



sommerfeltia

29

R.H. Økland, T. Økland & K. Rydgren

Vegetation-environment relationships of boreal
spruce swamp forests in Østmarka Nature Reserve,
SE Norway

2001



is owned and edited by the botanical departments at the Natural History Museums and Botanical Garden, University of Oslo.

SOMMERFELTIA is named in honour of the eminent Norwegian botanist and clergyman Søren Christian Sommerfelt (1794-1838). The generic name *Sommerfeltia* has been used in (1) the lichens by Flörke 1827, now *Solorina*, (2) Fabaceae by Schumacher 1827, now *Drepanocarpus*, and (3) Asteraceae by Lessing 1832, nom. cons.

SOMMERFELTIA is a series of monographs in plant taxonomy, phytogeography, phytosociology, plant ecology, plant morphology, and evolutionary botany. Authors of Norwegian institutions other than the Natural History Museums and Botanical Garden, University of Oslo pay a page charge of NOK 30, other authors pay NOK 100 per printed page.

SOMMERFELTIA appears at irregular intervals, normally one article per volume.

Editor: Rune Halvorsen Økland.

Editor of this volume: Per Sunding.

Editorial Board: Scientific staff of the botanical departments at the Natural History Museums and Botanical Garden, University of Oslo.

Address: SOMMERFELTIA, Natural History Museums and Botanical Garden, University of Oslo, P.O. Box 1172 Blindern, N-0318 Oslo 5, Norway.

Order: On a standing order (payment on receipt of each volume) SOMMERFELTIA is supplied at 30 % discount.

Separate volumes are supplied at the prices indicated on pages inserted before the back cover.

Copyright: The author(s) & Natural History Museums and Botanical Garden, University of Oslo.



sommerfeltia

29

R.H. Økland, T. Økland & K. Rydgren

**Vegetation-environment relationships of boreal
spruce swamp forests in Østmarka Nature Reserve,
SE Norway**

2001

ISBN 82-7420-043-8

ISSN 0800-6865

Økland, R.H., Økland, T. & Rydgren, K. 2001. Vegetation-environment relationships of boreal spruce swamp forests in Østmarka Nature Reserve, SE Norway. - *Sommerfeltia* 29: 1-190. Oslo. ISBN 82-7420-043-8. ISSN 0800-6865.

Swamp forests dominated by *Picea abies* contribute strongly to the total plant species richness in boreal forests. The variation in species composition and environmental conditions in swamp forests and the relationships of swamp forests to mires and upland forest, have, however, remained insufficiently known. From a preliminary survey of 57 spruce swamp forests, eleven localities were selected to represent the variation in the study area with respect to size and nutrient status, and altitude and position in the landscape. Physiographic and hydrotopographic descriptions were made. A total of 150 1-m² plots were distributed on the localities by a restricted random procedure. In each plot, the abundance of all vascular plants, bryophytes and macrolichens was recorded as frequency in 16 subplots, 53 variables (topographic and geographic, tree influence, water-table, water chemical and physical, and soil chemical and physical) were measured. The gradient (coenocline) structure of vegetation was found by parallel DCA and LNMDS ordinations, interpreted ecologically by analysis of correlations and geostatistical patterns. The two main coenoclines were the same for the full species composition and for vascular plant and cryptogams considered separately. The first gradient was related to soil acidity and nutrient concentrations: plots segregated into relatively poor (and intermediate) and richer swamp forests. Nitrogen availability is considered a decisive factor for species' responses to this gradient. The second gradient was related to depth to the water table and mesotopographic relief of the swamp-forest surface, varying mostly on fine (0.75-1.5 m) scales. Vascular plants segregate along this gradient due to a trade-off between tolerances to waterlogging and drought, bryophyte are influenced by a complex set of factors. Two minor vegetation gradients were also found; one related to microtopography (extending from flat, lawn-like areas dominated by large bryophytes to more strongly sloping sites dominated by small mosses and hepatics; 'pocket species') and one weakly related to the annual water-table amplitude. Relatively strong coenoclines were found that separated entire swamp forests but were uncorrelated with measured variables. These occurred because all swamp forests, notably the richer, had a strong element of uniqueness in species composition, probably because species are recruited from a large species pool during thousands of years. Swamp forest is proposed as a broad term for all peatlands with trees, including mire margin, from which it is essentially indistinguishable. Similarities with, and differences from, open mire and forest on mineral soil are discussed. Some unique features of swamp forests are pointed out. A classification of swamp forests into eight site-types by division of the two main gradients is proposed. Descriptions are provided for the six site-types encountered in the study area. All intact richer swamp forests and a representative selection of poor swamp forests should be protected if maintenance of the biological diversity of (coniferous) forests in general, and swamp forests in particular, is aimed at.

Keywords: Boreal coniferous forests, DCA, Environmental factors, Gradient, LNMDS, Norway, Ordination, Swamp forest, Vegetation.

Rune H. Økland, Botanical Museum, Univ. of Oslo, Sars' gt. 1, N-0562 Oslo, Norway and Norwegian Institute of Land Inventory, P.O. Box 115, N-1430 Ås, Norway; Tonje Økland, Norwegian Institute of Land Inventory; and Knut Rydgren, Department of Biology, Division of Botany and Plant Physiology, University of Oslo, P.O. Box 1045, Blindern, N-0316 Oslo, Norway and Norwegian Institute of Land Inventory (present address: Sogn og Fjordane College, P.O. Box 133, N-6851 Sogndal, Norway).

CONTENTS

INTRODUCTION	6
THE INVESTIGATION AREA	9
MATERIALS AND METHODS	11
THE SAMPLING DESIGN	11
<i>Selection of swamp-forest localities</i>	11
<i>Placement of 1-m² plots</i>	11
RECORDING OF VEGETATION	14
RECORDING OF DESCRIPTIVE CHARACTERISTICS, GEOGRAPHICAL CO-	
ORDINATES AND EXPLANATORY VARIABLES	19
<i>Geographical co-ordinates</i>	19
<i>Physiographic characteristics, microtopography and related variables</i>	19
<i>Tree-layer influence</i>	20
<i>Water-table fluctuations and hydrological characteristics</i>	22
<i>In situ measurements of ground water properties</i>	24
<i>Chemical composition and physical properties of soil</i>	24
RECORDING OF SPECIES RICHNESS VARIABLES	25
STATISTICAL ANALYSES	25
<i>Data manipulation: transformation of variables</i>	25
<i>Relationships between explanatory variables</i>	26
Correlation analysis	26
PCA ordination	26
<i>Ordination of vegetation</i>	26
DCA	27
LNMDS	27
Comparison of ordination results	27
<i>Environmental interpretation of variation in vegetation</i>	28
<i>Variation in species richness and species abundance</i>	28
<i>Analysis of spatial structure</i>	29
CLASSIFICATION OF VEGETATION	30
NOMENCLATURE AND TAXONOMIC NOTES	31
RESULTS	32
PHYSIOGRAPHIC AND HYDROLOGICAL DESCRIPTION OF	
SWAMP-FOREST LOCALITIES	32
DISTRIBUTION OF SPECIES ON THE STUDIED SWAMP-FOREST	
LOCALITIES	42
RELATIONSHIPS BETWEEN EXPLANATORY VARIABLES	46
ORDINATION OF VEGETATION	58
<i>Characteristics of ordinations and comparison of ordination axes</i>	58
DCA ordination of the full data set	58
LNMDS ordination of the reduced data set	60

DCA ordinations of data subsets	62
<i>Relationships between ordination axes and explanatory variables</i>	66
DCA ordination of the full data set	66
LNMDs ordination of the reduced data set	74
DCA ordinations of data subsets	75
<i>Positions of species optima and variation in species abundance along axes in the DCA ordination of the full data set</i>	75
Positions of species optima	112
Variation in species abundances along ordination axes	112
<i>Variation in species density along axes in the DCA ordination of the full data set</i>	122
SPATIAL STRUCTURE	124
<i>Explanatory variables</i>	124
<i>Ordination axes</i>	132
<i>Species density</i>	133
DISCUSSION	134
ENVIRONMENTAL INTERPRETATION OF GRADIENTS IN VEGETATION	134
<i>The main gradient related to soil acidity and nutrient concentrations</i>	134
Environmental interpretation	134
Is there a natural bipartition into 'poor' and 'rich' swamp forests?	138
<i>The second gradient related to depth to the water table</i>	139
<i>The third gradient related to microtopography</i>	142
<i>Existence of a fourth gradient related to the annual water-table amplitude</i>	144
<i>Among swamp-forest locality variation in species composition that is not correlated with explanatory variables</i>	145
THE RELATIONSHIP OF SWAMP FORESTS TO MIRES AND FORESTS	146
SITE-TYPE CLASSIFICATION OF SWAMP FORESTS	148
<i>The soil acidity and nutrient gradient</i>	148
<i>The water-table gradient</i>	148
CONSERVATION OF SPRUCE SWAMP FORESTS – BIODIVERSITY HOT SPOTS IN THE BOREAL CONIFEROUS FOREST LANDSCAPE	150
DESCRIPTION OF SITE TYPES	152
INTRODUCTION	152
THE WET, (MODERATELY) POOR (PW) SITE TYPE	152
THE DRY, (MODERATELY) POOR (PD) SITE TYPE	153
THE WET, INTERMEDIATELY RICH (IW) SITE TYPE	159
THE DRY, INTERMEDIATELY RICH (ID) SITE TYPE	164
THE WET, RICH (RW) SITE TYPE	169
THE DRY, RICH (RD) SITE TYPE	171
ACKNOWLEDGEMENTS	176
REFERENCES	177
APPENDIX	189

INTRODUCTION

Coniferous forests cover extensive areas and make up the key ecological element in the circumboreal zone. A century of forest ecological research has provided a fundament of basic knowledge about the patterns of variation in species composition and ecological conditions in these forests while, at the same time, new gaps of insufficient knowledge have been identified. At present, the status of our knowledge varies considerably, among regions, among forest types and among plant and animal groups.

Identification of the main gradients in forest understorey vegetation on mineral soil and their environmental basis attracted considerable interest in the 1990s (Lahti & Väisänen 1987, Carleton 1990, T. Økland 1990, 1996, Tonteri et al. 1990, R. Økland & Eilertsen 1993, Rydgren 1993, 1996). Few studies (Kenkel 1987, Jeglum 1991, Jeglum & He 1995, Korpela & Reinikainen 1996a) have, however, addressed the variation in species composition and environmental conditions in paludified forests (Hörnberg et al. 1998). This is notably the case for Norway and Sweden (Fremstad 1997, Anonymous 1999).

Swamp forests, in this study used as an inclusive term for wetlands with a more or less closed tree canopy, i.e. with a ground-water table permanently present near or close to the ground surface (R. Økland et al. 2000, 2001), occupy a small fraction of the total forested area in Norway and in Sweden (c. 4% of the productive forest area; Anonymous 1996, 1999). The area occupied by such forests increases eastwards in N Europe (Eurola et al. 1991) where the climate is drier and the topography more even. In spite of low areal importance, swamp forests are rich in red-listed species (Gundersen & Rolstad 1998a, 1998b), contain a large fraction of the species pool of boreal forests (Korpela & Reinikainen 1996b, Ohlson et al. 1997), and stand out as biodiversity hotspots in the otherwise often species-poor boreal forest landscape (Korpela & Reinikainen 1996b, Kuusinen 1996, Ohlson et al. 1997, Hörnberg et al. 1998).

Virgin swamp forests with a high, stagnant water table mostly have low tree productivity. Ditching often improves tree production strongly, turning an impediment into a highly productive site (Hänell 1988, Humphrey & Pluth 1996). Extensive, governmental funded ditching programmes have, however, considerably reduced the already small area covered by swamp forests, and the conflict between economic and conservation interests is now obvious (Ohlson et al. 1997, Hörnberg et al. 1998). Knowledge of the local distribution of species and relationships to variation in environmental factors are important for development of management strategies for the remnant, still intact swamp forests (Sjöberg & Ericson 1997).

The only vegetation gradient known to be important both in mires and forests on mineral soil is the 'poor - rich gradient' i.e. the response(s) to soil acidity, calcium, nitrogen and/or phosphorus concentrations. The presence of prominent poor - rich gradient(s) is well-documented, e.g. for mires by Sjörs (1948, 1950), Malmer (1962a), Daniels (1978), Heikkilä (1987), R. Økland (1989a, 1990b), Singaas (1990), Gignac & Vitt (1990), Glaser et al. (1990), Vitt et al. (1990), Gignac et al. (1991) and Anderson & Davis (1997), for *Salix*-dominated peatlands by Cottrell (1996) and for spruce forests on mineral soil by Eneroth (1931), Tonteri et al. (1990), R. Økland & Eilertsen (1993), Rydgren (1993), and T. Økland (1996). High importance of 'poor - rich gradient(s)' also in swamp forests is demonstrated in several extra-Scandinavian studies (Kenkel 1987, Jeglum 1991, Jeglum & He 1995, Korpela & Reinikainen 1996a, Bedford et al. 1999, Prieditis 1999).

Despite the omnipresence of distinct 'poor - rich direction of variation in species composi-

tion', the ecological basis for this variation, notably the relative importance of soil acidity and concentrations of calcium, nitrogen and other nutrients, has remained obscure. Recently, however, Bridgham et al. (1996) and Wheeler & Proctor (2000) have called for a new paradigm in peatland ecology: replacement of the single vegetation gradient in response to a complex-gradient that includes variation in acid-base status, base cation content and nutrient availability, by a two-gradient representation. According to their view, distinct vegetation gradients occur as responses to: (1) the 'acid, calcium-poor to alkaline, calcareous and carbonate-rich gradient', and (2) the 'low fertility to high fertility gradient' related to N and P availability. Shortage of relevant empirical data does, however, preclude this controversy from being finally settled (R. Økland et al. 2001).

According to Wheeler & Proctor (2000), a 'natural division' of the gradient from acidic to calcareous exists due to the bimodal distribution of calcium concentrations and, notably, water pH, which coincides with distinct vegetation types: 'poor fens' with water pH < 5.0 and 'rich fens' with water pH > 6.0. Wheeler & Proctor (2000) justify their view ecologically by pointing to differences between poor and rich fen waters with respect to buffering mechanism: *Sphagnum*-produced acidity in the former mainly being buffered by humic material, rich-fen waters by a bicarbonate system (Gorham et al. 1984, Kuhry et al. 1993). Empirical support for a natural bipartition of wetlands is, however, still available for a handful of investigated sites only. The radical suggestion of Bridgham et al. (1996) and Wheeler & Proctor (2000) to redefine the bog and fen concepts therefore awaits the results of further studies.

Coniferous swamp forests share with mires a high water-table and water-logged soils, with forests on mineral soils the presence of a tree layer. Thus, in their general appearance, swamp forests are transitional between mire and mineral-soil forests. In mires, the (median) depth to the water table, i.e. the gradient from wetter depressions (hollows and flarks with low depth to the water table) to drier hummocks has been shown to be important for species composition (Sjörs 1948, Malmer 1962a, Slack et al. 1980, Karlin & Bliss 1984, R. Økland 1989a, 1990b, Vitt & Chee 1990, Johnson 1996, Nordbakken 1996a). In mineral-soil forests variation in soil moisture on several scales in space and time affects species composition: variation in danger of extreme drought, conditioned on differences in topography and thickness and type of quaternary deposits, is assumed to be the most important cause of the gradient in conifer forest from spruce forest to pine forest (R. Økland & Eilertsen 1993, 1996), while variation in degree of paludification, dependent on median soil moisture, causes shifts in species composition in spruce- as well as pine-dominated forests (Malmström 1931, R. Økland & Eilertsen 1993, T. Økland 1996, Rydgren 1996). Variation along a hydrotopographical gradient is assumed to be important also in swamp forests, among others for species richness (Glaser et al. 1990, Ehrenfeld 1995b, Hörnberg et al. 1998). Insufficient empirical data are however still available on variation in factors related to water supply and soil moisture in swamp forests.

Local importance, either in mires or in forests on mineral soil, has been demonstrated for three other gradients in vegetation and environmental conditions: (1) The fine-scale gradient in mires from strongly peat-producing patches dominated by *Sphagnum* spp. to patches dominated by hepatics or lichens (Malmer 1962a, R. Økland 1989a, Nordbakken 1996a). (2) The fine-scale gradient in forests on mineral soil; from the 'normal' cryptogamic vegetation of even, planar forest floor dominated by large mosses, to small 'pocket sites' (R. Økland & Bendiksen 1985), e.g. steep ledges underneath stones and adjacent to tree bases, and dead wood (R. Økland 1994, Rydgren et al. 1999). (3) The gradient in forest on mineral soil related to tree-layer structure; from between trees to underneath trees and dense forest stands (R. Økland & Eilertsen 1993, T. Økland 1996, R. Økland et al. 1999). Thus Ehrenfeld (1995a) observed differences in several

important environmental factors between *Sphagnum*-dominated and litter-covered swamp forest hummocks, and demonstrated that surface topographic variation on scales finer than 25 cm may impact species composition of in swamp forests (Ehrenfeld 1995b). Nevertheless, the eventual relevance of the above-mentioned gradients for variation in species composition in swamp forests remains unclear.

Peatlands with trees are often included in mire vegetation studies under the name 'mire margin' (Sjörs 1948, Malmer 1962a, Fransson 1972), while in studies of forest vegetation they are included as 'swamp forest' (e.g. Kielland-Lund 1981). In North American studies, the terms 'treed bogs', 'treed fens' and 'forested wetlands' are commonly encountered (Kenkel 1987, Jeglum & He 1995). Several different classifications of the vegetation of swamp-forests (in a wide, inclusive sense) have been proposed to fill practical needs. In the recent survey of Norwegian vegetation types by Fremstad (1997), a distinction is made between 'mire margin' vegetation as a subcategory of mire vegetation and 'swamp scrub and swamp forest' vegetation as subcategories of forest vegetation. While admitting that the two categories are hardly separable by their floristic composition, Fremstad (1997) stated that 'mire margin vegetation' and 'swamp forest vegetation' can be separated on the basis of soil profile type; mires having a peat soil profile with extensive organic layers while swamp forests have a 'swamp soil profile' with a wet or water-saturated humus layer overlying gleyed mineral soils. A strongly contrasting view on the importance of the gradient from open mire expanse via treed mire margin and paludified forests to forest on mineral soil is expressed by Wheeler & Proctor (2000), who consider the gradient from mire expanse to mire margin 'not in itself clearly definable or ecologically useful'. Empirical data that can be used to settle this controversy hardly exist; demonstrating a strong need for further research on variation in species composition and environmental factors at the transition from mire to forest on mineral soil.

The main aim of the present study is (1) to identify the main gradients in vegetation and environmental factors in a representative sample of SE Norwegian swamp forests, and to discuss these gradients in relation to current theories of vegetation-environment relationships in peatland ecosystems. Secondary aims of this study are (2) to describe the distribution of species' abundances and species richness along the main gradients; and (3) to provide basis for a site-type classification of swamp forests (in a wide sense) that integrates information on variation in species composition, environmental conditions and species density.

THE INVESTIGATION AREA

The study was carried out in Østmarka Nature Reserve, Akershus county, SE Norway (11°01–02'E, 59°49–50'N; Fig. 1). The Nature Reserve was protected by law in 1990 and comprises an area of ca. 12.5 km² (plans exist for expanding the protected area).

The bedrock is of proterozoic age and quartz diorite, tonalite and gneisses of diverse origins are dominating (Sigmond et al. 1984). The main morphological relief type in the area is undulating hills with relative heights of 50–100(–150) m (Abrahamsen et al. 1984). The main direction of hills and valleys is N–S. Minor valleys often dissect the landscape further, resulting in a broken topography with structure on several scales. Below the upper coastal line (about 200–210 m a.s.l.), marine deposits occasionally occur (Holtedahl 1974). Above the upper coastal line the bedrock is usually covered by thin quaternary deposits of glaciofluvial origin (Holmsen 1951, Sigmond et al. 1984).

The area is covered by coniferous forests, which occur interspersed with topogeneous mires, swamp forests and many small lakes. Due to large topographic variation over short distances, the variation in forest types on mineral soil is extensive (T. Økland 1996). Both above- and below-ground traces of forest fires (fire scars and charcoal, respectively) occur. The area has been selectively cut, most recently *c.* 60 years ago (B. Økland 1994). Up to about 1900, Østmarka was affected by summer pasture practising, of which few signs are still left (Senje 1987).

The study area is situated in the southern boreal vegetation zone (lower part), the slightly oceanic section (Moen et al. 1998). Annual mean precipitation (1961–90 normal) at the station Enebakk (*c.* 10 km SE of the area) is 816 mm. Precipitation peaks in autumn and early winter (Førland 1993). Annual mean temperature (1961–90 normal) at the station Hakadal - Bliksrudhagan (30 km NW of the area) is 3.9 °C (Aune 1993). July is the warmest (15.2 °C), January the coldest (–6.8 °C) month. November - March normally have temperatures below 0 °C (Aune 1993). The mean maximum snow depth during the winter is 50–74 cm; the normal duration of snow cover is 100–124 days (Bjørnbæk 1993).

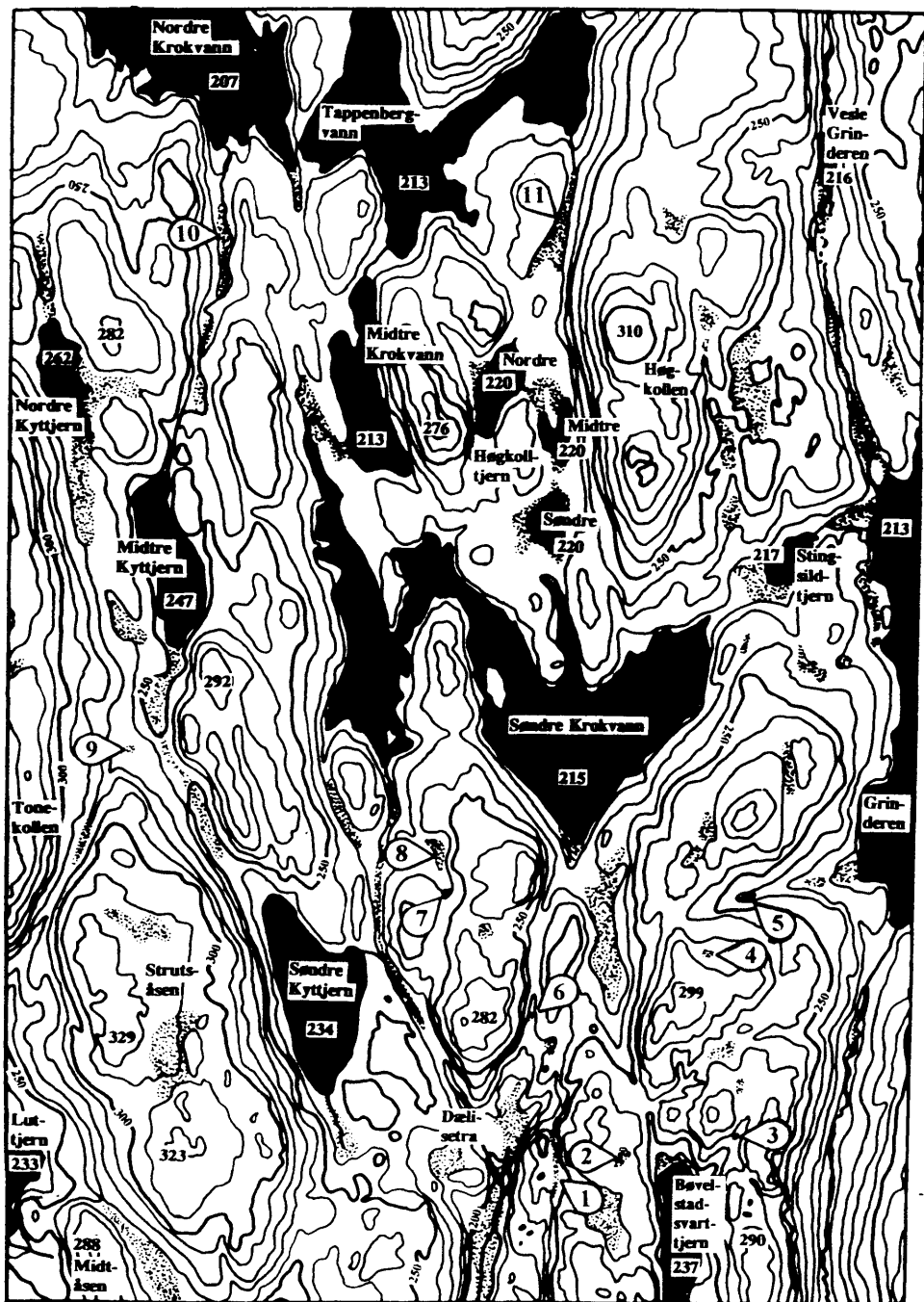


Fig. 1. Map of the investigation area showing swamp-forest localities 1-11.

MATERIALS AND METHODS

Selection of spruce swamp-forest localities, placement of plots and establishment of ground-water wells were performed in 1997. Field work was carried out in 1998 except for some supplementary recordings in 1999.

THE SAMPLING DESIGN

Selection of swamp-forest localities

An inventory of 57 spruce swamp forests in the study area made on 7-8 Oct. 1997 was used as basis for selecting eleven swamp-forest localities (swamp forests or parts of swamp forests) for further study (Tab. 1, Figs 1-2). The selected localities were considered to provide an adequate representation of the variation in swamp forests in the area, with respect to altitude (210-270 m a.s.l.; Tab. 1), size (160-5,860 m²), topographic position (valley bottom, plateau depression, catchment size), nutrient status, maximum peat depth (0.9-7.6 m), presence of springs, brooklets, etc. Swamp forests adjacent to tarns and lakes, with ground-water table fluctuations determined by those of the water basin, and swamp forests with largest length < 20 m, were not considered.

A description of the investigated swamp-forest localities is provided on pp. 00-00.

Placement of 1-m² plots

A restricted random procedure was used for plot placement (T. Økland 1988, R. Økland 1990a).

A *baseline* was placed along the longest axis of each of the 11 selected spruce swamp-forest localities, preferably from outlet to inlet. The baseline's length and compass direction was recorded and the baseline was divided into a minimum of 3 and a maximum of 10 *baseline segments*, the number depending on baseline length (20-30 m: 3; 30-50 m: 4; 50-80 m: 5; 80-120 m: 6; 120-160 m: 7; 170-230 m: 8; 230-300 m: 9; >300 m: 10). Within each baseline segment, the position for a *transverse line* perpendicular to the baseline was drawn at random from exact m positions along the baseline (positions ≤ 2 m from the border to the previous, and ≤ 3 m from the border to the next baseline segment along the baseline were discarded). For each swamp-forest locality, a *local co-ordinate system* was defined by taking the baseline as the ordinate (y axis) and the swamp-forest outlet as the origin. Sketch maps for all swamp-forest localities are given in Fig. 2.

Plots, each 1 m², were allocated to each spruce swamp-forest locality by two different criteria: (1) *Basic plots* were randomly placed along all transverse lines in all localities. The maximum number of basic plots in one swamp-forest locality was set to 20. The number of basic plots per transverse line was determined by transverse-line length (<5 m: 1; 5-10 m: 2; 10-20 m: 3; >20 m: 4). An exception was, however, made for swamp-forest locality No. 11, where the number of basic plots along all transverse lines was set to two to comply with the maximum number criterion. All plots had to be separated by a one-m buffer zone. In each swamp-forest locality, some basic plots were placed at the *highest hummock* to be found in each of a small

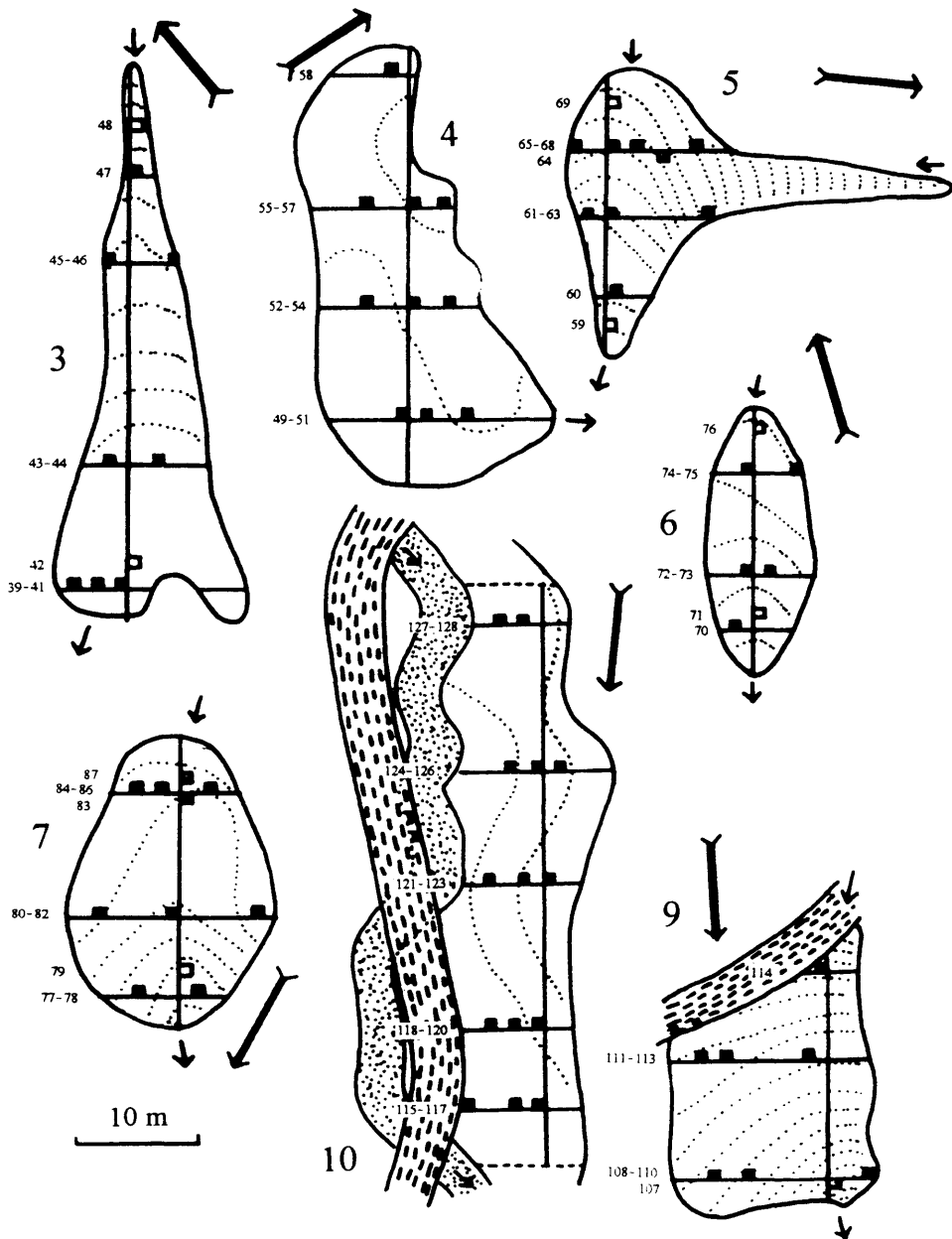
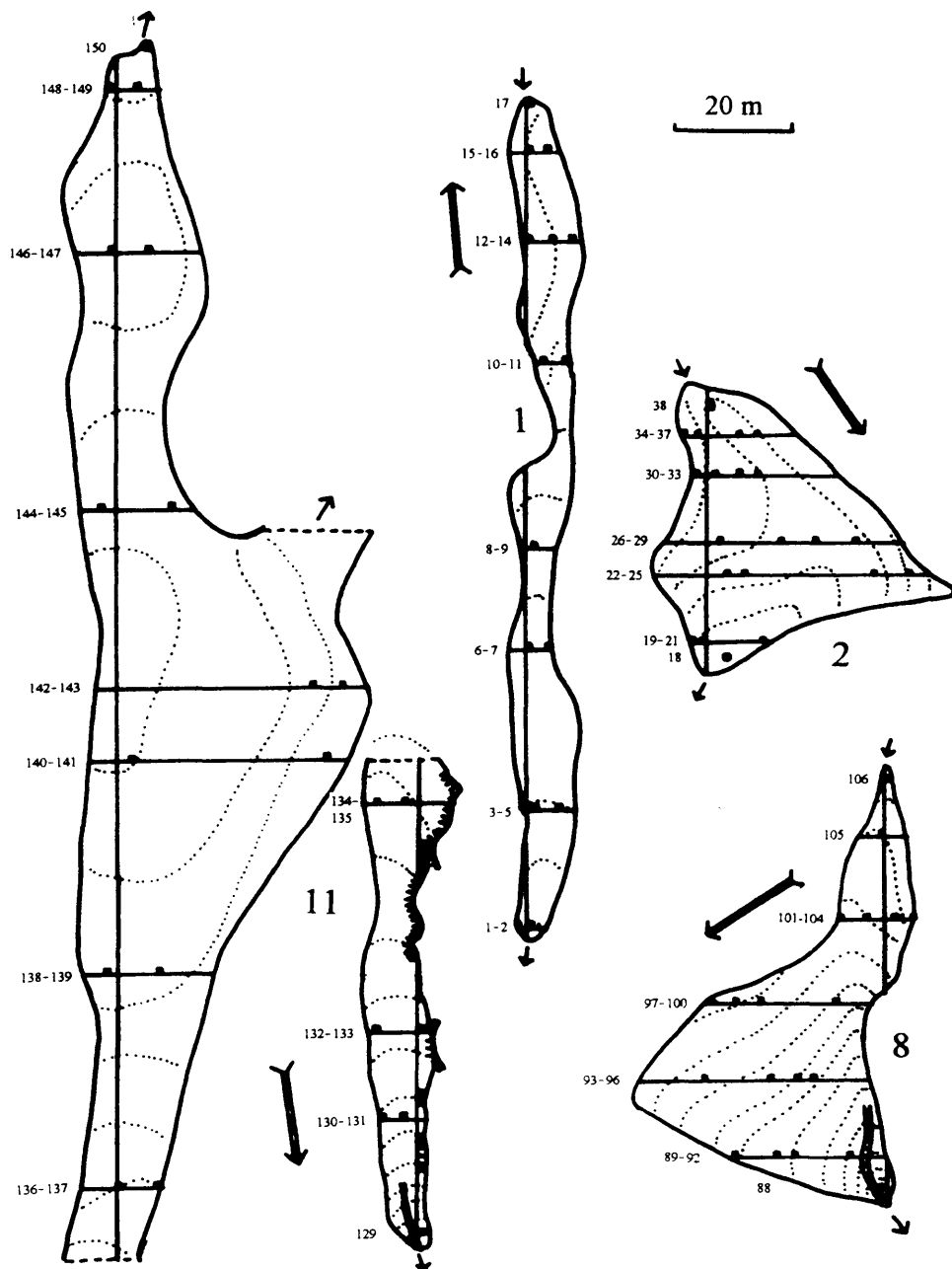


Fig. 2. Maps of investigated swamp-forest localities. The border onto adjacent forest on mineral soil is indicated by continuous line (comb-shaped line indicates escarpments). Brooks and ski tracks are indicated by enclosed shapes with dots and short, broken lines, respectively. Positions of all plots relative to the baseline and the transverse lines are shown. Plots placed by special



criteria are indicated by open squares. The topography of the median ground water table is indicated by dotted lines (contour interval = 0.1 m). Arrows point in northerly direction. Scales: 1: 500 (swamp-forest localities 3-7 and 9-10) and 1: 1,000 (swamp-forest localities 1-2, 8 and 11).

subset of randomly selected transverse lines (1 in swamp-forest localities with ≤ 7 plots; 2 in swamp-forest localities with 8-15 plots; 3 in swamp-forest localities with ≥ 16 plots; one plot along each transverse line). These plots were placed with the mid-point of one side edge at the position along the transverse line with the largest relative height above the adjacent depressions. The lower left corners of all other basic plots were drawn at random from exact m positions along the transverse lines. A plot with lower left corner position (-7,43) in the local co-ordinate system thus extended from positions -7 to -6 m along the abscissa and from 43 to 44 m along the ordinate in the local co-ordinate system. (2) *Additional plots* were allocated to swamp-forest on the basis of three special criteria: (i) presence of a well-defined *outlet*, (ii) presence of a well-defined *inlet*, and (iii) presence of well-defined *springs* and spring-influenced areas. A maximum of one plot could be attributed to each swamp-forest locality on basis of special criteria (i) and (ii). These plots were drawn at random from exact m positions along the baseline, conditioned on being situated 1-5 m from the start and the end of the baseline, respectively. Whenever present, well-defined springs and spring-influenced areas were mapped. Positions for the lower left corners of up to two plots per swamp-forest locality were drawn at random from exact m positions that corresponded to plots fully contained within the mapped areas, and that were separated from basic plots by a 1- m buffer zone.

Plot positions were rejected and replaced by the next available position if including (1) $> 25\%$ of open water (brook or small tarn), bare rock, large logs or stumps, (2) vertical walls higher than 0.25 m , and (3) trees with diameter at breast height (dbh > 15 cm). In each swamp-forest locality, up to 20% of the plots were allowed to include trees taller than 2 m but with dbh < 15 cm , rooted within the plot. After this limit had been reached, plot positions were rejected if containing trees taller than 2 m . Within each swamp-forest locality, plots were placed in the order: (1) additional plots, by criteria (i), (ii), and (iii), (2) basic plots by the largest-hummock criterion, and (3) other basic plots, transverse line by transverse line from low to high y coordinates.

All plots were permanently marked, using subterranean eloxed aluminium tubes.

RECORDING OF VEGETATION

Presence/absence of soil- and peat-dwelling vascular plants (the field layer; including lignified species < 80 cm high), bryophytes and lichens (the bottom layer) was recorded in each of 16 0.0625-m^2 subplots within each of the 150 plots. A species was recorded as present in a subplot when vertical projection of phytomass covered some part of the subplot. Frequency in the 16 subplots was used as a measure of species abundance (T. Økland 1988, R. Økland 1990a).

The following vegetation data sets were subjected to further analysis:

(1) The *full data set*, containing observations of frequency in subplots for 212 species (listed in Appendix 1) in 150 plots. (2) The *reduced data set*, similar to the full data set but with every sixth plot (6, 12, ..., 150) omitted (hence containing 125 plots). The full data set was divided into subsets in two different ways. By plots, a division was made into (3) *Subset A* (poor swamp forests) with 98 plots (and 152 species) and (4) *Subset B* (richer swamp forests) with 52 plots (and 166 species), was made according to plot positions along the first DCA axis in the ordination of the full data set (plots with DCA 1 score < 2.50 were assigned to Subset A; details are given below). By species, a division was made into (5) *Subset C* with 103 vascular plants (the

Tab. 1. Characteristics of investigated swamp forest localities. Direction refers to the direction of the baseline from outlet to inlet. n - number of 1-m² plots. Slope refers to the median ground-water table. Peat depth refers to the deepest peat deposit encountered for any plot in the swamp forest, measured from the median water table. Age is given as ¹⁴C-age of the initial (bottommost) peat deposited in the longest peat core (A.D. 1950 used for present time) and as calibrated age (years B.P.); further see text.

No.	Locality	UTM grid reference	Alt. (m)	Area (m ²)	Direction (°)	n	Slope (°)	Peat depth (m)	¹⁴ C age (yr B.P.)	Calibrated age (yr B.C.)
1	E of Dælisætra	PM 143,337-338	245	1,160	3	17	0-0.4	4.2	8,945±175	9,870±175
2	NW of Bøvelstadsvarttjern	PM 145,338	260	1,390	213	21	0-0.7	6.8	9,100±215	10,110±200
3	NE of Bøvelstadsvarttjern	PM 148,338	265	360	36	10	0-1.5	0.9	2,860±125	3,155±175
4	S of Grasdalen	PM 147,342	270	520	304	10	~0	1.1	3,005±120	3,155±165
5	Grasdalen	PM 148,343	235	250	265	11	3-6	1.2	2,420±115	2,530±190
6	E of Ørnehøgda	PM 143,341	225	160	16	7	1.0-1.5	1.6	5,045±125	5,785±135
7	NE of S Kytetjern	PM 140,343	235	360	151	11	0.5-1.5	2.8	6,595±105	7,455±85
8	SW of S Krok vann	PM 140,344	230	1,590	124	19	0.5-2.0	3.6	8,920±145	9,925±195
9	E of Tonekollidalen	PM 133,347	255	280	186	8	4-5	1.5	3,900±115	4,305±140
10	S of N Krok vann	PM 135,357	210	450	354	14	0(-0.5)	7.6	7,990±135	8,790±220
11	SE of Tappenbergvann	PM 142,358-360	230	5,860	188	22	0-0.7	6.3	7,750±135	8,490±210

Tab. 2. Explanatory variables measured for 1-m² plots and 0.0625-m² subplots: units of measurement, statistical properties, transformation applied (to give skewness = 0), and statistical properties of the transformed variable. S.D. – standard deviation; S.S. – standardized skewness; S.K. – standardized kurtosis. ppt – parts per thousand; ppm – parts per million.

Abbrev.	Variable	Unit of measurement	Summary statistics of untransformed variable			Transformation		Summary statistics of transformed variable		
			Range	S.S.	S.K.	Type	c value	Mean	S.D.	S.K.
Plots (1 m²)										
<i>Topographic and geographic variables</i>										
VertRan	Vertical range of plot	cm	6-53	4.75	1.82	ln(c+x)	1.684	0.526	0.204	-0.93
SlopeAvg	Average slope	° (400-g scale)	3-26	5.69	2.10	ln(c+x)	-1.682	0.594	0.188	-0.21
SlopeMa25	Maximum slope, 25-cm scale	° (400-g scale)	13-65	2.45	-0.85	ln(c+x)	16.47	0.502	0.230	-1.46
SlopeMa10	Maximum slope, 10-cm scale	° (400-g scale)	16-131	0.17	-2.02	ln(c+x)	1162	0.442	0.217	-2.08
DistMSoil	Distance to mineral soil	m	0.0-16.3	7.57	7.49	ln(c+x)	1.579	0.425	0.233	-1.06
SoilDMVL	Soil depth, measured from mean vertical position in the plot	cm	-16-777	5.78	-1.55	ln(c+x)	30.13	0.637	0.184	-0.90
SoilDMWT	As above, from median water table	cm	-22-760	5.73	-1.55	ln(c+x)	43.14	0.597	0.206	-1.55
<i>Tree influence variables</i>										
CanopyCAvg	Canopy coverage, averaged for 4 directions	%	22.0-84.8	-0.34	-1.23	e ^{c_x}	0.00213	0.563	0.229	-1.34
CanopyCMax	As above, maximum recorded for any of 4 directions	%	35.0-100.0	-2.38	0.94	e ^{c_x}	0.01745	0.439	0.203	-1.44
CanopyCMin	As above, minimum recorded for any of 4 directions	%	0.3-78.3	-0.34	0.78	e ^{c_x}	0.00158	0.559	0.225	0.89
TreeInfliv	Tree influence index, based upon living trees	-	0.000-0.826	6.54	2.31	ln(c+x)	0.0146	0.439	0.332	-3.65
TreeInflAll	Tree influence index, based living and standing and fallen dead trees, and stumps	-	0.000-0.976	1.34	-2.67	ln(c+x)	0.921	0.445	0.307	-3.08
Basal area	Basal area, as measured by relascope	-	8-37	-0.98	-1.36	e ^{c_x}	0.0148	0.483	0.219	-1.47
CrownI	Crown index (summed canopy coverage)	-	0-108	1.24	-1.70	ln(c+x)	134.7	0.456	0.238	-2.14
LitterI	Litter index (estimated litterfall)	-	0-22564	13.40	21.22	ln(c+x)	36.14	0.402	0.322	-3.64
<i>Water table variables</i>										
SnowD0423	Snow cover 23 April 1998	cm	0-100	0.87	-4.12	ln(c+x)	70.6	0.488	0.393	-4.20
WatTab100	Depth from average vertical level of bottom-layer surface to lowest measured water table; 100% exceedance level (minimum)	cm	4.7-54.7	4.18	2.39	ln(c+x)	9.93	0.470	0.215	-1.09
WatTab90	As above; 90% exc. level (lower decile)	cm	3.5-45.9	3.99	1.85	ln(c+x)	8.72	0.480	0.215	-1.23
WatTab50	As above; 50% exc. level (median)	cm	1.1-39.5	4.09	1.61	ln(c+x)	8.89	0.492	0.213	-1.18
WatTab10	As above; 10% exc. level (upper decile)	cm	-1.0-35.9	4.22	1.41	ln(c+x)	9.13	0.512	0.208	-1.04

Tab. 2 (continued).

Abbrev.	Variable	Unit of measurement	Summary statistics of untransformed variable			Transformation		Summary statistics of transformed variable		
			Range	S.S.	S.K.	Type	c value	Mean	S.D.	S.K.
Plots (1 m²) (continued)										
<i>Water table variables (continued)</i>										
WatTab0	As above; 0% exc. level (maximum)	cm	-2.8-34.5	3.99	1.41	ln(c+x)	11.58	0.495	0.205	-1.24
WatTabRan	Range of water table fluctuations	cm	2.0-29.5	3.25	0.47	ln(c+x)	8.69	0.470	0.213	-1.03
WatTabHMi	Depth from highest-situated level of bottom-layer surface to minimum water table	cm	9.6-69.5	3.90	1.50	ln(c+x)	8.68	0.498	0.211	-0.94
WatTabLMa	Depth from lowest-situated level of bottom-layer surface to maximum water table	cm	-19.6-13.1	0.19	-1.31	ln(c+x)	421	0.536	0.222	-1.29
<i>Water chemical and physical variables</i>										
WatTem0527	Temperature in tube water 27-28 May 1998	°C	2.4-9.5	0.31	2.06	ln(c+x)	70.4	0.553	0.159	2.13
WatTem0826	Temperature in tube water 26 Aug 1998	°C	7.0-10.0	1.86	-0.65	ln(c+x)	-4.59	0.481	0.208	-1.30
WatpH0527	pH in tube water 27-28 May 1998	-	3.14-6.31	-0.88	-2.48	e ^{cx}	0.162	0.474	0.243	-2.38
WatpH0826	pH in tube water 26 Aug 1998	-	3.33-5.95	-1.43	-2.76	e ^{cx}	0.317	0.461	0.264	-2.63
WatEC0527	Electric conductivity in t. wat. 27-28 May	μS·s ⁻¹	16.8-218.0	11.96	18.08	ln(c+ln(c+x))	-1.936	0.560	0.181	-0.19
WatEC0826	Electric conductivity in tube water 26 Aug	μS·s ⁻¹	21.2-176.3	11.93	16.59	ln(c+ln(c+x))	-2.513	0.522	0.206	-0.55
WatO0527	Dissolved O ₂ in tube water 27-28 May	ppm	0.3-10.0	20.24	68.24	ln(c+ln(c+x))	0.6375	0.552	0.127	5.77
WatO0826	Dissolved O ₂ in tube water 26 Aug	ppm	2.5-11.3	3.78	5.18	ln(c+x)	2.808	0.446	0.180	1.53
<i>Soil chemical and physical variables</i>										
SoilVolWt	Volume weight of sifted soil	g/dm ³	52-396	6.13	2.31	ln(c+x)	-39.17	0.525	0.242	-2.21
SoilLossOI	Loss on ignition	%	41.7-98.4	-8.95	8.54	e ^{cx}	0.106	0.460	0.290	-3.28
SoilpHH ₂ O	Soil pH measured in aqueous suspension	-	3.88-6.00	-0.92	-2.54	e ^{cx}	0.230	0.466	0.261	-2.54
SoilpHCaCl ₂	Soil pH measured in CaCl ₂ suspension	-	2.82-5.54	-0.58	-2.81	e ^{cx}	0.125	0.448	0.258	-2.79
SoilCEC	Cation exchange capacity of soil	mmol/kg soil	199-912	0.88	-0.83	ln(c+x)	1470	0.586	0.194	-0.52
SoilBaSat	Base saturation of soil	%	12.7-99.3	-5.67	1.30	e ^{cx}	0.0529	0.481	0.328	-3.85
HumusC	Extractable carbon in humus (in soil, corrected by division with SoilLossOI)	ppm	2451-8670	3.49	0.89	ln(c+x)	-185.5	0.515	0.197	-0.36
HumusN	Nitrogen in humus (corrected as above)	ppt	8.5-36.7	1.66	-2.53	ln(c+x)	7.79	0.558	0.239	-2.54
HumusP	Extractable phosphorus in humus (corr.)	ppm	3.2-189.0	4.32	-1.30	ln(c+x)	1.834	0.432	0.356	-4.08
HumusS	Extractable sulphur in humus (corr.)	ppm	112-425	5.24	2.21	ln(c+x)	-79.22	0.491	0.223	-1.88
HumusExAc	Extractable acidity (H ⁺) in humus (corr.)	ppm	0-481	5.79	2.20	ln(c+x)	22.95	0.465	0.280	-3.07

Tab. 2 (continued).

Abbrev.	Variable	Unit of measurement	Summary statistics of untransformed variable			Transformation		Summary statistics of transformed variable		
			Range	S.S.	S.K.	Type	c value	Mean	S.D.	S.K.
Plots (1 m²) (continued)										
<i>Soil chemical and physical variables (continued)</i>										
HumusCa	Extractable calcium in humus (corr.)	ppm	582-20455	1.08	-2.10	ln(c+x)	27119	0.481	0.248	-2.38
HumusMg	Extractable magnesium in humus (corr.)	ppm	153-1951	2.37	0.39	ln(c+x)	1173	0.503	0.198	-0.21
HumusK	Extractable potassium in humus (corr.)	ppm	258-1397	4.56	2.77	ln(c+x)	-20.8	0.509	0.190	-0.57
HumusNa	Extractable sodium in humus (corr.)	ppm	101-637	1.80	0.28	ln(c+x)	406.2	0.452	0.191	-0.66
HumusBa	Extractable barium in humus (corr.)	ppm	15.5-438.4	6.17	8.38	ln(c+x)	86.5	0.436	0.180	1.26
HumusFe	Extractable iron in humus (corr.)	ppm	0.6-376.9	17.20	38.05	ln(c+x)	-0.187	0.487	0.216	-0.47
HumusMn	Extractable manganese in humus (corr.)	ppm	19-1820	8.64	10.08	ln(c+x)	6.28	0.471	0.255	-3.24
HumusSr	Extractable strontium in humus (corr.)	ppm	3.0-77.7	0.79	-2.19	ln(c+x)	155	0.546	0.238	-2.04
HumusZn	Extractable zinc in humus (corr.)	ppm	8.7-249.5	14.52	38.23	ln(c+x)	7.17	0.429	0.156	3.83
HumusAl	Extractable aluminium in humus (corr.)	ppm	16-4260	13.09	18.57	ln(c+x)	-10.88	0.554	0.214	-1.19
Subplots (0.0625 m²)										
<i>Topographic variables</i>										
SVertRan	Vertical range of plot	cm	0-42	32.67	35.11	ln(c+x)	1.181	0.540	0.165	-1.75
SSlopeAvg	Average slope	°(400-g scale)	0-44	26.94	20.25	ln(c+x)	2.063	0.548	0.172	-2.69
SSlopeMa25	Maximum slope, 25-cm scale	°(400-g scale)	0-65	20.87	7.92	ln(c+x)	5.168	0.541	0.183	-4.63
<i>Water table variables</i>										
SWatTab100	Depth from average vertical level of bottom-layer surface to lowest measured water table; 100% exceedance level (minimum)	cm	-5.3-70.5	16.34	10.52	ln(c+x)	18.58	0.556	0.144	-0.66
SWatTab50	As above; 50% exc. level (median)	cm	-7.3-56.1	16.72	10.09	ln(c+x)	17.25	0.556	0.141	-0.11
SWatTab0	As above; 0% exc. level (maximum)	cm	-10.0-51.1	18.16	12.74	ln(c+x)	19.00	0.544	0.143	0.03
SWatTabHMi	Depth from highest-situated level of bottom-layer surface to minimum water table	cm	0.0-79.5	17.65	12.66	ln(c+x)	15.61	0.513	0.163	-1.44
SWatTabLMa	Depth from lowest-situated level of bottom-layer surface to maximum water table	cm	-16.0-44.0	13.94	7.91	ln(c+x)	32.13	0.531	0.137	3.03

C-layer) and (6) *Subset D* with 109 cryptogams (the D-layer).

(7) *The subplot data set*, containing presence/absence data for the 212 species in 2400 subplots (16 subplots per plot).

RECORDING OF DESCRIPTIVE CHARACTERISTICS, GEOGRAPHICAL CO-ORDINATES AND EXPLANATORY VARIABLES

Fifty-three explanatory variables – factors supposed to be important for the differentiation of vegetation – were measured or calculated for each of the 150 plots. These variables, making up five groups, were mainly recorded for environmental interpretation of gradients in species composition (ordination axes). Eight variables were recorded also for each of the 2400 subplots. A survey of explanatory variables, with abbreviations and summary statistics, is given in Tab. 2. Some additional physiographic and hydromorphological characteristics were recorded as background information for description of the swamp-forest localities.

We will stress that the term ‘explanatory’ is used in the statistical meaning of the word, to indicate the variables’ potential for explaining variation in other variables or data sets. Thus, no indication whatsoever of potential for biological or ecological causation is thereby implicitly assumed. Causal relationships will be discussed *a posteriori* by taking correlations with the explanatory variables as well as other relevant material into account (Shipley 1999).

Geographical co-ordinates

Co-ordinates for (the lower left corner of) all plots and subplots were determined relative to a co-ordinate system with the W–E direction as abscissa (x axis), the S–N axis as ordinate (y axis) and an origin arbitrarily placed south and west of the investigated swamp-forest localities. Co-ordinates in this co-ordinate system (x_0, y_0) for the origins of the 11 local co-ordinate systems, one for each swamp-forest locality, were determined (with accuracy ± 2 m) from topographic maps scaled 1:10 000. Plot co-ordinates relative to the local co-ordinate system (x_i, y_i) were related to the new origin by the translation formulae

$$x = x_0 + y_i \cdot \cos \alpha + x_i \cdot \sin \alpha \quad (1)$$

$$y = y_0 + y_i \cdot \sin \alpha - x_i \cdot \cos \alpha \quad (2)$$

where $\alpha = 90^\circ - \beta$, and β is the compass direction of the baseline. Co-ordinates for subplots were found by repeated application of the formulae on subplot positions within the plot, using the left corner of the plot as the origin in a plot-scale co-ordinate system.

Physiographic characteristics, microtopography and related variables

For each plot, the relative vertical level (microtopographic level) was recorded for 25 points as follows: The 1-m² steel frame used for recording of vegetation was levelled and the vertical distance from the levelled frame to the ground surface was measured at the corners of all

subplots, i.e. at the 25 intersection points for grid lines spaced 0.25 m and running in both directions, the outermost coinciding with plot edges. For each plot, the 25 measurements were centred, i.e. recalculated to heights z_i ($i = 1, \dots, 25$; the i 's ordered from low to high y co-ordinates and, for measurements with similar y, from low to high x co-ordinates) above the average vertical level, which was used as a reference point for relative vertical positions in the plot. The average vertical level was also calculated for each subplot as the mean of the 4 z_j values for the subplot corners.

The *vertical range* was determined as the difference between the largest and the smallest of the z_i values for each plot (VertRan) or subplot (SVertRan).

In each plot, the difference in vertical level between two points, i and j ,

$$\Delta z_{ij} = |z_i - z_j|, \quad (3)$$

was calculated for all 40 pairs of points spaced 0,25 m; 4 pairs along each of the five grid lines in two directions. For each of the 40 point pairs ij , this difference was converted to slope angle α :

$$\alpha_{ij} = \arctan (\Delta z_{ij}/25) \quad (4)$$

The mean of the 40 α_{ij} values, expressed on a 400-grade scale, was used as the variable *average slope* (SlopeAvg), and the maximum of the 40 α_{ij} values was recorded as *maximum slope on the 25-cm scale* (SlopeMa25).

The slope (mean of four α_{ij} values), and the maximum slope were also calculated for subplots (SSlopeAvg, SSlopeMax).

Maximum inclination in each plot (SlopeMa10) was also measured directly (on a 400°-scale) by a clinometer as the maximum measurable slope between two points in the plot, situated 10 cm apart.

Distance to mineral soil (DistMSoil) was measured as the shortest distance from the centre of each plot to mineral soil adjacent to the swamp forest.

The depth of the soil/peat deposits (from the ground surface down to the mineral soil) was determined at a fixed point 50 cm off the lower left corner of each plot by a peat corer. Soil depth was expressed in two ways, as *soil depth measured from average vertical level in the plot* (SoilDMVL), and as *soil depth measured from the median water table* (SoilDMWT); see below for further explanation.

In the longest peat core from each swamp-forest locality, a sample of the peat was collected just above the border onto mineral soil for radiocarbon dating at the Laboratory for Radiocarbon Dating, NTNU, Trondheim. The age of this sample is reported in two different ways: (1) as ^{14}C age; i.e. as time since the uptake of biogenic carbon ceased, and (2) as calibrated age, found by comparison with measurements of ^{14}C in tree-ring chronologies (method according to Stuiver & Reimer 1993).

Tree-layer influence

All trees - living, dead, and tree stumps - rooted within a 7 × 7-m tree plot around each plot and with the plot in the centre, as well as all larger trees (living, dead and stumps) outside this tree plot, that were sufficiently large and situated close enough to the plot to contribute to the tree

influence index (see below), were mapped. The crown perimeter of all mapped trees was drawn onto a sketch map and their height (h), crown height [ch; 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 (Anonymous 1998a)], diameter at breast height (dbh, in cm) and crown radius [cr; the mean of four measurements (in the four cardinal directions) of the distance from the stem centre to the crown perimeter; in dm], were measured. Crown area (ca) was estimated from the sketch map as the area encircled by the crown perimeter, and crown cover (cc) was estimated as percentage of the crown area covered by living phytomass. For stumps, diameter at stump height (dsh, in cm) was recorded, and converted to diameter at breast height according to Nyysönen (1955):

$$\text{dbh} = 0.75 \cdot \text{dsh} - 0.5 \quad (5)$$

Properties of the tree layer above and adjacent to all plots were used to calculate eight variables (all except the first three were recorded on arbitrary scales without denomination; Tab. 2).

Occurrence of gaps over each plot was measured by a convex, spherical densiometer (Lemmon 1956; Forestry Supplier Inc.) as the percentage of visible sky. Four measurements were performed for each plot, from the mid-points of plot edges, with the instrument directed towards the plot. Measurements were recalculated as percentage of canopy cover. The *average canopy cover* (CanopyCAvg), the *minimum canopy cover* (CanopyCMin) and the *maximum canopy cover* (CanopyCMax) were used as explanatory variables.

The model for *tree influence* developed by R. Økland et al. (1999) on basis of the principles of ecological field theory (Wu et al. 1985, Kuuluvainen & Pukkala 1989, Kuuluvainen et al. 1993) was used to calculate two tree influence indices for each plot, one *based upon living trees* (TreeInfLiv), and one *based upon all trees* (standing and fallen dead trees and stumps, in addition to living trees; TreeInfAll). By this model, the influence of a tree, I_i , at a particular point in space (in this case the plot centre) is assumed to depend on two independent factors: (1) the size of tree i relative to the size of the largest tree in the study area, and (2) the relative distance from the point to the stem centre of tree i . R. Økland et al. (1999) found the following equation for I_i to be optimal in terms of relative amounts of variation in understorey species composition 'explained' in a set of 175 plots from a SE Norwegian boreal spruce forest:

$$I_i = 0.0825 \cdot \text{dbh}^{0.6} \cdot \exp(-0.248 \cdot s^{2.2} \cdot \text{dbh}^{-1.52}) \quad (6)$$

where s is the distance from the plot centre to the centre of the stem of tree i (in dm) and dbh is the diameter of tree i at breast height. For each plot, tree influence is calculated from I_i values for single trees (all n trees with $I_i > 0$) as:

$$\text{TreeInf} = 1 - \prod_{i=1, \dots, n} [1 - I_i] \quad (7)$$

Basal area (BasalArea), a measure of the tree density, was measured at breast height by a relascope using the narrowest slit (relascope factor 1; Fitje & Strand 1973).

A *crown index* (CrownI) was calculated for the 5x5 m extended plot with the plot in its centre (T. Økland 1990, 1996, R. Økland and Eilertsen 1993) as:

$$\text{CrownI} = 0.04 \sum_{i=1, \dots, n} ca_i \cdot cc_i \quad (8)$$

where ca_i is the crown area of tree i within the 25-m² extended plot, cc_i is the crown cover of tree i and the sum is taken over all n trees that cover the extended plot.

A *litter index* (LitterI) was calculated by modifying the index of T. Økland (1990, 1996) and R. Økland & Eilertsen (1993) to incorporate trees rooted within the plot. For each tree i , the area of the crown projection within the 1-m² plot (ca_i) was measured and a line was drawn on the sketch map from the stem centre through the centre of the plot. Four different cases may be distinguished, the first three for trees with the stem centre within the crown perimeter, the fourth for eccentric trees. (1) The line intersects the plot margin at one point within the crown perimeter. (2) The line intersects the plot margin twice within the crown perimeter (relevant for some plots situated below large trees and for trees rooted within plots). (3) The tree crown covers a minor part of the plot only, and the line does not intersect the margin of the plot within the crown perimeter. (4) Eccentric trees (rooted outside the crown perimeter). In case (1) a distance d_i was measured along the line from its point of intersection with the crown perimeter to the point (within the crown perimeter) where it crosses the plot border. In case (2), d_i was measured to the proximal plot border, i.e. the border closest to the stem centre. Furthermore, the crown radius cr_i was measured along the line as the distance from the stem centre to the line's intersection with the crown perimeter. For cases (1) and (2), the contribution of a tree i to the litter index was calculated as:

$$I_i = (d_i/cr_i) \cdot cc_i \cdot ca_i \cdot (h_i - ch_{ki}) \quad (9)$$

The contribution of case (3) trees was by definition set to zero. The contribution of eccentric trees (case 4) was calculated as:

$$I_i = cc_i \cdot ca_i \cdot (h_i - ch_{ki}). \quad (10)$$

The litter index was obtained by summation over all trees i .

Water-table fluctuations and hydrological characteristics

One ground-water well was established in each plot in October 1997. A pit, c. 4 cm in diameter, was made by pressing a steel cylinder with pointed lower end into the peat. The cylinder was removed, and a perforated plastic tube, closed at the lower end, 2 cm in diameter and with walls perforated at 10-cm intervals, was inserted into the pit to a depth of maximum 2 m (less if the peat was shallower). The top of the tube was used as a reference point for measurements of depth to the ground-water table, and for relating water-table measurements to the vertical level of the ground surface.

The depth from the top of the tube to the ground-water table was measured for the first time 1 April 1998 (when many tube wells were still filled with ice). The next recording was made after most wells had become ice-free (23 April). Further recordings were made on average every tenth day until 5 November when ice was again present in most wells. All readings were always made within eight hours. Days without rainfall were chosen for water-table recordings whenever possible. In each plot, the distance from the top of the tube well to the ground-water table was determined (with accuracy 0.5 cm) by simultaneously lowering and gently blowing into a plastic

tube with diameter slightly smaller than that of the well tube, until a bubbling sound was heard (M. Ohlson, pers. comm.).

The 1998 growing season was extraordinarily wet. The smallest average depth from the mean vertical level in plots to the water table, 10.6 cm, was recorded 23 April. The water table sank until the largest average depth, 20.9 cm, was recorded 27 May. From 6 August, the water table remained high for the rest of the growing season (Fig. 3).

The depth from the average vertical level in plot k to the ground water table was treated as a function of time, $w_k(t)$, assuming linear change in depth to the water table between water-table recordings. The cumulative probability distribution function for depth from the average vertical level to the water table ($P_{x,k}$; the probability that the water table exceeded the level w_x) was found for each plot k as

$$P_{x,k}(w_x) = \text{Prob}(w_k(t) < w_x) \quad (11)$$

Negative w_x values were used to denote water tables *above* the ground surface.

Depths from the average vertical level to each of five characteristic water-table levels were calculated for each plot from the cumulative probability distribution functions: (1) *the 100% exceedance level* (WatTab100), i.e. the depth from the average vertical level to the lowest recorded (minimum) water table, (2) *the 90% exceedance level* (WatTab90), i.e. the depth to the level exceeded 90% of the ice-free season, the lower decile in the cumulative depth function, (3) *the 50% exceedance level* (WatTab50), i.e. the depth to the median water table, exceeded half the growing season, (4) *the 10% exceedance level* (WatTab10), i.e. the depth to the level exceeded 10% of the ice-free season, the upper decile in the cumulative depth function, and (5) *the 0% exceedance level* (WatTab0), i.e. the depth to the highest recorded (maximum) water table.

The *range of water-table fluctuations* (WatTabRan) was determined as

$$\text{WatTabRan} = \text{WatTab100} - \text{WatTab0}. \quad (12)$$

The *depth from the highest-situated level of bottom-layer surface to the minimum water table* (WatTabHMi) was calculated as

$$\text{WatTabHMi} = \text{WatTab100} + \max_{i=1,\dots,25} Z_i \quad (13)$$

and the *depth from the lowest-situated level of bottom-layer surface to the maximum water table* (WatTabLMa) was calculated as

$$\text{WatTabLMa} = \text{WatTab0} + \min_{i=1,\dots,25} Z_i, \quad (14)$$

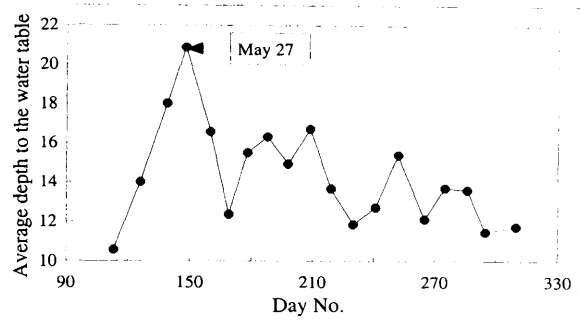


Fig. 3. Fluctuations of the average depth to the water-table in 150 tube wells in spruce swamp forest in Østmarka during the 1998 growing season.

where the z_i denote relative vertical levels (relative to the plot average), positive above and negative below the average level.

Five water-table variables were also recorded for subplots, viz. the 100%, 50% and 0% exceedance levels (SWatTab100, SWatTab50, and SWatTab0), and the depths from the highest-situated vertical level to the minimum water table (SWatTabHMi) and from the lowest-situated vertical level to the maximum water table (SWatTabLMa).

In August 1999, the vertical position of all water-well tube tops relative to fixed points on mineral soil adjacent to each swamp-forest locality were determined with an accuracy of ± 1 cm by an optical levelling instrument. From these measurements, the vertical position of the median water table (relative to the fixed point) was calculated for each plot, and hydrotopographic maps were drawn by assuming that the water table was planar between plots. The slope of the water-table at a particular point x in space was calculated as

$$\text{SlopeWT}(x) = \arctan(v_x/10) \quad (15)$$

where v_x is the difference in relative vertical level between points 5 m downstream and 5 m upstream of x .

Percentage *snow cover* (SnowC0423) was recorded in all plots on 23 April 1998, after a cold period.

In situ measurements of ground water properties

Four properties of the ground water were measured *in situ* on two occasions (27-28 May and 26 August 1998), by insertion of probes into the tube wells (to a depth where the probes were fully covered by water, i.e. c. 1-10 cm below the current water table: (1) *Water temperature* (WatTem0527, WatTem0826), measured by a Taylor probe, (2) *pH* (WatpH0527, WatpH0826), measured by a DigiSense S938-50 instrument with a Cole-Palmer G25 probe, (3) *electric conductivity* (WatECo0527, WatECo0826), measured by a Cole-Palmer 19820-00 probe, and (4) *dissolved O₂* (WatO0527, WatO0826), measured by a Cole-Palmer S946-75 Oxygen meter. Oxygen concentrations were not corrected for variation in temperature, as the temperature amplitude in water at the times of recording was very low compared to the variation in O₂ concentrations.

Chemical composition and physical properties of soil

Samples were collected on 27 August 1998 from the upper 5 cm of the humus layer (in peaty soil from the upper 5 cm below the surface layer of living bryophytes) for determination of loss on ignition and for chemical analyses. Several (5-10) subsamples collected outside the border of each plot were mixed in order to counteract fine-scale spatial variation in humus properties. Samples were brought to the laboratory the day after they were collected and kept frozen until analysis at the Soil Laboratory at the Norwegian Forest Research Institute, Ås (accredited procedures according to Ogner et al. 1991). Samples were dried at 25 °C, ground and sifted (2 mm mesh width).

Loss on ignition (SoilLossOI); in %, was determined by ashing ca. 1 g of sample at 550 °C in a muffle furnace (NISK: method GLT00000.M).

pH was measured in aqueous solution (pH_{H_2O}) and in calcium chloride (pH_{CaCl_2}). One part (by volume) of the dried sample was mixed with 2.5 parts distilled water or 0.01 M $CaCl_2$, the suspension was left overnight, and *pH* was measured the next day (NISK: methods PH-43200.M and PH-43500.M).

Total N (*Tot-N*; wt% of dry soil) was determined by the Kjeldahl method; digestion of the dried sample with H_2SO_4 and determination of N by flow injection analysis (method: FIA41000.M; Ogner et al. 1991). The *percentage of Total-N in humus (N/LI)* was determined from *Tot-N* by multiplication with 100/LossOI.

An NH_4NO_3 solution was used for extracting elements from soil (Stuanes et al. 1984): 10 g dried soil (1.08–6.67 g) was extracted using 50 ml 1 M NH_4NO_3 . The solution was left overnight and filtered. The sediment was washed with NH_4NO_3 until the volume of extract amounted to 250 cm^3 .

Extractable acidity (ExAc; ppm in humus) was determined by endpoint titration to *pH* = 7.00 of the soil extract with 0.05 M NaOH. The volume of titrant (NaOH) was corrected for the blank value of pure extractant (NISK: method TIT43000.M). Exchangeable concentrations of the cations Ca, Mg, K, Na, Ba, Fe, Mn, Sr, Zn, Al as well as C, P and S (NISK: method ICP43000.M), were determined by ICP. All element concentrations were recalculated as ppm of organic matter (from mg/kg dry sample to mg/kg organic matter, by multiplication with 100/SoilLossOI), as recommended by T. Økland (1988).

RECORDING OF SPECIES RICHNESS VARIABLES

Species density (Grace 1999) was recorded at the 1- m^2 plot and the 1/16- m^2 subplot scales as the number of species in each of four primary species groups in each plot.

The total number of species (in each group) recorded over all plots in a given swamp-forest locality was used as a measure of *species richness* at the locality scale.

STATISTICAL ANALYSES

STATGRAPHICS, Version 5.0 (Anonymous 1990) was used for all univariate statistical analyses.

Data manipulation: transformation of variables

For all recorded explanatory variables (Tab. 2), skewness and kurtosis standardised by division with their expected standard deviations, $(6/n)^{0.5}$ and $(24/n)^{0.5}$ respectively (Sokal & Rohlf 1995), were calculated. Homogeneity of variances (homoscedasticity) was achieved by transforming all variables to zero skewness. Three transformation formulae were used:

$$y_{kj}' = e^{c_k \times k_j} \quad (16)$$

$$y_{kj}' = \ln(c_k + x_{kj}) \quad (17)$$

$$y_{kj}' = \ln(c_k + \ln(c_k + x_{kj})) \quad (18)$$

where x_{kj} is the original value of variable k in plot j and c_k is a variable-specific parameter that gives the transformed variable $Y' = \{y_{kj}'\}$ zero skewness. Equation (16) was applied to left-skewed variables (standardised skewness < 0), equation (17) to right-skewed variables. Equation (18) was applied to right-skewed variables for which no c_k could be found by equation (17) that resulted in standardised skewness = 0. After transformation, all variables Y' were ranged to obtain new variables $Y = \{y_{kj}\}$ on a 0-1 scale:

$$y_{kj} = (y_{kj}' - \min(y_{kj}')) / (\max(y_{kj}') - \min(y_{kj}')) \quad (19)$$

Summary statistics for untransformed and transformed variables are given in Tab. 2. Species density variables were transformed using equation (17).

Relationships between explanatory variables

Correlation analysis

Correlations between environmental variables were calculated as Kendall's non-parametric correlation coefficients, τ (Kendall 1938, Sokal & Rohlf 1995). Kendall's τ was chosen because this coefficient only takes the ranks of variables into account. Relationships between variables were visualised graphically as (simplified) plexus diagrams (McIntosh 1978).

PCA ordination

PCA (Principal Component Analysis) ordination (Pearson 1901, ter Braak & Prentice 1988) was applied to a set of 106 variables (a conjugate variable was associated with each of the 53 explanatory variables; Ponge & Ferdy 1997) in 150 plots, using CANOCO, Version 4.0 (ter Braak & Šmilauer 1998). PCA was run on a correlation matrix (on centred and standardised transformed variables and conjugate variables). Correlation biplot scaling of PCA axes was used to optimise the fit of angles between variable vectors to inter-variable correlations.

Ordination of vegetation

Ordination methods were used to summarise the main gradients in vegetation. Because ordination methods may occasionally distort the true gradient structure in a data set (Minchin 1987, Wartenberg et al. 1987, R. Økland 1990a), representatives for both main families of ordination methods were used in parallel, as recommended by R. Økland (1990a, 1996). These families are: (1) multivariate statistical methods that find gradients in species composition (ordination axes) one by one, as the 'hypothetical environmental variable' that maximises the fit of species abundances to an explicit model for species' responses to environmental gradients, and (2) geometrical methods that seek a configuration of plots in an ordination space with fixed number of dimensions, that optimises the rank-order correspondence between sample-plot distances in

the ordination and floristic between-plot dissimilarities. We used DCA (detrended correspondence analysis; Hill 1979, Hill and Gauch 1980) and LNMDS (local, nonmetric multidimensional scaling; Kruskal 1964a, 1964b, Kruskal et al. 1973, Minchin 1987), respectively, because they are the generally most reliable methods within each family of methods (Minchin 1987, R. Økland 1990a).

DCA

DCA was applied to subplot frequency data of the full data set (150 plots) as well as subsets A, B, C and D (see p. 59), by means of CANOCO, Version 4.0 (ter Braak & Šmilauer 1998), debugged according to Oksanen & Minchin (1997). The following options were used: detrending by segments, non-linear rescaling, and proportional down-weighting of species with a frequency lower than the median frequency (as recommended by Eilertsen et al. 1990). Plot scores in ordinations are denoted $x_{\text{Subset, Axis}}$; thus $x_{\text{Full, 1}}$ refers to score with respect to the first DCA axis in the ordination of the full data set and $x_{\text{A, 2}}$ refers to DCA-axis 2 in the ordination of subset A.

Subplots were fit passively into the ordination of the full data set for the purpose of exploring the spatial structure of species composition at within-plot scales. This was accomplished by re-running DCA with the 150 plots of the full data set as active samples (options as above) and the 2400 subplots as passive samples (using presence/absence data, weighted by use of the species' frequencies in the full data set). The subplot scores obtained by passive ordination are the weighted averages of species optima along the ordination axes (R. Økland 1990a).

LNMDS

LNMDS was performed by use of DECODA, Version 2.04 (Minchin 1990). The largest subset to be appropriately handled by the program, the reduced data set (with 125 plots), was used with the following options: dimensionality (number of ordination axes) = 4, dissimilarity measure = percentage dissimilarity (Bray-Curtis), species abundances standardized by division with species maxima [as recommended by Faith et al. (1987)], at least 100 starting configurations, maximum number of iterations = 1000, stress reduction ratio for stopping of the iteration procedure (stress is a measure of correspondence between floristic dissimilarities between plots and the distance between plots in the ordination diagram) = 0.99999 [as recommended by T. Økland (1996)]. 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 (separate runs for each LNMDS axis, with the LNMDS scores as the only constraining variable) in CANOCO, in order to enhance comparability with the corresponding DCA axes (R. Økland 1990a, R. Økland & Eilertsen 1993, T. Økland 1996).

Comparison of ordination results

The degree of correspondence between the four first axes in the DCA ordination of the full data set and the four axes of DCA ordinations of subsets and LNMDS ordination of the reduced data set was assessed by calculating Kendall's rank correlation coefficients between scores of all plots included in both of the compared ordinations.

As a measure of outlier influence, the relative length of the *core* of each axis was calculated according to R. Økland (1990b) as the ratio

$$l_r = (\text{length of shortest interval along axis containing 90\% of the plots})/(\text{gradient length}) \quad (20)$$

Environmental interpretation of variation in vegetation

Ordination axes were interpreted ecologically by calculating Kendall's τ between axes (sample-plot scores) and explanatory variables.

DCA ordination axes (plot scores) were fit passively into the PCA ordination of explanatory variables. DCA axes were thus placed along the PCA axes so that the fit was optimized between (1) angles between DCA axis and explanatory variables in the PCA ordination, and (2) the correlations between axes and variables. The DCA axes were then generally placed together with the explanatory variables with which they were most strongly correlated.

For selected explanatory variables and ordination axes, observed explanatory variable values were overlaid on plot positions in the ordination. The resulting diagrams were used to make isoline diagrams for environmental variables. Isolines were constructed by block kriging interpolation using GS+, Version 3.1 for Windows (Anonymous 1998b). Plot scores in the two-dimensional space spanned by ordination axes 1 and 2 were used as geographic co-ordinates and an isotropic semivariance analysis of the transformed explanatory variable was performed, using an active lag of 4 S.D. units and steps of 0.25 S.D. units. Interpolation was performed from a grid with mesh width 0.25 S.D. units along both ordination axes. Goodness-of-fit of the three-dimensional surface (and the isolines) was assessed by a cross-validation, jackknifing procedure (Anonymous 1998b) whereby r^2 was calculated between the original and the predicted values for the variable. Interpolations were made by use of 8 as well as 16 neighbouring plots and the one with the highest goodness-of-fit was used further. After analysis, the fitted values for the explanatory variable were de-ranged and back-transformed to the original scale. De-ranging was performed by solving (19) for y_{kj}' , and back-transformation was performed by solving (16)–(18) for x_{kj} , viz.

$$y_{kj}' = e^{c_k z_{kj}}; z_{kj} = \ln(y_{kj}')/c_k \quad (21)$$

$$y_{kj}' = \ln(c_k + z_{kj}); z_{kj} = e^{y_{kj}'} - c_k \quad (22)$$

$$y_{kj}' = \ln[c_k + \ln(c_k + x_{kj})]; z_{kj} = e^{e^{y_{kj}'} - c_k} - c_k \quad (23)$$

Isolines were hand-fitted to de-ranged and back-transformed interpolated values.

Variation in species abundance and species richness

For all 139 species occurring in 5 or more of the 150 1-m² plots, species abundance (subplot frequency) was overlaid on plots' positions along DCA-axes 1 and 2. Similar diagrams were also made for selected species along DCA axes 1 and 4. Species distributions along axes were characterized by:

Range: The range of DCA scores for plots containing the species.

Optimum: The position along an axis at which the species' highest constancy was

Optimum range: The interval along an axis where the species' constancy was more than 50% of the constancy at optimum.

Species were classified to groups of similar distribution along each of DCA axes 1 and 2 by visual inspection of species abundance diagrams. A species' distribution was assessed on basis of occurrence in each of four intervals along DCA-axis 1 (0.00- 1.25 S.D. units, 1.25- 2.50 S.D., 2.50- 3.56 S.D., 3.56- 4.63 S.D.) and four intervals along DCA-axis 2 (0.00-0.87 S.D. units, 0.87- 1.75 S.D., 1.75- 2.70 S.D., 2.70- 3.64 S.D.).

Species density variables were related to ordination axes (sample-plot scores) by calculation of Kendall's τ .

Analysis of spatial structure

We used geostatistical methods (Rossi et al. 1992) to examine the spatial structure of explanatory variables, ordination axes and species density variables (all except ordination axes after transformation; Tab. 2, pp. 25-26). Data subset B were exempted from analysis because too many lag intervals had too low a number of observation pairs to allow reliable interpretation. All plot and subplot pairs situated less than 2048 m apart were grouped into distance classes d_i (properties given in Tab. 3); $[2^{i-4}, 2^{i-3}]$, $i = 1, \dots, 14$ (classes 1-4 relevant for subplots only).

Assuming that all variables and ordination axes had patterns of spatial variability that were

Tab. 3. Properties of distance-class partitioning for the four data sets subjected to analysis of spatial patterns.

Dist. class No.	Upper limit (m)	Data set							
		Subplots (n = 2400)		Full data set Subsets C, D (n = 150)		Reduced data set (n = 125)		Subset A (n = 98)	
Mean		No. of pairs	Mean dist. (m)	No. of pairs	Mean dist. (m)	No. of pairs	Mean dist. (m)	No. of pairs	Mean dist. (m)
	1	0.25	1905	0.25					
2	0.5	5980	0.36						
3	1	9815	0.68						
4	2	2762	1.62						
5	4	12846	2.92	58	2.71	40	2.71	29	2.77
6	8	25308	6.10	99	6.00	55	6.02	54	6.19
7	16	54515	11.96	211	11.85	144	11.81	123	12.00
8	32	73563	23.50	292	23.44	204	23.20	217	23.96
9	64	65329	44.82	253	44.80	157	44.94	156	43.71
10	128	100404	100.04	393	100.03	249	100.21	135	95.78
11	256	157653	192.27	619	192.75	390	193.23	350	177.43
12	512	235986	399.09	922	399.92	641	403.60	74	451.80
13	1024	926462	709.81	3616	710.21	2432	707.90	1383	712.11
14	2048	834247	1591.14	3257	1591.06	1597	1587.49	1204	1652.09

direction independent (isotropic), with mean and variance that did not vary with location in space (ergodic), we calculated ergodic, isotropic semivariance (γ_i ; half the variance of differences between plot pairs) for every distance class d_i . The semivariance was standardized by division with sample variance in order to enhance comparability among variables (Rossi et al. 1992). Calculations were made by use of GS+, Version 3.1 for Windows (Anonymous 1998b). As an aid in the interpretation of spatial patterns, we also calculated the Hausdorff-Besicovitch fractal dimension D as a measure of the degree of spatial structuring, for consecutive distance classes (Ohlson & R. Økland 1998, Skringo & R. Økland 1998). D was calculated from double logarithmic semivariograms (Palmer 1988) by the equation:

$$\begin{aligned} D_i &= 3 - 0.5 \cdot [\ln(\gamma_{i+1}) - \ln(\gamma_i)] / [\ln(i+1) - \ln(i)] \\ D_i &= 3 - 0.7213 \cdot [\ln(\gamma_{i+1}) - \ln(\gamma_i)] \end{aligned} \quad (24)$$

$D = 2.00$ indicates maximal spatial structure, i.e. that the value of the variable at a particular point p in space can be calculated from the point's geographical coordinates and the known value of the variable in a point a given distance $d \in d_i, d_{i+1}$ away from p . $D = 3.00$ indicates no spatial structuring (no increase in predictability from knowledge of the position of p and the value at a point a distance d away from p). $D > 3.00$ occurs when the semivariance decreases with increasing distance (from interval d_i to d_{i+1}); e.g. in periodic variables (Palmer 1988, Legendre 1993) for which the periodicity roughly coincides with the upper limit of the distance interval(s) for which $D > 3$.

A variable is spatially structured in a distance interval d_i if $\gamma(2^{i-4}) \gg \gamma(2^{i-3})$. No objective criteria do, however, exist by which the standardized semivariance as a function of distance can be used to determine the degree and *range* (i.e. upper limit of spatial structuring; Palmer 1988) of spatially dependent variation. Inference about spatial structure, notably the existence of a range, was therefore based upon inspection of the shape of semivariograms; the variation of γ as a function of lag distance (among others as summarized in the D statistic).

Interpretation of vegetational gradients by means of the explanatory variables was made by emphasising strength of correlations as well as similarity of spatial structure.

CLASSIFICATION OF VEGETATION

Classification of vegetation was performed *a posteriori*, i.e. by use of interpreted ordination results, by *detrended correspondence analysis space partitioning* (DCASP; Gauch 1982, R. Økland 1990a). The DCA ordination space was considered a good approximation for the *ecological space* (Whittaker 1967), i.e. the space with the main *ecoclines* (Whittaker 1960) as axes, because the DCA axes had been corroborated by LNMDS ordination and carefully interpreted by use of independent environmental explanatory variables. We partitioned the DCA ordination space by dividing the DCA axes, one by one, into segments. In this way, the multidimensional pattern of variation along ecoclines was converted into a reticulate, non-hierarchic classification (Tuomikoski 1942) with *site types* representing a simultaneous classification of vegetation and the environment (cf. Cajander 1926, Eneroth 1931, Whittaker 1962, R. Økland & Bendiksen 1985, R. Økland & Eilertsen 1993).

The site-types were named by the environmental conditions that characterised them.

All 150 plots were used to describe the site types (see the concluding, descriptive part on pp. 152–175). One vegetation table was compiled for each site-type. Constancy (frequency in the set of plots classified to the site type) and mean frequency in subplots was given for each species in each site type.

A majority of plots were placed at random (p. 11–14). Because inhomogeneous plots, with respect to species composition and/or environmental conditions, therefore occurred, species are expected to occur over a range of recorded (plot mean) environmental conditions that stretches beyond their habitat niche (Palmer & Dixon 1990). Furthermore, species may occasionally occur in plots classified by the dominant site-type to be outside the species' normal range. Inhomogeneous plots decreases the floristic distinctness of adjacent site-types.

NOMENCLATURE AND TAXONOMIC NOTES

The nomenclature follows Lid & Lid (1994), Frisvoll et al. (1995) and Krog et al. (1994) except for the genus *Polytrichastrum* G.L.Sm., which is not recognized as distinct from *Polytrichum* Hedw. Several groups of related taxa were treated collectively: *Betula* spp., comprising *B. pendula* Roth, *B. pubescens* Ehrh. and eventual hybrids; *Alchemilla* spp.; *Dryopteris expansa* agg., that may include *D. expansa* (C.Presl.) Fraser-Jenkins & Jermy, *D. dilatata* (Hoffm.) A.Gray, and *D. carthusiana* (Vill.) Fuchs.; *Hieracium* sp., probably comprising taxa belonging to the *Sylvatica* and *Vulgata* sections of subg. *Hieracium*; *Brachythecium rutabulum* agg, which includes *B. rivulare* Schimp. that was not always possible to distinguish with certainty from *B. rutabulum* (Hedw.) Schimp.; *Warnstorfia exannulata* agg., that includes *W. exannulata* (Schimp.) Loeske and that may also include *W. procera* (Ren. & H. Arn.) Tuom.; *Cephaloziella* sp.; *Lophozia ventricosa* agg., that includes *L. silvicola* Buch and *L. ventricosa* (Dicks.) Dum. and that may also include *L. longiflora* (Nees) Schiffn.; *Pellia* spp. that includes *P. epiphylla* (L.) Corda and *P. neesiana* (Nees) Limpr., not possible to separate in the sterile state; and *Cladonia chlorophaea* agg., that 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.

RESULTS

PHYSIOGRAPHIC AND HYDROLOGICAL DESCRIPTION OF SWAMP-FOREST LOCALITIES

Positions of swamp-forest localities in the forest landscape are shown in Fig. 1. Their hydrotopography appears from Fig. 2 and Tab. 1.

Swamp-forest locality 1 was situated in the bottom of a narrow (3–15 m wide and 150 m long) grove, separating a smaller from a larger hilltop. The swamp forest was made up by a northern and a southern part, both with peat depths up to c. 4 m, that were separated by a narrow strip of shallower peat. Swamp forest 1 had thus arose by coalescence of two formerly separate swamp forests. The onset of peat accumulation occurred almost simultaneously in the two basins (calibrated ages of c. 9,740 and 9,870 yrs B.P.). The swamp forest was almost level (slope < 0.4°), with a vertical difference of 0.8 m between the northern inlet and the outlet farthest south. The southern and central parts of the swamp forest were water-filled for most of the 1998 growing season, a small permanent brooklet occurred close to the outlet. The northern part was well stocked with *Picea abies*, the southern part was more open, with scattered *Picea abies*, *Betula* spp., *Alnus incana* and *A. glutinosa*.

Swamp-forest locality 2 was situated on the northeastern side of a hilltop in a broad, bowl-shaped, up to 6.8 m deep depression surrounded by low ridges. The onset of peat accumulation was dated to 10,110 yrs B.P. (Tab. 1). The water-table was almost level in central part of this swamp forest and gently sloping (up to 0.7°) near the outlet. The southern part of the swamp forest, close to the inlet, was very wet. The central part of this swamp forest was generally drier than the marginal parts. A seasonal brooklet occurred near the outlet. *Betula* spp. and *Picea abies* dominated in the tree layer; with scattered occurrences of *Alnus glutinosa*.

Swamp-forest locality 3 was situated on a nearly level terrace in an open, southwest-facing, V-shaped valley. The peat was shallow, only up to 0.9 m deep. Several large boulder stones (rising to 1.5 m above the peat surface) were distributed over the southern part of the swamp forest. The onset of peat accumulation was dated to 3,155 yrs B.P. The wet, central southern part of this swamp forest (near the outlet) was almost level, while the peripheral and northern parts were drier, with slopes up to 1.5°. The central southern part lacked a tree layer due to root upheaval of several large *Picea abies* trees. The tree layer consisted of *Picea abies* with scattered *Alnus incana*.

Swamp-forest locality 4 was situated on a small terrace (a shallow depression with maximum depth of 1.1 m) in a north-facing, gently sloping hillside, below a 3–5 m high vertical wall. The onset of peat accumulation was dated to 3,155 yrs B.P. The swamp forest had one distinct outlet, distinct inlets were lacking. This moderately wet to relatively dry swamp forest was stocked with *Picea abies* more or less the size of trees in the surrounding forest.

Swamp-forest locality 5 was situated in a gently sloping, open, east-facing valley, where a minor valley leads from the north into the main valley. The shallow, up to 1.2 m deep peat surface was frequently broken by the occurrence of boulder stones. The onset of peat accumulation was dated to 2,600 yrs B.P. A well-delimited spring area of c. 12 m² occurred close to the inlet of this swamp forest near its southwestern border onto mineral soil. An indistinct seasonal brooklet ran the length of the distinctly sloping (3–4°) swamp forest from inlet to outlet.

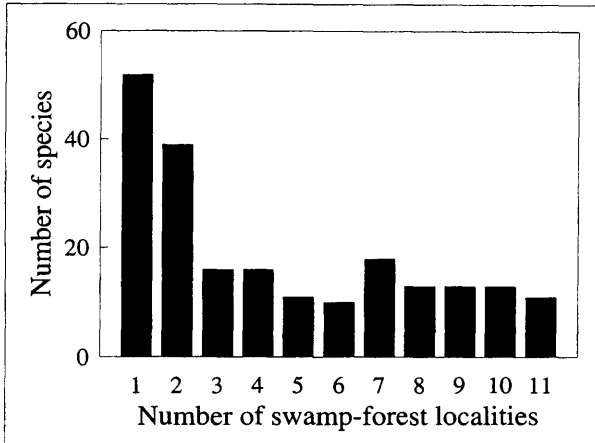


Fig. 4. The distribution of species on swamp-forest localities: the number of species recorded in each given number of swamp-forest localities (presence in a swamp-forest locality is based upon occurrence in at least one 1-m² plot in that locality).

depression up to 2.8 m deep. The time-point for onset of peat accumulation was dated to 7,455 yrs B.P. No distinct inlet occurred, but a well-delimited spring area, 20 m², occurred close to this swamp forest's southeastern margin. An open, wet central part connected the very gently sloping spring area and the outlet; slopes of 0.5–1.5° were encountered. Discharge was effected by a seasonal brooklet, emptying into swamp-forest locality 8. The marginal parts of this swamp forest was stocked with large *Picea abies* trees and scattered *Alnus glutinosa*.

Swamp-forest locality 8 was situated in a depression that to the east was bordered by a steep ledge and that otherwise passed into gentle slopes. The depression which was mostly 2–3 m, maximally 3.6 m deep. The onset of peat accumulation was dated to 9,925 yrs B.P. Swamp forest 8 was gently sloping from the inlet farthest southeast (discharge of water from the swamp-forest 7 brooklet) towards the outlet in its northwestern end. A wet soak ran the length of the western margin from inlet to outlet. Occasional water-filled depressions occurred along this soak, eventually amalgamating to form a distinct brooklet towards the outlet. Towards

Most of swamp forest 5 was wet, only the northern part was drier. *Picea abies* was the dominant tree species, *Alnus incana* occurred occasionally.

Swamp-forest locality 6 was the smallest of the investigated swamp forests, situated on a terrace in a deep, U-shaped, south-facing valley. The swamp forest covered a shallow depression, up to 1.6 m deep, where the onset of peat accumulation was dated to 5,785 yrs B.P. The water table in this swamp forest was gently sloping (1.0–1.5°), wet along the central axis, drier at margins, and with a seasonal brooklet emerging near the outlet. The centre was open, the margins were dominated by *Picea abies* and *Alnus incana*.

Swamp-forest locality 7 was situated in a U-shaped, N-facing grove below a steep hillside where it covers a

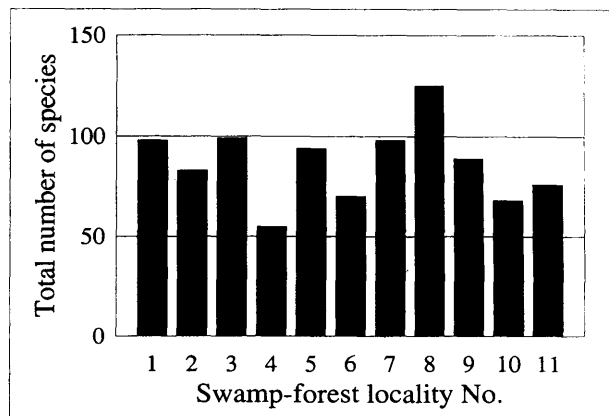
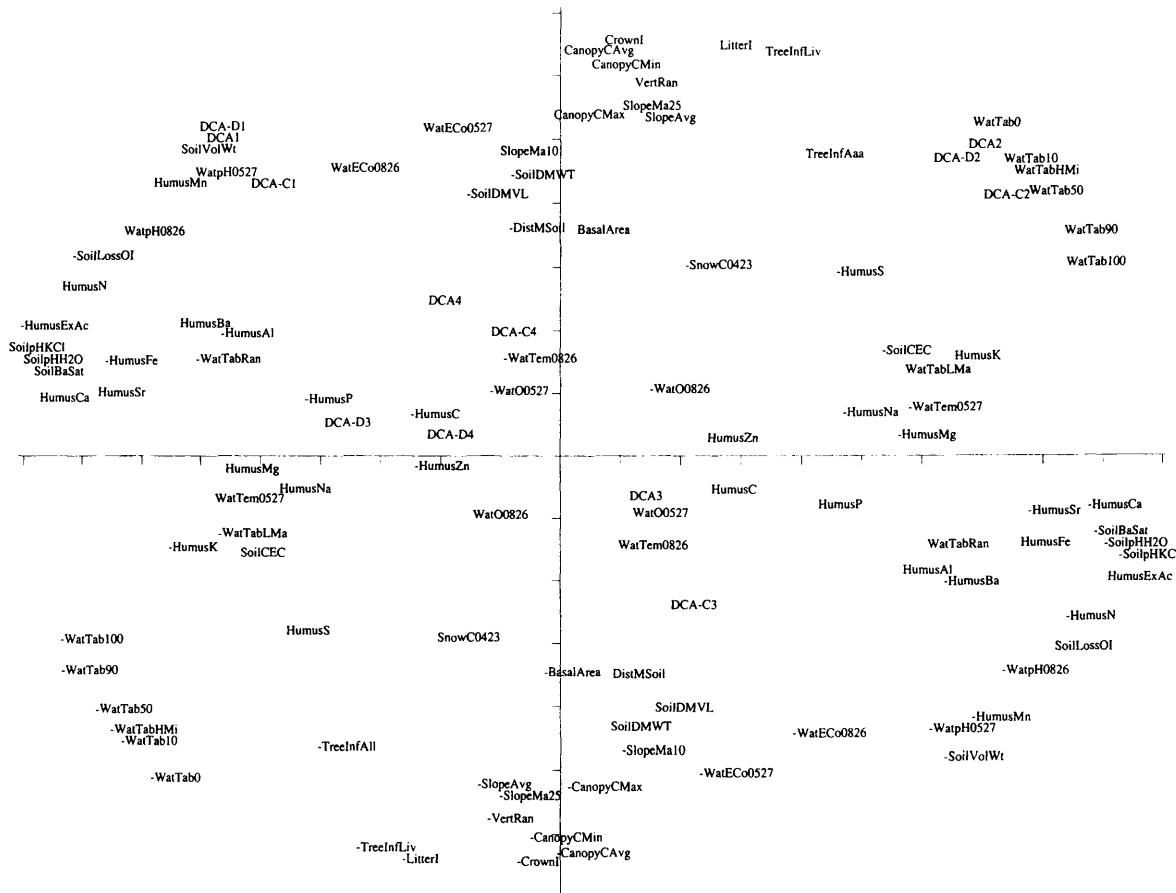


Fig. 5. Total number of species recorded in 1-m² plots in each of the eleven investigated swamp-forest localities.



Tab. 4. Species constancy (frequency in the 1-m² plots) and mean subplot frequency (given as exponent) in each of the 11 studied swamp forest localities, as well as total number of plots (out of 150) in which each species was recorded. Species occurring in 4 plots or less are listed at the bottom of the table. Swamp-forest localities are, for convenience, ordered by increasing mean soil pH. Four groups of species are indicated: preference for low-pH swamp-forest localities; preference for high-pH localities, ubiquitously distributed species and sparsely occurring species.

Species	Swamp forest No. (mean pH)											No. of plots
	4 (4.15)	2 (4.57)	11 (4.57)	1 (4.80)	8 (5.04)	10 (5.18)	6 (5.35)	3 (5.43)	5 (5.43)	7 (5.44)	9 (5.68)	
<i>Vaccinium myrtillus</i>	90 ¹³	76 ¹¹	82 ¹	53 ⁹	68 ⁹	43 ⁷	14 ³	60 ⁵	36 ⁴	27 ¹⁴	63 ⁸	90
<i>Vaccinium vitis-idaea</i>	80 ⁸	62 ⁹	68 ⁹	47 ⁶	68 ⁹	79 ⁷	-	20 ³	-	27 ⁴	38 ²	76
<i>Dactylorhiza maculata</i>	10 ¹	10 ¹	-	6 ²	5 ¹	-	-	-	-	-	-	5
<i>Lycopodium annotinum</i>	20 ⁴	48 ⁸	18 ⁴	12 ⁵	26 ⁷	14 ¹¹	-	40 ⁵	-	36 ¹⁰	13 ¹	34
<i>Melampyrum pratense</i>	-	14 ²	5 ¹	6 ⁶	5 ³	-	-	-	-	-	-	6
<i>Menyanthes trifoliata</i>	-	71 ⁹	32 ¹⁰	24 ⁷	42 ⁶	79 ¹³	-	-	-	-	-	45
<i>Potentilla palustris</i>	10 ¹	33 ³	14 ³	47 ⁸	26 ⁹	86 ⁹	-	-	-	-	-	36
<i>Rubus chamaemorus</i>	30 ⁵	57 ¹¹	23 ³	-	21 ⁷	36 ⁷	-	-	-	-	-	29
<i>Carex canescens</i>	20 ⁵	48 ⁹	41 ⁷	71 ⁹	37 ⁹	50 ⁸	-	20 ⁵	27 ²	73 ¹⁰	50 ⁷	64
<i>Carex echinata</i>	-	67 ⁶	23 ⁹	35 ⁹	53 ⁷	29 ⁴	-	30 ⁴	9 ¹⁰	36 ¹⁰	38 ³	50
<i>Carex rostrata</i>	-	62 ⁹	9 ¹⁰	6 ³	-	29 ¹²	-	-	-	9 ²	-	21
<i>Deschampsia flexuosa</i>	40 ⁹	10 ¹³	23 ⁷	18 ²	21 ⁸	29 ⁴	-	10 ⁷	-	-	-	23
<i>Eriophorum angustifolium</i>	-	10 ⁶	5 ¹⁵	18 ¹⁰	16 ¹²	7 ¹⁰	-	-	-	-	-	10
<i>Eriophorum vaginatum</i>	-	5 ¹³	-	-	42 ⁹	14 ¹⁰	-	-	-	-	-	11
<i>Aulacomnium palustre</i>	-	43 ⁵	32 ⁸	-	32 ⁷	14 ³	-	10 ¹	-	9 ²	-	26
<i>Pleurozium schreberi</i>	70 ¹⁰	38 ⁶	45 ⁴	29 ⁷	37 ³	57 ⁶	-	50 ⁴	18 ²	36 ⁷	38 ⁵	59
<i>Pohlia nutans</i>	-	10 ²	5 ³	-	5 ¹	7 ¹	-	-	-	-	-	5
<i>Polytrichum commune</i>	80 ¹¹	57 ¹⁰	36 ¹⁰	24 ¹⁵	5 ¹⁶	-	-	-	-	-	-	33
<i>Stramineum stramineum</i>	10 ¹¹	86 ¹²	41 ⁶	53 ⁵	53 ¹⁰	100 ⁸	-	-	9 ²	18 ⁴	-	64
<i>Sphagnum angustifolium</i>	80 ¹²	95 ¹²	95 ¹³	35 ¹³	63 ¹³	86 ¹⁰	-	-	-	-	-	79
<i>Sphagnum brevifolium</i>	-	57 ¹¹	14 ¹²	6 ⁹	-	-	-	-	-	-	-	16
<i>Sphagnum centrale</i>	30 ⁵	86 ¹⁴	86 ⁹	35 ¹¹	95 ¹³	86 ¹²	-	-	45 ⁶	45 ⁷	-	86
<i>Sphagnum girgensohnii</i>	90 ¹⁴	81 ¹³	100 ¹⁴	53 ¹¹	21 ⁹	79 ¹¹	14 ⁸	60 ⁸	9 ¹²	45 ¹³	-	85
<i>Sphagnum riparium</i>	-	52 ⁹	27 ¹²	-	-	-	-	-	-	-	-	17
<i>Cephalozia lunulifolia</i>	20 ¹	19 ²	23 ³	12 ³	11 ³	-	-	-	9 ¹	9 ¹	-	17
<i>Cephalozia pleniceps</i>	-	33 ⁴	14 ⁴	-	32 ⁷	-	-	-	-	-	-	16
<i>Ptilidium pulcherrimum</i>	10 ³	10 ¹	9 ²	-	-	-	-	-	9 ²	-	-	6
<i>Alnus incana</i>	-	-	-	12 ⁶	11 ³	-	43 ⁴	10 ²	36 ⁴	-	13 ¹	13
<i>Anemone nemorosa</i>	-	-	9 ⁶	12 ⁵	21 ⁸	-	71 ³	90 ¹⁰	82 ⁸	55 ⁴	100 ⁷	45
<i>Athyrium filix-femina</i>	-	-	5 ⁷	18 ²	-	-	71 ¹⁰	60 ⁷	27 ⁶	18 ⁷	-	20
<i>Caltha palustris</i>	-	-	5 ⁸	41 ⁹	16 ⁵	-	-	10 ³	55 ⁵	64 ⁶	75 ⁸	31
<i>Chrysosplenium alternifolium</i>	-	-	-	-	-	-	43 ¹	-	27 ¹	-	-	6
<i>Circaea alpina</i>	-	-	-	-	-	-	43 ⁵	-	36 ⁹	-	-	7
<i>Crepis paludosa</i>	-	-	-	6 ⁸	5 ³	-	14 ²	20 ⁴	64 ⁷	64 ¹¹	75 ⁸	25
<i>Epilobium palustre</i>	-	-	-	-	-	-	14 ²	-	18 ⁶	36 ⁷	-	7
<i>Filipendula ulmaria</i>	-	-	-	35 ⁸	32 ⁴	21 ²	86 ¹³	90 ¹⁰	64 ⁶	73 ⁹	63 ²	50
<i>Geum rivale</i>	-	-	-	-	-	-	14 ²	30 ⁵	9 ¹¹	-	-	5
<i>Gymnocarpium dryopteris</i>	-	-	14 ⁴	12 ²	5 ²	14 ²	43 ⁴	40 ⁷	73 ⁸	36 ⁹	38 ³	30
<i>Melampyrum sylvaticum</i>	10 ¹³	-	-	12 ³	-	-	86 ⁴	80 ⁶	-	9 ⁵	13 ¹	19
<i>Oxalis acetosella</i>	-	-	9 ²	18 ¹	26 ⁶	14 ²	100 ⁷	100 ¹¹	100 ¹⁰	82 ⁹	50 ⁴	53
<i>Paris quadrifolia</i>	-	-	-	-	5 ⁴	-	57 ³	10 ²	-	-	-	6
<i>Phegopteris connectilis</i>	10 ³	-	18 ⁵	12 ⁵	32 ⁸	7 ⁷	29 ³	100 ¹³	100 ¹²	73 ⁹	75 ⁷	51
<i>Ranunculus repens</i>	-	-	-	-	-	-	71 ¹²	40 ¹¹	27 ¹²	-	-	12
<i>Rubus saxatilis</i>	-	-	-	12 ³	32 ⁵	21 ³	-	80 ⁶	-	36 ²	50 ⁵	27
<i>Valeriana sambucifolia</i>	-	-	-	-	-	14 ⁶	57 ¹⁴	10 ¹	73 ⁷	-	-	15
<i>Agrostis canina</i>	-	-	5 ¹⁶	18 ¹⁰	42 ⁷	14 ⁸	-	50 ¹³	36 ¹²	64 ¹⁴	50 ⁵	34
<i>Agrostis capillaris</i>	-	-	-	-	-	-	-	50 ⁵	9 ¹	55 ⁶	-	12
<i>Carex flava</i>	-	5 ¹	-	-	-	14 ¹¹	-	20 ²	9 ⁴	45 ⁵	25 ⁴	13
<i>Carex loliacea</i>	-	-	-	-	5 ³	-	-	-	9 ¹⁰	-	63 ⁴	7
<i>Carex pallescens</i>	-	-	-	-	5 ¹	-	-	10 ²	9 ⁴	9 ⁷	25 ³	6
<i>Deschampsia cespitosa</i>	-	-	23 ⁴	12 ⁶	-	-	-	70 ¹⁰	45 ³	36 ⁹	75 ⁶	29
<i>Glyceria fluitans</i>	-	5 ¹	-	12 ⁹	5 ¹⁰	-	57 ⁷	-	9 ⁴	64 ⁶	13 ³	17

Tab. 4 (continued).

Species	Swamp forest No.										No. of plots	
	4	2	11	1	8	10	6	3	5	7		9
<i>Atrichum undulatum</i>	-	-	-	-	-	-	14 ¹	20 ⁸	55 ⁴	-	-	9
<i>Brachythecium rutabulum</i> agg.	-	-	-	12 ⁷	5 ²	-	86 ¹³	10 ³	27 ¹³	27 ³	13 ³	17
<i>Brachythecium salebrosum</i>	-	-	-	-	5 ¹	-	86 ³	-	18 ¹	27 ⁴	25 ³	14
<i>Bryum pseudotriquetrum</i>	-	-	-	18 ³	5 ⁴	-	-	60 ⁵	-	55 ⁹	38 ¹⁰	19
<i>Calliergon cordifolium</i>	-	10 ⁷	-	47 ⁵	5 ²	-	43 ⁴	40 ³	-	27 ⁷	13 ¹	22
<i>Calliergonella cuspidata</i>	-	5 ¹	-	6 ³	16 ³	-	-	40 ⁹	9 ³	9 ¹¹	75 ⁹	17
<i>Campylyum stellatum</i>	-	-	-	-	5 ¹⁰	-	-	30 ⁸	-	-	88 ¹⁰	11
<i>Cirriphyllum piliferum</i>	-	-	-	-	-	-	29 ⁶	60 ⁵	36 ⁵	-	25 ³	14
<i>Plagiomnium affine</i>	-	-	-	-	-	-	14 ¹¹	30 ¹¹	27 ⁸	-	13 ¹	8
<i>Plagiomnium elatum</i>	-	-	-	12 ⁷	5 ¹⁰	-	43 ²	70 ⁷	18 ²	9 ³	25 ⁷	18
<i>Plagiomnium ellipticum</i>	-	-	-	6 ¹	-	-	29 ²	-	18 ¹	9 ⁷	13 ²	7
<i>Plagiomnium medium</i>	-	-	-	12 ¹⁰	-	-	86 ¹³	-	27 ¹⁰	45 ⁶	13 ⁴	17
<i>Plagiothecium denticulatum</i>	-	5 ²	-	29 ³	11 ³	7 ¹	100 ⁶	40 ²	55 ⁶	36 ²	63 ⁷	35
<i>Pseudobryum cinclidioides</i>	-	14 ⁶	-	18 ²	-	43 ⁵	-	10 ¹	18 ⁵	27 ⁴	-	18
<i>Rhizomnium pseudopunctatum</i>	-	-	-	6 ³	11 ⁴	21 ²	14 ¹	-	36 ⁴	45 ⁶	63 ²	21
<i>Rhizomnium punctatum</i>	-	-	-	24 ³	5 ³	-	100 ⁶	60 ⁶	82 ⁷	36 ³	100 ³	39
<i>Rhodobryum roseum</i>	10 ⁴	-	-	-	-	-	29 ⁴	30 ⁵	27 ¹	-	-	9
<i>Rhytidiadelphus subpinnatus</i>	-	14 ¹	5 ¹	29 ⁴	26 ⁸	29 ³	57 ¹⁴	90 ¹³	82 ⁹	91 ⁹	63 ⁶	55
<i>Rhytidiadelphus triquetrus</i>	10 ¹	5 ¹	5 ²	-	21 ⁵	64 ⁵	-	90 ⁹	9 ¹¹	45 ⁴	75 ⁶	37
<i>Sphagnum warnstorffii</i>	-	33 ⁶	5 ⁸	47 ¹⁰	79 ¹²	71 ¹²	-	20 ³	64 ⁶	91 ¹⁰	63 ⁶	65
<i>Aneura pinguis</i>	-	-	-	-	21 ⁷	-	14 ³	10 ¹	18 ³	-	25 ⁵	10
<i>Blepharostoma trichophyllum</i>	-	10 ¹	5 ²	-	11 ³	7 ¹	29 ²	30 ¹	27 ⁴	27 ¹	63 ²	22
<i>Calyptogeia azurea</i>	-	-	-	6 ²	5 ⁴	7 ¹	-	20 ²	55 ³	18 ³	13 ¹	14
<i>Chiloscyphus polyanthos</i>	-	5 ²	-	24 ³	26 ⁴	-	86 ⁸	60 ⁷	64 ⁴	64 ⁶	75 ⁵	42
<i>Harpanthus flotovianus</i>	-	-	-	12 ⁴	16 ⁴	-	-	-	27 ¹	36 ⁶	-	12
<i>Jungermannia leiantha</i>	-	-	-	-	5 ²	-	-	10 ⁵	-	-	75 ³	8
<i>Riccardia latifrons</i>	-	-	9 ²	-	11 ²	-	-	-	9 ³	-	13 ¹	6
<i>Riccardia multifida</i>	-	-	-	-	5 ³	-	-	-	-	36 ¹⁰	25 ⁷	7
<i>Pellia</i> spp.	-	-	-	6 ¹⁵	5 ¹⁶	-	86 ¹⁵	20 ³	91 ¹⁰	73 ¹³	25 ⁸	30
<i>Betula</i> spp.	10 ¹	19 ⁵	18 ¹	6 ¹	21 ²	21 ¹	-	-	9 ¹	-	13 ¹	19
<i>Picea abies</i>	50 ³	43 ⁴	73 ⁴	29 ²	53 ⁴	43 ⁴	86 ²	60 ⁵	36 ³	73 ³	88 ⁶	82
<i>Sorbus aucuparia</i>	-	10 ³	23 ³	18 ²	5 ⁴	7 ²	43 ²	40 ³	9 ¹	18 ⁴	38 ⁴	25
<i>Dryopteris expansa</i> agg.	50 ⁴	5 ¹	14 ¹	24 ³	-	-	29 ⁸	30 ²	64 ⁶	36 ⁵	13 ⁷	30
<i>Equisetum sylvaticum</i>	70 ⁸	-	14 ¹¹	-	16 ⁵	36 ⁴	71 ⁷	80 ⁹	-	100 ⁹	100 ⁵	50
<i>Galium palustre</i>	-	-	5 ³	35 ⁹	42 ⁷	36 ⁷	57 ⁵	60 ⁵	27 ⁸	-	13 ²	34
<i>Linnaea borealis</i>	-	5 ¹	14 ⁸	18 ⁴	26 ²	7 ¹	-	50 ³	-	9 ⁸	-	19
<i>Maianthemum bifolium</i>	100 ⁷	86 ⁷	64 ⁸	65 ⁶	79 ⁹	57 ⁷	57 ³	80 ⁷	45 ⁵	91 ⁸	63 ²	108
<i>Orthilia secunda</i>	-	5 ³	5 ³	-	-	-	-	10 ¹	-	18 ⁷	-	5
<i>Trientalis europaea</i>	50 ³	57 ⁶	68 ⁷	53 ⁶	89 ⁶	64 ³	86 ⁴	70 ³	27 ²	91 ⁸	63 ⁴	98
<i>Pyrola minor</i>	-	5 ²	-	6 ⁶	21 ³	14 ⁴	-	-	-	-	-	8
<i>Viola palustris</i>	10 ²	19 ⁵	23 ¹¹	47 ⁷	42 ⁸	36 ⁸	14 ¹	40 ¹⁰	36 ¹¹	91 ¹⁰	-	50
<i>Calamagrostis arundinacea</i>	-	-	5 ⁴	6 ²	-	-	29 ⁶	60 ³	-	-	-	10
<i>Calamagrostis purpurea</i>	50 ⁸	71 ⁹	36 ¹⁰	53 ¹⁰	37 ⁵	71 ⁵	14 ¹	90 ¹⁰	18 ⁸	100 ⁹	-	77
<i>Luzula pilosa</i>	-	-	-	12 ³	-	-	14 ¹	40 ⁴	-	9 ²	-	8
<i>Brachythecium reflexum</i>	20 ⁶	19 ⁴	14 ⁴	18 ⁶	11 ⁵	-	29 ⁵	-	27 ⁶	9 ¹	50 ²	24
<i>Brachythecium starkei</i>	-	10 ³	-	6 ¹	5 ¹	-	29 ²	-	9 ¹	9 ¹	13 ²	9
<i>Dicranum fuscescens</i>	30 ³	38 ³	18 ³	-	16 ³	-	-	30 ³	9 ²	9 ²	25 ¹	25
<i>Dicranum majus</i>	70 ¹¹	57 ⁴	50 ⁶	35 ⁸	53 ⁶	50 ³	43 ⁵	90 ⁷	55 ⁹	55 ⁷	88 ⁹	84
<i>Dicranum scoparium</i>	70 ⁴	29 ⁵	23 ³	18 ³	37 ⁴	14 ¹	29 ²	40 ⁵	36 ³	36 ⁴	50 ³	48
<i>Hylacomiastrum umbratum</i>	30 ⁶	43 ⁵	18 ²	41 ⁶	32 ⁷	21 ⁴	29 ⁵	90 ⁷	64 ¹¹	64 ⁷	63 ⁸	62
<i>Hylacomium splendens</i>	60 ⁸	10 ⁶	32 ³	24 ³	42 ⁷	57 ⁶	-	30 ²	9 ⁴	45 ⁵	50 ¹¹	48
<i>Plagiothecium laetum</i>	60 ⁴	43 ⁵	36 ⁶	18 ¹⁰	37 ³	21 ²	71 ²	40 ⁴	36 ⁴	27 ⁶	38 ³	55
<i>Polytrichum formosum</i>	10 ¹	-	-	18 ⁵	5 ³	7 ³	29 ⁵	30 ⁴	36 ⁴	27 ³	-	18
<i>Rhizomnium magnifolium</i>	10 ¹	-	5 ¹	-	5 ¹³	-	14 ²	-	45 ⁵	45 ³	25 ⁹	16
<i>Sanionia uncinata</i>	-	5 ²	14 ²	12 ²	21 ³	29 ²	29 ³	20 ⁷	18 ⁴	9 ¹	50 ⁷	25
<i>Tetraphis pellucida</i>	50 ²	24 ⁴	23 ⁴	12 ⁷	5 ²	-	14 ⁶	30 ³	55 ⁴	27 ⁴	25 ⁹	33
<i>Warnstorfia exannulata</i> agg.	-	10 ¹	-	24 ⁴	16 ⁵	-	-	-	-	-	-	9
<i>Sphagnum russowii</i>	-	-	32 ⁹	18 ⁸	21 ¹²	-	-	-	-	-	25 ²	16
<i>Sphagnum squarrosom</i>	20 ⁹	10 ⁷	45 ⁵	71 ¹²	42 ¹¹	50 ¹⁴	71 ⁴	30 ⁶	91 ¹⁰	100 ¹⁰	25 ⁶	72
<i>Sphagnum teres</i>	-	43 ⁸	14 ¹¹	47 ¹²	79 ¹²	79 ¹⁴	-	-	-	55 ⁸	25 ²	54

Tab. 4 (continued).

Species	Swamp forest No.									No. of plots		
	4	2	11	1	8	10	6	3	5		7	9
<i>Barbilophozia attenuata</i>	10 ³	19 ⁴	9 ²	6 ³	5 ¹	-	-	-	9 ²	9 ¹	13 ⁴	12
<i>Calypogeia integristipula</i>	50 ⁴	48 ³	27 ⁶	18 ⁶	11 ⁵	7 ²	-	20 ³	45 ³	27 ²	25 ⁹	39
<i>Calypogeia muelleriana</i>	50 ⁶	52 ⁴	27 ⁵	53 ⁴	53 ⁹	21 ⁵	14 ¹	30 ¹	82 ⁶	82 ⁶	63 ⁶	71
<i>Calypogeia neesiana</i>	10 ⁴	24 ²	5 ¹	12 ³	5 ²	-	-	-	9 ¹	9 ¹	13 ⁵	13
<i>Cephalozia bicuspidata</i>	10 ²	29 ²	23 ⁴	29 ⁴	42 ⁵	21 ⁴	86 ⁷	30 ³	55 ⁸	27 ³	63 ⁷	51
<i>Chiloscyphus profundus</i>	10 ¹	14 ⁴	23 ⁶	6 ¹¹	21 ³	-	29 ²	-	91 ⁴	9 ⁶	75 ¹⁰	33
<i>Lepidozia reptans</i>	10 ¹	14 ³	18 ⁴	6 ²	16 ²	-	29 ¹	30 ²	45 ²	18 ⁴	25 ⁵	26
<i>Lophozia ventricosa</i> agg.	20 ²	10 ⁵	-	18 ²	16 ²	-	14 ¹	-	27 ³	9 ²	-	15
<i>Plagiochila asplenioides</i>	50 ⁵	-	9 ⁵	18 ⁵	16 ²	-	71 ⁷	90 ¹⁰	82 ¹⁰	45 ⁷	50 ⁸	45
<i>Scapania irrigua</i>	-	-	-	24 ³	5 ⁵	7 ¹	-	-	-	-	-	6
<i>Frangula alnus</i>	-	19 ⁴	-	-	5 ⁴	-	-	-	-	-	-	5
<i>Vaccinium oxycoccus</i>	-	-	-	-	32 ¹⁰	14 ⁴	-	-	-	-	-	8
<i>Equisetum fluviatile</i>	-	-	-	-	26 ⁴	29 ³	-	-	-	-	-	9
<i>Equisetum pratense</i>	-	-	-	-	-	-	-	-	45 ³	-	-	5
<i>Lysimachia thyrsoflora</i>	-	-	-	41 ⁷	-	7 ⁸	-	-	-	-	-	8
<i>Matteuccia struthiopteris</i>	-	-	-	-	-	-	86 ¹¹	-	-	-	-	6
<i>Tussilago farfara</i>	-	-	-	-	-	-	-	50 ⁶	-	-	50 ⁶	9
<i>Viola riviniana</i>	-	-	-	-	-	-	-	50 ⁴	-	-	13 ²	6
<i>Carex lasiocarpa</i>	-	-	-	-	26 ⁸	-	-	-	-	-	-	5
<i>Carex nigra</i>	-	29 ¹²	-	6 ⁴	-	-	-	-	-	-	-	7
<i>Molinia caerulea</i>	-	-	-	-	26 ¹³	-	-	-	-	-	-	5
<i>Phragmites australis</i>	-	-	-	-	53 ¹⁰	-	-	-	-	-	-	10
<i>Fissidens adianthoides</i>	-	-	-	-	-	-	-	20 ¹	-	-	38 ⁴	5
<i>Plagiothecium succulentum</i>	-	-	-	12 ¹	-	-	-	-	27 ⁵	-	-	5
<i>Thuidium tamariscinum</i>	-	-	-	-	-	-	-	90 ¹³	-	-	-	9
<i>Sphagnum magellanicum</i>	-	-	9 ⁵	-	26 ¹³	-	-	-	-	-	-	7
<i>Sphagnum subsecundum</i>	-	-	-	-	5 ¹⁵	-	-	-	-	36 ¹⁰	-	5

Additional species (occurring in less than 5 1-m² plots):

Acer platanoides 3:10¹ 1; *Alnus glutinosa* 7:9², 9:25¹ 3; *Pinus sylvestris* 2:5¹ 1; *Salix aurita* 10:14⁵, 8:5³ 3; *Salix aurita* × *caprea* 1:6³ 1; *Salix caprea* 10:7¹, 7:9⁴ 2; *Salix myrsinifolia* 1:6⁴ 1; *Viburnum opulus* 8:5¹ 1.

Calluna vulgaris 8:5¹ 1; *Empetrum nigrum* 8:11⁶ 2.

Alchemilla sp. 3:10² 1; *Bistorta vivipara* 7:9⁵ 1; *Cardamine pratensis* 3:40⁶ 4; *Cirsium helenioides* 7:36¹³ 4; *Cirsium palustre* 3:10¹ 1; *Corallorhiza trifida* 8:11² 2; *Dactylorhiza fuchsii* 7:18² 2; *Drosera rotundifolia* 8:11⁴ 2; *Fragaria vesca* 3:10⁸ 1; *Geranium sylvaticum* 7:9², 3:10³ 2; *Hieracium* sp. 7:9³, 3:20⁴ 3; *Listera cordata* 11:9², 3:10¹ 3; *Mycelis muralis* 3:30⁸ 3; *Polygonatum verticillatum* 9:13¹ 1; *Prunella vulgaris* 3:30⁸ 3; *Pteridium aquilinum* 4:10² 1; *Solidago virgaurea* 3:20⁵ 2.

Anthoxanthum odoratum 9:13¹ 1; *Carex canescens* × *loliacea* 8:11¹⁰ 2; *Carex chordorrhiza* 10:29¹² 4; *Carex digitata* 3:30¹, 6:14² 4; *Carex panicea* 8:5¹⁵ 1; *Carex pauciflora* 2:5¹, 8:5¹ 2; *Carex paupercula* 8:5⁹, 1:6² 2; *Festuca altissima* 5:9-2 1; *Festuca rubra* 7:9¹ 1; *Melica nutans* 8:5¹, 9:13⁶, 3:10⁴ 3.

Brachythecium populeum 6:14⁵ 1; *Calliergon richardsonii* 8:16¹, 1:6⁴ 4; *Climacium dendroides* 1:6¹, 3:10¹ 2; *Dicranum montanum* 10:7¹, 8:5¹ 2; *Herzogiella striatella* 8:5¹, 9:13¹ 2; *Hypnum cupressiforme* 7:9¹ 1; *Philonotis fontana* 7:9³ 1; *Plagiomnium undulatum* 5:9¹² 1; *Plagiothecium undulatum* 11:5², 8:5¹ 2; *Polytrichum strictum* 8:5² 1; *Pseudotaxiphyllum elegans* 8:5¹ 1; *Ptilium crista-castrensis* 4:10⁷, 1:6⁵, 9:13¹, 3:10¹ 4; *Rhytidadelphus loreus* 2:5¹ 1; *Scorpidium revolvens* 8:5⁷ 1; *Warnstorfia fluitans* 2:5¹ 1.

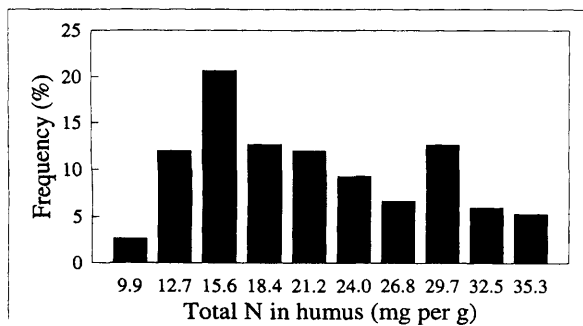
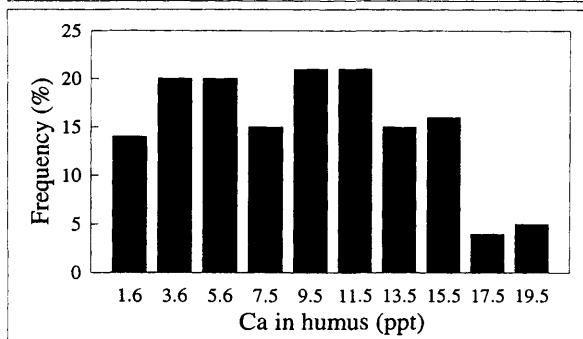
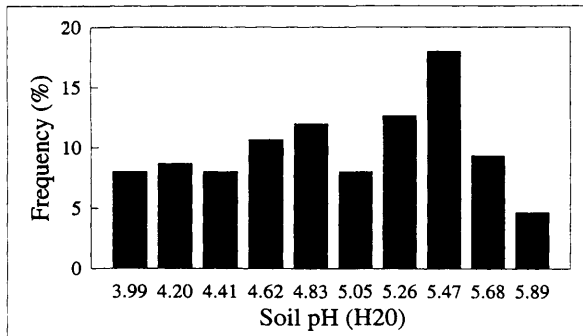
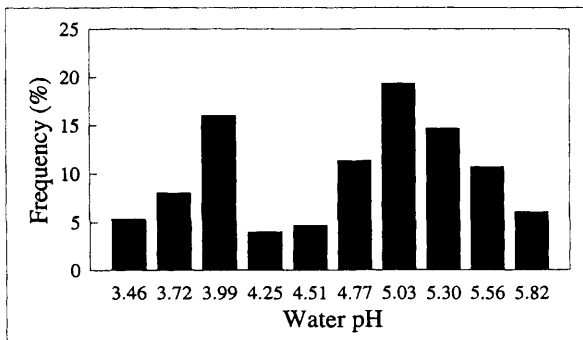
Sphagnum flexuosum 7:9¹⁶ 1; *Sphagnum quinquefarium* 4:20⁸, 3:10¹ 3.

Barbilophozia kunzeana 10:7² 1; *Barbilophozia lycopodioides* 9:13¹ 1; *Cephalozia* sp. 2:5¹, 5:9¹ 2; *Diptlophyllum albicans* 8:5¹, 6:14¹ 2; *Lophozia incisa* 7:9¹, 5:9³ 2; *Lophozia longidens* 4:10¹ 1; *Lophozia obtusa* 4:10¹, 5:9² 2; *Mylia taylorii* 9:13¹, 5:18¹ 3; *Ptilidium ciliare* 10:7², 8:5¹ 2; *Scapania paludosa* 8:5¹ 1; *Scapania scandica* 6:14² 1; *Scapania umbrosa* 7:9¹ 1; *Scapania undulata* 1:18¹, 9:18² 4.

Cladonia cenotea 2:5¹ 1; *Cladonia chlorophaea* 2:14², 4:10⁴ 4; *Cladonia coniocraea* 2:14², 4:10⁴ 4; *Cladonia digitata* 2:5¹, 11:5¹ 2; *Cladonia rangiferina* 2:5¹ 1; *Cladonia squamosa* 2:5¹ 1.

the outlet, the slope increased from c. 0.5° to c. 2°. The northern part of the swamp forest was open and mire-like, separated from the wet southeastern part by a forested, drier area dominated by *Picea abies* and with occurrence also of *Betula* spp. *Alnus incana* was frequent close to the wet soak.

Swamp-forest locality 9 was small, situated where a narrow, northeast-facing grove opened into a shallow, wider valley. The peat layer was shallow (to 1.5 m deep). The onset of peat

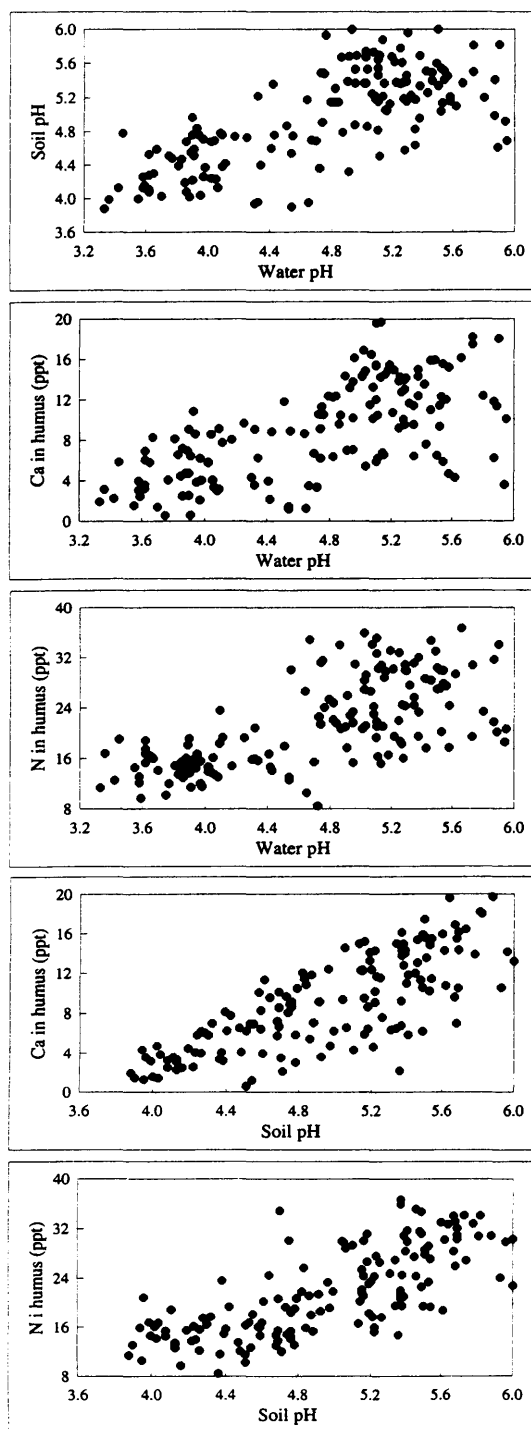


accumulation was dated to 4,305 yrs B.P. The western part of this swamp forest was open and wet, influenced by water from a diffuse spring. Towards the east, the ground gradually became drier and tree prominence increased, notably of *Picea abies* and *Alnus glutinosa*. The swamp forest was distinctly sloping (4–5°).

Swamp-forest locality 10 was selected as a part of a mire-swamp forest transitional area, extending for several hundred m along the bottom of a deep, north-facing, U-shaped valley with a central, permanent brook that discharged the lake Midtre Kyttjern and its extensive watershed. Peat layers up to 7.6 m deep were encountered. The slope of the subsoil surface increased strongly towards the border onto adjacent mineral soil. The onset of peat accumulation was dated to 8,790 yrs B.P. In the south-north direction (along the brook), this swamp-forest locality was almost level while from the brook to the valley side the surface ascended slightly. Wetness decreased and tree stand density increased from the mire-like areas along the brook towards the border onto mineral soil. *Picea abies* was the dominant tree, *Betula* spp. and *Alnus glutinosa* were also common.

Swamp-forest locality 11 was by far the largest among the swamp-forest

Figs 9–12. Frequency distributions for four variables of the soil nutrient/acidity group. Fig. 9. pH measured in tube water, 26 Aug 1998. Fig. 10. pH in aqueous soil suspension. Fig. 11. Calcium concentration in humus (ppt). Fig. 12. Total-N concentration in humus (ppt). up six compact groups, within which all pairs of variables were strongly correlated ($|\tau| > 0.40$; $P \ll 0.0001$; Fig. 8, Tab. 5).



localities investigated, being almost as large as the other ten localities taken together. This swamp forest filled a depression varying in breadth from a few m farthest north (near the outlet) to more than 40 m centrally. It was situated west of a prominent hill, which ascends quite steeply to the east., To the west, several smaller hills occur. A small extension of the swamp forest in between a couple of these hills were not included in the studied area. Peat depth was above 3 m along the entire long axis of the swamp-forest locality (mid-way between side margins), with a maximum depth of 6.3 m in the broadest, central part. The onset of peat accumulation was dated to 8,490 yrs B.P. This swamp-forest locality levelled off gently from the planar, south-central parts towards outlets near the southern and southwestern margins. Wetness increased northwards until a brooklet formed near the outlet. The southern and central parts of this swamp-forest locality were dry, densely stocked with *Picea abies* and with some *Betula* spp. occurring intermixed.

Figs 13–17. Patterns of co-ordinated variation in pairs of variables of the soil nutrient/acidity group. Fig. 13. pH measured in tube water, 26 Aug 1998 vs pH in aqueous soil suspension. Fig. 14. pH measured in tube water, 26 Aug 1998 vs calcium concentration in humus (ppt). Fig. 15. pH measured in tube water, 26 Aug 1998 vs total-N concentration in humus (ppt). Fig. 16. pH in aqueous soil suspension vs calcium concentration in humus (ppt). Fig. 17. pH in aqueous soil suspension vs total-N concentration in humus (ppt).

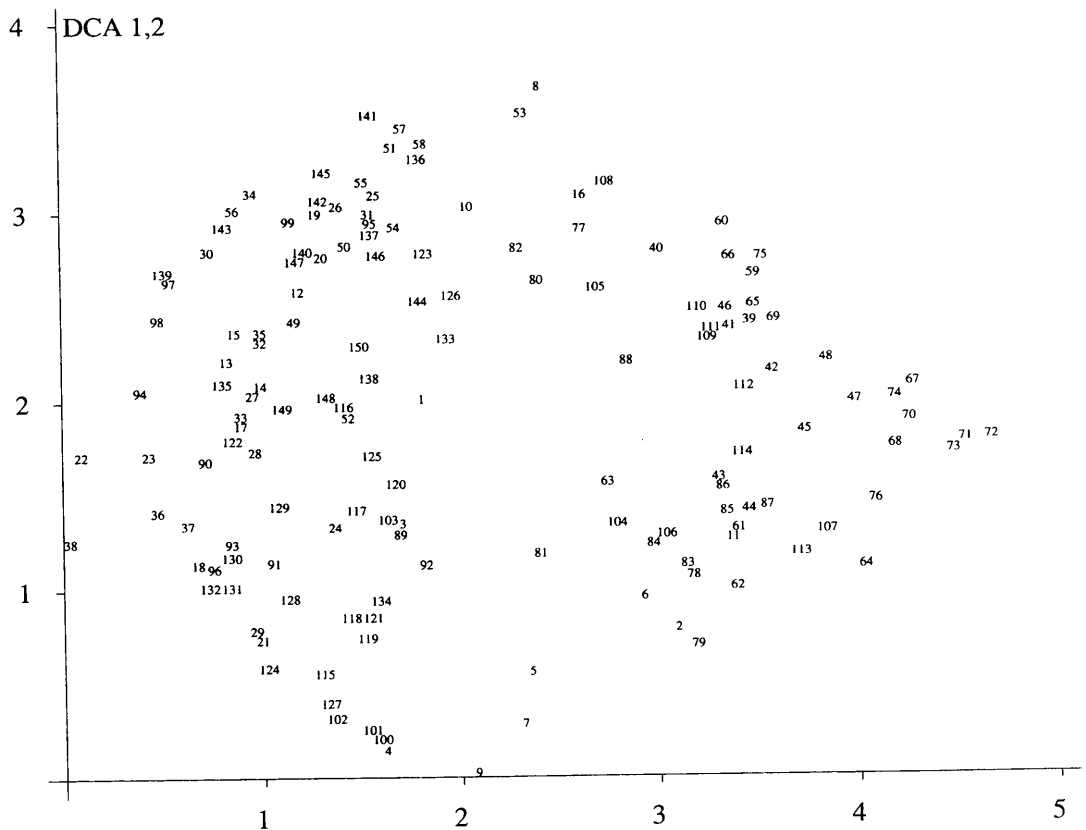
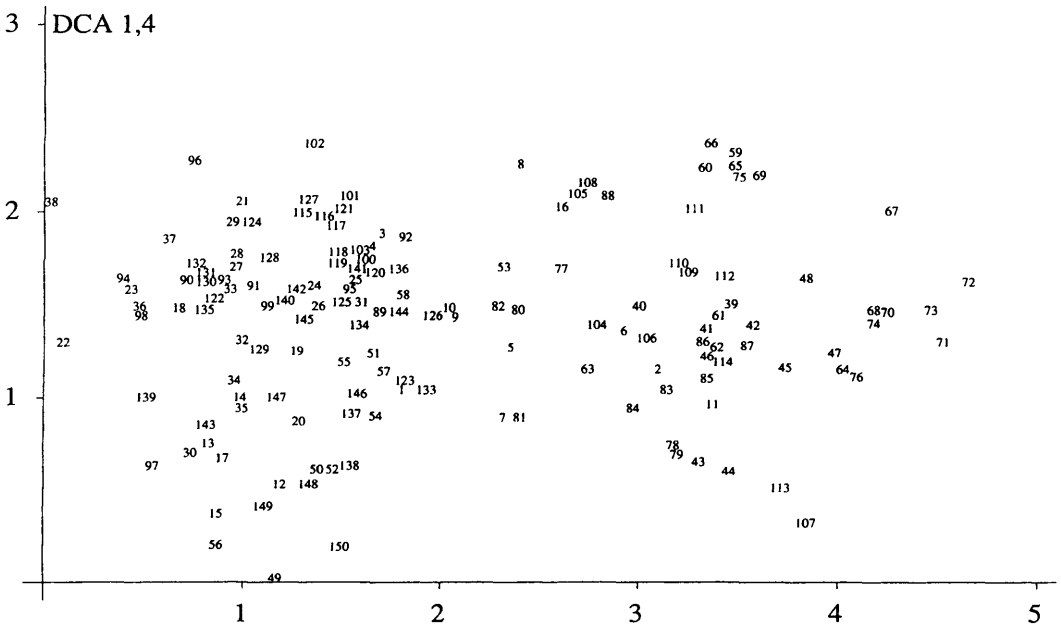
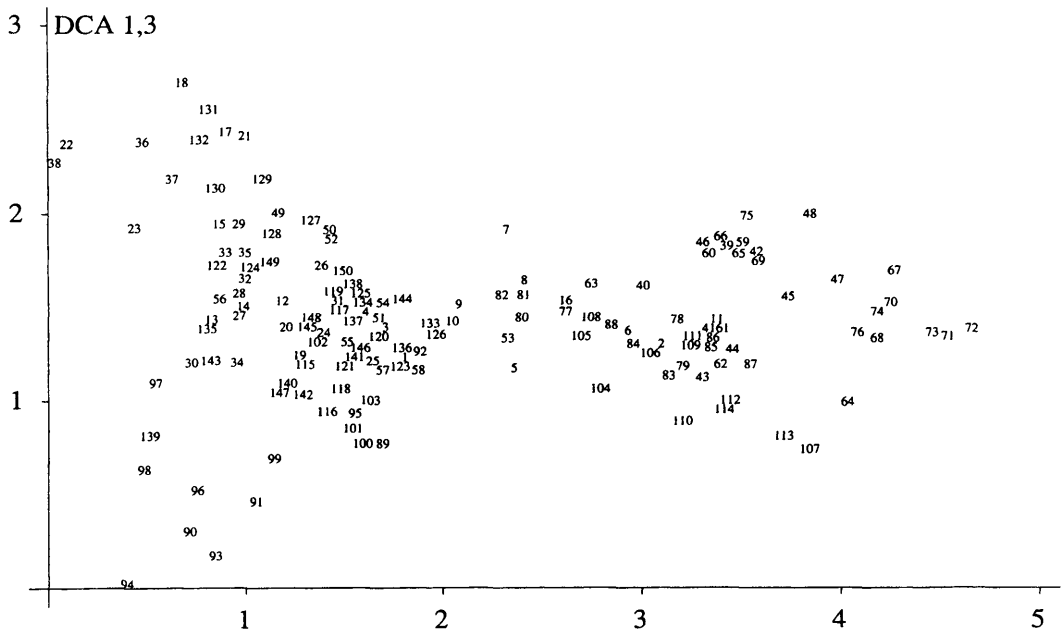


Fig. 18. DCA ordination of the full data set (150 1-m² plots), axes 1 (horizontal) and 2. Plot numbers are plotted onto plot positions. Scaling of axes in S.D. units.

DISTRIBUTION OF SPECIES ON THE STUDIED SWAMP-FOREST LOCALITIES

Fifty-two out of 212 species (24.5 %) were recorded in 1-m² plots from one swamp-forest locality only, and 39 (18.4 %) were only recorded in plots from two swamp-forest localities (Fig. 4). About one half of the species (107 out of 212) were recorded in 3 or fewer swamp-forest localities. Only 11 species (5.2 %) were recorded in all 11 swamp-forest localities (Fig. 4).

Tab. 4, showing for all species the constancy and mean subplot frequency in each swamp-forest locality, demonstrates that species were distributed on swamp-forest localities in a multitude of ways. Not even species that occurred in all or almost all swamp-forest localities, like *Vaccinium myrtillus*, *Sphagnum girgensohnii* and *S. squarrosum*, had high constancy throughout (Tab. 4). Many species had high constancy in one or a few swamp-forest localities while they had low constancy or were absent from others (e.g. *Athyrium filix-femina*, *Equisetum sylvaticum*, *Melampyrum sylvaticum*, *Menyanthes trifoliata*, *Agrostis capillaris*, *Carex rostrata*, *Deschampsia cespitosa*, *Brachythecium rutabulum* agg., *Bryum pseudotriquetrum*, *Calliergonella*



Figs 19-20. DCA ordination of the full data set (150 1-m² plots). Plot numbers are plotted onto plot positions. Scaling of axes in S.D. units. Fig. 19. Axes 1 (horizontal) and 3. Fig. 20. Axes 1 (horizontal) and 4.

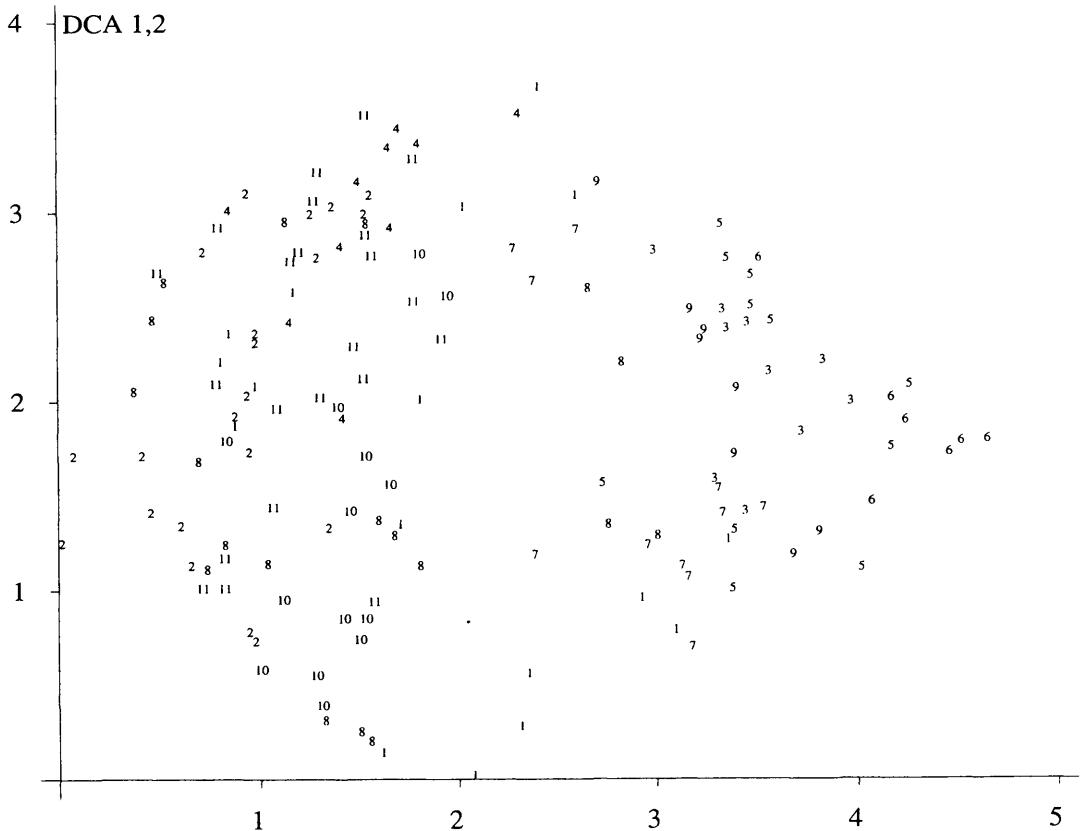
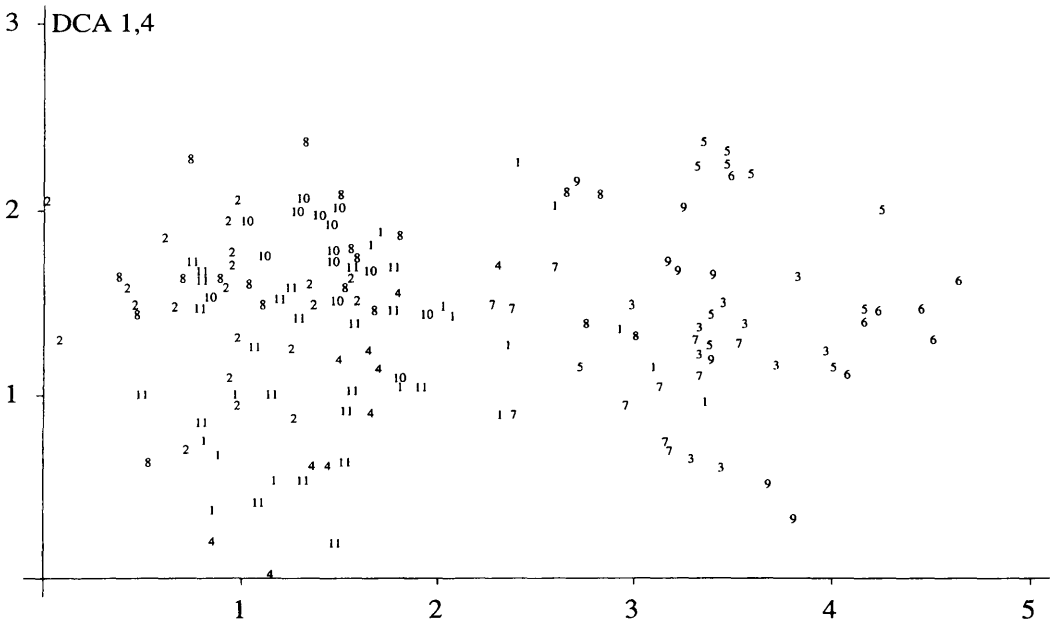
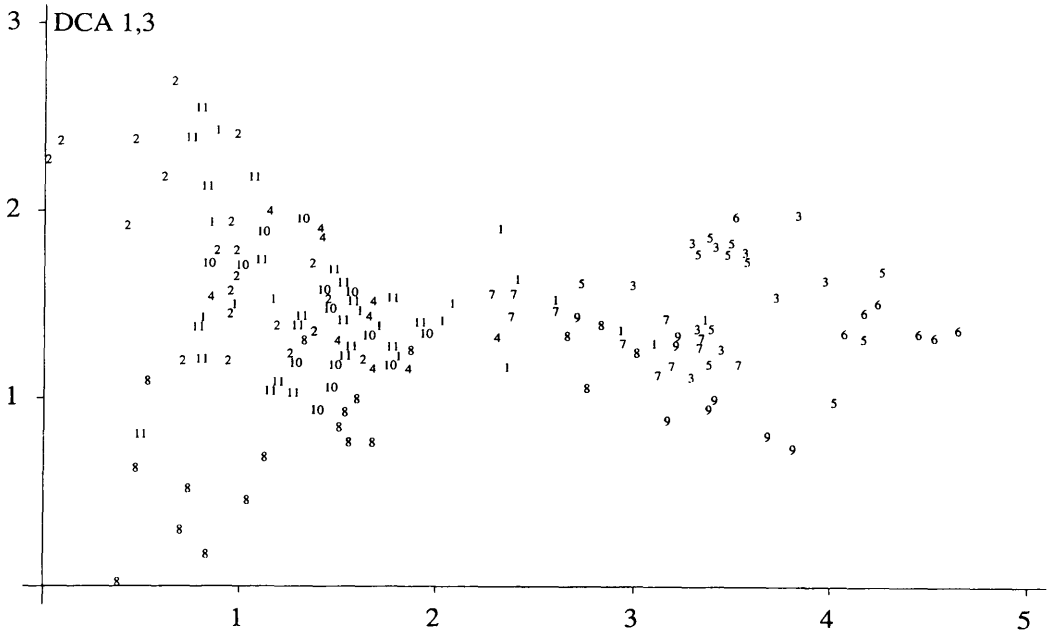


Fig. 21. DCA ordination of the full data set (150 1-m² plots), axes 1 (horizontal) and 2. Swamp-forest locality numbers are plotted onto plot positions. Scaling of axes in S.D. units.

cuspidata, *Plagiomnium elatum*, *P. medium*, *Polytrichum commune*, *Rhizomnium magnifolium*, *Sphagnum teres*, *S. warnstorffii* and *Chiloscyphus profundus* (Tab. 4). High constancy and/or subplot frequency was also observed for some species that were recorded in one or two swamp-forest localities only, such as *Vaccinium oxycoccos*, *Chrysosplenium alternifolium*, *Circaea alpina*, *Equisetum pratense*, *Lysimachia thyrsiflora*, *Matteuccia struthiopteris*, *Tussilago farfara*, *Viola riviniana*, *Phragmites australis*, *Sphagnum riparium* and *Thuidium tamariscinum*.

The total number of species recorded in 1-m² plots in each swamp-forest locality varied from 55 (swamp-forest locality 4) to 125 (swamp-forest locality 8; Fig. 5). The number of plots in a swamp-forest locality and the total number of species recorded in these plots were not correlated ($\tau = 0.112$, $p = 0.637$, $n = 11$).



Figs 22-23. DCA ordination of the full data set (150 1-m² plots). Swamp-forest locality numbers are plotted onto plot positions. Scaling of axes in S.D. units. Fig. 22. Axes 1 (horizontal) and 3. Fig. 23. Axes 1 (horizontal) and 4.

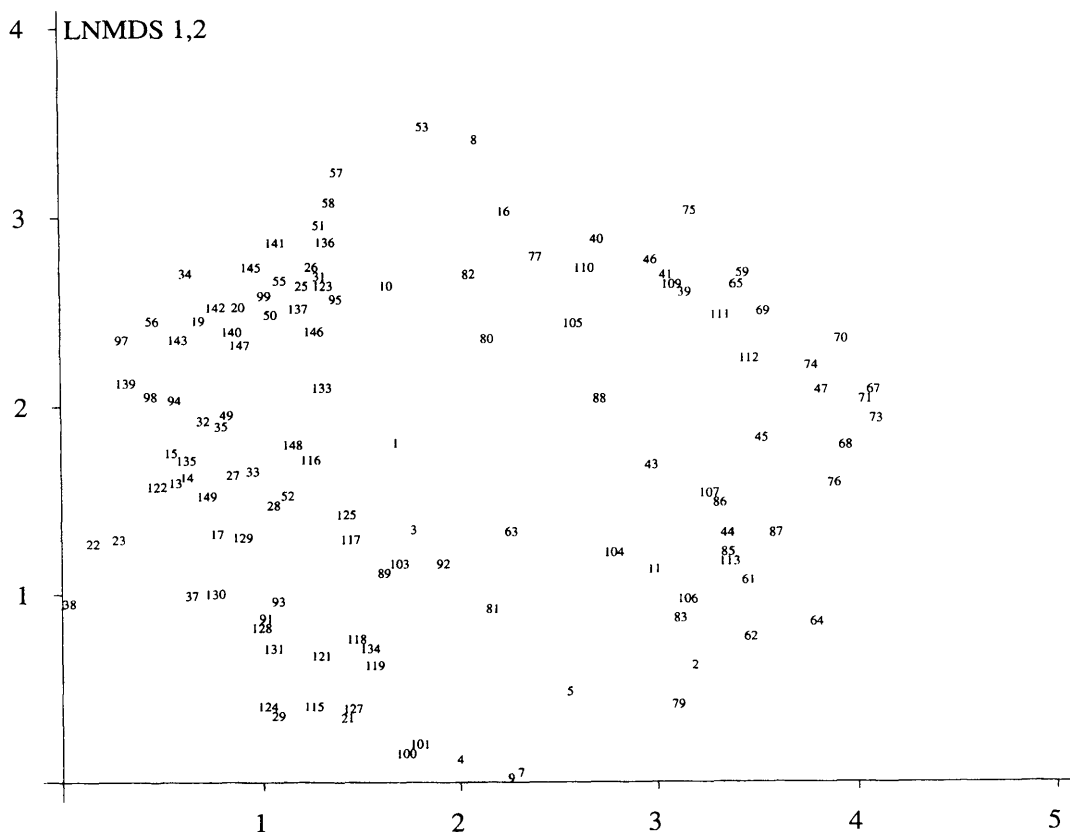
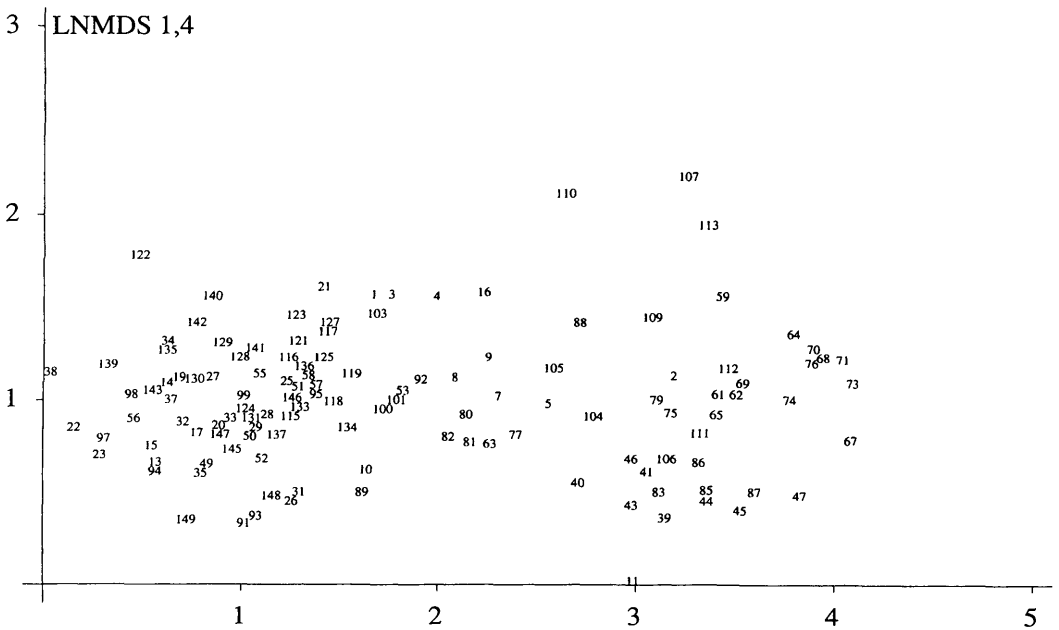
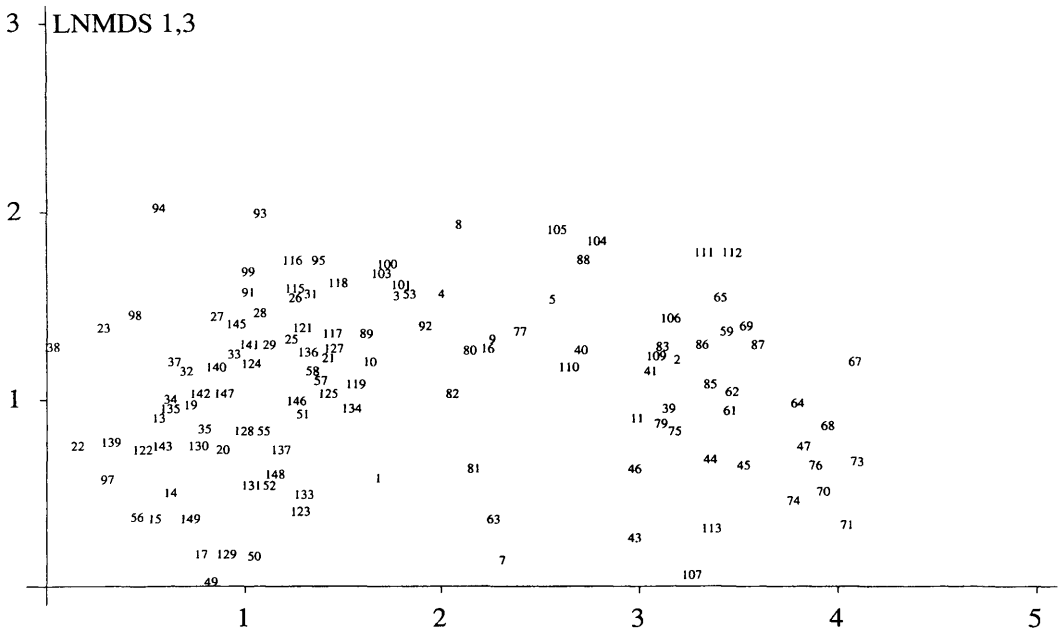


Fig. 24. LNMSD ordination of the reduced data set (125 1-m² plots), axes 1 (horizontal) and 2. Plot numbers are plotted onto plot positions. Axes rescaled in S.D. units.

RELATIONSHIPS BETWEEN EXPLANATORY VARIABLES

The first four axes of the PCA ordination of explanatory variables had eigenvalues (fractions of variation explained) of 0.306, 0.136, 0.079, and 0.063. More than one half (52.2%) of the total variation in the set of explanatory variables was thus explained by PCA axes 1–3. Figs 6–7 are therefore likely to provide a representative summary of the gradient structure in this data set.

The explanatory variables made up six compact groups, within which all pairs of variables were strongly correlated ($|\tau| > 0.40$; $P < 0.0001$; Fig. 8, Tab. 5). Members of the same group were to a large extent represented by vectors of more or less similar lengths and pointing in the same directions in the PCA ordination (Figs 6–7). The two largest groups both consisted of variables with high loadings [PCA 1 > (0.5–)0.7] on the first PCA axis (Fig. 6). Four smaller, compact groups with three or four variables each, that were characterized by low loadings on PCA-axis 1 and high loadings on PCA-axis 2 [PCA 1 > (0.3–)0.5], were separated along PCA-axis 3 (Fig. 7).



Figs 25-26. LNMDs ordination of the reduced data set (125 1-m² plots). Plot numbers are plotted onto plot positions. Axes rescaled in S.D. units. Fig. 25. Axes 1 (horizontal) and 3. Fig. 26. Axes 1 (horizontal) and 4.

Tab. 5. Kendall's rank correlation coefficients τ between 53 explanatory variables in the 150 plots (lower triangle), with significance probabilities (upper triangle). Very strong correlations ($|\tau| \geq 0.4, P < 0.0001$) in bold face, strong correlations ($|\tau| \geq 0.3, P < 0.0001$) italicized. Names of explanatory variables abbreviated in accordance with Tab. 2.

Variable	Vert Ran	Slope Avg	Slope Ma25	Slope Ma10	Dist MSoil	SoilD MVL	SoilD MWT	Canopy CAvg	Canopy CMax	Canopy CMin	Tree Infliv	Tree InfAll	Basal Area	Crown I	Lit- terl	SnowD 0423	Wat Tab100	Wat Tab90	Wat Tab50	Wat Tab10	Wat Tab0	Wat Tab Ran	WatTab HMi	WatTab LMa	WatTem 0527	WatTem 0826	
VertRan	*	.0000	.0000	.0000	.6337	.9132	.6361	.0704	.0892	.0196	.0000	.0000	.6206	.0044	.0007	.0233	.0046	.0006	.0000	.0000	.0000	.1409	.0000	.0029	.3556	.1753	
SlopeAvg	.6919	*	.0000	.0000	.7000	.3067	.5231	.1669	.1275	.1690	.0018	.0008	.7448	.0372	.0140	.0041	.0002	.0001	.0000	.0000	.0000	.9650	.0000	.0456	.6030	.2839	
SlopeMa25	.6949	.7167	*	.0000	.7167	.5516	.8478	.3279	.1188	.2711	.0017	.0003	.7471	.0728	.0297	.0039	.0026	.0005	.0000	.0000	.0000	.6733	.0000	.0081	.4801	.7057	
SlopeMa10	.4701	.5134	.5309	*	.3768	.2015	.1992	.5086	.2670	.4835	.1143	.0089	.5999	.0834	.3215	.0168	.7783	.6499	.1947	.0864	.0223	.0191	.0173	.0012	.0524	.5382	
DistMSoil	-.0267	.0214	.0204	-.0496	*	.0000	.0000	.0357	.2102	.0562	.1146	.1122	.1416	.0316	.0514	.5352	.9391	.9702	.9728	.9922	.3916	.1450	.8773	.6654	.2530	.1959	
SoilDMVL	-.0061	.0563	.0333	-.0712	.4189	*	.0000	.1745	.8908	.0501	.1060	.0991	.0042	.0051	.0393	.7504	.5684	.4960	.6905	.8812	.1998	.0141	.7761	.1332	.1778	.0001	
SoilDMWT	-.0263	.0352	.0107	-.0716	.4288	.9472	*	.1308	.9765	.0314	.0427	.0472	.0032	.0035	.0156	.5915	.7268	.7811	.5751	.4259	.0296	.0458	.5337	.0283	.3534	.0001	
CanopyCAvg	.1018	.0771	.0553	.0373	-.1177	-.0756	-.0841	*	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.1064	.3861	.0799	.0460	.0202	.0041	.0218	.1905	.1966	.1316	.0992	
CanopyCMax	.0987	.0877	.0909	.0646	-.0725	.0079	.0017	.7312	*	.0000	.0001	.0007	.0278	.0000	.0000	.0830	.5184	.0993	.0416	.0188	.0154	.0160	.3091	.4619	.1295	.1067	
CanopyCMin	.1341	.0783	.0635	.0404	-.1093	-.1115	-.1224	.7326	.4854	*	.0000	.0000	.0000	.0000	.0000	.1441	.1631	.0509	.0520	.0323	.0033	.1861	.0627	.4250	.1635	.2444	
TreeInfliv	.2283	.1740	.1772	.0890	-.0884	-.0900	-.1128	.3191	.2347	.3737	*	.0000	.0052	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0109	.0000	.0304	.0207	.4645	
TreeInfAll	.2403	.1850	.2005	.1458	-.0880	-.0908	-.1093	.2381	.1947	.2991	.5209	*	.0127	.0000	.0000	.0015	.0000	.0000	.0000	.0000	.0000	.0184	.0000	.0698	.1476	.0064	
BasalArea	.0281	-.0183	-.0184	.0298	-.0830	-.1607	-.1653	.2357	.1288	.2938	.1584	.1399	*	.0001	.0042	.2055	.7896	.9196	.8021	.8401	.3885	.5665	.6651	.3537	.4148	.3584	
CrownI	.1583	.1148	.1002	.0965	-.1191	-.1541	-.1607	.4020	.2730	.3950	.4224	.2459	.2225	*	.0000	.1789	.1113	.0540	.0341	.0202	.0055	.3755	.0207	.3972	.9404	.1634	
LitterI	.1924	.1385	.1241	.0565	-.1104	-.1160	-.1361	.3495	.2510	.3490	.5245	.2956	.1642	.5796	*	.0111	.0001	.0000	.0000	.0000	.0000	.4347	.0000	.0356	.0569	.4337	
SnowD0423	-.1300	-.1631	-.1658	-.1373	.0354	.0180	.0304	-.0926	-.1026	-.0856	-.2631	-.1799	-.0732	-.0762	-.1472	*	.0013	.0027	.0028	.0072	.0068	.0133	.0018	.4119	.9298	.7342	
WatTab100	.1579	.2024	.1685	.0157	.0042	.0314	-.0192	.0483	.0371	.0794	.2903	.2849	.0150	.0877	.2216	-.1822	*	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.7672
WatTab90	.1911	.2214	.1950	.0253	.0021	.0375	-.0153	.0975	.0947	.1111	.2904	.2975	-.0057	.1061	.2289	-.1700	.8699	*	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.7847
WatTab50	.2430	.2635	.2381	.0723	.0019	.0219	-.0309	.1111	.1171	.1105	.2864	.2902	-.0141	.1167	.2287	-.1694	.7686	.8806	*	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.8148
WatTab10	.2713	.2772	.2607	.0956	.0005	.0082	-.0439	.1294	.1350	.1218	.2826	.2783	-.0113	.1279	.2311	-.1523	.7065	.8135	.9159	*	.0000	.0000	.0000	.0000	.0000	.0000	.9702
WatTab0	.3102	.2912	.2741	.1275	-.0475	-.0706	-.1199	.1599	.1393	.1672	.2944	.2975	.0484	.1531	.2555	-.1535	.6282	.7159	.7798	.8307	*	.0254	.0000	.0000	.0000	.6279	
WatTabRan	-.0829	.0025	-.0238	-.1323	.0818	.1369	.1113	-.1294	-.1401	-.0762	.1434	.1315	-.0326	-.0494	.0445	-.1421	.5017	.3907	.2984	.2331	.1247	*	.0000	.0019	.0000	.1493	
WatTabHMi	.3380	.3522	.3150	.1327	-.0086	.0157	-.0343	.0729	.0584	.1059	.3290	.3214	.0243	.1274	.2445	-.1774	.7837	.7810	.7615	.7345	.6784	.3792	*	.0000	.0000	.5474	
WatTabLMa	-.1655	-.1102	-.1481	-.1802	-.0240	-.0827	-.1208	.0719	.0423	.0454	.1205	.0999	.0521	.0466	.1183	-.0465	.4697	.4996	.4991	.4973	.4982	.1729	.3983	*	.0000	.0406	
WatTem0527	.0517	.0288	.0397	.1088	-.0637	-.0746	-.0514	-.0844	-.0876	-.0797	-.1295	-.0802	-.0460	-.0041	-.1077	-.0050	-.3827	-.3844	-.3559	-.3364	-.3055	-.2644	-.3071	-.3284	*	.0000	
WatTem0826	.0763	.0598	.0213	.0347	.0725	.2157	.2153	-.0929	-.0938	-.0670	.0412	.1519	-.0522	.0777	.0446	-.0195	.0165	.0152	.0130	.0021	-.0270	.0813	.0335	-.1141	.2306	*	

Tab. 5 (continued).

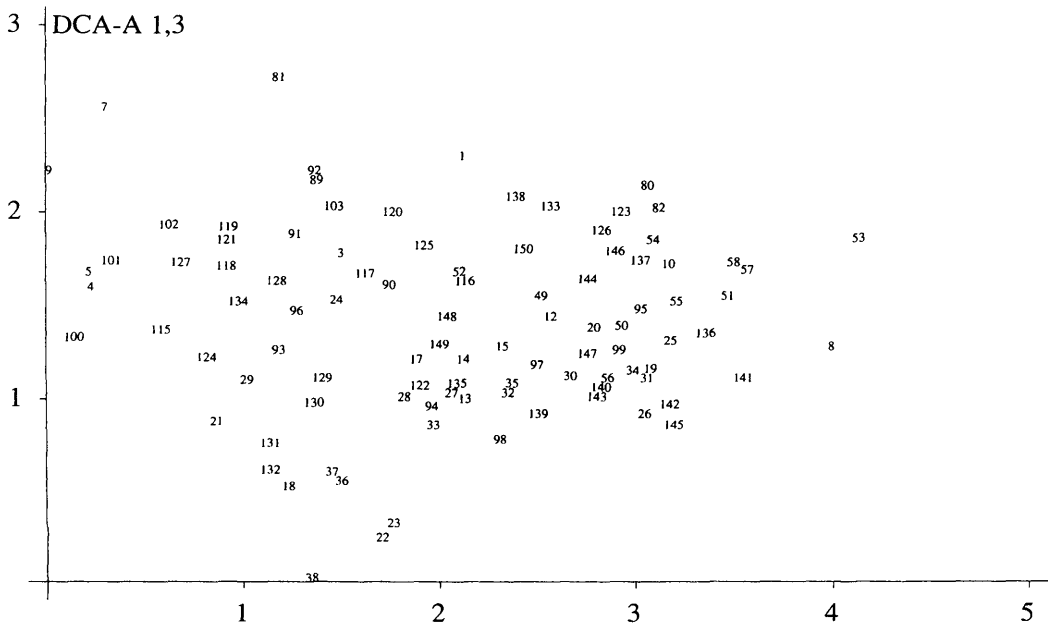
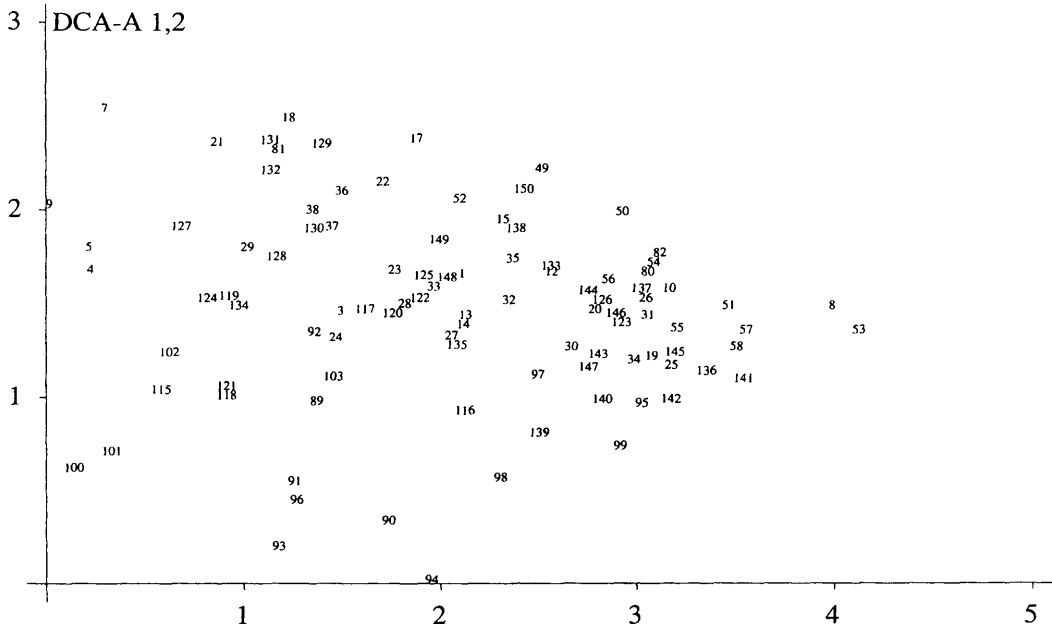
Variable	Vert Ran	Slope Avg	Slope Ma25	Slope Ma10	Dist MSoil	SoilD MVL	SoilD MWT	Canopy CAvg	Canopy CMax	Canopy CMin	Tree InfLiv	Tree InfAll	Basal Area	Crown I	Lit- terl	SnowD 0423	Wat Tab100	Wat Tab90	Wat Tab50	Wat Tab10	Wat Tab0	WatTab Ran	WatTab HMI	WatTab LMa	WatTem 0527	WatTem 0826
WatpH0527	.0540	.0594	.0677	.1402	-.1674	-.2204	-.2011	.1028	.1057	.0809	.0789	-.0099	.0871	.1291	.0932	-.0406	-.2565	-.2505	-.2185	-.1967	-.1415	-.2572	-.1791	-.1525	.3267	-.0371
WatpH0826	.0826	.0763	.0765	.1455	-.1337	-.1214	-.0990	.1100	.1284	.0380	-.0202	-.0889	-.0500	.0912	.0261	.0086	-.3338	-.3234	-.2682	-.2360	-.2194	-.3235	-.2526	-.2276	.3318	-.0018
WatEC0527	.0386	.0193	.0244	.0796	-.2160	-.2071	-.2048	.1368	.1029	.1340	.1403	.0336	.1550	.1707	.1612	-.1034	-.0185	-.0381	-.0382	-.0374	-.0162	-.0030	.0056	-.0267	.0575	-.0198
WatEC0826	.0238	.0065	.0126	.0871	-.1190	-.2028	-.1925	.1479	.0962	.1619	.0552	-.0614	.1254	.1602	.1422	.0054	-.1462	-.1318	-.0952	-.0642	-.0238	-.2492	-.1092	-.0219	.0842	-.1757
WatO0527	-.0217	-.0344	-.0052	.0166	-.0202	-.0780	-.0865	-.0036	-.0617	.0280	.0386	.0196	.0791	.0387	.0270	-.0348	.0393	.0430	.0400	.0214	.0400	.0167	.0134	.0578	-.0839	-.1111
WatO0826	-.0046	.0031	-.0026	.0733	-.0629	-.0276	-.0267	-.1546	-.1768	-.1505	-.0841	-.1222	.0331	-.0215	.0242	.0214	-.0520	-.0759	-.0866	-.0504	-.0402	-.0562	-.0402	.0830	-.0501	
SoilVolWt	.0481	.0274	.0442	.1673	-.1584	-.2449	-.2302	.1639	.1131	.1463	.0120	-.0681	.2261	.2003	.0900	.0385	-.2439	-.2533	-.2153	-.1944	-.1534	-.2618	-.1837	-.1704	.1730	-.1190
SoilLossOI	-.0184	-.0125	-.0161	-.1240	.1781	.2431	.2236	-.0544	-.0515	-.0091	.1071	.1982	-.0850	-.0588	.0157	-.0591	.3859	.3915	.3416	.3195	.2713	.3440	.3146	.2364	-.3053	.2153
SoilpHH ₂ O	-.0481	-.0449	-.0304	.0877	-.0882	-.1287	-.0962	.0203	.0333	-.0198	-.1556	-.2186	.0073	-.0198	-.1044	.0752	-.4775	-.4709	-.4081	-.3776	-.3465	-.4005	-.4049	-.2604	.3554	-.1908
SoilpHCaCl ₂	-.0391	-.0455	-.0281	.0909	-.0916	-.1418	-.1075	.0150	.0138	-.0178	-.1515	-.2110	.0068	-.0097	-.1050	.0928	-.4884	-.4843	-.4217	-.3939	-.3630	-.3903	-.4097	-.2813	.3728	-.1679
SoilCEC	-.0130	-.0073	.0108	.0242	.1586	.1570	.1819	-.0380	-.0029	-.0416	-.1385	-.0832	-.2139	-.1474	-.1983	.1341	-.2770	-.2547	-.2141	-.1992	-.2448	-.1310	-.2390	-.2248	.2040	.0799
SoilBaSat	-.0139	-.0128	.0086	.1149	.0212	-.0194	.0159	.0280	.0283	.0129	-.1246	-.1289	-.0240	-.0265	-.1360	.0964	-.4518	-.4517	-.3915	-.3673	-.3724	-.2918	-.3765	-.3379	.3250	-.0021
HumusC	.0229	.0499	.0453	-.0162	.0116	-.0472	-.0506	-.0907	-.0635	-.0888	.0362	.1137	-.0111	-.0302	-.0012	-.0919	.1351	.1146	.0987	.0857	.0628	.2219	.1198	.0430	.0197	.2068
HumusN	-.0128	-.0254	-.0049	.1331	-.1111	-.1789	-.1504	.0716	.0737	.0285	-.1400	-.1909	.1023	.0814	-.0338	.0995	-.4244	-.4241	-.3734	-.3514	-.3025	-.3577	-.3525	-.2732	.3208	-.0910
HumusP	-.0203	-.0125	-.0297	-.0118	.1390	.1210	.1065	.0636	.0104	.1038	.1169	.1287	.1265	.0677	.0221	.0409	.1964	.1856	.1618	.1488	.1112	.2028	.1572	.1145	-.2484	.1864
HumusS	-.0679	.0044	-.0345	-.0284	.0677	.0898	.1089	-.1236	-.0340	-.1985	-.2217	-.1545	-.2513	-.1332	-.1998	.0987	-.2948	-.2836	-.2587	-.2486	-.2722	-.1775	-.2779	-.2263	.2384	-.0065
HumusExAc	.0100	.0095	-.0115	-.1358	.0247	.0765	.0419	-.0514	-.0340	-.0400	.0923	.1198	-.0416	-.0241	.0909	-.0852	.4466	.4472	.3904	.3615	.3513	.3146	.3688	.3152	-.3458	.0199
HumusCa	.0090	.0039	.0291	.1247	.0271	-.0087	.0269	-.0014	.0011	-.0032	-.1298	-.1298	-.0685	-.0505	-.1421	.1156	-.4251	-.4207	-.3618	-.3410	-.3548	-.2602	-.3520	-.3516	.3320	.0049
HumusMg	.0014	.0499	.0507	.0841	.1349	.1234	.1458	.0550	.1129	.0014	-.1527	-.0844	-.1249	-.0650	-.1560	.1635	-.2430	-.2123	-.1531	-.1291	-.1746	-.2096	-.2034	-.1532	.0863	.0015
HumusK	.0534	.0632	.0609	-.0277	-.0021	-.0591	-.0890	.0412	.0139	.0574	.2196	.2102	.0864	.0958	.1657	-.1700	.3882	.3936	.3899	.3879	.3721	.2227	.3520	.3165	-.2839	.0014
HumusNa	-.0305	.0101	-.0022	.0796	.1001	.0148	.0307	.0244	.0440	-.0253	-.2094	-.1429	-.0153	-.0864	-.1425	.0839	-.2378	-.2265	-.1805	-.1521	-.1152	-.2809	-.2117	-.0906	.1308	-.0698
HumusBa	.0657	.0974	.0976	.1559	-.0156	-.0307	-.0126	-.0082	.0013	-.0205	-.0851	-.1400	-.0026	-.0013	-.0331	.0748	-.2051	-.2132	-.1762	-.1656	-.1900	-.1447	-.1528	-.2128	.2197	-.0377
HumusFe	.0251	.0194	-.0134	-.1039	.0278	.0915	.0642	-.0014	-.0032	.0224	.0925	.1769	-.0276	.0073	.0777	-.0543	.3494	.3661	.3165	.2971	.2797	.2682	.2920	.2098	-.2143	.1765
HumusMn	.0534	.0721	.0811	.1683	-.2034	-.2530	-.2385	.0691	.0579	.0402	.0017	-.1125	.0990	.1212	.0784	-.0058	-.2477	-.2329	-.1783	-.1573	-.1281	-.3003	-.1818	-.1337	.2616	-.1733
HumusSr	.0352	.0567	.0787	.1113	.0900	.0464	.0767	.0548	.0885	.0053	-.1460	-.1166	-.0957	-.0347	-.1289	.1452	-.3606	-.3323	-.2684	-.2431	-.2760	-.2776	-.2972	-.2775	.2595	.0043
HumusZn	.0759	.1318	.1274	.0823	.0205	.0250	.0191	-.0186	-.0150	.0057	.0133	.0402	.0137	-.0245	-.0541	-.0834	.1804	.1585	.1408	.1375	.1138	.1519	.1750	.0525	-.0316	.0114
HumusAl	-.0052	.0212	-.0042	-.1066	-.0576	.0266	.0038	-.0983	-.0522	-.1306	-.0034	-.0119	-.0641	-.1042	.0275	-.1235	.2538	.2481	.2064	.1824	.1852	.1777	.2050	.1710	-.1617	-.0955

Tab. 5 (continued).

Variable	WatpH 0527	WatpH 0826	WatECo 0527	WatECo 0826	WatO 0527	WatO 0826	Soil VolWt	Soil LossOI	SoilpH H ₂ O	SoilpH CaCl ₂	Soil CEC	Soil BaSat	Humus C	Humus N	Humus P	Humus S	Humus ExAc	Humus Ca	Humus Mg	Humus K	Humus Na	Humus Ba	Humus Fe	Humus Mn	Humus Sr	Humus Zn	Humus Al
VertRan	.3325	.1385	.4875	.6689	.7029	.9352	.3888	.7414	.3888	.4834	.8149	.8023	.6808	.8187	.7145	.2221	.8580	.8721	.9805	.3366	.5837	.2372	.6524	.3366	.5271	.1725	.9262
SlopeAvg	.2820	.1672	.7268	.9056	.5423	.9559	.6201	.8200	.4164	.4100	.8940	.8162	.3654	.6456	.8200	.9365	.8632	.9443	.3654	.2519	.8543	.0773	.7244	.1908	.3036	.0168	.7001
SlopeMa25	.2262	.1718	.6629	.8224	.9272	.9636	.4301	.7734	.5869	.6152	.8465	.8785	.4179	.9300	.5948	.5365	.8363	.6027	.3641	.2758	.9689	.0806	.8098	.1468	.1589	.0226	.9403
SlopeMa10	.0121	.0092	.1536	.1187	.7716	.1928	.0028	.0262	.1167	.1037	.6640	.0396	.7709	.0170	.8325	.6106	.0149	.0253	.1315	.6197	.1536	.0052	.0625	.0025	.0459	.1400	.0559
DistMSoil	.0026	.0161	.0001	.0320	.7224	.2610	.0044	.0013	.1126	.0989	.0042	.7024	.8339	.0450	.0122	.2222	.6560	.6246	.0150	.9702	.0709	.7785	.6155	.0002	.1044	.7121	.2989
SoilDMVL	.0001	.0279	.0002	.0002	.1662	.6200	.0000	.0000	.0198	.0102	.0044	.7244	.3918	.0012	.0280	.1031	.1652	.8747	.0250	.2828	.7886	.5773	.0964	.0000	.3990	.6503	.6294
SoilDMWT	.0003	.0730	.0002	.0005	.1249	.6315	.0000	.0000	.0815	.0514	.0010	.7736	.3586	.0063	.0531	.0480	.4469	.6248	.0081	.1059	.5773	.8188	.2440	.0000	.1637	.7292	.9443
CanopyCAvg	.0651	.0489	.0141	.0080	.9493	.0060	.0033	.3292	.7168	.7884	.4946	.6153	.1036	.1983	.2536	.0264	.3565	.9805	.3236	.4593	.9650	.8823	.9805	.2147	.3252	.7388	.0777
CanopyCMax	.0663	.0258	.0734	.0944	.2942	.0023	.0497	.3702	.5638	.8100	.9596	.6226	.2690	.1999	.8560	.5539	.5539	.9843	.0494	.8088	.4441	.9817	.9557	.3138	.1235	.7936	.3633
CanopyCMin	.1553	.5056	.0186	.0045	.6307	.0088	.0103	.8730	.7282	.7553	.4649	.8206	.1185	.6165	.0682	.0005	.4820	.9545	.9805	.3126	.6561	.7184	.6942	.4800	.9259	.9207	.0217
TreeInfLiv	.1567	.7178	.0118	.3223	.4983	.1344	.8298	.0543	.0053	.0066	.0129	.0254	.5160	.0119	.0357	.0001	.0975	.0197	.0061	.0001	.0002	.1264	.0965	.9753	.0087	.8109	.9520
TreeInfAll	.8581	.1073	.5423	.2656	.7274	.0280	.2174	.0003	.0001	.0001	.1307	.0194	.0389	.0005	.0195	.0050	.0297	.0184	.1254	.0001	.0095	.0110	.0013	.0411	.0342	.4656	.8289
BasalArea	.1213	.3743	.0058	.0256	.1686	.5589	.0001	.1298	.8964	.9041	.0001	.6699	.8426	.0684	.0242	.0000	.4591	.2223	.0260	.1237	.7846	.9637	.6231	.0278	.0881	.8072	.2533
CrownI	.0192	.0987	.0020	.0037	.4928	.6988	.0003	.2857	.7195	.8607	.0074	.6305	.5828	.1392	.2187	.0156	.6620	.3594	.2381	.0821	.1165	.9818	.8940	.0278	.5284	.6561	.0586
LitterI	.0983	.6432	.0042	.0116	.6389	.6703	.1109	.7808	.0644	.0625	.0004	.0158	.9830	.5481	.6945	.0004	.1066	.0116	.0056	.0032	.0113	.5568	.1677	.1637	.0220	.3367	.6246
SnowD0423	.4749	.8794	.0684	.9246	.5484	.7086	.4984	.2972	.1858	.1024	.0181	.0894	.1052	.0795	.4709	.0817	.1334	.0416	.0039	.0027	.1390	.1869	.3383	.9181	.0105	.1416	.0294
WatTab100	.0000	.0000	.7366	.0080	.4857	.3498	.0000	.0000	.0000	.0000	.0000	.0000	.0142	.0000	.0004	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0001	.0000
WatTab90	.0000	.0000	.4898	.0168	.4458	.1725	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0374	.0000	.0008	.0000	.0000	.0000	.0000	.0000	.0001	.0000	.0000	.0000	.0000	.0040
WatTab50	.0001	.0000	.4878	.0841	.4776	.1725	.0001	.0000	.0000	.0000	.0001	.0000	.0731	.0000	.0033	.0000	.0000	.0000	.0000	.0054	.0000	.0010	.0014	.0000	.0012	.0000	.0106
WatTab10	.0004	.0000	.4970	.2446	.7043	.1193	.0004	.0000	.0000	.0000	.0003	.0000	.1195	.0000	.0069	.0000	.0000	.0000	.0000	.0191	.0000	.0057	.0026	.0000	.0043	.0000	.0126
WatTab0	.0103	.0001	.7687	.6667	.4775	.3651	.0055	.0000	.0000	.0000	.0000	.0000	.2547	.0000	.0436	.0000	.0000	.0000	.0015	.0000	.0365	.0006	.0000	.0201	.0000	.0389	.0008
WatTabRan	.0000	.0000	.9572	.0000	.7692	.4750	.0000	.0000	.0000	.0000	.0188	.0000	.0001	.0000	.0003	.0015	.0000	.0000	.0002	.0001	.0000	.0094	.0000	.0000	.0000	.0064	.0014
WatTabHM	.0012	.0000	.9185	.0476	.8120	.3126	.0009	.0000	.0000	.0000	.0000	.0000	.0296	.0000	.0043	.0000	.0000	.0000	.0002	.0000	.0001	.0055	.0000	.0010	.0000	.0015	.0002
WatTabLM	.0057	.0000	.6282	.6917	.3055	.4703	.0020	.0000	.0000	.0000	.0000	.0000	.4354	.0000	.0377	.0000	.0000	.0000	.0004	.0000	.1001	.0001	.0001	.0152	.0000	.3410	.0019
WatTem0527	.0000	.0000	.2997	.1290	.1386	.1376	.0018	.0000	.0000	.0000	.0002	.0000	.7219	.0000	.0000	.0000	.0000	.0000	.1191	.0000	.0182	.0001	.0001	.0000	.0000	.5683	.0035
WatTem0826	.5060	.9740	.7229	.0016	.0514	.3734	.0331	.0001	.0006	.0026	.1519	.9702	.0002	.1025	.0008	.9068	.7217	.9300	.8504	.9792	.2105	.4987	.0015	.0019	.9378	.8376	.0865

Tab. 5 (continued).

Variable	WatpH 0527	WatpH 0826	WatECo 0527	WatCo 0826	WatO 0527	WatO 0826	Soil VolWt	Soil LossOI	SoilpH H ₂ O	SoilpH CaCl ₂	Soil CEC	Soil BaSat	Humus C	Humus N	Humus P	Humus S	Humus ExAc	Humus Ca	Humus Mg	Humus K	Humus Na	Humus Ba	Humus Fe	Humus Mn	Humus Sr	Humus Zn	Humus Al		
WatpH0527	*	.0000	.0000	.0000	.0143	.6119	.0000	.0000	.0000	.0000	.0016	.0000	.8276	.0000	.0000	.0005	.0000	.0000	.0189	.0003	.0096	.0000	.0000	.0000	.0000	.0994	.0000		
WatpH0826	.6387	*	.0000	.0000	.0134	.7785	.0000	.0000	.0000	.0000	.0000	.0000	.0246	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0012	.0000	.0000	.0000	.0000	.3352	.0000		
WatECo0527	.3461	.2669	*	.0000	.0066	.2346	.0000	.0000	.0027	.0008	.5940	.0025	.2162	.0000	.5895	.2009	.0002	.0062	.2126	.3864	.7961	.0185	.0011	.0000	.2601	.3468	.0024		
WatCo0826	.3052	.2734	.3510	*	.2729	.0857	.0000	.0000	.0000	.0000	.1481	.0000	.7961	.0000	.0793	.4063	.0000	.0000	.1423	.3468	.0741	.0019	.0002	.0000	.0038	.5553	.0000		
WatO0527	-.1382	-.1397	-.1533	-.0619	*	.0071	.1774	.4918	.4990	.2911	.0213	.0103	.7347	.1517	.6731	.0469	.0190	.0174	.0044	.0681	.0293	.4816	.3156	.4439	.0029	.8809	.0139		
WatO0826	.0283	-.0157	-.0661	-.0957	.1533	*	.1420	.0542	.0871	.1189	.0802	.6808	.8670	.1309	.2417	.5144	.3888	.9831	.2148	.4896	.6595	.9004	.1309	.2767	.4734	.4116	.7512		
SoilVolWt	.3681	.3695	.3410	.3299	-.0762	.0819	*	.0000	.0000	.0000	.8530	.0000	.0801	.0000	.2217	.3900	.0000	.0000	.0155	.0001	.0127	.0000	.0000	.0000	.0000	.2601	.0000		
SoilLossOI	-.4441	-.4677	-.2361	-.3063	.0388	-.1071	-.5919	*	.0000	.0000	.0308	.0000	.0047	.0000	.0000	.0004	.0000	.0000	.0015	.0000	.0001	.0000	.0000	.0000	.0000	.2720	.0006		
SoilpHH ₂ O	.4210	.4706	.1658	.2805	-.0382	.0954	.4095	-.6690	*	.0000	.0000	.0000	.0007	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0519	.0000	
SoilpHCaCl ₂	.4508	.4982	.1849	.2926	-.0596	.0869	.4533	-.7016	.9106	*	.0000	.0000	.0052	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0288	.0000	
SoilCEC	.1745	.2575	-.0294	.0798	-.1298	-.0973	.0102	-.1190	.3282	.3351	*	.0000	.9689	.0101	.1362	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0668	.0000	.0210	.0000
SoilBaSat	.3814	.4664	.1671	.2526	-.1447	.0229	.4419	-.4718	.6101	.6534	.5037	*	.1345	.0000	.0594	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0637	.0000	
HumusC	-.0120	-.1241	.0681	-.0142	-.0191	-.0093	-.0967	.1557	-.1881	-.1541	.0021	-.0825	*	.0510	.0292	.6156	.1105	.3811	.0383	.0000	.0067	.1345	.0000	.1215	.0455	.7936	.5167		
HumusN	.4219	.4564	.2451	.2918	-.0808	.0840	.6705	-.6677	.5514	.5894	.1418	.5341	-.1075	*	.0021	.0039	.0000	.0000	.0004	.0000	.0000	.0000	.0000	.0000	.0000	.1161	.0000		
HumusP	-.2318	-.2315	-.0297	-.0968	.0238	-.0651	-.0675	.2927	-.3472	-.3235	-.0821	-.1039	.1201	-.1695	*	.0000	.0437	.0162	.6632	.0005	.0157	.0046	.0000	.0000	.1127	.1509	.0007		
HumusS	.1925	.2612	-.0705	-.0458	-.1120	.0363	-.0475	-.1946	.2857	.2813	.2809	.2338	.0277	.1590	-.2706	*	.0009	.0000	.0000	.0002	.0000	.0000	.0000	.0050	.0000	.3535	.5488		
HumusExAc	-.4219	-.4839	-.2089	-.2855	.1323	-.0480	-.5372	.5353	-.6436	-.4056	-.8767	.0879	-.6130	.1111	-.1836	*	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.1001	.0000		
HumusCa	.3636	.4471	.1509	.2517	-.1341	.0012	.3856	-.4606	.5926	.6387	.5816	.8526	-.0482	.4847	-.1324	.2444	-.7857	*	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0801	.0000		
HumusMg	.1294	.2691	-.0687	.0809	-.1605	-.0690	.1336	-.1745	.3209	.3179	.4977	.4983	-.1141	.1955	.0240	.2637	.3605	.4899	*	.0010	.0000	.0000	.0000	.0000	.0083	.0000	.9339	.0000	
HumusK	-.2013	-.2940	-.0477	-.0519	.1028	-.0384	-.2194	.3170	-.3582	-.3702	-.2916	-.3904	.2818	-.3618	.1913	-.2020	.3605	-.3988	-.1805	*	.0149	.0000	.0000	.0597	.0000	.0004	.0022		
HumusNa	.1428	.1790	-.0142	.0985	-.1229	.0245	.1376	-.2205	.3173	.2895	.2273	.2684	-.1494	.2440	-.1330	.3355	-.2574	.2528	.3162	-.1341	*	.0000	.0000	.0013	.0000	.2886	.0142		
HumusBa	.2540	.3313	.1298	.1714	-.0397	.0070	.3650	-.4479	.4031	.4190	.2252	.4110	-.0824	.4438	-.1562	.2285	-.4259	.4543	.2281	-.2609	.2240	*	.0000	.0000	.0411	.0170			
HumusFe	-.3916	-.4542	-.1792	-.2067	.0566	-.0840	-.4102	.5089	-.6275	-.6246	-.2687	-.5818	.2256	-.4978	.2252	-.2338	.6087	-.5130	-.3301	.3299	-.2770	-.3707	*	.0000	.0000	.2671	.0000		
HumusMn	.4590	.4309	.2544	.3293	-.0432	.0605	.4450	-.5710	.5009	.5117	.1010	.3216	-.0853	.4867	-.2901	.1547	-.4076	.3473	.1454	-.1037	.1774	.3965	-.4198	*	.0000	.2211	.0004		
HumusSr	.3074	.4388	.0621	.1594	-.1680	-.0399	.3255	-.3820	.4959	.5196	.5485	.6985	-.1102	.4260	-.0873	.3278	-.6410	.7165	.6578	-.3541	.3498	.4776	-.4665	.2818	*	.2629	.0000		
HumusZn	-.0909	-.0532	-.0518	-.0325	.0084	.0457	-.0622	.0605	-.1073	-.1206	-.1271	-.1022	.0144	-.0865	.0791	.0511	.0906	-.0964	.0046	.1964	.0584	.1125	.0611	.0674	-.0617	*	.1657		
HumusAl	-.2360	-.2838	-.1672	-.2404	.1386	.0176	-.3555	.1892	-.2881	-.3254	-.3732	-.5902	.0357	-.3262	-.1865	.0330	.6010	-.5329	-.4012	.1683	-.1350	-.1315	.3562	-.1966	-.4087	.0763	*		



Figs 27–28. DCA ordination of Subset A (poor swamp forests; 98 1-m² plots). Plot numbers are plotted onto plot positions. Scaling of axes in S.D. units. Fig. 27. Axes 1 (horizontal) and 2. Fig. 28. Axes 1 (horizontal) and 3.

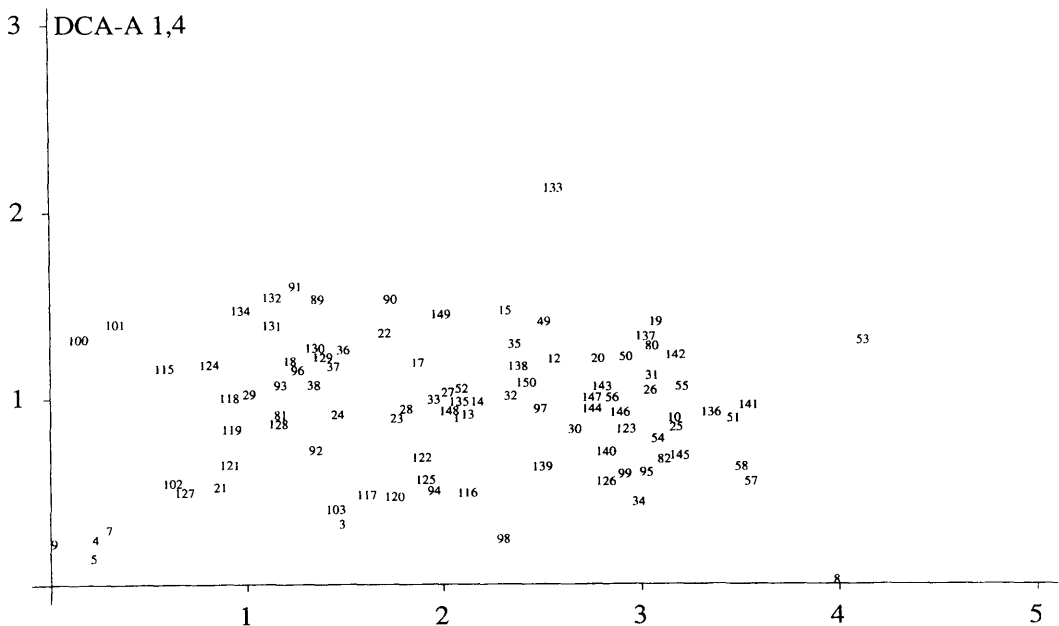


Fig. 29. DCA ordination of Subset A (poor swamp forests; 98 1-m² plots), axes 1 (horizontal) and 4. Plot numbers are plotted onto plot positions. Scaling of axes in S.D. units.

The largest compact group, *the soil nutrient/acidity group*, consisted of nine variables. Soil-pH (two variables), base saturation and the concentration of Ca were very strongly positively correlated with each other ($|\tau| > 0.50$) and strongly negatively correlated with exchangeable acidity and the concentration of Fe. pH measured in tube water on 26 August and Total N made up the rest of this group. Arrowheads representing the direction of strongest increase in these nine variables in the space spanned by PCA axes 1 and 2 were strongly clustered, all variables had negative loadings on PCA-axis 2 (Fig. 6). Eight other variables, also with high loadings on PCA-axis 1 and low loadings on PCA-axis 2 [PCA 2 < 0.0(-0.2)], were strongly correlated ($|\tau| > 0.40$) with four or more variables (most often Ca, base saturation, exchangeable acidity and pH) of the compact soil nutrient/acidity group (Tab. 5, Fig. 8). These eight variables were mostly not strongly correlated with each other (Tab. 5), but made up a gradient from Sr, Ba, Mg and cation exchange capacity which were most strongly correlated with Ca, via water-pH measured on 27 May which was most strongly correlated with water-pH 26 August; Al which was most strongly correlated with exchangeable acidity; volume weight which was most strongly correlated with total N; and Mn which was most strongly correlated with loss on ignition.

A closer look at four variables of the soil nutrient/acidity group (water-pH on 26 August, soil pH measured in H₂O, Ca and total N; all untransformed) revealed that the distribution of water pH was bimodal with modes for pH = 4.0 and 5.0 and a separating antimode at pH = 4.5 (Fig. 9), while the three others were more or less uniformly distributed (Figs 10–12). Due to the bimodality of water pH, the plots made up two (more or less distinct) clusters in a graph of water pH plotted against each of the other three variables (Figs 13–15). No clustering of plots could

be seen in graphs of soil pH vs calcium (Fig. 16) or soil pH vs total N (Fig. 17).

The other large compact group, *the water-table group*, consisted of six variables (depths from the average vertical level to five characteristic water-table levels, and depth from the highest level in a plot to the minimum water table) that were very strongly correlated ($|\tau| > 0.60$) and had closely similar loadings on the first two PCA ordination axes [PCA 1 > 0.7 , $0.3 < \text{PCA } 2 < 0.5$].

Considerable covariation occurred between variables of the soil nutrient/acidity and the water-table groups, as demonstrated by strong correlations between members of the two groups, most strongly between depth to the minimum (and lower decile) level(s) and soil pH ($|\tau| = -0.49$; Fig. 8, Tab. 5). pH, base saturation and the concentrations of total-nitrogen and calcium thus increased strongly while soil acidity and loss on ignition, among other variables, decreased with increasing depth to the water table. Six variables in addition to five of the eight variables that were strongly associated with the soil nutrient/acidity group had their vector arrowheads placed between those of variables in the two large compact groups in the space spanned by PCA-axes 1 and 2 (Figs 6, 8). These six variables made up a gradient from stronger relationship with the water-table group to stronger relationship with the soil nutrient/acidity group: the range of

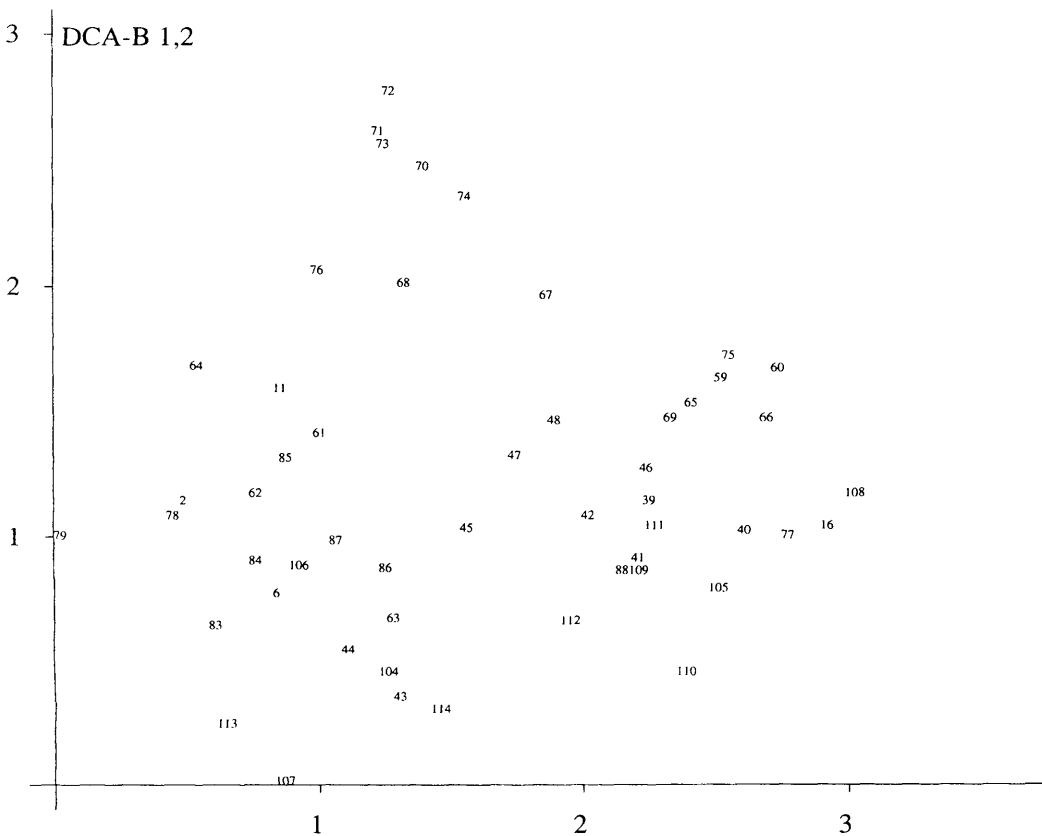


Fig. 30. DCA ordination of Subset B (richer swamp forests; 52 1-m² plots), axes 1 (horizontal) and 2. Plot numbers are plotted onto plot positions. Scaling of axes in S.D. units.

water-table fluctuations [PCA 2 \approx -0.15] and depth from the lowest-situated point on the bottom-layer surface to the maximum water table exemplify the former while the concentrations of sodium and sulphur are examples of the latter.

The *microtopography group* consisted of vertical range and the three slope measurements, with pair-wise correlations $|\tau| > 0.45$ (Tab. 5). This group was connected to the water-table group by positive, moderately strong correlations between several pairs of variables (largest $|\tau| = 0.35$).

The *tree influence group* consisted of seven variables of which six made up two compact, three-member subgroups with pair-wise $|\tau| > 0.40$ (Fig. 8, Tab. 5). The canopy coverage measurements (by densiometer) made up one subgroup, the other consisted of the litter and crown cover indices and the tree influence index based upon living trees. The subgroups were connected by the strong correlation between average canopy cover and the crown cover index. The seventh variable, the tree influence index based upon all (including dead) trees, was strongly correlated only with the tree influence index based upon living trees ($|\tau| = 0.52$). The eighth tree-layer variable, basal area, was only weakly correlated with the variables of this group ($0.13 < \tau < 0.29$).

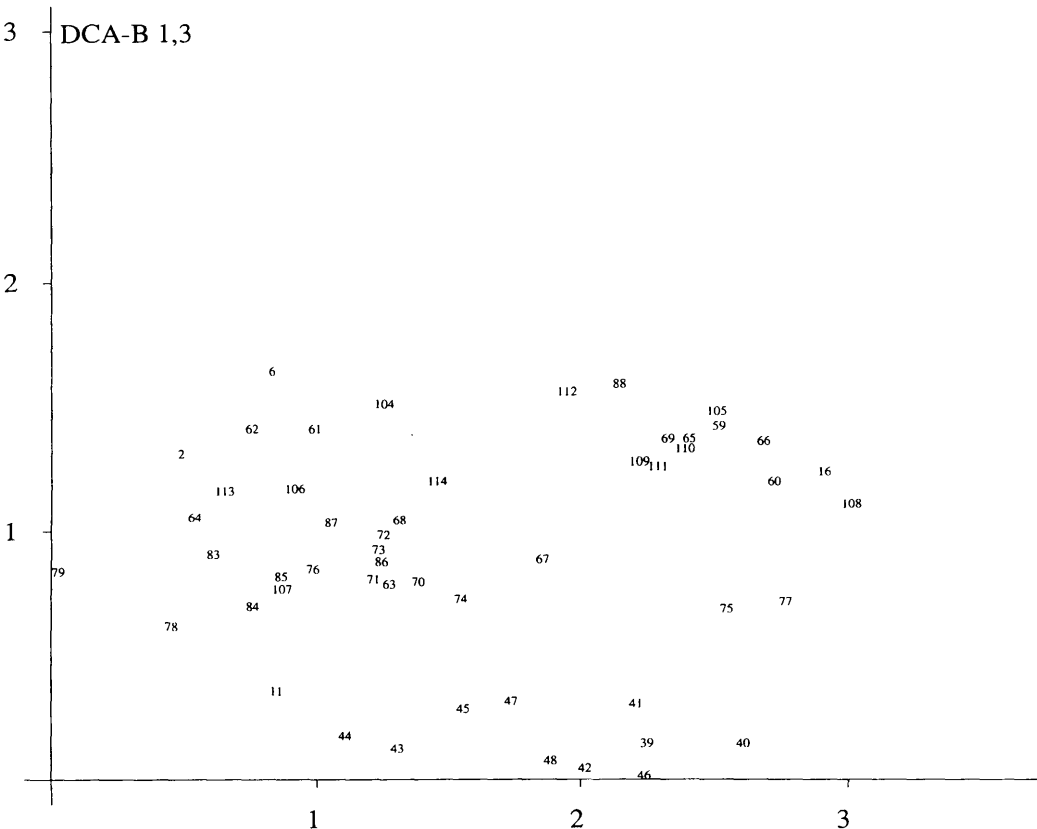


Fig. 31. DCA ordination of Subset B (richer swamp forests; 52 1-m² plots), axes 1 (horizontal) and 3. Plot numbers are plotted onto plot positions. Scaling of axes in S.D. units.

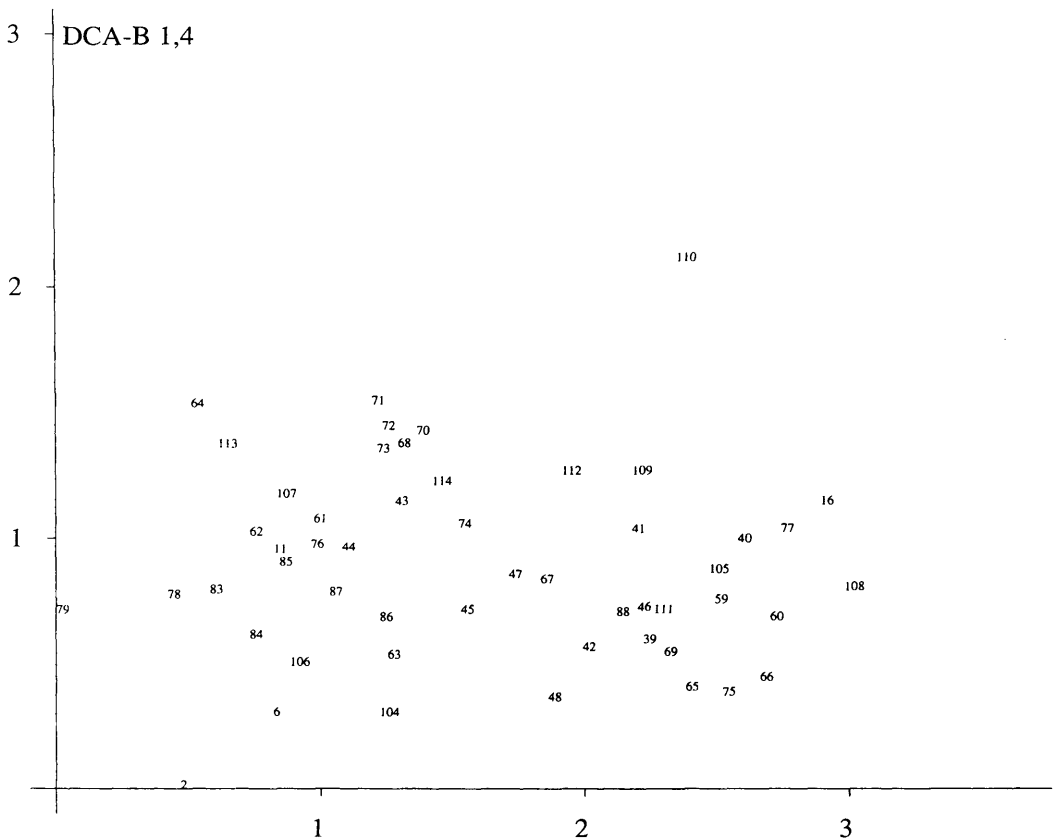
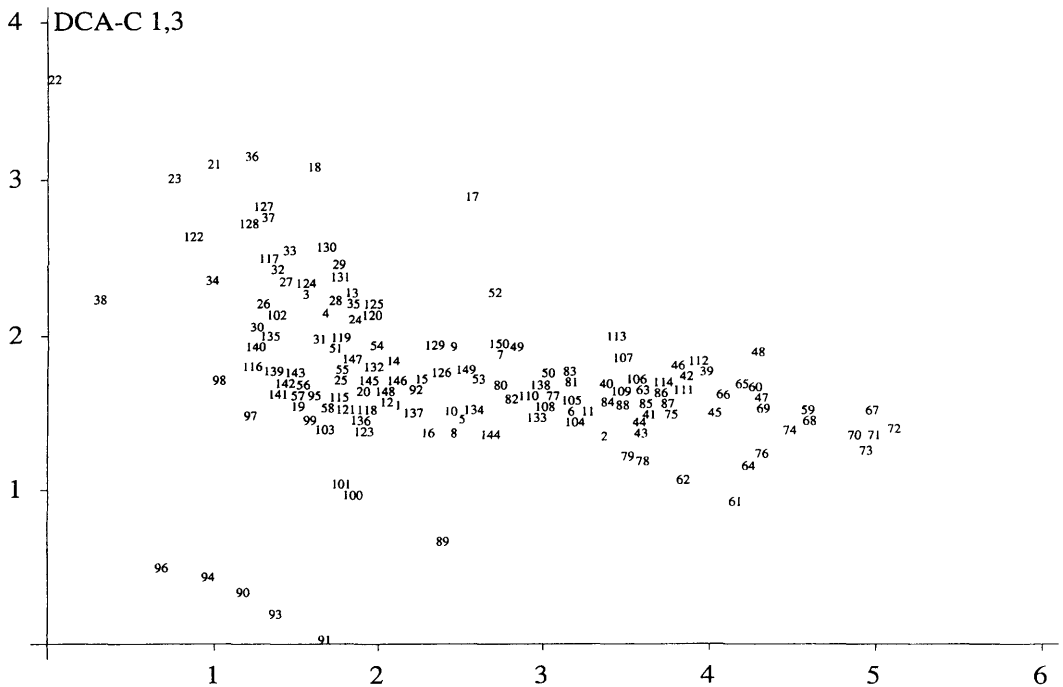
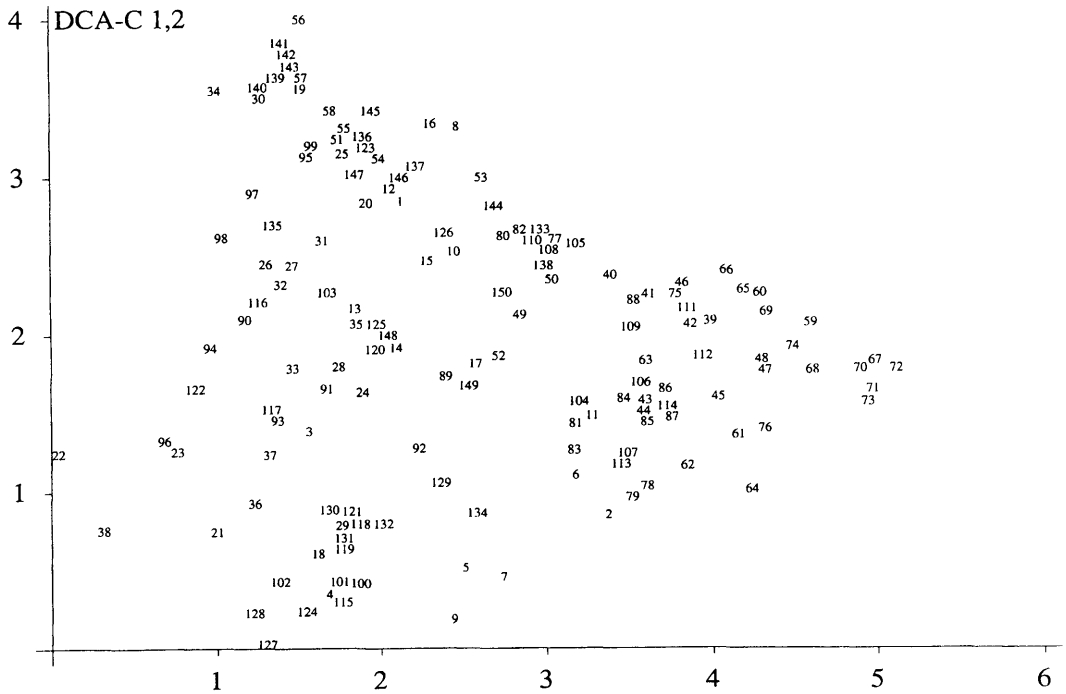


Fig. 32. DCA ordination of Subset B (richer swamp forests; 52 1-m² plots), axes 1 (horizontal) and 4. Plot numbers are plotted onto plot positions. Scaling of axes in S.D. units.

A positive relationship between tree influence and depth to the water table (stronger tree influence at large depths to the water table) was demonstrated by the correlations between the tree influence index based upon all trees and several variables of the water-table group (largest $|\tau| = 0.33$; Tab. 5, Fig. 8) and by arrowhead positions in the PCA ordination (Fig. 6). A weaker relationship was observed between the microtopography and tree influence groups (largest $|\tau| = 0.24$). Microtopographic variation thus tended to be more extensive (with steeper slope and higher vertical range) at sites beneath trees with high depths to the water table.

Distance from the plot to the border of the swamp-forest onto mineral soil made up the compact *soil-depth group* together with the two soil depth measurements (pair-wise $|\tau| > 0.40$). Variables in this group were weakly related to the soil nutrient/acidity group (by correlations with loss on ignition, volume weight and the concentration of Mn; largest $|\tau| = 0.25$), thus indicating a tendency for the uppermost layer of thick peat deposits to be looser and to have higher organic matter content than the uppermost layer of shallower peat layers.



Figs 33–34. DCA ordination of Subset C (vascular plants; 150 1-m² plots). Plot numbers are plotted onto plot positions. Scaling of axes in S.D. units. Fig. 33. Axes 1 (horizontal) and 2. Fig. 34. Axes 1 (horizontal) and 3.

ORDINATION OF VEGETATION

Characteristics of ordinations and comparison of ordination axes

DCA ordination of the full data set

The first two axes of the DCA ordination of the full data set had high eigenvalues (0.594 and 0.413) and gradient lengths of 4.63 and 3.64 S.D. units, respectively. No plots acted as outliers,

Tab. 6. Ordinations of vegetation: summary of axis properties. Gradient length is given in S.D. units. ETIR – eigenvalue-to-total inertia ratio. Core length – length of the shortest interval containing 90% of the plots relative to gradient length. Total inertia for the reduced data set is the sum of eigenvalues for all CA ordination axes. Gradient length and eigenvalue of LNMDS axes are calculated for the corresponding DCCA axis (see text).

Method	Data set		Ordination axis					
	Data set	No. of plots	Total inertia	Axis No.	Grad. length	Core length	Eigenvalue	ETIR
DCA	Full data set	150	5.521	1	4.628	0.713	0.594	0.108
				2	3.639	0.720	0.413	0.075
				3	2.672	0.541	0.215	0.039
				4	2.342	0.693	0.161	0.029
DCA-S	Full data set, subplots passive	150 +2400	5.521	1	5.547			
				2	4.504			
				3	3.709			
				4	3.640			
LNMDS	Reduced data set	125	5.404*	1	4.057	0.801	0.587	0.109
				2	3.454	0.728	0.424	0.078
				3	1.996	0.736	0.178	0.033
				4	2.184	0.519	0.134	0.025
DCA-A	Subset A (poor swamp forests)	98	4.341	1	4.091	0.721	0.498	0.115
				2	2.515	0.663	0.247	0.057
				3	2.699	0.570	0.198	0.046
				4	2.096	0.543	0.119	0.027
DCA-B	Subset B (richer swamp forests)	52	3.188	1	2.977	0.748	0.369	0.116
				2	2.763	0.743	0.267	0.084
				3	1.625	0.865	0.147	0.046
				4	2.095	0.536	0.099	0.031
DCA-C	Subset C (vascular plants)	150	5.996	1	5.070	0.654	0.609	0.102
				2	3.971	0.769	0.448	0.075
				3	3.615	0.472	0.291	0.049
				4	2.717	0.514	0.174	0.029
DCA-D	Subset D (cryptogams)	150	4.820	1	4.759	0.780	0.640	0.133
				2	3.746	0.674	0.406	0.084
				3	3.024	0.503	0.254	0.053
				4	2.569	0.543	0.177	0.037

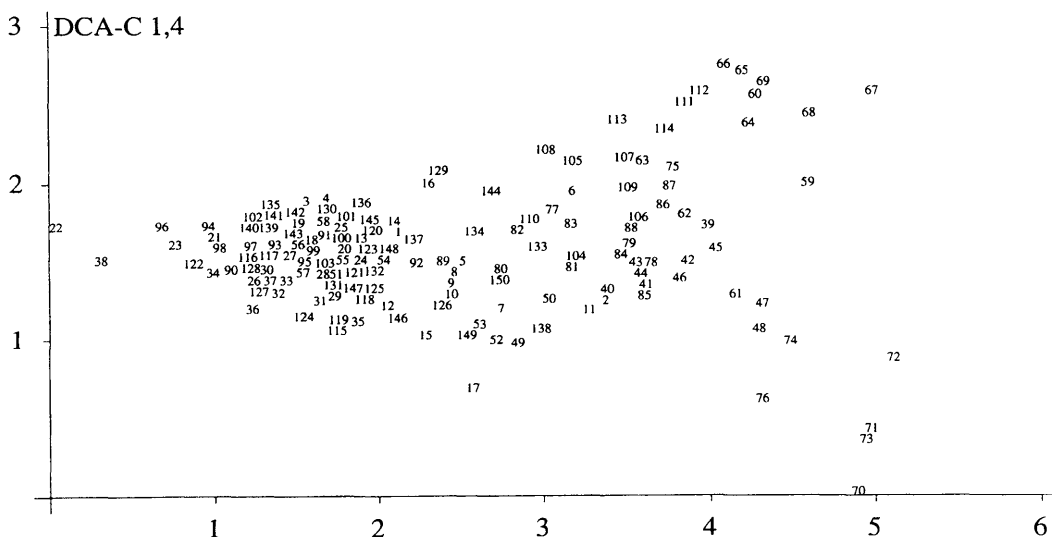


Fig. 35. DCA ordination of Subset C (vascular plants; 150 1-m² plots), axes 1 (horizontal) and 4. Plot numbers are plotted onto plot positions. Scaling of axes in S.D. units.

as judged by core length (Tab. 6). Considerable reduction of eigenvalue, gradient length and core length occurred from axis 2 to axis 3.

Two intervals along DCA 1 with high plot density (at 0.4–1.8 and at 3.2–4.3 S.D. units) were separated by a sparse region (relative discontinuity) at 1.9–2.6 S.D. units along the axis (Fig. 18). This motivated separate analyses of two subsets (Subset A, with DCA-axis 1 score, $x_{Full, 1} < 2.50$, and Subset B, with $x_{Full, 1} > 2.50$; p. 27). No sparse region was observed along DCA ordination axes 2–4 (Figs 18–20). DCA-1 scores below 0.7 were only obtained for plots from swamp-forest localities 2, 8 and 11 (Fig. 21). All plots from swamp-forest localities 2, 4, 10 and 11 had low DCA-1 scores ($x_{Full, 1} < 2.0$). The seven plots from swamp-forest locality 6 were among the nine plots with the highest DCA-axis 1 scores. All plots from the four swamp-forest localities 6, 3, 9 and 5 had high DCA-1 scores ($x_{Full, 1} > 2.5$), and all plots from swamp-forest locality 7 had $x_{Full, 1} > 2.0$. Only two swamp-forest localities, 1 and 8, were thus represented on both sides of the sparse region along DCA-axis 1.

The low- and high-score ends of DCA-axis 2 were occupied by plots 9 and 8, respectively (Fig. 18); two plots from swamp-forest locality 1 that were separated in space by just 1.3 m (Fig. 2). Plots in Subset A ($x_{Full, 1} < 2.5$) spanned a wider interval along DCA-axis 2 than plots in Subset B (Fig. 18). Most swamp-forest localities (3, 4 and 6 excepted) were represented by plots over most of DCA-axis 2 (Figs 18, 21).

Due to clustering of plots between 0.8 and 2.0 S.D. units (Fig. 19), DCA-axis 3 obtained a small relative core length (Tab. 6). The low-score end of this axis was made up by plots from swamp-forest locality 8. As for DCA-axis 2, plots in Subset A spanned a wider interval along DCA-axis 3 than plots in Subset B (the latter only spanning an interval of *c.* 1.2 S.D. units). Plots from the same swamp-forest locality tended to form clusters along this axis to such an extent that the swamp-forest localities replaced each other along the axis [in the order: 8; 4 and 10; 11, 1 and 2 (Subset A), and 9; 7 and 8; 6; 3 and 5 (Subset B; Fig. 22)].

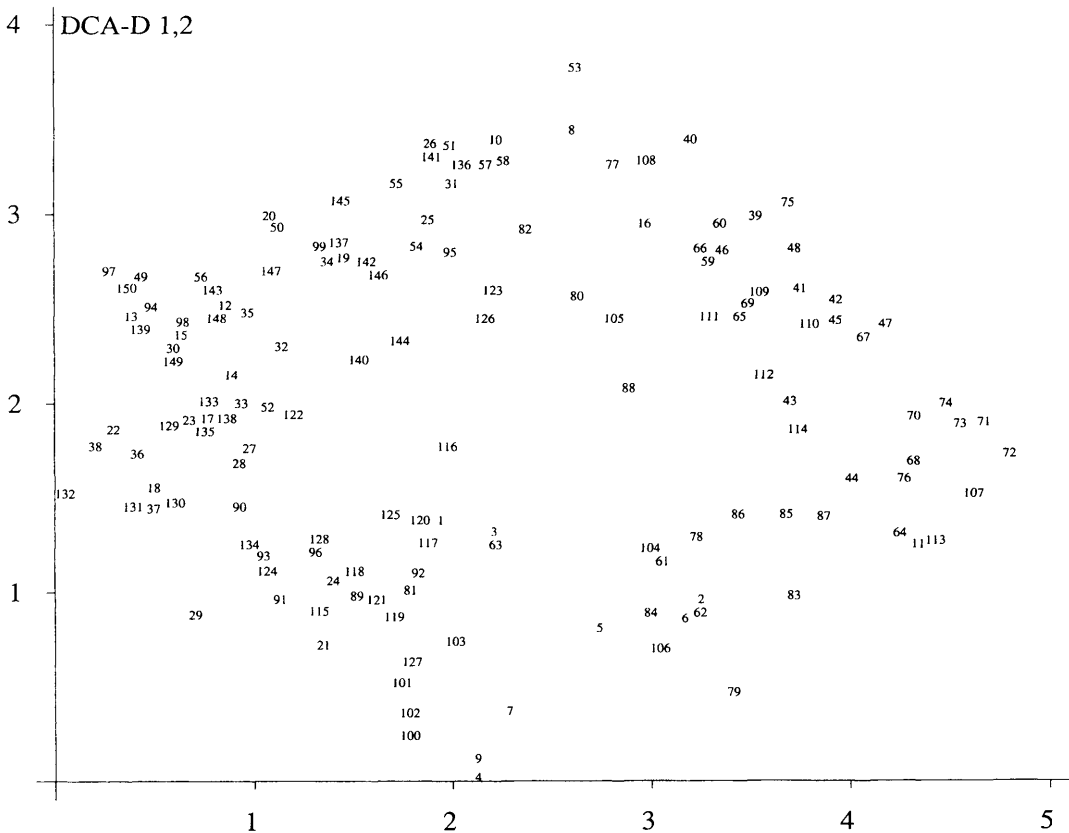


Fig. 36. DCA ordination of Subset D (cryptogams; 150 1-m² plots), axes 1 (horizontal) and 2. Plot numbers are plotted onto plot positions. Scaling of axes in S.D. units.

Within all intervals along DCA-axis 1, plots were relatively evenly distributed along DCA-axis 2 (relative core length = 0.693; Tab. 6, Fig. 20). A weak tendency was observed for plots from the same swamp-forest locality to form clusters along this axis (Fig. 23): plots from swamp-forest localities 4, 7 and 11 mostly obtained relatively low, and plots from 5, 8 and 10 relatively high, scores.

Plots placed by additional criteria (spring influence, outlet and inlet) did not form detectable patterns (aggregations) along any axis.

When the 2400 subplots were passively fit into the DCA ordination of the full data set, the gradient length of all axes increased by *c.* 1 S.D. unit (Tab. 6) due to the occurrence of subplots outside the range spanned by the 1-m² plots.

LNMSD ordination of the reduced data set

The first two axes in the LNMSD ordination of the reduced data set (125 plots) were very strongly correlated with the corresponding axes in the DCA ordination of the full data set ($\tau >$

0.8; Tab. 7). Apart from the smaller gradient length (as estimated by DCCA) of the first axis, the diagrams for the first two axes of the LNMDS and DCA ordinations were closely similar (compare Figs 18 and 24). Plots in Subset A spanned approximately the same interval along axes 1 (measured in S.D. units) in the two ordinations. The sparse region was, however, slightly broader and the interval spanned by Subset-B plots shorter (1.6 vs 2.2 S.D. units, respectively) along LNMDS 1 than along DCA 1.

The third LNMDS axis was strongly correlated with the fourth DCA axis ($\tau = 0.53$; Tab. 7). The two axes also had similar eigenvalues, gradient lengths, relative core lengths and patterns of plot scatter (Tab. 6). A comparison between Figs 25 and 20 showed that the correspondence between scores along LNMDS-axis 3 and DCA-axis 4 was better for plots with low scores than for plots with high scores along the two axes.

The fourth LNMDS axis was not strongly correlated with any of the axes in the DCA ordination of the full data set (Tab. 7). Low attributed eigenvalue (Tab. 6) and aggregation of the bulk of plots near the middle of the axis (Tab. 6, Fig. 26) indicated that this axis did not represent an important gradient in species composition.

Tab. 7. Kendall's rank correlation coefficients τ between plot scores along axes of the DCA ordination of the full data set and axes of other plot ordinations, and significance probabilities (P). Strong correlations ($|\tau| \geq 0.4$, $P < 0.0001$) in bold face. Highest absolute value of τ for each DCA axis with an axis in each of the other ordinations italicized. n - number of plots (in smallest data set).

Ordination	n	Axis No.	DCA 1		DCA 2		DCA 3		DCA 4	
			τ	P	τ	P	τ	P	τ	P
LMNDS	125	1	.8480	.0000	-.1288	.0332	-.0836	.1667	.0839	.1654
		2	.0991	.1012	.8390	.0000	-.0206	.7328	-.0054	.9286
		3	-.0316	.6011	-.0159	.7929	-.2262	.0002	.5287	.0000
		4	.0129	.8310	-.0075	.9015	-.0914	.1308	.2392	.0001
DCA-A	98	1	.1563	.0228	.9253	.0000	-.1285	.0612	-.2722	.0001
		2	.0270	.6944	-.1598	.0200	.7596	.0000	-.1977	.0040
		3	.6133	.0000	-.0711	.3009	-.1735	.0115	-.0318	.6430
		4	-.2046	.0029	-.0167	.8084	.1628	.0179	-.1535	.0256
DCA-B	52	1	-.1125	.2396	.9128	.0000	.4069	.0000	.6259	.0000
		2	.4370	.0000	.1340	.1623	.4036	.0000	.2370	.0135
		3	-.1474	.1238	-.0234	.8067	-.2019	.0351	.2941	.0021
		4	.2338	.0147	-.0129	.8932	-.3171	.0009	-.1082	.2590
DCA-C	150	1	.7299	.0000	-.0110	.8416	.0570	.3006	-.1017	.0647
		2	-.0548	.3200	.7940	.0000	-.1246	.0237	-.1037	.0603
		3	-.3512	.0000	-.0166	.7637	.3736	.0000	.0094	.8645
		4	.1097	.0463	.0666	.2267	-.1523	.0057	.1992	.0003
DCA-D	150	1	.8250	.0000	-.0040	.9417	-.1397	.0012	.0599	.2770
		2	.0268	.6271	.8081	.0000	.0794	.1495	-.0543	.3240
		3	.2802	.0000	-.3305	.0000	.2118	.0001	.2356	.0000
		4	-.0501	.3628	-.0916	.0961	-.1072	.0516	.4954	.0000

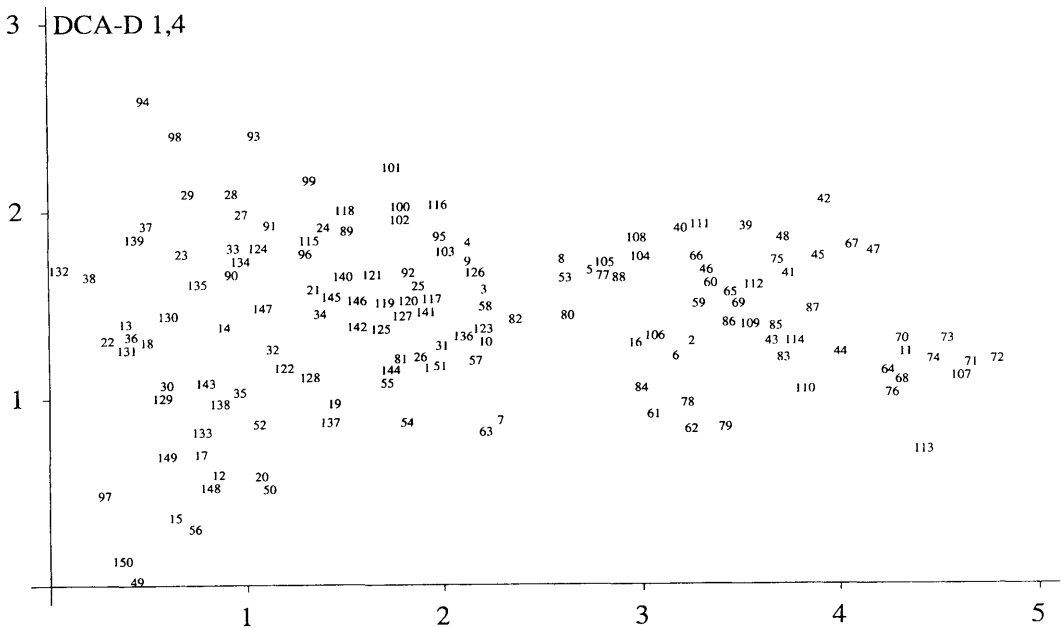


Fig. 38. DCA ordination of Subset D (cryptogams; 150 1-m² plots), axes 1 (horizontal) and 4. Plot numbers are plotted onto plot positions. Scaling of axes in S.D. units.

set were in close correspondence (Tab. 7, also compare Figs 18 and 30). The gradient length of DCA-B 1 did, however, exceed the interval (in S.D. units) along DCA-2 spanned by plots in Subset B. DCA-B 1 was also correlated with the third and fourth axes of the DCA ordination of the full data set, indicating that the coenoclines corresponding to axes 2-4 in the DCA ordination of the full data set together formed one vegetation gradient in Subset B. The considerably lower eigenvalue of DCA-B 1 than of DCA-2 indicated that the former coenocline was less strong in Subset B than in Subset A (and in the full data set).

The second DCA-B axis was correlated with the first as well as the third axis in the DCA ordination of the full data set (Tab. 7). The correlation between DCA-B 2 and DCA 1 mainly reflected the separation of plots from swamp-forest localities 5 and 6 from the remainder of plots near the high-score end of the axes (Figs 19, 30), while the correlation between DCA-B2 and DCA 3 was mainly due to the low scores along both axes attributed to several plots from swamp-forest locality 9. The third and fourth axes in the DCA ordination of Subset B had low eigenvalues and gradient lengths and were only weakly correlated with axes in the DCA ordination of the full data set (Tab. 7). In part, these axes were influenced by outliers or groups of outliers (Figs 31-32, Tab. 6).

Subset C (vascular plants). The first two axes in the ordination of vascular plants were strongly correlated ($0.7 < \tau < 0.8$) with the corresponding axes in the DCA ordination of the full data set (Tab. 7), but DCA-C axes had larger eigenvalues and gradient lengths than the DCA axes, and the two-dimensional point configurations were visually different (compare Figs 18 and 33). Although no sparse region occurred along DCA-C 1 (Fig. 33), no plot switched to the other side of the vaguely indicated subset divide in the ordination of vascular plants. The scattering of

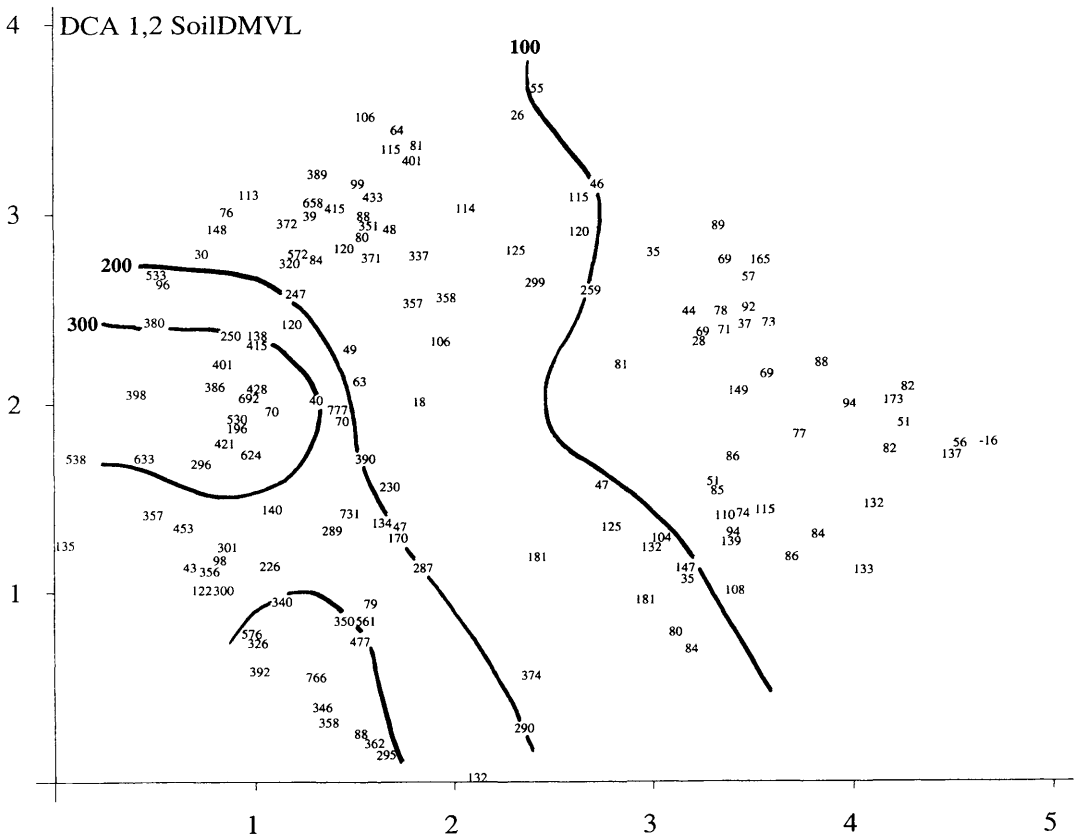


Fig. 39. DCA ordination of the full data set (150 1-m² plots), axis 1 (horizontal) and 2: values for soil depth (in cm), measured from mean vertical level in the plot, plotted onto plot positions, and isolines found by block kriging. Crossvalidation $r^2 = 0.323$.

Subset-B plots along DCA-C 2 was less strong than along DCA 2 (compare Figs 18 and 33).

The third axis in the ordination of vascular plants was correlated (although not strongly) with DCA 3 based upon the full data set (Tab. 7). The bulk of the plots were strongly clustered near the mid-point of the axis ($x_{C,3} \approx 1.5$ S.D. units; Fig. 34). The correlation between the third axes in the two ordinations mainly resulted from the aggregation of plots from swamp-forest locality 8 close to the low-score ends of both. Plots from swamp-forest locality 2 occupied the high-score end of DCA-C 3. The fourth axis in the ordination of vascular plants was only weakly correlated with any axis (most strongly with DCA 4) in the ordination of the full data set, and separation along DCA-C 4 was only observed for plots with high DCA-1 scores (Tab. 6, Fig. 35). The similarity between the two fourth axes mainly resulted from the high scores obtained by plots from swamp-forest locality 5 (Nos 59–69) along both.

Subset D (cryptogams). The first two axes in the DCA ordination of cryptogams corresponded closely to axes 1 and 2 in the ordination of the full data set, with respect to correlations between plot positions ($\tau > 0.8$; Tab. 7), eigenvalues and gradient lengths (Tab. 6),

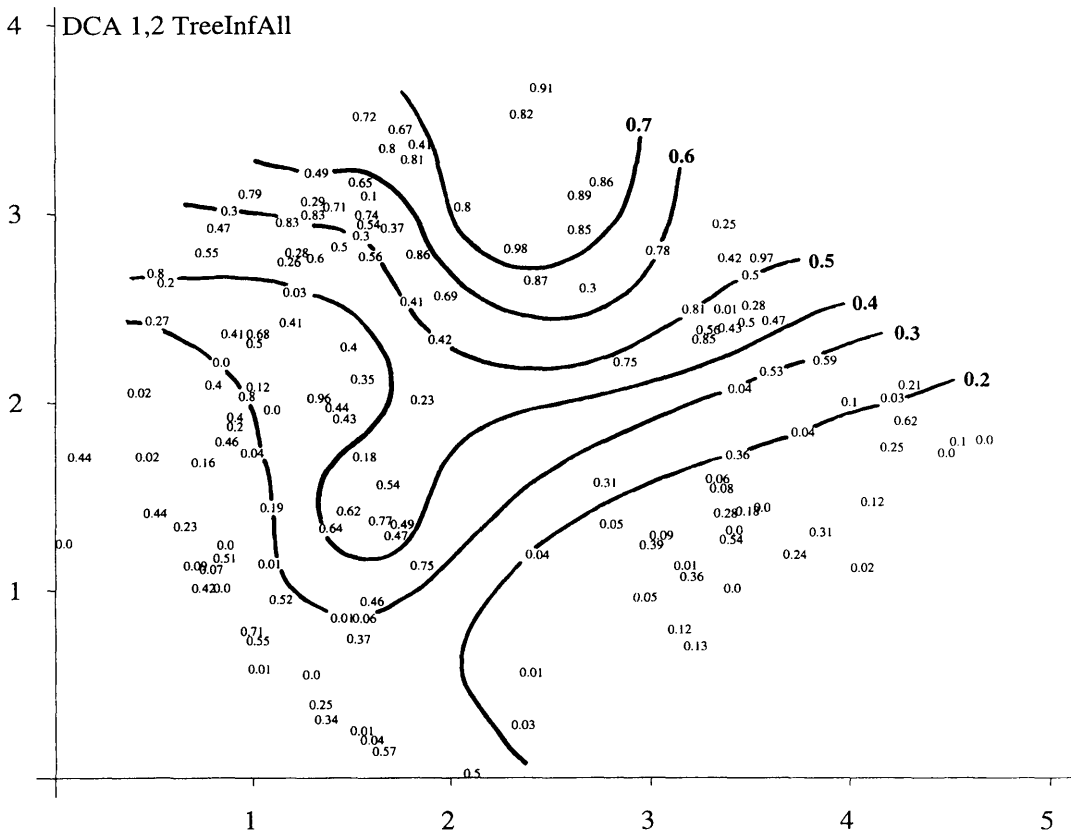


Fig. 40. DCA ordination of the full data set (150 1-m² plots), axis 1 (horizontal) and 2: values for the tree influence index, based upon living and standing and fallen dead trees, and stumps, plotted onto plot positions, and isolines found by block kriging. Crossvalidation $r^2 = 0.293$.

and point configurations (compare Figs 18 and 36). Noticeable differences between corresponding axes in the two ordinations were the sparse region along the first axis which was more displaced towards the high-score end of DCA-D 1, and the spread of Subset-A plots relative to Subset-B plots (relative compositional turnover) which was more extensive along DCA-D 1 than along DCA 1.

The third axis in the DCA ordination of cryptogams mainly separated plots in Subset B near the high-score end of DCA-D 1 (Fig. 37). This axis was not strongly correlated with any axis in the ordination of the full data set (Tab. 7). Low scores along this axis were obtained by plots in swamp-forest localities 3 and 9 while high scores were obtained by plots in swamp-forest locality 6 and some spring-influenced plots (plots 64, 67, 83, 85-87).

Even though DCA-D 4 was strongly correlated with DCA 4 (Tab. 7) and the point clouds in Figs 19 and 38 were similarly shaped, there were considerable differences as to the positions of individual plots along these axes.

Except for the slight tendency for spring-influenced plots to aggregate near the high-score

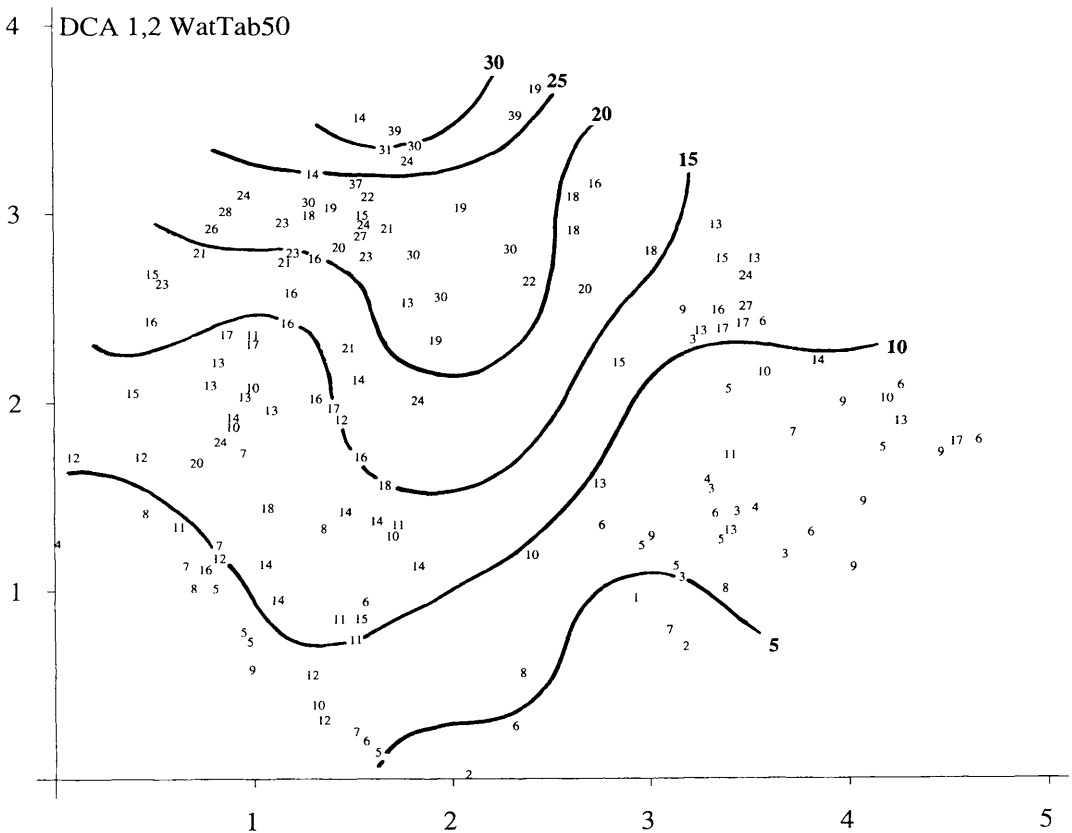


Fig. 41. DCA ordination of the full data set (150 1-m² plots), axis 1 (horizontal) and 2: values for depth from the average vertical level of bottom-layer surface to the median measured water table (i.e., the 50% exceedance level; in cm), plotted onto plot positions, and isolines found by block kriging. Crossvalidation $r^2 = 0.596$.

end of DCA-D 3, no tendencies for plots placed by additional criteria (spring influence, outlet and inlet) to show noticeable distributional patterns along any axis in any subset ordination could be observed.

Relationships between ordination axes and explanatory variables

DCA ordination of the full data set

Thirteen explanatory variables were strongly correlated ($|\tau| > 0.30$) with axis 1 in the DCA ordination of the full data set (see isoline diagrams; Figs 39–50): eight variables of the soil nutrient/acidity group, three variables associated with this group (soil volume weight, pH measured in tube water 27–28 May 1998, and the concentration of Mn in peat), and the two soil

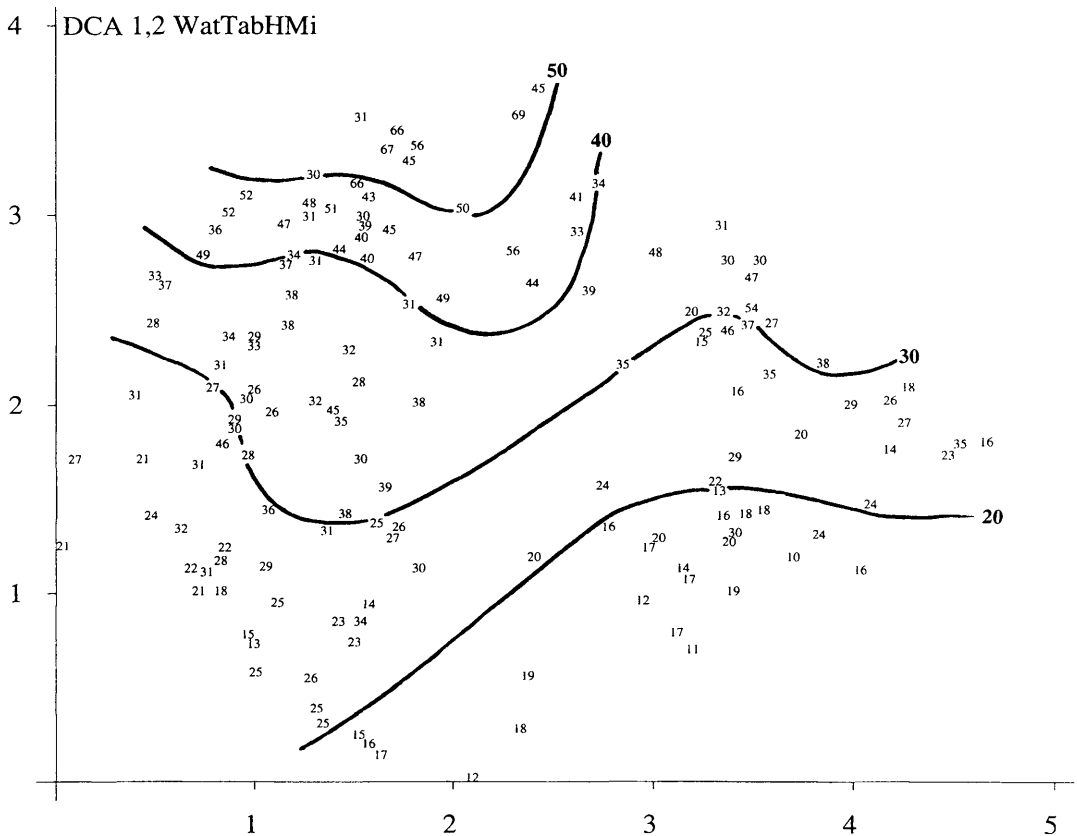


Fig. 42. DCA ordination of the full data set (150 1-m² plots), axis 1 (horizontal) and 2: values for depth from highest-situated level of bottom-layer surface to minimum water table (in cm), plotted onto plot positions, and isolines found by block kriging. Crossvalidation $r^2 = 0.610$.

depth variables (Tab. 8). As also indicated by the (passively obtained) position for the arrowhead of the DCA-1 vector in the PCA ordination of explanatory variables (Fig. 6), the variables most strongly correlated with this axis ($|\tau| > 0.45$) were soil volume weight, the concentrations of Mn (Fig. 50) and total N (Fig. 46), and loss on ignition (Fig. 44). Concentrations of most elements in peat increased along DCA-axis 1 (Fe and Al concentrations decreased), while acidity (of soil and tube water; Figs 43, 45), soil organic matter and soil depth (Fig. 39) decreased along the axis.

The patterns of variation along DCA-axis 1 varied considerably among variables strongly correlated with the axis. Loss on ignition (Fig. 44) and the concentrations of total N (Fig. 46) and Mn (Fig. 50) showed maximal rates of change per unit compositional change (S.D.-unit) at the transition from Subset A (poor swamp forests) to Subset B (richer swamp forests). For instance, loss on ignition was mostly above 88% for DCA-1 plot scores ($x_{Full,1}$) < 2.0 and rarely above 83% for $x_{Full,1} > 3.0$. Furthermore, the concentration of total N (in the organic peat fraction) was mostly below 22 ppt (2.2%) for $x_{Full,1} < 2.0$ and above 26 ppt for $x_{Full,1} > 3.0$. Within each subset neither loss on ignition nor the N concentration varied along DCA-axis 1 in a consistent manner.

Tab. 8. Kendall's rank correlation coefficients τ between plot scores along DCA axes (the full data set; $n = 150$) and LNMDS axes (the reduced data set; $m = 125$) and the 53 explanatory variables, with significance probabilities (P). Strong correlations ($|\tau| \geq 0.3$, $P < 0.0001$) in bold face. Highest absolute value of τ for each ordination axis is italicized. Names of explanatory variables abbreviated in accordance with Tab. 2.

Variable	DCA 1		DCA 2		DCA 3		DCA 4		LNMDS 1		LNMDS 2		LNMDS 3		LNMDS 4	
	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P
VertRan	.0638	.2517	.2517	.0000	-.0594	.2854	.2580	.0000	.0654	.2838	.3224	.0000	.1922	.0016	.1418	.0202
SlopeAvg	.0393	.4756	.2604	.0000	-.0691	.2102	.2301	.0000	.0291	.6311	.3307	.0000	.2214	.0003	.0797	.1879
SlopeMa25	.0656	.2402	.2272	.0000	-.0416	.4563	.2639	.0000	.0764	.2123	.2807	.0000	.2191	.0003	.1436	.0190
SlopeMa10	.1623	.0036	.1438	.0099	-.0772	.1662	.2093	.0002	.1993	.0011	.2228	.0003	<i>.2611</i>	<i>.0000</i>	.0385	.5286
DistMSoil	-.2484	.0000	-.0751	.1757	-.0834	.1327	.1192	.0315	-.2251	.0002	-.1068	.0793	.1410	.0205	-.0234	.7007
SoilDMVL	-.3457	.0000	-.1366	.0131	-.0382	.4878	.1638	.0029	-.3277	.0000	-.2018	.0008	.1607	.0079	.0764	.2065
SoilDMWT	-.3272	.0000	-.1773	.0013	-.0405	.4617	.1637	.0030	-.3032	.0000	-.2397	.0001	.1645	.0065	.0679	.2616
CanopyCAvg	-.1772	.0015	-.2205	.0001	.0573	.3033	-.0658	.2371	.0867	.1562	.2569	.0000	-.0630	.3023	.1987	.0012
CanopyCMax	-.1131	.0490	-.1665	.0038	.0765	.1832	-.0956	.0960	.0396	.5305	.1832	.0037	-.0213	.7359	.1748	.0056
CanopyCMin	-.1835	.0013	-.2644	.0000	.0070	.9026	-.0255	.6537	.0880	.1591	.3271	.0000	-.0884	.1572	.1860	.0029
TreeInfLiv	.0748	.1793	.3167	.0000	.0956	.0859	.1139	.0407	.0001	.9983	.3746	.0000	-.0408	.5047	.1802	.0032
TreeInfAll	-.0080	.8850	.3511	.0000	.0726	.1876	.0921	.0945	-.0637	.2918	.3832	.0000	.0587	.3316	.1515	.0122
BasalArea	.1779	.0015	.1567	.0052	.0692	.2174	-.0579	.3022	.1137	.0648	.2016	.0011	-.1236	.0448	.0000	1.0000
CrownI	.1956	.0004	.2058	.0002	-.0306	.5784	.0877	.1113	.1361	.0244	.2974	.0000	-.0240	.6914	.1483	.0142
LitterI	.1506	.0075	.2807	.0000	.0550	.3285	.0828	.1412	.0576	.3524	.3228	.0000	-.0337	.5860	.0888	.1516
SnowD0423	.0464	.4137	-.1263	.0260	-.0395	.4861	.0499	.3792	.0579	.3532	-.1539	.0136	.0810	.1938	.1250	.0450
WatTab100	-.1752	.0015	.5418	.0000	.0493	.3706	-.0960	.0812	-.2975	.0000	.4921	.0000	-.0883	.1444	-.0169	.7798
WatTab90	-.1771	.0013	.5513	.0000	.0083	.8799	-.0549	.3192	-.2870	.0000	.4939	.0000	-.0561	.3532	.0413	.4947
WatTab50	-.1476	.0074	.5350	.0000	-.0445	.4193	-.0092	.8671	-.2452	.0001	.4965	.0000	-.0174	.7733	.0754	.2127
WatTab10	-.1296	.0186	.5239	.0000	-.0773	.1603	.0013	.9818	-.2147	.0004	.4999	.0000	-.0061	.9201	.0813	.1788
WatTab0	-.0581	.2916	.5601	.0000	-.0581	.2916	-.0352	.5231	-.1360	.0245	.5426	.0000	-.0308	.6100	.0423	.4839
WatTabRan	-.2633	.0000	.2198	.0001	.1177	.0348	-.1331	.0170	-.3433	.0000	.1474	.0161	-.1206	.0489	-.0517	.3989
WatTabHMa	-.1130	.0401	.5580	.0000	.0277	.6156	-.0076	.8901	-.2220	.0002	.5356	.0000	-.0342	.5717	.0403	.5055
WatTabLMi	-.0958	.0821	.3151	.0000	-.0011	.9844	-.1831	.0009	-.1732	.0042	.2687	.0000	-.1697	.0050	-.0075	.9015
WatTem0527	.1178	.0334	-.3435	.0000	.0159	.7736	.1205	.0295	.2049	.0008	-.2814	.0000	.1012	.0959	.0512	.3991
WatTem0826	-.2758	.0000	-.0245	.6606	.0103	.8529	.1131	.0424	-.2102	.0006	-.0282	.6446	.1341	.0283	.0734	.2301
WatpH0527	.3651	.0000	-.2156	.0001	-.0622	.2594	.1106	.0449	.4170	.0000	-.1253	.0384	.0771	.2026	.0522	.3886
WatpH0826	.3093	.0000	-.3164	.0000	-.1304	.0182	.1797	.0011	.3946	.0000	-.2047	.0007	.1498	.0135	.0664	.2736

Tab. 8 (continued).

Variable	DCA 1		DCA 2		DCA 3		DCA 4		LNMDS 1		LNMDS 2		LNMDS 3		LNMDS 4	
	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P
WatO0527	.0015	.9792	.1063	.0592	.1142	.0427	-.0020	.9714	-.0099	.8725	.0830	.1797	-.0675	.2752	.0163	.7924
WatO0826	.0663	.2333	-.0366	.5102	-.0741	.1830	.0131	.8136	.0903	.1389	-.0231	.7055	.1621	.0079	-.2016	.0010
SoilVolWt	.5174	.0000	-.0557	.3129	-.0749	.1748	.1099	.0465	.5353	.0000	.0203	.7376	.0657	.2783	-.0087	.8863
SoilLossOI	-.4785	.0000	.2612	.0000	-.0077	.8889	-.1371	.0128	-.5648	.0000	.1895	.0017	-.0510	.3993	.0398	.5110
SoilpHH ₂ O	.4232	.0000	-.3740	.0000	-.0808	.1436	.1255	.0231	.5155	.0000	-.2766	.0000	.0839	.1666	.0038	.9506
SoilpHCaCl ₂	.4375	.0000	-.3817	.0000	-.0774	.1608	.1332	.0158	.5359	.0000	-.2791	.0000	.0905	.1352	.0219	.7183
SoilCEC	.0435	.4297	-.3054	.0000	-.1461	.0080	.1226	.0260	.1007	.0960	-.2883	.0000	.1207	.0460	.2323	.0001
SoilBaSat	.3218	.0000	-.3571	.0000	-.1469	.0077	.1761	.0014	.3999	.0000	-.2650	.0000	.1716	.0046	.0957	.1138
HumusC	-.1164	.0345	.0822	.1353	.0507	.3569	-.0149	.7861	-.0950	.1163	.0625	.3017	.0239	.6930	.0175	.7716
HumusN	.4835	.0000	-.2585	.0000	-.0298	.5884	.1375	.0125	.5618	.0000	-.1850	.0022	.0667	.2699	-.0023	.9694
HumusP	-.1750	.0015	.2148	.0001	-.0283	.6076	-.0365	.5073	-.2138	.0004	.1594	.0084	.0343	.5703	.0058	.9235
HumusS	-.0429	.4364	-.4151	.0000	-.0021	.9702	.1298	.0184	.0524	.3863	-.4008	.0000	.1439	.0173	-.0565	.3499
HumusExAc	-.3969	.0000	.3229	.0000	.1384	.0120	-.1683	.0023	-.4728	.0000	.2262	.0002	-.1596	.0083	-.0740	.2214
HumusCa	.2940	.0000	-.3668	.0000	-.1134	.0395	.1807	.0010	.3732	.0000	-.2818	.0000	.1565	.0096	.1254	.0381
HumusMg	.0609	.2685	-.2580	.0000	-.2548	.0000	.1689	.0022	.1205	.0462	-.2351	.0001	.2378	.0001	.1345	.0262
HumusK	-.1524	.0057	.3258	.0000	-.0353	.5210	-.0799	.1467	-.1874	.0019	.2880	.0000	-.0631	.2967	-.0196	.7457
HumusNa	.1109	.0441	-.1604	.0036	-.1443	.0088	.0115	.8340	.1559	.0099	-.1037	.0862	.0574	.3423	-.0929	.1244
HumusBa	.2634	.0000	-.2281	.0000	.1084	.0491	.1468	.0077	.3081	.0000	-.1817	.0027	.0040	.9472	.0392	.5165
HumusFe	-.4062	.0000	.2936	.0000	.1236	.0248	-.1751	.0015	-.4926	.0000	.2083	.0006	-.1369	.0236	.0225	.7104
HumusMn	.5039	.0000	-.1798	.0011	-.0455	.4082	.1422	.0098	.5505	.0000	-.1210	.0453	.0399	.5096	.0570	.3456
HumusSr	.2052	.0002	-.3485	.0000	-.1653	.0027	.1846	.0008	.2844	.0000	-.2834	.0000	.1746	.0039	.1197	.0477
HumusZn	-.0704	.2009	.0932	.0907	.0058	.9159	.0060	.9133	-.0800	.1858	.0655	.2783	.0646	.2850	-.0511	.3981
HumusAl	-.2521	.0000	.1331	.0157	.2766	.0000	-.1059	.0546	-.2877	.0000	.0715	.2371	-.1914	.0016	-.1695	.0050

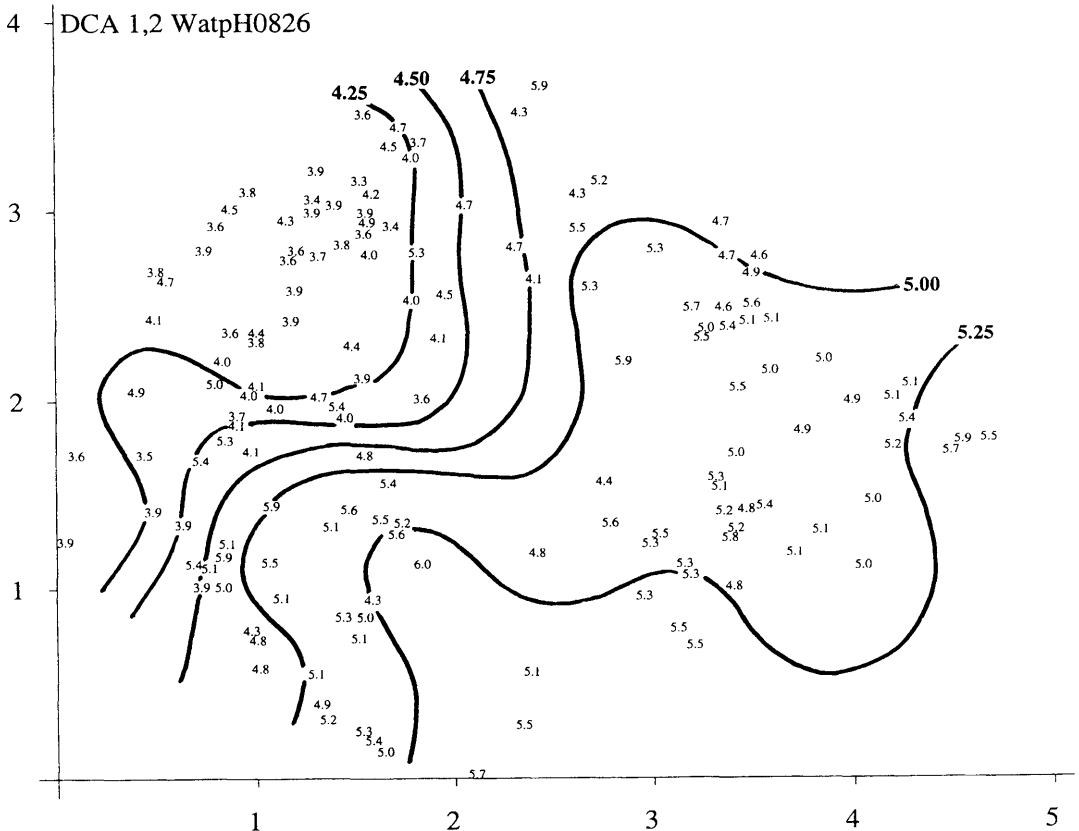


Fig. 43. DCA ordination of the full data set (150 1-m² plots), axis 1 (horizontal) and 2: values for pH in tube water, 26 Aug 1998, plotted onto plot positions, and isolines found by block kriging. Crossvalidation $r^2 = 0.441$.

Soil depth was mostly lower than 1.2 m in Subset B, while considerable variation in soil depth was observed in Subset-A plots (Fig. 39). High pH values, in tube water (Fig. 43) as well as in soil (Fig. 45), and low concentrations of Fe in soil (Fig. 49) were observed for $x_{Full, 1} > 3.0$, and also for low DCA-1 scores when $x_{Full, 2}$ was also low. The division into two subsets did not coincide with the bimodality in any of the explanatory variables, neither did it correspond with the two groups visible in the graphs of water pH vs soil pH or water pH vs total-N concentration (Figs 51–52).

The weak, negative, relationship ($-0.18 < \tau < -0.12$, $0.001 < P < 0.02$) between depth to the water table and position along DCA 1 (Tab. 8) arose because a majority of Subset-B plots had low depths to the water table (Figs 42, 45). Plots with high DCA-1 score also had a narrower range of water-table fluctuation in the 1998 season than Subset-A plots, as demonstrated by the negative correlation between water-table range and DCA 1 (Tab. 8).

The six variables of the water-table group, among which DCA 2 was placed in the PCA ordination (Fig. 6), were particularly strongly correlated with DCA-axis 2 ($\tau > 0.50$). As many

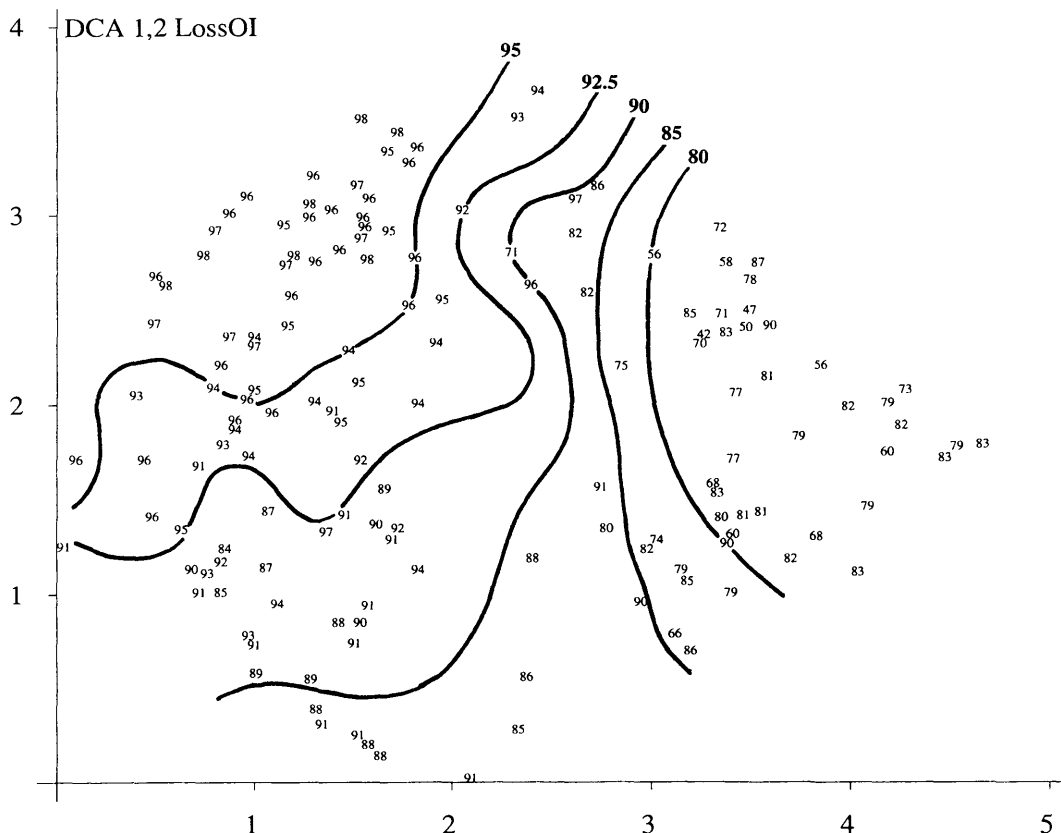


Fig. 44. DCA ordination of the full data set (150 1-m² plots), axis 1 (horizontal) and 2: loss on ignition in surface peat (in %), plotted onto plot positions, and isolines found by block kriging. Crossvalidation $r^2 = 0.641$.

as fourteen additional explanatory variables were strongly correlated ($|\tau| > 0.30$) with DCA-axis 2 (Figs 41–42, Tab. 8): the two tree influence indices (positively; Fig. 40) and several variables of, and associated with, the soil nutrient/acidity group (Tab. 8, Figs 43, 45, 47, 48). Depth to the water table, tree influence and peat acidity thus increased with increasing plot score along DCA-axis 2, while the concentrations of N, S and Ca in surface peat decreased.

Relative to DCA ordination axes 1 and 2, isolines for depth to the water table ran more or less parallel with the second axis (Figs 41–42) except for some deflection towards lower DCA-2 scores between 1 and 2 S.D. units along DCA 1. This indicated a tendency for plots with DCA-2 score of a given magnitude to be situated at a relatively greater depth to the water table if it was placed in this interval along DCA-axis 1. A deflection in the opposite direction occurred for $x_{Full, 1} > 3.0$, i.e. in Subset B (richer swamp forest), where plots with DCA-2 score of a given magnitude had relatively lower depths to the water table than plots with lower $x_{Full, 1}$. Soil concentrations of sulfur decreased regularly with increasing DCA-2 score for plots in Subset A, while this relationship was less strong in Subset B (Fig. 47).

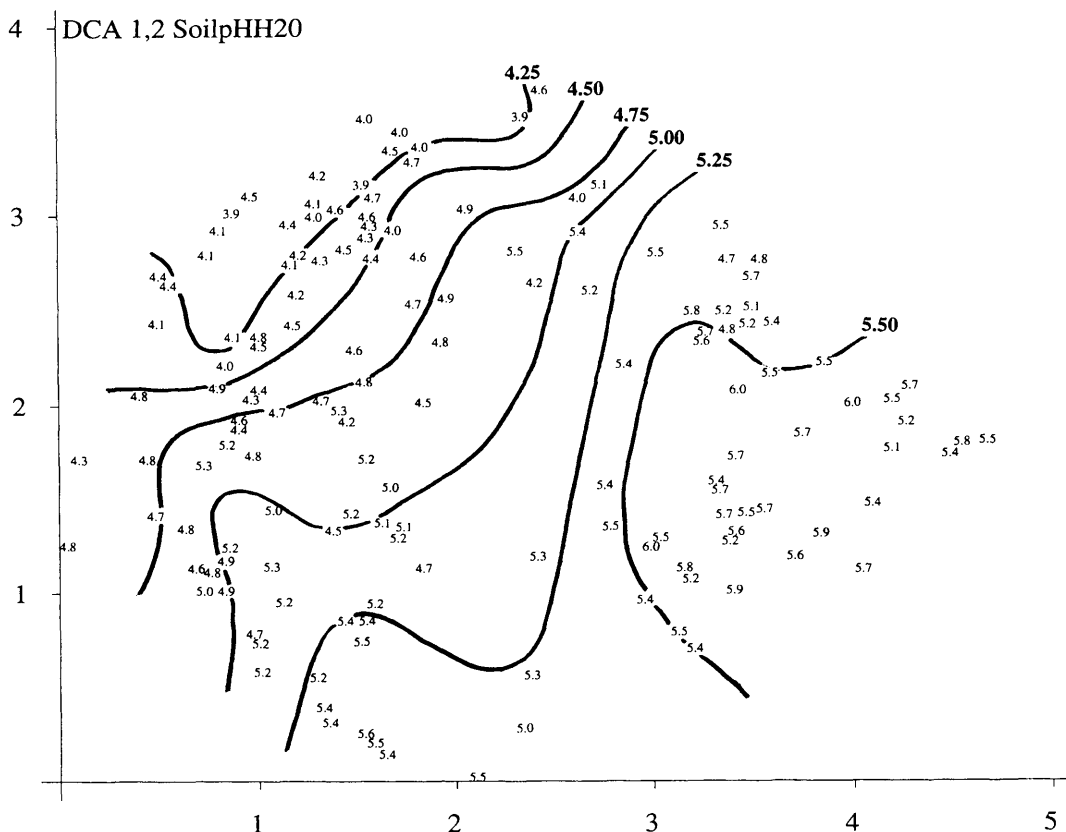


Fig. 45. DCA ordination of the full data set (150 1-m² plots), axis 1 (horizontal) and 2: pH in aqueous suspension of surface peat, plotted onto plot positions, and isolines found by block kriging. Crossvalidation $r^2 = 0.574$.

Variables strongly correlated with one or both of the first two DCA ordination axes could be ordered along a three-step gradient: (1) Variables strongly positively correlated with DCA 1 and not or only weakly correlated with DCA 2, and hence with direction of steepest descent more or less parallel with DCA-axis 1. Typical examples were the concentrations of total N (Fig. 46) and Mn (Fig. 50) and loss on ignition (Fig. 44), which obtained high, positive, loadings on PCA-axis 2 (for variables strongly negatively correlated with DCA-axis 1, the loadings of conjugate variables were high and positive). (2) Variables more or less strongly correlated both with DCA axes 1 and 2 and hence with directions of steepest descent coinciding with the diagonal in the ordination diagram [e.g. pH (Figs 43, 45), Fe (Fig. 49) and Ca concentrations (Fig. 48) and the range of water-table fluctuations]. Most of these variables showed variation along DCA-axis 2 in Subset A but hardly in Subset B. (3) Variables such as depth to the water table (several variables; see Figs 41–42 for examples), S concentration (Fig. 47) and tree influence (Fig. 40), which were strongly positively correlated with DCA 2 and not or only weakly correlated with DCA 1, and that obtained high positive loadings on both of PCA-axes 1 and 2 (Fig. 6).

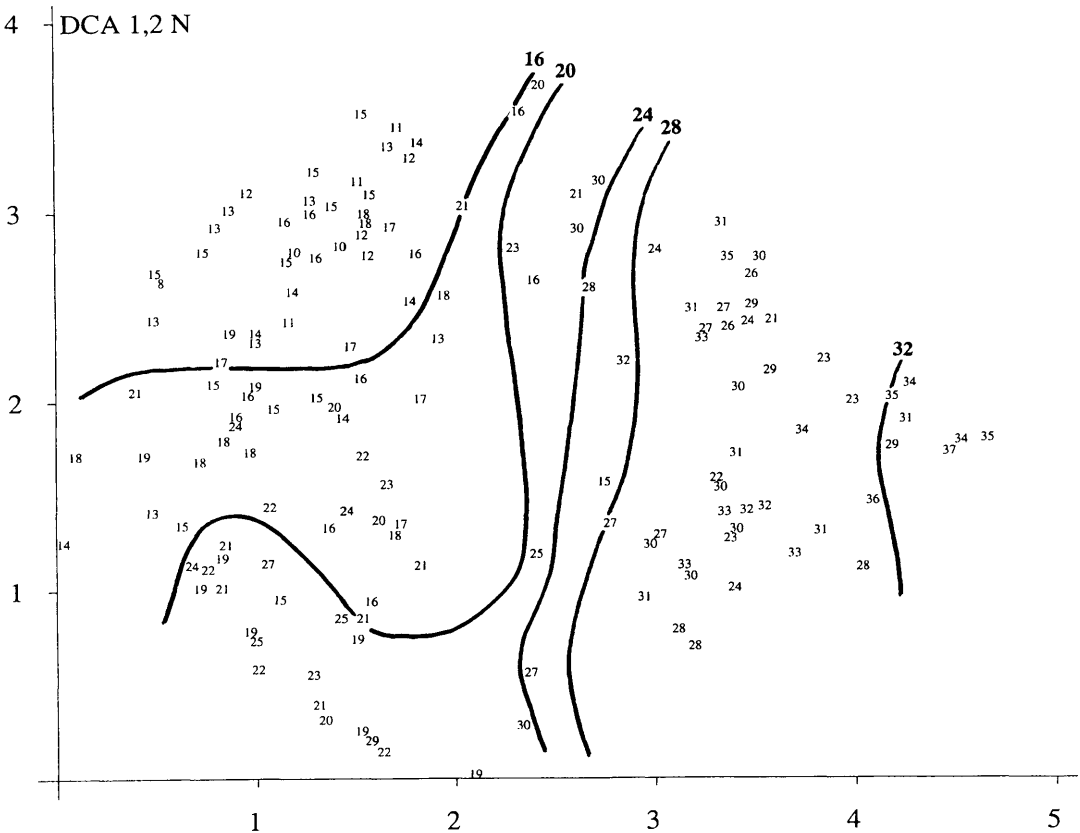


Fig. 46. DCA ordination of the full data set (150 1-m² plots), axis 1 (horizontal) and 2: total N in organic fraction of surface peat (ppt), plotted onto plot positions, and isolines found by block kriging. Crossvalidation $r^2 = 0.697$.

None of the 53 explanatory variables were strongly correlated with DCA-axes 3 or 4. Only two variables (Al and Mg concentrations; Tab. 8) had correlation coefficients with DCA-axis 3 larger than 0.20. DCA 3 obtained low loadings on the first three axes in the PCA ordination of explanatory variables (Figs 6–7). All four variables of the microtopography group were moderately ($\tau > 0.20$; Tab. 8) correlated with DCA-axis 4, indicating a tendency for plots with high DCA-axis 4 scores to possess more strongly sloping microsites and have larger vertical amplitudes. The weak positive correlations ($0.12 < \tau < 0.20$) with pH and concentrations of Ca, Mg, N and Mn explained the position of the arrowhead of the DCA-4 vector in the PCA ordination of explanatory variables among variables of the microtopography and soil acidity/nutrient groups.

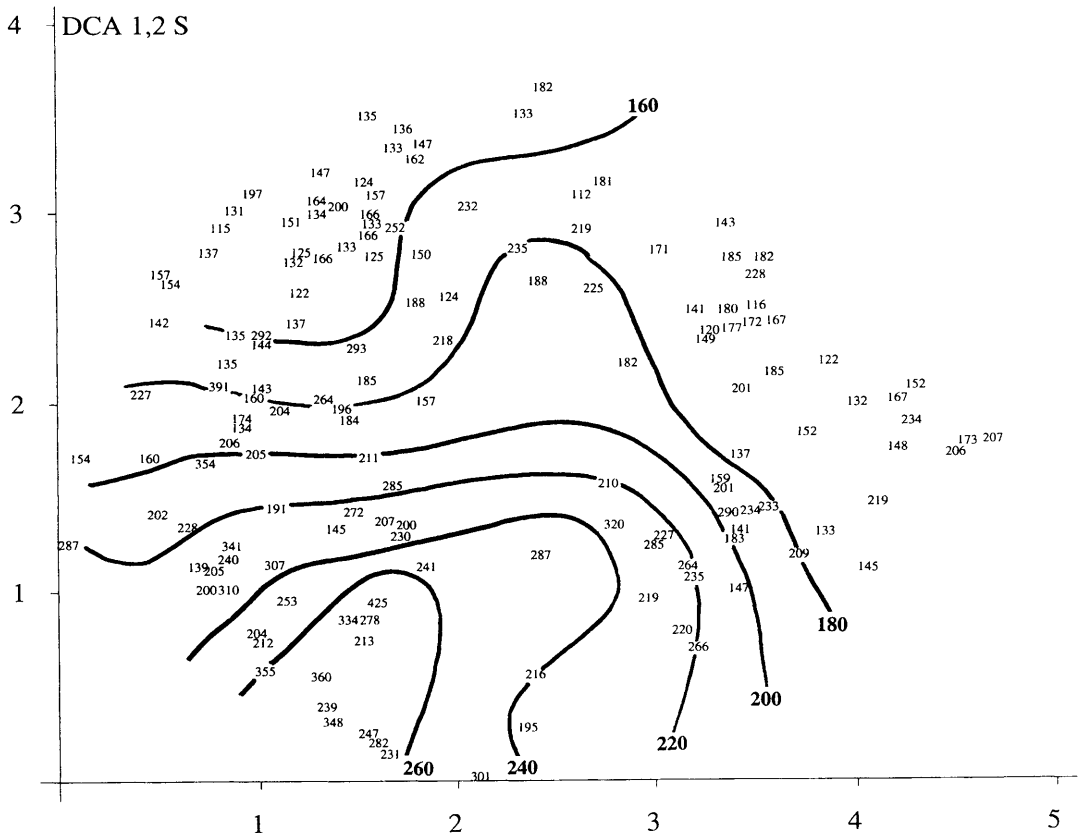


Fig. 47. DCA ordination of the full data set (150 1-m² plots), axis 1 (horizontal) and 2: extractable sulfur in organic fraction of surface peat (ppm), plotted onto plot positions, and isolines found by block kriging. Crossvalidation $r^2 = 0.275$.

LNMSD ordination of the reduced data set

The correlations between axes in the LNMSD ordination of the reduced data set (125 plots) and explanatory variables were closely similar to those obtained for the corresponding DCA axes (Tab. 8). Only minor differences in correlation strength were observed for the most strongly correlated variables; in favour of LNMSD for the first axes (the highest absolute value of the correlation coefficient, $\tau = 0.565$, was found between LNMSD 1 and loss on ignition, while the maximum for DCA 1 was $\tau = 0.517$, obtained for soil volume weight), in favour of DCA for the second axes (the highest $\tau = 0.560$, compared to $\tau = 0.543$ for LNMSD 2; both obtained for depth to the maximum water table). Like DCA 4, LNMSD 3 was most strongly correlated with the microtopography variables ($\tau = 0.261$ for maximum slope). No correlation coefficients higher than 0.25 were found between LNMSD 4 and explanatory variables.

The close correspondence between the first two axes obtained by the two ordination methods, DCA and LNMSD, is interpreted as a manifestation of strong gradient structure in the

Tab. 9. Kendall's rank correlation coefficients τ between plot scores along DCA axes in ordinations of subsets A (poorer swamp forest; $n = 98$) and B (richer swamp forest; $n = 52$) and the 53 explanatory variables, with significance probabilities (P). Strong correlations [$|\tau| \geq 0.3$; $P < 0.0001$ (Subset A), $P < 0.002$ (Subset B)] in bold face. Highest absolute value of τ for each ordination axis italicized. Names of explanatory variables abbreviated in accordance with Tab. 2.

Variable	DCA-A 1		DCA-A 2		DCA-A 3		DCA-A 4		DCA-B 1		DCA-B 2		DCA-B 3		DCA-B 4	
	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P
VertRan	.2543	.0002	-.1572	.0234	.0377	.5866	-.1519	.0287	.3728	.0001	.1067	.2718	.1832	.0588	.0391	.6868
SlopeAvg	.2607	.0001	-.2190	.0014	.0580	.3986	-.1401	.0418	.3235	.0007	.0955	.3199	.1014	.2902	-.0727	.4485
SlopeMa25	.2288	.0010	-.1633	.0193	.0494	.4795	-.1839	.0085	.2964	.0022	.1272	.1895	.1393	.1504	.0168	.8620
SlopeMa10	.1579	.0225	-.1800	.0093	.0164	.8130	-.1407	.0423	.2007	.0411	.0478	.6278	.0516	.5999	.0070	.9430
DistMSoil	-.0825	.2312	-.1727	.0122	-.1702	.0136	.0358	.6038	-.1454	.1331	-.0269	.7820	.0820	.3976	.2224	.0219
SoilDMVL	-.1656	.0158	-.1543	.0246	-.1997	.0037	-.1328	.0535	-.1820	.0572	-.0008	.9937	.1429	.1358	-.0719	.4533
SoilDMWT	-.1913	.0053	-.1395	.0421	-.2089	.0024	-.1227	.0745	-.2499	.0090	-.0295	.7582	.1127	.2396	-.0446	.6414
CanopyCAvg	.2253	.0011	-.0679	.3272	.1335	.0541	.0546	.4317	.2510	.0099	.0602	.5369	.1511	.1208	.1621	.0964
CanopyCMax	.1628	.0225	-.0848	.2345	.1620	.0232	-.0071	.9213	.1919	.0551	.0455	.6499	.1970	.0493	.0918	.3599
CanopyCMin	.2744	.0001	.0089	.8995	.0865	.2213	.0146	.8365	.3221	.0012	-.0079	.9366	.0759	.4455	.1915	.0544
TreeInfLiv	.2971	.0000	-.0062	.9290	.1445	.0371	-.0764	.2711	.4726	.0000	.0177	.8555	-.1068	.2711	.0085	.9306
TreeInfAll	.3485	.0000	-.0384	.5764	.0837	.2230	-.1383	.0444	.3783	.0001	-.0462	.6301	-.0718	.4534	-.0704	.4629
BasalArea	.2046	.0035	.0904	.1965	-.0293	.6758	.0293	.6758	.1803	.0642	-.2844	.0036	-.1528	.1172	-.0973	.3188
CrownI	.2435	.0004	-.0932	.1749	.1609	.0192	.0264	.7012	.3012	.0016	.0492	.6079	.0915	.3396	-.0235	.8067
LitterI	.2915	.0000	-.0482	.4923	.1625	.0207	.1072	.1272	.3602	.0002	.1562	.1102	.0023	.9810	-.0365	.7088
SnowD0423	-.1542	.0296	.0291	.6814	-.1002	.1575	-.0993	.1620	-.0760	.4377	.1322	.1781	.3347	.0006	.0404	.6804
WatTab100	.6569	.0000	-.1006	.1431	.0844	.2195	-.0334	.6276	.4356	.0000	.1674	.0811	-.1943	.0425	-.0795	.4072
WatTab90	.6721	.0000	-.1383	.0440	.0921	.1798	-.0475	.4897	.4794	.0000	.2067	.0312	-.0552	.5645	-.0568	.5538
WatTab50	.6084	.0000	-.1964	.0042	.1170	.0885	-.0720	.2952	.4960	.0000	.1825	.0571	.0038	.9685	-.0356	.7106
WatTab10	.5934	.0000	-.2222	.0012	.1217	.0765	-.0771	.2625	.4758	.0000	.1909	.0467	.0454	.6358	.0242	.8006
WatTab0	.6322	.0000	-.1564	.0227	.0968	.1588	-.0234	.7333	.4753	.0000	.1523	.1126	.0204	.8312	.0477	.6190
WatTabRan	.2584	.0002	.0081	.9070	-.0077	.9119	-.0272	.6963	.1287	.1841	-.0154	.8743	-.3584	.0002	-.1398	.1501
WatTabHMa	.6396	.0000	-.1454	.0342	.0888	.1963	-.0889	.1962	.5111	.0000	.1446	.1316	-.1157	.2272	-.0734	.4439
WatTabLMi	.3603	.0000	-.0430	.5312	.0989	.1500	.0636	.3555	.1662	.0825	.0591	.5381	-.0787	.4117	-.0833	.3852
WatTem0527	-.3979	.0000	.1535	.0262	.0032	.9633	-.0051	.9412	-.1527	.1125	-.1730	.0730	.0943	.3275	.1957	.0424
WatTem0826	-.1448	.0372	-.0331	.6339	-.1823	.0088	-.0156	.8225	.1186	.2206	-.0269	.7820	-.0360	.7103	.0621	.5220

Tab. 9 (continued).

Variable	DCA-A 1		DCA-A 2		DCA-A 3		DCA-A 4		DCA-B 1		DCA-B 2		DCA-B 3		DCA-B 4	
	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P
WatpH0527	-.2716	.0001	.0633	.3571	.3510	.0000	-.1845	.0074	-.0220	.8189	-.1117	.2458	-.0205	.8312	.1708	.0756
WatpH0826	-.3747	.0000	-.0634	.3571	.2695	.0001	-.1788	.0095	-.1607	.0942	-.0654	.4970	.1640	.0881	.1322	.1694
WatEC0527	-.0266	.6989	-.0198	.7729	.1496	.0295	-.1118	.1044	.1528	.1108	.0395	.6814	-.2212	.0212	.1683	.0797
WatEC0826	-.0027	.9682	-.0150	.8275	.1534	.0258	-.1216	.0775	-.0944	.3239	.1038	.2795	-.0462	.6302	.2401	.0123
WatO0527	.1130	.1081	.1330	.0587	-.0875	.2136	.1117	.1128	.1478	.1304	.0132	.8929	.1721	.0787	-.0962	.3260
WatO0826	.0000	1.0000	-.0804	.2457	-.0626	.3665	.0098	.8876	-.1012	.2967	-.1123	.2483	-.0638	.5116	-.2306	.0177
SoilVolWt	-.1191	.0844	-.0699	.3109	.1539	.0258	-.1879	.0066	.1635	.0882	.0729	.4485	.0288	.7642	.1866	.0521
SoilLossOI	.5197	.0000	-.1244	.0701	-.2052	.0028	.0695	.3125	-.1103	.2492	-.0167	.8621	-.0212	.8251	.0742	.4392
SoilpHH ₂ O	-.5505	.0000	.0543	.4301	.2051	.0029	-.0847	.2194	-.2325	.0157	-.1616	.0940	.0670	.4871	.1356	.1597
SoilpHCaCl	-.5737	.0000	.0739	.2826	.2060	.0028	-.1060	.1240	-.2502	.0092	-.1749	.0693	.0805	.4026	.1687	.0796
SoilCEC	-.3245	.0000	-.0367	.5933	.1276	.0633	-.2739	.0001	-.2840	.0030	-.1121	.2427	.0877	.3599	.2937	.0022
SoilBaSat	-.4372	.0000	-.0540	.4320	.1656	.0160	-.2554	.0002	-.2840	.0031	-.1861	.0530	.0645	.5022	.2102	.0287
HumusC	.0594	.3867	.0476	.4879	.0592	.3884	.0467	.4975	.1291	.1772	-.0326	.7343	-.0416	.6642	-.0189	.8436
HumusN	-.4555	.0000	.0780	.2561	.1453	.0344	-.1201	.0807	-.1034	.2796	.0856	.3724	.0733	.4439	.1884	.0494
HumusP	.2153	.0017	-.0940	.1710	-.1267	.0651	-.0534	.4374	.0219	.8190	.0280	.7702	-.0839	.3810	.0976	.3086
HumusS	-.4475	.0000	.0502	.4650	.1326	.0535	.0137	.8418	-.2892	.0025	-.0977	.3085	-.0189	.8436	-.1627	.0897
HumusExAc	.4319	.0000	.0599	.3833	-.1895	.0058	.2578	.0002	.2263	.0186	.1813	.0601	-.0578	.5482	-.2352	.0146
HumusCa	-.4454	.0000	-.0093	.8926	.1537	.0252	-.2527	.0002	-.2378	.0129	-.1189	.2152	.1036	.2796	.2641	.0059
HumusMg	-.2667	.0001	-.2061	.0027	.1491	.0300	-.2299	.0008	-.2559	.0075	-.2098	.0288	.1429	.1358	.0779	.4162
HumusK	.3468	.0000	-.1610	.0190	.0074	.9144	.1015	.1398	.3133	.0011	.0507	.5969	-.1308	.1721	-.0764	.4253
HumusNa	-.1437	.0363	-.1345	.0502	.0023	.9731	.0179	.7941	-.2544	.0078	-.0659	.4922	-.1338	.1624	.1657	.0839
HumusBa	-.3080	.0000	.1615	.0187	.1103	.1084	-.0754	.2731	-.0340	.7225	.3143	.0011	-.0945	.3238	.1733	.0707
HumusFe	.3737	.0000	.1066	.1204	-.2338	.0007	.1577	.0218	.2242	.0191	.1037	.2795	.1656	.0839	-.0008	.9937
HumusMn	-.2431	.0004	-.0304	.6585	.3586	.0000	-.1569	.0226	.1351	.1578	.1810	.0592	-.0749	.4346	-.0144	.8808
HumusSr	-.3982	.0000	-.0527	.4428	.1870	.0065	-.1944	.0047	-.2469	.0099	-.1295	.1771	.1732	.0707	.2323	.0154
HumusZn	.0940	.1710	-.1315	.0554	.0200	.7706	-.0260	.7057	.1080	.2591	-.0038	.9685	-.2866	.0028	-.1233	.1982
HumusAl	.0952	.1653	.2791	.0000	-.0753	.2731	.3316	.0000	.1820	.0572	.1598	.0958	-.1006	.2938	-.2051	.0324

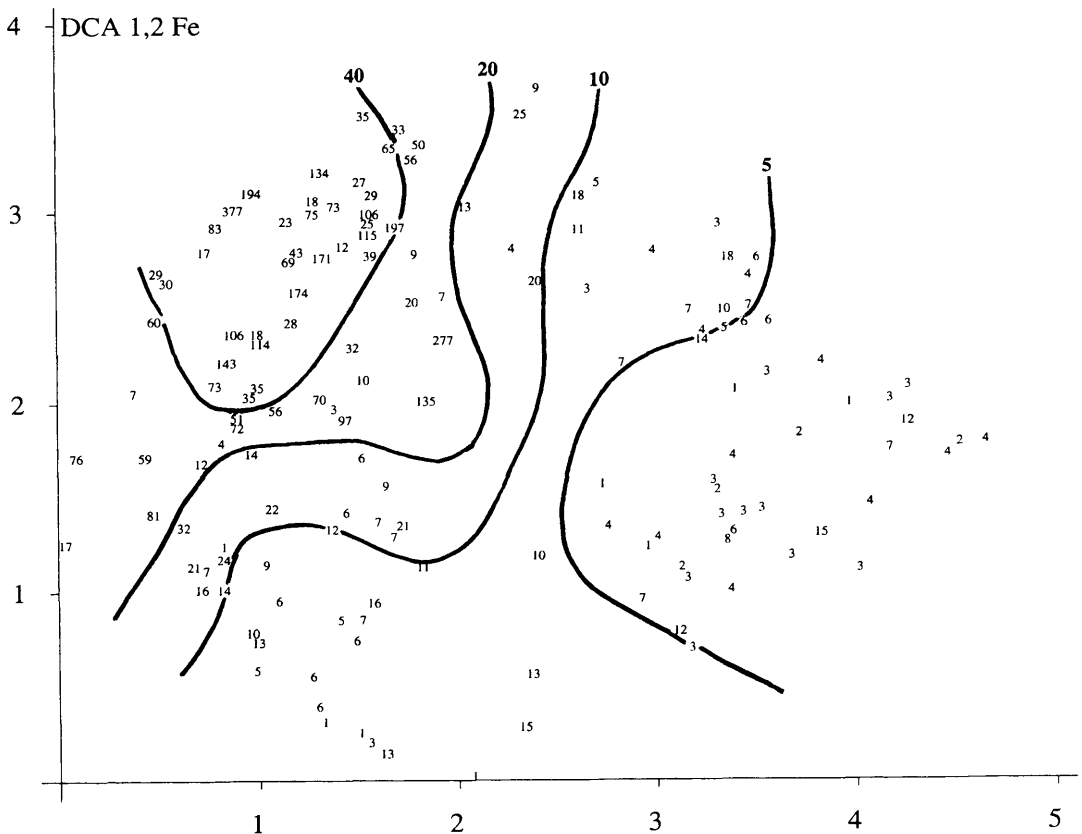


Fig. 49. DCA ordination of the full data set (150 1-m² plots), axis 1 (horizontal) and 2: extractable iron in organic fraction of surface peat (ppm), plotted onto plot positions, and isolines found by block kriging. Crossvalidation $r^2 = 0.490$.

= -0.259). Tree influence and three variables of the microtopography group were about equally strongly correlated with DCA-A 1 and DCA 2.

Like DCA 3 with which it was strongly correlated (Tab. 7), DCA-A 2 was not strongly correlated with any explanatory variable. The highest correlation coefficient ($\tau = 0.279$; Tab. 9) with DCA-A 2 was observed for the concentration of Al in peat.

Even though the third axis in the DCA ordination of Subset A was strongly correlated with the first axis in the ordination of the full data set ($\tau = 0.613$), only two strong correlations ($\tau > 0.30$; with Mn concentration and tube-water pH on 27–28 May 1998) were found between DCA-A 3 and explanatory variables (in contrast to the 13 for DCA 1; Tabs 8–9).

Like DCA-A 2, few significant correlations with explanatory variables was observed for DCA-A 4; the strongest with the concentration of Al ($\tau = 0.332$; Tab. 9).

Subset B (richer swamp forest). DCA-B 1 were equally strongly correlated with the second axis in the DCA ordination of the full data set as was DCA-A 1 (Tab. 7), but showed different patterns of correlations with explanatory variables (Tab. 8). DCA-B 1 was less strongly

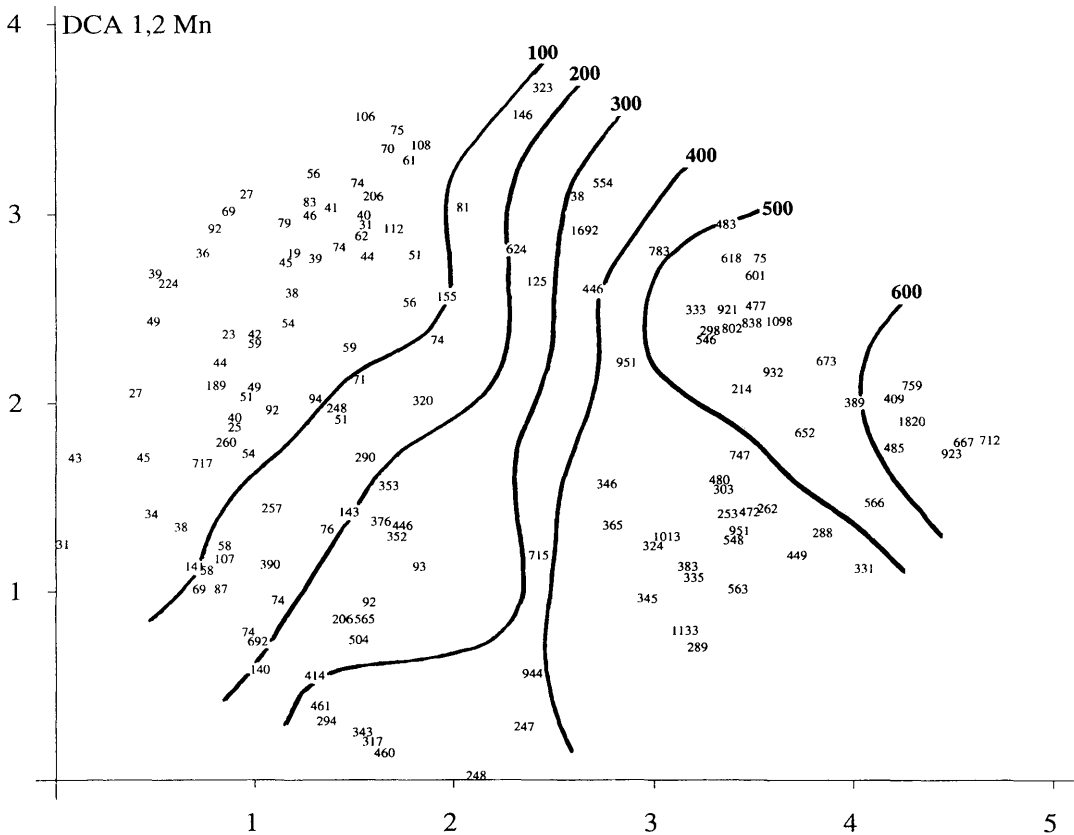


Fig. 50. DCA ordination of the full data set (150 1-m² plots), axis 1 (horizontal) and 2: extractable manganese in organic fraction of surface peat (ppm), plotted onto plot positions, and isolines found by block kriging. Crossvalidation $r^2 = 0.598$.

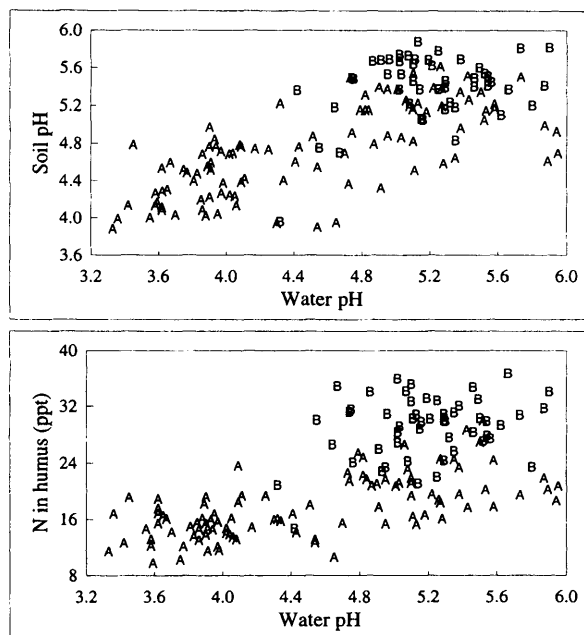
correlated with variables of the water-table group [$\tau > 0.43$ vs $\tau > 0.59$ (Tab. 9); the strongest correlation was found for depth from the highest vertical level to the minimum water table ($\tau = 0.511$)] and the soil nutrient/acidity group (no strong correlations, compared to the eleven observed for DCA-A 1). Moderately strong correlations ($0.2 < |\tau| < 0.3$) were, however, found for nine variables of the extended soil nutrient/acidity group. DCA-B 1 was correlated more strongly than DCA-A 1 with variables of the tree influence and microtopography groups (also note that DCA-B 1 was more strongly correlated with DCA 4 than was DCA-A 1). Five of seven variables in the tree influence group were strongly correlated ($|\tau| > 0.3$) with DCA-B 1 and, in contrast to DCA 2 and DCA-A 1, DCA-B 1 was much more strongly correlated with the tree influence index based upon living trees than with the index based upon all (also including dead) trees (compare Tabs 8 and 9). In fact, the correlation between DCA-B 1 and the tree influence index based upon living trees was equally strong as the correlations between this axis and water-table variables. Vertical range and average slope (both with $\tau > 0.3$) were the microtopography variables most strongly correlated with this axis.

Tab. 10. Kendall's rank correlation coefficients τ between plot scores along DCA axes in ordinations of subsets C (vascular plants; $n = 150$) and D (cryptogams; $n = 150$) and the 53 explanatory variables, with significance probabilities (P). Strong correlations [$|\tau| \geq 0.3$; $P < 0.0001$] in bold face. Highest absolute value of τ for each ordination axis italicized. Names of explanatory variables abbreviated in accordance with Tab. 2.

Variable	DCA-C 1		DCA-C 2		DCA-C 3		DCA-C 4		DCA-D 1		DCA-D 2		DCA-D 3		DCA-D 4	
	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P
VertRan	-.0189	.7340	.2134	.0001	-.0278	.6177	.0745	.1803	.1090	.0501	.2316	.0000	-.0524	.3465	.1574	.0047
SlopeAvg	-.0506	.3585	.2166	.0001	-.0592	.2828	.0065	.9069	.0852	.1222	.2479	.0000	-.0852	.1222	.1835	.0009
SlopeMa25	-.0320	.5669	.1862	.0009	-.0436	.4349	.0046	.9339	.1067	.0562	.2094	.0002	-.0227	.6843	.1657	.0030
SlopeMa10	.0611	.2735	.1002	.0725	-.0875	.1164	.0191	.7326	.2180	.0001	.1378	.0135	.0240	.6663	.1735	.0019
DistMSoil	-.2580	.0000	-.0658	.2354	.1349	.0150	-.0786	.1563	-.1969	.0004	-.0799	.1493	-.0929	.0937	.1777	.0013
SoilDMVL	-.3860	.0000	-.0974	.0771	.1819	.0010	-.0521	.3443	-.2852	.0000	-.1656	.0026	-.0436	.4287	.2275	.0000
SoilDMWT	-.3661	.0000	-.1384	.0120	.1732	.0017	-.0519	.3459	-.2635	.0000	-.2030	.0002	-.0237	.6667	.2370	.0000
CanopyCAvg	.1792	.0013	.2264	.0000	-.1436	.0099	.2123	.0001	.1483	.0078	.1865	.0008	-.0283	.6107	-.0413	.4583
CanopyCMax	.1056	.0661	.1711	.0029	-.1210	.0352	.2096	.0003	.0887	.1227	.1375	.0167	-.0009	.9869	-.0027	.9622
CanopyCMin	.1920	.0007	.2612	.0000	-.0866	.1280	.1737	.0023	.1621	.0044	.2416	.0000	-.0760	.1815	-.0611	.2831
TreeInfliv	.0021	.9701	.2871	.0000	.0503	.3663	.0500	.3689	.0999	.0726	.3103	.0000	-.1115	.0451	.0254	.6485
TreeInfAll	-.0890	.1059	.3279	.0000	.1094	.0469	.0403	.4646	.0142	.7961	.3289	.0000	-.1519	.0058	.0261	.6351
BasalArea	.1982	.0004	.1352	.0160	.0466	.4066	.1975	.0004	.1742	.0019	.1684	.0027	-.0394	.4821	-.0448	.4243
CrownI	.1700	.0020	.2011	.0003	-.1366	.0131	.1279	.0202	.2074	.0002	.1962	.0004	-.0027	.9611	-.0135	.8062
LitterI	.1357	.0159	.2688	.0000	-.0793	.1588	.0663	.2386	.1421	.0116	.2682	.0000	-.0226	.6884	-.0205	.7163
SnowD0423	.0752	.1847	-.1338	.0183	.0062	.9130	.0705	.2138	.0204	.7184	-.1207	.0333	.0748	.1869	.0091	.8730
WatTab100	-.1854	.0008	.5260	.0000	.0781	.1560	-.1323	.0163	-.1859	.0007	.5098	.0000	-.3390	.0000	-.0818	.1375
WatTab90	-.2030	.0002	.5582	.0000	.0559	.3098	-.0718	.1925	-.1868	.0007	.4887	.0000	-.3260	.0000	-.0822	.1358
WatTab50	-.1907	.0005	.5487	.0000	.0153	.7811	-.0265	.6305	-.1511	.0061	.4677	.0000	-.2975	.0000	-.0566	.3044
WatTab10	-.1788	.0012	.5443	.0000	-.0054	.9223	.0035	.9495	-.1285	.0196	.4559	.0000	-.2853	.0000	-.0518	.3468
WatTab0	-.0919	.0951	.5703	.0000	-.0235	.6691	.0312	.5717	-.0697	.2056	.4910	.0000	-.2566	.0000	-.0799	.1472
WatTabRan	-.2540	.0000	.2128	.0001	.1728	.0019	-.3230	.0000	-.2470	.0000	.2261	.0001	-.2457	.0000	-.0356	.5228
WatTabHMa	-.1476	.0074	.5252	.0000	.0566	.3037	-.0714	.1947	-.1105	.0448	.5197	.0000	-.2926	.0000	-.0331	.5477
WatTabLMi	-.0780	.1565	.3368	.0000	.0127	.8175	.0003	.9961	-.1359	.0136	.2678	.0000	-.1996	.0003	-.1727	.0017
WatTem0527	.0969	.0800	-.3879	.0000	-.0444	.4230	.0081	.8837	.1524	.0059	-.2895	.0000	.2213	.0001	.0877	.1134
WatTem0826	-.3037	.0000	-.0173	.7561	.1408	.0115	-.0996	.0739	-.2019	.0003	-.0339	.5431	-.0602	.2802	.1242	.0258

Tab. 10 (continued).

Variable	DCA-C 1		DCA-C 2		DCA-C 3		DCA-C 4		DCA-D 1		DCA-D 2		DCA-D 3		DCA-D 4	
	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P	τ	P
WatpH0527	.2934	.0000	-.2374	.0000	-.1606	.0036	.0831	.1320	.3805	.0000	-.1943	.0004	.2509	.0000	.0705	.2009
WatpH0826	.2511	.0000	-.3234	.0000	-.2299	.0000	.0653	.2368	.3295	.0000	-.2960	.0000	.2789	.0000	.1258	.0227
WatECo0527	.2216	.0001	-.0265	.6305	-.0148	.7886	.0768	.1632	.3044	.0000	.0099	.8569	.0993	.0715	-.0516	.3493
WatECo0826	.2970	.0000	-.0620	.2608	-.0990	.0725	.1190	.0309	.3857	.0000	-.0340	.5380	.1343	.0149	-.0577	.2953
WatO0527	.0369	.5126	.0745	.1865	.0529	.3481	.0265	.6378	-.0222	.6934	.1016	.0716	-.0182	.7470	-.0284	.6147
WatO0826	.0724	.1928	-.0277	.6188	-.1256	.0239	.0501	.3677	.0949	.0881	-.0460	.4079	.0706	.2041	.1409	.0113
SoilVolWt	.4750	.0000	-.1030	.0621	-.2115	.0001	.1650	.0028	.5561	.0000	-.0258	.6409	.2537	.0000	.0725	.1891
SoilLossOI	-.4860	.0000	-.3098	.0000	.1876	.0007	-.1165	.0345	-.4556	.0000	.2085	.0002	-.3854	.0000	-.1179	.0323
SoilpHH ₂ O	.3773	.0000	-.4041	.0000	-.1849	.0008	.1019	.0651	.4248	.0000	-.3371	.0000	.3525	.0000	.1085	.0494
SoilpHCaCl ₂	.3893	.0000	-.4163	.0000	-.1864	.0007	.1004	.0687	.4449	.0000	-.3383	.0000	.3582	.0000	.1132	.0403
SoilCEC	-.0670	.2242	-.2799	.0000	.0111	.8403	-.0482	.3811	.0925	.0929	-.3228	.0000	.0915	.0968	.0828	.1328
SoilBaSat	.2295	.0000	-.3776	.0000	-.1383	.0122	.0663	.2292	.3843	.0000	-.3230	.0000	.2786	.0000	.1729	.0017
HumusC	-.1485	.0070	.0664	.2279	.0812	.1405	-.0990	.0723	-.0871	.1139	.0887	.1073	-.0613	.2657	-.0383	.4867
HumusN	.4629	.0000	-.3028	.0000	-.2170	.0001	.1086	.0485	.5043	.0000	-.2202	.0001	.3940	.0000	.0829	.1324
HumusP	-.1942	.0004	.2299	.0000	.0879	.1105	-.0321	.5596	-.1299	.0183	.1743	.0015	-.1899	.0006	.0103	.8518
HumusS	-.0559	.3098	-.3909	.0000	-.0504	.3603	-.0558	.3106	-.0511	.3535	-.3840	.0000	.2131	.0001	.1153	.0364
HumusExAc	-.3014	.0000	.3468	.0000	.1689	.0022	-.0900	.1024	-.4624	.0000	.2912	.0000	-.3052	.0000	-.1688	.0022
HumusCa	.2000	.0003	-.3875	.0000	-.0908	.0991	.0140	.7999	.3498	.0000	-.3296	.0000	.2775	.0000	.1691	.0021
HumusMg	-.0180	.7440	-.2035	.0002	-.1302	.0181	.0532	.3344	.0978	.0757	-.2752	.0000	.0874	.1124	.1835	.0009
HumusK	-.1594	.0038	.3612	.0000	.0090	.8696	.0120	.8276	-.1703	.0020	.2847	.0000	-.2462	.0000	-.0761	.1672
HumusNa	.0785	.1541	-.1503	.0063	-.1168	.0340	.0242	.6608	.1230	.0255	-.1461	.0080	.1127	.0408	.0433	.4316
HumusBa	.2600	.0000	-.2774	.0000	-.0509	.3552	-.1129	.0403	.2666	.0000	-.1837	.0008	.3367	.0000	.0605	.2720
HumusFe	-.3505	.0000	.3207	.0000	.2431	.0000	-.0807	.1427	-.4291	.0000	.2721	.0000	-.3060	.0000	-.1829	.0009
HumusMn	.4346	.0000	-.1994	.0003	-.2517	.0000	.1043	.0581	.4856	.0000	-.1705	.0020	.3271	.0000	.0906	.1001
HumusSr	.1399	.0111	-.3399	.0000	-.1417	.0101	.0229	.6774	.2406	.0000	-.3289	.0000	.2191	.0001	.1480	.0072
HumusZn	-.0663	.2285	.1228	.0258	.0294	.5929	-.1196	.0299	-.0794	.1495	.0828	.1328	-.0579	.2931	.1265	.0216
HumusAl	-.1191	.0306	.1265	.0216	.1252	.0230	-.1015	.0654	-.3369	.0000	.1531	.0054	-.0810	.1414	-.1695	.0021



Figs 51–52. Patterns of co-ordinated variation in pairs of variables of the soil nutrient/acidity group, with subset classification of plots (A or B) as labels. Fig. 51. pH measured in tube water, 26 Aug 1998 vs pH in aqueous soil suspension. Fig. 52. pH measured in tube water, 26 Aug 1998 vs total-N concentration in humus (ppt).

explanatory variables in the order DCA-D 1 (cryptogams), DCA 1, and DCA-C 1 (vascular plants) was observed, while for axis 2 the order was reversed (compare Tabs 8 and 10). Soil depth and water temperatures in summer were strongly correlated with DCA-C 1 but not with DCA-D 1.

The variable most strongly correlated with DCA-C 2 was depth to the maximum water table, while depth from the highest levels in the plot to the minimum water table was most strongly correlated with DCA-D 2. The close correspondence between the first two axes in the ordinations of the full species composition and the separate ordinations of layers was also reflected in the positions of arrowheads in the PCA ordination of explanatory variables (Fig. 6).

DCA-C 3 was not strongly correlated with any of the explanatory variables while DCA-C 4 (like DCA-B 3) was correlated with the range of water-table fluctuations (Tab. 10).

Like DCA-D 1, DCA-D 3 was strongly correlated with several variables of, or associated with, the soil nutrient/acidity group. But unlike DCA-D 1, DCA-D 3 was also moderately correlated with variables of the water-table group. These correlation patterns resembled those found for DCA 1, with which DCA-D 3 was weakly but significantly positively correlated, and were inverse to those found for DCA 2, which was negatively correlated with DCA-D 3.

DCA-D 4 was strongly correlated with DCA 4 (Tab. 7), but unlike the latter DCA D-4 was most strongly correlated with soil depth ($\tau > 0.22$) and the correlations with microtopography variables were weaker (in the range $0.15 < \tau < 0.2$).

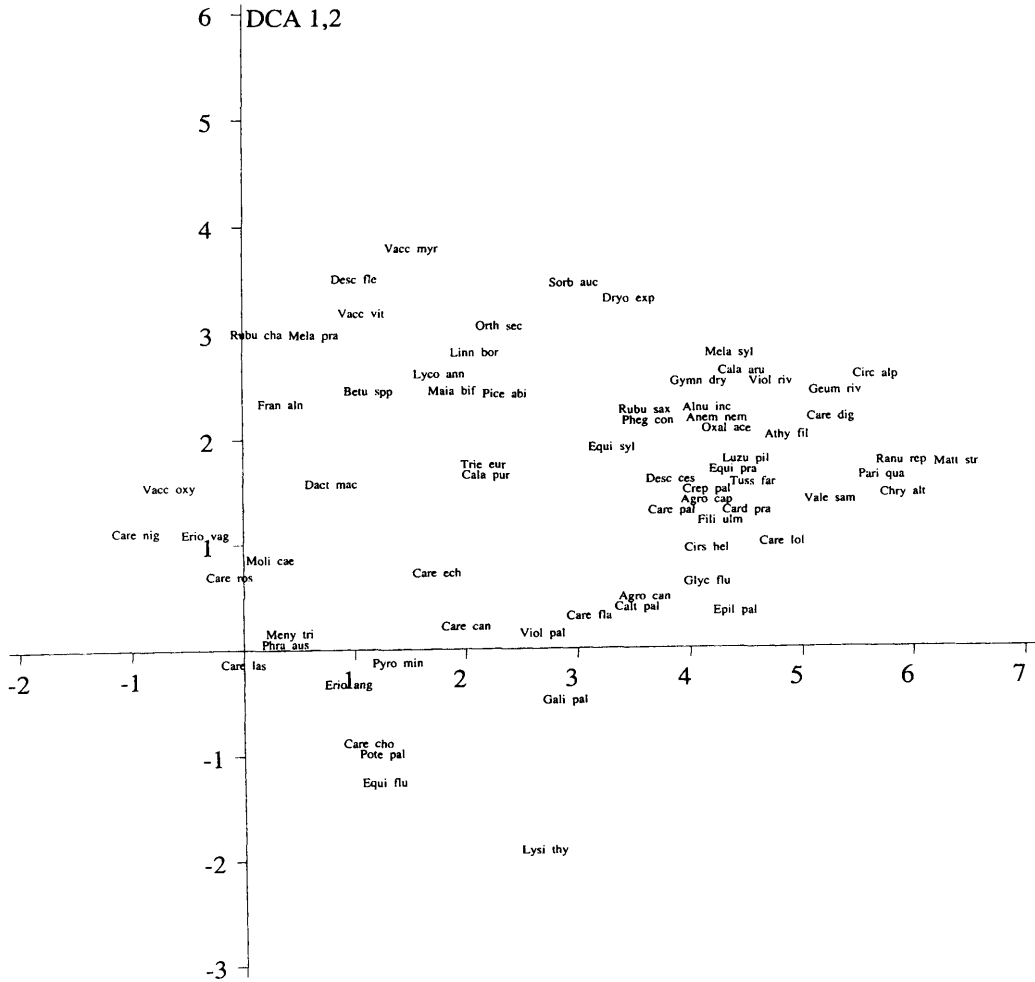


Fig. 53. DCA ordination of the full data set (150 1-m² plots), axis 1 (horizontal) and 2: optima for vascular plant species that occur in 4 or more plots. Scaling of axes in S.D. units. Species names are indicated by the first four letters of the generic and the first three letters of the specific epithet (see Appendix 1).

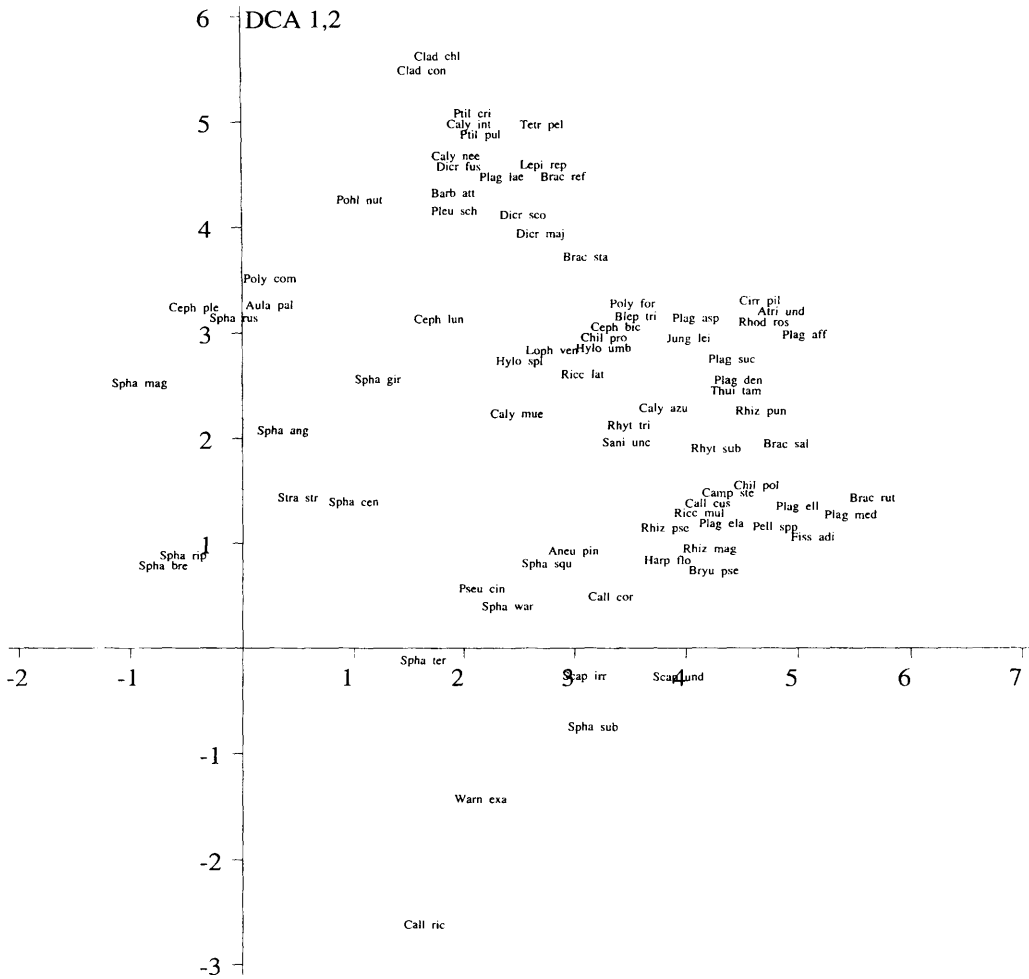


Fig. 54. DCA ordination of the full data set (150 1-m² plots), axis 1 (horizontal) and 2: optima for cryptogams that occur in 4 or more plots. Scaling of axes in S.D. units. Species names are indicated by the first four letters of the generic and the first three letters of the specific epithet (see Appendix 1).

Positions of species optima and variation in species abundances along axes in the DCA ordination of the full data set

Positions of species optima

Optima close to the low-score end of DCA-axis 1 were obtained by species typical of (poorer) mires (e.g., *Vaccinium oxycoccos*, *Menyanthes trifoliata*, *Carex lasiocarpa*, *C. nigra*, *C. rostrata*, *Eriophorum vaginatum*, *Phragmites communis* and *Sphagnum magellanicum*) while optima close

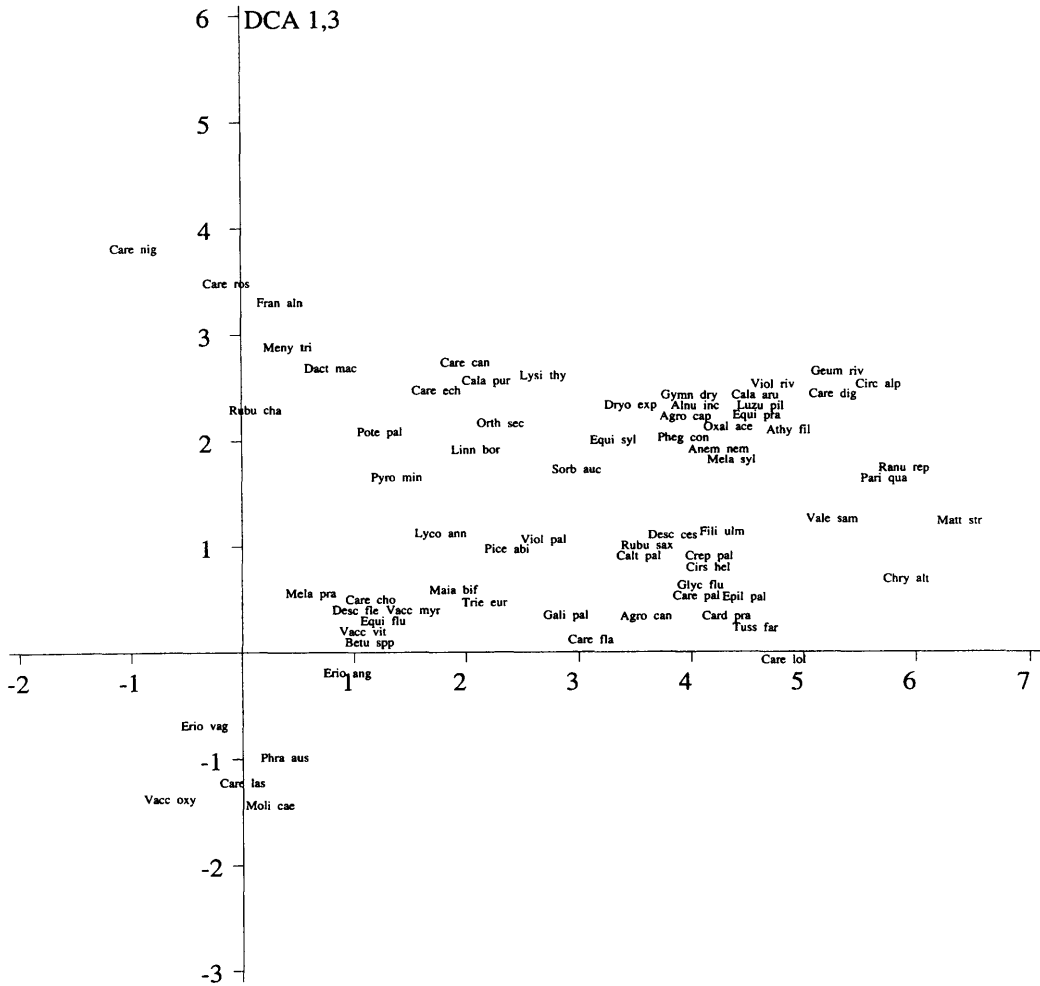


Fig. 55. DCA ordination of the full data set (150 1-m² plots), axis 1 (horizontal) and 3: optima for vascular plant species that occur in 4 or more plots. Scaling of axes in S.D. units. Species names are indicated by the first four letters of the generic and the first three letters of the specific epithet (see Appendix 1).

to the high-score end were obtained by species characteristic of meadows, deciduous forests and springs (e.g. *Chrysosplenium alternifolium*, *Circaea alpina*, *Matteuccia struthiopteris*, *Paris quadrifolia*, *Ranunculus repens*, *Brachythecium rutabulum* agg. and *Plagiomnium medium*; Figs 53–54). Unlike plots, species optima did not segregate into two clusters along DCA-axis 1.

Optima along DCA-axis 2 close to the low-score end were observed for species characteristic of wet swamps, tarn margins and wet mire sites, such as *Equisetum fluitans*, *Galium palustre*, *Lysimachia thyrsiflora*, *Potentilla palustris*, *Carex chordorrhiza*, *Calliargon richardsonii*, *Warnstorfia exannulata* and *Sphagnum subsecundum* (Figs 53–54). Optima close

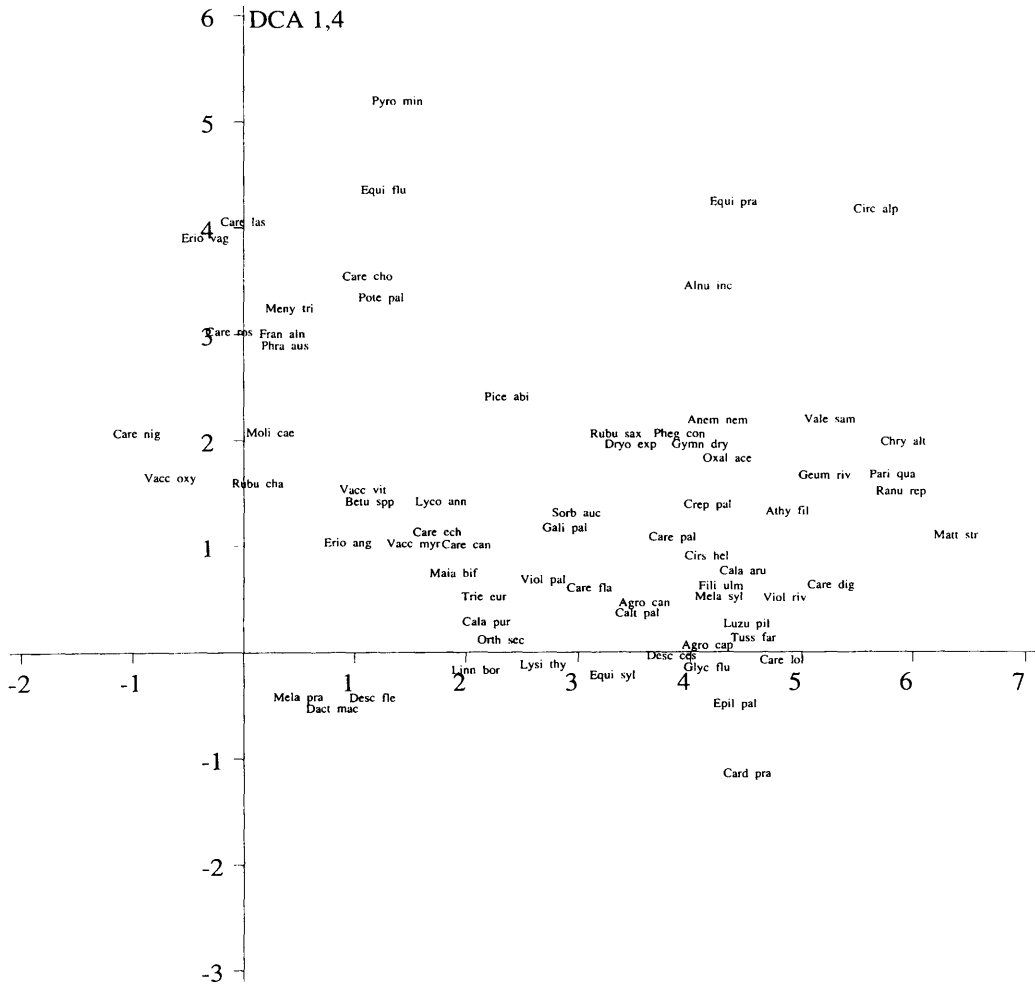


Fig. 57. DCA ordination of the full data set (150 1-m² plots), axis 1 (horizontal) and 4: optima for vascular plant species that occur in 4 or more plots. Scaling of axes in S.D. units. Species names are indicated by the first four letters of the generic and the first three letters of the specific epithet (see Appendix 1).

strongly correlated with the range of water-table fluctuations, decreasing along the axis ($\tau = -0.358$), and snow depth ($\tau = 0.335$). Strong correlations were not found between the fourth axis in the DCA ordination of Subset B and any explanatory variable (Tab. 9).

Subset C (vascular plants) and Subset D (cryptogams). Correlations between the first two axes in the separate ordinations of vascular plants and cryptogams (all 150 plots) and explanatory variables were closely similar to those found for the first two axes in the ordination of the full species composition. A noteworthy decrease in the strength of correlations between axis 1 and explanatory variables in the order DCA-D 1 (cryptogams), DCA 1, and DCA-C 1 (vascular

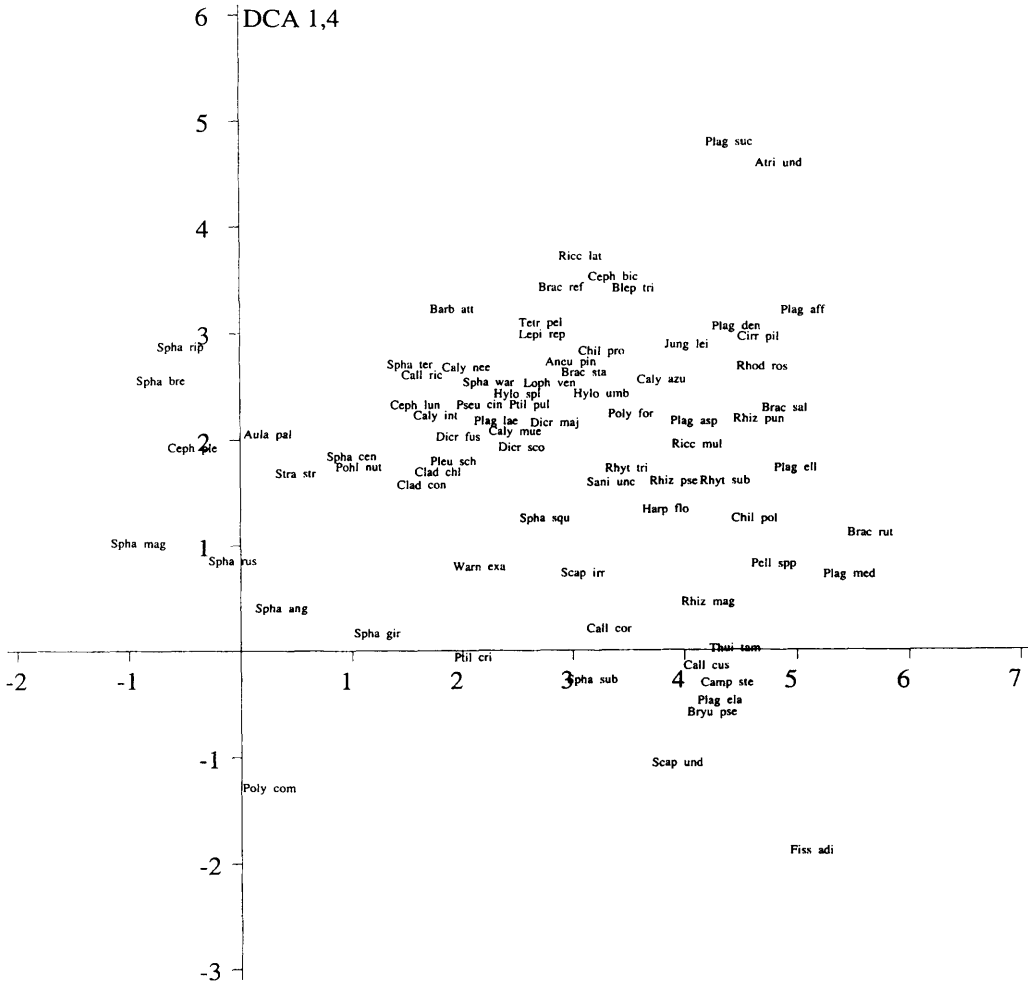
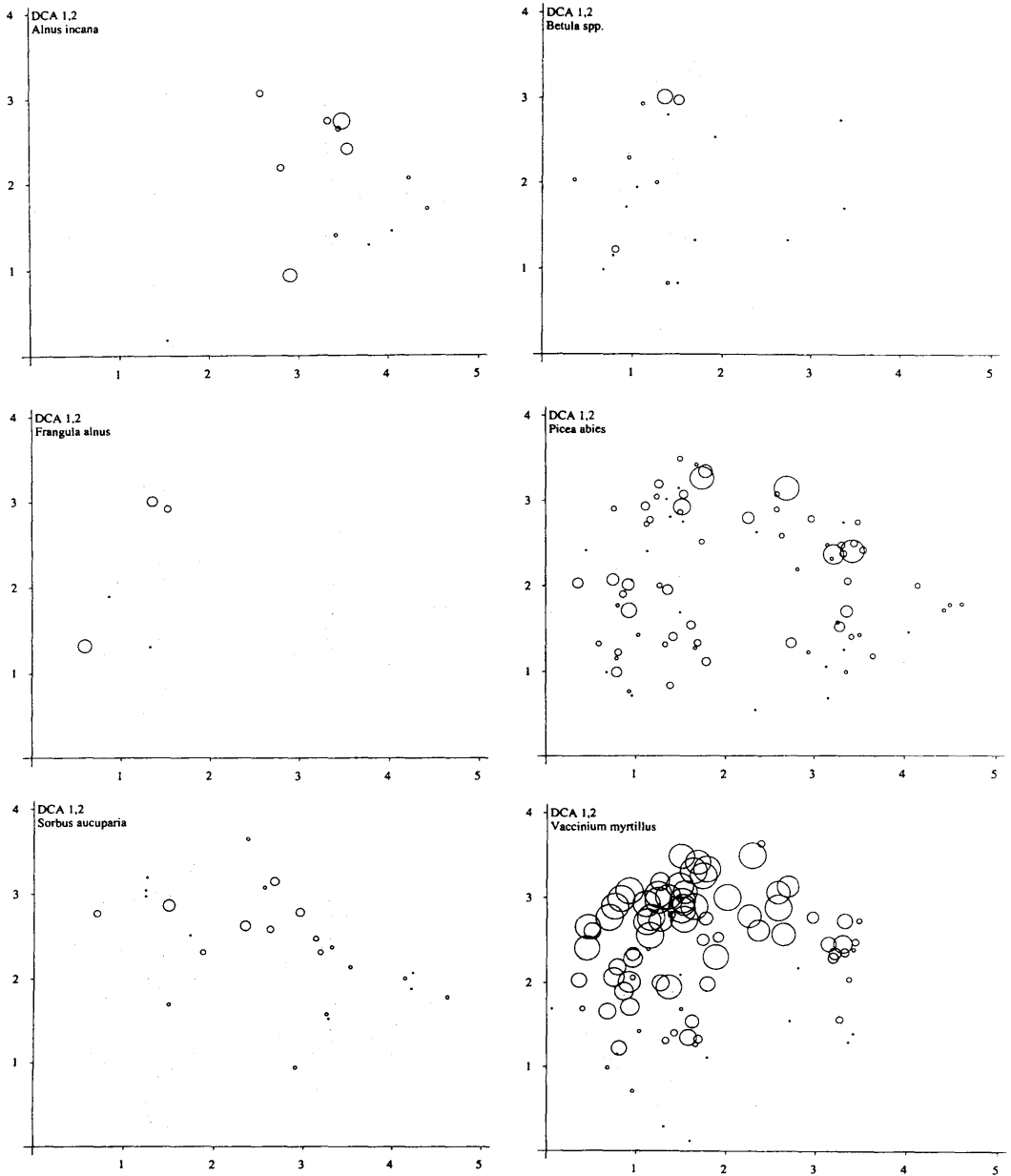


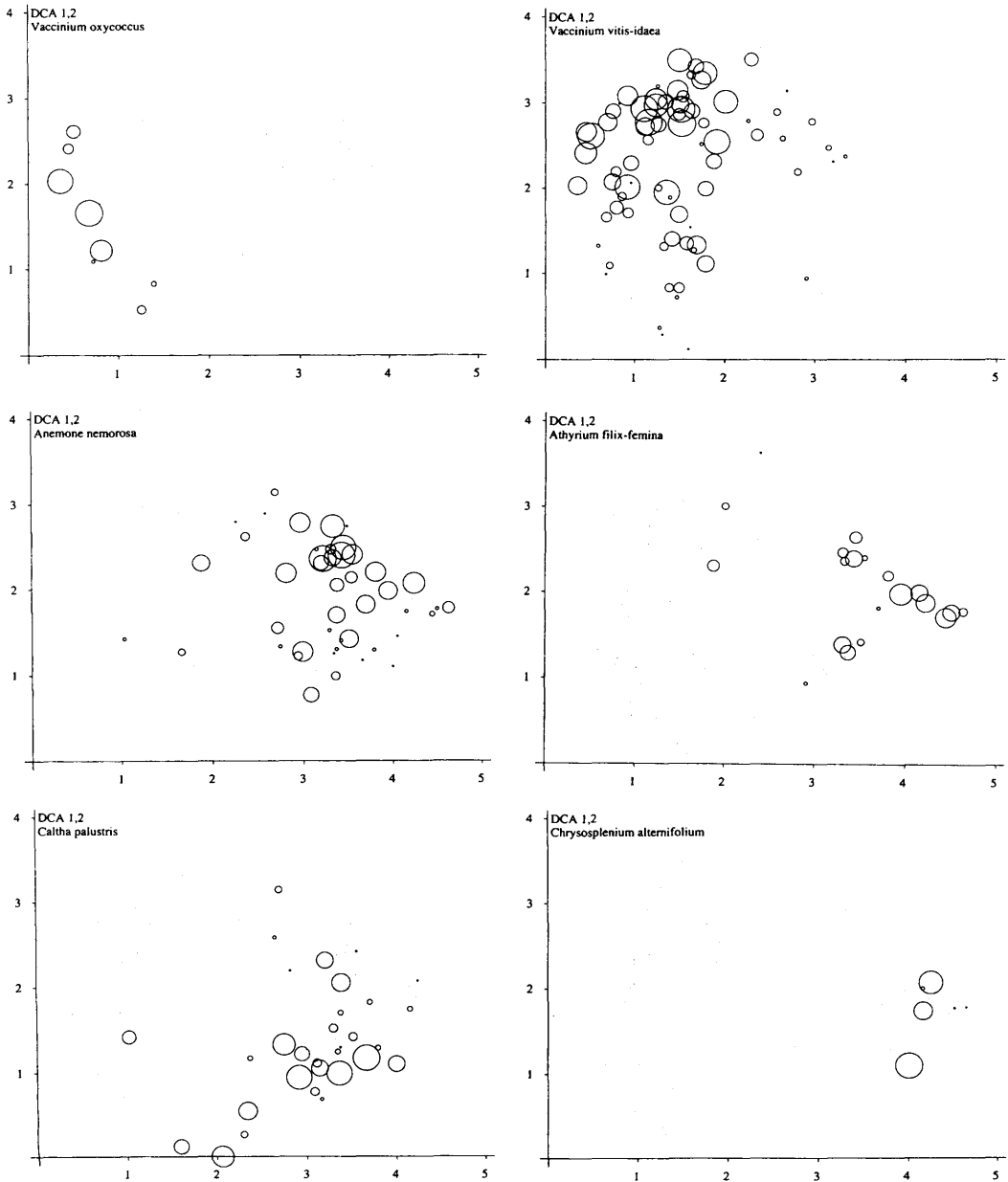
Fig. 58. DCA ordination of the full data set (150 1-m² plots), axis 1 (horizontal) and 4: optima for cryptogams that occur in 4 or more plots. Scaling of axes in S.D. units. Species names are indicated by the first four letters of the generic and the first three letters of the specific epithet (see Appendix 1).

plants) was observed, while for axis 2 the order was reversed (compare Tabs 8 and 10). Soil depth and water temperatures in summer were strongly correlated with DCA-C 1 but not with DCA-D 1.

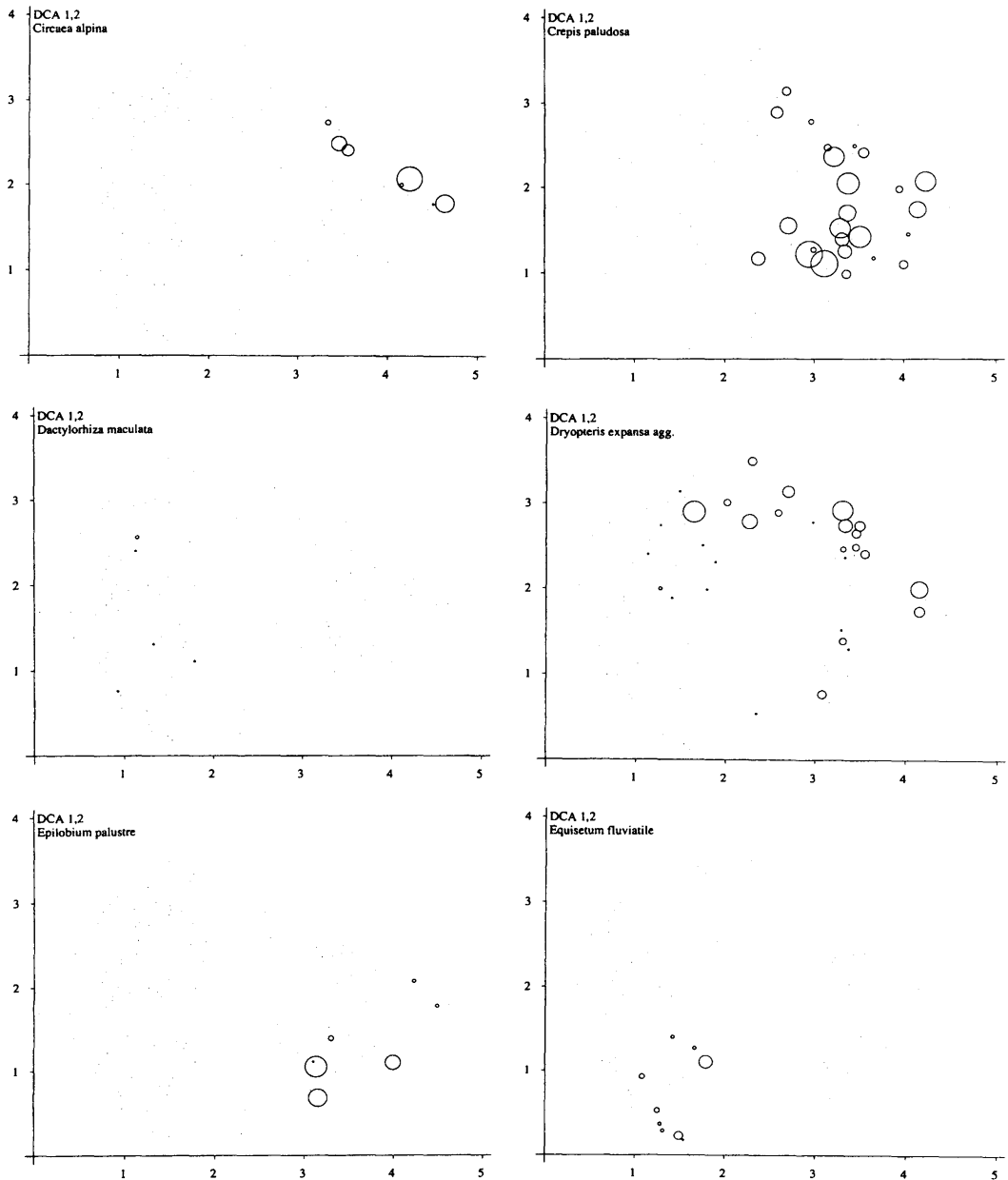
The variable most strongly correlated with DCA-C 2 was depth to the maximum water table, while depth from the highest levels in the plot to the minimum water table was most strongly correlated with DCA-D 2. The close correspondence between the first two axes in the ordinations of the full species composition and the separate ordinations of layers was also reflected in the positions of arrowheads in the PCA ordination of explanatory variables (Fig. 6).



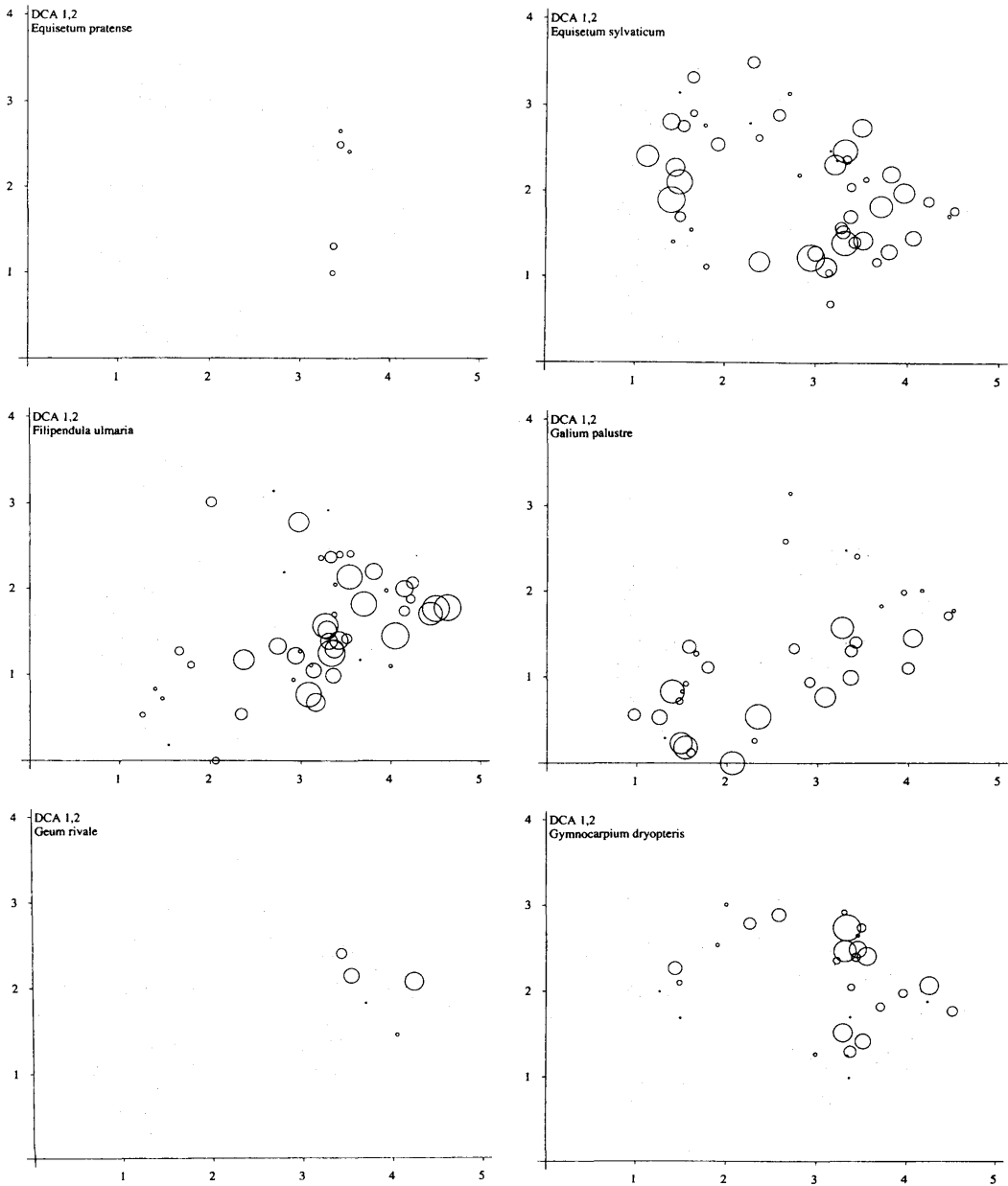
Figs 59–64. Distribution of species abundances in the DCA ordination of the full data set, axes 1 (horizontal) and 2 (vertical). Subplot frequency for each species in each plot proportional to circle size. Scaling of axes in S.D. units. Fig. 59. *Alnus incana*. Fig. 60. *Betula spp.* Fig. 61. *Frangula alnus*. Fig. 62. *Picea abies*. Fig. 63. *Sorbus aucuparia*. Fig. 64. *Vaccinium myrtillus*.



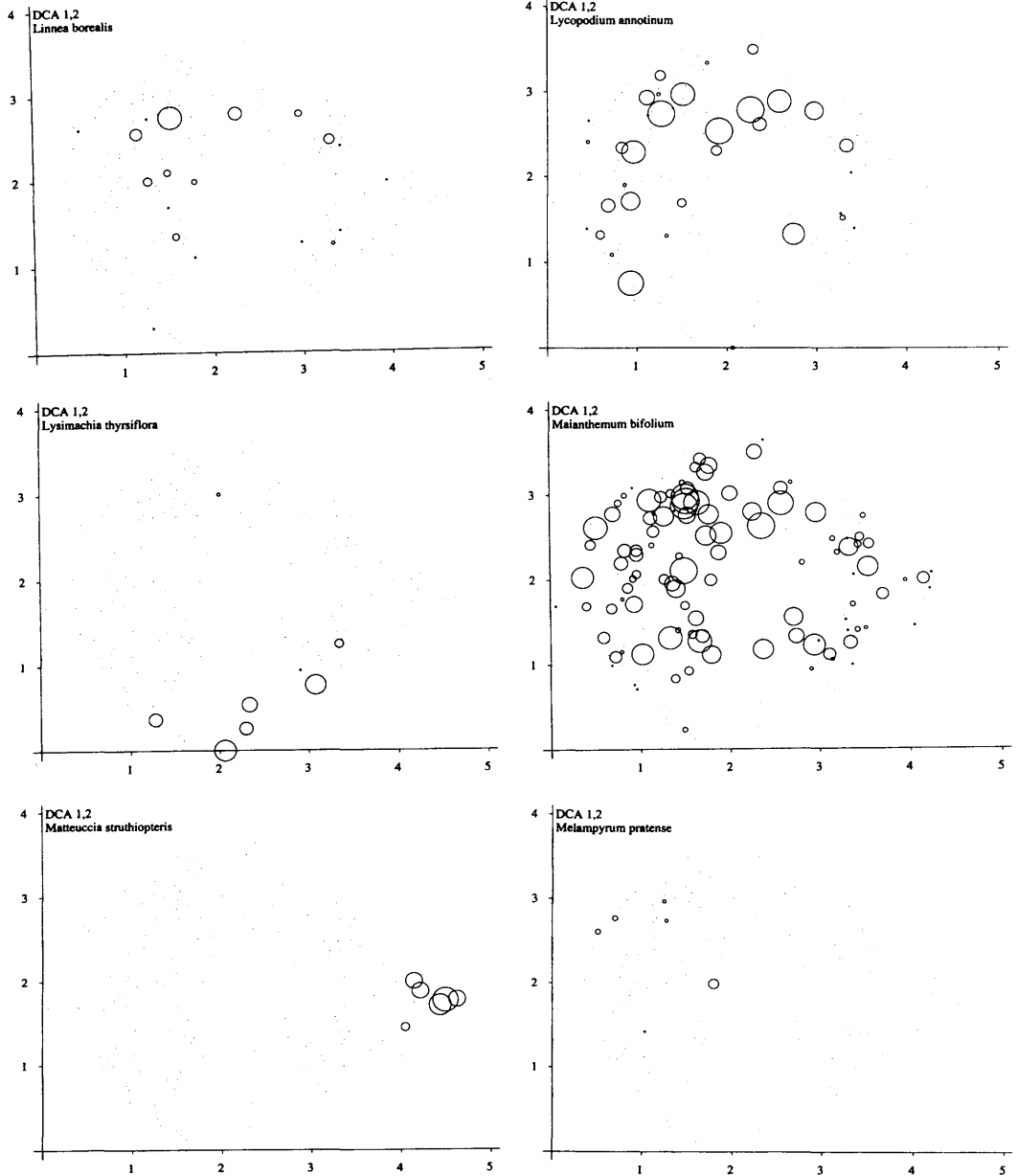
Figs 65–70. Distribution of species abundances in the DCA ordination of the full data set, axes 1 (horizontal) and 2 (vertical). Subplot frequency for each species in each plot proportional to circle size. Scaling of axes in S.D. units. Fig. 65. *Vaccinium oxycoccus*. Fig. 66. *Vaccinium vitis-idaea*. Fig. 67. *Anemone nemorosa*. Fig. 68. *Athyrium filix-femina*. Fig. 69. *Caltha palustris*. Fig. 70. *Chrysosplenium alternifolium*.



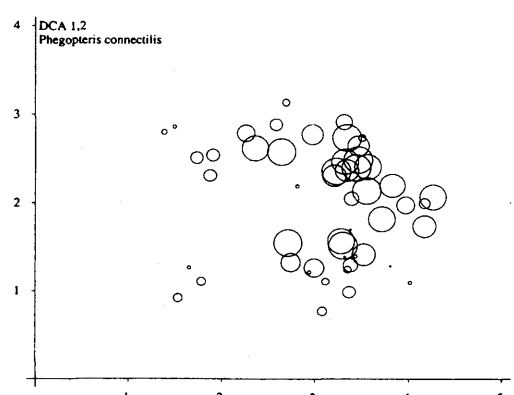
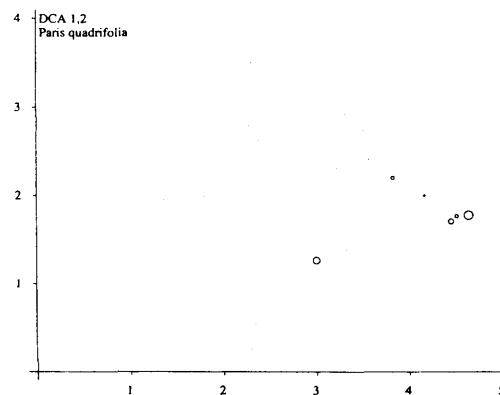
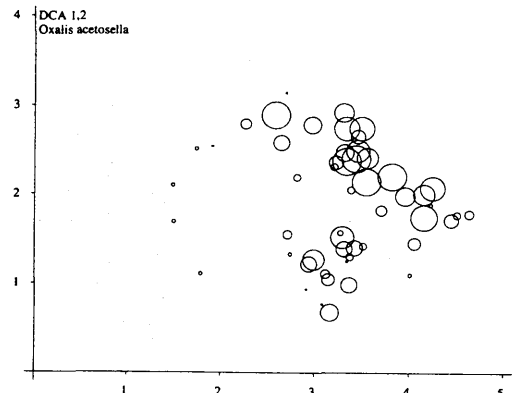
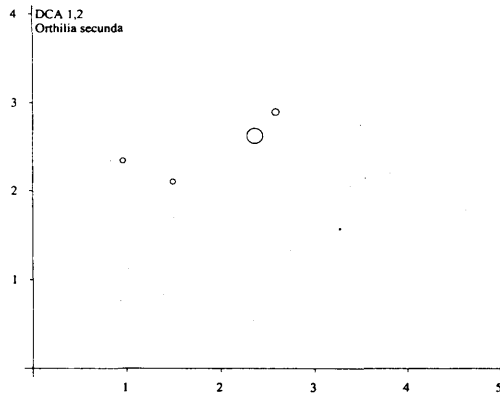
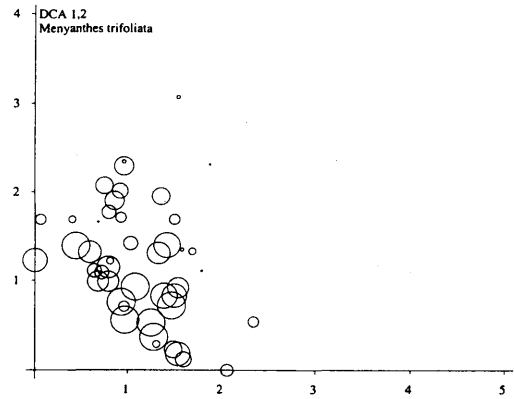
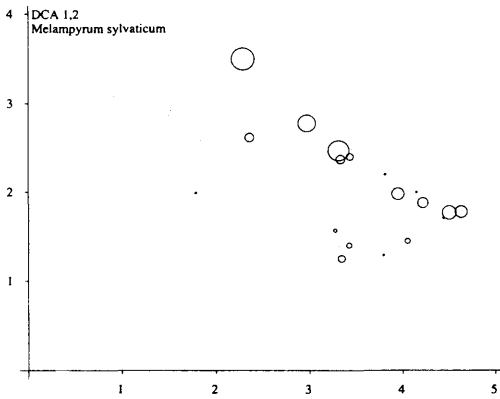
Figs 71–76. Distribution of species abundances in the DCA ordination of the full data set, axes 1 (horizontal) and 2 (vertical). Subplot frequency for each species in each plot proportional to circle size. Scaling of axes in S.D. units. Fig. 71. *Circaea alpina*. Fig. 72. *Crepis paludosa*. Fig. 73. *Dactylorhiza maculata*. Fig. 74. *Dryopteris expansa* agg.. Fig. 75. *Epilobium palustre*. Fig. 76. *Equisetum fluviatile*.



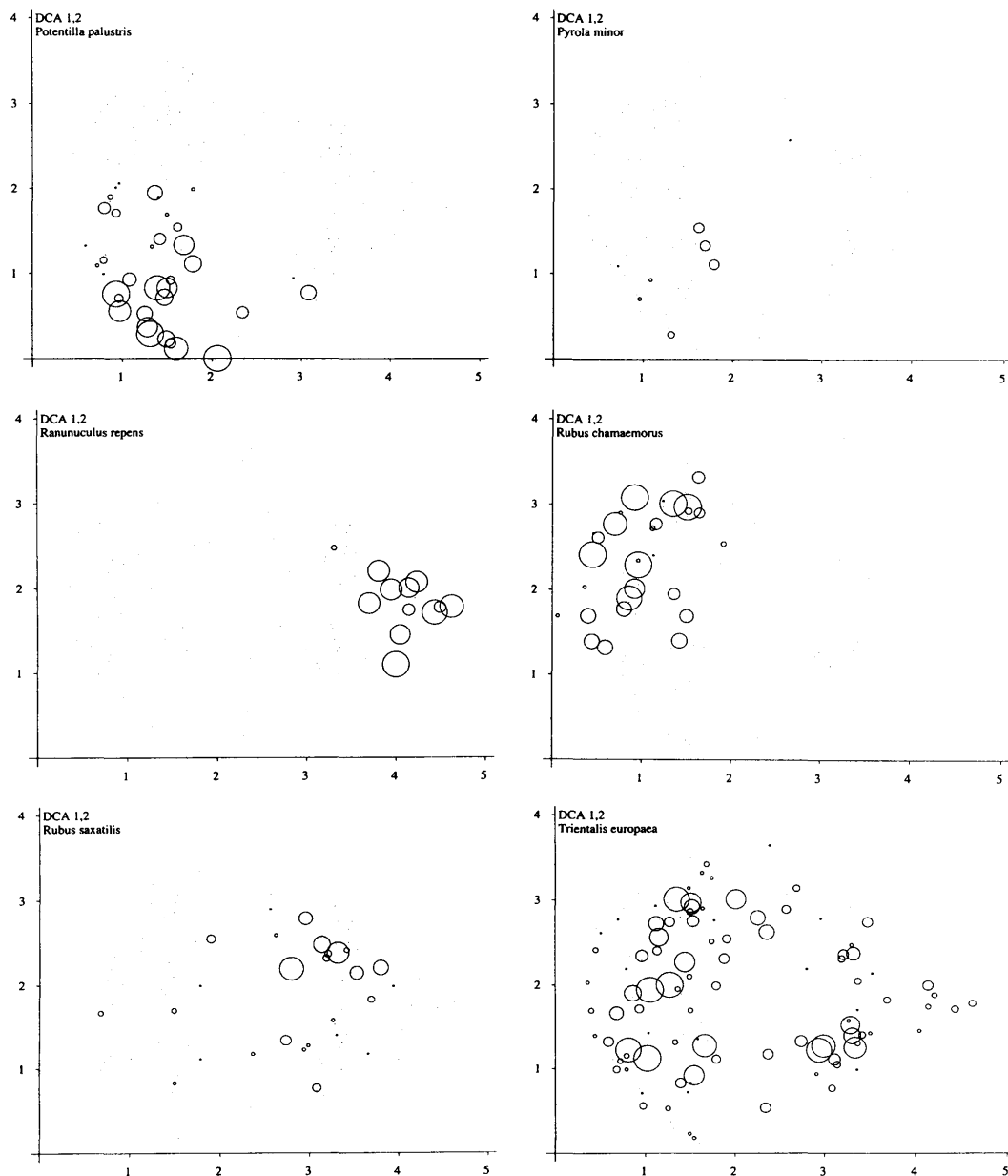
Figs 77–82. Distribution of species abundances in the DCA ordination of the full data set, axes 1 (horizontal) and 2 (vertical). Subplot frequency for each species in each plot proportional to circle size. Scaling of axes in S.D. units. Fig. 77. *Equisetum pratense*. Fig. 78. *Equisetum sylvaticum*. Fig. 79. *Filipendula ulmaria*. Fig. 80. *Galium palustre*. Fig. 81. *Geum rivale*. Fig. 82. *Gymnocarpium dryopteris*.



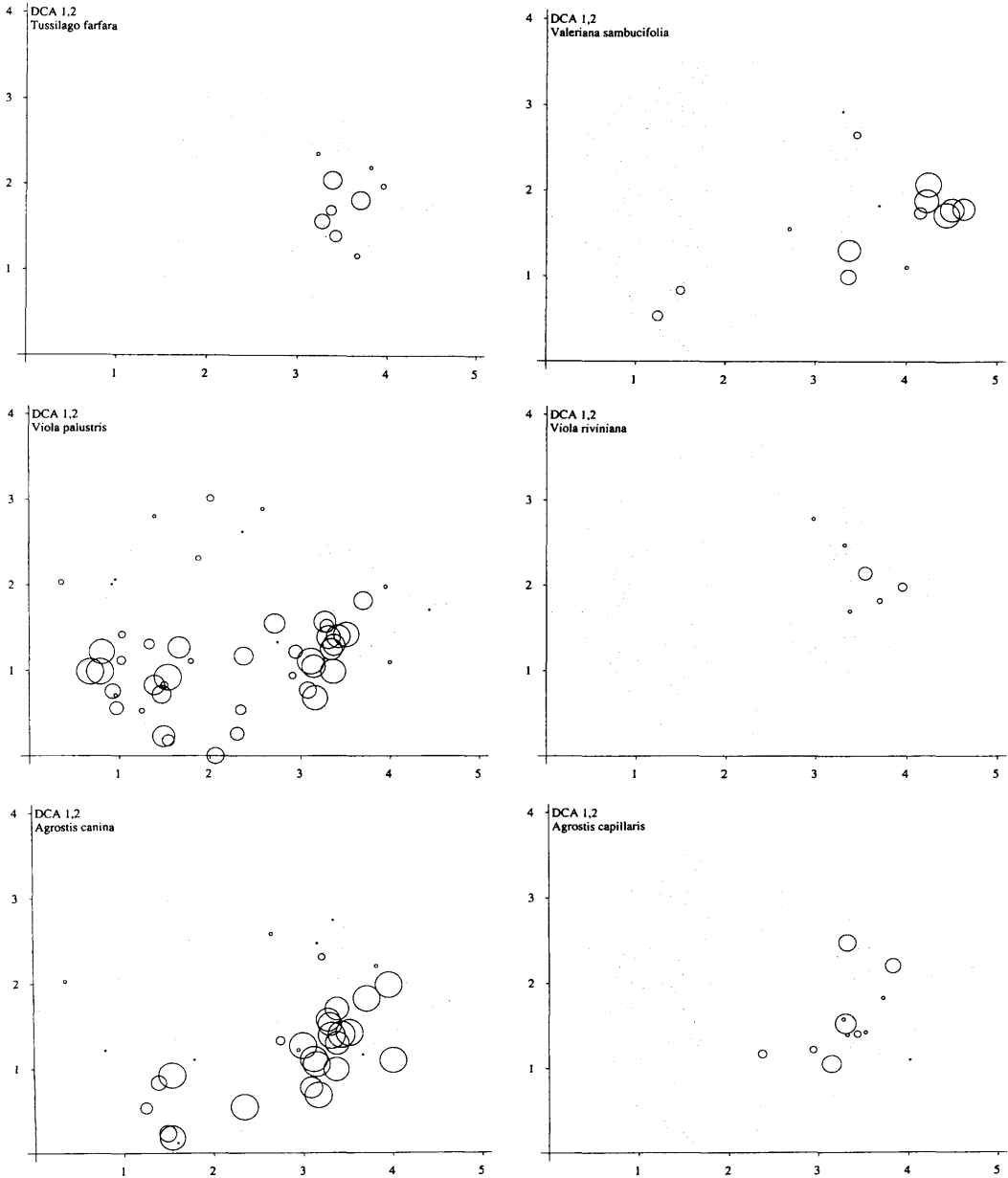
Figs 83–88. Distribution of species abundances in the DCA ordination of the full data set, axes 1 (horizontal) and 2 (vertical). Subplot frequency for each species in each plot proportional to circle size. Scaling of axes in S.D. units. Fig. 83. *Linnaea borealis*. Fig. 84. *Lycopodium annotinum*. Fig. 85. *Lysimachia thysiflora*. Fig. 86. *Maianthemum bifolium*. Fig. 87. *Matteuccia struthiopteris*. Fig. 88. *Melampyrum pratense*.



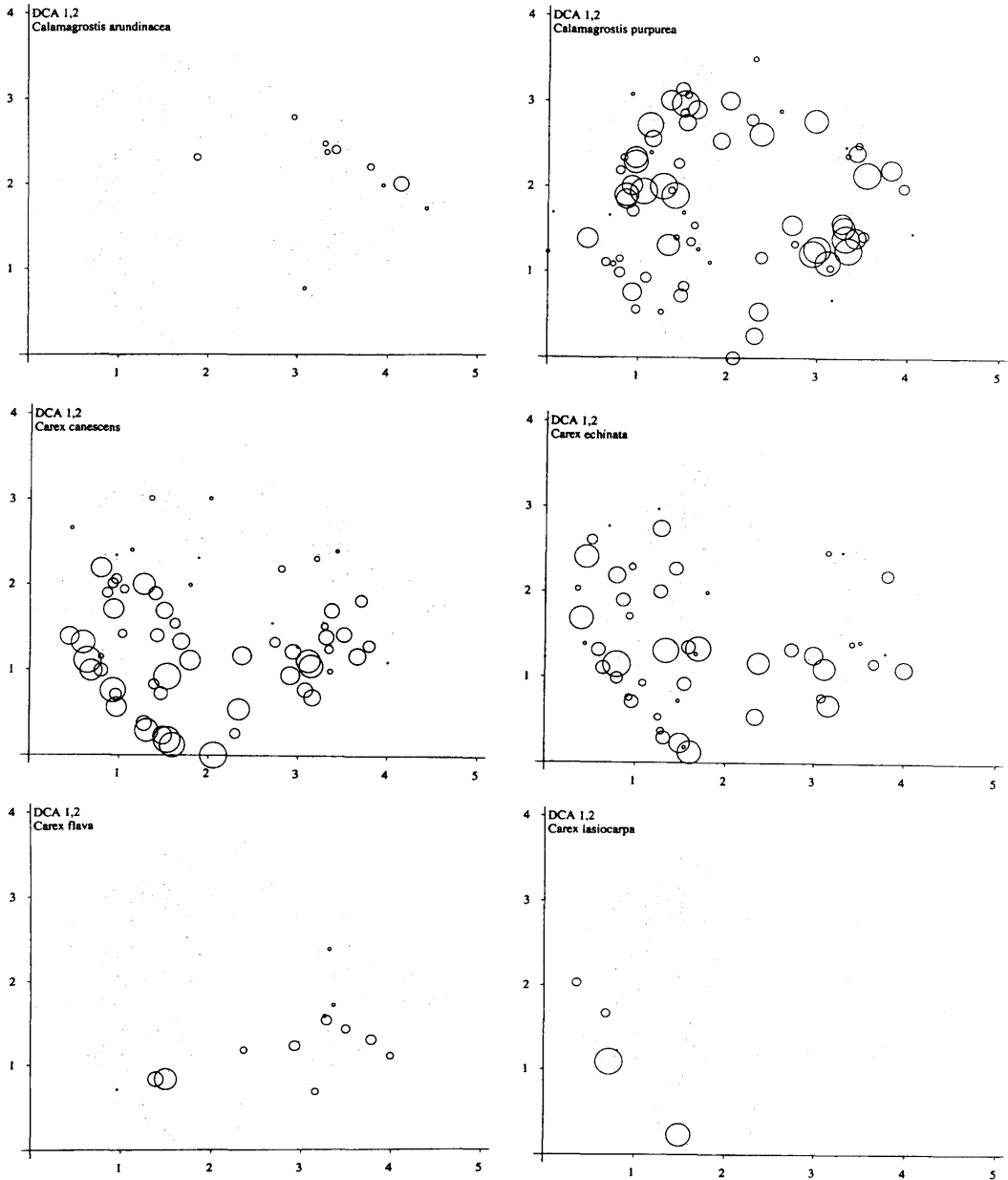
Figs 89–94. Distribution of species abundances in the DCA ordination of the full data set, axes 1 (horizontal) and 2 (vertical). Subplot frequency for each species in each plot proportional to circle size. Scaling of axes in S.D. units. Fig. 89. *Melampyrum sylvaticum*. Fig. 90. *Menyanthes trifoliata*. Fig. 91. *Orthilia secunda*. Fig. 92. *Oxalis acetosella*. Fig. 93. *Paris quadrifolia*. Fig. 94. *Phegopteris connectilis*.



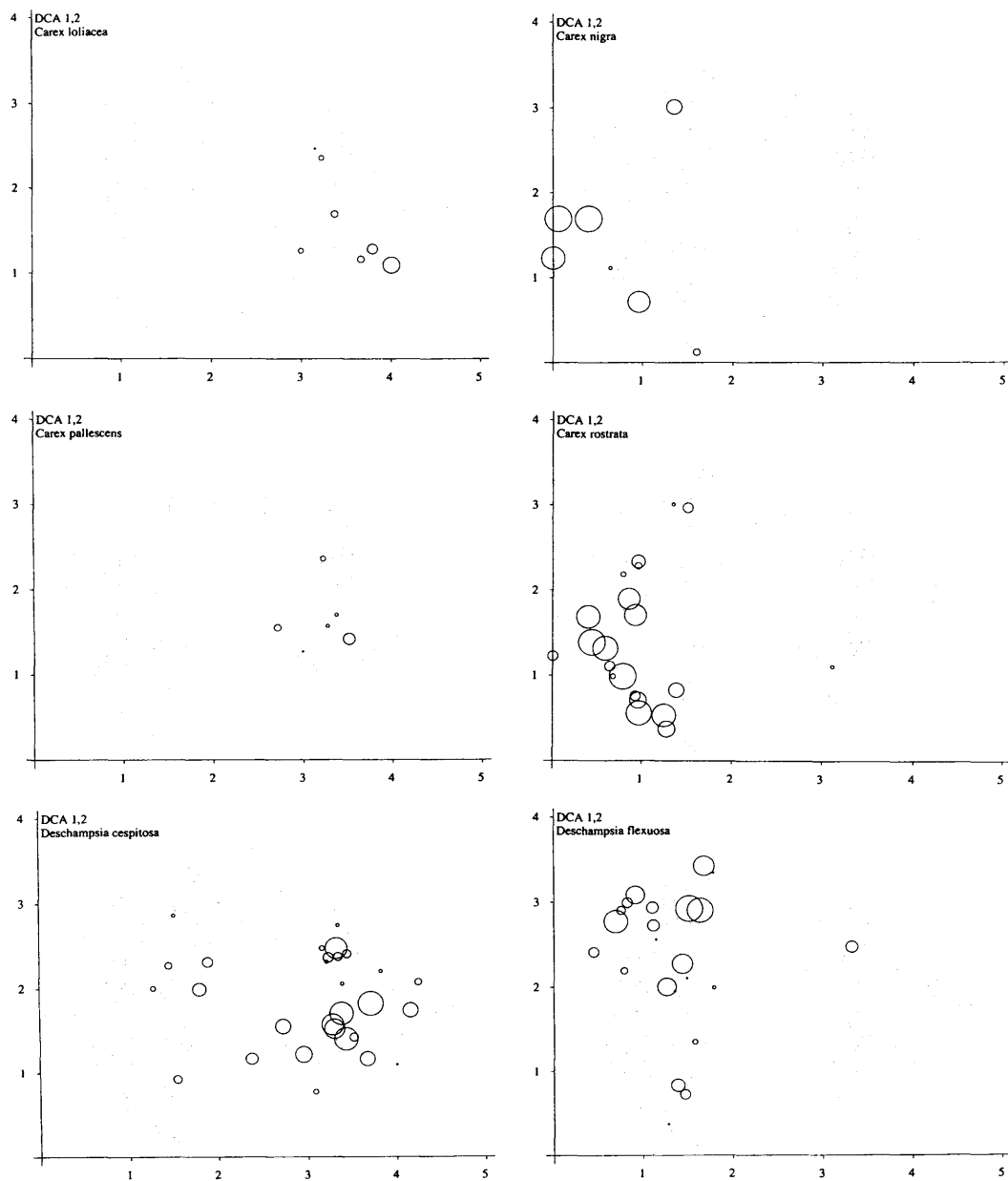
Figs 95–100. Distribution of species abundances in the DCA ordination of the full data set, axes 1 (horizontal) and 2 (vertical). Subplot frequency for each species in each plot proportional to circle size. Scaling of axes in S.D. units. Fig. 95. *Potentilla palustris*. Fig. 96. *Pyrola minor*. Fig. 97. *Ranunculus repens*. Fig. 98. *Rubus chamaemorus*. Fig. 99. *Rubus saxatilis*. Fig. 100. *Trientalis europaea*.



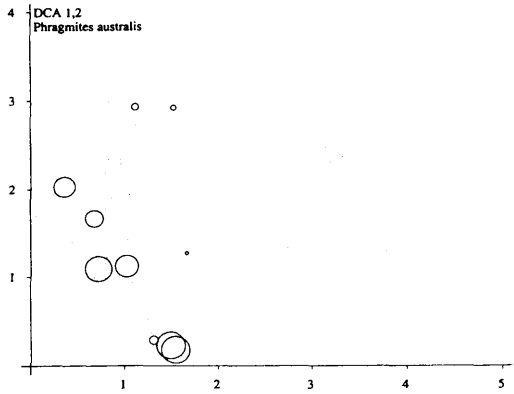
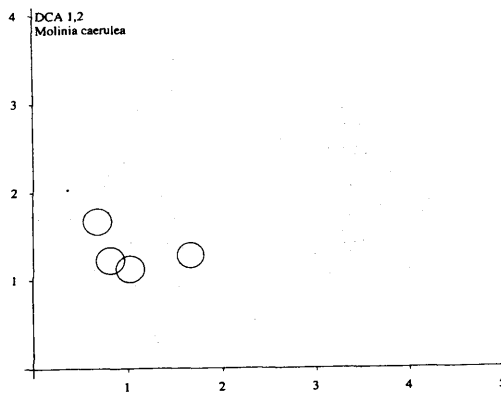
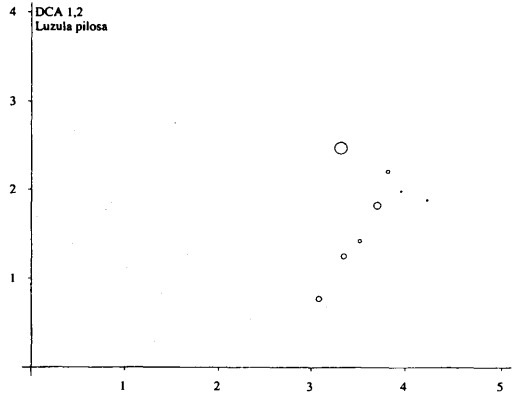
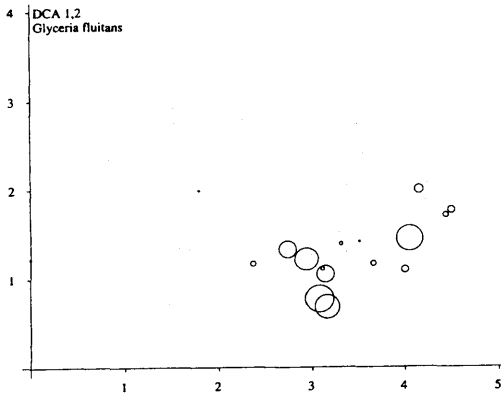
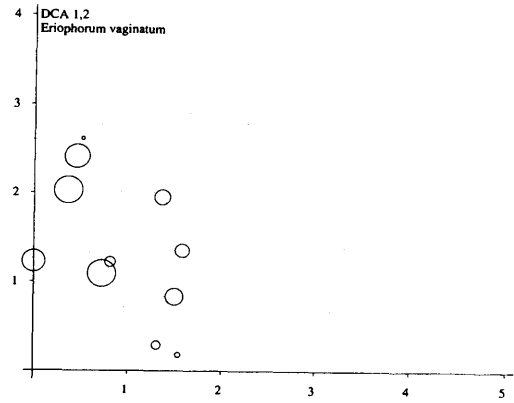
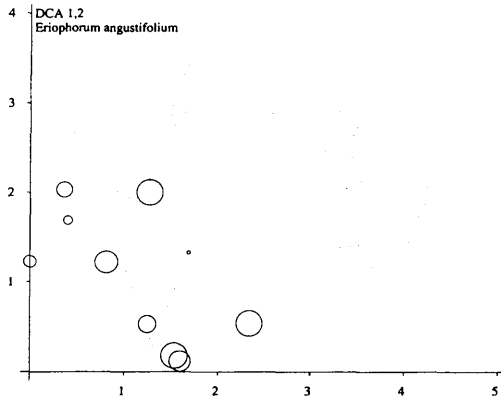
Figs 101–106. Distribution of species abundances in the DCA ordination of the full data set, axes 1 (horizontal) and 2 (vertical). Subplot frequency for each species in each plot proportional to circle size. Scaling of axes in S.D. units. Fig. 101. *Tussilago farfara*. Fig. 102. *Valeriana sambucifolia*. Fig. 103. *Viola palustris*. Fig. 104. *Viola riviniana*. Fig. 105. *Agrostis canina*. Fig. 106. *Agrostis capillaris*.



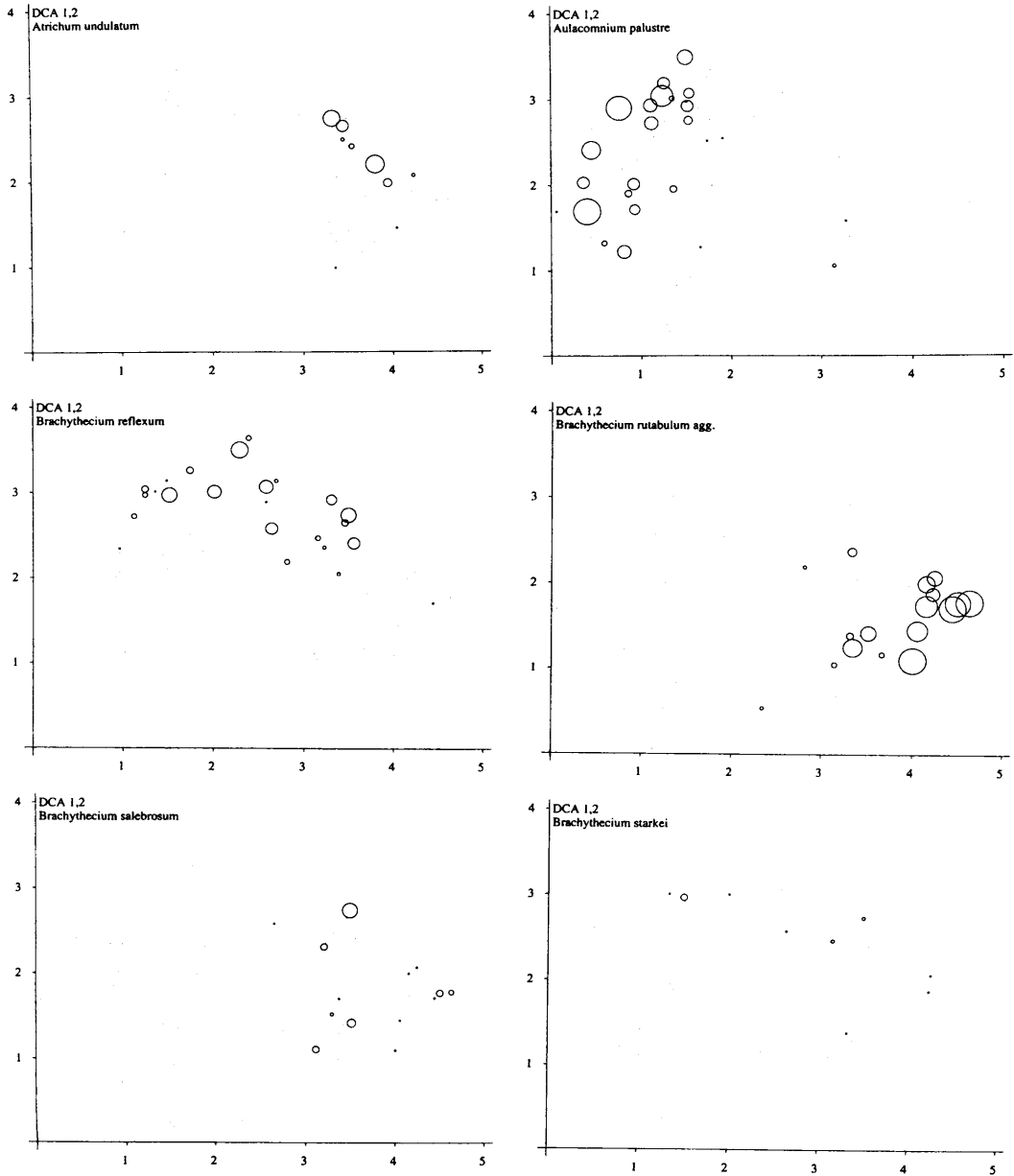
Figs 107–112. Distribution of species abundances in the DCA ordination of the full data set, axes 1 (horizontal) and 2 (vertical). Subplot frequency for each species in each plot proportional to circle size. Scaling of axes in S.D. units. Fig. 107. *Calamagrostis arundinacea*. Fig. 108. *Calamagrostis purpurea*. Fig. 109. *Carex canescens*. Fig. 110. *Carex echinata*. Fig. 111. *Carex flava*. Fig. 112. *Carex lasiocarpa*.



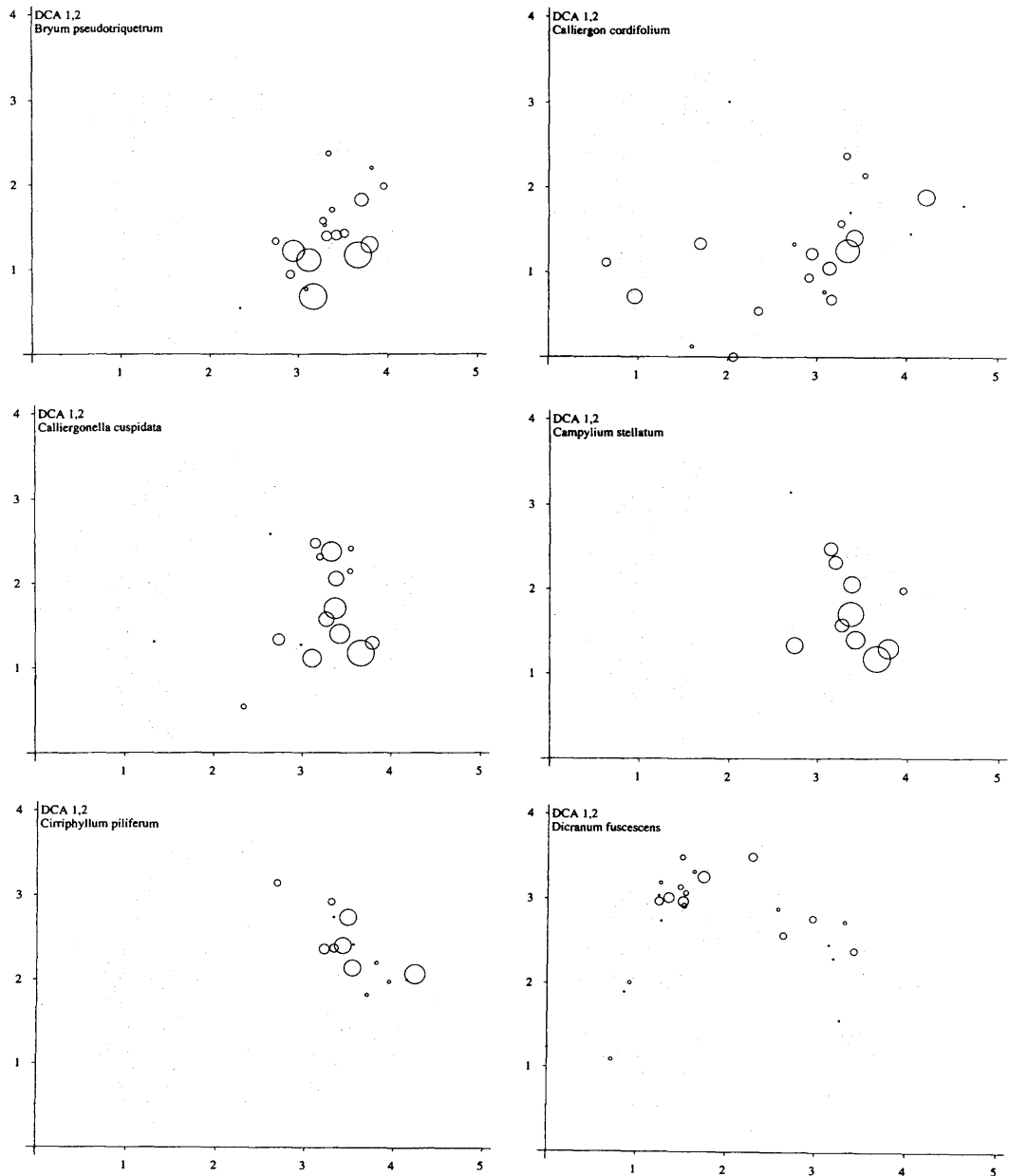
Figs 113–118. Distribution of species abundances in the DCA ordination of the full data set, axes 1 (horizontal) and 2 (vertical). Subplot frequency for each species in each plot proportional to circle size. Scaling of axes in S.D. units. Fig. 113. *Carex loliacea*. Fig. 114. *Carex nigra*. Fig. 115. *Carex pallescens*. Fig. 116. *Carex rostrata*. Fig. 117. *Deschampsia cespitosa*. Fig. 118. *Deschampsia flexuosa*.



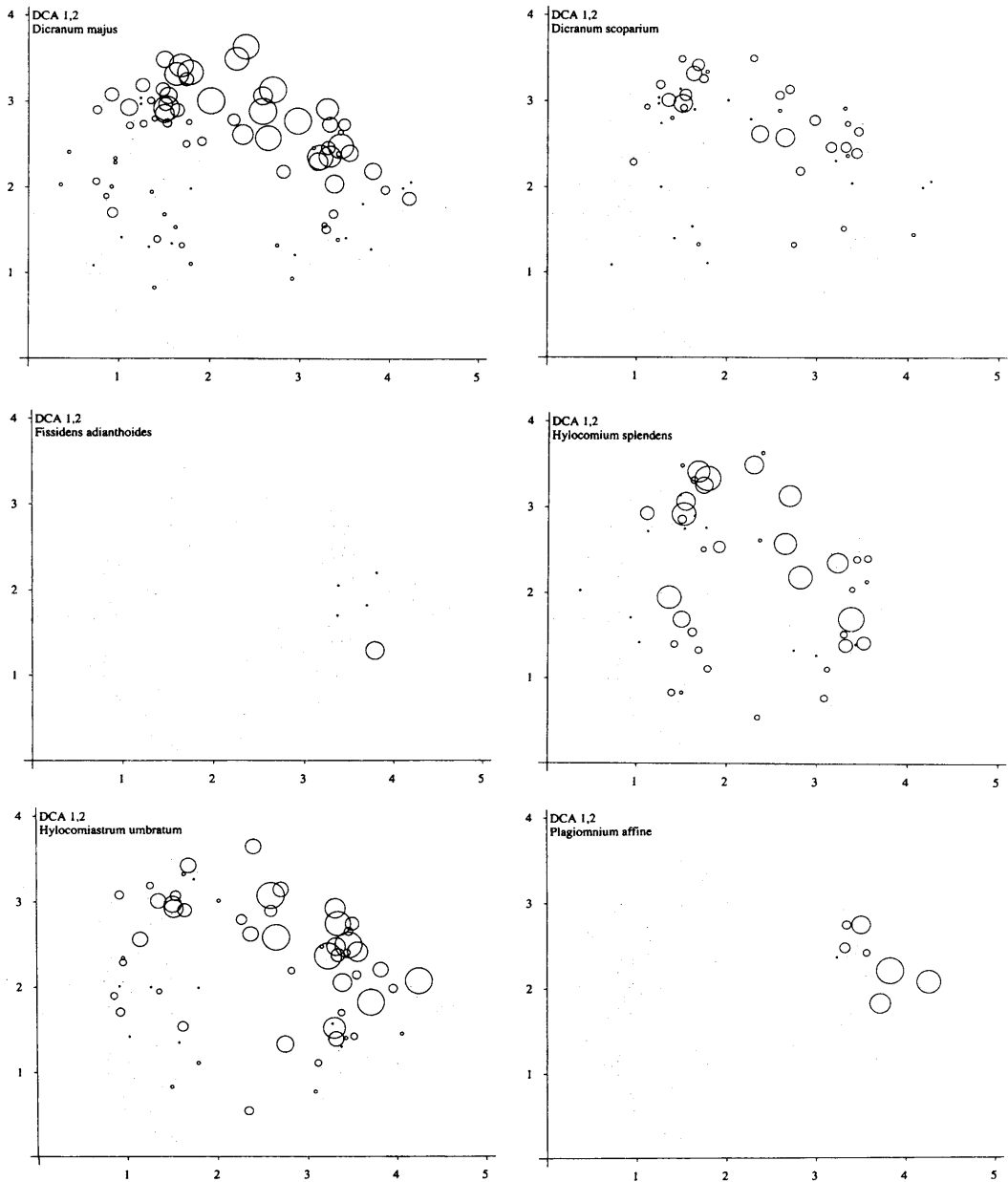
Figs 119–124. Distribution of species abundances in the DCA ordination of the full data set, axes 1 (horizontal) and 2 (vertical). Subplot frequency for each species in each plot proportional to circle size. Scaling of axes in S.D. units. Fig. 119. *Eriophorum angustifolium*. Fig. 120. *Eriophorum vaginatum*. Fig. 121. *Glyceria fluitans*. Fig. 122. *Luzula pilosa*. Fig. 123. *Molinia caerulea*. Fig. 124. *Phragmites australis*.



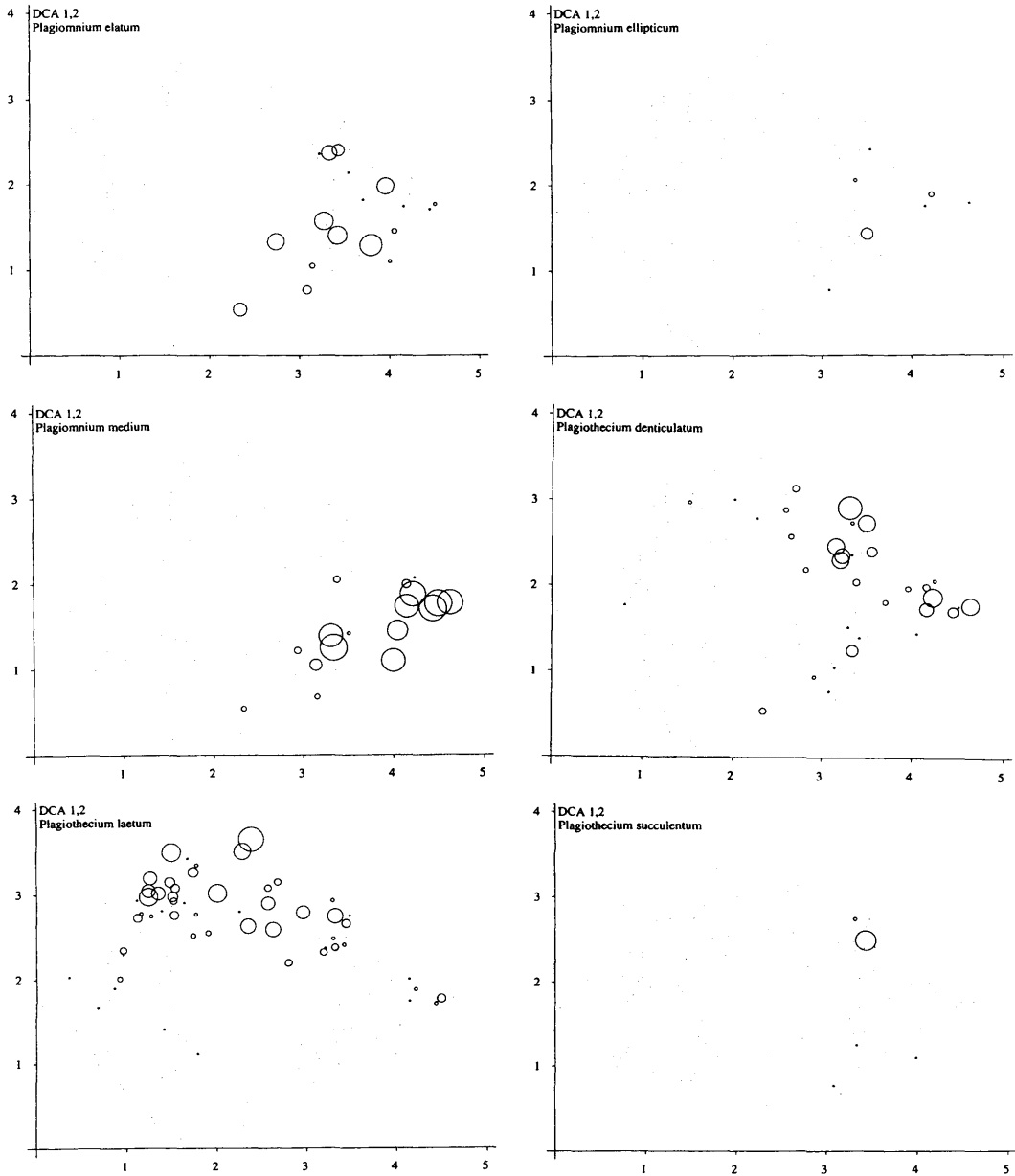
Figs 125–130. Distribution of species abundances in the DCA ordination of the full data set, axes 1 (horizontal) and 2 (vertical). Subplot frequency for each species in each plot proportional to circle size. Scaling of axes in S.D. units. Fig. 125. *Atrichum undulatum*. Fig. 126. *Aulacomnium palustre*. Fig. 127. *Brachythecium reflexum*. Fig. 128. *Brachythecium rutabulum* agg.. Fig. 129. *Brachythecium salebrosum*. Fig. 130. *Brachythecium starkei*.



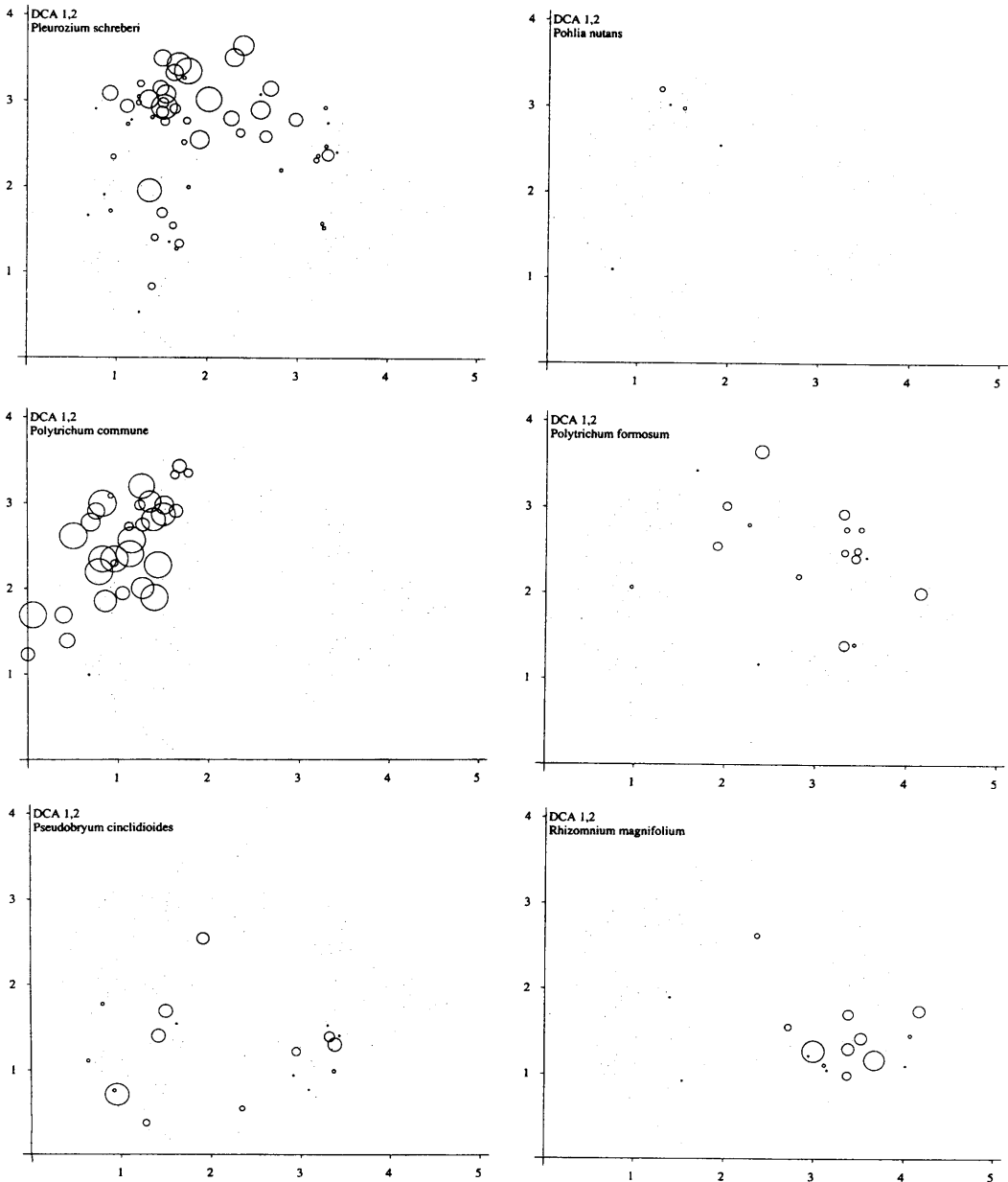
Figs 131–136. Distribution of species abundances in the DCA ordination of the full data set, axes 1 (horizontal) and 2 (vertical). Subplot frequency for each species in each plot proportional to circle size. Scaling of axes in S.D. units. Fig. 131. *Bryum pseudotriquetrum*. Fig. 132. *Calliergon cordifolium*. Fig. 133. *Calliergonella cuspidata*. Fig. 134. *Campylium stellatum*. Fig. 135. *Cirriphyllum piliferum*. Fig. 136. *Dicranum fuscescens*.



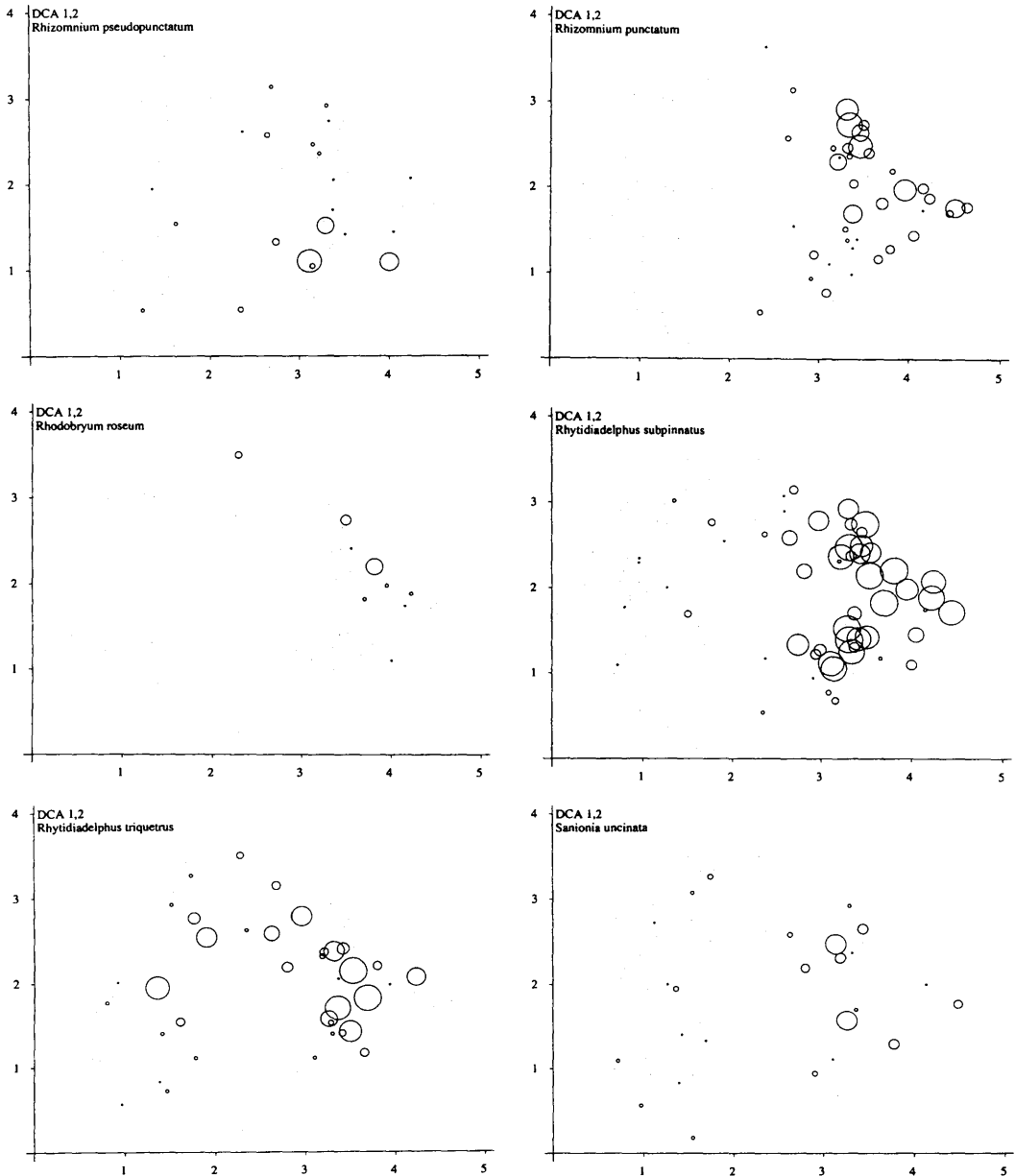
Figs 137–142. Distribution of species abundances in the DCA ordination of the full data set, axes 1 (horizontal) and 2 (vertical). Subplot frequency for each species in each plot proportional to circle size. Scaling of axes in S.D. units. Fig. 137. *Dicranum majus*. Fig. 138. *Dicranum scoparium*. Fig. 139. *Fissidens adianthoides*. Fig. 140. *Hylocomium splendens*. Fig. 141. *Hylocomiastrum umbratum*. Fig. 142. *Plagiomnium affine*.



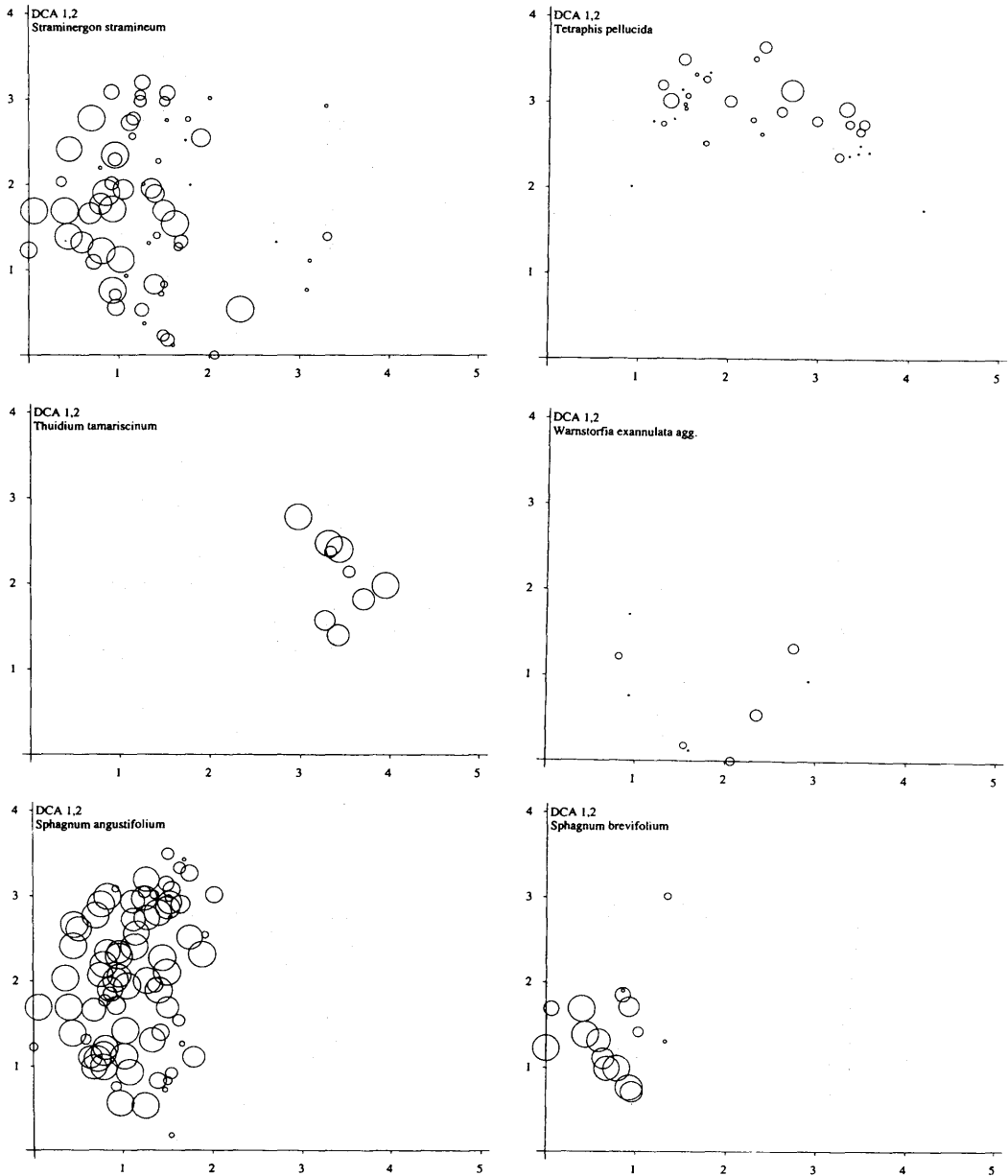
Figs 143- 148. Distribution of species abundances in the DCA ordination of the full data set, axes 1 (horizontal) and 2 (vertical). Subplot frequency for each species in each plot proportional to circle size. Scaling of axes in S.D. units. Fig. 143. *Plagiomnium elatum*. Fig. 144. *Plagiomnium ellipticum*. Fig. 145. *Plagiomnium medium*. Fig. 146. *Plagiothecium denticulatum*. Fig. 147. *Plagiothecium laetum*. Fig. 148. *Plagiothecium nemorale*.



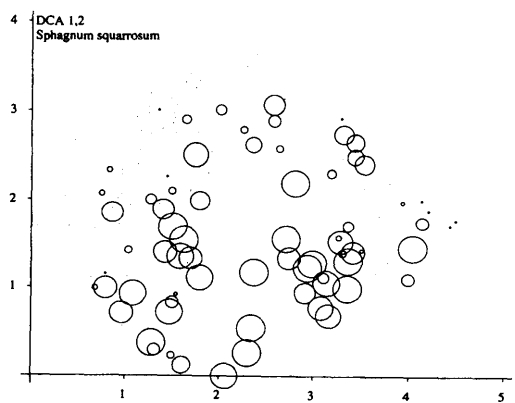
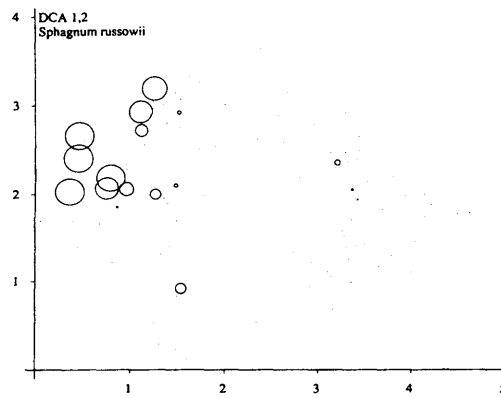
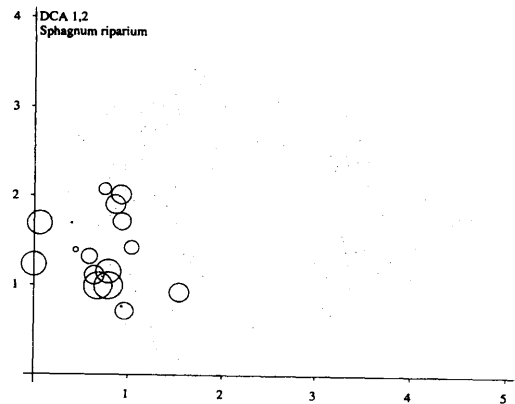
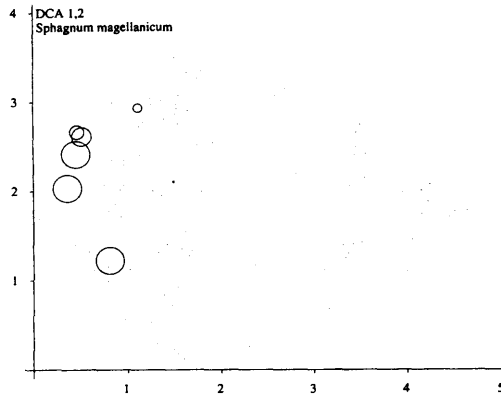
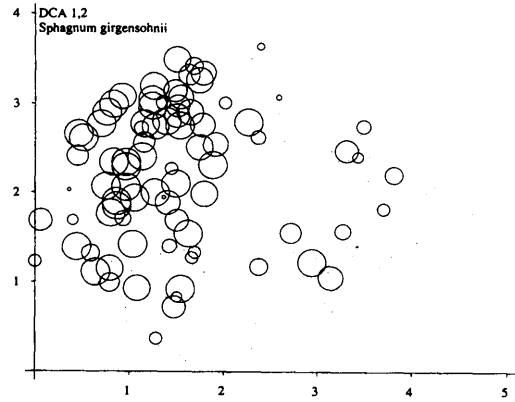
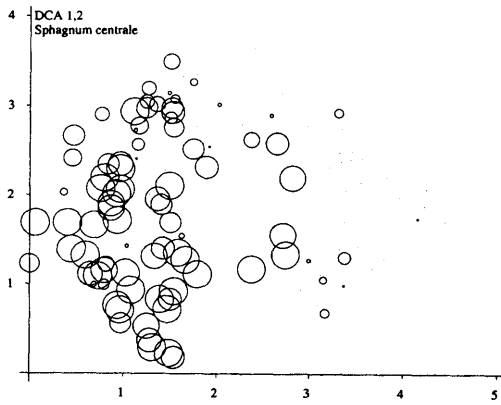
Figs 149–154. Distribution of species abundances in the DCA ordination of the full data set, axes 1 (horizontal) and 2 (vertical). Subplot frequency for each species in each plot proportional to circle size. Scaling of axes in S.D. units. Fig. 149. *Pleurozium schreberi*. Fig. 150. *Pohlia nutans*. Fig. 151. *Polytrichum commune*. Fig. 152. *Polytrichum formosum*. Fig. 153. *Pseudobryum cinclidioides*. Fig. 154. *Rhizomnium magnifolium*.



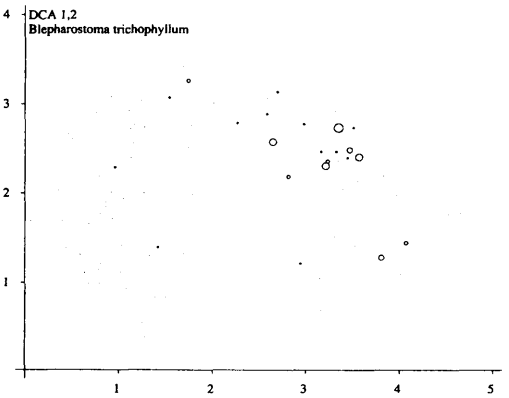
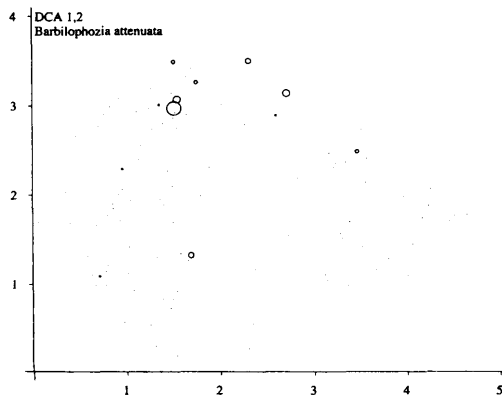
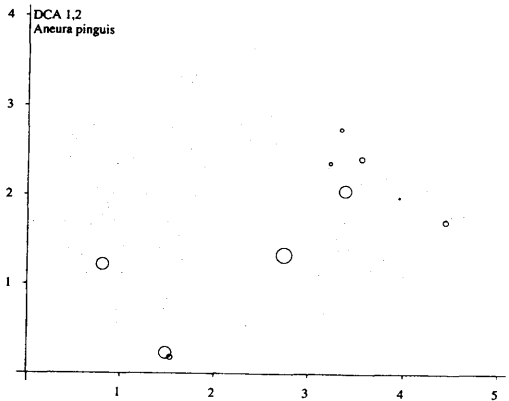
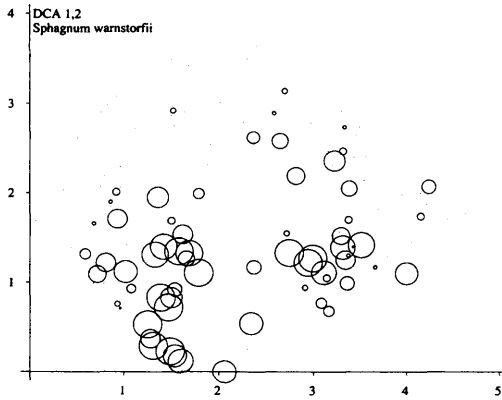
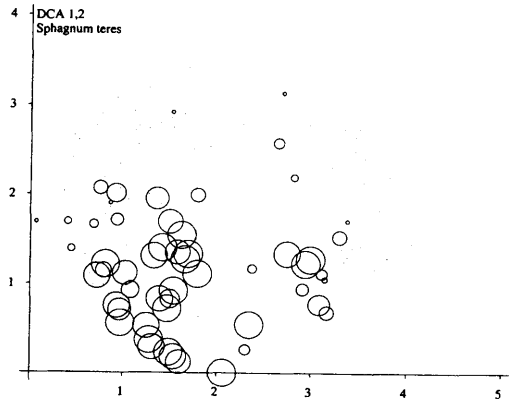
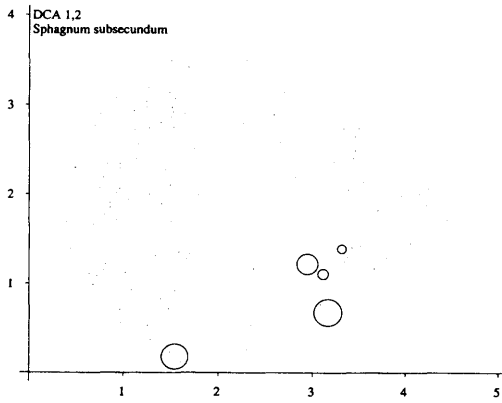
Figs 155–160. Distribution of species abundances in the DCA ordination of the full data set, axes 1 (horizontal) and 2 (vertical). Subplot frequency for each species in each plot proportional to circle size. Scaling of axes in S.D. units. Fig. 155. *Rhizomnium pseudopunctatum*. Fig. 156. *Rhizomnium punctatum*. Fig. 157. *Rhodobryum roseum*. Fig. 158. *Rhytidiadelphus subpinnatus*. Fig. 159. *Rhytidiadelphus triquetrus*. Fig. 160. *Sanionia uncinata*.



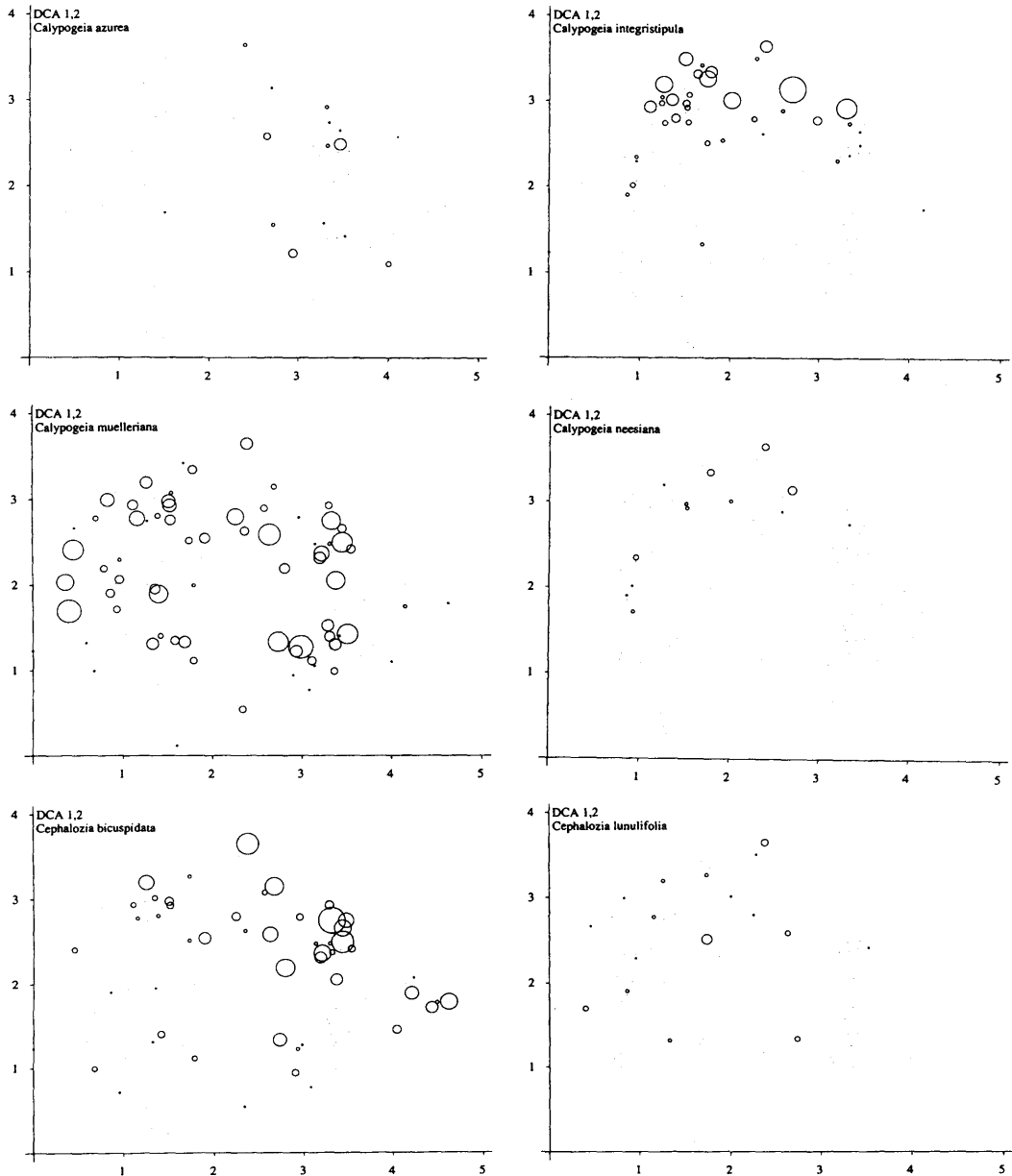
Figs 161- 166. Distribution of species abundances in the DCA ordination of the full data set, axes 1 (horizontal) and 2 (vertical). Subplot frequency for each species in each plot proportional to circle size. Scaling of axes in S.D. units. Fig. 161. *Straminergon stramineum*. Fig. 162. *Tetraphis pellucida*. Fig. 163. *Thuidium tamariscinum*. Fig. 164. *Warnstorfia exannulata* agg.. Fig. 165. *Sphagnum angustifolium*. Fig. 166. *Sphagnum brevifolium*.



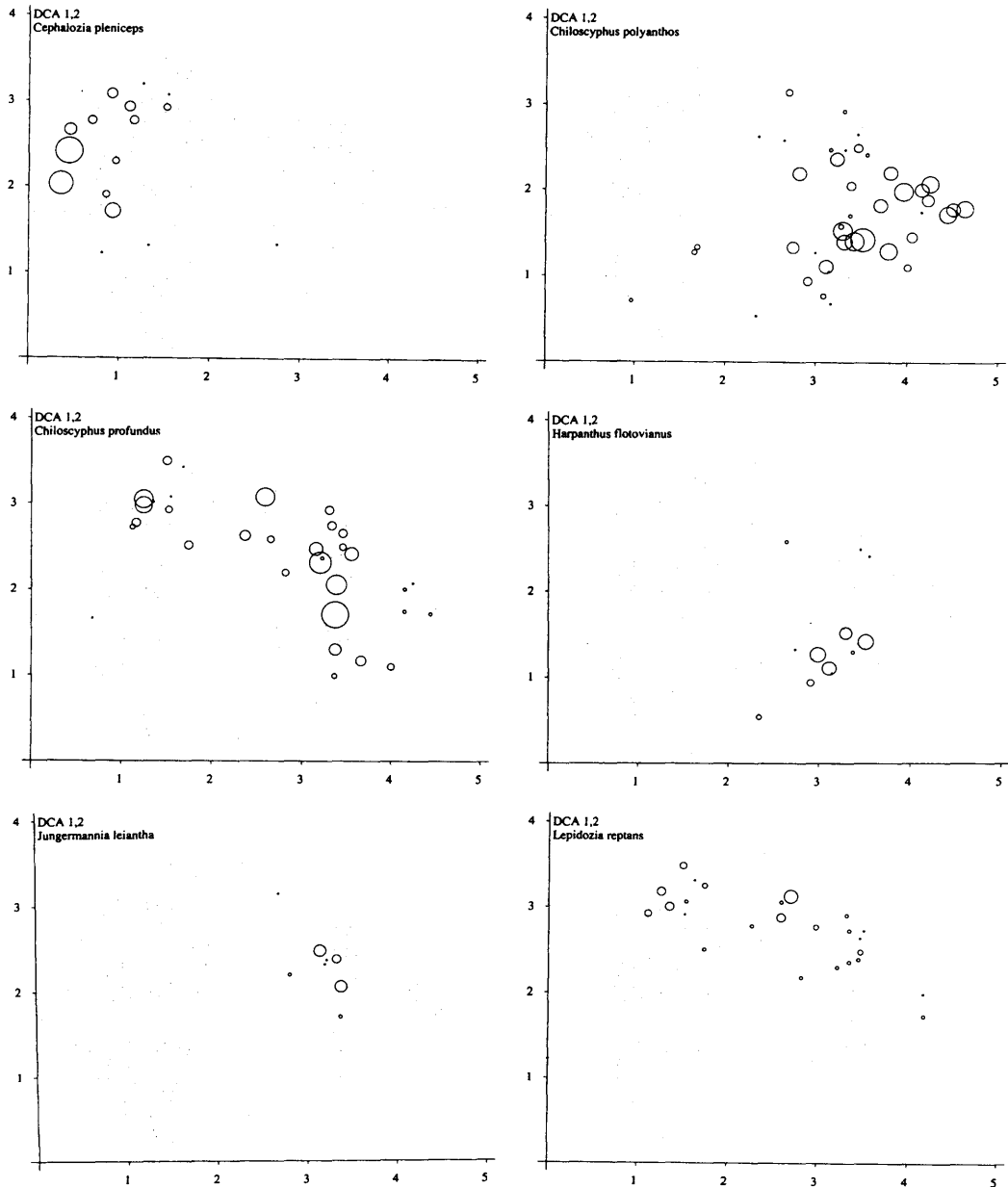
Figs 167–172. Distribution of species abundances in the DCA ordination of the full data set, axes 1 (horizontal) and 2 (vertical). Subplot frequency for each species in each plot proportional to circle size. Scaling of axes in S.D. units. Fig. 167. *Sphagnum centrale*. Fig. 168. *Sphagnum girgensohnii*. Fig. 169. *Sphagnum magellanicum*. Fig. 170. *Sphagnum riparium*. Fig. 171. *Sphagnum russowii*. Fig. 172. *Sphagnum squarrosum*.



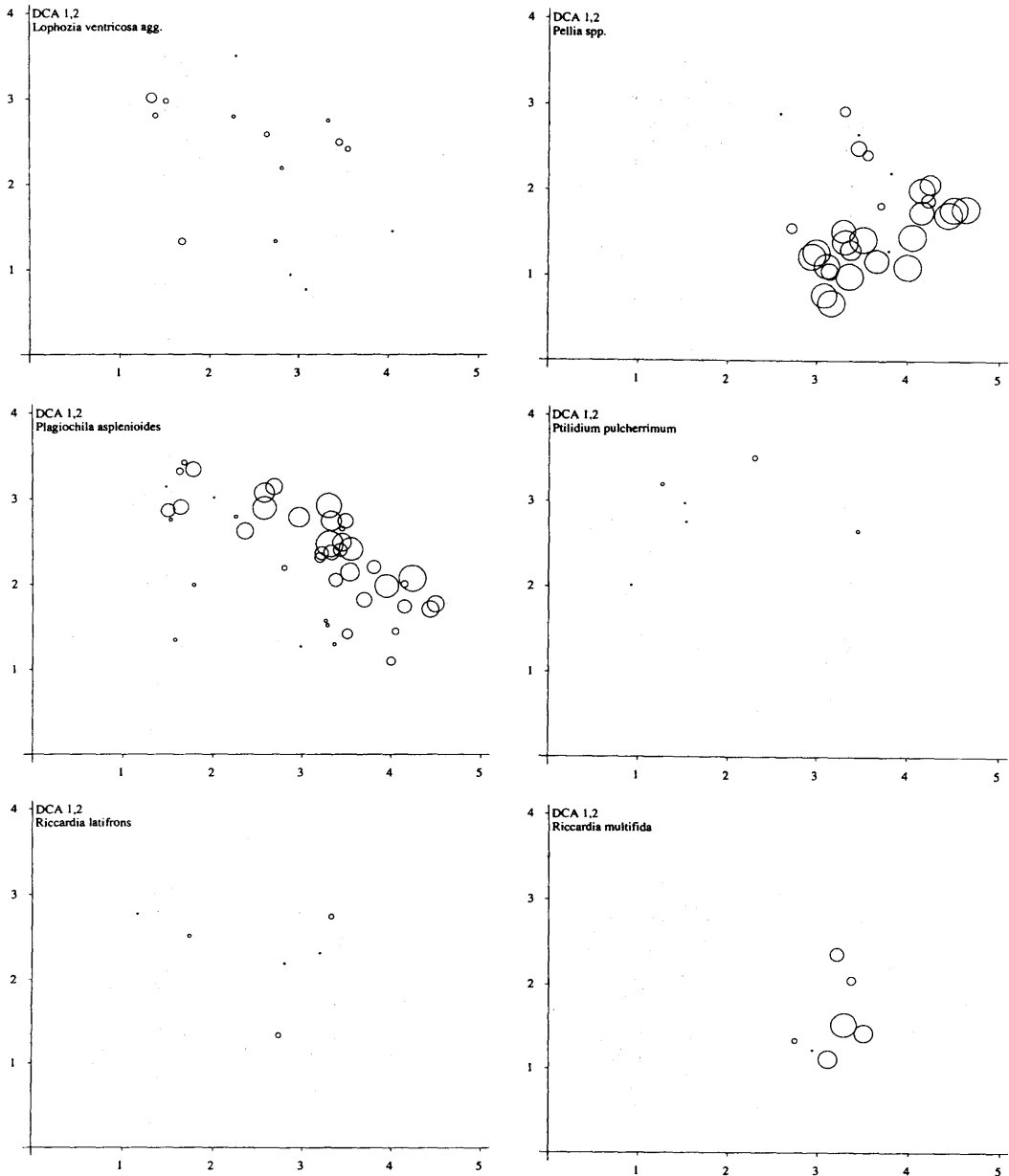
Figs 173–178. Distribution of species abundances in the DCA ordination of the full data set, axes 1 (horizontal) and 2 (vertical). Subplot frequency for each species in each plot proportional to circle size. Scaling of axes in S.D. units. Fig. 173. *Sphagnum subsecundum*. Fig. 174. *Sphagnum teres*. Fig. 175. *Sphagnum warnstorffii*. Fig. 176. *Aneura pinguis*. Fig. 177. *Barbilophozia attenuata*. Fig. 178. *Blepharostoma trichophyllum*.



Figs 179–184. Distribution of species abundances in the DCA ordination of the full data set, axes 1 (horizontal) and 2 (vertical). Subplot frequency for each species in each plot proportional to circle size. Scaling of axes in S.D. units. Fig. 179. *Calypogeia azurea*. Fig. 180. *Calypogeia integristipula*. Fig. 181. *Calypogeia muelleriana*. Fig. 182. *Calypogeia neesiana*. Fig. 183. *Cephalozia bicuspidata*. Fig. 184. *Cephalozia lunulifolia*.



Figs 185–190. Distribution of species abundances in the DCA ordination of the full data set, axes 1 (horizontal) and 2 (vertical). Subplot frequency for each species in each plot proportional to circle size. Scaling of axes in S.D. units. Fig. 185. *Cephalozia pleniceps*. Fig. 186. *Chiloscypus polyanthos*. Fig. 187. *Chiloscypus profundus*. Fig. 188. *Harpanthus flotovianus*. Fig. 189. *Jungermannia leiantha*. Fig. 190. *Lepidozia reptans*.

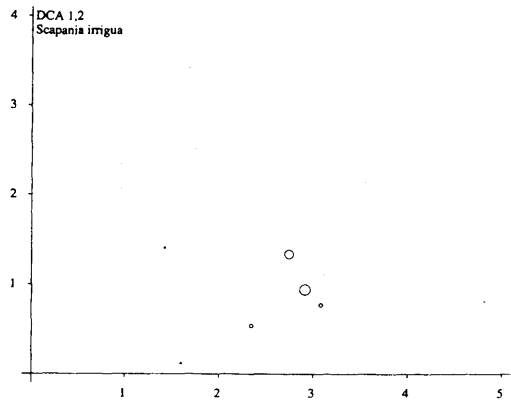


Figs 191–196. Distribution of species abundances in the DCA ordination of the full data set, axes 1 (horizontal) and 2 (vertical). Subplot frequency for each species in each plot proportional to circle size. Scaling of axes in S.D. units. Fig. 191. *Lophozia ventricosa* agg. Fig. 192. *Pellia* spp. Fig. 193. *Plagiochila asplenioides*. Fig. 194. *Ptilidium pulcherrimum*. Fig. 195. *Riccardia latifrons*. Fig. 196. *Riccardia multifida*.

DCA-C 3 was not strongly correlated with any of the explanatory variables while DCA-C 4 (like DCA-B 3) was correlated with the range of water-table fluctuations (Tab. 10).

Like DCA-D 1, DCA-D 3 was strongly correlated with several variables of, or associated with, the soil nutrient/acidity group. But unlike DCA-D 1, DCA-D 3 was also moderately correlated with variables of the water-table group. These correlation patterns resembled those found for DCA 1, with which DCA-D 3 was weakly but significantly positively correlated, and were inverse to those found for DCA 2, which was negatively correlated with DCA-D 3.

DCA-D 4 was strongly correlated with DCA 4 (Tab. 7), but unlike the latter DCA D-4 was most strongly correlated with soil depth ($\tau > 0.22$) and the correlations with microtopography variables were weaker (in the range $0.15 < \tau < 0.2$).



Figs 197. Distribution of abundance of *Scapania irrigua* in the DCA ordination of the full data set, axes 1 (horizontal) and 2 (vertical). Subplot frequency in each plot proportional to circle size. Scaling of axes in S.D. units.

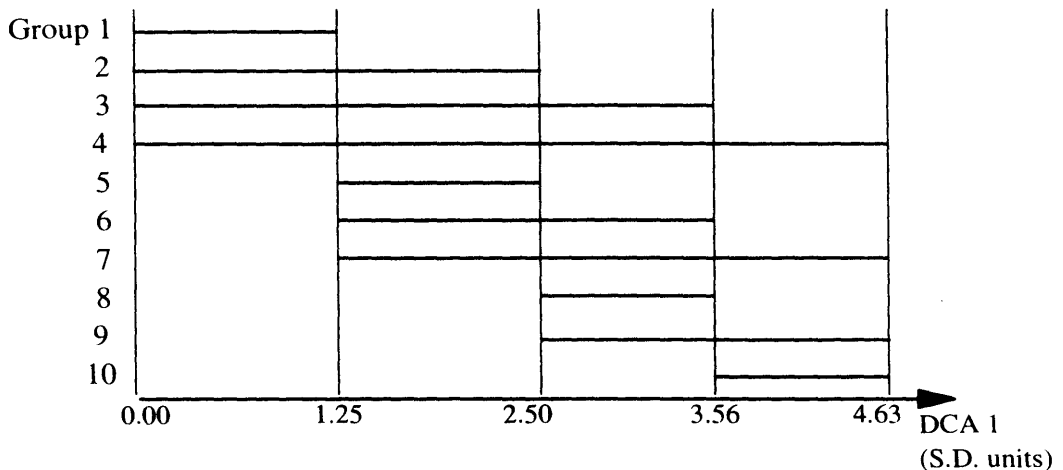
Positions of species optima and variation in species abundances along axes in the DCA ordination of the full data set

Positions of species optima

Optima close to the low-score end of DCA-axis 1 were obtained by species typical of (poorer) mires (e.g., *Vaccinium oxycoccos*, *Menyanthes trifoliata*, *Carex lasiocarpa*, *C. nigra*, *C. rostrata*, *Eriophorum vaginatum*, *Phragmites communis* and *Sphagnum magellanicum*) while optima close

Tab. 11. Kendall's rank correlation coefficients τ between plot scores along DCA axes ($n = 150$) and four primary and two secondary species richness variables (number of plant species of a given group present in the plot), with significance probabilities (P). Strong correlations ($|\tau| \geq 0.3$, $P < 0.0001$) in bold face.

Variable	DCA 1		DCA 2		DCA 3		DCA 4	
	τ	P	τ	P	τ	P	τ	P
Vascular plants	.4034	.0000	-.2558	.0000	-.1483	.0087	.0248	.6612
Mosses	.4696	.0000	.2327	.0000	-.1117	.0491	.1206	.0337
<i>Sphagnum</i>	-.4654	.0000	-.2782	.0000	.0360	.5408	.0758	.1979
Hepatics	.3733	.0000	.2481	.0000	-.1007	.0825	.1936	.0008
Cryptogams	.3789	.0000	.2074	.0002	-.0904	.1075	.1997	.0004
All species	.4648	.0000	.0260	.6375	-.1183	.0317	.1464	.0078

**Species group 1**

Vaccinium oxycoccos
Sphagnum brevifolium
Sphagnum magellanicum
Sphagnum riparium

Species group 2

Frangula alnus
Vaccinium vitis-idaea
Dactylorhiza maculata
Melampyrum pratense
Menyanthes trifoliata
(Pyrola minor)
Rubus chamaemorus
Carex lasiocarpa
Carex nigra
Carex rostrata
Deschampsia flexuosa
Eriophorum angustifolium
Eriophorum vaginatum
Molinia caerulea
Phragmites australis
Aulacomnium palustre
Pohlia nutans
Polytrichum commune
Sphagnum angustifolium
Sphagnum russowii
Cephalozia lunulifolia
Cephalozia pleniceps

Species group 3

Betula spp.
Vaccinium myrtillus
Lycopodium annotinum

Orthilia secunda
Potentilla palustris
Dicranum fuscescens
Pleurozium schreberi
Straminergon stramineum
Sphagnum centrale
Sphagnum girgensohnii
Calypogeia integrispula
Calypogeia neesiana
Lepidozia reptans
Ptilidium pulcherrimum

Species group 4

Picea abies
Sorbus aucuparia
Linnaea borealis
Maianthemum bifolium
Trientalis europaea
Viola palustris
Calamagrostis purpurea
Carex canescens
Carex echinata
Dicranum majus
Dicranum scoparium
Plagiothecium laetum
Sanionia uncinata
Sphagnum squarrosum
Calypogeia muelleriana
Cephalozia bicuspidata

Species group 5

(Equisetum fluviale)

Species group 6

Lysimachia thyrsoiflora

Hylocomium splendens
Pseudobryum cinclidioides
Tetraphis pellucida
Warnstorfia exannulata agg.
Sphagnum subsecundum
Sphagnum teres
Barbilophozia attenuata
(Riccardia latifrons)
Scapania irrigua

Species group 7

Anemone nemorosa
Athyrium filix-femina
Caltha palustris
Dryopteris expansa agg.
Equisetum sylvaticum
Filipendula ulmaria
Galium palustre
Gymnocarpium dryopteris
Melampyrum sylvaticum
Oxalis acetosella
Phegopteris connectilis
Rubus saxatilis
Valeriana sambucifolia
Agrostis canina
Calamagrostis arundinacea
Carex flava
Deschampsia cespitosa
Brachythecium reflexum
Brachythecium starkei
Calliergon cordifolium
Hylocomiastrum umbratum
Plagiothecium

denticulatum
Polytrichum formosum
Rhizomnium pseudopunctatum
Rhytidadelphus squarrosus agg.
Rhytidadelphus triquetrus
Sphagnum warnstorffii
Aneura pinguis
Blepharostoma trichophyllum
Calypogeia azurea
Chiloscyphus polyanthos
Chiloscyphus profundus
Lophozia ventricosa agg.
Plagiochila asplenioides

Species group 8

(Equisetum pratense)
(Carex pallescens)
(Harpanthus flotovianus)
(Jungermannia leiantha)
(Riccardia multifida)

Species group 9

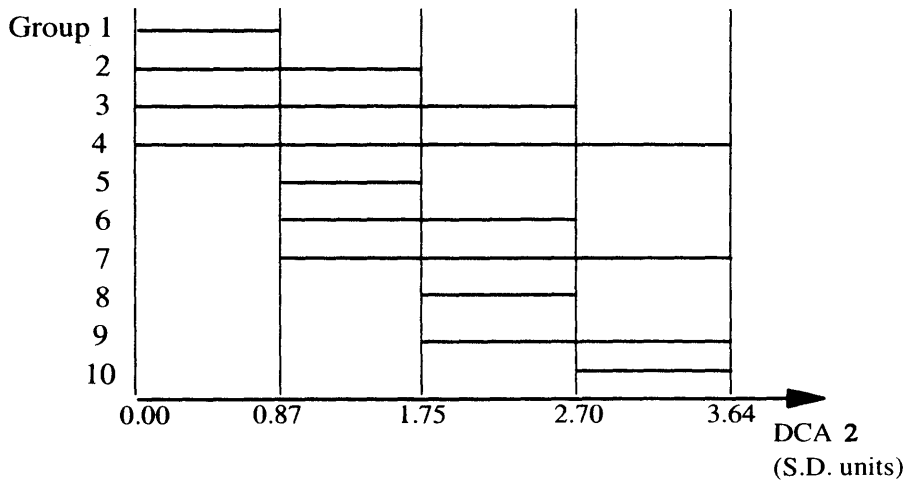
Alnus incana
Circaea alpina
Crepis paludosa
Epilobium palustre
Geum rivale
Tussilago farfara

Viola riviniana
Agrostis capillaris
Carex loliacea
Glyceria fluitans
Luzula pilosa
Atrichum undulatum
Brachythecium rutabulum agg.
Brachythecium salebrosum
Bryum pseudotriquetrum
Calliergonella cuspidata
Campyllum stellatum
Cirriphyllum piliferum
Fissidens adianthoides
Plagiomnium affine
Plagiomnium elatum
Plagiomnium ellipticum
Plagiomnium medium
Plagiothecium nemorale
Rhizomnium cuspidata
Rhizomnium magnifolium
Rhizomnium punctatum
Rhodobryum roseum
Thuidium tamariscinum
Pellia spp.

Species group 10

Chryso-splenium alternifolium
Matteuccia struthiopteris
Paris quadriflora
Ranunculus repens

Fig. 198. Species distributions along axis 1 in the DCA ordination of the full data set (150 1-m² plots). Species with few occurrences and hence with uncertain affiliation to group are given in brackets.



Species group 1
(none)

Species group 2

Epilobium palustre
Equisetum fluviatile
Lysimachia thyrsoflora
Potentilla palustris
(*Pyrola minor*)
Carex flava
Carex lasiocarpa
Glyceria fluitans
Pseudobryum
cinclidioides
Warnstorfia exannulata
agg.
Sphagnum brevifolium
Sphagnum riparium
Sphagnum subsecundum
Scapania irrigua

Species group 3

Vaccinium oxycoccos
Caltha palustris
Dactylorhiza maculata
Galium palustre
Menyanthes trifoliata
Valeriana sambucifolia
Viola palustris
Agrostis canina
Carex canescens
Carex echinata
Eriophorum
angustifolium
Eriophorum vaginatum
Molinia caerulea
Brachythecium

rutabulum agg.

Bryum

pseudotriquetrum
Calliergon cordifolium
Plagiomnium elatum
Plagiomnium medium
Sphagnum teres
Sphagnum warnstorffii
Aneura pinguis

Species group 4

Filipendula ulmaria
Oxalis acetosella
Trientalis europaea
Calamagrostis purpurea
Carex nigra
Carex rostrata
Phragmites australis
Hylocomium splendens
Plagiothecium
denticulatum
Pleurozium schreberi
Rhizomnium
pseudopunctatum
Rhizomnium punctatum
Rhytidiadelphus
subpinnatus agg.
Sanionia uncinata
Straminergon
stramineum
Sphagnum
angustifolium
Sphagnum centrale
Sphagnum girgensohnii
Sphagnum squarrosum
Cephalozia bicuspidata
Chiloscyphus
polyanthos

Pellia spp.

Species group 5
(none)

Species group 6

Chrysopterygium alternifolium
Equisetum pratense
Matteuccia
struthiopteris
Paris quadrifolia
Ranunculus repens
Tussilago farfara
Agrostis capillaris
Carex loliacea
Carex pallenscens
Luzula pilosa
Calliergonella
cuspidata
Campyllum stellatum
Fissidens adianthoides
Plagiomnium ellipticum
Rhizomnium
magnifolium
Harpanthus flotovianus
Riccardia latifrons
Riccardia multifida

Species group 7

Alnus incana
Betula spp.
Frangula alnus
Picea abies
Vaccinium myrtillus
Vaccinium vitis-idaea
Anemone nemorosa

Athyrium filix-femina
Crepis paludosa
Dryopteris expansa agg.
Equisetum sylvaticum
Gymnocarpium
dryopteris
Linnaea borealis
Lycopodium annotinum
Maianthemum bifolium
Melampyrum sylvaticum
Phegopteris connectilis
Rubus chamaemorus
Rubus saxatilis
Deschampsia cespitosa
Deschampsia flexuosa
Aulacomnium palustre
Brachythecium
salebrosum
Dicranum majus
Dicranum scoparium
Hylocomiastrum
umbratum
Plagiothecium nemorale
Polytrichum commune
Polytrichum formosum
Rhodobryum roseum
Rhytidiadelphus
triquetrus
Thuidium tamariscinum
Sphagnum
magellanicum
Blepharostoma
trichophyllum
Calypogeia azurea
Calypogeia muelleriana
Cephalozia lunulifolia
Chiloscyphus profundus
Lophozia ventricosa

agg.
Plagiochila
asplesioides

Species group 8

Geum rivale
Jungermannia leiantha

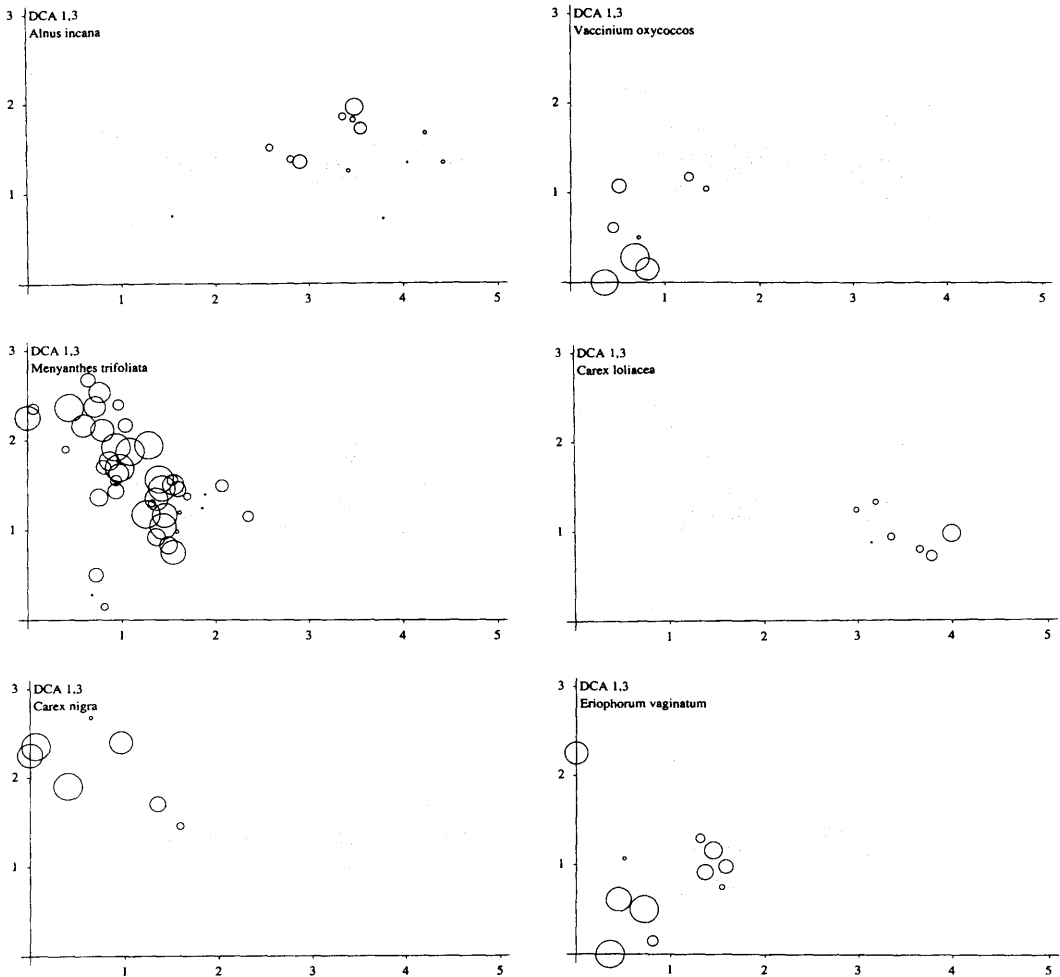
Species group 9

Sorbus aucuparia
Circaea alpina
Melampyrum pratense
Orthilia secunda
Viola riviniana
Calamagrostis
arundinacea
Atrichum undulatum
Brachythecium reflexum
Brachythecium starkei
Cirriphyllum piliferum
Dicranum fuscescens
Plagiomnium affine
Plagiothecium laetum
Tetraphis pellucida
Sphagnum russowii
Barbilophozia attenuata
Calypogeia
integristipula
Calypogeia neesiana
Cephalozia pleniceps
Lepidozia reptans
Ptilidium pulcherrimum

Species group 10

Pohlia nutans

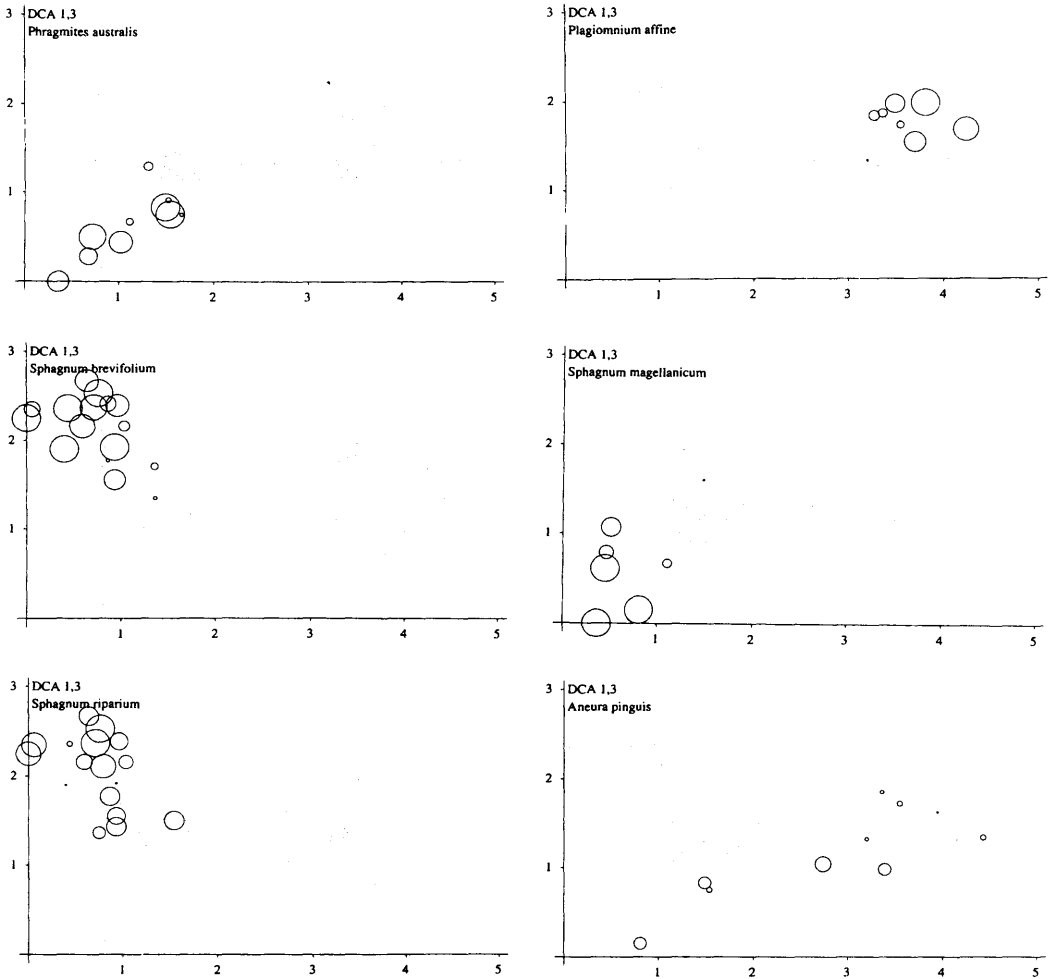
Fig. 199. Species distributions along axis 2 in the DCA ordination of the full data set (150 1-m² plots). Species with few occurrences and hence with uncertain affiliation to group are given in brackets.



Figs 200–205. Distribution of species abundances in the DCA ordination of the full data set, axes 1 (horizontal) and 3 (vertical). Subplot frequency for each species in each plot proportional to circle size. Scaling of axes in S.D. units. Fig. 200. *Alnus incana*. Fig. 201. *Vaccinium oxycoccos*. Fig. 202. *Menyanthes trifoliata*. Fig. 203. *Carex loliacea*. Fig. 204. *Carex nigra*. Fig. 205. *Eriophorum vaginatum*.

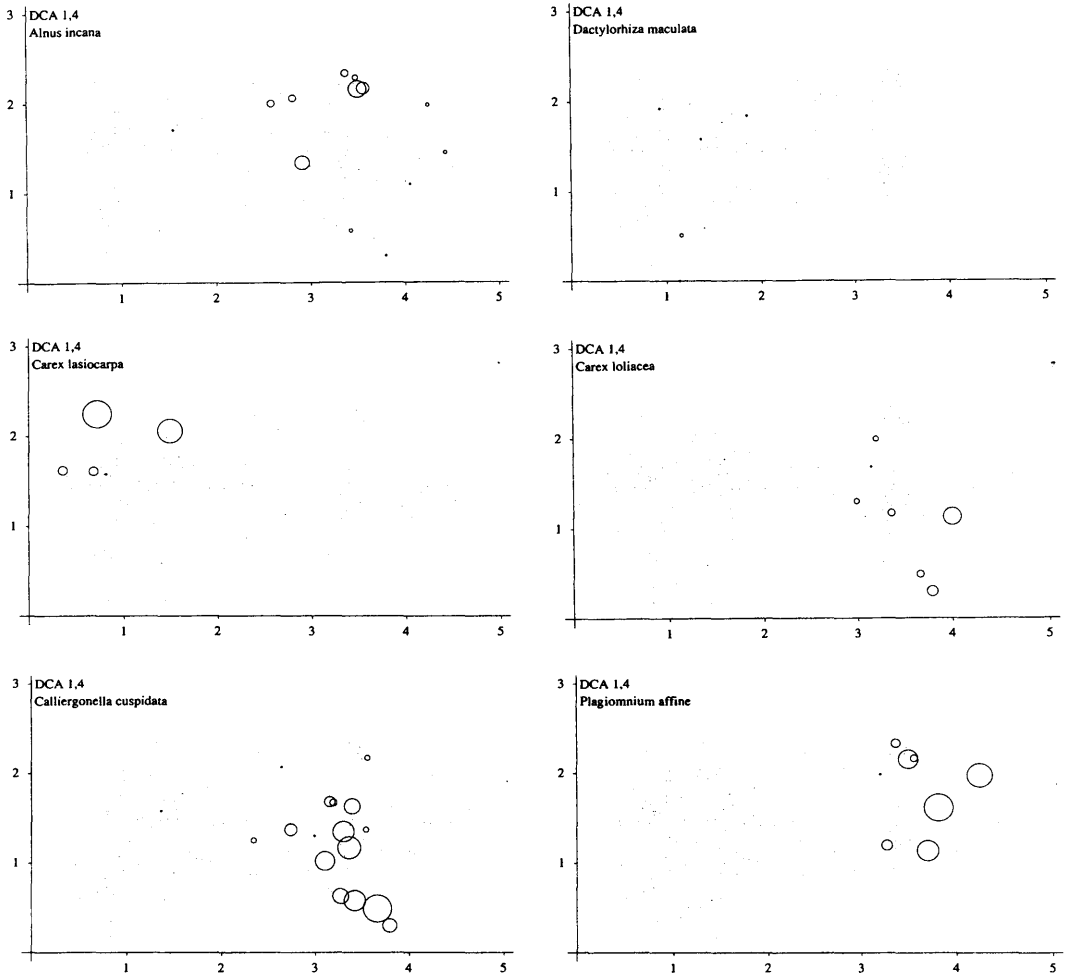
to the high-score end were obtained by species characteristic of meadows, deciduous forests and springs (e.g. *Chrysosplenium alternifolium*, *Circaea alpina*, *Matteuccia struthiopteris*, *Paris quadrifolia*, *Ranunculus repens*, *Brachythecium rutabulum* agg. and *Plagiomnium medium*; Figs 53–54). Unlike plots, species optima did not segregate into two clusters along DCA-axis 1.

Optima along DCA-axis 2 close to the low-score end were observed for species characteristic of wet swamps, tarn margins and wet mire sites, such as *Equisetum fluitans*, *Galium palustre*, *Lysimachia thyrsoiflora*, *Potentilla palustris*, *Carex chordorrhiza*, *Calliergon*



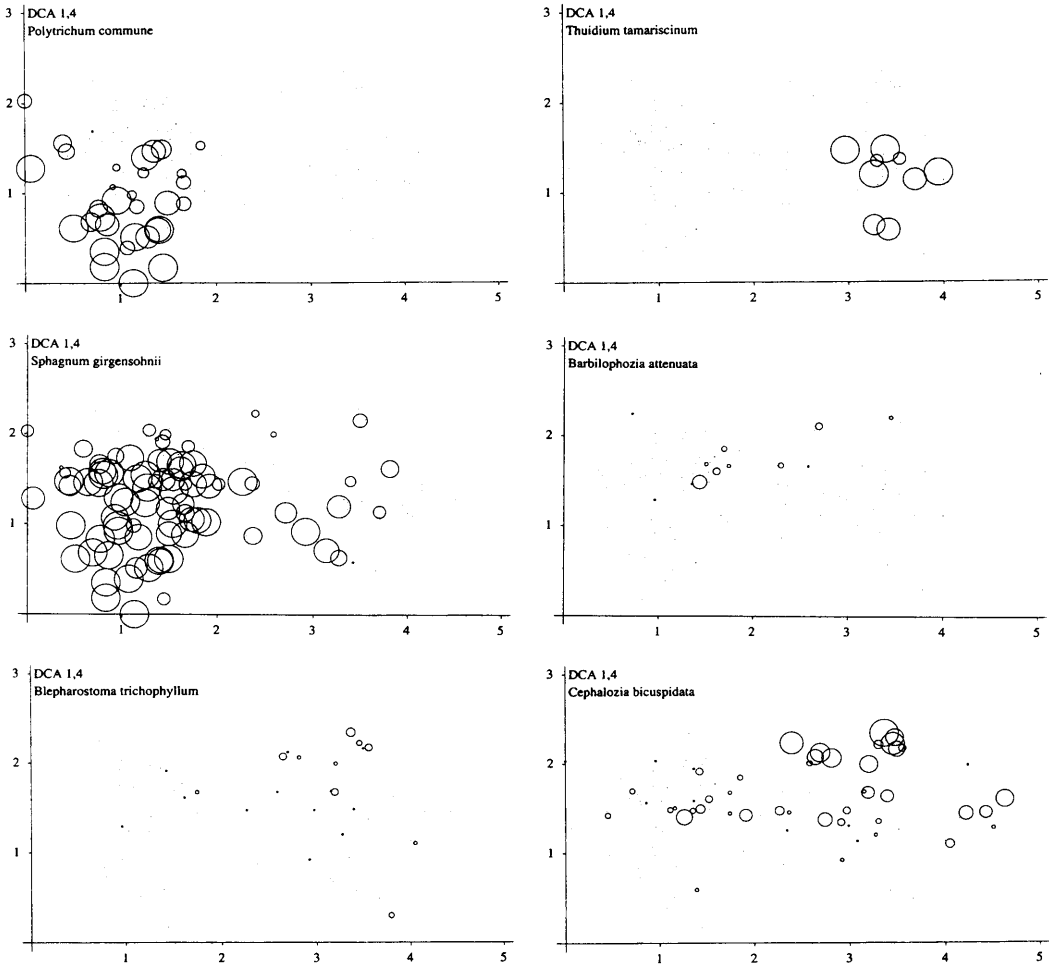
Figs 206–211. Distribution of species abundances in the DCA ordination of the full data set, axes 1 (horizontal) and 3 (vertical). Subplot frequency for each species in each plot proportional to circle size. Scaling of axes in S.D. units. Fig. 206. *Phragmites australis*. Fig. 207. *Plagiomnium affine*. Fig. 208. *Sphagnum brevifolium*. Fig. 209. *Sphagnum magellanicum*. Fig. 210. *Sphagnum riparium*. Fig. 211. *Aneura pinguis*.

richardsonii, *Warnstorfia exannulata* and *Sphagnum subsecundum* (Figs 53–54). Optima close to the high-score end were mostly observed for cryptogams typical of dry, non-paludified forests, e.g. *Ptilium crista-castrensis*, *Tetraphis pellucida*, *Calypogeia integristipula*, *Ptilidium pulcherrimum*, *Cladonia chlorophaea* and *C. coniocraea* (Fig. 54). The sixteen species (species occurring in 3 or fewer plots disregarded) with optimum closest to the high-score end of this axis were all cryptogams. Among vascular plants, *Vaccinium myrtilus* obtained the highest optimum (Fig. 54).



Figs 212–217. Distribution of species abundances in the DCA ordination of the full data set, axes 1 (horizontal) and 4 (vertical). Subplot frequency for each species in each plot proportional to circle size. Scaling of axes in S.D. units. Fig. 212. *Alnus incana*. Fig. 213. *Dactylorhiza maculata*. Fig. 214. *Carex lasiocarpa*. Fig. 215. *Carex loliacea*. Fig. 216. *Calliergonella cuspidata*. Fig. 217. *Plagiomnium affine*.

With the exception of a group of species with optima near the low-score end of DCA-axis 1, most species' optima along DCA-axis 3 were clumped in the interval 0–3 S.D. units (Figs 55–56). Species with optima near the low-score end of DCA-axis 3, such as *Vaccinium oxycoccos*, *Carex lasiocarpa*, *Eriophorum vaginatum*, *Molinia caerulea*, *Phragmites australis*, *Sphagnum magellanicum*, *Sphagnum russowii* and *Cephalozia pleniceps* were particularly common in swamp-forest locality 8, while species with optima along DCA-axis 3 near the high-score end, such as *Carex nigra*, *Carex rostrata*, *Sphagnum brevifolium* and *S. riparium* had their



Figs 218–223. Distribution of species abundances in the DCA ordination of the full data set, axes 1 (horizontal) and 4 (vertical). Subplot frequency for each species in each plot proportional to circle size. Scaling of axes in S.D. units. Fig. 218. *Polytrichum commune*. Fig. 219. *Thuidium tamariscinum*. Fig. 220. *Sphagnum girgensohnii*. Fig. 221. *Barbilophozia attenuata*. Fig. 222. *Blepharostoma trichophyllum*. Fig. 223. *Cephalozia bicuspidata*.

main occurrences in swamp-forest localities 2 and 11 (Tab. 4). Species with optima along DCA-axis 1 near the high-score end of that axis segregated along DCA-axis 3 according to their relative abundance in swamp-forest locality 9 vs 3 and 5 (low scores for species like *Carex loliacea* and *Fissidens adianthoides* which preferred the former, and high scores for species like *Atrichum undulatum*, *Plagiomnium affine* and *Thuidium tamariscinum* which preferred the latter two).

Optima for vascular plants as well as cryptogams were well separated along DCA-axis 4

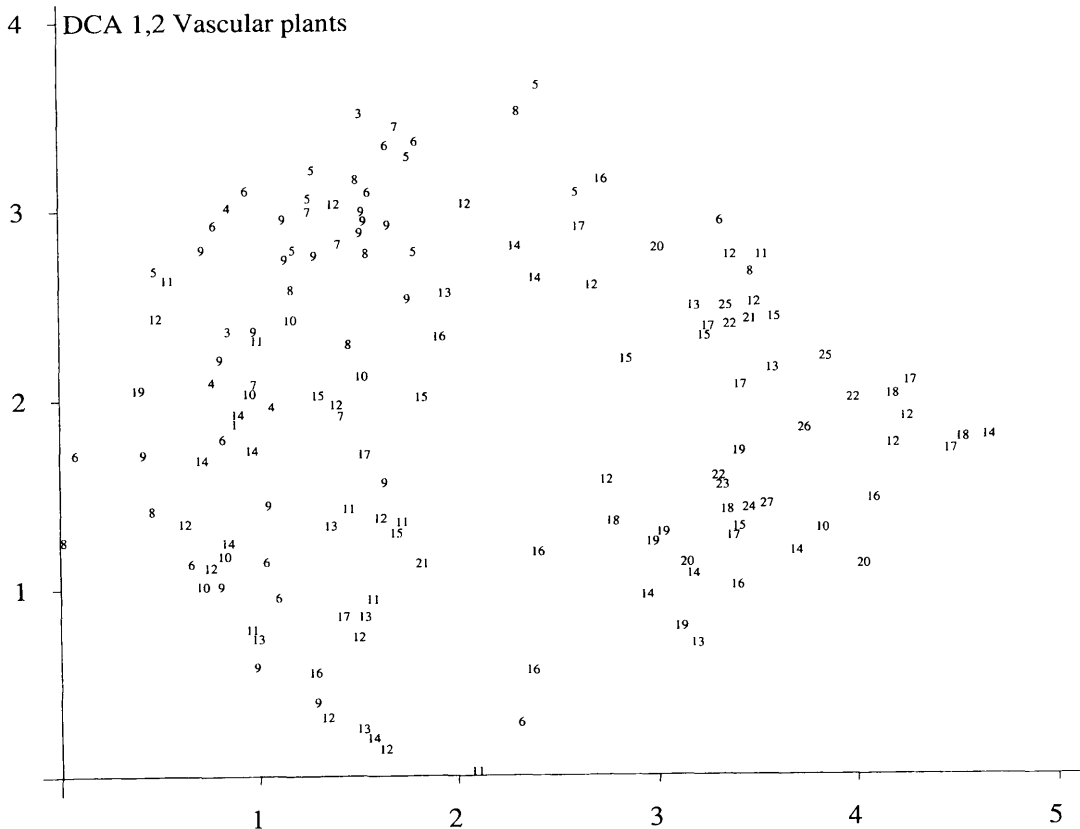


Fig. 224. DCA ordination of the full data set (150 1-m² plots), axis 1 (horizontal) and 2: number of vascular plant species plotted onto plot positions.

(Figs 57–58). Optima close to the low-score end were found for *Cardamine pratensis*, *Fissidens adianthoides*, *Polytrichum commune* and *Scapania undulata*, while optima close to the high-score end were found for vascular plants such as *Circaea alpina*, *Equisetum fluviatile*, *E. pratense*, *Pyrola minor* and *Carex lasiocarpa* and for cryptogams such as *Atrichum undulatum* and *Plagiothecium succulentum*.

Variation in species abundances along ordination axes

Almost all species showed systematic variation in constancy and subplot frequency along the first two axes in the DCA ordination of the full data set. Patterns of distributions along DCA axes 1 and 2 (as shown in Figs 59–197) were summarized in separate classifications for each axis of 139 species (recorded in 5 or more plots) into 10 groups (Figs 198–199).

Twenty-seven species (19% of the total number of species recorded in 5 or more plots) were more or less confined to poor-site plots (DCA 1 scores, $x_{Full, 1} < 2.5$ S.D.; Species groups 1, 2 and 5; Fig. 198), while 38 (27% of the total) were more or less confined to richer sites

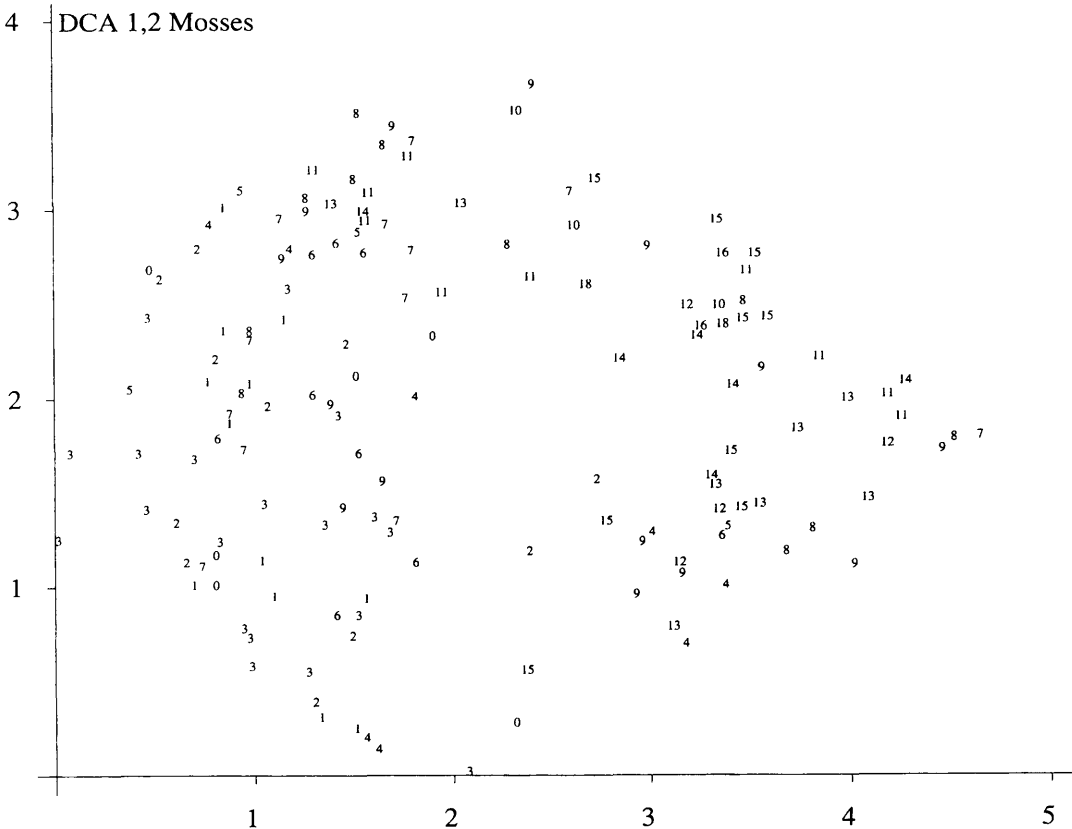


Fig. 225. DCA ordination of the full data set (150 1-m² plots), axis 1 (horizontal) and 2: number of moss species plotted onto plot positions.

(Species groups 8–10; Fig. 198). Four species were more or less confined to each of the lower (Species group 1) and upper (Species group 10) quarters of DCA-axis 1, respectively. Species group 7, with 34 species (24% of total) that preferred richer sites but that also occurred in the interval 1.25–2.50 along DCA-axis 1, was the largest group in terms of number of species. Sixteen species (Group 4) occurred all along DCA-axis 1.

Fourteen species (10% of total) were more or less confined to wetter sites (DCA 2 scores, $x_{Full,2} < 1.75$ S.D.; Species groups 1, 2 and 5; Fig. 199), 24 (17%) to drier sites (Species groups 8–10; Fig. 199). No species was confined to the lower quarter of DCA-axis 2 (Species group 1), while one species, *Pohlia nutans* (Fig. 150) was more or less confined to the upper quarter. The largest group in terms of number of species was Species group 7 (avoidance of plots with DCA-axis 2 scores in the lower quarter), with 40 species (29% of total), twenty-one species (15% of total) avoided plots with DCA-axis 2 scores in the upper quarter. Twenty species (14% of total; Group 4) occurred all along DCA-axis 2.

Relatively few species showed distinct patterns of variation in abundance along DCA ordination axes 3 and 4; selected examples are illustrated in Figs 200–211 and Figs 212–223,

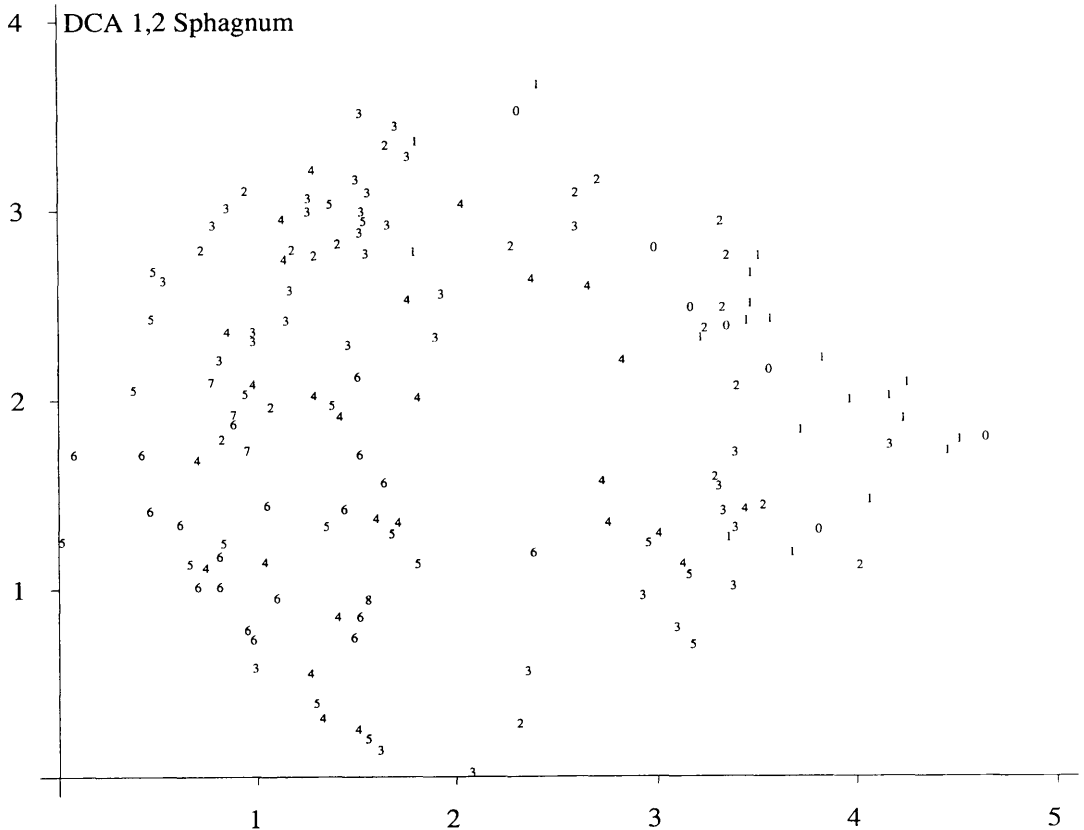


Fig. 226. DCA ordination of the full data set (150 1-m² plots), axis 1 (horizontal) and 2: number of *Sphagnum* species plotted onto plot positions.

respectively. Species more or less completely restricted to swamp-forest locality 8, e.g. *Vaccinium oxycoccos* (Fig. 201), *Phragmites australis* (Fig. 206) and *Sphagnum magellanicum* (Fig. 209), were more or less restricted to plots with low DCA-1 and low DCA-3 scores (Tab. 4, Fig. 22). Species mainly occurring in swamp-forest localities 2 and/or 11, e.g. *Carex nigra* (Fig. 204), *Sphagnum brevifolium* (Fig. 208) and *Sphagnum riparium* (Fig. 210), typically occurred in plots with low DCA-1 and high DCA-3 scores. With its main occurrence in swamp-forest locality 9, *Carex loliacea* (Fig. 203) was more or less restricted to plots with high DCA-1 and low DCA-3 scores. *Plagiomnium affine* (Fig. 207), most common in swamp-forest locality 3, had its main occurrence in plots with high DCA-1 and high DCA-3 scores.

The constancy and abundance of the common species of poor, dry sites (low DCA-1, high DCA-2 scores), *Polytrichum commune* (Fig. 218), declined abruptly in the interval 1.0–1.4 S.D. units along DCA 4 and the species was almost totally absent from plots with $x_{Full,4} > 1.5$ S.D. The opposite pattern, preference for plots with high DCA-4 scores, was seen for hepatics (and some mosses) typical of ‘pocket sites’, such as *Barbilophozia attenuata* (Fig. 221), *Blepharostoma trichophyllum* (Fig. 222) and *Cephalozia bicuspidata* (Fig. 223), as well as for other species such

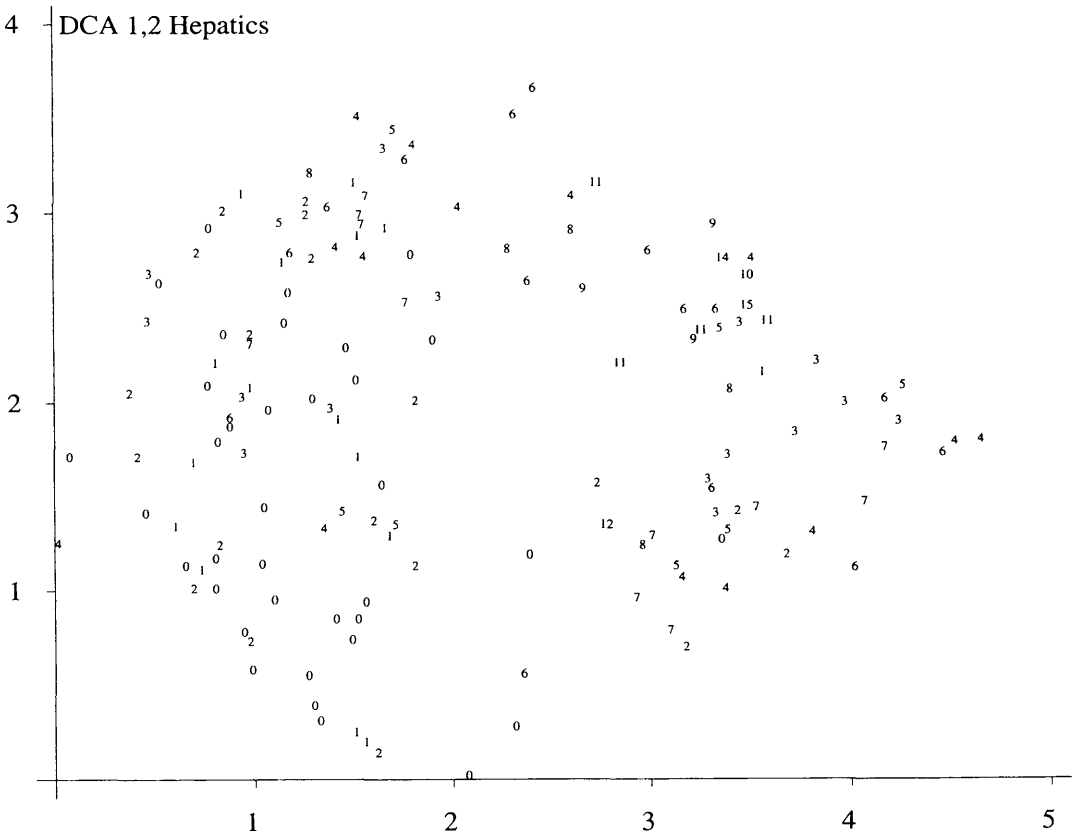


Fig. 227. DCA ordination of the full data set (150 1-m² plots), axis 1 (horizontal) and 2: number of hepatic species plotted onto plot positions.

as *Alnus incana* (Fig. 212) and *Carex lasiocarpa* (Fig. 214).

Variation in species density along axes in the DCA ordination of the full data set

Species density at the 1-m² scale increased along DCA-axis 1 for all plant groups except peat mosses (Figs 224–229); peat moss density decreased from 4–6 species per plot for $x_{Full,1} < 1.0$ S.D. units to 0–1(–3) species for $x_{Full,1} > 3.5$ S.D. (Fig. 226). A typical Subset-A plot typically contained 6–12 vascular plant species, 1–8 moss species and 0–4 species of hepatics, while Subset-B plots contained 12–22 vascular plant species, 7–15 moss species and 3–8 species of hepatics. The total number of species per plot was mostly 12–25 in Subset A and 24–45 in Subset B (Fig. 229).

For all plant groups, species density at the 1-m² scale was less strongly correlated with DCA 2 than with DCA 1 (Tab. 11). Subset-B plots showed almost no systematic variation in species density along DCA 2 (except peat-moss species density which decreased along DCA 2

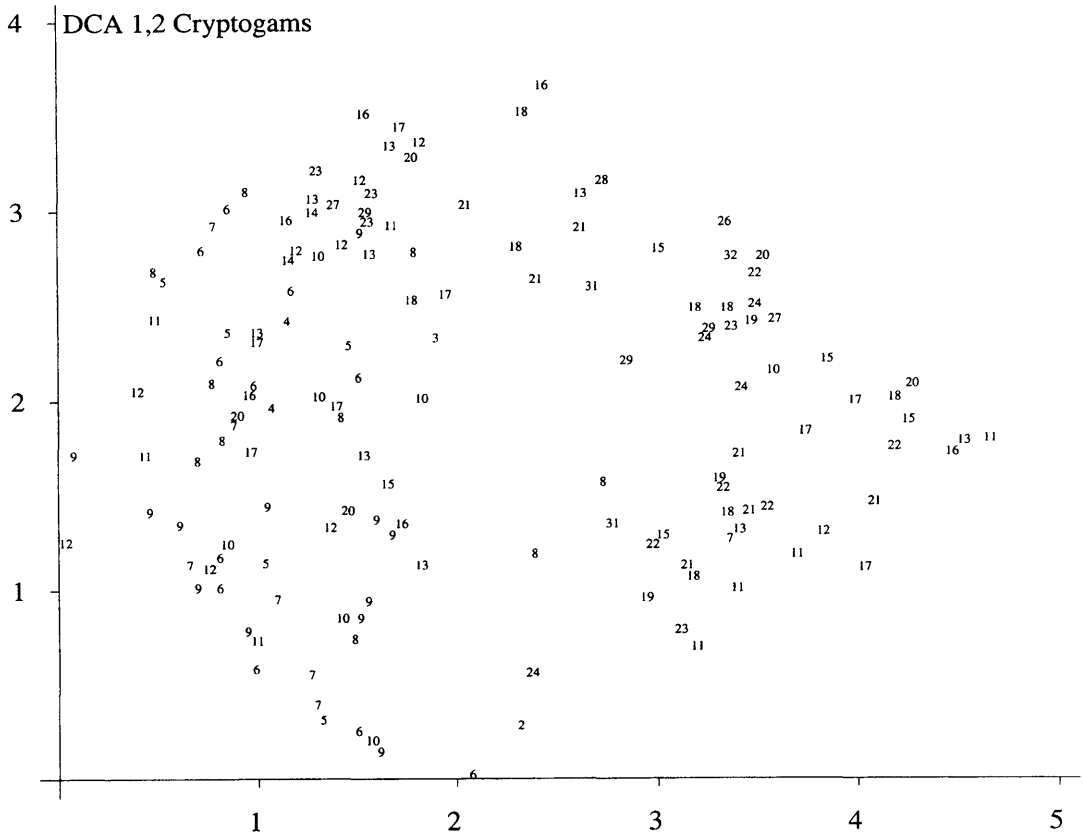


Fig. 228. DCA ordination of the full data set (150 1-m² plots), axis 1 (horizontal) and 2: total number of cryptogam species plotted onto plot positions.

in both subsets; Fig. 226). For plots in Subset A, vascular plant species density decreased from 9–14 for $x_{Full,2} < 1.0$ S.D. units to 5–9 for $x_{Full,2} > 2.5$ S.D. units (Fig. 224) while high moss and hepatic species densities were observed for Subset-A plots with $x_{Full,2} > 2.5$ (Figs 225, 227). As a result of these opposite trends, total species density was uncorrelated with plot position along DCA 2.

Except for a slight increase in hepatic (and cryptogam, partly also moss) species density along DCA-axis 4, no clear species richness trends were observed along DCA-axes 3 and 4 (Tab. 11).

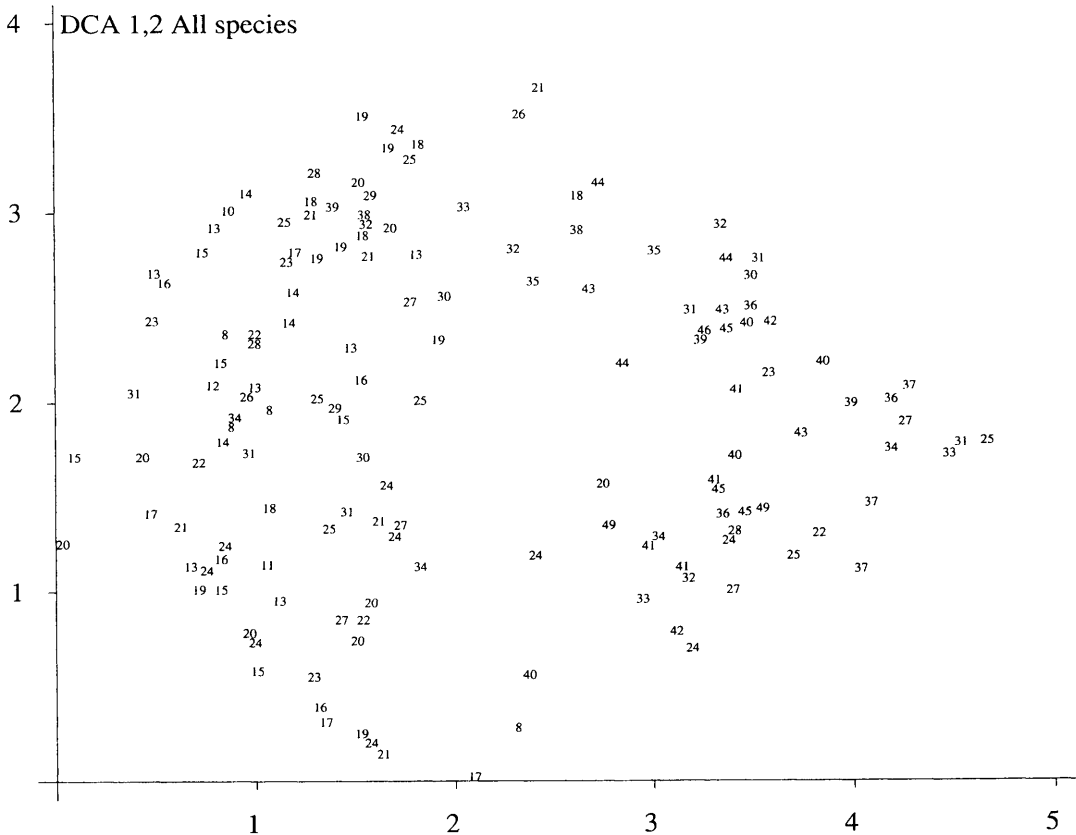


Fig. 229. DCA ordination of the full data set (150 1-m² plots), axis 1 (horizontal) and 2: total number of species plotted onto plot positions.

SPATIAL STRUCTURE

Explanatory variables

All variables belonging to, or associated with, the *soil nutrient/acidity group* (Fig. 8) had more or less strong spatially dependent variation at scales up to the range, 50–100(–200) m (Tabs 12–13). These variables were, however, not recorded at the subplot scale, and the data did therefore not allow analysis of spatially dependent variation at scales finer than 3 m. The concentrations of Ca, Mg, Ba, Sr and Al and base saturation (and K) were strongly spatially structured in two intervals, 3–6 m and 25–100 m (between swamp-forest localities), and had irregular spatial dependence patterns at broader scales. The other variables of the soil nutrient/acidity group (all pH measurements and the concentrations of N and Fe), electric conductivity in tube water, the concentration of Mn and water temperature in spring, showed little variation in degree of spatial dependence for distances shorter than the range. The concentrations of S, P and Na (of which

Tab. 12. Standardized semivariance (γ) and Hausdorff-Besicovitch fractal dimension (D) for explanatory variables (see Tab. 2 for abbreviations, transformation and summary statistics) in the full data set ($n = 150$) and the set of subplots ($n = 2400$). D values < 2.80 in bold face, $D > 3.20$ italicized. Properties of the distance-class partitioning are summarized in Tab. 3.

	Standardized semivariance for distance classes (indicated by number, with upper limit in m in brackets)														Hausdorff-Besicovitch fractal dimension D for pairs of distance classes (indicated by number, with upper limits i m in brackets)														
	1 (0.25)	2 (0.5)	3 (1)	4 (2)	5 (4)	6 (8)	7 (16)	8 (32)	9 (64)	10 (128)	11 (256)	12 (512)	13 (1024)	14 (2048)	2 (0.25 -0.5)	3 (0.5 -1)	4 (1 -2)	5 (2 -4)	6 (4 -8)	7 (8 -16)	8 (16 -32)	9 (32 -64)	10 (64 -128)	11 (128 -256)	12 (256 -512)	13 (512 -1024)	14 (1024 -2048)		
Plots (1 m²)																													
<i>Topographic and geographic variables</i>																													
VertRan					0.898	1.070	1.127	1.016	1.002	1.043	1.214	0.894	1.098	0.873						2.874	2.963	3.075	3.010	2.971	2.890	3.221	2.852	3.165	
SlopeAvg					1.001	0.998	1.078	0.889	1.131	1.166	1.029	1.001	1.134	0.864						3.002	2.944	3.139	2.826	2.978	3.090	3.020	2.910	3.196	
SlopeMa25					1.096	1.036	1.051	0.862	0.957	1.133	0.891	1.064	1.111	0.938						3.041	2.990	3.143	2.925	2.878	3.173	2.872	2.969	3.196	
SlopeMa10					0.915	1.010	1.045	1.059	0.823	1.005	0.992	1.145	1.044	0.951						2.929	2.975	2.990	3.182	2.856	3.009	2.897	3.067	3.122	
DistMSoil					0.375	0.661	0.874	1.274	1.067	0.837	1.448	0.963	1.017	0.908						2.591	2.799	2.728	3.128	3.175	2.605	<i>3.294</i>	2.961	3.067	
SoilDMVL					0.273	0.415	0.566	0.734	0.701	0.621	1.256	1.205	0.850	1.136						2.698	2.776	2.813	3.033	3.087	2.492	3.030	3.252	3.082	
SoilDMWT					0.292	0.391	0.573	0.750	0.695	0.642	1.272	1.089	0.895	1.114						2.789	2.724	2.806	3.055	3.057	2.507	3.112	3.142	2.791	
<i>Tree influence variables</i>																													
CanopyCAvg					0.419	0.578	0.567	0.682	0.763	0.766	0.975	0.853	0.858	1.205						2.768	3.014	2.867	2.919	2.997	2.826	3.096	2.996	2.842	
CanopyCMax					0.491	0.751	0.687	0.693	0.667	0.843	0.868	0.828	1.023	0.970						2.693	3.064	2.994	3.028	2.831	2.979	3.034	2.847	2.755	
CanopyCMin					0.466	0.564	0.679	0.676	0.903	0.856	0.807	0.789	0.823	1.347						2.862	2.866	3.003	2.791	3.039	3.043	3.016	2.970	3.038	
TreeInfliv					0.603	0.871	1.073	0.932	0.921	1.056	0.850	0.985	1.076	1.023						2.735	2.850	3.102	3.009	2.901	3.157	2.894	2.936	2.645	
TreeInflAll					0.640	1.107	1.065	1.037	0.977	1.007	1.046	1.196	1.021	0.961						2.605	3.028	3.019	3.043	2.978	2.973	2.903	3.114	3.036	
Basal area					0.202	0.287	0.615	0.754	1.281	1.248	0.872	1.000	1.060	1.088						2.747	2.450	2.853	2.618	3.019	3.259	2.901	2.958	3.044	
CrownI					0.340	0.608	0.995	0.899	1.030	0.983	0.929	0.922	0.998	1.149						2.581	2.645	3.073	2.902	3.034	3.041	3.005	2.943	2.981	
LitterI					0.599	0.828	1.073	0.859	0.954	1.043	0.900	1.088	1.034	1.015						2.766	2.813	3.160	2.924	2.936	3.106	2.863	3.037	2.898	
<i>Water table variables</i>																													
SnowD0423					0.656	0.666	0.824	0.894	1.121	0.993	0.966	1.063	1.057	1.008						2.989	2.846	2.941	2.837	3.087	3.020	2.931	3.004	3.013	
WatTab100					0.362	0.553	0.700	0.590	0.692	1.624	0.737	1.016	1.117	1.095						2.694	2.830	3.123	2.885	2.385	<i>3.570</i>	2.768	2.932	3.034	
WatTab90					0.456	0.641	0.842	0.684	0.743	1.476	0.769	1.031	1.077	1.059						2.754	2.803	3.150	2.940	2.505	3.470	2.789	2.969	3.014	
WatTab50					0.545	0.658	0.917	0.741	0.792	1.366	0.817	0.980	1.079	1.004						2.864	2.761	3.154	2.952	2.607	<i>3.371</i>	2.869	2.931	3.012	
WatTab10					0.608	0.639	0.944	0.774	0.848	1.276	0.856	0.968	1.091	0.957						2.964	2.719	3.143	2.934	2.705	3.288	2.911	2.914	3.052	

Tab. 12 (continued).

	Standardized semivariance for distance classes (indicated by number, with upper limit in m in brackets)														Hausdorff-Besicovitch fractal dimension D for pairs of distance classes (indicated by number, with upper limits i m in brackets)														
	1 (0.25)	2 (0.5)	3 (1)	4 (2)	5 (4)	6 (8)	7 (16)	8 (32)	9 (64)	10 (128)	11 (256)	12 (512)	13 (1024)	14 (2048)	2 (0.25 -0.5)	3 (0.5 -1)	4 (1 -2)	5 (2 -4)	6 (4 -8)	7 (8 -16)	8 (16 -32)	9 (32 -64)	10 (64 -128)	11 (128 -256)	12 (256 -512)	13 (512 -1024)	14 (1024 -2048)		
Plots (1 m²) (continued)																													
<i>Water table variables (continued)</i>																													
WatTab0					0.683	0.679	0.916	0.938	0.839	1.044	0.975	0.963	1.112	0.929						3.004	2.767	3.017	3.063	2.842	3.049	3.009	2.896	3.095	
WatTabRan					0.216	0.277	0.365	0.305	0.489	1.752	0.637	1.103	1.143	1.199						2.821	2.801	3.130	2.659	2.079	3.730	2.604	2.974	3.130	
WatTabHMi					0.517	0.744	0.917	0.738	0.801	1.405	0.843	0.982	1.149	0.993						2.737	2.849	3.157	2.941	2.595	3.368	2.890	2.887	2.965	
WatTabLMa					0.617	0.747	0.824	0.831	0.864	1.000	0.981	1.019	1.020	0.992						2.862	2.929	2.994	2.972	2.895	3.014	2.973	2.999	3.105	
<i>Water chemical and physical variables</i>																													
WatTem0527					0.296	0.390	0.548	0.791	0.461	0.926	0.873	0.961	0.944	1.033						2.801	2.755	2.735	3.389	2.497	3.043	2.931	3.013	3.020	
WatTem0826					0.112	0.207	0.543	0.599	0.469	0.829	0.846	0.905	1.222	0.961						2.557	2.304	2.929	3.176	2.589	2.985	2.951	2.783	2.935	
WatpH0527					0.204	0.388	0.379	0.609	0.753	0.748	1.579	1.109	0.903	1.101						2.536	3.017	2.658	2.847	3.005	2.461	3.255	3.148	3.173	
WatpH0826					0.224	0.274	0.330	0.483	0.698	0.908	1.317	1.094	1.003	1.039						2.855	2.866	2.725	2.734	2.810	2.732	3.134	3.063	2.857	
WatEC00527					0.480	0.536	0.697	0.936	0.730	0.895	1.199	1.195	0.983	0.986						2.920	2.811	2.787	3.179	2.853	2.789	3.002	3.141	2.975	
WatEC00826					0.464	0.709	0.524	0.617	0.949	0.909	1.144	1.345	0.886	1.106						2.694	3.218	2.882	2.689	3.031	2.834	2.883	3.301	2.998	
WatO0527					0.851	0.768	0.979	1.049	0.905	0.786	1.023	0.609	1.045	1.136						3.074	2.825	2.950	3.107	3.102	2.810	3.374	2.611	2.840	
WatO0826					0.396	0.341	0.562	0.580	0.529	0.727	0.447	0.459	0.658	1.496						3.108	2.640	2.977	3.066	2.771	3.351	2.981	2.740	2.940	
<i>Soil chemical and physical variables</i>																													
SoilVolWt					0.206	0.304	0.377	0.347	0.556	1.056	0.939	1.433	0.871	1.313						2.719	2.845	3.060	2.660	2.537	3.085	2.695	3.359	2.408	
SoilLossO1					0.138	0.213	0.365	0.330	0.522	1.524	1.306	1.486	1.000	1.048						2.687	2.611	3.073	2.669	2.227	3.111	2.907	3.286	2.704	
SoilpHH ₂ O					0.257	0.305	0.453	0.406	0.472	1.665	0.914	1.343	1.061	1.115						2.876	2.715	3.079	2.891	2.091	3.433	2.722	3.170	2.966	
SoilpHCaCl ₂					0.273	0.271	0.408	0.417	0.502	1.544	1.025	1.333	1.016	1.166						3.005	2.705	2.984	2.866	2.190	3.296	2.810	3.196	2.964	
SoilCEC					0.555	0.909	0.484	0.427	0.669	0.768	0.590	0.881	1.039	1.315						2.644	3.455	3.090	2.676	2.900	3.190	2.711	2.881	2.901	
SoilBaSat					0.230	0.484	0.404	0.430	0.664	1.079	0.797	1.157	1.002	1.260						2.463	3.130	2.955	2.687	2.650	3.219	2.731	3.104	2.830	
HumusC					0.518	0.611	0.609	0.823	0.992	1.144	0.718	1.189	0.952	1.037						2.881	3.002	2.783	2.865	2.897	3.336	2.636	3.160	2.835	
HumusN					0.162	0.236	0.398	0.391	0.537	1.561	0.858	1.721	0.935	1.219						2.729	2.623	3.013	2.771	2.230	3.432	2.498	3.460	2.938	
HumusP					0.311	0.465	0.762	0.837	1.007	1.373	1.131	1.052	1.007	0.894						2.710	2.644	2.932	2.867	2.776	3.140	3.052	3.032	2.809	
HumusS					0.562	0.372	0.722	0.717	0.707	0.821	0.677	0.633	1.127	1.062						3.298	2.522	3.005	3.010	2.892	3.139	3.048	2.584	3.086	
HumusExAc					0.227	0.372	0.352	0.382	0.560	1.152	0.817	1.287	0.955	1.337						2.644	3.040	2.941	2.724	2.480	3.248	2.672	3.275	3.043	
HumusCa					0.274	0.480	0.387	0.353	0.540	1.026	0.653	1.228	0.949	1.422						2.596	3.155	3.066	2.693	2.537	3.326	2.544	3.186	2.757	

Tab. 13. Inferred spatial structure (strength and range) of explanatory variables and vegetation gradients (DCA axes in ordination of the full data set), based on standardized semivariances and Hausdorff-Besicovitch fractal dimensions as given in Tabs 12-14. Names of explanatory variables abbreviated in accordance with Tab. 2.

Variable	Inferred spatial pattern
<i>Topographic and geographic variables</i>	
VertRan	Strong spatial dependence, range 1.5 m
SlopeAvg	Strong spatial dependence, range 1.5 m
SlopeMa25	Strong spatial dependence, range 1.5 m
SlopeMa10	No spatial dependence > 2 m; probably moderate or strong spatial dependence to range \leq 1.5 m
DistMSoil	Very strong spatial dependence to c. 12 m, strong spatial dependence to range \approx 25 m
SoilDMVL	Strong spatial dependence to possible range \approx 32 m, irregular at broader scales
SoilDMWT	Strong spatial dependence to possible range \approx 32 m, irregular at broader scales
<i>Tree influence variables</i>	
CanopyCAvg	Strong spatial dependence to 6 m, moderate to no spatial dependence at broader scales, range indistinct
CanopyCMax	Strong spatial dependence to 6 m, moderate to no spatial dependence at broader scales, range indistinct
CanopyCMin	Moderate spatial dependence, range \approx 50 m
TreeInFLiv	Strong spatial dependence, range \approx 12 m
TreeInfAll	Strong spatial dependence, range 6 m
BasalArea	Strong to very strong spatial dependence, range \approx 50 m
CrownI	Strong to very strong spatial dependence, range \approx 12 m
LitterI	Strong spatial dependence to 6 m, moderate to range \approx 12 m
<i>Water table variables</i>	
SnowC0423	Weak spatial dependence, range \approx 50 m
WatTab100	Very strong spatial dependence to 1.5 m (notably in the 0.75-1.5 m interval), moderate spatial dependence to range \approx 100 m
WatTab90	Very strong spatial dependence to 1.5 m (notably in the 0.75-1.5 m interval), moderate spatial dependence to range \approx 100 m
WatTab50	Very strong spatial dependence to 1.5 m (notably in the 0.75-1.5 m interval), moderate spatial dependence to range \approx 100 m
WatTab10	Very strong spatial dependence to 1.5 m (notably in the 0.75-1.5 m interval), moderate spatial dependence to range \approx 100 m
WatTab0	Very strong spatial dependence to 1.5 m (notably in the 0.75-1.5 m interval), moderate spatial dependence to range \approx 100 m
WatTabRan	Moderate to strong spatial dependence to range \approx 100 m
WatTabHMi	Very strong spatial dependence to 1.5 m, moderate spatial dependence to range \approx 100 m
WatTabLMa	Very strong spatial dependence to 1.5 m, moderate spatial dependence to range \approx 100 m
<i>Water chemical and physical variables</i>	
WatTem0527	Moderate to strong spatial dependence to range \approx 100 m
WatTem0826	Very strong spatial dependence to c. 12 m and from c. 50 to range \approx 100 m
WatpH0527	Strong spatial dependence to range \approx 200 m
WatpH0826	Strong spatial dependence to range \approx 200 m
WatEC0527	Moderate spatial dependence to range \approx 200 m
WatEC0826	Moderate spatial dependence to range \approx 200 m
WatO0527	None
WatO0826	Irregular; apparent spatial dependence from 6 to 12 m, and at scales > 1 km (range?)

Tab. 13 (continued).

Variable	Inferred spatial pattern
<i>Soil chemical and physical variables</i>	
SoilVolWt	Strong spatial dependence to range \approx 100 m
SoilLossOI	(Very) strong spatial dependence to range \approx 100 m
SoilpHH ₂ O	Moderate spatial dependence to c. 50 m, very strong from 50 to range \approx 100 m; irregular at broader scales
SoilpHCaCl ₂	Moderate spatial dependence to c. 50 m, very strong from 50 to range \approx 100 m; irregular at broader scales
SoilCEC	None (irregular)
SoilBaSat	Strong spatial dependence to 6 m and from c. 25 to range \approx 100 m; irregular at broader scales
HumusC	Moderate spatial dependence, range \approx 50 m, irregular at broader scales
HumusN	Strong spatial dependence, range \approx 100 m, irregular at broader scales
HumusP	Strong spatial dependence to 12 m, moderate to range \approx 50 m
HumusS	Irregular but spatially dependent variation below possible range \approx 1 km
HumusExAc	Strong spatial dependence, range \approx 100 m, irregular at broader scales
HumusCa	Very strong spatial dependence c. 3-6 m and from 25 m to range \approx 100 m, irregular at broader scales
HumusMg	Very strong spatial dependence c. 3-6 m and from 25 m to range \approx 100 m, irregular at broader scales
HumusK	Very strong spatial dependence c. 3-6 m and from 25 m to range \approx 100 m, irregular at broader scales
HumusNa	Very strong spatial dependence, range \approx 6 m
HumusBa	Very strong spatial dependence c. 3-6 m and from 25 m to range \approx 100 m, irregular at broader scales
HumusFe	Moderate spatial dependence, range \approx 100 m
HumusMn	Very strong spatial dependence to range \approx 100 m
HumusSr	Very strong spatial dependence c. 3-6 m and from 25 m to range \approx 100 m, irregular at broader scales
HumusZn	Irregular but spatially dependent variation to range \approx 400 m
HumusAl	Strong spatial dependence c. 3-6 m and from 25 m to range \approx 100 m, irregular at broader scales
<i>Vegetation gradients (DCA ordination axes)</i>	
DCA 1	Strong spatial dependence to 3 m and, particularly strongly, from 25 m to range \approx 100 m
DCA 2	Very strong spatial dependence to 1.5 m, moderate to range c. 75 m
DCA 3	Moderate to strong spatial dependence, range \approx 200 m
DCA 4	Strong spatial dependence, notably in the 1.5-3, and 50-100 m, intervals, range \approx 100 m
<i>Species richness (species number)</i>	
Vascular plants	Moderate spatial dependence to c. 1.5 m, weak and irregular to range \approx 200 m
Mosses	Strong spatial dependence to 1.5 m, weak to range \approx 50 m
<i>Sphagnum</i>	Strong spatial dependence to 1.5 m and at c. 200 m, but irregular at broad scales (> 200 m)
Hepatics	Strong spatial dependence to 8 m, irregular at broader scales
Cryptogams	Some spatial dependence to indicative range \approx 25 m
All species	Moderate spatial dependence to range \approx 200 m

none belonged to the soil nutrient/acidity group but all were more or less strongly correlated with variables of that group) showed different patterns of spatial variability: the strength of spatial dependence varied irregularly for S, with signs of periodicity for the 3–6 m interval (Tab. 12); P was strongly spatially dependent to c. 12 m and weakly spatially dependent to the approximate range of c. 50 m; and Na was very strongly spatially dependent to the range, c. 6 m (Tab. 13).

Tab. 14. Standardized semivariance (γ) and Hausdorff-Besicovitch fractal dimension (D) for plot scores along axes in the DCA and LNMDS ordinations. D values < 2.80 in bold face, D > 3.20 italicized. Properties of the distance-class partitioning are summarized in Tab. 3. Ordination axes abbreviated in accordance with Tab. 6.

	Standardized semivariance for distance classes (indicated by number, with upper limit in m in brackets)														Hausdorff-Besicovitch fractal dimension D for pairs of distance classes (indicated by number, with upper limits i m in brackets)														
	1 (0.25)	2 (0.5)	3 (1)	4 (2)	5 (4)	6 (8)	7 (16)	8 (32)	9 (64)	10 (128)	11 (256)	12 (512)	13 (1024)	14 (2048)	2 (0.25)	3 (0.5)	4 (1)	5 (2)	6 (4)	7 (8)	8 (16)	9 (32)	10 (64)	11 (128)	12 (256)	13 (512)	14 (1024)		
Plots (1 m²), full data set (n = 150)																													
DCA 1					0.119	0.113	0.159	0.192	0.379	1.126	1.166	2.221	0.877	1.123						3.037	2.754	2.864	2.509	2.215	2.975	2.535	<i>3.670</i>	2.822	
DCA 2					0.535	0.638	0.744	0.886	0.942	1.054	1.063	0.806	1.097	0.927						2.873	2.889	2.874	2.956	2.919	2.994	3.200	2.778	3.121	
DCA 3					0.215	0.498	0.528	0.626	0.866	0.954	0.852	0.649	1.195	1.118						2.394	2.958	2.877	2.766	2.930	3.082	3.196	2.560	3.048	
DCA 4					0.539	0.731	0.813	0.693	0.840	1.603	0.881	0.854	1.104	1.048						2.780	2.923	3.115	2.861	2.534	<i>3.432</i>	3.022	2.815	3.038	
Subplots (0.0625 m²; n = 2400)																													
DCA-S 1	0.029	0.035	0.057	0.100	0.157	0.151	0.205	0.220	0.397	1.125	1.151	2.215	0.882	1.126	2.864	2.648	2.595	2.675	3.028	2.779	2.949	2.574	2.249	2.984	2.528	<i>3.664</i>	2.824		
DCA-S 2	0.057	0.085	0.164	0.444	0.579	0.685	0.781	0.930	0.962	1.044	1.084	0.826	1.088	0.935	2.712	2.526	2.282	2.808	2.879	2.905	2.874	2.976	2.941	2.973	3.196	2.801	3.109		
DCA-S 3	0.112	0.146	0.229	0.299	0.358	0.596	0.640	0.757	0.885	0.890	1.015	0.721	1.174	1.027	2.809	2.675	2.808	2.870	2.632	2.949	2.879	2.887	2.996	2.905	3.247	2.648	3.096		
DCA-S 4	0.115	0.151	0.251	0.296	0.648	0.708	0.837	0.724	0.797	1.384	0.862	0.887	1.061	1.132	2.804	2.633	2.881	2.435	2.936	2.879	3.105	2.931	2.602	<i>3.342</i>	2.979	2.871	2.953		
Reduced data set (1 m²; n = 125)																													
LNMDS 1					0.133	0.128	0.183	0.197	0.440	1.388	1.170	1.902	0.893	1.200						3.028	2.742	2.947	2.420	2.171	3.123	2.649	<i>3.545</i>	2.787	
LNMDS 2					0.617	0.781	0.814	0.875	0.883	1.027	1.054	0.948	1.089	0.912						2.830	2.970	2.948	2.993	2.891	2.981	3.076	2.900	3.128	
LNMDS 3					0.503	0.486	0.692	0.695	0.664	0.968	0.822	1.212	1.097	1.083						3.025	2.745	2.997	3.033	2.728	3.118	2.720	3.072	3.009	
LNMDS 4					0.359	0.371	0.541	0.659	0.785	0.800	0.956	0.841	0.930	1.242						2.976	2.728	2.858	2.874	2.986	2.871	3.092	2.927	2.791	
Subset A (poorer swamp forest; 1 m²; n = 98)																													
DCA-A 1					0.750	0.476	0.594	0.733	0.845	1.001	1.072	1.000	1.180	0.962						3.328	2.840	2.848	2.897	2.878	2.951	3.050	2.881	3.147	
DCA-A 2					0.238	0.401	0.449	0.521	0.761	1.450	0.683	0.749	1.382	1.113						2.624	2.918	2.893	2.727	2.535	3.543	2.933	2.558	3.156	
DCA-A 3					0.305	0.375	0.543	0.599	0.681	1.146	1.540	0.987	1.152	0.774						2.851	2.733	2.929	2.907	2.625	2.787	<i>3.321</i>	2.888	3.287	
DCA-A 4					0.533	0.407	0.698	0.696	0.881	1.230	1.337	0.660	1.066	0.910						3.195	2.611	3.002	2.830	2.759	2.940	3.509	2.654	3.114	
Subset C (vascular plants; 1 m²; n = 150)																													
DCA-C 1					0.115	0.115	0.189	0.243	0.424	1.163	1.110	2.146	0.949	1.072						3.000	2.642	2.819	2.598	2.272	3.034	2.524	<i>3.589</i>	2.912	
DCA-C 2					0.510	0.593	0.745	0.900	0.908	1.038	1.131	0.714	0.926	1.014						2.891	2.835	2.864	2.994	2.903	2.938	3.332	2.812	2.935	
DCA-C 3					0.259	0.425	0.614	0.805	0.748	0.752	1.423	0.828	1.292	0.831						2.643	2.735	2.805	3.053	2.996	2.540	<i>3.391</i>	2.679	3.318	
DCA-C 4					0.304	0.578	0.451	0.251	0.306	1.080	0.361	1.759	1.079	1.279						2.537	3.179	<i>3.423</i>	2.857	2.090	<i>3.790</i>	1.858	<i>3.353</i>	2.877	
Subset D (cryptogams; 1 m²; n = 150)																													
DCA-D 1					0.172	0.183	0.207	0.233	0.384	1.017	1.190	1.995	0.809	1.216						2.955	2.911	2.915	2.640	2.297	2.887	2.627	<i>3.651</i>	2.706	
DCA-D 2					0.489	0.653	0.739	0.852	0.939	1.075	1.017	0.903	1.214	0.851						2.791	2.911	2.897	2.930	2.902	3.040	3.086	2.787	3.256	
DCA-D 3					0.314	0.386	0.503	0.540	0.471	0.995	0.576	1.805	0.917	1.320						2.851	2.809	2.949	3.099	2.461	<i>3.394</i>	2.176	<i>3.489</i>	2.737	
DCA-D 4					0.533	0.525	0.700	0.942	0.790	1.356	0.874	1.082	1.179	0.966						3.011	2.792	2.786	3.127	2.610	<i>3.317</i>	2.846	2.938	3.144	

Tab. 15. Standardized semivariance (γ) and Hausdorff-Besicovitch fractal dimension (D) for species density of different plant groups (for 1-m² plots and 1/16 m² subplots). D values < 2.80 in bold face, D > 3.20 italicized. Properties of the distance-class partitioning are summarized in Tab. 3. Ordination axes abbreviated in accordance with Tab. 5.

	Standardized semivariance for distance classes (indicated by number, with upper limit in m in brackets)														Hausdorff-Besicovitch fractal dimension D for pairs of distance classes (indicated by number, with upper limits i m in brackets)														
	1 (0.25)	2 (0.5)	3 (1)	4 (2)	5 (4)	6 (8)	7 (16)	8 (32)	9 (64)	10 (128)	11 (256)	12 (512)	13 (1024)	14 (2048)	2 (0.25 -0.5)	3 (0.5 -1)	4 (1 -2)	5 (2 -4)	6 (4 -8)	7 (8 -16)	8 (16 -32)	9 (32 -64)	10 (64 -128)	11 (128 -256)	12 (256 -512)	13 (512 -1024)	14 (1024 -2048)		
Plots (1 m²), full data set (n = 150)																													
Vascular plants					0.274	0.354	0.448	0.431	0.519	0.879	1.230	1.517	0.909	1.014						2.815	2.830	3.028	2.866	2.620	2.758	2.849	3.369	2.921	
Mosses					0.486	0.691	0.659	0.628	0.991	0.982	1.019	1.076	0.933	1.109						2.746	3.034	3.035	2.671	3.007	2.973	2.961	3.103	2.875	
<i>Sphagnum</i>					0.362	0.372	0.642	0.594	0.399	0.429	1.353	1.454	0.871	1.068						2.980	2.606	3.056	3.287	2.948	2.171	2.948	<i>3.370</i>	2.853	
Hepatics					0.484	0.772	0.558	0.677	0.939	1.141	0.780	0.637	0.920	1.327						2.663	<i>3.234</i>	2.861	2.764	2.859	<i>3.274</i>	3.146	2.735	2.736	
Cryptogams					0.596	0.758	0.713	0.776	1.093	1.188	0.950	0.811	0.994	1.145						2.827	3.044	2.939	2.753	2.940	3.161	3.114	2.853	2.898	
All species					0.396	0.467	0.541	0.593	0.754	1.129	1.068	1.212	0.933	1.119						2.881	2.894	2.934	2.827	2.709	3.040	2.909	3.189	2.869	
Subplots (0.0625 m²; n = 2400)																													
Vascular plants	0.211	0.250	0.333	0.512	0.573	0.536	0.654	0.647	0.761	1.028	1.079	1.251	1.009	0.978	2.878	2.793	2.690	2.919	3.048	2.856	3.008	2.883	2.783	2.965	2.893	3.155	3.023		
Mosses	0.190	0.237	0.347	0.533	0.581	0.789	0.773	0.681	0.918	0.857	0.949	1.071	0.902	1.125	2.841	2.725	2.690	2.938	2.779	3.015	3.091	2.785	3.050	2.926	2.913	3.124	2.841		
<i>Sphagnum</i>	0.134	0.181	0.241	0.434	0.436	0.491	0.573	0.610	0.570	0.659	1.115	1.381	0.941	1.088	2.783	2.793	2.576	2.997	2.914	2.889	2.955	3.049	2.895	2.621	2.846	3.277	2.895		
Cryptogams	0.330	0.379	0.542	0.659	0.744	0.830	0.980	0.892	0.947	1.091	0.914	0.944	1.041	1.081	2.900	2.742	2.859	2.912	2.921	2.880	3.068	2.957	2.898	3.128	2.977	2.929	2.973		
All species	0.229	0.270	0.390	0.426	0.580	0.565	0.766	0.745	0.702	1.080	0.943	1.151	1.011	1.061	2.881	2.735	2.936	2.777	3.019	2.780	3.020	3.043	2.689	3.098	2.856	3.094	2.965		

All variables of the *water-table group* showed very strong spatially dependent variation to 1.5 m, particularly in the 0.75–1.50 m interval, and moderately strong spatial structuring to the range ≈ 100 m (Tabs 12-13). The lowest standardized semivariance recorded for any explanatory variable in any distance class was observed for depth from the highest vertical position in a subplot to the minimum water table, in the 0.25–0.50 m interval (Tab. 12). The range of water table fluctuations, which was correlated with variables in the soil nutrient/acidity group as well as with variables in the water-table group, showed spatially dependent variation up to 100 m but lacked strong spatial dependence at fine scales.

Variables of the *microtopography group* were spatially structured up to 1.5 m (Tab. 12).

All variables of the *tree influence group* had spatially dependent variation at fine scales, at least up to 6 m (Tabs 12-13). A gradient was present among the tree influence variables, from the tree influence index based upon all trees and the litter index which were strongly spatially structured up to ranges of 6(–12) m, via the tree influence index based upon living trees and the crown index with ranges of *c.* 12 m, to the canopy indices and basal area with spatial dependence on all within swamp-forest scales (Tab. 13).

Variables of the *soil depth group* had strong spatial dependence within swamp-forest localities, and ranges of *c.* 25 m (Tab. 12).

Ordination axes

Ordination axes (including the passive ordination of subplots; Tab. 14) generally showed stronger spatial structuring than the variables with which they were most strongly correlated (compare Tabs 12 and 14), particularly at the finest scales (< 3 m).

The first axis in the DCA ordination of the full data set and some ordination axes strongly correlated with this axis (LNMDS 1, DCA-C 1 and DCA-D 1) showed similar patterns of spatial dependence: spatial structure up to *c.* 100 m, particularly strongly in the 25–100 m interval (Tab. 14), and, as demonstrated by the DCA ordination of subplots (DCA-S 1), strong spatial structure also in the 0.5–3.0 m interval. The third axis in the DCA ordination of Subset A, which was also strongly correlated with DCA 1, differed in having a weaker spatial structure and by having a broader range (≈ 200 m).

DCA 2, LNMDS 2, DCA-C 2, DCA-D 2 and DCA-A 1, which were strongly correlated with each other (Tab. 7), were all weakly spatially structured from 3 to 50–100 m. Furthermore, the subplot ordination (DCA-S 2) revealed very strong spatial structuring up to 1.5 m, notably in the 0.75–1.50 m interval. Nevertheless, the standardized semivariance at the finest scale (0.25 m) was twice as large for DCA-S 2 than for DCA-S 1 (Tab. 14).

The correlated axes DCA 4, LNMDS 3 and DCA-D 4 shared the range of spatial dependence of *c.* 100 m and particularly strong spatial dependence in the 50–100 m interval (Tabs 13, 14). As demonstrated by the subplot ordination (DCA-S 4), spatial dependence was stronger at finer scales, most notably in the 1.5–3 m interval. DCA 3 showed a similar pattern of spatial dependence, but with wider range (*c.* 200 m) and without intervals in which the spatial dependence was particularly strong (Tab. 14).

Species density

Species density at the 1-m² scale (as well as the 1/16-m² scale) was less strongly spatially structured than ordination axes and, generally, also less strongly structured than the explanatory variables (compare Tab. 15 with Tabs 12 and 14). Vascular plant, moss and *Sphagnum* (and total) species density was strongly spatially dependent up to *c.* 1.5 m and weakly spatially structured from 1.5 m to the range, 50–200 m. Hepatic and moss species density were less strongly spatially structured than those of vascular plants and *Sphagnum* at all lag distances (Tab. 15), and also tended to have shorter ranges of spatially dependent variation (Tab. 13).

DISCUSSION

ENVIRONMENTAL INTERPRETATION OF GRADIENTS IN VEGETATION

The first two axes of the DCA and LNMDS ordinations represent the responses of vegetation to the two main environmental complex-gradients in swamp forests: a gradient in soil acidity and nutrient concentrations and a gradient in depth to the water table. A minor vegetation gradient related to fine-scale microtopographic heterogeneity and a vegetation gradient possibly related to the annual range of variation in depth to the water-table were also revealed by ordination. We will consider each of these four ecoclines in turn, and also briefly discuss possible causes of vegetation gradients identified by ordination that are uncorrelated with any of the recorded explanatory variables.

The main gradient related to soil acidity and nutrient concentrations

Environmental interpretation

The main coenocline in the investigated spruce swamp forests is related to a complex-gradient that includes soil acidity and concentrations of N and base cations. This is evident from the strong correlations between first axis in ordinations of the full species composition, vascular plants and cryptogams, and variables of the soil nutrient/acidity group, and from the more or less coincident patterns of spatial dependence [notably the strong spatial dependence in the interval (25–)50–100 m, i.e. between swamp-forest localities, and the range of spatially dependent variation of c. 100 m.] of these ordination axes and explanatory variables. Ecoclines [gradients in vegetation and the environment; Whittaker (1967)] that correspond to this main gradient in our study are treated as the ‘poor – rich direction of variation in vegetation’ in studies of Fennoscandian mire and/or paludified forest vegetation by traditional methods (Sjörs 1948, 1950, 1952, Malmer 1962a, 1986).

Considerable shifts in species composition occur along the ‘poor – rich gradient’ from (ombrogenous) bog to extremely rich fen (Sjörs 1948, Fransson 1972, Fremstad 1997), and different ecological factors may restrict species’ distributions in different sections of the gradient. We therefore start the discussion of ecological relationships by establishing correspondence between the range of variation encountered in our study and previous studies.

Most divisions of the full range of variation along the ‘poor – rich gradient’ are variation over a common theme; a partitioning into six classes (Fransson 1972, R. Økland 1989a, R. Økland et al. 2001): bog, extremely and moderately poor fen, intermediate fen, moderately and extremely rich fen. None of the investigated swamp-forest localities are exclusively fed by ombrogenous water (rain water); all receive additional supplies of minerogenous water (water enriched with respect to many elements by contact with mineral soil; Sjörs 1948, R. Økland 1989b). This is obvious from the hydrotopography of the investigated localities (Fig. 2), from the lack of soil pH < 3.9 in any dry plot (Malmer 1962a, Kielland-Lund 1981), and from the abundant presence of fen plants (indicators of minerogenous water supply; Du Rietz 1954) in all parts of all investigated swamp-forest localities. Our material does, however, not include

extremely poor fen sites either. In SE Norway such sites most often have a tree layer dominated by Scots pine (*Pinus sylvestris*), an understorey vegetation that differ from truly ombrogenous sites only by the scattered occurrence of fen plants like *Melampyrum pratense*, *Carex globularis*, *Polytrichum commune*, *Sphagnum brevifolium*, *S. riparium* and *S. russowii*, and a peat mineral content only slightly higher than in ombrogenous peat (Sjörs 1948, Malmer 1962a, Fransson 1972, R. Økland 1989a). The opposite end-point along the gradient, the extremely rich fen, is also absent from our material: only one of the species mentioned by Fremstad (1997; also see Moen 1990) as typical of extremely rich sites, *Fissidens adianthoides*, is present in our material, and no plot has the high soil cation concentrations and the high pH typical of extremely rich sites (Sjörs 1952). The variation encompassed by our data therefore corresponds to moderately poor, intermediate and moderately rich fens in previous studies.

The traditional Scandinavian view, later adopted by mire ecologists from other parts of the world, is that variation in species composition along the 'poor - rich gradient' is primarily due to variation in soil acidity and/or concentrations of 'base minerals' like Ca and Mg (Thunmark 1942, Sjörs 1952, Du Rietz 1949, 1954, Malmer 1962a, 1962b, 1986, 1993, Persson 1962, Sonesson 1970b, Fransson 1972, Karlin & Bliss 1984, R. Økland 1989a, 1990b, Glaser et al. 1990, Gignac et al. 1991). At a first glance, the strong correlations between these variables and the main coenocline in our study seems to support this hypothesis. A closer look, however, reveals that pH, Ca and most other variables of the soil nutrient/acidity group are correlated both with the main coenocline and with the (second) coenocline related to depth to the water table [similar results were also obtained by Jeglum & He (1995) for Canadian forested wetlands; and can be inferred from Vitt & Chee (1990)]. These variables therefore do not strictly reflect variation from 'poor' to 'rich', but have their main direction of variation from 'poor-and-dry' to 'rich-and-wet' sites. This indicates that other or additional factors have to be taken into account to explain variation along the 'poor - rich gradient'. Bridgham et al. (1996) hold against this explanation that the concentrations of Ca and Mg are sufficient for plant growth even in ombrogenous peat (Clymo & Hayward 1982, Malmer 1986) and that mire and swamp-forest plants respond insignificantly to Ca fertilization (Clymo & Hayward 1982, Kooijman & Bakker 1995).

An alternative view [reviewed by Bridgham et al. (1996)], is that variation in species composition in swamp forests, just like in coniferous forests on mineral soil (R. Økland & Eilertsen 1993, T. Økland 1996, Giesler et al. 1998), is determined mainly by nitrogen availability. This view is supported by the N-restricted growth experimentally demonstrated for several wetland vascular plants and bryophytes (Bridgham et al. 1996: Tab. 2, Li & Vitt 1997). Our results are consistent with this explanation: the concentration of total N deviates from all other measured variables (except extractable Mn) in being more or less unrelated to depth to the water table, by differing strongly between the 'poor' and the 'rich' subsets, and total nitrogen is also one among the variables most strongly correlated with the relevant ordination axes.

While inorganic nitrogen was previously considered to be the only nitrogen source that could be utilised by plants (e.g. Ingestad 1973), recent studies have demonstrated that organic nitrogen, abundantly present in the soil as free amino acids (Kielland 1995), is also taken up by boreal forest and mire vascular plants (Chapin et al. 1993, Kielland 1994, Näsholm et al. 1998) and bryophytes (Kielland 1997). Nitrogen is rapidly sequestered by, and for some years tightly recycled within, the living bryophyte layer and becomes available to vascular plant roots by decomposition of dead bryophyte material (Malmer et al. 1994, Li & Vitt 1997). The variation in availability of different chemical forms of nitrogen along this gradient is not known (Malmer 1993, Bridgham et al. 1996, 1998), but wetland vegetation is, in general, adapted to nitrogen

uptake from multiple sources and minimisation of losses. Characteristics of the plants themselves are therefore more important for the functioning of the system than nutrient cycling at the stand level (Jonasson & Shaver 1999). The strong correlation between total nitrogen and ordination axes in our study accords with overall nitrogen supplies, organic and inorganic, as the important factor.

In addition to direct measures of soil acidity and N and base cation concentrations, the main coenocline is correlated with loss on ignition and soil depth; both decrease abruptly from poor to richer swamp forests (Figs 39, 44) in accordance with a change of soil profile (Fremstad 1997) from a more organic type (Fibrisol, Mesisol) to a Gleysol [terminology according to Anonymous (1987)]. Similar observations are made in Finland by Korpela & Reinikainen (1996a) and in Latvia by Prieditis (1999), and are indicated by Green et al. (1993) from North America. However, in none of these studies, including ours, is there a one-to-one relationship between soil type and position along the gradient (e.g. Sims et al. 1982).

Soil organic matter content reflects the rates of fundamental biological processes in the soil, as determined by the balance between rates of input and decay of organic matter. From 'poor' to 'rich', input of vascular plant litter increases due to increasing vascular plant species density (this study) and production (Bradbury & Grace 1983, Clymo 1983). However, this is of minor importance for peat accumulation, which is governed by the production and, most notably, decay, of *Sphagnum* spp.; the single most important factor controlling the rate of peat accumulation (Clymo 1983, 1984, Damman 1986, Malmer 1986). Because of unique chemical properties (Coulson & Butterfield 1978, Clymo 1984, Bridgham et al. 1996), *Sphagnum* litter is inert to decomposition (recalcitrant), and decomposes more slowly than litters from any other growth form present on mires (Coulson & Butterfield 1978, Malmer et al. 1994, Aerts et al. 1999). *Sphagnum* productivity increases from ombrotrophic to 'poor' minerotrophic sites (Damman 1986, Rochefort et al. 1990), but decreases again from 'poor' to 'rich' sites as indicated by the decrease in *Sphagnum* species density and the abundance of most *Sphagnum* species. The preference of most *Sphagnum* species for acid fens is due to their low physiological tolerance for high cation concentrations (Skene 1915) due to overstress of the cation exchange mechanism (Brehm 1968). Ample production of the cation exchanger PGA (polygalacturonic acid) by *Sphagnum* regulates pH internally in the living cells (Kilham 1982), aids in efficient trapping of supplied nutrients (Malmer 1993), reduces the ambient pH and thus deteriorates growth conditions for most other species (Andrus 1986). The effect of decreasing *Sphagnum* production from 'poor' to 'rich' sites on peat accumulation is accentuated by an even stronger increase in the rate of decay (Malmer 1962b, Damman 1986, Verhoeven et al. 1990, Johnson & Damman 1993, Aerts et al. 1999).

Following the classification of German mires by Succow (1988), studies in North Carolina peatlands by Bridgham et al. (1996) and British and Dutch studies, Wheeler & Proctor (2000) suggest that two, major, more or less independent gradients related to 'richness' exist in mires: in addition to, and distinct from, the "acid, calcium-poor - alkaline, calcareous and carbonate-rich gradient" there exists a gradient in species composition associated with variation in 'fertility' [or productivity, Austin & Gaywood (1994); the position along which may, as demonstrated by Wheeler & Shaw (1995), be quantified by a phytometer estimate (Wheeler et al. 1992)]. Following suggestions by Bridgham & Richardson (1993) and Bridgham et al. (1995, 1998), Wheeler & Proctor (2000) ascribe this 'fertility' gradient mainly to phosphorus deficiency in 'rich' swamp forests and mires.

Our results, as well as those of Cooper & Andrus (1994) from Wyoming, U.S., contain no indications of a 'fertility' gradient that is independent of the 'poor - rich' gradient. Instead,

several observations suggest that phosphorus availability is not an important factor for the differentiation of swamp forest vegetation in Østmarka, neither along the 'poor - rich' gradient nor as an independent gradient within 'rich' sites: (1) Extractable phosphorus varies strongly among plots (Tab. 2), and is not correlated with relevant ordination axes, not even in the ordination of the 'rich' Subset B (Tab. 9). (2) Species occurrence limits are sharper towards the 'poor' than towards the 'rich' end of the gradient [K. Rydgren, R. Økland & T. Økland, unpublished results]. This indicates that species are restricted from occurring in poorer sites rather than the converse, and questions the ecological importance attributed by Bridgham et al. (1996) to the observation that P and N mineralization rates are higher in bogs than in fens when calculated per unit soil volume and by Bedford et al. (1999) to the correlation between N:P ratios in plant tissue and surface soils of N American wetlands. (3) The lack of any relationship between extractable amounts of P and Ca indicates that P immobilisation because of precipitation with calcite, as described from calcareous fens (Boyer & Wheeler 1989), does not occur in the investigated swamp forests.

A close look at the results of published studies reveal considerable variation in the relationship between P, other peat constituents and position along the 'poor-rich gradient'; from positive pair-wise relationships between Ca, N, P and gradient position in Finnish pine-dominated swamp forests (Schneider & Westman 1987), via no relationship between P and the gradient in our study, to negative relationships between P and Ca in studies of calcareous fens by Boyer & Wheeler (1989) and Vitt & Chee (1990). Nevertheless, there exists a simple, unifying solution (with three elements) for these seemingly inconsistent results: (1) The apparent discrepancy between English, C European and some N American studies on one hand and the Fennoscandian and some other N American studies on the other is due to regional differences in the supply of nutrients to mires (R. Økland et al. 2001): C Europe, S England and S Sweden differ from C and N Fennoscandia by receiving so large amounts of N that P has replaced N as the growth-limiting nutrient (Aerts et al. 1992). One 'poor - rich' gradient in mire vegetation from bog to moderately rich fen [correlated with several single environmental factors, among them soil and water acidity (pH), electric conductivity, and concentrations of Ca, Mg, Mn, total N and even P] is typical for regions with low deposition of airborne pollutants, while more or less independent gradients related to 'fertility' (P availability) and alkalinity typically occurs elsewhere. (2) Additional variation in the strength of pair-wise correlations between variables, and between each variable and the coenocline, is brought about by differences in the range of environmental variation and wetland types that is included in the studies that are compared. (3) At all latitudes there is a complex gradient structure (in species composition and environmental conditions) within rich fens that depends on local conditions (Fransson 1972, Vitt et al. 1995). This explains why correlations among environmental variables vary strongly from one data set to another: one, two or even three distinct gradients may be discerned, of which a 'fertility' gradient related to P availability and inversely related to pH and Ca concentrations (Boyer & Wheeler 1989, Vitt & Chee 1990) may be one; and fertility gradients that are independent of the 'poor - rich' gradient (Wheeler & Proctor 2000) are others. The results obtained for spruce swamp forests in Østmarka fit into this pattern.

Vitt & Chee (1990) suggest that different factor complexes govern the variation, at least within rich fens, of vascular plants and bryophytes: the former mainly respond to a gradient in availability of important nutrients (notably P and N), while soil acidity and availability most notably of Ca and Mg are more important for the latter. This is neither supported by our results nor by the results of Anderson & Davis (1997): coincident gradient patterns of vascular plants and of cryptogams indicate that common or strongly related explanations apply to the two groups

over the range of variation along the 'poor-rich' coenocline we have studied. In fact, both soil acidity and soil nutrient concentrations are generally more strongly correlated with plot positions along the cryptogam than along the vascular plant coenocline in separate ordinations.

Is there a natural bipartition into 'poor' and 'rich' swamp forests?

A careful examination of species abundance distributions along DCA axes 1 and 2 (our full data set) reveals that many species with optima in richer swamp forest occur more or less regularly also in plots from the poor swamp-forest subset. Typical examples are *Sphagnum teres* and *S. warnstorffii*, which occur in swamp-forest localities 1, 8 and 10 in plots with DCA-1 scores > 1.0 and low DCA-2 scores. *Caltha palustris*, *Filipendula ulmaria*, *Galium palustre* and *Lysimachia thyrsoiflora* are less common but follow the same pattern. The isoline diagrams (Figs 43, 45) show that these plots differ from other poor swamp-forest plots by having soil and water pH > 5.0 . Plots with DCA-1 scores > 1.5 and high DCA-2 scores most often contain a variable number of species typical of richer spruce [i.e. low herb and fern-dominated; Kielland-Lund (1981) and Fremstad (1997)] forests on mineral soil, such as *Anemone nemorosa*, *Dryopteris expansa* agg., *Gymnocarpium dryopteris*, *Oxalis acetosella* and *Phegopteris connectilis*. These plots mostly have soil pH > 4.5 , while water pH varies strongly (Fig. 43). With their mixture of species characteristic of 'moderately poor' and 'rich' sites, plots in the 1.5–2.5 S.D. interval along DCA-axis 1 are typical for 'intermediate fens' as defined by Sjörs (1952); see Sjörs (1947, 1948), Persson (1961) and Fransson (1972).

Even though typical 'intermediate-fen plots' are abundant in our material, the sparse region midway along DCA axis 1 shows that the floristic limit between 'poor' and 'rich' swamp forests is relatively sharp, most strongly so for cryptogams as indicated by separate ordinations of plant-group subsets. Several authors have claimed or demonstrated a 'natural' bipartition of fens along these lines: Du Rietz (1949) states that the limit between 'poor' and 'rich' sites is one of the sharpest borderlines in mires, Prieditis (1999) makes a first bipartition of spruce swamp forests into 'poor' and 'rich', and Wheeler & Proctor (2000: 194) state that "... if there is a primary 'natural' subdivision within mires, it is (high Ca, high pH) rich fen vs (low Ca, low pH) poor fen+bog ...". Other authors, however, take the opposite position: Sjörs (1952) characterises the 'poor-rich limit' as indistinct, and plots from Canadian 'wooded peatlands' (and subsets) make up continuous clouds along the first DCA ordination axis related to soil nutrient content in the study by Jeglum (1991).

Our data seem to comply fully with the 'natural division' of fens as characterised by Wheeler & Proctor (2000): not only is there a distinct floristic limit, but in addition water pH is bimodally distributed. Upon careful examination, however, our results turn out to deviate from the Wheeler & Proctor (2000) in two important respects: (1) The separating antimode in the distribution of water pH is at c. 4.3 pH units, not at c. 5.5 units as suggested by Wheeler & Proctor (2000) from own data and data in Gorham et al. (1985), Gorham & Janssens (1992) and Proctor (1995). (2) The separating antimode for water pH does not correspond with the 'poor - rich split' in the ordination; instead plots classified as 'poor' and 'rich' overlap broadly over a range of water-pH values from 4.5 to 6.0 (Fig. 51).

A close examination of available material reveals that our results, as well as those reported by Wheeler & Proctor (2000), may fit into a broad-scale geographical pattern. 'Intermediate fen waters' characterized by high water pH (up to 6.5) and low base mineral content (Witting 1949, Sjörs 1952, Vitt et al. 1975, Cooper & Andrus 1994) typically occur in the boreal zone. Typically, they are associated with vegetation of an intermediate type (Sjörs 1950, Fransson

1965, 1972), but they may occasionally support poor-fen vegetation without rich-fen indicators (Vitt et al. 1975). The transitions in vegetation (Cooper & Andrus 1994) and chemical characteristics (Sjörs 1952) are often described as gradual. In the boreo-nemoral and nemoral zones, however, intermediate fen vegetation is more or less lacking (Sjörs 1950, 1952, Malmer 1962a, Fransson 1972) and the pH of mire water more closely follows its base cation content (Witting 1947, Sjörs 1952, Wheeler & Proctor 2000). Our study area has 'intermediate swamp-forest plots' with a prominent element of 'rich-fen species' and with higher pH than 'poor swamp-forest plots'. On the other hand, the concentrations of base cations hardly differ and the floristic limit is distinct, but does not correspond to the separating antimode in the bimodal distribution of water pH. Thus, northern and southern traits are mixed in Østmarka Nature Reserve, which is situated close to the border of the south boreal onto the boreo-nemoral zone. The general geographic pattern of variation does, however, not apply without exceptions: while one set of water-pH data from the northern hardwood region of the U.S. (Vitt & Slack 1984) shows no bimodality, data from boreal Canada (Vitt et al. 1995) show a clear gap for $5.0 < \text{pH} < 6.0$. Furthermore, the combination of $\text{pH} > 6.0$ and low Ca concentrations is reported to occur in mires developed under special hydrological conditions (Yabe & Onimaru 1997). We therefore support Sjörs' (1952) view that there is a strong degree of individuality among study areas with respect to the sharpness of the 'poor - rich transition' and of covariation pattern among single environmental variables that make up the gradient from acid, base-poor sites to alkaline, base-rich sites.

The second gradient related to depth to the water table

The second most important coenocline in the investigated spruce swamp forests is related to the complex-gradient in depth to the water table, as demonstrated by the correlations between variables of the water-table group and the first axis in separate ordinations of poor and richer spruce swamp-forest subsets (A and B) and the second axis in all other ordinations. In fact, these correlations are the strongest observed between ordination axes and explanatory variables in this study.

This coenocline is a swamp-forest parallel to the 'hummock-to-mud bottom-direction of variation' in mire vegetation (Sjörs 1948, Malmer 1962a, Fransson 1972), because: (1) the corresponding coenocline in mires is also strongly correlated with (median) depth to the water table (Malmer 1962a, R. Økland 1989a, 1990b, Nordbakken 1996a); and (2) the strong spatial dependence in the interval 0.75–1.5 m observed in this study both for the coenocline and for water-table variables have parallels in *Chamaecyparis* swamps in New Jersey (Ehrenfeld 1995b) as well as treeless bogs in SE Norway (Ohlson & R. Økland 1998). Variation in vegetation in response to variation in depth to the water table is described in several studies of forested mire ('mire margin') vegetation (e.g. Sjörs 1948, Malmer 1962a, Fransson 1972, Johnson 1996) in which small-square techniques, e.g. of the Fennoscandian phytosociological tradition (Whittaker 1962, Trass & Malmer 1978, R. Økland 1990a), have been used.

The comparable magnitudes of standardized semivariances for water-table variables and for ordination axes at scales finer than 1.5 m indicate that fine-scaled species patterns are mainly determined by depth to the water table and that contiguity of biological processes such as dispersal and mortality, that give rise to floristic self-similarity (Legendre 1993) by a fine-scaled mass effect (Shmida & Ellner 1984), does not overrule the effects of fine-scaled ecological variation. The alteration of drier, elevated sites and wetter depressions in swamp forests and

mires at scales of one to a few metres (R. Økland 1989b) will be referred to as *mesotopographic* structure, while variation in surface topography at very fine scales will be referred to as *microtopographic* structure.

This coenocline has spatial structure also on broader scales, reflecting the multi-scale patterns of variation in physiographic conditions, hydrology and, hence, (average) depth to the water table: in the studied swamp forests at the 10–25 m scale due to the low frequency in richer swamp-forest localities of sites with high depth to the water table, and at scales up to c. 75 m due to differences in wetness among entire swamp forests (Ehrenfeld 1995b). Local variation in the scales of these patterns explains why coenoclines and water-table variables are correlated in some studies where plot sizes of 5 × 5 m (Anderson et al. 1995, Anderson & Davis 1997) or 10 × 20 m (Vitt et al. 1990) are used and not in others (e.g. Kielland-Lund 1981, Jeglum 1991, Jeglum & He 1995, Korpela & Reinikainen 1996a, Prieditis 1999).

Acidity, organic matter content and K concentration increase, while pH, base saturation and extractable amounts of Ca, Mg, N and, notably, S, decrease from wetter to drier sites along the second coenocline, in accordance with relationships reported in previous studies (e.g. Malmer 1962a, 1962b, Vitt et al. 1975, Damman 1978, 1986, Clymo 1983, Karlin & Bliss 1984, Jeglum 1991). Concordance over peat types ranging from bog to rich fen indicates that these relationships between peat properties and depth to the water table apply to peat in general. For instance, K tends to be concentrated in the upper peat layers due to accumulation in living bryophytes (Damman 1978, Clymo 1983), and concentrations of several elements are influenced by the relationship between redox potential and depth to the watertable: drier sites offer an oxidizing, while flooded, anoxic sites offer a reducing environment (Pearsall 1938, Malmer 1962a, Damman 1978, Clymo 1984, Ehrenfeld 1995a). The redox potential determines the chemical state of many elements, cations as well as anions, and, hence, the solubility of their salts. One example is sulfur, which at drier sites occurs in the oxidized state as soluble sulphate (+VI) anions, in anoxic sites as less soluble sulphide (-II) anions (Clymo 1983, Devito & Hill 1999). Base cations are leached from drier sites and precipitate in wetter sites as low-soluble sulphides. This explains why extractable S is particularly strongly correlated with this coenocline. Differences in dominant chemical processes between the aerated drier and the waterlogged wetter areas in peatlands (Malmer 1962a) also explain why the uppermost peat layer is more acid in drier than in wetter swamp-forest sites.

Contrary to observations by Damman (1978), our data contain no evidence for accumulation of bi- or trivalent cations such as Fe, Zn and Al at levels close to the water table. This may be due to: (1) sampling method; we collected the uppermost peat layer while in other studies peat monoliths have been analysed; (2) the way element concentrations are expressed; as weight ratios in our study, as volumetric molar concentrations in other studies (e.g. Malmer 1962a); (3) differences between peat types (Clymo 1983), notably that minerogeneous swamp-forest peat differs from the ombrogenous open mire peat most often subjected to peat chemical studies (e.g. Malmer 1962a, 1962b, Damman 1978, Clymo 1983); and (4) regional differences (Clymo 1983).

The higher pH and nutrient concentrations of wetter than adjacent drier sites, reflected in the negative correlation between relevant variables and the second coenocline, explains why the strong fine-scaled spatial structure of the second coenocline has a counterpart in spatially dependent variation of the main coenocline at scales < 3 m. This relationship is an important reason why levels along the 'poor - rich' coenocline cannot be unequivocally characterized in terms of measured water or soil chemical variables.

The correlations among variables of the water-table and tree influence groups arise because

trees mainly occur in drier micro-sites in swamp forests (Karlin & Bliss 1984, Glaser et al. 1990, Johnson 1996). This is due to a bidirectional causality: (1) Establishment of trees, i.e. successful germination and survival of seedlings and saplings, is mainly restricted to elevated, well-aerated soils (Huenneke & Sharitz 1986, Ehrenfeld 1995b, Hörnberg et al. 1997). Once established, however, *Picea abies* seedlings become more tolerant of seasonal waterlogging (Pelkonen 1979). (2) The basal part and the expanding rooting system of an established tree sapling provides scaffolding for bryophyte growth (Malmer et al. 1994). An elevated, hummock-shaped structure may therefore build up around a tree in some years.

The considerably broader scales of spatially dependent variation observed for tree-influence variables (based upon living trees as well as all trees) than for the second coenocline and the water-table variables show that past or present occurrence of a tree is not a *necessary* condition for development of an undulating swamp-forest surface. Only a small fraction of suitable microsites are in fact occupied by trees (Ohlson & Zackrisson 1992, Hörnberg et al. 1997), because: (1) germination success depends on microhabitat conditions, and is higher under favourable moisture conditions; (2) seedling and sapling mortality is very high, among others due to high danger of overgrowth by *Sphagnum*, and (3) recruitment is dependent on favourable macroclimatic conditions, and therefore only occurs intermittently (Rydgren et al. 1998). This accords with the occurrence of mesotopographic structure also on open mires (R. Økland 1989a). The well-documented pattern-forming processes in mires (e.g. Granlund 1932, Aartolahti 1965, Tolonen 1967, Barber 1981, Foster & Fritz 1987, R. Økland 1989b, Malmer et al. 1994, Malmer & Wallén 1999) may well apply also to swamp forests, but empirical data to support this are lacking.

Although some hummocks have an overstorey while others do not, the studied swamp-forests lack a vegetation gradient related to tree influence as is often found in spruce forests on mineral soil (e.g. R. Økland & Eilertsen 1993, T. Økland 1996, Rydgren 1996, Rydgren et al. 1999). This may be due to: (1) trees in swamp forests mostly growing singly or in small groups; sufficient light thus reaches the understorey; (2) capillary uptake of water from the ground-water reservoir by peat mosses (Granlund 1932, Ehrenfeld 1995a) counteracts the potentially negative effects of rainfall interception on plants growing underneath trees; and (3) the fact that in swamp forests the number of trees that are sufficiently large to produce the shade, litterfall and rainfall interception required for a change in understorey species composition away from dominance by *Sphagnum* spp. is too low for a gradient on its own to be recognised by ordination.

The correlation between the second coenocline and depth to the water table is strongest in the separate ordination of poor swamp forests; most likely because the greater range of variation in depths to the water table in poor than in richer swamp forests provides for a higher β -diversity. High hummocks in poor swamp forests are largely composed of the remains of decomposition-resistant *Sphagnum* spp., while in richer swamp forests more rapidly decomposing mosses dominate and elevated sites are therefore most often restricted to bases of large trees.

The second coenocline is, both in ordinations of vascular plants and of cryptogams, generally most strongly correlated with depth to the *maximum* water table. This accords with the hypothesis of Malmer (1962a) and R. Økland (1989a, 1990b) that duration of water-logging is the decisive factor for species' responses to this coenocline. The slightly stronger correlations observed for vascular plants than for cryptogams show that 'moisture gradients' are not more important to bryophytes and lichens than to vascular plants, as suggested by Glaser et al. (1990) and Anderson et al. (1995). Although species density patterns demonstrate that vascular plants and *Sphagnum* generally prefer wetter while mosses and hepatics prefer drier sites (Andrus et al. 1983, R. Økland 1989a, 1990c), species can be found in all groups that have optima that do not

fit into this general pattern.

Vascular plants of drier swamp-forest sites (and mire hummocks) are sensitive to waterlogging (Malmer 1962a, Bannister 1964a, Bell & Tallis 1974) and differ from wetter-growing species by possession of mycorrhiza and/or by lacking root aerenchyma (Metsävainio 1931). Vascular plants with preference for wetter sites (depressions) have (deep) rooting systems with aerenchyma but may instead be sensitive to drought (Malmer 1962a, Bannister 1964b).

Ectohydric cryptogams, i.e. the majority of bryophyte and lichen species, take up water and nutrients over their entire surface (Buch 1947, Blum 1973). Because the growth of ectohydric bryophytes under normal field conditions is primarily limited by moisture supply (Stålfelt 1937, R. Økland 1997a), they are expected in general to prefer wetter sites. This is, however, not the case for mosses and hepatics in swamp forests in Østmarka, for which several reasons may apply: (1) Many forest and mire mosses are intolerant to waterlogging (Birse 1958, Busby et al. 1978), which inhibits photosynthesis by increasing the resistance to CO₂ diffusion (Rundel & Lange 1980). The group optima for mosses and hepatics is therefore displaced away from the wettest, waterlogged sites. (2) *Sphagnum* spp. monopolise the physiologically optimal, wet, habitat. Their higher growth rates in such habitats (Pakarinen & Rinne 1979) enable them to overtop mosses and hepatics there (Sirén 1955, Viereck 1970, Foster 1984). As a result, smaller moss and hepatic species are displaced to drier habitats that are suboptimal for *Sphagnum* ('centrifugal organisation'; Keddy & Shipley 1989, Keddy 1990). (3) Differences in ability to colonise patches of naked peat (R. Økland 1990c). No thorough, long-term, field observational and experimental data on mire and swamp forest vegetation dynamics are, however, available to assess the relative importance of mechanisms that may determine the distribution of *Sphagnum*, mosses and hepatics (and lichens), as groups or as single species, along this gradient. Careful studies designed to address similar questions for open bogs have, however, not yet come up with clear answers (Rydin 1986, 1993a, 1993b, 1997, R. Økland 1989a, 1990c, Nordbakken 1996b, 1997) and simple answers to these questions are therefore not likely to exist. If, however, control of ectohydric cryptogam growth rates by moisture availability turns out to be an important factor for the segregation of bryophytes along the depth-to-the-water-table gradient, the generally much higher growth rates of bryophytes in paludified than in non-paludified forests (Pakarinen & Rinne 1979) will make up a difference of considerable importance for the ecological functioning of these systems. Furthermore, the high growth rates probably explain why bryophytes have much lower danger of becoming buried in litter in spruce swamp forests (During & Verschuren 1988, R. Økland 1995, 1997a), and why swamp forests often have a nearly continuous bryophyte cover.

The third gradient related to microtopography

A third coenocline related to the extent of microtopographic variation (correlated with vertical range and maximum slope), considerably less strong than the two most important coenoclines, appears in the DCA and LNMSD ordinations of the full data set as axis 4 and 3, respectively, and in the ordination of cryptogams. Even though the two microtopographic variables are as strongly correlated with the axis related to depth to the water table, the independence of DCA ordination axes makes this coenocline represent a unique component of variation related to microtopography which is independent of the variation related to depth to the water table. This gradient extends from continuous, flat, lawn-like, drier sites dominated by large bryophytes like *Polytrichum commune* and *Sphagnum girgensohnii* to more or less convex, hummock-like, drier sites with a strong microrelief (i.e. considerable vertical variation over short distances and high maximum

slope on a fine scale), dominated by small mosses and hepatics. Examples of these so-called 'pocket species' (R. Økland & Bendiksen 1985) are *Barbilophozia attenuata*, *Blepharostoma trichophyllum*, and *Tetraphis pellucida*. This gradient is most prominent in poor swamp forests, where drier sites have considerably higher areal importance than in rich swamp forests.

Small acrocarpous mosses and hepatics abound among the 'pocket species', as demonstrated by the correlation of this coenocline with species densities of mosses and hepatics but not of vascular plants and *Sphagnum* (the latter decreasing along DCA-axis 4 in the ordination of the full data set). A floristically similar coenocline, mostly with the same 'pocket species' occupying the gradient end-point is found in coniferous forests on mineral soil (R. Økland & Bendiksen 1985, Goth & Røeggen 1994, R. Økland 1994, Rydgren et al. 1999). This is not unexpected, as the microsites with 'pocket species' in the swamp-forest localities investigated by us are the same as in forests on mineral soils: adjacent to large trees, i.e. at the side of, or underneath, exposed roots (Rydgren et al. 1999); on the top and sides of fallen logs and tree stumps (Söderström 1988, Kryus et al. 1999); adjacent to large, exposed stones and rock outcrops (Rydgren et al. 1999); and litter-covered patches underneath trees, that differ from *Sphagnum*-covered patches in moisture content and several other environmental conditions (Ehrenfeld 1995a). One kind of microsite, mechanically damaged peat, for instance brought about by trampling by mammals (T. Økland 1996), is common to mire, swamp forest and forest on mineral soil.

This coenocline shows strong spatial dependence on fine scales, notably in the 1.5–3 m interval, and has a range of spatially dependent variation at c. 100 m. We interpret the combination of strong spatial structure of the coenocline, weak correlations between microtopographic variables and ordination axes, and weak spatial structure of microtopographic variables at all scales, as indications that many 'pocket species' have localised distributions (Söderström 1989, Goth & Røeggen 1994), and that variation in microtopography (as represented by the measured variables) is neither sufficient nor necessary for 'pocket species' to occur. The overall frequency of 'pocket species' in 1-m² plots is low; subplot frequency in single plots or groups of neighbouring plots is high; and distributions have strong elements of apparent randomness (Fowler 1990, R. Økland 1990a) that arise because many 'pocket species' are dispersal limited (Söderström 1989).

Two mechanisms may explain the preference, or restriction, of 'pocket species' to 'pocket sites' (R. Økland 1994): (1) 'Pocket sites' are gaps of short duration, created by fine-scale disturbance. 'Pocket species' are early colonisers, i.e. ruderal species in the terminology of Grime (1979) and fugitive and shuttle species in the terminology of During (1979, 1992), occupying 'pocket sites' until overtopped by larger, more competitive species. (2) 'Pocket sites' persist for decades, centuries or millennia, but are extreme with respect to important environmental factors such as inclination, radiation, soil depth, soil organic matter content, or soil stability. 'Pocket species' are stress tolerators (Grime 1979) with specialized traits that make them able to establish and survive in 'pocket sites' that act as refugia from which more competitive forest-floor species are excluded by lack of tolerance to the extreme conditions. Most 'pocket species' combine ruderal (1–2) and stress-tolerator (3–5) traits such as: (1) production of copious spores and/or gemmae [specialized vegetative propagules; Correns (1899), Schuster (1983), Söderström (1987)]; (2) ability of propagules to remain attached to, and germinate on, steep, unstable surfaces with low organic matter content (van Tooren & During 1988); (3) small individual shoots with reduced probability of becoming detached by gravity (aided by attached ice and water drops; Watson 1960, van Tooren & During 1988), implying a spread of the risk of extinction on a large number of ramets (Eriksson & Jerling 1990); (4) closely appressed growth form (R. Økland 1994, Bates 1998), implying substrate stabilisation and a reduction of the danger of detachment by substrate

slides and other fine-scale disturbances (During & ter Horst 1987, van Tooren & During 1988); and (5) high shade and drought-stress tolerance (Grime 1979). Empirical data for assessment of the relative frequency of the two kinds of 'pocket sites' (and transitions) are not available, but the combination of ruderal and stress-tolerator traits possessed by most 'pocket species' indicates ability to enter 'pocket sites' regardless of origin and duration. We assume that 'pocket sites' arise in swamp forests in many different ways and comprise the full range from ephemeral sites such as mechanically damaged *Sphagnum* which is colonized by, e.g., *Cephalozia pleniceps* (Vitt et al. 1975, T. Økland 1996), to sites adjacent to large trees, stones, rock outcrops and underneath tree roots, that last for centuries or millennia. Furthermore, we believe that the species composition of a 'pocket site' at a given time-point is the result of a unique combination of dispersal events, successful establishments and population survivals.

This coenocline displays shifts in stature, taxonomic composition and life-history traits similar to those observed for the coenocline in mires associated with peat-producing ability (Malmer 1962a, R. Økland 1989a, 1990b, 1990c, Nordbakken 1996a). A closer comparison does, however, reveal that the two coenoclines differ in several respects: (1) The mire coenocline is more weakly or not at all dependent on microtopographic heterogeneity; in fact the weakly peat-producing patches, the mire parallel to 'pocket sites', occur adjacent to, and without any measurable ecological difference from, the strongly peat-producing, *Sphagnum*-dominated patches. (2) A coenocline associated with peat-producing ability occurs in mires at all depths to the water table while in swamp forests 'pocket species' are abundant in drier sites only. (3) Except for *Cephalozia lunulifolia*, spruce swamp-forest 'pocket species' do not occur as 'poor peat producers' in mires; mires and swamp forests even differ with respect to small *Cladonia* spp. (4) A gradient in peat-producing ability is typical of mire sites very poor in nutrients; the characteristic, weakly peat-producing vegetation rapidly becomes less important towards mire sites richer in nutrients (R. Økland 1989a). We conclude that the apparent similarity between the mire gradient related to peat-producing ability and the coenocline in spruce swamp forests related to microtopography does not have a common ecological cause. On the other hand, the common presence of coenoclines related to microtopography indicates affinity between spruce-dominated swamp forests and forests on mineral soil.

Existence of a fourth gradient related to the annual water-table amplitude

A fourth vegetation gradient, relevant to richer swamp forests only and correlated with the annual water-table range, appears as the third axis in the ordination of plots from richer swamp-forest sites and as the fourth axis in the ordination of vascular plants. Plots from swamp-forest localities 3 and 6, that lack spring horizons and have a more strongly fluctuating water-table, are separated from plots, many of which are spring influenced, from localities 5, 7, 8 and 9. The moderately strong spatial structure up to the range of 100–200 m observed for both the fourth vascular plant ordination axis and the range of water-table fluctuations supports the interpretation that this coenocline separates richer swamp-forest patches or entire swamp-forest localities with a less fluctuating water table (due, among others, to spring influence) from patches or localities with higher probability of drying out in summer.

No relationship between the annual water-table amplitude (or this coenocline) and peat depth is found in this study despite the water table is reported to fluctuate more strongly in marginal than in open bog areas and with increasing proximity to the adjacent mineral soil (Malmer 1962a, 1986, Mörnsjö 1969). The most likely reason is that variation in peat depth at

the between-localities scale, on which variation along the coenocline is expressed, is masked by the large variation in peat depth within each swamp-forest locality. The lack of significant correlations with peat depth does not therefore rule out the possibility that swamp-forest size and peat depth are important determinants of the water-table fluctuation pattern and, hence, the species composition.

The annual water-table amplitude influences the rate of decay, which in turn controls the rate of peat accumulation (Clymo 1984), by determining the residence time of the organic matter in the periodically aerated surface peat layer, the acrotelm [terminology according to Ingram (1978)]. In the permanently waterlogged catotelm, decay is hampered by oxygen deficiency (Clymo 1965, Heal et al. 1978). Thus peat will accumulate at a lower rate the larger the annual water-table amplitude is, because the longer does the organic matter stay in the acrotelm (Clymo 1983), and the more strongly decomposed will it be when it enters the catotelm (Malmer 1986).

The relationship between this and other coenoclines described from richer sites remains unclear. This coenocline may be an independent swamp-forest (or mire) parallel to the gradient in richer, sloping forest sites on mineral soil, from 'normal', non-flushed sites to tall fern and herb sites with 'wet flushing' by ground water, i.e. with flow of ground water parallel to, or upwards in, the soil profile (Samuelsson 1917, Nordhagen 1928, Malmström 1949, Rydgren 1993, R. Økland 1997b). The observed gradient may as well represent one part of a gradient in richer sites from mires with low annual water-table amplitude to non-paludified forests on mineral soil that are only periodically saturated with water, or it may correspond to the 'mire expanse - mire margin' gradient (Sjörs 1983, Malmer 1986, R. Økland et al. 2001). The relationship with rate of decay also opens for the possibility that this coenocline is associated with variation in nutrient turnover rates and, hence, in productivity (Mörnsjö 1969, Malmer 1964, 1986). Further studies are needed to sort out patterns of variation in vegetation, environmental conditions and derived vegetation traits such as productivity, in 'rich', paludified sites (R. Økland et al. 2001).

No gradient in poor swamp forests is clearly related to water-table fluctuations and/or runs from more mire-like to more forest-like sites. Analysis of a combined data set with plots from poor swamp forests and plots from spruce forest on mineral soil (T. Økland et al. in prep.) instead reveals that the vegetation gradient in swamp forest related to depth to the water table continues into forest on mineral soil over a sharp vegetational transition (further see p. 147).

Among swamp-forest locality variation in species composition that is not correlated with explanatory variables

Plots from the same swamp-forest locality tend to be clustered together along several ordination axes, the third for the full data set (separating plots in poor as well as richer swamp-forest localities), the second for poor swamp-forests, and the third for vascular plants, that are not correlated with any measured environmental variable. There is always a risk that such coenoclines have an ecological explanation, but that this is left undetected because the relevant complex gradient is not represented by any recorded explanatory variable (R. Økland 1990a). Although existence of such complex gradients can never be ruled completely out, we consider this explanation unlikely because of the large number (53) of carefully chosen variables we have recorded.

An alternative explanation for these coenoclines is that swamp forests are geographically separated habitat islands, each with its own developmental and disturbance history, that over

thousands of years have accumulated sets of species that are sufficiently distinct to warrant recognition as independent ordination axes. This explanation is supported by: (1) the high total species richness in spruce swamp forests, with many species that only occur in one or very few swamp-forest localities; (2) the high number of alternative dominants at all positions along the two main gradients; (3) the results of a separate study of floristic relationships among plots, within and among swamp-forest localities (R. Økland et al., unpubl. results), showing that ecologically similar sites are floristically significantly more dissimilar if situated in different than if situated in the same swamp-forest locality, and (4) a parallel palaeoecological study of the studied swamp-forest localities (Korbøl 2000), in which traces of recurrent wildfires are shown to occur in a fine-grained spatial pattern and hence to give rise to invasion windows (Eriksson & Fröborg 1996) of small spatial extent and short temporal duration in this productive environment (R. Økland et al. 2000).

THE RELATIONSHIP OF SWAMP FORESTS TO MIRES AND FORESTS

The concepts of 'mire expanse' and 'mire margin', coined by Sjörs (1948), have been extensively adopted by Scandinavian mire ecologists (Malmer 1962a, Fransson 1972, Moen 1973, Sjörs 1983, R. Økland 1989a, R. Økland et al. 2001). The relationship between mire margin (in Sjörs' sense) and swamp forest has, however, remained unclear. For instance, Fremstad (1997) distinguishes two parallel series of vegetation types, a mire margin series characterized by peaty soil and a swamp forest series (in a strict sense) on 'swamp soil', with parallel vegetation types at all acidity/nutrient levels. She admits, though, that the floristic differences between the two series are indeed small. We do not find any ordination axis that corresponds to a gradient from 'mire margin' to 'swamp forest' and therefore recommend that the two-series representation of vegetation at the transition from open mire to forest on mineral soil is abandoned. The same conclusions are drawn from similar observations in corresponding vegetation in other countries [e.g. Korpela & Reinikainen (1996a) from Finland; Prieditis (1999) from Latvia]. The strong variation in dominance relationships among cryptogams, and thus in peat accumulation rates on fine spatial scales (Ohlson & R. Økland 1998) and soil type, provide additional arguments against maintenance of mire margin and swamp forest as separate site-type series. To our knowledge, the study of Jeglum (1991) from Canada is the only study in which a slight separation of plots into two series, a conifer swamp series and treed fen series, with parallel poor, intermediate and rich vegetation types, has been indicated (along the second DCA axis). This indicates that floristic variation along a gradient from 'swamp forest' via 'mire margin' (that extends further into open mire or 'mire expanse') may occasionally be possible to trace, but that this gradient is associated with too little compositional turnover, and ecologically too indistinct, to make separation of two series practically tenable. We therefore suggest that 'swamp forest' is used as a collective term for sites with trees, with a permanent water table situated close to the surface, and with soil with high organic matter content (R. Økland et al. 2001).

A widely circumscribed concept of swamp forest makes the term 'mire margin' superfluous. Another arguments for abandoning 'mire margin' and 'mire expanse' as scientific terms is the lack of any necessary relationship between 'vegetation of a mire margin type' and proximity to the border between peatland and adjacent mineral soil (Fransson 1972). This is exemplified by pine bogs, treated as 'mire margin' according to the Scandinavian tradition

(Fransson 1972) and as 'mire expanse' according to the Finnish (Korpela & Reinikainen 1996a). Pine bogs frequently occur as islands within peatland complexes, separated from the peatland matrix or the adjacent mineral soil by a wet lagg zone with vegetation of a 'mire expanse' type (Fransson 1972, R. Økland 1989b). R. Økland et al. (2001) propose the term 'open mire' as a replacement for 'mire expanse', as the latter term has failed to gain general acceptance outside Scandinavia (Wheeler & Proctor 2000).

While a broad swamp-forest concept obliterates the problem of distinguishing between swamp forest in a strict sense and 'mire margin', the problem of defining a limit along the cline from swamp forest (in the wide sense) to open mire (e.g. R. Økland 1989a, 1990b) still remains. Extensive lists of differential species for open mire against swamp forest (in a wide sense) and *vice versa* are given by Fransson (1972), Moen (1990) and Fremstad (1997). No species with preference for open mire according to these lists are found in our plots; thus the spruce swamp-forest localities we have studied all clearly belong to swamp forest.

Analysis of a combined set of vegetation data from Østmarka Nature Reserve, with plots from spruce swamp forest and spruce forest on mineral soil (T. Økland et al. in prep.; also see R. Økland et al. 2000), demonstrates that the vegetation gradient from wet to drier swamp-forest sites continues via paludified to dry spruce forest on mineral soil. T. Økland et al. (in prep.) demonstrate a relatively sharp discontinuity in species composition at the ecological limit between sites with permanent presence of a ground-water table and sites that dry up, at least occasionally [long-term observations of depths to the water table in Malmström (1931) support this interpretation ecologically]. Because the factors restricting species' distributions shift along this coenocline, from the duration of waterlogging in peatland sites (Malmer 1962a, R. Økland 1989b, 1990b) to soil moisture availability (e.g. expressed as median soil moisture) in forests on mineral soil (R. Økland & Eilertsen 1993, T. Økland 1996, Rydgren 1996), one can hardly consider this as one ecocline. T. Økland et al. (in prep.) predict that the limit at the transition from swamp forest to forest on mineral soil becomes less sharp towards more humid climates, because the demand of mire and swamp-forest species for high and constant substrate moisture is increasingly fulfilled even on shallow, inorganic soils (R. Økland & Bendiksen 1985, T. Økland 1996).

The presence of a permanent, high ground water table and (mostly) deep soil layers with a high organic matter content, at least on sites with low pH and low base cation concentrations, indicate that swamp forests have ecological affinities to mires. The coenocline related to median soil moisture in mineral soil sites is related although principally different (T. Økland et al. in prep.). Presence of a tree layer is, on the other hand, shared with forests on mineral soil although a gradient from between trees to underneath trees, which usually occurs on mineral soil with one independent component of variation and one component co-varying with the soil moisture gradient (T. Økland 1996), fails to be recognisable in swamp forests. The complex-gradient in soil acidity and nutrient concentrations has a prominent role for variation in species composition in all relevant ecosystems. We demonstrate that spruce swamp forests share with forests on mineral soil a gradient in vegetation that is related to microtopography, while no parallel to the peat productivity gradient on the open mire is present. We therefore conclude that swamp forests do not only have affinities with mires and with forests on mineral soil; they also possess strong, unique, ecological characteristics that make them merit treatment as an ecosystem type on its own.

SITE-TYPE CLASSIFICATION OF SWAMP FORESTS

The strong gradient structure of swamp forests in Østmarka Nature Reserve leaves no doubt that a gradient-based site-type classification of swamp forests is more appropriate from an ecological point of view than a hierarchical phytosociological classification. This accords with the opinions of many other authors (Tuomikoski 1942, Fransson 1972, Lahti 1995, Bridgham et al. 1996, Korpela & Reinikainen 1996a). The two main ecoclines (ecologically interpreted ordination axes) stand out as the natural fundament for such a site-type classification.

The soil acidity and nutrient gradient

Supplementing our results with information on pine-dominated swamp forests poorer in nutrients than the poor spruce-dominated swamp forests investigated by us (Fransson 1972, R. Økland 1989b, Fremstad 1997), we suggest that the gradient in soil acidity and nutrient concentrations is divided into five or six levels: (1) ombrogenous, (2) extremely poor minerogeneous, (3) moderately poor minerogeneous, (4) intermediate minerogeneous, and (5) rich minerogeneous. The rich minerogeneous level may be divided again into moderately rich and extremely rich. Our results show that levels (3)–(5) are typically encountered in spruce swamp forests in areas with weathering-resistant Precambrian bedrock.

In accordance with the discussion of the relationship between DCA-axis 1 and the soil acidity and nutrient gradient on pp. 134–139, we have used DCA-axis 1 score = 1.25 S.D. units as the limit between the (moderately) poor and the intermediate site-types, and DCA-axis 1 score = 2.50 as the limit between the intermediate and rich site-types.

A majority of species tend to have sharper distributional limits towards poorer than towards richer sites (Fransson 1972, Jeglum 1991). This is consistent with the Fennoscandian practice of dividing this coenocline by a 'lower-tolerance-limit approach', i.e. by emphasising species limits towards sites poorer in nutrients.

We suggest inclusion of intermediate fens in a wide concept of poor fens rather than in rich fens *sensu lato*, as motivated by their positive characterisation by presence of typical rich-fen species (Du Rietz 1949). Our view gains some support by soil chemical data (intermediate fens are characterised by variable but often relatively high water and peat pH but low concentrations of total N in humus) and is strongly supported by ordination results (plots with intermediate and plots with poor vegetation make up one cluster together along relevant DCA axes). Further support for this view comes from the separation of typical moderately poor fen and typical intermediate fen vegetation along axis 3 in the DCA ordination of poor fens in a wide sense (Subset A), despite this axis is only weakly and insignificantly correlated with environmental variables. This indicates that occurrence of patches with 'intermediate species composition' in a matrix of typical 'poor vegetation' is hardly predictable from the chemistry of the soil.

The water-table gradient

Our results demonstrate a gradual change in species composition along the second coenocline related to water-table depth. In mires, the corresponding gradient is usually divided into three levels, carpet, lawn and hummock (Sjörs 1948, Fransson 1972), or five levels, carpet, lower and

upper lawn, and lower and upper hummock (Malmer 1962a, R. Økland 1989a, 1990b). Each of level makes up a mire *subfeature* (R. Økland 1989b) with uniform physiognomy and site conditions (Malmer 1962a, R. Økland 1989a, 1990b). On open bogs, the subfeature levels are well characterized by differential species (Fransson 1972, R. Økland 1989a) and water-table duration properties (Malmer 1962a, R. Økland 1989a). The hydrological definitions of mire subfeatures (Malmer 1962a, R. Økland 1989a) is applied to spruce swamp forests by R. Økland et al. (2000), who perform a division into wet depressions that are periodically flooded and hence correspond to carpets and lawns (plot scores along DCA-axis 2 < 1.75 S.D. units), and drier sites (parallelling hummocks), with permanently aerated surface soil. The same criterion is used here to separate wet from dry site-types at each level along the soil acidity and nutrient gradient.

Opinions differ with respect to which transition between levels that is the most distinct or ecologically the most important: (1) between hummocks and lawns (Du Rietz 1949, Malmer 1962a, 1986, Fransson 1972), i.e. where the upper limit for periodic peat-surface inundation coincides with the lower limit for establishment and dominance of *Calluna vulgaris*, which is very sensitive to waterlogging (Bannister 1964a, Wallén 1987); (2) between high and low lawns (R. Økland 1989a); i.e. where the upper limit for inundation after moderate rainfall coincides with frequency limits for a large number of species and the shift from dominance by species with mycorrhizae (and devoid of root aerenchyma) to species devoid of mycorrhizae (but with root aerenchyma); (3) between carpets and lawns (Sjörs 1948); and (4) none; no obvious discontinuities appear along this coenocline and that the levels are difficult to characterize in terms of water-table properties (Wheeler & Shaw 1995, Wheeler 1999, Wheeler & Proctor 2000). A strong criticism against (4) is presented by R. Økland et al. (2001).

Water-table variables are more strongly correlated with a coenocline (R. Økland 1990b, Nordbakken 1996a), and species' response curves more predictable as functions of depth to the water table (compare Rydgren et al. in prep. a with R. Økland 1986b, 1989a), in open bogs and poor fens than in spruce swamp forests. This indicates that the subfeature levels are floristically less distinct in spruce swamp forests. In our opinion, this is primarily due to hydrological differences between swamp forest and open mire, such as stronger but less predictable fluctuations of the water-table throughout the year in the former, affect the predictability of species' abundances as a function of depth to the water-table. This is supported by the weekly recordings of depth to the water table made over a fifteen-year period at the beginning of the 20th century, over a range of N Swedish sites from paludified spruce forest to open mire, by Malmström (1931), and by water-table recordings over periods of years by Malmer (1962a) and Mörnsjö (1969). Our data from swamp forests in Østmarka cannot be used to evaluate this hypothesis, partly because comparable measurements in adjacent open mire sites are not available, partly because water-table data collected in the unusually wet 1998 growing season are unlikely to be representative for the investigated swamp forests or comparable with data from mires in other years. Furthermore, the difference from open mire is likely to be accentuated by properties of our swamp-forest data in two ways: (1) Variation, and spatial structure, along the gradient in swamp forest in depth to the water table occurs down to the finest scales addressed in our study (0.25 m). Plots smaller than our subplots are therefore needed if most of this variation shall be captured at between-plot scales (compare Nordbakken 1996a, 1996b). (2) Species abundances become less strongly dependent on depths to the water table along the gradient from ombrogenous, via poorer, to richer minerogenous sites, in mires as well as swamp forests. The range of habitat conditions (moderately poor and richer) included in our study therefore explains part of the difference from bogs and the poorest of fens. The first axes related to water-table depth in separate ordinations of 'poor' and 'rich' plots support existence

of such a relationship in swamp forests: the poor-subset coenocline has higher β diversity, higher eigenvalue and is more strongly correlated with water-table variables. This relationship is further accentuated by the generally sharper lower than upper limits of plants along this gradient (R. Økland 1989a) in combination with the majority of (rich-)fen plants preferring wetter sites and the majority of bog plants preferring drier sites (Malmer 1962a, Sonesson 1970a, 1970b, R. Økland 1990b). The shift from poorer to richer sites therefore implies a shift towards a species composition with a less specific response to depth to the water table. For instance, species with distinct lower limits in the hummock-to-hollow zonation because of intolerance to waterlogging, such as *Calluna vulgaris* and *Empetrum nigrum* (Bell & Tallis 1973, 1974), are restricted to ombrogenous and extremely poor minerogeous spruce swamp forests, and the abundances of the waterlogging-sensitive *Vaccinium* spp. (Metsävainio 1931) decrease from poorer to richer swamp forests.

The more frequent occurrence of extensive, hydromorphologically uniform, drier areas in swamp forests than on open mires, makes the mire terms hummock, lawn and carpet which pertain to the varied mesotopography of the mire surface, less well suited for swamp forests (including pine bogs) than for open mires. We therefore provisionally suggest that the gradient in depth to the water table in swamp forests is divided into two levels: (1) wet depressions and (2) drier sites. These are, by intention, parallels to the terms hollows and hummocks in bogs and flarks and hummocks in fens used, among others, by Sjörs (1948) and R. Økland (1989b).

Because the wet depression level hardly occurs in ombrogenous and extremely poor minerogeous swamp forests (Sjörs 1948, Malmer 1972, Fransson 1972, R. Økland 1989a), a gradient reference frame (R. Økland & Bendiksen 1985) with eight realised types seems adequate for variation in swamp forests (R. Økland et al. 2000): three for wet depressions and five for drier sites along the gradient in soil acidity and nutrient concentrations. Descriptions of the six site-types encountered in the study area are provided on pp. 152–175.

CONSERVATION OF SPRUCE SWAMP FORESTS - BIODIVERSITY HOTSPOTS IN THE BOREAL CONIFEROUS FOREST LANDSCAPE

The lack of any relationship between the number of 1-m² plots in a swamp-forest locality and the total number of species recorded in these plots indicate (1) that the plots capture a representative fraction of the species composition at each swamp-forest locality; (2) that this captured fraction is comparable among localities; and (3) that species richness at the scale of swamp-forest localities is not primarily determined by locality size.

The investigated spruce swamp forests have high local species richness compared to the surrounding spruce forests on mineral soil (T. Økland 1990, 1996, 1999; Rydgren 1996, Rydgren et al. 1998; T. Økland et al. in prep.). This also accords with the results of studies from Sweden (Ohlson et al. 1997, Hörnberg et al. 1998) and Finland (Korpela & Reinikainen 1996a), showing that swamp forests have very high species richness compared to other coniferous forest types, thus being biodiversity hotspots (Reid 1998) in the boreal forest landscape. Our study points to variation along several important environmental complex-gradients as one important reason for the high plant species richness of swamp forests (Paratley & Fahey 1986, Kenkel 1987, Vitt et al. 1995, Korpela & Reinikainen 1996a, Anderson & Davis 1997, Hörnberg et al. 1998), but also opens for high importance of the history of each swamp-forest site, more or less independent of

present-day environmental conditions (R. Økland et al. in prep.).

The floristic uniqueness of richer swamp-forests, apparently without relationship with present-day ecological conditions (R. Økland et al. in prep.), offers a special challenge to conservation swamp-forest biodiversity because a significant number of species must be expected to be absent from any set of swamp-forest reserves selected to represent the natural ecological variation. Given the low areal importance of intact, richer swamp forests, an aim of maintaining the biological diversity of (coniferous) forests in general, and swamp forests in particular, implies that all intact swamp forests with vegetation of a 'rich type' should be protected against drainage and other irreversible impacts (Korpela & Reinikainen 1996a). Swamp-forest localities poor in nutrients may also be species rich by local standards, and thus important for maintenance of a high species diversity at finer landscape scales (Sjöberg & Ericson 1997).

DESCRIPTION OF SITE TYPES

INTRODUCTION

The six site types make up a reticulate classification of the variation in spruce-dominated swamp forests, representing a tripartition of the gradient in soil acidity and nutrient status and a bipartition of the water-table gradient. Tab. 16 provides a survey of the vegetation of the site types, in which groups of differential species are indicated. The standardised descriptions of the site types are based upon material from the investigation area only. Comparisons with other authors are restricted to Kielland-Lund (1981) and Fremstad (1997).

THE WET, (MODERATELY) POOR (PW) SITE TYPE

Species composition. The floristic composition of the PW site type is shown in Tab. 17. The only constant species (occurring in $\geq 80\%$ of the plots) were *Menyanthes trifoliata* in the field layer and *Sphagnum angustifolium* and *S. centrale* in the bottom layer. Frequent species (occurring in 60–80% of the plots) were *Trientalis europaea*, *Calamagrostis purpurea*, *Carex echinata*, *C. rostrata*, *Straminergon stramineum*, *Sphagnum brevifolium*, *S. girgensohnii*, *S. riparium*, and *S. teres*. The most important species in the field layer, with locally high subplot frequency, were *Menyanthes trifoliata*, *Potentilla palustris*, *Carex canescens*, *C. nigra* and *C. rostrata*. Local dominants in the bottom layer were *Sphagnum angustifolium*, *S. centrale*, *S. brevifolium*, *S. girgensohnii* and *S. riparium*. *Straminergon stramineum* had locally high subplot frequency. All other bryophyte species were quantitatively unimportant.

The number of species per plot varied from 11 to 31, with a median of 19. The number of vascular plant species was (6–)10(–16), and the number of cryptogamic species was (5–)9(–17).

Physiognomy. A tree layer was most often lacking. The field layer was open, mostly without dominants, typically with herbs and graminoids as the most prominent species groups. Ericaceous species were quantitatively unimportant. Most often, the bottom layer consisted of a more or less continuous *Sphagnum* carpet that occasionally was dominated by a single species (e.g. *Sphagnum riparium*; plot 132). In most cases, however, a patchy mosaic with changing dominance relationships was observed. The *Sphagnum* carpet was often devoid of moss and hepatic species (other than *Straminergon stramineum*). Mud-bottom patches and water-filled hollows occurred locally.

Occurrence. The PW site type typically covered extensive areas in the central, low-lying water-tracks of larger swamp forests, with increasing areal cover towards the outlet (e.g. swamp-forest locality 11). This site-type also occurred in peripheral parts of swamp forests fed by seepage water from the adjacent mineral soil (localities 2 and 8). A mosaic of the PW and the PD site types was often observed.

Soil type. A peat soil profile typically occurred; occasionally with transitions to swamp soil.

Environment. Median depth to the water table = (4–)9(–20) cm; the bottom-layer level

was typically flooded after snow melt and after long, wet periods.

The organic content of the soil was high; loss on ignition = (84-)91(-96) %.

The topsoil was (moderately) acid, $\text{pH}_{\text{H}_2\text{O}} = (4.3-)4.9(-5.3)$.

The soil was poor in nitrogen [(1.1-)1.9(-3.1) % of organic matter].

Variation. Tab. 17 demonstrates considerable variation in field-layer composition of which some was related to wetness: plot 90, dominated by *Molinia caerulea* and with a prominent element of *Vaccinium* spp., represented the dry, while plot 38, with a very sparse field layer, represented the wet end of the range spanned by the plots. Plot 18, situated near the outlet of swamp-forest locality 2, had a sparse bottom layer.

Many local dominance variants occur, e.g.: plots 90-96, with prominence of *Molinia caerulea* and/or *Phragmites communis*; plot 22, with high importance of *Polytrichum commune* but otherwise typical of the PD site type; and plot 23 with high importance of *Aulacomnium palustre*. Plot 28 contained several species typical of the PD site type because it comprises a broad range of depths to the water-table.

Comments. (1) *Sphagnum teres* and *S. warnstorffii*, species typical for intermediate and rich swamp forests (Tab. 16), regularly occurred among species typical of poor sites in plots from several swamp-forest localities that were classified to the PW site type (see Tab. 17: e.g. plots 22, 23, 28, 36, 37 and 130). These plots had topsoil pH below 5.0 and thus represented typical poor sites. This indicates that the two *Sphagnum* species have a broader tolerance towards poorer sites in the study area than previously assumed (Fransson 1972, Fremstad 1997). Plots 21, 115, 128 and 129, in which one or a few of the species *Carex flava*, *Filipendula ulmaria*, *Galium palustre*, *Pyrola minor*, *Valeriana sambucifolia*, *Calliergon cordifolium*, *Pseudobryum cinclidioides* and *Rhizomnium pseudopunctatum* occurred sparsely, had topsoil $\text{pH} \geq 5.0$ and formed a transition to the intermediate wet (IW) site type.

(2) This study documents that the main habitat niche of the less well known species *Sphagnum brevifolium* (Flatberg 1993) is poor, *Sphagnum*-dominated carpets in swamp forests, situated close to the median water table.

Corresponding site types: Kielland-Lund (1981): Chamaemoro-Piceetum, typical subassociation, p.p. Fremstad (1997): K1a Forest- or shrub-dominated poor fen, forest fen variant, p.p. E1a Poor swamp forest, typical variant, p.p.

THE DRY, (MODERATELY) POOR (PD) SITE TYPE

Species composition. The floristic composition of the PD site type is shown in Tab. 18. Constant species were *Vaccinium myrtillus*, *V. vitis-idaea* and *Maianthemum bifolium* in the field layer and *Sphagnum angustifolium* and *S. girgensohnii* in the bottom layer. The only additional frequent species was *Sphagnum centrale*. Local dominants, occasionally with high subplot frequency, were *Rubus chamaemorus* in the field layer, and *Sphagnum angustifolium*, *S. girgensohnii*, *Polytrichum commune*, *Sphagnum centrale*, *S. magellanicum* and *S. russowii* in the bottom layer. *Straminergon stramineum* and *Aulacomnium palustre* also reached locally high subplot frequency in the bottom layer.

The number of species per plot varied from 8 to 34, with a median of 15. The number of vascular plant species was (1-)8(-19), and the number of cryptogamic species was (4-)8(-20).

Physiognomy. A tree layer was most often present, dominated by *Picea abies* and with

Tab. 16. Species constancy (frequency in 1-m² plots) and mean subplot frequency (given as exponent) in each of the six site types. Abbreviations: PW – wet, poor; PD – dry, poor, IW – wet, intermediately rich; ID – dry, intermediately rich; RW – wet, rich; RD – dry, rich). Species are ordered primarily to reflect preference for types along the soil acidity and nutrient gradient, secondarily to reflect preference for wet vs dry site types. Species occurring in few plots or with inconsistent pattern of distribution on site types are listed at the bottom of the table.

Site type	PW	PD	IW	ID	RW	RD
Number of plots	20	27	20	31	24	28
<i>Sphagnum brevifolium</i>	60 ¹⁴	7 ⁶	5 ²	3 ⁴	-	-
<i>Sphagnum riparium</i>	65 ¹⁰	11 ¹⁰	5 ¹¹	-	-	-
<i>Vaccinium oxycoccus</i>	20 ⁹	11 ¹⁰	5 ³	-	-	-
<i>Sphagnum magellanicum</i>	5 ¹⁶	19 ¹¹	-	3 ¹	-	-
<i>Menyanthes trifoliata</i>	95 ¹⁰	22 ⁹	80 ¹⁰	12 ⁵	-	-
<i>Carex lasiocarpa</i>	15 ⁷	4 ⁵	5 ¹⁴	-	-	-
<i>Carex nigra</i>	25 ¹²	-	5 ⁴	3 ⁹	-	-
<i>Eriophorum angustifolium</i>	20 ⁹	4 ⁹	20 ¹¹	3 ¹⁵	-	-
<i>Carex rostrata</i>	60 ¹¹	15 ⁷	10 ¹⁰	6 ⁴	4 ²	-
<i>Phragmites australis</i>	15 ¹³	7 ⁸	20 ¹⁰	3 ³	-	-
<i>Molinia caerulea</i>	15 ¹⁶	4 ¹	5 ¹⁵	-	-	-
<i>Eriophorum vaginatum</i>	15 ¹²	11 ¹¹	20 ⁷	3 ⁹	-	-
<i>Dactylorhiza maculata</i>	5 ¹	7 ²	10 ¹	-	-	-
<i>Frangula alnus</i>	5 ⁸	4 ¹	5 ¹	6 ⁵	-	-
<i>Sphagnum angustifolium</i>	95 ¹⁴	96 ¹⁴	50 ⁸	77 ¹¹	-	-
<i>Pohlia nutans</i>	5 ¹	-	-	13 ²	-	-
<i>Aulacomnium palustre</i>	25 ⁷	30 ⁹	5 ¹	32 ⁴	8 ²	-
<i>Melampyrum pratense</i>	5 ¹	15 ³	-	3 ⁶	-	-
<i>Polytrichum commune</i>	25 ⁹	59 ¹¹	-	39 ¹²	-	-
<i>Vaccinium vitis-idaea</i>	25 ⁴	81 ¹⁰	65 ⁵	87 ⁹	4 ²	29 ³
<i>Deschampsia flexuosa</i>	-	33 ⁷	20 ⁵	29 ⁸	-	4 ⁷
<i>Cephalozia pleniceps</i>	10 ⁵	33 ⁷	5 ¹	10 ²	4 ¹	-
<i>Rubus chamaemorus</i>	20 ⁷	59 ⁸	5 ⁹	26 ⁸	-	-
<i>Sphagnum russowii</i>	-	33 ¹²	5 ⁶	13 ⁶	-	7 ²
<i>Cephalozia lunulifolia</i>	5 ³	19 ¹	5 ²	23 ²	4 ³	7 ²
<i>Potentilla palustris</i>	50 ⁶	15 ³	80 ¹⁰	13 ⁴	8 ⁵	-
<i>Viola palustris</i>	45 ⁹	11 ²	65 ⁹	13 ³	75 ¹⁰	11 ⁵
<i>Carex canescens</i>	55 ¹¹	30 ⁵	80 ¹¹	23 ⁶	75 ⁷	14 ⁴
<i>Carex echinata</i>	60 ⁷	33 ⁶	65 ⁹	10 ⁶	42 ⁷	11 ⁴
<i>Sphagnum squarrosum</i>	30 ⁸	11 ⁶	80 ¹²	39 ⁷	88 ¹¹	50 ⁷
<i>Straminergon stramineum</i>	75 ¹²	59 ¹⁰	70 ⁷	45 ⁶	17 ³	4 ²
<i>Sphagnum centrale</i>	100 ¹³	74 ¹¹	55 ¹⁴	11 ⁹	33 ⁶	14 ⁹
<i>Calamagrostis purpurea</i>	65 ⁵	44 ¹⁰	60 ⁷	55 ⁹	58 ¹⁰	32 ⁸
<i>Betula</i> spp.	20 ²	15 ²	15 ¹	16 ⁴	8 ¹	4 ¹
<i>Trientalis europaea</i>	75 ⁵	48 ⁶	60 ⁵	77 ⁶	79 ⁵	54 ⁴
<i>Sanionia uncinata</i>	10 ²	4 ¹	20 ¹	13 ²	21 ⁴	32 ⁵
<i>Picea abies</i>	45 ³	48 ⁴	40 ⁵	58 ⁴	58 ³	71 ⁵
<i>Lycopodium annotinum</i>	30 ⁷	33 ⁶	10 ²	29 ⁹	17 ⁵	14 ⁹
<i>Calypogeia muelleriana</i>	25 ⁴	44 ⁶	35 ⁴	52 ⁶	63 ⁵	57 ⁶
<i>Linnaea borealis</i>	-	11 ³	15 ²	19 ⁵	13 ¹	14 ³
<i>Sphagnum girgensohnii</i>	60 ¹¹	89 ¹⁵	5 ¹⁰	94 ¹³	21 ¹⁰	21 ⁸
<i>Orthilia secunda</i>	-	4 ³	-	6 ⁶	4 ¹	4 ⁴
<i>Maianthemum bifolium</i>	55 ⁵	81 ⁷	55 ⁸	94 ⁹	63 ⁴	71 ⁵
<i>Barbilophozia attenuata</i>	5 ¹	4 ¹	5 ³	19 ³	-	11 ²

Tab. 16 (continued).

Site type	PW	PD	IW	ID	RW	RD
Number of plots	20	27	20	31	24	28
<i>Cephalozia bicuspidata</i>	15 ²	15 ²	20 ²	39 ⁵	29 ⁴	75 ⁷
<i>Vaccinium myrtillus</i>	45 ⁵	85 ¹³	45 ⁴	94 ¹²	17 ²	57 ⁸
<i>Chiloscyphus profundus</i>	5 ¹	15 ⁷	-	23 ³	29 ⁶	50 ⁶
<i>Dicranum majus</i>	15 ³	52 ⁴	35 ²	84 ⁹	38 ²	89 ⁹
<i>Pleurozium schreberi</i>	15 ¹	33 ³	30 ³	84 ⁸	8 ²	46 ⁴
<i>Dicranum scoparium</i>	5 ¹	19 ²	20 ¹	58 ⁵	13 ³	61 ⁴
<i>Lepidozia reptans</i>	5 ¹	4 ⁴	-	29 ³	4 ²	50 ³
<i>Dicranum fuscescens</i>	10 ²	19 ²	-	32 ⁴	4 ¹	25 ³
<i>Sorbus aucuparia</i>	-	11 ²	-	23 ³	13 ²	43 ³
<i>Plagiothecium laetum</i>	5 ¹	41 ⁴	10 ¹	68 ⁶	8 ²	64 ⁴
<i>Calypogeia neesiana</i>	5 ²	11 ²	-	19 ³	-	11 ²
<i>Calypogeia integristipula</i>	5 ¹	30 ³	5 ²	61 ⁵	4 ¹	32 ⁵
<i>Ptilidium pulcherrimum</i>	-	4 ¹	-	13 ²	-	4 ²
<i>Riccardia latifrons</i>	-	4 ¹	-	3 ²	4 ³	11 ²
<i>Equisetum fluviatile</i>	10 ³	-	35 ³	-	-	-
<i>Warnstorfia exannulata</i> agg.	15 ²	-	20 ⁴	-	8 ³	-
<i>Sphagnum subsecundum</i>	-	-	5 ¹⁵	-	17 ¹⁰	-
<i>Scapania irrigua</i>	-	-	15 ¹	-	13 ⁴	-
<i>Carex flava</i>	5 ¹	-	15 ⁹	-	33 ⁴	4 ²
<i>Lysimachia thyrsiflora</i>	-	-	20 ¹⁰	3 ²	13 ⁶	-
<i>Pseudobryum cinclidioides</i>	15 ⁶	4 ²	20 ⁴	6 ⁸	33 ³	-
<i>Sphagnum teres</i>	70 ¹⁰	11 ⁷	100 ¹⁴	13 ⁹	42 ⁹	10 ⁴
<i>Caltha palustris</i>	5 ⁸	-	25 ⁸	-	71 ⁷	29 ⁴
<i>Galium palustre</i>	10 ⁸	-	70 ⁸	-	42 ⁸	29 ²
<i>Calliargon cordifolium</i>	10 ⁷	-	20 ⁵	3 ¹	46 ⁵	14 ⁵
<i>Agrostis canina</i>	10 ⁴	4 ²	35 ¹⁰	-	70 ¹³	25 ⁶
<i>Sphagnum warnstorffii</i>	50 ⁸	7 ³	95 ¹³	16 ⁶	83 ⁸	32 ⁷
<i>Filipendula ulmaria</i>	5 ³	-	40 ⁵	3 ⁶	92 ⁹	64 ⁷
<i>Aneura pinguis</i>	5 ⁷	-	10 ⁵	-	8 ⁶	18 ³
<i>Rubus saxatilis</i>	5 ³	-	15 ²	10 ³	29 ²	46 ⁶
<i>Deschampsia cespitosa</i>	-	-	10 ⁶	16 ⁵	46 ⁹	39 ⁵
<i>Anemone nemorosa</i>	5 ²	-	5 ⁴	10 ⁵	75 ⁴	79 ⁹
<i>Hylocomium splendens</i>	10 ¹	11 ³	35 ⁴	61 ⁷	38 ⁵	29 ⁸
<i>Rhytidiadelphus squarrosus</i> agg.	5 ¹	11 ¹	10 ²	19 ³	83 ⁹	82 ¹¹
<i>Equisetum sylvaticum</i>	-	4 ¹³	20 ⁵	45 ⁷	63 ⁸	57 ⁷
<i>Rhytidiadelphus triquetrus</i>	5 ¹	7 ²	25 ²	23 ⁶	33 ⁷	50 ⁸
<i>Lophozia ventricosa</i> agg.	-	-	5 ⁴	16 ³	17 ¹	18 ³
<i>Oxalis acetosella</i>	-	-	5 ²	16 ³	88 ⁶	93 ¹⁰
<i>Phegopteris connectilis</i>	-	-	15 ⁴	23 ⁷	75 ⁷	82 ¹²
<i>Calypogeia azurea</i>	-	-	-	6 ²	21 ²	25 ³
<i>Melampyrum sylvaticum</i>	-	-	-	10 ⁶	25 ²	36 ⁶
<i>Hylocomiastrum umbratum</i>	10 ³	22 ⁴	25 ³	52 ⁶	46 ⁵	79 ¹⁰
<i>Blepharostoma trichophyllum</i>	-	4 ¹	5 ¹	10 ¹	13 ²	50 ²
<i>Athyrium filix-femina</i>	-	-	-	10 ⁴	21 ⁷	43 ⁷
<i>Gymnocarpium dryopteris</i>	-	-	-	23 ³	29 ⁵	57 ⁷
<i>Dryopteris expansa</i> agg.	-	7 ¹	5 ¹	32 ⁴	21 ³	43 ⁶
<i>Polytrichum formosum</i>	-	4 ²	5 ¹	16 ⁴	8 ⁴	32 ⁴
<i>Calamagrostis arundinacea</i>	-	-	-	3 ⁴	8 ²	25 ⁴
<i>Plagiochila asplenioides</i>	-	-	5 ²	35 ⁵	38 ⁴	86 ¹⁰
<i>Brachythecium starkei</i>	-	-	-	10 ²	4 ¹	18 ¹
<i>Brachythecium reflexum</i>	-	15 ³	-	23 ⁵	4 ¹	43 ⁵
<i>Tetraphis pellucida</i>	-	11 ²	-	55 ⁴	4 ¹	43 ⁵

Tab. 16 (continued).

Site type	PW	PD	IW	ID	RW	RD
Number of plots	20	27	20	31	24	28
<i>Rhizomnium magnifolium</i>	-	-	5 ¹	6 ²	54 ⁵	-
<i>Glyceria fluitans</i>	5 ¹	-	5 ³	3 ¹	50 ⁸	7 ⁵
<i>Cirsium helenioides</i>	-	-	-	-	17 ¹³	-
<i>Carex pallescens</i>	-	-	-	-	21 ³	4 ³
<i>Bryum pseudotriquetrum</i>	-	-	5 ¹	-	58 ⁸	14 ⁴
<i>Epilobium palustre</i>	-	-	-	-	21 ⁷	7 ²
<i>Carex loliacea</i>	-	-	-	-	21 ⁵	7 ²
<i>Riccardia multifida</i>	-	-	-	-	21 ⁸	7 ⁷
<i>Agrostis capillaris</i>	-	-	5 ⁵	-	33 ⁵	11 ⁷
<i>Harpanthus flotovianus</i>	-	-	5 ³	-	33 ⁵	11 ¹
<i>Plagiomnium medium</i>	-	-	5 ³	-	42 ¹⁰	21 ⁹
<i>Plagiothecium nemorale</i>	-	-	-	-	13 ¹	7 ⁷
<i>Pellia spp.</i>	-	-	-	-	75 ¹⁴	43 ⁸
<i>Crepis paludosa</i>	-	-	5 ⁸	-	58 ⁹	36 ⁷
<i>Plagiomnium elatum</i>	-	-	5 ⁸	-	42 ⁶	25 ⁴
<i>Brachythecium rutabulum</i> agg.	-	-	5 ²	-	38 ¹⁰	25 ⁹
<i>Calliergonella cuspidata</i>	-	-	10 ²	-	33 ¹⁰	25 ⁵
<i>Campylium stellatum</i>	-	-	-	-	25 ¹²	18 ⁶
<i>Brachythecium salebrosum</i>	-	-	-	-	29 ²	25 ³
<i>Cardamine pratensis</i>	-	-	-	-	8 ⁹	7 ³
<i>Chiloscyphus polyanthos</i>	5 ²	-	15 ²	3 ¹	75 ⁶	68 ⁶
<i>Rhizomnium pseudopunctatum</i>	5 ²	-	10 ²	6 ¹	33 ⁶	29 ²
<i>Valeriana sambucifolia</i>	5 ⁶	-	5 ⁵	-	25 ⁸	25 ⁹
<i>Geranium sylvaticum</i>	-	-	-	-	4 ²	4 ³
<i>Tussilago farfara</i>	-	-	-	-	17 ⁶	18 ⁶
<i>Plagiomnium ellipticum</i>	-	-	-	-	13 ³	14 ²
<i>Alnus incana</i>	-	-	5 ¹	-	21 ³	25 ⁵
<i>Rhizomnium punctatum</i>	-	-	5 ³	3 ¹	67 ³	75 ⁷
<i>Equisetum pratense</i>	-	-	-	-	8 ⁴	11 ³
<i>Fissidens adianthoides</i>	-	-	-	-	8 ⁶	11 ¹
<i>Luzula pilosa</i>	-	-	-	-	13 ³	18 ³
<i>Ranunculus repens</i>	-	-	-	-	17 ¹³	29 ¹¹
<i>Matteuccia struthiopteris</i>	-	-	-	-	8 ⁹	14 ¹¹
<i>Paris quadrifolia</i>	-	-	-	-	8 ⁴	14 ³
<i>Chrysoplenium alternifolium</i>	-	-	-	-	8 ¹⁴	14 ⁵
<i>Hieracium</i> sp.	-	-	-	-	4 ³	7 ⁴
<i>Plagiothecium denticulatum</i>	-	4 ¹	5 ⁴	10 ¹	38 ³	75 ⁵
<i>Rhodobryum roseum</i>	-	-	-	3 ⁴	8 ¹	21 ⁴
<i>Carex digitata</i>	-	-	-	-	4 ¹	11 ²
<i>Atrichum undulatum</i>	-	-	-	-	8 ¹	25 ⁶
<i>Thuidium tamariscinum</i>	-	-	-	-	8 ¹³	25 ¹³
<i>Geum rivale</i>	-	-	-	-	4 ²	14 ⁷
<i>Viola riviniana</i>	-	-	-	-	4 ²	18 ⁴
<i>Jungermannia leiantha</i>	-	-	-	-	4 ²	25 ³
<i>Circaea alpina</i>	-	-	-	-	-	25 ⁷
<i>Plagiomnium affine</i>	-	-	-	-	-	29 ⁹
<i>Cirriphyllum piliferum</i>	-	-	-	-	-	50 ⁵

Tab. 16 (continued).

Additional species:

Acer platanoides RD 4¹; *Alnus glutinosa* IW 5², RD 7¹; *Pinus sylvestris* PD 4¹; *Salix aurita* PW 10⁵, IW 5²; *Salix aurita* × *caprea* IW 5²; *Salix caprea* PW 5¹, RW 4⁴; *Salix myrsinifolia* IW 5⁴; *Viburnum opulus* RD 4⁷.

Calluna vulgaris PD 4¹; *Empetrum nigrum* PD 7⁸.

Alchemilla sp. RD 4²; *Bistorta vivipara* RW 4⁵; *Cirsium palustre* RW 4³; *Corallorhiza trifida* PW 10²; *Dactylorhiza fuchsii* RW 8¹; *Drosera rotundifolia* PW 5⁷, PD 4¹; *Fragaria vesca* RD 4⁸; *Listera cordata* ID 6², RD 4¹; *Mycelis muralis* RD 11⁸; *Polygonatum verticillatum* RD 4¹; *Pteridium aquilinum* ID 3²; *Prunella vulgaris* RD 11⁸; *Pyrola minor* PW 15², IW 20⁶, RD 4¹; *Solidago virgaurea* RD 7⁵.

Anthoxanthum odoratum RD 4¹; *Carex canescens* × *loliacea* IW 5¹⁶, RW 4³; *Carex chordorrhiza* PW 5¹², IW 10¹⁵, ID 3⁴; *Carex panicea* PW 5¹⁵; *Carex pauciflora* PW 5¹, PD 4¹; *Carex paupercula* IW 10⁶; *Festuca altissima* RD 4²; *Festuca rubra* RW 4¹; *Melica nutans* 11⁴; *Phragmites australis* PW 15¹³, PD 7⁸, IW 20¹⁰, ID 3³.

Brachythecium populeum RD 4⁵; *Calliergon richardsonii* IW 15², RW 4¹; *Climacium dendroides* RW 4⁷, RD 3¹; *Dicranum montanum* PD 4¹, ID 3¹; *Herzogiella striatella* RD 7¹; *Hypnum cupressiforme* RW 4¹; *Philonotis fontana* RW 4³; *Plagiomnium undulatum* RW 4¹²; *Plagiothecium undulatum* PD 4¹, ID 3²; *Polytrichum strictum* PD 4²; *Pseudotaxiphyllum elegans* RD 4¹; *Ptilium crista-castrensis* ID 6⁵, RW 4¹, RD 4¹; *Rhytidiadelphus loreus* PD 4¹; *Scorpidium revolvens* 4⁷; *Warnstorfia fluitans* PW 5¹.

Sphagnum flexuosum IW 5¹⁶; *Sphagnum quinquefarium* PD 4⁸, ID 3¹⁰, RW 4¹.

Barbilophozia kunzeana IW 5²; *Barbilophozia lycopodioides* RD 4¹; *Cephalozia* spp. PD 4¹, RW 4¹; *Diplophyllum albicans* RW 4¹, RD 4¹; *Lophozia incisa* RW 4¹, RD 4³; *Lophozia longidens* ID 3⁷; *Lophozia obtusa* ID 3¹, RD 4²; *Mytilia taylorii* 11¹; *Ptilidium ciliare* ID 3³, RD 4¹; *Scapania paludosa* RW 4¹; *Scapania scandica* RW 4²; *Scapania umbrosa* RW 4¹; *Scapania undulata* IW 5¹, RW 13²; *Cladonia cenotea* ID 3¹; *Cladonia chlorophaea* agg. ID 13³; *Cladonia coniocraea* ID 13²; *Cladonia digitata* ID 6²; *Cladonia rangiferina* ID 3⁴; *Cladonia squamosa* ID 3³.

Betula spp. as a prominent element. The field layer varied from open and species-deficient (plots 15 and 17) to, more typically, dense and dominated by *Vaccinium myrtillus*, with or without co-dominance of *Vaccinium vitis-idaea* and/or *Empetrum nigrum*. Herbs and graminoids were locally important. The bottom layer consisted of a more or less continuous bryophyte carpet, dominated by *Sphagnum* spp. and often with *Polytrichum commune* as a prominent element. Patches covered by litter or naked peat were observed in some places.

Occurrence. The PD site type covered extensive areas in swamp forests, most typically where the ground-water table was level or almost level, and shelter from direct influence of seepage water was present (e.g. the northern part of swamp-forest locality 1, the central-western part of swamp-forest 2, the central-eastern part of swamp-forest 8 and the central and southern parts of swamp-forest locality 11; see Fig. 2). Such sites were characterised by a more or less planar bottom-layer surface, above which some distinct hummocks might rise. The surface typically became more undulating towards the border onto mineral soil. The PD site type also occurred as distinct, often high, domed, hummock islands in a matrix of the PW site type (swamp-forest localities 2, 4, 11).

Soil type. A peat soil profile, often strongly humified, typically occurred.

Environment. Median depth to the water table = (10–)16(–30) cm; the bottom layer was not flooded.

The organic content of soil was invariably high; loss on ignition = (93–)96(–98) %.

The topsoil was (moderately) acid, pH_{H₂O} = (3.9–)4.4(–5.2).

The soil was poor in nitrogen [(0.8–)1.5(–2.4) % of organic matter].

Variation. The vegetation of level segments and elevated hummocks differed in several respects. The bottom layer of the former was usually poorer in species, with dominance of *Sphagnum angustifolium*, *S. girgensohnii* and *Polytrichum commune*, while in the latter *Sphagnum centrale* (and *S. magellanicum*) played important parts and the number of bryophyte species was higher due to a prominent element of forest-floor bryophytes like *Dicranum majus*, *Plagiothecium laetum*, *Pleurozium schreberi*, *Calypogeia* and *Cephalozia* spp. (see Tab. 18). This

Tab. 17 (continued).

Additional species (occurring in one plot only):

Frangula alnus 37:8; *Salix caprea* 115:7.

Anemone nemorosa 129:2; *Caltha palustris* 129:8; *Dactylorhiza maculata* 29:1; *Drosera rotundifolia* 93:7; *Filipendula ulmaria* 115:3; *Melampyrum pratense* 129:1; *Rubus saxatilis* 90:3; *Valeriana sambucifolia* 115:6.

Carex chordorrhiza 115:12; *Carex flava* 21:1; *Carex panicea* 93:15; *Carex pauciflora* 28:1; *Glyceria fluitans* 38:1.

Dicranum scoparium 96:1; *Plagiothecium laetum* 90:1; *Pohlia nutans* 96:1; *Rhizomnium pseudopunctatum* 115:2; *Rhytidadelphus squarrosus* agg. 96:1; *Rhytidadelphus triquetrus* 124:1; *Warnstorfia fluitans* 36:1.

Sphagnum magellanicum 36:16.

Aneura pinguis 93:7; *Barbilophozia attenuata* 115:1; *Calyptogeia integrispula* 38:1; *Calyptogeia neesiana* 28:2; *Cephalozia lunulifolia* 23:3; *Chiloscyphus polyanthos* 21:2; *Chiloscyphus profundus* 91:1; *Lepidozia reptans* 38:1.

variation was not clearly related to depth to the water table at the scale of 1-m² plots. Wetness was, however, reflected in variation in species composition from plots with *Menyanthes trifoliata*, *Carex rostrata* and *Sphagnum riparium* situated close to the median water table (e.g. 33, 35 and 135), to the bryophyte-rich plot 142 situated on a tall hummock.

“Pocket sites” (e.g. small vertical walls, cracks in the peat surface, cavities underneath tree roots and adjacent to tree boles) occurred more frequently towards higher hummocks and were associated with high bryophyte species richness (e.g. plots 32, 33, 99 and 140). Apart from the occurrence of species typical of richer site types in the maximum-pH plot 122 (see Tab. 18), variation related to soil acidity and nutrient status was not observed.

Comments. (1) There were very few occurrences in plots classified to the PD site-type of species typical of forest sites characterised as ‘slightly rich’ by R. Økland & Eilertsen (1993) and as low-fern spruce forest (Eu-Piceetum dryopteridetosum) by Kielland-Lund (1981). The soil acidity and nutrient status of PD plots therefore corresponds to that of the poor series of forest site types of R. Økland & Eilertsen (1993).

Corresponding site types: Kielland-Lund (1981): Chamaemoro-Piceetum, typical subassociation, p.p. Fremstad (1997): K1a Forest- or shrub-dominated poor fen, forest fen variant, p.p.; K1b *Carex globularis*-variety. E1a Poor swamp forest, typical variant, p.p.

THE WET, INTERMEDIATELY RICH (IW) SITE TYPE

Species composition. The floristic composition of the IW site type is shown in Tab. 19. Constant species were *Menyanthes trifoliata*, *Potentilla palustris* and *Carex canescens* in the field layer and *Sphagnum squarrosum*, *S. teres* and *S. warnstorffii* in the bottom layer. Frequent species were *Vaccinium vitis-idaea*, *Galium palustre*, *Trientalis europaea*, *Viola palustris*, *Calamagrostis purpurea* and *Carex echinata* in the field layer and *Straminergon stramineum* and *Sphagnum centrale* in the bottom layer. The frequent and constant species were the most important species in the respective layers, except for locally high abundance also of *Lysimachia thyrsiflora*, *Agrostis canina*, *Carex chordorrhiza*, *Eriophorum angustifolium* and *Phragmites australis*. *Sphagnum flexuosum* dominated the bottom layer of plot 81.

The number of species per plot varied from 8 to 40, with a median of 23. The number of vascular plant species was (3–)9(–17), and the number of cryptogamic species was (3–)16(–29).

Physiognomy. A tree layer was most often lacking. The field layer was sometimes open (plots 7, 120), although typically dominated by a multi-species mixture of herbs and/or graminoids. Examples of herb-rich plots are 89 and 117, of plots rich in graminoids 5, 100 and

Tab. 18. Species composition of plots classified to the dry, (moderately) poor (PD) site type. Species abundance is given as frequency in subplots. Constancy and mean frequency is given (as exponent) in column to the right.

Plot	12	13	14	15	17	19	20	27	30	32	33	34	35	49	56	94	97	98	99	122	135	139	140	142	143	147	149		
<i>Betula</i> spp.	2	2	.	.	2	1	15 ²
<i>Picea abies</i>	.	.	1	.	.	.	7	.	.	4	.	.	.	1	.	6	.	1	5	2	7	.	4	3	3	3	.	48 ⁴	
<i>Sorbus aucuparia</i>	1	.	.	4	1	.	.	.	11 ²	
<i>Vaccinium myrtillus</i>	16	10	3	.	.	16	14	13	16	11	11	16	8	2	16	9	10	15	16	.	12	15	16	16	16	16	.	85 ¹³	
<i>Vaccinium oxycoccus</i>	15	8	6	11 ¹⁰	
<i>Vaccinium vitis-idaea</i>	6	6	1	.	.	14	9	15	11	9	5	12	.	.	1	11	16	13	16	8	10	12	16	13	9	11	.	81 ¹⁰	
<i>Linnaea borealis</i>	7	1	1	11 ³	
<i>Lycopodium annotinum</i>	.	.	.	7	.	2	16	.	.	14	2	2	9	.	.	1	.	.	.	1	.	33 ⁶	
<i>Maianthemum bifolium</i>	7	8	5	8	.	7	12	4	9	8	6	1	7	3	3	13	14	6	14	2	.	.	2	.	4	8	.	81 ⁷	
<i>Melampyrum pratense</i>	2	2	.	3	3	15 ³	
<i>Menyanthes trifoliata</i>	9	.	11	11	.	2	8	10	22 ⁹	
<i>Potentilla palustris</i>	.	.	1	.	.	.	1	.	.	3	7	15 ³	
<i>Rubus chamaemorus</i>	12	14	16	15	16	2	1	.	2	7	16	.	9	.	1	7	1	2	3	.	59 ⁸		
<i>Trientalis europaea</i>	11	1	.	.	.	6	1	1	10	.	7	5	.	2	1	3	1	9	16	48 ⁶	
<i>Viola palustris</i>	.	.	1	.	.	.	1	3	11 ²	
<i>Calamagrostis purpurea</i>	10	5	.	4	12	.	.	12	.	14	14	2	13	2	15	16	44 ¹⁰	
<i>Carex canescens</i>	.	12	6	.	.	.	6	.	.	6	.	1	2	2	.	.	.	5	.	30 ⁵	
<i>Carex echinata</i>	.	10	.	.	.	1	10	.	1	4	8	3	6	14	33 ⁶	
<i>Carex rostrata</i>	.	3	4	13	.	8	15 ⁷	
<i>Deschampsia flexuosa</i>	1	4	14	.	.	11	.	.	.	6	.	6	7	5	7	.	33 ⁷	
<i>Eriophorum vaginatum</i>	16	2	14	11 ¹¹	
<i>Aulacomnium palustre</i>	7	.	.	4	7	.	11	8	13	15	8	.	30 ⁹	
<i>Brachythecium reflexum</i>	3	1	4	.	3	.	.	15 ³	
<i>Dicranum fuscescens</i>	5	1	2	.	.	1	1	19 ²	
<i>Dicranum majus</i>	1	4	2	.	2	3	8	2	.	.	2	.	2	10	.	4	.	3	.	1	5	4	.	52 ⁴	
<i>Dicranum scoparium</i>	1	1	.	.	4	3	1	19 ²	
<i>Hylocomium splendens</i>	1	.	8	1	.	11 ³	
<i>Hylocomiastrum umbratum</i>	9	1	.	4	4	5	2	22 ⁴	
<i>Plagiothecium laetum</i>	11	2	3	.	1	1	.	4	.	1	.	1	.	1	.	1	.	.	2	8	.	5	.	41 ⁴	
<i>Pleurozium schreberi</i>	3	1	9	3	8	1	2	1	2	.	33 ³	
<i>Polytrichum commune</i>	16	16	.	16	13	6	8	.	11	4	.	3	16	16	.	16	10	5	8	59 ¹¹	
<i>Rhytidadelphus squarrosus</i> agg.	1	.	1	1	11 ¹	
<i>Straminergon stramineum</i>	4	2	.	.	.	7	.	8	16	8	16	9	16	.	6	.	15	.	13	.	.	8	6	.	10	12	59 ¹⁰		
<i>Tetraphis pellucida</i>	3	1	1	11 ²	
<i>Sphagnum angustifolium</i>	15	16	14	15	8	15	15	15	16	16	15	4	14	16	16	16	15	16	14	7	15	16	.	7	16	14	16	96 ¹⁴	
<i>Sphagnum centrale</i>	7	16	16	12	15	12	.	16	.	16	15	.	14	1	.	4	.	10	16	.	16	12	10	8	8	2	.	74 ¹¹	
<i>Sphagnum girgensohnii</i>	12	.	16	16	16	16	15	.	16	16	16	15	16	16	16	2	16	12	.	16	16	16	16	16	16	8	16	89 ¹⁵	
<i>Sphagnum magellanicum</i>	16	11	16	5	.	.	.	8	19 ¹¹	

Tab. 18 (continued).

Plot	12	13	14	15	17	19	20	27	30	32	33	34	35	49	56	94	97	98	99	122	135	139	140	142	143	147	149	
<i>Sphagnum riparium</i>	-	-	-	-	-	-	-	11	-	-	11	-	-	-	-	-	-	-	-	-	7	-	-	-	-	-	-	11 ¹⁰
<i>Sphagnum russowii</i>	-	16	8	-	1	-	-	-	-	-	-	-	-	-	-	16	-	16	13	-	13	16	-	-	-	7	-	33 ¹²
<i>Sphagnum squarrosum</i>	-	-	-	3	12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	11 ⁶
<i>Sphagnum teres</i>	-	-	-	-	-	-	-	11	-	-	2	-	-	-	-	-	-	-	-	-	8	-	-	-	-	-	-	11 ⁷
<i>Calypogeia integristipula</i>	-	-	-	-	-	3	3	3	-	1	2	-	2	-	-	-	-	-	7	-	-	-	-	2	-	-	-	30 ²
<i>Calypogeia muelleriana</i>	-	4	5	-	-	-	1	-	3	2	5	-	-	-	8	10	-	12	6	-	-	1	9	-	-	-	-	44 ⁶
<i>Calypogeia neesiana</i>	-	-	-	-	-	-	-	1	-	-	1	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11 ¹
<i>Cephalozia bicuspidata</i>	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	3	3	-	-	-	2	-	-	-	-	15 ²
<i>Cephalozia lunulifolia</i>	-	-	-	-	-	-	-	-	-	1	2	-	-	-	1	-	-	-	-	-	-	1	2	-	-	-	-	19 ¹
<i>Cephalozia pleniceps</i>	-	-	-	-	-	-	-	-	5	4	4	6	-	-	-	14	-	16	6	-	-	7	5	-	-	-	-	33 ⁷
<i>Chiloscyphus profundus</i>	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	11	-	3	-	15 ⁷

Additional species (occurring in one or two plots only):

Frangula alnus 33:1 4¹; *Pinus sylvestris* 4¹.

Calluna vulgaris 32:1 4¹; *Empetrum nigrum* 94:14, 98:2 7⁸.

Dactylorhiza maculata 12:2 7¹; *Drosera rotundifolia* 94:1 4¹; *Dryopteris expansa* agg. 20:1, 49:1 7¹; *Equisetum sylvaticum* 49:13 4¹³; *Orthilia secunda* 35:3 4³.

Agrostis canina 94:2 4²; *Carex lasiocarpa* 94:5 4²; *Carex pauciflora* 94:1 4¹; *Eriophorum angustifolium* 94:9 4⁹; *Molinia caerulea* 94:1 4¹; *Phragmites australis* 94:12, 99:4 7⁸.

Dicranum montanum 122:1 4¹; *Plagiothecium denticulatum* 122:1 4¹; *Plagiothecium undulatum* 97:1 4¹; *Polytrichum formosum* 14:2 4²; *Polytrichum strictum* 99:2 4²; *Pseudobryum cinclidioides* 122:2 4²; *Rhytidiadelphus loreus* 19:1 4¹; *Rhytidiadelphus triquetrus* 27:1, 122:2 7¹; *Sanionia uncinata* 147:1 4¹.

Sphagnum brevifolium 17:9, 33:2 7³; *Sphagnum quinquefarium* 56:8 4⁸; *Sphagnum warnstorffii* 27:4, 33:2 7³.

Barbilophozia attenuata 32:1 4¹; *Blepharostoma trichophyllum* 32:1 4¹; *Cephaloziella* sp. 32:1 4¹; *Lepidozia reptans* 99:1 4⁴; *Ptilidium pulcherrimum* 27:1 4¹; *Riccardia latifrons* 140:1 4¹.

Tab. 19. Species composition of plots classified to the wet, intermediately rich (IW) site type. Species abundance is given as frequency in subplots. Constancy and mean frequency is given (as exponent) in column to the right.

Plot	3	4	5	7	9	24	81	89	92	100	101	102	103	117	118	119	120	121	127	134	
<i>Betula</i> spp.	1	2	.	.	1	.	.	15 ¹
<i>Picea abies</i>	4	.	1	.	.	3	.	2	5	5	4	.	5	.	.	40 ⁴
<i>Vaccinium myrtillus</i>	5	1	.	.	.	4	.	3	1	.	.	1	10	4	.	.	8	.	.	.	45 ⁴
<i>Vaccinium vitis-idaea</i>	11	1	.	.	.	5	.	3	10	.	.	1	8	9	5	2	1	6	2	.	65 ⁵
<i>Caltha palustris</i>	.	9	11	4	13	.	3	25 ⁸
<i>Dactylorhiza maculata</i>	1	.	.	1	10 ¹
<i>Equisetum fluviatile</i>	2	8	1	5	2	.	2	2	.	35 ³
<i>Equisetum sylvaticum</i>	12	.	3	2	.	.	2	.	.	.	20 ⁵
<i>Filipendula ulmaria</i>	.	.	7	.	4	.	12	5	4	1	2	2	40 ⁵
<i>Galium palustre</i>	.	5	15	3	14	.	.	3	7	14	13	1	8	.	14	4	.	2	.	3	70 ⁸
<i>Linnaea borealis</i>	1	.	.	1	4	15 ²
<i>Lycopodium annotinum</i>	2	2	10 ²
<i>Lysimachia thyrsoflora</i>	.	.	9	8	13	8	.	20 ¹⁰
<i>Maianthemum bifolium</i>	8	14	12	14	11	.	3	.	5	3	5	.	9	.	.	5	55 ⁸
<i>Menyanthes trifoliata</i>	4	9	6	.	7	13	.	.	1	14	10	4	2	15	15	16	.	14	16	12	80 ¹⁰
<i>Phegopteris connectilis</i>	2	5	5	15 ⁴
<i>Potentilla palustris</i>	12	14	7	.	16	2	.	.	10	6	10	16	.	7	15	10	5	12	12	5	80 ¹⁰
<i>Pyrola minor</i>	6	6	.	.	4	6	.	.	.	20 ⁶
<i>Rubus saxatilis</i>	2	.	1	2	.	.	15 ²
<i>Trientalis europaea</i>	.	.	6	.	.	3	6	14	5	2	2	.	1	.	6	1	.	1	.	12	60 ⁵
<i>Viola palustris</i>	.	.	6	8	10	6	11	13	3	7	13	.	.	.	12	11	.	4	.	16	65 ⁹
<i>Agrostis canina</i>	.	1	16	1	15	10	.	.	.	9	16	35 ¹⁰
<i>Calamagrostis purpurea</i>	.	.	11	10	8	13	7	2	2	.	.	.	5	3	.	8	4	6	.	.	60 ⁷
<i>Carex canescens</i>	10	15	13	6	16	.	11	.	12	16	11	14	.	8	6	8	6	.	9	16	80 ¹¹
<i>Carex chordorrhiza</i>	16	14	10 ¹⁵
<i>Carex echinata</i>	15	14	10	.	.	15	13	2	.	2	12	8	8	.	.	2	.	.	4	8	65 ⁹
<i>Carex flava</i>	4	9	15 ⁹
<i>Carex paupercula</i>	.	2	9	10 ⁶
<i>Carex rostrata</i>	9	.	.	.	10	.	10 ¹⁰
<i>Deschampsia cespitosa</i>	7	5	10 ⁶
<i>Deschampsia flexuosa</i>	3	.	8	6	.	.	1	.	.	20 ⁵
<i>Eriophorum angustifolium</i>	2	12	15	15	20 ¹¹
<i>Eriophorum vaginatum</i>	3	.	5	8	10	.	.	20 ⁷
<i>Phragmites australis</i>	2	.	16	16	5	20 ¹⁰
<i>Calliergon cordifolium</i>	7	2	5	.	5	20 ⁵
<i>Calliergon richardsonii</i>	.	4	1	.	1	15 ²
<i>Calliergonella cuspidata</i>	.	.	3	.	.	1	10 ²
<i>Dicranum majus</i>	3	1	.	.	2	.	.	.	1	4	2	.	2	.	.	.	35 ²
<i>Dicranum scoparium</i>	2	1	.	.	.	1	.	.	.	1	.	.	.	20 ¹
<i>Hylocomium splendens</i>	4	.	3	4	.	.	.	4	4	.	5	2	.	.	.	35 ⁴
<i>Hylocomiastrum umbratum</i>	.	.	5	2	.	.	.	1	.	.	.	6	2	.	.	25 ³
<i>Plagiothecium laetum</i>	1	.	.	.	1	10 ¹
<i>Pleurozium schreberi</i>	5	2	.	.	.	1	4	4	.	4	.	.	.	30 ³	
<i>Pseudobryum cinclidioides</i>	.	.	3	8	.	.	1	.	4	.	.	20 ⁴
<i>Rhizomnium pseudopunctatum</i>	.	.	3	2	.	.	.	10 ³
<i>Rhytiadelphus squarrosus</i> agg.	.	.	2	.	.	.	1	10 ²
<i>Rhytiadelphus triquetrus</i>	2	2	1	2	5	25 ²
<i>Sanionia uncinata</i>	1	2	.	.	.	1	1	20 ¹
<i>Straminergon stramineum</i>	8	2	16	.	5	2	.	5	.	8	7	.	4	12	3	16	4	2	.	.	70 ⁷
<i>Warnstorfia exannulata</i> agg.	.	1	7	.	5	4	20 ⁴
<i>Sphagnum angustifolium</i>	15	.	3	13	3	.	.	.	10	10	3	7	5	.	7	50 ⁸
<i>Sphagnum centrale</i>	15	16	16	16	13	16	16	16	13	16	16	3	13	14	16	75 ¹⁴
<i>Sphagnum girgensohnii</i>	7	10	7	8	.	13	16	6	7	16	.	45 ¹⁰
<i>Sphagnum squarrosum</i>	13	10	16	16	15	.	16	.	15	.	4	7	15	13	.	15	16	7	16	2	80 ¹²
<i>Sphagnum teres</i>	16	14	16	6	16	15	5	16	16	15	16	15	14	16	15	16	11	16	16	.	100 ¹⁴
<i>Sphagnum warnstorffii</i>	15	14	13	.	13	15	8	9	16	13	16	16	16	15	16	16	11	12	11	8	95 ¹³

Tab. 19 (continued).

Plot	3	4	5	7	9	24	81	89	92	100	101	102	103	117	118	119	120	121	127	134	
<i>Aneura pinguis</i>	3	7	10 ⁵
<i>Calypogeia muelleriana</i>	7	1	4	.	.	7	.	.	4	.	.	.	5	3	35 ⁴
<i>Cephalozia bicuspidata</i>	.	.	1	.	.	1	.	.	3	4	20 ²
<i>Chiloscyphus polyanthos</i>	3	.	1	3	15 ²
<i>Scapania irrigua</i>	.	1	2	1	15 ¹

Additional species (occurring in one plot only):

Alnus glutinosa 81:2; *Alnus incana* 100:1; *Frangula alnus* 24:1; *Salix aurita* 121:2; *Salix aurita* × *caprea* 5:3; *Salix myrsinifolia* 9:4; *Vaccinium oxycoccus* 118:3.
Anemone nemorosa 89:4; *Crepis paludosa* 81:8; *Dryopteris expansa* agg. 5:1; *Oxalis acetosella* 92:2; *Rubus chamaemorus* 117:9; *Valeriana sambucifolia* 121:5.
Agrostis capillaris 81:5; *Carex canescens* × *loliacea* 103:16; *Carex lasiocarpa* 101:14; *Carex nigra* 4:4; *Glyceria fluitans* 81:3; *Molinia caerulea* 89:15.
Aulacomnium palustre 89:1; *Brachythecium rutabulum* agg. 5:2; *Bryum pseudotriquetrum* 5:1; *Plagiomnium elatum* 5:8; *Plagiomnium medium* 5:3; *Plagiothecium denticulatum* 5:4; *Polytrichum formosum* 81:1; *Rhizomnium magnifolium* 134:1; *Rhizomnium punctatum* 5:3.
Sphagnum brevifolium 24:2; *Sphagnum flexuosum* 81:16; *Sphagnum riparium* 134:11; *Sphagnum russowii* 134:6; *Sphagnum subsecundum* 100:15.
Barbilophozia attenuata 3:3; *Barbilophozia kunzeana* 117:2; *Blepharostoma trichophyllum* 117:1; *Calypogeia integristipula* 3:2; *Cephalozia lunulifolia* 24:2; *Cephalozia pleneiceps* 24:1; *Harpanthus flotovianus* 5:3; *Lophozia ventricosa* agg. 3:4; *Plagiochila asplenioides* 103:2; *Scapania undulata* 5:1.

101. Ericaceous species were quantitatively unimportant. The bottom layer varied considerably with respect to cover and species composition, from a continuous carpet mostly with several *Sphagnum* species (see Tab. 19), to a carpet interrupted by naked (mud-bottom) peat (e.g. 5, 9, 100).

Occurrence. The IW site type was most often encountered as a minor element in swamp-forest localities dominated by poor site types, in sites with particularly high water through-flow rates. Typical examples are the water-tracks, with more or less distinct discharge rivulets, that lead from the central parts of swamp forests 1 and 8 to the respective outlets. In swamp-forest locality 10, which was part of a valley-bottom fen with high water through-flow rates, developed along a brooklet, the central, open areas adjacent to the brooklet was occupied by the IW site type. The IW site type also occurred as occasional patches within the PW site type (e.g. plots 24 and 134).

Soil type. The soil profile varied from *Sphagnum* peat to typical swamp soil, often with considerable vertical and/or horizontal fine-scaled variation.

Environment. Median depth to the water table = (2-)10(-18); the bottom layer was typically flooded after snow melt and after long, wet periods.

The organic content of soil was high; loss on ignition = (85-)91(-97) %.

Topsoil pH_{H₂O} = (4.5-)5.3(-5.6).

The soil was moderately poor in nitrogen [(1.6-)2.1(-3.0) % of organic matter].

Variation. The abundance and occurrence of field-layer species varied considerably among plots (Tab. 19). The composition of both layers varied in accordance with depth to the water table. The wettest extreme was made up by plot 9, with a sparsely developed bottom layer mainly consisting of stunted *Sphagnum* shoots, and with high prominence of *Caltha palustris*, *Galium palustre*, *Potentilla palustris*, and *Viola palustris*. Regularly flooded plots (4, 5, 7, 9, 24, 100, 101, 134; with median depth to the water-table ≤ 10 cm) lacked the element of forest-floor and dry swamp-forest species typical of other plots (e.g. *Picea abies* (saplings), *Vaccinium* spp.,

Maianthemum bifolium, *Trientalis europaea*, *Deschampsia flexuosa*, *Dicranum* spp., *Hylocomium splendens*, *Hylocomiastrum umbratum*, *Pleurozium schreberi*, *Rhytidiadelphus triquetrus*, *Sphagnum angustifolium* and, notably, *S. girgensohnii*). Some variation related to soil acidity and nutrient status was observed, but the lower importance of nutrient-demanding species and the higher prominence of *Vaccinium* spp. and other species with optimum in poor forests on mineral soil in plots with soil pH \leq 5.0 (24, 92, 120) may also be a result of these plots being among the driest ones classified to the IW site type.

Comments. (1) The main difference between the IW and PW site types is the replacement of *Sphagnum brevifolium* and *S. riparium* as bottom-layer dominants (in the latter site type) by *S. teres*, *S. warnstorffii* and *S. squarrosum*.

Corresponding site types: Kielland-Lund (1981): Chamaemoro-Piceetum, typical subassociation, p.p. Calamagrostio purpureae-Salicetum pentandrae calthetosum, typical variant, p.p. Fremstad (1997): L1a Forest- or shrub-dominated intermediate fen, forest variant, p.p. E1a Poor swamp forest, typical variant, p.p. E3a *Alnus incana*-*Betula*-*Salix* swamp shrub and forest, *Alnus incana*-*Salix pentandra* variant, p.p.

THE DRY, INTERMEDIATELY RICH (ID) SITE TYPE

Species composition. The floristic composition of the ID site type is shown in Tab. 20. Constant species were *Vaccinium myrtillus*, *V. vitis-idaea* and *Maianthemum bifolium* in the field layer and *Dicranum majus*, *Pleurozium schreberi* and *Sphagnum girgensohnii* in the bottom layer. Frequent species were *Trientalis europaea*, *Hylocomium splendens*, *Plagiothecium laetum*, *Sphagnum angustifolium* and *Calypogeia integristipula*. Local dominants, with high subplot frequency, were the field-layer constants. Dominance relationships in the bottom layer varied considerably among plots. Local dominants that reached high subplot frequency in some plots were, in order of decreasing overall importance, *Sphagnum girgensohnii*, *S. angustifolium*, *S. centrale*, *Polytrichum commune*, *Dicranum majus* and *Pleurozium schreberi*.

The number of species per plot varied from 13 to 39, with a median of 25. The number of vascular plant species was (3-)9(-17), and the number of cryptogamic species was (3-)16(-29).

Physiognomy. A tree layer was most often present; dominated by *Picea abies* and with *Betula* spp., sometimes also *Alnus incana* or *A. glutinosa*, as additional species. Total cover in the field layer was mostly high, with dominance of ericaceous species (*Vaccinium myrtillus* with co-dominance of *Vaccinium vitis-idaea*) and a prominent element of herbs, in some plots also of the graminoids *Calamagrostis purpurea* and *Deschampsia flexuosa*. The physiognomy of the bottom layer varied considerably, e.g.: a more or less continuous bryophyte carpet, dominated by *Sphagnum* spp. (plots 1, 123, 138); *Sphagnum* spp. with *Polytrichum commune* as co-dominant (plots 26, 50, 52, 137, 150); and dominance by mosses (*Dicranum* spp., *Hylocomium splendens*, *Pleurozium schreberi*; plots 8, 51, 53, 80). Small patches occurred that were covered by litter or naked peat.

Occurrence. In swamp-forest localities 1 and 8, the ID site type occurred as high hummocks, built up around tree bases, in a matrix of the IW site type. More frequently, however,

the ID site type covered extensive areas in almost level sites sheltered from the direct influence of seepage water, where it often made up a mosaic with, or formed transitions to, the PD site type (swamp-forest localities 2, 4 and 11). Some occurrences of the ID site type in rich swamp forests, close to the border onto mineral soil, were also observed (swamp-forest locality 7: plots 80, 82). In swamp-forest locality 10, the ID site type occupied a narrow zone between the IW-dominated area close to the central brooklet and the adjacent mineral soil.

Soil type. Strongly humified peat, with transitions to swamp soil (e.g. plot 82).

Environment. Median depth to the water table = (13–)21(–40); the bottom-layer surface was normally not flooded.

The organic content of soil was high in all plots except 82; loss on ignition = (72–)96(–98).

The topsoil was moderately acid; $\text{pH}_{\text{H}_2\text{O}}$ = (3.9–)4.6(–5.5).

The soil was poor in nitrogen [(1.0–)1.5(–2.3) % of organic matter].

Variation. At level sites, the bottom layer was mostly poor in species, with a vigorous, more or less continuous layer of *Sphagnum girgensohnii* with lesser (plots 1, 133) or higher (plots 137, 148) importance of *S. angustifolium* and *S. centrale*, or dominated by *Polytrichum commune* (plots 52, 150). *Menyanthes trifoliata* and *Potentilla palustris* were typical of plots (125, 133) situated relatively close to the median water table, adjacent to, or with an element of, the IW site type. Distinctly elevated hummocks (e.g. 51, 55, 57) were most often dominated by forest-floor mosses (*Dicranum majus*, *Pleurozium schreberi*, *Hylocomium splendens*, *Hylocomiastrum umbratum*). Many plots, tall hummocks in particular, had a strong element of “pocket species” such as *Calyptogeia integristipula*, *C. neesiana*, *Cephalozia bicuspadata*, *Lepidozia reptans*, *Tetraphis pellucida* and *Plagiothecium laetum* agg.

Variation related to soil acidity and nutrient status was observed in the field as well as the bottom layer. Plots with topsoil $\text{pH} < 4.4$ (e.g. 52–58, 137, 141, 145, 146) were more or less deficient in differential species for the intermediate site types (compare Tabs 16 and 20), while species like *Oxalis acetosella*, *Phegopteris connectilis* and *Sphagnum squarrosum* regularly occurred in plots with $\text{pH} \geq 4.7$ (e.g. 10, 82, 116, 125, 126, 138, 144).

Comments. (1) The ID and PD site types overlapped broadly, both with respect to environmental conditions and species composition. These site types are similar partly because a large majority of differential species for intermediate swamp forests [which are forest-floor species characteristic of the ‘slightly rich’ forest sites of R. Økland & Eilertsen (1993) and the low-fern spruce forest (Eu-Piceetum dryopteridetosum) of Kielland-Lund (1981)] preferred wet sites (see Tab. 16). Species like *Anemone nemorosa*, *Athyrium filix-femina*, *Gymnocarpium dryopteris*, *Melampyrum sylvaticum*, *Oxalis acetosella* and *Rubus saxatilis* did, however, failed completely to occur in ID plots with $\text{pH} < 4.5$. We interpret this as an indication that the ID site type, as here defined by the DCASP method, includes mis-classified PD plots. This applies to plots from swamp-forest localities 4 and 11. The group of plots with species indicating intermediately rich sites correspond to the slightly rich series of forest site types of R. Økland & Eilertsen (1993), both with respect to species composition and soil acidity and nutrient status.

Corresponding site types: Kielland-Lund (1981): Chamaemoro-Piceetum, typical subassociation, p.p., and *Dryopteris phegopteris*-subassociation. Calamagrostio purpureae-Salicetum pentandrae hylocomietosum, p.p. Fremstad (1997): L1a Forest- or shrub-dominated intermediate fen, forest variant, p.p. E1a Poor swamp forest, typical variant, p.p. E3a *Alnus incana*-*Betula*-*Salix* swamp shrub and forest, *Alnus incana*-*Salix pentandra* variant, p.p.

Tab. 20. Species composition of plots classified to the dry, intermediately rich (ID) site type. Species abundance is given as frequency in subplots. Constancy and mean frequency is given (as exponent) in column to the right.

Plot	1	8	10	25	26	31	50	51	52	53	54	55	57	58	80	82	95	116	123	125	126	133	136	137	138	141	144	145	146	148	150	
<i>Betula</i> spp.	9	6	1	1	2	.	16 ⁴
<i>Picea abies</i>	.	.	.	5	1	.	1	1	2	8	1	7	10	6	.	1	.	.	14	3	.	3	3	5	1	3	.	58 ⁴
<i>Sorbus aucuparia</i>	.	2	6	2	.	3	.	7	.	.	1	1	.	23 ³	
<i>Vaccinium myrtillus</i>	9	4	16	14	15	15	4	16	.	16	16	16	15	16	13	14	13	15	8	2	6	15	16	16	1	15	7	11	16	10	.	94 ¹²
<i>Vaccinium vitis-idaea</i>	9	.	14	7	9	10	.	5	2	8	9	12	9	14	7	2	16	15	6	10	15	9	11	7	.	14	2	2	16	4	.	87 ⁹
<i>Dryopteris expansa</i> agg.	1	.	4	1	5	13	1	9	1	1	.	2	.	32 ⁴
<i>Equisetum sylvaticum</i>	10	7	16	7	4	1	.	.	4	1	.	.	2	6	8	.	.	.	15	.	.	.	7	.	11	45 ⁷
<i>Gymnocarpium dryopteris</i>	.	.	2	7	.	.	.	1	2	.	.	.	3	1	8	23 ³
<i>Linnaea borealis</i>	3	8	1	.	.	.	4	.	.	.	14	5	.	19 ⁶
<i>Lycopodium annotinum</i>	14	6	.	.	.	2	8	16	.	.	.	5	16	6	6	.	.	29 ⁹	
<i>Maianthemum bifolium</i>	7	1	9	8	5	16	1	6	11	9	15	3	7	10	16	11	16	9	12	5	13	9	10	16	16	.	12	.	10	6	4	94 ⁹
<i>Menyanthes trifoliata</i>	.	.	.	2	10	.	.	6	.	1	13 ⁵
<i>Oxalis acetosella</i>	6	.	.	.	2	1	.	.	.	2	.	2	16 ³
<i>Phegopteris connectilis</i>	3	15	10	7	7	.	2	.	7	.	.	.	23 ⁷	
<i>Potentilla palustris</i>	2	1	9	.	2	13 ⁴
<i>Rubus chamaemorus</i>	16	16	.	7	.	.	6	4	7	.	8	3	26 ⁸
<i>Trientalis europaea</i>	5	1	12	.	15	12	.	2	.	.	2	2	3	.	9	9	3	1	3	5	6	2	4	3	.	3	.	7	16	12	77 ⁶	
<i>Viola palustris</i>	.	.	4	.	.	.	2	1	3	13 ³
<i>Calamagrostis purpurea</i>	.	.	11	4	12	16	.	.	16	3	11	8	.	.	14	7	.	4	.	2	10	.	.	5	10	16	6	55 ⁹
<i>Carex canescens</i>	2	.	2	.	3	.	.	.	8	10	13	.	23 ⁶
<i>Deschampsia cespitosa</i>	8	6	.	2	3	4	16 ⁵
<i>Deschampsia flexuosa</i>	2	15	.	12	1	.	.	16	1	1	.	.	.	11	12	.	29 ⁸
<i>Aulacomnium palustre</i>	.	.	.	6	3	1	7	4	.	.	1	9	1	7	5	.	.	32 ⁴
<i>Brachythecium reflexum</i>	.	3	8	.	1	9	.	.	10	.	1	4	23 ⁵
<i>Dicranum fuscescens</i>	.	.	.	3	6	6	.	2	.	5	.	3	3	7	.	.	3	.	2	.	.	.	32 ⁴
<i>Dicranum majus</i>	1	15	16	10	4	8	3	14	.	14	8	8	14	15	12	7	15	2	3	2	5	.	8	11	.	10	4	8	5	.	84 ⁹	
<i>Dicranum scoparium</i>	.	.	1	7	8	11	2	9	.	4	1	1	7	2	10	1	4	5	.	.	4	.	5	.	1	.	.	58 ⁵
<i>Hylocomium splendens</i>	.	2	.	11	.	.	.	4	.	11	1	1	13	15	2	.	14	14	1	10	7	.	10	5	.	2	3	.	1	.	61 ⁷	
<i>Hylocomiastrum umbratum</i>	1	9	2	6	9	10	.	2	.	.	8	.	9	.	9	6	11	3	1	4	.	1	.	52 ⁶
<i>Plagiothecium laetum</i>	.	15	11	5	8	6	1	.	10	1	6	1	2	9	1	4	.	2	.	3	.	6	.	.	11	3	8	5	.	.	68 ⁶	
<i>Pleurozium schreberi</i>	2	12	15	11	11	6	2	10	.	11	6	9	14	16	5	9	15	14	4	6	11	.	2	7	.	10	3	4	5	.	84 ⁸	
<i>Pohlia nutans</i>	1	2	1	3	.	.	13 ²
<i>Polytrichum commune</i>	13	11	14	5	16	.	8	.	8	5	14	.	.	15	.	13	16	39 ¹²
<i>Polytrichum formosum</i>	.	8	5	1	.	.	.	2	5	16 ⁴
<i>Rhytidiadelphus squarrosus</i> agg.	2	3	4	4	1	1	.	19 ²
<i>Rhytidiadelphus triquetrus</i>	4	2	.	2	14	7	.	12	.	2	23 ⁶
<i>Sanionia uncinata</i>	.	.	.	2	3	3	1	.	13 ²
<i>Stramineogon stramineum</i>	1	.	2	9	.	6	.	11	12	3	13	11	1	9	2	2	3	45 ⁶
<i>Tetraphis pellucida</i>	.	7	7	3	9	2	1	2	.	3	.	1	.	1	2	3	2	4	.	.	7	3	6	.	.	.	55 ⁴

Tab. 20 (continued).

Plot	1	8	10	25	26	31	50	51	52	53	54	55	57	58	80	82	95	116	123	125	126	133	136	137	138	141	144	145	146	148	150		
<i>Sphagnum angustifolium</i>	.	.	10	10	5	4	16	7	16	.	11	9	2	.	.	.	14	9	.	13	4	16	10	14	16	7	15	15	2	16	16	77 ¹¹	
<i>Sphagnum centrale</i>	.	.	2	5	9	12	.	.	12	.	.	2	.	.	9	.	13	14	.	12	1	13	4	7	16	9	12	8	11	.	.	61 ⁹	
<i>Sphagnum girgensohnii</i>	15	4	7	14	8	13	16	12	14	.	15	13	10	14	8	16	.	2	14	13	14	16	15	14	16	15	15	16	16	16	7	94 ¹³	
<i>Sphagnum russowii</i>	2	14	.	6	.	13 ⁶
<i>Sphagnum squarrosum</i>	11	.	6	.	1	.	.	.	12	.	5	.	.	.	9	4	16	4	.	14	.	.	6	1	39 ⁷
<i>Sphagnum teres</i>	8	2	13	.	14	13 ⁹
<i>Sphagnum warnstorffii</i>	6	7	.	3	12	.	4	16 ⁶
<i>Barbilophozia attenuata</i>	.	.	.	4	1	8	.	.	.	3	2	.	.	2	19 ³
<i>Calypogeia integristipula</i>	.	7	10	3	7	4	5	5	.	2	.	.	2	7	1	3	3	2	.	10	.	.	8	3	10	3	.	.	61 ⁵
<i>Calypogeia muelleriana</i>	2	7	.	2	.	8	3	.	11	.	.	.	1	5	5	10	8	6	.	.	6	4	7	6	.	.	52 ⁶
<i>Calypogeia neesiana</i>	.	4	2	.	.	2	2	1	.	.	19 ³
<i>Cephalozia bicuspadata</i>	.	13	.	.	3	5	2	2	5	4	1	.	.	.	7	.	2	.	.	.	2	9	.	.	39 ⁵	
<i>Cephalozia lunulifolia</i>	.	4	1	1	1	2	6	2	.	.	23 ²
<i>Chiloscyphus profundus</i>	.	.	.	1	1	1	.	6	.	4	5	5	.	.	.	23 ³	
<i>Lepidozia reptans</i>	.	.	.	2	5	.	.	1	2	1	3	.	.	.	4	2	5	.	.	29 ³	
<i>Lophozia ventricosa</i> agg.	6	3	3	.	.	1	2	16 ³
<i>Plagiochila asplenioides</i>	2	.	1	4	.	.	9	1	3	9	10	2	8	2	.	35 ⁵	
<i>Ptilidium pulcherrimum</i>	1	.	.	.	3	2	1	.	.	13 ²
<i>Cladonia chlorophaea</i> agg.	.	.	.	2	3	1	.	.	.	4	13 ³
<i>Cladonia coniocraea</i>	.	.	.	1	3	1	.	.	.	2	13 ²

Additional species (occurring in three or fewer plots):

Frangula alnus 26:6, 95:4 6⁵.

Anemone nemorosa 80:5, 82:1, 133:10 10⁵; *Athyrium filix-femina* 8:1, 10:4, 133:7 10⁴; *Filipendula ulmaria* 10:6 3⁶; *Listera cordata* 133:2, 138:1 6²; *Lysimachia thyrsoiflora* 10:2 3²; *Melampyrum pratense* 1:6 3⁶; *Melampyrum sylvaticum* 1:1, 53:10, 80:5 10⁶; *Orthilia secunda* 80:9, 138:3 6⁶; *Pteridium aquilinum* 57:2 3²; *Rubus saxatilis* 1:1, 125:3, 126:5 10².

Calamagrostis arundinacea 133:4 3⁴; *Carex chordorrhiza* 116:4 3⁴; *Carex echinata* 1:2, 148:8, 150:8 10⁶; *Carex nigra* 25:9 3⁹; *Carex rostrata* 26:2, 31:6 6⁴; *Eriophorum angustifolium* 148:15 3¹⁵; *Eriophorum vaginatum* 116:9 3⁹; *Glyceria fluitans* 1:1 3¹; *Phragmites australis* 95:3 3³.

Brachythecium starkei 10:1, 26:1, 31:4 10²; *Calliergon cordifolium* 10:1 3¹; *Dicranum montanum* 95:1 3¹; *Plagiothecium denticulatum* 10:1, 31:2, 82:1 10¹; *Plagiothecium undulatum* 137:2 3²;

Pseudobryum cinclidioides 125:8, 126:7 6⁸; *Ptilium crista-castrensis* 10:3, 57:7 6⁵; *Rhizomnium magnifolium* 52:1, 80:3 6²; *Rhizomnium pseudopunctatum* 80:1, 116:1 6¹; *Rhizomnium punctatum* 8:1 3¹; *Rhodobryum roseum* 53:4 3⁴.

Sphagnum brevifolium 26:4 3⁴; *Sphagnum magellanicum* 138:1 3¹; *Sphagnum quinquefarium* 57:10 3¹⁰.

Blepharostoma trichophyllum 25:1, 82:1, 136:2 10¹; *Calypogeia azurea* 125:1 6²; *Cephalozia pleniceps* 25:1, 95:4, 145:1 10²; *Chiloscyphus polyanthos* 80:1 3¹; *Lophozia longidens* 51:7 3²; *Lophozia obtusa* 57:1 3¹; *Ptilidium ciliare* 116:3 3³; *Riccardia latifrons* 144:3 3².

Cladonia cenotea 31:1 3¹; *Cladonia digitata* 26:3, 141:1 6²; *Cladonia rangiferina* 31:4 3⁴; *Cladonia squamosa* 31:3 3³.

Tab. 21. Species composition of plots classified to the wet, rich (RW) site type. Species abundance is given as frequency in subplots. Constancy and mean frequency is given (as exponent) in column to the right.

Plot	2	6	11	43	44	61	62	63	64	68	73	76	78	79	83	84	85	86	87	104	106	107	113	114		
<i>Alnus incana</i>	.	8	.	.	2	2	1	1	.	.	21 ³
<i>Picea abies</i>	.	.	1	2	3	.	2	.	.	.	2	1	1	1	.	2	.	6	2	6	.	.	.	3	7	58 ³
<i>Sorbus aucuparia</i>	.	2	.	2	1	13 ²
<i>Vaccinium myrtillus</i>	.	.	.	4	1	1	.	1	17 ²
<i>Anemone nemorosa</i>	9	.	1	.	2	2	5	7	1	2	3	1	.	.	.	5	.	2	11	2	12	2	1	10	75 ⁴	
<i>Athyrium filix-femina</i>	.	2	.	.	.	9	12	10	.	4	21 ⁷
<i>Caltha palustris</i>	5	15	3	.	.	1	15	.	10	3	.	.	10	2	5	9	.	5	5	13	.	3	16	3	71 ⁷	
<i>Cirsium helenioides</i>	10	.	16	14	10	17 ¹³
<i>Crepis paludosa</i>	.	.	8	.	.	5	10	5	10	.	2	.	.	.	16	16	8	12	13	.	3	.	2	10	58 ⁹	
<i>Dryopteris expansa</i> agg.	5	1	.	.	.	6	21 ³
<i>Epilobium palustre</i>	9	.	.	.	13	11	1	.	3	21 ⁷
<i>Equisetum sylvaticum</i>	.	.	.	7	7	2	9	4	4	12	16	15	8	11	.	9	9	5	8	.	.	62 ⁸
<i>Filipendula ulmaria</i>	15	2	16	15	11	11	9	.	2	6	14	16	9	11	2	10	10	11	6	10	2	.	1	3	92 ⁹	
<i>Galium palustre</i>	12	6	.	13	7	7	9	.	7	.	5	11	6	42 ⁸
<i>Gymnocarpium dryopteris</i>	.	.	1	.	7	1	11	9	.	2	.	.	1	29 ⁵	
<i>Linnaea borealis</i>	.	.	2	.	1	1	13 ¹
<i>Lycopodium annotinum</i>	.	.	.	1	1	3	.	13	17 ⁵
<i>Lysimachia thyriflora</i>	12	1	5	13 ⁶
<i>Maianthemum bifolium</i>	.	2	8	.	3	.	1	11	.	.	.	1	2	.	7	13	1	1	2	9	1	.	.	3	62 ⁴	
<i>Melampyrum sylvaticum</i>	.	.	4	2	3	1	3	1	.	.	.	25 ²
<i>Oxalis acetosella</i>	1	1	1	3	9	4	9	5	2	15	8	7	7	10	5	9	9	13	4	2	12	88 ⁶
<i>Phegopteris connectilis</i>	5	.	4	15	2	8	7	16	2	13	4	2	1	16	13	11	11	1	.	1	75 ⁷	
<i>Ranunculus repens</i>	16	7	15	12	17 ¹³
<i>Rubus saxatilis</i>	5	.	.	2	2	1	.	.	6	2	.	1	.	.	29 ²
<i>Trientalis europaea</i>	4	2	13	2	4	3	1	.	.	3	4	2	4	.	7	15	10	11	2	7	14	.	.	1	79 ⁶	
<i>Tussilago farfara</i>	.	.	.	9	7	3	6	17 ⁶
<i>Valeriana sambucifolia</i>	13	9	2	2	7	15	25 ⁸
<i>Viola palustris</i>	10	4	13	13	14	13	15	12	2	.	1	.	14	15	16	8	14	8	15	1	75 ¹⁰
<i>Agrostis canina</i>	13	.	.	14	16	14	15	.	16	.	.	.	16	16	16	2	16	14	16	5	16	.	1	14	71 ¹³	
<i>Agrostis capillaris</i>	.	.	.	2	4	.	.	.	1	.	.	.	11	.	.	4	2	12	2	33 ⁵
<i>Calamagrostis purpurea</i>	.	.	16	12	12	.	.	12	.	.	.	1	4	1	15	16	16	13	6	4	16	58 ¹⁰
<i>Carex canescens</i>	9	11	5	.	.	.	3	1	1	.	.	.	14	10	14	9	9	4	9	6	1	7	10	9	75 ⁷	
<i>Carex echinata</i>	5	.	.	.	3	.	.	.	10	13	13	2	8	11	1	6	.	42 ⁷
<i>Carex flava</i>	.	.	.	2	4	4	.	6	.	6	5	.	.	6	.	2	.	33 ⁴
<i>Carex loliacea</i>	10	3	6	4	4	.	21 ⁵
<i>Carex pallescens</i>	.	.	.	2	.	.	.	4	7	.	1	.	.	2	.	21 ³
<i>Deschampsia cespitosa</i>	3	.	.	13	14	.	.	9	1	9	10	.	12	5	.	.	.	9	14	46 ⁹	
<i>Glyceria fluitans</i>	16	4	.	3	15	10	14	2	13	2	.	1	10	.	.	3	.	.	50 ⁸	
<i>Luzula pilosa</i>	3	.	3	2	12 ³
<i>Brachythecium rutabulum</i> agg.	.	.	11	16	13	16	12	3	.	.	.	4	.	9	.	.	.	3	.	.	38 ¹⁰	
<i>Brachythecium salebrosum</i>	1	.	1	1	.	.	4	.	.	2	5	1	.	.	29 ²
<i>Bryum pseudotriquetrum</i>	2	5	.	4	6	16	14	13	6	2	5	4	.	10	16	3	.	58 ⁸	
<i>Calliergon cordifolium</i>	2	5	14	4	10	1	8	6	.	7	.	.	.	2	1	.	46 ⁵	
<i>Calliergonella cuspidata</i>	.	.	.	9	12	11	7	1	8	16	13	33 ¹⁰	
<i>Campylium stellatum</i>	.	.	.	8	11	10	.	12	16	15	25 ¹²	
<i>Dicranum majus</i>	.	2	.	3	2	1	.	5	1	2	.	1	.	5	38 ²	
<i>Dicranum scoparium</i>	2	3	.	3	12 ³
<i>Hylocomium splendens</i>	4	.	.	1	3	.	8	4	8	1	1	.	15	38 ⁵		
<i>Hylocomiastrum umbratum</i>	2	.	.	1	2	1	2	.	.	4	.	9	13	4	10	.	.	.	4	.	46 ⁵	
<i>Plagiommium elatum</i>	5	.	.	11	11	.	.	.	2	1	1	3	3	10	.	13	.	.	.	42 ⁶	
<i>Plagiommium ellipticum</i>	1	1	7	13 ³
<i>Plagiommium medium</i>	.	.	16	14	14	16	12	7	3	.	4	14	.	2	42 ¹⁰	
<i>Plagiothecium denticulatum</i>	1	2	7	.	1	.	.	.	8	6	1	1	1	38 ³	
<i>Plagiothecium succulentum</i>	1	.	1	1	13 ¹
<i>Pseudobryum cinclidioides</i>	1	1	.	.	1	8	2	5	6	1	33 ³	
<i>Rhizomnium magnifolium</i>	7	5	4	1	7	.	2	1	.	2	1	.	.	7	.	13	.	12	6	.	54 ⁵	
<i>Rhizomnium pseudopunctatum</i>	11	.	.	.	1	3	.	14	.	.	10	1	4	.	.	.	1	.	33 ⁶	
<i>Rhizomnium punctatum</i>	5	2	.	.	1	1	1	1	.	1	4	6	.	.	1	5	2	3	.	.	.	5	5	11	67 ³	

Tab. 21 (continued).

Plot	2	6	11	43	44	61	62	63	64	68	73	76	78	79	83	84	85	86	87	104	106	107	113	114	
<i>Rhytidiadelphus squarrosus</i> agg	3	1	15	·	14	6	·	·	6	2	15	9	15	4	15	6	16	16	14	13	7	·	2	8	83 ⁹
<i>Rhytidiadelphus triquetrus</i>	·	·	·	10	4	·	·	·	·	·	·	·	·	·	2	·	2	3	13	·	·	·	5	15	33 ⁷
<i>Sanionia uncinata</i>	·	3	·	12	·	·	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·	·	6	·	21 ⁵
<i>Straminergon stramineum</i>	2	·	·	·	·	·	·	·	·	·	·	·	·	·	·	2	·	5	·	·	1	·	·	·	17 ³
<i>Sphagnum centrale</i>	·	·	·	·	·	7	1	15	·	1	·	·	·	4	5	·	·	·	·	·	16	2	·	·	33 ⁶
<i>Sphagnum girgensohnii</i>	·	·	·	9	1	·	12	·	·	·	·	·	14	·	·	16	·	·	·	·	·	·	·	·	21 ¹⁰
<i>Sphagnum squarrosus</i>	14	12	·	3	13	16	16	16	7	7	1	16	15	14	6	16	4	14	2	13	16	·	·	6	88 ¹¹
<i>Sphagnum subsecundum</i>	·	·	·	·	·	·	·	·	·	·	·	·	·	·	16	6	12	5	·	·	·	·	·	·	17 ¹⁰
<i>Sphagnum teres</i>	12	7	·	·	·	·	·	·	·	·	·	·	·	3	8	6	16	·	8	·	15	16	·	2	42 ⁹
<i>Sphagnum warnstorffii</i>	6	3	11	·	1	2	8	3	13	4	·	4	6	14	16	14	10	15	16	16	·	2	4	·	83 ⁸
<i>Blepharostoma trichophyllum</i>	·	·	·	·	·	·	·	·	·	·	·	·	2	·	·	·	1	·	·	·	·	·	3	·	13 ²
<i>Calyptogeia azurea</i>	·	·	·	1	·	·	2	3	·	·	·	·	·	·	·	5	·	·	1	·	·	·	·	·	21 ²
<i>Calyptogeia muelleriana</i>	1	1	·	1	7	4	·	1	2	·	1	·	5	7	6	7	12	12	14	·	·	·	·	·	63 ⁵
<i>Cephalozia bicuspidata</i>	1	4	·	·	·	·	·	·	·	7	5	·	·	·	·	2	·	·	·	8	1	·	·	·	29 ⁴
<i>Chiloscyphus polyanthos</i>	3	5	·	3	11	·	·	4	1	10	6	1	1	8	·	9	11	14	7	1	10	·	2	·	75 ⁶
<i>Chiloscyphus profundus</i>	·	·	·	·	7	3	·	4	2	2	·	·	·	·	·	·	·	·	·	·	·	·	6	16	29 ⁶
<i>Harpanthus flotovianus</i>	·	4	·	·	2	·	·	·	·	·	·	·	1	·	8	·	·	7	9	1	9	·	·	·	33 ⁵
<i>Lophozia ventricosa</i> agg.	1	1	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·	·	2	·	·	·	·	·	17 ¹
<i>Pellia</i> spp.	15	·	·	·	12	16	6	16	14	16	16	10	16	15	16	15	14	16	·	16	1	14	·	·	75 ¹⁴
<i>Plagiochila asplenoides</i>	·	·	·	2	·	2	·	5	8	10	4	·	·	·	·	·	2	6	·	1	·	·	·	·	38 ⁴
<i>Riccardia multifida</i>	·	·	·	·	·	·	·	·	·	·	·	·	·	11	1	·	15	11	3	·	·	·	·	·	21 ⁸
<i>Scapania irrigua</i>	2	6	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	5	·	·	·	·	13 ⁴
<i>Scapania undulata</i>	2	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	2	·	·	13 ²

Additional species (occurring in one plot only):

Betula spp. 104:1, 114:1 8¹; *Salix caprea* 83:4 4⁴.

Vaccinium vitis-idaea 6:2 4².

Bistorta vivipara 83:5 4²; *Cardamine pratensis* 43:7, 44:11 8⁹; *Chrysosplenium alternifolium* 64:16, 68:11 8¹⁴; *Cirsium palustre* 44:3 4³; *Dactylorhiza fuchsii* 83:1, 87:1 8¹; *Equisetum pratense* 61:4, 62:3 8⁴; *Geranium sylvaticum* 87:2 4²; *Geum rivale* 76:2 4²; *Hieracium* sp. 86:3 4³; *Matteuccia struthiopteris* 73:13, 76:5 8⁹; *Orthilia secunda* 43:1 4¹; *Paris quadrifolia* 73:3, 106:4 8⁴; *Potentilla palustris* 2:9, 6:1 8⁵; *Viola riviniana* 114:2 4².

Calamagrostis arundinacea 2:2, 73:2 8²; *Carex canescens* x *loliacea* 106:3 4³; *Carex digitata* 44:1 4¹; *Carex rostrata* 83:2 4²; *Festuca rubra* 87:1 4¹.

Atrichum undulatum 62:1, 76:1 8¹; *Aulacomnium palustre* 43:1, 78:2 8²; *Brachythecium reflexum* 73:1 4¹; *Brachythecium starkei* 85:1 4¹; *Calliergon richardsonii* 104:1 4¹; *Climacium dendroides* 2:7 4⁷; *Dicranum fuscescens* 43:1 4¹; *Fissidens adianthoides* 107:11, 114:1 8⁶; *Hypnum cupressiforme* 84:1 4¹; *Philonotis fontana* 87:1 4³; *Plagiommium undulatum* 68:12 4¹²; *Plagiothecium laetum* 68:1, 73:2 8²; *Pleurozium schreberi* 43:2, 86:2 8²; *Polytrichum formosum* 44:2, 85:6 8⁴; *Ptilium crista-castrensis* 43:1 4¹; *Rhodobryum roseum* 64:1, 68:1 8¹; *Scorpidium revolvens* 104:7 4⁷; *Tetraphis pellucida* 68:1 4¹; *Thuidium tamariscinum* 43:12, 44:13 8¹³; *Warnstorfia exannulata* agg. 6:1, 104:6 8⁴.

Sphagnum quinquefarium 44:1 4¹.

Aneura pinguis 73:3, 104:9 8⁶; *Calyptogeia integrispula* 68:1 4¹; *Cephalozia lunulifolia* 104:3 4³; *Cephalozia pleniceps* 104:1 4¹; *Cephalozia* sp. 62:1 4¹; *Diplophyllum albicans* 104:1 4¹; *Jungermannia leiantha* 114:2 4²; *Lepidozia reptans* 68:2 4²; *Lophozia incisa* 84:1 4¹; *Riccardia latifrons* 104:3 4³; *Scapania paludosa* 106:1 4¹; *Scapania scandica* 76:2 4²; *Scapania umbrosa* 84:1 4¹.

THE WET, RICH (RW) SITE TYPE

Species composition. The floristic composition of the RW site type is shown in Tab. 21. Constant species were *Filipendula ulmaria* and *Oxalis acetosella* in the field layer and *Rhytidiadelphus squarrosus* agg., *Sphagnum squarrosus* and *S. warnstorffii* in the bottom layer. Frequent species were *Anemone nemorosa*, *Caltha palustris*, *Equisetum sylvaticum*, *Maianthemum bifolium*, *Phegopteris connectilis*, *Trientalis europaea*, *Viola palustris*, *Agrostis canina* and *Carex canescens* in the field layer and *Rhizomnium punctatum*, *Chiloscyphus polyanthos* and *Pellia* spp. in the bottom layer. The main local dominants in the field layer, with high subplot frequency, were the frequent and constant species and *Crepis paludosa*, *Ranunculus*

repens, *Calamagrostis purpurea* and *Glyceria fluitans* (see Tab. 21). In the bottom layer, locally high subplot frequency was obtained by a large number of species, among which the most important were *Sphagnum squarrosum*, *Pellia* spp., *Rhytidiadelphus squarrosus* agg., *Sphagnum warnstorffii*, *S. teres*, *Brachythecium rivulare* (included in '*B. rutabulum* agg.), *Plagiomnium medium* and *Bryum pseudotriquetrum*.

The number of species per plot varied from 20 to 49, with a median of 35. The number of vascular plant species was (10-)-17(-27), and the number of cryptogamic species was (7-)-19(-31).

Physiognomy. The tree layer was sparse, with *Alnus* spp., *Betula* spp. and/or stunted *Picea abies*, or lacking. The more or less dense field layer was dominated by herbs and had a prominent graminoid element. The bottom layer varied considerably with respect to cover and species composition. Typical examples are continuous carpets dominated by *Sphagnum squarrosum* (e.g. plots 61-63, 84, 106), moss-dominated carpets (e.g. plots 73, 113, 114) and sparse bryophyte carpets with patch-wise high cover of naked peat (e.g. plots 6, 107).

Occurrence. When present, rich site types most often dominated small swamp forests entirely, filling terraces and shallow depressions in long, narrow valleys (e.g. swamp-forest localities 3, 5, 9), occurring at low-lying sites in the landscape with large catchment areas (localities 6, 7 and 9). Some rich swamp-forest sites have developed around spring horizons (localities 5 and 7).

The RW site type typically occupies the central, wetter parts of swamp forests with low soil acidity, rich in nutrients. In the study area, rich site types rarely occurred together with the intermediate and poor site types (swamp-forest locality 8 made a noticeable exception).

Soil type. A swamp soil profile typically occurred; transitions to peat soil were occasionally observed.

Environment. Median depth to the water table = (1-)-6(-)-13; the bottom layer was flooded after wet periods.

The organic content of soil was variable; loss on ignition = (60-)-81(-)-91.

The topsoil was weakly acid; $\text{pH}_{\text{H}_2\text{O}}$ = (5.1-)-5.5(-6.0).

The soil was mostly moderately rich in nitrogen [(1.5-)-3.0(-3.7) % of organic matter].

Variation. There was considerable variation in species occurrence and abundance, and dominance relationships, both among plots and among swamp-forest localities. Some of this variation was related to influence by spring water (high in plots 64, 68, 83, 85-87). Species with preference for spring-influenced plots were *Chrysosplenium alternifolium*, *Cirsium helenioides*, *Crepis paludosa*, *Bryum pseudotriquetrum*, *Plagiomnium* spp., *Rhizomnium pseudopunctatum* and *Riccardia multifida*. No consistent variation in species composition or dominance relationships related to soil acidity and nutrient status, depth to the water table or other environmental factors were observed, except for slightly increasing importance of forest-floor species with decreasing distance to the border onto adjacent mineral soil.

Comments. (1) The species composition of rich (wet as well as dry) swamp-forest sites varies considerably, both at the within- and between swamp-forest scales. How much of this variation that is due to variation in the environment and how much is due to other reasons, is analysed in a separate study (R. Økland et al., in prep.).

Corresponding site types: Kielland-Lund (1981): *Calamagrostio purpureae-Salicetum pentandrae calthetosum*, typical variant, p.p. Fremstad (1997): M1: Forest- or shrub-dominated rich fen, p.p. E4 Rich swamp forest p.p.

THE DRY, RICH (RD) SITE TYPE

Species composition. The floristic composition of the RD site type is shown in Tab. 22. Constant species were *Oxalis acetosella* and *Phegopteris connectilis* in the field layer and *Dicranum majus*, *Rhytidiadelphus squarrosus* agg. and *Plagiochila asplenioides* in the bottom layer. Frequent species were *Picea abies* (saplings), *Anemone nemorosa*, *Filipendula ulmaria* and *Maianthemum bifolium* in the field layer, and *Dicranum scoparium*, *Hylocomiastrum umbratum*, *Plagiothecium denticulatum*, *P. laetum*, *Rhizomnium punctatum*, *Cephalozia bicuspidata* and *Chiloscyphus polyanthos* in the bottom layer. Locally important (dominant) species, in addition to the constant and frequent species, were *Matteuccia struthiopteris*, *Valeriana sambucifolia*, *Athyrium filix-femina* and *Plagiomnium medium* in swamp-forest locality 6 (plots 70–72, 74) and *Ranunculus repens*, *Deschampsia cespitosa*, *Rhytidiadelphus triquetrus* and *Thuidium tamariscinum* in swamp-forest locality 3 (plots 39–42, 45–48).

The number of species per plot varied from 20 to 49, with a median of 35. The number of vascular plant species was (10–)17(–27), and the number of cryptogamic species was (7–)19(–31).

Physiognomy. A tree layer was most often present, consisting of *Picea abies* and/or *Alnus* spp. and *Betula* spp. Tree-layer density mostly increased towards the peripheral, drier parts of the swamp-forests. The field-layer was often dense, dominated by herbs (ferns) and with a prominent element of graminoids. The cover and species composition of the bottom layer varied considerably. Typically, the development of the bottom layer was inversely related to field-layer cover. Mosses were the most important species group in the bottom layer.

Occurrence. The occurrence of rich swamp-forest localities in general is described under the RW site type. The RD site type typically occupied the peripheral, drier parts of rich swamp forests which, in extreme cases (swamp-forest localities 3, 6, 9) comprised all except the inlet, the outlet and a central water track. In some of the investigated swamp-forest localities (e.g. 7), the ID site type occasionally replaced the RD site type towards the border onto adjacent mineral soil.

Soil type. The soil profile was mostly a typical, dark swamp soil. Transitions to brown forest soils with mull humus occurred near the border onto mineral soil.

Environment. Median depth to the water table = (3–)14(–27) cm; a flooded bottom-layer surface occurred in sites with particularly strongly fluctuating water table only.

The organic content of soil was variable; loss on ignition = (42–)79(–97).

The topsoil was weakly acid; $\text{pH}_{\text{H}_2\text{O}}$ = (4.0–)5.5(–6.0).

The soil was moderately rich in nitrogen [(2.1–)3.0(–3.5) % of organic matter].

Variation. Tab. 22 displays considerable variation in species composition among swamp-forest localities. Several species were abundant in some swamp forests while being absent from others, without obvious ecological explanations. Plot 16 (with topsoil $\text{pH}_{\text{H}_2\text{O}}$ = 4.0) differed from all other plots classified to the RD site type ($\text{pH}_{\text{H}_2\text{O}} \geq 4.7$) by lacking species typical of rich sites (compare Tabs 16 and 22). Otherwise, variation related to soil acidity or nutrient status was not observed.

Considerable variation in species composition was, however, observed in relation to depth to the water table. Species typical of occasionally flooded plots (median depth to the water table < 10 cm; 45, 47, 67, 69, 72, 74, 109, 110, 112) include, among others, *Chrysosplenium alternifolium* and *Ranunculus repens* (which were particularly important in the spring-influenced plot 67), *Tussilago farfara* and *Campylium stellatum*. Forest-floor species (e.g. *Vaccinium* spp.,

Tab. 22. Species composition of plots classified to the dry, rich (RD) site type. Species abundance is given as frequency in subplots. Constancy and mean frequency is given (as exponent) in column to the right.

Plot	16	39	40	41	42	45	46	47	48	59	60	65	66	67	69	70	71	72	74	75	77	88	105	108	109	110	111	112		
<i>Alnus incana</i>	4	3	.	.	4	2	7	10	.	4	25 ⁵	
<i>Picea abies</i>	3	14	4	4	.	.	4	4	1	.	4	.	2	2	3	3	3	2	3	15	2	2	12	4	71 ⁵	
<i>Sorbus aucuparia</i>	2	.	5	2	2	1	.	1	.	2	2	4	5	3	3	.	43 ³	
<i>Vaccinium myrtillus</i>	14	2	7	5	.	.	11	4	9	3	16	1	14	13	6	9	7	3	57 ⁸	
<i>Vaccinium vitis-idaea</i>	.	.	4	2	4	4	3	1	1	3	.	.	29 ³	
<i>Anemone nemorosa</i>	.	16	12	10	7	11	6	11	12	.	.	15	14	13	12	.	2	7	.	1	1	12	.	4	9	2	16	8	79 ⁹	
<i>Athyrium filix-femina</i>	.	10	.	5	.	2	6	13	6	7	3	11	10	5	10	43 ⁷
<i>Caltha palustris</i>	3	1	1	1	2	4	10	.	.	11	29 ⁴	
<i>Chrysosplenium alternifolium</i>	14	.	.	1	1	2	14 ⁵
<i>Circaea alpina</i>	9	3	15	7	.	1	11	2	25 ⁷
<i>Crepis paludosa</i>	.	.	3	4	.	.	.	2	.	12	6	7	.	.	5	.	4	12	13	36 ⁷	
<i>Dryopteris expansa</i> agg.	.	.	1	1	.	.	3	.	.	5	12	4	8	.	5	.	.	.	10	6	4	.	.	7	43 ⁶	
<i>Equisetum pratense</i>	2	.	4	.	.	2	11 ³
<i>Equisetum sylvaticum</i>	.	.	5	3	13	14	12	10	6	5	.	.	11	7	2	.	2	12	1	1	5	57 ⁷	
<i>Filipendula ulmaria</i>	.	4	12	7	15	15	.	2	10	.	1	.	.	7	4	5	16	16	10	.	.	1	.	1	.	.	3	2	64 ⁷	
<i>Galium palustre</i>	.	3	.	.	.	2	1	3	2	.	2	3	2	29 ²
<i>Geum rivale</i>	.	6	.	.	9	1	11	14 ⁷
<i>Gymnocarpium dryopteris</i>	.	5	.	.	5	13	5	.	2	3	10	16	11	11	1	6	.	.	.	5	8	4	4	57 ⁷	
<i>Linnaea borealis</i>	.	1	4	.	.	6	1	14 ³
<i>Lycopodium annotinum</i>	.	.	11	8	14	14 ⁹
<i>Maianthemum bifolium</i>	8	4	12	11	12	7	1	2	.	.	.	5	.	1	6	1	.	.	.	7	3	15	3	.	2	3	3	.	71 ⁵	
<i>Matteuccia struthiopteris</i>	10	15	10	10	14 ¹¹
<i>Melampyrum sylvaticum</i>	.	4	10	5	.	.	12	7	1	6	8	7	1	36 ⁶
<i>Mycelis muralis</i>	.	.	.	5	.	.	.	7	11	11 ⁸
<i>Oxalis acetosella</i>	.	16	10	16	16	6	10	11	16	8	11	13	14	14	12	2	4	5	12	14	16	4	9	1	4	.	8	4	93 ¹⁰	
<i>Paris quadrifolia</i>	2	2	5	1	14 ³
<i>Phegopteris connectilis</i>	.	16	12	13	16	15	15	10	14	12	9	16	16	15	15	6	4	7	2	16	4	13	.	16	8	82 ¹²
<i>Prunella vulgaris</i>	.	4	.	.	.	6	.	.	13	11 ⁸
<i>Ranunculus repens</i>	13	3	13	13	29 ¹¹
<i>Rubus saxatilis</i>	.	3	8	13	8	4	.	1	9	1	14	2	.	4	10	4	46 ⁶
<i>Trientalis europaea</i>	.	.	1	8	1	4	2	3	.	4	6	6	5	1	.	4	4	.	.	6	4	54 ⁴
<i>Tussilago farfara</i>	11	.	3	2	2	11	18 ⁶
<i>Valeriana sambucifolia</i>	1	.	.	.	4	1	.	.	15	.	14	14	13	.	.	.	2	25 ⁹
<i>Viola palustris</i>	11	.	2	2	11 ⁵
<i>Viola riviniana</i>	.	.	2	.	8	3	2	5	18 ⁴
<i>Agrostis canina</i>	16	.	16	2	.	.	.	1	2	.	4	1	.	.	25 ⁶
<i>Agrostis capillaris</i>	2	10	.	9	11 ⁷
<i>Calamagrostis arundinacea</i>	.	5	3	3	.	.	3	2	4	9	25 ⁴
<i>Calamagrostis purpurea</i>	.	10	14	3	16	.	1	6	12	.	.	4	2	32 ⁸

Tab. 22 (continued).

Plot	16	39	40	41	42	45	46	47	48	59	60	65	66	67	69	70	71	72	74	75	77	88	105	108	109	110	111	112		
<i>Carex canescens</i>	.	2	.	.	.	7	4	.	.	3	.	.	14 ⁴		
<i>Carex digitata</i>	.	.	1	2	2	11 ²		
<i>Carex echinata</i>	1	7	3	.	11 ⁴		
<i>Deschampsia cespitosa</i>	.	5	.	5	.	15	13	.	2	.	.	2	4	2	3	6	2	39 ⁵	
<i>Luzula pilosa</i>	4	7	1	2	1	18 ³		
<i>Melica nutans</i>	4	1	6	11 ⁴	
<i>Atrichum undulatum</i>	5	11	7	.	2	10	2	3	25 ⁶		
<i>Brachythecium reflexum</i>	8	4	6	.	.	.	7	9	1	3	7	2	.	3	2	2	43 ⁵	
<i>Brachythecium rutabulum</i> agg.	.	.	.	5	9	.	8	15	16	10	.	.	2	25 ⁹		
<i>Brachythecium salebrosum</i>	1	.	4	3	1	9	.	.	1	.	4	.	.	.	25 ³		
<i>Brachythecium starkei</i>	1	.	1	.	.	.	2	.	1	.	.	4	2	.	18 ¹		
<i>Bryum pseudotriquetrum</i>	.	.	.	3	.	8	.	4	2	14 ⁴		
<i>Calliergon cordifolium</i>	.	.	.	4	3	10	.	1	14 ⁵		
<i>Calliergonella cuspidata</i>	.	.	.	12	3	3	1	.	4	6	.	9	25 ⁵	
<i>Campyllum stellatum</i>	4	1	8	8	10	18 ⁶	
<i>Cirriphyllum piliferum</i>	.	10	.	5	10	2	.	2	2	.	4	.	1	12	1	.	.	.	1	10	.	.	.	4	.	.	6	50 ⁵		
<i>Dicranum fuscescens</i>	.	4	4	2	2	.	4	.	1	1	.	25 ²	
<i>Dicranum majus</i>	11	3	16	13	.	1	8	5	10	3	13	15	9	1	10	8	.	1	7	16	8	15	16	11	2	15	11	89 ⁹		
<i>Dicranum scoparium</i>	5	6	6	2	.	6	.	.	5	2	.	3	1	1	.	2	5	11	5	1	6	.	1	61 ⁴		
<i>Fissidens adianthoides</i>	1	.	.	1	11 ¹	
<i>Hylocomium splendens</i>	.	4	.	.	2	4	14	13	13	.	.	12	3	29 ⁸
<i>Hylocomiastrum umbratum</i>	16	4	.	8	5	16	11	5	9	5	12	16	15	16	12	.	.	.	8	7	4	16	9	.	2	16	11	79 ¹⁰		
<i>Plagiomnium affine</i>	12	6	.	16	.	.	.	5	14	4	11	1	29 ⁹	
<i>Plagiomnium elatum</i>	.	7	.	9	1	1	.	10	2	1	.	25 ⁴	
<i>Plagiomnium ellipticum</i>	1	3	.	1	2	14 ²	
<i>Plagiomnium medium</i>	1	15	16	15	5	4	21 ⁹	
<i>Plagiothecium denticulatum</i>	.	.	.	1	.	3	.	3	.	1	14	.	2	2	6	11	1	10	4	10	3	3	3	4	10	10	9	4	75 ⁵	
<i>Plagiothecium laetum</i>	4	2	8	4	.	2	.	5	2	.	9	.	.	2	5	.	1	1	8	4	9	4	4	.	1	.	.	64 ⁴		
<i>Pleurozium schreberi</i>	1	1	8	7	.	2	.	2	.	2	.	1	11	2	7	9	3	.	2	.	46 ⁴		
<i>Polytrichum formosum</i>	.	5	4	.	.	.	6	4	3	.	1	.	.	.	7	3	.	3	32 ⁴		
<i>Rhizomnium pseudopunctatum</i>	2	.	1	1	3	2	.	2	2	1	29 ²
<i>Rhizomnium punctatum</i>	.	.	.	3	.	7	6	13	3	10	13	14	15	.	6	6	11	6	6	6	.	.	3	3	10	3	1	5	75 ⁷	
<i>Rhodobryum roseum</i>	2	.	2	10	1	2	6	21 ⁴	
<i>Rhytidiadelphus squarrosus</i> agg.	1	12	12	6	16	16	16	13	16	6	12	13	7	14	12	15	.	.	.	16	1	9	9	5	2	.	15	.	82 ¹¹	
<i>Rhytidiadelphus triquetrus</i>	.	7	12	12	16	16	.	1	5	11	6	9	5	3	.	5	1	50 ⁸
<i>Sanionia uncinata</i>	.	.	.	1	6	2	5	.	1	.	.	.	5	3	.	6	12	.	.	32 ⁵	
<i>Tetraphis pellucida</i>	.	1	6	1	5	9	1	5	.	1	6	6	.	.	13	.	.	5	.	43 ⁵	
<i>Thuidium tamariscinum</i>	.	16	16	7	7	13	16	16	25 ¹³	
<i>Sphagnum centrale</i>	5	2	15	13	14 ⁹	
<i>Sphagnum girgensohnii</i>	3	6	.	.	.	7	13	.	10	8	21 ⁸	
<i>Sphagnum squarrosum</i>	12	2	.	10	1	9	11	.	11	1	1	.	1	.	7	16	4	.	5	.	.	50 ⁷		

Tab. 22 (continued).

Plot	16	39	40	41	42	45	46	47	48	59	60	65	66	67	69	70	71	72	74	75	77	88	105	108	109	110	111	112	
<i>Sphagnum teres</i>	4	6	2	.	.	.	11 ⁴	
<i>Sphagnum warnstorffii</i>	4	2	8	2	10	9	3	.	.	12	9	32 ⁷
<i>Aneura pinguis</i>	1	2	.	3	2	7	18 ³	
<i>Barbilophozia attenuata</i>	2	1	.	.	4	.	.	.	11 ²	
<i>Blepharostoma trichophyllum</i>	.	1	1	.	.	.	1	.	.	.	3	5	.	4	1	1	2	4	1	4	1	2	50 ²	
<i>Calypogeia azurea</i>	2	.	.	1	2	7	1	4	1	.	.	.	25 ²	
<i>Calypogeia integristipula</i>	.	.	5	1	1	12	1	2	2	.	.	16	2	.	.	32 ⁵	
<i>Calypogeia muelleriana</i>	.	.	1	.	.	.	2	.	.	5	4	12	11	.	5	.	.	1	.	.	4	6	13	3	7	1	9	11	57 ⁶
<i>Calypogeia neesiana</i>	1	1	.	.	5	.	.	.	11 ²	
<i>Cephalozia bicuspidata</i>	3	.	4	3	.	.	2	.	.	10	5	13	16	1	4	8	2	10	.	9	.	11	9	11	7	2	10	7	75 ⁷
<i>Chiloscyphus polyanthos</i>	8	1	11	8	1	2	5	.	10	2	7	8	10	8	.	.	8	1	4	.	2	8	5	68 ⁶
<i>Chiloscyphus profundus</i>	11	5	5	4	5	1	8	.	.	.	2	.	.	4	4	.	13	8	2	12	50 ⁶
<i>Harpanthus flotovianus</i>	1	.	.	1	2	11 ¹
<i>Jungermannia leiantha</i>	.	.	.	5	2	.	1	1	7	1	7	25 ³
<i>Lepidozia reptans</i>	2	2	3	2	1	2	3	2	1	1	5	2	.	8	2	.	50 ³	
<i>Lophozia ventricosa</i> agg.	4	2	.	3	2	3	18 ³	
<i>Mytilia taylorii</i>	1	1	1	.	11 ¹
<i>Pellia</i> spp.	4	.	.	1	1	6	9	.	12	6	8	16	16	15	.	1	43 ⁸	
<i>Plagiochila asplenioides</i>	12	8	12	9	11	9	16	14	8	3	15	11	12	16	14	.	10	.	4	9	14	3	.	10	6	.	8	8	86 ¹⁰
<i>Riccardia latifrons</i>	3	1	.	.	1	.	.	.	11 ²

Additional species (occurring in one or two plots):

Acer platanoides 42:1 4¹; *Alnus glutinosa* 108:1 7¹; *Betula* spp. 66:1 4¹; *Viburnum opulus* 88:7 4⁷.

Achemilla sp. 46:2 4²; *Cardamine pratensis* 39:1, 41:4 7³; *Epilobium palustre* 67:2, 71:2 7²; *Fragaria vesca* 48:8 4⁸; *Geranium sylvaticum* 48:3 4³; *Hieracium* sp. 39:6, 48:1 7⁴; *Listera cordata* 45:1 4¹;

Orthilia secunda 77:4 4⁴; *Polygonatum verticillatum* 111:1 4¹; *Pyrola minor* 105:1 4¹; *Solidago virgaurea* 45:4, 46:5 7⁵.

Anthoxanthum odoratum 111:1 4¹; *Carex flava* 41:2 4²; *Carex loliacea* 110:1, 111:3 7²; *Carex pallescens* 111:3 4³; *Deschampsia flexuosa* 46:7 4⁷; *Festuca altissima* 69:2 4².

Brachythecium populeum 75:5 4⁴; *Climacium dendroides* 39:1 4¹; *Herzogiella striatella* 105:1, 109:1 7¹; *Plagiothecium nemorale* 65:12, 66:2 7⁷; *Pseudotaxiphyllum elegans* 88:1 4¹; *Ptilium*

crista-castrensis 111:1 4¹; *Straminergon stramineum* 60:2 4².

Sphagnum russowii 111:3, 112:1 7².

Barbilophozia lycopodioides 111:1 4¹; *Cephalozia lunulifolia* 69:1, 105:3 7²; *Diplophyllum albicans* 74:1 4¹; *Lophozia incisa* 66:3 4³; *Lophozia obtusa* 65:2 4²; *Ptilidium ciliare* 88:1 4¹; *Ptilidium*

pulcherrimum 59:2 4²; *Riccardia multifida* 111:8, 112:5 7⁷.

Dryopteris expansa agg., *Hylocomium splendens*, *Polytrichum formosum*, *Tetraphis pellucida* and *Lepidozia reptans*) preferred drier sites. Within drier sites, particularly high cryptogam species richness was observed in stony sites and other kinds of “pocket sites”, as exemplified by plots 46, 59, 60, 65, 66, 88 and 108.

Comments. (1) The species-poor low-pH plot 16, which was devoid of species typical of rich site types, was mis-classified by DCA due to its high abundance of *Hylocomiastrum umbratum*, *Sphagnum squarrosum* and *Plagiochila asplenioides*; species with optima in rich sites.

(2) Variation, both at within- and between swamp-forest scales, typical for rich swamp forests in the study area (see the RW site type, comment 1), is even stronger in the RD than in the RW site type.

Corresponding site types: Kielland-Lund (1981): Calamagrostio purpureae-Salicetum pentandrae, a.o. *Glyceria (lithuanica)* variant. Fremstad (1997): M1: Forest- or shrub-dominated rich fen, p.p. E4 Rich swamp forest p.p.

ACKNOWLEDGEMENTS

This study is a co-operation between the Norwegian Institute of Land Inventory and the University of Oslo, and is a part of the forest biodiversity project 'Miljøregistreringer i skog' of the Norwegian Forest Research Institute (NISK) and financially supported by the Norwegian Ministry of Agriculture. We thank all persons, too many to mention by their names, for help and support during the project. Kjell Ivar Flatberg is thanked for inspiring field advice on identification of *Sphagnum*. Harald Bratli, Gunnar Engan, Kjell Tore Hansen, Johnny Hofsten, John Haaland, Auen Korbøl, Hans Petter Kristoffersen, John Y. Larsson and Astrid Skrindo are thanked for enthusiastic participation, most notably in field work. Ivar Gjerde and Camilla Baumann at NISK and Rune Askvik and Rigmor Johannesen of the forest administration of Oslo municipality are thanked for kind cooperation and logistic assistance. Juha-Pekka Hotanen and asbjørn Moen are thanked for constructive criticism of an earlier version of the manuscript.

REFERENCES

- Aartolahti, T. 1965. Oberflächenformen von Hochmoore und ihre Entwicklung in Südwest-Häme und Nord-Satakunta. - *Fennia* 93: 1-268.
- Abrahamsen, J., Jacobsen, N. K., Kalliola, R., Dahl, E., Wilborg, L. & Pålsson, L. 1984. Naturgeografisk regioninndeling av Norden, ed.2. - Nordiska Ministerrådet, Helsingfors.
- Aerts, R., Verhoeven, J. T. A. & Whigham, D. E. 1999. Plant-mediated controls on nutrient cycling in temperate fens and bogs. - *Ecology* 80: 2170-2181.
- Aerts, R., Wallén, B. & Malmer, N. 1992. Growth-limiting nutrients in *Sphagnum*-dominated bogs subject to low and high atmospheric nitrogen supply. - *J. Ecol.* 80: 131-140.
- Anderson, D. S. & Davis, R. B. 1997. The vegetation and its environments in Maine peatlands. - *Can. J. Bot.* 75: 1785-1805.
- Anderson, D. S., Davis, R. B. & Janssens, J. A. 1995. Relationships of bryophytes and lichens to environmental gradients in Maine peatlands. - *Vegetatio* 120: 147-159.
- Andrus, R. E. 1986. Some aspects of *Sphagnum* ecology. - *Can. J. Bot.* 64: 416-426.
- Anonymous, 1987. The canadian system of soil classification, ed. 2. - *Agric. Can. Publs* 1646: 1-164.
- Anonymous, 1990. GS+: geostatistics for the environmental sciences Version 2.1. - Gamma Design Software, Exeter, Mass.
- Anonymous, 1996. Skog 96. Statistikk over skogforhold og -ressurser i Norge. - Norsk Inst. Jord-Skogkartlegging, Ås.
- Anonymous, 1998a. Feltinstruks 1998. Landsskogtaksering og overvåking av skogens sunnhetstilstand. - Ås, Unpubl. (Internal note, Norw. Inst. Land Inventory).
- Anonymous, 1998b. GS+ (+ hevet): geostatistics for the environmental sciences. - Gamma Design Software, Plainwell, Mich.
- Anonymous, 1999. Sveriges sumpskogar. Resultat av sumpskogsinventeringen 1990-1998. - Skogsstyrelsen Medd. 1999: 1-41.
- Aune, B. 1993. Temperaturnormaler, normalperiode 1961-1990. - Norske Meteorol. Inst. Rapp. Klima 1993: 1-63.
- Austin, M. P. & Gaywood, M. J. 1994. Current problems of environmental gradients and species response curves in relation to continuum theory. - *J. Veg. Sci.* 5: 473-482.
- Bannister, P. 1964a. The water relations of certain heath plants with references to their ecological amplitude. I. Introduction: germination and establishment. - *J. Ecol.* 52: 423-432.
- Bannister, P. 1964b. The water relations of certain heath plants with reference to their ecological amplitude. II. Field studies. - *J. Ecol.* 52: 481-497.
- Barber, K.E. 1981. Peat stratigraphy and climatic change: a palaeoecological test of the theory of cyclic bog regeneration. - Balkema, Rotterdam.
- Bates, J. W. 1998. Is 'life-form' a useful concept in bryophyte ecology? - *Oikos* 82: 223-237.
- Bedford, B. L., Walbridge, M. R. & Aldous, A. 1999. Patterns in nutrient availability and plant diversity of temperate North American wetlands. - *Ecology* 80: 2151-2169.
- Bell, J. N. B. & Tallis, J. H. 1973. Biological flora of the British Isles. *Empetrum nigrum* L. - *J. Ecol.* 61: 289-305.
- Bell, J.N.B. & Tallis, J. H. 1974. The response of *Empetrum nigrum* L. to different mire water regimes, with special reference to Wybunbury Moss, Cheshire and Featherbed Moss, Derbyshire. - *J. Ecol.* 62: 75-95.

- Birse, E. M. 1958. Ecological studies on growth-form in bryophytes. III. The relationship between the growth-form of mosses and ground-water supply. - J. Ecol. 46: 9-27.
- Bjørnbæk, G. 1993. Snø 1: 7 mill. Nasjonalatlas for Norge kartblad 3.1.4. - Statens Kartverk, Hønefoss.
- Blum, O.B. 1973. Water relations. - In: Ahmadjian, V. and Hale, M. E. (eds.), The lichens, Academic Press, New York, pp. 381-400.
- Boyer, M. L. H. & Wheeler, B. D. 1989. Vegetation patterns in spring-fed calcareous fens: calcite precipitation and constraints on fertility. - J. Ecol. 77: 597-607.
- Bradbury, I.K. & Grace, J. 1983. Primary production in wetlands. - In: Gore, A. J. P. (ed.), Ecosystems of the world. 4A. Mires: swamp, bog, fen and moor, General studies, Elsevier, Amsterdam, pp. 285-310.
- Brehm, K. 1968. Die Bedeutung des Kationenaustausches für den Kationengehalt lebender Sphagnen. - Planta 79: 324-345.
- Bridgham, S. D., Pastor, J., Janssens, J. A., Chapin, C. & Malterer, T. J. 1996. Multiple limiting gradients in peatlands: a call for a new paradigm. - Wetlands 16: 45-65.
- Bridgham, S. D., Pastor, J., McClaugherty, C. A. & Richardson, C. J. 1995. Nutrient-use efficiency: a litterfall index, a model, and a test along a nutrient-availability gradient in North Carolina peatlands. - Am. Nat. 145: 1-21.
- Bridgham, S. D. & Richardson, C. J. 1993. Hydrology and nutrient gradients in North Carolina peatlands. - Wetlands 13: 207-218.
- Bridgham, S. D., Updegraff, K. & Pastor, J. 1998. Carbon, nitrogen, and phosphorus mineralization in northern wetlands. - Ecology 79: 1545-1561.
- Buch, H. 1947. Über die Wasser- und Mineralstoffversorgung der Moose. II. - Soc. Scient. Fenn. Commentnes Biol. 20: 1-49.
- Busby, J. R., Bliss, L. C. & Hamilton, C. D. 1978. Microclimate control of growth rates and habitats of the boreal forest mosses, *Tomenthypnum nitens* and *Hylocomium splendens*. - Ecol. Monogr. 48: 95-110.
- Cajander, A. K. 1926. The theory of forest types. - Acta for. Fenn. 29: 1-108.
- Carleton, T. J. 1990. Variation in terricolous bryophyte and macrolichen vegetation along primary gradients in Canadian boreal forests. - J. Veg. Sci. 1: 585-594.
- Chapin, F. S. III., Moilanen, L. & Kielland, K. 1993. Preferential use of organic nitrogen for growth by a nonmycorrhizal arctic sedge. - Nature 361: 150-153.
- Clymo, R. S. 1965. Experiments on breakdown of *Sphagnum* in two bogs. - J. Ecol. 53: 747-758.
- Clymo, R. S. 1983. Peat. - In: Gore, A. J. P. (ed.), Ecosystems of the world. 4A. Mires: swamp, bog, fen and moor: general studies, Elsevier, Amsterdam, pp. 159-224.
- Clymo, R. S. 1984. The limits to peat bog growth. - Phil. Trans. R. Soc. Lond. Ser. B. 303: 605-654.
- Cooper, D. J. & Andrus, R. E. 1994. Patterns of vegetation and water chemistry in peatlands of the west-central Wind River Range, Wyoming, U.S.A. - Can. J. Bot. 72: 1586-1597.
- Correns, C. 1899. Untersuchungen über Vermehrung der Laubmoose durch Brutorgane und Stecklinge. - Bryophyt. Bibliotheca 7: 1-472 (Reprinted in 1976).
- Cottrell, T. R. 1996. Use of plant strategy ordination, DCA and ANOVA to elucidate relationships among habitats of *Salix planifolia* and *Salix monticola*. - J. Veg. Sci. 7: 237-246.
- Coulson, J. C. & Butterfield, J. E. 1978. An investigation of the biotic factors determining the rates of plant decomposition on blanket bog. - J. Ecol. 66: 631-650.
- Damman, A. W. H. 1978. Distribution and movement of elements in ombrotrophic peat bogs. -

Oikos 30: 480-495.

- Damman, A. W. H. 1986. Hydrology, development, and biogeochemistry of ombrogenous peat bogs with special reference to nutrient conditions in a western Newfoundland bog. - Can. J. Bot. 64: 384-394.
- Daniels, R. E. 1978. Floristic analyses of British Mires and mire communities. - J. Ecol. 66: 773-802.
- Devito, K. J. & Hill, A. R. 1999. Sulphate mobilization and pore water chemistry in relation to groundwater hydrology and summer drought in two conifer swamps on the Canadian shield. - Wat. Air Soil Pollut. 113: 97-144.
- Du Rietz, G. E. 1949. Huvudenheter och huvudgränser i svensk myrvegetation. - Svensk Bot. Tidskr. 43: 274-309.
- Du Rietz, G. E. 1954. Die Minerlabodenwasserzeigergerne als Grundlage einer natürlichen Zweigliederung der nord- und mitteleuropäischen Moore. - Vegetatio 5-6: 571-585.
- During, H. J. 1979. Life strategies of bryophytes. - Lindbergia 5: 2-18.
- During, H. J. 1992. Ecological classifications of bryophytes and lichens. - In: Bates, J. W. and Farmer, A. M. (eds.), Bryophytes and lichens in a changing environment, Clarendon Press, Oxford, pp. 1-31.
- During, H. J. & ter Horst, B. 1987. Diversity and dynamics in bryophyte communities on earth banks in a Dutch forest. - Symp. Biol. Hung. 35: 447-455.
- During, H.J. & van Tooren, B.F. 1988. Pattern and dynamics in the bryophyte layer of a chalk grassland. - In: During, H. J.; Werger, M. J. A., and Willems, J. H. (eds.), Diversity and pattern in plant communities, SPB Acad. Publ., The Hague, pp. 195-208.
- Ehrenfeld, J. G. 1995a. Microsite differences in surface substrate characteristics in Chamaecyparis swamps of the New Jersey pinelands. - Wetlands 15: 183-189.
- Ehrenfeld, J.G. 1995. Microtopography and vegetation in Atlantic white cedar swamps: the effects of natural disturbances. - Can. J. Bot. 73: 474-484.
- Eilertsen, O., Økland, R. H., Økland, T. & Pedersen, O. 1990. Data manipulation and gradient length estimation in DCA ordination. - J. Veg. Sci. 1: 261-270.
- Eneroth, O. 1931. Om skogstyper och föryngringsförhållanden inom Lappmarken. I. - Norrl. Skogsvårdsförb. Tidskr. 1931: 113-182.
- Eriksson, O. & Fröborg, H. 1996. "Windows of opportunity" for recruitment in long-lived clonal plants: experimental studies of seedling establishment in *Vaccinium* shrubs. - Can. J. Bot. 74: 1369-1374.
- Eriksson, O. & Jerling, L. 1990. Hierarchical selection and risk spreading in clonal plants. - In: van Groenendael, J. and de Kroon, H. (eds.), Clonal growth in plants: regulation and function, SPB Academic Publ., The Hague, pp. 79-94.
- Eurola, S., Aapala, K., Kokko, A. & Nironen, M. 1991. Mire type statistics in the bog and southern aapa mires of Finland (60-66°N). - Annls Bot. Fenn. 28: 15-36.
- Faith, D. P., Minchin, P. R. & Belbin, L. 1987. Compositional dissimilarity as a robust measure of ecological distance. - Vegetatio 69: 57-68.
- Fitje, A. & Strand, L. 1973. Tremålingslære, ed. 2. - Universitetsforlaget, Oslo.
- Flatberg, K.I. 1993. The European taxa in the *Sphagnum recurvum* complex. 2. Amended descriptions of *Sphagnum brevifolium* and *S. fallax*. - Lindbergia 17: 96-110.
- Førland, E. J. 1993. Nedbørnormaler, normalperiode 1961-1990. - Norske Meteorol. Inst. Rapp. Klima 39: 1-63.
- Foster, D. R. 1984. The dynamics of *Sphagnum* in forest and peatland communities in southeastern Labrador, Canada. - Arctic 37: 133-140.

- Foster, D. R. & Fritz, S. C. 1987. Mire development, pool formation and landscape processes on patterned fens in Dalarna, Central Sweden. - *J. Ecol.* 75: 409-437.
- Fowler, N.L. 1990. Disorderliness in plant communities: comparisons, causes, and consequences. - In: Grace, J. B. and Tilman, D. (eds.), *Perspectives on plant competition*, Academic Press, San Diego, pp. 291-306.
- Fransson, S. 1965. The borderland. - *Acta Phytogeogr. Suec.* 50: 167-175.
- Fransson, S. 1972. Myrvegetation i sydvästra Värmland. - *Acta Phytogeogr. Suec.* 57: 1-133.
- Fremstad, E. 1997. Vegetasjonstyper i Norge. - *Norsk Inst. Naturforsk. Temahefte* 12: 1-279.
- Frisvoll, A. A., Elvebakk, A., Flatberg, K. I. & Økland, R. H. 1995. Sjekklister over norske mosar. Vitskapleg og norsk namneverk. - *Norsk Inst. Naturforsk. Temahefte* 4: 1-104.
- Gauch, H. G. Jr. 1982. Multivariate analysis in community ecology. - *Camb. Stud. Ecol.* 1: 1-298.
- Giesler, R., Högberg, M. & Högberg, P. 1998. Soil chemistry and plants in Fennoscandian boreal forest as exemplified by a local gradient. - *Ecology* 79: 119-137.
- Gignac, L. D. & Vitt, D. H. 1990. Habitat limitations of *Sphagnum* along climatic, chemical, and physical gradients in mires of western Canada. - *Bryologist* 93: 7-22.
- Gignac, L. D., Vitt, D. H. & Bayley, S. E. 1991. Bryophyte response surfaces along ecological and climatic gradients. - *Vegetatio* 93: 29-45.
- Glaser, P. H., Janssens, J. A. & Siegel, D. I. 1990. The response of vegetation to chemical and hydrological gradients in the Lost River peatland, northern Minnesota. - *J. Ecol.* 78: 1021-1048.
- Gorham, E., Bayley, S. E. & Schindler, D. W. 1984. Ecological effects of acid deposition upon peatlands: a neglected field in "acid-rain" research. - *Can. J. Fish. Aquat. Sci.* 41: 1256-1268.
- Gorham, E., Eisenreich, S.J., Ford, J. & Santelmann, M.V. 1985. The chemistry of bog waters. - In: Stumm, W. (ed.), *Chemical processes in lakes*, Wiley, New York, NY, pp. 339-363.
- Gorham, E. & Janssens, J. A. 1992. Concepts of fen and bog re-examined in relation to bryophyte cover and the acidity of surface water. - *Acta Soc. Bot. Pol.* 61: 7-20.
- Goth, B.M.T. & Røeggen, O. 1994. Micro-scale vegetation-environment relations in a boreal spruce forest site in the Solhomfjell area, Gjerstad, S Norway. - *Cand. scient. Thesis*, Univ. Oslo, Oslo, unpubl.
- Grace, J. B. 1999. The factors controlling species density in herbaceous plant communities: an assessment. - *Perspect. Pl. Ecol. Syst.* 2: 1-28.
- Granlund, E. 1932. De svenska högmossarnas geologi. - *Sver. Geol. Unders. Ser. C* 26: 1-193.
- Green, R. N., Trowbridge, R. L. & Klinka, K. 1993. Towards a taxonomic classification of humus forms. - *For. Sci. Monogr.* 29: 1-49.
- Grime, J.P. 1979. *Plant strategies and vegetation processes*. - Wiley, Chichester.
- Gundersen, V. & Rolstad, J. 1998a. Nøkkelbiotoper i skog. - *Norsk Inst. Skogforsk. Oppdragsrapp.* 1998: 5: 1-61.
- Gundersen, V. & Rolstad, J. 1998b. Truete arter i skog. - *Norsk Inst. Skogforsk. Oppdragsrapp.* 1998: 6: 1-74.
- Hånell, B. 1988. Postdrainage forest productivity of peatlands in Sweden. - *Can. J. For. Res.* 18: 1443-1456.
- Heal, O. W., Swift, M. J. & Anderson, J. M. 1982. Nitrogen cycling in United Kingdom forests: the relevance of basic ecological research. - *Phil. Trans. R. Soc. Lond. Ser. B.* 296: 427-444.
- Heikkilä, H. 1987. The vegetation and ecology of mesotrophic and eutrophic fens in western

- Finland. - *Annls Bot. Fenn.* 24: 155-175.
- Hill, M.O. 1979. DECORANA - A FORTRAN program for detrended correspondence analysis and reciprocal averaging. - Cornell University, Ithaca, NY.
- Hill, M. O. & Gauch, H. G. Jr. 1980. Detrended correspondence analysis: an improved ordination technique. - *Vegetatio* 42: 47-58.
- Holmsen, G. 1951. Oslo. Beskrivelse til kvartærgeologisk landgeneralkart. - *Norg. Geol. Unders.* 176: 1-62.
- Holtedahl, O. 1974. Noen glasifluviale israndavsetninger i den sydlige del av Glomma-vaassdragets (nåværende) dreneringsområde. - *Norg. Geol. Unders.* 306: 1-85.
- Hörnberg, G., Ohlson, M. & Zackrisson, O. 1997. Influence of bryophytes and microrelief conditions on *Picea abies* seed regeneration patterns in boreal old-growth swamp forests. - *Can. J. For. Res.* 27: 1015-1023.
- Hörnberg, G., Zackrisson, O., Segerström, U., Svensson, B. W., Ohlson, M. & Bradshaw, R. H. W. 1998. Boreal swamp forests: biodiversity "hotspots" in an impoverished forest landscape. - *BioScience* 48: 795-802.
- Huenneke, L. F. & Sharitz, R. R. 1986. Microsite abundance and distribution of woody seedlings in a South Carolina cypress-tupelo swamp. - *Am. Midl. Nat.* 115: 328-335.
- Humphrey, W. D. & Pluth, D. J. 1996. Net nitrogen mineralization in natural and drained fen peatlands in Alberta, Canada. - *Soil Sci. Soc. Am. J.* 60: 932-940.
- Ingestad, T. 1973. Mineral nutrient requirements of *Vaccinium vitis-idaea* and *Vaccinium myrtillus*. - *Physiol. Pl.* 29: 239-246.
- Ingram, H. A. P. 1978. Soil layers in mires: function and terminology. - *J. Soil Sci.* 29: 224-227.
- Jeglum, J. K. 1991. Definition of trophic classes in wooded peatlands by means of vegetation types and plant indicators. - *Annls Bot. Fenn.* 28: 175-192.
- Jeglum, J. K. & He, F. 1995. Pattern and vegetation-environment relationships in a boreal forested wetland in northeastern Ontario. - *Can. J. Bot.* 73: 629-637.
- Johnson, J. B. 1996. Phytosociology and gradient analysis of a subalpine treed fen in Rocky Mountain National Park, Colorado. - *Can. J. Bot.* 74: 1203-1218.
- Johnson, L. C. & Damman, A. W. H. 1993. Decay and its regulation in *Sphagnum* peatlands. - *Adv. Bryol.* 5: 249-296.
- Jonasson, S. & Shaver, G. R. 1999. Within-stand nutrient cycling in arctic and boreal wetlands. - *Ecology* 80: 2139-2150.
- Karlin, E. & Bliss, L. C. 1984. Variation in substrate chemistry along microtopographical and water chemistry gradients in peatlands. - *Can. J. Bot.* 62: 142-153.
- Keddy, P.A. 1990. Competitive hierarchies and centrifugal organization in plant communities. - In: Grace, J. B. and Tilman, D. (eds.), *Perspectives on plant competition*, Academic Press, San Diego, pp. 265-290.
- Keddy, P. A. & Shipley, B. 1989. Competitive hierarchies in herbaceous plant communities. - *Oikos* 54: 234-241.
- Kendall, M. G. 1938. A new measure of rank correlation. - *Biometrika* 30: 81-93.
- Kenkel, N. C. 1987. Trends and interrelationships in boreal wetland vegetation. - *Can. J. Bot.* 65: 12-22.
- Kielland, K. 1994. Amino acid absorption by arctic plants: implication for plant nutrient and nitrogen cycling. - *Ecology* 75: 2373-2383.
- Kielland, K. 1995. Landscape patterns of free amino acids in arctic tundra soils. - *Biogeochemistry* 31: 85-98.
- Kielland, K. 1997. Role of free amino acids in the nitrogen economy of arctic cryptogams. -

- Écoscience 4: 75-79.
- Kielland-Lund, J. 1981. Die Waldgesellschaften SO-Norwegians. - *Phytocoenologia* 9: 53-250.
- Kilham, P. 1982. The biogeochemistry of bog ecosystems and the chemical ecology of *Sphagnum*. - *Mich. Bot.* 21: 159-168.
- Kooijman, A. M. & Bakker, C. 1995. Species replacement in the bryophyte layer in mires: the role of water type, nutrient supply and interspecific interactions. - *J. Ecol.* 83: 1-8.
- Korbøl, A. 2000. Fine-scale distribution patterns of macroscopic charcoal in boreal swamp forests in Østmarka nature reserve, SE Norway. - Oslo, Botanical Museum, Natural History Museums and Botanical Garden, University of Oslo. .
- Korpela, L. & Reinikainen, A. 1996a. A numerical analysis of mire margin forest vegetation in South and Central Finland. - *Annls Bot. Fenn.* 33: 183-197.
- Korpela, L. & Reinikainen, A. 1996b. Patterns of diversity in boreal mire margin vegetation. - *Suo* 47: 17-28.
- Krog, H., Østhagen, H. & Tønsberg, T. 1994. Lavflora. Norske busk- og bladlav. Ny revidert utgave ved Hildur Krog og Tor Tønsberg, ed. 2. - Oslo, Norway, Universitetsforlaget. .
- Kruskal, J. B. 1964a. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. - *Psychometrika* 29: 1-27.
- Kruskal, J. B. 1964. Nonmetric multidimensional scaling: a numerical method. - *Psychometrika* 29: 115-129.
- Kruskal, J.B., Young, F. W. & Seery, J. B. 1973. How to use KYST, a very flexible program to do multidimensional scaling and unfolding. - Murray Hill, New Jersey, unpubl., Bell Labs.
- Kruys, N., Fries, C., Jonsson, B. G., Lämås, T. & Ståhl, G. 1999. Wood-inhabiting cryptogams on dead Norway spruce (*Picea abies*) trees in managed Swedish boreal forests. - *Can. J. For. Res.* 29: 178-186.
- Kuhry, P., Nicholson, B. J., Gignac, L. D., Vitt, D. H. & Bayley, S. E. 1993. Development of *Sphagnum*-dominated peatlands in boreal continental Canada. - *Can. J. Bot.* 71: 10-22.
- Kuuluvainen, T., Hokkanen, T. J., Järvinen, E. & Pukkala, T. 1993. Factors related to seedling growth in a boreal Scots pine stand: a spatial analysis of a vegetation soil system. - *Can. J. For. Res.* 23: 2101-2109.
- Kuuluvainen, T. & Pukkala, T. 1989. Effect of Scots pine seed trees on the density of ground vegetation and tree seedlings. - *Silva Fenn.* 23: 159-167.
- Kuusinen, M. 1996. Importance of spruce swamp-forests for epiphyte diversity and flora on *Picea abies* in southern and middle boreal Finland. - *Ecography* 19: 41-45.
- Lahti, T. 1995. Understorey vegetation as an indicator of forest site potential in Southern Finland. - *Acta for. Fenn.* 246: 1-68.
- Lahti, T. & Väisänen, R. A. 1987. Ecological gradients of boreal forests in South Finland; an ordination test of Cajanders's forest site type theory. - *Vegetatio* 68: 145-156.
- Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm. - *Ecology* 74: 1659-1673.
- Lemmon, P. E. 1956. A spherical densiometer for estimating forest overstorey density. - *For. Sci.* 2: 314-320.
- Li, Y. & Vitt, D. H. 1997. Patterns of retention and utilization of aerially deposited nitrogen in boreal peatlands. - *Écoscience* 4: 106-116.
- Lid, J. & Lid, D. T. 1994. Norsk flora. 6 utgåve ved R. Elven. - Det Norske Samlaget, Oslo, Norway.
- Malmer, N. 1962a. Studies on mire vegetation in the Archaean area of Southwestern Götaland (South Sweden). I. Vegetation and habitat conditions on the Åkhult mire. - *Opera Bot.* 7:

1-322.

- Malmer, N. 1962b. Studies on mire vegetation in the Archaean area of Southwestern Götaland (South Sweden). II. Distribution and seasonal variation in elementary constituents on some mire sites. - *Opera Bot.* 7: 1-62.
- Malmer, N. 1964. On the circulation of elementary constituents in the *Sphagnum*-mires of S.W. Sweden. - In: Burt, B. L. (ed.), Abstracts of papers, Tenth international botanical congress Edinburgh, Publication committee of Tenth international botanical congress, Edinburgh, pp. 246-247.
- Malmer, N. 1986. Vegetational gradients in relation to environmental conditions in northwestern European mires. - *Can. J. Bot.* 64: 375-383.
- Malmer, N. 1993. Mineral nutrients in vegetation and surface layers of *Sphagnum*-dominated peat-forming systems. - *Adv. Bryol.* 5: 223-248.
- Malmer, N., Svensson, B. M. & Wallén, B. 1994. Interactions between *Sphagnum* mosses and field layer vascular plants in the development of peat-forming systems. - *Folia Geobot. Phytotax.* 29: 483-496.
- Malmer, N. & Wallén, B. 1999. The dynamics of peat accumulation on bogs: mass balance of hummocks and hollows and its variation throughout a millennium. - *Ecography* 22: 736-750.
- Malmström, C. 1931. Om faran för skogsmarkens försumpning i Norrland. En studie från Kulbäckslidens och Roklidens försöksfält. - *Meddn St. SkogsförsAnst.* 26: 1-162.
- Malmström, C. 1949. Studier över skogstyper och trädslagsfördelning Västerbottens län. - *Meddn St. SkogsförsInst.* 37: 1-231.
- McIntosh, R. P. 1978. Matrix and plexus techniques. - In: Whittaker, R. H. (ed.), *Ordination of plant communities*, Junk, The Hague, pp. 151-184.
- Metsävainio, K. 1931. Untersuchungen über das Wurzelsystem der Moorpflanzen. - *Annlis Bot. Soc. Zool.-Bot. Fenn. Vanamo* 1: 1-422.
- Minchin, P. R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. - *Vegetatio* 69: 89-107.
- Minchin, P. R. 1990. DECODA Version 2.01. - Canberra, Dept. Biogeogr. Geomorph.. Aust. natn. Univ. .
- Moen, A. 1973. Landsplan for myrreservater i Norge. - *Norsk Geogr. Tidsskr.* 27: 173-193.
- Moen, A. 1990. The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands. - *Gunneria* 63: 1-451.
- Moen, A., Lillethun, A. & Odland, A. 1998. Nasjonalatlas for Norge: Vegetasjon. - Statens Kartverk, Hønefoss.
- Mörnsjö, T. 1969. Studies on vegetation and development of a peatland in Scania, South Sweden. - *Opera Bot.* 24: 1-187.
- Näsholm, T., Ekblad, A., Nordin, A., Giesler, R., Högberg, M. & Högberg, P. 1998. Boreal forest plants take up organic nitrogen. - *Nature* 392: 914-916.
- Nordbakken, J.-F. 1996a. Fine-scale patterns of vegetation and environmental factors on an ombrotrophic mire expanse: a numerical approach. - *Nord. J. Bot.* 16: 197-209.
- Nordbakken, J.-F. 1996b. Plant niches along the watertable gradient on an ombrotrophic mire expanse. - *Ecography* 19: 114-121.
- Nordbakken, J.-F. 1997. Småskala endringer i ombrotrof myrvegetasjon i SO-Norge 1990/91-96. *Bot. Hage Mus. Univ. Oslo Rapp.* 1: 1-34.
- Nordhagen, R. 1928. Die Vegetation und Flora des Sylenegebietes. - *Skr. Norske Vidensk.-Akad. Oslo Mat.-Naturvid. Klasse* 1927: 1-612.

- Nyyssönen, A. 1955. Hakuuäärän arviointi kannoista (Eng. summ.: Estimation of the cut from stumps). - *Communitnes Inst. for. Fenn.* 45: 1-68.
- Ogner, G., Opem, M., Remedios, G., Sjøtveit, G. & Sørli, B. 1991. The chemical analysis program of The Norwegian Forest Research Institute, 1991. - Ås, The Norwegian Forest Research Institute. .
- Ohlson, M. & Økland, R. H. 1998. Spatial variation in rates of carbon and nitrogen accumulation in a boreal bog. - *Ecology* 79: 2745-2758.
- Ohlson, M., Söderström, L., Hörnberg, G., Zackrisson, O. & Hermansson, J. 1997. Habitat qualities versus long-term continuity as determinants of biodiversity in boreal old-grown swamp forest. - *Biol. Conserv.* 81: 221-231.
- Ohlson, M. & Zackrisson, O. 1992. Tree establishment and microhabitat relationships in north Swedish peatlands. - *Can. J. For. Res.* 22: 1869-1877.
- Økland, B. 1994. Mycetophilidae (Diptera), an insect group vulnerable to forestry practices? A comparison of clearcut, managed and semi-natural spruce forests in southern Norway. - *Biodiv. Conserv.* 3: 68-85.
- Økland, R. H. 1989a. A phytoecological study of the mire Northern Kisselbergmosen, SE Norway. I. Introduction, flora, vegetation and ecological conditions. - *Sommerfeltia* 8: 1-172.
- Økland, R. H. 1989b. Hydromorphology and phytogeography of mires in inner Østfold and adjacent part of Akershus, SE Norway, in relation to SE Fennoscandian mires. - *Op. Bot.* 97: 1-122.
- Økland, R. H. 1990a. Vegetation ecology: theory, methods and applications with reference to Fennoscandia. - *Sommerfeltia Suppl.* 1: 1-233.
- Økland, R. H. 1990b. A phytoecological study of the mire Northern Kisselbergmosen, SE Norway. II. Identification of gradients by detrended (canonical) correspondence analysis. - *Nord. J. Bot.* 10: 79-108.
- Økland, R. H. 1990c. A phytoecological study of the mire Northern Kisselbergmosen, SE Norway. III. Diversity and habitat niche relationships. - *Nord. J. Bot.* 10: 191-220.
- Økland, R. H. 1994. Patterns of bryophyte associations at different scales in a Norwegian boreal spruce forest. - *J. Veg. Sci.* 5: 127-138.
- Økland, R. H. 1995. Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal spruce forests. I. Demography. - *J. Ecol.* 83: 697-712.
- Økland, R. H. 1996. Are ordination and constrained ordination alternative or complementary strategies in general ecological studies? - *J. Veg. Sci.* 7: 289-292.
- Økland, R. H. 1997a. Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal spruce forests. III. Six-year demographic variation in two areas. - *Lindbergia* 22: 49-68.
- Økland, R. H. 1997b. Vegetasjonsøkologi. Plantenes respons på økologiske gradienter - teorier, metoder og mønstre. - Oslo, Bot. Hage Mus, Univ. Oslo. .
- Økland, R. H. & Bendiksen, E. 1985. The vegetation of the forest-alpine transition in the Grunningsdalen area, Telemark, SE Norway. - *Sommerfeltia* 2: 1-224.
- Økland, R. H. & Eilertsen, O. 1993. Vegetation-environment relationships of boreal coniferous forests in the Solhomfjell area, Gjerstad, S Norway. - *Sommerfeltia* 16: 1-254.
- Økland, R. H. & Eilertsen, O. 1996. Dynamics of understory vegetation in an old-growth boreal coniferous forest, 1988-1993. - *J. Veg. Sci.* 7: 747-762.
- Økland, R. H., Økland, T. & Rydgren, K. 2000. Biologisk mangfold i bunnvegetasjonen i gransumpskog. - *Norsk Inst. Jord- Skogkartlegging Rapp.* 2000: 3: 1-79.

- Økland, R. H., Økland, T. & Rydgren, K. 2001. A Scandinavian perspective on ecological gradients in north-west European mires: reply to Wheeler and Proctor. - *J. Ecol.* 89: 481-486.
- Økland, R. H., Rydgren, K. & Økland, T. 1999. Single-tree influence on understorey vegetation in a Norwegian boreal spruce forest. - *Oikos* 87: 488-498.
- Økland, T. 1988. An ecological approach to the investigation of a beech forest in Vestfold, SE Norway. - *Nord. J. Bot.* 8: 375-407.
- Økland, T. 1990. Vegetational and ecological monitoring of boreal forests in Norway. I. Rausjømarka in Akershus county, SE Norway. - *Sommerfeltia* 10: 1-52.
- Økland, T. 1996. Vegetation-environment relationships of boreal spruce forest in ten monitoring reference areas in Norway. - *Sommerfeltia* 22: 1-349.
- Økland, T. 1999. Intensivovervåking i granskog: Endringer i undervegetasjonen i fem overvåkingsområder i løpet av en fem-års-periode. - *Norsk Inst. Jord- Skogkartlegging Rapp.* 1999: 1-33.
- Oksanen, J. & Minchin, P. R. 1997. Instability of ordination results under changes in input data order: explanations and remedies. - *J. Veg. Sci.* 8: 447-454.
- Pakarinen, P. & Rinne, R. J. K. 1979. Growth rates and heavy metal concentrations of five moss species in paludified spruce forests. - *Lindbergia* 5: 77-83.
- Palmer, M. W. 1988. Fractal geometry: a tool for describing spatial patterns of plant communities. - *Vegetatio* 75: 91-102.
- Palmer, M. W. & Dixon, P. M. 1990. Small-scale environmental heterogeneity and the analysis of species distributions along gradients. - *J. Veg. Sci.* 1: 57-65.
- Paratley, R. D. & Fahey, T. J. 1986. Vegetation-environment relations in a conifer swamp in central New York. - *Bull. Torrey Bot. Club* 113: 357-371.
- Pearsall, W. H. 1938. The soil complex in relation to plant communities. III. Moorlands and bogs. - *J. Ecol.* 26: ?
- Pearson, K. 1901. On lines and planes of closest fit to systems of points in space. - *Phil. Mag.* 6. Ser. 2: 559-572.
- Pelkonen, E. 1979. Männyn ja kuusen taimien kyvystä sietää tulva vuoden eri aikoina [Eng. Summ.: Seasonal flood tolerance of Scots pine and Norway spruce seedlings]. - *Suo* 30: 35-42.
- Persson, Å. 1961. Mire and spring vegetation in an area north of Lake Torneträsk, Torne Lappmark, Sweden. I. Description of the vegetation. - *Opera Bot.* 6: 1-187.
- Persson, Å. 1962. Mire and spring vegetation in an area north of Lake Torneträsk, Torne Lappmark, Sweden. II. Habitat conditions. - *Opera Bot.* 6:3: 1-100.
- Ponge, J.-F. & Ferdy, J.-B. 1997. Growth of *Fagus sylvatica* saplings in an old-growth forest as affected by soil and light conditions. - *J. Veg. Sci.* 8: 789-796.
- Prieditis, N. 1999. *Picea abies*- and *Fraxinus excelsior*-dominated wetland forest communities in Latvia. - *Pl. Ecol.* 144: 49-70.
- Proctor, M.C.F. 1995. Hydrochemistry of the raised bog and fens at Malham Tarn National Nature Reserve, Yorkshire, UK. - In: Hughes, J. M. R. and Heathwaite, A. L. (eds.), *Hydrology and hydrochemistry of British wetlands*, Wiley, Chichester, UK, pp. 273-289.
- Reid, W. 1998. Biodiversity hotspots. - *Trends Ecol. Evol.* 13: 275-280.
- Rochefort, L., Vitt, D. H. & Bayley, S. E. 1990. Growth, production, and decomposition dynamics of *Sphagnum* under natural and experimentally acidified conditions. - *Ecology* 71: 1986-2000.
- Rossi, R. E., Mulla, D. J., Journel, A. G. & Franz, E. H. 1992. Geostatistical tools for modeling

- and interpreting ecological spatial dependence. - Ecol. Monogr. 62: 277-314.
- Rundel, P. W. & Lange, O. L. 1980. Water relations and photosynthetic response of a desert moss. - Flora 169: 329-335.
- Rydgren, K. 1993. Herb-rich spruce forests in W Nordland, N Norway: an ecological and methodological study. - Nord. J. Bot. 13: 667-690.
- Rydgren, K. 1997. Vegetation-environment relationships of old-growth spruce forest vegetation in Østmarka Nature Reserve, SE Norway, and comparison of three ordination methods. - Nord. J. Bot. 16: 421-439.
- Rydgren, K., Økland, R. H. & Økland, T. 1998. Population biology of the clonal moss *Hylocomium splendens* in Norwegian boreal spruce forests. IV. Effects of experimental fine-scale disturbance. - Oikos 82: 5-19.
- Rydgren, K., Økland, T., Økland, R. H. & Storaunet, K. O. 1999. Hogstpåvirkning på biologisk mangfold og undervegetasjonens sammensetning i granskog. - Norsk Inst. Jord-Skogkartlegging Rapp. 1999: 1-35.
- Rydin, H. 1986. Competition and niche separation in *Sphagnum*. - Can. J. Bot. 64: 1817-1824.
- Rydin, H. 1993a. Interspecific competition between *Sphagnum* mosses on a raised bog. - Oikos 66: 413-423.
- Rydin, H. 1993b. Mechanisms of interactions among *Sphagnum* species along water-level gradients. - Adv. Bryol. 5: 153-185.
- Rydin, H. 1997. Competition among bryophytes. - Adv. Bryol. 6: 135-168.
- Samuelsson, G. 1917. Studien über die Vegetation der Hochgebirgsgegenden von Dalarna. - Nova Acta Regiae Soc. Scient. Upsal. Ser. 4 4: 1-252.
- Schneider, H. & Westman, C. J. 1987. Relation of peat nutrients to ground vegetation communities on sedge pine fens. - Suo 38: 29-36.
- Schuster, R. M. 1983. Reproductive biology, dispersal mechanisms, and distribution patterns in Hepaticae and Anthocerotae. - Sonderbände Naturw. Ver. Hamb. 7: 119-162.
- Senje, S. 1987. Østmarka. - Oslo, Gyldendal. .
- Shmida, A & Ellner, S. 1984. Coexistence of plants with similar niches. - Vegetatio 58: 29-55.
- Sigmond, E.M.O., Gustavson, M. & Roberts, D. 1984. Berggrunnskart over Norge 1: 1 000 000. - Trondheim, Norg. geol. Unders. .
- Sims, R. A., Cowell, D. W. & Wickware, G. M. 1982. Classification of fens near southern James Bay, Ontario, using vegetational physiognomy. - Can. J. Bot. 60: 2608-2623.
- Singsaas, S. 1990. Classification and ordination of the mire vegetation of Stormyra near Tynset, S Norway. - Nord. J. Bot. 9: 413-423.
- Sirén, G. 1955. The development of spruce forest on raw humus sites in northern Finland and its ecology. - Acta for. Fenn. 62: 1-408.
- Sjöberg, K. & Ericson, L. 1997. Mosaic boreal landscapes with open and forested wetlands. - Ecol. Bull. 46: 48-60.
- Sjörs, H. 1947. Myrvegetationen i övre Långanområdet i Jämtland. - Ark. Bot. K. Svenska VetenskAkad. 33A: 1-96.
- Sjörs, H. 1948. Myrvegetation i Bergslagen. - Acta Phytogeogr. Suec. 21: 1-299.
- Sjörs, H. 1950. Regional studies in north Swedish mire vegetation. - Bot. Not. 103: 173-222.
- Sjörs, H. 1952. On the relation between vegetation and electrolytes in north Swedish mire waters. - Oikos 2: 241-258.
- Sjörs, H. 1983. Mires of Sweden. - In: Gore, A. J. P. (ed.), Ecosystems of the world. 4B. Mires: swamp, bog, fen and moor: regional studies, Elsevier, Amsterdam, pp. 69-94.
- Skene, M. 1915. The acidity of *Sphagnum* and its relation to chalk and mineral salts. - Ann. Bot.

- (Lond.) 29: 65-87.
- Skrindo, A. & Økland, R. H. 1998. Fertilization effects and vegetation-environment relationships in a boreal pine forest in Åmli, S Norway. - *Sommerfeltia* 25: 1-90.
- Slack, N. G., Vitt, D. H. & Horton, D. G. 1980. Vegetation gradients of minerotrophically rich fens in western Alberta. - *Can. J. Bot.* 58: 330-350.
- Söderström, L. 1987. Dispersal as a limiting factor for distribution among epixylic bryophytes. - *Symp. Biol. Hung.* 35: 475-483.
- Söderström, L. 1988. The occurrence of epixylic bryophyte and lichen species in an old natural and managed forest stand in northeast Sweden. - *Biol. Conserv.* 45: 169-178.
- Söderström, L. 1989. Regional distribution patterns of bryophyte species on spruce logs in northern Sweden. - *Bryologist* 92: 349-355.
- Sokal, R.R. & Rohlf, F. J. 1995. *Biometry*, ed. 3. - New York, Freeman. .
- Stålfelt, M. G. 1937. Die bedeutung der Vegetation im Wasserhaushalt des Bodens. - *Svenska Skogsvårdsfören. Tidskr.* 35: 161-195.
- Stuanes, A., Ognér, G. & Opem, M. 1984. Ammonium nitrate as an extractant for soil exchangeable cations, exchangeable acidity and aluminium. - *Communs Soil Sci. Pl. Anal.* 15: 773-778.
- Stuiver, M. & Reimer, P. J. 1993. Extended ¹⁴C data base and revised Calib 3.0 age calibration programme. - *Radiocarbon* 35: 214-230.
- Succow, M. 1988. *Landschaftsökologische Moorkunde*. - Fischer, Jena.
- ter Braak, C. J. F. & Prentice, I. C. 1988. A theory of gradient analysis. - *Adv. Ecol. Res.* 18: 271-317.
- ter Braak, C.J.F. & Smilauer{v over s}, P. 1998. *CANOCO reference manual and userÇs guide to Canoco for Windows: software for canonical community ordination (version 4)*. - Ithaca, N.Y., Microcomputer Power. .
- Thunmark, S. 1942. Über rezente Eisenocker und ihre Mikro-organismengemeinschaften. - *Bull. Geol. Instn Univ. Uppsala* 29: 1-285.
- Tolonen, K. 1967. Über die Entwicklung der Moore im finnischen Nordkarelien. - *Annls Bot. Fenn.* 4: 219-416.
- Tonteri, T., Mikkola, K. & Lahti, T. 1990. Compositional gradients in the forest vegetation of Finland. - *J. Veg. Sci.* 1: 691-698.
- Trass, H. & Malmer, N. 1978. North European approaches to classification. - In: Whittaker, R. H. (ed.), *Classification of plant communities*, Junk, The Hague, pp. 201-245.
- Tuomikoski, R. 1942. Untersuchungen über die Untervegetation der Bruchmoore in Ostfinnland I. Zur Methodik der pflanzensoziologischen Systematik. - *Annls Bot. Soc. Zool.-Bot. Fenn. Vanamo* 17: 1-203.
- van Tooren, B. F. & During, H. J. 1988. Early succession of bryophyte communities on dutch forest earth banks. - *Lindbergia* 14: 40-46.
- Verhoeven, J. T. A., Maltby, E. & Schmitz, M. B. 1990. Nitrogen and phosphorus mineralization in fens and bogs. - *J. Ecol.* 78: 713-726.
- Viereck, L. A. 1970. Forest succession and soil development adjacent to the Chene river in interior Alaska. - *Arct. Alp. Res.* 2: 1-26.
- Vitt, D. H. & Chee, W.-L. 1990. The relationships of vegetation to surface water chemistry and peat chemistry in fens of Alberta, Canada. - *Vegetatio* 89: 87-106.
- Vitt, D. H., Crum, H. & Snider, J. A. 1975. The vertical zonation of *Sphagnum* species in hummock-hollow complexes in northern Michigan. - *Mich. Bot.* 14: 190-200.
- Vitt, D. H., Horton, D. G., Slack, N. G. & Malmer, N. 1990. *Sphagnum*-dominated peatlands of

- the hyperoceanic British Columbia coast: patterns in surface water chemistry and vegetation. - *Can. J. For. Res.* 20: 696-711.
- Vitt, D. H., Li, Y. & Belland, R. J. 1995. Patterns of bryophyte diversity in peatlands of continental western Canada. - *Bryologist* 98: 218-227.
- Vitt, D. H. & Slack, N. G. 1984. Niche diversification of *Sphagnum* relative to environmental factors in northern Minnesota peatlands. - *Can. J. Bot.* 62: 1409-1430.
- Wallén, B. 1987. Growth pattern and distribution of biomass of *Calluna vulgaris* (L.) Hull on an ombrotrophic peat-bog. - *Holarct. Ecol.* 10: 73-79.
- Wartenberg, D., Ferson, S. & Rohlf, F. J. 1987. Putting things in order: a critique of detrended correspondence analysis. - *Am. Nat.* 129: 434-448.
- Watson, E. V. 1960. Further observations on the bryophyte flora of the Isle of May. II. Rate of succession in selected communities involving bryophytes. - *Trans. Proc. Bot. Soc. Edinburgh* 39: 85-106.
- Wheeler, B. D. & Proctor, M. C. F. 2000. Ecological gradients, subdivisions and terminology of north-west European mires. - *J. Ecol.* 88: 187-203.
- Wheeler, B.D. & Shaw, S.C. 1995. A focus on fens - controls on the composition of fen vegetation in relation to restoration. - In: Wheeler, B. D.; Shaw, S. C.; Fojt, W. J., and Robertson, R. A. (eds.), *Restoration of temperate wetlands*, Wiley, Chichester, UK, pp. 49-72.
- Wheeler, B. D., Shaw, S. C. & Cook, R. E. D. 1992. Phytometric assessment of the fertility of undrained rich-fen soils. - *J. Appl. Ecol.* 29: 466-475.
- Whittaker, R. H. 1960. Vegetation in the Siskiyou Mountains, Oregon and California. - *Ecol. Monogr.* 30: 279-338.
- Whittaker, R. H. 1962. Classification of natural communities. - *Bot. Rev.* 28: 1-239.
- Whittaker, R. H. 1967. Gradient analysis of vegetation. - *Biol. Rev. Camb. Phil. Soc.* 42: 207-264.
- Witting, M. 1947. Katjonsbestämningar i myrvatten. - *Bot. Not.* 100: 287-304.
- Witting, M. 1949. Kalciumhalten i några nordsvenska myrvatten. - *Svensk Bot. Tidskr.* 43: 715-739.
- Wu, H., Sharpe, P. J. H., Walker, J. & Penridge, L. K. 1985. Ecological field theory: a spatial analysis of resource interference among plants. - *Ecol. Modelling* 29: 215-243.
- Yabe, K. & Onimaru, K. 1997. Key variables controlling the vegetation of a cool-temperate mire in northern Japan. - *J. Veg. Sci.* 8: 29-36.

APPENDIX

Appendix 1. List of the 212 species recorded in the 150 1-m² plots

- Acer platanoides*
Alnus glutinosa
Alnus incana
Betula spp.
Frangula alnus
Picea abies
Pinus sylvestris
Salix aurita
Salix aurita × *caprea*
Salix caprea
Salix myrsinifolia
Sorbus aucuparia
Viburnum opulus
Calluna vulgaris
Empetrum nigrum
Vaccinium myrtillus
Vaccinium oxycoccus
Vaccinium vitis-idaea
Alchemilla spp.
Anemone nemorosa
Athyrium filix-femina
Bistorta vivipara
Caltha palustris
Cardamine pratensis
Chrysosplenium alternifolium
Circaea alpina
Cirsium helenioides
Cirsium palustre
Corallorhiza trifida
Crepis paludosa
Dactylorhiza fuchsii
Dactylorhiza maculata
Drosera rotundifolia
Dryopteris expansa agg.
Epilobium palustre
Equisetum fluviatile
Equisetum pratense
Equisetum sylvaticum
Filipendula ulmaria
Fragaria vesca
Galium palustre
Geranium sylvaticum
Geum rivale
Gymnocarpium dryopteris
Hieracium spp.
Linnaea borealis
Listera cordata
Lycopodium annotinum
Lysimachia thyrsiflora
Maianthemum bifolium
Matteuccia struthiopteris
Melampyrum pratense
Melampyrum sylvaticum
Menyanthes trifoliata
Mycelis muralis
Orthilia secunda
Oxalis acetosella
Paris quadrifolia
Phegopteris connectilis
Polygonatum verticillatum
Potentilla palustris
Pteridium aquilinum
Prunella vulgaris
Pyrola minor
Ranunculus repens
Rubus chamaemorus
Rubus saxatilis
Solidago virgaurea
Trientalis europaea
Tussilago farfara
Valeriana sambucifolia
Viola palustris
Viola riviniana
Agrostis canina
Agrostis capillaris
Anthoxanthum odoratum
Calamagrostis arundinacea
Calamagrostis purpurea
Carex canescens
Carex canescens × *loliacea*
Carex chordorrhiza
Carex digitata
Carex echinata
Carex flava
Carex lasiocarpa
Carex loliacea
Carex nigra
Carex pallescens
Carex panicea
Carex pauciflora
Carex paupercula
Carex rostrata
Deschampsia cespitosa
Deschampsia flexuosa
Eriophorum angustifolium
Eriophorum vaginatum
Festuca altissima
Festuca rubra

- Glyceria fluitans*
Luzula pilosa
Melica nutans
Molinia caerulea
Phragmites australis
Atrichum undulatum
Aulacomnium palustre
Brachythecium populeum
Brachythecium reflexum
Brachythecium rutabulum agg.
Brachythecium salebrosum
Brachythecium starkei
Bryum pseudotriquetrum
Calliergon cordifolium
Calliergon richardsonii
Calliergonella cuspidata
Campylium stellatum
Cirriphyllum piliferum
Climacium dendroides
Dicranum fuscescens
Dicranum majus
Dicranum montanum
Dicranum scoparium
Fissidens adianthoides
Herzogiella striatella
Hylocomium splendens
Hylocomiastrum umbratum
Hypnum cupressiforme
Philonotis fontana
Plagiomnium affine
Plagiomnium elatum
Plagiomnium ellipticum
Plagiomnium medium
Plagiomnium undulatum
Plagiothecium denticulatum
Plagiothecium laetum
Plagiothecium succulentum
Plagiothecium undulatum
Pleurozium schreberi
Pohlia nutans
Polytrichum commune
Polytrichum formosum
Polytrichum strictum
Pseudobryum cinclidioides
Pseudotaxiphyllum elegans
Ptilium crista-castrensis
Rhizomnium magnifolium
Rhizomnium pseudopunctatum
Rhizomnium punctatum
Rhodobryum roseum
Rhytidiadelphus loreus
Rhytidiadelphus subpinnatus
Rhytidiadelphus triquetrus
Sanionia uncinata
Scorpidium revolvens
Straminergon stramineum
Tetraphis pellucida
Thuidium tamariscinum
Warnstorfia exannulata agg.
Warnstorfia fluitans
Sphagnum angustifolium
Sphagnum brevifolium
Sphagnum centrale
Sphagnum flexuosum
Sphagnum girgensohnii
Sphagnum magellanicum
Sphagnum quinquefarium
Sphagnum riparium
Sphagnum russowii
Sphagnum squarrosum
Sphagnum subsecundum
Sphagnum teres
Sphagnum warnstorffii
Aneura pinguis
Barbilophozia attenuata
Barbilophozia kunzeana
Barbilophozia lycopodioides
Blepharostoma trichophyllum
Calypogeia azurea
Calypogeia integristipula
Calypogeia muelleriana
Calypogeia neesiana
Cephalozia bicuspidata
Cephalozia lunulifolia
Cephalozia pleniceps
Cephaloziella spp.
Chiloscyphus polyanthos
Chiloscyphus profundus
Diplophyllum albicans
Harpanthus flotovianus
Jungermannia leiantha
Lepidozia reptans
Lophozia incisa
Lophozia longidens
Lophozia obtusa
Lophozia ventricosa agg.
Mylia taylorii
Pellia spp.
Plagiochila asplenioides
Ptilidium ciliare
Ptilidium pulcherrimum
Riccardia latifrons
Riccardia multifida
Scapania irrigua
Scapania paludosa
Scapania scandica
Scapania umbrosa
Scapania undulata
Cladonia cenotea
Cladonia chlorophaea agg.
Cladonia coniocraea
Cladonia digitata
Cladonia rangiferina
Cladonia squamosa

SOMMERFELTIA AND SOMMERFELTIA SUPPLEMENT

Vol. 1. A. Hansen & P. Sunding: Flora of Macaronesia. Checklist of vascular plants. 3. revised edition. 167 pp. NOK 140. (Jan. 1985; out of stock).

Vol. 2. R.H. Økland & E. Bendiksen: The vegetation of the forest-alpine transition in Gruningsdalen, S. Norway. 224 pp. NOK 170. (Nov. 1985).

Vol. 3. T. Halvorsen & L. Borgen: The perennial Macaronesian species of *Bubonium* (Compositae-Inuleae). 103 pp. NOK 90. (Feb. 1986).

Vol. 4. H.B. Gjørum & P. Sunding: Flora of Macaronesia. Checklist of rust fungi (Uredinales). 42 pp. NOK 50. (Dec. 1986).

Vol. 5. J. Middelborg & J. Mattsson: Crustaceous lichenized species of the Caliciales in Norway. 71 pp. NOK 70. (May 1987).

Vol. 6. L.N. Derrick, A.C. Jermy & A.C. Paul: Checklist of European Pteridophytes. xx + 94 pp. NOK 95. (Jun. 1987).

Vol. 7. L. Malme: Distribution of bryophytes on Fuerteventura and Lanzarote, the Canary Islands. 54 pp. NOK 60. (Mar. 1988).

Vol. 8. R.H. Økland: A phytoecological study of the mire Northern Kisselbergmosen, SE. Norway. I. Introduction, flora, vegetation, and ecological conditions. 172 pp. NOK 140. (Oct. 1989).

Vol. 9. G. Mathiassen: Some corticolous and lignicolous Pyrenomycetes s. lat. (Ascomycetes) on *Salix* in Troms, N Norway. 100 pp. NOK 85. (Oct. 1989).

Vol. 10. T. Økland: Vegetational and ecological monitoring of boreal forests in Norway. I. Rausjømarka in Akershus county, SE Norway. 52 pp. NOK 55. (June 1990).

Vol. 11. R.H. Økland (ed.): Evolution in higher plants: patterns and processes. Papers and posters presented on a symposium arranged on occasion of the 175th anniversary of the Botanical Garden in Oslo, June 5-8, 1989. 183 pp. NOK 150. (Dec. 1990).

Vol. 12. O. Eilertsen: Vegetation patterns and structuring processes in coastal shell-beds at Akerøya, Hvaler, SE Norway. 90 pp. NOK 85. (June 1991).

Vol. 13. G. Gulden & E.W. Hanssen: Distribution and ecology of stipitate hydneous fungi in Norway, with special reference to the question of decline. 58 pp. NOK 110. (Feb. 1992).

Vol. 14. T. Tønsberg: The sorediate and isidiate, corticolous, crustose lichens in Norway. 300 pp. NOK 330. (May 1992).

Vol. 15. J. Holtan-Hartwig: The lichen genus *Peltigera*, exclusive of the *P. canina* group, in Norway. 77 pp. NOK 90. (March 1993).

Vol. 16. R.H. Økland & O. Eilertsen: Vegetation-environment relationships of boreal coniferous forests in the Solhomfjell area, Gjerstad, S Norway. 254 pp. NOK 170. (March 1993).

Vol. 17. A. Hansen & P. Sunding: Flora of Macaronesia. Checklist of vascular plants. 4. revised edition. 295 pp. NOK 250. (May 1993).

Vol. 18. J.F. Ardévol Gonzáles, L. Borgen & P.L. Péres de Paz: Checklist of chromosome numbers counted in Canarian vascular plants. 59 pp. NOK 80. (Sept. 1993).

Vol. 19. E. Bendiksen, K. Bendiksen & T.E. Brandrud: *Cortinarius* subgenus *Myxaciium* section *Colliniti* (Agaricales) in Fennoscandia, with special emphasis on the Arctic-alpine zones. 37 pp. NOK 55. (Nov. 1993).

Vol. 20. G. Mathiassen: Corticolous and lignicolous Pyrenomycetes s.lat. (Ascomycetes) on *Salix* along a mid-Scandinavian transect. 180 pp. NOK 180. (Nov. 1993).

Vol. 21. K. Rydgren: Low-alpine vegetation in Gutulia National Park, Engerdal, Hedmark, Norway, and its relation to the environment. 47 pp. NOK 65. (May 1994).

Vol. 22. T. Økland: Vegetation-environment relationships of boreal spruce forests in ten monitoring reference areas in Norway. 349 pp. NOK 230. (May 1996).

Vol. 23. T. Tønsberg, Y. Gauslaa, R. Haugan, H. Holien & E. Timdal: The threatened macrolichens of Norway - 1995. 258 pp. NOK 220. (June 1996).

Vol. 24. C. Brochmann, Ø.H. Rustan, W. Lobin & N. Kilian: The endemic vascular plants of the Cape Verde islands, W Africa. 356 pp. NOK 230. (Dec. 1997).

Vol. 25. A. Skrindo & R.H. Økland: Fertilization effects and vegetation-environment relationships in a boreal pine forest in Åmli, S Norway. 90 pp. NOK 90. (Dec. 1998).

Vol. 26. A. Granmo: Morphotaxonomy and chorology of the genus *Hypoxylon* (Xylariaceae) in Norway. 81 pp. NOK 120. (Sept. 1999).

Vol. 27. A. Granmo, T. Læssøe & T. Schumacher: The genus *Nemania* s.l. (Xylariaceae) in Norden. 96 pp. NOK 135 (Sept. 1999).

Vol. 28. H. Krog: Corticolous macrolichens of low montane rainforests and moist woodlands of eastern Tanzania. 75 pp. NOK 135 (July 2000).

Vol. 29. Økland, R.H., Økland, T. & Rydgren, K. 2001: Vegetation-environment relationships of boreal spruce swamp forests in Østmarka Nature Reserve, SE Norway. 190 pp. NOK 155 (Sept. 2001).

Supplement Vol. 1. R.H. Økland: Vegetation ecology: theory, methods and applications with reference to Fennoscandia. 233 pp. NOK 180. (Mar. 1990).

Supplement Vol. 2. R.H. Økland: Studies in SE Fennoscandian mires, with special regard to the use of multivariate techniques and the scaling of ecological gradients. (Dissertation summary). 22 pp. NOK 35. (Dec. 1990).

Supplement Vol. 3. G. Hestmark: To sex, or not to sex... Structures and strategies of reproduction in the family Umbilicariaceae (Lecanorales, Ascomycetes). (Dissertation summary). 47 pp. NOK 55. (Dec. 1991).

Supplement Vol. 4. C. Brochmann: Polyploid evolution in arctic-alpine *Draba* (Brassicaceae). 37 pp. NOK 60. (Nov. 1992).

Supplement Vol. 5. A. Hansen & P. Sunding: Botanical bibliography of the Canary Islands. 116 pp. NOK 130. (May 1994).

Supplement Vol. 6. R.H. Økland: Boreal coniferous forest vegetation in the Solhomfjell area, S Norway: structure, dynamics and change, with particular reference to effects of long distance airborne pollution. 33 pp. NOK 43. (May 1995).

Supplement Vol. 7. K. Rydgren: Fine-scale disturbance in an old-growth boreal forest - patterns and processes. 25 pp. NOK 40. (May 1997).





INSTRUCTIONS TO AUTHORS:

SOMMERFELTIA accepts scientific papers of 32 printed pages or more, in English. The abstract must not exceed 300 words. The author is responsible for ensuring that the English is linguistically correct.

Manuscripts to SOMMERFELTIA must not have been published or accepted for publication elsewhere.

Manuscripts are subjected to peer reviewing by at least two reviewers, before acceptance or rejection is decided.

Authors of planned contributions to SOMMERFELTIA are recommended to contact the editor early in the writing process: manuscripts should, as far as possible, be prepared by the author to fit the layout of the series. Relevant WordPerfect codes on a discette, as well as further instructions, are obtained from the editor. The manuscript should be submitted in three paper copies or, by agreement with the editor, electronically.

Figures (incl. line drawings) should preferably be 16.0 cm broad and not higher than 23.6 cm – the type area. They are reduced to 87 % during the printing process. Narrower and broader figures may be accepted. Legends to figures should be included as a separate file. Tables (including headings) should be enclosed on a separate file. Tabulator stops should be used for vertical alignment of table columns. One open line should be left between the table heading and the table proper. Tables placed at right angles to normal text should be 23.6 cm broad and not more than 16.0 cm high. Tables divided on more pages can be accepted; on the second and later pages the table heading should be Tab. x (continued).

Figures and tables should be numbered separately and consecutively with Arabic numerals. Black and white photographs can be accepted after agreement with the editor. Coloured illustrations are normally accepted only when paid for by the author. Taxonomic keys should have right margins and be based on dichotomies. References should be written according to current practice in SOMMERFELTIA. SOMMERFELTIA prefers abbreviations of titles in accordance with the World List of Scientific Periodicals. Recent issues of SOMMERFELTIA (Vols 22-27) should be consulted for details of layout.

An author is supplied with ten copies free of charge. When there are more than one author, each receives eight copies free of charge. Additional copies may be ordered at subscription cost.

