	.0030	-.0619	n.s.	-.0433	n.s.	.0875	n.s.	-.3650	.0004
19 pH_{CaCl2}	**.4736**	**.0000**	-.0406	n.s.	.0262	n.s.	.0099	n.s.	.3149	.0027	-.3022	.0040
20 Ca	.0400	n.s.	.3224	.0010	-.2368	.0153	.1788	.0670	.2571	.0084	.2882	.0031
21 Mg	-.2898	.0030	.1755	.0721	-.0457	n.s.	-.0106	n.s.	-.1118	n.s.	.3306	.0007
22 K	-.0090	n.s.	.3747	.0001	.1356	n.s.	.2278	.0196	.0873	n.s.	.2131	.0290
23 Na	-.2147	.0278	-.0498	n.s.	**-.4181**	**.0000**	.0514	n.s.	-.0041	n.s.	.2980	.0023
24 H^+	.0269	n.s.	**-.3959**	**.0000**	.1470	n.s.	-.0694	n.s.	-.1771	.0695	-.3780	.0001
25 Al	.1853	.0576	-.1918	.0493	.2450	.0121	-.1657	.0895	-.0514	n.s.	-.3829	.0001
26 Fe	-.1037	n.s.	-.2457	.0118	.1241	n.s.	-.0955	n.s.	-.2653	.0066	-.2180	.0255
27 Mn	-.0073	n.s.	.1967	.0438	-.1078	n.s.	.3176	.0011	.1053	n.s.	.1265	n.s.
28 Zn	-.3437	.0004	.3208	.0010	-.1241	n.s.	.1902	n.s.	-.0873	n.s.	**.4531**	**.0000**
29 Total N	**.6424**	**.0000**	-.0971	n.s.	.1405	n.s.	.0269	n.s.	.3404	.0005	**-.4122**	**.0000**
30 P Al	-.1641	.0927	-.0188	n.s.	-.0098	n.s.	.0465	n.s.	-.1102	n.s.	.1657	.0895
31 P	-.0645	n.s.	.1755	.0721	-.1323	n.s.	.0351	n.s.	.1037	n.s.	.3020	.0020
32 S	.1510	n.s.	-.0759	n.s.	.3414	.0005	.0710	n.s.	-.0661	n.s.	-.2767	.0046

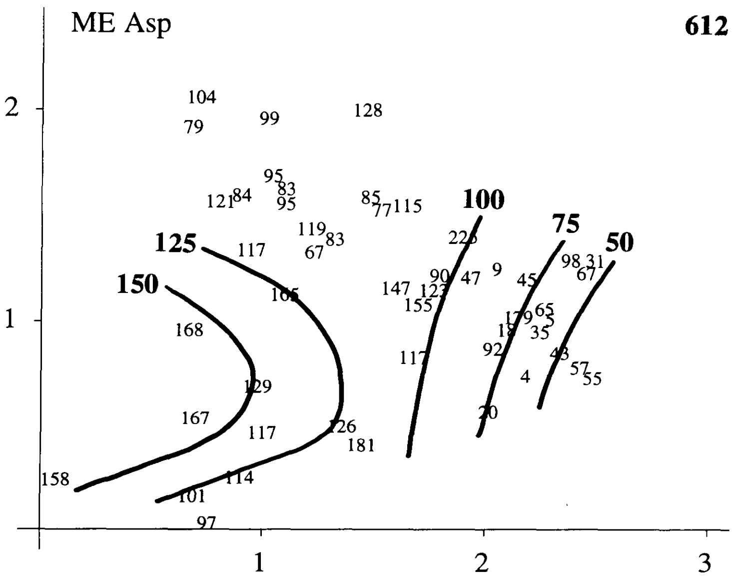
meso plot aspect unfavourability (Fig. 612) and loss on ignition were also strongly correlated with DCA 1; the two first mentioned positively, and the two last mentioned negatively correlated. Other variables that were positively correlated with DCA 1 were macro plot incli-



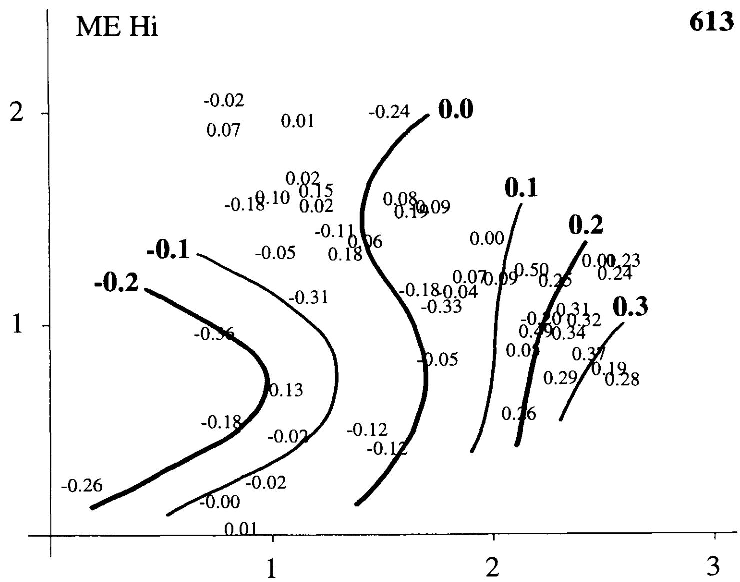


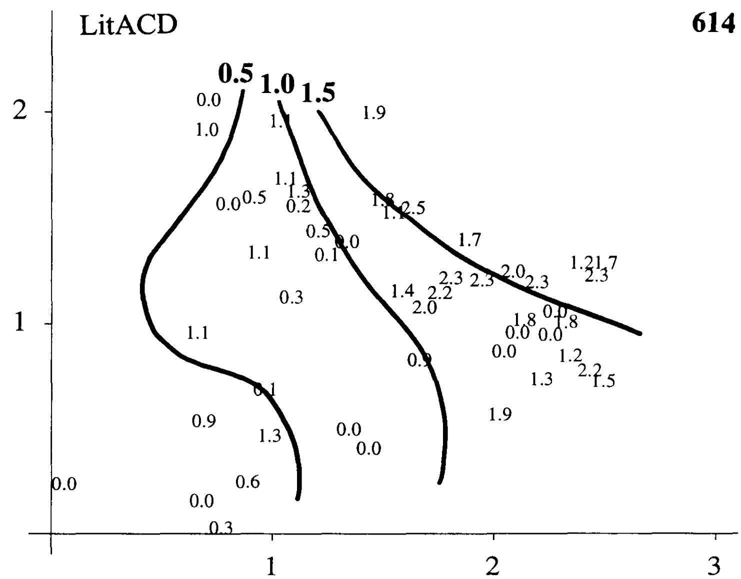
Figs 609-610. Øyenskavelen: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 609. MA Inc (R^2 = 0.571). Fig. 610. MA Asp (R^2 = 0.724). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.



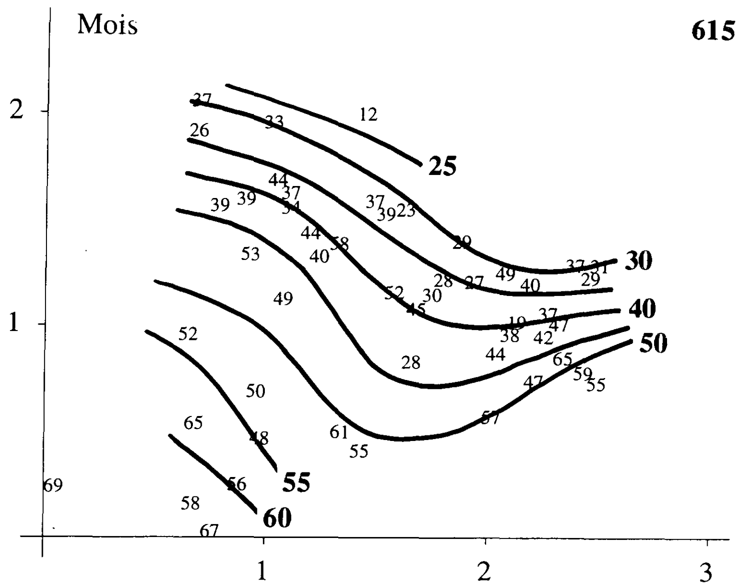


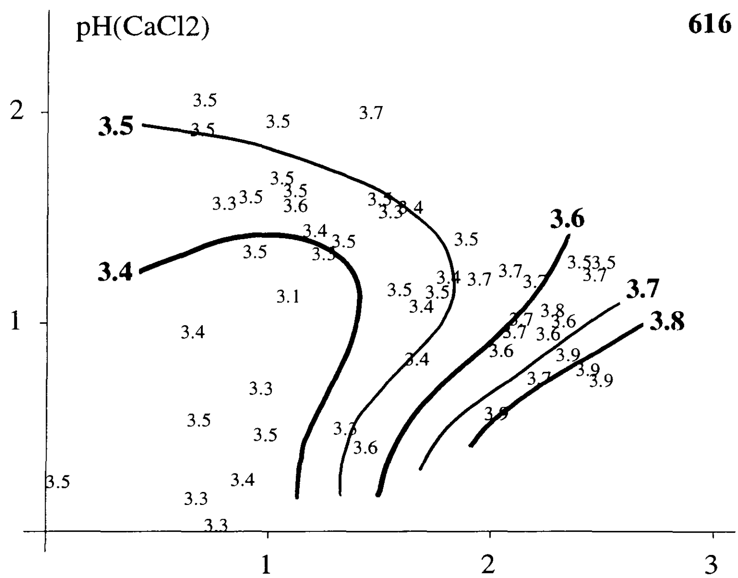
Figs 611-612. Øyenskavelen: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 611. MA Hi (R^2 = 0.674). Fig. 612. ME Asp (R^2 = 0.432). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.



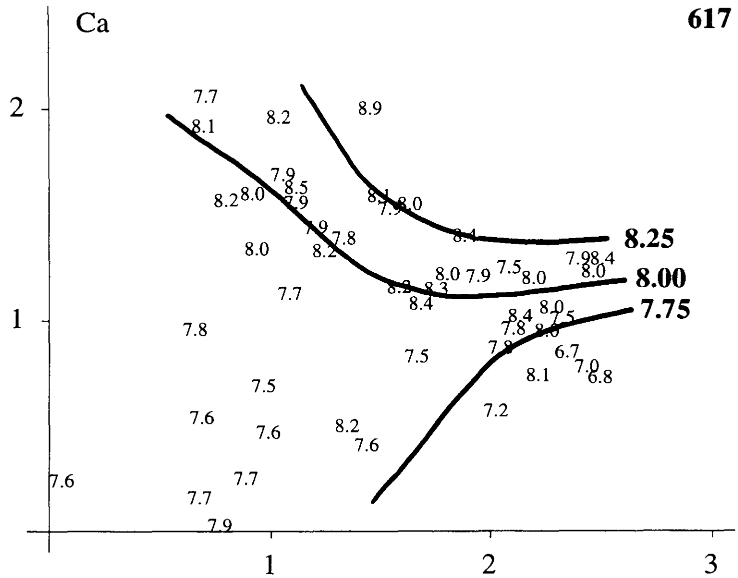


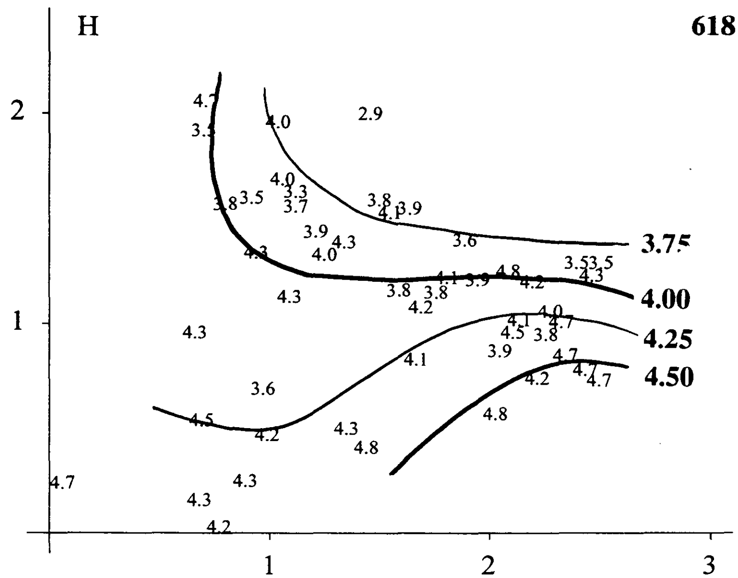
Figs 613-614. Øyenskavelen: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots' positions. Scaling of axes in S.D. units. Fig. 613. ME Hi (R^2 = 0.527). Fig. 614. Lit ACD (R^2 = 0.379). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.



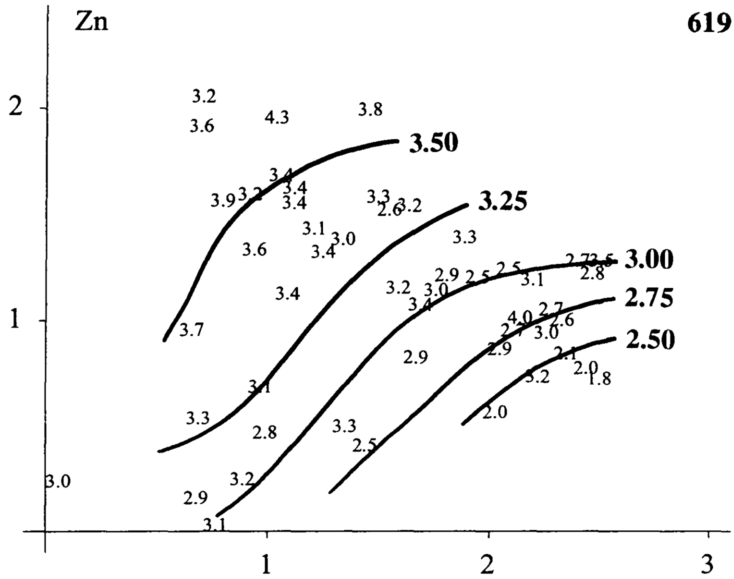


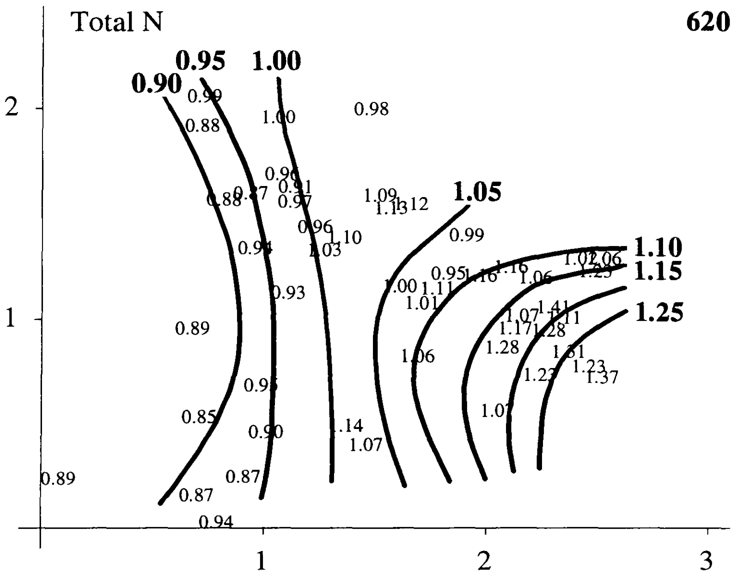
Figs 615-616. Øyenskavelen: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 615. Mois (R^2 = 0.669). Fig. 616. pH_{CaCl2} (R^2 = 0.694). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.



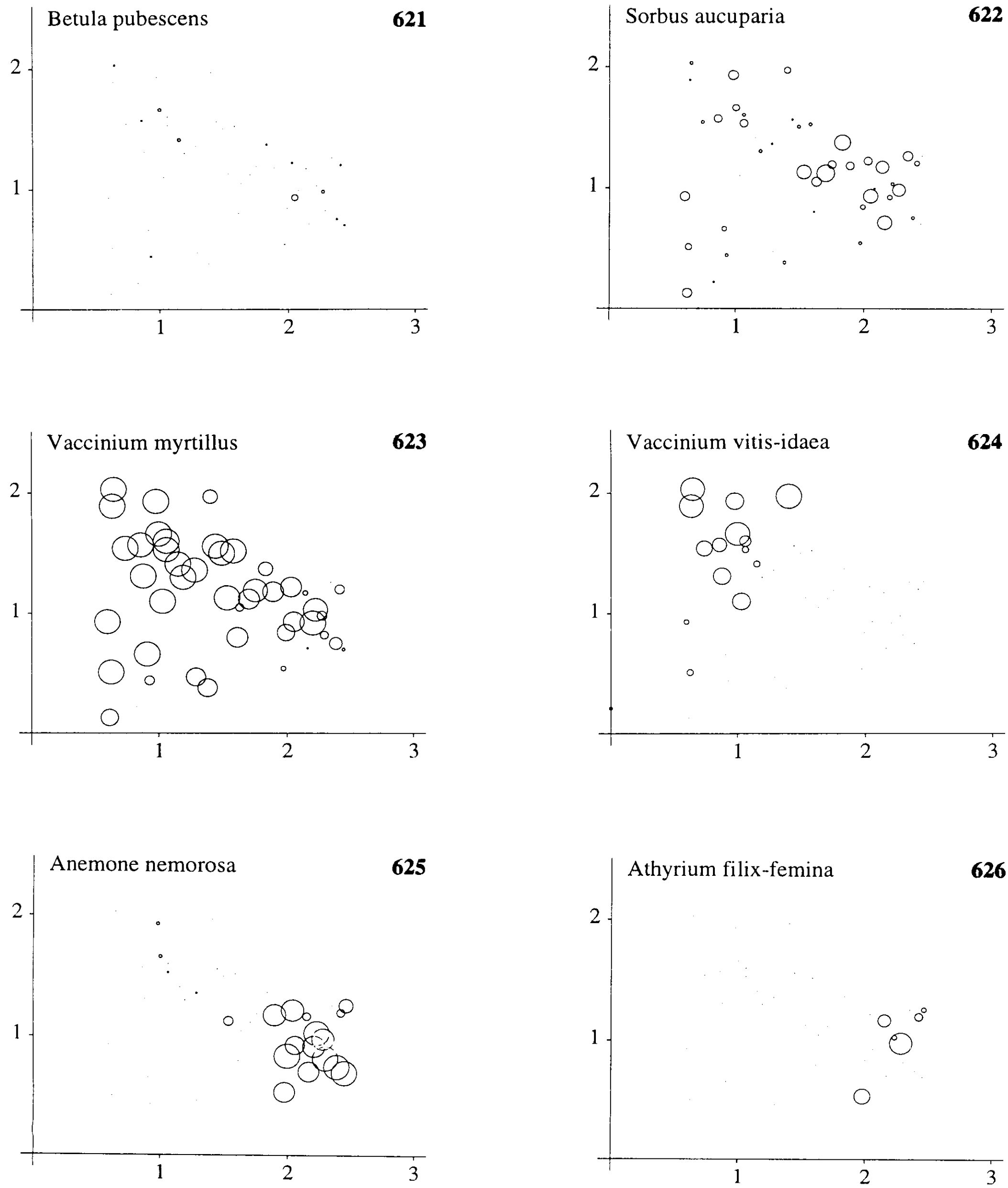


Figs 617-618. Øyenskavelen: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 617. Ca (R^2 = 0.521). Fig. 618. H^+ (R^2 = 0.435). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.

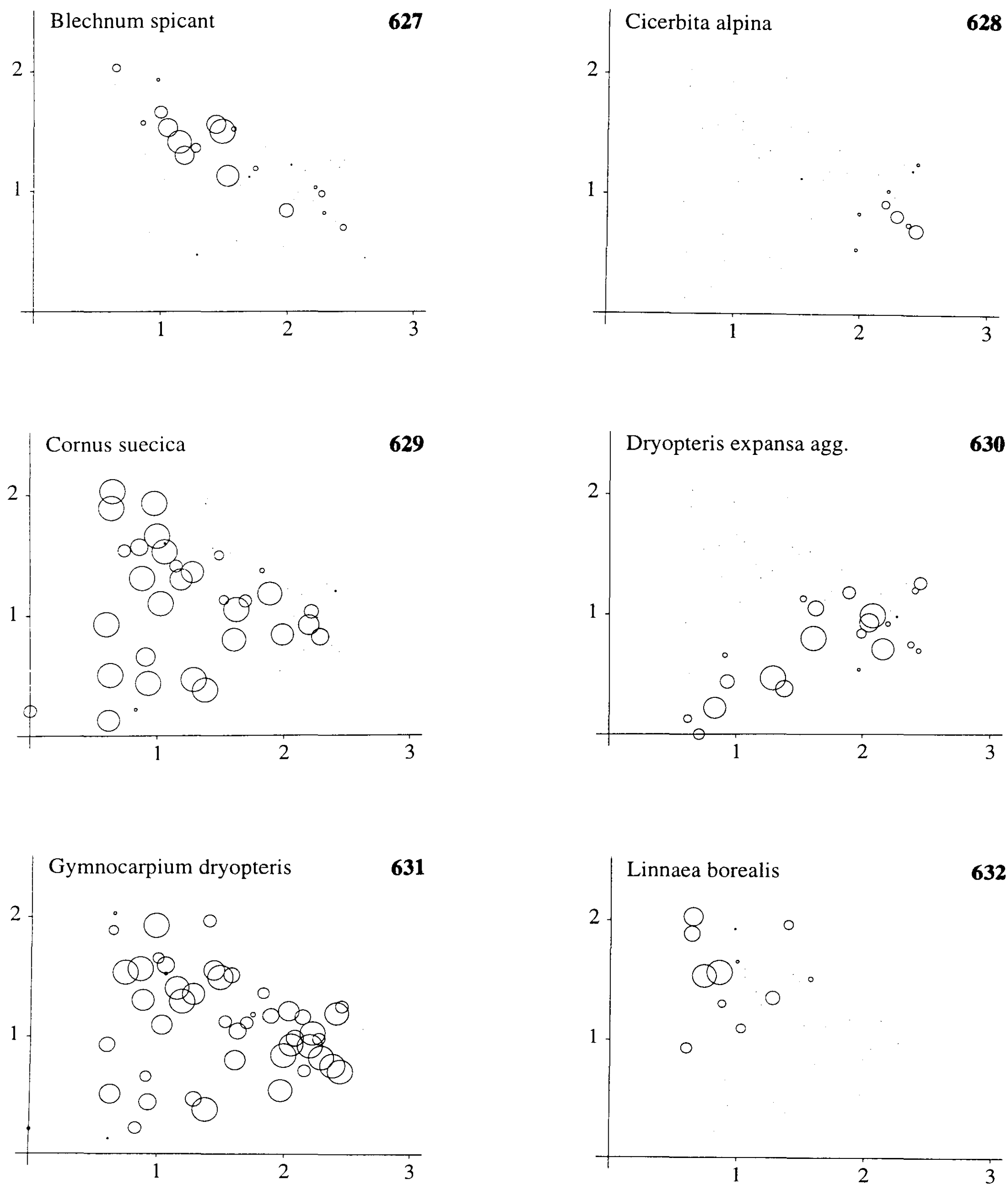




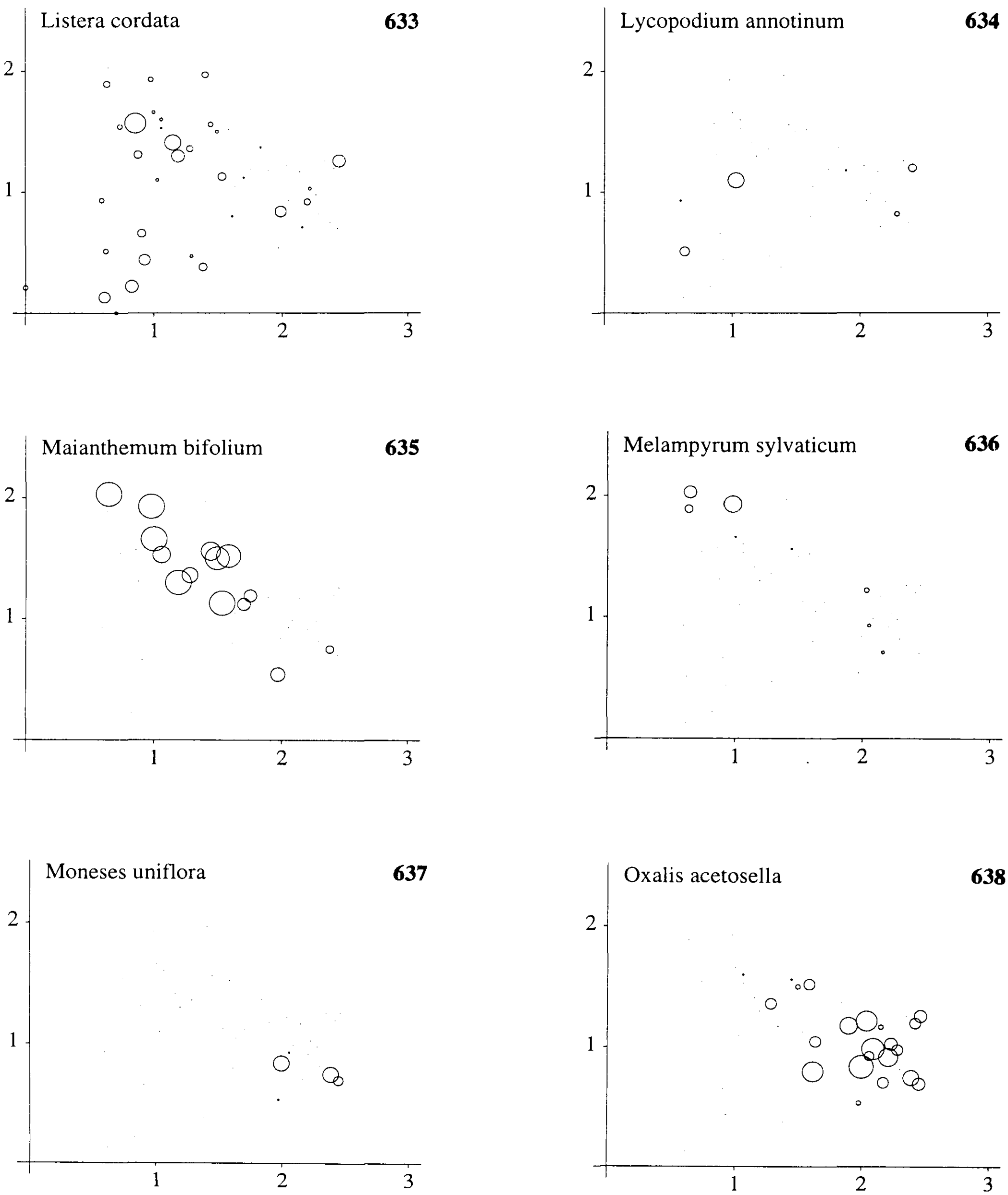
Figs 619-620. Øyenskavelen: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 619. Zn (R^2 = 0.528). Fig. 620. Total N (R^2 = 0.668). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.



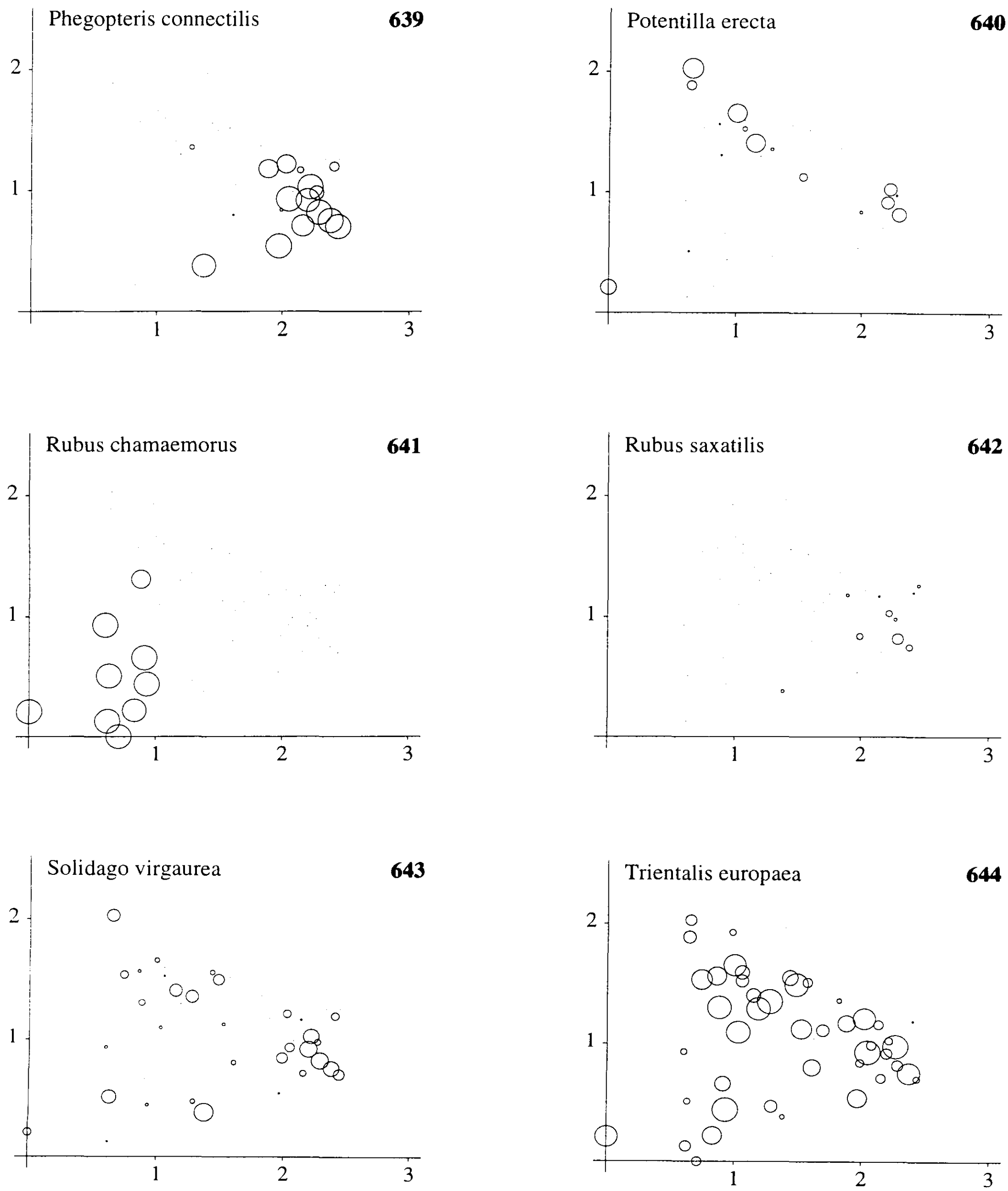
Figs 621-626. Øyenskavelen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 621. *Betula pubescens.* Fig. 622. *Sorbus aucuparia.* Fig. 623. *Vaccinium myrtillus.* Fig. 624. *Vaccinium vitis-idaea.* Fig. 625. *Anemone nemorosa.* Fig. 626. *Athyrium filix-femina.*



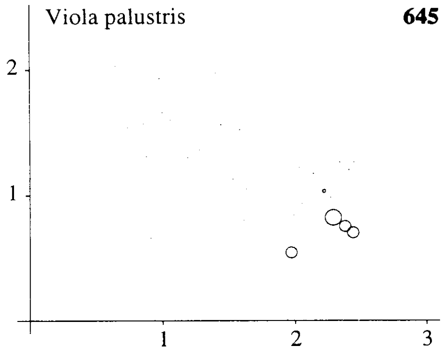
Figs 627-632. Øyenskavelen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 627. *Blechnum spicant*. Fig. 628. *Cicerbita alpina*. Fig. 629. *Cornus suecica*. Fig. 630. *Dryopteris expansa* agg. Fig. 631. *Gymnocarpium dryopteris*. Fig. 632. *Linnaea borealis*.

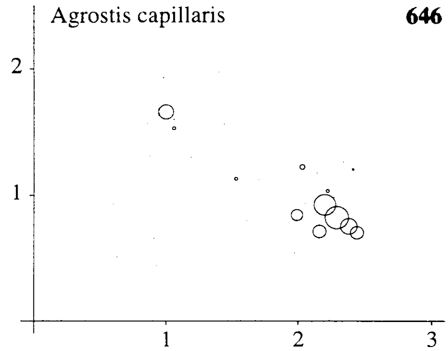


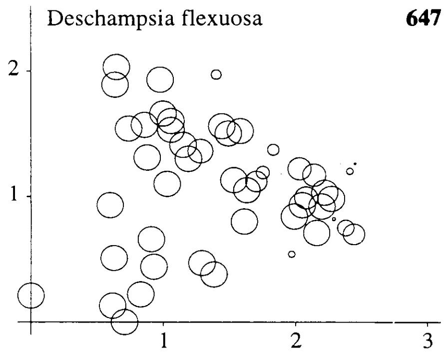
Figs 633-638. Øyenskavelen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 633. *Listera cordata.* Fig. 634. *Lycopodium annotinum.* Fig. 635. *Maianthemum bifolium.* Fig. 636. *Melampyrum sylvaticum.* Fig. 637. *Moneses uniflora.* Fig. 638. *Oxalis acetosella.*

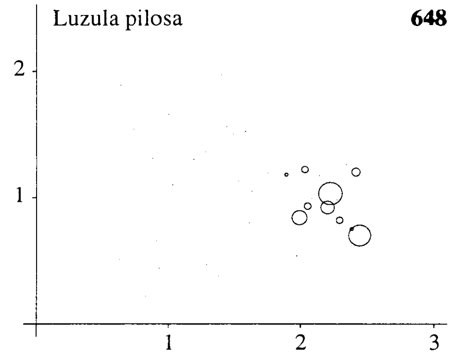


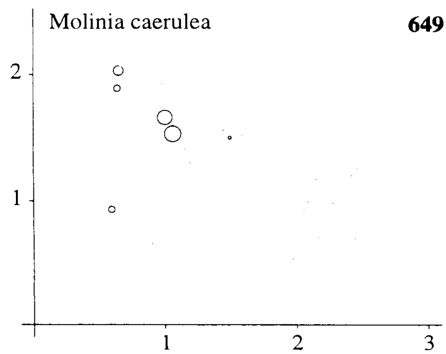
Figs 639-644. Øyenskavelen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 639. *Phegopteris connectilis*. Fig. 640. *Potentilla erecta*. Fig. 641. *Rubus chamaemorus*. Fig. 642. *Rubus saxatilis*. Fig. 643. *Solidago virgaurea*. Fig. 644. *Trientalis europaea*.

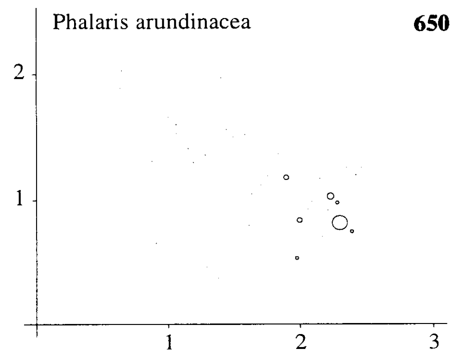




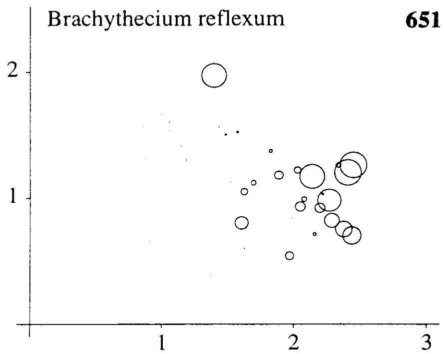


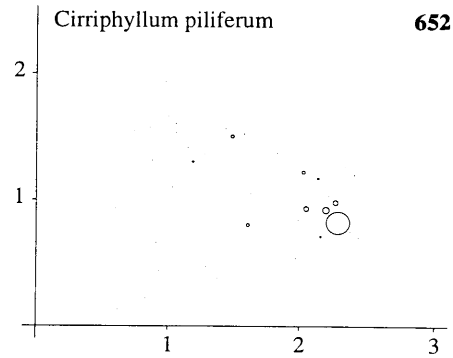


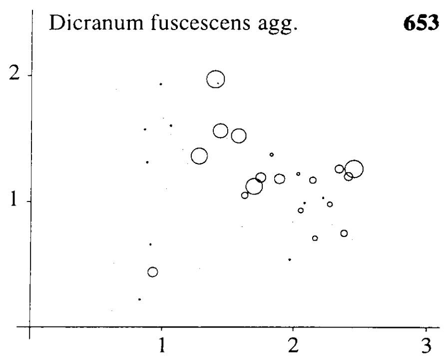


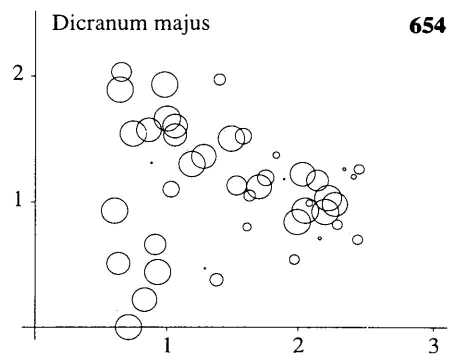


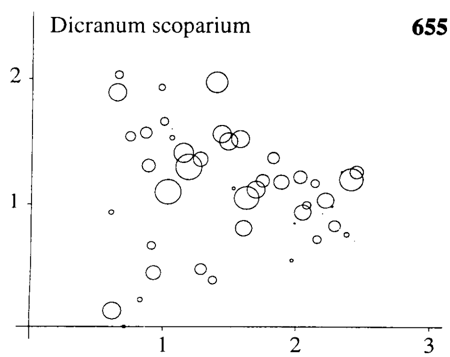
Figs 645-650. Øyenskavelen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 645. *Viola palustris*. Fig. 646. *Agrostis capillaris*. Fig. 647. *Deschampsia flexuosa*. Fig. 648. *Luzula pilosa*. Fig. 649. *Molinia caerulea*. Fig. 650. *Phalaris arundinacea*.

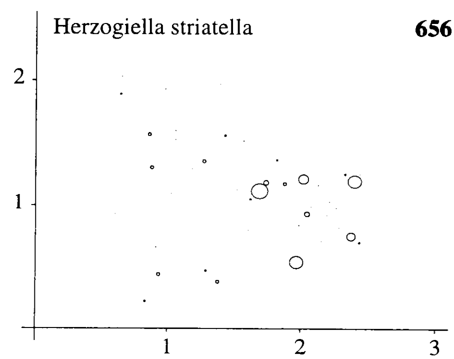




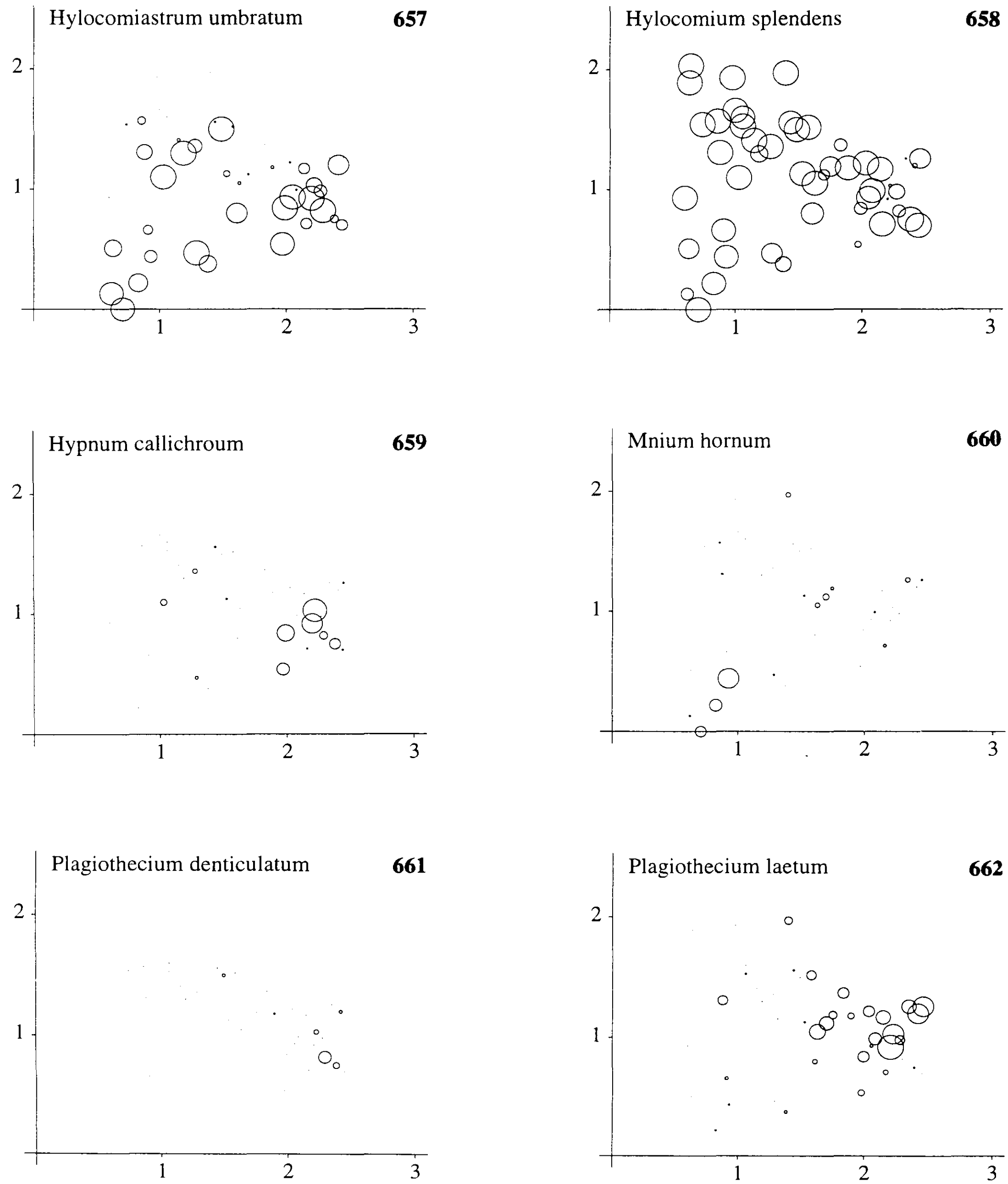




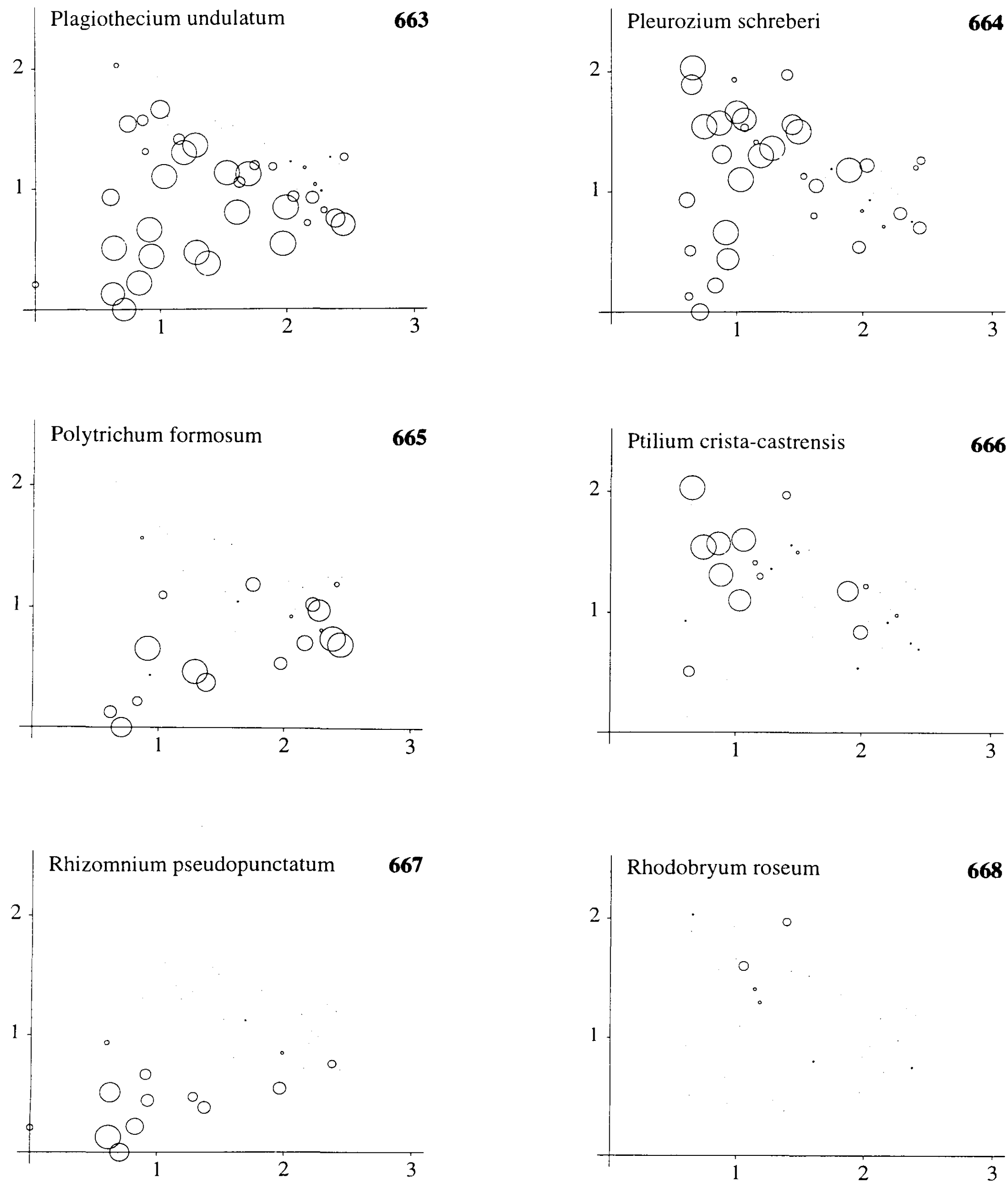




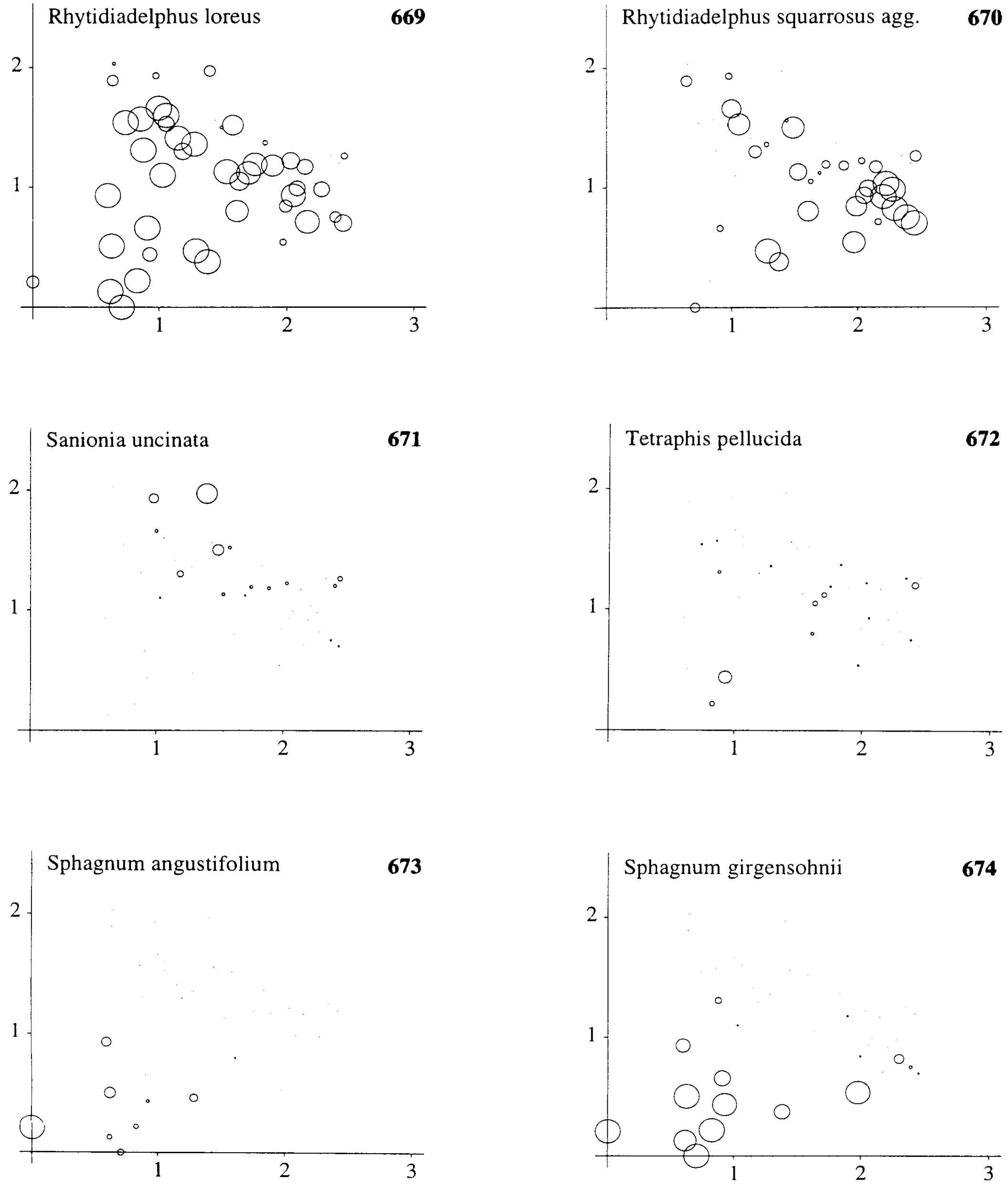
Figs 651-656. Øyenskavelen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency insubplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 651. *Brachythecium reflexum*. Fig. 652. *Cirriphyllum piliferum*. Fig. 653. *Dicranum fuscescens* agg. Fig. 654. *Dicranum majus*. Fig. 655. *Dicranum scoparium*. Fig. 656. *Herzogiella striatella*.



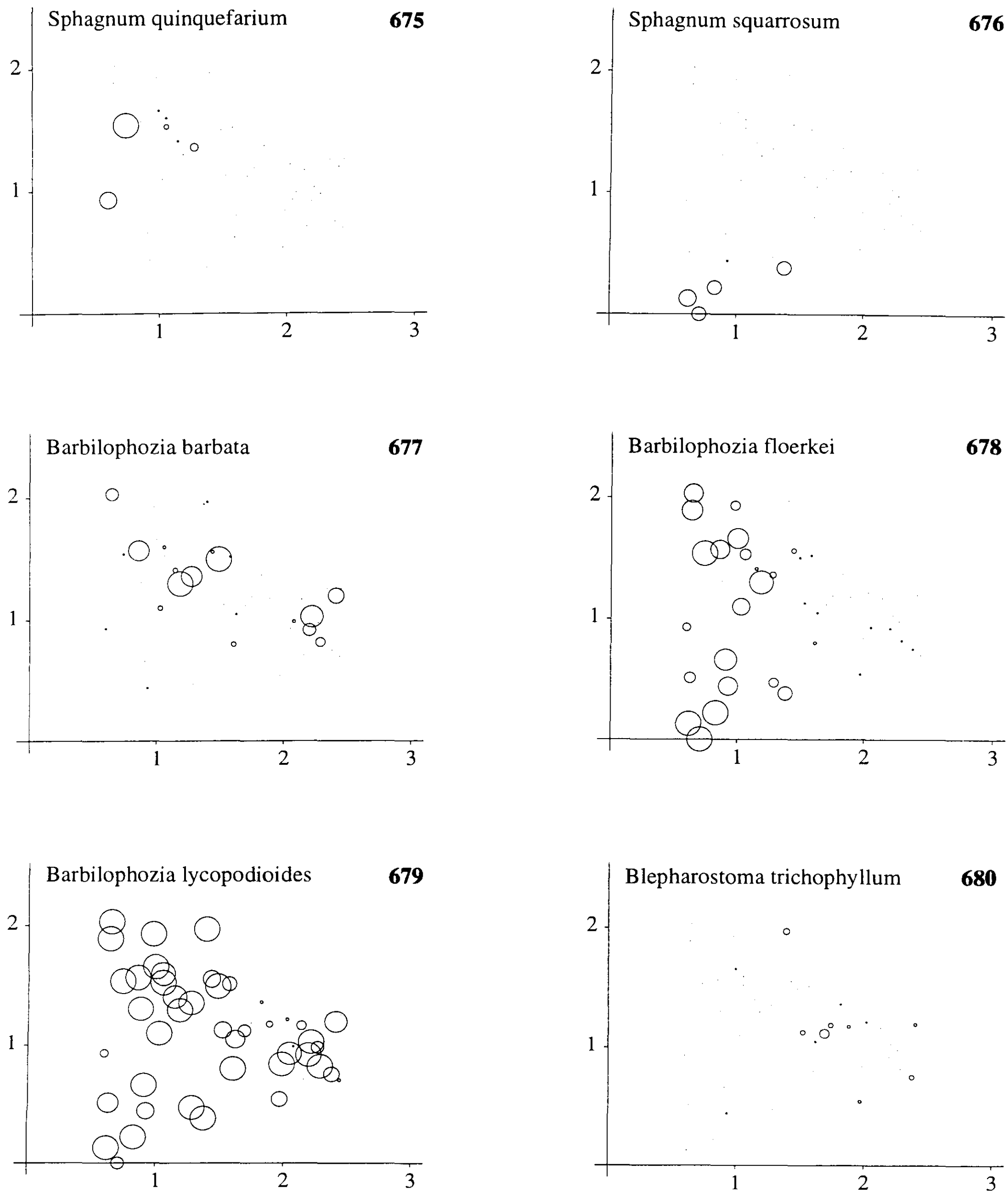
Figs 657-662. Øyenskavelen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 657. *Hylocomiastrum umbratum*. Fig. 658. *Hylocomium splendens*. Fig. 659. *Hypnum callichroum*. Fig. 660. *Mnium hornum*. Fig. 661. *Plagiothecium denticulatum*. Fig. 662. *Plagiothecium laetum*.



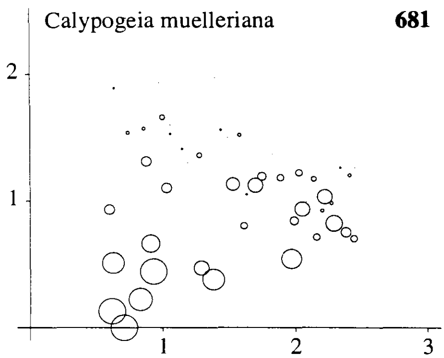
Figs 663-668. Øyenskavelen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 663. *Plagiothecium undulatum*. Fig. 664. *Pleurozium schreberi*. Fig. 665. *Polytrichum formosum*. Fig. 666. *Ptilium crista-castrensis*. Fig. 667. *Rhizomnium pseudopunctatum*. Fig. 668. *Rhodobryum roseum*.

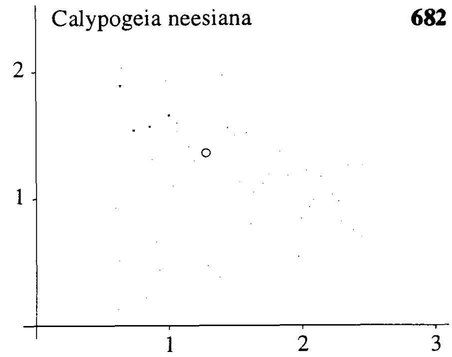


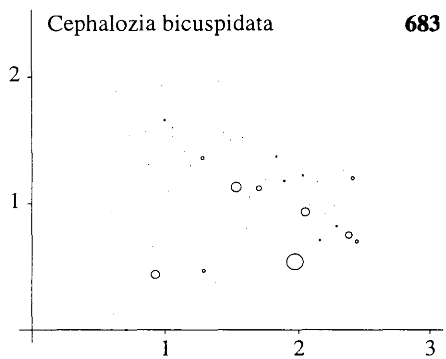
Figs 669-674. Øyenskavelen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 669. *Rhytidiadelphus loreus*. Fig. 670. *Rhytidiadelphus squarrosus* agg. Fig. 671. *Sanionia uncinata*. Fig. 672. *Tetraphis pellucida*. Fig. 673. *Sphagnum angustifolium*. Fig. 674. *Sphagnum girgensohnii*.

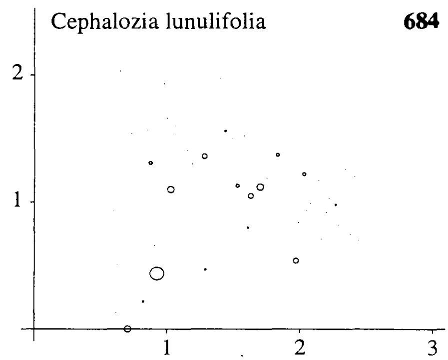


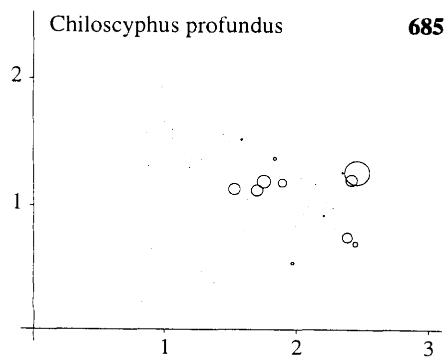
Figs 675-680. Øyenskavelen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 675. *Sphagnum quinquefarium*. Fig. 676. *Sphagnum squarrosum*. Fig. 677. *Barbilophozia barbata*. Fig. 678. *Barbilophozia floerkei*. Fig. 679. *Barbilophozia lycopodioides*. Fig. 680. *Blepharostoma trichophyllum*.

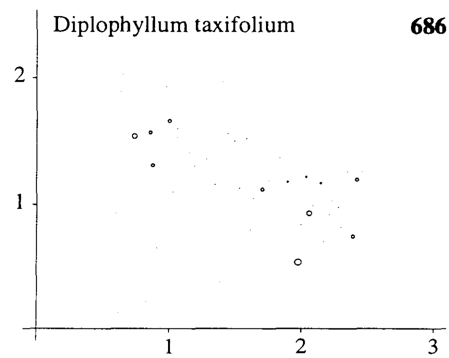




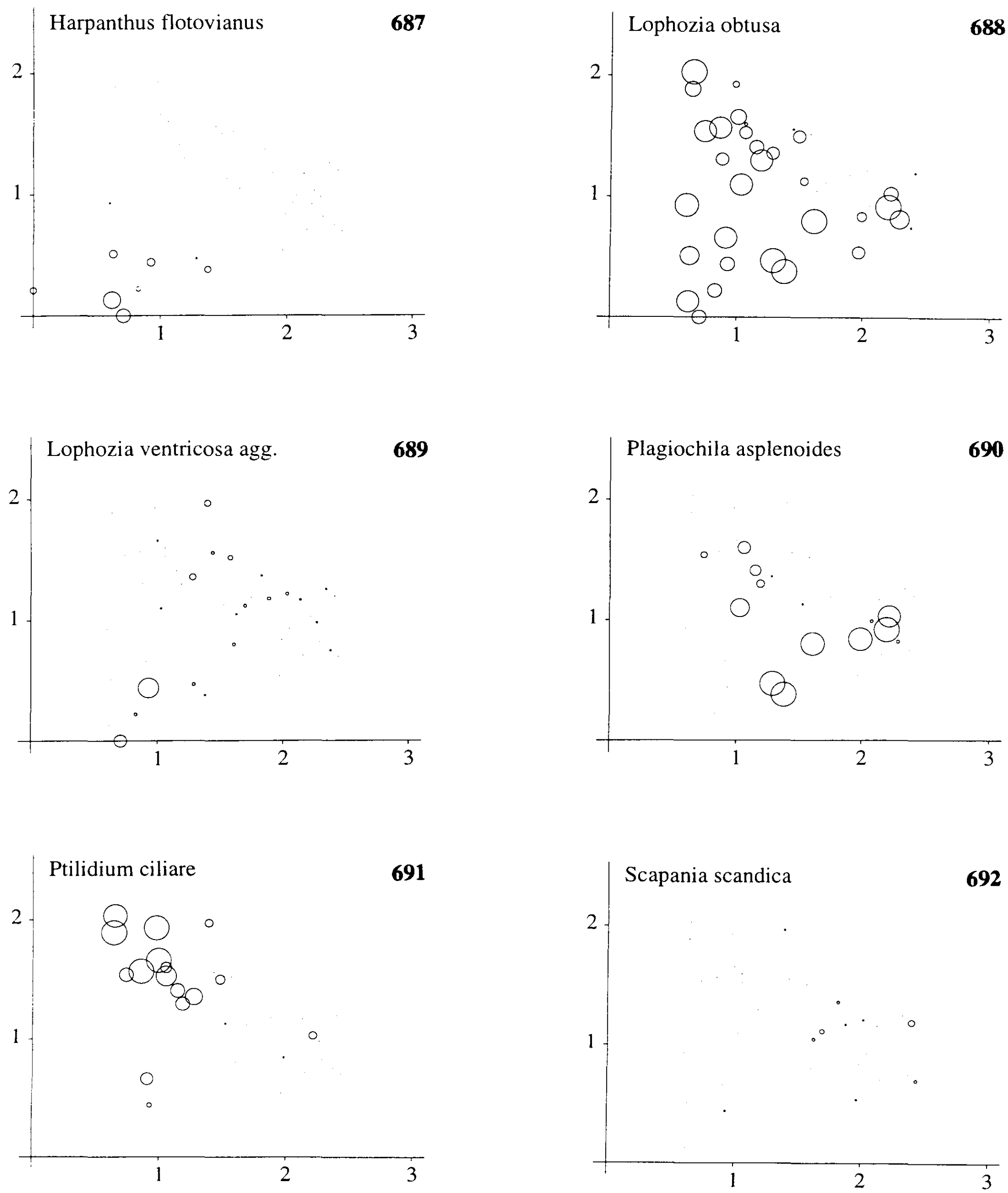




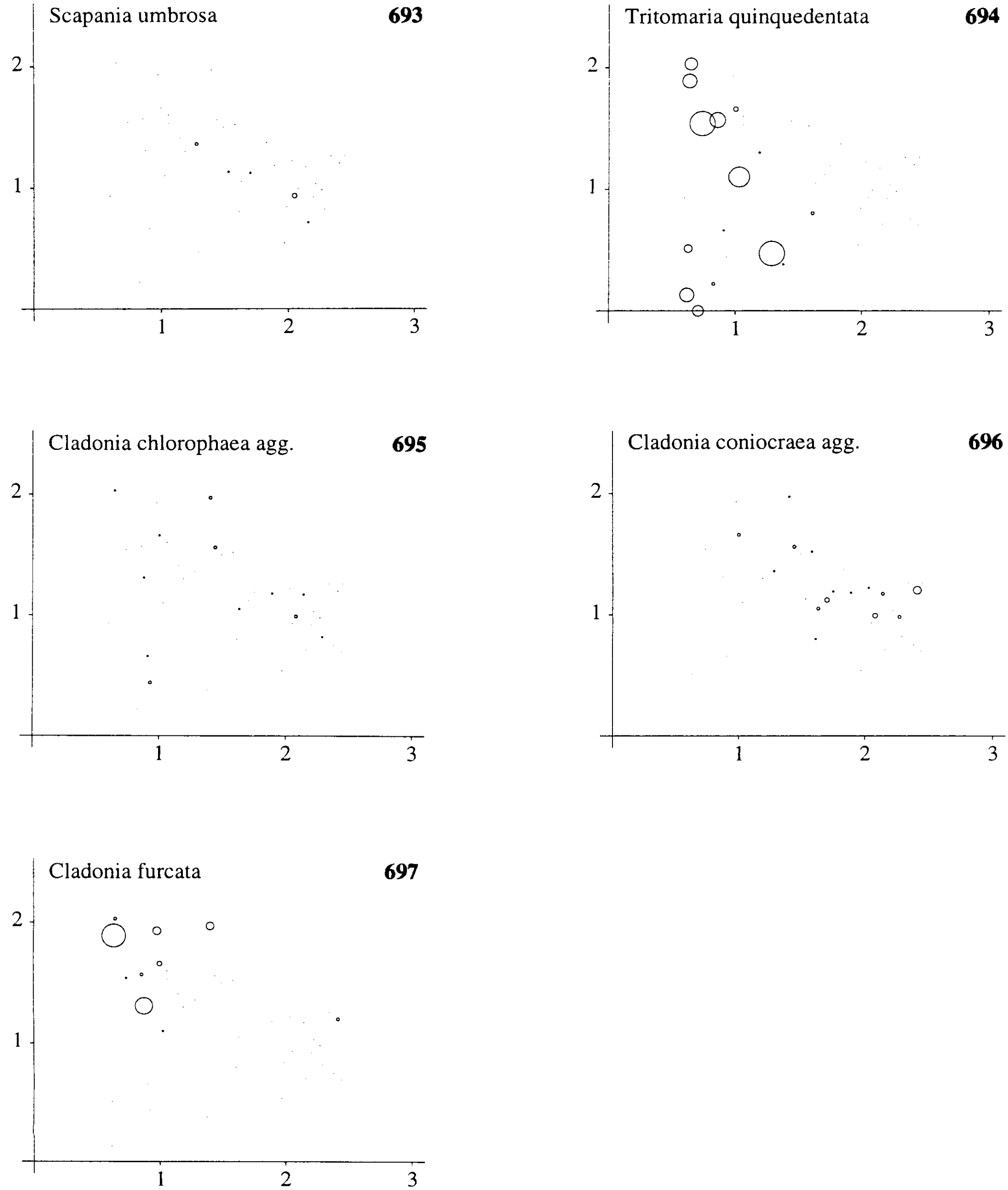




Figs 681-686. Øyenskavelen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 681. *Calypogeia muelleriana*. Fig. 682. *Calypogeia neesiana*. Fig. 683. *Cephalozia bicuspidata*. Fig. 684. *Cephalozia lunulifolia*. Fig. 685. *Chiloscyphus profundus*. Fig. 686. *Diplophyllum taxifolium*.



Figs 687-692. Øyenskavelen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 687. *Harpanthus flotovianus*. Fig. 688. *Lophozia obtusa*. Fig. 689. *Lophozia ventricosa*. Fig. 690. *Plagiochila asplenoides* agg. Fig. 691. *Ptilidium ciliare*. Fig. 692. *Scapania scandica*.



Figs 693-697. Øyenskavelen: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 693. *Scapania umbrosa*. Fig. 694. *Tritomaria exsectiformis*. Fig. 695. *Cladonia chlorophaea* agg. Fig. 696. *Cladonia coniocraea* agg. Fig. 697. *Cladonia furcata*.

nation (Fig. 609), meso plot aspect unfavourability (Fig. 610) and the litter indices (Fig. 614), while the concentration of Zn (Fig. 619) was negatively correlated with DCA 1. The variables most strongly correlated with LNMDS 1 were the litter indices (positively), aspect favourability and soil moisture (both negatively).

Soil moisture (Fig. 615) and the concentration of H^+ (Fig. 618) were strongly negatively correlated with DCA 2, while concentrations of Ca (Fig. 617), K and Zn (Fig. 619) were positively correlated with this axis. Most strongly correlated with LNMDS 2 were the concentration of total N and macro plot heat index (both negatively) and the concentration of Zn (positively). The litter indices and Na were strongly negatively correlated with DCA 3, while Mn was the only variable significantly correlated with DCA 4.

The distribution of species abundance in the DCA ordination

Seventy-seven of a total of 128 species occurred in 5 or more of the 50 meso plots (Figs 621-697).

Vaccinium myrtillus (Fig. 623), *Deschampsia flexuosa* (Fig. 647), *Hylocomium splendens* (Fig. 658) and *Barbilophozia lycopodioides* (Fig. 679), typical examples of species with wide ecological amplitude in bilberry-dominated spruce forest, were abundant in most plots.

Several species were mostly restricted to the left part of the DCA ordination; species with high abundance in plots from sites with unfavourable aspect, low pH and low N content: *Vaccinium vitis-idaea* (Fig. 624), *Linnaea borealis* (Fig. 632) and *Cladonia furcata* (Fig. 697) were more or less restricted to dry sites (upper left part of the DCA ordination diagram); *Rubus chamaemorus* (Fig. 641), *Sphagnum angustifolium* (Fig. 673) and *Harpanthus flotovianus* (Fig. 687) occurred in moist sites (lower left); and *Barbilophozia floerkei* (Fig. 678) and *Tritomaria quinquedentata* (Fig. 694) occurred in dry as well as moist sites.

Examples of species restricted to meso plots with favourable aspect, high pH and high N content (right-hand half of the DCA ordination), were *Athyrium filix-femina* (Fig. 626), *Cicerbita alpina* (Fig. 628), *Luzula pilosa* (Fig. 648), *Phalaris arundinacea* (Fig. 650), *Cirriphyllum piliferum* (Fig. 652) and *Plagiothecium denticulatum* (Fig. 661).

Examples of species that appeared to occur irrespective of aspect, pH and N content, but that had preference for plots from moist sites (low DCA 2 scores), were *Sphagnum girgensohnii* (Fig. 674) and *Rhizomnium pseudopunctatum* (Fig. 667).

GRANNESET

Correlations between environmental variables

pH and concentrations of the cations Ca, Zn and Mn made up a group of more or less strongly positively correlated variables (Tab. 30, Fig. 698). The macro plot light index was positively correlated with the litter indices, in turn positively correlated with concentrations of Ca and Zn.

Soil moisture content was negatively correlated with each of pH, concentrations of Ca, Mn and Zn, and the litter indices. The concentrations of Al and Fe were strongly positively

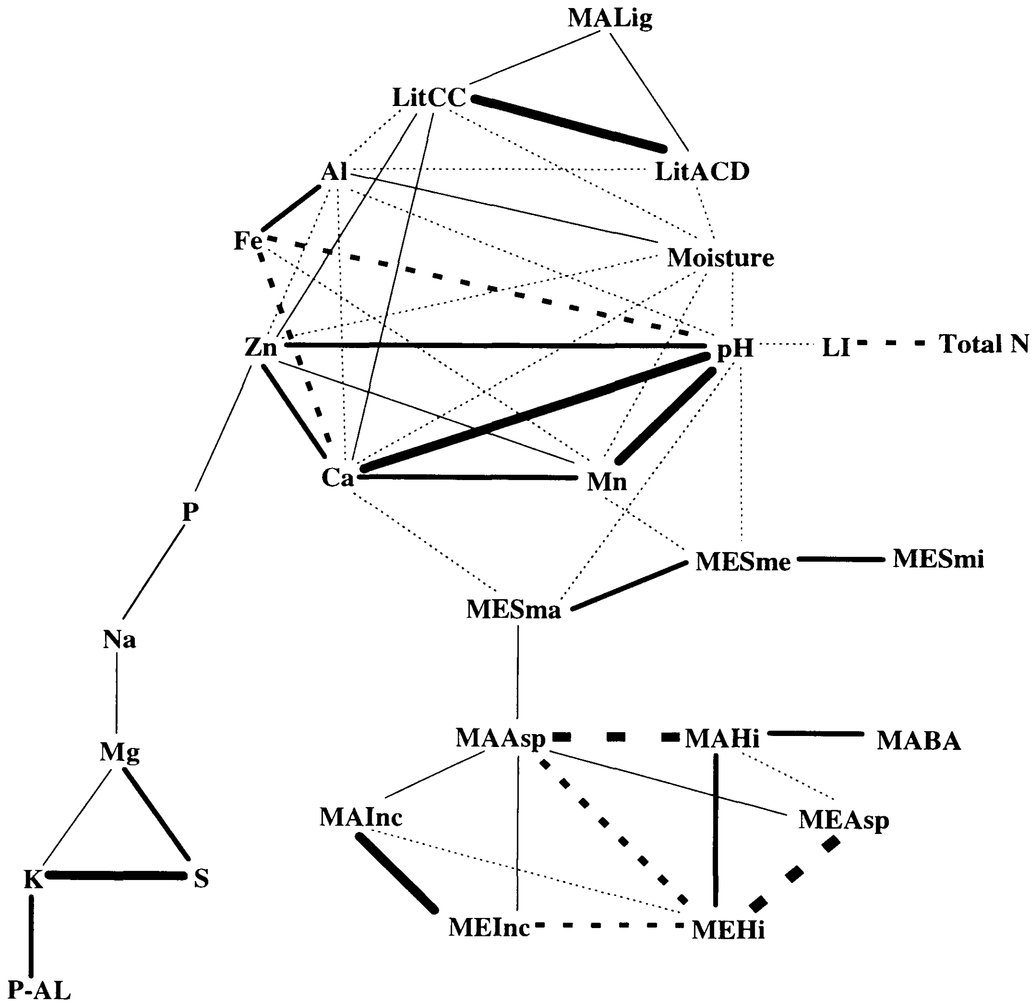


Fig. 698. Granneset: plexus diagram visualizing Kendall's τ between pairs of environmental variables. Significance probabilities for τ are indicated by lines with different thickness (in order of decreasing thickness): $|\tau| \geq 0.60$, $0.45 \leq |\tau| < 0.60$, $0.35 \leq |\tau| < 0.45$. Continuous lines refer to positive correlations, broken lines to negative.

correlated, and both were positively correlated with soil moisture and negatively correlated with pH and concentrations of Ca and Zn.

The concentration of total N was strongly negatively correlated with loss on ignition and positively correlated with pH, while loss on ignition was negatively correlated with pH.

A second group of correlated variables consisted of macro and meso plot aspect, inclination and heat index which were pairwise correlated, and macro plot basal area, which was strongly positively correlated with macro plot heat index. The two groups of correlated

Tab. 30. Granneset: Kendall's nonparametric correlation coefficient τ between 32 environmental variables in the 50 meso sample plots (lower triangle), with significance probabilities (upper triangle). Correlations significant at level P < 0.0001 in bold face. n.s. - significance probability > 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 2.

Variable	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
01 MA Inc	*	.0003	.0044	.0896	n.s.	**.0000**	.0341	.0001	.0189	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0131	.0295	.0669	n.s.	.0792	.0736	.0048	.0085	.0137	n.s.	n.s.	.0181	.0282	.0098	.0227	n.s.
02 MA Asp	.3857	*	**.0000**	.0109	n.s.	.0007	.0001	**.0000**	n.s.	n.s.	n.s.	.0202	.0003	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0043	n.s.	n.s.	n.s.	n.s.	.0522	n.s.	n.s.	n.s.
03 MA Hi	-.3010	**-.7089**	*	**.0000**	n.s.	.0069	.0005	**.0000**	n.s.	n.s.	n.s.	.0384	.0047	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0048	n.s.	n.s.	.0131	n.s.	n.s.	n.s.	n.s.	n.s.
04 MA BA	.1795	-.2697	**.5191**	*	n.s.	n.s.	.0368	.0143	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0461	.0157	.0461	.0269	n.s.	n.s.	.0787	n.s.	.0377	n.s.	n.s.	n.s.
05 MA Lig	.0000	-.1348	.1198	-.0222	*	n.s.	.0213	.0137	n.s.	n.s.	.0459	n.s.	n.s.	.0001	.0002	.0056	n.s.	n.s.	.0664	n.s.	n.s.	n.s.	.0181	n.s.	.0021	n.s.	.0080	.0165	n.s.	n.s.	.0333	n.s.
06 ME Inc	**.7788**	.3509	-.2759	.0758	-.0740	*	.0444	**.0000**	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0053	.0357	n.s.	.0990	n.s.	n.s.	.0072	.0010	.0573	n.s.	n.s.	.0072	.0123	.0117	.0148	n.s.
07 ME Asp	.2168	.3955	-.3553	-.2122	-.2191	.1989	*	**.0000**	n.s.	n.s.	n.s.	.0816	.0050	.0395	.0864	.0681	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0308	n.s.	n.s.	.0200	n.s.	n.s.	.0335	n.s.	n.s.
08 ME Hi	-.4007	**-.5048**	**.4821**	.2479	.2496	**-.4167**	**-.7167**	*	n.s.	n.s.	n.s.	n.s.	.0114	.0722	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0576	.0088	n.s.	n.s.	.0037	n.s.	n.s.	.0041	.0316	n.s.
09 ME Rou	-.2453	-.0861	.0140	-.1000	-.1263	-.1360	.0659	.0092	*	n.s.	.0596	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
10 ME Con	.1042	-.0722	.1176	.1264	.0404	.0975	-.0969	.0198	.0144	*	n.s.	n.s.	n.s.	n.s.	n.s.	.0010	n.s.		.0129	.0200	.0132	n.s.	n.s.	n.s.	n.s.	n.s.	.0908	.0182	n.s.	n.s.	n.s.	n.s.n.s.
11 ME Smi	.1015	.1200	-.0609	.1023	.2037	.0241	.0745	-.0354	-.1900	-.0765	*	**.0000**	.0857	n.s.	n.s.	n.s.	n.s.	.0666	n.s.	n.s.	.0135	.0552	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0223
12 ME Sme	.0380	.2381	-.2102	-.0342	.0514	-.0224	.1714	-.1222	-.1428	-.0787	**.4743**	*	**.5446**	n.s.	n.s.	.0774	.0179	.0157	**.0000**	.0010	.0255	.0694	n.s.	n.s.	n.s.	.0088	.0002	.0357	n.s.	n.s.	n.s.	.0136
13 ME Sma	.1607	.3760	-.2887	-.1153	.0534	.0934	.2276	-.2491	-.0603	-.1415	.1706	**.5446**	*	n.s.	n.s.	.0786	n.s.	.0895	.0003	.0003	n.s.	n.s.	n.s.	n.s.	n.s.	.0070	.0017	n.s.	n.s.	n.s.	n.s.	n.s.
14 LitCC	.0307	-.1212	.0832	-.0139	.3944	.0244	-.2049	.1781	.0291	.1160	.1084	-.0393	-.1068	*	**.0000**	.0001	n.s.	.0779	.0031	.0001	n.s.	n.s.	.0097	n.s.	.0001	.0195	.0048	.0001	n.s.	n.s.	n.s.	n.s.
15 LitACD	-.0403	-.0316	-.0321	-.1137	.3864	-.0168	-.1705	.1489	.0917	.0781	.1495	.0134	-.0605	**.8104**	*	.0003	n.s.	n.s.	.0114	.0009	n.s.	n.s.	.0077	n.s.	**.0000**	.0565	.0295	.0015	n.s.	n.s.	n.s.	n.s.
16 Mois	-.1307	.0913	-.1029	-.0946	-.2803	-.1477	.1788	-.0890	.0328	-.3230	.0700	.1731	.1732	-.3829	-.3570	*	.0959	.0161	.0001	**.0000**	n.s.	n.s.	n.s.	n.s.	**.0000**	.0011	.0001	**.0000**	n.s.	.0834	.0994	n.s.
17 LI	-.2532	-.1536	.0417	-.1459	.1203	-.2752	.0246	.0973	.1154	-.1552	.1526	.2325	.1322	.0800	.1309	.1627	*	.0001	.0005	.0076	.0179	.0149	n.s.	.0804	n.s.	.0833	.0015	.0023	**.0000**	.0171	n.s.	.0008
18 pH_{H_2O}	.2369	.1497	-.0762	-.0400	.0307	.2210	-.0072	-.0312	.0046	.2613	-.1927	-.2529	-.1785	.1866	.1619	-.2508	-.3987	*	**.0000**	**.0000**	.0009	n.s.	n.s.	.0161	.0147	.0002	**.0000**	.0003	.0002	n.s.	n.s.	.0010
19 pH_{CaCl_2}	.1952	-.0173	.0584	.0450	.1943	.1559	-.0866	.0681	.0240	.2393	-.1557	**-.4391**	-.3762	.3067	.2618	-.3956	-.3531	**.7669**	*	**.0000**	.0070	.0529	n.s.	.0127	.0002	**.0000**	**.0000**	**.0000**	.0010	n.s.	n.s.	.0019
20 Ca	.1617	-.0517	.0400	.0656	.1150	.1626	-.1132	.0694	-.0126	.2439	-.079	-.3224	-.3530	.3929	.3303	**-.3959**	-.2608	**.5738**	**.7162**	*	n.s.	n.s.	n.s.	.0084	**.0000**	**.0000**	**.0000**	**.0000**	.0014	n.s.	n.s.	n.s.
21 Mg	-.1789	-.0414	.0196	-.2019	-.0434	-.1427	-.0246	.1020	.0546	.1104	-.2430	-.2190	-.1386	-.0816	-.0857	.1004	-.2314	.3454	.2749	.1314	*	**.0000**	.0001	n.s.	.0062	n.s.	.0019	n.s.	.0927	.0164	.0187	**.0000**
22 K	-.1823	.0500	-.1148	-.2445	.0332	-.1559	-.0459	.0612	.0530	.1384	-.1886	-.1780	-.1551	-.1066	-.0890	-.0743	-.2379	.1597	.1974	.0253	**.4465**	*	.0031	n.s.	n.s.	n.s.	.0016	n.s.	n.s.	**.0000**	**.0000**	**.0000**
23 Na	-.2872	-.0844	.0298	-.2019	.2394	-.2649	-.1017	.1853	.0967	-.0082	-.1211	-.0205	.0462	.2564	.2638	-.0351	.1071	.0919	.0681	-.0139	.3747	.2882	*	n.s.	n.s.	n.s.	.0171	n.s.	.0994	.0118	.0007	.0027
24 H^+	-.2683	-.2912	.2849	.2240	.1031	-.3243	-.2116	.2555	-.0177	-.0231	.1277	.0566	-.0016	.0466	.0691	.0547	.1709	-.2508	-.2542	-.2571	.0073	.0090	.1200	*	.0051	n.s.	n.s.	.0474	n.s.	.0834	n.s.	n.s.
25 Al	-.2511	-.1275	.1046	.0656	-.3109	-.1873	.0066	.0547	-.0328	-.0791	-.0651	.0829	.1353	-.3896	**-.4086**	**.4155**	.0155	-.2543	-.3784	**-.4024**	.2669	.1053	.1053	.2735	*	**.0000**	.0179	.0001	n.s.	n.s.	n.s.	n.s.
26 Fe	-.1668	.0276	.0009	-.0315	-.1116	-.0784	-.0394	.0563	-.0815	-.1665	.0387	.2568	.2656	-.2314	-.1889	.3192	.1693	-.3846	**-.5283**	**-.4661**	.0433	-.0302	.1069	.1314	**.5053**	*	.0002	.0035	.0834	n.s.	n.s.	n.s.
27 Mn	-.0034	-.1620	.2508	.1780	.2683	-.0305	-.2280	.2833	.0109	.2324	-.1475	-.3700	-.3085	.2797	.2155	-.3910	-.3099	**.5096**	**.6886**	**.5249**	.3029	.3078	.2327	-.0629	-.2310	-.3698	*	**.0000**	.0041	.0007	.0002	.0007
28 Zn	.2408	.0913	-.0876	-.0043	.2428	.2649	-.0984	.0057	-.1135	.1302	-.0173	-.2059	-.1237	.3929	.3137	**-.4171**	-.2984	.3739	**.5007**	**.5086**	.0547	.0531	.1184	-.1935	-.3845	-.2849	**.4155**	*	.0033	n.s.	.0234	.0493
29 Total N	.2236	.1981	-.1165	.2104	-.1354	.2467	-.0049	-.0482	-.0731	.1500	.0189	-.0993	-.1254	.0117	-.0175	-.0922	**-.5912**	.3918	.3353	.3110	.1641	.1200	-.1608	-.1461	-.0139	-.1690	.2800	.2865	*	.0303	n.s.	.0645
30 P Al	-.2631	-.1327	.1046	.0775	.1167	-.2484	-.2083	.2800	.0109	.0956	-.0074	-.0468	-.1303	.0183	.0275	-.1690	-.2330	.0009	.1129	-.0302	.2343	**.4515**	.2457	.1690	.1249	.0514	.3306	.1249	.2114	*	**.6947**	.3029
31 P	-.2322	-.0586	-.0094	-.0247	.2155	-.2401	-.1607	.2098	.0193	.1236	.1236	.0140	-.0205	-.0132	.1115	.1340	-.1608	-.1529	.0027	.1198	.0106	.2294	**.4498**	.3290	.1445	.0057	-.0351	.3616	.2212	.1478	*	.0080
32 S	.0155	.1585	-.1301	-.1457	-.0520	.0239	.0312	-.0351	-.0109	.1253	-.2249	-.2420	-.1452	-.1032	-.1090	-.0661	-.3279	.3418	.3163	.1118	**.4743**	**.6229**	.2931	-.0384	.1233	-.0220	.3290	.1918	.1804	.3029	.2588	*

variables were connected via the soil depth variables, negatively correlated with pH and concentrations of Ca and Mn, see Fig. 698.

PCA ordination of environmental variables

Eigenvalues of the first two PCA axes were 0.240 and 0.173, thus 41.3% of the variation in measured environmental variables was explained by the first two PCA axes.

The strongly positively correlated variables pH, Ca, Zn and Mn obtained high loadings on PCA 1 (Fig. 699). Median and maximum soil depth, Fe, loss on ignition, Al and soil moisture content, i.e. the variables most strongly negatively correlated with the group mentioned above, obtained the lowest loadings on PCA 1.

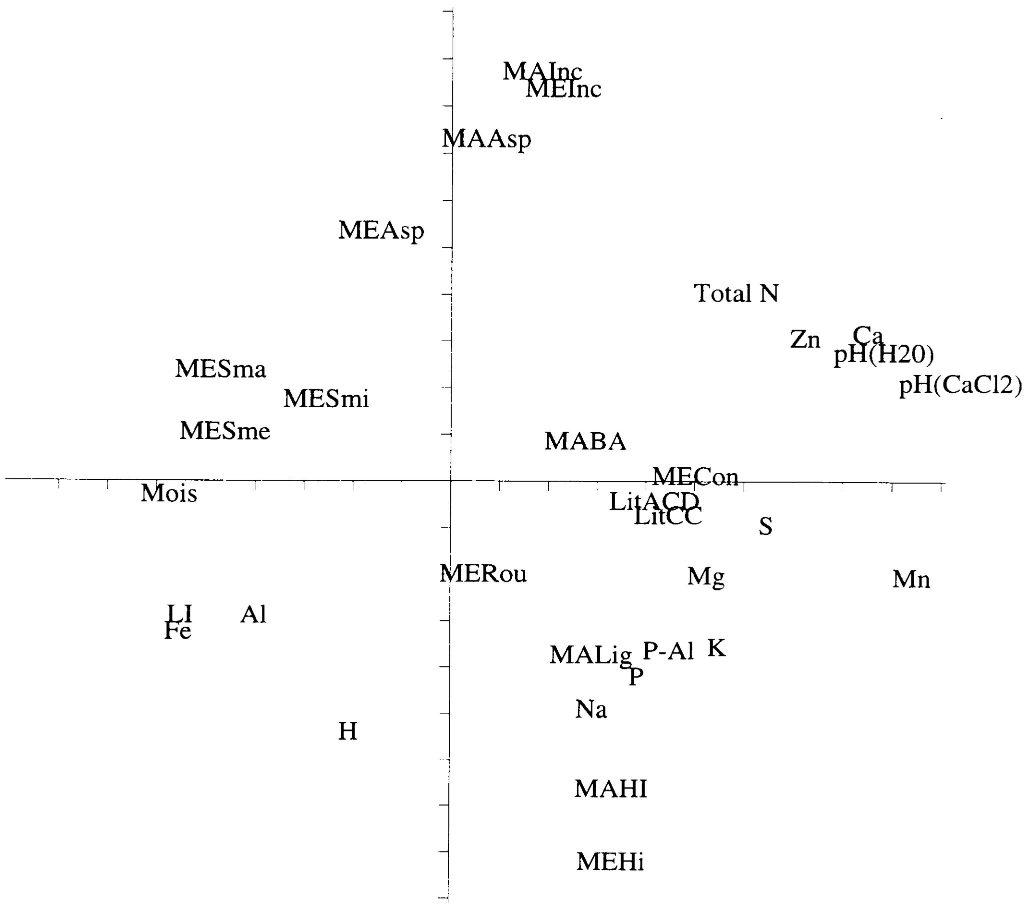


Fig. 699. Granneset: PCA ordination of 32 environmental variables (names abbreviated in accordance with Tab. 2), axes 1 (horizontal) and 2 (vertical). Positions of variables in the ordination give the head of variable vectors.

Macro and meso plot inclination and macro plot aspect unfavourability obtained the highest loadings on PCA 2, while macro and meso plot heat indices obtained the lowest loadings on PCA 2.

PCA ordination results were mainly consistent with the correlations between variables (Tab. 30, Fig. 698).

DCA and LNMDS ordination

The plots were relatively evenly distributed along the first two DCA axes (Fig. 700), while the LNMDS ordination (Fig. 701) was influenced by outliers (plot Nos 41 and 43). Thus 90% of the plots were concentrated between 1.3 and 2.8 S.D. units along LNMDS 1 and between 0.5 and 2.2 S.D. units along LNMDS 2. Due to these outliers, the gradients were somewhat longer for LNMDS axes than for comparable DCA axes. The outliers had few species (6 and 11, respectively, against an area average of 22.1) and few species-in-subplot occurrences.

The fraction of variation explained by DCA 1 was 15.9% (Tab. 31), decreasing by ca. 50% from DCA 1 to DCA 2 and from DCA 2 to DCA 3. The eigenvalues (Tab. 31) of DCA 3 and DCA 4 were low (0.099 and 0.067, respectively), corresponding to explained fractions of variation below 5%.

Correlations between DCA and LNMDS ordination axes and between ordination axes and environmental variables

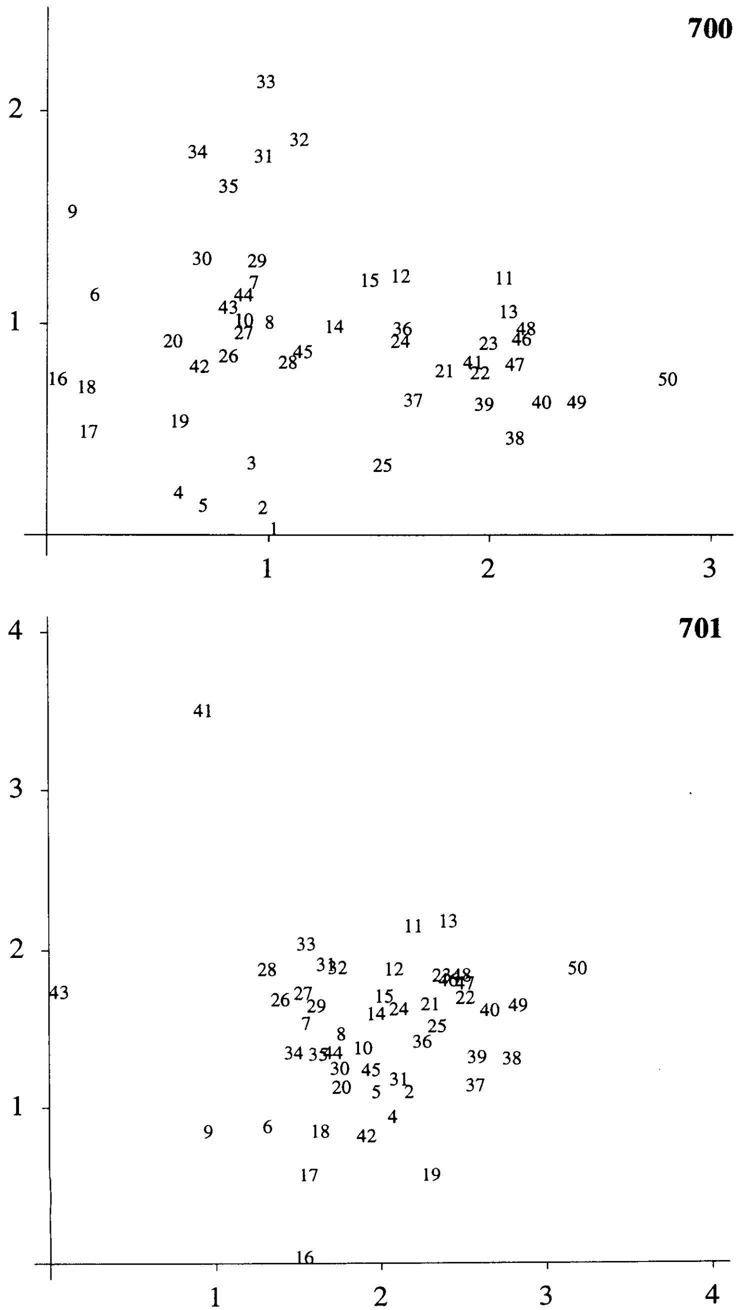
DCA 1 was strongly correlated with both LNMDS 1 and LNMDS 2 (τ = 0.568 and τ = 0.476, respectively, Tab. 32); i.e. the variation along DCA 1 was partly represented by LNMDS 1 and partly by LNMDS 2. Variables strongly correlated with DCA 1 were thus correlated with LNMDS 1 and/or LNMDS 2. DCA 2 was only weakly correlated with the LNMDS axes.

The variables most strongly correlated with DCA 1 were pH (Fig. 710) and concentrations of Ca (Fig. 711) and Zn (Fig. 714), with positive correlations, and loss on ignition (Fig. 709), which was negatively correlated with this axis. Other correlated variables were Mn and total N (Fig. 715) which were positively correlated, and soil depth median (Fig. 705) and maximum (Fig. 706), soil moisture (Fig. 708) and Fe (Fig. 713), all negatively correlated. The variable most strongly correlated with LNMDS 1 was loss on ignition.

The variables most strongly correlated with DCA 2 were the macro plot light index (Fig. 704) and the litter index based on crown cover (Fig. 707), both with positive correlations, and

Tab. 31. Granneset: Eigenvalues and the fraction of variation explained for DCA axes 1-4.

	DCA 1	DCA 2	DCA 3	DCA 4
Eigenvalues	0.350	0.188	0.099	0.067
Fraction of variation explained	0.159	0.086	0.045	0.031

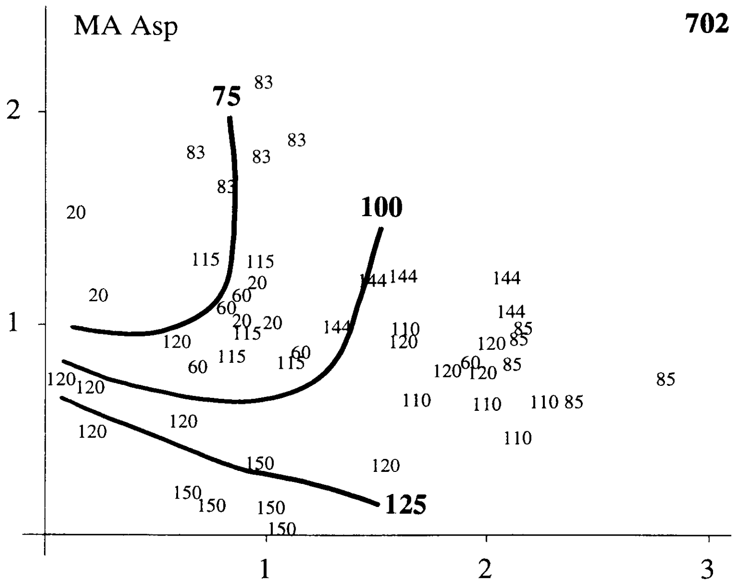


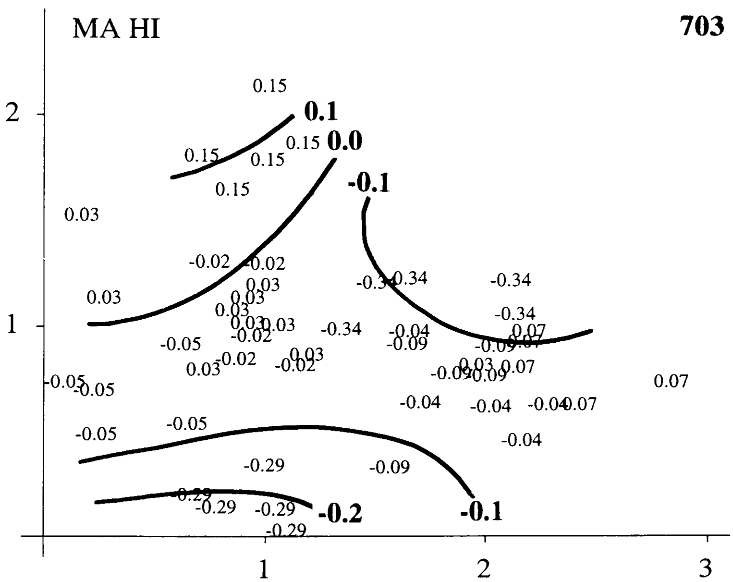
Figs 700-701. Granneset: ordinations of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Meso plot numbers are plotted onto the sample plot positions. Fig. 700. DCA ordination. Scaling of axes in S.D. units. Fig. 701. LNMDS ordination. Axes linearly rescaled in S.D. units.

Tab. 32. Granneset: Kendall's nonparametric correlation coefficient τ between DCA and LNMDS axes, and between 32 environmental variables in the 50 meso sample plots and sample plot positions with respect to DCA and LNMDS axes, and their significance probabilities. Correlations significant at level $P < 0.0001$ in bold face. n.s. - significance probability > 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 2.

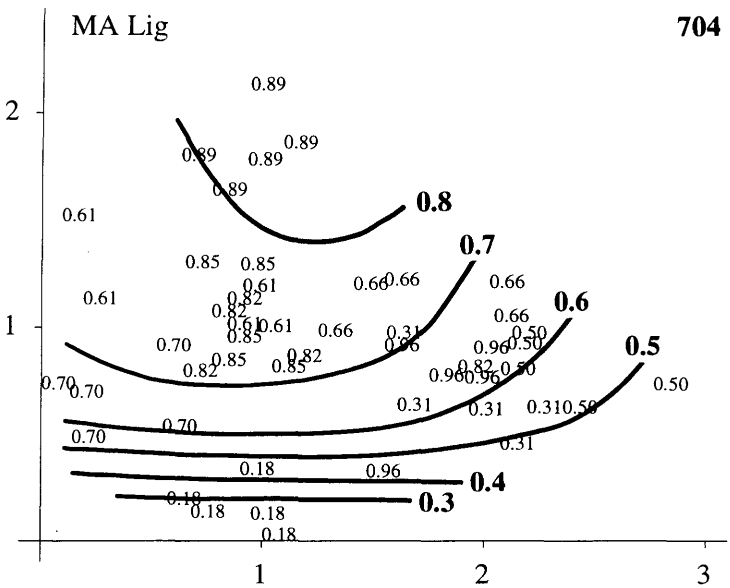
Variable	DCA 1		DCA 2		DCA 3		DCA 4		LNMDS 1		LNMDS 2	
	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P
LNMDS 1	**.5684**	**.0000**	-.3250	.0009	.1699	.0819	.1895	.0523				
LNMDS 2	**.4759**	**.0000**	.2816	.0039	-.1461	n.s.	-.1314	n.s.				
01 MA Inc	.1875	.0658	-.0120	n.s.	-.2064	.0428	.1049	n.s.	.1893	.0634	.2511	.0137
02 MA Asp	.0155	n.s.	-.3429	.0008	-.3808	.0002	.0310	n.s.	.1991	.0512	-.0810	n.s.
03 MA Hi	-.0213	n.s.	.3495	.0005	.2883	.0044	.0604	n.s.	-.1803	.0745	.1454	n.s.
04 MA BA	.0434	n.s.	.2121	.0362	.1218	n.s.	.1286	n.s.	-.1057	n.s.	.2240	.0269
05 MA Lig	-.0775	n.s.	.3671	.0003	-.1491	n.s.	-.0877	n.s.	-.2761	.0064	.2223	.0281
06 ME Inc	.2847	.0039	-.0074	n.s.	-.2022	.0402	.0338	n.s.	.2361	.0166	.2929	.0030
07 ME Asp	-.0246	n.s.	-.1755	.0733	.0180	n.s.	.1558	n.s.	.2125	.0302	-.2804	.0042
08 ME Hi	-.0922	n.s.	.2065	.0343	.0988	n.s.	-.0988	n.s.	-.2858	.0034	.1380	n.s.
09 ME Rou	-.0261	n.s.	-.0345	n.s.	.0647	n.s.	-.1925	.0543	-.0370	n.s.	-.0311	n.s.
10 ME Con	.1335	n.s.	.1599	n.s.	.0989	n.s.	-.0115	n.s.	.0453	n.s.	.1352	n.s.
11 ME Smi	-.1260	n.s.	.2117	.0314	-.2447	.0129	.0008	n.s.	-.2472	.0120	.0750	n.s.
12 ME Sme	-.3864	.0001	.0911	n.s.	-.2715	.0056	-0960	n.s.	-.3266	.0009	-.1731	.0774
13 ME Sma	-.3547	.0003	-.0924	n.s.	-.2144	.0294	-.0957	n.s.	-.1791	.0691	-.2276	.0208
14 LitCC	.1165	n.s.	.3763	.0001	-.2447	.0135	-.2214	.0254	-.1957	.0483	**.4712**	**.0000**
15 LitACD	.0940	n.s.	.3154	.0015	-.2971	.0027	-.2355	.0174	-.2048	.0387	**.4086**	**.0000**
16 Mois	-.3094	.0015	-.2947	.0025	.0416	n.s.	.1053	n.s.	-.0719	n.s.	**-.4939**	**.0000**
17 LI	**-.4064**	**.0000**	.2167	.0266	-.1267	n.s.	.0041	n.s.	**-.4384**	**.0000**	-.1889	.0533
18 pH_{H2O}	**.4489**	**.0000**	-.1526	n.s.	-.0152	n.s.	-.0669	n.s.	.3446	.0009	.2883	.0057
19 pH_{CaCl2}	**.5507**	**.0000**	-.0250	n.s.	.0198	n.s.	.0319	n.s.	.3259	.0014	**.4249**	**.0000**
20 Ca	**.5053**	**.0000**	.1445	n.s.	-.0449	n.s.	.0351	n.s.	.2417	.0133	**.4873**	**.0000**
21 Mg	.1135	n.s.	-.3355	.0006	.1608	.0994	-.0857	n.s.	.1862	.0565	-.1429	n.s.
22 K	.0629	n.s.	-.2882	.0031	.1559	n.s.	.0302	n.s.	.1748	.0734	-.1510	n.s.
23 Na	-.1886	.0533	-.0629	n.s.	-.0139	n.s.	-.1886	.0533	-.1748	.0734	-.0922	n.s.
24 H^+	-.2131	.0290	.0465	n.s.	.1967	.0438	.0090	n.s.	-.2630	.0071	-.1592	n.s.
25 Al	-.2702	.0056	-.2620	.0073	.2473	.0113	.0204	n.s.	-.0915	n.s.	**-.4351**	**.0000**
26 Fe	-.3698	.0002	-.0743	n.s.	.0269	n.s.	-.0792	n.s.	-.2368	.0153	-.2931	.0027
27 Mn	3600	.0002	.0318	n.s.	.1102	n.s.	-.0188	n.s.	.1421	n.s.	.3845	.0001
28 Zn	**.4678**	**.0000**	.0580	n.s.	-.1445	n.s.	-.0939	n.s.	.1944	.0465	**.4759**	**.0000**
29 Total N	.3682	.0002	-.1690	.0834	-.0253	n.s.	.0351	n.s.	.2858	.0034	.2751	.0048
30 P-AL	.0400	n.s.	-.0824	n.s.	.1331	n.s.	-.0971	n.s.	-.0245	n.s.	.0188	n.s.
31 P	-.0041	n.s.	-.0482	n.s.	.0400	n.s.	-.1020	n.s.	-.0588	n.s.	.0106	n.s.
32 S	.1984	.0421	-.3649	.0002	.1641	.0927	.0416	n.s.	.3234	.0009	-.0873	n.s.

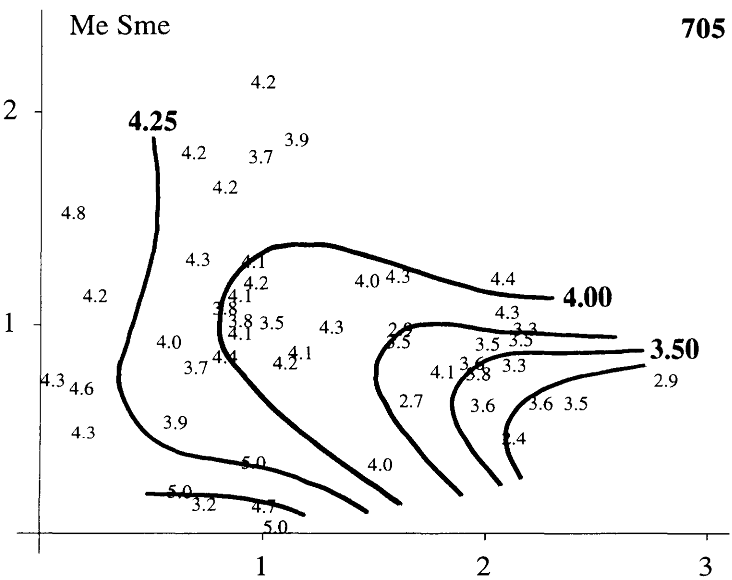
the concentration of S, with negative correlation. Other variables correlated with DCA 2 were macro plot heat index, positively correlated (Fig. 703), and macro plot aspect unfavourability (Fig. 702) and the concentration of Mg (Fig. 712), both negatively correlated. Soil moisture (Fig. 708) was also correlated with DCA 2, and the correlation was only slightly less strong



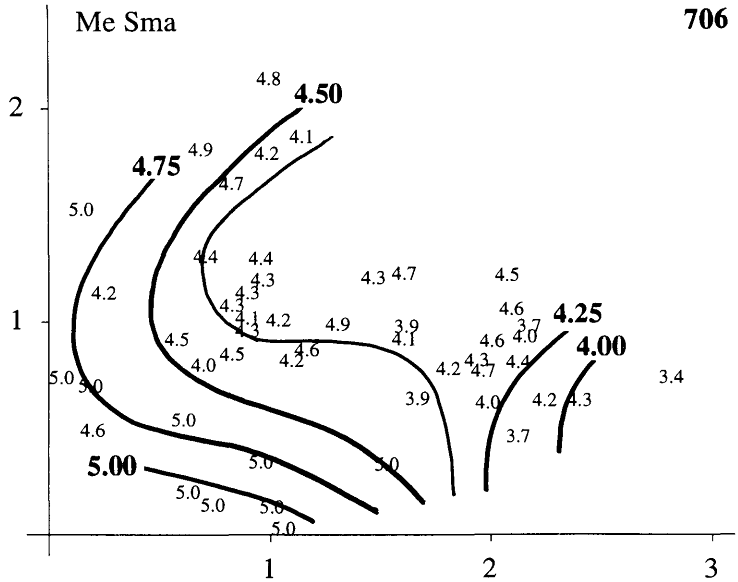


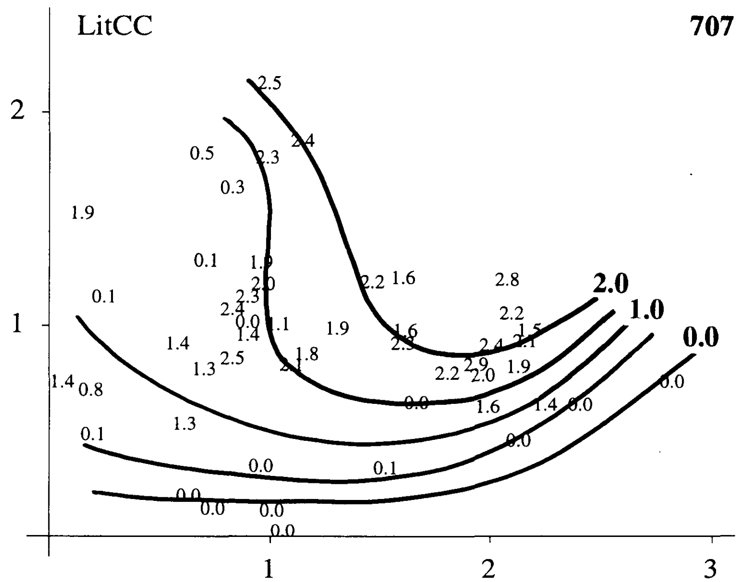
Figs 702-703. Granneset: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots' positions. Scaling of axes in S.D. units. Fig. 702. MA Asp (R^2 = 0.472). Fig. 703. MA Hi (R^2 = 0.613). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.





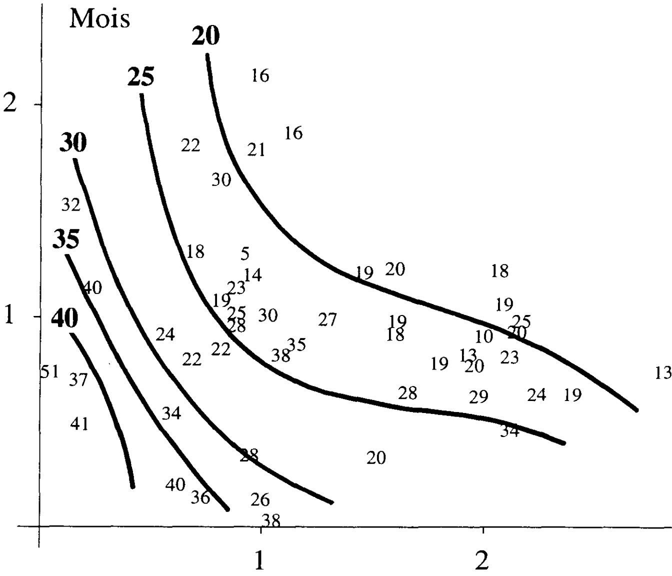
Figs 704-705. Granneset: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots' positions. Scaling of axes in S.D. units. Fig. 704. MA Lig (R^2 = 0.495). Fig. 705. ME Sme (R^2 = 0.490). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.





Figs 706-707. Granneset: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 706. ME Sma (R^2 = 0.572). Fig. 707. Lit CC (R^2 = 0.590). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.

708



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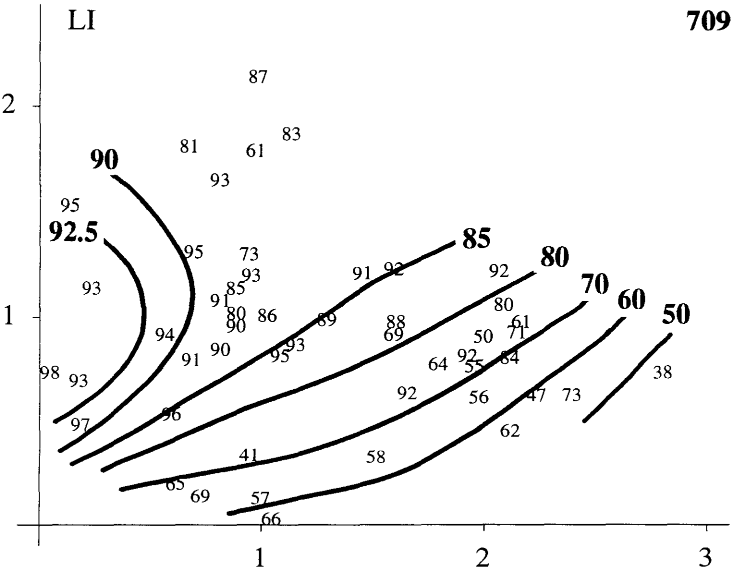
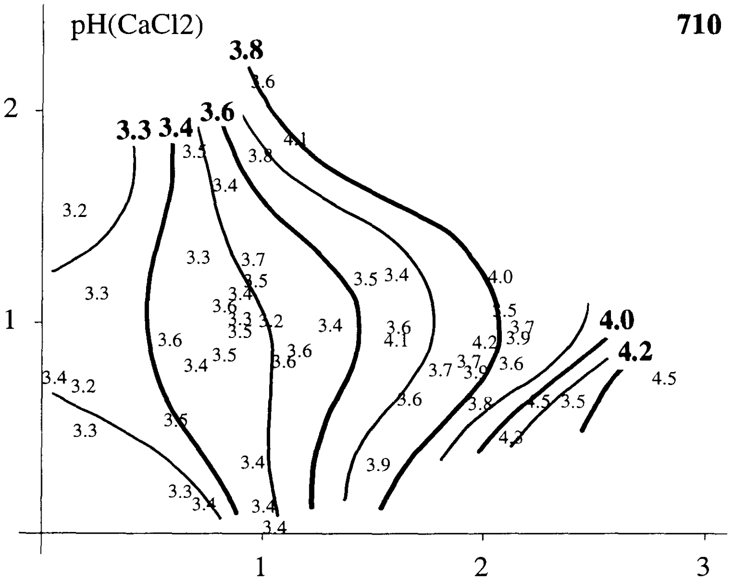
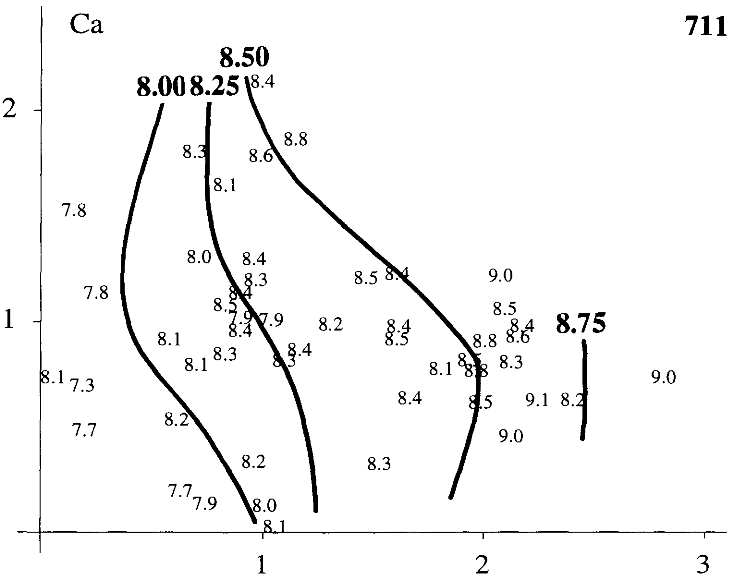
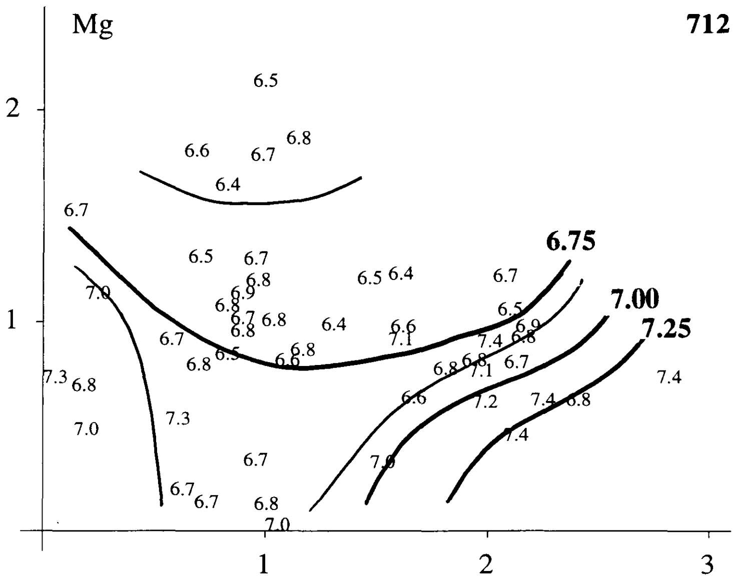


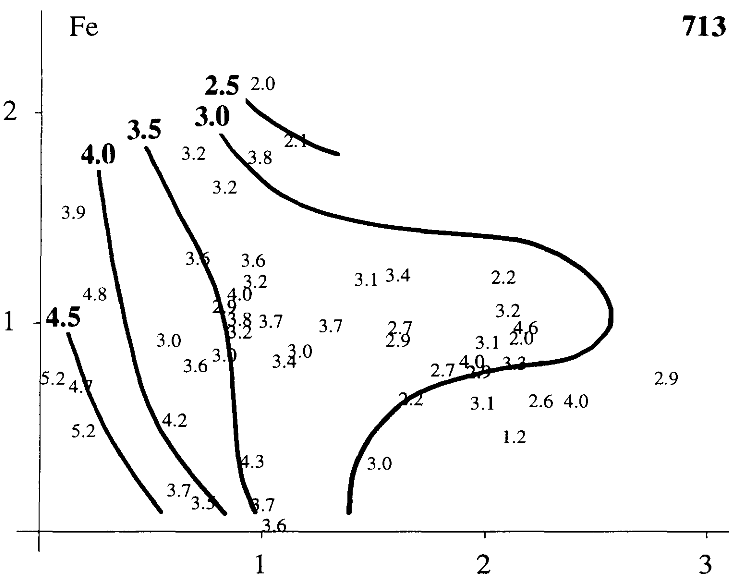
Figs 708-709. Granneset: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 708. Mois (R^2 = 0.606). Fig. 709. LI (R^2 = 0.580). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.



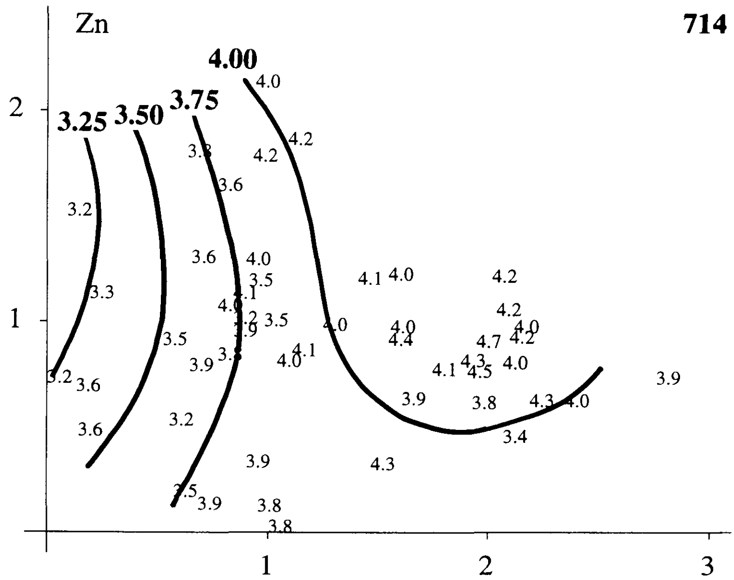


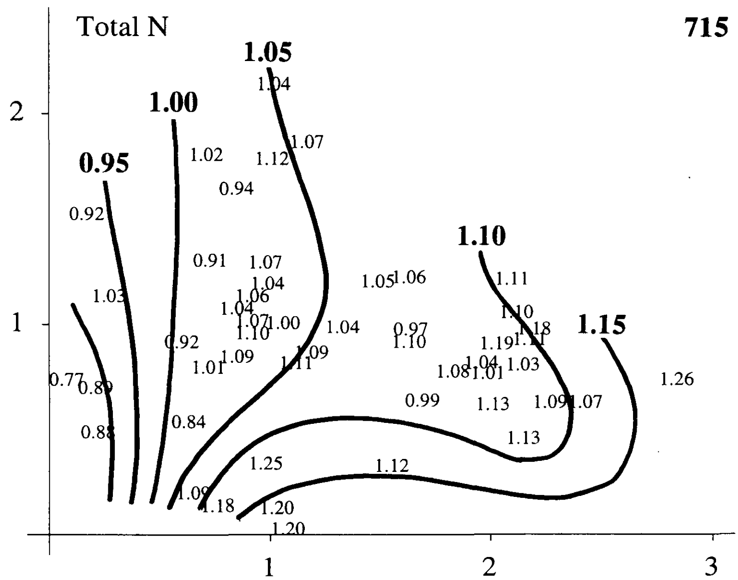
Figs 710-711. Granneset: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots' positions. Scaling of axes in S.D. units. Fig. 710. pH_{CaCl2} (R^2 = 0.598). Fig. 711. Ca (R^2 = 0.645). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.



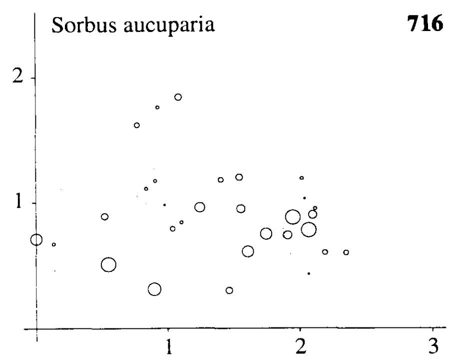


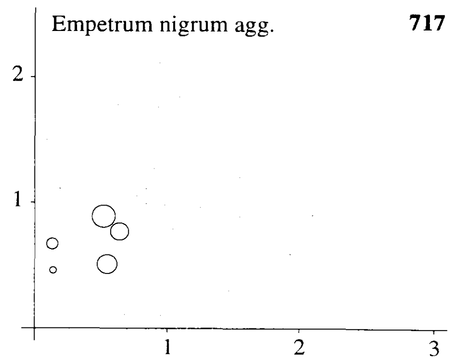
Figs 712-713. Granneset: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 712. Mg (R^2 = 0.451). Fig. 713. Fe (R^2 = 0.536). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.

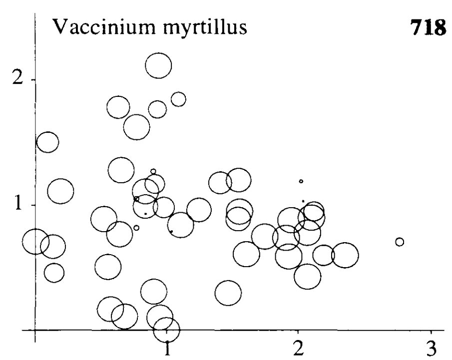


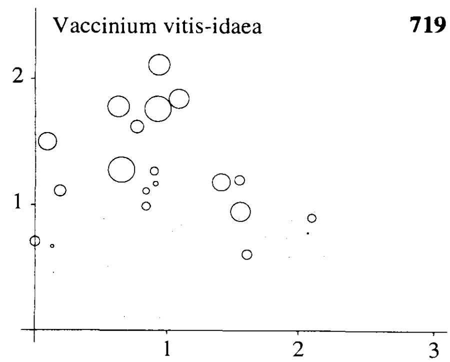


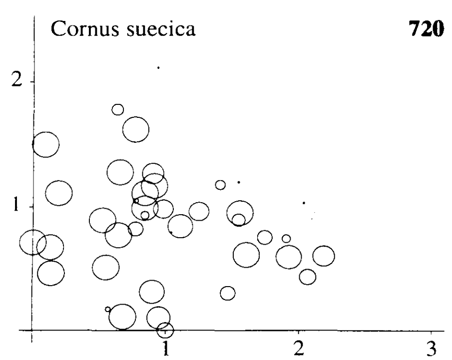
Figs 714-715. Granneset: isolines for environmental variables in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Values for the environmental variables are plotted onto the meso plots′ positions. Scaling of axes in S.D. units. Fig. 714. Zn ($R^2 = 0.564$). Fig. 715. Total N ($R^2 = 0.668$). R^2 refers to the coefficient of determination between original and smoothened values as interpolated from the isolines. Names of environmental variables in accordance with Tab. 2.

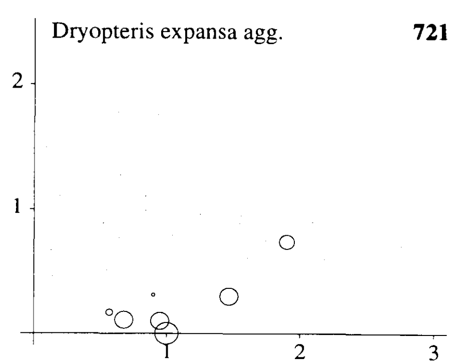




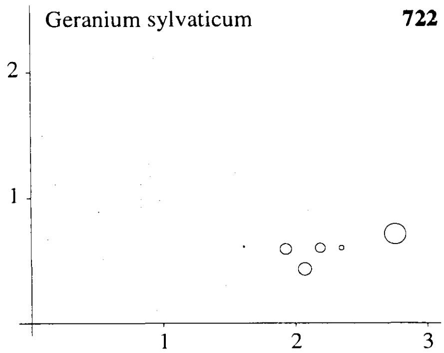


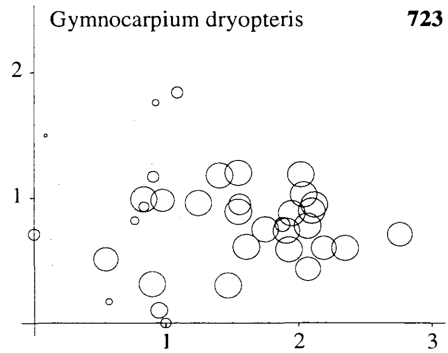


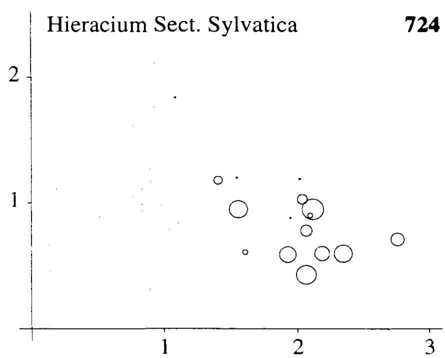


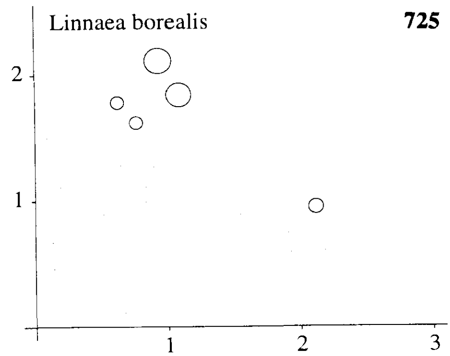


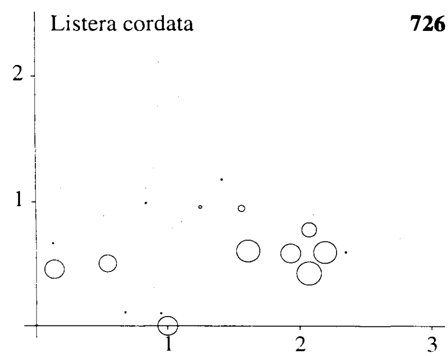
Figs 716-721. Granneset: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 716. *Sorbus aucuparia*. Fig. 717. *Empetrum nigrum*. Fig. 718. *Vaccinium myrtillus*. Fig. 719. *Vaccinium vitis-idaea*. Fig. 720. *Cornus suecica*. Fig. 721. *Dryopteris expansa* agg.

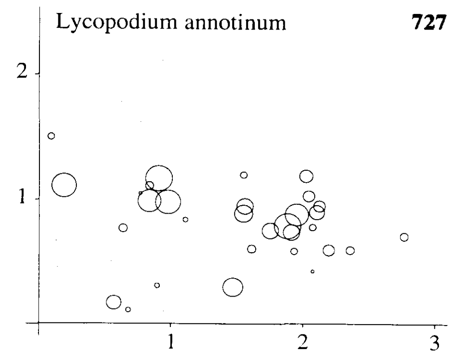




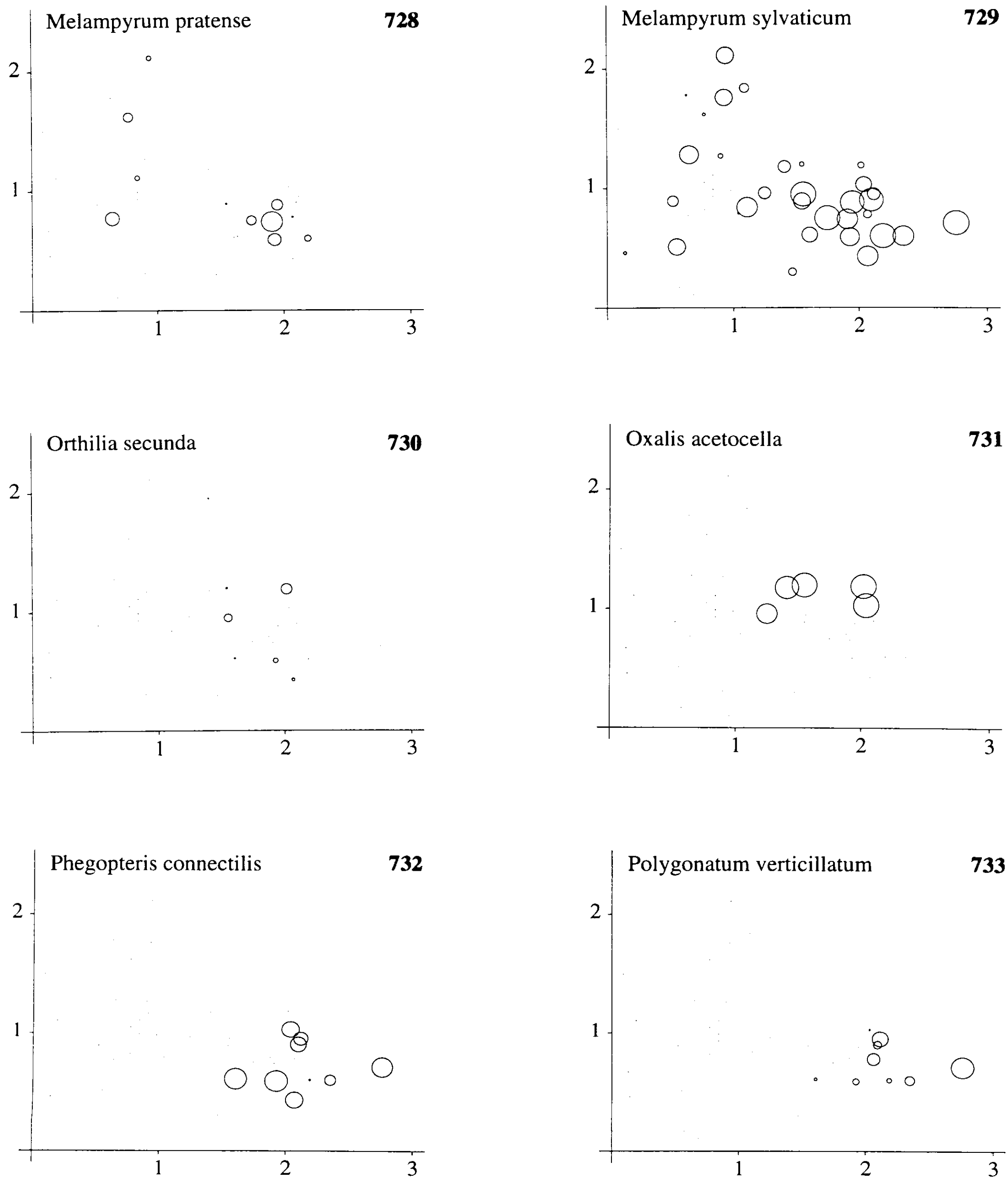




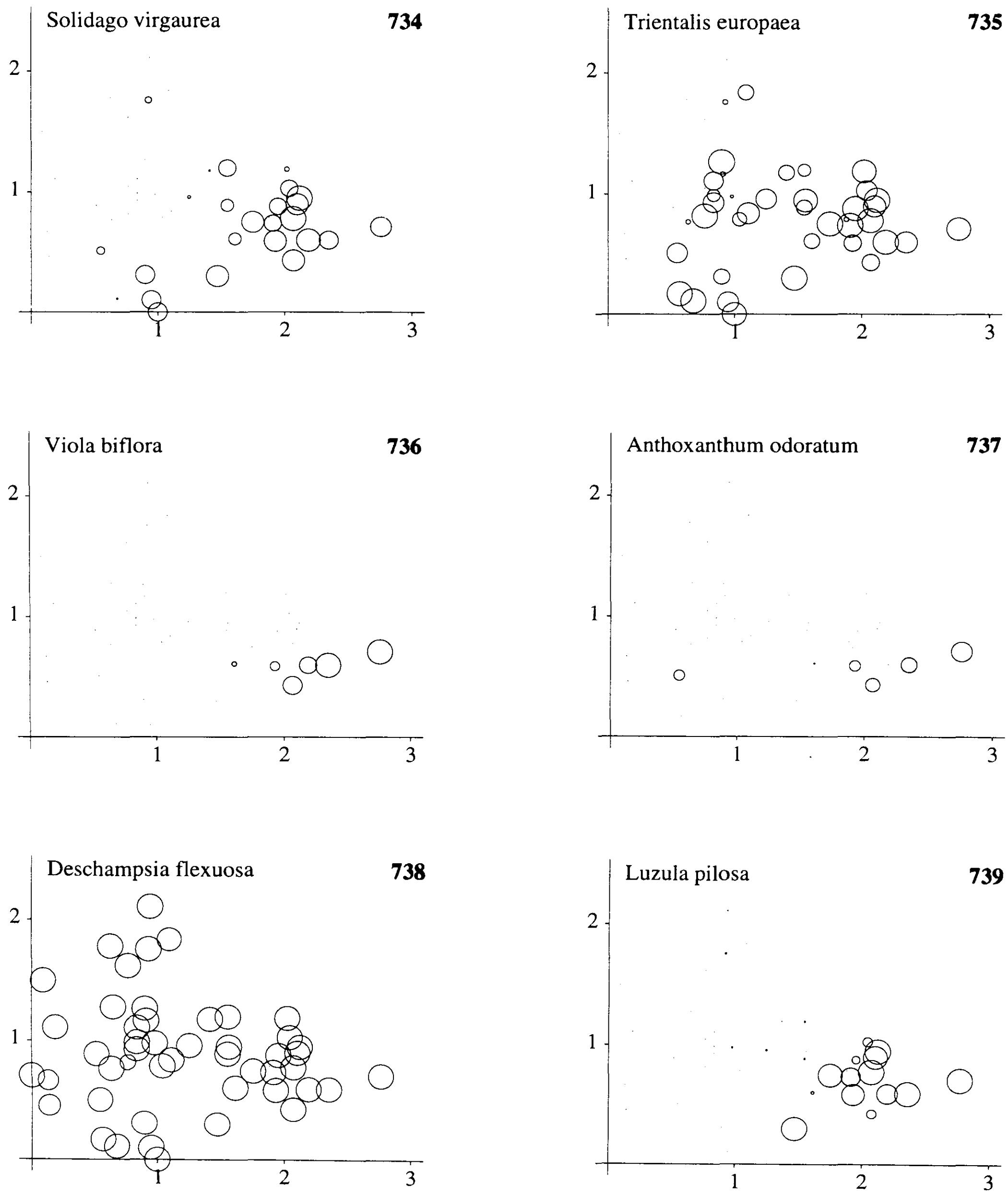




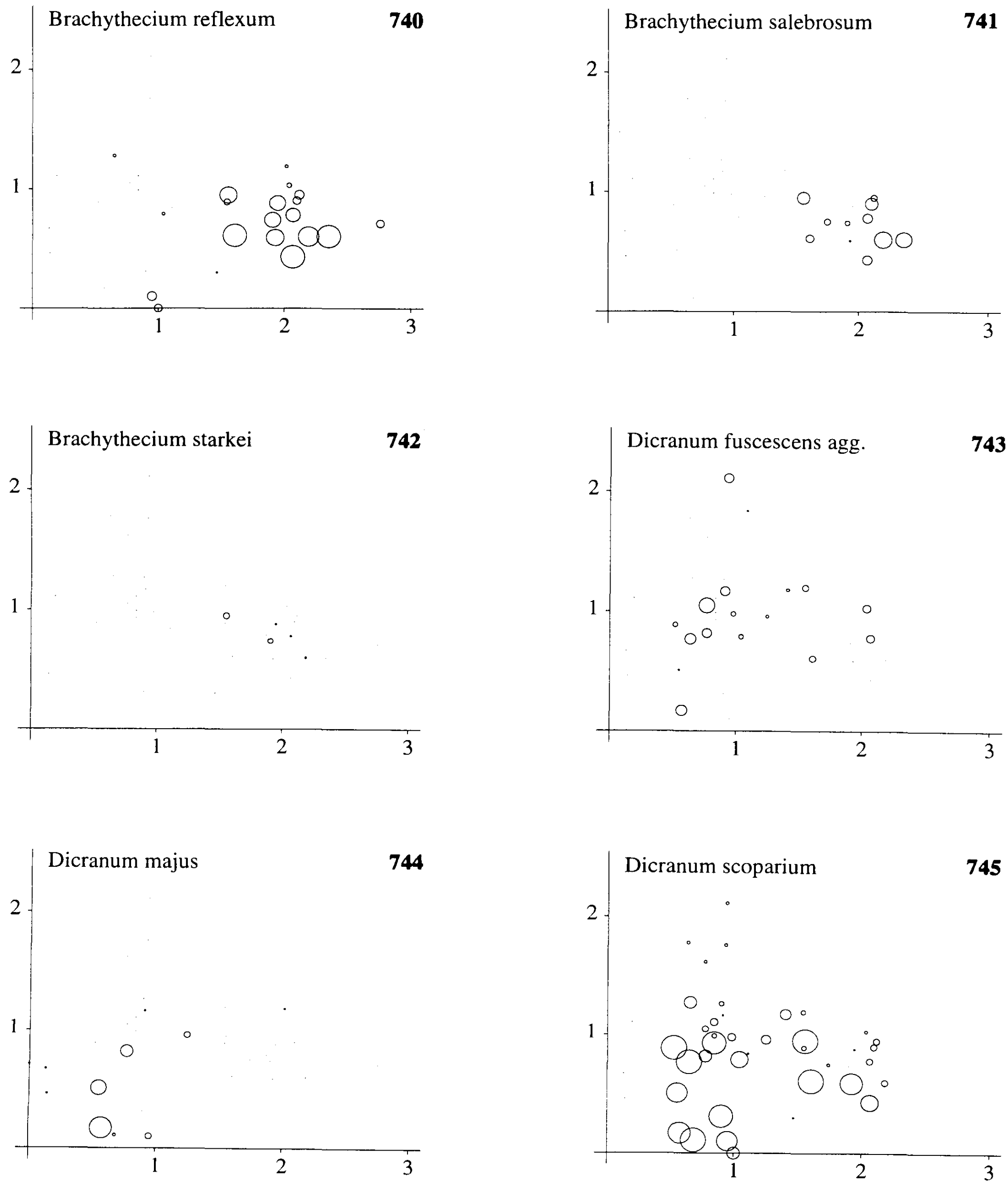
Figs 722-727. Granneset: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 722. *Geranium sylvaticum*. Fig. 723. *Gymnocarpium dryopteris*. Fig. 724. *Hieracium Sect. Sylvatica*. Fig. 725. *Linnaea borealis*. Fig. 726. *Listera cordata*. Fig. 727. *Lycopodium annotinum*.



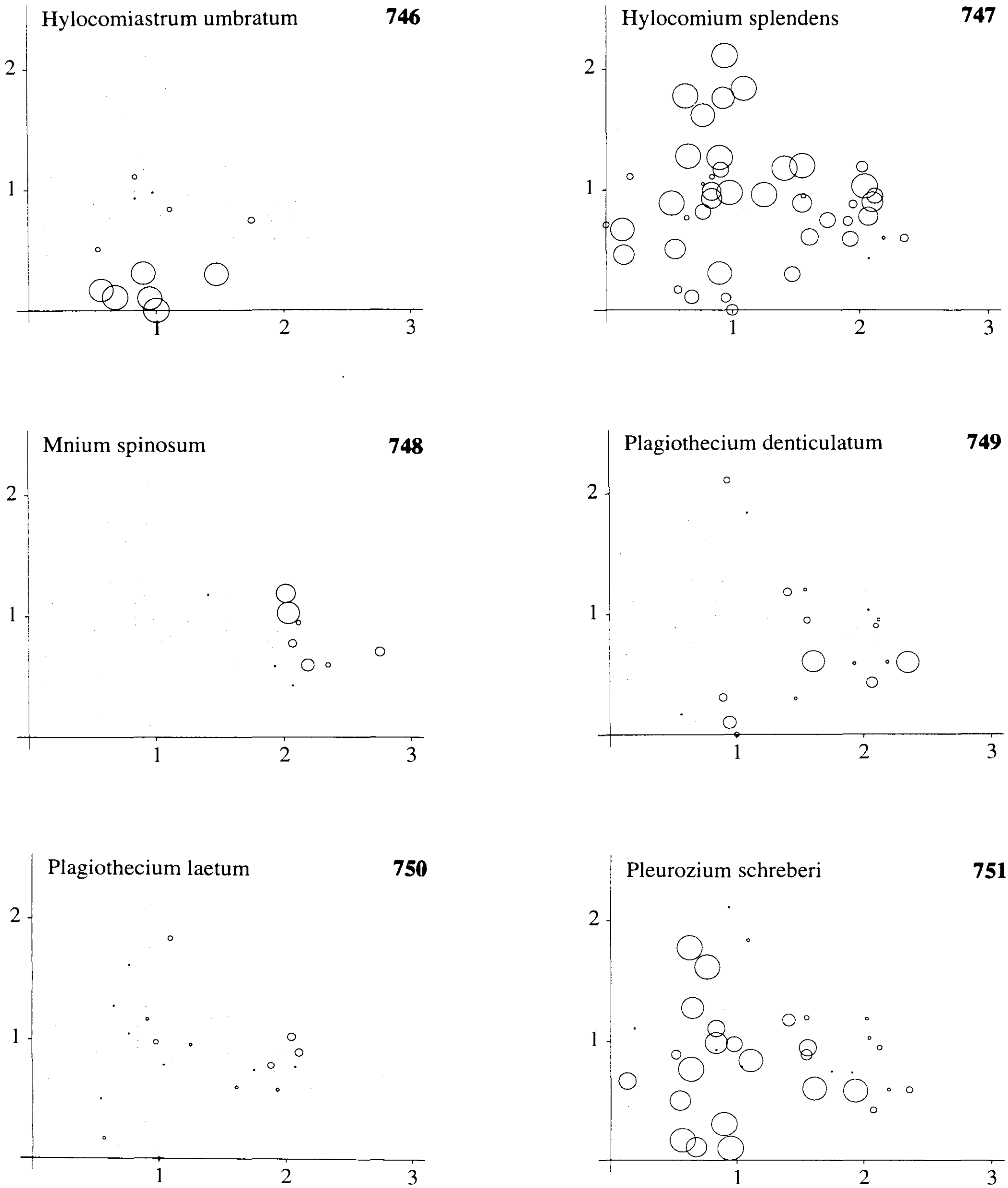
Figs 728-733. Granneset: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 728. *Melampyrum pratense*. Fig. 729. *Melampyrum sylvaticum*. Fig. 730. *Orthilia secunda*. Fig. 731. *Oxalis acetosella*. Fig. 732. *Phegopteris connectilis*. Fig. 733. *Polygonatum verticillatum*.



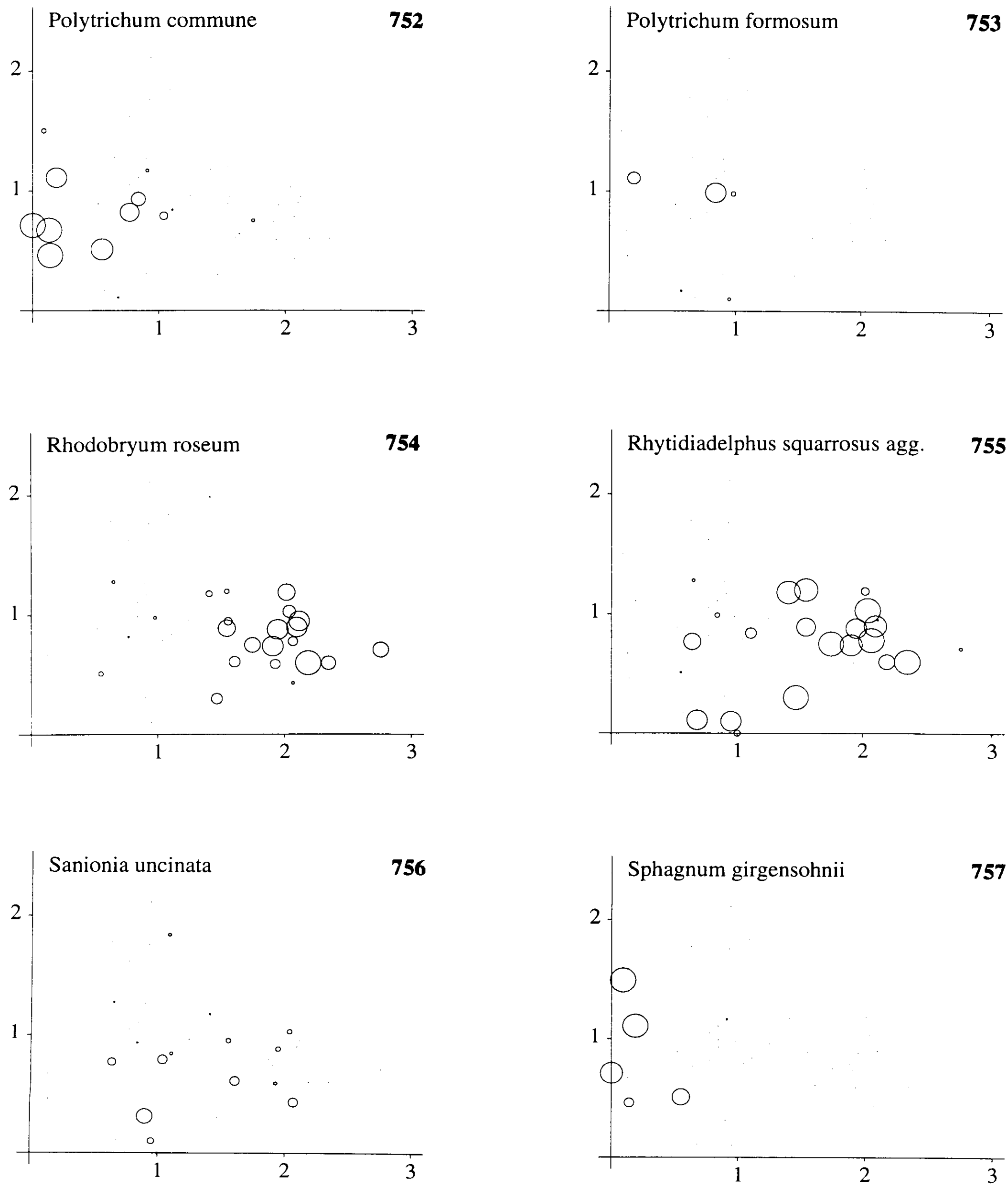
Figs 734-739. Granneset: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 734. *Solidago virgaurea*. Fig. 735. *Trientalis europaea*. Fig. 736. *Viola biflora*. Fig. 737. *Anthoxanthum odoratum*. Fig. 738. *Deschampsia flexuosa*. Fig. 739. *Luzula pilosa*.



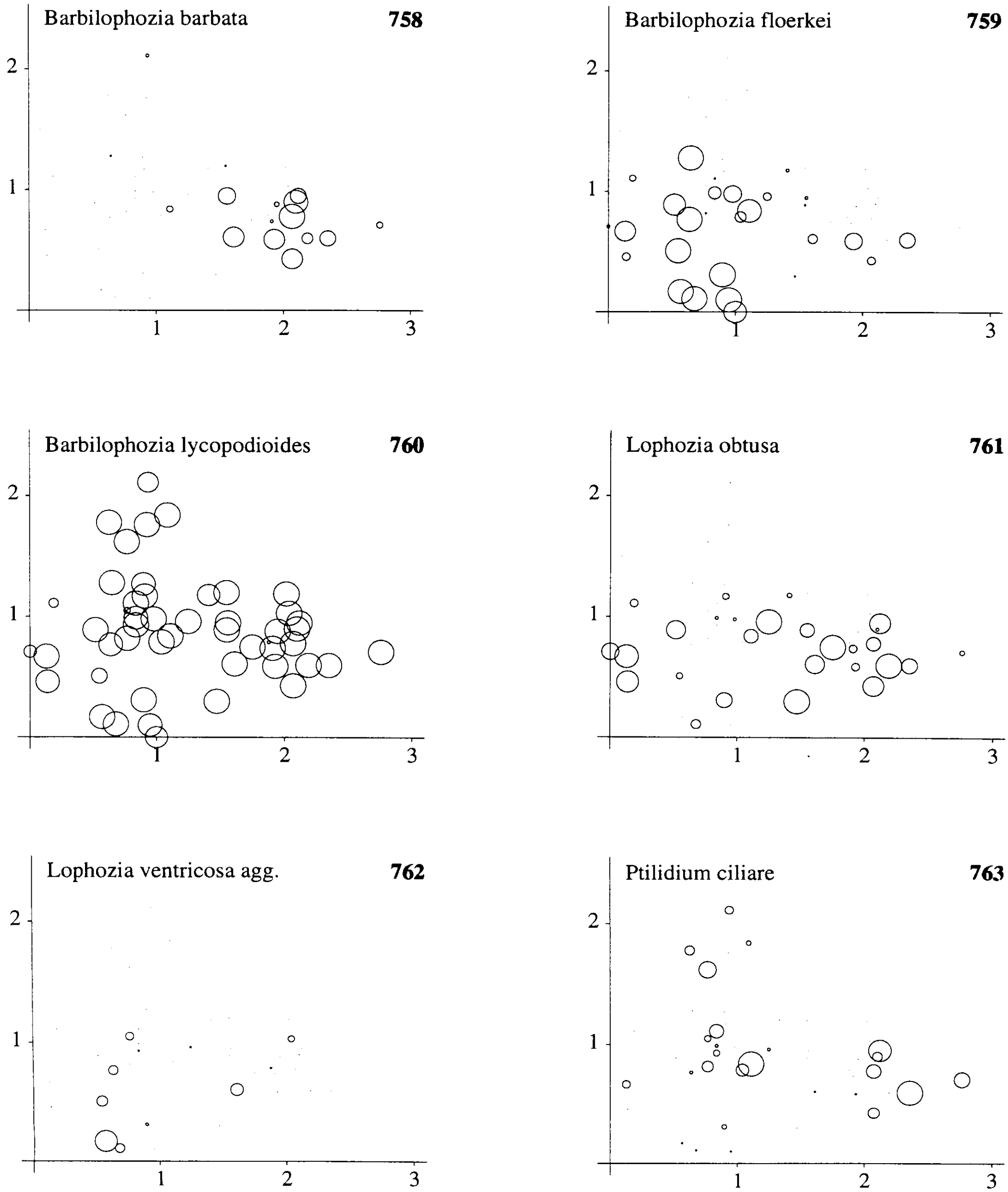
Figs 740-745. Granneset: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 740. *Brachythecium reflexum*. Fig. 741. *Brachythecium salebrosum*. Fig. 742. *Brachythecium starkei*. Fig. 743. *Dicranum fuscescens* agg. Fig. 744. *Dicranum majus*. Fig. 745. *Dicranum scoparium*.



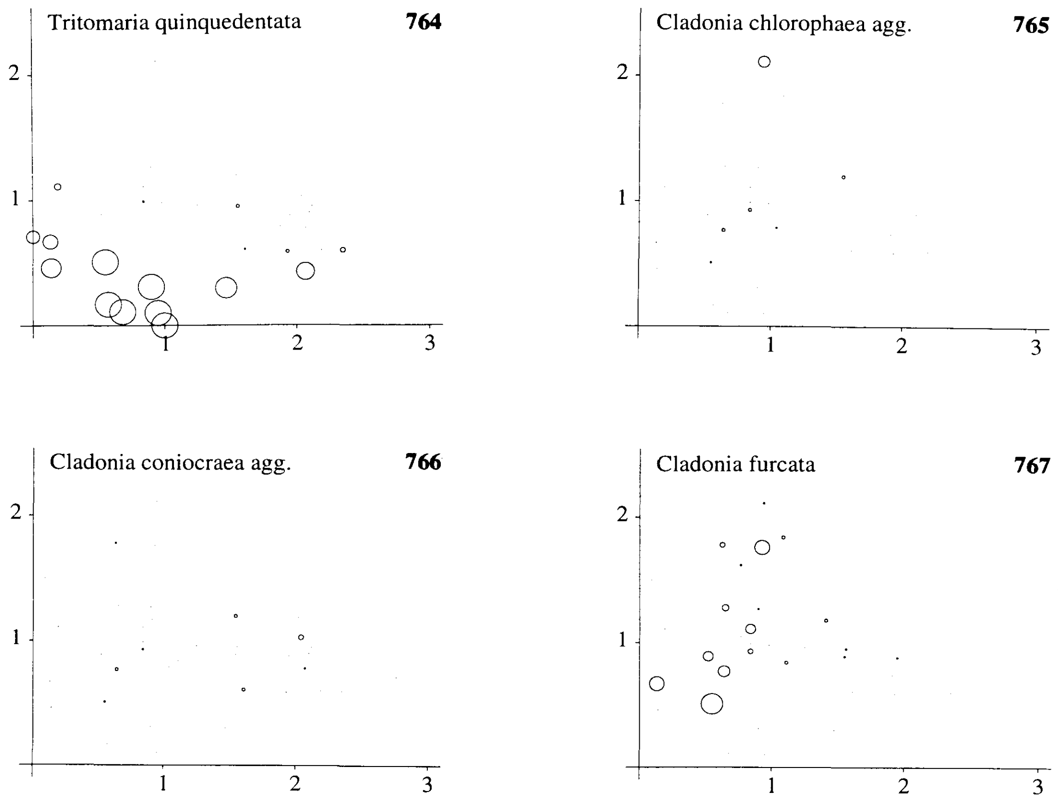
Figs 746-751. Granneset: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 746. *Hylocomiastrum umbratum*. Fig. 747. *Hylocomium splendens*. Fig. 748. *Mnium spinosum*. Fig. 749. *Plagiothecium denticulatum*. Fig. 750. *Plagiothecium laetum*. Fig. 751. *Pleurozium schreberi*.



Figs 752-757. Granneset: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 752. *Polytrichum commune*. Fig. 753. *Polytrichum formosum*. Fig. 754. *Rhodobryum roseum*. Fig. 755. *Rhytidiadelphus squarrosus* agg. Fig. 756. *Sanionia uncinata*. Fig. 757. *Sphagnum girgensohnii*.



Figs 758-763. Granneset: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 758. *Barbilophozia barbata*. Fig. 759. *Barbilophozia floerkei*. Fig. 760. *Barbilophozia lycopodioides*. Fig. 761. *Lophozia obtusa*. Fig. 762. *Lophozia ventricosa* agg. Fig. 763. *Ptilidium ciliare*.



Figs 764-767. Granneset: distributions of species abundances in the DCA ordination of 50 meso plots, axes 1 (horizontal) and 2 (vertical). Frequency in subplots for each species in each meso plot proportional to circle size. Scaling of axes in S.D. units. Fig. 764. *Tritomaria quinquedentata*. Fig. 765. *Cladonia chlorophaea* agg. Fig. 766. *Cladonia coniocraea* agg. Fig. 767. *Cladonia furcata*.

than with DCA 1. The variables most strongly correlated with LNMDS 2 were the litter indices, soil moisture, pH and concentrations of Ca, Al and Zn.

Only macro plot aspect was strongly correlated with DCA 3 (which was also correlated with DCA 2).

The distribution of species abundance in the DCA ordination

Fifty-two of a total of 102 species occurred in 5 or more of the 50 meso plots (Figs 716-767).

Vaccinium myrtillus (Fig. 718), a typical example of a species with wide ecological amplitude, was abundant in most plots. Other examples of abundant species were *Deschampsia flexuosa* (Fig. 738), *Hylocomium splendens* (Fig. 747) and *Barbilophozia lycopodioides* (Fig. 760).

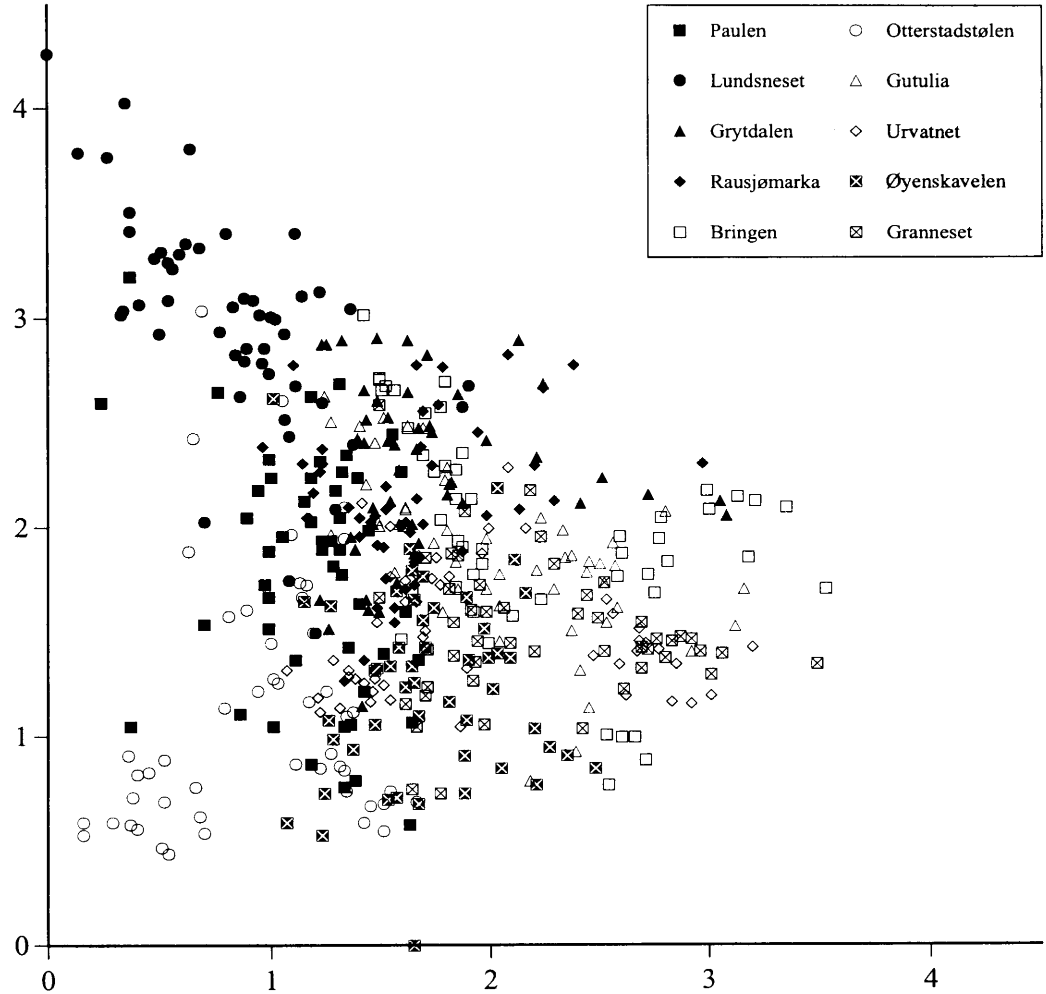


Fig. 768. The total data set: DCA of 500 sample plots, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

Examples of species restricted to the plots on relatively dry sites with high nutrient contents and high pH (lower right part of the DCA ordination) were *Geranium sylvaticum* (Fig. 722), *Polygonatum verticillatum* (Fig. 733), *Phegopteris connectilis* (Fig. 732), *Viola biflora* (Fig. 736), *Brachythecium reflexum* (Fig. 740), *B. salebrosum* (Fig. 741) and *Mnium spinosum* (Fig. 748).

Polytrichum commune (Fig. 752) was restricted to plots on relatively moist sites, poor in nutrients (lower left part of the ordination diagram). *Hylocomiastrum umbratum* (Fig. 746) was restricted to plots on moist sites but with relatively low to moderately high pH and nutrient content.

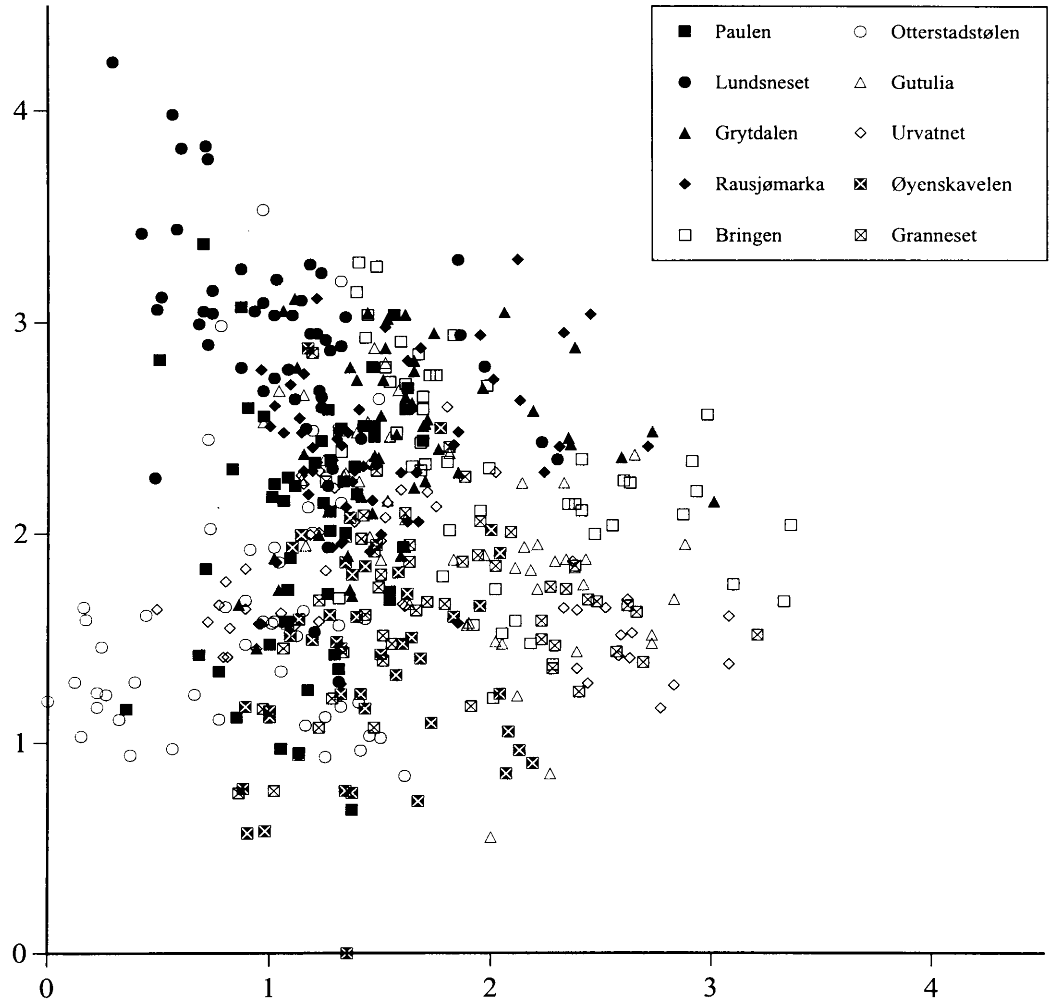


Fig. 769. The total data set: DCA of 500 sample plots with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

THE TOTAL DATA SET

Variation in species abundances between reference areas

Twenty-seven species showed decreasing, while thirty species showed increasing frequency from the Boreo-nemoral to the Northern Boreal zone (Tab. 33). *Calamagrostis arundinacea*

Tab. 33. Abundance and distribution of species in the total data set; reference areas ordered according to vegetation zone from the Boreo-Nemoral to the Northern Boreal, species ordered by preference for warmer and colder zones, respectively. Indifferent and infrequent species are listed at the bottom of the table. Reference areas abbreviated by the first three letters of their names, see Tab. 1. Quantity for each species in each reference area is given as F^{MSF} where F is frequency % in the area, MSF is the mean frequency in subplots (calculated for the plots in which the species occurs).

Species	PAU	LUN	RAU	OTT	ØYE	URV	GRY	GRA	BRI	GUT	Total
Frangula alnus	6^{3}	4^{4}	·	·	·	·	·	·	·	·	1.0^{3}
Calamagrostis arundinacea	·	18^{7}	50^{13}	·	·	·	·	·	·	·	6.8^{11}
Hypnum cupressiforme agg.	42^{2}	40^{7}	2^{1}	38^{6}	·	·	·	·	·	·	12.2^{5}
Thuidium tamariscinum	8^{4}	·	·	8^{12}	·	·	·	·	·	·	1.6^{8}
Diplophyllum albicans	16^{3}	·	·	22^{3}	·	·	·	·	·	·	3.8^{3}
Heterocladium heteropterum	·	6^{5}	·	4^{1}	·	·	·	·	·	·	1.0^{3}
Leucobryum glaucum	·	2^{2}	·	12^{4}	·	·	·	·	·	·	1.4^{4}
Dicranodontium denudatum	6^{2}	·	·	44^{4}	2^{1}	·	·	·	·	·	5.2^{4}
Mylia taylorii	4^{2}	·	2^{1}	20^{2}	2^{1}	·	·	·	·	·	2.8^{2}
Pseudotaxiphyllum elegans	12^{5}	2^{1}	4^{2}	10^{3}	8^{2}	·	·	·	·	·	3.6^{3}
Mnium hornum	10^{2}	4^{5}	·	·	32^{3}	·	·	·	·	·	4.6^{3}
Herzogiella striatella	10^{1}	4^{1}	·	10^{1}	42^{3}	·	·	·	·	·	6.6^{2}
Carex pilulifera	8^{2}	8^{3}	·	10^{3}	·	8^{1}	·	·	·	·	3.4^{2}
Plagiothecium undulatum	58^{8}	12^{3}	·	74^{12}	78^{10}	56^{12}	·	·	·	·	27.8^{10}
Pteridium aquilinum	40^{4}	4^{1}	8^{9}	10^{5}	·	·	2^{2}	·	·	·	6.4^{5}
Plagiochila asplenoides	22^{3}	·	60^{7}	26^{7}	30^{9}	30^{7}	2^{1}	·	·	·	17.0^{7}
Rhytidiadelphus loreus	28^{3}	·	2^{6}	90^{13}	88^{12}	70^{10}	22^{7}	·	·	·	30.0^{10}
Chiloscyphus coadunatus	14^{4}	·	4^{3}	34^{5}	6^{10}	8^{9}	4^{2}	·	·	·	7.0^{5}
Calypogeia azurea	6^{3}	·	8^{3}	4^{1}	4^{2}	2^{1}	6^{4}	·	·	·	3.0^{2}
Calypogeia muelleriana	40^{6}	4^{3}	20^{2}	78^{8}	80^{6}	28^{4}	18^{2}	·	·	·	26.8^{6}
Anemone nemorosa	10^{2}	·	30^{5}	16^{4}	40^{10}	40^{10}	10^{6}	·	·	·	14.6^{7}
Lepidozia reptans	16^{3}	18^{3}	12^{2}	·	4^{2}	6^{1}	6^{2}	·	4^{2}	·	6.6^{2}
Tetraphis pellucida	30^{3}	20^{4}	16^{1}	20^{1}	34^{2}	·	14^{2}	·	4^{1}	·	13.8^{2}
Polytrichum formosum	60^{6}	12^{4}	12^{7}	82^{9}	40^{8}	8^{3}	6^{3}	10^{5}	2^{4}	·	23.2^{7}
Dicranum polysetum	8^{1}	62^{8}	6^{3}	6^{2}	·	·	·	·	·	2^{2}	8.4^{7}
Sphagnum quinquefarium	16^{4}	10^{7}	22^{7}	42^{13}	14^{5}	24^{9}	24^{11}	·	6^{8}	2^{9}	16.0^{9}
Maianthemum bifolium	80^{9}	20^{6}	86^{11}	52^{5}	28^{12}	74^{8}	42^{7}	·	52^{9}	6^{9}	44.0^{9}
Tritomaria quinquedentata	12^{2}	·	2^{4}	22^{6}	30^{7}	54^{7}	24^{4}	34^{10}	22^{4}	32^{6}	23.2^{6}
Lycopodium annotinum	6^{2}	·	2^{1}	6^{5}	12^{4}	·	28^{8}	62^{8}	20^{10}	32^{5}	16.8^{7}
Rhodobryum roseum	2^{1}	·	2^{1}	·	14^{3}	22^{4}	6^{1}	46^{8}	28^{5}	34^{6}	15.4^{5}
Barbilophozia lycopodioides	2^{12}	·	46^{8}	38^{4}	90^{12}	84^{10}	92^{11}	98^{15}	90^{11}	100^{14}	64.0^{12}
Solidago virgaurea	10^{3}	2^{1}	8^{3}	4^{1}	66^{5}	36^{7}	20^{4}	50^{10}	42^{5}	50^{4}	28.8^{6}
Orthilia secunda	2^{1}	·	·	·	·	18^{2}	·	12^{3}	32^{6}	32^{8}	9.6^{6}
Barbilophozia floerkei	·	6^{4}	24^{5}	48^{8}	62^{7}	60^{9}	40^{5}	56^{9}	12^{3}	66^{7}	37.4^{7}
Brachythecium reflexum	·	·	26^{2}	12^{2}	46^{7}	2^{10}	30^{9}	40^{8}	32^{8}	30^{3}	21.8^{6}
Linnaea borealis	·	·	20^{7}	12^{3}	24^{8}	56^{8}	16^{5}	10^{11}	76^{9}	68^{8}	28.2^{8}
Lophozia obtusa	·	·	14^{2}	18^{4}	66^{10}	58^{6}	28^{4}	54^{9}	44^{9}	70^{8}	35.2^{7}
Melampyrum sylvaticum	·	·	34^{6}	·	16^{4}	62^{9}	28^{3}	64^{9}	10^{2}	48^{9}	26.2^{8}
Brachythecium starkei	·	·	6^{2}	·	2^{5}	2^{1}	22^{5}	10^{2}	14^{8}	·	5.6^{5}
Listera cordata	·	·	·	18^{4}	68^{4}	52^{3}	·	32^{7}	22^{4}	44^{3}	23.6^{4}
Cephalozia pleniceps	·	·	·	4^{2}	·	12^{6}	2^{1}	·	10^{5}	14^{4}	4.2^{4}
Empetrum nigrum	·	·	·	2^{1}	6^{7}	2^{1}	8^{6}	10^{10}	2^{1}	28^{6}	5.8^{6}
Brachythecium salebrosum	·	·	·	·	6^{7}	6^{6}	·	22^{6}	20^{5}	8^{10}	6.2^{6}
Nardus stricta	·	·	·	·	2^{1}	·	·	6^{11}	·	8^{6}	1.6^{7}

Tab. 33 (cont.)

Species	PAU	LUN	RAU	OTT	ØYE	URV	GRY	GRA	BRI	GUT	Total
Carex vaginata	·	·	·	·	21	4^{4}	2^{5}	·	2^{9}	16^{9}	2.6^{7}
Deschampsia cespitosa	·	·	·	·	8^{6}	8^{6}	·	·	8^{6}	30^{5}	5.4^{5}
Rubus chamaemorus	·	·	·	·	18^{15}	·	·	8^{8}	·	2^{3}	2.8^{12}
Polygonatum verticillatum	·	·	·	·	6^{3}	·	6^{7}	18^{6}	4^{5}	·	3.4^{5}
Moneses uniflora	·	·	·	·	10^{6}	10^{7}	2^{1}	8^{6}	4^{2}	10^{6}	4.4^{5}
Geranium sylvaticum	·	·	·	·	2^{6}	20^{7}	6^{4}	12^{6}	22^{5}	20^{4}	8.2^{5}
Rhizomnium pseudopunctatum	·	·	·	·	28^{7}	14^{4}	·	4^{2}	10^{5}	26^{5}	8.2^{6}
Harpanthus flotovianus	·	·	·	·	18^{5}	·	·	·	·	6^{5}	2.4^{5}
Aconitum septentrionale	·	·	·	·	·	2^{1}	·	·	8^{4}	·	1.0^{3}
Ranunculus acris	·	·	·	·	·	4^{6}	·	2^{5}	·	10^{3}	1.6^{4}
Trichostomum tenuirostre	·	·	·	·	·	·	2^{1}	·	10^{2}	·	1.2^{2}
Mnium spinosum	·	·	·	·	·	·	4^{7}	20^{5}	16^{8}	18^{6}	5.8^{6}
Viola biflora	·	·	·	·	·	·	·	12^{11}	·	·	1.2^{11}
Betula pubescens	2^{1}	·	·	8^{2}	24^{2}	2^{2}	8^{5}	2^{1}	12^{1}	2^{1}	6.0^{2}
Picea abies	12^{3}	32^{3}	64^{4}	2^{1}	8^{2}	10^{3}	20^{3}	6^{4}	28^{3}	4^{6}	18.6^{3}
Pinus sylvestris	·	4^{2}	14^{3}	2^{2}	4^{1}	·	30^{2}	2^{2}	2^{1}	·	5.8^{2}
Populus tremula	10^{3}	10^{2}	14^{1}	6^{3}	·	·		·	6^{2}	·	4.6^{2}
Sorbus aucuparia	92^{6}	24^{2}	46^{4}	82^{5}	84^{4}	36^{2}	56^{7}	60^{4}	44^{3}	26^{2}	55.0^{4}
Vaccinium myrtillus	90^{12}	62^{12}	96^{13}	100^{13}	88^{12}	96^{13}	98^{15}	98^{13}	96^{13}	100^{15}	92.4^{13}
Vaccinium vitis-idaea	60^{7}	60^{10}	46^{6}	40^{7}	30^{9}	94^{9}	92^{11}	42^{8}	92^{9}	100^{12}	65.6^{9}
Athyrium filix-femina	·	·	·	·	12^{7}	10^{4}	·	4^{3}	2^{1}	·	2.8^{5}
Blechnum spicant	4^{16}	·	·	84^{11}	42^{6}	10^{4}	6^{4}	·	·	·	14.6^{9}
Cicerbita alpina	·	·	·	·	20^{4}	·	·	·	·	4^{2}	2.4^{4}
Convallaria majalis	·	·	20^{7}	·	·	·	8^{8}	·	16^{4}	·	4.4^{6}
Cornus suecica	·	·	·	18^{10}	68^{12}	40^{11}	2^{2}	80^{11}	·	·	20.8^{11}
Dryopteris expansa agg.	·	·	14^{4}	8^{3}	44^{8}	12^{4}	12^{4}	14^{9}	6^{3}	·	11.0^{6}
Equisetum sylvaticum	·	·	·	·	8^{4}	·	·	8^{5}	·	14^{4}	3.0^{4}
Fragaria vesca	·	·	·	·	·	8^{6}	·	·	12^{4}	4^{3}	2.4^{4}
Goodyera repens	·	·	·	·	·	14^{3}	·	·	·	·	1.4^{3}
Gymnocarpium dryopteris	24^{10}	·	2^{1}	22^{7}	96^{11}	58^{10}	16^{5}	70^{13}	64^{12}	60^{9}	41.2^{10}
Hieracium Sect. Sylvatica	·	·	4^{2}	·	·	·	·	32^{6}	22^{7}	8^{2}	6.6^{6}
Hieracium Sect. Vulgata	·	8^{4}	8^{3}	·	6^{1}	22^{5}	·	·	10^{5}	26^{4}	8.0^{4}
Huperzia selago	2^{1}	2^{1}	·	6^{2}	·	2^{4}	·	·	·	·	1.2^{2}
Lycopodium clavatum	6^{5}	·	·	·	8^{6}	·	·	·	·	·	1.4^{5}
Melampyrum pratense	18^{2}	16^{2}	16^{2}	30^{3}	6^{1}	48^{7}	46^{6}	22^{6}	6^{2}	46^{6}	25.4^{5}
Oreopteris limbosperma	·	·	·	32^{13}	2^{1}	·	·	·	·	·	3.4^{12}
Oxalis acetosella	·	·	34^{3}	32^{11}	44^{8}	48^{11}	12^{14}	10^{15}	44^{12}	56^{9}	28.0^{9}
Paris quadrifolia	·	·	·	·	·	·	·	2^{1}	10^{3}	·	1.2^{3}
Phegopteris connectilis	22^{7}	·	·	10^{3}	34^{11}	16^{8}	2^{10}	18^{10}	14^{12}	·	11.6^{9}
Potentilla erecta	20^{4}	4^{2}	·	36^{7}	32^{6}	10^{2}	2^{6}	2^{6}	·	6^{4}	11.2^{5}
Rubus saxatilis	6^{2}	·	·	·	20^{3}	16^{12}	10^{9}	2^{9}	24^{7}	2^{1}	8.0^{7}
Trientalis europaea	42^{8}	14^{5}	48^{6}	54^{10}	90^{9}	44^{6}	18^{4}	78^{12}	40^{8}	58^{6}	48.6^{8}
Veronica officinalis	·	·	2^{5}	·	·	12^{8}	·	4^{2}	6^{2}	·	2.4^{5}
Viola palustris	·	·	·	·	10^{7}	·	·	·	·	·	1.0^{7}
Viola riviniana	·	2^{1}	4^{2}	·	·	22^{8}	8^{4}	·	16^{5}	6^{2}	5.8^{5}
Agrostis capillaris	24^{7}	8^{4}	·	18^{4}	24^{7}	22^{4}	·	·	·	6^{3}	10.2^{5}
Anthoxanthum odoratum	·	2^{7}	·	·	·	10^{4}	·	12^{8}	·	16^{6}	4.0^{6}
Calamagrostis purpurea	10^{4}	·	·	·	2^{3}	·	·	·	12^{3}	2^{1}	2.6^{3}
Carex digitata	·	·	20^{4}	·	·	6^{5}	6^{3}	·	14^{7}	·	4.6^{5}
Deschampsia flexuosa	90^{14}	32^{10}	72^{14}	94^{14}	96^{14}	88^{13}	72^{11}	96^{16}	84^{14}	94^{15}	81.8^{14}

Tab. 33 (cont.)

Species	PAU	LUN	RAU	OTT	ØYE	URV	GRY	GRA	BRI	GUT	Total
Juncus filiformis	·	·	·	·	4^{7}	·	·	6^{6}	·	·	1.0^{6}
Luzula pilosa	2^{4}	8^{3}	18^{6}	12^{4}	20^{7}	48^{9}	·	38^{9}	30^{6}	42^{2}	21.8^{6}
Luzula sylvatica	·	·	·	10^{2}	·	·	·	·	·	·	1.0^{2}
Melica nutans	·	·	·	·	·	8^{8}	8^{9}	·	18^{6}	6^{6}	4.0^{7}
Milium effusum	·	·	·	·	·	·	·	4^{9}	10^{5}	·	1.4^{6}
Molinia caerulea	·	14^{4}	·	12^{5}	12^{6}	·	10^{12}	·	·	·	4.8^{6}
Phalaris arundinacea	·	·	·	·	14^{4}	·	·	·	·	·	1.4^{4}
Trichophorum cespitosum	·	·	·	16^{5}	·	·	·	·	·	·	1.6^{5}
Aulacomnium palustre	·	6^{3}	·	·	·	·	·	·	2^{3}	4^{6}	1.2^{4}
Cirriphyllum piliferum	·	2^{4}	6^{5}	2^{8}	20^{3}	14^{8}	4^{5}	6^{5}	·	4^{2}	5.8^{5}
Dicranum fuscescens agg.	44^{4}	88^{10}	20^{2}	14^{5}	56^{4}	20^{2}	58^{5}	34^{4}	60^{5}	36^{5}	43.0^{6}
Dicranum majus	90^{10}	94^{13}	96^{14}	86^{11}	90^{11}	80^{9}	62^{9}	22^{4}	24^{5}	30^{9}	67.4^{11}
Dicranum montanum	·	·	4^{1}	·	·	·	4^{2}	·	2^{2}	·	1.0^{1}
Dicranum scoparium	70^{6}	92^{8}	32^{3}	48^{6}	90^{7}	84^{8}	96^{10}	78^{7}	88^{9}	84^{10}	76.2^{8}
Hylocomiastrum umbratum	2^{3}	·	24^{5}	44^{6}	74^{9}	20^{8}	6^{5}	24^{9}	4^{9}	14^{6}	21.2^{7}
Hylocomium splendens	26^{6}	60^{6}	86^{9}	80^{7}	98^{13}	96^{15}	88^{9}	90^{10}	84^{13}	98^{15}	80.6^{11}
Hypnum callichroum	·	·	·	22^{6}	28^{5}	6^{13}	·	·	·	·	5.6^{6}
Mnium stellare	·	·	·	·	·	·	·	·	12^{4}	·	1.2^{4}
Plagiomnium affine	4^{2}	6^{9}	2^{1}	·	·	·	·	·	·	2^{11}	1.4^{6}
Plagiothecium denticulatum	6^{1}	8^{2}	16^{2}	10^{1}	12^{3}	·	30^{4}	36^{4}	46^{4}	28^{3}	19.2^{4}
Plagiothecium laetum	56^{4}	84^{5}	62^{4}	38^{4}	60^{6}	12^{2}	78^{8}	36^{2}	52^{4}	32^{4}	51.0^{5}
Plagiothecium nemorale	·	4^{1}	2^{1}	·	·	·	2^{1}	4^{4}	4^{2}	·	1.6^{2}
Pleurozium schreberi	66^{6}	92^{11}	94^{12}	76^{6}	76^{9}	86^{9}	82^{10}	68^{8}	78^{11}	84^{10}	80.2^{9}
Pohlia cruda	·	·	·	·	2^{2}	·	·	·	4^{2}	4^{2}	1.0^{2}
Pohlia nutans	2^{1}	34^{4}	·	8^{2}	8^{4}	4^{4}	2^{1}	4^{2}	6^{1}	14^{3}	8.2^{3}
Polytrichum commune	4^{10}	4^{1}	4^{7}	12^{7}	8^{12}	·	·	26^{8}	12^{4}	10^{10}	8.0^{8}
Polytrichum juniperinum	·	6^{1}	2^{1}	2^{1}	·	·	·	·	·	·	1.0^{1}
Ptilium crista-castrensis	2^{1}	26^{3}	40^{7}	32^{7}	44^{7}	76^{12}	14^{5}	2^{9}	32^{13}	6^{10}	27.4^{9}
Rhizomnium punctatum	2^{2}	·	2^{5}	4^{3}	·	·	4^{2}	·	10^{3}	4^{6}	2.6^{3}
Rhytidiadelphus squarrosus agg.	2^{1}	·	14^{8}	48^{8}	64^{10}	32^{8}	10^{3}	46^{10}	6^{7}	12^{9}	23.4^{9}
Rhytidiadelphus triquetrus	·	·	·	6^{9}	2^{1}	26^{10}	·	2^{1}	·	·	3.6^{9}
Sanionia uncinata	·	2^{1}	·	·	32^{3}	14^{6}	4^{2}	32^{4}	14^{1}	16^{4}	11.4^{3}
Straminergon stramineum	·	·	·	·	8^{4}	·	·	2^{1}	·	10^{8}	2.0^{5}
Sphagnum angustifolium	·	2^{1}	·	·	18^{5}	·	·	·	12^{11}	12^{6}	4.4^{7}
Sphagnum centrale	·	·	·	2^{1}	6^{8}	·	2^{11}	·	·	·	1.0^{7}
Sphagnum girgensohnii	38^{6}	12^{7}	16^{7}	6^{2}	34^{9}	6^{3}	4^{11}	12^{11}	20^{14}	20^{7}	16.8^{8}
Sphagnum rubiginosum	·	·	·	·	·	20^{12}	·	·	·	·	2.0^{12}
Sphagnum russowii	·	6^{7}	·	·	4^{11}	6^{5}	4^{2}	2^{5}	10^{4}	20^{7}	5.2^{6}
Sphagnum squarrosum	·	·	·	·	10^{8}	·	·	2^{1}	·	·	1.2^{7}
Anastrepta orcadensis	·	·	·	44^{6}	·	·	·	·	·	·	4.4^{6}
Barbilophozia attenuata	28^{2}	32^{3}	24^{2}	4^{1}	8^{3}	14^{2}	38^{3}	6^{2}	10^{3}	22^{2}	18.6^{2}
Barbilophozia barbata	6^{1}	6^{4}	2^{1}	20^{4}	42^{6}	52^{7}	38^{4}	32^{8}	36^{5}	6^{1}	24.0^{5}
Barbilophozia hatcheri	2^{1}	·	·	·	2^{1}	·	·	·	4^{2}	2^{2}	1.0^{2}
Barbilophozia kunzeana	·	2^{1}	·	2^{1}	·	8^{1}	·	·	·	10^{3}	2.2^{2}
Blepharostoma trichophyllum	6^{2}	8^{3}	24^{2}	4^{2}	26^{2}	6^{2}	18^{3}	6^{3}	26^{5}	22^{3}	14.6^{3}
Calypogeia integristipula	6^{1}	4^{4}	24^{2}	4^{2}	8^{2}	·	14^{2}	·	14^{2}	26^{3}	10.0^{2}
Calypogeia neesiana	2^{2}	2^{3}	2^{1}	12^{1}	10^{2}	8^{2}	26^{2}	4^{2}	10^{2}	10^{5}	8.6^{2}
Calypogeia sphagnicola	·	2^{1}	·	·	·	·	·	2^{10}	4^{7}	4^{1}	1.2^{5}
Cephalozia bicuspidata	16^{3}	·	14^{1}	44^{4}	34^{3}	12^{3}	8^{2}	2^{1}	6^{2}	16^{2}	15.2^{3}
Cephalozia loitlesbergeri	·	·	·	·	4^{2}	2^{1}	·	·	4^{9}	2^{1}	1.2^{4}
Cephalozia lunulifolia	8^{3}	2^{2}	12^{1}	18^{2}	32^{3}	6^{2}	30^{2}	4^{2}	20^{2}	34^{4}	16.6^{2}

Tab. 33 (cont.)

Species	PAU	LUN	RAU	OTT	ØYE	URV	GRY	GRA	BRI	GUT	Total
Chiloscyphus minor	·	·	·	·	·	·	·	·	12^{2}	·	1.2^{2}
Chiloscyphus profundus	64^{3}	28^{8}	68^{4}	60^{5}	26^{5}	4^{2}	80^{7}	·	50^{7}	2^{13}	38.2^{5}
Diplophyllum taxifolium	2^{1}	·	2^{2}	14^{2}	24^{2}	·	6^{2}	·	·	2^{1}	5.0^{2}
Lepidozia pearsonii	·	·	·	38^{11}	·	·	·		·	·	3.8^{11}
Lophozia incisa	·	·	2^{1}	·	4^{4}	2^{1}	·	·	2^{1}	·	1.0^{2}
Lophozia longidens	·	·	2^{1}	·	6^{2}	·	10^{2}	·	8^{1}	2^{1}	2.8^{2}
Lophozia ventricosa agg.	10^{3}	6^{2}	4^{2}	30^{4}	42^{3}	28^{2}	28^{2}	22^{5}	42^{5}	54^{5}	26.6^{4}
Moerckia blyttii	·	·	·	16^{2}	·	·	·	2^{1}	·	·	1.8^{2}
Plagiochila porelloides	10^{1}	2^{2}	2^{1}	6^{2}	2^{2}	·	·	·	2^{4}	·	2.4^{2}
Ptilidium ciliare	6^{1}	34^{4}	18^{3}	14^{6}	36^{9}	4^{4}	18^{3}	52^{6}	42^{3}	4^{2}	22.8^{5}
Ptilidium pulcherrimum	6^{1}	·	·	·	·	2^{1}	16^{1}	2^{1}	34^{2}	2^{3}	6.2^{2}
Scapania irrigua	·	·	·	4^{1}	6^{2}	·	·	·	·	6^{1}	1.6^{1}
Scapania scandica	·	·	·	·	20^{2}	·	·	·	·	4^{1}	2.4^{2}
Scapania umbrosa	·	·	·	·	12^{2}	4^{3}	·	·	·	·	1.6^{2}
Cladonia bellidiflora	·	16^{3}	·	8^{2}	2^{1}	·	4^{1}	6^{3}	·	12^{2}	4.8^{2}
Cladonia cenotea	·	4^{1}	·	·	·	2^{1}	·	2^{1}	6^{2}	4^{2}	1.8^{2}
Cladonia chlorophaea agg.	8^{2}	16^{2}	2^{1}	12^{1}	24^{1}	4^{1}	26^{5}	12^{3}	32^{3}	34^{2}	17.0^{2}
Cladonia coniocraea agg.	2^{1}	40^{2}	10^{1}	12^{3}	30^{2}	16^{1}	26^{3}	16^{2}	26^{3}	10^{1}	18.8^{2}
Cladonia digitata	·	4^{4}	·	·	·	·	2^{1}	·	6^{2}	·	1.2^{3}
Cladonia furcata	2^{6}	16^{4}	·	14^{4}	20^{5}	12^{3}	16^{3}	36^{4}	18^{2}	36^{5}	17.0^{4}
Cladonia gracilis	·	2^{2}	·	·	·	·	·	2^{1}	2^{5}	6^{1}	1.2^{2}
Cladonia rangiferina	·	12^{7}	·	·	2^{2}	·	·	8^{2}	10^{3}	10^{3}	4.2^{4}

Additional species (occurring in 5 or fewer sample plots; Area: F^{FSP} $TotF^{FSP}$):

Juniperus communis GUT 4^2, GRA 2^1 0.6^1; Quercus sp. LUN 8^2 0.8^2; Phyllodoce carulea GRA 2^9 0.2^9; Calluna vulgaris OTT 2^1, 2^9 0.4^5; Vaccinium uliginosum OTT 4^2, GUT 4^6 0.8^4.

Actaea spicata BRI 2^4 0.2^4; Alchemilla sp. GUT 4^3, URV 2^2 0.3^3; Antennaria dioica LUN 2^2 0.2^2; Athyrium distentifolium ØYE 2^4 0.2^4; Campanula rotundifolia URV 2^3 0.2^3; Circium helenioides URV 2^8 0.2^8; Dactylorhiza fuchsii GRA 4^1 0.4^1; Dactylorhiza maculata RAU 2^2, 2^1 0.4^2; Digitalis purpurea OTT 2^2 0.2^2; Epilobium angustifolium GRA 4^5 0.4^5; Equisetum pratense GRA 8^2 0.8^2; Eriophorum vaginatum GRA 2^6 0.2^6; Filipendula ulmaria URV 6^7 0.6^7; Galium boreale URV 2^1 0.2^1; Galium saxatile OTT 2^1 0.2^1; Geum rivale GUT 2^3, URV 6^2 0.8^2; Lonicera periclymenum PAU 2^2 0.2^2; Narthecium ossifragum OTT 6^6 0.2^2; Platanthera sp. RAU 2^2 0.2^2; Prunella vulgaris URV 4^1 0.4^1; Pyrola minor GUT 2^2 0.2^2; Selaginella selaginoides GUT 2^2, GRA 4^5 0.6^4; Taraxacum sp. GUT 2^2 0.2^2; Trollius europaeus GRA 8^3 0.8^3.

Agrostis canina RAU 4^4, GUT 2^8 0.6^5; Carex binervis OTT 8^3 0.8^3; Carex brunnescens GRA 4^4 0.4^4; Carex panicea OTT 4^2 0.4^2; Carex paupercula OTT 4^4 0.4^4; Festuca rubra LUN 2^8 0.2^8.

Andreaea rupestris OTT 2^2 0.2^2; Antitrichia curtipendula RAU 2^1 0.2^1; Bartramia ithyphylla BRI 2^2 0.2^2; Bartramia pomiformis BRI 2^1 0.2^1 Brachythecium oedipodium LUN 4^6 0.4^6; Brachythecium populeum PAU 6^1 0.6^1; Brachythecium rivulare GRY 2^1 0.2^1; Brachythecium rutabulum GRY 6^4, RAU 2^1 0.8^4; Bryum sp. GUT 2^2 0.2^2; Campylopus atrovirens OTT 2^1 0.2^1; Eurhynchium angustirete RAU 2^3 0.2^3; Herzogiella seligeri LUN 2^3, RAU 2^1 0.4^2; Hylocomiastrum pyrenaicum GUT 2^7, GRA 4^1 0.6^3; Isopterygiopsis pulchella GUT 2^1 0.2^1; Paraleucobryum longifolium OTT 2^1 0.2^1; Polytrichum alpinum GUT 2^1 0.2^1; Racomitrium canescens agg. OTT 2^3 0.2^3; Racomitrium heterosticum agg. PAU 2^1, OTT 2^1 0.4^1; Racomitrium lanuginosum; OTT 2^2 0.2^2; Rhabdoweisia crenulata OTT 2^1 0.2^1; Schistidium apocarpum agg. OTT 4^2 0.4^2; Thuidium delicatulum OTT 2^2 0.2^2.

Anastrophyllum minutum PAU 2^1, 2^1 0.4^1; Barbilophozia atlantica OTT 2^1 0.2^1; Bazzania tricrenata GRY 2^1, OTT 4^3 0.6^2; Bazzania trilobata OTT 6^7 0.6^7; Cephalozia connivens GRY 2^1 0.2^1; Cephalozia lacinulata ØYE 2^1 0.2^1; Cephalozia leucantha URV 2^2 0.2^2; Cephaloziella sp. GRY 2^1, GUT 4^3 0.6^2; Kurzia trichoclados OTT 4^2 0.4^2; Lophozia adscendens PAU 2^1, GRY 2^2 0.4^2; Lophozia collaris OTT 2^1 0.2^1; Lophozia excisa GUT 6^1, 2^1 0.8^1; Lophozia sudetica GRY 2^1, OTT 2^2, GUT 2^1 0.6^1; Lophozia wenzelii GUT 2^2 0.2^2; Marsupella emarginata ØYE 2^1 0.2^1; Metzgeria furcata GRY 2^1 0.2^1; Nowellia curvifolia LUN 2^1 0.2^1; Pellia sp. GUT 2^1 0.2^1; Radula complanata BRI 4^2 0.4^2; Scapania paludosa ØYE 6^2 0.6^2; Scapania uliginosa ØYE 2^4 0.2^4; Tritomaria exsectiformis OTT 2^1 0.2^1.

Cetraria pinastri BRI 4^2 0.4^2; Cladonia arbuscula agg. GUT 2^5 0.2^5; Cladonia cariosa GUT 2^2 0.2^2; Cladonia coccifera agg. GUT 4^1, ØYE 2^1 0.6^1; Cladonia cornuta BRI 4^1, GUT 4^2 0.8^1; Cladonia deformis GUT 4^2 0.4^2; Cladonia macilenta LUN 2^4 0.2^4; Cladonia phyllophora LUN 2^2, GUT 2^1 0.4^2; Cladonia squamosa LUN 6^3, OTT 2^1 0.8^2; Cladonia sulphurina GUT 8^3 0.8^3; Cladonia uncialis LUN 4^3, GUT 4^3 0.2^1; Hypogymnia physodes BRI 2^1 0.2^1; Nephroma arcticum GUT 2^1 0.2^1; Nephroma parile BRI 2^1 0.2^1; Peltigera aphthosa GRA 6^4 0.6^4; Peltigera canina GUT 2^6 0.2^6; Peltigera degenii BRI 4^5 0.4^5; Peltigera membranacea BRI 2^1 0.2^1.

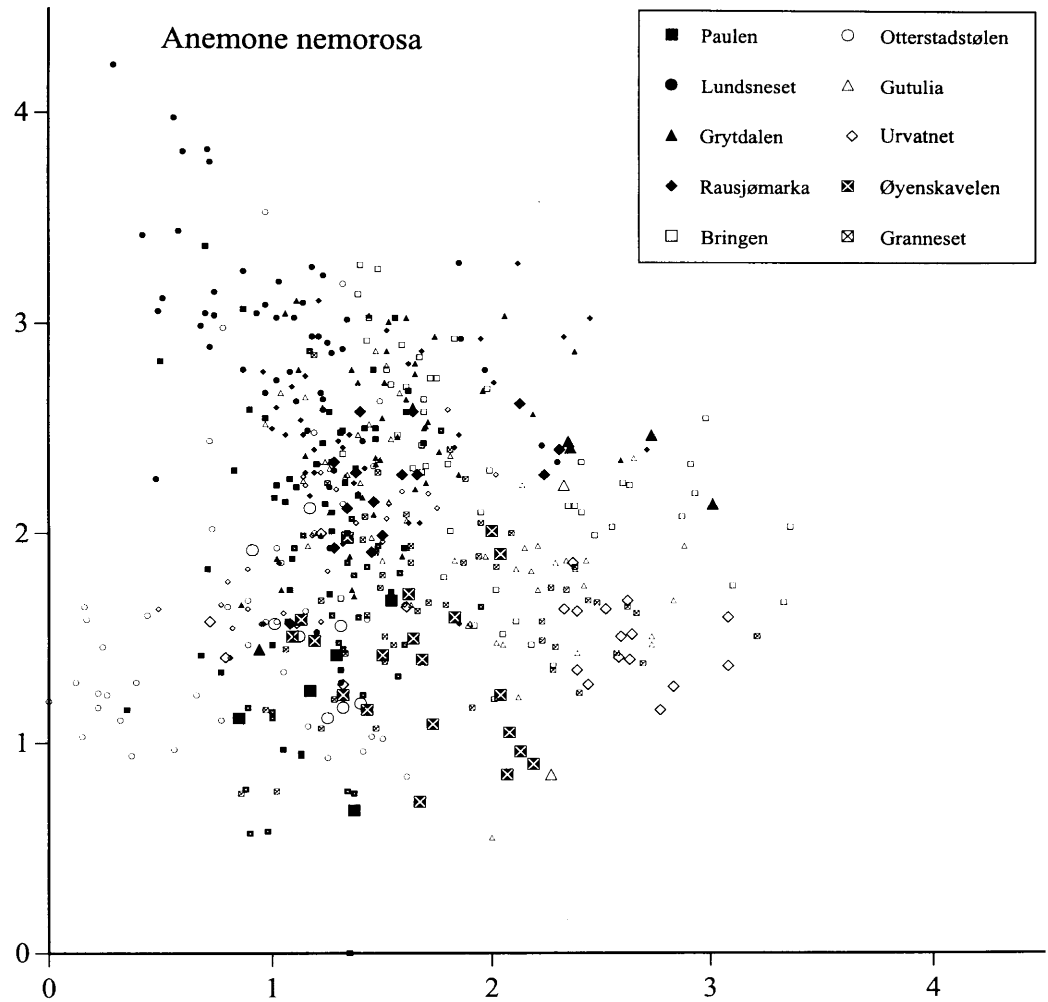


Fig. 770. The total data set: distribution of *Anemone nemorosa* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

exemplifies locally frequent species concentrated to the Boreo-Nemoral and Southern Boreal zones. *Plagiothecium undulatum, Plagiochila asplenoides, Rhytidiadelphus loreus, Calypogeia muelleriana, Polytrichum formosum* and *Dicranum majus* extend into the Middle Boreal zone. Several species, all with low frequency, were concentrated to the Middle and Northern Boreal zones. Several species which were frequent in the Middle and Northern Boreal zones, decreased in frequency in the Southern Boreal zone and were more or less absent in the Boreo-nemoral zone, e.g. *Listera cordata, Lophozia obtusa, Barbilophozia floerkei, Barbilop-*

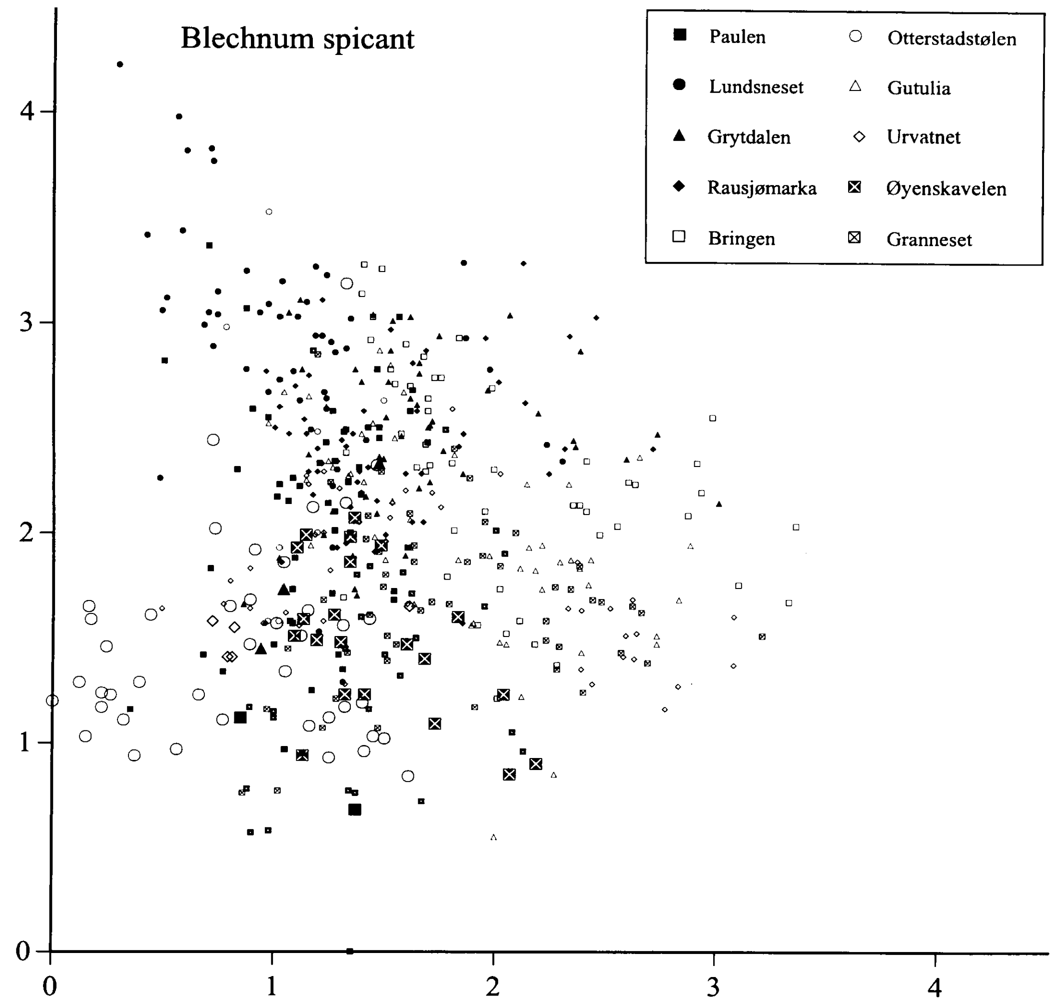


Fig. 771. The total data set: distribution of *Blechnum spicant* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

hozia lycopodioides and *Tritomaria quinquedentata*.

Thirty species showed preference for oceanic areas (Tab. 34). Examples of locally frequent species of this kind were, in order of decreasing restriction to oceanic areas: *Anastrepta orcadensis, Lepidozia pearsonii, Oreopteris limbosperma, Dicranodontium denudatum, Blechnum spicant, Plagiothecium undulatum, Rhytidiadelphus loreus* and *Calypogeia muelleriana*. Twenty species showed preference for a more continental climate. Most species of this kind had low local frequency.

Tab. 34. Abundance and distribution of species in the total data set; reference areas ordered according to vegetation section from the more oceanic to the more continental, species ordered by preference for more oceanic and more continental zones, respectively. Indifferent and infrequent species are listed at the bottom of the table. Reference areas abbreviated by the first three letters of their names, see Tab. 1. Quantity for each species in each reference area is given as F^{MSF} where F is frequency in the area, MSF is the mean frequency in subplots (calculated for the plots in which the species occurs).

Species	OTT	ØYE	PAU	URV	GRY	LUN	RAU	GRA	GUT	BRI	Total
Anastrepta orcadensis	44^{6}	·	·	·	·	·	·	·	·	·	4.4^{6}
Lepidozia pearsonii	38^{11}	·	·	·	·	·	·	·	·	·	3.8^{11}
Trichophorum cespitosum	16^{5}	·	·	·	·	·	·	·	·	·	1.6^{5}
Oreopteris limbosperma	32^{13}	2^{1}	·	·	·	·	·	·	·	·	3.4^{12}
Dicranodontium denudatum	44^{4}	2^{1}	6^{2}	·	·	·	·	·	·	·	5.2^{4}
Lycopodium clavatum	·	8^{6}	6^{5}	·	·	·	·	·	·	·	1.4^{5}
Diplophyllum albicans	22^{3}	·	16^{3}	·	·	·	·	·	·	·	3.8^{3}
Thuidium tamariscinum	8^{12}	·	8^{4}	·	·	·	·	·	·	·	1.6^{8}
Hypnum callichroum	22^{6}	28^{5}	·	6^{13}	·	·	·	·	·	·	5.6^{6}
Blechnum spicant	84^{11}	42^{6}	4^{16}	10^{4}	6^{4}	·	·	·	·	·	14.6^{9}
Herzogiella striatella	10^{1}	42^{3}	10^{1}	·	·	4^{1}	·	·	·	·	6.6^{2}
Plagiothecium undulatum	74^{12}	78^{10}	58^{8}	56^{12}	·	12^{3}	·	·	·	·	27.8^{10}
Carex pilulifera	10^{3}	·	8^{2}	8^{1}	·	8^{3}	·	·	·	·	3.4^{2}
Molinia caerulea	12^{5}	12^{6}	·	·	10^{12}	14^{4}	·	·	·	·	4.8^{6}
Heterocladium heteropterum	4^{1}	·	·	·	·	6^{5}	·	·	·	·	1.0^{3}
Leucobryum glaucum	12^{4}	·	·	·	·	2^{2}	·	·	·	·	1.4^{4}
Mnium hornum	·	32^{3}	10^{2}	·	·	4^{5}	·	·	·	·	4.6^{3}
Rhytidiadelphus loreus	90^{13}	88^{12}	28^{3}	70^{10}	22^{7}	·	2^{6}	·	·	·	30.0^{10}
Chiloscyphus profundus	34^{5}	6^{10}	14^{4}	8^{9}	4^{2}	·	4^{3}	·	·	·	7.0^{5}
Mylia taylorii	20^{2}	2^{1}	4^{2}	·	·	·	2^{1}	·	·	·	2.8^{2}
Hypnum cupressiforme agg.	38^{6}	·	42^{2}	·	·	40^{7}	2^{1}	·	·	·	12.2^{5}
Pseudotaxiphyllum elegans	10^{3}	8^{2}	12^{5}	·	·	2^{1}	4^{2}	·	·	·	3.6^{3}
Pteridium aquilinum	10^{5}	·	40^{4}	·	2^{2}	4^{1}	8^{9}	·	·	·	6.4^{5}
Calypogeia muelleriana	78^{8}	80^{6}	40^{6}	28^{4}	18^{2}	4^{3}	20^{2}	·	·	·	26.8^{6}
Calypogeia azurea	4^{1}	4^{2}	6^{3}	2^{1}	6^{4}	·	8^{3}	·	·	·	3.0^{2}
Anemone nemorosa	16^{4}	40^{10}	10^{2}	40^{10}	10^{6}	·	30^{5}	·	·	·	14.6^{7}
Plagiochila asplenoides	26^{7}	30^{9}	22^{3}	30^{7}	2^{1}	·	60^{7}	·	·	·	17.0^{7}
Cornus suecica	18^{10}	68^{12}	·	40^{11}	2^{2}	·	·	80^{11}	·	·	20.8^{11}
Potentilla erecta	36^{7}	32^{6}	20^{4}	10^{2}	2^{6}	4^{2}	·	2^{6}	6^{4}	·	11.2^{5}
Polytrichum formosum	82^{9}	40^{8}	60^{6}	8^{3}	6^{3}	12^{4}	12^{7}	10^{5}	·	2^{4}	23.2^{7}
Cladonia rangiferina	·	2^{2}	·	·	·	12^{7}	·	8^{2}	10^{3}	10^{3}	4.2^{4}
Rhodobryum roseum	·	14^{3}	2^{1}	22^{4}	6^{1}	·	2^{1}	46^{8}	34^{6}	28^{5}	15.4^{5}
Lepidozia reptans	·	4^{2}	16^{3}	6^{1}	6^{2}	18^{3}	12^{2}	·	·	4^{2}	6.6^{2}
Orthilia secunda	·	·	2^{1}	18^{2}	·	·	·	12^{3}	32^{8}	32^{6}	9.6^{6}
Carex digitata	·	·	·	6^{5}	6^{3}	·	20^{4}	·	·	14^{7}	4.6^{5}
Melica nutans	·	·	·	8^{8}	8^{9}	·	·	·	6^{6}	18^{6}	4.0^{7}
Viola riviniana	·	·	·	22^{8}	8^{4}	2^{1}	4^{2}	·	6^{2}	16^{5}	5.8^{5}
Veronica officinalis	·	·	·	12^{8}	·	·	2^{5}	4^{2}	·	6^{2}	2.4^{5}
Cladonia cenotea	·	·	·	2^{1}	·	4^{1}	·	2^{1}	4^{2}	6^{2}	1.8^{2}
Cladonia digitata	·	·	·	·	2^{1}	4^{4}	·	·	·	6^{2}	1.2^{3}
Plagiothecium nemorale	·	·	·	·	2^{1}	4^{1}	2^{1}	4^{4}	·	4^{2}	1.6^{2}
Mnium spinosum	·	·	·	·	4^{7}	·	·	20^{5}	18^{6}	16^{8}	5.8^{6}
Calypogeia sphagnicola	·	·	·	·	·	2^{1}	·	2^{10}	4^{1}	4^{7}	1.2^{5}
Cladonia gracilis	·	·	·	·	·	2^{2}	·	2^{1}	6^{1}	2^{5}	1.2^{2}

Tab. 34 (cont.)

Species	OTT	ØYE	PAU	URV	GRY	LUN	RAU	GRA	GUT	BRI	Total
Aulacomnium palustre	·	·	·	·	·	6^{3}	·	·	4^{6}	2^{3}	1.2^{4}
Hieracium Sect. Sylvatica	·	·	·	·	·	·	4^{2}	32^{6}	8^{2}	22^{7}	6.6^{6}
Milium effusum	·	·	·	·	·	·	·	4^{9}	·	10^{5}	1.4^{6}
Paris quadrifolia	·	·	·	·	·	·	·	2^{1}	·	10^{3}	1.2^{3}
Chiloscyphus minor	·	·	·	·	·	·	·	·	·	12^{2}	1.2^{2}
Mnium stellare	·	·	·	·	·	·	·	·	·	12^{4}	1.2^{4}
Betula pubescens	8^{2}	24^{2}	2^{1}	2^{2}	8^{5}	·	·	2^{1}	2^{1}	12^{1}	6.0^{2}
Frangula alnus	·	·	6^{3}	·	·	4^{4}	·	·	·	·	1.0^{3}
Picea abies	2^{1}	8^{2}	12^{3}	10^{3}	20^{3}	32^{3}	64^{4}	6^{4}	4^{6}	28^{3}	18.6^{3}
Pinus sylvestris	2^{2}	4^{1}	·	·	30^{2}	4^{2}	14^{3}	2^{2}	·	2^{1}	5.8^{2}
Populus tremula	6^{3}	·	10^{3}	·	·	10^{2}	14^{1}	·	·	6^{2}	4.6^{2}
Sorbus aucuparia	82^{5}	84^{4}	92^{6}	36^{2}	56^{7}	24^{2}	46^{4}	60^{4}	26^{2}	44^{3}	55.0^{4}
Empetrum nigrum	2^{1}	6^{7}	·	2^{1}	8^{6}	·	·	10^{10}	28^{6}	2^{1}	5.8^{6}
Vaccinium myrtillus	100^{13}	88^{12}	90^{12}	96^{13}	98^{15}	62^{12}	96^{13}	98^{13}	100^{15}	96^{13}	92.4^{13}
Vaccinium vitis-idaea	40^{7}	30^{9}	60^{7}	94^{9}	92^{11}	60^{10}	46^{6}	42^{8}	100^{12}	92^{9}	65.6^{9}
Aconitum septentrionale	·	·	·	2^{1}	·	·	·	·	·	8^{4}	1.0^{3}
Athyrium filix-femina	·	12^{7}	·	10^{4}	·	·	·	4^{3}	·	·	2.8^{5}
Convallaria majalis	·	·	·	·	8^{8}	·	20^{7}	·	·	16^{4}	4.4^{6}
Dryopteris expansa agg.	8^{3}	44^{8}	·	12^{4}	12^{4}	·	14^{4}	14^{9}	·	6^{3}	11.0^{6}
Equisetum sylvaticum	·	8^{4}	·	·	·	·	·	8^{5}	14^{4}	·	3.0^{4}
Fragaria vesca	·	·	·	8^{6}	·	·	·	·	4^{3}	12^{4}	2.4^{4}
Geranium sylvaticum	·	2^{6}	·	20^{7}	6^{4}	·	·	12^{6}	20^{4}	22^{5}	8.2^{5}
Goodyera repens	·	·	·	14^{3}	·	·	·	·	·	·	1.4^{3}
Gymnocarpium dryopteris	22^{7}	96^{11}	24^{10}	58^{10}	16^{5}	·	2^{1}	70^{13}	60^{9}	64^{12}	41.2^{10}
Hieracium Sect. Vulgata	·	6^{1}	·	22^{5}	·	8^{4}	8^{3}	·	26^{4}	10^{5}	8.0^{4}
Huperzia selago	6^{2}	·	2^{1}	2^{4}	·	2^{1}	·	·	·	·	1.2^{2}
Linnaea borealis	12^{3}	24^{8}	·	56^{8}	16^{5}	·	20^{7}	10^{11}	68^{8}	76^{9}	28.2^{8}
Listera cordata	18^{4}	68^{4}	·	52^{3}	·	·	·	32^{7}	44^{3}	22^{4}	23.6^{4}
Lycopodium annotinum	6^{5}	12^{4}	6^{2}	·	28^{8}	·	2^{1}	62^{8}	32^{5}	20^{10}	16.8^{7}
Maianthemum bifolium	52^{5}	28^{12}	80^{9}	74^{8}	42^{7}	20^{6}	86^{11}	·	6^{9}	52^{9}	44.0^{9}
Melampyrum pratense	30^{3}	6^{1}	18^{2}	48^{7}	46^{6}	16^{2}	16^{2}	22^{6}	46^{6}	6^{2}	25.4^{5}
Melampyrum sylvaticum	·	16^{4}	·	62^{9}	28^{3}	·	34^{6}	64^{9}	48^{9}	10^{2}	26.2^{8}
Moneses uniflora	·	10^{6}	·	10^{7}	2^{1}	·	·	8^{6}	10^{6}	4^{2}	4.4^{5}
Oxalis acetosella	32^{11}	44^{8}	·	48^{11}	12^{14}	·	34^{3}	10^{15}	56^{9}	44^{12}	28.0^{9}
Phegopteris connectilis	10^{3}	34^{11}	22^{7}	16^{8}	2^{10}	·	·	18^{10}	·	14^{12}	11.6^{9}
Polygonatum verticillatum	·	6^{3}	·	·	6^{7}	·	·	18^{6}	·	4^{5}	3.4^{5}
Ranunculus acris	·	·	·	4^{6}	·	·	·	2^{5}	10^{3}	·	1.6^{4}
Rubus chamaemorus	·	18^{15}	·	·	·	·	·	8^{8}	2^{3}	·	2.8^{12}
Rubus saxatilis	·	20^{3}	6^{2}	16^{12}	10^{9}	·	·	2^{9}	2^{1}	24^{7}	8.0^{7}
Solidago virgaurea	4^{1}	66^{5}	10^{3}	36^{7}	20^{4}	2^{1}	8^{3}	50^{10}	50^{4}	42^{5}	28.8^{6}
Phegopteris connectilis	10^{3}	34^{11}	22^{7}	16^{8}	2^{10}	·	·	18^{10}	·	14^{12}	11.6^{9}
Trientalis europaea	54^{10}	90^{9}	42^{8}	44^{6}	18^{4}	14^{5}	48^{6}	78^{12}	58^{6}	40^{8}	48.6^{8}
Viola biflora	·	·	·	·	·	·	·	12^{11}	·	·	1.2^{11}
Viola palustris	·	10^{7}	·	·	·	·	·	·	·	·	1.0^{7}
Agrostis capillaris	18^{4}	24^{7}	24^{7}	22^{4}	·	8^{4}	·	·	6^{3}	·	10.2^{5}
Anthoxanthum odoratum	·	·	·	10^{4}	·	2^{7}	·	12^{8}	16^{6}	·	4.0^{6}
Calamagrostis arundinacea	·	·	·	·	·	18^{7}	50^{13}	·	·	·	6.8^{11}
Calamagrostis purpurea	·	2^{3}	10^{4}	·	·	·	·	·	2^{1}	12^{3}	2.6^{3}
Carex vaginata	·	2^{1}	·	4^{4}	2^{5}	·	·	·	16^{9}	2^{9}	2.6^{7}
Deschampsia cespitosa	·	8^{6}	·	8^{6}	·	·	·	·	30^{5}	8^{6}	5.4^{5}

Tab. 34 (cont.)

Species	OTT	ØYE	PAU	URV	GRY	LUN	RAU	GRA	GUT	BRI	Total
Deschampsia flexuosa	94^{14}	96^{14}	90^{14}	88^{13}	72^{11}	32^{10}	72^{14}	96^{16}	94^{15}	84^{14}	81.8^{14}
Juncus filiformis	·	4^{7}	·	·	·	·	·	6^{6}	·	·	1.0^{6}
Luzula pilosa	12^{4}	20^{7}	2^{4}	48^{9}	·	8^{3}	18^{6}	38^{9}	42^{2}	30^{6}	21.8^{6}
Nardus stricta	·	2^{1}	·	·	·	·	·	6^{11}	8^{6}	·	1.6^{7}
Phalaris arundinacea	·	14^{4}	·	·	·	·	·	·	·	·	1.4^{4}
Brachythecium reflexum	12^{2}	46^{7}	·	2^{10}	30^{9}	·	26^{2}	40^{8}	30^{3}	32^{8}	21.8^{6}
Brachythecium salebrosum	·	6^{7}	·	6^{6}	·	·	·	22^{6}	8^{10}	20^{5}	6.2^{6}
Brachythecium starkei	·	2^{5}	·	2^{1}	22^{5}	·	6^{2}	10^{2}	·	14^{8}	5.6^{5}
Cirriphyllum piliferum	2^{8}	20^{3}	·	14^{8}	4^{5}	2^{4}	6^{5}	6^{5}	4^{2}	·	5.8^{5}
Dicranum fuscescens agg.	14^{5}	56^{4}	44^{4}	20^{2}	58^{5}	88^{10}	20^{2}	34^{4}	36^{5}	60^{5}	43.0^{6}
Dicranum majus	86^{11}	90^{11}	90^{10}	80^{9}	62^{9}	94^{13}	96^{14}	22^{4}	30^{9}	24^{5}	67.4^{11}
Dicranum montanum	·	·	·	·	4^{2}	·	4^{1}	·	·	2^{2}	1.0^{1}
Dicranum polysetum	6^{2}	·	8^{1}	·	·	62^{8}	6^{3}	·	2^{2}	·	8.4^{7}
Dicranum scoparium	48^{6}	90^{7}	70^{6}	84^{8}	96^{10}	92^{8}	32^{3}	78^{7}	84^{10}	88^{9}	76.2^{8}
Hylocomiastrum umbratum	44^{6}	74^{9}	2^{3}	20^{8}	6^{5}	·	24^{5}	24^{9}	14^{6}	4^{9}	21.2^{7}
Hylocomium splendens	80^{7}	98^{13}	26^{6}	96^{15}	88^{9}	60^{6}	86^{9}	90^{10}	98^{15}	84^{13}	80.6^{11}
Plagiomnium affine	·	·	4^{2}	·	·	6^{9}	2^{1}	·	2^{11}	·	1.4^{6}
Plagiothecium denticulatum	10^{1}	12^{3}	6^{1}	·	30^{4}	8^{2}	16^{2}	36^{4}	28^{3}	46^{4}	19.2^{4}
Plagiothecium laetum	38^{4}	60^{6}	56^{4}	12^{2}	78^{8}	84^{5}	62^{4}	36^{2}	32^{4}	52^{4}	51.0^{5}
Pleurozium schreberi	76^{6}	76^{9}	66^{6}	86^{9}	82^{10}	92^{11}	94^{12}	68^{8}	84^{10}	78^{11}	80.2^{9}
Pohlia cruda	·	2^{2}	·	·	·	·	·	·	4^{2}	4^{2}	1.0^{2}
Pohlia nutans	8^{2}	8^{4}	2^{1}	4^{4}	2^{1}	34^{4}	·	4^{2}	14^{3}	6^{1}	8.2^{3}
Polytrichum commune	12^{7}	8^{12}	4^{10}	·	·	4^{1}	4^{7}	26^{8}	10^{10}	12^{4}	8.0^{8}
Polytrichum juniperinum	2^{1}	·	·	·	·	6^{1}	2^{1}	·	·	·	1.0^{1}
Ptilium crista-castrensis	32^{7}	44^{7}	2^{1}	76^{12}	14^{5}	26^{3}	40^{7}	2^{9}	6^{10}	32^{13}	27.4^{9}
Rhizomnium pseudopunctatum	·	28^{7}	·	14^{4}	·	·	·	4^{2}	26^{5}	10^{5}	8.2^{6}
Rhizomnium punctatum	4^{3}	·	2^{2}	·	4^{2}	·	2^{5}	·	4^{6}	10^{3}	2.6^{3}
Rhytidiadelphus squarrosus agg.	48^{8}	64^{10}	2^{1}	32^{8}	10^{3}	·	14^{8}	46^{10}	12^{9}	6^{7}	23.4^{9}
Rhytidiadelphus triquetrus	6^{9}	2^{1}	·	26^{10}	·	·	·	2^{1}	·	·	3.6^{9}
Sanionia uncinata	·	32^{3}	·	14^{6}	4^{2}	2^{1}	·	32^{4}	16^{4}	14^{1}	11.4^{3}
Straminergon stramineum	·	8^{4}	·	·	·	·	·	2^{1}	10^{8}	·	2.0^{5}
Tetraphis pellucida	20^{1}	34^{2}	30^{3}	·	14^{2}	20^{4}	16^{1}	·	·	4^{1}	13.8^{2}
Trichostomum tenuirostre	·	·	·	·	2^{1}	·	·	·	·	10^{2}	1.2^{2}
Sphagnum angustifolium	·	18^{5}	·	·	·	2^{1}	·	·	12^{6}	12^{11}	4.4^{7}
Sphagnum centrale	2^{1}	6^{8}	·	·	2^{11}	·	·	·	·	·	1.0^{7}
Sphagnum girgensohnii	6^{2}	34^{9}	38^{6}	6^{3}	4^{11}	12^{7}	16^{7}	12^{11}	20^{7}	20^{14}	16.8^{8}
Sphagnum quinquefarium	42^{13}	14^{5}	16^{4}	24^{9}	24^{11}	10^{7}	22^{7}	·	2^{9}	6^{8}	16.0^{9}
Sphagnum rubiginosum	·	·	·	20^{12}	·	·	·	·	·	·	2.0^{12}
Sphagnum russowii	·	4^{11}	·	6^{5}	4^{2}	6^{7}	·	2^{5}	20^{7}	10^{4}	5.2^{6}
Sphagnum squarrosum	·	10^{8}	·	·	·	·	·	2^{1}	·	·	1.2^{7}
Barbilophozia attenuata	4^{1}	8^{3}	28^{2}	14^{2}	38^{3}	32^{3}	24^{2}	6^{2}	22^{2}	10^{3}	18.6^{2}
Barbilophozia barbata	20^{4}	42^{6}	6^{1}	52^{7}	38^{4}	6^{4}	2^{1}	32^{8}	6^{1}	36^{5}	24.0^{5}
Barbilophozia floerkei	48^{8}	62^{7}	·	60^{9}	40^{5}	6^{4}	24^{5}	56^{9}	66^{7}	12^{3}	37.4^{7}
Barbilophozia hatcheri	·	2^{1}	2^{1}	·	·	·	·	·	2^{2}	4^{2}	1.0^{2}
Barbilophozia kunzeana	2^{1}	·	·	8^{1}	·	2^{1}	·	·	10^{3}	·	2.2^{2}
Barbilophozia lycopodioides	38^{4}	90^{12}	2^{12}	84^{10}	92^{11}	·	46^{8}	98^{15}	100^{14}	90^{11}	64.0^{12}
Blepharostoma trichophyllum	4^{2}	26^{2}	6^{2}	6^{2}	18^{3}	8^{3}	24^{2}	6^{3}	22^{3}	26^{5}	14.6^{3}
Calypogeia integristipula	4^{2}	8^{2}	6^{1}	·	14^{2}	4^{4}	24^{2}	·	26^{3}	14^{2}	10.0^{2}
Calypogeia neesiana	12^{1}	10^{2}	2^{2}	8^{2}	26^{2}	2^{3}	2^{1}	4^{2}	10^{5}	10^{2}	8.6^{2}
Cephalozia bicuspidata	44^{4}	34^{3}	16^{3}	12^{3}	8^{2}	·	14^{1}	2^{1}	16^{2}	6^{2}	15.2^{3}
Cephalozia loitlesbergeri	·	4^{2}	·	2^{1}	·	·	·	·	2^{1}	4^{9}	1.2^{4}

Tab. 34 (cont.)

Species	OTT	ØYE	PAU	URV	GRY	LUN	RAU	GRA	GUT	BRI	Total
Cephalozia lunulifolia	18^{2}	32^{3}	8^{3}	6^{2}	30^{2}	2^{2}	12^{1}	4^{2}	34^{4}	20^{2}	16.6^{2}
Cephalozia pleniceps	4^{2}	·	·	12^{6}	2^{1}	·	·	·	14^{4}	10^{5}	4.2^{4}
Chiloscyphus profundus	60^{5}	26^{5}	64^{3}	4^{2}	80^{7}	28^{8}	68^{4}	·	2^{13}	50^{7}	38.2^{5}
Diplophyllum taxifolium	14^{2}	24^{2}	2^{1}	·	6^{2}	·	2^{2}	·	2^{1}	·	5.0^{2}
Harpanthus flotovianus	·	18^{5}	·	·	·	·	·	·	6^{5}	·	2.4^{5}
Lophozia incisa	·	4^{4}	·	2^{1}	·	·	2^{1}	·	·	2^{1}	1.0^{2}
Lophozia longidens	·	6^{2}	·	·	10^{2}	·	2^{1}	·	2^{1}	8^{1}	2.8^{2}
Lophozia obtusa	18^{4}	66^{10}	·	58^{6}	28^{4}	·	14^{2}	54^{9}	70^{8}	44^{9}	35.2^{7}
Lophozia ventricosa agg.	30^{4}	42^{3}	10^{3}	28^{2}	28^{2}	6^{2}	4^{2}	22^{5}	54^{5}	42^{5}	26.6^{4}
Moerckia blyttii	16^{2}	·	·	·	·	·	·	2^{1}	·	·	1.8^{2}
Plagiochila porelloides	6^{2}	2^{2}	10^{1}	·	·	2^{2}	2^{1}	·	·	2^{4}	2.4^{2}
Ptilidium ciliare	14^{6}	36^{9}	6^{1}	4^{4}	18^{3}	34^{4}	18^{3}	52^{6}	4^{2}	42^{3}	22.8^{5}
Ptilidium pulcherrimum	·	·	6^{1}	2^{1}	16^{1}	·	·	2^{1}	2^{3}	34^{2}	6.2^{2}
Scapania irrigua	4^{1}	6^{2}	·	·	·	·	·	·	6^{1}	·	1.6^{1}
Scapania scandica	·	20^{2}	·	·	·	·	·	·	4^{1}	·	2.4^{2}
Scapania umbrosa	·	12^{2}	·	4^{3}	·	·	·	·	·	·	1.6^{2}
Tritomaria quinquedentata	22^{6}	30^{7}	12^{2}	54^{7}	24^{4}	·	2^{4}	34^{10}	32^{6}	22^{4}	23.2^{6}
Cladonia bellidiflora	8^{2}	2^{1}	·	·	4^{1}	16^{3}	·	6^{3}	12^{2}	·	4.8^{2}
Cladonia chlorophaea agg.	12^{1}	24^{1}	8^{2}	4^{1}	26^{5}	16^{2}	2^{1}	12^{3}	34^{2}	32^{3}	17.0^{2}
Cladonia coniocraea agg.	12^{3}	30^{2}	2^{1}	16^{1}	26^{3}	40^{2}	10^{1}	16^{2}	10^{1}	26^{3}	18.8^{2}
Cladonia furcata	14^{4}	20^{5}	2^{6}	12^{3}	16^{3}	16^{4}	·	36^{4}	36^{5}	18^{2}	17.0^{4}

Additional species (occurring in 5 or fewer sample plots; Area: F^{FSP} $TotF^{FSP}$):

Juniperus communis GUT 4^{2}, GRA 2^{1} 0.6^{1}; Quercus sp. LUN 8^{2} 0.8^{2}; Calluna vulgaris OTT 2^{1}, ØYE 2^{9} 0.4^{5}; Phyllodoce caerulea GRA 2^{9} 0.2^{9}; Vaccinium uliginosum OTT 4^{2}, GUT 4^{6} 0.8^{4}.

Actaea spicata BRI 2^{4} 0.2^{4}; Alchemilla sp. GUT 4^{3}, URV 2^{2} 0.3^{3}; Antennaria dioica LUN 2^{2} 0.2^{2}; Athyrium distentifolium ØYE 2^{4} 0.2^{4}; Campanula rotundifolia URV 2^{3} 0.2^{3}; Circium helenioides URV 2^{8} 0.2^{8}; Dactylorhiza fuchsii GRA 4^{1} 0.4^{1}; Dactylorhiza maculata RAU 2^{2}, ØYE 2^{1} 0.4^{2}; Digitalis purpurea OTT 2^{2} 0.2^{2}; Epilobium angustifolium GRA 4^{5} 0.4^{5}; Equisetum pratense GRA 8^{2} 0.8^{2}; Eriophorum vaginatum GRA 2^{6} 0.2^{6}; Filipendula ulmaria URV 6^{7} 0.6^{7}; Galium boreale URV 2^{1} 0.2^{1}; Galium saxatile OTT 2^{1} 0.2^{1}; Geum rivale GUT 2^{3}, URV 6^{2} 0.8^{2}; Lonicera periclymenum PAU 2^{2} 0.2^{2}; Narthecium ossifragum OTT 6^{6} 0.2^{2}; Platanthera sp. RAU 2^{2} 0.2^{2}; Prunella vulgaris URV 4^{1} 0.4^{1}; Pyrola minor GUT 2^{2} 0.2^{2}; Selaginella selaginoides GUT 2^{2}, GRA 4^{5} 0.6^{4}; Taraxacum sp. GUT 2^{2} 0.2^{2}; Trollius europaeus GRA 8^{3} 0.8^{3}.

Agrostis canina RAU 4^{4}, GUT 2^{8} 0.6^{5}; Carex binervis OTT 8^{3} 0.8^{3}; Carex brunnescens GRA 4^{4} 0.4^{4}; Carex panicea OTT 4^{2} 0.4^{2}; Carex paupercula OTT 4^{4} 0.4^{4}; Festuca rubra LUN 2^{8} 0.2^{8}.

Bartramia ithyphylla BRI 2^{2} 0.2^{2}; Bartramia pomiformis BRI 2^{1} 0.2^{1}; Andreaea; rupestris OTT 2^{2} 0.2^{2}; Antitrichia curtipendula RAU 2^{1} 0.2^{1}; Brachythecium oedipodium LUN 4^{6} 0.4^{6}; Brachythecium populeum PAU 6^{1} 0.6^{1}; Brachythecium; rivulare GRY 2^{1} 0.2^{1}; Brachythecium rutabulum GRY 6^{4}, RAU 2^{1} 0.8^{4}; Bryum sp. GUT 2^{2} 0.2^{2}; Campylopus atrovirens OTT 2^{1} 0.2^{1}; Eurhynchium angustirete RAU 2^{3} 0.2^{3}; Herzogiella seligeri LUN 2^{3}, RAU 2^{1} 0.4^{2}; Hylocomiastrum pyrenaicum GUT 2^{7}, GRA 4^{1} 0.6^{3}; Isopterygiopsis pulchella GUT 2^{1} 0.2^{1}; Paraleucobryum longifolium OTT 2^{1} 0.2^{1}; Polytrichum alpinum GUT 2^{1} 0.2^{1}; Racomitrium canescens agg. OTT 2^{3} 0.2^{3}; Racomitrium heterostichum agg. PAU 2^{1}, OTT 2^{1} 0.4^{1}; Racomitrium lanuginosum; OTT 2^{2} 0.2^{2}; Schistidium apocarpum agg. OTT 4^{2} 0.4^{2}; Thuidium delicatulum OTT 2^{2} 0.2^{2}.

Sphagnum aongstroemii GRA 2^{1} 0.2^{1}; Sphagnum palustre LUN 2^{1} 0.2^{1}; Sphagnum papillosum OTT 2^{4} 0.2^{4}.

Barbilophozia atlantica OTT 2^{1} 0.2^{1}; Bazzania tricrenata GRY 2^{1}, OTT 4^{3} 0.6^{2}; Bazzania trilobata OTT 6^{7} 0.6^{7}; Cephalozia connivens GRY 2^{1} 0.2^{1}; Cephalozia lacinulata ØYE 2^{1} 0.2^{1}; Cephalozia leucantha OTT 2^{2} 0.2^{2}; Cephaloziella sp. GRY 2^{1}, GUT 4^{3} 0.6^{2}; Kurzia trichoclados OTT 4^{2} 0.4^{2}; Lophozia adscendens PAU 2^{1}, GRY 2^{2} 0.4^{2}; Lophozia collaris OTT 2^{1} 0.2^{1}; Lophozia excisa GUT 6^{1}, ØYE 2^{1} 0.8^{1}; Lophozia sudetica GRY 2^{1}, OTT 2^{2}, GUT 2^{1} 0.6^{1}; Lophozia wenzelii GUT 2^{2} 0.2^{2}; Marsupella emarginata ØYE 2^{1} 0.2^{1}; Metzgeria furcata GRY 2^{1} 0.2^{1}; Nowellia curvifolia LUN 2^{1} 0.2^{1}; Pellia sp. GUT 2^{1} 0.2^{1}; Radula complanata BRI 4^{2} 0.4^{2}; Rhabdoweisia crenulata OTT 2^{1} 0.2^{1}; Scapania paludosa ØYE 6^{2} 0.6^{2}; Scapania uliginosa ØYE 2^{4} 0.2^{4}; Anastrophyllum minutum PAU 2^{1}, ØYE 2^{1} 0.4^{1}; Tritomaria exsectiformis OTT 2^{1} 0.2^{1}.

Cetraria pinastri BRI 4^{2} 0.4^{2}; Cladonia arbuscula agg. GUT 2^{5} 0.2^{5}; Cladonia cariosa GUT 2^{2} 0.2^{2}; Cladonia coccifera agg. GUT 4^{1}, ØYE 2^{1} 0.6^{1}; Cladonia cornuta BRI 4^{1}, GUT 4^{2} 0.8^{1}; Cladonia deformis GUT 4^{2} 0.4^{2}; Cladonia macilenta LUN 2^{4} 0.2^{4}; Cladonia phyllophora LUN 2^{2}, GUT 2^{1} 0.4^{2}; Cladonia squamosa LUN 6^{3}, OTT 2^{1} 0.8^{2}; Cladonia sulphurina GUT 8^{3} 0.8^{3}; Cladonia uncialis LUN 4^{3}, GUT 4^{3} 0.2^{1}; Hypogymnia physodes BRI 2^{1} 0.2^{1}; Nephroma arcticum GUT 2^{1} 0.2^{1}; Nephroma parile BRI 2^{1} 0.2^{1}; Peltigera aphthosa GRA 6^{4} 0.6^{4}; Peltigera canina GUT 2^{6} 0.2^{6}; Peltigera degenii BRI 4^{5} 0.4^{5}; Peltigera membranacea BRI 2^{1} 0.2^{1}.

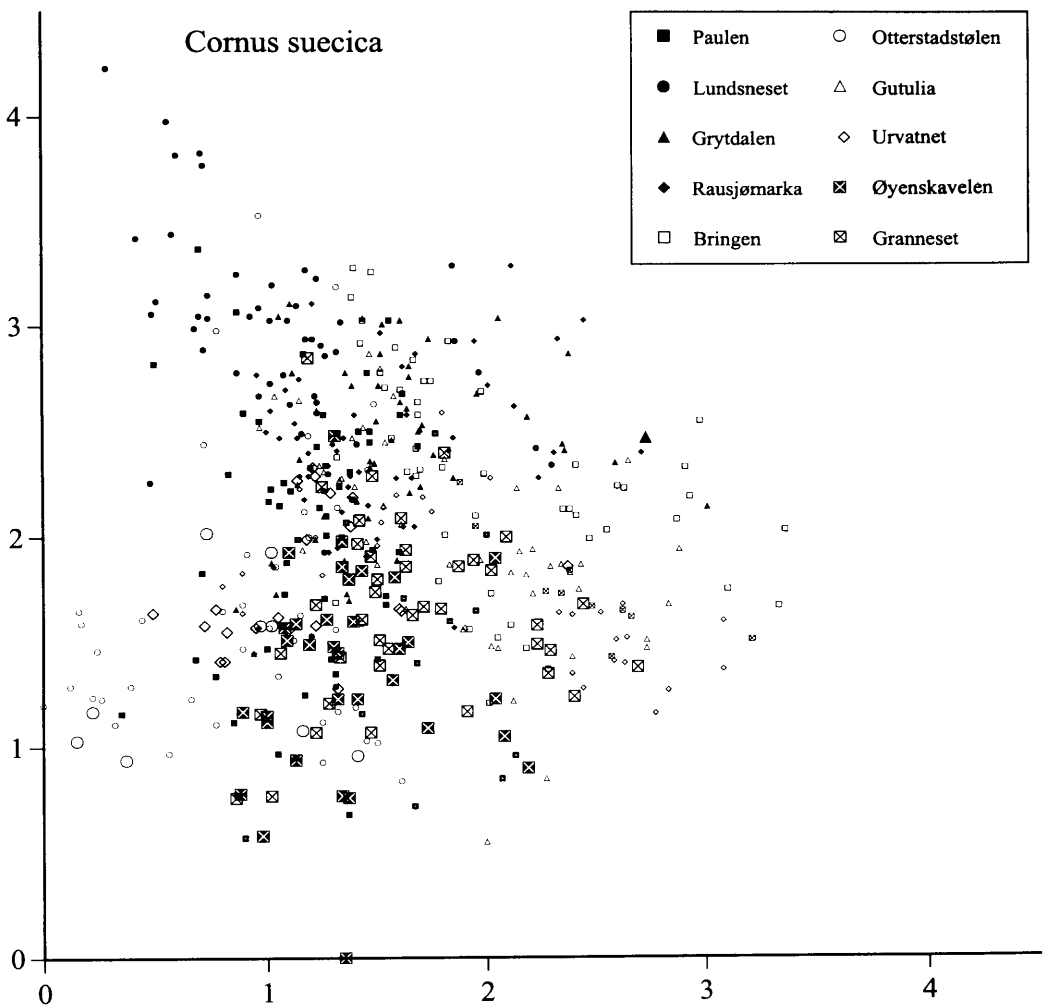


Fig. 772. The total data set: distribution of *Cornus suecica* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

Variation in environmental variables between reference areas

The reference areas differed considerably with respect to the range and median values for several of the measured environmental variables (Tab. 35). Among the topographic variables, inclination was particularly high in Otterstadstølen and Grytdalen, aspects were generally more unfavourable in Paulen and Grytdalen, and meso plot roughness was particularly low in Granneset. The soil depth was generally higher in the three northernmost reference areas. The

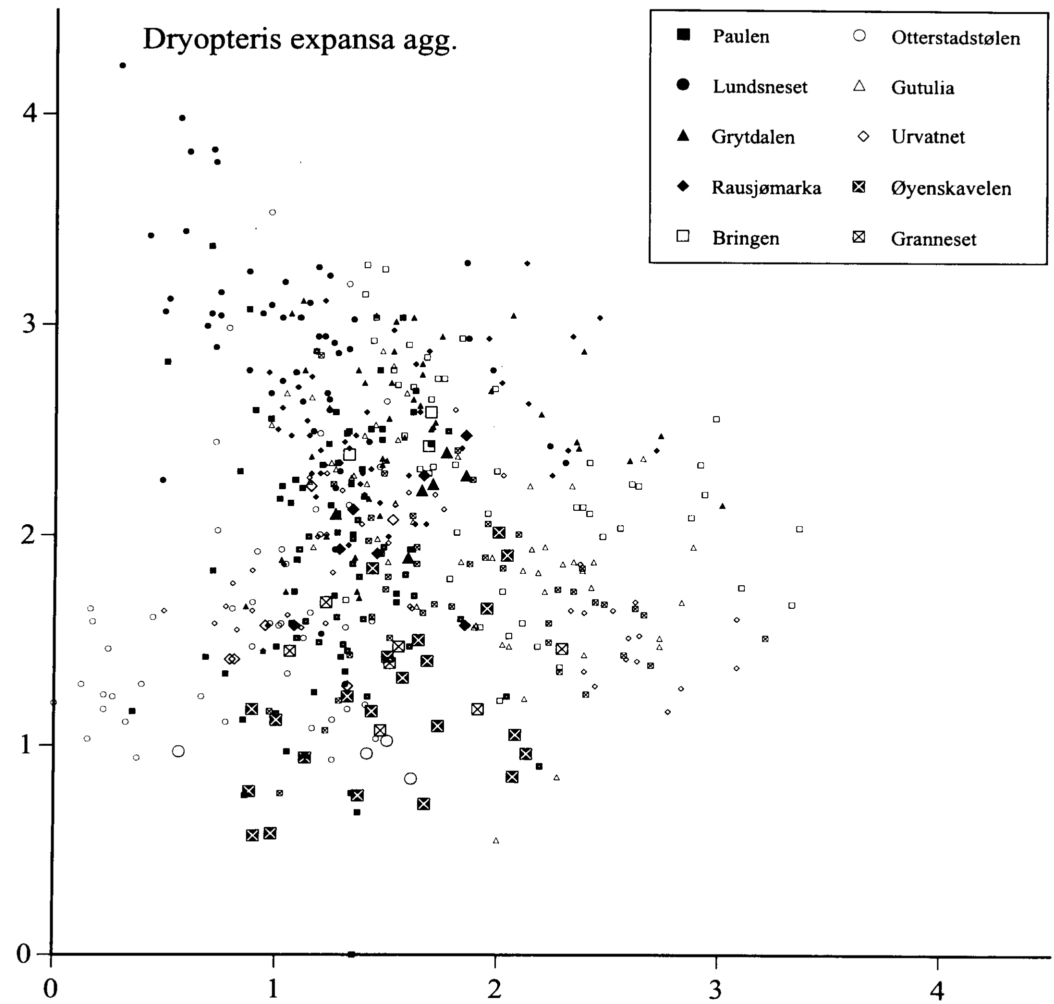


Fig. 773. The total data set: distribution of *Dryopteris expansa* agg. (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

recorded soil moisture was highest in Otterstadstølen and Øyenskavelen, the most humid reference areas. Lowest pH values were recorded in the southernmost reference areas, notably in Paulen and Lundsneset. The lowest concentrations of Ca were recorded in the humid and in the southernmost reference areas, while higher concentrations were recorded in the more continental and/or northernmost areas. The highest Mg and Na concentrations were recorded in Øyenskavelen. The highest concentrations of total N were recorded in Otterstadstølen.

Tab. 35. Variation of environmental variables within monitoring areas: minimum, median (in bold face) and maximum.

	01 MA Inc			02 MA Asp			03 MA H i			04 MA BA			05 MA Lig			06 ME Inc			07 MA Asp			08 ME H i		
	Min	**Med**	Max	Min	**Med**	Max	Min	**Med**	Max	Min	**Med**	Max	Min	**Med**	Max	Min	**Med**	Max	Min	**Med**	Max	Min	**Med**	Max
Paulen	9	**23**	31	70	**138**	185	-0.52	**-0.21**	0.01	6.8	**8.6**	15.3	0.34	**0.67**	1.21	3	**22**	46	35	**130**	198	-0.88	**-0.18**	0.09
Lundneset	5	**20**	38	10	**105**	200	-0.34	**0.09**	0.66	12.3	**15.9**	27.5	0.20	**0.43**	0.67	5	**20**	42	1	**99**	199	-0.42	**0.10**	0.72
Grytdalen	3	**29**	51	60	**130**	198	-0.63	**-0.08**	0.41	11.5	**14.9**	21.5	0.13	**0.38**	0.63	6	**31**	51	17	**129**	196	-0.95	**-0.17**	0.43
Rausjømarka	8	**16**	25	10	**100**	177	-0.29	**-0.02**	0.23	11.8	**15.9**	27.2	0.13	**0.32**	0.49	4	**21**	45	0	**98**	175	-0.72	**-0.01**	0.66
Bringen	3	**24**	44	20	**100**	168	-0.45	**-0.06**	0.46	10.0	**11.8**	15.5	0.26	**0.57**	0.79	0	**24**	48	5	**114**	198	-0.68	**-0.11**	0.60
Otterstadstølen	26	**38**	54	10	**86**	178	-1.58	**-0.09**	0.89	5.3	**10.8**	13.8	0.21	**0.57**	1.11	5	**32**	48	7	**118**	196	-0.80	**-0.13**	0.80
Gutulia	4	**15**	30	10	**70**	165	-0.29	**0.06**	0.29	9.5	**17.6**	26.5	0.15	**0.35**	0.36	2	**15**	35	5	**95**	175	-0.40	**0.00**	0.55
Urvatnet	1	**15**	30	10	**109**	195	-0.43	**-0.07**	0.36	9.0	**18.0**	25.0	0.35	**0.50**	0.79	1	**14**	42	0	**108**	198	-0.54	**-0.06**	0.47
Øyenskavlen	2	**11**	18	5	**87**	135	-0.13	**-0.08**	0.47	6.0	**11.6**	17.8	0.37	**0.59**	0.97	0	**20**	34	4	**96**	200	-0.36	**0.04**	0.50
Granneset	19	**25**	33	20	**101**	150	-0.34	**-0.06**	0.15	5.8	**10.2**	16.3	0.18	**0.65**	0.96	0	**18**	39	5	**118**	200	-0.53	**-0.11**	0.12

	09 ME Rou			10 ME Con			11 ME Smi			12 ME Sme			13 ME Sma			14 LitCC			15 LitACD			16 Mois		
	Min	**Med**	Max	Min	**Med**	Max	Min	**Med**	Max	Min	**Med**	Max	Min	**Med**	Max	Min	**Med**	Max	Min	**Med**	Max	Min	**Med**	Max
Paulen	0.00	**1.31**	2.15	-6.7	**-0.5**	8.1	0.0	**1.9**	3.5	2.2	**3.0**	4.1	3.0	**4.0**	4.5	0.00	**1.92**	2.81	0.00	**1.77**	2.63	5	**11**	56
Lundneset	0.53	**1.28**	2.27	-7.8	**-0.3**	11.5	0.0	**2.1**	3.7	1.1	**3.0**	4.1	2.4	**3.7**	4.4	0.00	**1.05**	2.37	0.00	**1.04**	2.36	6	**11**	36
Grytdalen	0.88	**1.42**	2.23	7.9	**0.1**	4.8	0.0	**1.7**	4.0	0.0	**2.7**	4.3	2.2	**3.5**	4.5	0.00	**0.95**	2.99	0.00	**0.92**	2.93	18	**35**	60
Rausjømarka	0.83	**1.46**	2.52	-5.7	**0.7**	16.4	0.0	**1.7**	3.6	1.6	**2.8**	4.2	1.6	**3.4**	4.4	0.00	**1.22**	2.76	0.00	**1.17**	2.82	11	**30**	54
Bringen	0.88	**1.47**	2.12	-10.8	**0.1**	6.6	0.0	**2.3**	4.0	2.3	**3.3**	4.4	3.0	**4.0**	4.9	0.00	**1.11**	2.63	0.00	**1.12**	2.60	4	**12**	28
Otterstadstølen	0.67	**1.28**	2.31	-6.6	**-0.4**	4.6	0.0	**2.1**	3.7	2.1	**3.3**	4.1	3.3	**3.9**	4.7	0.00	**1.22**	2.93	0.00	**1.17**	2.81	33	**46**	65
Gutulia	0.88	**1.44**	2.19	-6.6	**-1.0**	5.7	0.0	**1.6**	3.3	0.9	**2.7**	4.3	2.2	**3.5**	4.6	0.00	**0.88**	2.81	0.00	**0.78**	2.58	6	**27**	59
Urvatnet	0.53	**1.30**	2.19	-6.2	**-1.0**	5.7	0.0	**3.0**	4.3	2.8	**3.8**	4.5	3.0	**4.2**	4.8	0.00	**1.22**	2.79	0.00	**1.04**	2.36	14	**37**	61
Øyenskavlen	0.00	**1.35**	2.14	-4.4	**0.1**	9.2	0.0	**2.6**	4.7	0.0	**3.6**	4.7	0.0	**4.0**	4.7	0.00	**1.24**	2.65	0.00	**1.05**	2.53	12	**43**	69
Granneset	0.41	**0.98**	1.59	-2.8	**0.1**	4.2	0.7	**3.0**	5.0	2.4	**3.9**	5.0	3.4	**4.4**	5.0	0.00	**1.32**	2.85	0.00	**1.10**	2.62	5	**25**	51

Tab. 35 (cont.)

	17 LI			18 pH_{H2O}			19 pH_{CaCl2}			20 Ca			21 Mg			22 K			23 Na			24 H^+		
	Min	**Med**	Max	Min	**Med**	Max	Min	**Med**	Max	Min	**Med**	Max	Min	**Med**	Max	Min	**Med**	Max	Min	**Med**	Max	Min	**Med**	Max
Paulen	56.9	**91.3**	96.2	3.6	**4.0**	4.8	2.9	**3.2**	4.0	5.81	**7.56**	8.13	4.62	**6.17**	6.74	5.69	**6.76**	7.32	4.46	**5.24**	5.67	4.22	**4.79**	5.28
Lundneset	30.7	**88.9**	98.7	3.8	**4.2**	5.0	2.9	**3.2**	4.0	5.31	**7.67**	8.91	4.80	**6.18**	6.76	6.22	**6.90**	7.19	4.86	**5.51**	5.98	2.33	**4.75**	5.56
Grytdalen	64.8	**87.9**	97.5	3.9	**4.4**	5.2	3.0	**3.4**	4.5	7.16	**8.15**	9.08	5.17	**5.70**	6.04	6.48	**6.83**	7.22	4.09	**4.74**	5.51	4.76	**5.64**	6.29
Rausjømarka	13.2	**60.5**	94.7	3.3	**4.2**	5.0	3.0	**3.4**	4.4	6.37	**7.99**	9.65	5.16	**5.88**	6.94	5.99	**6.85**	7.43	4.03	**4.72**	5.27	3.71	**5.81**	6.54
Bringen	28.7	**75.3**	97.3	3.6	**4.4**	5.6	2.8	**3.6**	5.0	7.18	**8.26**	9.77	5.25	**6.05**	7.12	5.67	**6.73**	7.35	4.03	**4.69**	6.36	0.23	**3.78**	4.56
Otterstadstølen	33.4	**85.6**	97.9	3.9	**4.3**	4.9	3.2	**3.5**	3.8	6.77	**7.59**	8.38	6.11	**6.91**	7.59	6.30	**6.78**	7.19	4.93	**5.31**	5.73	4.08	**4.63**	5.68
Gutulia	44.2	**85.6**	96.9	2.8	**4.6**	5.5	3.0	**4.0**	5.2	7.28	**8.49**	9.45	5.38	**6.00**	6.56	6.72	**7.17**	7.86	4.08	**4.72**	5.69	0.11	**3.17**	4.69
Urvatnet	30.5	**81.0**	98.2	4.0	**4.8**	6.8	4.1	**4.4**	4.9	6.97	**8.47**	10.25	6.41	**6.82**	7.47	6.69	**7.10**	7.55	5.48	**6.02**	6.82	0.19	**3.96**	5.05
Øyenskavlen	59.5	**89.0**	97.9	4.1	**4.4**	4.9	4.0	**4.3**	5.0	6.74	**7.88**	8.92	6.13	**7.12**	7.53	6.57	**7.19**	9.14	5.29	**6.07**	6.69	2.93	**4.11**	4.83
Granneset	37.7	**78.7**	97.7	4.0	**4.3**	5.0	3.2	**3.6**	4.5	7.32	**8.30**	9.14	6.37	**6.81**	7.43	6.54	**7.16**	8.08	4.95	**5.42**	6.17	0.10	**3.48**	5.63

	25 Al			26 Fe			27 Mn			28 Zn			29 Total N			30 P-Al			31 P			32 S		
	Min	**Med**	Max	Min	**Med**	Max	Min	**Med**	Max	Min	**Med**	Max	Min	**Med**	Max	Min	**Med**	Max	Min	**Med**	Max	Min	**Med**	Max
Paulen	4.15	**5.99**	7.75	2.62	**3.59**	5.76	2.59	**4.34**	5.30	2.86	**4.20**	4.92	0.92	**1.09**	1.40	3.67	**4.73**	5.15	0.00	**4.78**	5.21	4.29	**4.54**	5.02
Lundneset	4.18	**5.23**	7.67	2.62	**3.59**	5.76	3.24	**4.85**	7.58	3.08	**4.17**	5.76	0.88	**0.99**	1.28	3.98	**4.52**	5.31	3.11	**4.48**	5.11	4.52	**4.96**	5.61
Grytdalen	0.25	**3.47**	7.48	0.00	**2.05**	4.37	4.84	**6.46**	7.93	3.72	**4.42**	5.35	0.86	**1.06**	1.21	3.97	**4.76**	5.06	2.49	**4.79**	7.25	4.07	**4.45**	4.79
Rausjømarka	2.94	**6.27**	8.04	0.00	**4.23**	6.25	3.76	**5.63**	6.98	2.94	**4.23**	4.98	0.92	**1.12**	1.31	4.30	**4.81**	5.65	1.79	**3.99**	5.69	3.56	**4.32**	4.80
Bringen	3.65	**4.90**	7.59	0.00	**3.13**	5.50	4.85	**6.42**	7.71	2.95	**4.04**	5.11	0.68	**0.95**	1.26	3.71	**4.84**	5.40	1.34	**4.49**	5.44	4.81	**5.21**	6.24
Otterstadstølen	3.53	**5.22**	7.71	1.66	**3.13**	5.89	2.92	**4.03**	7.77	2.91	**3.85**	4.57	0.96	**1.16**	1.48	3.89	**4.65**	5.21	1.93	**4.57**	5.48	3.45	**4.16**	4.67
Gutulia	3.14	**4.56**	6.54	0.70	**2.35**	5.13	4.98	**6.87**	7.98	3.15	**3.76**	4.59	0.85	**1.01**	1.28	4.33	**5.09**	6.18	2.33	**4.89**	5.99	3.69	**4.50**	5.02
Urvatnet	2.67	**4.03**	6.48	2.42	**3.07**	4.70	3.95	**5.94**	7.48	1.86	**3.12**	3.85	0.60	**0.91**	1.12	3.65	**4.59**	5.30	3.34	**4.55**	5.43	4.68	**5.01**	5.46
Øyenskavlen	2.85	**5.35**	7.43	2.11	**4.12**	7.02	3.35	**4.10**	5.85	1.83	**3.07**	4.27	0.85	**1.05**	1.41	4.32	**4.86**	5.54	1.63	**4.30**	5.63	4.47	**5.18**	5.71
Granneset	2.98	**3.98**	4.86	1.23	**3.36**	5.22	4.45	**6.20**	7.96	3.15	**3.87**	4.68	0.77	**1.06**	1.26	4.60	**5.78**	6.29	4.94	**5.86**	6.79	4.25	**4.62**	5.48

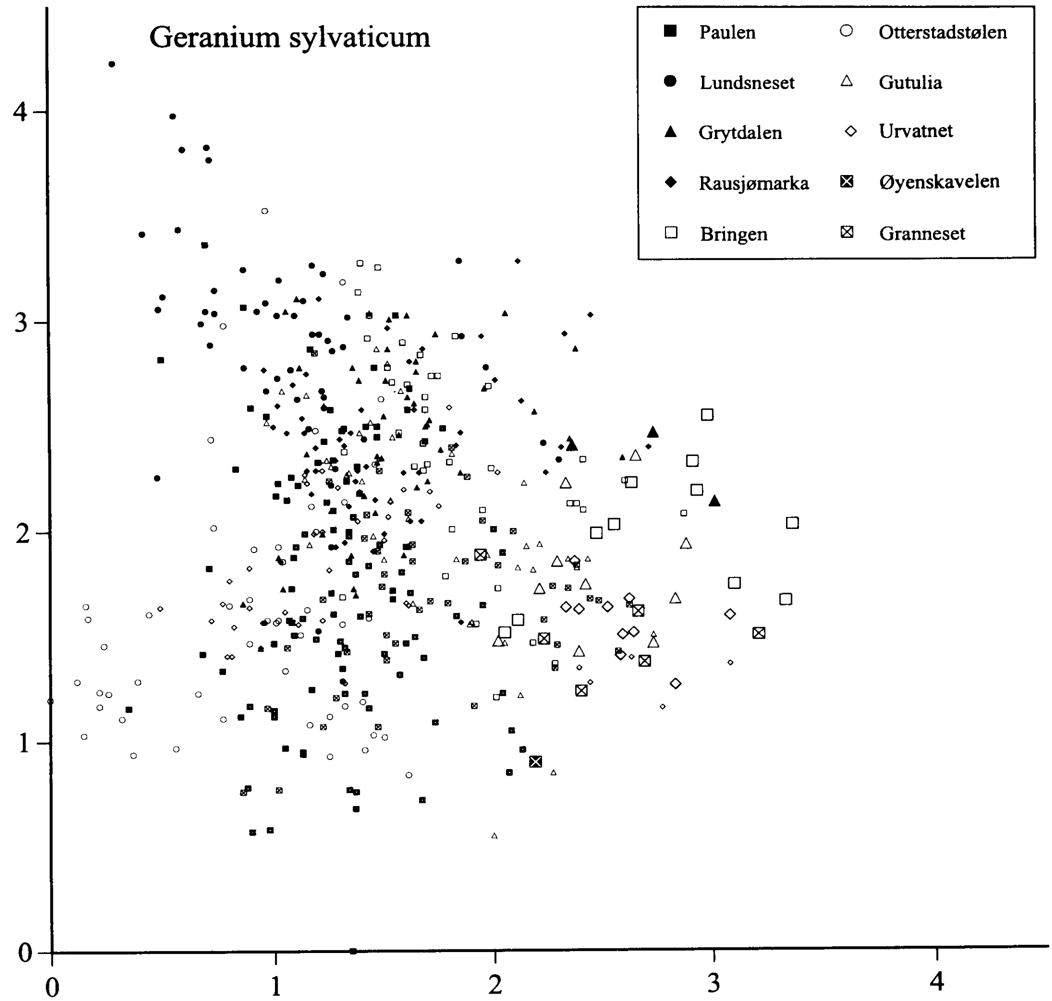


Fig. 774. The total data set: distribution of *Geranium sylvaticum* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

Variation partitioning

The total variation in the data set (total inertia) was 6.242.

(1) *CCA with seven climatic/geographical variables as constraining variables, and using forward selection of variables. A*ll variables contributed significantly to explain variation in vegetation ($P < 0.001$). The variation explained by these variables, C ($C = C|E + C \cap E$), was 0.791, corresponding to an explained fraction of variation of 0.791/6.242 = 0.127 (12.7%).

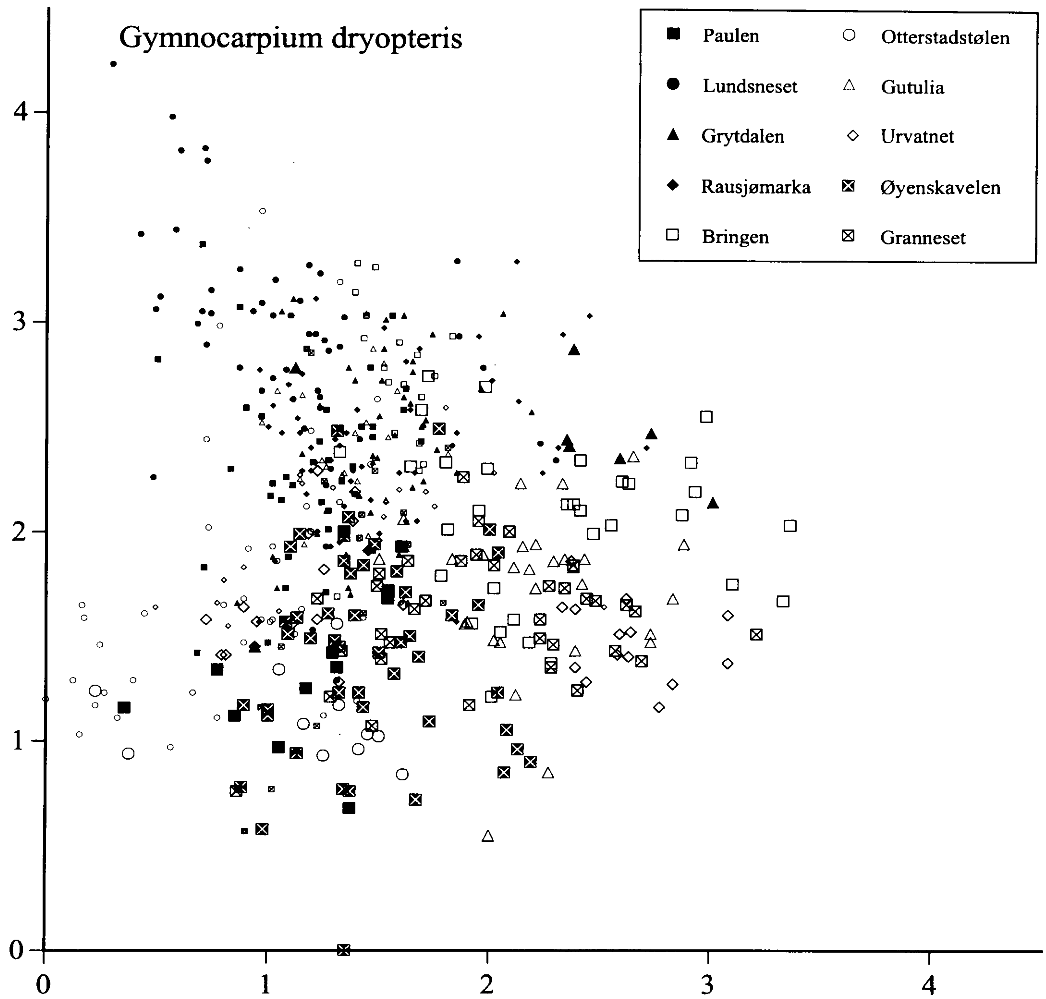


Fig. 775. The total data set: distribution of *Gymnocarpium dryopteris* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

(2) *CCA with 32 environmental variables as constraining variables, and using forward selection of variables*: Twenty-six of 32 variables (all except: ME Con, ME Sma, LitACD, ME Asp, ME Smi and pH_{H2O}) contributed significantly to explain variation in vegetation ($P < 0.001$). The variation explained by these variables; E ($E = E|C + E \cap C$), was 1.569, corresponding to an explained fraction of variation of 1.569/6.242 = 0.251 (25.1%).

(3) *CCA with seven climatic/geographical variables as covariables and 26 significant environmental explanatory variables as constraining variables*: The variation explained by en-

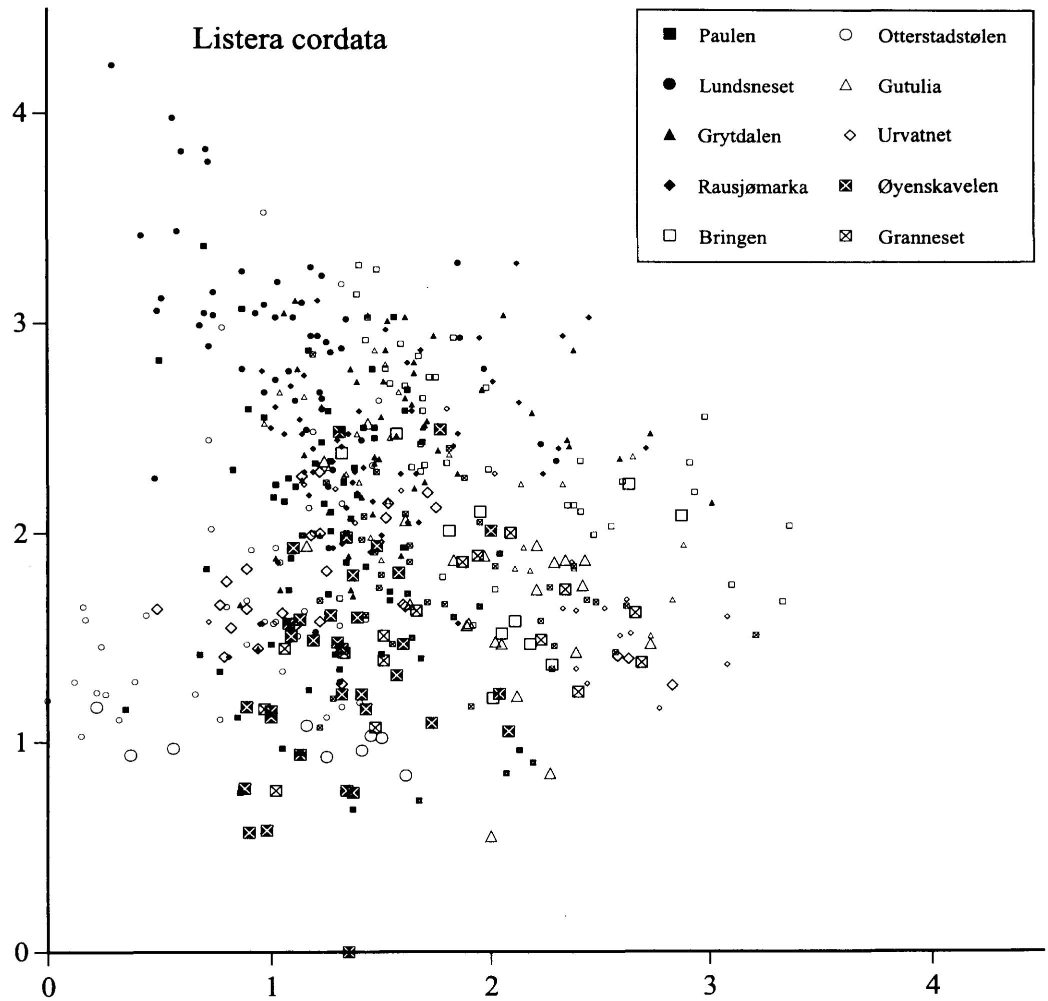


Fig. 776. The total data set: distribution of *Listera cordata* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

vironmental variables after removal of variation due to climatic/geographical variables; E|C was 1.071, corresponding to an explained fraction of variation of 1.071/6.242 = 0.172 (17.2%).

The fraction of variation explained by environmental as well as climatic/geographical variables (variation shared between the two sets of explanatory variables), E∩C = E - E|C, was 0.498, corresponding to an explained fraction of variation of 0.498/6.242 = 0.080 (8.0%). The variation exclusively due to climatic/geographical variables, C - E∩C, was 0.293, corresponding to an explained fraction of variation of 0.293/6.242 = 0.047 (4.8 %).

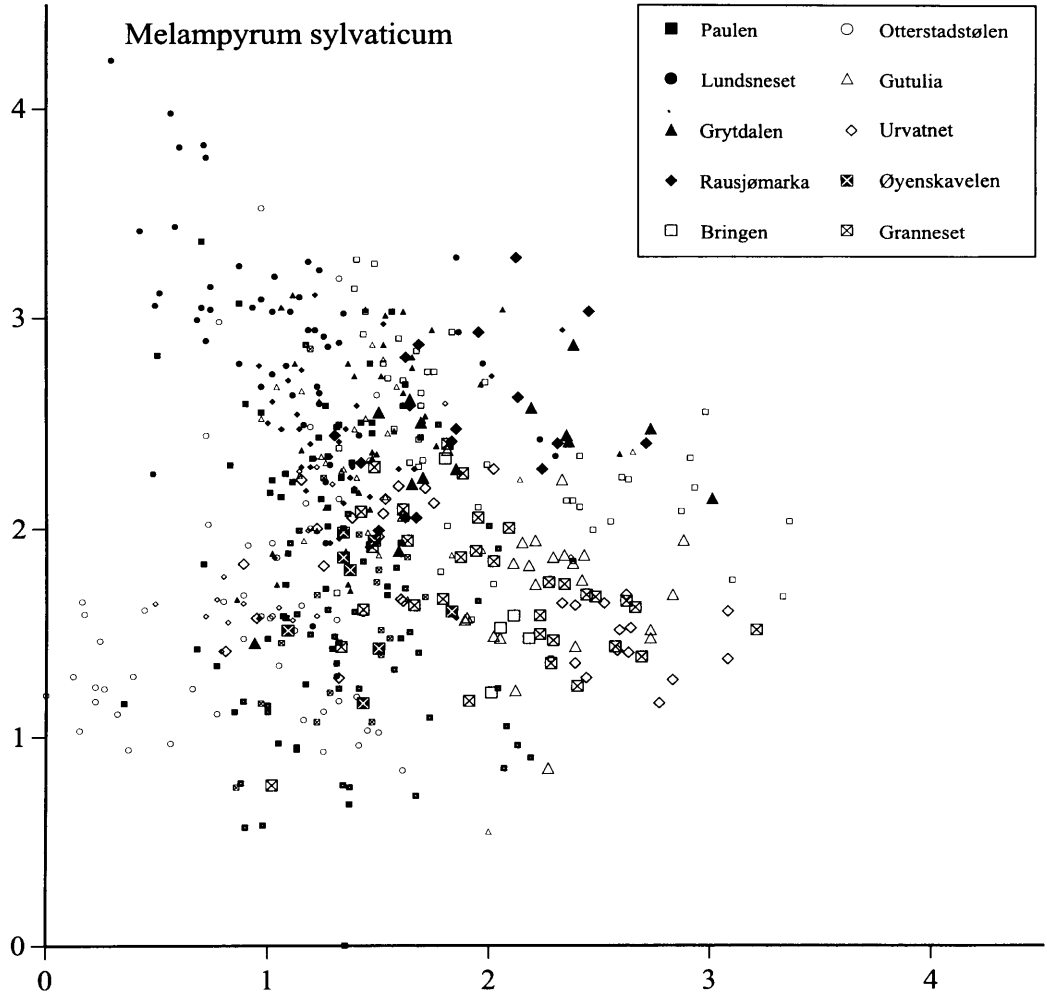


Fig. 777. The total data set: distribution of *Melampyrum sylvaticum* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

DCA ordination of the total data set

Seventeen plots from Otterstadstølen were separated from the other plots by having low DCA 1 and low DCA 2 scores, while most plots from Lundsneset had low DCA 1 and high DCA 2 scores in the DCA ordination of the total data set (Fig. 768). The highest DCA 1 scores were obtained in plots from Bringen, Gutulia, Urvatnet and Granneset.

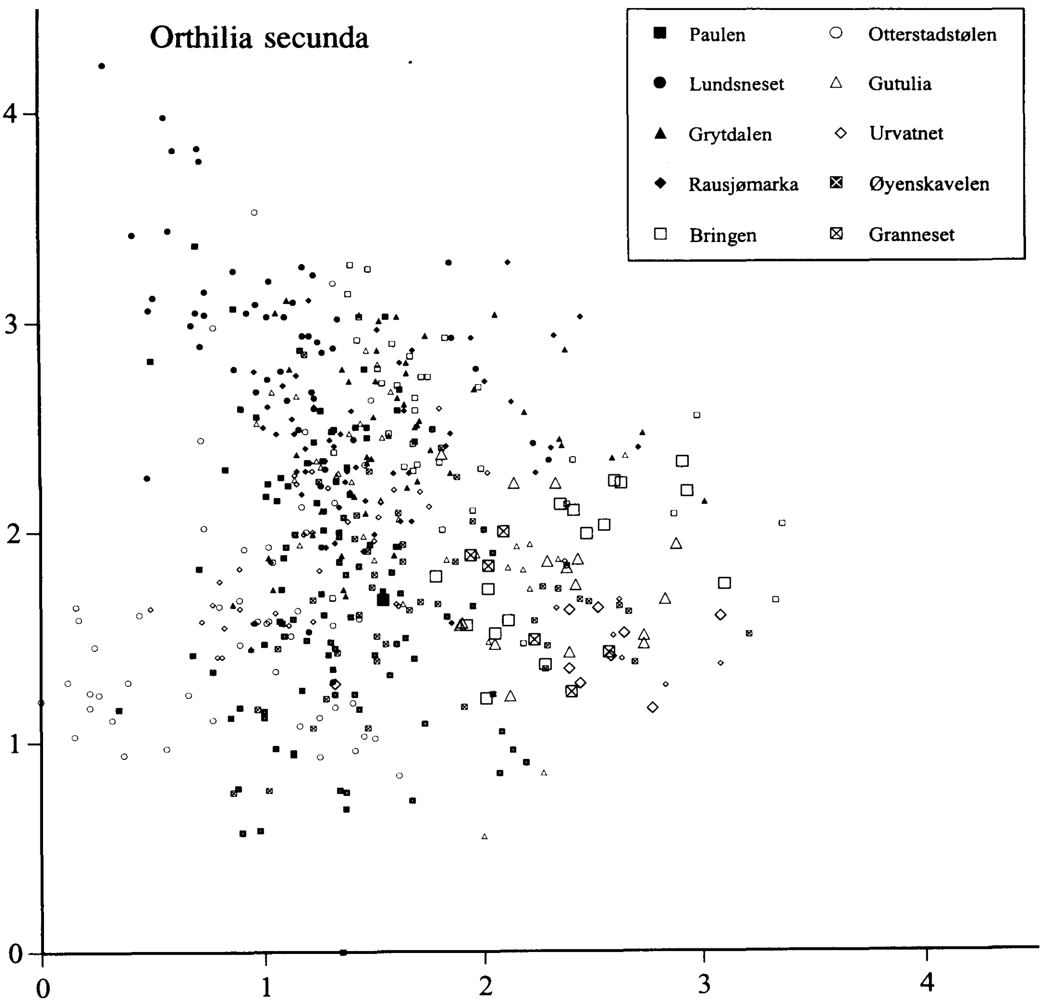


Fig. 778. The total data set: distribution of *Orthilia secunda* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

Correlations between DCA axes (ordination of the total data set) and environmental/climatic and geographical variables

pH and concentrations of Ca, and Mn were the variables most strongly positively correlated with DCA 1, while the concentration of H^+, the mean annual temperature and effective temperature sum were most strongly negatively correlated, all with $|\tau| > 0.3$, $P \ll 0.0001$ (Tab. 36). Zn was the variable most strongly positively correlated with DCA 2 while soil

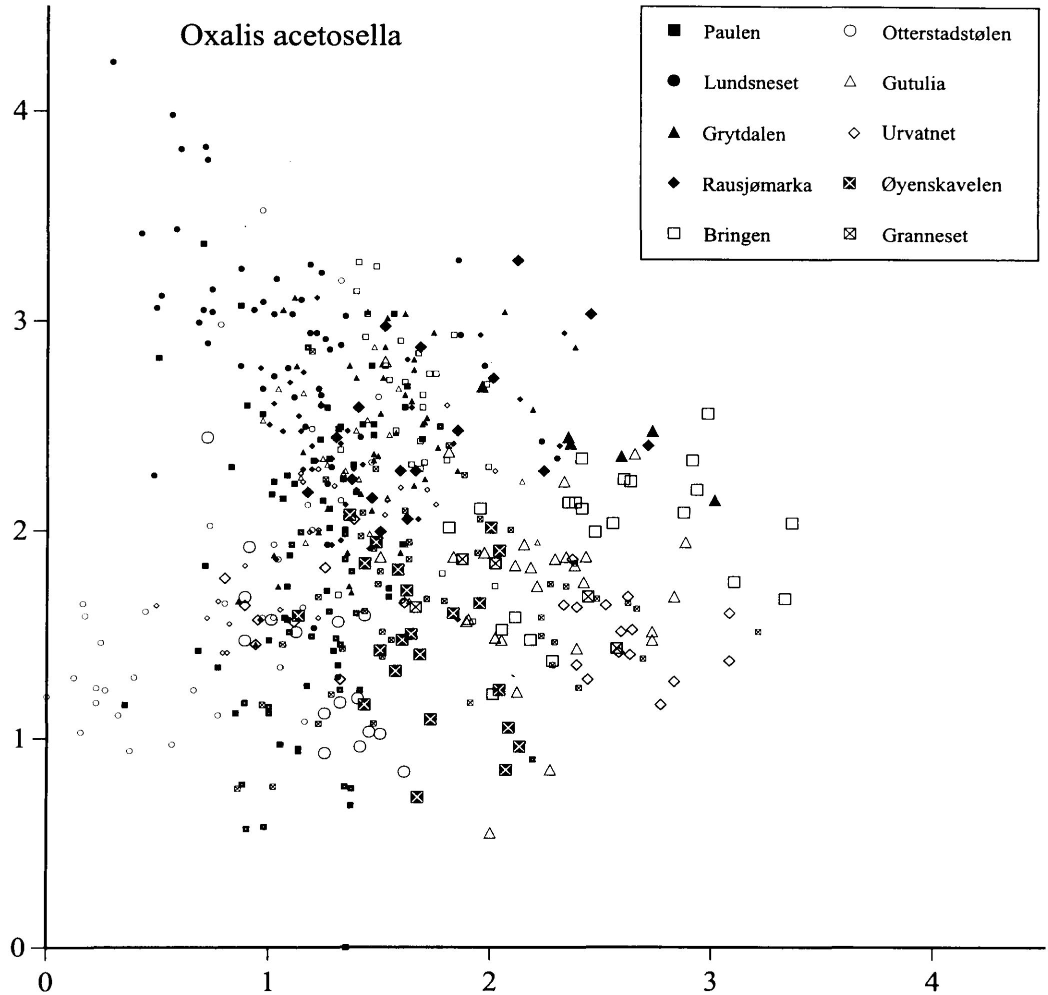


Fig. 779. The total data set: distribution of *Oxalis acetosella* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

moisture, the concentration of Mg, mean annual precipitation, Tamm's humidity index and latitude were the variables most strongly negatively correlated ($|\tau| > 0.3$, $P << 0.0001$). The variables most strongly correlated with DCA 3 were the concentration of P (positively correlated), effective temperature sum and the concentration of total N (both negatively correlated).

Tab. 36. The total material: Kendall's nonparametric correlation coefficients τ with significance probabilities (P) between 32 environmental and 7 climatic/geographical variables in the 500 meso sample plots and sample plot positions with respect to DCA axes. Correlations significant at level $P < 0.0001$ in bold face. n.s. - significance probability > 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 2.

Variable	DCA 1		DCA 2		DCA 3		DCA 4	
	τ	P	τ	P	τ	P	τ	P
01 MA Inc	-.1143	.0002	-.0277	n.s.	**-.2131**	**.0000**	**.2120**	**.0000**
02 MA Asp	**-.1853**	**.0000**	-.0983	.0012	.0064	n.s.	-.0603	.0473
03 MA Hi	.1027	.0007	**.1416**	**.0000**	-.0284	n.s.	.0928	.0021
04 MA BA	.0673	n.s.	**.1999**	**.0000**	.0093	n.s.	**-.2259**	**.0000**
05 MA Lig	.0460	n.s.	-.0492	n.s.	-.1015	.0008	**.2413**	**.0000**
06 ME Inc	-.0926	.0023	.0450	n.s.	**-.1989**	**.0000**	**.1912**	**.0000**
07 ME Asp	**-.1279**	**.0000**	**-.1266**	**.0000**	.0520	.0849	-.0287	n.s.
08 ME Hi	.0899	.0027	**.1450**	**.0000**	-.0511	n.s.	.0241	n.s.
09 ME Rou	-.0435	n.s.	.0615	.0414	-.0108	n.s.	.0413	n.s.
10 ME Con	.0150	n.s.	.0166	n.s.	-.0069	n.s.	-.0048	n.s.
11 ME Smi	.0521	.0873	**-.1482**	**.0000**	**.1312**	**.0000**	-.0881	.0038
12 ME Sme	.0750	.0128	**-.2540**	**.0000**	.0841	.0052	-.0171	n.s.
13 ME Sma	.0953	.0016	**-.2013**	**.0000**	.0841	.0053	.0350	n.s.
14 LitCC	-.0072	n.s.	**.1289**	**.0000**	**-.1385**	**.0000**	.1150	.0002
15 LitACD	.0282	n.s.	**.1494**	**.0000**	**-.1635**	**.0000**	.1101	.0003
16 Mois	.0039	n.s.	**-.4158**	**.0000**	-.0217	n.s.	-.0214	n.s.
- Ranked Mois	-.0161	n.s.	**-.2263**	**.0000**	-.0927	.0022	-.0887	.0034
17 LI	**-.2933**	**.0000**	.0314	n.s.	**.2633**	**.0000**	-.0545	.0700
18 pH_{H2O}	**.3863**	**.0000**	**-.2819**	**.0000**	-.0713	.0224	-.0488	n.s.
19 pH_{CaCl2}	**.4667**	**.0000**	**-.2327**	**.0000**	-.0955	.0022	.1191	.0001
20 Ca	**.4548**	**.0000**	.0976	.0011	.0567	.0588	.0199	n.s.
21 Mg	-.0384	n.s.	**-.3179**	**.0000**	-.0358	n.s.	.1213	.0001
22 K	**.2162**	**.0000**	**-.1381**	**.0000**	**.2077**	**.0000**	-.0086	n.s.
23 Na	**-.1269**	**.0000**	**-.2393**	**.0000**	.0394	n.s.	.0401	n.s.
24 H^+	**-.3495**	**.0000**	**.1466**	**.0000**	**-.2098**	**.0000**	-.0937	.0018
25 Al	**-.1440**	**.0000**	-.1107	.0002	**-.2245**	**.0000**	-.1027	.0006
26 Fe	**-.1322**	**.0000**	-.0483	n.s.	**-.1738**	**.0000**	-.0133	n.s.
27 Mn	**.4445**	**.0000**	**.1784**	**.0000**	**.1695**	**.0000**	-.0556	.0640
28 Zn	-.0644	.0319	**.3802**	**.0000**	**-.1526**	**.0000**	.0453	n.s.
29 Total N	.0594	.0477	-.1008	.0008	**-.4095**	**.0000**	**.1933**	**.0000**
30 P-Al	**.2321**	**.0000**	-.0236	n.s.	**.2370**	**.0000**	**.1396**	**.0000**
31 P	.0758	.0115	.0364	n.s.	**.3072**	**.0000**	**.1624**	**.0000**
32 S	**.1938**	**.0000**	-.0534	.0748	.1067	.0004	.0077	n.s.
C1 Prec.	**-.2364**	**.0000**	**-.3162**	**.0000**	**-.2192**	**.0000**	**.2612**	**.0000**
C2 T	**-.4828**	**.0000**	.0958	.0017	**-.3974**	**.0000**	-.0139	n.s.
C3 ETS	**-.4561**	**.0000**	**.1336**	**.0000**	**-.4147**	**.0000**	-.0839	.0056
C4 Tamm's H	**-.1333**	**.0000**	**-.3691**	**.0000**	-.0791	.0093	**.3018**	**.0000**
C5 Lat.	**.3482**	**.0000**	**-.3854**	**.0000**	**.2458**	**.0000**	.0937	.0029
C6 Long.	**.2470**	**.0000**	.0096	.0015	**.3140**	**.0000**	.0937	.0440
C7 Alt.	**.3119**	**.0000**	.0172	n.s.	**.2966**	**.0000**	-.0228	n.s.

Tab. 37. The total material: Kendall's nonparametric correlation coefficients τ with significance probabilities (P) between 32 environmental and 7 climatic/geographical variables in the 500 meso sample plots and sample plot positions with respect to axes in the DCA ordination with 7 covariables, representing the variation exclusively due to climatic variables. Correlations significant at level $P < 0.0001$ in bold face. n.s. - significance probability > 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 2.

Variable	DCA 1		DCA 2		DCA 3		DCA 4	
	τ	P	τ	P	τ	P	τ	P
01 MA Inc	-.0903	.0030	-.0062	n.s.	**-.2507**	**.0000**	**.2103**	**.0000**
02 MA Asp	**-.1921**	**.0000**	-.0906	.0028	-.0060	n.s.	-.0393	n.s.
03 MA Hi	**.1434**	**.0000**	**.1376**	**.0000**	-.0333	n.s.	.0377	n.s.
04 MA BA	.0963	.0015	**.1944**	**.0000**	.0533	.0787	**-.2233**	**.0000**
05 MA Lig	.0379	n.s.	-.0424	n.s.	**-.1348**	**.0000**	**.2304**	**.0000**
06 ME Inc	-.0573	.0591	.0697	.0217	**-.2375**	**.0000**	**.1838**	**.0000**
07 ME Asp	**-.1482**	**.0000**	**-.1300**	**.0000**	.0418	n.s.	.0063	n.s.
08 ME Hi	**.1246**	**.0000**	**.1431**	**.0000**	-.0470	n.s.	-.0160	n.s.
09 ME Rou	-.0311	n.s.	.0672	n.s.	-.0231	n.s.	.0046	n.s.
10 ME Con	.0257	n.s.	.0286	n.s.	-.0189	n.s.	-.0267	n.s.
11 ME Smi	.0125	n.s.	**-.1544**	**.0000**	**.1388**	**.0000**	-.0563	.0649
12 ME Sme	.0236	n.s.	**-.2671**	**.0000**	.0939	.0018	.0193	n.s.
13 ME Sma	.0471	n.s.	**-.2115**	**.0000**	.0861	.0043	.0652	.0308
14 LitCC	.0477	n.s.	**.1461**	**.0000**	**-.1512**	**.0000**	.0914	.0026
15 LitACD	.0374	n.s.	**.1661**	**.0000**	**-.1753**	**.0000**	.0826	.0066
16 Mois	-.0897	.0028	**-.4003**	**.0000**	-.0058	n.s.	-.0322	n.s.
- Ranked Mois	-.0778	.0101	**-.2526**	**.0000**	.0647	.0326	-.0850	.0050
17 LI	**-.3304**	**.0000**	.0443	n.s.	**.2183**	**.0000**	-.0154	n.s.
18 pH_{H2O}	**.3380**	**.0000**	**-.3165**	**.0000**	-.0739	.0179	-.0136	n.s.
19 pH_{CaCl2}	**.4423**	**.0000**	**-.2706**	**.0000**	-.0904	.0037	.0542	.0821
20 Ca	**.4777**	**.0000**	.0658	.0282	.0964	.0013	.0540	.0720
21 Mg	-.0240	n.s.	**-.3123**	**.0000**	-.0396	n.s.	**.2035**	**.0000**
22 K	**.1617**	**.0000**	**-.1728**	**.0000**	**.2538**	**.0000**	.0692	.0211
23 Na	**-.1873**	**.0000**	**-.2286**	**.0000**	.0141	n.s.	.0944	.0017
24 H^+	**-.2986**	**.0000**	**.1816**	**.0000**	**-.2102**	**.0000**	**-.1726**	**.0000**
25 Al	**-.1373**	**.0000**	-.1069	.0004	**-.2390**	**.0000**	**-.1956**	**.0000**
26 Fe	**-.1473**	**.0000**	-.0339	n.s.	**-.1752**	**.0000**	-.0400	n.s.
27 Mn	**.4781**	**.0000**	**.1324**	**.0000**	**.2214**	**.0000**	-.0257	n.s.
28 Zn	.0435	n.s.	**.3918**	**.0000**	**-.1554**	**.0000**	.0408	n.s.
29 Total N	.1018	.0007	-.0980	.0011	**-.4226**	**.0000**	.1143	.0001
30 P-Al	**.2123**	**.0000**	-.0413	n.s.	**.2568**	**.0000**	**.2619**	**.0000**
31 P	.0435	n.s.	.0351	n.s.	**.3075**	**.0000**	**.2949**	**.0000**
32 S	**.1765**	**.0000**	-.0692	.0211	.1067	.0004	.0446	n.s.
C1 Prec.	**-.2608**	**.0000**	**-.2800**	**.0000**	**-.2422**	**.0000**	**.2349**	**.0000**
C2 Temp.	**-.3547**	**.0000**	.1208	.0001	**-.3864**	**.0000**	-.0167	n.s.
C3 ETS	**-.3328**	**.0000**	**.1601**	**.0000**	**-.3636**	**.0000**	-.0940	.0019
C4 Tamm's H	**-.1791**	**.0000**	**-.3355**	**.0000**	**-.1238**	**.0000**	**.2669**	**.0000**
C5 Latitude	**.1834**	**.0000**	**-.3803**	**.0000**	**.2532**	**.0000**	**.1493**	**.0000**
C6 Longitude	**.1814**	**.0000**	.0293	n.s.	**.2992**	**.0000**	-.0385	n.s.
C7 Altitude	**.2649**	**.0000**	.0129	n.s.	**.2781**	**.0000**	-.0374	n.s.

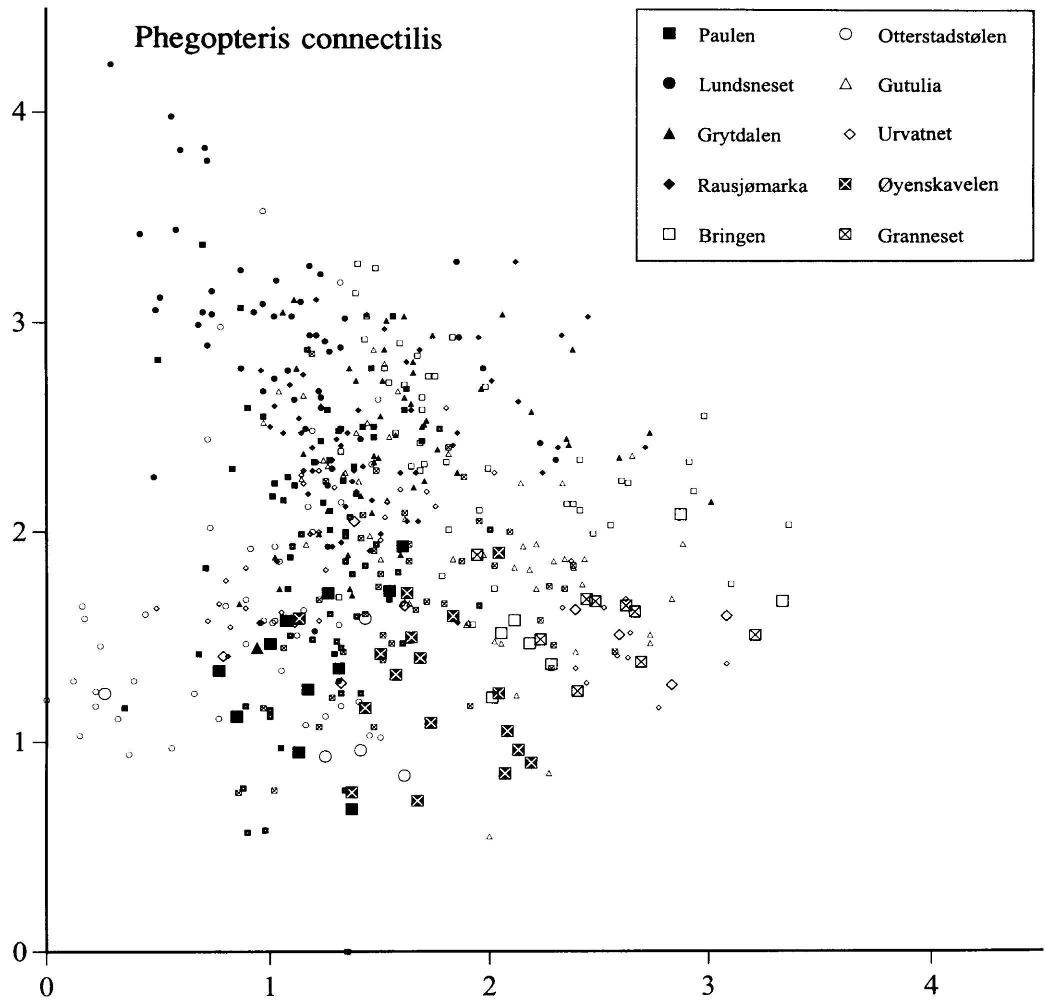


Fig. 780. The total data set: distribution of *Phegopteris connectilis* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

DCA ordination of the total data set with variation exclusively due to climatic/geographical variables removed

The distribution of plots in the DCA ordination of the total data set, using the 7 CCA axes that represent variation exclusively explained by climatic/geographical variables as covariables (compare Figs 768 and 769), was in most respects similar to the DCA ordination of the total data set (without covariables, Fig. 768). Correlations between corresponding DCA axes for or-

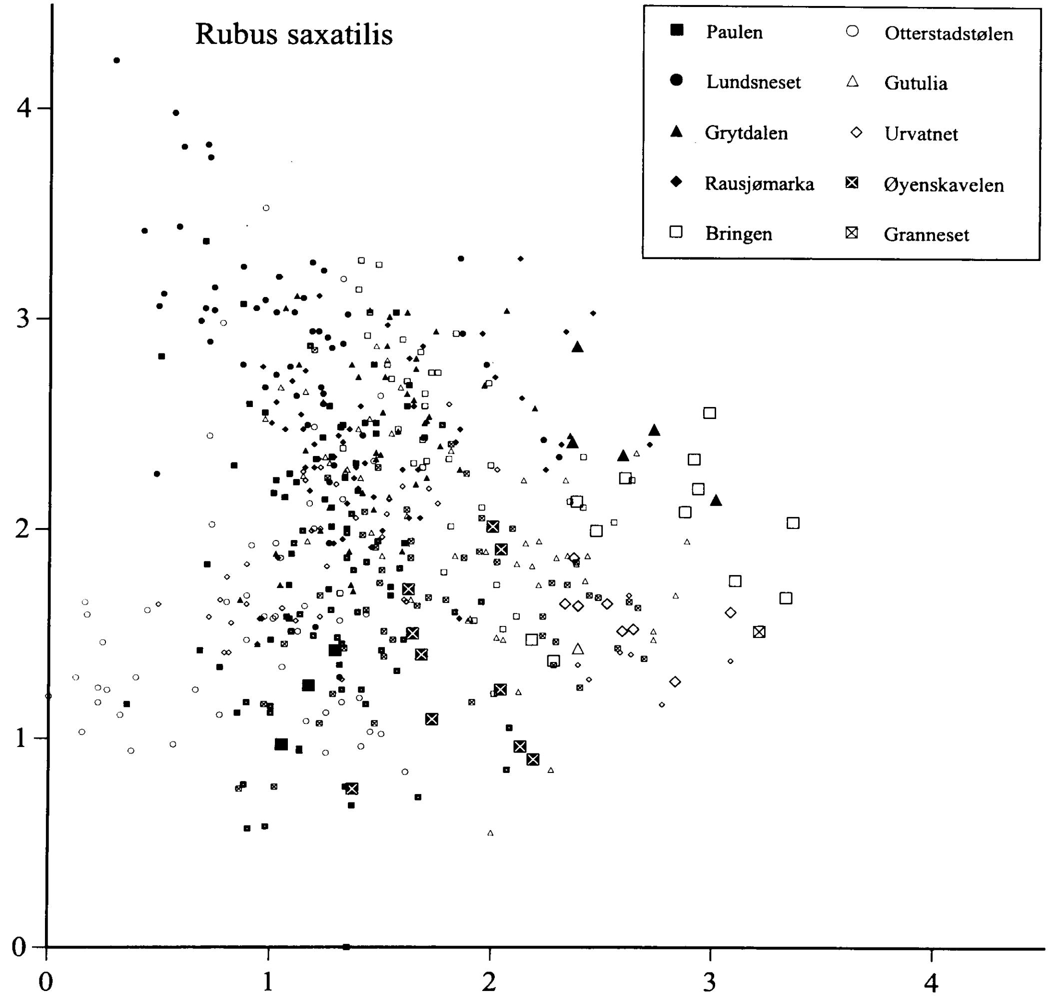


Fig. 781. The total data set: distribution of *Rubus saxatilis* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

dinations of the total data set with and without covariables (Tab. 38) were high; 0.749 for the first and 0.841 for the second DCA axes. However, plots from Otterstadstølen generally obtained higher DCA 2 scores (> 1 S.D.). Otherwise, differences between ordinations with respect to plot positions were small in most cases.

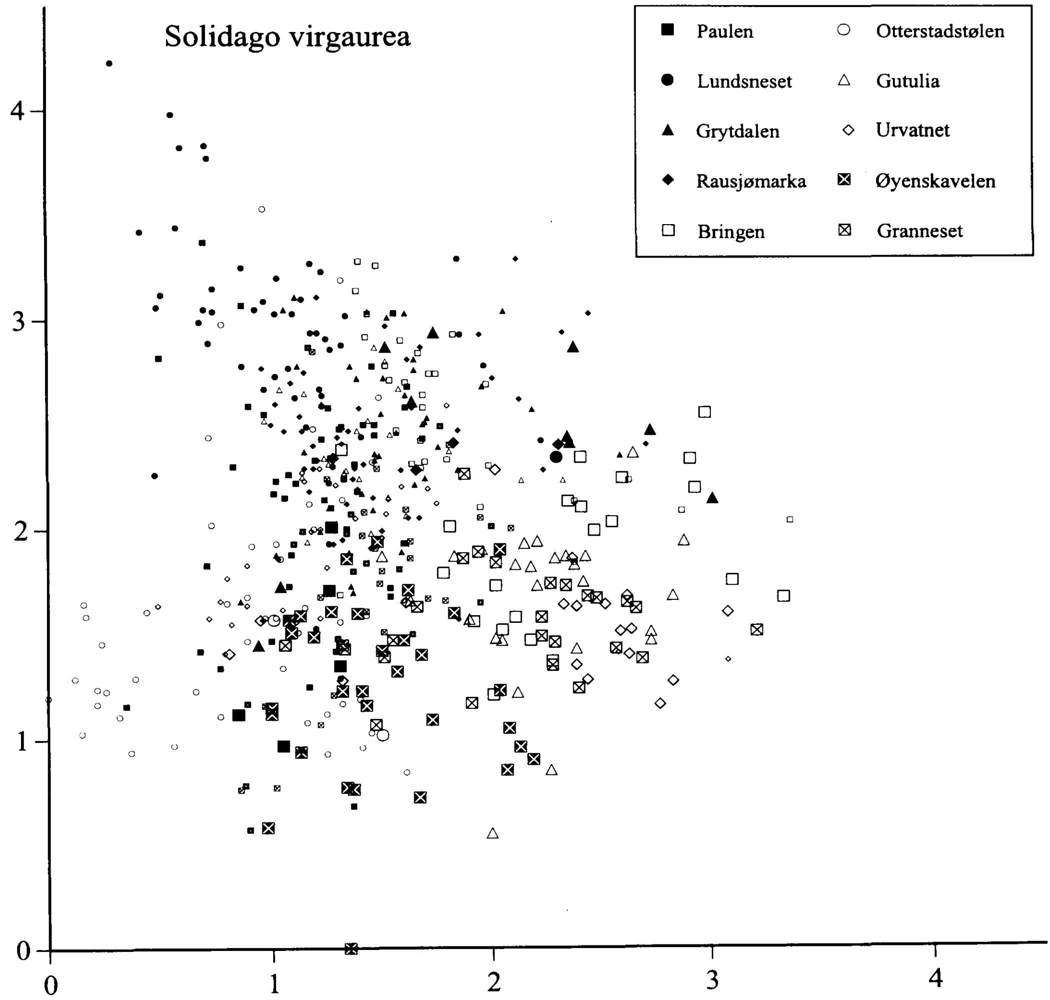


Fig. 782. The total data set: distribution of *Solidago virgaurea* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

Correlations between DCA axes for ordination of the total data set with variation exclusively due to climatic/geographical variables removed, and environmental and climatic/geographical variables

Relationships between DCA axes and explanatory variables (Tab. 37) closely resembled those of the DCA ordination of the total data set (without covariables; Tab. 36). However, correlations of most climatic/geographical variables were less strong, while correlations of most

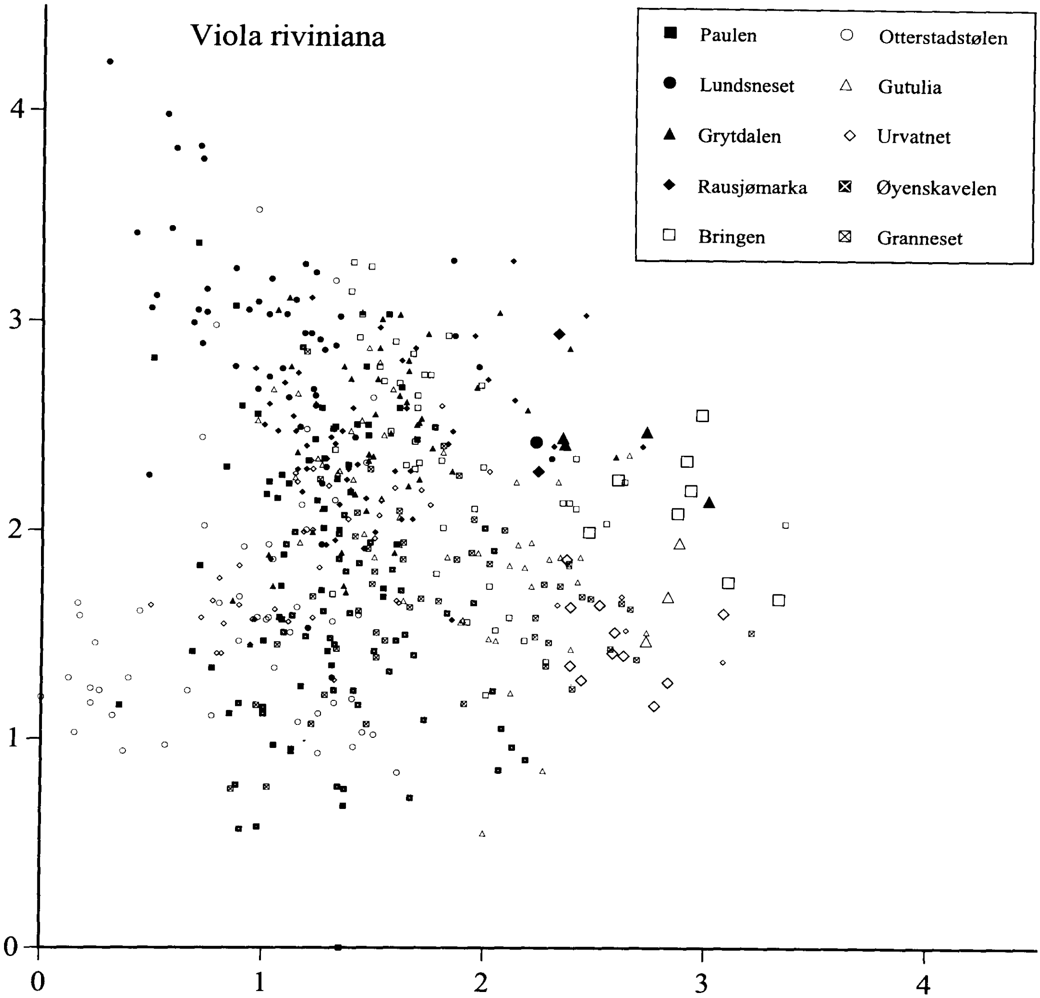


Fig. 783. The total data set: distribution of *Viola riviniana* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

environmental variables were strengthened.

Total N was not correlated with DCA 1 in either of the ordinations of the total data set, but strongly correlated with DCA 3 (Tabs 36, 37). *Within* six reference areas, however, total N was significantly correlated with each of DCA 1 and DCA 3 (Tab. 39; $P < 0.01$; all except Paulen and Lundsneset, and Otterstadstølen (DCA 1) and Gutulia (DCA 3)).

Tab. 38. The total material: Kendall's nonparametric correlation coefficients τ with significance probabilities (P) between axes in the DCA ordination of 500 sample plots (no covariables) and axes in the DCA ordination with 7 covariables, representing the variation exclusively due to climatic variables. Correlations significant at level P < 0.0001 in bold face. n.s. - significance probability > 0.1.

	DCA ordination without covariables							
DCA ordination with covariables	DCA 1		DCA 2		DCA 3		DCA 4	
	τ	P	τ	P	τ	P	τ	P
DCA 1	**.7485**	**.0000**	-.0179	n.s.	.0142	n.s.	.0179	n.s.
DCA 2	**.1698**	**.0000**	**.8407**	**.0000**	-.0081	n.s.	.0240	n.s.
DCA 3	**.1485**	**.0000**	-.0241	n.s.	**.7416**	**.0000**	**-.2206**	**.0000**
DCA 4	.0020	n.s.	.0384	n.s.	.0003	n.s.	**.6886**	**.0000**

Distribution of species abundance in the DCA ordination of the total data set with variation exclusively due to climatic/geographical variables removed

Several species were more or less restricted to, or most abundant in, moist sites (low DCA 2 scores), e.g.: *Blechnum spicant* (Fig. 771), *Cornus suecica* (Fig. 772), *Listera cordata* (Fig.

Tab. 39. Kendall's nonparametric correlation coefficients τ with significance probabilities (P), calculated for each of the ten monitoring areas (n = 50) between Total N and sample plot positions along axes 1 and 3 in the DCA ordination of 500 sample plots with 7 covariables, representing the variation exclusively due to climatic variables. Correlations significant at level P < 0.0001 in bold face. n.s. - significance probability > 0.1.

Monitoring area	DCA 1		DCA 3	
	τ	P	τ	P
Paulen	.0933	n.s.	-.1727	.0775
Lundsneset	.0680	n.s.	-.1272	n.s.
Grytdalen	.3569	.0003	-.3943	.0001
Rausjømarka	.2884	.0033	**-.4755**	**.0000**
Bringen	**.4365**	**.0000**	**-.4906**	**.0000**
Otterstadstølen	.0033	n.s.	-.3010	.0021
Gutulia	**.4871**	**.0000**	-.1707	.0817
Urvatnet	.3756	.0001	.3630	.0002
Øyenskavlen	**.4998**	**.0000**	**.5790**	**.0000**
Granneset	.3190	.0011	**-.4025**	**.0000**

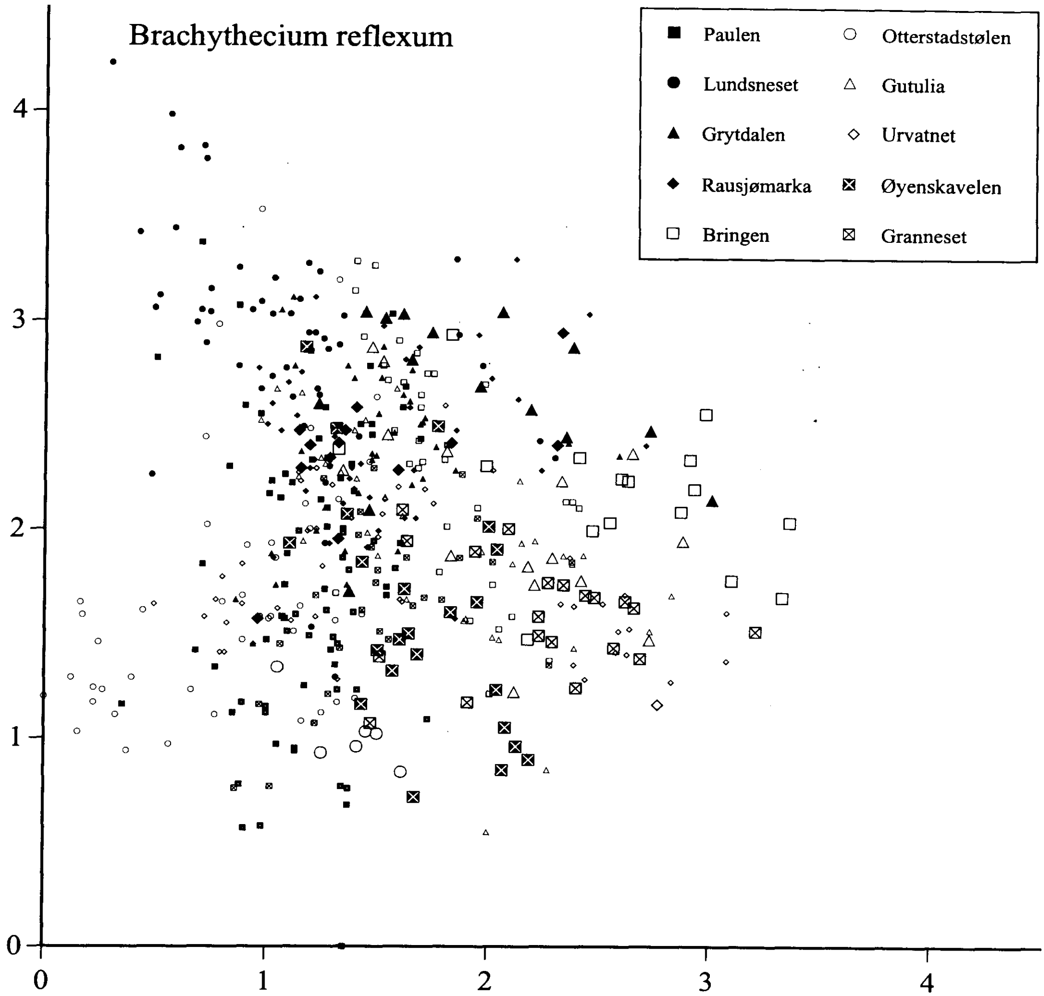


Fig. 784. The total data set: distribution of *Brachythecium reflexum* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

776), *Phegopteris connectilis* (Fig. 780), *Hypnum callichroum* (Fig. 789), *Plagiothecium undulatum* (Fig. 794), *Polytrichum commune* (Fig. 795), *Rhytidiadelphus loreus* (Fig. 798), *Sphagnum girgensohnii* (Fig. 801), *S. quinquefarium* (Fig. 802) and *Calypogeia muelleriana* (Fig. 804).

Blechnum spicant (Fig. 771) had its optimum in the most humid reference areas (Otterstadstølen and Øyenskavelen) and was, within these areas, almost completely absent from plots on very dry sites (high DCA 2 scores) and from sites rich in nutrients (high DCA

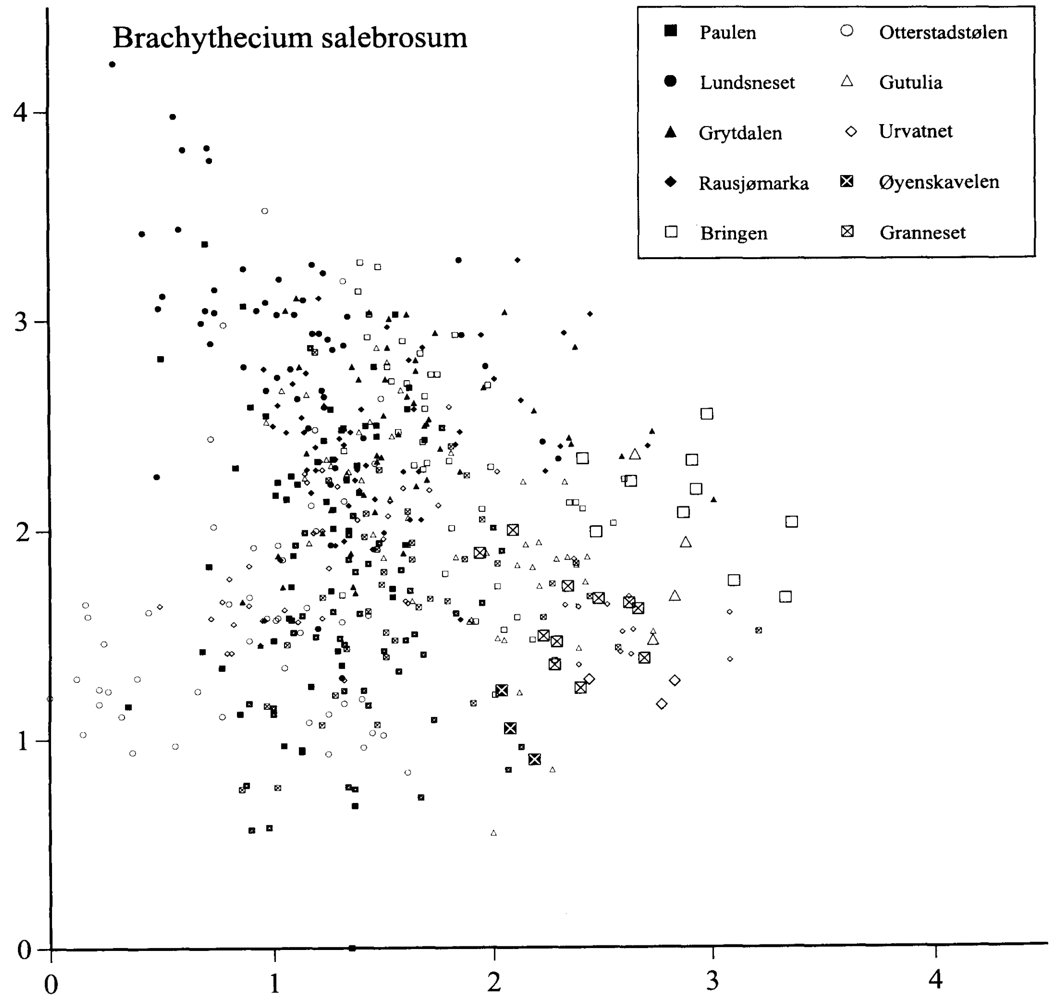


Fig. 785. The total data set: distribution of *Brachythecium salebrosum* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

1 scores). *Cornus suecica* was most abundant in Øyenskavelen and Granneset, and less abundant in sites rich in nutrients. *Listera cordata* (Fig. 776) occurred along most of DCA 1, but decreased in abundance towards plots from the most nutrient-rich sites (the right-hand part of the ordination). Except from occurrence in a few plots in Urvatnet, *Hypnum callichroum* (Fig. 789) was restricted to plots in Otterstadstølen and Øyenskavelen, while *Plagiothecium undulatum* (Fig. 794) was also abundant in Paulen. *Polytrichum commune* was most abundant on sites relatively poor in nutrients (low DCA 1 scores). *Rhytidiadelphus loreus* (Fig. 798) oc-

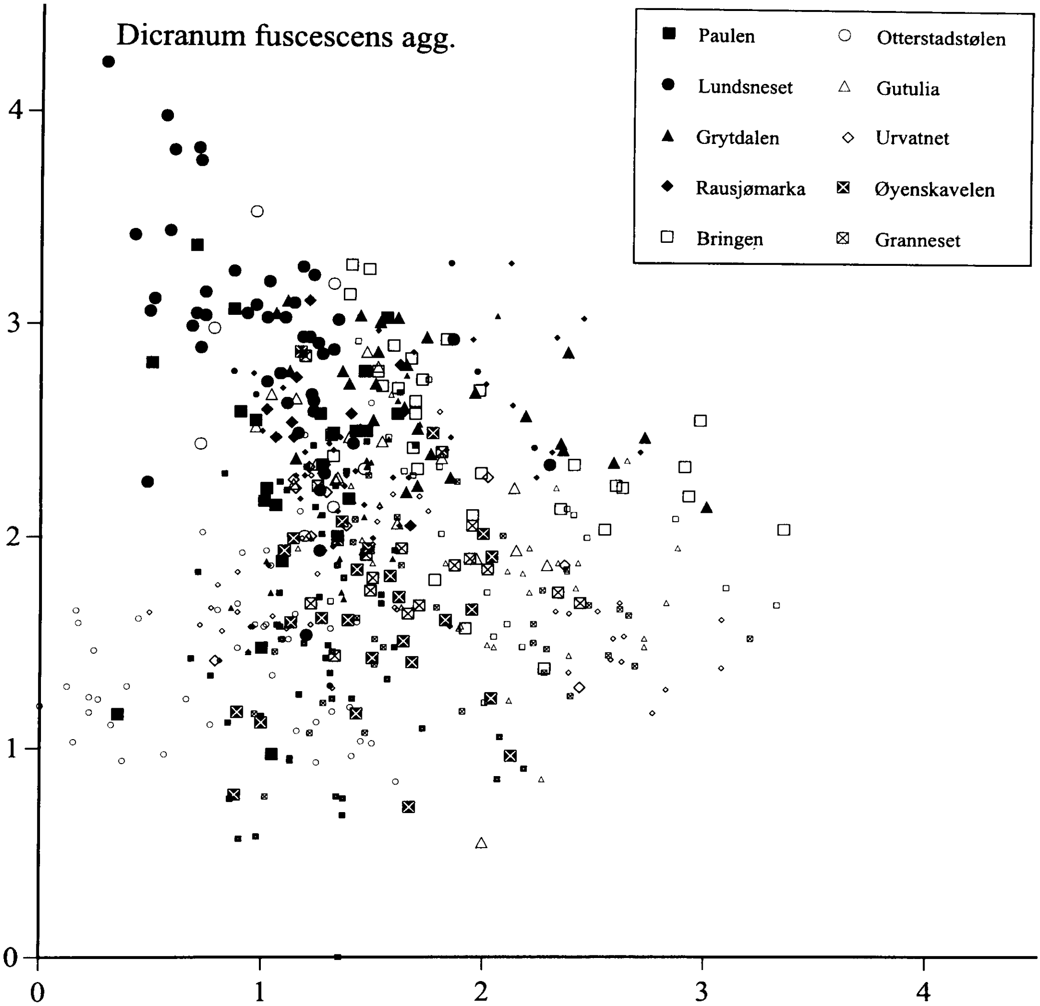


Fig. 786. The total data set: distribution of *Dicranum fuscescens* agg. (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

curred on moist sites (low DCA 2 scores) along all of DCA 1, in Otterstadstølen also on some of the driest sites. *Sphagnum girgensohnii* (Fig. 801) was absent from the sites most rich in nutrients (high DCA 1 scores). High abundance of *Calypogeia muelleriana* (Fig. 804) was recorded in Paulen, Otterstadstølen and Øyenskavelen only.

Dicranum polysetum (Fig. 788) and *Hypnum cupressiforme* agg. (Fig. 790) were most abundant on dry sites, poor in nutrients (upper right in the DCA ordination). The latter was almost entirely restricted to Paulen, Lundsneset and Otterstadstølen.

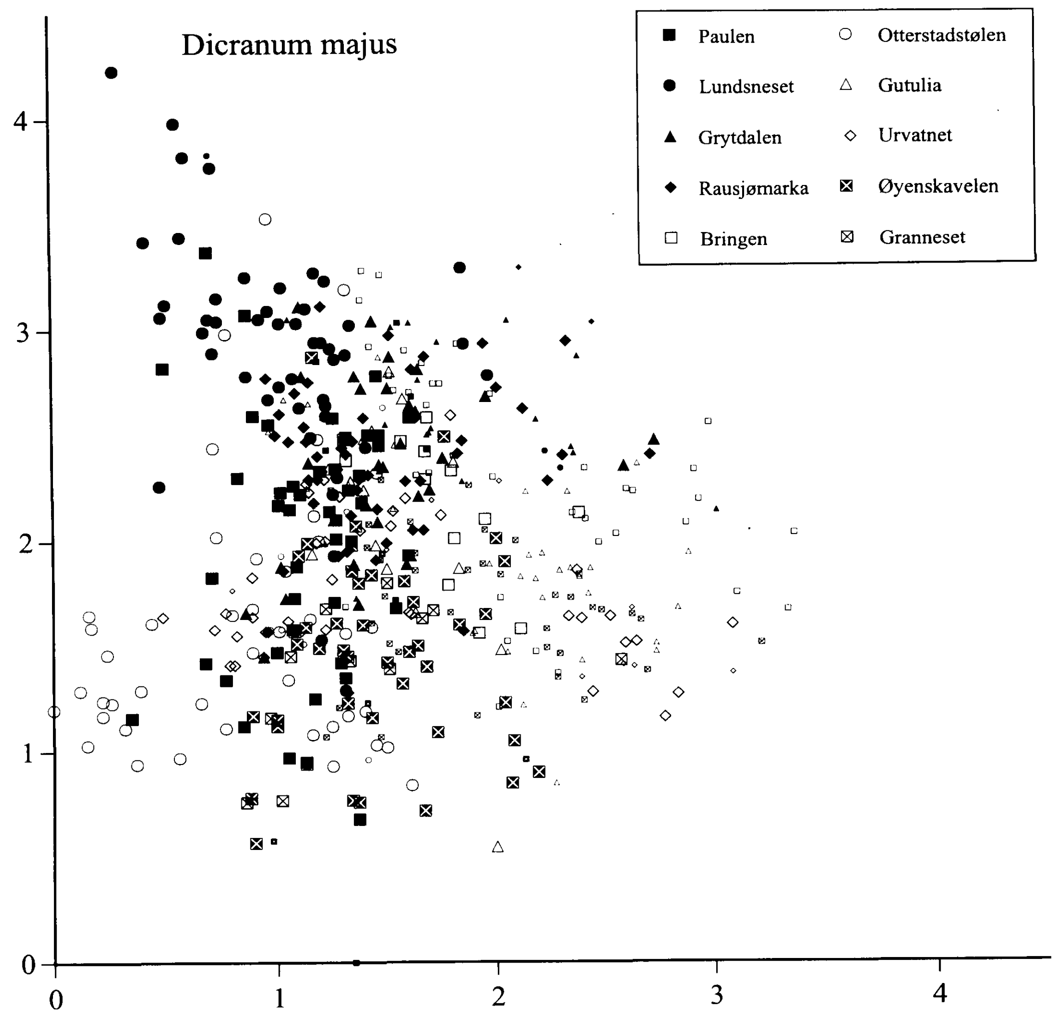


Fig. 787. The total data set: distribution of *Dicranum majus* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

Some species were widely distributed along DCA 2, occurring both in dry and moist sites, e.g. *Dicranum majus* (Fig. 787) and *Tetraphis pellucida* (Fig. 800). *Dicranum fuscescens* agg. (Fig. 786) and *Plagiothecium laetum* (Fig. 793) were somewhat more concentrated to drier sites (high DCA 2 scores). All four species were also widely distributed along DCA 1, although less abundant on sites rich in nutrients.

Several species were more or less restricted to sites rich in nutrients (high DCA 1 scores), e.g. *Geranium sylvaticum* (Fig. 774), *Orthilia secunda* (Fig. 778), *Solidago virgaurea*

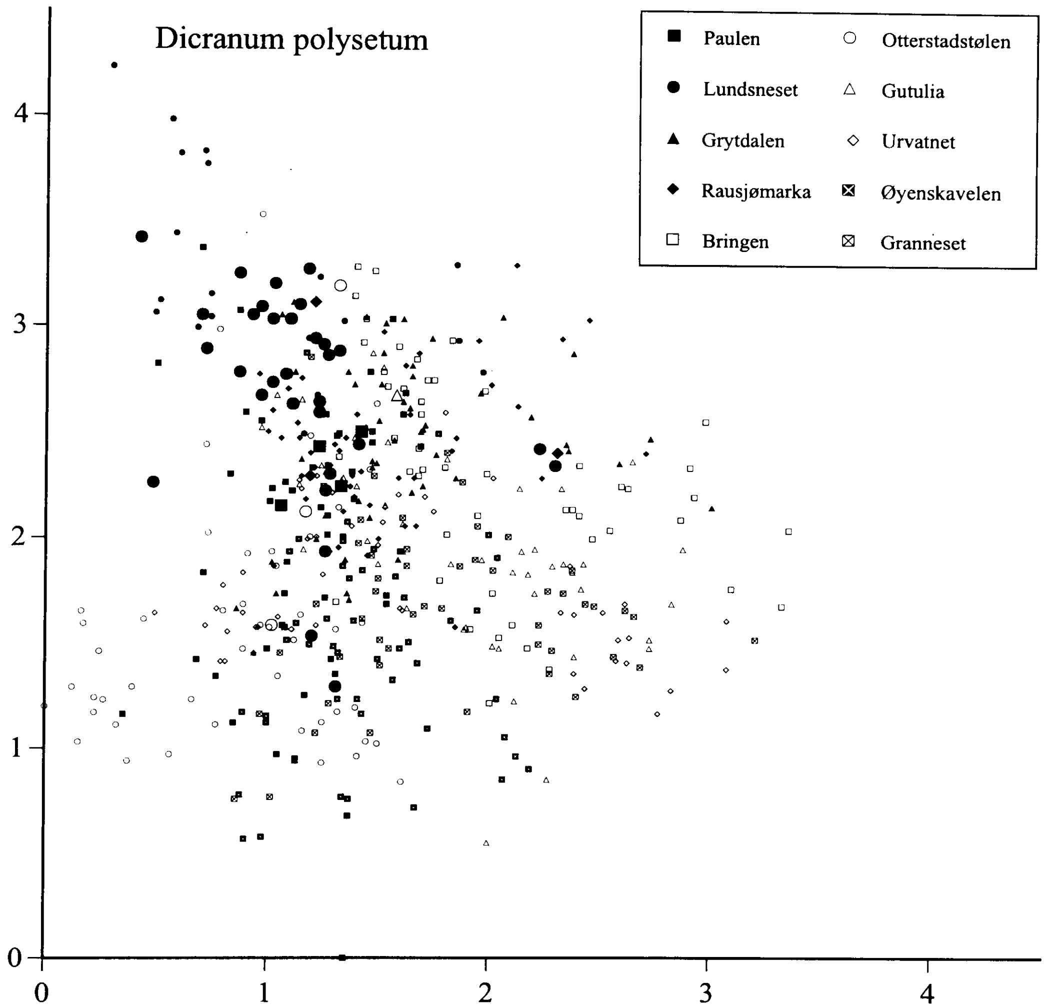


Fig. 788. The total data set: distribution of *Dicranum polysetum* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

(Fig. 782), *Viola riviniana* (Fig. 783), *Brachythecium salebrosum* (Fig. 785), *Plagiothecium denticulatum* (Fig. 792), *Rhodobryum roseum* (Fig. 797) and *Mnium spinosum* (Fig. 791) However, their amplitudes towards sites poorer in nutrients varied.

Geranium sylvaticum (Fig. 774), *Orthilia secunda* (Fig. 778), *Viola riviniana* (Fig. 783), *Brachythecium salebrosum* (Fig. 785), and *Mnium spinosum* (Fig. 791) were most strongly restricted to sites rich in nutrients. With a few exceptions, these species were absent from the most humid reference areas. Less distinct limits towards poorer sites were demonstrated by *Solidago virgaurea* (Fig. 782), *Rhodobryum roseum* (Fig. 797) and *Plagiothecium denticulatum*

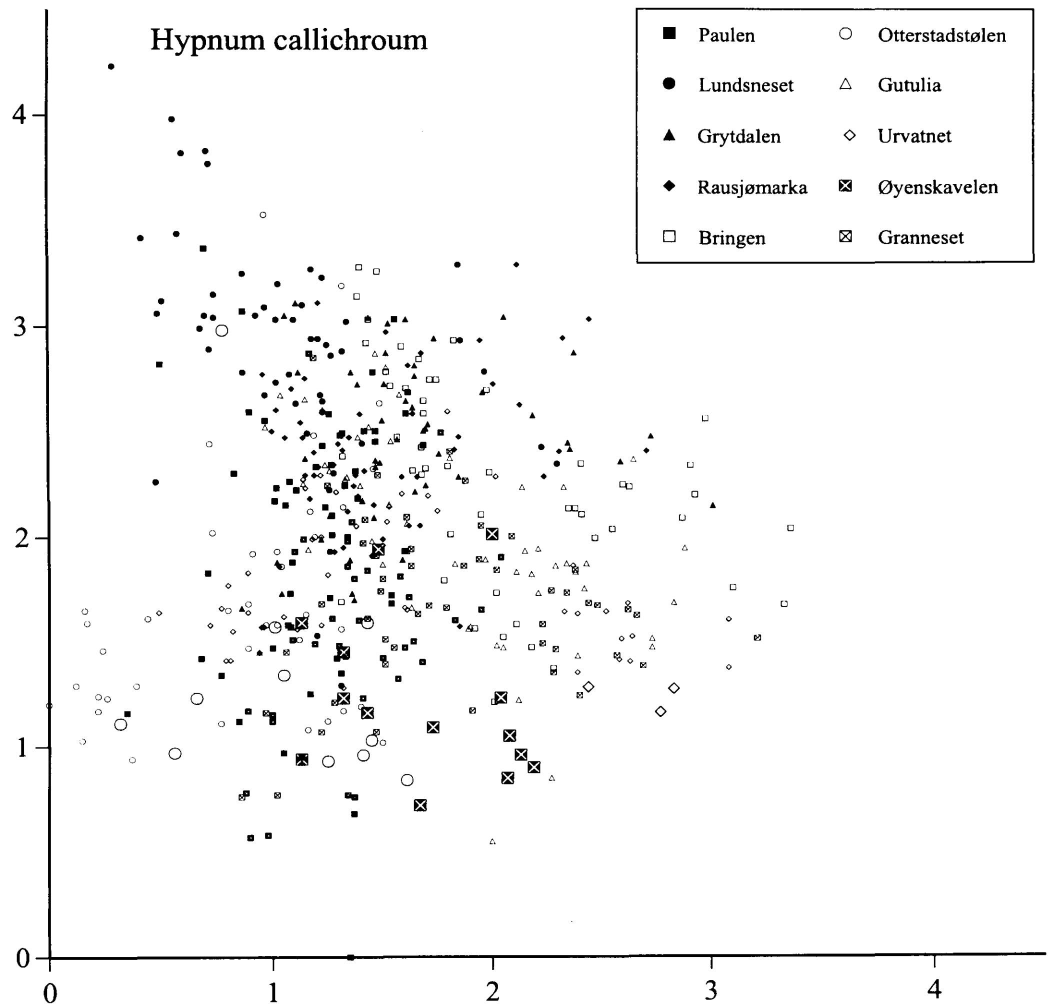


Fig. 789. The total data set: distribution of *Hypnum callichroum* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

(Fig. 792), but they were all most abundant on sites rich in nutrients. These three species were present in all reference areas, although *R. roseum* and *P. denticulatum* both decreased in abundance towards the more humid reference areas. *Solidago virgaurea* was also present on sites poor in nutrients, but then mainly restricted to moist sites. All three species were absent from the driest sites (high DCA 2 scores).

Some species, e.g. *Cephalozia bicuspidata* (Fig. 805) and *Cephalozia lunulifolia* (Fig. 806) appeared to be more or less randomly distributed in the ordination. However, *Cephalozia*

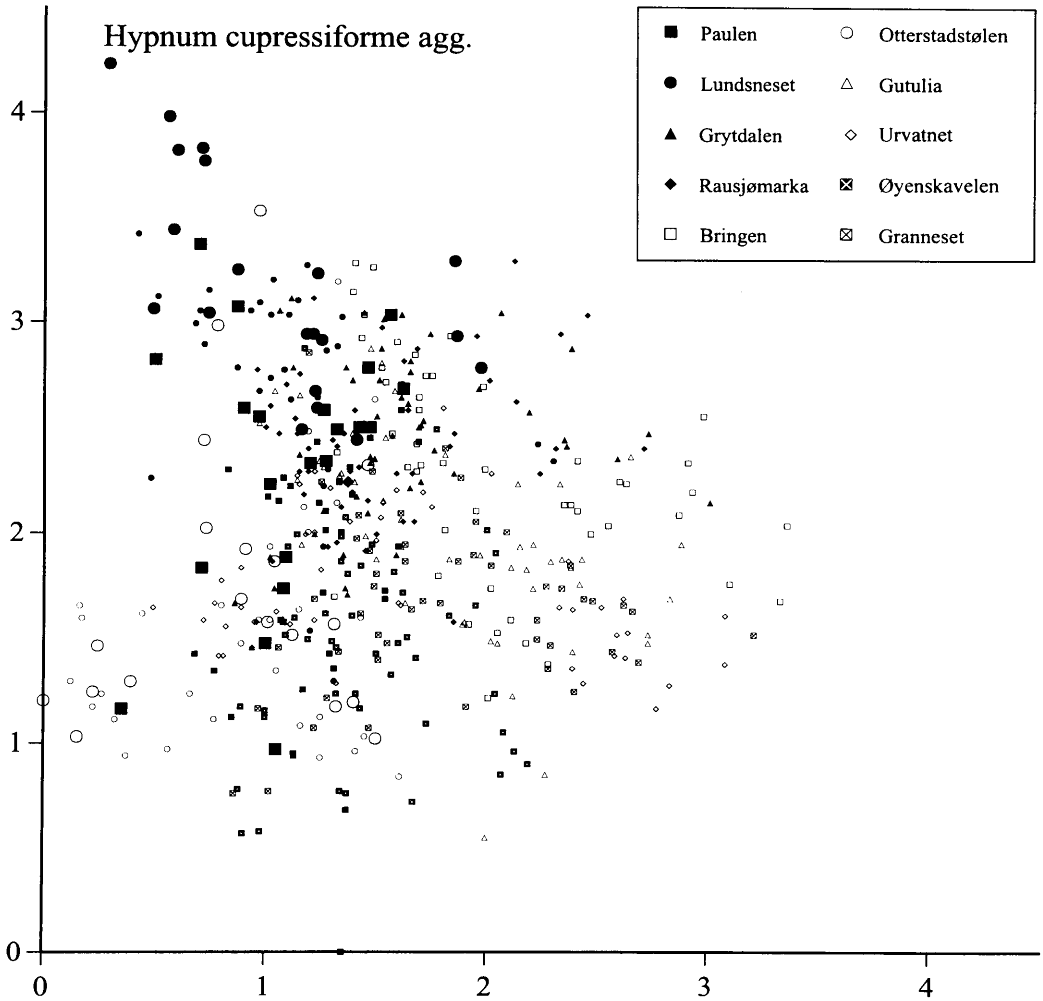


Fig. 790. The total data set: distribution of *Hypnum cupressiforme* agg. (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

bicuspidata was more abundant on moist sites and in humid reference areas.

Between-area differences in the distribution in the ordination were shown by several species, e.g. *Anemone nemorosa* (Fig. 770), *Dryopteris expansa* agg. (Fig. 773), *Gymnocarpium dryopteris* (Fig. 775), *Melampyrum sylvaticum* (Fig. 777), *Oxalis acetosella* (Fig. 779), *Phegopteris connectilis* (Fig. 780), *Rubus saxatilis* (Fig. 781), *Brachythecium reflexum* (Fig. 784), *Polytrichum formosum* (Fig. 796), *Rhytidiadelphus squarrosus agg.* (Fig.

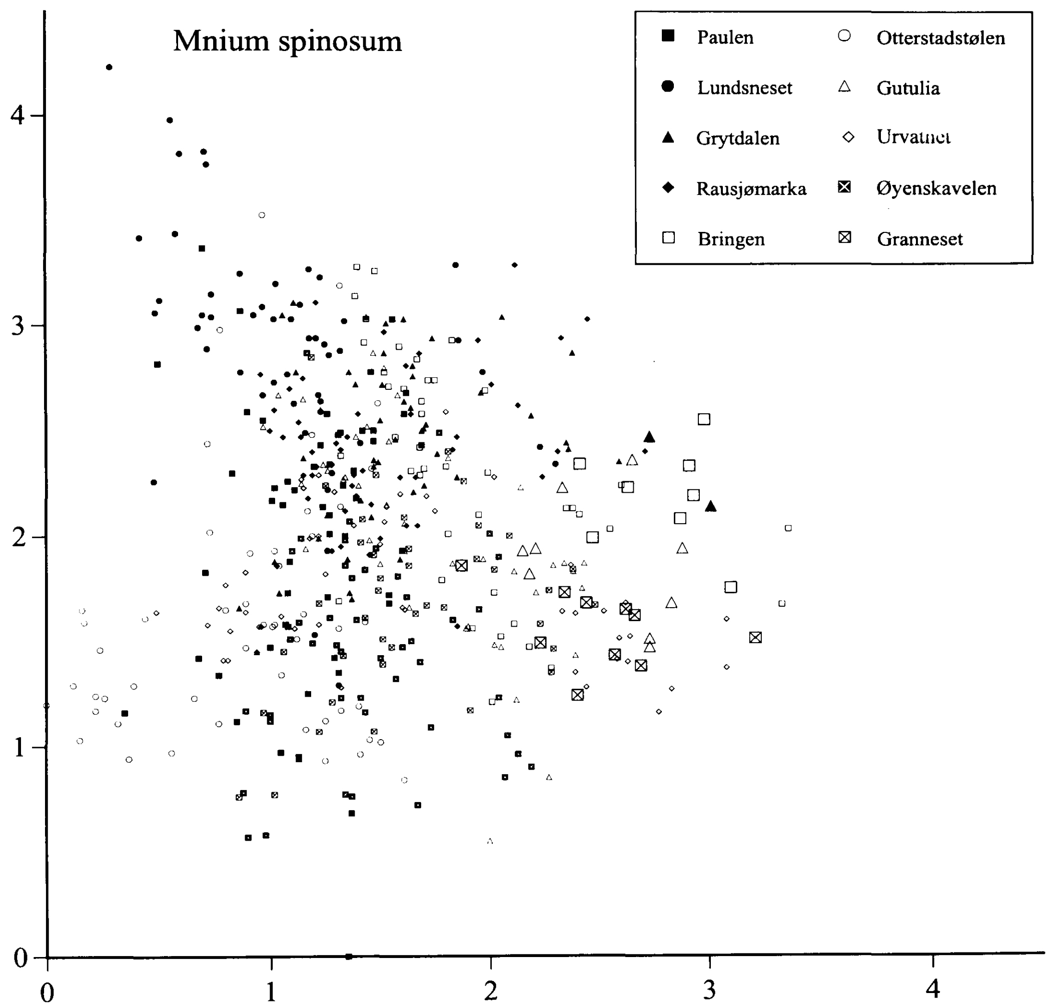


Fig. 791. The total data set: distribution of *Mnium spinosum* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

799), *Sphagnum quinquefarium* (Fig. 802), *Barbilophozia floerkei* (Fig. 803), *Lophozia obtusa* (Fig. 807) and *Tritomaria quinquedentata* (Fig. 808).

Anemone nemorosa (Fig. 770) was more or less restricted to moist sites in the most humid reference areas (Paulen, Otterstadstølen, Øyenskavelen, Urvatnet), while it was indifferent with respect to soil moisture in Grytdalen and Rausjømarka. This species had a wide amplitude with respect to soil nutrient content (DCA 1) in most areas, but with considerable variation in abundance. Thus, high abundance was noted in sites rich in nutrients

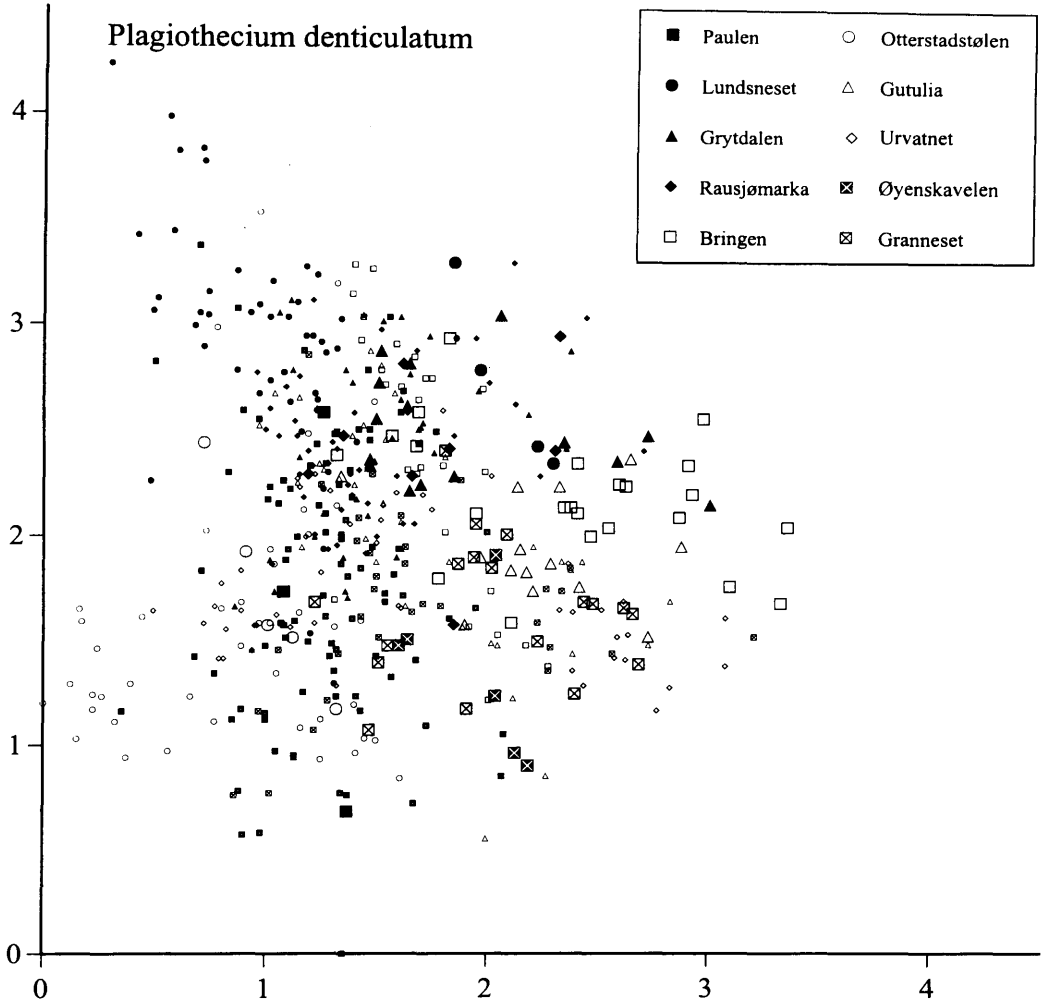


Fig. 792. The total data set: distribution of *Plagiothecium denticulatum* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

in Grytdalen, Gutulia and Urvatnet, in sites poor in nutrients in Paulen and Otterstadstølen.

Dryopteris expansa agg. (Fig. 773) was almost completely restricted to moist sites in the most humid reference areas and in Granneset, while it was absent from moist sites in Grytdalen and Bringen, where it was restricted to medium-dry sites. This species is also absent from the sites most rich in nutrients in Grytdalen, Bringen and Rausjømarka, while in Øyenskavelen and Otterstadstølen it occurred in the plots with the highest DCA 1 scores recorded

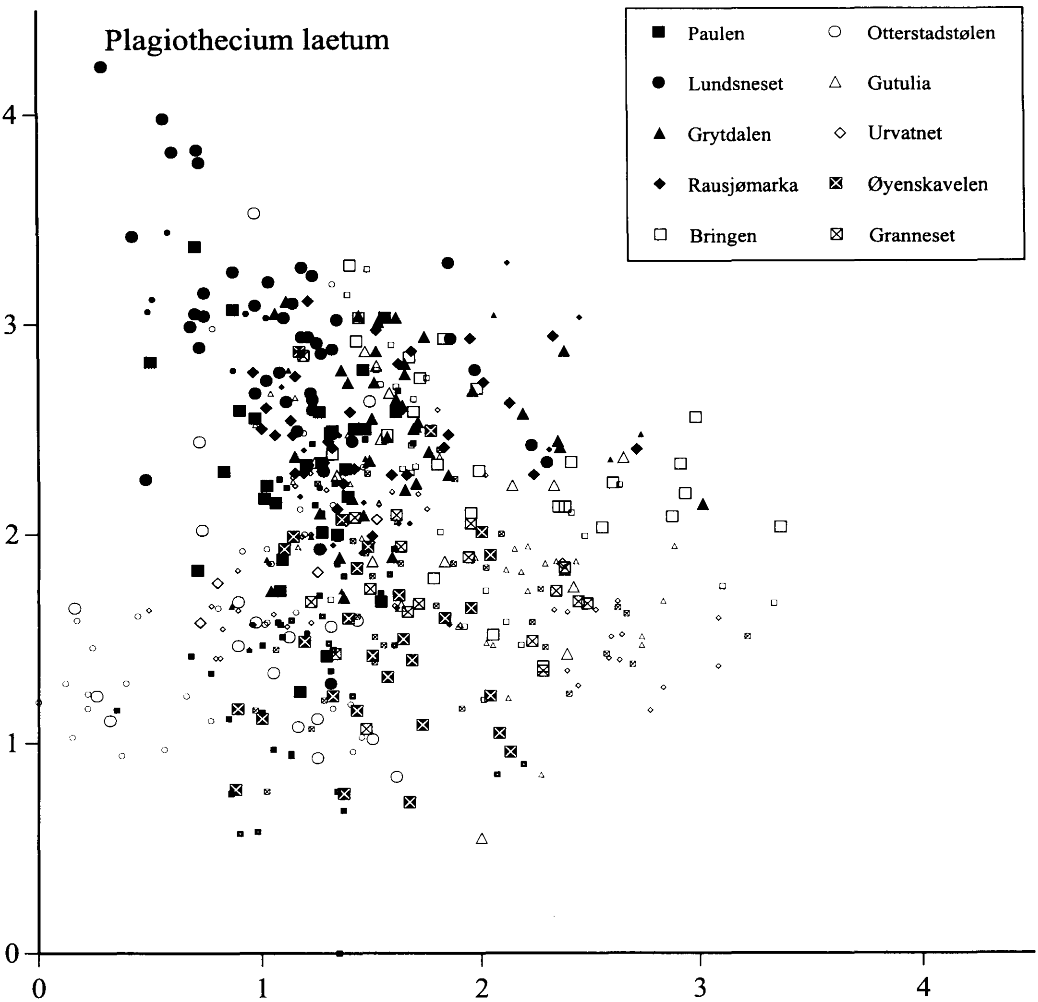


Fig. 793. The total data set: distribution of *Plagiothecium laetum* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

recorded for these areas, i.e. on the sites most rich in nutrients.

Gymnocarpium dryopteris (Fig. 775) was relatively evenly distributed along DCA *1*, except for lower abundance in plots from sites poor in nutrients (low DCA 1 scores). The species was absent from the most dry sites in all reference areas. However, *Gymnocarpium dryopteris* was more abundant on sites poor in nutrients in Øyenskavelen, Otterstadstølen and Paulen than in Bringen, Gutulia and Granneset, where it was mainly restricted to moist sites.

The highest abundance of *Melampyrum sylvaticum* (Fig. 777) was recorded in Gutulia, Urvatnet and Granneset in sites rich in nutrients, but it also occurred in Grytdalen, Rausjømar-

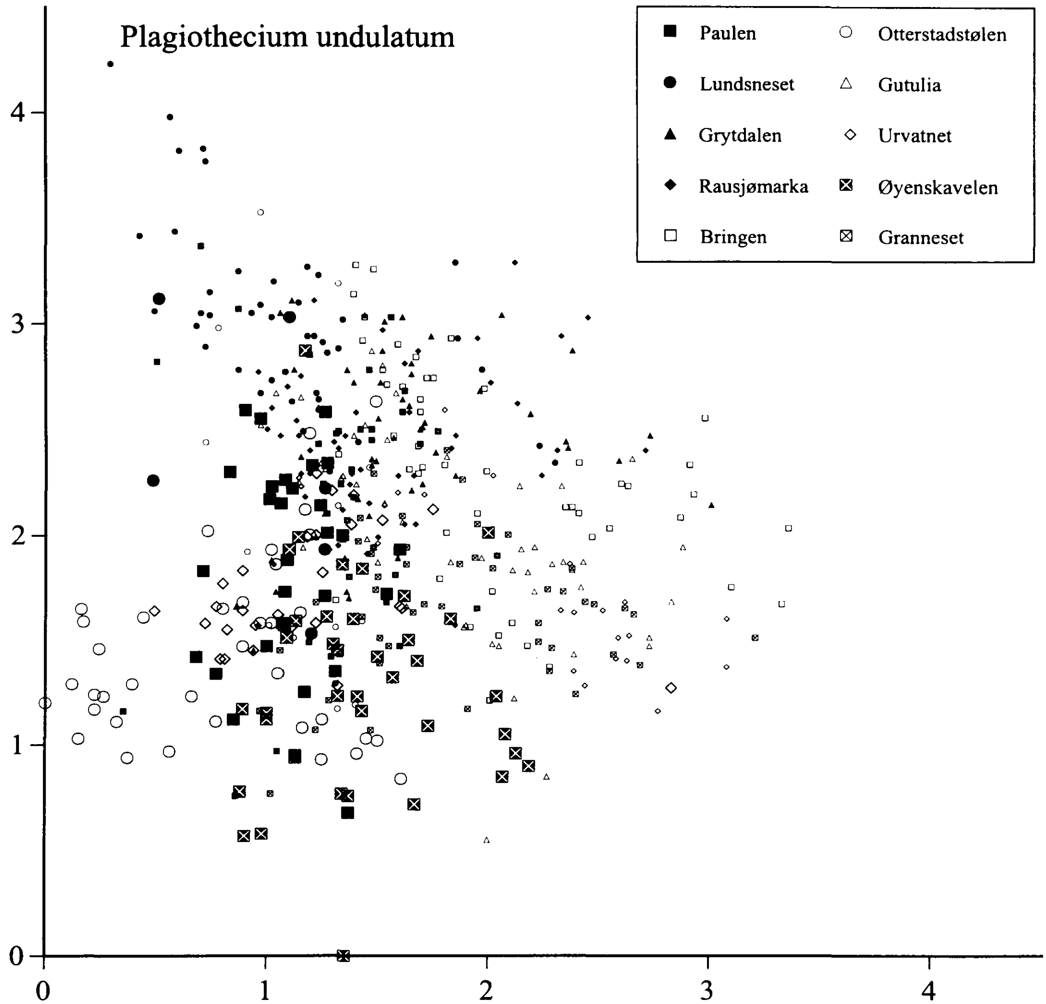


Fig. 794. The total data set: distribution of *Plagiothecium undulatum* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

ka, Bringen and Øyenskavelen. This species had a distinct limit in the ordination towards plots from sites poor in nutrients (low DCA 1 scores) in Grytdalen, Rausjømarka, and Gutulia, while it was present both on poor and rich sites in Urvatnet and Granneset, although with declining abundance towards poor sites. The species was absent from the sites most rich in nutrients in Øyenskavelen. Except for a few plots in Rausjømarka, *Melampyrum sylvaticum* was also absent from most of the dry sites in all reference areas.

Oxalis acetosella (Fig. 779) was most abundant on sites rich in nutrients (high DCA 1

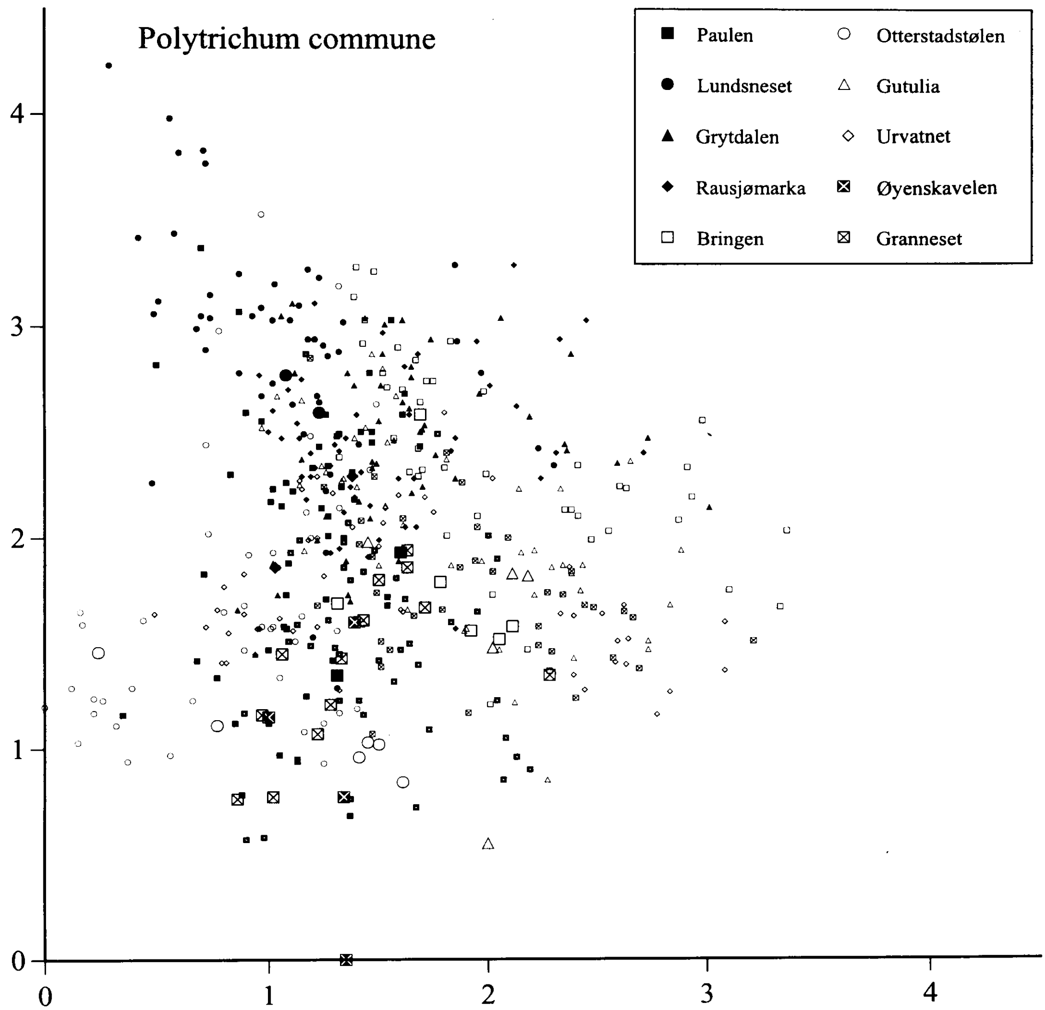


Fig. 795. The total data set: distribution of *Polytrichum commune* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

scores), mostly with a distinct limit in the ordination towards plots from sites poor in nutrients. The limit was particularly clear in Grytdalen and Bringen. The species was also present on poorer sites in Otterstadstølen and Urvatnet, but preferably on moist sites. *Oxalis acetosella* was absent from the driest sites in most reference areas, but it occurred in a few plots from relatively dry sites in Rausjømarka.

Phegopteris connectilis (Fig. 780) was restricted to moist or relatively moist sites in all reference areas where it was present (low DCA 2 scores). In humid reference areas this spe-

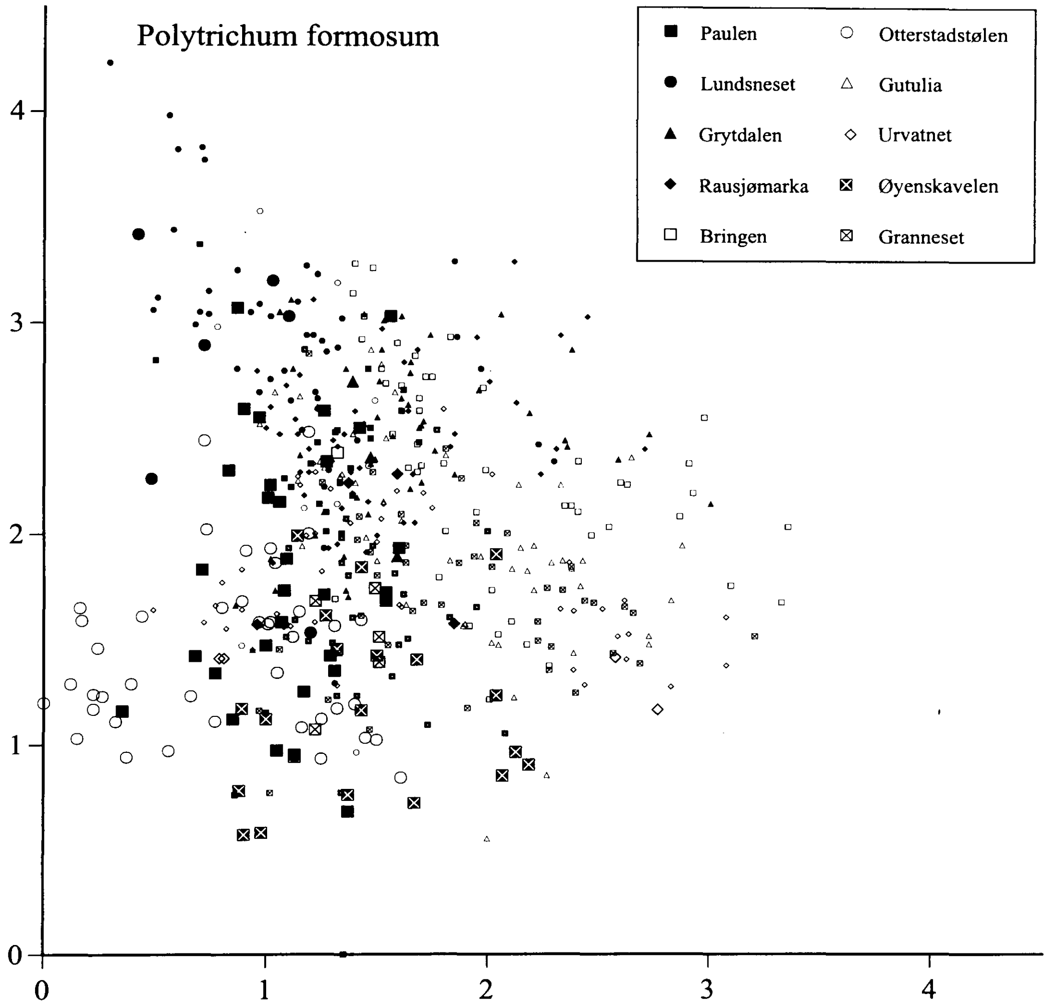


Fig. 796. The total data set: distribution of *Polytrichum formosum* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

cies was also present on sites relatively poor in nutrients (low DCA 1 scores).

Rubus saxatilis (Fig. 781) had a limit of occurrence towards sites poor in nutrients (low DCA 1 scores) in all reference areas where it was present. In Paulen and Øyenskavelen, however, this species even occurred in sites with relatively low content of nutrients when there was a high soil moisture.

Brachythecium reflexum (Fig. 784) was most abundant on sites rich in nutrients. In Otterstadstølen this species was restricted to moist sites, while it had wider amplitude along

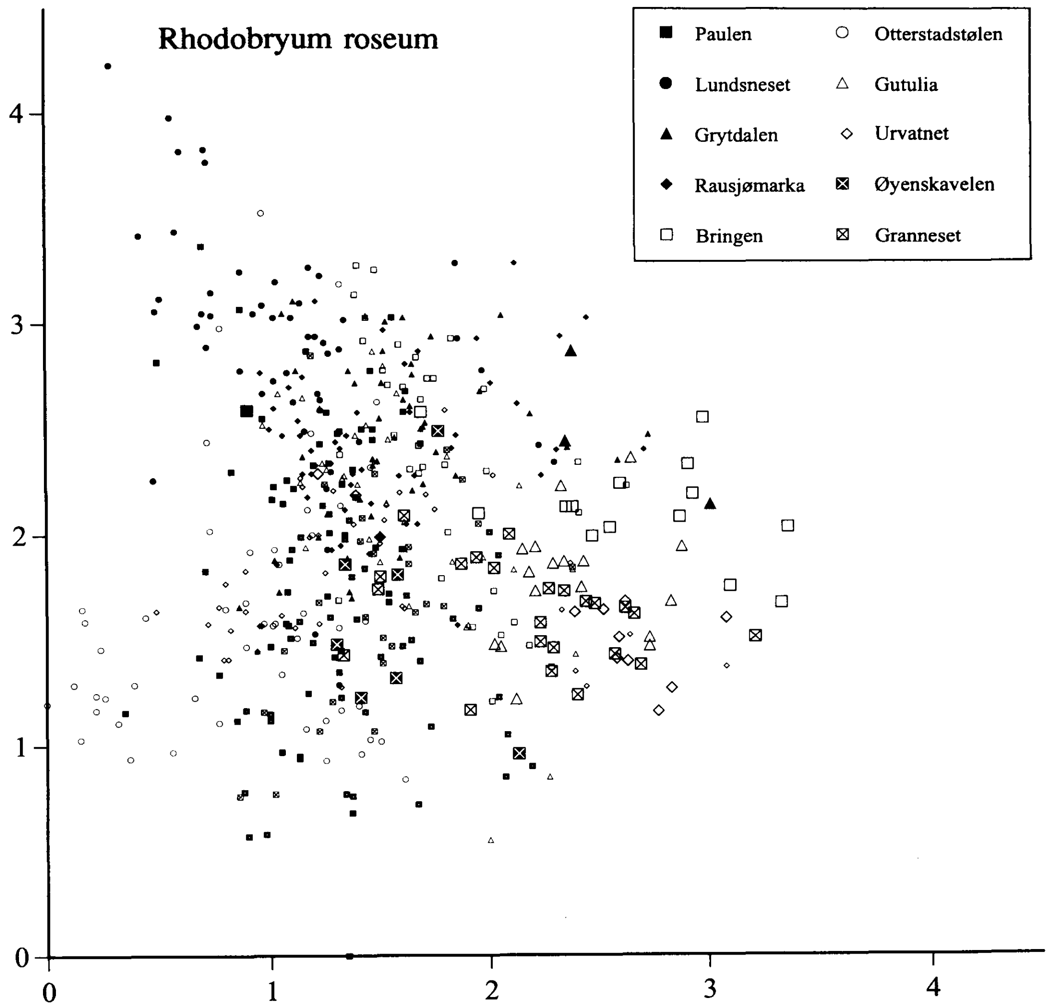


Fig. 797. The total data set: distribution of *Rhodobryum roseum* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

the soil moisture gradient (along DCA 2) in Øyenskavelen. In Grytdalen and Rausjømarka the species was most abundant on relatively dry sites.

Polytrichum formosum (Fig. 796) was most abundant on sites poor in nutrients (low DCA 1 scores). This species preferred moist sites in the most humid reference areas, in Urvatnet (few plots) and in Granneset. In the southernmost reference areas on lower altitudes, *Polytrichum formosum* was also abundant on relatively dry sites. *Polytrichum formosum* had low abundance in reference areas with a more continental climate and/or situated in the Nor-

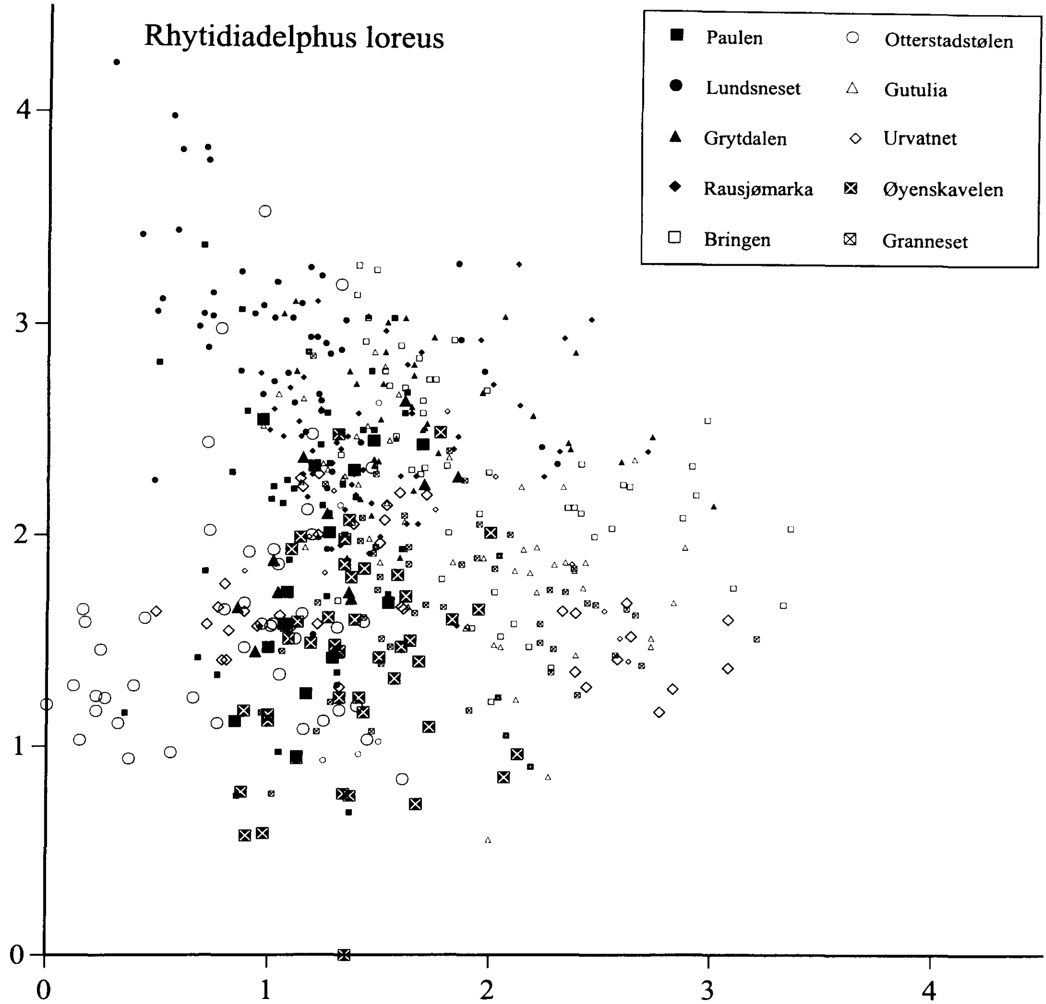


Fig. 798. The total data set: distribution of *Rhytidiadelphus loreus* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

thern Boreal zone.

Rhytidiadelphus squarrosus agg. (Fig. 799) was most abundant on moist sites (low DCA 2 scores). In Bringen, Gutulia, Urvatnet and Granneset, this species had a distinct limit in the ordination towards plots from sites poor in nutrients, while in Otterstadsølen and Øyenskavelen its amplitude along DCA 1 was wider, implying a higher tolerance for poor sites.

Sphagnum quinquefarium (Fig. 802) was mainly restricted to the left part of the ordina-

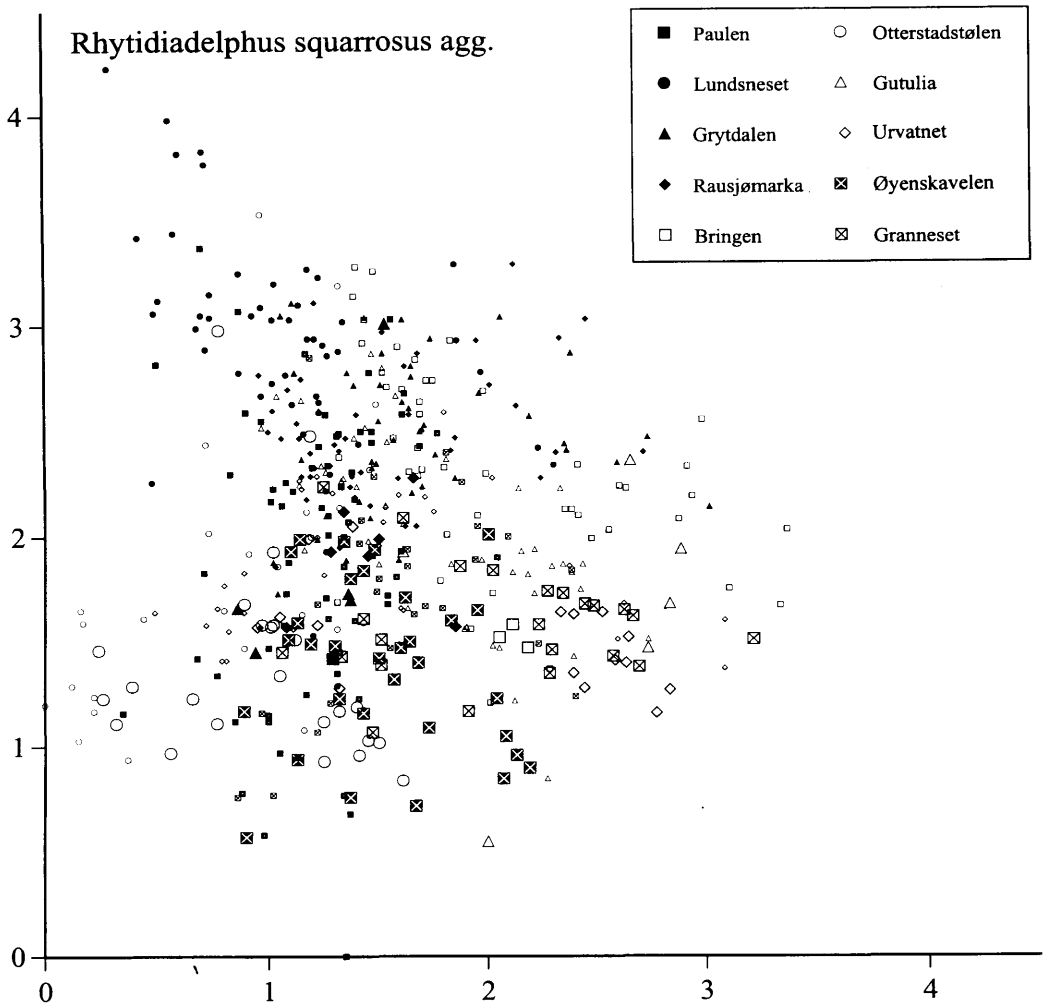


Fig. 799. The total data set: distribution of *Rhytidiadelphus squarrosus* agg. (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

tion; to sites poor in nutrients. In Otterstadstølen and Øyenskavelen this species was restricted to moist sites, while also present on medium dry sites in the other less humid reference areas.

Barbilophozia floerkei (Fig. 803) was most abundant on moist sites (low DCA 2 scores), especially in the humid reference areas. In reference areas from the Middle and Northern Boreal zones, e.g. Grytdalen, Bringen and Gutulia, a shift towards higher abundance in drier sites (higher DCA 2 scores) was noted.

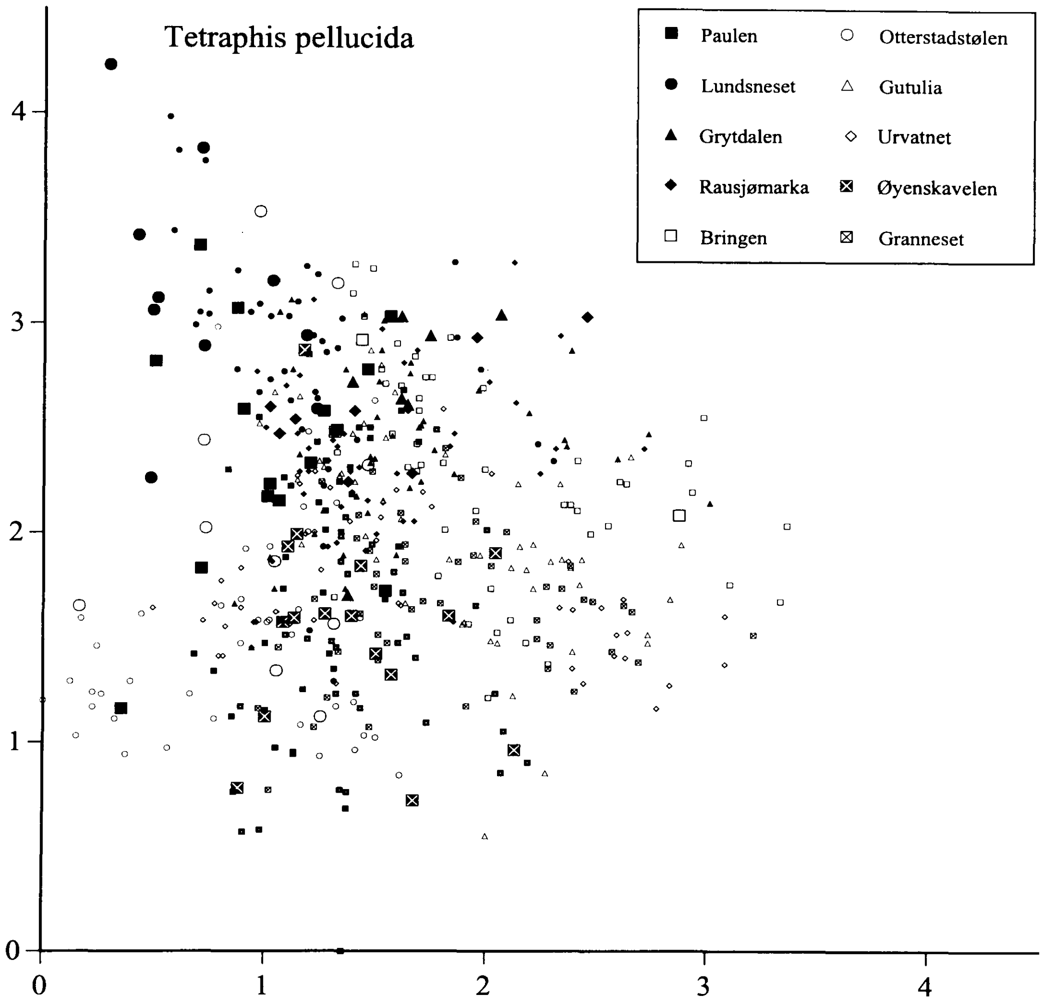


Fig. 800. The total data set: distribution of Tetraphis pellucida (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

Lophozia obtusa (Fig. 807) was restricted to moist sites in Otterstadstølen and mainly also in Øyenskavelen and Granneset. In Grytdalen, Bringen and Gutulia, this species expanded its range towards plots on drier sites (higher DCA 2 scores).

Tritomaria quinquedentata (Fig. 808) was most abundant on moist sites (low DCA 2 scores), but also occurred on medium-dry sites in the Middle and Northern Boreal zones; in Grytdalen, Bringen, Gutulia and Urvatnet.

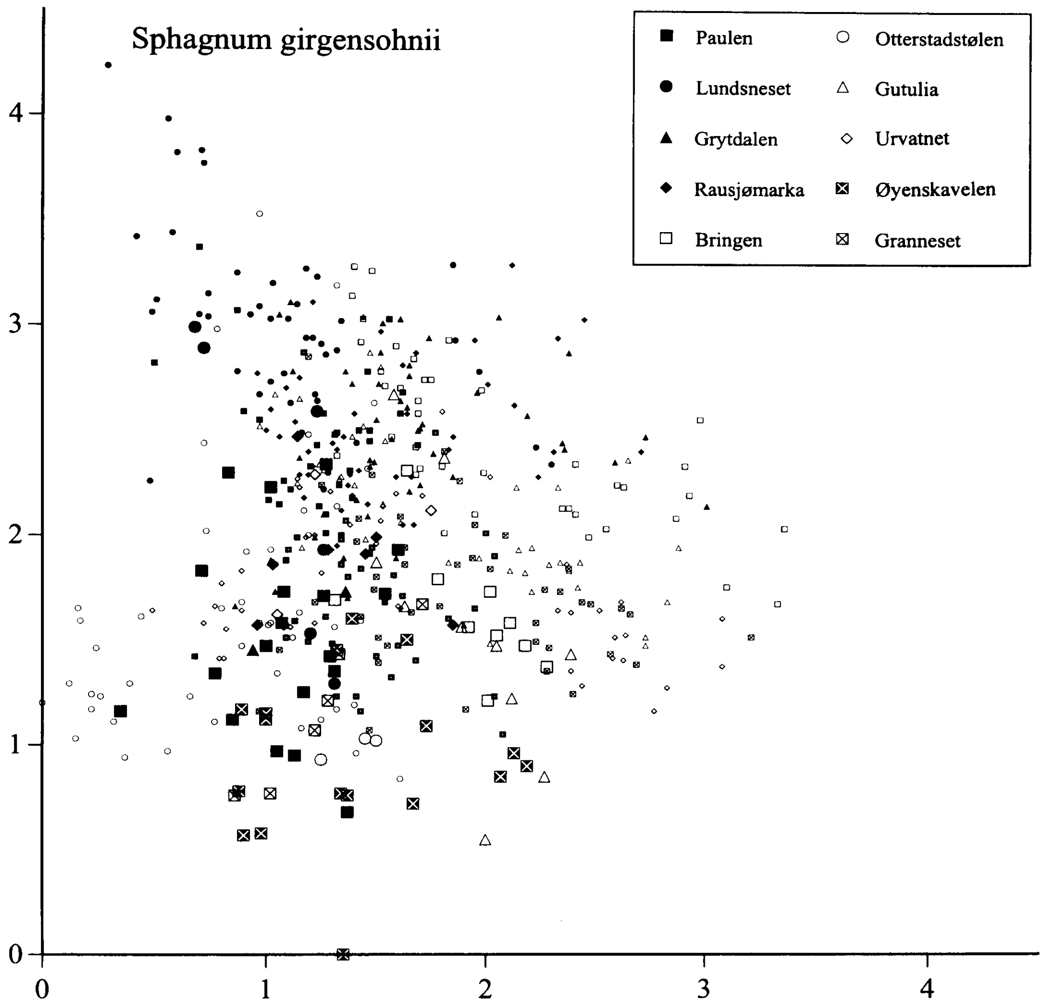


Fig. 801. The total data set: distribution of *Sphagnum girgensohnii* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

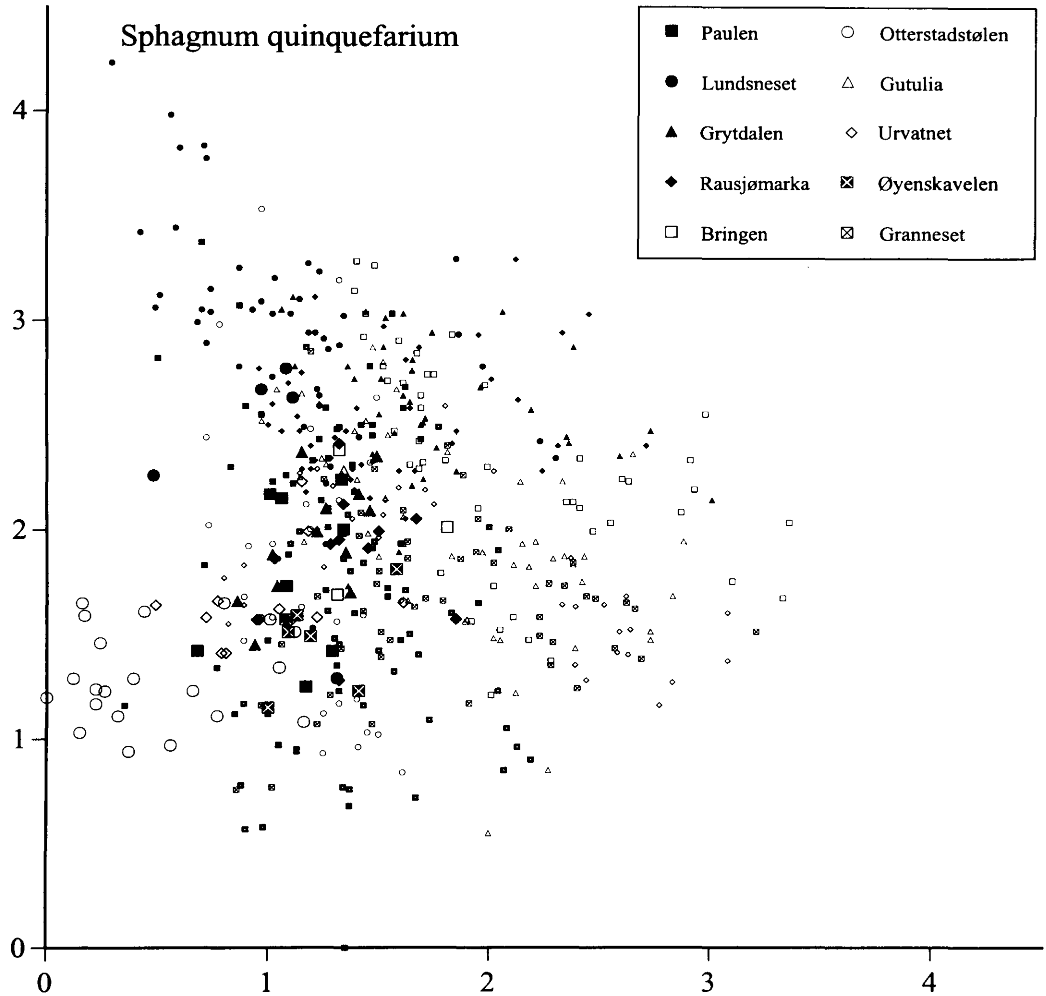


Fig. 802. The total data set: distribution of *Sphagnum quinquefarium* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

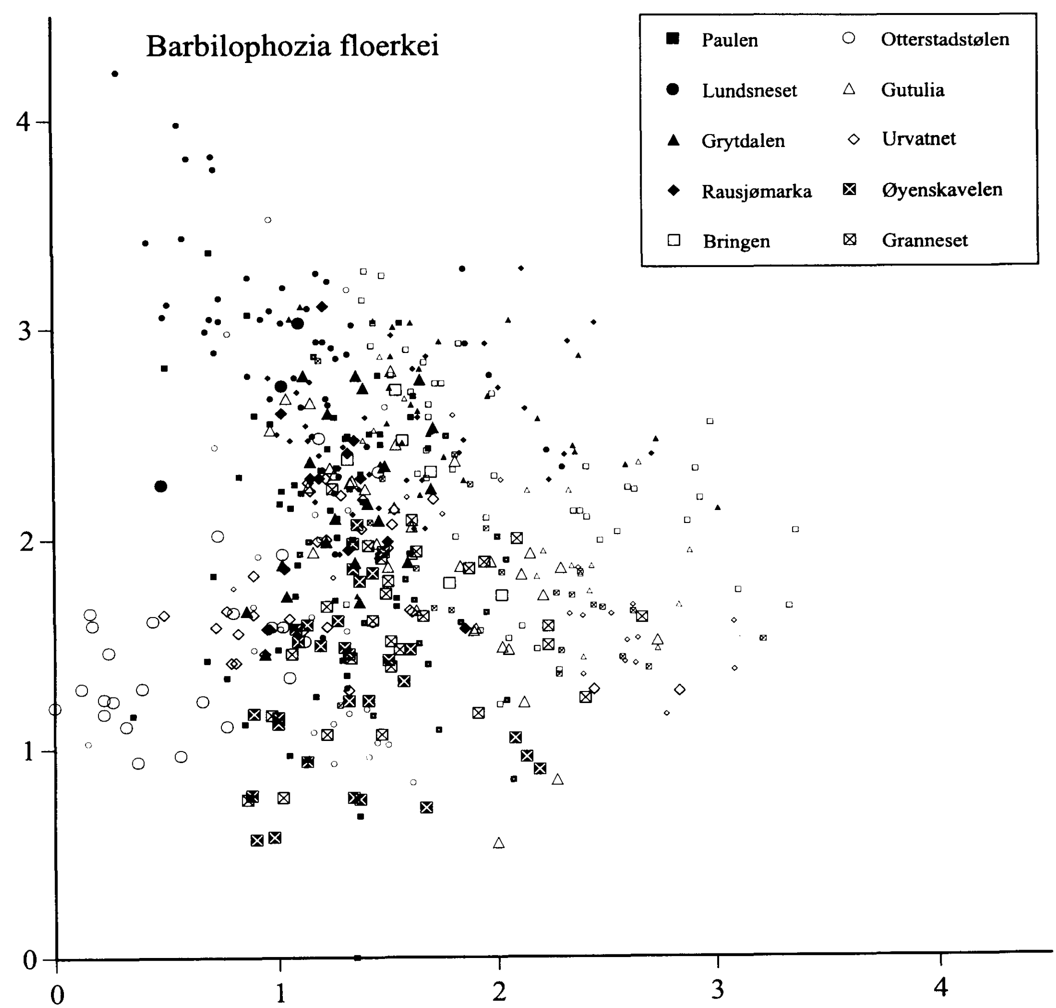


Fig. 803. The total data set: distribution of *Barbilophozia floerkei* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

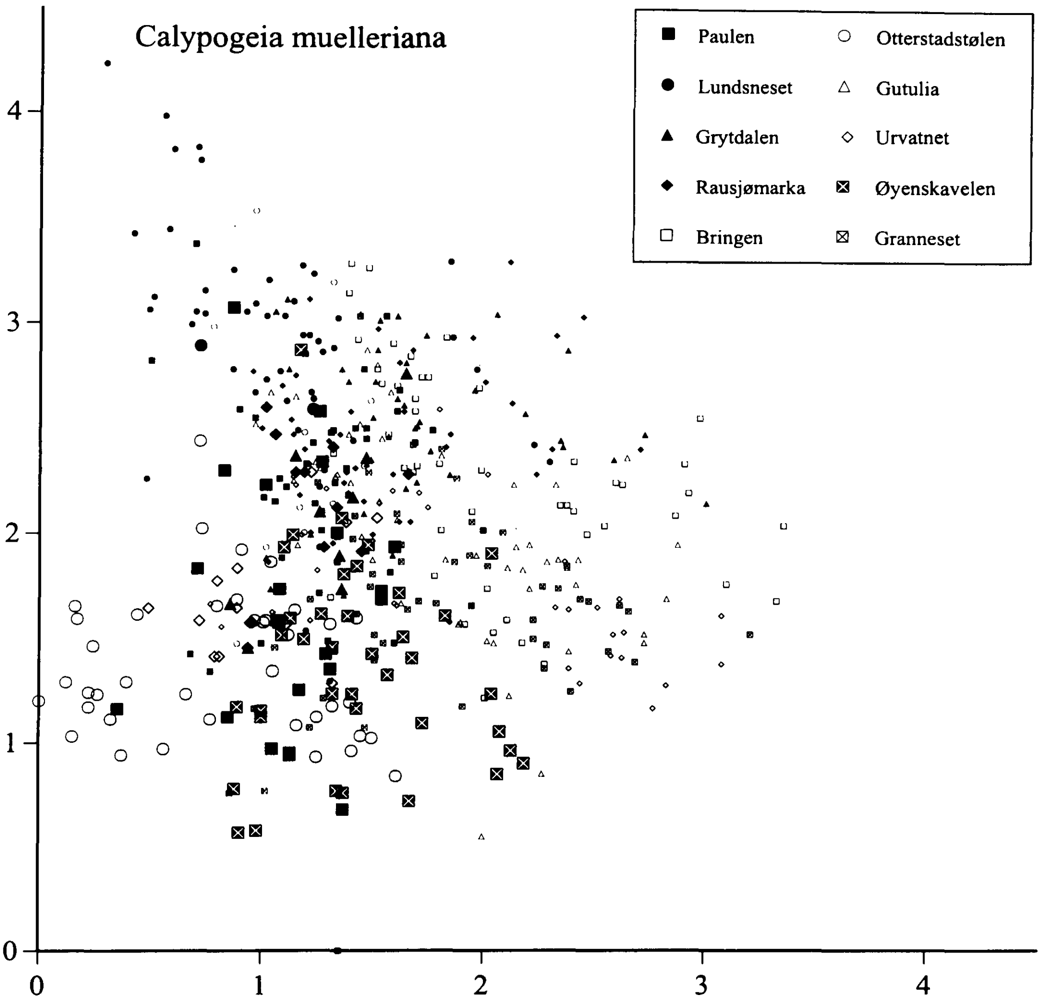


Fig. 804. The total data set: distribution of *Calypogeia muelleriana* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

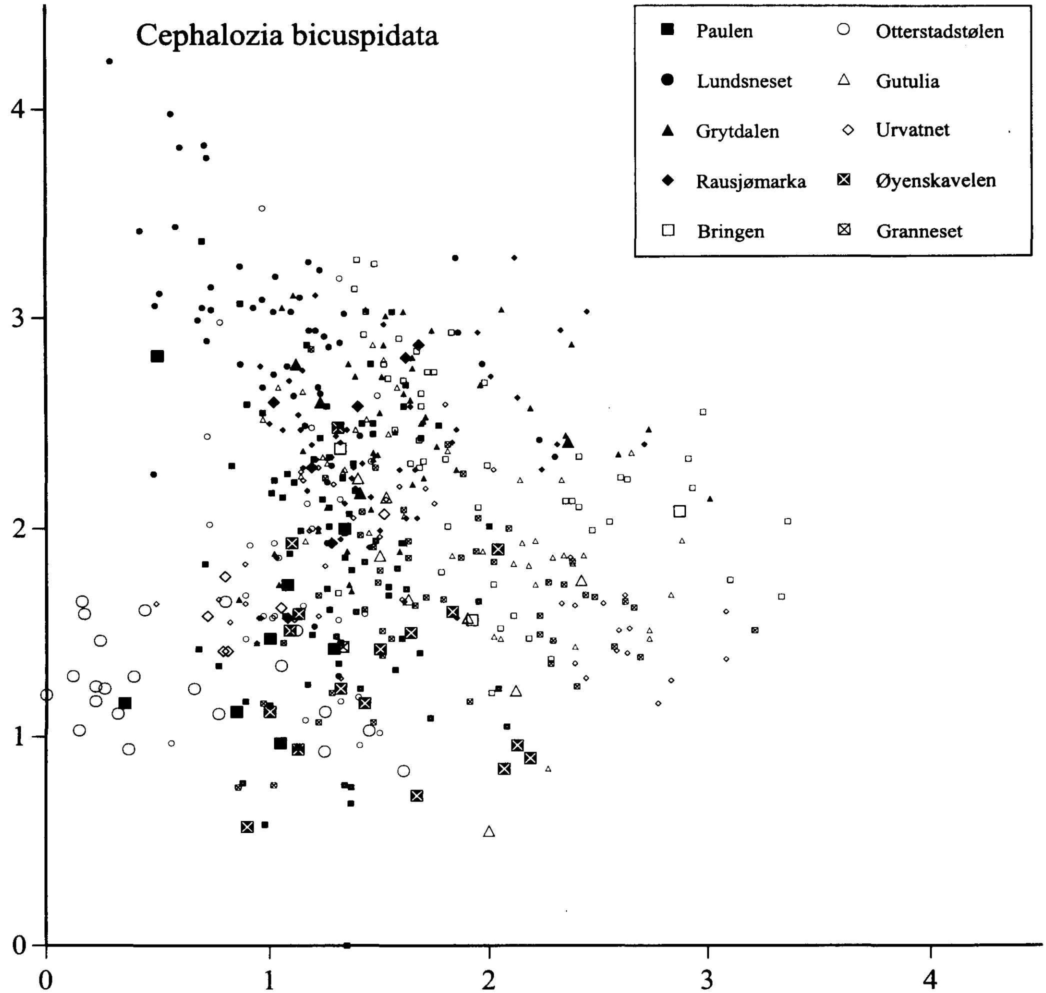


Fig. 805. The total data set: distribution of *Cephalozia bicuspidata* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

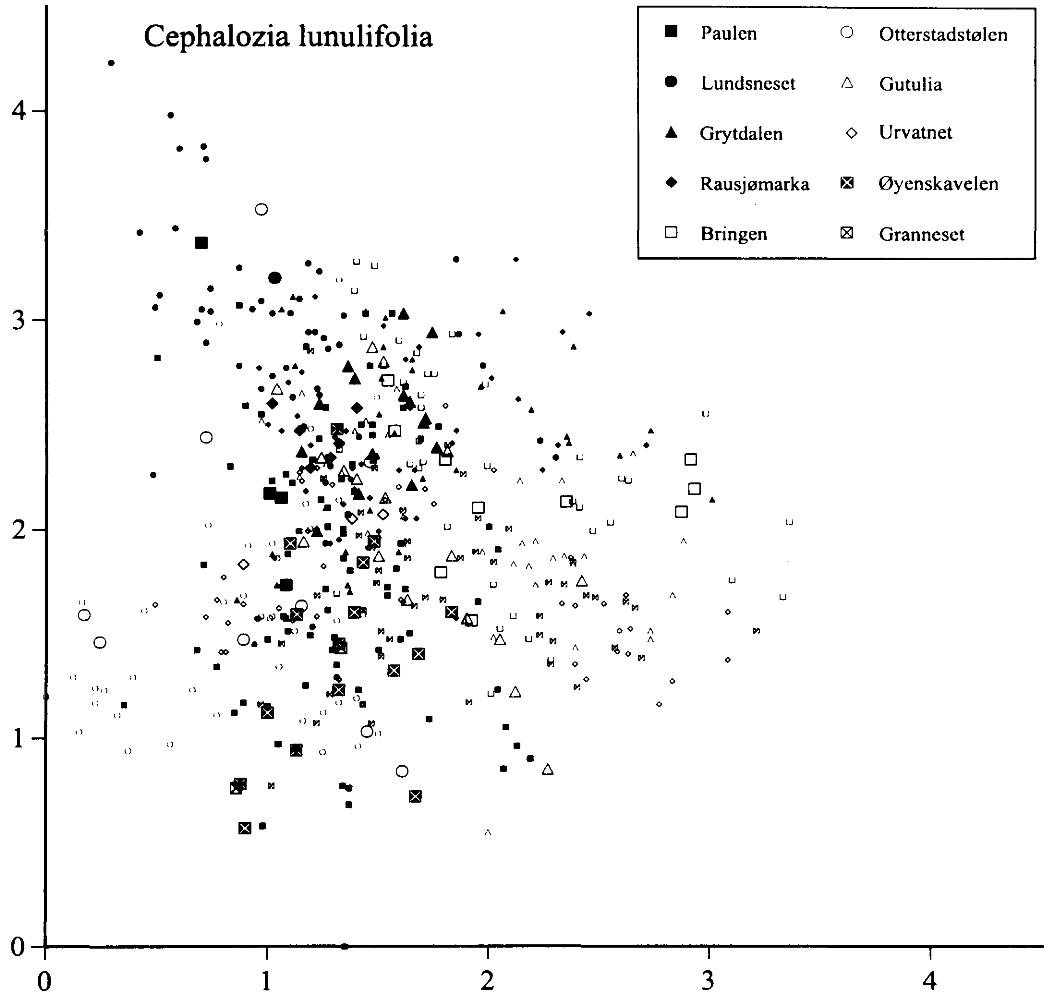


Fig. 806. The total data set: distribution of *Cephalozia lunulifolia* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

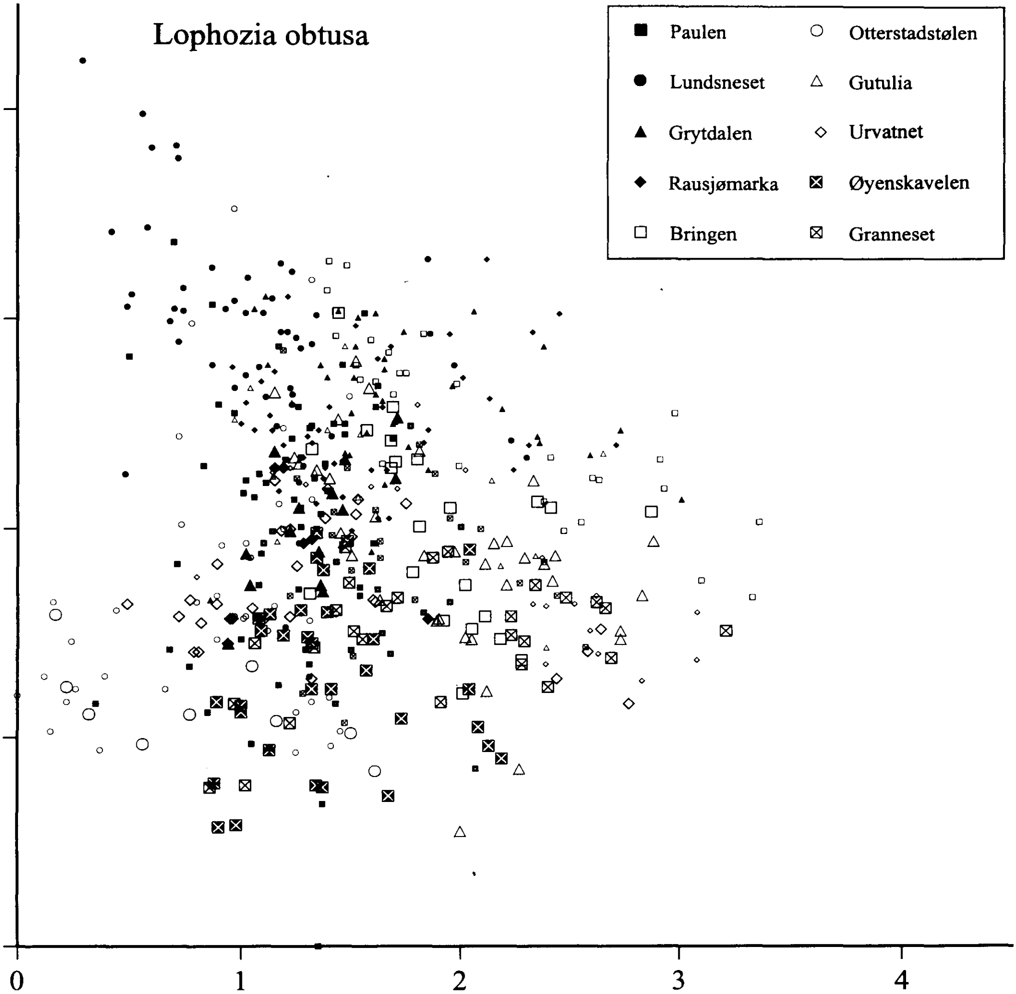


Fig. 807. The total data set: distribution of *Lophozia obtusa* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

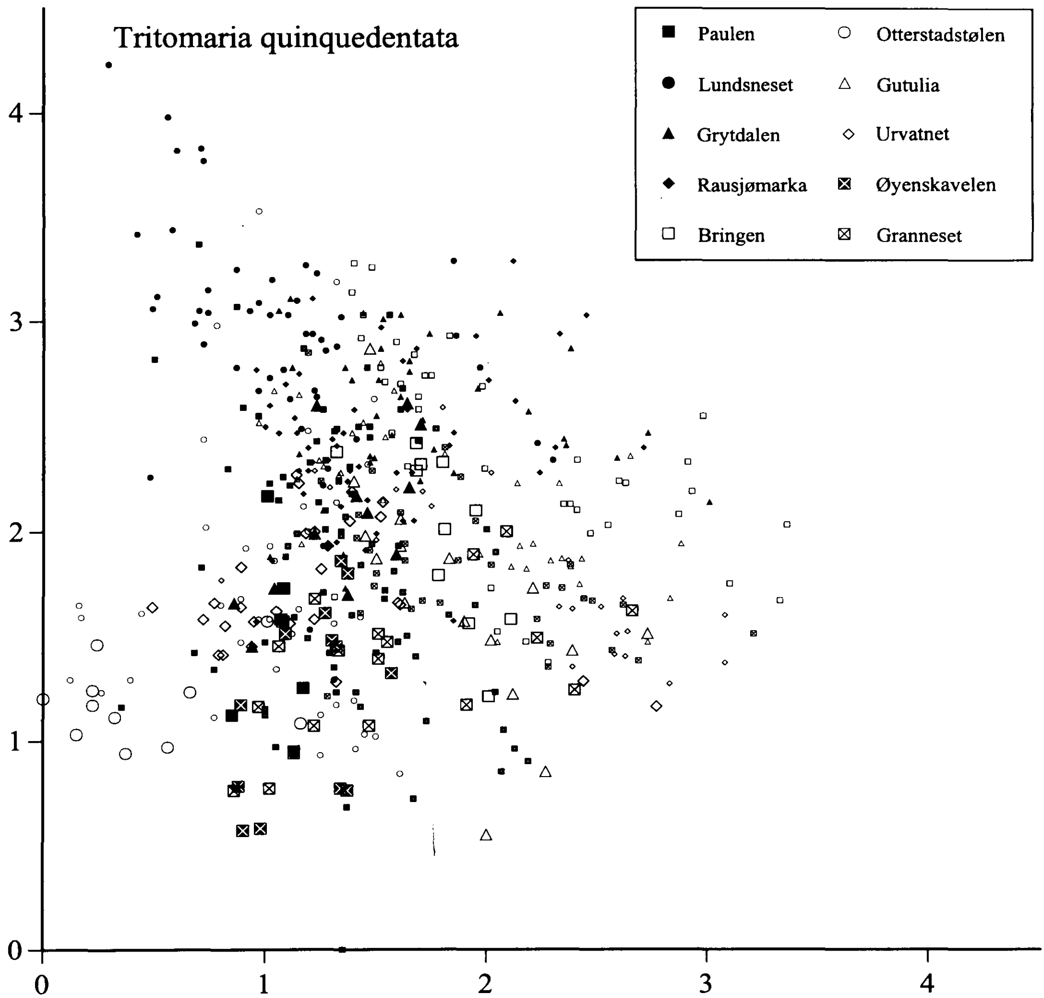


Fig. 808. The total data set: distribution of *Tritomaria quinquedentata* (presence indicated by large symbol) in the DCA ordination with variation exclusively due to climatic/geographical variables removed, axes 1 (horizontal) and 2 (vertical). Scaling of axes in S.D. units.

DISCUSSION

EVALUATION OF THE RELATIVE PERFORMANCE OF DCA AND LNMDS ORDINATION METHODS

The parallel use of DCA and LNMDS methods on the data sets from the ten reference areas shows that the main complex-gradients are recovered by both methods. The correlations with environmental variables are somewhat stronger for DCA 1 than for LNMDS 1 for seven of the reference areas, while the converse is true for two areas. DCA thus apparently recovers the variation in vegetation along the first ordination axis, which usually corresponds to a complex-gradient in nutrient conditions, better than LNMDS 1. For the second axis, environmental variables are more strongly correlated with LNMDS 2 than DCA 2 for four reference areas, while the converse is true for three areas. Variation in vegetation corresponding to the complex-gradient with soil moisture, litter conditions and/or tree density as important single variables, is thus occasionally recovered somewhat better by LNMDS than by DCA. These results do not support the view of Minchin (1987) that LNMDS is superior to DCA in recovering main gradients in vegetation. Other authors, however, suggest parallel application of both methods (Kenkel & Orlóci 1986, R. Økland 1990a, R. Økland & Eilertsen 1993, Rydgren 1993).

Outlying plots occur in both DCA and LNMDS ordinations. However, when outliers in the initial DCA ordinations (50 plots) are removed and new ordination analyses performed, new outliers appear in LNMDS ordination only. Careful examination of the outlying plots reveals three points of interest: (1) plots with deviating species compositions may give rise to outliers in DCA ordination, both when the species number is low compared to the other plots, as in Rausjømarka, and when high, as in Lundsneset; (2) plots with deviating number of species (α diversity) give rise to outliers irrespective of species composition in LNMDS ordination; and (3) LNMDS seems to be more vulnerable than DCA to plots with deviating α diversity, as plots with somewhat deviating number of species appear as new outliers only in LNMDS ordinations, as in Lundsneset, Grytdalen, Rausjømarka, Urvatnet, Øyenskavelen and Granneset.

The sensitivity of LNMDS to plots with deviating α diversity is likely to be an effect of the way floristic dissimilarities are used in the ordination algorithm. While the final plot position in DCA is determined by species optima (plot scores are weighted averages of species optima; Hill & Gauch 1980, ter Braak & Prentice 1988), the rank order of floristic dissimilarities between plots is used in LNMDS (Minchin 1987). This difference between the methods can be exemplified by two ecologically similar plots, both thus having the same weighted average of species optima using species abundances as weights, but the first containing half of the species occurring in the second. In DCA, these two plots obtain the same position along the ordination axis. In LNMDS, however, these two plots are likely to be placed far apart, as the floristic dissimilarity beween them will inevitably be high. The same applies to two plots with the same species, but with low abundances in one and high abundances in the other. These examples also explain the results of this study, that α-diversity gradients tend to be represented along ordination axes in LNMDS ordination.

The results strongly support the view that tests on simulated data sets are not sufficient for proper evaluation of the relative performance of ordination methods (R. Økland 1990a), as DCA on ten field data sets generally give axes that are more strongly related to measured environmental variables than LNMDS, despite the inferior gradient recovery of DCA in tests with simulated data (Kenkel & Orlóci 1986, Minchin 1987). This is not suprising, as unrealistic properties of simulated data sets may influence the ordination results and, hence, performance in tests (R. Økland & Eilertsen 1993). Thus, evaluation of ordination methods should also be based on results and experience gained by use on field data sets.

INTERPRETATION OF MAIN GRADIENTS IN REFERENCE AREAS

The results demonstrate variation between the ten reference areas with respect to which environmental variables are included in the complex environmental gradient that is most important for differentiation of the vegetation. The generally most important complex-gradient (Tab. 40) consists of single gradients in pH, total N and cation concentrations and is usually named the gradient in nutrient conditions or the fertility gradient (Malmström 1949, Dahl et al. 1967, Kielland-Lund 1981, Sepponen 1985, R. Økland & Eilertsen 1993, among others). In some of the reference areas, however, pH and total N on one hand, and cation concentrations on the other, are parts of different complex-gradients. Variation in vegetation related to a more or less strong soil moisture gradient is usually present, but the relationship of soil moisture with other environmental parameters varies. In some areas soil moisture and light and litter conditions vary along the same vegetational gradient, while in others the gradient in soil moisture is related to the same vegetational gradient (ordination axis) as pH, nitrogen content and/or cation concentrations. These differences may partly be due to differences in local environmental variation from one reference area to another, partly to regional variation. The litter index may express variation from under trees to below trees in some areas, while expressing variation on a broader scale when correlated with the macro plot variables.

Paulen

The main complex-gradient corresponds to variation in vegetation (DCA 1) from sites with low pH, low Al and total N concentrations, but high concentrations of P and cations like Ca, Mn, Zn, Mg and K (low DCA 1 scores) to vice versa. Some variation along DCA 1 corresponds to variation in vegetation from sites below trees and/or from sites in dense forest to gaps and/or open forest.

The second complex-gradient corresponds to variation in vegetation (DCA 2) from sites with low inclination and favourable aspects (low DCA 2 scores), to vice versa.

Some of the variation in vegetation along both DCA 1 and DCA 2 corresponds to variation in soil moisture, from moderately moist to dry sites (DCA 2) at the low-pH end of the main gradient, to the wettest sites which have high pH.

Tab. 40. Summary of environmental variables correlated with DCA axes 1 and 2 in ordinations of each reference area. Bold face - $\tau \geq 0.4$, normal letters - $0.3 \leq \tau < 0.4$, brackets - $0.25 \leq \tau < 0.3$. Italics - negative correlations. Variables in order of decreasing τ. Abbreviations for names of environmental variables in accordance with Tab. 2.

Reference area	DCA 1				DCA 2			
	pH/nutrients	Moisture	Light/Litter	Other	pH/nutrients	Moisture	Light/Litter	Other
Paulen	***Ca***, **Al**, ***Mn***, ***P-Al***, **pH_{H_2O}**, **Al**, **H^+**, ***Zn***, ***P***, *K*, *Mg*, Total N, S	Mois	*LitCC*			*Mois*		MA Inc, ***MA Hi*** *MEHi*
Lundsneset	***H^+***, Ca, Mg, Mn, (Na), *(Al)*	*Mois*	**MA Lig**	**MA Hi**, ***MA Asp***, **MA Inc**, MEInc, ME Smi			***MABA***, LI	
Grytdalen	**pH_{CaCl_2}**, **Zn**, **Ca**, ***Al***, **Mn**, **Total N**, ***Na***, ***H^+***, P-AL, (S)	*(Mois)*	MA Lig, (LitCC,LitACD)	**MA Hi**, ***MA Asp*** ***MEAsp***, MEHi, (LI)	*(pH_{CaCl_2})*, *(Ca)*, *(Mg)*			
Rausjømarka	**Ca**, **Mn**, **Mg**, *H^+*, pH_{CaCl_2}, (Zn)	***Mois***	**MA Lig**, **MA BA**, LitACD	*ME Asp*, (MAHi), (ME Hi)	*Total N*, K, *pH_{CaCl_2}*, (P), (H^+)		*MA Lig*,	MA Asp, (LI, ME Asp)
Bringen	**pH_{CaCl_2}**, **Mg**, **Total N**, (Ca) *P*, (Mn)			*LI*, MA Inc, MEInc, *(ME Smi)*	Zn, (Ca, P, P-AL)	*Mois*	MALig	**MA Hi**, ***MA Asp***, *MEAsp*, (MEHi),*(LI)*
Otterstadstølen	**pH_{CaCl_2}**, Fe, Total N, K, Al		MA Lig	*LI*, ***ME Smi***, *MA Hi*, (ME Asp), (MA Asp), (ME Hi)	**Ca**, Mn, *Na*, *S*	***Mois***	**LitACD**	MA Inc, (ME Sma)
Gutulia	pH_{CaCl_2}, Mn, Ca, *H^+*, Total N, Mg, *Fe*, S, *P*, *(P-AL)*			***LI***		P, *Al*, *P-AL*, *Na*, *Mg*, Zn		*Mois*MA Lig
Urvatnet	**pH_{CaCl_2}**, **Ca**, **H^+**, **P**, **P-AL**, Mn, Total N		MA Lig, MA BA	***LI***, **MA Hi**, *MA Asp*, MEHi, MEAsp	*(Mg)*	*Mois*	MA BA, LitCC	*ME Smi*
Øyenskavelen	**Total N**, **pH_{CaCl_2}**, *Zn*, *(Mg)*		LitACD, (MA Lig)	***MA Asp***, **MA Hi**, **ME Hi**, ***LI***, MA Inc, MEAsp	***H^+***, K, Ca, Zn, pH_{H_2O}	***Mois***		(MA Inc)
Granneset	**pH_{CaCl_2}**, **Ca**, **Zn**, *Fe*, Total N, Mn, *(Al)*	*Mois*		***LI***, ME Sma, Me Sme, (ME Inc)	*S*, *Mg*, *(K)*, *(Al)*	(*Mois*)	MA Lig, LitCC	MA Hi, *MA Asp*

Lundsneset

The main complex-gradient corresponds to variation in vegetation (DCA 1) from sites with low inclination and low content of Ca (and Mg and Mn) in open forest on unfavourable aspects (low DCA 1 scores), to vice versa. Some of the variation in vegetation along the main gradient corresponds to variation in soil moisture and minimum soil depth. Thus, the wettest sites have unfavourable aspects with low inclination and contents of cations and high minimum soil depth, while dry sites occur both on slopes with high inclination, favourable aspects and high contents of cations on shallow soils, and on sites which are intermediate in these conditions.

The second gradient corresponds to variation in vegetation (DCA 2) related to variation in tree density.

Grytdalen

Only one gradient in vegetation (DCA 1) is interpretable by means of the environmental variables. Thus, only one complex environmental gradient can be identified; from sites with unfavourable aspects in open forest, with low pH and contents of nutrients like Ca, Mn, Zn and nitrogen, but high contents of Na and Al, to vice versa.

This simple gradient structure is partly due to the narrow range of variation in soil moisture (also along DCA 1): the more moist sites (with dominance of *Sphagnum* spp.) are restricted to the low-pH end of the main gradient.

Rausjømarka

The main complex-gradient corresponds to a gradient in vegetation (DCA 1) from open and moist sites with (relatively) low pH and contents of nutrients (Ca, Mg and Mn), to vice versa. Aspect unfavourabilty and litter indices also have some variation along the main gradient (DCA 1), corresponding to variation in vegetation from sites with unfavourable aspects in gaps (with low pH and content of nutrients), to sites with favourable aspects below trees (with high pH and contents of nutrients).

pH varies also along the second gradient (corresponding to variation in vegetation along DCA 2), while nitrogen content only varies along this gradient. Thus, the second gradient expresses variation in vegetation from sites with moderate to low pH and high to low nitrogen content in the nutrient-poor end of the main complex-gradient.

Bringen

The main complex-gradient corresponds to variation in vegetation (DCA 1) from sites with low inclination, pH and contents of nutrients (nitrogen and Mg) and a high content of organic matter, to sites with high pH, inclination and content of nutrients, and a low content of organic matter in the soil, to vice versa.

The second gradient corresponds to variation in vegetation (DCA 2) from moist sites with unfavourable aspects in open forest, to dry sites with favourable aspects in more dense forest. Variation in soil moisture appears to be mainly independent of variation in pH and nutrients, as vegetation on both dry and moist sites occurs in the low-pH and nutrient-poor end of the gradient, and on sites with intermediate pH and contents of nutrients.

Otterstadstølen

The main complex-gradient corresponds to variation in vegetation (DCA 1) from sites with low pH, high soil depth and content of organic matter in the humus layer, to vice versa. Contents of nutrients like nitrogen, K, Fe and Al also increase along this gradient, although less consistently.

The second complex-gradient corresponds to variation in vegetation (DCA 2) from moist sites between trees, mostly with low inclination, and low content of nutrients like Ca and Mn but a high content of Na (low DCA 2 scores), to vice versa. Inclination and the cations Mn and Na also vary along the gradient, though less strongly correlated. The most strongly sloping sites below trees are thus dry, with a high content of Ca.

The two complex-gradients are largely independent of each other.

Gutulia

The main complex-gradient corresponds to variation in vegetation (DCA 1) from sites with low pH and low contents of nutrients (nitrogen, Ca, Mn, Mg) and a high content of organic matter in the humus layer, to vice versa.

The second complex-gradient corresponds to variation in vegetation (DCA 2) from sites in open forest, with high soil moisture and contents of Na and Al (low DCA 2 scores) to dry sites, with low contents of Al and Na, in more dense forest. Except for the wettest sites which have relatively high pH and content of nutrients, the variation in soil moisture is to a large extent independent of the variation in pH and nutrients, although the wettest sites have relatively high pH and content of nutrients. Vegetation on dry sites (DCA 2) occurs both on sites with low and high pH and content of nutrients.

Urvatnet

The main complex-gradient corresponds to variation in vegetation (DCA 1) from sites with unfavourable aspects, low pH and contents of nutrients (Ca, Mn and total N) and a high content of organic matter in the humus layer (low DCA 1 scores), to vice versa.

The second gradient corresponds to variation in vegetation (DCA 2) from sites with a high soil moisture content (low DCA 2 scores) to dry sites, to a large extent independent of variation in pH and nutrients.

Tree stand density and light conditions vary along both gradients; the most open forest is restricted to moist sites with low pH and nutrient content, while dense forest occurs both on sites with low and high pH and contents of nutrients, and on dry as well as moist sites.

Øyenskavelen

The main complex-gradient corresponds to variation in vegetation (DCA 1) from sites with unfavourable aspects, low pH and a low content of nitrogen, and a high content of organic matter in the humus layer (low DCA 1 scores), to vice versa. The (weak) correlation of this vegetation gradient with litter indices, indicate some variation from below to between trees and/or from open to more dense forest.

The second gradient corresponds to variation in vegetation (DCA 2) from moist sites with low content of Ca (low DCA 2 scores) to dry sites with a high content of Ca. Soil moisture and Ca content are both unrelated to variation along the main complex-gradient, while inclination (and content of Zn) varies to some degree along both gradients.

Inclination and Zn are, to some degree, correlated with both gradients. Thus, moist sites with low pH also have low inclination, and dry sites with high pH also have high inclination.

The strong correlation between the litter indices (and Na) and DCA 3 (and LNMDS 1) indicate variation in vegetation from below to between trees, that is independent variation along the main gradients.

Granneset

The main complex-gradient corresponds to variation in vegetation (DCA 1) from sites with low pH and contents of nutrients (nitrogen, Ca, Mn and Zn) and a high content of organic matter in the humus layer (low DCA 1 scores), to vice versa. Soil moisture is partly related to this main complex-gradient, as high soil moisture is invariably associated with low pH and content of nutrients, while dry sites are restricted mainly to sites with intermediate to high pH and content of nutrients.

The second gradient corresponds to variation in vegetation (DCA 2) partly due to differences in soil moisture among sites with low pH and content of nutrients. These differences are also related to aspect, which is unfavourable on moist sites. Variation in vegetation along this gradient is also partly related to variation in light and litter. The correlation between the light index and the litter indices, may indicate that both reflect variation in tree density, i.e. on a broader scale than from below to between individual trees. Highest tree density occurs on some of the driest sites with intermediate pH and content of nutrients, while more open forest occurs on the wettest sites, with low pH and content of nutrients.

MAIN COMPLEX-GRADIENTS IN BOREAL SPRUCE FORESTS

The gradient in nutrient conditions

The high importance of a complex-gradient in nutrient conditions for differentiation of the understory in boreal forests is documented in several investigations (e.g. Malmström 1949, Dahl et al. 1967, Kuusipalo 1985, Sepponen 1985, Taylor et al. 1987, R. Økland & Eilertsen 1993, among others), and is considered to be the most important complex-gradient for the structuring of vegetation in boreal spruce forests (cf. Dahl et al. 1967, Tonteri et al. 1990, Kuusipalo 1983a, 1983b, 1985, R. Økland & Eilertsen 1993, among others). Although the relative importance of different parameters that make up this complex-gradient varies between different studies, pH, content of nitrogen and concentration of exchangeable Ca are usually described as important (cf. Malmström 1949, Dahl et al. 1967, Kuusipalo 1983b, 1984, 1985, R. Økland & Eilertsen 1993, among others). Considerable variation in parameters contributing to this gradient occurs also between the ten reference areas (Tab. 40), but pH and total N are almost invariably among the most important parameters. Some differences are regional, mainly caused by climatic differences, and some differences are due environmental variation on a local scale.

In this study pH contributes to variation in vegetation (DCA 1) along the main complex-gradient in nine of ten reference areas. In six of these, pH is the variable which is most strongly correlated with the first DCA axis (Grytdalen, Bringen, Otterstadstølen, Urvatnet and Granneset (Tab. 40): i.e. pH is the parameter which best reflects variation along the main vegetational gradient. Similar results are found by Sepponen (1985), Lahti & Väisänen (1987), Taylor et al. (1987), Tyler (1989), T. Økland (1990), R. Økland & Eilertsen (1993), among others. However, pH mainly affects plants indirectly through the influence on soil fauna and availability of mineral nutrients (cf. Glømme 1932).

The soil fauna, and thus the decomposition rate, is dependent on pH: on acid soils fungi dominate as decomposers, while on sites with higher pH bacteria and earthworms dominate (cf. Glømme 1932, Romell 1935, Hesselmann 1937, Nykvist 1961b, Lindgren 1975). Important nutrients thus become available to plants more readily on soils with high pH.

The content of nitrogen (total N) contributes to the main complex-gradient in all reference areas except Lundsneset and Rausjømarka (Tab. 40). In Lundsneset neither nitrogen nor pH vary along the main gradient, while in Rausjømarka pH varies along both DCA 1 and DCA 2, and content of nitrogen varies along DCA 2. Inclusion of nitrogen content in humus in the main complex-gradient is in accordance with several other studies from boreal forests (Hesselman 1926, Malmström 1949, Kuusipalo 1983b, 1985, Lahti & Väisänen 1987, R. Økland & Eilertsen 1993). In all reference areas pH and nitrogen content are more or less strongly correlated. In Lundsneset this correlation is mainly due to five meso plots with higher pH and content of nitrogen than the other plots. After removing these plots, no significant variation in pH and nitrogen is left along DCA 1.

Nitrogen is usually considered to be the most important limiting resource in boreal forests (cf. Hesselman 1937, Malmstrøm 1949, Kuusipalo 1984, Tamm 1991). Nitrogen is important for building up new organic material in plants (Kubin 1983), but also for the microbiological activity in the humus (Olsen 1990), as the microbes need nitrogen for their synthesis of organic matter (Kubin 1983). However, nitrogen is available in two forms, as NH_4^+ and NO_3^- (Glømme 1932, Gigon & Rorison 1972, Ingestad 1973). As plants differ in their ability to utilize NH_4^+ and NO_3^- (Gigon & Rorison 1972, Falkengren-Grerup & Lakkenborg-Kristensen 1994), the species composition may be dependent on the relative availability of nitrogen in each of the two forms; i.e. the rate of nitrification. However, the strong relationship between total amounts of nitrogen and main gradients in vegetation, suggests that also the total amounts of available nitrogen, regardless of chemical state, i.e. the nitrogen mineralization rates, are important for the species composition. A strong positive relationship between total amounts of nitrogen and nitrification rates is demonstrated by Simard & N'dayegamiye (1993). Both nitrification rates and nitrogen mineralization rates are dependent on pH (cf. Glømme 1932). However, more research is needed to assess species' responses to variation in nitrification rates.

One hypothesis that has been repeatedly forwarded is that the dependence of pH on the nitrogen mineralization process is due to the cation Ca, claimed to be the primary environmental variable limiting nitrogen mineralization rates in humus (Hesselman 1926, Dahl et al. 1967, see also R. Økland & Eilertsen 1993). In most studies Ca is one of the most important parameters contributing to the main complex-gradient, usually more or less strongly correlated with pH (cf. Hesselman 1937, Malmström 1949, Kuusipalo 1983b, Taylor et al. 1987, among others). In this study Ca is positively correlated with pH in six of the ten reference areas: in Grytdalen, Rausjømarka, Bringen, Gutulia, Urvatnet and Granneset. In Bringen, Gutulia, Urvatnet and Granneset Ca is also more or less strongly correlated with nitrogen content. However, in Otterstadstølen and Øyenskavelen, the two reference areas with most strongly humid climate, Ca is neither correlated with pH nor nitrogen content, nor does Ca vary along the same DCA axis as pH or nitrogen content. In both areas Ca and soil moisture vary along the same vegetational gradient (high concentrations of Ca near the dry end). In Øyenskavelen Ca is also negatively correlated with soil moisture. In Paulen, also an reference area with a humid climate, though less strongly so, Ca is negatively correlated with all of pH, nitrogen and soil moisture, while positively correlated with the litter index. Ca varies along the same vegetational gradient (DCA 1) as pH and nitrogen in Paulen, but with opposite signs, and soil moisture varies along both DCA 1 and DCA 2. The negative correlation between Ca and pH, and between Ca and nitrogen content in Paulen, demonstrate similarity with results from Øyenskavelen and Otterstadstølen, and suggest that in a humid climate, Ca does not contribute to a gradient in nutrient conditions as is normally the case in less humid areas.

These results from reference areas with a humid climate contradict the hypothesis that Ca content in the humus layer is *the* primary environmental parameter limiting the rate of nitrogen mineralization via its effects on pH. Other parameters are likely to be involved. The result that Ca is usually correlated with pH and often also with nitrogen content in reference areas with less humid climate, while uncorrelated in more humid areas, suggests regional variation in the importance of parameters affecting nitrogen mineralization or that the availability of Ca is partly climatically conditioned. Possible explanations why Ca, litter indices and soil moisture are related to the same gradient in vegetation are further discussed in connection with the gradient in soil moisture conditions (pp. 332-333).

In five reference areas; Paulen, Grytdalen, Rausjømarka, Otterstadstølen and Granneset, positive correlations between litter indices and content of Ca are found. In Paulen and Otterstadstølen this is likely to be due to higher concentrations of Ca below trees (as also reported by Kubin 1983, from northern Finland) where the amount of litter is greater than between trees. In Grytdalen and Rausjømarka, however, variation in the amount of Ca is related to variation in light and tree density on a broader scale than from below to between trees. This is evident from the positive correlations between Ca and the macro plot light index in both areas, the positive correlation between Ca and tree density in Rausjømarka, and the correlations of Ca and light index with the main gradient in vegetation (DCA 1) in both areas. In these areas dense forest occurs on sites with a high content of nutrients and high pH, as also reported in other studies (cf. Kuusipalo 1983b, 1985, 1988, R. Økand & Eilertsen 1993, among others).

The effect of the plants themselves on the humus is often stressed (Hesselman 1937, Sepponen 1985, Lahti & Väisänen 1987, R. Økland & Eilertsen 1993). Even if the subsoil is important for the availability of nutrients during the initial stages of the humus formation

(Romell 1935), its influence diminishes gradually and mostly becomes less important in old spruce stands, as the plants themselves contribute to the type of humus formed (cf. Hesselman 1937, Sirén 1955). For instance, the herbs contribute to favourable nutrient conditions by their rapidly decomposable litter (cf. Lähde 1974), while the decomposition of some feather mosses is very slow due to high lignin content (Mikola 1955, Berg 1984, Oechel & van Cleve 1986).

According to Staaf (1982), both Ca and Mg are immobile ions, dependent on organic matter as carrier substance. The type and amount of litter and the decompositon rate thus plays an important role for the content of these cations in the humus (cf. Buldgen et al. 1983, T. Økland 1988, 1990, 1993, R. Økland & Eilertsen 1993). Many parameters influence the rate of litter decomposition (e.g. pH, temperature, soil moisture and humus type). Litter decomposition rates also vary between species (Mikola 1955), and litter from deciduous trees and vascular plants (which are generally more abundant in forests rich in nutrients) decompose more rapidly than spruce litter (cf. Nykvist 1961a, 1961b, Lähde 1974, Havas & Kubin 1983). Variation in litter decomposition rates may thus contribute to consolidate the gradient in nutrient conditions.

Decomposition rates are higher on sites with favourable aspects due to high incoming radiation (Kuusipalo 1985, R. Økland & Eilertsen 1993). This can explain the negative correlation between aspect unfavourability and the gradient in nutrient conditions in Grytdalen, Rausjømarka and Urvatnet. The content of organic matter in the humus layer (measured as loss on ignition) reflects the litter decomposition rates. This explains the negative correlation between loss on ignition and both pH and content of nutrients in Bringen, Otterstadstølen, Gutulia, Urvatnet and Granneset, and the variation from low contents of organic matter on sites rich in nutrients to high contents on poorer sites and beneath trees where litter accumulates (cf. Hesselman 1926, Dahl et al. 1967, Bergseth 1977, Sepponen 1985, R. Økland & Eilertsen 1993).

The gradient in soil moisture

A complex-gradient in soil moisture conditions is of major importance for the differentiation of vegetation in most boreal forests (cf. Arnborg 1964, Kuusipalo 1983b, 1985, Lahti & Väisänen 1987, Taylor et al. 1987, Carleton 1990, T. Økland 1990, R. Økland & Eilertsen 1993, Rydgren 1993). The soil moisture gradient is in principle independent of the complex-gradient in nutrient conditions (R. Økland & Eilertsen 1993), but the two gradients may be correlated (Lähti & Väisänen 1987, Carleton 1990). The two complex-gradients are more or less unrelated in Bringen, Otterstadstølen, Gutulia, Urvatnet and Øyenskavelen. One example is Gutulia, where all combinations of dry and moist sites, and sites both poor and rich in nutrients occur. In Paulen, Grytdalen (where the gradient in soil moisture is less strong), Rausjømarka and Granneset, the two complex-gradients are more or less strongly correlated. In Paulen, the wettest sites have a high pH and high nitrogen content. In the other reference areas, on the other hand, the sites rich in nutrients are mostly dry while moist sites are invariably poor. Thus, in Granneset, nutrient-rich sites with high moisture content are restricted to long slopes with springs and open luxuriant tall-herb and tall-fern vegetation (cf. Malmström 1949, R. Økland & Bendiksen 1985), which are not included in this investigation. Differences between reference areas with respect to combinations of major gradients may also partly be due to variation between areas in the terrain conditions encountered, e.g. variation in aspects and inclination occurring in each area. In Otterstadstølen, for instance, the sites are generally more steep, and in Granneset the soil surface is more even than in other reference areas. Sparsely occurring combinations of site conditions may also have escaped inclusion among the plots.

The soil moisture content, as measured in the present study, intentionally represents median or normal values (T. Økland 1990, R. Økland & Eilertsen 1993). The results thus indicate that paludified sites maintain a relatively high soil water content throughout most of the year. The wettest sites included in this investigation are paludified patches or slopes, usually with a high abundance of one or more species of *Sphagnum*, such as *S. girgensohnii* and *S. quinquefarium*, with or without ferns as *Phegopteris connectilis* (cf. also Kuusipalo 1985). The abundance and occurrence of small hepatics like *Cephalozia* spp., *Calypogeia* spp., *Lophozia* spp. and *Harpanthus flotovianus*, vary among the *Sphagnum* shoots. *Sphagnum* carpets entirely devoid of hepatics mostly occur on plane surfaces (e.g. in plot Nos 4 and 5 in Grytdalen). In *Sphagnum* carpets with more uneven surface, hepatics are usually abundant (e.g. in plot Nos 6 and 7 in Bringen, and plot Nos 12 and 33 in Gutulia). The establishment and maintenance of hepatic populations is likely to be dependent on retarded or stagnant *Sphagnum* growth (cf. R. Økland 1989, 1990b). In turn, this stagnation may be due to fine-scale disturbance, e.g. caused by trampling and urination by large animals (Ericson 1977, Frisvoll & Flatberg 1990), burial in litter (Kujala 1926, During & Verschuren 1988, R. Økland 1995b) and frost damage (Collins 1976), or be the result of parasitism by fungi (Redhead 1981) or algal overgrowth (cf. During & van Tooren 1990). High abundance of hepatics may further retard growth of *Sphagnum* (Pakarinen 1978).

The sizes of the paludified patches and slopes vary from one reference area to another, and also within each reference area. This variation is mainly due to variation in terrain forms. R. Økland & Eilertsen (1993) stress the difference between *topogenous* paludification, which occurs in small depressions with poor drainage and stagnant water; and *soligenous* paludification, which is favoured by a cold and humid climate and occurs in slopes where the terrain determines the speed and direction of water movement. Significant correlations between soil moisture and inclination do not occur in any of the ten reference areas. According to R. Økland & Eilertsen (1993), this is typical of areas with both types of paludification. In Lundsneset, Paulen and Otterstadstølen, inclination varies along the same gradient as soil moisture, but in the opposite direction (stronger inclination on the drier sites). This relationship may indicate higher importance of topogenous than soligenous paludification (cf. R. Økland & Eilertsen 1993). However, a more likely explanation of these relationships is the presence of very steep, well-drained macro plots in all these areas.

In all ten reference areas paludified sites most often occur in smaller or greater gaps in the forest, i.e. between trees, or in open stands in more or less sloping terrain (cf. R. Økland & Eilertsen 1993). Soil moisture and litter indices are inversely related to the same vegetational gradient (more or less strongly correlated with the same ordination axis) in seven of the reference areas (Paulen, Lundsneset, Grytdalen, Rausjømarka, Otterstadstølen, Urvatnet, and Granneset). This demonstrates that the soil is drier below trees than in the gaps between trees, and that the understory species vary in their tolerance to the dry conditions below trees, as several species are restricted to the more moist sites in the gaps between trees (cf. Taylor et al. 1987, Schaetzl et al. 1989, R. Økland & Eilertsen 1993). The variation in soil moisture from below to between trees is due to the impact of tree canopies (cf. R. Økland & Eilertsen 1993): (1) a strong gradient in throughfall precipitation (low close to tree stems), caused by canopy interception (C.O. Tamm 1953, Beier et al. 1993), (2) stronger water uptake by trees close to stems (cf. Stålfelt 1937b) and (3) large amounts of spruce litter, particularly close to stems, that give rise to a loose and thick humus which dries up rapidly after rainfall, due to low capacity for retaining moisture (cf. Malmström 1937, Stålfelt 1937b).

The probability of burial of cryptogamic species also increases from gaps between trees to below trees, where the amount of litter is considerably higher (Tarkhova & Ipatov 1975, R. Økland & Eilertsen 1993). Thus, few species can establish and survive on the thick and generally dry humus just below trees, except occasionally for some bryophytes, such as *Barbilophozia lycopodioides* and *Plagiothecium laetum*. Length of the period in hydrated state is assumed to be the most important parameter limiting growth of ectohydric bryophytes (cf. Stålfelt 1937b, C.O. Tamm 1953). In a superhumid climate such as in Otterstadstølen and Øyenskavelen, more species survive below trees, e.g. *Dicranum majus*, *Hylocomium splendens*, *Hypnum cupressiforme* agg., *Polytrichum formosum* and *Rhytidiadelphus loreus*, due to: (1) the high air humidity, in turn caused by the high precipitation frequency, (2) the high (absolute amounts of) throughfall precipitation, and, in several places, (3) recurrent irrigation by surface run-off water.

In Lundsneset, Grytdalen, Rausjømarka, Bringen, Gutulia, Urvatnet and Granneset, the light index and/or basal area are positively correlated, while soil moisture is negatively correlated with the same vegetational gradient. Thus, low light supply also contributes to make sites just below trees unfavourable for a majority of species.

Soil moisture is negatively correlated with the concentration of Ca in five reference areas; relatively strongly so in Lundsneset, Rausjømarka, Øyenskavelen and Granneset ($|\tau| > 0.35$, $P < 0.0003$). In Paulen the correlation coefficient is weaker ($\tau = -0.292$, $P = 0.003$). In the other reference areas this correlation is even weaker or insignificant. The negative correlations between Ca concentration and soil moisture in Lundsneset, Rausjømarka and Granneset are likely to be due to the negative correlation between the main complex-gradients; all the moist sites are relatively poor in nutrients. Thus in these reference areas the correlation between soil moisture and the concentration of Ca is considered not to be related to differences in soil moisture on a fine scale (from below to between trees).

The strong positive correlation between the concentration of Ca and the litter indices, and the correlations between the concentration of Ca, the litter indices and soil moisture with DCA 2 in Otterstadstølen, indicate a higher content of Ca on dry sites below trees (cf. also Kubin 1983) than on more moist sites between trees. In Otterstadstølen this gradient in Ca concentration is independent of pH and content of nitrogen, which are related to DCA 1. In Øyenskavelen, the strong negative correlation between Ca and moisture and the correlation between moisture (negative) and Ca (positive, but weaker) with DCA 2 indicate higher Ca concentration on dry sites than on moist sites, irrespective of the main gradient in nutrient conditions. The concentration of Ca is thus largely independent of pH and content of nitrogen as in Otterstadstølen. However, in Øyenskavelen no relationship seems to exist between the Ca concentration and gradients in litterfall. In Paulen all of soil moisture, pH and concentrations of Ca and nitrogen vary along DCA 1 (see discussion of the gradient of nutrient conditions, pp. 327-330). In this area, the concentration of Ca is negatively correlated with the three other variables, and positively correlated with litter indices. In Paulen the highest Ca concentrations thus occur on dry sites with low pH.

The results indicate no relationship or a negative correlation between Ca concentrations and (1) pH and nitrogen contents, (2) the main gradient in vegetation (DCA 1, strongly correlated with pH) in spruce forests with an oceanic climate (see p. 329). At the same time, the Ca concentration decreases with increasing soil moisture and/or from below to between trees in these areas. The reasons for these results are likely to be complex. Ca may be supplied to the humus in different ways: (1) directly from precipitation; (2) by leakage from trees and other plants; (3) by decomposition of litter; and (4) by weathering of the subsoil. The relative importance of the different sources for Ca varies regionally and locally. Several points may be relevant: (1) Precipitation, and thus also leakage from trees and understory vegetation, is more important in oceanic than in more continental areas, due to considerably higher annual precipitation and higher concentrations of marine Ca in precipitation, decreasing with the distance from the coast (Varskog 1995). (2) The amount of precipitation reaching the ground is higher in open (and mostly wetter) sites than (in the often drier sites) between trees, as the canopy interception is considerable (C.O. Tamm 1953, Beier et al. 1993). However, the deposition of most cations (Ca included) increases from between to below trees in spruce forests (C.O. Tamm 1953, Rosén & Lundmark-Thelin 1985, Carleton & Kavanagh 1990, Beier et al. 1993), because the gradient in Ca concentrations in throughfall is even stronger. (3) The higher precipitation causes stronger leakage of Ca and other cations from the humus in the humid areas. Open and moist sites in Paulen and Otterstadstølen, and moist sites in Øyenskavelen, are likely to be subjected to strong leakage, as they receive run-off surface water from large catchment areas, and thus have high water throughflow rates. (4) The Ca concentration in humus in more continental areas is more strongly dependent on litter decomposition and the availability of Ca in the humus (cf. Varskog 1995). In such areas the Ca concentration in the humus is also dependent on properties of the subsoil in sites with less thick humus layers and higher pH. The large amounts of litter contribute to increase the availablity of Ca below trees. Reasons why Ca concentrations tend to be positively correlated with other variables of the complex-gradient in nutrient conditions when litter is the most important source of Ca, are discussed in connection with the nutrient gradient (pp. 329-330).

Similar relationships between Ca, litter and soil moisture are observed by R. Økland & Eilertsen (1993) in the Solhomfjell area, also with a humid climate. R. Økland & Eilertsen (1993) explain the correlation between Ca and soil moisture in the Solhomfjell area, and the higher Ca concentrations below trees found by Kubin (1983), by the higher Ca concentrations in throughfall than in incident rain due to leakage from spruce needles. Additional explanations, as discussed above, are, however, likely to be involved. Since investigations of humid boreal spruce forests are few, no conclusion about the relative importance of these and other possible causes can yet be drawn.

Dry sites frequently occur below trees, but very dry sites may also be topographically conditioned. Steep slopes, southerly to westerly aspects and convex terrain forms enhance drainage and give rise to dry sites extending over macro plots or even wider. This is exemplified by the following macro plots: Lundsneset (macro plot No. 7), Grytdalen (macro plot Nos 3 and 6), Rausjømarka (macro plot No. 6), Bringen (macro plot No. 9), Gutulia (macro plot No. 8), Urvatnet (macro plot No. 7) and Granneset (macro plot Nos 3 and 7). The dry sites on southerly to westerly aspects are often also rich in nutrients. Due to high incoming radiation, such sites dry up rapidly.

The concentration of Al is positively correlated with soil moisture in Paulen, Lundsneset, Gutulia and Granneset, and the concentration of Fe is positively correlated with soil moisture in Øyenskavelen and Granneset ($\tau > 0.3$). The strongest correlation between soil moisture and the Al concentration is found in Granneset, where the concentration of Al is also strongly negatively correlated with the litter indices, indicating accumulation of Al on open sites. R. Økland & Eilertsen (1993: 157) claim existence of a positive correlation between concentrations of each of Al and Fe and soil moisture in the Solhomfjell area. However, careful inspection of their data (R. Økland & Eilertsen 1993: Tab. 5) reveals that Fe concentrations are not significantly correlated with soil moisture in Solhomfjell. On the other hand, both of Al and Fe concentrations are correlated with DCA 2, the vegetational gradient interpreted as due to variation in soil moisture (R. Økland & Eilertsen 1993: Tab. 11). R. Økland & Eilertsen (1993) suggest that a positive relationship between soil moisture and concentrations of Al and Fe may be due to less strong leakage of water soluble organic acids with chelatized cations in paludified sites. More investigations are needed to judge the strength and regional validity of relationships between soil moisture and concentrations of Al and Fe.

A positive correlation between soil moisture and Na is observed in Grytdalen, Rausjømarka, Bringen, Otterstadstølen and Gutulia. In Grytdalen and Bringen the correlation is strong ($\tau > 0.4$). This is likely to be due to the combination of high solubility of monovalent ions like Na, and the higher supply by precipitation and surface water to moist than to drier sites (cf. R. Smith 1978).

MAIN GRADIENTS AND VARIATION IN TOTAL DATA SET

Relative importance of environmental and climatic/geographical variation

The variation in the total data set explained exclusively by environmental variables is more than three times the variation explained exclusively by climatic and geographical variables. The total variation explained by environmental variables (which is the sum of the variation exclusively attributed to this set of explanatory variables and the variation shared by both sets, cf. pp. 33-34) is twice the total variation explained by climatic/geographical variables. This demonstrates high importance of local environmental variables for the differentiation of the investigated vegetation. The analysis and interpretation of variation within each reference area demonstrate some variation as to which environmental parameters are related to the main gradients, although DCA 1 is interpreted as related to a complex-gradient in nutrient conditions in nine of ten reference areas. In addition, soil moisture and gradients from below to between trees are important for the vegetational variation in most areas. According to these results the main complex-gradients important for the differentiation of vegetation is largely similar for spruce forests over most of Norway, despite considerable variation as to which variables that make up these gradients. The order of magnitude of variation explained exclusively by environmental variables is about the same as found in spruce forest in Solhomfjell, Gjerstad, southern Norway, by R. Økland & Eilertsen (1994).

Strong correlations exist between gradients in vegetation (DCA axes, ordination of total data set) and climatic/geographical variables, and numerous species show variation in occurrence and abundance along regional gradients. The variation exclusively explained by climatic variables is low, because a major part of the variation in vegetation explained by the climatic/geographical variables is jointly explained by the two sets of explanatory variables. Variation due to differences in climate between reference areas is thus to a large extent reflected in the local environmental variables that make up the complex-gradients important to vegetation. One example is the difference between oceanic areas and more continental areas in the relationship between Ca and pH.

The fraction of variation explained by any set of explanatory variables depends on the number of variables selected and their properties. For instance, several climatic variables other than the seven used in this study might have been chosen. However, effective temperature sum and humidity are likely to be strongly correlated with other climatic variables, such as variables that represent summer temperatures (e.g. mean July temperature) and frost exposure (e.g. mean January temperature). The independent contribution of such supplementary variables to the explained fraction of variation is thus expected to be low.

The large size of the total data set contributes to the high percentage of unexplained variation, just as the amount of random variation in a vegetational data set increases with increasing data set size (cf. T. Smith & Urban 1988, R. Økland et al. 1990, R. Økland & Eilertsen 1994). Vegetational responses to environmental gradients and other conditions acting on finer scales than one square meter (e.g. fine-scale disturbances) also contribute to the unexplained variation (cf. R. Økland & Eilertsen 1994). One example is the microtopographical variation at very fine scales, that provides conditions favourable for many small hepatics and mosses like *Tetraphis pellucida*, and thereby gives rise to a vegetational gradient from the normal forest floor to patches dominated by small bryophytes (cf. Carleton 1990, R. Økland 1994, 1995a). This gradient does not, however, appear in any ordinations in this study (see also R. Økland & Eilertsen 1993). These species often appear as *rural species*, i.e. species with low frequency but wide range along a complex-gradient (cf. Hanski 1991, Collins et al. 1993), in the ordinations (see species distribution plots). The reason for this is likely to be that the main complex-gradients are mostly of low importance for such species, and that the relevant microtopographical features are more or less independent of these main gradients. These species are likely to have a narrower amplitude, restricted to, for example, pockets in the forest floor, and thus being *satellite species* in the terminology of Collins et al. (1993) with respect to relevant complex-gradients.

Interpretation of main gradients in the total data set

The corresponding DCA axes in the two ordinations of the total data set (one without covariables and one with variation exclusively due to climatic/geographical variables removed) are strongly correlated and are also correlated with the same environmental and climatic/geographical variables, demonstrating high similarity between the two ordinations. This is probably due to the relatively high fraction of variation in vegetation that is jointly explained by both sets of explanatory variables, and the low fraction of variation that is explained exclusively by climatic/geographical variables. The main difference between the ordinations is the less strong correlations between climatic/geographical variables and DCA axes after removing variation exclusively due to these variables. As a consequence of the similarity between the two ordinations only one interpretation (that applies to both) will be presented here.

The main complex-gradient corresponds to variation in vegetation (DCA 1) from sites with low pH and low content of nutrients (cations like Ca and Mn) and areas with high mean annual temperature and high effective temperature sum (low DCA 1 scores) to vice versa. This complex-gradient thus combines environmental variation from low to high pH and nutrient content, with variation from reference areas in S and W Norway (Paulen, Lundsneset and Otterstadstølen) to reference areas at higher altitudes and further north (Bringen, Gutulia, Urvatnet and Granneset).

These relationships may partly be due to the differences in bedrock; the Precambrian bedrock prevailing in southern and parts of western Norway is resistant to weathering and gives rise to a soil poor in nutrients. This situation is likely to be maintained because low weathering rates prevent establishment of the more nutrient-demanding species, that would have given rise to a rapidly decomposing and nutrient-rich litter (Hesselman 1926, Mikola 1955, Taylor et al. 1991). Favourable temperatures contribute to increased rate of litter decomposition (Mikola 1960, Kubin 1983, Johansson 1986), but not to an extent that is sufficient for the formation of a more nutrient-rich humus in these areas. High temperatures may also increase the danger of desiccation of the humus layer and thereby contribute to prevent humus formation, and to maintenance of a shallow humus in these areas.

Local conditions may also contribute to accentuate the gradient. The more favourable southwesterly aspects are absent from the investigated vegetation in Paulen, because spruce forest is mainly restricted to northerly and easterly aspects in the southern boreal zone (cf. Sjörs 1963, Ahti et al. 1968). In reference areas further north, such as Gutulia, Urvatnet and Granneset, the bedrock is more favourable, and spruce forest occurs on all aspects. Humus with a higher content of nutrients thus develops readily on favourable aspects, in sloping terrain, sometimes also enhanced by flushing of oxygen-rich water. However, on less favourable aspects in these areas, a thicker humus layer will normally build up, due to the low decomposition rates (cf. van Cleve et al. 1983, Havas & Kubin 1983, Oechel & van Cleve 1986). The influence of the bedrock on the properties of the humus then decreases with time, and humus with a relatively low pH and a low content of nutrients builds up (cf. Romell 1935). This explains the wider amplitude in vegetational response (distribution of plots along DCA 1) to the main complex-gradient, i.e. a stronger gradient in nutrient conditions, in these areas.

Interpretation of the main vegetational gradient in the ordination of the total data set mainly as a response to a complex-gradient in nutrient conditions confirms the results obtained by separate analyses of data from each reference area, although the variables contributing to the complex-gradient vary between reference areas. In addition the ordination of the total data set orders the reference areas along the same gradient.

A second complex-gradient corresponds to variation in vegetation (DCA 2) from sites with high soil moisture and Mg concentrations but low Zn concentrations and areas with high annual precipitation and humidity (low DCA 2 scores), to vice versa. This complex-gradient thus combines environmental variation, e.g. in soil moisture, with regional variation from the humid/oceanic reference areas close to the west or southwest coast (Paulen, Otterstadstølen and Øyenskavelen), to less humid reference areas (e.g. Lundsneset and Bringen), with a high share of dry plots. The presence of a regional component of variation in soil moisture is confirmed by the higher correlation of DCA 2 with soil moisture than with ranked soil moisture. The correlation between soil moisture and DCA 2 might have been even higher if strict comparability of soil moisture values from all reference areas could be obtained. (The results of Tab. 35 do for instance indicate that Paulen and Lundsneset may have been sampled in periods somewhat drier than corresponding to median soil moisture.)

The variation in Mg (and Na, cf. Odland et al. 1990) concentrations is likely to be due to the combination of higher Mg concentrations in precipitation in areas close to the coast (sea-salt effect), and to higher annual precipitation in these areas (cf. Varskog 1995). The strong gradient in mean annual precipitation from the most humid reference areas (Otterstadstølen and Øyenskavelen) to the least humid reference area (Bringen) seems to accentuate the differences in soil moisture between reference areas (cf. Tab. 35).

The nitrogen content is uncorrelated with DCA 1 (ordination of total data set) despite positive correlations between nitrogen and the main gradient in vegetation (DCA 1) in eight of the reference areas when ordinated separately. Nitrogen content is, however, strongly correlated with DCA 3 in both ordinations of the total data set. However, nitrogen content and DCA 1 scores (the ordination of the total data set) are significantly correlated for seven of the reference areas, when calculated separately for each area. The remaining three areas, Paulen, Lundsneset and Otterstadstølen, are the areas most strongly exposed to long-distance airborne pollutants (cf. Statens Forurensningstilsyn 1992). The absence of a relationship between nitrogen concentrations and DCA 1 in the most polluted areas, and the high median value of nitrogen in Paulen and Otterstadstølen relative to pH, may indicate excess of nitrogen in these areas.

The reason why nitrogen content and DCA 1 (ordination of the total data set) are uncorrelated is likely to be that regional differences in nitrogen supply (decreasing from SW towards N and E in Norway), outweigh the increases in nitrogen along this axis in seven of the reference areaas.

The strong correlations between nitrogen content and DCA 3 in ordinations of the total data set are likely to reflect a response to residual variation in nitrogen content, which neither coincides with local variation along the complex-gradient in nutrient conditions, nor can be ascribed to differences in deposition of airborne pollutants.

Regional variation in occurrence and abundance of species

Species with similar responses to main complex-gradients in most reference areas

Similar responses to the main environmental complex-gradients in spruce forests in the different regions of Norway represented by the reference areas are demonstrated for several species. Some species, both vascular plants such as *Geranium sylvaticum*, *Orthilia secunda* and *Viola riviniana*, and bryophytes like *Brachythecium salebrosum* and *Mnium spinosum,* have a relatively sharp distributional limit against sites poor in nutrients. Although these species are more or less absent from the most humid reference areas and from the southernmost reference areas, they may be used as indicators of nutrient-rich sites.

The use of vascular plants as indicators of nutrient-rich sites in spruce forest is well accepted (cf. Kielland-Lund 1981, Fremstad & Elven 1987, Kuusipalo 1985, R. Økland & Eilertsen 1993, 1994, among others). Although the bryophytes also vary along this complex-gradient, as documented in this study (see also Carleton 1990, R. Økland & Eilertsen 1993), the causes of this response remain controversial, due to the ectohydric nature of most bryophytes (Kuusipalo 1988, Brown & Bates 1990, Bates 1992, R. Økland & Eilertsen 1993). Thus Carleton (1990) reports bryophytes to be among the best indicators of nutrient status in his study area, while Kuusipalo (1988) maintains that the effect of soil fertility on bryophytes is indirect and due to the increase in tree density (and reduced light supply to the forest floor) with increasing fertility. R. Økland & Eilertsen (1993) discuss eight hypotheses for the response of bryophytes to a gradient in nutrient conditions. They conclude that several conditions contribute, but do not agree with the view of Kuusipalo (1988). One of the favoured hypotheses is that some direct uptake of nutrients does occur for several species, e.g. *Hylocomium splendens* (showed experimentally by Stålfelt 1937a), many acrocarps and *Brachythecium* spp. and *Plagiothecium* spp. which are closely appressed to the substrate (cf. Bates 1987). Some support for a causal relationship between soil fertility and the occurrence of bryophytes is provided by the distribution plots of species such as *Brachythecium salebrosum* and *Plagiothecium denticulatum*, both avoiding sites with the lowest content of nutrients in all reference areas. Variation in intensity of competition for space, properties of the humus layer, litterfall and several other conditions are likely to contribute to the response of bryophytes (cf. R. Økland & Eilertsen 1993), but field experiments are probably necessary before a conclusion can be drawn.

Species are also used as indicators of soil moisture conditions (cf. R. Økland & Eilertsen 1993). However, several of the species most clearly restricted to moist sites (with sharp limits towards high DCA 2 scores in the ordination of the total data set), like *Blechnum spicant* and *Hypnum callichroum*, are more or less also restricted to the humid reference areas. Such combined responses to regional and local complex-gradients explain the high fraction of joint variation (i.e. the variation explained both by environmental and climatic/geographical variables) in the analyses of total data set. *Sphagnum girgensohnii* has its optimum in moist sites in most reference areas, apparently without any regional differences, but the limit of this species towards medium dry sites is not very sharp.

In all reference areas only few species are restricted to dry sites and/or sites poor in nutrients. Rather than possessing indicators, these sites are characterized by the absence, or lower frequency of species that are more abundant in more moist sites and/or sites more rich in nutrients.

Species with regional variation in response to main complex-gradients

Several species occur with different ranges in the different reference areas in the ordination of the total data, i.e. they have a regional variation in response to the main environmental complex-gradients. According to Boyko's geo-ecological law of distribution (the law of relative constancy of site conditions, Boyko 1947), a species will maintain its amplitude with respect to the environmental conditions which are physiologically important over a wide range of climatic conditions. A species may thus displace its distribution with respect to a measured environmental variable from one climatic region to another, if the measured variable and the condition of primary physiological importance are affected differently by climate.

Species such as *Anemone nemorosa*, *Gymnocarpium dryopteris*, *Oxalis acetoella*, *Rubus saxatilis*, *Phegopteris connectilis* and *Rhytidiadephus squarrosus* agg. occur on sites with lower pH and lower contents of nutrients in the humus layer in the humid reference areas compared to the more continental, where they reach an optimum on sites with higher pH and higher contents of nutrients. However, in the humid reference areas these species are more or less restricted to moist sites. In a literature study of regional variation in coniferous forest vegetation in S Norway, R. Økland & Bendiksen (1985) report similar differences in the distribution of some species in their "submesic series", which largely corresponds to the range of spruce forest vegetation included in this study. Apparently, high soil moisture compensates for lower pH and lower content of nutrients in the humus layer in a humid climate. According to Boyko's law the amount of nutrients available for these species should be the same on the sites where they occur, in the humid reference areas as well as in the more continental. The rate of nutrient availability may, however, differ between the humid and less humid areas. Water flow rates through the humus are considerably higher in humid areas due to higher precipitation, thus contributing to higher supply of nutrients from precipitation (cf. Varskog 1995), and probably also to higher nutrient turnover rates. Thus, in the humid areas the amounts of available nutrients may be higher throughout the year, despite the lower pH and contents of nutrients measured at one point of time. An alternative hypothesis is that different environmental conditions are important for species distributions in humid and more continental areas, and in this case the premises for Boyko's geo-ecological law are not fulfilled. More investigations of vegetation-environment relationships in humid spruce forests are needed to draw any conclusion. Analyses of flow of nutrient fluxes in the soil throughout the year would be particularly useful.

Anemone nemorosa, *Gymnocarpium dryopteris*, *Oxalis acetosella* and *Phegopteris connectilis* are all considered as typical species for the phytososiological entity called "small-fern spruce forest" (Eu-Picetum dryopteridetosum; Kielland-Lund 1981). In this study they are associated either with medium-dry sites with high pH and content of nutrients, or with moist sites with from medium-high to low pH, possibly with relatively high supply of nutrients from precipitation in humid areas. The regional variation in their distributions along main complex-gradients, and the sparse knowledge we have of their physiological needs, imply that these species should not be used as general indicators, neither of particular nutrient conditions nor of particular soil moisture conditions.

Other species with preference for moist sites in the humid areas, such as *Dryopteris expansa* agg., *Barbilophozia floerkei*, *Sphagnum quinquefarium* and *Tritomaria quinquedentata,* have a different pattern of regional variation. These species are present on drier sites in less humid areas and at higher altitudes, particularly in Grytdalen, Bringen and Gutulia. They are less frequent or absent from nutrient-rich sites in most reference areas, and from the driest sites in the humid reference areas and from Lundsneset. These species thus extend their range into locally drier sites towards higher altitudes, while they are restricted to moist sites at lower altitudes. The reason for this is unknown, but may partly be due to lower evapotranspiration at higher altitudes.

CONCLUSION

Both of the ordination methods DCA and LNMDS reveal the main structure in vegetation, but LNMDS is considerably more vulnerable to sample plots with deviating species number, which often act as outliers in the LNMDS ordinations.

The main complex environmental gradients, and the variation in spruce forest vegetation along these gradients, are similar for spruce forests in different parts of Norway, but considerable variation occur in: (1) environmental parameters contributing to the complex-gradient, and (2) species responses to local and regional, environmental and climatic, variation. In nine out of ten reference areas the main complex-gradient important for vegetational structure is the gradient in nutrient conditions, best expressed by pH and nitrogen concentrations. Other contributing parameters, like concentrations of Ca and Mn, vary to some extent between reference areas. In humid areas, the concentration of Ca is related to the gradient in soil moisture and the gradient from below to between trees, which is the secondmost important complex-gradient in most areas, rather than the complex-gradient in nutrient conditions.

The variation in spruce forest vegetation due to local environmental conditions is considerable. Even though some of the variation in vegetation is exclusively due to variation in climatic conditions, a considerable fraction of the variation between and within reference areas can be explained by both of local environmental and regional climatic/geographical parameters.

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