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Vegetation-environment relationships of boreal coniferous forests in the Solhomfjell area, Gjerstad, S Norway

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Editor: Rune Halvorsen Økland.
Editor of this volume: Per Sunding.
Editorial Board: Scientific staff of the Botanical Garden and Museum.
Address: SOMMERFELTIA, Botanical Garden and Museum, University of Oslo, Trondheimsveien 23B, N-0562 Oslo 5, Norway.
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Publication from the TVLF (Supplies and Effects of Long-Distance Airborne Pollutants) programme of NMF (National Committee for Environmental Research): the project "Effects of Long-Distance Airborne Pollution on Boreal Coniferous Forest Vegetation".

Publication No. 27 from TOV (Terrestrial Monitoring Programme of the Directorate for Nature Management).

ISBN 82-7420-018-7

ISSN 0800-6865

Økland, R.H. & Eilertsen, O. 1993. Vegetation-environment relationships of boreal coniferous forests in the Solhomfjell area, Gjerstad, S Norway. - Sommerfeltia 16: 1-254. Oslo. ISBN 82-7420-018-7. ISSN 0800-6865.

The understory vegetation (vascular plants, bryophytes and lichens) in an area dominated by boreal coniferous forests is subjected to detailed ecological analysis. Two hundred meso sample plots (1 m^2) are used as basis for vegetation sampling, and provided with measurements of 33 environmental variables. Species abundance is recorded as frequency in 16 subplots. Parallel DCA and 2-dimensional LNMDS ordinations of meso sample plots were largely identical, both provided two coenocline axes interpretable in ecological terms. The first axis is interpreted as the response to a broad-scale topographical complex-gradient, made up of two independent complex-gradients; (1) a topography-soil depth complex-gradient in the pine forest (running from lichen-rich pine forests to submesic *Vaccinium myrtillus*-dominated spruce forests), and (2) a complex-gradient in soil nutrient status in the spruce forest. The second axis, mainly affecting the species composition of the bottom layer, is interpreted as a fine-scale paludification gradient. The causes of variation along these gradients are discussed: Desiccation tolerance is considered to act directly on the physiology of vascular plant species, setting their limits towards xeric sites. Similarly, cryptogams with optima in the more mesic sites are considered to be excluded from drier sites by physiological tolerance. Limits of cryptogams towards more mesic sites are, however, considered to be set by competitive ability (growth rates) in accordance with the competitive hierarchy theory. N availability is assumed to be the most important factor for differentiation of vascular plants along the nutrient gradient, while bryophytes are expected to respond to a complex of factors, including structural properties of the humus layer. Increasing N accumulation in the humus towards xeric sites may indicate oversaturation due to deposition of airborne NO_3^- or NH_4^+. Fine-scale paludification, mainly of a soligenous type, occurred in sloping terrain with shallow soil. The cryptogams apparently make up a competitive hierarchy also along the paludification gradient. No other coenoclines could be identified by analysis of 0.0625 m^2 micro sample plots, most probably because the response of vegetation to micro-scale environmental gradients (probably most important: the variation in microtopography) not essentially different from the meso-scale gradients, and because the importance of random processes increase towards finer scales. Structuring processes are discussed with reference to the observed patterns. The lack of a closed bottom layer in almost all sample plots is considered a strong indication of high importance of fine-scale disturbance and density-independent mortality in the investigated system, while interspecific competition is of lower importance. The methodology in vegetation ecological studies is discussed with particular reference to monitoring. The potential of an integrated concept using permanent plots, parallel investigation of vegetation and environmental parameters, and gradient analysis, is stressed. Several suggestions for future studies, based on this integrated approach, are made.

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

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CONTENTS

INTRODUCTION

During the 20th century, European forest soils have experienced considerable acidification, apparently due to the effects of long distance airborne pollutants (e.g., von Zeszchwitz 1982, C.O. Tamm & Hallbäcken 1988, Battarbee et al. 1989). Changes in the pH of topsoil and subsoil layers in a wide range of South Swedish deciduous and coniferous forest types have been documented by Falkengren-Grerup (1986, 1987), Hallbäcken & C.O. Tamm (1986), Falkengren-Grerup et al. (1987), and Falkengren-Grerup & Tyler (1991b). Indications of soil acidification in Norway have been provided by Dahl (1988) and Aune et al. (1989). Soil acidification has normally been accompanied by cation leaching (e.g., Falkengren-Grerup et al. 1987, Falkengren-Grerup & Tyler 1991b), and increased deposition of nitrate and ammonia has resulted in increased N content of the humus layer (cf. Abrahamsen 1980, 1984, Bjørnstad 1991).

Since the first reports of "new forest damages" from Central Europe, the causes and extent of forest decline have remained contorversial issues, particularly in Fennoscandia (see, e.g., reviews by Ulrich et al. (1979), Abrahamsen (1984), Schütt & Cowling (1985), Aamlid et al. (1990), and Abrahamsen et al. (1990)). The causal relationship between pollution and forest decline is, however, obvious in parts of Czechoslovakia, Poland and the former DDR (cf. Kubiková 1991). The relationship between airborne pollutants and vegetational change in these areas is also unanimous (Kubiková 1991). Well-documented vegetational changes due to airborne pollutants have also been reported by Wittig & Neite (1985) from Germany and Falkengren-Grerup (1989b) from S Sweden, in beech forest microsites receiving ample acidified stemflow water. Furthermore, regional trends in the heavy metal content of plants, notably mosses, have been found to be strongly correlated with atmospheric deposition patterns (Gydesen et al. 1983, Rühling et al. 1987, Rinne & Mäkinen 1988, Steinnes et al. 1988). More recently, "new moss damages" have been reported from Norwegian boreal coniferous forests, particularly in regions and at times when the deposition rates have been high (R. Økland & Eilertsen 1988, Frisvoll 1989, Frisvoll & Flatberg 1990, Flatberg & Frisvoll 1991).

Several recent studies have addressed the extent of vegetational response to the changing environmental conditions in European forests. Most studies have reported increase in acid-tolerating and/or nitrophilous species (e.g., Wittig et al. 1985, Falkengren-Grerup 1986, Wittig & Werner 1986, Falkengren-Grerup & Eriksson 1990, Falkengren-Grerup & Tyler 1991a), although other, more or less contradictory trends have also been reported (e.g., Kuhn et al. 1987, Lähde & Nieppola 1987, Bjørnstad 1991). Reasons for these apparent controversies may be (1) insufficient material for statistical significance of trends, (2) interactions with other temporal trends, e.g., natural acidification in response to ageing of the forest stand (C.O. Tamm & Hallbäcken 1988), (3) inexact localization of plots, and (4) subjective interpretation of temporal trends.

The ground vegetation is an important part of the forest ecosystem, both in terms of biomass and function (Hesselman 1937, Stålfelt 1937a, Sirén 1955, van Cleve et al. 1983, Oechel & van Cleve 1986). There are good reasons to believe that the ground vegetation is more sensitive than trees to environmental change: (1) The number of vascular plant species in forests is high, representing a considerable number of vegetative and generative strategies (cf. Grime 1979, Grime & J. Anderson 1986). (2) Vascular plants depend on the humus layer for uptake of water and nutrients (cf. Kujala 1926a, Kivenheimo 1947). (3) The number of species in the bottom layer (bryophytes and lichens) and the strategies they represent is also high (cf. Kujala 1926b, During 1979, Slack 1988, 1990, Rincon & Grime 1989, Grime et al. 1990, R. Økland 1990c, Rogers 1990). (4) The uptake of water and nutrients in most cryptogamic species is directly from the atmosphere (C.O. Tamm 1953, Rühling & Tyler 1970).

In Norway, sample plots used for vegetation studies have only exceptionally been permanently marked (Sunding 1985), and no short-cuts to the answers of questions relating to vegetation change are therefore possible. The extent of vegetational change in Fennoscandian boreal coniferous forests due to airborne pollution is at present not known. Thus there is an urgent need for establishment of scientific reference sites in boreal coniferous forests, allowing for simultaneous monitoring of vegetation, environmental conditions and tree variables (T. Økland 1990). In this starting phase of vegetation monitoring, particular attention should be paid to choice of methods, in order to enable identification of the smallest possible changes as early as possible (T. Økland 1990).

Understanding the causes of changes in vegetation and environmental factors prerequisites in-depth knowledge of the vegetational response to variation along environmental gradients. Furthermore, the extent of "natural" dynamics in vegetation and the environment has to be known (C.O. Tamm & Hallbäcken 1988, T. Økland 1990).

Each of the Fennoscandian countries have developed independent traditions of forest ecological research, but all share a strong emphasis on detailed description of fine-scale patterns (Whittaker 1962, R. Økland & Bendiksen 1985, R. Økland 1990a).

In Finland, vegetation ecology has remained an integral part of forest research. The system of forest site-types, proposed by Cajander (1909), has been most influential for the whole 20th century. According to the Cajanderian view, the ground vegetation in forests closely reflects the site conditions, thus the site and its vegetation should be jointly classified (Cajander 1921). The forest site-types normally occurring on bedrock poor in nutrients were ordered in an ecological series from dry-and-poor to wet-and-rich (Cajander 1909, Ilvessalo 1922, Kujala 1929, Kalela 1961, Kujala 1961, cf. also Frey 1978). The existence of such a main gradient in environment and vegetation has been taken as the basis for many subsequent studies (e.g., Valmari 1921, Aaltonen 1925, Kujala 1926a, 1926b, Sirén 1955, Kivenheimo 1947, Yli-Vakkuri 1961).

In Sweden, as well as in Finland, forest vegetation ecology has maintained an important position in forest research. Classification of forest vegetation has partly been made by description of "plant communities" of local validity (e.g., Hesselman 1936, Malmström 1937), more or less in accordance with the Uppsala school of phytosociology (cf. Whittaker 1962, Trass & Malmer 1978, R. Økland & Bendiksen 1985), partly by development of a distinctive N Swedish forest site-type classification (Eneroth 1931, 1934, 1937, Arnborg 1964, 1989, Arnborg & Ebeling 1978). The latter resembles the Finnish forest site-type system, but the unidimensional gradient model is replaced by a model including two perpendicular axes; soil moisture and soil nutrient status. Highlights of Swedish forest ecological research were the studies of processes in the humus layer and their importance for the vegetation (e.g., Hesselman 1917, 1926, 1937, O. Tamm 1920, 1931, Romell 1935, Romell & Malmström 1945).

In the early history of forest ecological research in Norway (as well as in Sweden), the focus was on ecological problems and vegetation description was informal. The important papers and monographs by Glømme and Mork (e.g., Glømme 1928, 1932, Mork 1938, 1942, 1946), are highlights of this period. But unlike the other Nordic countries, the Norwegian forest ecological research during the 1960s and 1970s split into one forestry-related branch emphasizing soil processes and the abiotic environment (e.g., Bjor 1963, 1971, Mork 1968), and another branch strongly emphasizing vegetation classification by the methods of the Braun-Blanquet school. The latter line of research has resulted in the publication of several local or regional phytosociological surveys (e.g., Dahl et al. 1967, Kielland-Lund 1967, 1973, 1981, Aune 1973, Bjørndalen 1980). Focus has been on characterization of phytocoena and their relationships to the environment rather than on vegetational responses to environmental factors (cf. R. Økland & Bendiksen 1985, R. Økland 1990a). In a continuously varying vegetation, the adequacy of devoting most of the research effort to classification (as a goal in itself) should be seriously questioned (R. Økland & Bendiksen 1985 and references quoted therein).

The development of numerical techniques in vegetation ecology during the last 30 years has enabled testing of hypotheses emerging from subjective observations. However, the number of recent studies of Fennoscandian boreal coniferous forests using multivariate methods is remarkably low (e.g., Bjørndalen 1981, Oksanen 1983, Kuusipalo 1985, R. Økland & Bendiksen 1985, Lahti & Väisänen 1987, T. Økland 1990, Tonteri et al. 1990a, 1990b, Heikkinen 1991). There are indications in some of these studies that the main gradient in boreal forest vegetation is the gradient from lichen-rich pine forests to mesic or wet herb- and fern rich spruce forests, as assumed in the Finnish site-type approach (Lahti & Väisänen 1987, Tonteri et al. 1990a), although the ecological basis for this differentiation remains obscure (cf. R. Økland & Bendiksen 1985). The results of T. Økland (1990) indicate that several environmental gradients may be of importance for the differentiation of vegetation within a restricted area, including gradients in soil nutrient status and soil moisture. The environmental variables mostly vary in a complex and multidimensional manner (T. Økland 1988, 1990, Allen & Peet 1990), and their intercorrelations are often difficult to understand.

The fundamental tasks of forest vegetation ecological research in a vegetational continuum (in response to continuous variation in environmental variables, cf. R. Økland & Bendiksen 1985) is the establishment of major coenoclines (vegetational gradients), the complex-gradients causing them, and the spatial scales on which they operate. A gradient reference frame (R. Økland & Bendiksen 1985) is necessary to systematize our present knowledge, and to improve our understanding of patterns and processes (including species responses to major complex-gradients, interactions between layers, relative importance of competitive interactions (between and within species) and abiotic factors for the vegetation structure, rate of vegetation change under natural conditions, etc.). Furthermore, improved knowledge of present gradient relationships is necessary to interpret temporal changes. The methodological challenges involved in objectivization of sample placement, quantification of species abundances and data treatment are considerable (cf. T. Økland 1988, 1990, R. Økland 1990a).

After thirty years with access to ordination techniques, there has been a considerable rationalization among available methods (cf. Gauch et al. 1977, 1981, Minchin 1987). The two methods most popular at present are detrended correspondence analysis (DCA) and variants of (local nonmetric) multidimensional scaling (LNMDS), preferred by different authors for different reasons. Claims for favourability of LNMDS variants have mostly been based upon performance in tests with simulated data (e.g., Kenkel & Orlóci 1986, Minchin 1987), while DCA has mainly been preferred for its apparent success with field data and its practical advantages (Kent & Ballard 1988, Peet et al. 1988). The relative success of different ordination techniques appears to be dependent on data set properties (Minchin 1987, R. Økland 1990a), indicating that parallell use of the two methodological concepts for ordination of the same data-set is advantageous (R. Økland 1990a, 1990b). However, such a combined approach is, however, rarely seen (cf. Oksanen 1983).

The aim of the present study is to establish a reference site for forest vegetation ecological studies in a S Norwegian area with high deposition rates for airborne pollutants. This implies: (1) to give a thorough description of the present vegetation patterns and variation in environmental variables at the reference site, (2) to find the most important gradients in vegetation and discuss (a) their dependence on ecological complex-gradients and (b) important processes in the boreal forest ecosystem, and (3) to evaluate different methods for use in vegetation ecological monitoring studies, including (a) sampling strategies, and (b) ordination techniques.

THE INVESTIGATION AREA

The investigation area is situated within the Solhomfjell forest reserve, Gjerstad municipality, Aust-Agder county, S Norway (Fig. 1). The distance to the outer coastal line is ca. 38 km. The area of the reserve is 10.25 km^2, of which the investigation area comprises about 2 km^2 in the altitudinal interval 350-480 m (Fig. 2). The UTM grid reference is 32V ML 86-92, 33-36, and the geographic position is 8°58´E, 58°58´N.

GEOLOGY AND GEOMORPHOLOGY

The area belongs to the central-southern Norwegian Precambrian, consisting mainly of gneisses with intrusions of granites and pegmatite (Oftedahl 1980, Sigmond et al. 1984). According to Børset (1979) the area around Svarttjern (the eastern part of the investigation area) consists of gneissic granites with large pegmatite intrusions, while the Solhomfjell area

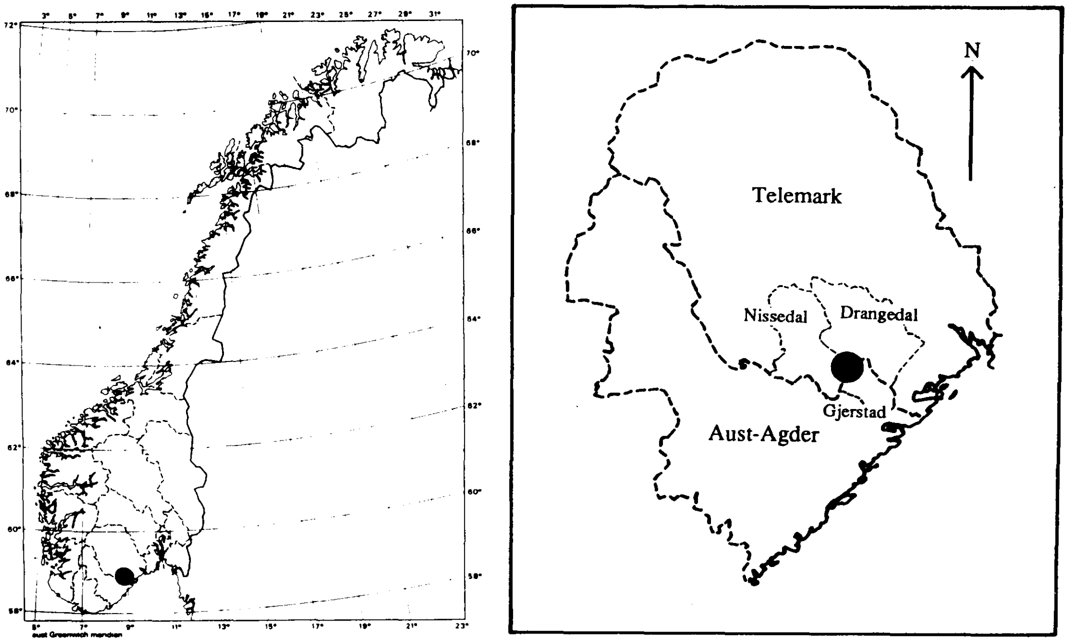


Fig. 1. Maps of Norway (left) and the counties Aust-Agder and Telemark (right) showing the position of the investigation area (dot) close to the border between Gjerstad, Drangedal and Nissedal municipalities.

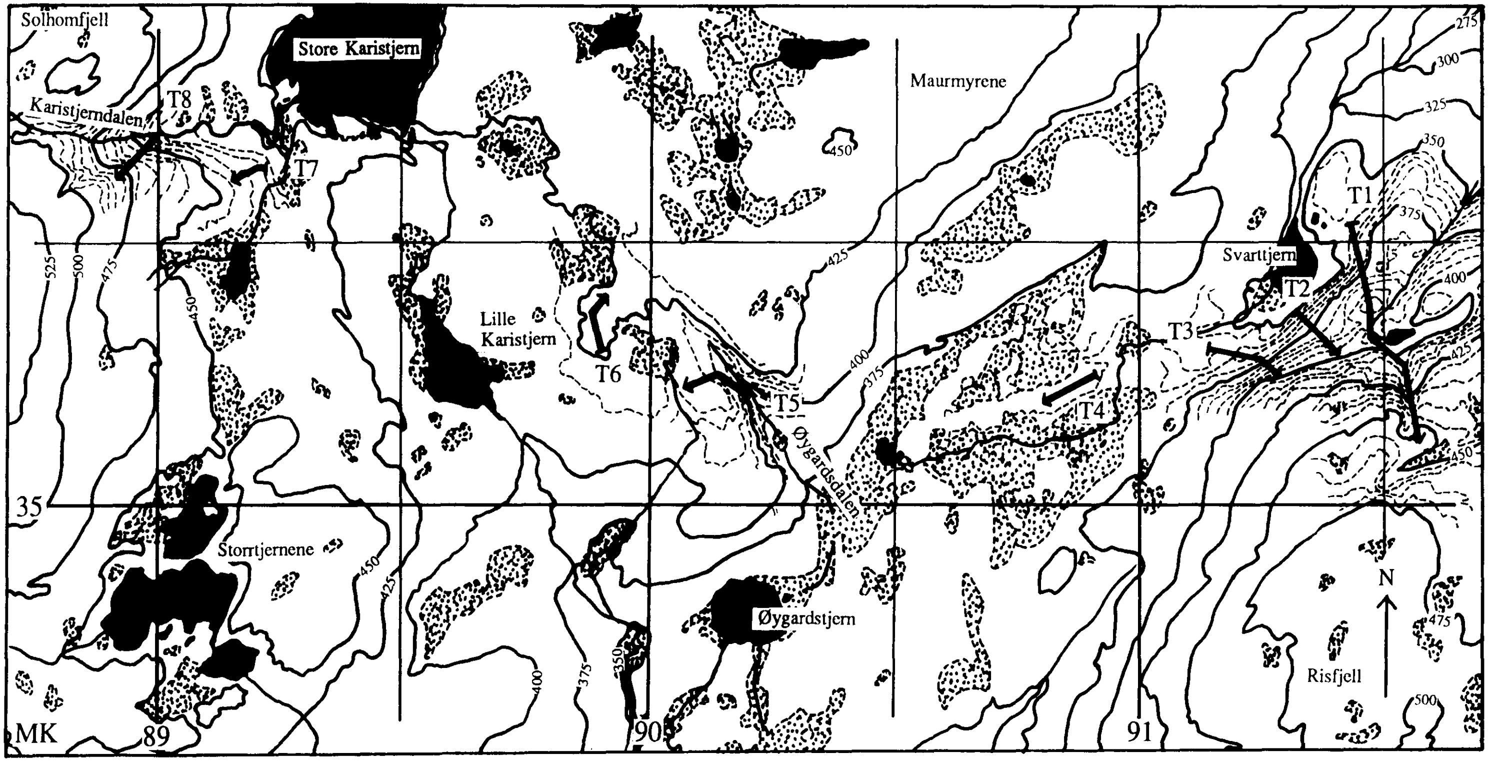


Fig. 2. The investigation area, with transects T1-T8 and UTM grid (500·500 m) superimposed (part of 100·100 km square 32V:MK). Contour interval 25 m; interval between additional contours (broken lines) 5 m. Altitudes in m. Black - lakes and tarns. Dots enclosed within broken line - mires.

(the western part of the investigation area) consists of pale granites with numerous pegmatite intrusions and locally a more gneissic structure.

The investigation area is situated in a hilly landscape, with peaks up to 653 m (Solhomfjell), rising from a plateau at 350-400 m, and surrounded by deep valleys at all margins.

Morainic deposits in the investigation area are sparse and generally very shallow or absent, except from sheltered sites. Thicker deposits are encountered southeast of Svarttjern, but even there the deposits are interrupted by rock outcrops and talus slopes. West and north of Svarttjern, in the direction of Solhomfjell, the deposits are generally very shallow and form a mosaic with bare rock. Extensive areas devoid of morainic deposits occur. The soil is thin, soil depths above 50 cm are rarely encountered except southwest of Svarttjern.

Peat covers extensive areas. Mires are quantitatively most important on the plateaux, but also occur in sloping terrain. The peat is mostly shallow. The mires mostly belong to the sloping (soligenous) fen complex type (cf. R. Økland 1989a), often consisting of several narrow segments splitting the forest into smaller stands.

CLIMATE

Temperature. The nearest meteorological station, Tveitsund, is situated at 250 m, 20 km WNW of Svarttjern. Tab. 1 shows temperature normals 1961-90 at Tveitsund, corrected for altitude according to Laaksonen (1976). Annual mean temperature in the normal period is 4.2 °C, mean temperatures for the warmest (July) and coldest (February) months are 14.4 and -5.5 °C, respectively, giving an annual temperature amplitude of 19.9 °C.

Precipitation. Precipitation normals 1961-90 for the nearest station, Gjerstad (some 12 km ESE of the investigation area, at 250 m, ca. 25 km from the coast), are given in Tab. 1. The annual precipitation normal, 1290 mm, indicates a humid climate. Precipitation peaks in autumn, as typical of oceanic and suboceanic climates. Own observations indicate that the general cloudiness and rainfall intensity increases from the Gjerstad village (with the rain gauge) in direction of the investigation area. However, Førland (1976), in his account of the

Tab. 1. Normals and means for some meteorological parameters measured at stations close to the investigation area.

Parameter	Station	Month												Year
		1	2	3	4	5	6	7	8	9	10	11	12	
Precipitation	Gjerstad 1961-90	105	77	82	65	89	81	106	127	145	165	146	101	1290
Temperature	Tveitsund 1961-90	-4.8	-5.5	-1.5	2.4	8.0	12.8	14.4	13.2	9.1	5.2	0.1	-2.8	4.2
Wind force (m/s)	Tveitsund 1967-91	1.3	1.0	1.2	1.1	1.1	1.3	1.1	0.9	1.2	1.4	1.1	1.5	1.2
Main wind direction (°)	Tveitsund 1967-91	150	300	300	300	210	210	210	210	300	210	150	300	

Tab. 2. Wind directions, percentage distribution. Mean 1967-91 for the meteorological station Tveitsund.

0°	30°	60°	90°	120°	150°	180°	210°	240°	270°	300°	330°
3.6	2.6	4.3	2.7	1.8	5.9	4.9	7.6	3.3	5.2	7.7	6.0

altitudinal dependence of precipitation, indicates a precipitation maximum 20 km off the outer coastal line in the Sørlandet region.

Wind. Tab. 1 gives a survey of the prevailing wind directions at Tveitsund throughout the year; NW vinds dominate in winter, SW winds in summer. On an annual basis, the dominant wind directions are SE-SW-NW.

Snow cover. The area has a stable snow cover, normally lasting from November to April.

CONSERVATIONAL STATUS, FOREST HISTORY AND HUMAN INFLUENCE

Svarttjern and Solhomfjell Forest Reserve has been owned by the Norwegian state from 1956. The area was administratively protected 13 August 1970. In 1976, a proposal for protection of a 10.25 km^2 by law as a Nature Reserve was forwarded. Only a small deciduous forest area, Napane, 1 km N of Svarttjern, was included in the deciduous forest reserve plan, passing Parliament in 1977, while the proposal for a large reserve was temporarily postponed, awaiting a national plan for coniferous forest reserves. This plan has now been forwarded, and is expected to pass the Parliament in June 1993. The investigation is in its entirety included in the future Solhomfjell Nature Reserve.

The present forest reserve and its immediate surroundings belonged to Eikeland ironworks until 1878. In general, upper Gjerstad was an important area for forestry and for haymaking. Information on logging, mowing and other activities in the forests of this area in the second half of the 19th century, have been collected by Lars Skjeldsø (in Vestad 1979) and by Gjerstad Historielag (1974). None of these references indicate that logging took place prior to year 1900 within the limits of the reserve.

Several private owners possessed the area between 1878 and 1956. A log cabin for forest workers was built close to Svarttjern in 1912. No organized logging was, however, undertaken in the present reserve. J. von Ubisch, forester in charge employed by the last private owner (Harboe, from 1932), assessed the pristine forest in the Svarttjern area so valuable that no logging was performed (K. Espeland, pers. comm.). Extensive logging has been performed outside the reserve in all directions after the takeover by the Norwegian state.

There are no reports of large forest fires from the investigation area (Directorate for State forests, Sørlandet forvaltning, unpubl.). Fire scars have been observed on some pine trees close to the border onto the reserve as well as within the reserve, in the Svarttjern area. Trees with fire scars do not occur in the vicinity of investigated sample plots.

Hafsten (1985) estimated the spruce immigration in the area to have taken place around A.D. 1000 (a radiocarbon dating from Vegårshei some 20 km S of the investigation area is at 1130±70 BP.).

In 1993, the reserve area appears an old pristine forest. The only tree-felling agent of importance is, and has been, beaver, *Castor fiber*, which has selectively cut *Betula pubescens*, *Populus tremula* and other deciduous trees. Fallen logs occur frequently. There was a considerable variety of forest age and structure within the investigation area. In the Svarttjern area, mature spruce individuals were measured to be 50-200 years old (Børset 1979), with trunk diameters of 25-50(-90) cm and heights up to 30 m (cf. also Appendix 3). Pine trees were generally older than the spruce, with trunk diameters up to 70 cm, heights up to 25 m, and measured ages up to 470 years.

PHYTOGEOGRAPHY

The humid, suboceanic climate and the poor bedrock with shallow quaternary deposits provided basis for a flora with predominance of more or less oceanic plant species. In the phytogeographic terminology of Bendiksen & Halvorsen (1981), later amended by R. Økland & Bendiksen (1985) and R. Økland (1989a), the western species were the most important. The mires were dominated by the slightly western *Erica tetralix* and *Narthecium ossifragum*, while the more widespread species *Blechnum spicant* and *Sphagnum molle* occurred frequently. Eastern species were few (*Scheuchzeria palustris* occurred on poor mires), as were warmth-demanding, southeastern species (*Hepatica nobilis* not infrequent on lower slopes, with *Acer platanoides*). Southern species were prominent in the low-situated parts of the area; e.g., *Festuca altissima*, *Quercus* spp., *Sanicula europaea* and *Taxus baccata*. *Betula nana* was the most prominent among the northern species, frequent in mires all over the area.

Abrahamsen et al. (1984) and Dahl et al. (1986) considered the area to belong to the boreo-nemoral (or hemiboreal) zone in the system of vegetation regions by Ahti et al. (1968). However, the area possessed several traits suggesting its inclusion in the southern boreal zone: (1) The dominant position of coniferous forest, deciduous forest fragments only occurring when aspect and local conditions were particularly favourable. (2) The presence of southern species in favourable sites, mostly at lower altitudes. (3) The common occurrence of *Betula nana* in mires throughout the area. (4) The temperature climate. Above 450 m, the vegetation and climatic conditions suggested middle boreal conditions, and the deciduous forest element disappeared.

PREVIOUS INVESTIGATIONS IN THE AREA

Mires have been described by Moen (1972, 1974). The vegetation was surveyed by O. Børset and O.O. Moss in 1977, and the bird fauna in 1978 (Børset 1979). Studies of the macromycetes have been published by Brandrud (1988) and Gulden et al. (1992).

MATERIALS AND METHODS

The field work was carried out in 1988.

THE SAMPLING DESIGN

A combination of systematic and restricted random sampling techniques was used for placement of sample plots. Eight transects were selected subjectively to cover the variation in boreal forest vegetation in the investigation area, as well as the variation in topography, slope, aspect, etc. Most transects were running from hilltop to valley bottom, but level transects were also included. Each tenth meter along the transects was a potential site for the lower left corner of a macro sample plot, 16 m^2, with its left margin along the transect line (Fig. 3). Positions were rejected if they included (1) mires, tarns or elements of ecosystems other than forest, (2) more than 50 % naked rock, (3) walls higher than 1 m, or (4) boulder stones with diameter larger than 1 m. The total number of macro sample plots, 100, was distributed on the transects according to transect length. Within each transect, the desired number of sample plots were randomly chosen from the accepted transect positions.

Each macro sample plot was divided into 16 subplots, 1 m^2 each. Two randomly chosen subplots, constrained to be situated along the margin of the macro plot, were fixed to be taken as meso sample plots (Fig. 3). Meso plots were rejected if they included (1) more than 25 % naked rock, (2) walls higher than 0.25 m, (3) boulder stones with diameter larger than 0.25 m, or (4) a tree higher than 2 m, rooted within the plot. A rejected meso plot was replaced by another macro subplot, selected from a fixed priority list. Meso plot corners were permanently marked by subterranean aluminium tubes.

Each meso sample plot was divided into 16 subplots, 0.0625 m^2 each. As with the meso plots, two subplots were fixed to be used as micro sample plots. The corners of the micro sample plot were permanently marked.

The sample sets included 100 macro sample plots, numbered MA 1-100. The number of meso sample plots was 200, the 100 meso plots along the lower edge of the macro plot (cf. Fig. 3) were numbered ME 1-100, the 100 plots along the upper edge numbered ME 101-200. The last two figures of the meso sample plot number thus equalled the macro plot number. The number of micro sample plots was 400. The 100 micro sample plots along the lower edge of ME 1-100 were numbered MI 1-100, the 100 micro sample plots along the upper edge of ME 1-100 were numbered MI 101-200. similarly, the micro sample plots along the lower edge of ME 101-200 were numbered MI 201-300 and the micro plots along the upper edge of ME 101-200 were numbered MI 301-400.

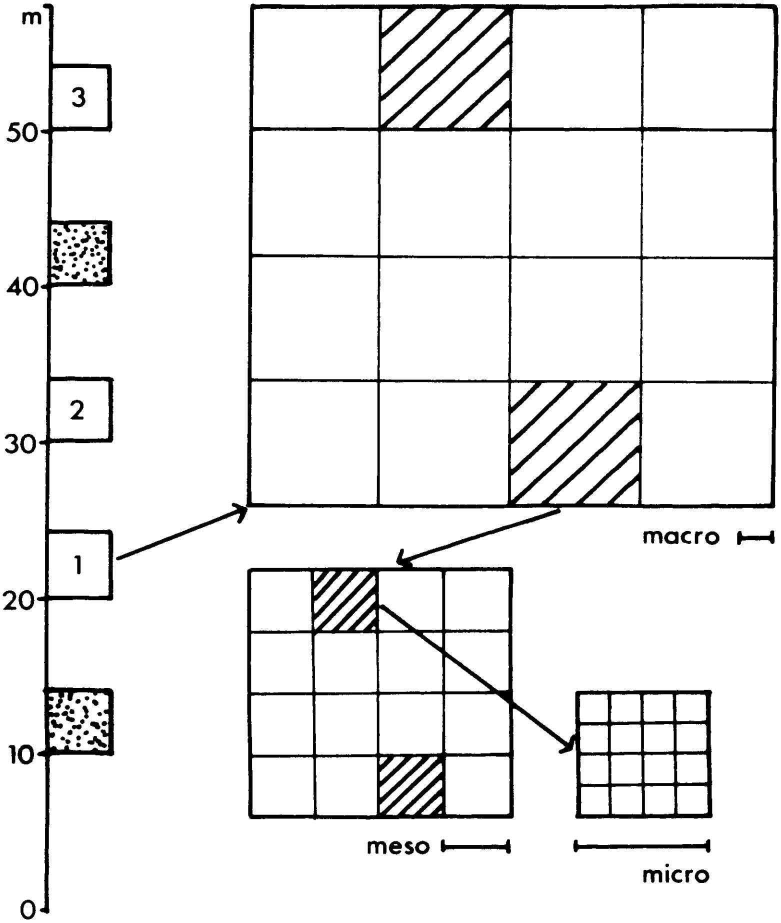


Fig. 3. The sampling scheme. Left: One transect with 3 accepted (numbered) and 2 rejected (dotted) macro sample plots. Above right: Sampling within the macro sample plots; two meso sample plots hatched. Below right: Sampling within the meso sample plot; meso subplots taken as micro plots hatched. Rule = 0.25 m.

RECORDING OF VEGETATION

As the vegetation of the field and bottom layers (vascular plants including lignified species less than 80 cm high, bryophytes and lichens) was the main object of this study, the tree and shrub layers were treated as environmental variables influencing the lower layers, see pp. 21-23. Vegetation was analyzed at the meso and micro scales (plot sizes 1 and 0.0625 m^2, respectively). Presence/absence of all species was recorded for each subplot. For vascular plants, presence by cover and presence by rooting were both recorded. Frequency in subplots was calculated for each species and each meso and micro sample plot. For vascular plants, frequency was calculated from presence by cover. Advantages of frequency in subplots over cover estimation as a method for recording species abundances, are discussed by T. Økland (1988), also see R. Økland (1990a).

The following vegetational data sets were subjected to further analysis:

ME 200, containing frequency in subplots data for 171 species in 200 meso sample plots. The ME 200 data set was divided into two subsets; *Subset A* (spruce forest) with 121 and *Subset B* (pine forest) with 79 sample plots, according to sample plot positions along the first DCA axis in the ordination of the ME 200 data set (cf. p. 48 and Appendix 1). Fifty sample plots in Subset A are included in the "Terrestrial monitoring programme" (TOV) of the Directorate for Nature Management (see Appendix 1). The ME 200 data set was split onto two subsets; *MEV 200* with 65 vascular plant species and *MEB 200* with 106 cryptogamic species (bryophytes and lichens). As two of the MEB 200 sample plots were devoid of species, this data set only includes 198 samples.

ME S3200, presence/absence data for 171 species in 3198 meso subplots (2 subplots were devoid of species).

MI 400, containing frequency in subplots data for 144 species in 400 micro sample plots.

For each plot, several biotic variables were recorded:

CC - total cover in the field layer.

CD - total cover in the bottom layer.

N-TOT - total number of species in the sample plot.

N-VAS - number of vascular plants in the sample plot.

N-BOT - number of bryophytes (*N-BRY*) and lichens (*N-LIC*) in the sample plot.

RECORDING OF ENVIRONMENTAL VARIABLES

Environmental variables were registered for (1) background information, (2) interpretation of variation in vegetation, and (3) monitoring changes in vegetation and environmental variables over time. The environmental parameters of the first and second groups mainly follow T. Økland (1989, 1990), and are described below. Variables exclusively belonging to the third group are the same as recorded in NIJOS' national grid of forest monitoring sites (Rørå et al. 1988, also see T. Økland 1990), and will not be further treated here. The environmental variables included (Tab. 3) can conveniently be divided into macro scale variables, meso scale variables, and meso scale humus layer variables.

Background information and tree measurements

For each macro sample plot, the exact position of all trees, their canopy perimeters, fallen logs, stumps, boulder stones, naked rock, as well as special details, were mapped. All trees (> 2 m high) rooted within a 64 m^2 plot having the 16 m^2 macro sample plot in the centre, and all other trees with canopies covering the macro plot, were mapped as well. Mapped trees were numbered consecutively, and subjected to the following measurements:

Tab. 3. Environmental parameters; number, abbreviation, unit of measurement, range of scale, frequency distribution, and transformation applied.

No	Abbrev.	Parameter	Unit	Range	Distribution	Transformation
01	MA Slo	Slope	°	0-90	uniform	no
02	MA Asf	Heat index		0-200	uniform	no
03	MA Ter	Terrain form		0-5	uniform	no
04	MA Une	Surface unevenness		1-4	uniform	no
05	MA S d	Soil depth		1-4	uniform	no
06	MA Bas	Basal area		0-∞	uniform	no
07	MA Can	Canopy cover		0-∞	uniform	no
08	ME Slo	Slope	°	0-90	normal-uniform	no
09	ME Asf	Heat index		0-200	uniform	no
10	ME Une	Unevenness		0-∞	lognormal	ln (1+x)
11	ME Con	Convexity		-∞-+∞	normal	no
12	ME Smi	Soil depth, minimum	cm	0-∞	lognormal	ln (1+x)
13	ME Sme	Soil depth, median	cm	0-∞	lognormal	ln (1+x)
14	ME Sma	Soil depth, maximum	cm	0-∞	lognormal	ln (1+x)
15	ME Lit	Litter index		0-∞	lognormal	ln (1+x)
16	ME Bas	Basal area		0-∞	uniform	no
17	Mois	Soil moisture	vol. %	0-100	normal	no
18	LI	Loss on ignition	%	0-100	bimodal	no
19	pH_{H20}	pH, aquous solution		0-14	normal	no
20	pH_{CaCl2}	pH, measured in $CaCl_2$		0-14	normal	no
21	Ca	Exchangeable Ca	ppm/LI	0-∞	lognormal	ln (1+x)
22	Mg	Exchangeable Mg	ppm/LI	0-∞	lognormal	ln (1+x)
23	Na	Exchangeable Na	ppm/LI	0-∞	lognormal	ln (1+x)
24	K	Exchangeable K	ppm/LI	0-∞	lognormal	ln (1+x)
25	H	Exchangeable H	ppm/LI	0-∞	± lognormal	ln (1+x)
26	N	Total N	weight %/LI	0-100	± lognormal	ln (1+x)
27	P-AL	Total P	ppm/LI	0-∞	lognormal	ln (1+x)
28	Al	Exchangeable Al	ppm/LI	0-∞	lognormal	ln (1+x)
29	Fe	Exchangeable Fe	ppm/LI	0-∞	lognormal	ln (1+x)
30	Mn	Exchangeable Mn	ppm/LI	0-∞	lognormal	ln (1+x)
31	Zn	Exchangeable Zn	ppm/LI	0-∞	± lognormal	ln (1+x)
32	P	Exchangeable P	ppm/LI	0-∞	lognormal	ln (1+x)
33	S	Exchangeable S	ppm/LI	0-∞	± lognormal	ln (1+x)

Stand age was estimated by taking core samples from representative trees outside the 64 m^2 enlarged macro sample plot.

Site quality (height at 40 years of age), H_{40}, was determined from nomograms in Tveite & Braastad (1981); expressing relationships between H_{40}, age at breast height (according to cores) and dominant height of the stand.

Diameter at breast height (1.3 m) was calculated from measurements of stem perimeter in mm.

Height, h, from normal stump height to top, in dm.

Height to the crown, h_c, the distance from normal stump height to the point on the stem where the lower green whorl of branches not separated from the rest of the canopy by more than one whorl of dead branches originate.

Crown area, a, the area of the crown projection, estimated from a map.

Crown cover, b, the projection of living phytomass on the crown area, visually estimated on a percentage scale.

Social status of the trees was recorded by classification into six groups; 0 - suppressed, 1 - dominated, 2 - codominator, 3 - dominator, 4 - standard, x - free-standing (Rørå 1988, T. Økland 1990).

Mechanical and biotic damage, was classificed into seven categories in accordance with Rørå (1988): 1 - broken top, 2 - broken top; new top regenerated, 3 - dry top, 4 - dry top; new top regenerated, 5 - insect damage, 6 - physical damage, 7 - stem cleft.

Tree stand data, including data on individual mapped trees, are given in Appendix 2. Macro sample plot sketches showing positions of trees as well as special details, are given in Appendix 3.

Macro scale variables

The following variables were measured to be representative for the macro sample plots.

(1) Slope (MA Slo) was measured by a compass (90° scale).

(2) Aspect favourability (MA Asf) was calculated from aspect measured by a clinometer (400^g scale). The measurements were converted to a heat index on a linear scale, following Dargie (1984), Parker (1988) and Heikkinen (1991): SSW (225^g) was considered the most favourable aspect, and given the heat index value of 0; NNE (25^g) was considered the least favourable aspect and given the heat index value of 200. Intermediate values were calculated by the following formulae:

$$\begin{aligned} h_i &= 175^g + a_i && 0^g \leq a_i \leq 25^g \\ h_i &= |a_i - 225^g| && 25^g \leq a_i \leq 400^g \end{aligned} \qquad (1)$$

where a_i is the recorded aspect in macro plot i and h_i is the heat index.

(3) Terrain shape (MA Ter) was scored on a six point scale: 0 - valley bottom or concave terrace, 1 - concave valleyside, 2 - plane valleyside, 3 - convex valleyside, 4 - ridge, 5 - hilltop.

(4) Surface unevenness (MA Une) was scored on a four point scale (cf. Rørå et al. 1988): 1 - relatively even (6 terrain roughnesses or less within the 64 m^2 plot enclosing the macro plot; a roughness defined to deviate more than 0.35 m from the surrounding terrain surface), 2 - uneven (7 or more roughnesses), 3 - boulderfield, 4 - coarse, with vertical walls, clefts and cliffs.

(5) Soil depth (MA S d) was scored on a four point scale, based on observations of the surface relief within the 64 m^2 plot (cf. Rørå et al. 1988): 1 - < 25 cm (extensive rock outcrops), 2 - 25-50 cm (localized rock outcrops), 3 - 50-100 cm (no rock outcrops, terrain uneven), 4 - > 100 cm (even surface, glaciofluvial material totally concealing unevennesses of the parent material).

(6) Basal area (MA Bas) was determined by a relascope (Fitje & Strand 1973). Basal

area was measured at breast height from the lower left corner of each meso sample plot (*16 ME Bas*), using relascope factor 2. Values for the two meso sample plots were averaged to give MA Bas. Basal area is an expression of tree density and thus gives information of the light supply to the understory.

(7) Canopy cover (MA Can), c, was calculated by the following formula:

$$c = (\Sigma_{i = 1,\ldots,n} a_i b_i)/16 \qquad (2)$$

where a_i and b_i are the crown area and crown cover for tree i, and $i = 1,\ldots,n$ are the n trees covering the macro sample plot. c is an expression of the relative canopy cover of the macro sample plot, also taking into account trees with overlapping crown projections.

Meso scale variables

The following variables were measured to be representative for the meso sample plots:

(8) Slope (ME Slo) was measured by a compass (see 1).

(9) Aspect favourability (ME H i) was calculated from aspect measured by a clinometer (see 2).

(10) Unevenness (ME Une). For each meso sample plot, microtopography was recorded in the field as follows: A 1 m^2 steel frame, used for recording vegetation, was levelled, and the vertical distance from the levelled frame to the soil surface at the centre of each of the 16 subplots was measured. These 16 observations were recalculated to heights above the lowest relative level in the meso plot, z_i, $i = 1,\ldots,16$. The z_i values can be considered as a function of x, position in sample plot from left to right (0,1,2,3) and y, position from bottom to top (0,1,2,3); $z_i = f(x_i,y_i)$. The plane of best fit to the observation was estimated by bivariate regression taking the z_i values as the dependent variable and x and y as independent variables; the model for the systematic part of the regression being

$$Ez = a_1x + a_2y + a_0 \qquad (3)$$

The regression was used to estimated fitted values z';

$$z_i' = a_1x_i + a_2y_i + a_0. \qquad (4)$$

The deviation of the soil surface from the plane of best fit was

$$k_i = z_i' - z_i. \qquad (5)$$

In even terrain, the k_i values of adjacent subplots (subplots sharing one edge) differ only slightly in absolute value. There are 24 pairs of adjacent subplots within one meso plot. The following equation was used to measure unevenness, u:

$$u = (\Sigma_{i,j} \mid k_i - k_j \mid)/24 \qquad (6)$$

where the sum is over all pairs of adjacent subplots.

(11) Convexity (ME Con). The microtopography measurements (see 10 above) were

used. Convex and concave sample plots will have k_i values that are systematically distributed over the plot (as a function of x and y). Convex plots will have a maximum of k_i close to the centre of the plot, while concave plots will have a minimum in this region. The deviation from fitted values near the centre of the plot is calculated as

$$k_0 = (k_6 + k_7 + k_{10} + k_{11})/4, \tag{7}$$

where the subscripts i refer to subplot numbers, counted from the lower left of the plot. Subplots 6, 7, 10 and 11 are the four subplots bordering on the plot centre. The mean deviation of k_i from k_0 for the remaining 12 subplots can be used as an index of the convexity of the meso plot:

$$co = (\Sigma_i\ k_0 - k_i)/12, \tag{8}$$

where i is the values from 1 to 16 different from 6, 7, 10 and 11. Values of $co > 0$ indicate convex plots, values < 0 indicate concave plots, while values ≈ 0 indicate plane, uneven or saddle-shaped plots.

(12-14) Soil depth. Soil depth was measured as the distance possible to drive a steel rod into the soil. Measurements were made at eight fixed points 25 cm off the egde of the meso sample plot; 2 points along each edge. The set of measurements was used to make three variables: *(12) Soil depth, minimum (ME Smi), (13) Soil depth, median (ME Sme),* and *(14) Soil depth, maximum (ME Sma).*

(15) Litter index (ME Lit). Amount of litterfall was estimated for each meso sample plot by consideration of the position of the plot relative to all trees covering the plot, and to characteristics of the trees. Crowns of trees rooted within the crown perimeter were assumed to be conical and gradually tapering. The amount of litter falling on one sample plot then should be proportional with: (1) the crown height; the height of the canopy over the sample plot ($h - h_c$), (2) the fraction of the sample plot lying within the crown perimeter (f), (3) the crown cover (b), and (4) the relative position of the proximal end of the sample plot (the end most close to the centre of the stem), i.e., d_r/d, calculated as follows: A line was drawn from the stem centre, through the centre of the sample plot. The line was extended till it crossed the crown perimeter. The distance along the line from stem centre to the crown perimeter was termed d, the distance along the line from the proximal end of the sample plot to the crown perimeter was d_r. For "excentric trees", i.e. trees with stem positioned outside the crown perimeter, a cylindrical crown was assumed and point (4) was left out. The following equation was used for the litter index:

$$l = \Sigma_i\ [(d_{ri}/d_i)\cdot b_i \cdot f_i \cdot (h_i - h_{ci})] \qquad \text{stem rooted within crown perimeter} \tag{9}$$

$$l = \Sigma_i\ [b_i \cdot f_i \cdot (h_i - h_{ci})] \qquad \text{stem not rooted within crown perimeter,}$$

where the sum is taken over all trees i covering the sample plot.

(16) Basal area (ME Bas) was determined by a relascope (Fitje & Strand 1973). Basal area was measured at breast height from the lower left corner of each meso sample plot using relascope factor 1 (also see 6 MA Bas).

Meso scale humus layer variables

The following set of variables were measured to be representative for the humus layer (or the upper 5 cm of the humus layer, if thicker). Two sets of samples were collected; one set for determination of soil moisture, and one set for determination of chemical and physical properties of the humus layer.

Samples for determination of soil moisture were collected on 15-16 Oct 1988, after several days without precipitation. Two cores, 5 cm high and 98 cm^3 each, were collected just below the sample plot. The cores were transferred to plastic bags and kept frozen until analysis.

Samples for chemical and physical analysis were taken on 15-16 Sept 1988. Several (5-10) small samples, 50-100 cm^3 each, were collected and mixed. They were kept in the frozen state for several months. Before analysis at Landbrukets Analysesenter, Ås (procedures according to A.R. Selmer-Olsen (pers. comm.)) they were dried at 38°C, grounded and sifted with 2 mm mesh width.

Exchangeable cations were determined by adding 50 cm^3 1 M NH_4NO_3 solution to 10 g dried soil (cf. Stuanes et al. 1984). The solution was left overnight, filtered, and the sediment washed with 1 M NH_4NO_3 until the volume of extract amounted to 250 cm^3. Element concentrations *((21) Ca, (22) Mg, (23) Na, (24) K, (28) Al, (30) Mn, (31) Zn, (32) P*, and *(33) S*, were determined in the extract by a Jarrell Ash ICAP 1100 instrument.

(17) Soil Moisture (Mois). Volumetric soil moisture was determined by weighting the fresh samples, drying the samples at 110°C until constant weight, and reweighting.

(18) Loss on ignition (LI) was determined by ashing a sample at 550°C in a muffle furnace.

(19) pH, aquous solution (pH_{H2O}). One part dried sample was mixed with 2.5 parts distilled water and left overnight. pH was measured the next day with an Orion SA 720 meter.

(20) pH, measured in $CaCl_2$ (pH_{CaCl2}). One part dried sample was mixed with 2.5 parts 0.01 M $CaCl_2$, otherwise as (19).

(25) Echangeable H [H_3O^+]. 50 ml of the extract was titrated with 0.05 M NaOH until pH = 7.0. The volume of NaOH was corrected for the value used with pure extractant, to obtain the result.

(26) Total N. Kjeldahl-N was determined by digestion of the dried sample with H_2SO_4, and use of a Se catalyst in a Tecator FIA system.

(27) Total P (P-AL). One part dried sample was mixed with 20 parts of a solution 0.1 M with respect to ammoniumlactate and 0.4 M with respect to acetic acid. pH was adjusted to 3.75. P was determined in the extract by Jarell Ash ICAP 1100.

DATA MANIPULATION: TRANSFORMATION OF ENVIRONMENTAL VARIABLES

All entering of data on the computer and most data manipulation was performed using Biological Data Program/PC Version 1.01 (Pedersen 1988).

Meso sample plots belonging to the same macro plot were given equal values for macro scale variables. The units of measurement for the 33 environmental variables are given in Tab. 3. All element concentrations (variables 21-33) were converted from ppm (mg/kg dry sample) to fraction of organic content by multiplication with 100/LI, as recommended by T. Økland (1988).

The frequency distributions of the 33 variables over the 200 meso sample plots were inspected (Tab. 3). The transformation ln (1+x) was applied to more or less lognormal or lograndomly distributed variables. The resulting data set, containing transformed values for 33 environmental variables in 200 meso sample plots is referred to as the *ME ENTR* data set.

CLASSIFICATION OF VEGETATION

Terminology and basic assumptions

Gradient terminology follows Whittaker (1967), also see R. Økland & Bendiksen (1985) and R. Økland (1990a). Single environmental gradients, changing more or less parallel in space, form *complex-gradients* (Whittaker 1956). The directions of variation (Sjörs 1947) in vegetation are termed *coenoclines* (Whittaker 1960). Together coenoclines and the underlying complex-gradients constitute *ecoclines* (Whittaker 1960).

The boreal forests are conceived as a vegetational and ecological continuum, in accordance with R. Økland & Bendiksen (1985).

When the major ecoclines can be considered as well-known, the *direct gradient approach to classification* (R. Økland & Bendiksen 1985, R. Økland 1989b, 1990a, also see Whittaker 1967, 1978) is well suited for description of vegetation. The direct gradient approach implies a conversion of the multidimensional pattern into a reticulate, non-hierarchic classification by division of the gradient axes (Tuomikoski 1942, Webb 1954). Each combination of segments (positions) along the gradients is considered one *site-type*, the basic (and only) unit of the classification system.

Classification of the vegetation of the investigation area by the direct gradient approach

Basic assumptions

The direct gradient approach to classification of vegetation assumes that the main ecoclines are known. So far, a regionally valid generalisation of major gradients in boreal coniferous forests cannot be made, as the number of studies emphasizing both vegetation and environmental variables are still far too few. R. Økland & Bendiksen (1985) considered two ecoclines to be the most important on a local scale; (1) the topographic moisture complex-gradient, composed of several single environmental gradients, and (2) the complex-gradient in nutrient status. Furthermore, a third complex-gradient, (3) fine-scale variation in moisture status, can be added (cf. Gjærevoll 1956, Bendiksen & Salvesen 1992, R. Økland & Bendiksen 1985). R. Økland & Bendiksen (1985) sum up correlations and circumstantial evidence in favour of considering the topographic moisture gradient and the complex-gradient in nutrient status as the most important. Important circumstantial evidence also comes from the strong congruence of the different classificatory constructions, as shown by R. Økland & Bendiksen (1985): the main types can be ordered along the mentioned ecoclines.

The three ecoclines mentioned were taken as the basis of a direct gradient approach to classification. As the role of these gradients had not been decisively established *a priori* and no ecological measurements were used to perform the classification, the classification must be considered a subjective, tentative division of vegetational variation along the three ecoclines (like the other direct gradient approaches to Fennoscandian forest vegetation). Accumulated circumstantial evidence of species' responses to the three complex-gradients considered was used for separation of site-types. Thus the classification was based on local criteria, strictly applicable to the investigation area only. Affilation of the meso sample plots to site-types was done in the field in 1988, prior to numerical analysis. Thus the classification could be used as a means of interpretation of the results of subsequent analyses, independent of the measured environmental variables.

Separation of site-types

The topographic moisture gradient. This gradient was divided into seven categories, termed *series.* These series correspond to the four series distinguished by R. Økland & Bendiksen (1985) to be applicable to boreal forest vegetation over S Fennoscandia, with transitional types included. Thus series 1 here is intended to correspond to the xeric series of R. Økland & Bendiksen (1985), series 3 to the subxeric series, series 5 to the submesic series, and series 7 to the mesic series.

The complex-gradient in nutrient status. No division of this gradient was suggested by R. Økland & Bendiksen (1985). The phytosociological classification by Kielland-Lund (1981), and later on, the systems of Fremstad & Elven (1987) and Kielland-Lund et al. (1989), recognized four (or fewer) categories along this gradient: (1) Poor forests, negatively characterized. (2) Slightly rich forests, for instance including the "low fern types". (3) Rich forests, including the poor forms of "low herb types". (4) Extremely rich forests, including the rich forms of "low herb and tall fern" types. A division along these lines was easily carried out for the investigation area.

The complex-gradient in fine-scale moisture. This gradient was tentatively divided into two categories; type 1 (dry) and type 2 (moist).

Site-type codes

Every unique combination of positions along the topographic moisture gradient, the complex-gradient in nutrient status and the gradient in fine-scale moisture, was considered a site-type. The site-types were coded as follows: The first figure indicated the series. In the presence of variation along the nutrient complex-gradient (series 5), position along the latter was indicated by a dot followed by a number. Variation along the fine-scale gradient in moisture was indicated by a hyphen followed by another number. Examples are 3-2, the moist subxeric site-type; 4-1, the dry subxeric-submesic transitional site-type; and 5.2-2, the moist, slightly rich submesic site-type.

Description of site-types: material and presentation

The 200 meso sample plots were used to describe the vegetation of the site-types. Site-type descriptions are collected in the concluding, descriptive part (pp. 169-199). One vegetation table was compiled for each site-type. For each sample plot, the values of some biotic and tree layer variables (see p. 19 and 21-23) were also tabulated, as well as frequency in subplots for all species. Mean and standard deviation was tabulated for the biotic and tree layer variables; constancy and mean frequency in subplots was given for the species. Untransformed environmental variables for all meso sample plots classified to the same site-type are given in Appendix 4.

ORDINATION OF VEGETATION

The two ordination methods now considered most appropriate for extracting the major coenoclines in a vegetational data set, LNMDS (local non-metric multidimensional scaling) and DCA (detrended correspondence analysis) (Kenkel & Orlóci 1986, Minchin 1987, Kent & Ballard 1988, R. Økland 1990a), were used for this study.

Ordination methods

DCA (Hill 1979, Hill & Gauch 1980), as implemented into CANOCO, Version 2.2 (ter Braak 1987a), was applied to the ME 200, MI 400, and ME S3200 data sets, Subsets A and B of ME 200, and subsets MEV 200 (vascular plants) and MEB 200 (bryophytes and lichens). Species with frequency in the data sets less than the median frequency were downweighted in proportion to their frequency (Eilertsen & Pedersen 1989, Eilertsen et al. 1990). Detrending-by-segments was used, as recommended by Knox (1989), R. Økland (1990a) and Eilertsen (1991). Otherwise, standard options were used.

LNMDS (Kruskal 1964a, 1964b, Minchin 1987) was applied to the ME 200 data set, using the program KYST (Kruskal et al. 1973), as modified and implemented into the DECODA program package (Minchin 1986). Percentage dissimilarity (Bray-Curtis, or Czekanowski measure), standardized by division with species maxima, was used as a measure of between-sample dissimilarity, as recommended by Faith et al. (1987) and R. Økland (1990a). Two- and three-dimensional LNMDS solutions were found (termed LNMDS 2, and LNMDS 3, respectively). At least ten different initial configurations were used for both of the LNMDS ordinations, of which one in each case based on prior DCA ordination (see below). No solution was accepted unless reached from at least two different starting configurations (cf. Minchin 1987). LNMDS axes were linearly rescaled in S.D. units by the nonlinear rescaling procedure of the DECORANA and CANOCO programs (cf. Hill 1979, ter Braak 1987a), by use of rescaled hybrid canonical correspondence analysis (cf. ter Braak 1987b, 1987c), with the original LNMDS scores as constraining variables (R. Økland 1990a, Eilertsen et al. 1990).

Comparison of ordination results

Axes of different ordinations were subjected to pair-wise comparison using Pearson's product-moment correlation coefficient (cf. Sokal & Rohlf 1981).

RELATIONSHIPS BETWEEN ENVIRONMENTAL VARIABLES

Correlation analysis

After transformation (cf. p. 25), all environmental variables were normally or uniformly distributed or almost so, except 17 LI, that was slightly bimodal (cf. Tab. 3). The variables then were suited for correlation analysis by a statistical model assuming linear relationships between the variables and normal distribution of errors. Pearson's product-moment correlation coefficient (cf. Sokal & Rohlf 1981) was used. For comparison, Kendall's τ (Kendall 1938) was calculated between a subset of the environmental variables, but the ranking of the coefficients differed but very slightly from Pearson's r, and attention was therefore restricted to the latter. Pearson's r was calculated between all pairs of environmental variables in the ME ENTR data set.

The correlative structure of the ME ENTR data set was also displayed by use of plexus diagrams (McIntosh 1978, T. Økland 1988).

PCA ordination

PCA (Principal component analysis) ordination (e.g., Orlóci 1978, ter Braak & Prentice 1988) was applied to the ME ENTR data set using CANOCO, Version 2.2 (ter Braak 1987a). PCA was run on a correlation matrix, and Euclidean biplot scaling of axes was used. The resulting PCA axes (principal components) thereby summarize correlations between environmental variables.

RELATONSHIPS BETWEEN VEGETATION AND ENVIRONMENTAL VARIABLES. INTERPRETATION OF ORDINATION RESULTS

Correlation analysis

Pearson's product-moment correlation coefficients were calculated between ordination axes (the sample plot scores) and (transformed) environmental variables, and between ordination axes and biotic variables. In some cases, separate correlation coefficients were calculated for the whole ME 200 data set and for Subsets A and B.

Visual aids to interpretation of ordination diagrams

Several visual aids to interpretation of ordination diagrams were used (cf. R. Økland 1990a):

(1) *Plotting the classification into site-types onto the sample plot positions.*

(2) *Vector fitting.* Vectors of steepest descent (direction of strongest change) of environmental variables were fitted to some ordination diagrams (cf. Bowman & Minchin 1987, ter Braak 1987a, 1987c, R. Økland 1990a).

(3) *Plotting of values for environmental variables onto the sample plot positions* was carried out for all environmental variables with correlations with any axis, $r > 0.4$.

(4) *Isolines for environmental variables.* Based on (3). Isolines were constructed by fitting a three-dimensional surface to environmental variable z (or the transformed value, for variables that were transformed, cf. Tab. 3) by multiple (polynomial) regression: z was taken as the dependent variable, products of x and y, the sample scores with respect to ordination axes 1 and 2, of order up to 3, were taken as independent variables (R. Økland 1990a):

$$Ez = a_0 + a_1x^3 + a_2x^2y + a_3xy^2 + a_4y^3 + a_5x^2 + a_6xy + a_7y^2 + a_8x + a_9y \qquad (10)$$

After determination of the regression coefficients a_j, isolines were hand-fitted to a plot of predicted values for z by the regression model (back-transformed for transformed variables). Goodness-of-fit of the three-dimensional surface (and the isolines) assessed by calculating the multiple correlation coefficient, r, between the original and predicted values.

Variation in species abundance along DCA axes

Frequency in subplots as a function of sample plot position along DCA 1 and DCA 2 was depicted for all species occurring in 10 or more meso sample plots. The following descriptors of species response were noted for each species and each DCA axis:

Range: Range of DCA scores of sample plots containing the species.

Optimum range: Range of DCA scores of sample plots in which the species regularly reaches frequency in subplots higher than or equal to 10.

Optimum: Mid-point of optimum range.

Frequency: Approximate frequency of species within range; 4 - > 80% (constant); 3 -50-80% (frequent); 2 - 25-50% (scattered); 1 - < 25% (occasional).

NOMENCLATURE AND TAXONOMIC NOTES

The nomenclature of vascular plants follows Flora Europaea (Tutin et al. 1964, 1968, 1972, 1976, 1980, D. Moore 1982). *Empetrum nigrum* L. is ssp. *nigrum*, as only dioecious flowers have been observed on *Empetrum* in the investigation area. *Dryopteris expansa* agg. includes *D. expansa* (C. Presl.) Fraser-Jenkins & Jermy, *D. dilatata* (Hoffm.) A. Gray, and *D. carthusiana* (Vill.) Fuchs. *Hieracium* is classified to "group" (cf. Lid 1985).

Mosses and *Sphagnum* L. follow Corley et al. (1981). *Plagiothecium laetum* agg. includes *Plagiothecium laetum* B., S. & G. and *P. curvifolium* Schlieph. ex Limpr. *Pohlia nutans* agg. includes *P. nutans* (Hedw.) Lindb. and *P. sphagnicola* (B., S. & G.) Broth. *Racomitrium heterostichum* agg. includes *R. heterostichum* (Hedw.) Brid. and *R. affine* (Web. & Mohr) Lindb. *Rhytidiadelphus subpinnatus* agg. includes *R. subpinnatus* (Lindb.) Kop. and *R. squarrosus* (Hedw.) Warnst. Hepatics follow Grolle (1983). *Lophozia ventricosa* agg. includes *L. ventricosa* (Dicks.) Dum. and *L. longiflora* (Nees) Schiffn. Lichens follow Santesson (198?). *Cladonia chlorophaea* agg. includes *C. chlorophaea* (Flörke ex Sommerf.) Spreng., *C. merochlorophaea* Asah., *C. cryptochlorophaea* Asah., *C. grayi* Merr. ex Sandst.

and *C. pyxidata* (L.) Hoffm. *Cladonia coccifera* agg. includes *C. coccifera* (L.) Willd. and *C. pleurota* (Flörke) Schaer. *Cladonia coniocraea* agg. includes *C. coniocraea* (Flörke) Spreng. and *C. ochrochlora* Flörke.

Critical specimens were collected for microscopic determination. After the field work it turned out that *Dicranum scoparium* with falcato-secund leaves had, in some cases, been mistaken for *D. majus*. This error has not been corrected in the present material.

RESULTS

CLASSIFICATION

The classification system

Among the seven series along the topographic moisture gradient, the most mesic series (series 7) hardly occurred in the investigation area, and was not represented by any meso sample plots. Six series were thus encountered along this gradient. The rich extreme along the complex-gradient in nutrient status was only sporadically encountered, and therefore merged with the third, moderately rich category.

The maximum number of site-types was thus reduced from 56 (7·4·2) to 36 (6·3·2). Only fourteen of these were, however, encountered in the ME 200 data set (Fig. 4). Differentiation along the nutrient gradient only occurred within series 5; series 1-4 always were poor, while series 6 always was rich. In all types except the rich series 5 (only dry) and series 6 (only wet or transitional), both dry and moist sites occurred.

6 ▨	5.3 ▩					
	5.2-1 ◈ 5.2-2 ◇					
	5.1-1 ◍ 5.1-2 ○	4-1 ○ 4-2 ◍	3-1 ⭘ 3-2 ●	2-1 ⭘ 2-2 ●	1-1 ⭘ 1-2 ●	

Fig. 4. The classification system adopted in the present study; site-type codes are given within boxes. Horizontal sequence of types according to position along the topographic moisture gradient, and vertical sequence according to position along the complex-gradient in nutrient status. Site-types separating along the complex-gradient in fine-scale moisture are boxed together; the dry type above, the moist type below. Empty (dotted) boxes indicate combinations not met with in the investigation area. Symbols associated with codes refer to Fig. 15.

Tab. 4. Survey vegetation table. For each species and site-type, constancy and mean frequency in subplots is tabulated (the latter given as an exponent). Species are ordered to reflect variation along major gradients.

	1-1	1-2	2-1	2-2	3-1	3-2	4-1	4-2	5.1-1	5.1-2	5.2-1	5.2-2	5.3	6
Carex panicea	.	33^{7}	.	.	.	.	.	.	.	.	.	.	.	.
Scirpus cespitosus	.	33^{5}	.	.	.	.	.	.	.	.	.	.	.	.
Dicranum montanum	17^{6}	.	8^{2}	.	.	.	.	.	.	.	.	.	.	.
Dicranum drummondii	50^{2}	33^{7}	23^{5}	25^{8}	10^{6}	.	.	13^{4}	.	.	.	.	.	.
Dicranum spurium	50^{7}	33^{1}	23^{3}	13^{1}	.	.	.	.	.	.	.	.	.	.
Leucobryum glaucum	33^{1}	.	23^{2}	25^{3}	5^{1}	9^{2}	.	13^{3}	.	.	.	.	.	.
Cetraria islandica	75^{11}	67^{16}	77^{7}	63^{8}	24^{4}	9^{6}	.	.	.	.	.	.	.	.
Cladina arbuscula	75^{8}	67^{5}	54^{5}	38^{3}	24^{4}	.	.	.	.	.	.	.	.	.
Cladina mitis	33^{11}	67^{11}	46^{5}	13^{2}	.	.	.	.	.	.	.	.	.	.
Cladonia bellidiflora	83^{10}	67^{10}	39^{6}	63^{3}	5^{5}	9^{2}	.	.	.	.	.	.	.	.
Cladonia cornuta	8^{3}	.	8^{1}	.	.	.	.	.	.	.	.	.	.	.
Cladonia gracilis	50^{4}	.	8^{1}	13^{2}	5^{3}	.	.	.	.	.	.	.	.	.
Cladonia squamosa	83^{6}	67^{3}	15^{2}	50^{5}	.	18^{2}	6^{1}	.	.	.	.	.	.	.
Cladonia sulphurina	25^{4}	33^{1}	15^{4}	13^{2}	.	9^{4}	.	.	.	.	.	.	.	.
Cladonia uncialis	75^{9}	100^{5}	54^{4}	38^{6}	.	.	.	.	.	.	.	.	.	.
Carex pilulifera	17^{2}	67^{8}	15^{2}	38^{3}	.	.	.	.	.	.	.	.	6^{1}	.
Racomitrium lanuginosum	42^{3}	66^{6}	8^{5}	50^{5}	10^{2}	.	5^{1}	.	.	.	.	.	.	.
Sphagnum compactum	.	33^{2}	.	25^{6}	.	.	.	.	.	.	.	.	.	.
Dicranum polysetum	50^{7}	33^{4}	46^{3}	25^{4}	71^{6}	18^{7}	22^{8}	.	.	11^{1}	.	.	.	.
Polytrichum juniperinum	8^{3}	.	.	13^{11}	.	27^{10}	.	13^{4}	.	.	.	.	.	.
Cephaloziella sp.	25^{4}	33^{3}	38^{2}	25^{5}	.	9^{12}	6^{3}	.	.	.	.	.	.	.
Cladina rangiferina	100^{11}	100^{8}	85^{6}	63^{9}	62^{5}	.	.	.	.	.	.	.	.	.
Cladonia chlorophaea agg.	100^{11}	100^{4}	92^{7}	75^{8}	29^{4}	27^{7}	6^{3}	.	.	.	4^{2}	.	.	.
Pohlia nutans agg.	83^{4}	100^{5}	31^{4}	75^{2}	14^{2}	45^{5}	6^{3}	.	.	.	8^{2}	.	13^{2}	.
Sphagnum capillifolium	17^{1}	67^{5}	23^{2}	100^{11}	14^{2}	82^{12}	.	.	.	.	.	.	.	.
Pinus sylvestris	100^{4}	100^{4}	46^{3}	88^{4}	29^{2}	45^{2}	6^{2}	25^{3}	4^{2}	.	.	.	6^{1}	.
Calluna vulgaris	92^{9}	67^{11}	85^{10}	100^{12}	100^{12}	100^{14}	33^{11}	50^{6}	.	.	.	.	.	.
Ptilidium ciliare	50^{3}	33^{9}	85^{3}	63^{4}	67^{9}	64^{7}	56^{4}	38^{2}	17^{3}	.	.	.	.	.
Barbilophozia floerkei	25^{9}	33^{2}	38^{10}	63^{7}	38^{5}	64^{4}	6^{14}	38^{8}	4^{3}	22^{5}	.	.	.	.
Dicranum fuscescens	17^{3}	.	23^{2}	.	.	9^{9}	6^{16}	12^{4}	9^{2}	11^{4}	13^{2}	.	.	.
Vaccinium vitis-idaea	92^{10}	100^{6}	100^{14}	75^{11}	100^{16}	100^{16}	100^{13}	100^{13}	78^{11}	100^{10}	42^{5}	67^{10}	44^{5}	40^{7}
Dicranum scoparium	83^{5}	100^{9}	85^{6}	75^{7}	57^{8}	91^{6}	61^{4}	63^{5}	30^{2}	11^{1}	25^{4}	17^{3}	6^{3}	40^{2}
Barbilophozia attenuata	.	33^{1}	8^{3}	13^{3}	5^{2}	9^{1}	.	13^{1}	9^{2}	11^{1}	.	.	.	20^{2}
Lophozia ventricosa agg.	8^{7}	.	23^{6}	50^{5}	.	27^{2}	11^{1}	.	20^{2}	22^{1}	17^{2}	.	31^{3}	20^{2}
Betula pubescens	.	33^{2}	.	13^{1}	.	9^{8}	.	.	.	44^{3}	4^{3}	50^{3}	13^{2}	40^{3}
Empetrum nigrum	8^{3}	33^{12}	46^{10}	50^{9}	52^{13}	64^{8}	17^{8}	13^{16}	.	.	.	.	.	.
Erica tetralix	.	.	8^{12}	.	5^{1}	27^{8}	.	.	.	.	.	.	.	.
Cladonia furcata	.	.	23^{3}	25^{2}	10^{1}	9^{1}	.	.	.	.	.	.	.	.
Vaccinium uliginosum	.	.	38^{10}	25^{8}	50^{12}	73^{13}	22^{11}	25^{11}	2^{16}	.	.	.	6^{3}	.
Melampyrum pratense	8^{3}	.	23^{4}	50^{2}	33^{5}	27^{2}	39^{4}	25^{5}	9^{3}	11^{1}	4^{4}	.	13^{4}	.
Aulacomnium palustre	.	.	8^{1}	.	.	9^{1}	.	13^{4}	.	.	.	.	.	.
Calypogeia sphagnicola	.	.	.	25^{7}	.	45^{4}	.	13^{6}	.	.	.	.	.	.
Cephalozia loitlesbergeri	.	.	.	13^{2}	.	.	.	13^{1}	.	.	.	.	.	.
Calypogeia neesiana	.	.	25^{3}	25^{1}	5^{1}	27^{6}	11^{2}	13^{6}	13^{3}	11^{1}	8^{5}	.	13^{3}	.

Tab. 4 (continued).

	1-1	1-2	2-1	2-2	3-1	3-2	4-1	4-2	5.1-1	5.1-2	5.2-1	5.2-2	5.3	6
Pleurozium schreberi	75^{7}	33^{12}	100^{12}	100^{11}	100^{14}	100^{13}	78^{12}	100^{10}	80^{8}	100^{6}	63^{5}	67^{9}	69^{6}	20^{3}
Cephalozia lunulifolia	.	.	.	13^{2}	.	9^{1}	.	13^{3}	9^{3}	11^{2}	17^{2}	17^{2}	13^{3}	.
Vaccinium myrtillus	75^{6}	67^{4}	77^{15}	88^{11}	100^{15}	100^{14}	100^{16}	100^{16}	98^{15}	100^{16}	100^{14}	100^{15}	88^{12}	60^{15}
Picea abies	8^{2}	.	15^{1}	50^{3}	5^{1}	64^{3}	28^{2}	50^{2}	43^{2}	89^{3}	29^{2}	83^{5}	50^{2}	80^{4}
Ptilium crista-castrensis	.	.	.	.	10^{3}	27^{9}	61^{7}	50^{5}	13^{3}	56^{4}	8^{1}	17^{12}	.	.
Calliergon stramineum	.	.	.	.	.	18^{14}	.	.	.	.	.	17^{4}	.	.
Sphagnum quinquefarium	.	.	8^{5}	.	.	36^{11}	11^{5}	88^{15}	4^{5}	33^{10}	.	17^{9}	6^{1}	.
Hylocomium splendens	.	.	8^{2}	.	9^{5}	55^{3}	61^{9}	88^{9}	76^{8}	89^{6}	54^{4}	67^{2}	63^{6}	40^{5}
Cephalozia bicuspidata	.	.	.	.	.	9^{2}	6^{4}	.	11^{2}	33^{2}	17^{2}	50^{2}	19^{2}	20^{1}
Plagiothecium laetum agg.	.	.	.	.	5^{1}	9^{1}	17^{3}	63^{2}	50^{5}	33^{3}	75^{6}	17^{7}	50^{6}	.
Polytrichum formosum	.	.	.	.	.	.	.	38^{8}	11^{5}	78^{7}	42^{6}	17^{5}	31^{3}	20^{1}
Barbilophozia lycopodioides	8^{2}	.	8^{3}	13^{1}	29^{6}	18^{3}	67^{10}	75^{9}	67^{10}	89^{13}	79^{7}	67^{11}	69^{5}	.
Calypogeia integristipula	.	.	.	.	.	.	6^{2}	13^{2}	13^{3}	.	13^{3}	33^{2}	13^{3}	.
Rhytidiadelphus loreus	.	.	.	.	.	.	6^{2}	38^{5}	20^{4}	67^{9}	13^{6}	17^{4}	25^{3}	.
Lophozia obtusa	.	.	.	.	.	.	28^{4}	50^{6}	15^{6}	22^{3}	8^{4}	33^{3}	25^{5}	.
Lophocolea heterophylla	.	.	.	.	5^{2}	.	50^{4}	38^{7}	78^{4}	33^{2}	71^{8}	67^{5}	75^{6}	40^{6}
Sorbus aucuparia	.	.	.	25^{2}	5^{1}	18^{2}	67^{6}	63^{8}	91^{6}	100^{4}	100^{8}	83^{3}	100^{7}	100^{6}
Pteridium aquilinum	.	.	.	.	.	.	22^{12}	.	46^{10}	33^{7}	42^{6}	67^{9}	31^{12}	80^{9}
Trientalis europaea	.	.	.	.	.	18^{3}	6^{3}	50^{7}	63^{5}	100^{7}	88^{7}	67^{10}	100^{6}	100^{5}
Deschampsia flexuosa	.	.	.	.	.	18^{11}	50^{10}	75^{14}	93^{13}	100^{16}	79^{13}	83^{13}	81^{11}	60^{6}
Dicranum majus	.	.	.	13^{4}	5^{2}	36^{12}	56^{11}	100^{9}	87^{14}	100^{14}	96^{12}	83^{12}	94^{13}	80^{4}
Hypnum cupressiforme	.	.	.	.	.	.	.	.	2^{1}	.	4^{1}	.	.	.
Cornus suecica	.	.	.	.	.	.	.	.	2^{6}	11^{9}	4^{16}	33^{14}	.	.
Diplophyllum taxifolium	.	.	.	.	.	.	.	.	4^{2}	22^{5}	8^{1}	.	.	.
Potentilla erecta	.	.	.	.	.	.	.	.	2^{2}	22^{7}	4^{3}	33^{3}	.	.
Plagiothecium undulatum	.	.	.	.	.	9^{2}	.	25^{5}	24^{10}	67^{9}	29^{8}	67^{8}	13^{4}	.
Sphagnum girgensohnii	.	.	.	.	.	9^{8}	.	.	.	78^{11}	.	50^{12}	.	.
Calypogeia azurea	.	.	.	.	.	.	.	.	.	44^{2}	8^{1}	17^{1}	.	.
Calypogeia muellerana	.	.	.	.	.	18^{2}	6^{3}	25^{3}	26^{3}	78^{5}	46^{4}	83^{6}	25^{2}	20^{6}
Tritomaria quinquedentata	.	.	.	.	.	.	6^{2}	.	2^{5}	22^{2}	13^{1}	33^{6}	6^{1}	.
Lepidozia reptans	.	.	.	.	.	.	.	.	4^{2}	.	4^{2}	.	6^{1}	.
Tetraphis pellucida	.	.	.	.	.	.	.	.	4^{2}	11^{1}	4^{1}	.	6^{1}	.
Barbilophozia barbata	.	.	.	.	.	.	.	.	11^{2}	22^{1}	8^{1}	17^{7}	6^{1}	.
Convallaria majalis	.	.	.	.	.	.	.	.	13^{4}	33^{1}	29^{4}	.	56^{4}	60^{6}
Linnaea borealis	.	.	.	.	.	.	6^{2}	13^{3}	11^{4}	22^{2}	13^{3}	.	31^{6}	40^{3}
Maianthemum bifolium	.	.	.	.	.	.	33^{4}	37^{5}	96^{12}	100^{12}	100^{14}	83^{11}	100^{14}	100^{10}
Solidago virgaurea	.	.	.	.	.	.	.	.	7^{2}	22^{3}	38^{3}	33^{1}	56^{4}	100^{4}
Luzula pilosa	8^{1}	.	.	.	.	.	.	.	4^{3}	22^{2}	33^{4}	.	63^{4}	80^{6}
Plagiothecium denticulatum	.	.	.	.	.	.	6^{5}	.	26^{3}	11^{1}	42^{4}	33^{4}	50^{6}	60^{4}
Blepharostoma trichophyllum	.	.	.	.	.	.	6^{4}	.	7^{1}	11^{1}	8^{3}	.	31^{1}	20^{2}
Plagiochila asplenioides	.	.	.	.	.	.	6^{2}	25^{1}	41^{6}	78^{6}	79^{8}	50^{3}	81^{8}	80^{11}
Lycopodium annotinum	.	.	.	.	.	.	.	.	13^{5}	56^{8}	38^{6}	100^{5}	25^{7}	40^{2}
Hylocomium umbratum	.	.	.	.	.	.	.	.	37^{7}	67^{9}	71^{9}	83^{12}	69^{9}	60^{4}
Oxalis acetosella	.	.	.	.	.	.	.	.	.	.	46^{5}	.	75^{9}	80^{11}
Brachythecium reflexum	.	.	.	.	.	.	.	12^{1}	15^{4}	.	46^{6}	17^{3}	44^{7}	40^{8}
Anemone nemorosa	.	.	.	.	.	.	.	.	2^{3}	.	50^{3}	17^{1}	81^{8}	80^{10}
Dryopteris expansa agg.	.	.	.	.	.	.	.	.	.	11^{2}	67^{8}	17^{1}	63^{5}	40^{4}
Gymnocarpium dryopteris	.	.	.	.	.	.	.	.	17^{4}	22^{8}	71^{6}	83^{10}	88^{11}	80^{10}
Milium effusum	.	.	.	.	.	.	.	.	.	.	13^{4}	.	13^{10}	20^{3}
Cirriphyllum piliferum	.	.	.	.	.	.	.	.	2^{3}	.	13^{3}	.	13^{5}	100^{9}
Plagiomnium affine	.	.	.	.	.	.	.	.	.	11^{2}	25^{6}	.	56^{6}	100^{8}
Thelypteris phegopteris	.	.	.	.	.	.	.	.	.	.	17^{6}	50^{9}	25^{8}	80^{10}
Calamagrostis purpurea	.	.	.	.	.	.	.	.	11^{5}	44^{7}	79^{9}	100^{8}	94^{13}	100^{14}

Tab. 4 (continued).

	1-1	1-2	2-1	2-2	3-1	3-2	4-1	4-2	5.1-1	5.1-2	5.2-1	5.2-2	5.3	6
Festuca altissima	.	.	.	.	.	.	.	.	.	.	8^{1}	.	44^{10}	.
Populus tremula	.	.	.	13^{6}	.	.	.	.	7^{3}	.	4^{6}	.	31^{5}	40^{5}
Dryopteris filix-mas	.	.	.	.	.	.	.	.	.	.	4^{6}	.	19^{9}	20^{7}
Melampyrum sylvaticum	.	.	.	.	.	.	.	.	2^{1}	.	13^{2}	.	44^{3}	40^{3}
Rubus saxatilis	.	.	.	.	.	.	.	.	.	11^{4}	8^{3}	.	50^{4}	80^{7}
Viola riviniana	.	.	.	.	.	.	.	.	.	.	.	.	50^{5}	80^{6}
Carex digitata	.	.	.	.	.	.	.	.	.	.	.	.	6^{1}	40^{4}
Melica nutans	.	.	.	.	.	.	.	.	.	.	4^{3}	.	25^{7}	80^{7}
Rhodobryum roseum	.	.	.	.	.	.	.	.	.	.	4^{1}	.	13^{5}	80^{7}
Rhytidiadelphus subpinnatus	.	.	.	.	.	.	.	.	15^{4}	33^{3}	33^{2}	17^{4}	63^{7}	80^{16}
Rhytidiadelphus triquetrus	.	.	.	.	.	.	.	.	15^{4}	11^{1}	29^{3}	.	44^{5}	40^{6}
Athyrium filix-femina	.	.	.	.	.	.	.	.	.	.	4^{6}	.	.	80^{11}
Crepis paludosa	.	.	.	.	.	.	.	.	.	.	.	.	.	60^{13}
Geranium sylvaticum	.	.	.	.	.	.	.	.	.	.	4^{10}	.	6^{1}	80^{7}
Hepatica nobilis	.	.	.	.	.	.	.	.	.	.	.	.	.	60^{5}
Polygonatum verticillatum	.	.	.	.	.	.	.	.	.	.	.	.	.	60^{9}
Valeriana sambucifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	60^{9}
Chiloscyphus polyanthos	.	.	.	.	.	.	.	.	.	.	.	.	.	20^{16}

Differentiation of site-types

A survey of the vegetation of the site-types is given in Tab. 4. A full description of site-types, including an account of their relationships to the measured environmental factors, is given in the concluding, descriptive part (pp. 169-199). The following criteria were found suitable for differentiation of site-types in the investigation area:

The topographic moisture gradient

The 1-2 limit. Series 1 contained exposed crags with low soil depth. The series was mostly negatively characterized by lack, or low importance, of the main dwarf shrub species of the more mesic site-types (*Empetrum nigrum*, *Vaccinium myrtillus*, and *V. uliginosum*). Lichens dominated the bottom layer, while bryophytes were quantitatively less important.

The 2-3 limit. Lichens retained a prominent position in type 2, while in type 3 they played an unimportant role. Several characteristic species of the dry, open crags, e.g., *Dicranum drummondii*, *D. spurium*, and *Racomitrium lanuginosum*, were almost absent from series 3. On the other hand, the latter was characterized by sparse presence of the species typical of spruce forests, e.g., *Hylocomium splendens*, *Ptilium crista-castrensis* and *Sphagnum quinquefarium.*

The 3-4 limit. This limit was characterized by considerably increased importance of spruce over pine (from 3 to 4), by a group a species, e.g., *Dicranum polysetum* and *Sphagnum capillifolium*, that were almost absent from series 4, and by the more or less frequent appearance of several species in type 4 that were typical of the bilberry-dominated spruce forests, e.g., *Trientalis europaea*, *Deschampsia flexuosa*, *Dicranum majus*, *Polytrichum formosum*, *Barbilophozia lycopodioides*, and *Lophocolea heterophylla*.

The 4-5 limit. The last-mentioned species group further increased in abundance from type 4 to type 5. Several pine forest species, in particular *Calluna vulgaris*, but also *Pinus sylvestris* and *Ptilidium ciliare*, were absent from type 5. A considerable number of species typical of submesic forests appeared. The quantitatively most important was *Maianthemum bifolium*, other important species were *Lycopodium annotinum*, *Hylocomium umbratum*, *Plagiothecium denticulatum*, *P. undulatum*, *Sphagnum girgensohnii*, and *Plagiochila asplenioides*.

The 5-6 limit. The limit was characterized by increasing importance of hygrophilous species like *Athyrium filix-femina*, *Crepis paludosa*, *Valeriana sambucifolia*, and several others.

The gradient in nutrient status

Important criteria on the three resulting categories were as follows:

The 1-2 limit. The following species were used as indicators of type 2: *Anemone nemorosa*, *Calamagrostis purpurea*, *Dryopteris expansa* agg., *Gymnocarpium dryopteris*, *Oxalis acetosella*, and *Brachythecium reflexum.*

The 2-3 limit. The most important indicators of type 3 were: *Carex digitata*, *Festuca altissima*, *Melampyrum sylvaticum*, *Melica nutans*, *Rubus saxatilis*, and *Viola riviniana.*

The gradient in fine-scale moisture

The two categories along this gradient differ in the occurrence of hygrophilous species. Type 2 (moist) is characterized by prominence of hygrophilous species, e.g., *Sphagnum capillifolium*, *S. compactum*, *S. girgensohnii*, *S, quinquefarium*, *Calypogeia muellerana*, *C. sphagnicola*, *Tritomaria quinquedentata*, and the vascular plants *Cornus suecica* and *Potentilla erecta.* Type 1 (dry) is mostly negatively characterized, but several species showed some preference for this type (e.g., *Plagiothecium laetum* agg., *Brachythecium reflexum* and *Lophocolea heterophylla*).

RELATIONSHIPS BETWEEN ENVIRONMENTAL VARIABLES

Correlation analysis

Pairwise correlations between environmental variables are shown in Tab. 5. Correlations significant at level $P < 0.0001$ having $r > 0.35$ were shown in the plexus diagram in Fig. 5. The 33 environmental variables make up groups of correlated variables, more or less connected with each other by pair-wise between-group correlations. Eight E-groups could be discerned:

(1) Six variables, 03 MA Ter, 05 MA S d, 18 LI, 19 pH_{H2O}, 20 pH_{CaCl2}, and 26 N made up a group of correlated variables. The two pH measurements were almost perfectly correlated, $r = 0.9437$. Very strong correlations were observed between these and either of LI (negative), MA Ter (negative) and N (positive). MA S d was strongly correlated with MA Ter ($r = -0.7750$). The subgroup of pair-wise positively correlated variables, MA S d, pH_{H2O},

Tab. 5. Pearson's product-moment correlation coefficients between the 33 environmental variables in the 200 meso sample plots (lower triangle), and their significance probabilities (upper triangle). Correlations significant at level P < 0.0001 in bold face. n.s. - significance probability less than 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 3.

Variable	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
01 MA Slo	*	.0019	**.0000**	**.0000**	**.0000**	.0416	.0051	**.0000**	.0001	**.0000**	n.s.	.0251	n.s.	n.s.	.0044	.0017	n.s.	**.0000**	.0001	**.0000**	.0043	.0154	.0234	**.0000**	n.s.	**.0000**	**.0000**	.0014	.0021	**.0000**	.0009	**.0000**	**.0000**
02 MA Asf	.2185	*	.0220	.0046	n.s.	n.s.	n.s.	.0015	**.0000**	.0432	n.s.	n.s.	n.s.	.0503	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
03 MA Ter	**-.4219**	-.1619	*	.0038	**.0000**	.0002	**.0000**	.0001	.0081	.0056	n.s.	.0658	**.0000**	**.0000**	.0002	**.0000**	.0142	**.0000**	**.0000**	**.0000**	.0003	.0126	n.s.	**.0000**	.0002	**.0000**	n.s.	n.s.	n.s.	.0002	n.s.	n.s.	.0232
04 MA Une	**.5115**	.1995	-.2037	*	n.s.	n.s.	n.s.	**.0000**	n.s.	.0022	n.s.	.0167	.0051	n.s.	.0883	.0067	n.s.	.0002	.0099	.0030	.0091	.0347	.0196	.0004	.0164	.0003	.0504	n.s.	n.s.	**.0000**	.0032	.0190	.0001
05 MA S d	**.3063**	n.s.	**-.7750**	.0092	*	**.0000**	**.0000**	.0199	.0868	.0837	n.s.	.0014	**.0000**	**.0000**	**.0000**	**.0000**	n.s.	.0001	**.0000**	**.0000**	**.0000**	.0003	n.s.	.0001	**.0000**	**.0000**	.0225	n.s.	.0174	.0023	n.s.	n.s.	.0478
06 MA Bas	.1442	.0178	-.2641	.0790	**.3040**	*	**.0000**	n.s.	n.s.	n.s.	n.s.	n.s.	.0139	.0015	**.0000**	**.0000**	.0007	.0412	n.s.	.0044	**.0000**	.0004	n.s.	.0005	.0006	n.s.	.0669	.0004	.0184	.0032	n.s.	n.s.	n.s.
07 MA Can	.1974	-.0777	**-.3175**	.0402	**.4522**	**.5805**	*	n.s.	n.s.	.0577	n.s.	n.s.	.0020	.0002	**.0000**	**.0000**	**.0000**	n.s.	n.s.	.0128	**.0000**	.0001	n.s.	.0002	.0001	n.s.	.0023	**.0000**	.0023	.0042	n.s.	n.s.	n.s.
08 ME Slo	**.7188**	.2234	-.2691	**.3597**	.1646	.0053	.0910	*	.0001	**.0000**	n.s.	.0504	.0084	n.s.	0.419	n.s.	.0530	.0004	.0007	.0012	.0636	n.s.	n.s.	.0037	n.s.	**.0000**	.0003	.0096	.0090	**.0000**	n.s.	.0812	.0007
09 ME Asf	.2719	**.5554**	-.1869	.1020	.1214	.0456	-.0034	.2698	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0612	.0486	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0661	n.s.	.0487	n.s.	n.s.	.0553
10 ME Une	**.3662**	.1431	-.1952	.2152	.1226	.0853	.1344	**.4064**	.0834	*	n.s.	n.s.	n.s.	.0387	.0040	n.s.	n.s.	n.s.	n.s.	n.s.	.0021	.0018	n.s.	.0004	.0672	n.s.	.0131	n.s.	n.s.	.0068	n.s.	n.s.	n.s.
11 ME Con	.1097	-.0110	-.0632	.0858	.0088	.1061	.0744	.0830	.0791	-.0034	*	n.s.	n.s.	n.s.	n.s.	.0791	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0320	n.s.	.0807	n.s.	n.s.	n.s.	n.s.	.0896
12 ME Smi	-.1584	.0953	-.1304	-.1691	.2249	.0614	.0607	-.1385	-.0080	-.0394	-.0789	*	**.0000**	**.0000**	n.s.	n.s.	n.s.	.0176	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	.0373	n.s.	.0183	n.s.	.0411	n.s.	n.s.	n.s.
13 ME Sme	-.1160	.1017	**-.2966**	-.1974	**.4404**	.1736	.2168	-.1858	.0031	.0948	-.0809	**.6664**	*	**.0000**	.0095	.0092	.0008	n.s.	n.s.	n.s.	.0150	.0022	n.s.	n.s.	.0226	.0923	n.s.	**.0000**	.0022	n.s.	n.s.	n.s.	n.s.
14 ME Sma	-.0360	-1386	**-.4026**	-.0844	**.4728**	.2234	.2648	-.1054	.0780	.1463	-.0968	**.4751**	**.8240**	*	.0019	.0040	.0027	n.s.	n.s.	n.s.	.0055	.0019	n.s.	.0814	.0098	n.s.	n.s.	.0001	.0014	n.s.	n.s.	n.s.	n.s.
15 ME Lit	.2007	.0350	-.2575	.1208	**.3425**	**.5801**	**.7357**	.1440	.1038	.2015	-.0106	-.0170	.1831	.2192	*	**.0000**	**.0000**	n.s.	n.s.	.0310	**.0000**	.0057	n.s.	.0038	.0003	n.s.	.0586	**.0000**	.0050	.0041	n.s.	n.s.	n.s.
16 ME Bas	.2200	.0412	**-.3902**	.1911	**.3875**	**.8511**	**.4759**	.0144	.0395	.0678	.1245	.1020	.1838	.2014	**.4920**	*	.0946	.0018	.0163	.0003	**.0000**	.0001	n.s.	.0001	**.0000**	.0137	.0369	.0152	.0611	.0061	n.s.	n.s.	n.s.
17 Mois	.0259	.0432	-.1731	-.0708	.0141	-.2390	**-.3529**	.1370	.0626	-.1161	-.0111	-.0662	-.2361	-.2111	**-.3474**	-.1185	*	.0976	.0001	.0078	n.s.	.0753	n.s.	n.s.	.0204	.0025	n.s.	**.0000**	.0582	n.s.	n.s.	.0273	n.s.
18 LI	**-.3267**	.0401	**.3049**	-.2607	-.2758	-.1445	-.0294	-.2461	-.0262	-.0847	-.0673	.1677	.0783	.0316	-.0527	-.2192	-.1175	*	**.0000**	**.0000**	**.0000**	.0001	.0158	**.0000**	**.0000**	**.0000**	**.0000**	**.0000**	.0008	**.0000**	.0015	n.s.	**.0000**
19 pH_{H2O}	.2794	.0272	**-.5109**	.1821	**.3927**	.1112	.0727	.2374	.1326	.0836	.0898	-.0585	-.0043	.0372	.0484	.1697	.2823	**-.5491**	*	**.0000**	.0001	.0614	.0002	.0005	**.0000**	**.0000**	n.s.	**.0000**	n.s.	**.0000**	n.s.	**.0000**	**.0000**
20 pH_{CaCl2}	**.2995**	.0516	**-.5500**	.2090	**.4642**	.2004	.1758	.2280	.1397	.0940	.0975	-.0072	.0536	.1128	.1525	.2504	.1878	**-.5819**	**.9437**	*	**.0000**	.0142	.0006	.0006	**.0000**	**.0000**	n.s.	.0002	.0487	**.0000**	n.s.	.0045	**.0000**
21 Ca	.2011	.0075	-.2559	.1840	**.3178**	**.3404**	**.3497**	.1314	.0275	.2159	-.0140	.0562	.1718	.1957	**.3195**	**.3473**	-.0944	**-.3532**	.2665	**.3616**	*	**.0000**	**.0000**	**.0000**	**.0000**	.0003	**.0000**	.0019	.0009	**.0000**	**.0000**	.0001	**.0000**
22 Mg	.1712	-.0456	-.1762	.1494	.2540	.2471	.2750	.0828	-.0146	.2197	-.0309	.0870	.2149	.2179	.1950	.2658	-.1261	-.2683	.1325	.1732	**.9045**	*	**.0000**	**.0000**	**.0000**	.0642	**.0000**	.0223	.0317	**.0000**	**.0000**	**.0000**	**.0000**
23 Na	.1602	-.0421	-.0713	.1649	.1024	.0801	.0414	.1033	.0239	.1012	.0129	.0281	.0693	.0289	.0126	.0732	.0579	-.1705	.2605	.2401	**.7377**	**.8092**	*	**.0000**	.0018	.0458	n.s.	n.s.	n.s.	**.0000**	**.0000**	**.0000**	**.0000**
24 K	**.3448**	-.0115	**-.2937**	.2468	.2662	.2427	.2639	.2046	.0741	.2488	.0021	-.0206	.0882	.1235	.2040	.2762	-.0869	**-.2866**	.2429	.2412	**.7549**	**.8375**	**.7593**	*	**.0000**	.0027	.0011	n.s.	n.s.	**.0000**	**.0000**	**.0000**	**.0000**
25 H	-.1006	-.0768	.2580	-.1696	**-.3390**	-.2416	-.2751	-.0045	-.0162	-.1297	-.0242	-.0353	-.1612	-.1823	-.2556	**-.2903**	.1639	**.3138**	**-.3724**	**-.5243**	**-.5531**	**-.3897**	-.2192	**-.2838**	*	.0008	.0009	.0090	**.0000**	**.0000**	**.0000**	.0186	**.0000**
26 N	**.3572**	-.0128	**-.4211**	.2539	**.3901**	.0799	.0801	**.3151**	.0880	.0545	.1517	-.1474	-.1194	-.0446	.0898	.1741	.2128	**-.7441**	**.6393**	**.6658**	.2511	.1311	.1414	.2109	-.2347	*	**.0000**	.0001	n.s.	**.0000**	n.s.	n.s.	.0001
27 P-AL	**.2908**	-.0357	-.0930	.1385	.1614	.1298	.2140	.2503	.0644	.1752	.0865	.0235	-.0686	-.0551	.1340	.1476	-.0729	**-.3448**	-.0308	.0946	**.3187**	**.3032**	.0871	.2296	-.2334	**.3146**	*	.0034	n.s.	**.0000**	.0002	**.0000**	.0011
28 Al	.2246	-.0577	-.0856	.1142	-.0751	-.2480	**-.3447**	.1827	.1302	-.1035	.1238	-.1667	**-.2827**	-.2738	**-.3230**	-.1715	**.3399**	**-.3045**	**.3518**	.2613	-.2183	-.1616	.1153	.0413	.1842	.2753	-.2063	*	**.0000**	.0008	.0001	n.s.	**.0000**
29 Fe	.2165	-.0473	.0955	.1019	-.1680	-.1666	-.2142	.1843	.0667	-.0513	.0543	-.1125	-.2152	-.2251	-.1978	-.1327	.1342	-.2344	-.0887	-.1396	-.2323	-.1520	-.0337	-.0115	**.2862**	.0336	.0920	**.6463**	*	.0129	**.0000**	**.0000**	**.0000**
30 Mn	**.4011**	.0088	-.2643	**.3407**	.2147	.2078	.2018	**.2945**	.1396	.1944	.1085	-.1446	-.0993	.0187	.2019	.1932	-.1099	**-.5292**	**.4399**	**.5515**	**.5734**	**.4635**	**.4150**	**.5181**	**-.5483**	**.4242**	**.3434**	.2359	.1755	*	**.0000**	**.0000**	**.0000**
31 Zn	.2332	.0140	-.0416	.2075	.0538	-.0478	-.0267	.0914	.1010	.0702	.0890	-.0730	-.0942	-.0191	-.0850	-.0263	-.0471	-.2231	-.0056	.0696	**.3385**	**.3748**	**.3346**	**.3873**	**-.2887**	.0700	.2600	.2799	.3510	**.6652**	*	**.0000**	**.0000**
32 P	**.2930**	.0372	.0138	.1657	.0296	.0217	.0800	.1236	.0912	.0483	.1047	-.0787	-.1048	-.0698	.0218	.0290	-.1561	.0226	**-.2844**	-.2001	.2706	**.3646**	**.2964**	**.4051**	-.1663	.1073	**.4087**	.0785	**.2828**	**.4877**	**.7576**	*	**.0000**
33 S	**.3484**	-.0263	-.1604	.2743	.1401	.0548	-.0076	.2384	.1357	.1074	.1204	-.0585	-.0796	-.0288	-.0353	.0432	-.0538	**-.3835**	**.2837**	**.3390**	**.3671**	**.3527**	**.4509**	**.4553**	**-.3013**	.2719	.2290	**.4725**	**.4356**	**.7697**	**.7919**	**.6044**	*

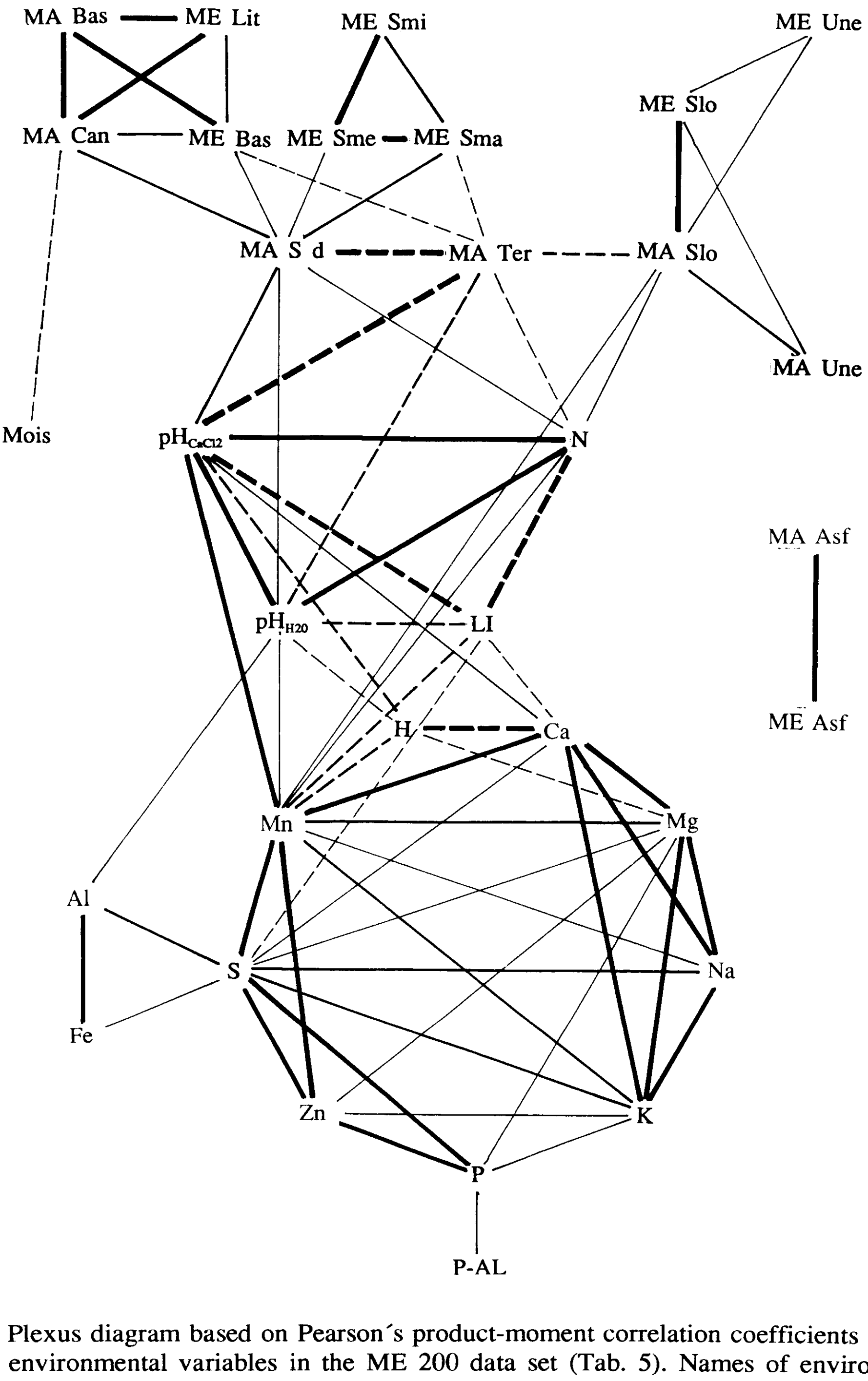


Fig. 5. Plexus diagram based on Pearson's product-moment correlation coefficients between the 33 environmental variables in the ME 200 data set (Tab. 5). Names of environmental variables in accordance with Tab. 3. Thick lines - $r > 0.55$, medium lines - $0.45 < r < 0.55$, thin lines - $0.35 < r < 0.45$. Broken lines - negative correlations.

pH_{CaCl2}, and N was denoted 1+, the variables MA Ter and LI negatively correlated with subgroup 1+ was termed 1-.

(2) Nine variables, all chemical properties of the humus layer; 21 Ca, 22 Mg, 23 Na, 24 K, 25 H, 30 Mn, 31 Zn, 32 P and 33 S belonged to this group. Eight of these (all except H) made up a tight group of positively correlated variables. Out of 28 pairs, 17 had $r > 0.45$. Two subgroups of variables with pairwise r mostly > 0.6 could be discerned: (a) Ca, Mg, Na, and K. (b) Mn, Zn, P, and S. H made up a subgroup on its own. It was negatively correlated with all other variables, strongly so ($r < -0.5$) with Ca and Mn. By its strong correlation with pH_{CaCl2}, H provided a link between groups 1 and 2. Also Mn and Ca showed strong correlations with variables of group 1, and provided a brigde between the two groups. 27 P-AL was correlated with P ($r = 0.4242$), but otherwise showed no $r > 0.35$. It could be considered a satellite to group 2.

(3) 28 Al and 29 Fe were strongly positively correlated ($r = 0.6463$), but apart from positive correlations with S of group 2 ($r > 0.43$), they showed no $r > 0.36$.

(4) 04 MA Une, 01 MA Slo, 08 ME Slo, and 10 ME Une made up a series of positively correlated variables, adjacent pairs along the series most strongly correlated. This group was connected to group 1 by MA Slo, negatively correlated with MA Ter ($r = -0.4219$).

(5) The meso scale soil depth variables, 12 ME Smi, 13 ME Sme, and 14 ME Sma, were more strongly correlated with each other, than were any of the three with some other variable. The group was connected to group 1 through a strong positive correlation between ME Sma and MA S d ($r = 0.4728$), a positive correlation between ME Sme and MA S d ($r = 0.4404$) and a negative correlation between ME Sma and MA Ter ($r = -0.4026$).

(6) The variables characterizing the closure of the tree layer, 06 MA Bas, 07 MA Can, 15 ME Lit, and 16 ME Bas made up a group of strongly positively correlated variables (all pairwise correlations with $r > 0.45$). They were connected to group 1 through positive correlations with MA S d, less so through negative correlations with MA Ter.

(7) 17 Mois made up a group on its own. It was most strongly correlated with MA Can ($r = -0.3529$), less so with the other members of group 6. It was positively correlated with AL ($r = 0.3399$).

(8) The heat indices (02 MA Asf and 09 ME Asf) were not correlated with any other variables at level $P < 0.0001$. Te two heat indices had $r = 0.5554$.

PCA ordination

Eigenvalues of the PCA ordination are given in Tab. 6.

PCA 1. The first PCA axis accounted for 22.8 % of the variance in the ME ENTR correlation matrix. High (positive) loadings were obtained by the variables of E-groups 1+ and 2+ (Figs 6, 7). Equally high negative loadings were obtained by subgroups 1- and 2-. Relatively high loadings were also obtained by E-groups 4, the slope/unevenness variables, and 6, the canopy closure variables. The remaining variables (E-groups 3, 5, 6, 8) obtained very low loadings.

PCA 2. The second PCA axis accounted for 13.5 % of the variance. Particularly high (positive) loadings were obtained by Al and Fe of E-group 3, Mois (E-group 7), and some of the variables of E-group 2, notably S and Zn, but also Mn and P (Figs 6, 7). The highest negative loadings were obtained by the soil depth variables (E-group 5), in particular ME Sme, partly also ME Sma. The polarization along PCA 2: Al, Fe and Mois on the one hand, and

Tab. 6. Eigenvalues of PCA axes in ordination of 33 environmental variables (cf. Tab. 3).

Axis	Eigenv.
1	0.2281
2	0.1348
3	0.1009
4	0.0721

ME Sme and ME Sma on the other, reflected pairwise negative correlations ($r > 0.2$, $P < 0.005$). Relatively high negative loadings were obtained by E-group 6 variables (canopy closure). Most of the E-group 1, 2, 4 and 7 variables obtained low loadings on PCA 2.

PCA 3. The third PCA axis accounted for 10.1 % of the variance. This axis mainly separated variables of E-group 1 from variables of E-group 2; high positive loadings were obtained by E-group 1+, high negative loadings by E-group 2+ and 1- (Figs 8, 9). The low

Tab. 7. Pearson's product-moment correlation coefficients between the 9 vegetational variables in the 200 meso sample plots (lower triangle), and their significance probabilities (upper triangle). Correlations significant at level $P < 0.0001$ in bold face. n.s. - significance probability less than 0.1. Vegetational variables: N-TOT - total number of species, N-VAS - number of vascular plant species, N-BOT - number of species in the bottom layer, N-BRY - number of bryophyte species, N-LIC - number of lichen species, CC - percentage cover of the field layer, CD - percentage cover of the bottom layer. The variables MA Can and ME Lit equal environmental variables 07 and 15, respectively (cf. Tab. 3).

Variable	N-TOT	N-VAS	N-BOT	N-BRY	N-LIC	MA Can	ME Lit	CC	CD
N-TOT	*	*	*	*	*	.0091	.0375	*	*
N-VAS	*	*	.0086	**.0000**	**.0000**	*	n.s.	.0617	n.s.
N-BOT	*	.1855	*	*	*	**.0000**	**.0000**	**.0000**	*
N-BRY	*	**.4068**	*	*	.0057	.0098	.0386	n.s.	*
N-LIC	*	**-.3910**	*	-.1947	*	**-.0000**	**.0000**	**.0000**	*
MA Can	-.1840	.0740	**-.3523**	-.1823	**-.3383**	*	*	n.s.	**.0000**
ME Lit	-.1472	.0810	**-.3031**	-.1464	**-.3102**	*	*	n.s.	**.0000**
CC	*	*	**-.3484**	-.1015	**-.4788**	.0067	-.0556	*	**.0000**
CD	*	.0141	*	*	*	**-.3864**	**-.3274**	**-.3089**	*

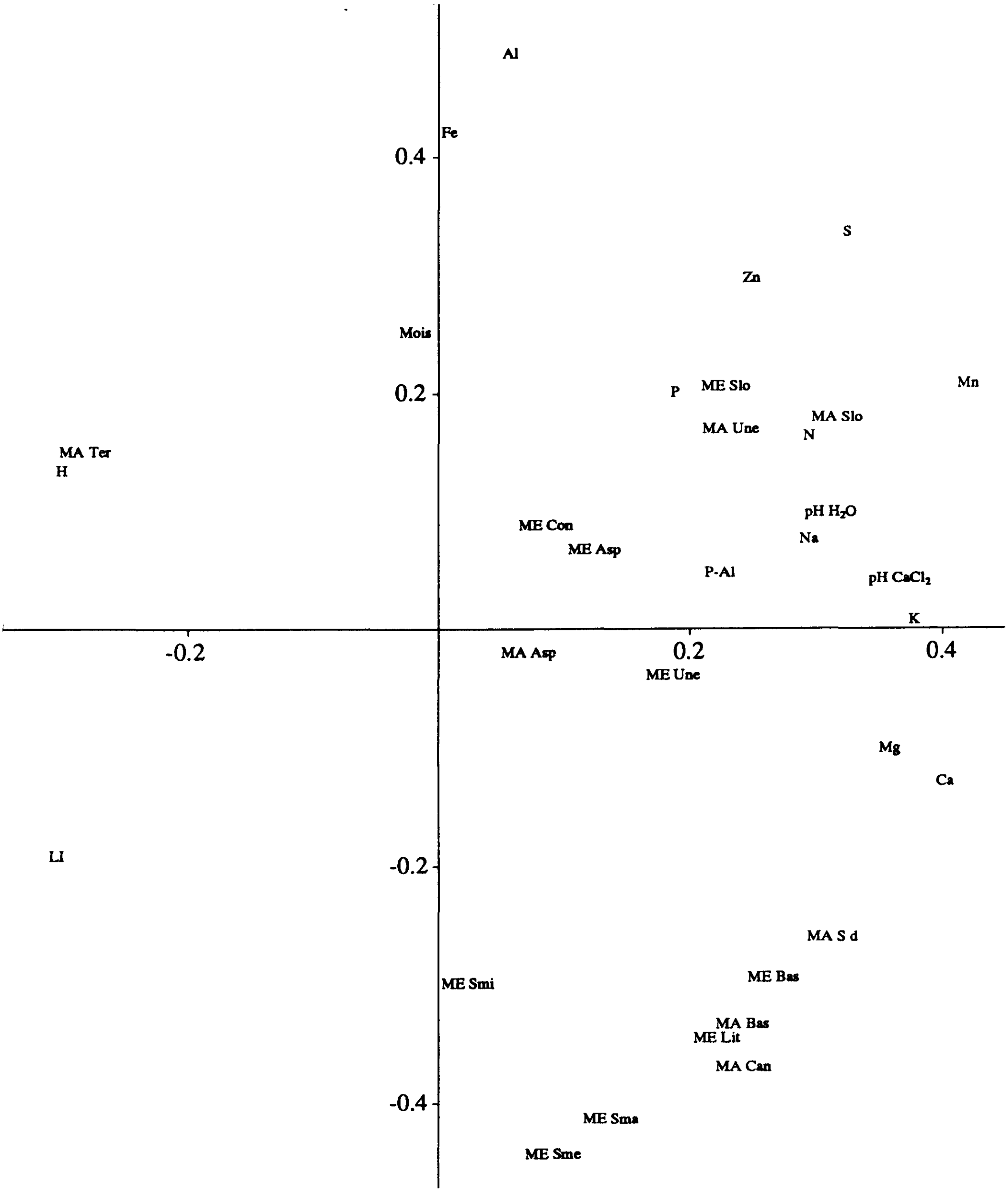


Fig. 6. PCA ordination of 33 environmental variables in the ME 200 data set: loadings for variables on axes 1 and 2. Names of environmental variables are abbreviated in accordance with Tab. 3.

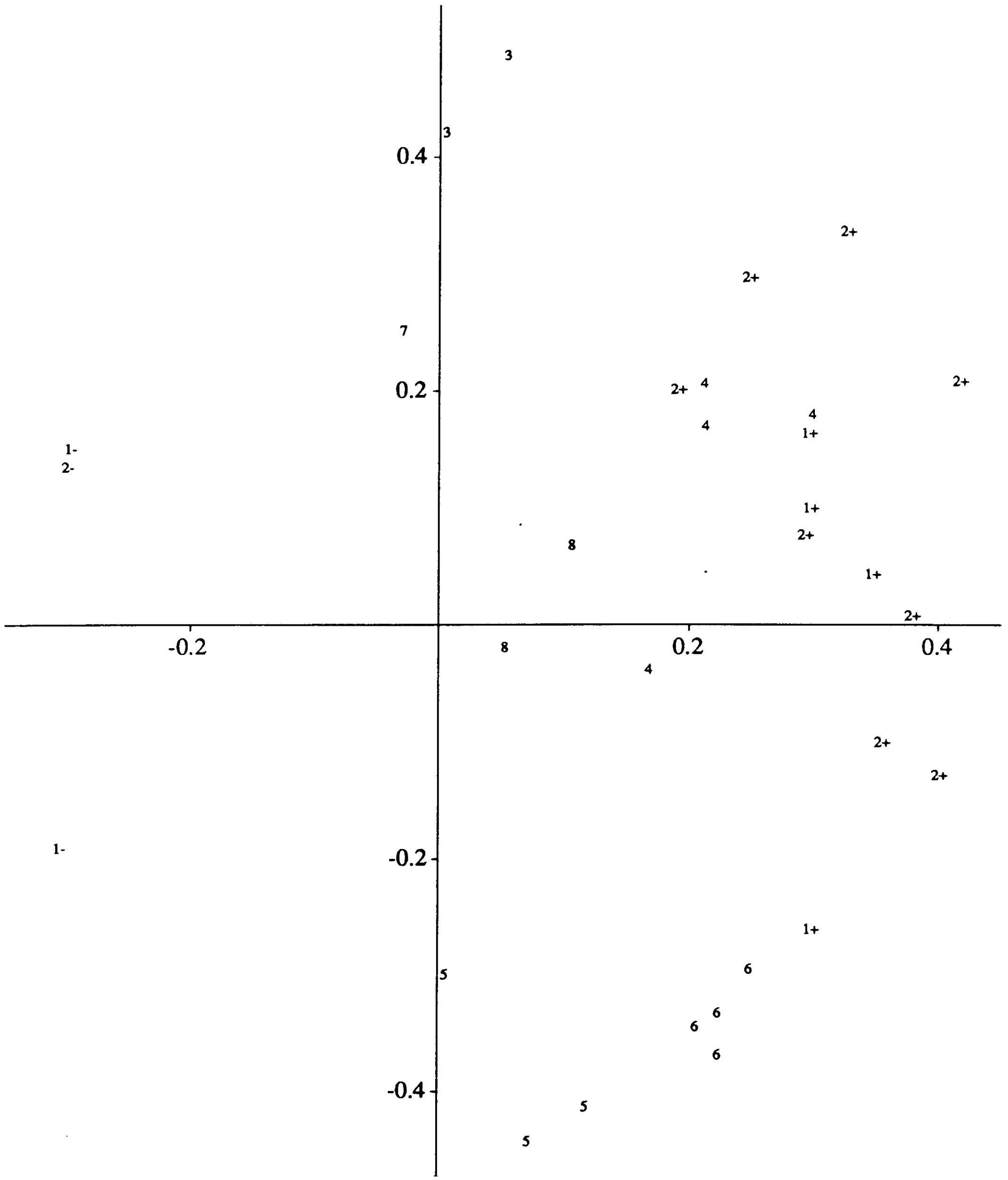


Fig. 7. PCA ordination of 33 environmental variables in the ME 200 data set: loadings for variables on axes 1 and 3. Names of environmental variables are abbreviated in accordance with Tab. 3.

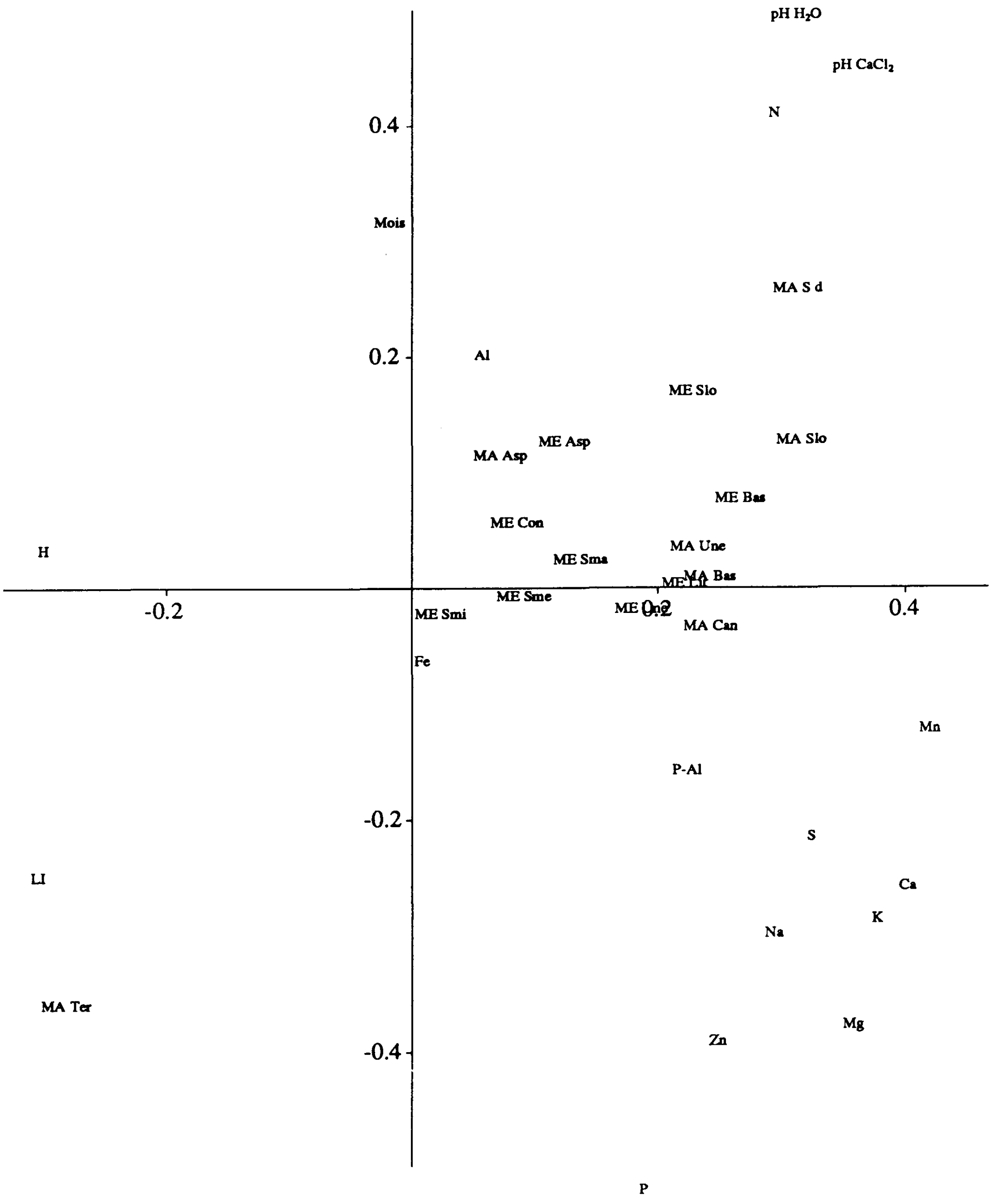


Fig. 8. PCA ordination of 33 environmental variables in the ME 200 data set: E-group affilation of variables plotted onto the variable loadings; axes 1 and 2.

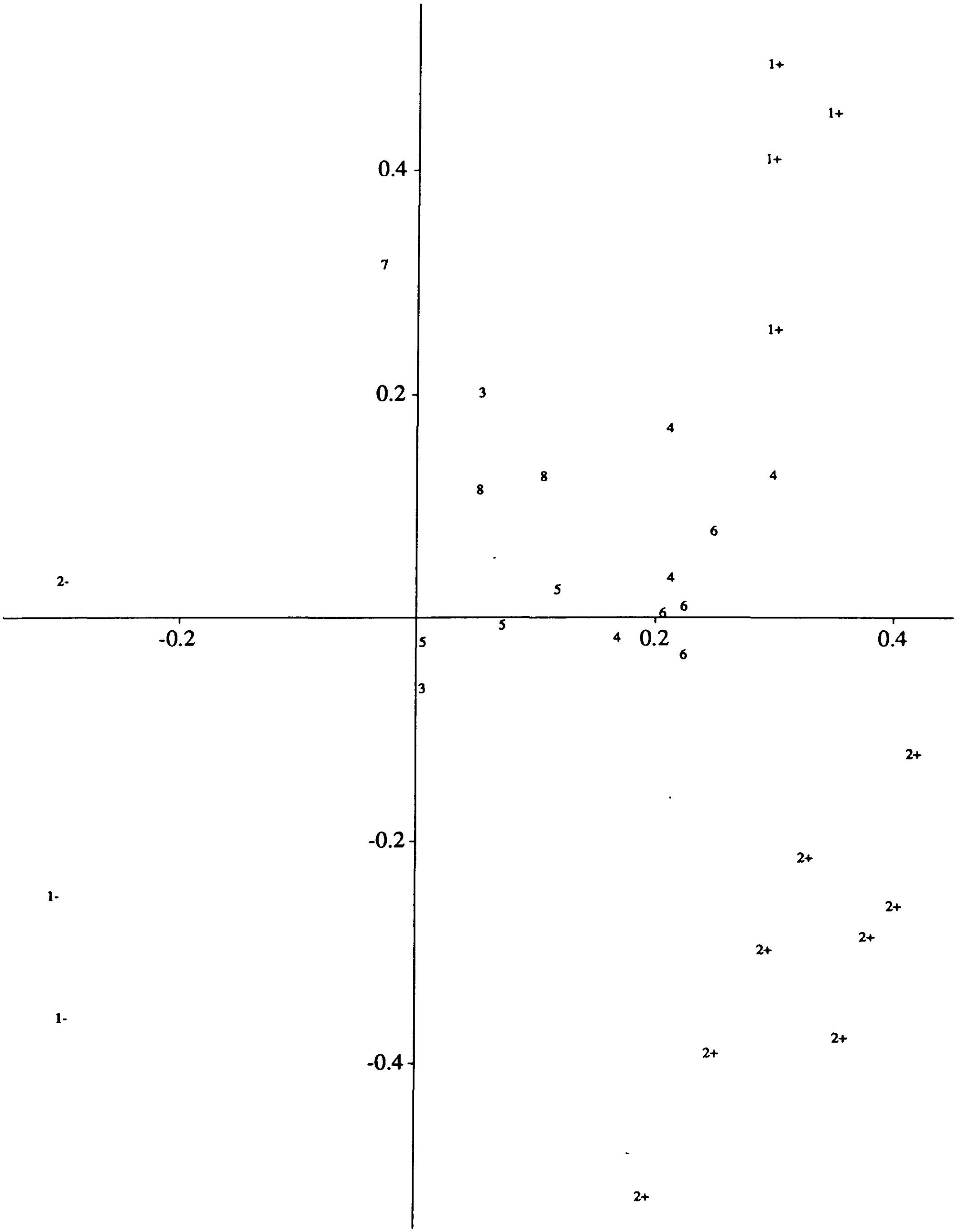


Fig. 9. PCA ordination of 33 environmental variables in the ME 200 data set: E-group affilation of variables plotted onto the variable loadings; axes 1 and 3.

loading of H (E-group 2-) showed the somewhat transitional position of this variable in the group 1-2 continuum. Mois also obtained a relatively high, positive loading, also reflected in positive correlations between Mois and N and the two pH measurements ($P < 0.01$).

PCA 4. Accounting for only 7.2 % of the variance, this axis produced a polarization of variables not followed by significant correlations.

RELATIONSHIPS BETWEEN BIOTIC VARIABLES

Correlation coefficients between the biotic variables (including the environmental variables 07 MA Can and 15 ME Lit) are shown in Tab. 7.

Number of species in the field and bottom layers were only slightly positively correlated ($r = 0.1855$, $P = 0.0086$), as a result of two opposing trends; a strong positive correlation between species number in the field layer with number of bryophyte species ($r = 0.4068$, $P < 0.0001$) and a strong negative correlation with number of lichen species ($r = -0.3910$, $P < 0.0001$). The number of bryophte and lichen species were slightly negatively correlated ($r = -0.1947$, $P = 0.0057$).

Increasing canopy cover implied a slight lowering of N-TOT; a result of an increase in N-VAS and a strong decrease in N-BOT ($P < 0.0001$), in turn a result of a slight decrease in N-BRY ($P < 0.05$) and a strong decrease in N-LIC ($P < 0.0001$). Similarly, increasing cover of the field layer (CC) implied a strong decrease in N-BOT, this time mostly caused by a strong lowering of N-LIC ($r = -0.4788$, $P < 0.0001$). Cover of the bottom layer was not correlated with N-VAS.

The cover of the different layers showed similar relationships: There was no correlation between canopy cover and field layer cover, but a strong negative correlation between canopy cover and CD ($r = -0.3864$, $P < 0.0001$), and CC and CD ($r = -0.3089$, $P < 0.0001$).

ORDINATION OF THE MESO SAMPLE PLOTS: THE FULL SPECIES COMPOSITION

Characteristics of the ordinations

DCA

Characteristics of the DCA ordination are given in Tab. 8. The first DCA axis had a gradient length of 6.19 S.D. units; more than double the length of the second axis. The eigenvalues differed by a factor of four (0.70 vs 0.17). The third DCA axis was slightly shorter than the second axis and the eigenvalue slightly lower (0.14).

Lowest score along DCA 1 was obtained by sample plot 153, followed by plot 53 (Fig. 10); both mesic plots very rich in species (site-type 6), see Fig. 10. Sample plot 179 made up the other end of the axis, followed by 63 and 163 (all belonging to site-types 1-1 and 1-2). The sample plots made up two clusters of high sample plot density along the axis, with centres about 2.0 S.D. and 4.5 S.D. and a relative discontinuity at about 3.3 S.D. These two

Tab. 8. The vegetational ordinations - characteristics of data sets and ordination axes. NSa - number of sample plots, NSp - number of species, NOc - number of occurrences in data matrix, No - axis number, Gr.l. - gradient length, in LNMDS calculated by rescaled constrained correspondence analysis (rCCA), Eig.v. - eigenvalue.

Ordination	Data set characteristics				Axis characteristics		
	Sample plot type	NSa	NSp	NOc	No	Gr.l.	Eig.v.
DCA	Meso sample plots	200	171	3754	1	6.19	0.7011
					2	2.64	0.1728
					3	2.46	0.1303
					4	2.18	0.1200
LNMDS2	Meso sample plots	200	171	3754	1	7.19	
					2	2.52	
LNMDS3	Meso sample plots	200	171	3754	1	5.69	
					2	3.47	
					3	2.44	
DCAV	Meso sample plots, vascular plants	200	65	1661	1	5.34	0.6393
					2	2.57	0.2185
					3	2.82	0.1413
					4	2.54	0.1208
DCAB	Meso sample plots, bottom layer	198	106	2093	1	6.53	0.7763
					2	2.85	0.2890
					3	3.54	0.2258
					4	2.45	0.1676
DCAS	Meso sample plot subplots	3198	171	27162	1	7.62	0.7234
					2	3.23	0.2572
					3	4.16	0.1947
					4	3.75	0.1845
DCAM	Micro sample plots	400	144	3837	1	6.99	0.7367
					2	3.88	0.2886
					3	3.55	0.2531
					4	3.22	0.2313

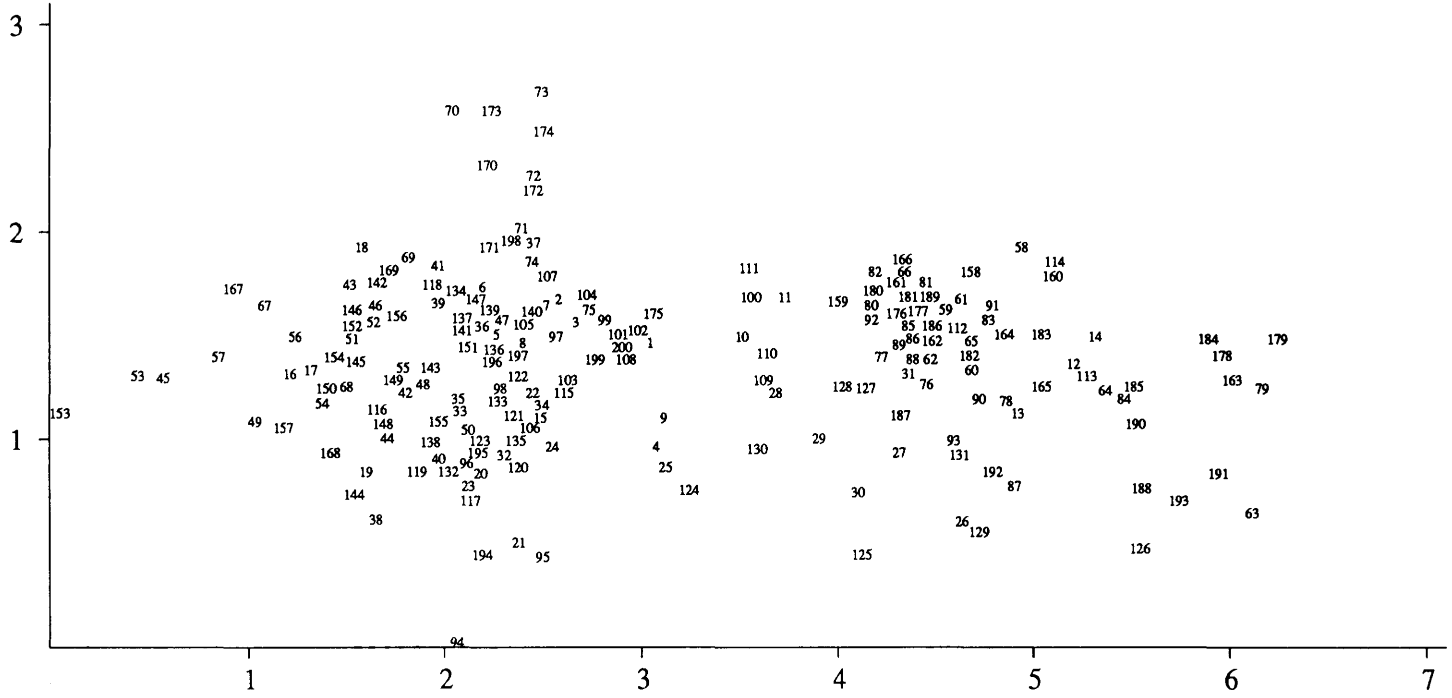


Fig. 10. DCA ordination of the ME 200 data set, axes 1 and 2. Meso sample plot numbers plotted onto the sample plot positions. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures.

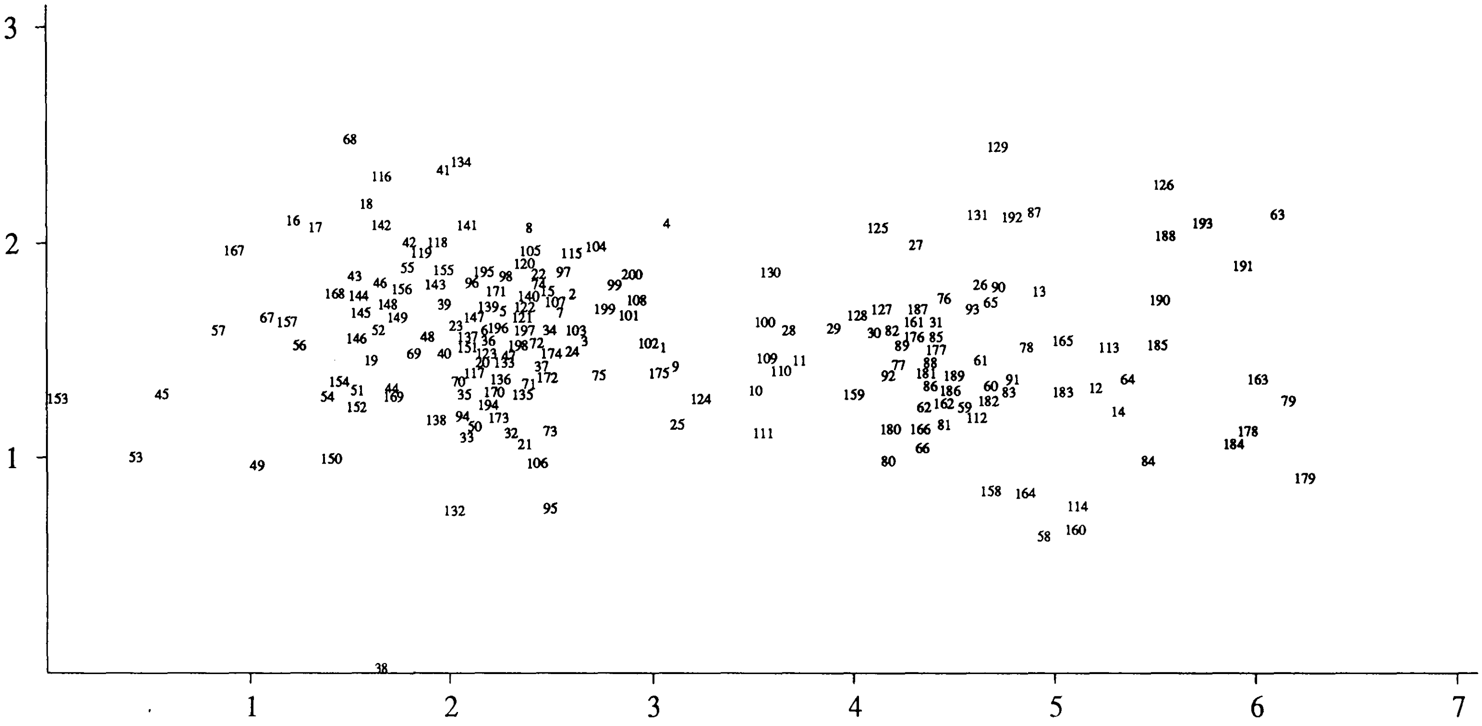


Fig. 11. DCA ordination of the ME 200 data set, axes 1 and 3. Meso sample plot numbers plotted onto the sample plot positions. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures.

clusters roughly corresponded to spruce and pine forest, respectively. The relative discontinuity was used to divide the ME 200 data set into two subsets: Subset A with DCA 1 < 3.3 comprising 121 sample plots and Subset B with DCA 1 > 3.3 comprising 79 sample plots (Appendix 1).

DCA 2 showed low values for sample plots 94, 194, 95, 121, 126 etc., all classified as moist plots (site-types 3-2 and 5.1-2). Sample plots 73, 173, 70, 174, and 70 of the SE-facing Transect 5, belonging to site-types 4-1 and 5.1-1, reached highest DCA 2 scores (Fig. 10).

Sample plot 38 (site-type 5.2-2) obtained an isolated position at the lower end of DCA 3, separated by the rest of the sample plots by more than 0.5 S.D. units. Sample plots 68 and 129 made up the opposite end (Fig. 11).

DCA 4 had sample plots 12 and 193 at the respective ends.

LNMDS, two-dimensional solution

The lengths of the LNMDS2 axes were 7.19 and 2.52 S.D. units, respectively (Tab. 8). The sample plots defining the ends of DCA 1 also occupied end positions along LNMDS2 1, except that the maximum score was reached by sample plot 79 (Fig. 12). Lowest score along LNMDS2 2 was reached by sample plot 38 (site-type 5.2-2), highest scores by plots 73 and 173. The sample plots made up two intergrading clusters of high sample plot density as is DCA (above). Subsets A and B separated at ca. 4.15 S.D. along LNMDS2 1.

LNMDS, three-dimensional solution

The lengths of the LNMDS3 axes were 5.69, 3.47 and 2.44 S.D. units (Tab. 8). The first LNMDS3 axis differed somewhat from LNMDS2 1; the lower end was again defined by sample plots 53 and 153; the upper end by sample plot 63 (Fig. 13). Some clustering of sample plots along the axis was observed. The second axis approached a second order polynomial function of positions along axis 1; the LNMDS3 1 end-point sample plots (53 and 79) obtained low values also along LNMDS3 2. Two sample plots of the LNMDS2 1 middle, Nos 155 and 95, obtained the highest values. From Fig. 13 it can be seen that the sequence of sample plots along the arch approaches the sequence along LNMDS2 1 (Fig. 12). LNMDS3 3 had lowest score for sample plot 94, highest scores for sample plots 73 and 173 (Fig. 14).

Correlations between ordination axes and environmental variables

Tab. 9 shows correlations between ordination axes and the 33 environmental variables.

DCA

Sample plot scores along DCA 1 were most strongly correlated with environmental variables of E-group 1. The highest correlation, r = 0.8047, was obtained by 03 MA Ter; indicating a shift in topography along DCA 1 from valley bottom (low value of MA Ter) at low DCA 1 values to rigdes and hilltops at high DCA 1. Other strongly correlated variables were 05 MA S d (r = -0.7280) and 20 pH_{CaCl2} (r = -0.6212). High negative correlations with DCA 1 were also shown by slope (E-group 4), canopy cover (E-group 6), soil depth (E-group 5), and several of the E-group 2+ variables (cation concentrations).

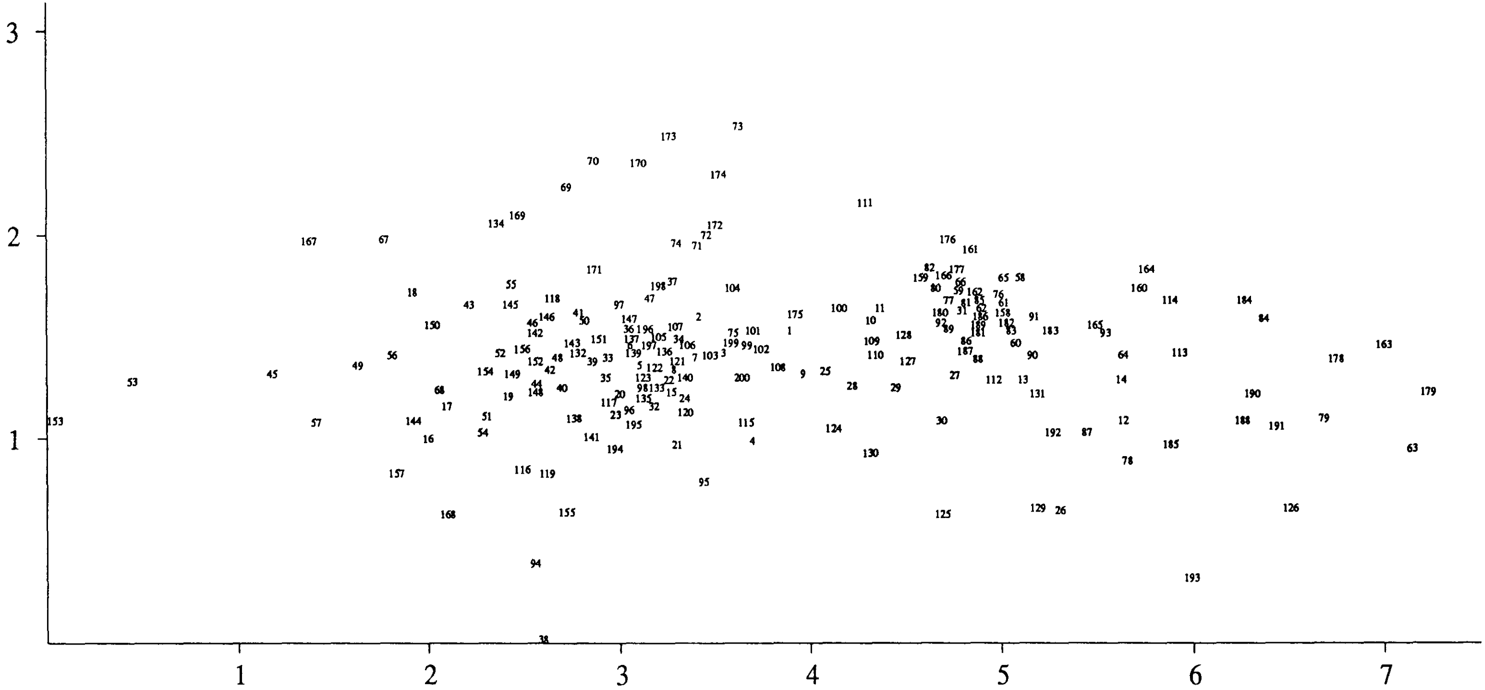


Fig. 12. LNMDS2 ordination of the ME 200 data set, axes 1 and 2. Meso sample plot numbers plotted onto the sample plot positions. Axes linearly rescaled in S.D. units by rhCCA.

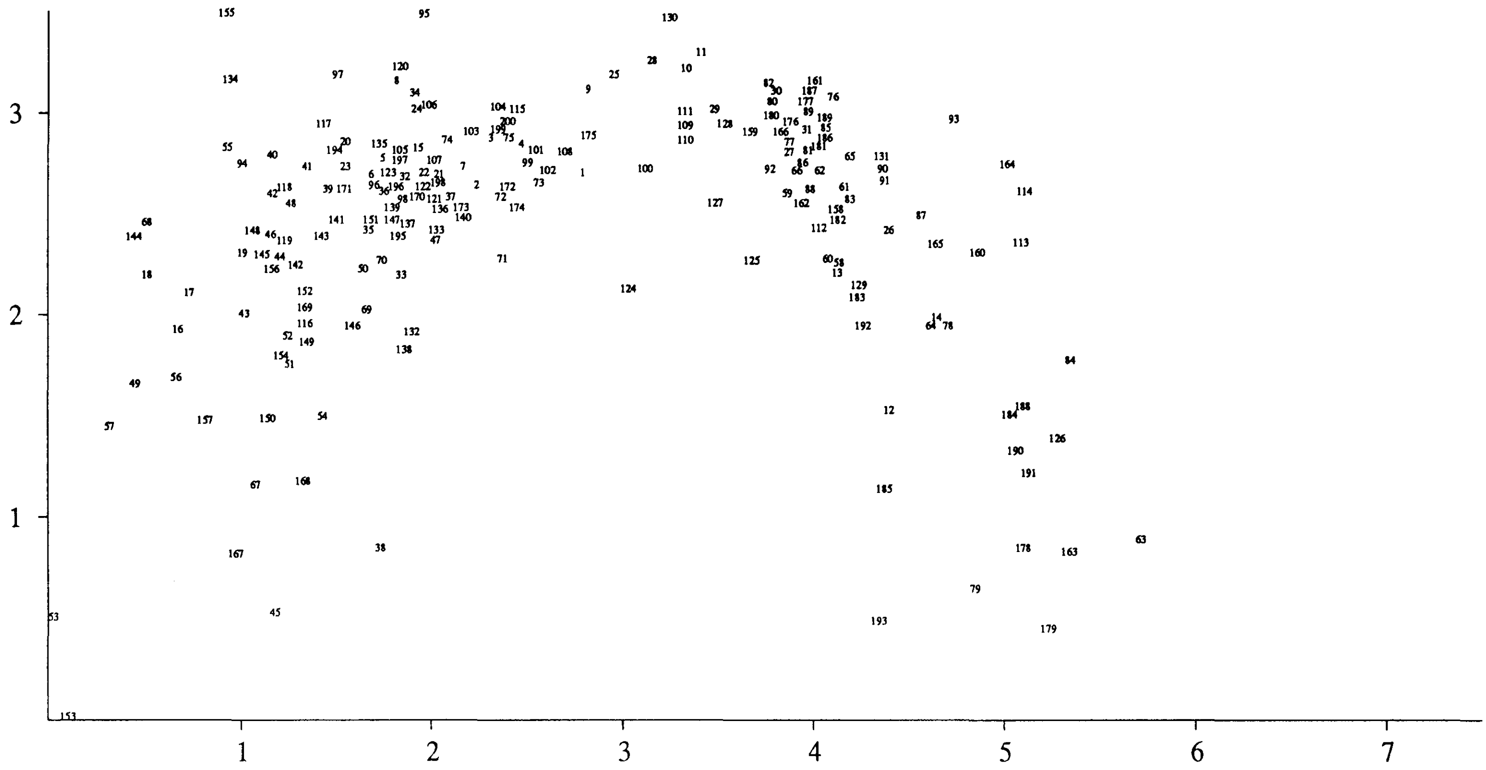


Fig. 13. LNMDS3 ordination of the ME 200 data set, axes 1 and 2. Meso sample plot numbers plotted onto the sample plot positions. Axes linearly rescaled in S.D. units by rhCCA.

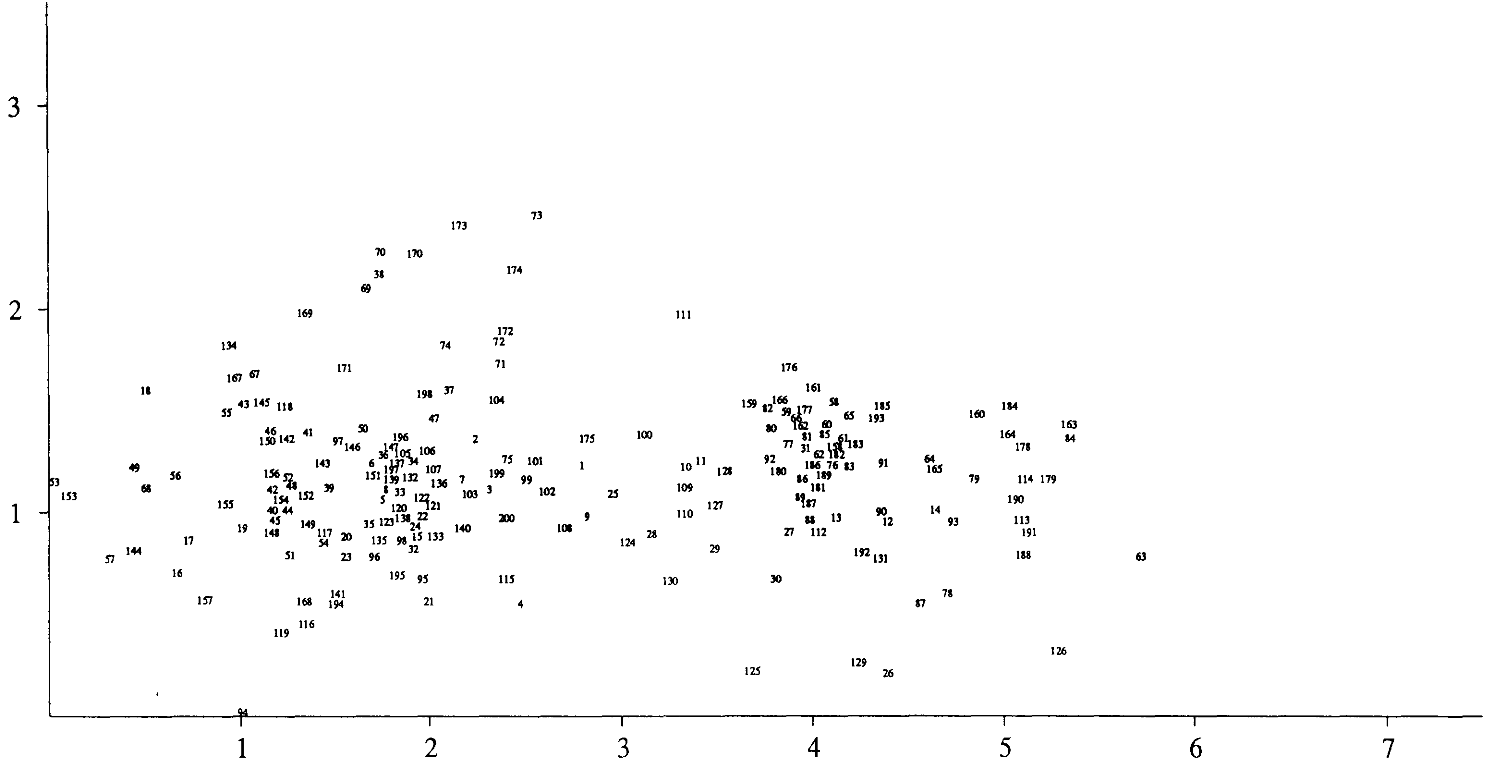


Fig. 14. LNMDS3 ordination of the ME 200 data set, axes 1 and 3. Meso sample plot numbers plotted onto the sample plot positions. Axes linearly rescaled in S.D. units by rhCCA.

Tab. 9. Pearson's product-moment correlation coefficients between meso sample plot scores relative to ordination axes and the 33 environmental variables (r), with significance probabilities (P). Correlations significant at level $P < 0.0001$ in bold face. n.s. - significance probability less than 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 3. DCA - DCA ordination, downweighting of species with frequency lower than median. LNMDS2 - LNMDS ordination, two-dimensional solution. LNMDS3 - LNMDS ordination, three-dimensional solution.

Variable	DCA 1		DCA 2		DCA 3		DCA 4		LNMDS2 1		LNMDS2 2		LNMDS3 1		LNMDS3 2		LNMDS3 3	
	r	P	r	P	r	P	r	P	r	P	r	P	r	P	r	P	r	P
01 MA Slo	**-.5848**	**.0000**	-.2283	.0011	.2533	.0003	-.2824	.0001	**-.5538**	**.0000**	-.1975	.0051	**-.5947**	**.0000**	.1234	.0816	-.2644	.0002
02 MA Asf	-.1871	.0080	-.2030	.0039	.2515	.0003	-.0272	n.s.	-.1941	.0059	-.1838	.0092	-.1924	.0063	.1990	.0047	-.2784	.0001
03 MA Ter	**.8047**	**.0000**	.0680	n.s.	.0008	n.s.	.0942	n.s.	**.7761**	**.0000**	.1095	n.s.	**.7809**	**.0000**	.0770	n.s.	.0168	n.s.
04 MA Une	**-.3248**	**.0000**	-.1047	n.s.	.1446	.0411	-.2091	.0030	**-.3262**	**.0000**	-.1215	.0865	**-.3682**	**.0000**	.0634	n.s.	-.1304	.0657
05 MA S d	**-.7280**	**.0000**	.1858	.0084	-.0003	n.s.	-.0082	n.s.	**-.6997**	**.0000**	.1310	.0645	**-.6925**	**.0000**	-.1099	n.s.	.2274	.0012
06 MA Bas	**-.4030**	**.0000**	**.3473**	**.0000**	.1608	.0230	-.0169	n.s.	**-.4010**	**.0000**	.2733	.0001	**-.4023**	**.0000**	.0968	n.s.	**.2974**	**.0000**
07 MA Can	**-.3748**	**.0000**	**.4799**	**.0000**	.0843	n.s.	.0607	n.s.	**-.3533**	**.0000**	**.4454**	**.0000**	**-.3524**	**.0000**	.1081	n.s.	**.4922**	**.0000**
08 ME Slo	**-.4097**	**.0000**	-.2184	.0019	.2443	.0005	-.1767	.0123	**-.3842**	**.0000**	-.1610	.0027	**-.4158**	**.0000**	.0816	n.s.	-.2286	.0011
09 ME Asf	-.1767	.0123	-.1481	.0364	.1731	.0142	-.0993	n.s.	-.1763	.0125	-.1116	n.s.	-.1882	.0076	.1036	n.s.	-.1738	.0138
10 ME Une	-.2792	.0001	.0283	n.s.	.0674	n.s.	-.0685	n.s.	-.2675	.0001	.0531	n.s.	-.2654	.0001	**.2917**	**.0000**	-.0658	n.s.
11 ME Con	-.0668	n.s.	-.0166	n.s.	-.0188	n.s.	-.1280	.0709	-.0379	n.s.	-.0697	n.s.	-.0578	n.s.	-.0271	n.s.	-.0392	n.s.
12 ME Smi	-.1598	.0238	.2688	.0001	-.1345	.0576	.2556	.0003	-.1726	.0145	.2544	.0003	-.1163	n.s.	.2020	.0041	.2631	.0002
13 ME Sme	**-.3494**	**.0000**	**.4146**	**.0000**	-.2078	.0032	.2735	.0001	**-.3550**	**.0000**	**.4187**	**.0000**	**-.2872**	**.0000**	.2238	.0014	**.3996**	**.0000**
14 ME Sma	**-.4344**	**.0000**	**.3881**	**.0000**	-.1555	.0279	.2349	.0006	**-.4405**	**.0000**	**.3866**	**.0000**	**-.3824**	**.0000**	.1827	.0096	**.3444**	**.0000**
15 ME Lit	**-.3630**	**.0000**	**.4163**	**.0000**	.1694	.0165	.0342	n.s.	**-.3525**	**.0000**	**.4034**	**.0000**	**-.3641**	**.0000**	.1364	.0542	**.4266**	**.0000**
16 ME Bas	**-.5220**	**.0000**	.2648	.0002	.1698	.0162	-.1314	.0637	**-.5040**	**.0000**	.1524	.0312	**-.5256**	**.0000**	.0707	n.s.	.2095	.0029
17 Mois	-.0623	n.s.	**-.5649**	**.0000**	-.0060	n.s.	-.1385	.0505	-.0694	n.s.	**-.5502**	**.0000**	-.0925	n.s.	**-.2914**	**.0000**	**-.4228**	**.0000**
18 LI	**.4928**	**.0000**	.0990	n.s.	-.0606	n.s.	.1558	.0276	**.5018**	**.0000**	.2137	.0024	**.4991**	**.0000**	**.5284**	**.0000**	.1429	.0435
19 pH$_{H2O}$	**-.5477**	**.0000**	-.1966	.0053	-.1065	n.s.	.0821	n.s.	**-.5723**	**.0000**	-.2353	.0008	**-.5190**	**.0000**	**-.4362**	**.0000**	-.1034	n.s.
20 pH$_{CaCl2}$	**-.6212**	**.0000**	-.0823	n.s.	-.0507	n.s.	.0297	n.s.	**-.6482**	**.0000**	-.1544	.0291	**-.5944**	**.0000**	**-.4187**	**.0000**	-.0403	n.s.
21 Ca	**-.4135**	**.0000**	**.3017**	**.0000**	.1212	.0874	-.1340	.0584	**-.4239**	**.0000**	.1976	.0050	**-.4013**	**.0000**	-.0444	n.s.	.1911	.0067
22 Mg	**-.3267**	**.0000**	**.3011**	**.0000**	.0965	n.s.	-.0956	n.s.	**-.3289**	**.0000**	.2171	.0020	**-.3045**	**.0000**	.0230	n.s.	.1589	.0246
23 Na	-.1718	.0150	.0604	n.s.	.0411	n.s.	-.0525	n.s.	-.1786	.0114	.0238	n.s.	-.1514	.0323	-.0504	n.s.	.0126	n.s.
24 K	**-.4002**	**.0000**	.1546	.0288	.1198	.0911	-.1910	.0068	**-.3863**	**.0000**	.0954	n.s.	**-.3854**	**.0000**	.0822	n.s.	.0238	n.s.
25 H	**.3752**	**.0000**	-.2581	.0002	-.0802	n.s.	.1169	.0991	**.3942**	**.0000**	-.1514	.0324	**.3581**	**.0000**	.1045	n.s.	-.1294	.0678
26 N	**-.5565**	**.0000**	-.1355	.0557	.1108	n.s.	-.1738	.0138	**-.5548**	**.0000**	-.1943	.0058	**-.5666**	**.0000**	**-.4944**	**.0000**	-.9088	n.s.
27 P-AL	-.2470	.0004	.1803	.0106	.1979	.0050	-.2308	.0010	-.2377	.0007	.1067	n.s.	-.2729	.0001	.0029	n.s.	.0844	n.s.
28 Al	-.0384	n.s.	**-.4997**	**.0000**	-.0984	n.s.	-.1387	.0501	-.0335	n.s.	**-.4987**	**.0000**	-.0239	n.s.	**-.2830**	**.0000**	**-.4542**	**.0000**
29 Fe	.0933	n.s.	**-.3111**	**.0000**	.0244	n.s.	-.0643	n.s.	.1116	n.s.	**-.3406**	**.0000**	.0905	n.s.	-.0812	n.s.	-.2477	.0004
30 Mn	**-.4260**	**.0000**	.0596	n.s.	.1419	.0451	-.2318	.0010	**-.4373**	**.0000**	-.0647	n.s.	**-.4245**	**.0000**	-.1415	.0456	-.0973	n.s.
31 Zn	-.0936	n.s.	.0465	n.s.	.0758	n.s.	**-.3256**	**.0000**	-.0936	n.s.	-.0731	n.s.	-.1024	n.s.	.0025	n.s.	-.1641	.0203
32 P	-.0318	n.s.	.1074	n.s.	.1521	.0316	**-.3403**	**.0000**	-.0067	n.s.	.0378	n.s.	-.0489	n.s.	.2363	.0008	-.0596	n.s.
33 S	-.2221	.0016	-.0330	n.s.	.0500	n.s.	-.2369	.0007	-.2190	.0018	-.1303	.0659	-.2125	.0025	-.0822	n.s.	-.1814	.0102

The environmental variable most strongly correlated with DCA 2 was 17 Mois (r = -0.5649), indicating decreasing soil moisture along the axis. High correlations were also noted for E-group 3 (notably Al; r = -0.4997). Canopy cover (E-group 6) and soil depth (E-group

5) increased along the axis, all correlations significant at $P \leq 0.0001$.

No environmental variable was correlated with DCA 3 score at significance level $P < 0.0001$. The highest correlations (all positive) were obtained by MA Slo ($r = 0.2533$, $P = 0.0003$), MA Asf ($r = 0.2515$, $P = 0.0003$) and ME Slo ($r = 0.2443$, $P = 0.0005$).

The environmental variables ZN and P of E-group 2+ were most strongly correlated with DCA 4 ($r = -0.3256$ and $r = -0.3403$, respectively). Other significant correlations were obtained by variables of E-groups 4 and 5.

LNMDS, two-dimensional solution

Correlations between LNMDS2 1 and environmental variables closely approached those described for DCA 1. The highest correlation, $r = 0.7761$, was noted for MA Ter. Similarly, correlations between LNMDS2 2 and environmental variables were similar to those of DCA 2, but in most cases the value of r for corresponding variables were lower (for instance, the highest value, with Mois, was $r = -0.5502$).

LNMDS, three-dimensional solution

Correlations between LNMDS3 1 and environmental variables again closely approached those described for DCA 1. The highest correlation noted was 0.7809 for MA Ter.

Variables of E-group 2 were strongly correlated with LNMDS3 2; the highest correlations were noted for LI ($r = 0.5284$), N ($r = -0.4944$), and the two pH measurements. Correlations significant at level $P < 0.0001$ were also noted by Mois ($r = -0.2914$) and AL ($r = 0.2830$).

MA Can was most strongly correlated with LNMDS3 3 ($r = 0.4922$), followed by AL ($r = -0.4542$), ME Lit ($r = 0.4266$) and Mois ($r = -0.4228$). Positive correlations were also noted by other variables of E-group 6 and the soil depth variables (E-group 5).

Comparison of ordinations

Tab. 10 shows pairwise correlations between sample scores of the three ordinations. The first axes of the three ordinations were virtually identical ($r \geq 0.98$!). Very similar, but not identical, were DCA 2, LNMDS2 2 and LNMDS3 3 ($r \geq 0.78$). LNMDS3 2, a curvilinear function of LNMDS3 1, did not approach any of the other axes, neither did DCA 3 nor DCA 4.

The close similarity of the two first axes in DCA and two-dimensional LNMDS indicated that the vegetational gradients reflected by these axes were the dominant trends in the ME 200 data-set. The higher correlations between DCA axes and environmental variables motivated the DCA solution to be preferred over LNMDS. Very low correlations between DCA 3 and environmental parameters motivated restriction of further attention to the first two axes.

Tab. 10. Pearson's product-moment correlation coefficients between meso sample plot scores relative to ordination axes (lower triangle) and significance probabilities (upper triangle). Correlations significant at level $P < 0.0001$ in bold face. n.s. - significance probability less than 0.1. DCA - DCA ordination, downweighting of species with frequency lower than median. MDS2 - LNMDS ordination, two-dimensional solution. MDS3 - LNMDS ordination, three-dimensional solution.

	DCA 1	DCA 2	DCA 3	DCA 4	MDS2 1	MDS2 2	MDS3 1	MDS3 2	MDS3 3
DCA 1	*	*	*	*	**.0000**	n.s.	**.0000**	n.s.	n.s.
DCA 2	*	*	*	*	n.s.	**.0000**	n.s.	.0439	**.0000**
DCA 3	*	*	*	*	.0913	.0105	.0171	n.s.	**.0000**
DCA 4	*	*	*	*	n.s.	.0001	.0217	n.s.	**.0000**
MDS2 1	**.9876**	-.0617	-.1197	.0893	*	*	**.0000**	n.s.	n.s.
MDS2 2	.0010	**.8473**	-.1807	.2698	*	*	n.s.	.0001	**.0000**
MDS3 1	**.9817**	-.0263	-.1685	.1622	**.9800**	.0467	*	*	*
MDS3 2	.0023	.1427	.1101	.0333	.0200	.2753	*	*	*
MDS3 3	-.0345	**.7870**	**-.3022**	**.3893**	-.0342	**.8131**	*	*	*

Interpretation of the DCA ordination by means of the classification into site-types

The site-types segregated along the first two DCA axes, as shown in Fig. 15. It is readily apparent from the figure that the series (and site-types along the nutrient gradient, within series 5) made up a sequence along DCA 1 from 6, via 5.3, 5.2, 5.1, 4, 3, 2 to 1. The sequence was not fully discrete, the site-types overlapped in transitional zones from 0.15 to 0.50 S.D. units wide. Each series (or site-type within series 5) occupied roughly equal intervals along the axis; 0.7-1.0 S.D. units. The narrowest intervals were occupied by 3 and 5.3, the widest by 2 and 4. Subset A corresponded to site-types 5.1, 5.2, 5.3 and 6 and Subset B to series 1, 2 and 3. The relative discontinuity at DCA 1 = 3.3 divided site-type 4 almost equally onto the subsets. The results showed that the topographic moisture gradient and the gradient in nutrient status, forming the basis for the classification system, joined to form one complex coenocline. The variation along the fine-scale moisture gradient was clearly expressed along DCA 2 (Fig. 15). Dry (-1) site-types occurred at DCA 2 > ca. 1.0; somewhat lower for site-types of series 5, somewhat higher for series 1-3.

Interpretation of the DCA ordination by means of the environmental variables

Correlations between environmental variables and DCA axes (Tab. 9) have been treated above (pp. 48-53).

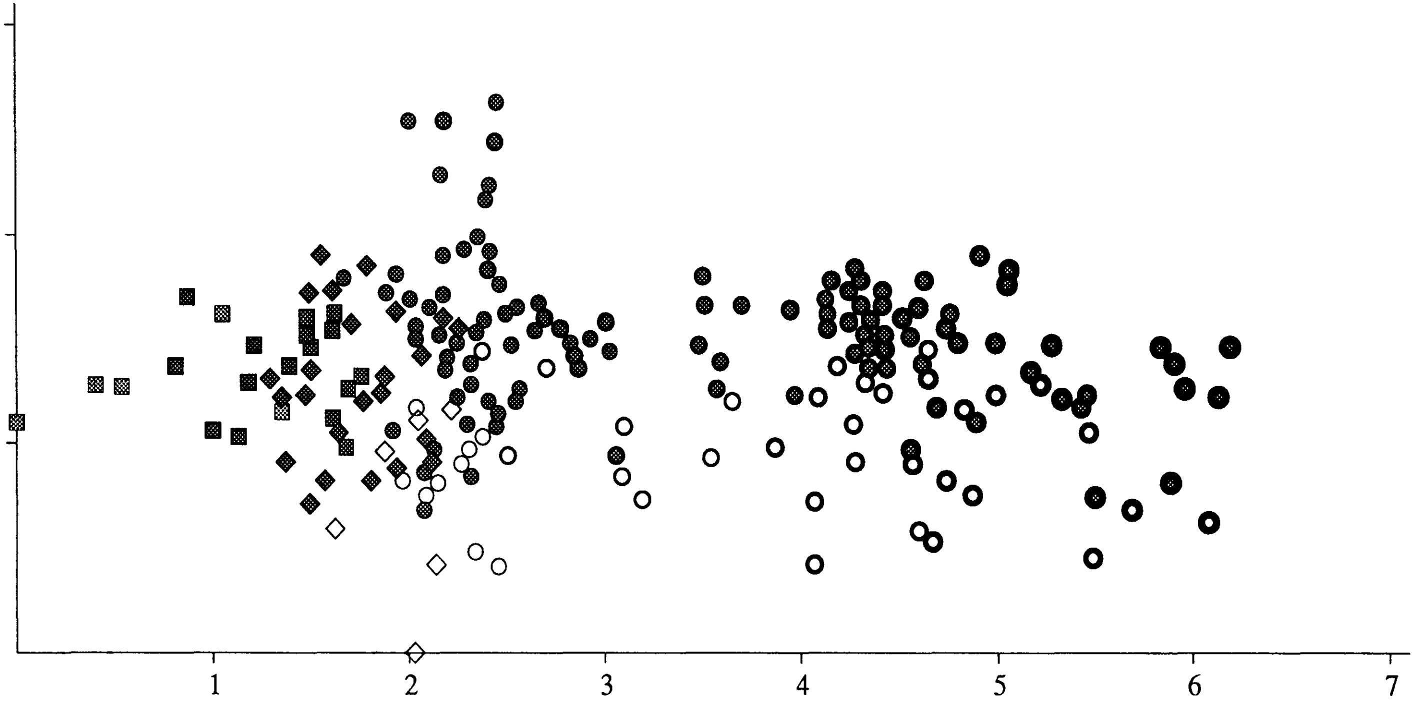


Fig. 15. DCA ordination of the ME 200 data set, axes 1 and 2. Site-type classification of sample plots plotted onto the sample plot positions. For explanation of symbols, see Fig. 4 (p. 31). Axes scaled in S.D. units.

Vector fitting

Fig. 16 shows vectors for the direction of steepest increase in the environmental variables plotted onto the DCA 12 ordination diagram. Long arrows indicate high correlations between the variable in question and the ordination axes. Fig. 16 amplifies the results of the correlation analysis. Most arrows were extended in the direction of DCA 1, indicating generally stronger correlations of the environmental variables with this axis. Vectors representing variables of E-group 1 (MA S d, pH_{CaCl2}, N and pH_{H2O} pointing left (negatively correlated), and MA Ter and LI pointing right) had the longest components along DCA 1, while their components along DCA 2 were short. A high number of variables had relatively long components along both axes; negatively correlated with DCA 1 and positively correlated with DCA 2 (and thus pointing towards the upper left of the diagram). These were Mn, K, Ca, and Mg of E-group 2+ (H of E-group 2- pointing in the opposite direction), the canopy cover group of variables (E-group 6), and the soil depth variables (E-group 5); ME Sma most closely approached DCA 1 and displayed the longest vector, ME Sme only slightly shorter, while ME Smi had a short arrow more closely approaching DCA 2. The slope variables (MA Slo and ME Slo of E-group 4) pointed towards the lower left; strongly negatively correlated with DCA 1, but also negatively correlated with DCA 2. The Mois vector was long and almost parallel with DCA 2. Also aligning to DCA 2, pointing in the negative direction, and having relatively long arrows, were Al and Fe of E-group 3.

Variation of environmental variables

Twenty of the 33 environmental variables had correlations with DCA 1 or DCA 2 higher than 0.35. The variation of these variables along DCA 1 and DCA 2 are shown in Figs 17-37.

E-group 1 parameters showed variation along DCA 1. The variation of MA Ter, the variable most strongly correlated with DCA 1, is shown in Fig. 18. Sample plots with the lowest DCA 1 values (belonging to site-type 6) represented valley bottoms or concave slopes. The 5.2-2 site-type ($1.0 < \text{DCA } 1 < 2.5$; $\text{DCA } 2 < 1.0$) represented concave or straight valley sides; the 5.2-1 and 5.3 site-types mostly represented straight valley sides; 5.1-1 and 4 straight or convex valley-sides, while site-types 3, 2 and 1 were confined to ridges and hilltops. There was no distinct tendency to variation in MA Ter along DCA 2 for $\text{DCA } 1 > 2.5$. MA S d (Fig. 19) was low (value 1 of the MA S d parameter) at $\text{DCA } 1 > 3.7$ (site-types 1-3), with an indistinct tendency for increasing frequency of the deepest soils (parameter value 3) towards lower DCA 1 values. LI (Fig. 28) showed a complex pattern of variation. The organic content of the humus layer was low at DCA 1 = 0, increasing rapidly to DCA 1 = 3.0. Maximum (close to 100 %) were reached about DCA 1 = 2.0, DCA 2 = 0.0 and in the region $3.2 < \text{DCA } 1 < 4.5$, $\text{DCA } 2 > 1.2$. LI decreased slightly towards higher DCA values, but the variation between neighbouring points in the ordination diagram was considerable. pH_{H2O} (Fig. 29) showed insignificant variation (3.9-4.2) for $\text{DCA } 1 > 2.5$ (site-types 1-4), except for a trend to increasing pH from high to low DCA 2 position (ca. 3.9 in the uppermost, 4.0-4.2 in the lowermost DCA 2 positions). At low DCA 2 positions pH_{H2O} was 4.1-4.2 in site-type 5.1 and 4.2-4.4 in 5.2, in both cases decreasing towards higher DCA 2 scores (and thus giving rise to slightly oblique isolines in Fig. 29). pH_{H2O} was distinctly higher in site-type 5.3 (4.4-4.8), and reached the highest values (5.0-5.5) in site-type 6. pH_{CaCl2} (Fig. 30) closely followed pH_{H2O}, but the variation along DCA 2 (for constant position along DCA 1) was insignificant (vertical isolines in Fig. 30). N (Fig. 34) showed a pattern of variation approaching the inverse of LI

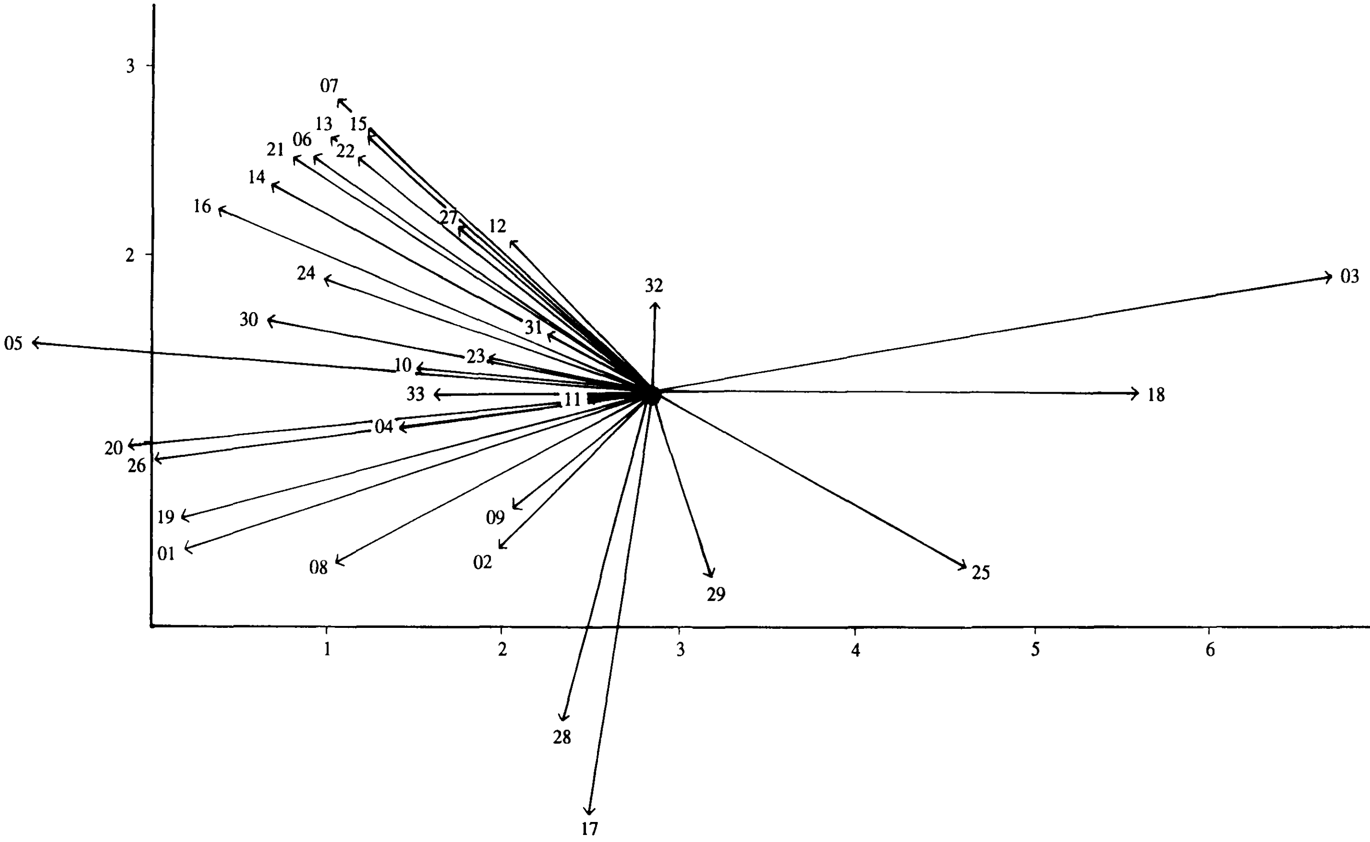


Fig. 16. DCA ordination of the ME 200 data set, axes 1 and 2. Vectors for environmental variables (numbers in accordance with Tab. 3) fitted. Axes scaled in S.D. units.

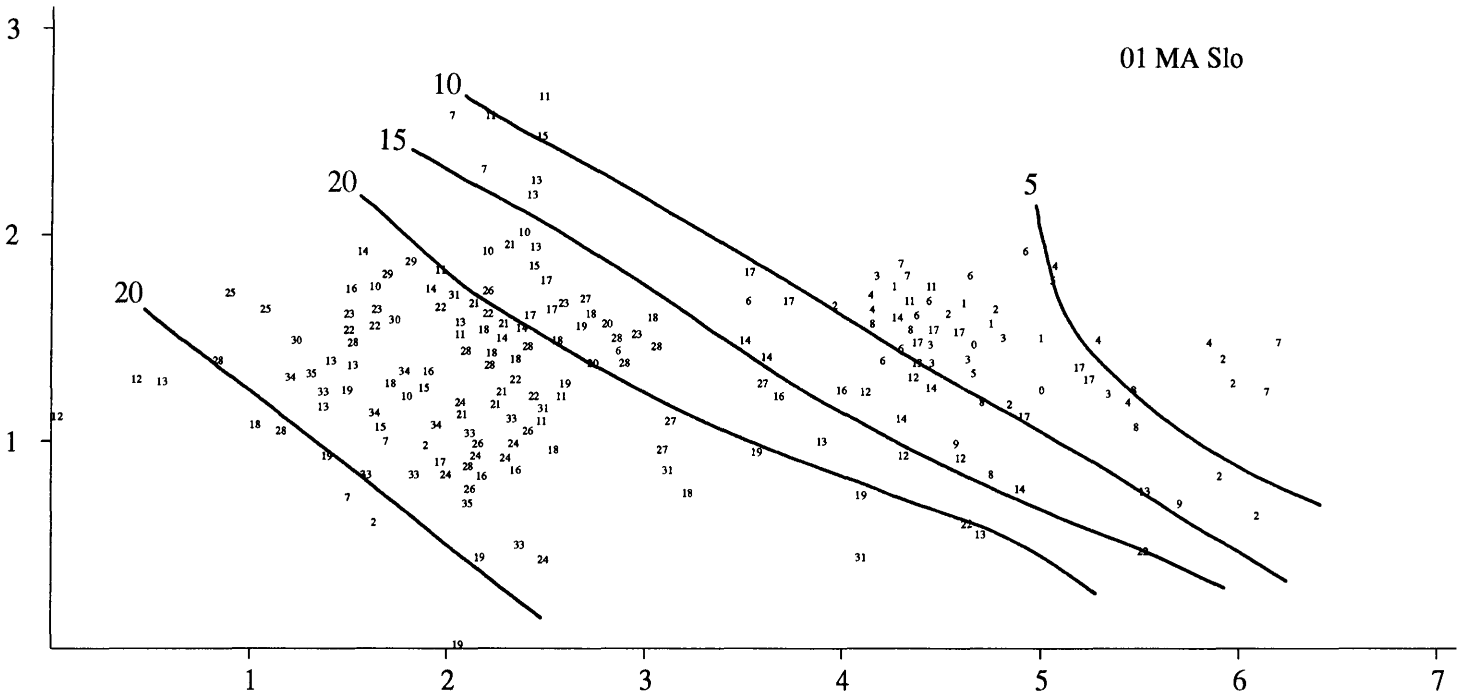


Fig. 17. DCA ordination of the ME 200 data set, axes 1 and 2. Values for 01 MA Slope (°) plotted onto the sample plot positions. Isolines based on fitting third-order polynomials in x and y. Correlation between original values and predicted values as calculated from the multiple regression model, r = 0.729. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures.

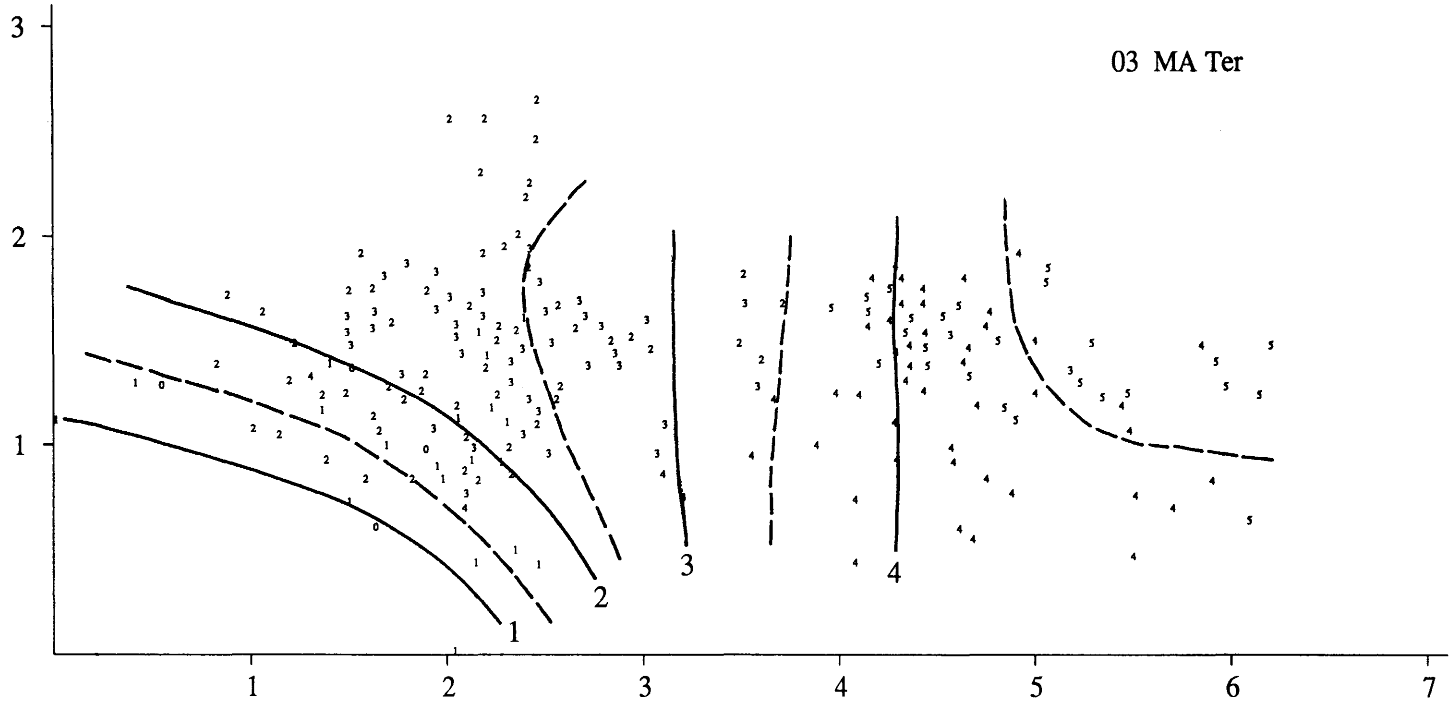


Fig. 18. DCA ordination of the ME 200 data set, axes 1 and 2. Values for 03 MA Terrain form (recorded on a 0-5 scale, cf. p. 21) plotted onto the sample plot positions. Isolines based on fitting third-order polynomials in x and y. Correlation between original values and predicted values as calculated from the multiple regression model, r = 0.841. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures.

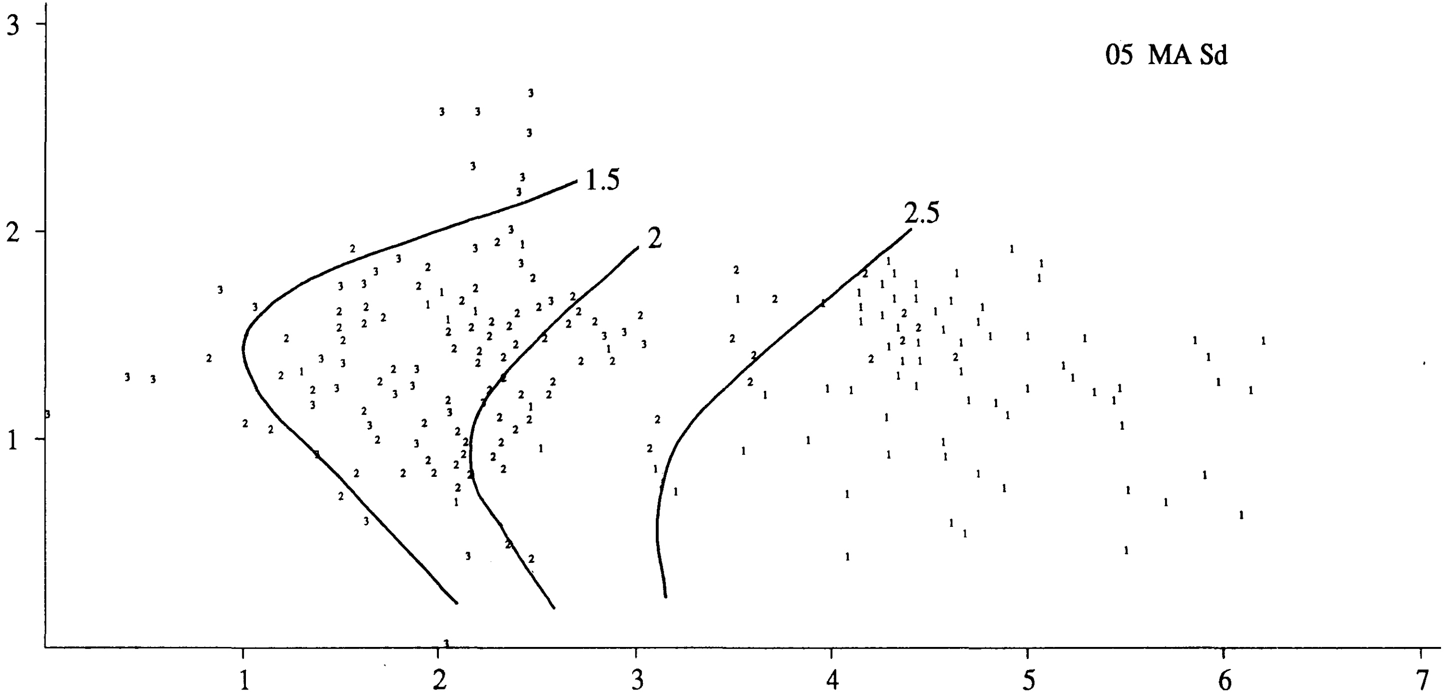


Fig. 19. DCA ordination of the ME 200 data set, axes 1 and 2. Values for 05 MA (recorded on a 1-4 scale, cf. p. 21) plotted onto the sample plot positions. Isolines based on fitting third-order polynomials in x and y. Correlation between original values and predicted values as calculated from the multiple regression model, r = 0.785. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures.

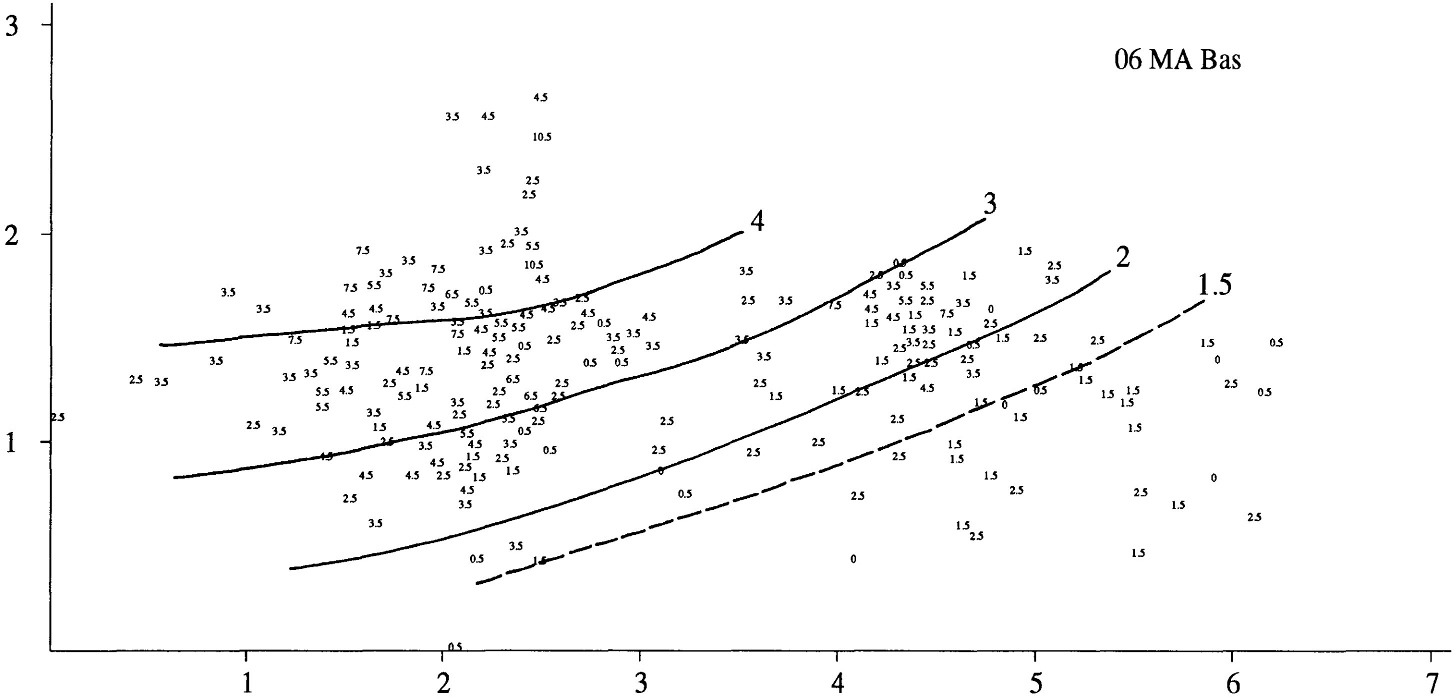


Fig. 20. DCA ordination of the ME 200 data set, axes 1 and 2. Values for 06 MA Basal area (cf. p. 21-22) plotted onto the sample plot positions. Isolines based on fitting third-order polynomials in x and y. Correlation between original values and predicted values as calculated from the multiple regression model, r = 0.535. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures.

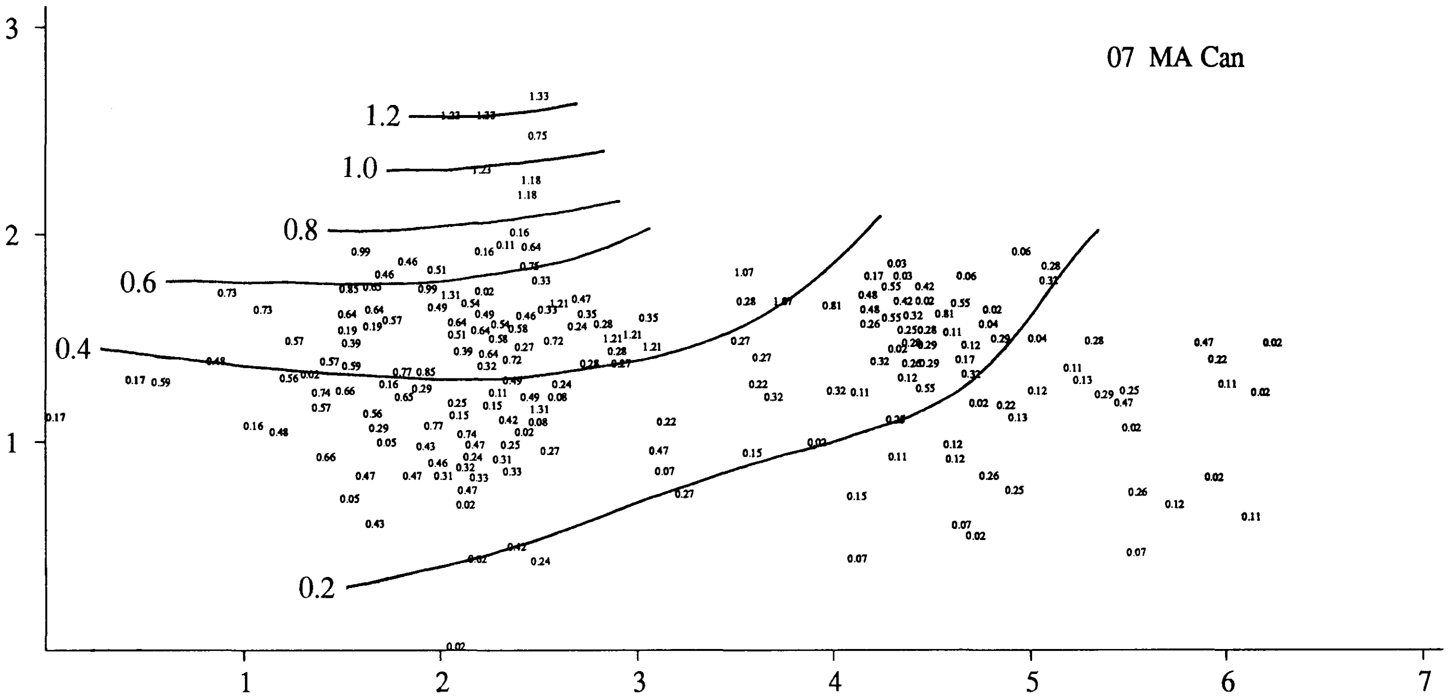


Fig. 21. DCA ordination of the ME 200 data set, axes 1 and 2. Values for 07 MA Canopy cover (cf. p. 22) plotted onto the sample plot positions. Isolines based on fitting third-order polynomials in x and y. Correlation between original values and predicted values as calculated from the multiple regression model, r = 0.640. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures.

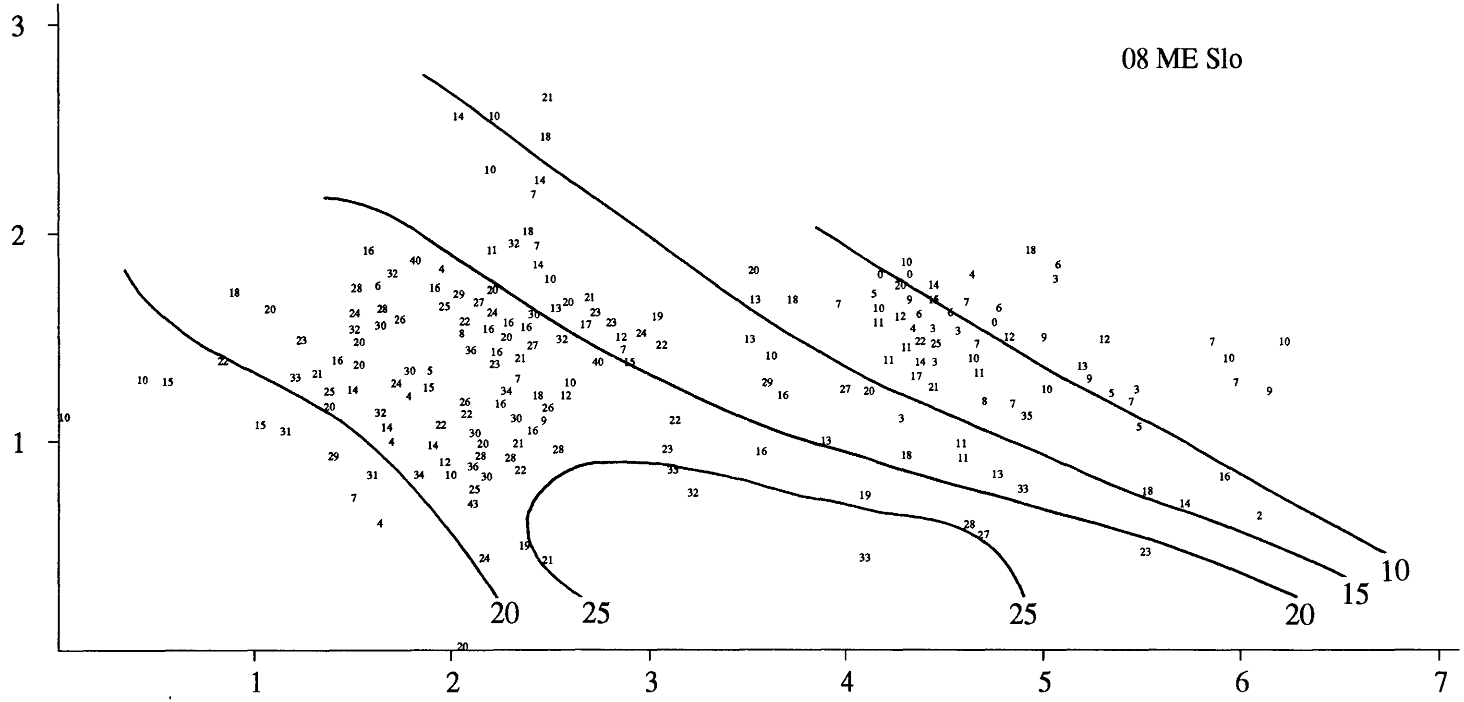


Fig. 22. DCA ordination of the ME 200 data set, axes 1 and 2. Values for 08 ME Slope (°) plotted onto the sample plot positions. Isolines based on fitting third-order polynomials in x and y. Correlation between original values and predicted values as calculated from the multiple regression model, r = 0.588. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures.

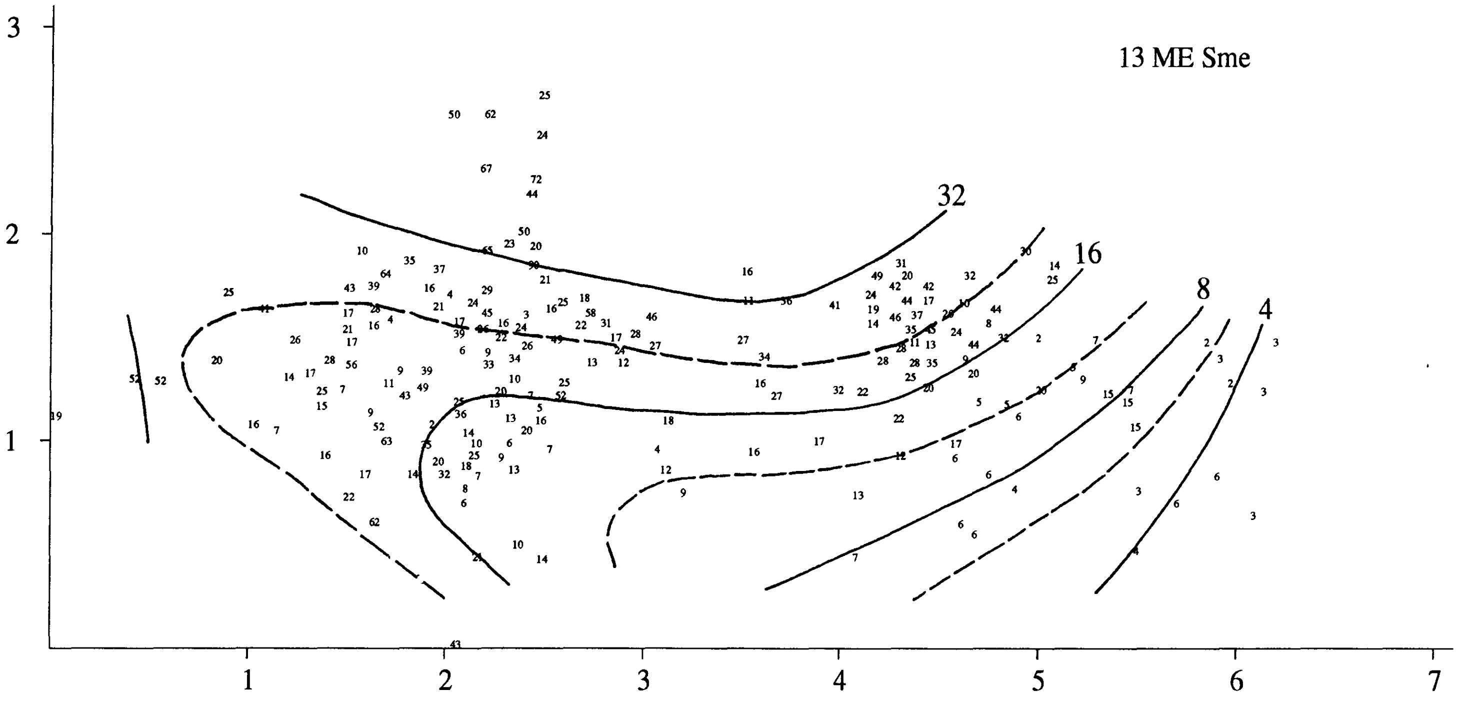


Fig. 23. DCA ordination of the ME 200 data set, axes 1 and 2. Values for 13 ME Soil depth, median (cm), plotted onto the sample plot positions. Isolines based on fitting third-order polynomials in x and y to original, ln-transformed values. Correlation between original (ln-transformed) values and predicted values as calculated from the multiple regression model, r = 0.652. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures.

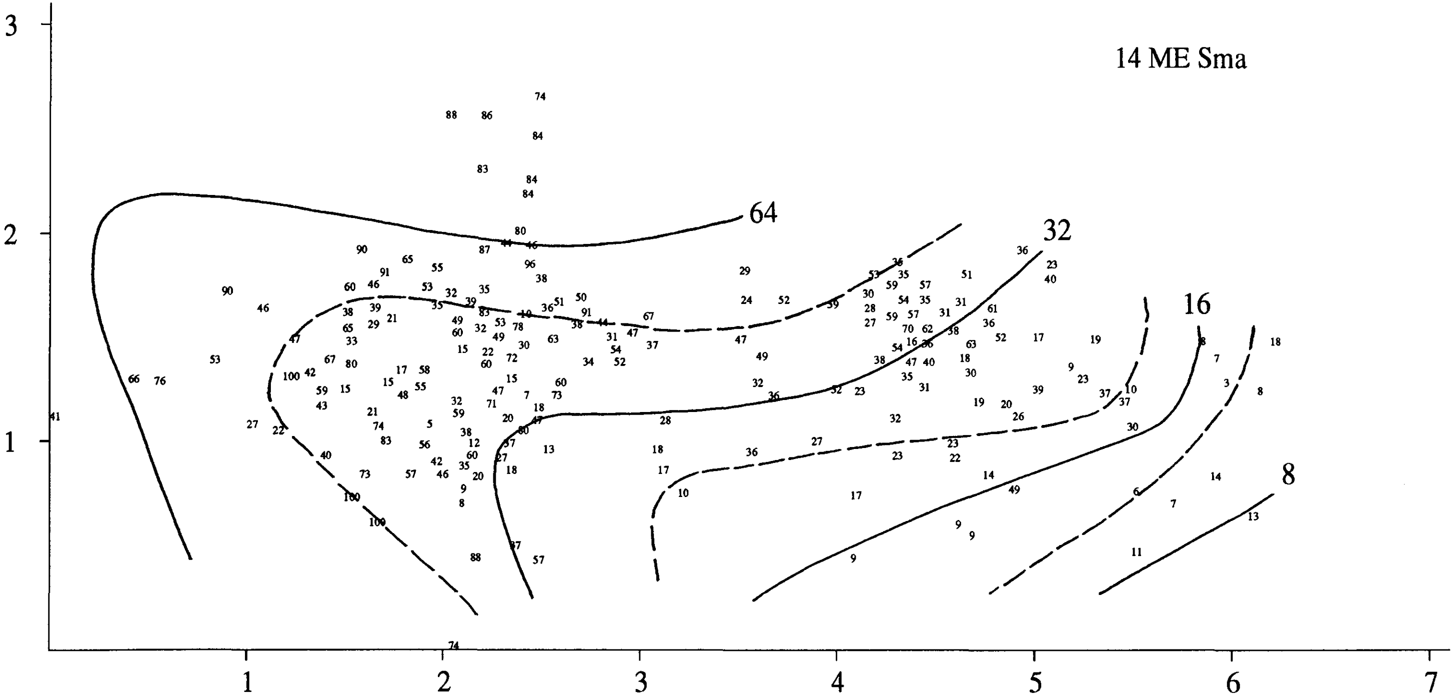


Fig. 24. DCA ordination of the ME 200 data set, axes 1 and 2. Values for 14 ME Soil depth, minimum (cm), plotted onto the sample plot positions. Isolines based on fitting third-order polynomials in x and y to original, ln-transformed values. Correlation between original (ln-transformed) values and predicted values as calculated from the multiple regression model, r = 0.660. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures.

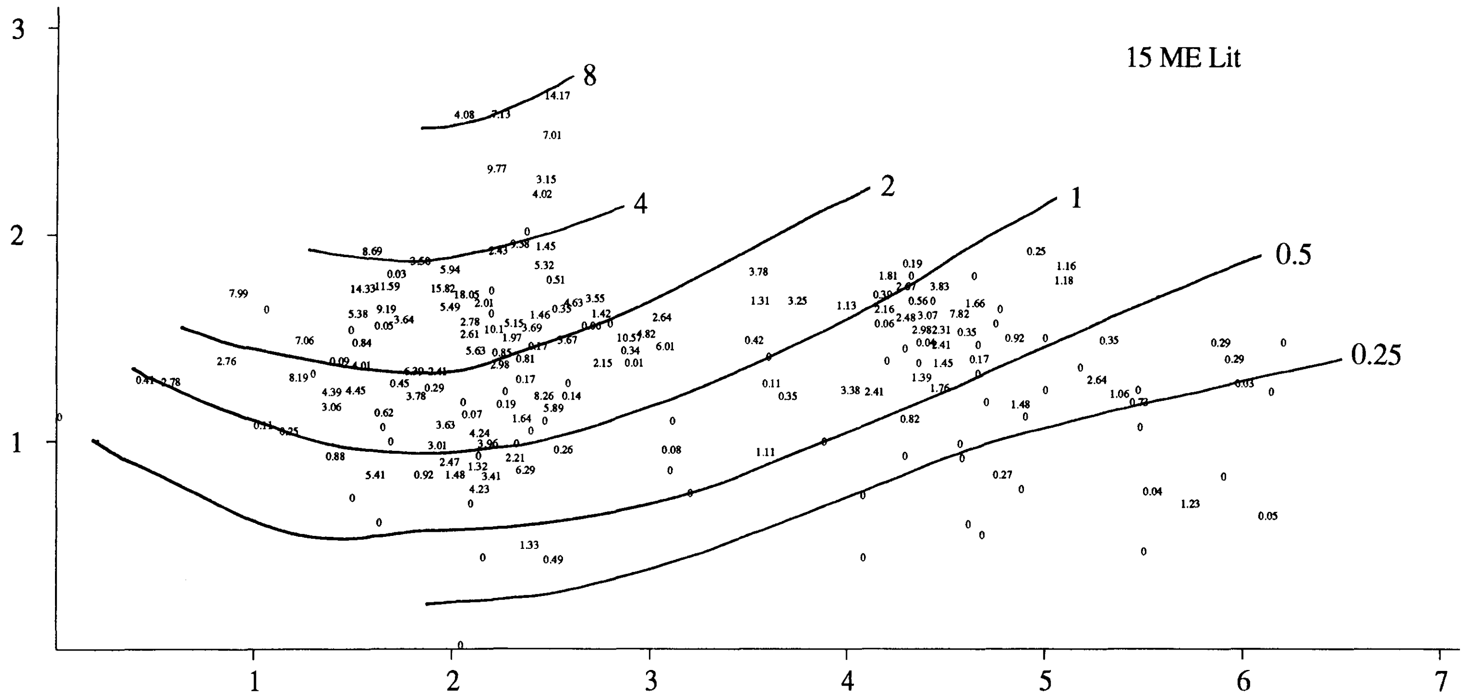


Fig. 25. DCA ordination of the ME 200 data set, axes 1 and 2. Values for 15 ME Litter index (cf. p. 23) plotted onto the sample plot positions. Isolines based on fitting third-order polynomials in x and y. Correlation between original values and predicted values as calculated from the multiple regression model, r = 0.560. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures.

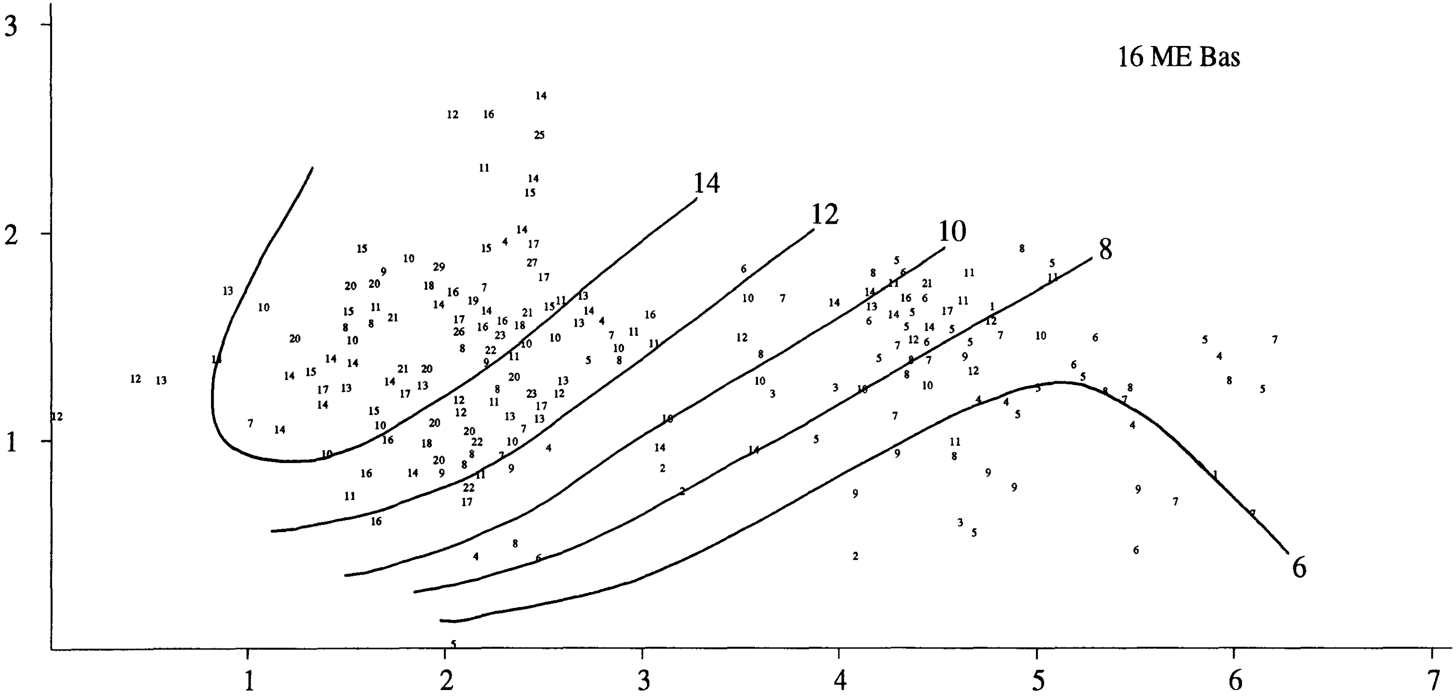


Fig. 26. DCA ordination of the ME 200 data set, axes 1 and 2. Values for 16 ME Basal area (cf. p. 24) plotted onto the sample plot positions. Isolines based on fitting third-order polynomials in x and y. Correlation between original values and predicted values as calculated from the multiple regression model, r = 0.607. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures.

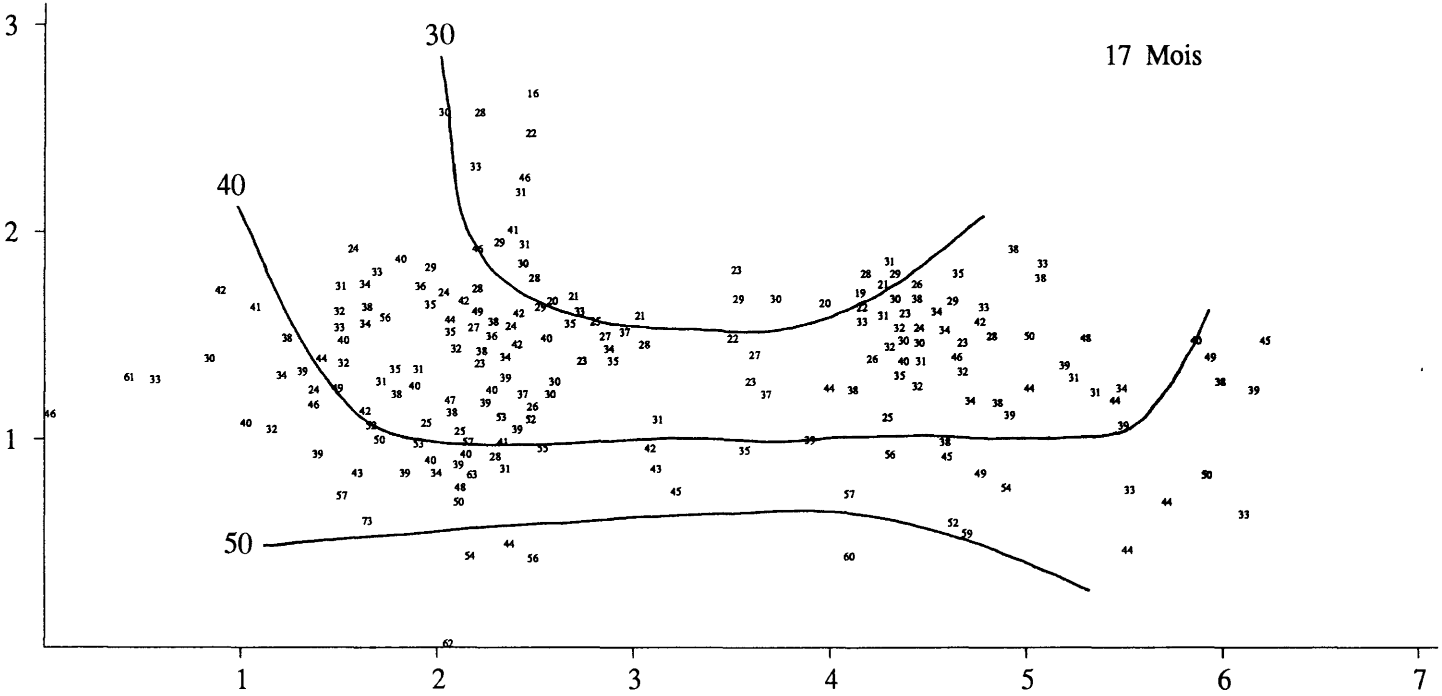


Fig. 27. DCA ordination of the ME 200 data set, axes 1 and 2. Values for 17 Volumetric soil moisture (%) plotted onto the sample plot positions. Isolines based on fitting third-order polynomials in x and y. Correlation between original values and predicted values as calculated from the multiple regression model, r = 0.666. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures.

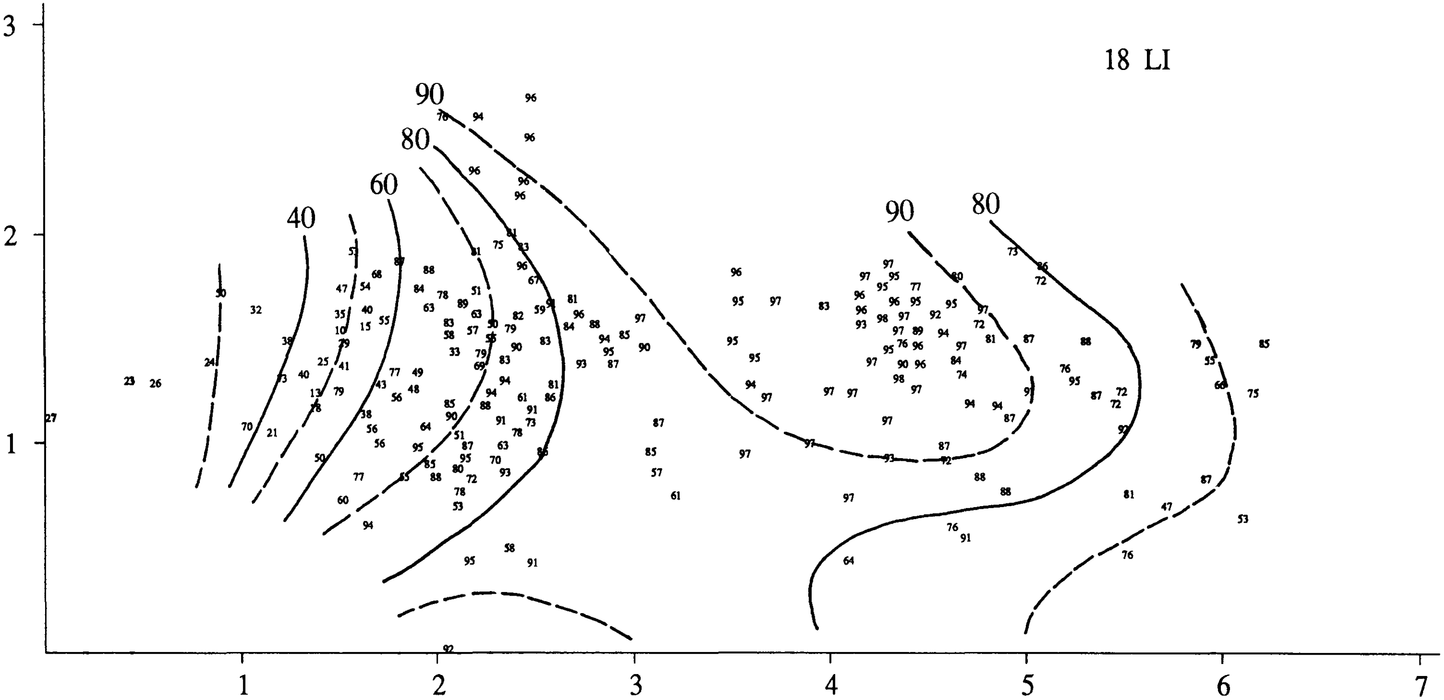


Fig. 28. DCA ordination of the ME 200 data set, axes 1 and 2. Values for 18 Loss on ignition (%) plotted onto the sample plot positions. Isolines based on fitting third-order polynomials in x and y. Correlation between original values and predicted values as calculated from the multiple regression model, r = 0.786. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures.

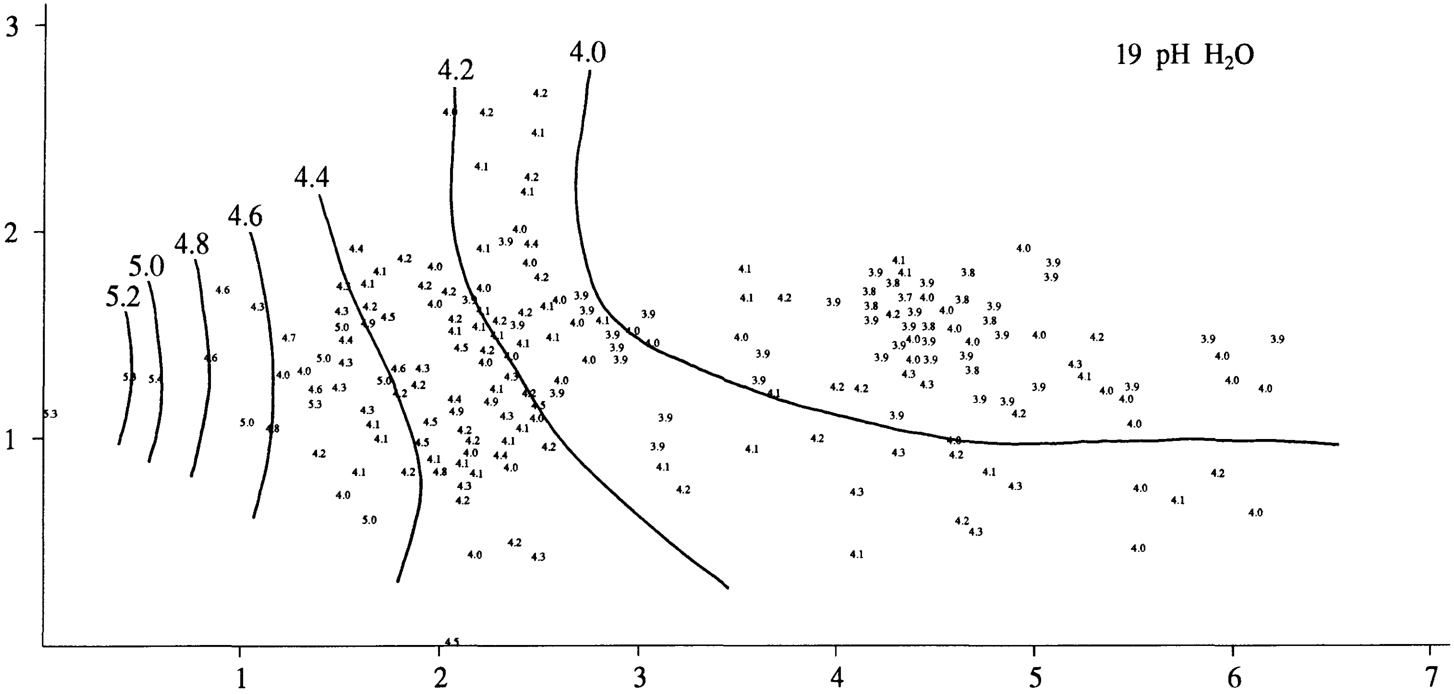


Fig. 29. DCA ordination of the ME 200 data set, axes 1 and 2. Values for 19 pH_{H20} plotted onto the sample plot positions. Isolines based on fitting third-order polynomials in x and y. Correlation between original values and predicted values as calculated from the multiple regression model, r = 0.738. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures.

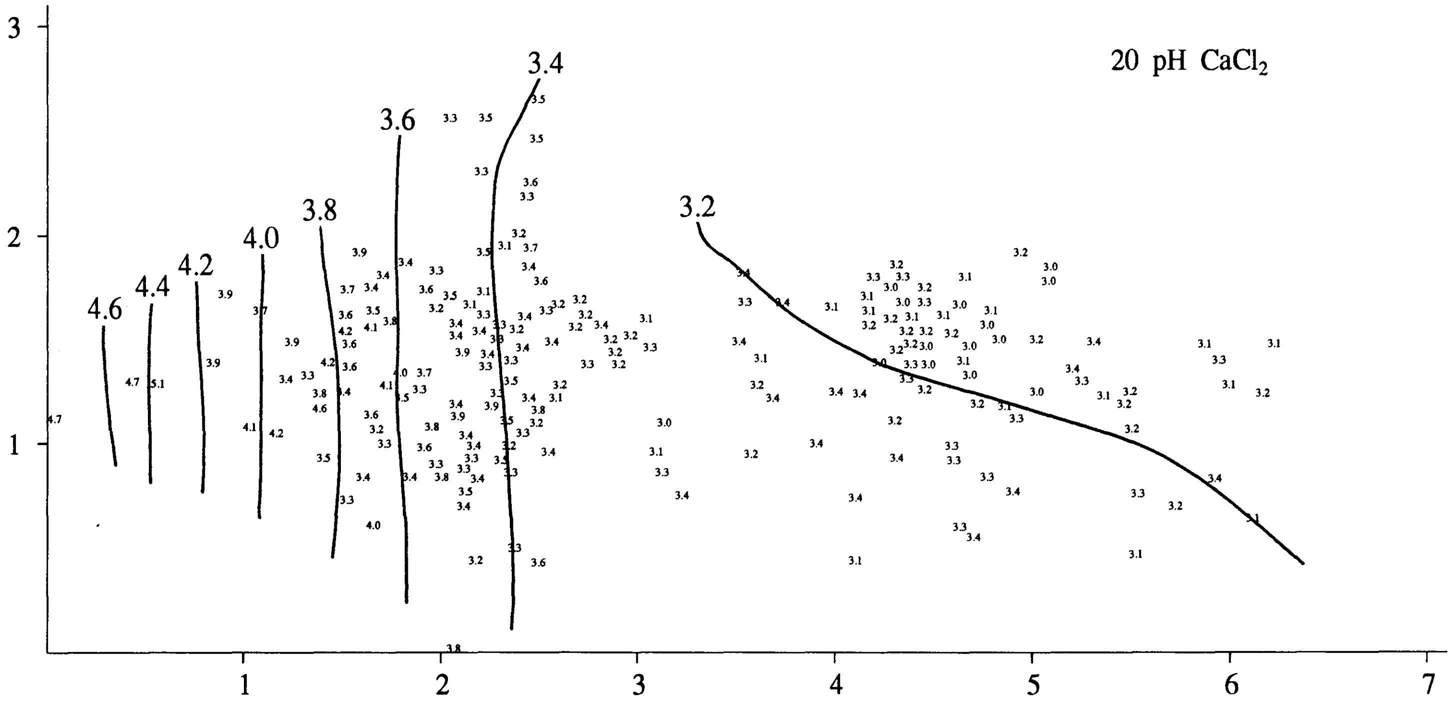


Fig. 30. DCA ordination of the ME 200 data set, axes 1 and 2. Values for 20 pH$_{CaCl2}$ plotted onto the sample plot positions. Isolines based on fitting third-order polynomials in x and y. Correlation between original values and predicted values as calculated from the multiple regression model, r = 0.787. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures.

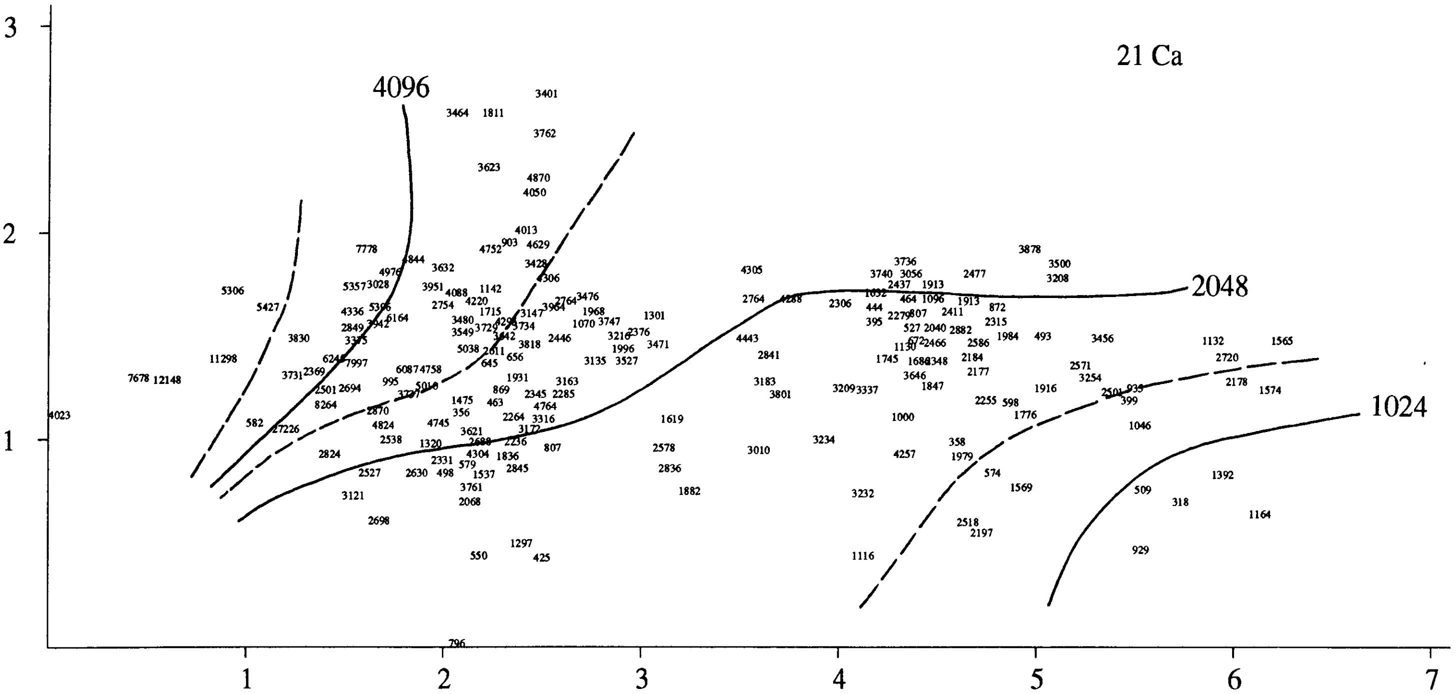


Fig. 31. DCA ordination of the ME 200 data set, axes 1 and 2. Values for 21 Exchangeable Ca (divided by loss on ignition; given as ppm in organic fraction of the humus), plotted onto the sample plot positions. Isolines based on fitting third-order polynomials in x and y to original, ln-transformed values. Correlation between original, ln-transformed values and predicted values as calculated from the multiple regression model, r = 0.550. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures.

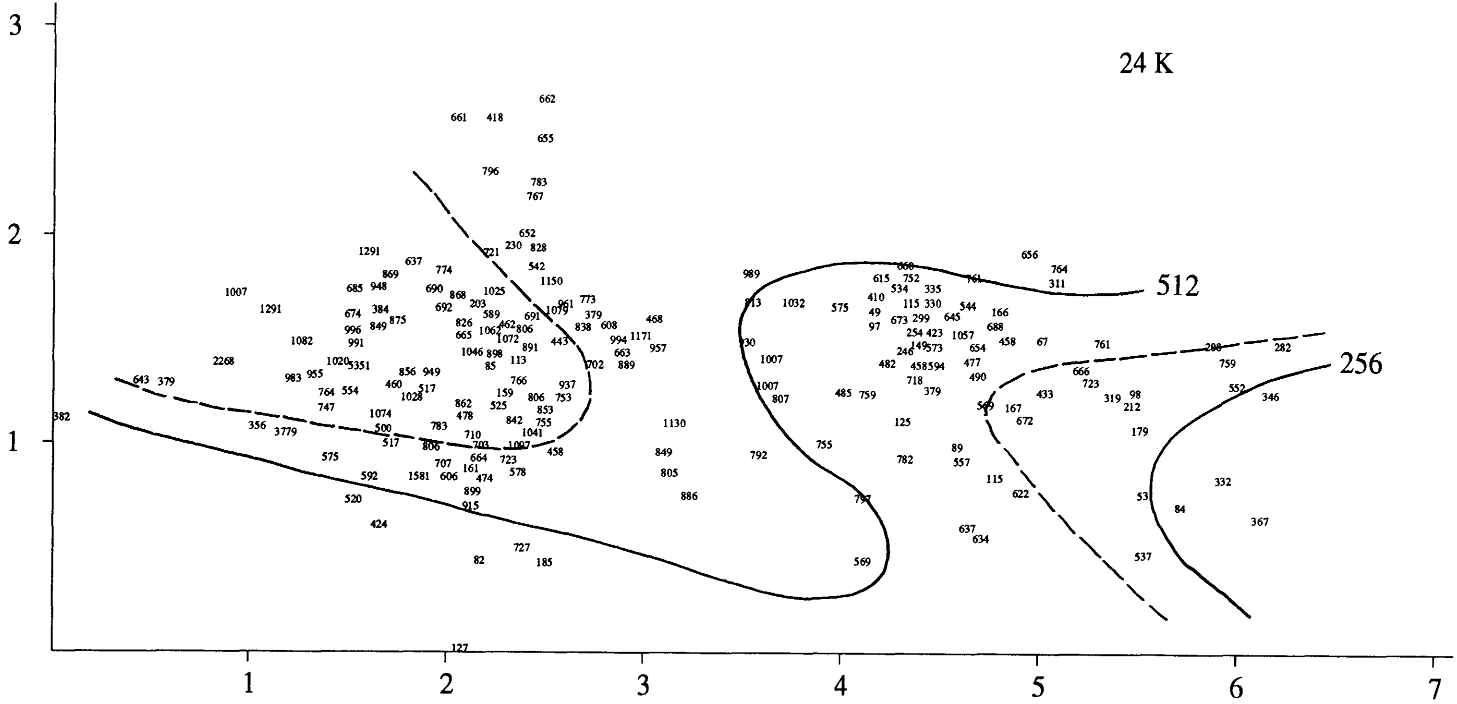


Fig. 32. DCA ordination of the ME 200 data set, axes 1 and 2. Values for 24 Exchangeable K (divided by loss on ignition; given as ppm in organic fraction of the humus), plotted onto the sample plot positions. Isolines based on fitting third-order polynomials in x and y to original, ln-transformed values. Correlation between original, ln-transformed values and predicted values as calculated from the multiple regression model, r = 0.506. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures.

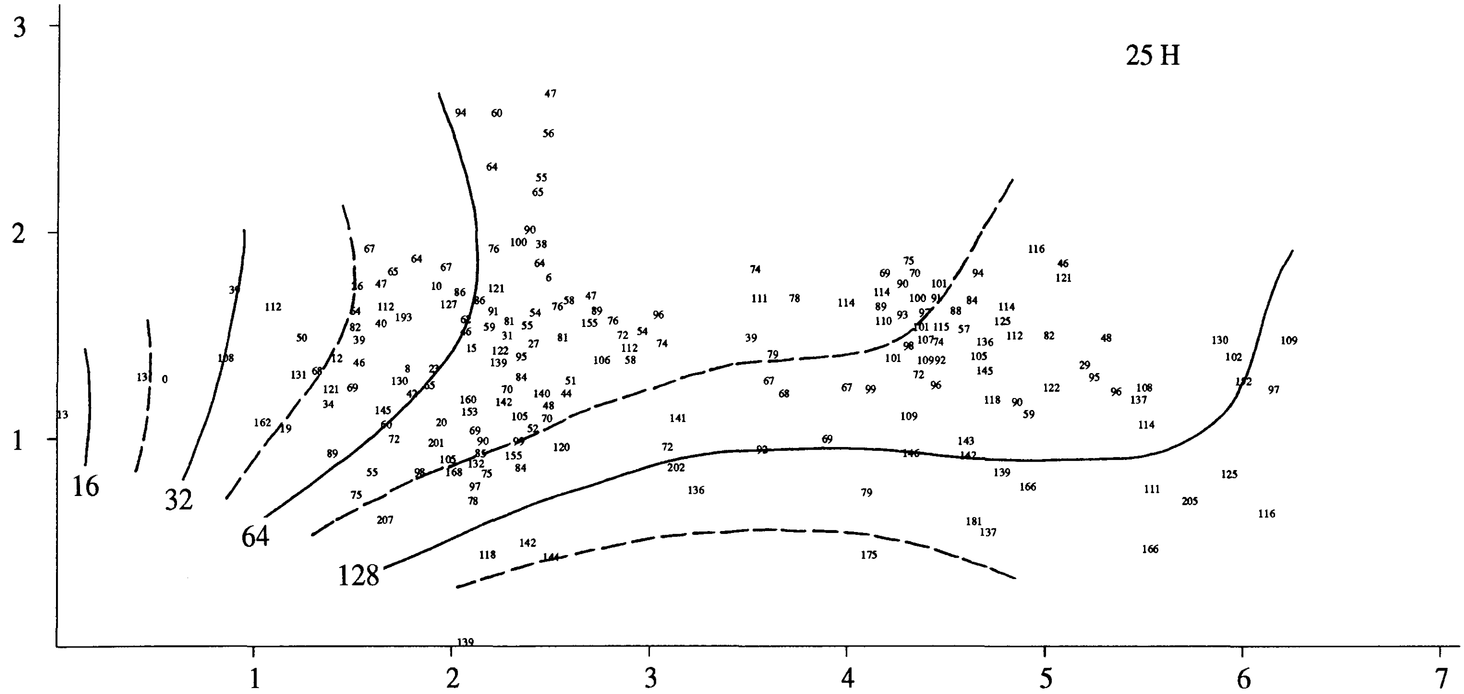


Fig. 33. DCA ordination of the ME 200 data set, axes 1 and 2. Values for 25 Exchangeable H (divided by loss on ignition; given as ppm in organic fraction of the humus), plotted onto the sample plot positions. Isolines based on fitting third-order polynomials in x and y to original, ln-transformed values. Correlation between original, ln-transformed values and predicted values as calculated from the multiple regression model, r = 0.544. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures.

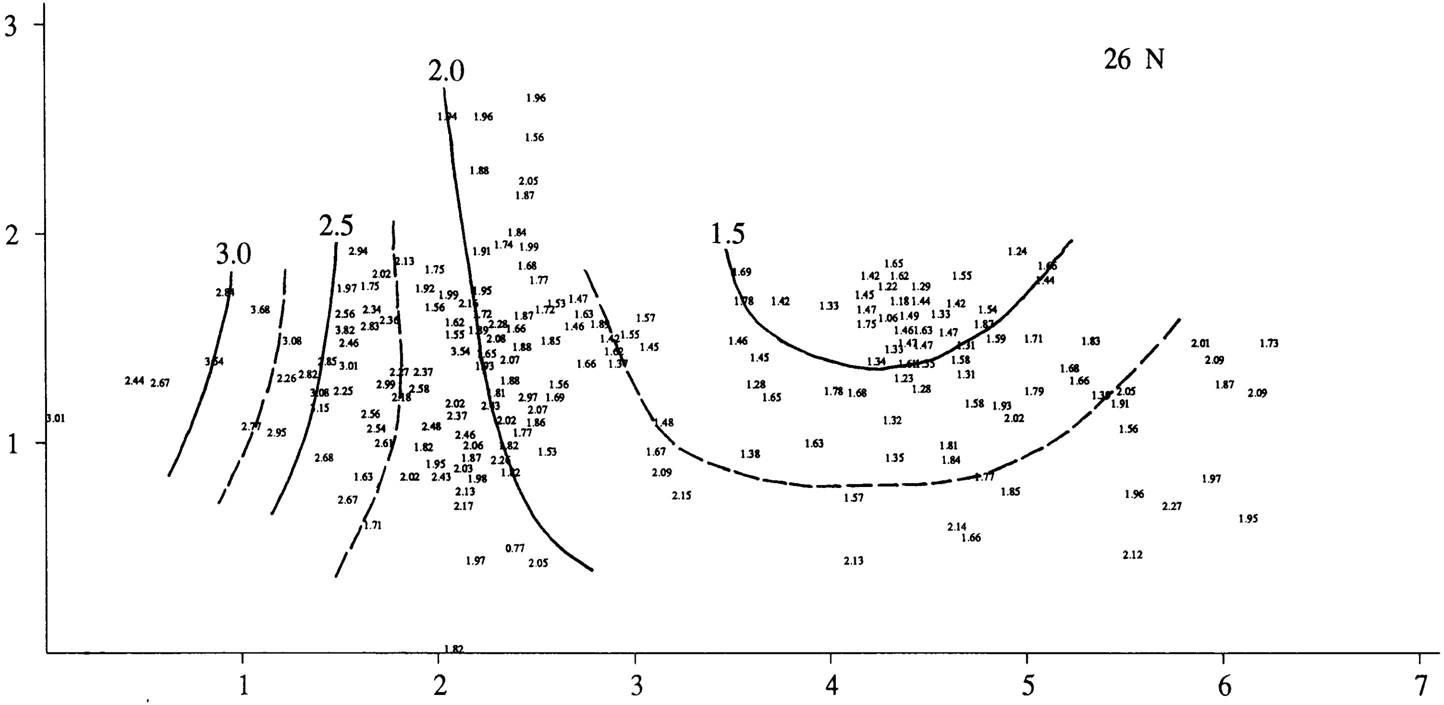


Fig. 34. DCA ordination of the ME 200 data set, axes 1 and 2. Values for 26 Total N (in % of loss on ignition), plotted onto the sample plot positions. Isolines based on fitting third-order polynomials in x and y to original, ln-transformed values. Correlation between original, ln-transformed values and predicted values as calculated from the multiple regression model, r = 0.789. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures.

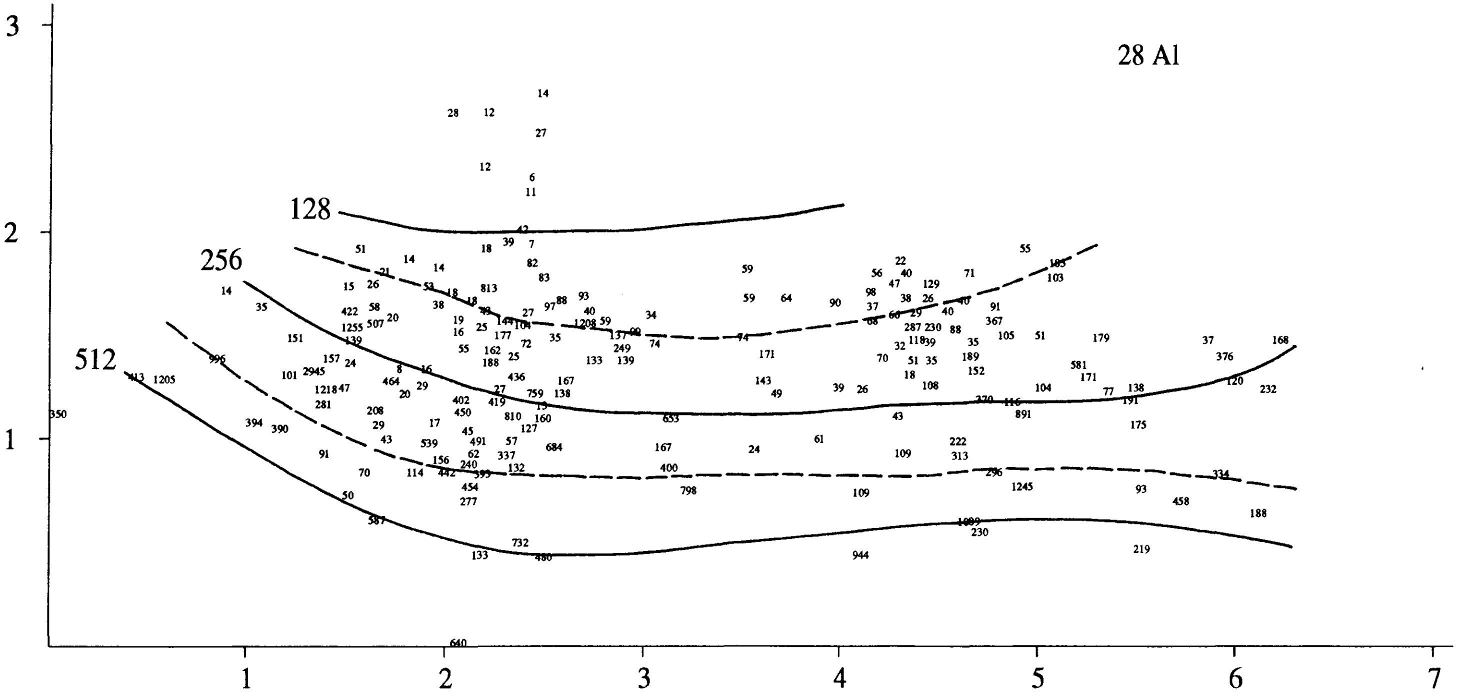


Fig. 35. DCA ordination of the ME 200 data set, axes 1 and 2. Values for 28 Exchangeable Al (divided by loss on ignition; given as ppm in organic fraction of the humus), plotted onto the sample plot positions. Isolines based on fitting third-order polynomials in x and y to original, ln-transformed values. Correlation between original, ln-transformed values and predicted values as calculated from the multiple regression model, r = 0.547. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures.

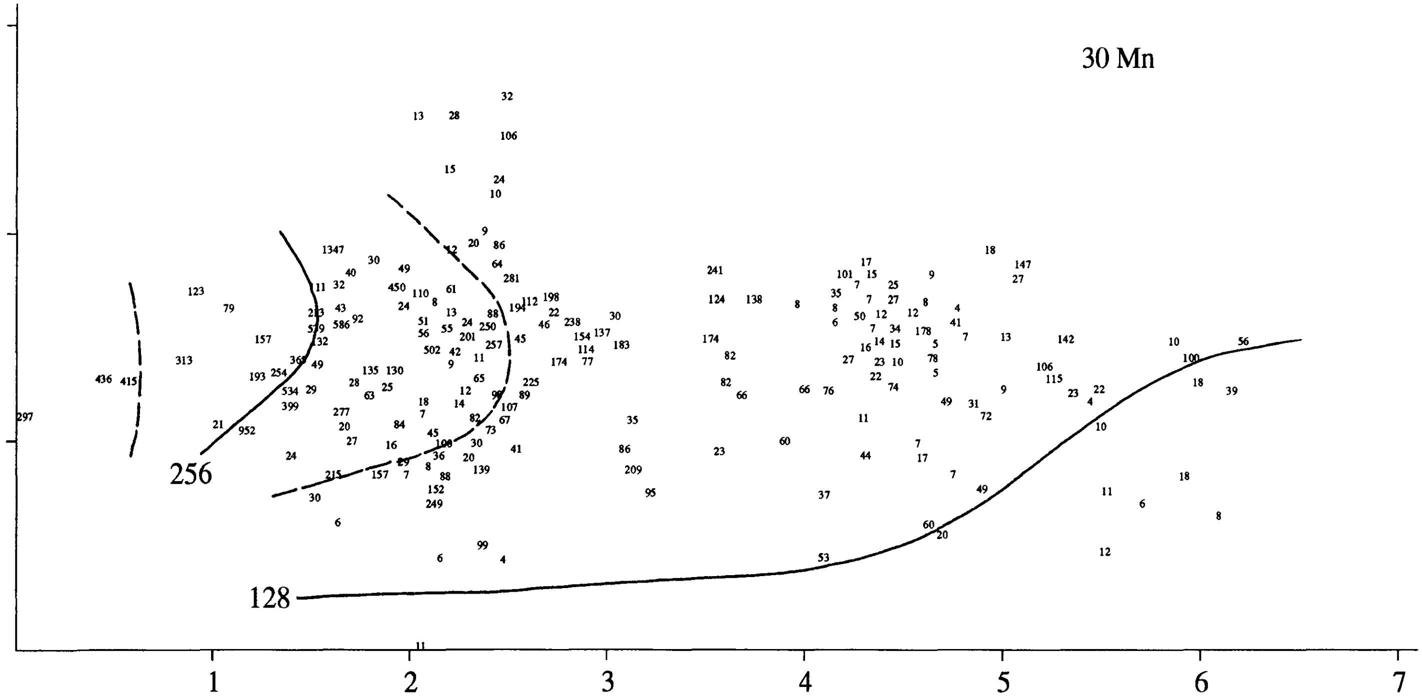


Fig. 36. DCA ordination of the ME 200 data set, axes 1 and 2. Values for 30 Exchangeable Mn (divided by loss on ignition; given as ppm in organic fraction of the humus), plotted onto the sample plot positions. Isolines based on fitting third-order polynomials in x and y to original, ln-transformed values. Correlation between original, ln-transformed values and predicted values as calculated from the multiple regression model, r = 0.522. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures.

(Fig. 28): Lowest values were reached for 3.0 < DCA 1 < 5.0, DCA 2 > 1.0, increasing slightly in all directions. N increased steeply from site-type 4 via 5.1, 5.2 and 5.3 to 6. There were no significant trends along DCA 2 for DCA 1 < 2.5.

E-group 2 showed variation along DCA 2 as well as along DCA 1, but the variables differred somewhat with respect to the direction of steepest increase in the ordination diagram (cf. Fig. 16). The four variables with r > 0.4 with DCA 1 made the following sequence according to increasing alignment to DCA 1: Ca, H, K, Mn. Ca (Fig. 31) showed a strong trend along both axes; lowest values were recorded for the 1-2 site-type (lower right), relatively low values were noted for all -2 site-types, as well as for the 1-1 and 2-1 site-types, and high values were noted in the 5.1-1 sample plots from Transect 5 (DCA 2 > 2.0), the 5.2-1, 5.3 and 6 site-types. K (Fig. 32) showed a slight tendency for lower values in the -2 site-types, but the dominant trend was the increase from high to low DCA 1 scores. The highest values were encountered in the 5.3 site-type. The variation between neighbouring sample plots was considerable, as indicated by the relatively low correlation between K and DCA 1 (r =-0.4002). H (Fig. 33) showed a pattern almost perfectly inverse to the one shown by Ca, except perhaps for a stronger alignment of isolines to DCA 1 (variation along DCA 2) for high DCA 1 values, gradually changing to alignment to DCA 2 towards low DCA 1 values. Mn (Fig. 36) showed very low values for site-types 1-3, as well as for very low and very high DCA 2 values (and DCA 1 < 4). Mn increased considerably from DCA 1 = 3.0 to DCA 1 = 0, the generally highest values were observed in site-type 6.

E-group 3. Al (Fig. 35) showed considerable variation along DCA 2, with the lowermost values (close to zero) in the 4-1 and 5.1-1 sample plots of Transect 5 (DCA 2 > 2.0). High values were encountered in the -2 site-types and in the 6 site-type as well.

E-group 4. The slope parameters (Figs 17, 22) showed similar overall trends of variation in the ordination diagram. Low values (< 10°) were typical of the 1-1, 1-2, 2-1 and partly the 3-1 site-types, i.e. the upper right part of the diagram. The slope increased to a maximum of 25-30° in the 4-2, 5.1-2, 5.1-1, 5.2 and 5.3 site-types, i.e. along a broad zone from the middle of DCA 1 (low DCA 2 score) to low DCA 1 and high DCA 2 scores. The slope of site-types 5.2-2 and 6 was mostly below 20°.

E-group 5. Meso scale soil depth varied along both DCA axes, with the lowest values both for ME Sme (Fig. 23) and ME Sma (Fig. 24) in the lower right, the highest values in the upper left. Me Sme showed a slightly stronger tendency than ME Sma to alignment of isolines along DCA 1 (strongest correlation with DCA 2). Occasional low values were encountered for single sample plots also for low DCA 1 scores, and occasional high values were also noted in the 2-1 site-type.

E-group 6, the canopy cover variables, showed variation along both DCA axes. Basal area, both on the macro and the meso scales (Figs 20, 26), obtained their lowest values for high DCA 1 and low DCA 2 scores, gradually increasing to a maximum at DCA 1 = 2, DCA 2 > 2. At DCA 1 < ca. 2.5, most variation occurred along DCA 2, indicating that increasing soil fertility (cf. Ca, Mn, etc.) did not lead to increased canopy cover. The pattern of variation in MA Can (Fig. 21) closely resembled MA Bas. The same pattern reappeared in ME Lit (Fig. 25), but in this case the trend along DCA 2 was strengthened and the variation between adjacent sample plots was larger.

E-group 7, Mois (Fig. 27), showed considerable variation along DCA 2, with the highest figures (> 60%) in the 3-2, 5.1-2 and 5.2-2 site-types (DCA 2 < 0.8). Mois values were somewhat higher for sample plots with low DCA 2 scores at the extreme right in the diagram. The lowest values (< 30%) were noted in the 3-1, 4-1, 5.1-1 and 5.2-1 site-types (1.5 < DCA 1 < 4.5, DCA 2 > 1.5).

Tab. 11. Pearson's product-moment correlation coefficients between meso sample plot scores relative to the first two DCA ordination axes and the 33 environmental variables (r), with significance probabilities (P). Correlations are given for all sample plots (Subsets A+B; n = 200), for plots with DCA 1 < 3.3 (Subset A; n = 121) and for sample plots with DCA 1 > 3.3 (Subset B; n = 79). Correlations significant at level P < 0.0001 in bold face. n.s. - significance probability less than 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 3.

Variable	DCA 1						DCA 2					
Subset	A+B		A		B		A+B		A		B	
	r	P	r	P	r	P	r	P	r	P	r	P
01 MA Slo	**-.5848**	**.0000**	.0248	n.s.	-.3642	.0010	-.2283	.0011	-.2695	.0028	-.4313	.0001
02 MA H i	-.1871	.0080	-.0760	n.s.	-.3267	.0033	-.2030	.0039	-.2694	.0028	-.1329	n.s.
03 MA Ter	**.8047**	**.0000**	.3335	.0002	**.4632**	**.0000**	.0680	n.s.	.2324	.0103	.0120	n.s.
04 MA Une	**-.3248**	**.0000**	-.1062	n.s.	-.0281	n.s.	-.1047	n.s.	-.1537	.0923	..0571	n.s.
05 MA S d	**-.7280**	**.0000**	-.2638	.0035	-.3823	.0005	.1858	.0084	.2170	.0168	.2391	.0338
06 MA Bas	**-.4030**	**.0000**	-.1508	.0987	-.3929	.0003	**.3473**	**.0000**	.3514	.0001	.3617	.0011
07 MA Can	**-.3748**	**.0000**	.0456	n.s.	-.3356	.0025	**.4799**	**.0000**	**.5383**	**.0000**	.3997	.0003
08 ME Slo	**-.4097**	**.0000**	.0601	n.s.	-.2185	.0531	-.2184	.0019	-.1800	.0482	**-.4409**	**.0000**
09 ME H i	-.1767	.0123	-.0102	n.s.	-.1623	n.s.	-.1481	.0364	-.1461	n.s.	-.1869	.0995
10 ME Une	-.2792	.0001	.0896	n.s.	**-.4722**	**.0000**	.0283	n.s.	-.1073	n.s.	.2736	.0147
11 ME Con	-.0668	n.s.	-.0186	n.s.	-.0411	n.s.	-.0166	n.s.	-.0059	n.s.	-.0462	n.s.
12 ME Smi	-.1598	.0238	-.0165	n.s.	**-.6341**	**.0000**	.2688	.0001	.2151	.0178	.3749	.0007
13 ME Sme	**-.3494**	**.0000**	-.0972	n.s.	**-.6456**	**.0000**	**.4146**	**.0000**	.3492	.0001	**.5450**	**.0000**
14 ME Sma	**-.4344**	**.0000**	-.1598	.0800	**-.5778**	**.0000**	**.3881**	**.0000**	.3144	.0004	**.5573**	**.0000**
15 ME Lit	**-.3630**	**.0000**	-.0505	n.s.	-.3027	.0068	**.4163**	**.0000**	**.4455**	**.0000**	.3823	.0005
16 ME Bas	**-.5320**	**.0000**	-.1532	.0935	-.2733	.0148	.2648	.0002	.2720	.0025	.3052	.0062
17 Mois	-.0623	n.s.	-.2302	.0111	.3768	.0006	**-.5649**	**.0000**	**-.5465**	**.0000**	**-.6260**	**.0000**
18 LI	**.4928**	**.0000**	**.6723**	**.0000**	**-.6314**	**.0000**	.0990	n.s.	.0855	n.s.	.3118	.0052
19 pH$_{H2O}$	**-.5477**	**.0000**	**-.6605**	**.0000**	-.0429	n.s.	-.1966	.0053	-.1865	.0405	**-.4781**	**.0000**
20 pH$_{CaCl2}$	**-.6212**	**.0000**	**-.7020**	**.0000**	-.1730	n.s.	-.0823	n.s.	-.0850	n.s.	-.3090	.0056
21 CA	**-.4135**	**.0000**	-.3401	.0001	-.3120	.0051	**.3017**	**.0000**	.3358	.0002	.2414	.0321
22 MG	**-.3267**	**.0000**	-.2146	.0181	-.3256	.0034	**.3011**	**.0000**	.3328	.0002	.2569	.0023
23 NA	-.1718	.0150	-.2506	.0056	-.2155	.0565	.0604	n.s.	.1295	n.s.	-.0395	n.s.
24 K	**-.4002**	**.0000**	-.0832	n.s.	-.3292	.0031	.1546	.0288	.1750	.0549	.1180	n.s.
25 H	**.3752**	**.0000**	.3307	.0002	.2977	.0077	-.2581	.0002	-.2267	.0124	-.4259	.0001
26 N	**-.5565**	**.0000**	**-.6885**	**.0000**	**.5306**	**.0000**	-.1355	.0557	-.0693	n.s.	**-.5376**	**.0000**
27 P-AL	-.2470	.0004	-.0871	n.s.	-.1497	n.s.	.1803	.0106	.2072	.0226	.1044	n.s.
28 AL	-.0384	n.s.	-.1262	n.s.	.3547	.0013	**-.4997**	**.0000**	**-.4868**	**.0000**	**-.5508**	**.0000**
29 FE	.0933	n.s.	.1716	.0598	.2605	.0204	**-.3111**	**.0000**	-.2639	.0034	-.4286	.0001
30 MN	**-.4260**	**.0000**	-.2990	,0009	-.2559	.0228	.0596	n.s.	.0199	n.s.	.1521	n.s.
31 ZN	.0936	n.s.	.0681	n.s.	-.0357	n.s.	.0465	n.s.	-.0217	n.s.	.1908	.0922
32 P	-.0318	n.s.	**.3928**	**.0000**	-.2002	.0769	.1074	n.s.	.0302	n.s.	.2565	.0225
33 S	-.2221	.0016	-.0794	n.s.	-.0944	n.s.	-.0330	n.s.	-.0655	n.s.	-.0160	n.s.

Correlations between ordination axes and environmental variables within Subsets A and B

Correlation coefficients between environmental variables and DCA axes, calculated separately for each subset (Tab. 11), showed that several environmental variables had independent patterns of variation within each subset, at least along DCA 1.

DCA 1. For the whole material, twenty of the 33 variables showed correlations with DCA 1 significant at $P < 0.0001$. Only two of these variables were significantly correlated with DCA 1 ($P < 0.0001$) within both subsets, but the trends shown by LI and N in the two subsets were opposing; masked in the overall trend! Thus the only variable showing more or less monotonous variation in both subsets and correlations significant at $P < 0.001$, was MA Ter. Monotonous variation but lower significance ($P < 0.01$) was shown by MA S d Ca and H. DCA 1 thus could be interpreted as a topography-soil depth gradient, but with complex co-variation with several other factors.

Completely different sets of environmental variables were correlated with DCA 1 within each subset; the differences being so great that the vegetational variation along DCA 1 in the two subsets appeared to be dependent on separate complexes of environmental variables. A nutrient variable complex including the two pH measurements and N (E-group 1), to a lesser degree also Ca, Mg, Na, Mn and H (E-group 2), showed nutrient concentrations in the soil to increase within Subset A towards lower DCA 1 values. LI increased strongly from low to higher DCA 1 values within Subset A (cf. Fig. 28). A soil depth variable complex including the three ME S variables (E-group 5) showed the highest correlations with DCA 1 in Subset B. High correlations were also shown by LI (decreasing), N (increasing), MA Ter (increasing)

Tab. 12. Pearson's product-moment correlation coefficients between meso sample plot scores relative to DCA ordination axes and the 9 biotic variables (r), with significance probabilities (P). Correlations significant at level $P < 0.0001$ in bold face. n.s. - significance probability less than 0.1. Biotic variables: N-TOT - total number of species, N-VAS -number of vascular plant species, N-BOT - number of species in the bottom layer, N-BRY - number of bryophyte species, N-LIC - number of lichen species, CC - percentage cover of the field layer, CD - percentage cover of the bottom layer. The variables MA Can and ME Lit equal environmental variables 07 and 15, respectively (cf. Tab. 3).

Variable	DCA 1		DCA 2		DCA 3		DCA 4	
	r	P	r	P	r	P	r	P
N-TOT	**-.4382**	**.0000**	**-.5008**	**.0000**	.1947	.0057	**-.3013**	**.0000**
N-VAS	**-.7148**	**.0000**	-.1644	.0200	.0278	n.s.	.0210	n.s.
N-BOT	.0311	n.s.	**-.6015**	**.0000**	.2689	.0001	**-.4788**	**.0000**
N-BRY	**-.3892**	**.0000**	**-.5534**	**.0000**	**-.3371**	**.0000**	**-.4177**	**.0000**
N-LIC	**.7719**	**.0000**	-.1343	.0580	-.1043	n.s.	-.1486	.0357
MA Can	**-.3748**	**.0000**	**.4799**	**.0000**	.0843	n.s.	.0607	n.s.
ME Lit	**-.3630**	**.0000**	**.4163**	**.0000**	.1694	.0165	.0342	n.s.
CC	-.2223	.0016	.2335	.0009	-.0968	n.s.	**.2875**	**.0000**
CD	.1132	n.s.	**-.5385**	**.0000**	.0163	n.s.	-.2551	.0003

Tab. 13. Pearson's product-moment correlation coefficients between meso sample plot scores relative to the first two DCA ordination axes and the 9 biotic variables (r), with significance probabilities (P). Correlations are given for all sample plots (Subsets A+B; n = 200), for plots with DCA 1 < 3.3 (Subset A; n = 121) and for sample plots with DCA 1 > 3.3 (Subset B; n = 79). Correlations significant at level P < 0.0001 in bold face. n.s. - significance probability less than 0.1. Biotic variables: N-TOT - total number of species, N-VAS -number of vascular plant species, N-BOT - number of species in the bottom layer, N-BRY - number of bryophyte species, N-LIC - number of lichen species, CC - percentage cover of the field layer, CD - percentage cover of the bottom layer. The variables MA Can and ME Lit equal environmental variables 07 and 15, respectively (cf. Tab. 3).

Variable	DCA 1						DCA 2					
Subset	A+B		A		B		A+B		A		B	
	r	P	r	P	r	P	r	P	r	P	r	P
N-TOT	**-.4382**	**.0000**	**-.6150**	**.0000**	.3889	.0005	**-.5008**	**.0000**	**-.4973**	**.0000**	**-.7266**	**.0000**
N-VAS	**-.7148**	**.0000**	**-.8405**	**.0000**	-.3020	.0068	-.1644	.0200	-.2089	.0215	-.4040	.0002
N-BOT	.0311	n.s.	-.1100	n.s.	**.4985**	**.0000**	**-.6015**	**.0000**	**-.5840**	**.0000**	**-.6564**	**.0000**
N-BRY	**-.3892**	**.0000**	-.1262	n.s.	-.0436	n.s.	**-.5534**	**.0000**	**-.5912**	**.0000**	**-.6933**	**.0000**
N-LIC	**.7719**	**.0000**	.1582	.0830	**.8529**	**.0000**	-.1343	.0580	-.0715	n.s.	-.2408	.0325
MA Can	**-.3748**	**.0000**	.0456	n.s.	-.3356	.0025	**.4799**	**.0000**	**.5383**	**.0000**	.3997	.0003
ME Lit	**-.3630**	**.0000**	-.0505	n.s.	-.3027	.0068	**.4163**	**.0000**	**.4455**	**.0000**	.3823	.0005
CC	-.2223	.0016	.0059	n.s.	**-.8122**	**.0000**	.2335	.0009	.1358	n.s.	.3934	.0003
CD	.1132	n.s.	.0963	n.s.	.3439	.0019	**-.5385**	**.0000**	**-.5727**	**.0000**	**-.4621**	**.0000**

and ME Une (decreasing). Relatively high correlations were also shown by MA Slo, MA Asf, MA S d, the litter and canopy cover variables, and some of the cations (Ca, Mg, K, Mn), all decreasing along DCA 1, while Mois, H and Al increased slightly.

DCA 2. Two variables; Mois and Al, were strongly negatively correlated with DCA 2 ($P < 0.0001$) within both subsets. The other variables significantly correlated with DCA 2 in ME 200 at $P < 0.0001$ also showed significant correlations with DCA 2 in both subsets, mostly at $P < 0.001$. Additional variables showing particularly high correlations with DCA 2 in Subset A were MA Bas and ME Lit (increasing along DCA 2), in Subset B ME Slo and MA Slo (decreasing), the ME S variables (increasing), pH_{H20} and N (decreasing along DCA 2). DCA 2 could therefore be interpretated as a fine-scale moisture gradient, in Subset A mostly followed by a gradient in canopy closure, in Subset B followed by gradients in decreasing soil depth and increasing pH.

Interpretation of the DCA ordination by means of the biotic variables

The biotic variables mostly showed consistent trends of variation in the ordination space (cf. Tabs 12, 13). N-TOT was significantly correlated with both axes, most strongly so with DCA 2 (Fig. 37). The highest number of species was reached in site-type 6 (low DCA 1 score); N-TOT was about 25 in site-type 5.2-2, 18-25 in the other -2 site-types, while N-TOT decreased along DCA 2 to ca. 15 for DCA 2 > 1, and to 5 for DCA 2 > 2.

N-VAS (Fig. 38) decreased from ca. 30 at DCA 1 = 0 to ca. 8 at DCA 1 = 2.5. The correlation between N-VAS and DCA 1 in Subset A was r = - 0.8405! For DCA 1 > 2.5,

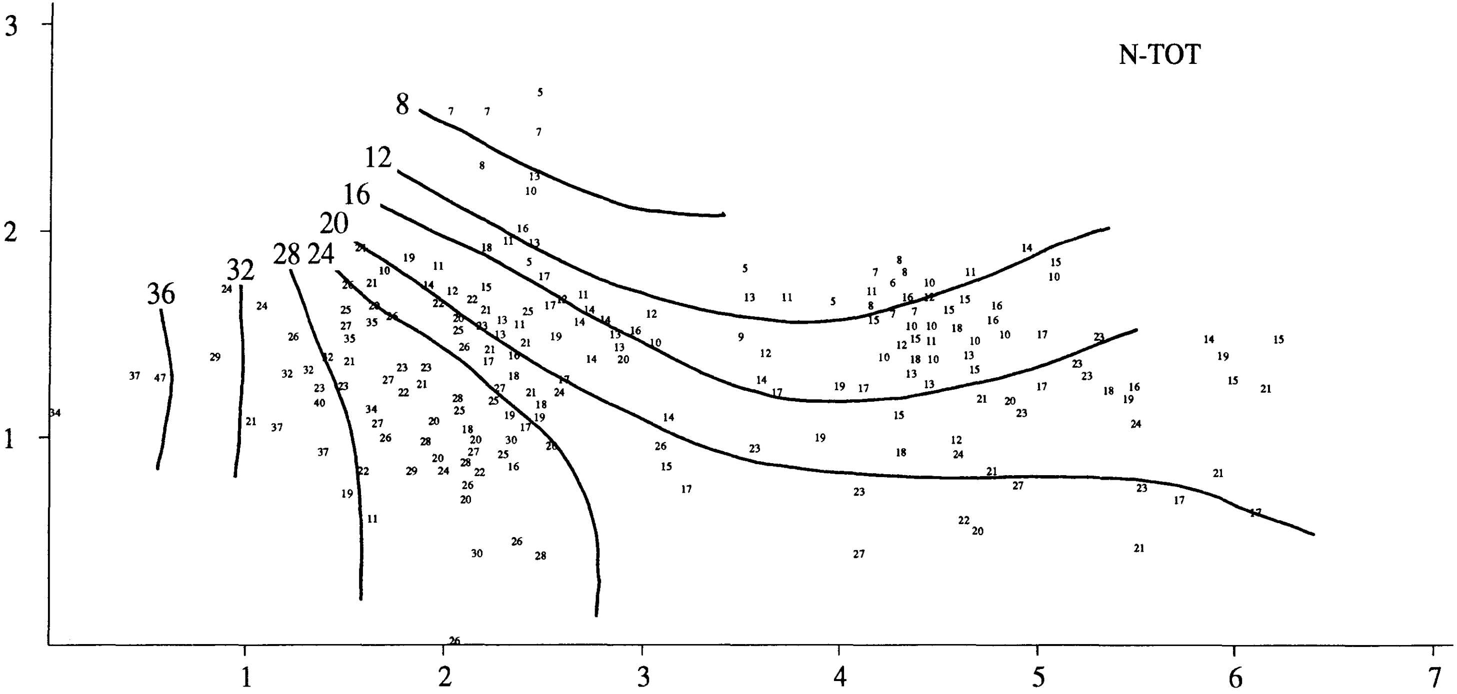


Fig. 37. DCA ordination of the ME 200 data set, axes 1 and 2. Values for N-TOT, total number of species, plotted onto the sample plot positions. Isolines based on fitting third-order polynomials in x and y. Correlation between original values and predicted values as calculated from the multiple regression model, r = 0.816. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures.

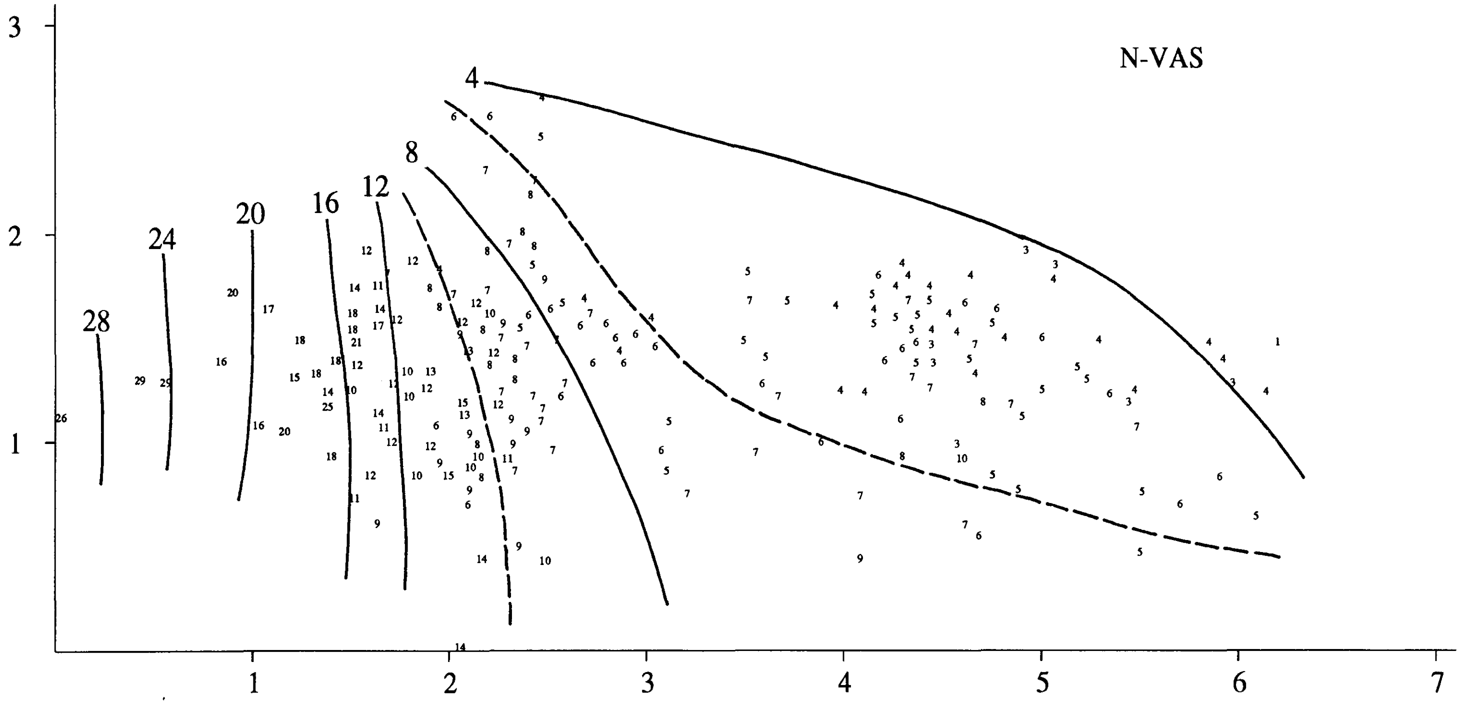


Fig. 38. DCA ordination of the ME 200 data set, axes 1 and 2. Values for N-VAS, number of vascular plant species, plotted onto the sample plot positions. Isolines based on fitting third-order polynomials in x and y. Correlation between original values and predicted values as calculated from the multiple regression model, r = 0.898. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures.

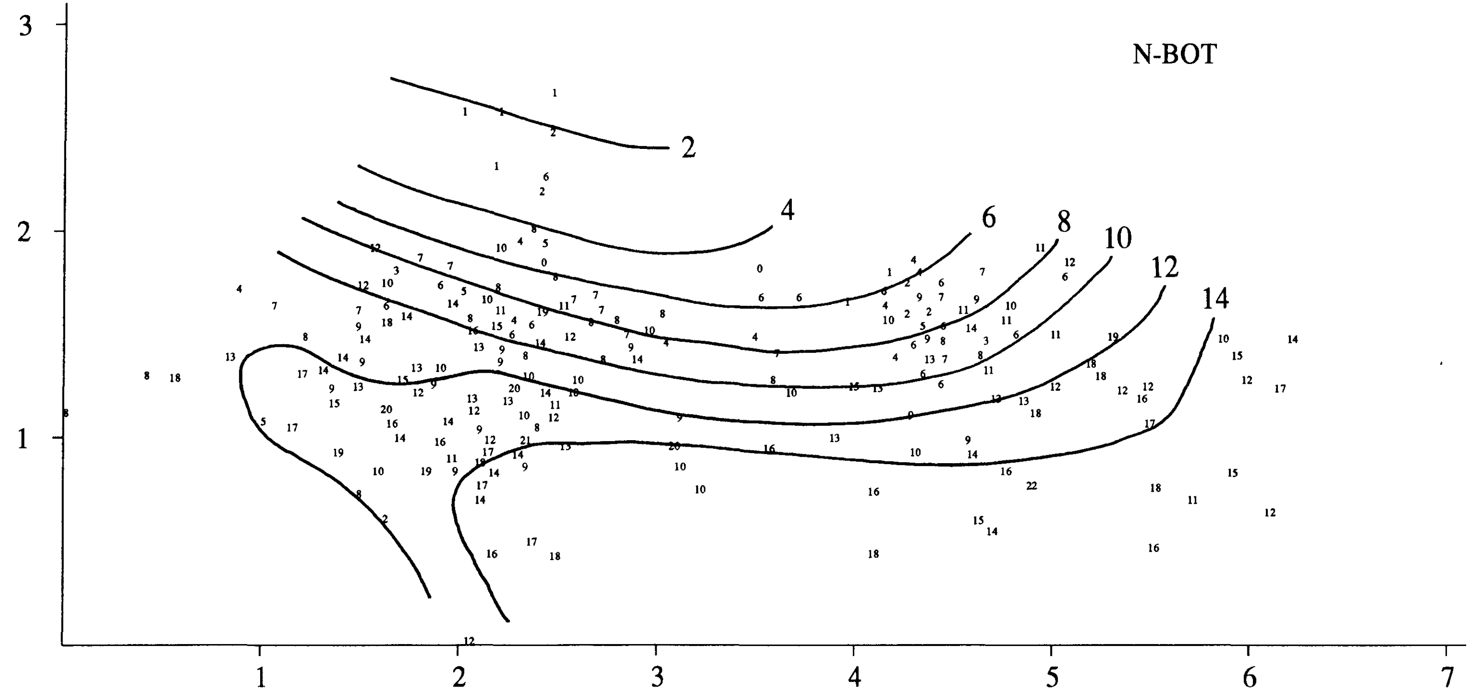


Fig. 39. DCA ordination of the ME 200 data set, axes 1 and 2. Values for N-BOT, number of cryptogamic species, plotted onto the sample plot positions. Isolines based on fitting third-order polynomials in x and y. Correlation between original values and predicted values as calculated from the multiple regression model, r = 0.695. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures.

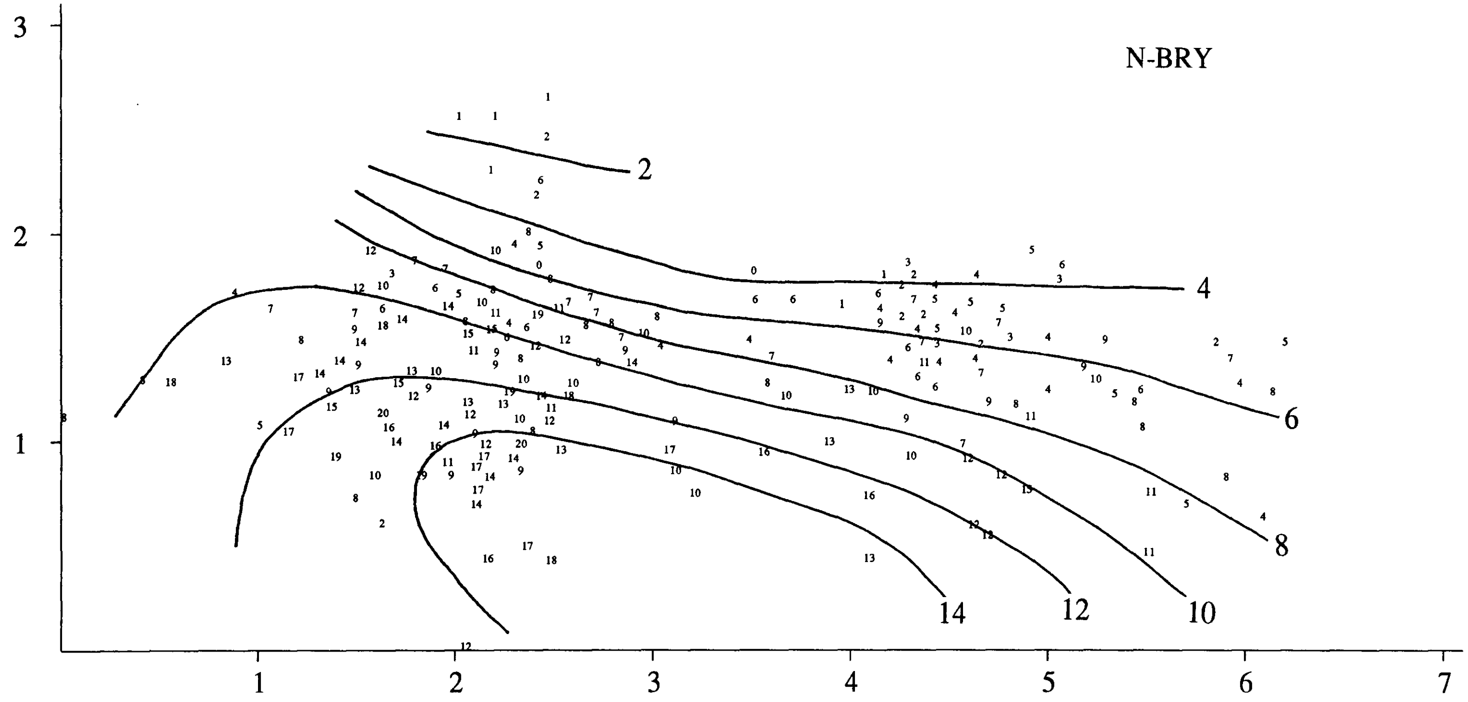


Fig. 40. DCA ordination of the ME 200 data set, axes 1 and 2. Values for N-BRY, number of bryophyte species, plotted onto the sample plot positions. Isolines based on fitting third-order polynomials in x and y. Correlation between original values and predicted values as calculated from the multiple regression model, r = 0.751. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures.

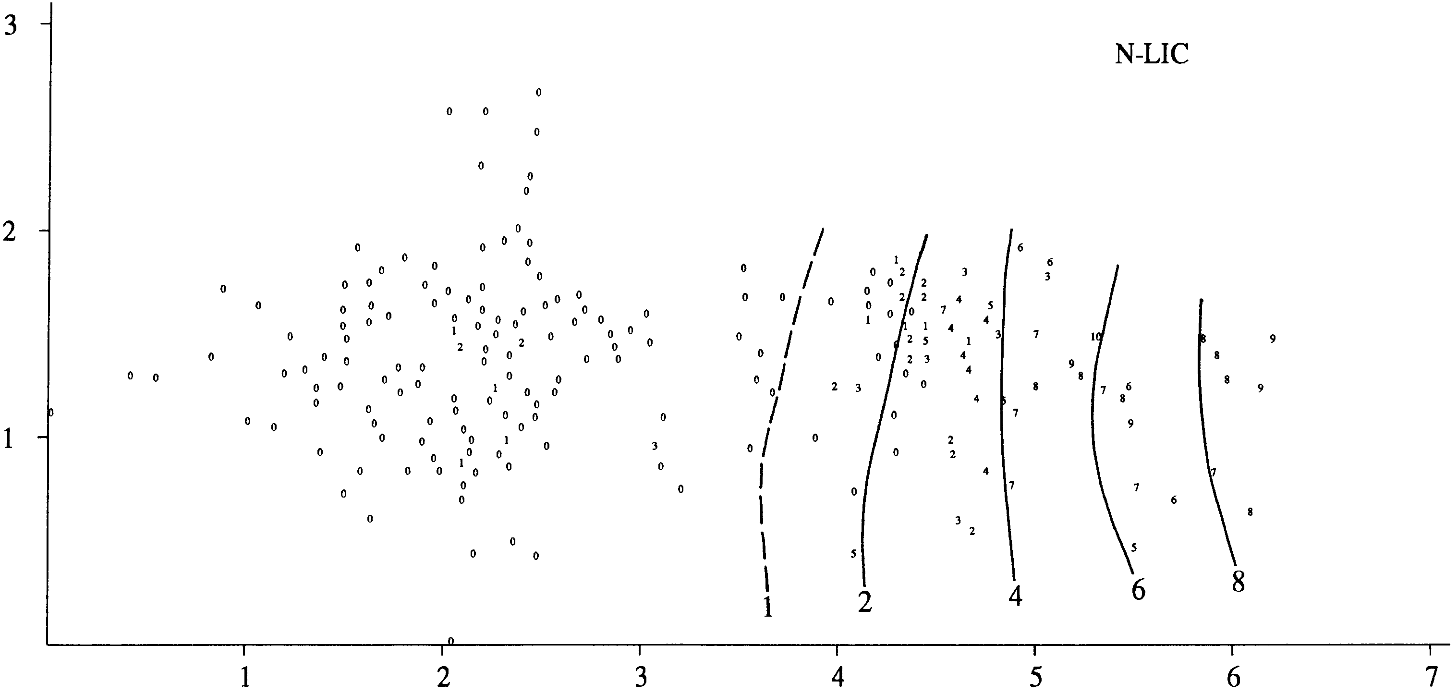


Fig. 41. DCA ordination of the ME 200 data set, axes 1 and 2. Values for N-LIC, number of lichen species, plotted onto the sample plot positions. Isolines based on fitting third-order polynomials in x and y. Correlation between original values and predicted values as calculated from the multiple regression model, r = 0.898. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures.

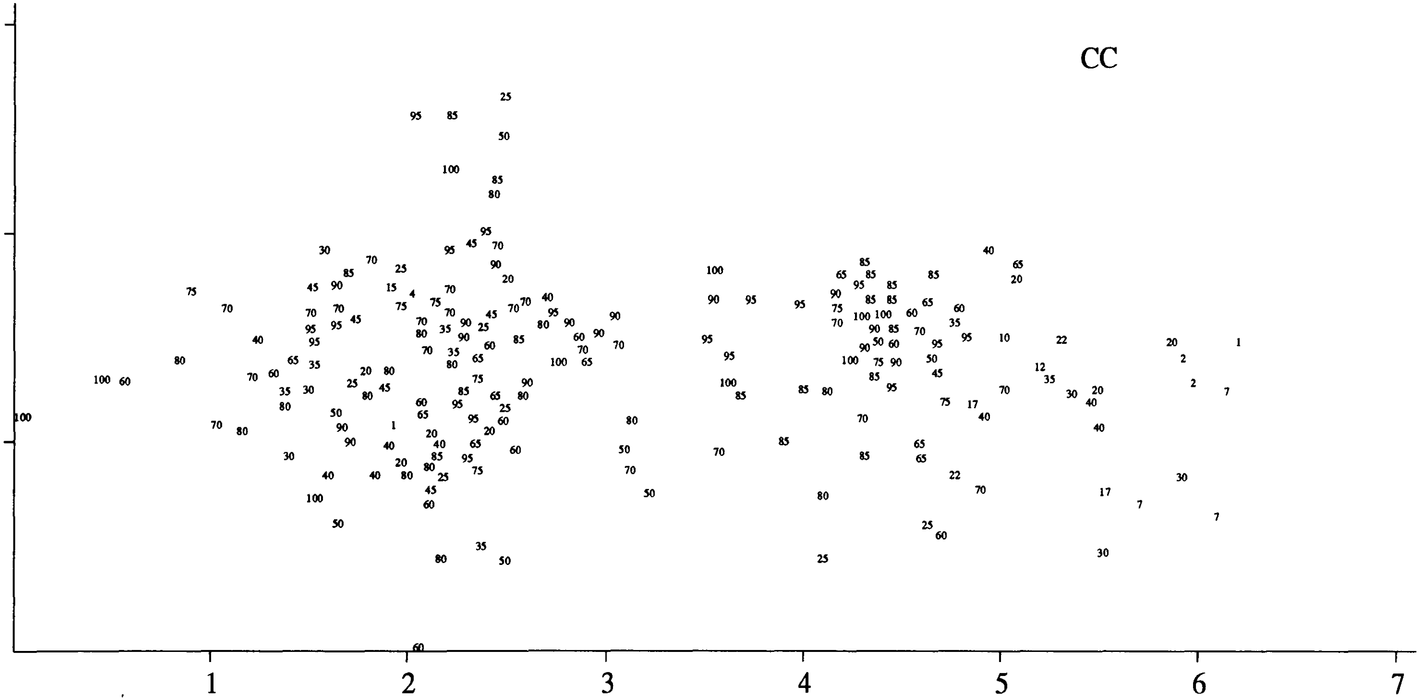


Fig. 42. DCA ordination of the ME 200 data set, axes 1 and 2. Values for CC, percent cover in the field layer, plotted onto the sample plot positions. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures.

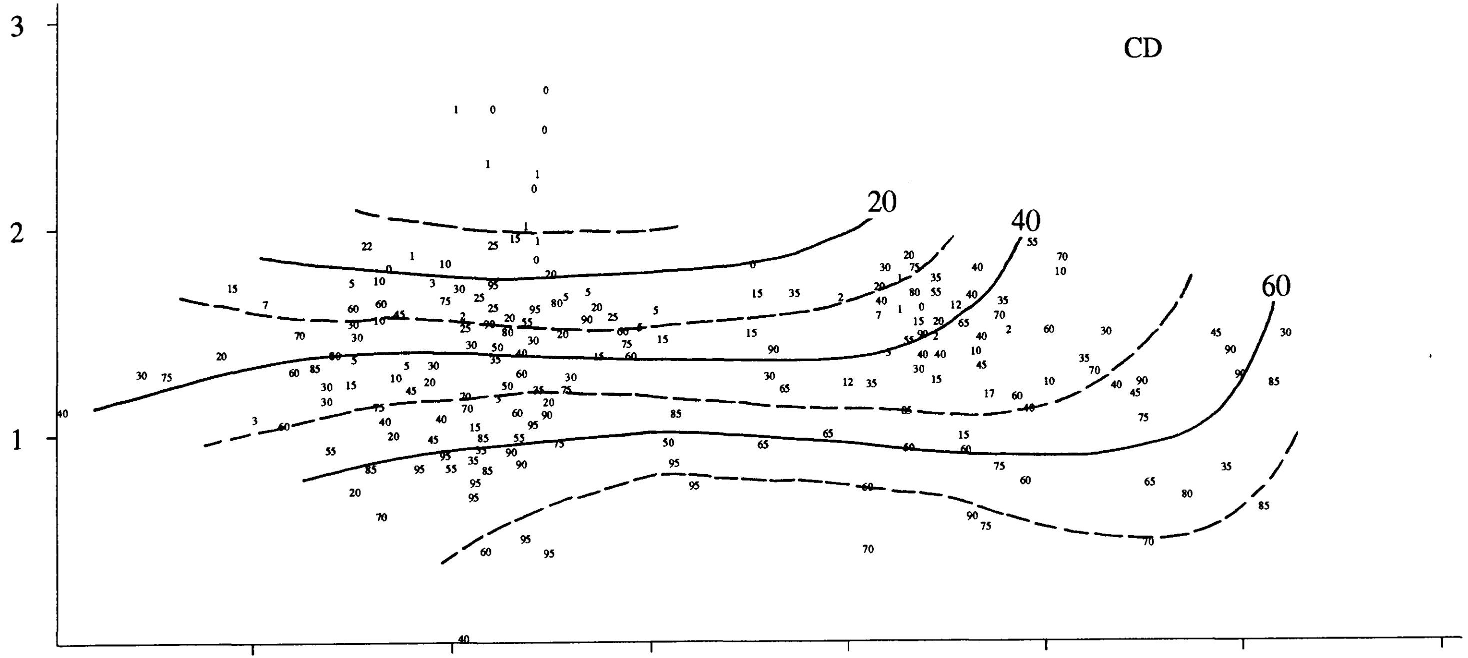


Fig. 43. DCA ordination of the ME 200 data set, axes 1 and 2. Values for CD, percent cover in the bottom layer, plotted onto the sample plot positions. Isolines based on fitting third-order polynomials in x and y. Correlation between original values and predicted values as calculated from the multiple regression model, r = 0.589. Axes scaled in S.D. units. Sample plot positions slightly adjusted in order to avoid overlapping figures.

N-VAS decreased slightly along DCA 1 and DCA 2 to give a minimum of N-VAS = 1-4 in the upper right corner (site-type 1-1).

N-BOT (Fig. 39) occasionally reached above 15, for DCA 1 > 2.0 and DCA 2 < 1.0 (site-types 1-2, 2-2, 3-2, 4-2 and 5.1-2). There was a slight increase in N-BOT for DCA 2 < 1 when DCA 1 passed from 0 towards 2. N-BOT increased significantly with increasing DCA 1 in Subset B (Tab. 13). N-BOT decreased as a function of DCA 2 for DCA 2 > 1. The lowest values, N-BOT = 0-2 were reached in site-types 4-1 and 5.1-1. N-BRY (Fig. 40) showed no clear trend along DCA 1 within any subset, but a weak decrease was present in the total material. N-BRY was strongly negatively correlated with DCA 2. N-LIC (Fig. 41) increased along DCA 1 in Subset B (Tab. 13); lichens were more or less absent from site-types 4, 5 and 6, while rapidly increasing in number of species towards the right end of the diagram. N-LIC showed no trend along DCA 2. N-BOT could be explained as a result of trends in N-BRY and N-LIC.

The significance probability of correlations between CC and the DCA axes was low (r = -0.2223, P = 0.0016 for DCA 1; r = 0.2335, P = 0.0009 for DCA 2, cf. Tab. 12). Fig. 42 and Tab. 13 demonstrate a complex pattern of variation: High CC values (mostly above 70) were found in site-types 4-1, 5.1-1, 5.2-1, partly also 5.3 and 6. However, the variation between adjacent sample plots was large, and CC values below 25 occurred over most of the ordination space, except for the area occupied by site-types 3-1 and 4-1 (2.8 < DCA 1 < 4.4, DCA 2 < 1.2). For DCA 1 > 4.8, CC was mostly below 50. There was a marked tendency for low CC values to the extreme right in the ordination, manifest in the highly significant negative correlation between CC and DCA 1 in Subset B (r = -0.8122, P < 0.0001).

CD was strongly correlated with DCA 2, as shown by the horizontal isolines for CD in the diagram (Fig. 43) and the high, negative correlations between CD and DCA 2 within both subsets (Tab. 13). CD decreased from generally above 60 at DCA 2 < 0.7 to generally below 30 at DCA 2 > 1.6 (except for DCA 1 > 4.5). The sample plots for which DCA 2 > 2.0, were almost devoid of a bottom layer.

Variation in species abundance along the axes of the DCA ordination

The variation in frequency in subplots for all 82 species occurring in 10 or more of the meso sample plots is shown in Figs 44-125. The relationships of the species to the classification into site-types is shown in Tab. 4, also see Fig. 15. Tab. 14 summarizes the characteristics of species responses to the first two DCA axes. The autecology of the individual species in the investigation area can be confidently deduced from the tables and figures referred to above. Here only points of more general interest will be considered.

The spread of species optima (as estimated by DCA) in the ordination follows the trends in biotic variables N-VAS, N-BRY and N-LIC, as given in Tab. 12, and will not be further commented. In general, there was a strong tendency to a positive relationship between range and total frequency in the data set, although no attempts have been made to quantify this (many species have ranges extending outside the sampled portion of the gradient).

Simultaneous consideration of frequency within range and optimal range gave good indications of the dominant species within different portions of the axes (cf. Tab. 14). In the field layer, seven species were constant within their ranges. They did not show any clear segregation along DCA 2, but segregated considerably along DCA 1. The most important species in the field layer, constant over most of DCA 1, was *Vaccinium myrtillus* (Fig. 51).

Tab. 14. Characteristics of species responses to DCA axes: DCA species scores, range of occurrence of species along axes, and frequency of species within range. Fig. - Number of figure showing frequency in subplots as a function of position in ordination diagram. Freq. Tot. - total frequency in the ME 200 data set. Freq. Range - frequency of species within its range, given on a 1-4 scale (cf. pp. 00).

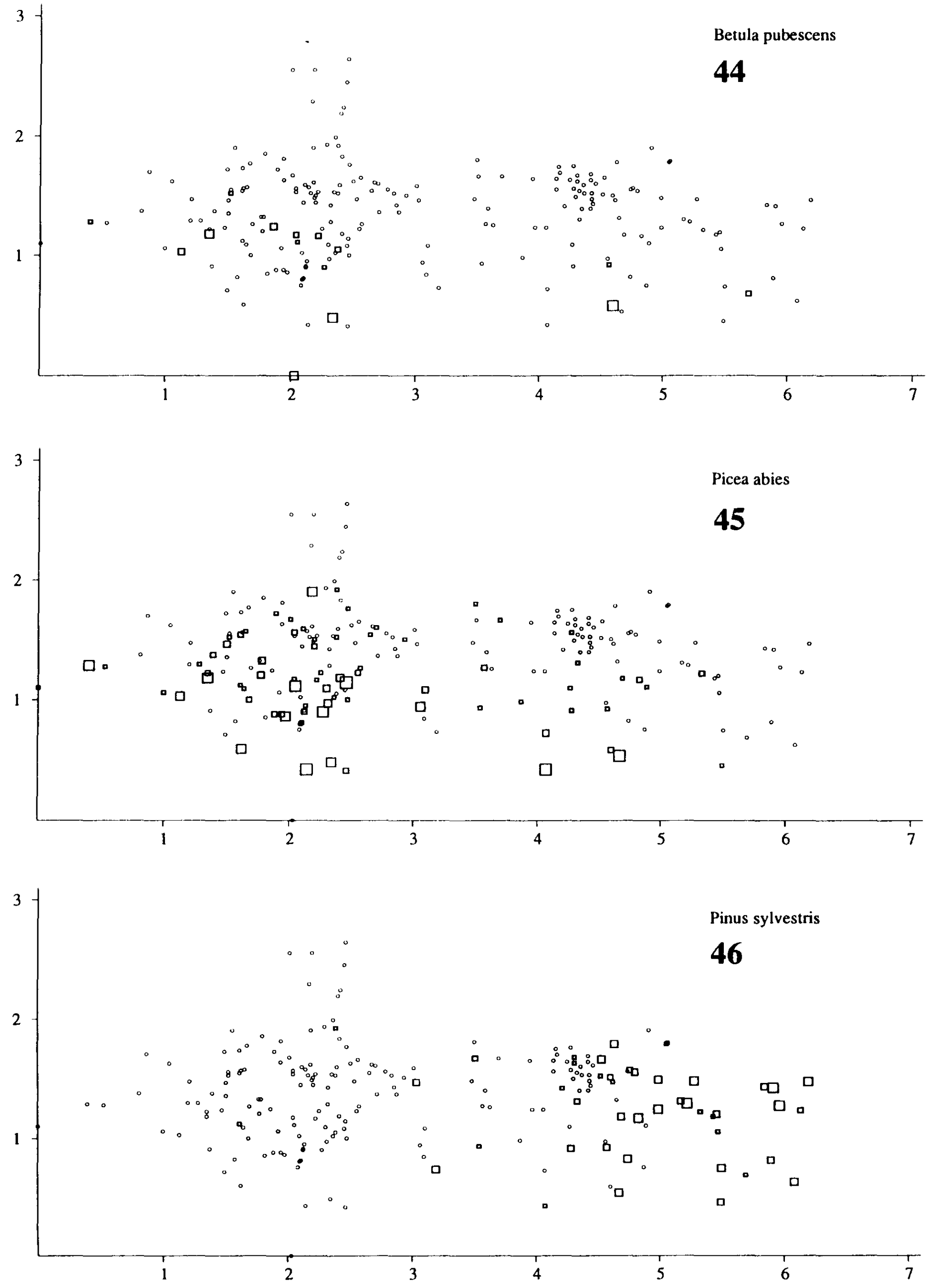
Species	Fig.	Freq. Tot.	Species scores		Range		Freq. Range	Comments
			DCA 1	DCA 2	DCA 1	DCA 2		
Betula pubescens	44	7.5	2.93	-0.74	(0.3-)1.1-2.3(-5.6)	-1.5	1	Saplings
Picea abies	45	38.0	2.66	-0.32	-5.4	0.4-1.9	3	Saplings
Pinus sylvestris	46	22.5	5.60	0.79	(1.6-)3.0-	0.4-1.9	3	Saplings
Populus tremula	47	6.0	1.65	2.07	0.7-2.3(-5.4)	0.9-2.2	2	Saplings
Sorbus aucuparia	48	61.5	1.65	2.81	-**1.2-2.4**-4.1(-4.8)	-**1.2-1.6**-	4	Saplings
Calluna vulgaris	49	37.0	5.14	1.00	2.7-**3.4-5.5**-	**0.4-2.0**	4	
Empetrum nigrum	50	17.0	5.01	1.76	3.7-**4.1-4.9**-5.4	0.4-**0.5-1.8**	3	
Vaccinium myrtillus	51	93.5	3.22	1.81	0.5-**1.2-5.1**-6.2	-	4	
V. uliginosum	52	16.5	4.77	1.39	(1.7-)**3.4-4.9**-5.4	**0.7-1.8**	3	
V. vitis-idaea	53	79.0	3.99	1.98	(0.5-)1.3-**2.0-5.4**-	**0.4-2.2**-	4	
Anemone nemorosa	54	15.5	0.22	1.62	-**1.4**-2.1	0.8-**1.1-1.5**-1.7	3	
Convallaria majalis	55	14.0	0.54	2.65	-2.6	0.8-1.9	2	
Dryopteris expansa agg.	56	17.5	0.93	0.49	0.9-2.3	0.4-1.8	3	
Gymnocarpium dryopteris	57	25.0	0.65	0.48	0.4-**0.8-1.6**-2.1(-2.9)	-**0.9-1.9**-	3	
Linnaea borealis	58	9.5	1.29	2.83	-2.9	0.8-1.8	2	
Lycopodium annotinum	59	16.0	1.51	-0.44	-**0.8-1.6**-2.4(-3.0)	-**0.6-1.9**-	3	
Maianthemum bifolium	60	56.0	1.47	2.09	-**0.4-2.4**-3.2	-**0.4-2.0**-	4	
Melampyrum pratense	61	17.5	4.10	2.82	(0.9-)2.3-5.9	0.4-1.8	2	
M. sylvaticum	62	6.5	0.55	1.88	-2.1(-3.0)	1.0-1.9	2	
Oxalis acetosella	63	13.5	0.20	1.61	-**1.4**(-2.1)	0.7-**0.9-1.5**-1.7	3	
Pteridium aquilinum	64	25.5	1.57	3.70	-**1.7-2.4**-3.0	0.4-**1.8**-	3	
Rubus saxatilis	65	7.5	0.05	1.08	-1.9	0.8-1.6	2	
Solidago virgaurea	66	15.0	0.72	2.46	-2.3	0.9-1.9	2	
Thelypteris phegopteris	67	7.5	0.14	-0.30	-2.0	-1.8	2	
Trientalis europaea	68	45.5	1.47	0.09	-**1.4-2.4**(-4.6)	-**1.1**-	4	
Viola riviniana	69	6.0	-0.38	1.40	-1.6	1.0-1.7	3	
Calamagrostis purpurea	70	27.0	0.74	0.77	-**0.3-1.9**-2.3	-**0.7-1.8**-1.9	3	
Carex pilulifera	71	5.0	6.39	-0.31	(1.4-)4.5-	0.4-1.6	1	
Deschampsia flexuosa	72	54.5	1.94	0.80	-**1.2-3.2**-4.6	-**1.9**-2.3	4	
Luzula pilosa	73	13.0	0.61	2.29	-2.2(-5.1)	0.7-1.9	2	
Brachythecium reflexum	74	14.5	0.76	2.82	-2.5(-3.5)	0.7-2.2	2	
Cirriphyllum piliferum	75	5.5	-0.46	1.41	-**0.6**-2.0	1.0-**1.1-1.3**-1.7	2	
Dicranum drummondii	76	7.5	5.60	1.08	(3.5-)4.3-	0.8-1.8	2	
D. fuscescens	77	8.0	3.76	-0.20	1.4-	0.4-1.7	1	
D. majus	78	60.0	2.05	1.15	-**1.4-3.0**-4.7	-**0.4-1.9**-2.0	4	
D. polysetum	79	18.5	5.19	2.53	(2.3-)3.7-**4.1-5.2**-	0.4-**1-3-1.8**-1.9	3	
D. scoparium	80	46.5	4.85	0.34	1.0-	-	3	
D. spurium	81	5.5	7.19	1.73	4.7-	-	2	
Hylocomium splendens	82	49.5	2.50	1.95	0.6-**1.9-3.7**-5.0	0.4-**0.9-1.8**-2.2	3	
H. umbratum	83	29.5	1.30	-0.16	-**1.1-2.6**	-**1.3**-1.8	3	
Leucobryum glaucum	84	6.0	5.49	-0.29	(3.1-)4.3-	-1.5	2	
Plagiomnium affine	85	10.5	-0.06	0.72	-2.0	0.8-1.8	3	
Plagiothecium denticulatum	86	18.5	1.20	0.89	-2.0	0.8-2.2	2	
P. laetum agg.	87	31.5	1.54	2.30	1.2-4.1	0.7-2.2	3	
P. undulatum	88	16.5	1.75	-0.45	1.3-**2.0-2.4**-2.5(-3.9)	-**0.4-1.1**-1.6	2	
Pleurozium schreberi	89	81.0	3.89	1.42	1.1-**2.1-5.3**-	0.4-**0.8-2.0**	4	
Pohlia nutans agg.	90	18.0	5.50	-0.10	(1.4-)3.9-	0.4-1.9	3	
Polytrichum commune	91	8.0	3.07	-0.89	1.6-2.5,4.2-5.5	-1.6	1	Bimodal
P. formosum	92	16.0	1.63	-0.37	(0.0-)1.2-3.2	0.4-1.8	2	
Ptilium crista-castrensis	93	17.0	3.37	0.11	(1.3-)1.9-4.3	0.4-1.7	2	

Tab. 14 (continued).

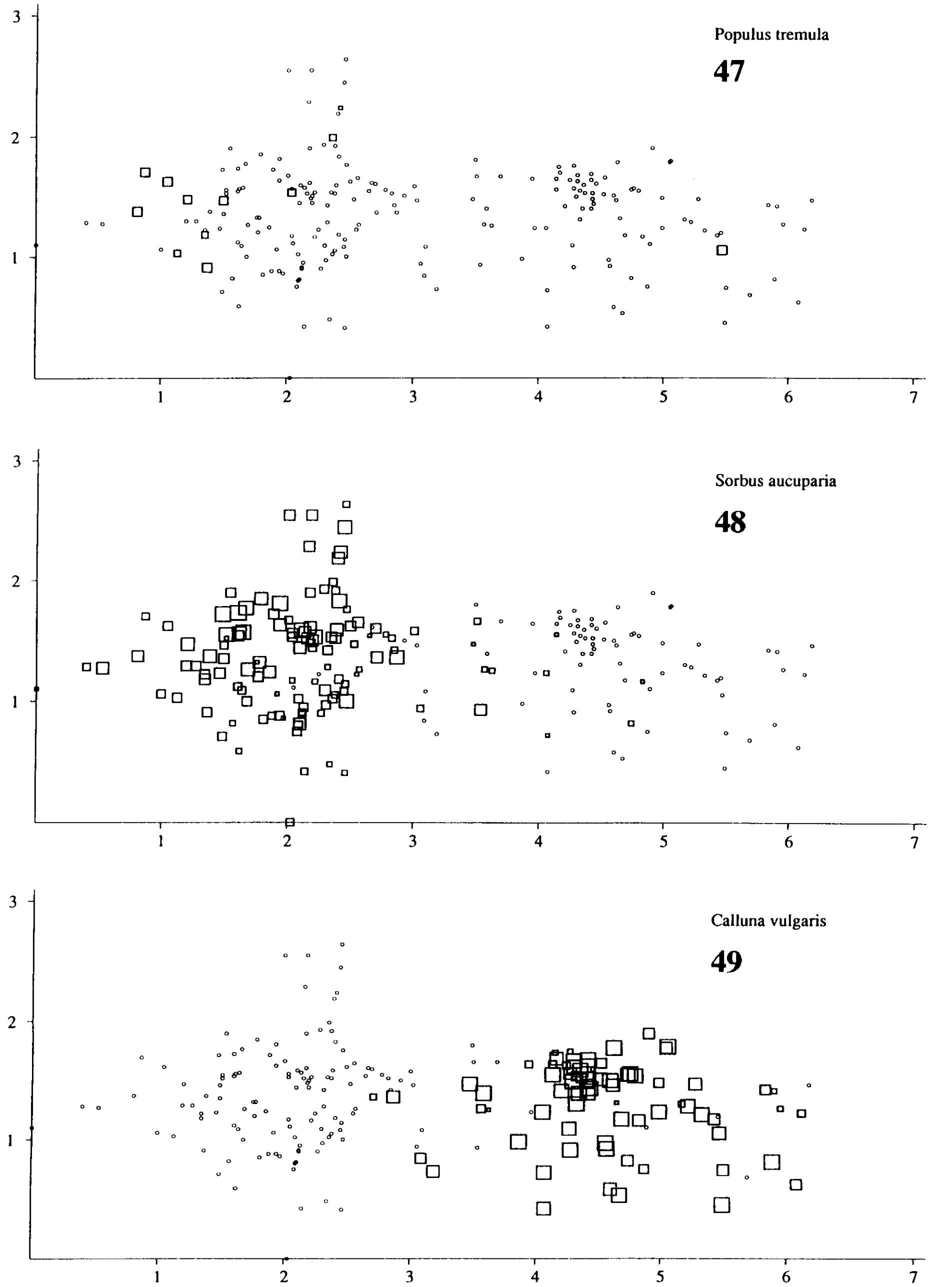
Species	Fig.	Freq. Tot.	Species scores		Range		Freq. Range	Comments
			DCA 1	DCA 2	DCA 1	DCA 2		
Racomitrium lanuginosum	94	7.5	6.03	-0.34	4.0-	0.4-1.7	2	
Rhytidiadelphus loreus	95	13.5	1.95	-0.37	0.8-3.1	0.4-1.8	2	
R. subpinnatus agg.	96	16.5	0.34	0.74	**-1.4**-2.5	0.4-**1.0-1.5**-2.0	2	
Rhytidiadelphus triquetrus	97	12.0	1.13	2.96	-2.7	1.1-1.9	2	
Sphagnum capillifolium	98	13.5	5.18	-0.40	**4.0-5.0**-5.9	**0.4-1.5**-1.6	3	
S. girgensohnii	99	5.5	2.11	-0.76	**1.6-2.5**(-4.0)	**-1.2**	2	
S. quinquefarium	100	10.5	3.40	-0.59	1.7-**2.4-4.1**-4.9	**-1.1**-1.4	3	
Barbilophozia attenuata	101	6.0	3.70	0.51	(1.3-)2.1-2.5,4.2-5.2	0.8-1.9	1	Weakly bimodal
B. barbata	102	5.5	2.33	1.39	1.3-3.0	0.8-1.6	1	
B. floerkei	103	18.5	4.96	-0.39	2.3-5.9	-1.7	2	
B. lycopodioides	104	51.0	2.50	0.86	0.8-**2.0-4.0**-4.8(-5.3)	**-0.8-1.6**-1.9	3	
Blepharostoma trichophyllum	105	6.5	1.56	0.49	0.5-3.0	0.8-1.6	1	
Calypogeia integristipula	106	7.5	1.78	1.48	1.4-2.9	0.8-1.9	1	
C. muellerana	107	23.0	1.76	-0.51	1.2-3.0(-4.3)	-2.0	2	
C. neesiana	108	11.0	3.52	-0.46	1.6-5.4	-1.5	1	Weakly bimodal
Cephalozia bicuspidata	109	10.5	2.01	-0.46	-2.9(-4.3)	-1.6	1	
C. lunulifolia	110	7.5	2.09	0.43	1.2-2.4(-4.6)	0.5-1.7	1	
Cephaloziella spp.	111	6.5	5.91	-0.46	4.0-	-1.3	2	
Lophocolea heterophylla	112	43.5	1.59	2.54	-3.5(-4.3)	0.4-	3	
Lophozia obtusa	113	13.0	2.20	0.03	1.1-3.6	0.4-1.6	2	
L. ventricosa agg.	114	17.0	4.00	-0.36	1.1-5.5	-	2	Weakly bimodal
Plagiochila asplenioides	115	34.0	1.06	0.85	**-0.4-2.0**-2.6(-3.6)	0.4-**0.8-1.5**-2.0	4	
Ptilidium ciliare	116	32.5	4.84	1.81	2.1-5.9	-	3	
Tritomaria quinquedentata	117	5.0	1.97	-0.79	1.3-3.1	-1.6	1	
Cetraria islandica	118	16.0	6.28	0.47	4.0-**5.3-**	**-1.6-**	3	
Cladina arbuscula	119	13.0	5.86	3.32	4.3-	(0.6-)1.2-	4	
C. mitis	120	6.5	7.06	1.22	4.5-**5.8-**	**0.6-1.5**-2.0	2	
C. rangiferina	121	22.0	5.95	2.45	4.1-**4.7-**	**-1.0-**	4	
Cladonia bellidiflora	122	12.0	6.52	0.76	4.0-	-	3	
C. chlorophaea agg.	123	22.0	5.91	1.40	(2.0-)4.0-**5.1-**	**-0.7-**	4	
C. squamosa	124	10.5	6.55	0.09	(3.0-)4.0-	-	3	
C. uncialis	125	11.0	6.68	0.51	4.4-	0.6-1.5	4	

The species was absent from the extreme ends of DCA 1, but dominated almost every sample plot from 1.2 to 5.1 along the axis. Although subordinate to *Vaccinium myrtillus* in cover, *V. vitis-idaea* occurred along most of DCA 1 (Fig. 53) and its optimum range was somewhat displaced towards the right in the ordination (2.0-5.4 S.D. along DCA 1). *Calluna vulgaris* (Fig. 49) was the constant dominant in site-types 2 and 3 (optimum range 3.4-5.5). Towards the more mesic end of axis 1, *Deschampsia flexuosa* (Fig. 72) was constant over the range 1.2-3.2, followed by *Trientalis europaea* (Fig. 68), *Sorbus aucuparia* saplings (Fig. 48), constant in the optimum range ca. 1.3-2.4, and, above all, *Maianthemum bifolium* (Fig. 60), present in almost every meso subplot in the range 0.5-2.2 along DCA 1. Towards the left end of DCA 1, several species of vascular plants were important and locally dominant, but no one reached constancy on 1 m^2 plots.

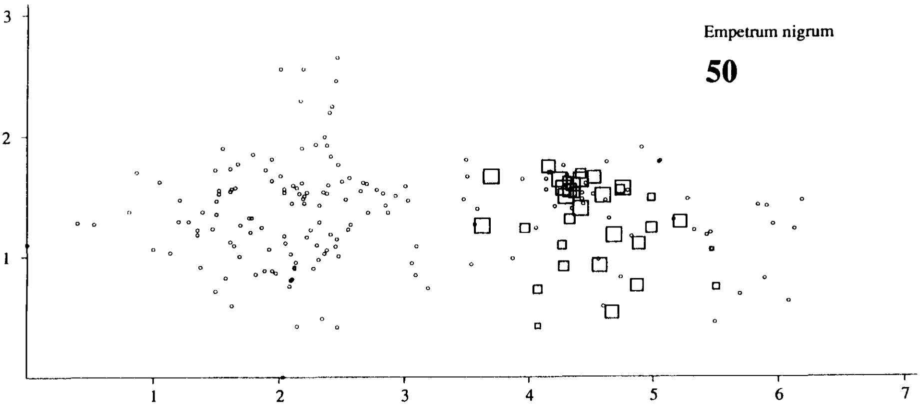
The vascular plants were generally indifferent to DCA 2, although some exceptions could be noted: *Picea abies* saplings and seedlings (Fig. 45) were concentrated at low DCA 2 values, in particular when occurring at high DCA 1 values. A similar tendency to restriction to low DCA 2 values for high DCA 1 scores, was noted for *Trientalis europaea* and indicated for *Deschampsia flexuosa*. *Carex pilulifera* (Fig. 71), restricted to high DCA 1 values,

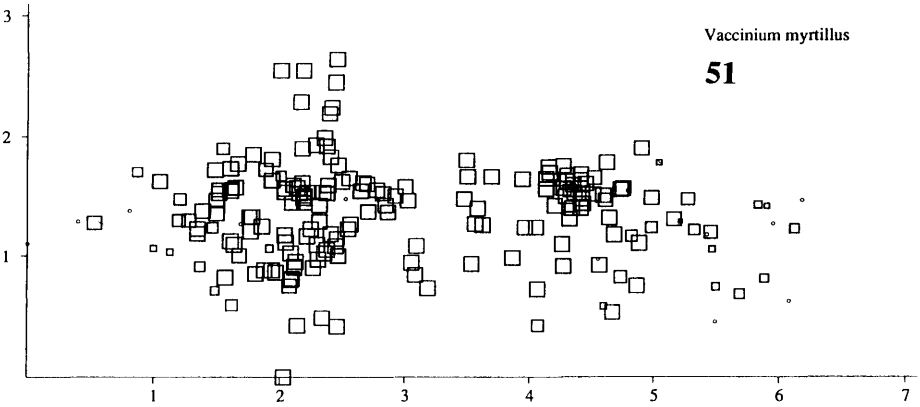


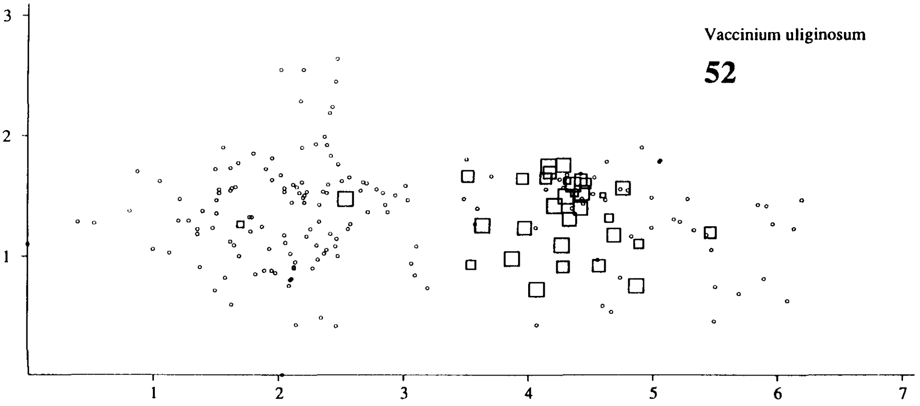
Figs 44-46. DCA of the ME 200 data set, axes 1 and 2. Frequency in subplots for each species in the meso sample plots plotted on to the meso sample plot positions. Scaling of axes in S.D. units. Small circle - absent. Square - present; area of square proportional to frequency in subplots. Fig. 44. *Betula pubescens* (saplings and seedlings). Fig. 45. *Picea abies* (saplings and seedlings). Fig. 46. *Pinus sylvestris* (saplings and seedlings).



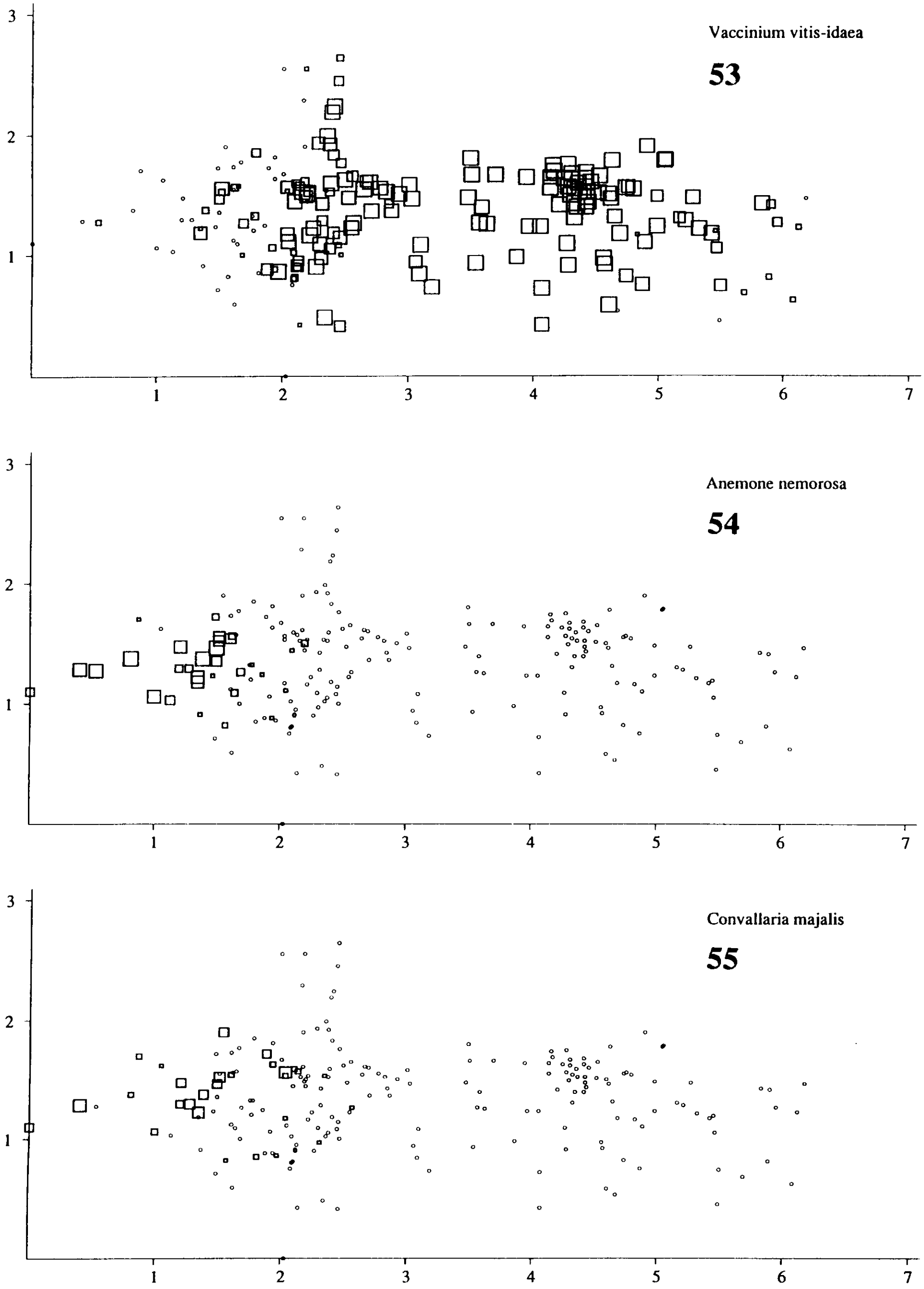
Figs 47-49. DCA of the ME 200 data set, axes 1 and 2. Frequency in subplots for each species in the meso sample plots plotted on to the meso sample plot positions. Scaling of axes in S.D. units. Small circle - absent. Square - present; area of square proportional to frequency in subplots. Fig. 47. *Populus tremula* (saplings and seedlings). Fig. 48. *Sorbus aucuparia* (saplings and seedlings). Fig. 49. *Calluna vulgaris.*



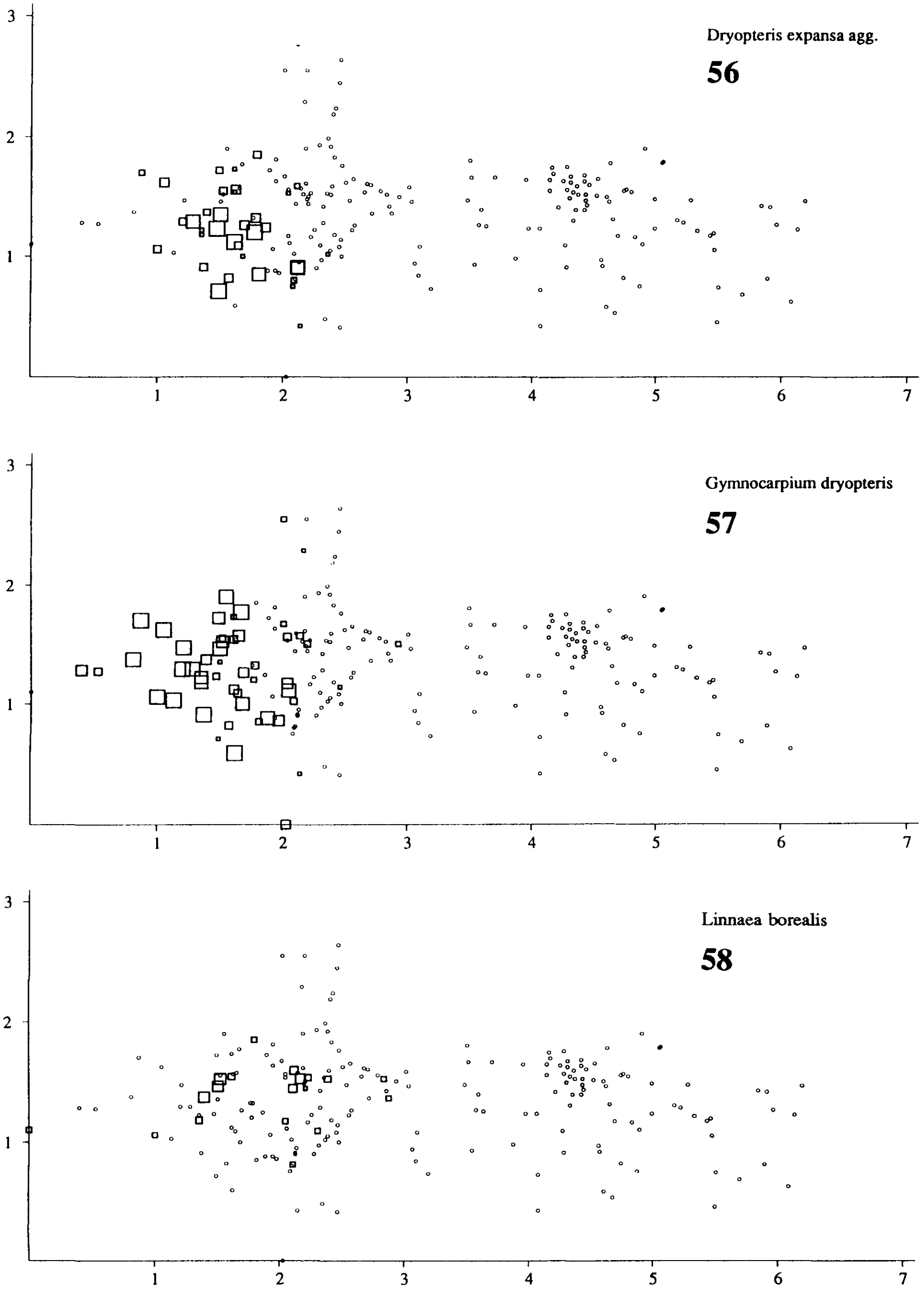




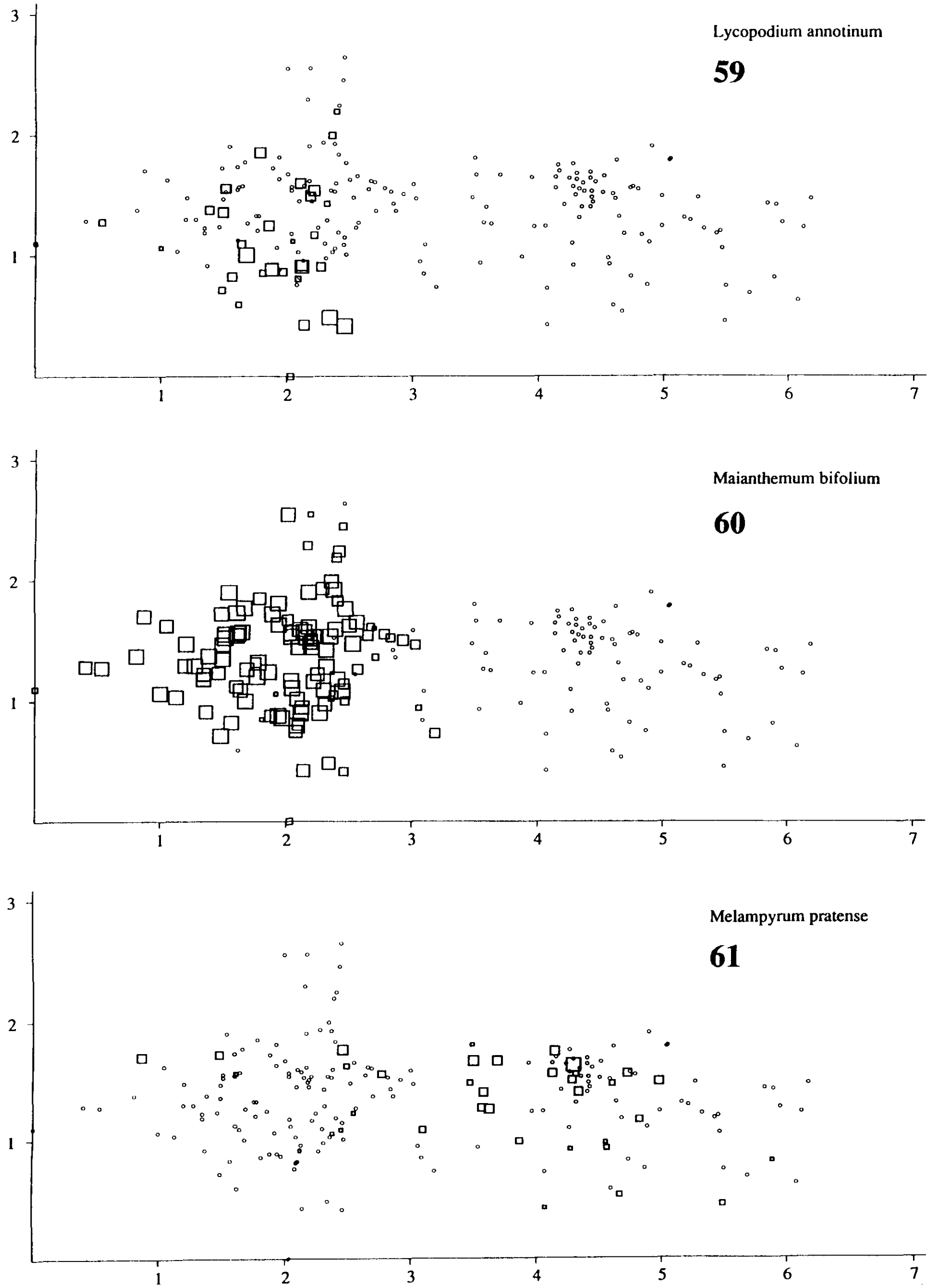
Figs 50-52. DCA of the ME 200 data set, axes 1 and 2. Frequency in subplots for each species in the meso sample plots plotted on to the meso sample plot positions. Scaling of axes in S.D. units. Small circle - absent. Square - present; area of square proportional to frequency in subplots. Fig. 50. *Empetrum nigrum*. Fig. 51. *Vaccinium myrtillus*. Fig. 52. *Vaccinium uliginosum*.



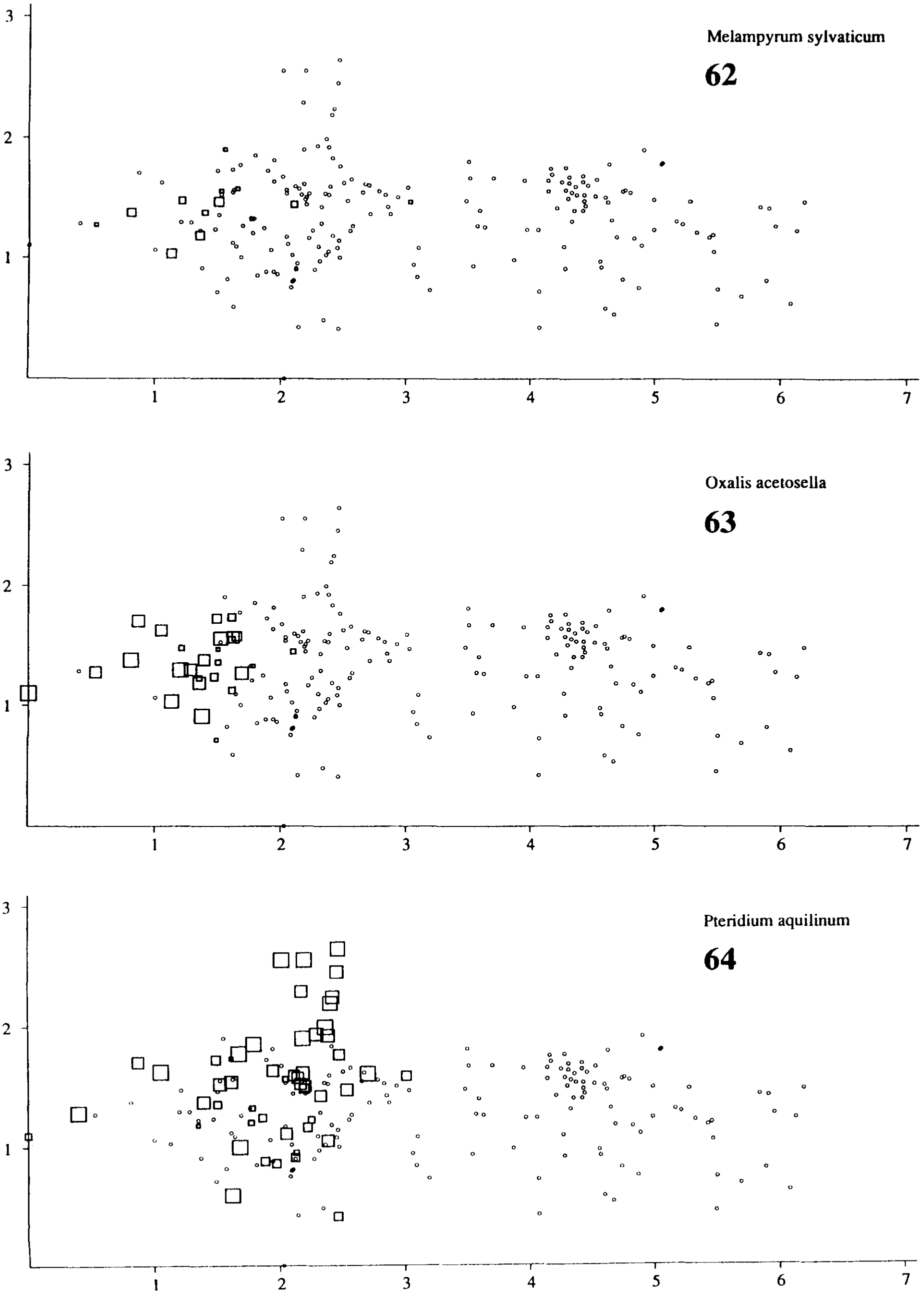
Figs 53-55. DCA of the ME 200 data set, axes 1 and 2. Frequency in subplots for each species in the meso sample plots plotted on to the meso sample plot positions. Scaling of axes in S.D. units. Small circle - absent. Square - present; area of square proportional to frequency in subplots. Fig. 53. *Vaccinium vitis-idaea*. Fig. 54. *Anemone nemorosa*. Fig. 55. *Convallaria majalis*.



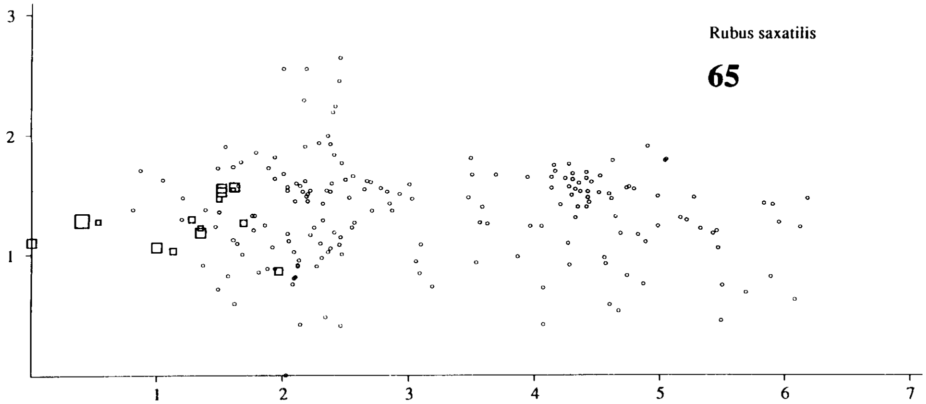
Figs 56-58. DCA of the ME 200 data set, axes 1 and 2. Frequency in subplots for each species in the meso sample plots plotted on to the meso sample plot positions. Scaling of axes in S.D. units. Small circle - absent. Square - present; area of square proportional to frequency in subplots. Fig. 56. *Dryopteris expansa* agg. Fig. 57. *Gymnocarpium dryopteris*. Fig. 58. *Linnaea borealis*.

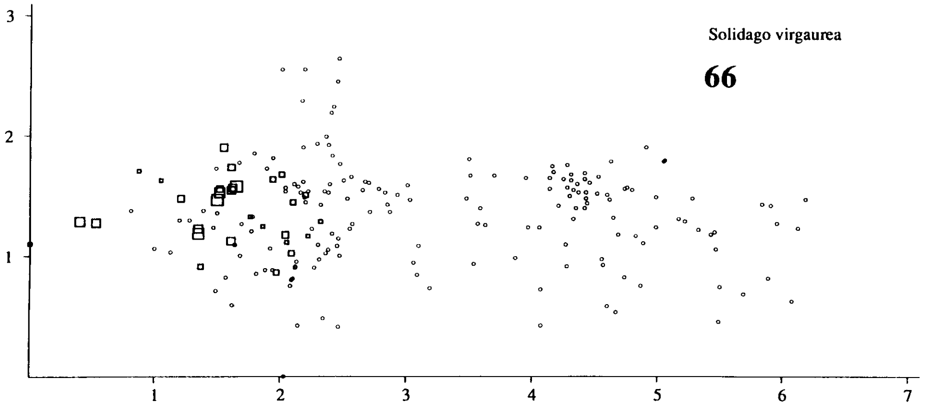


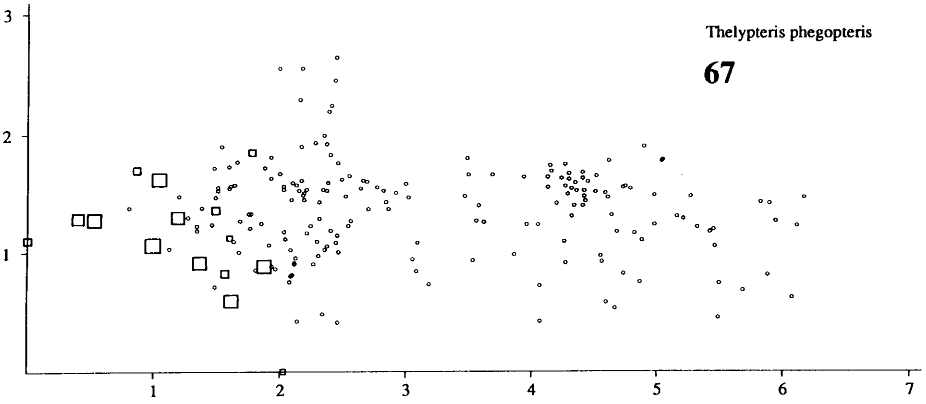
Figs 59-61. DCA of the ME 200 data set, axes 1 and 2. Frequency in subplots for each species in the meso sample plots plotted on to the meso sample plot positions. Scaling of axes in S.D. units. Small circle - absent. Square - present; area of square proportional to frequency in subplots. Fig. 59. *Lycopodium annotinum*. Fig. 60. *Maianthemum bifolium*. Fig. 61. *Melampyrum pratense*.



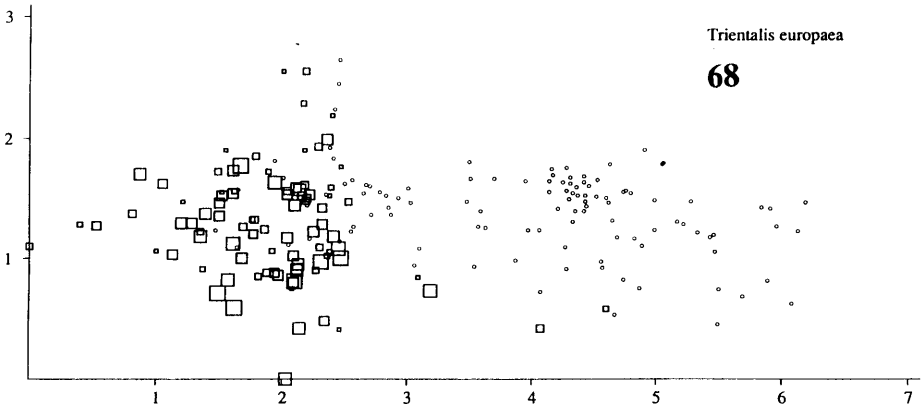
Figs 62-64. DCA of the ME 200 data set, axes 1 and 2. Frequency in subplots for each species in the meso sample plots plotted on to the meso sample plot positions. Scaling of axes in S.D. units. Small circle - absent. Square - present; area of square proportional to frequency in subplots. Fig. 62. *Melampyrum sylvaticum*. Fig. 63. *Oxalis acetosella*. Fig. 64. *Pteridium aquilinum*.

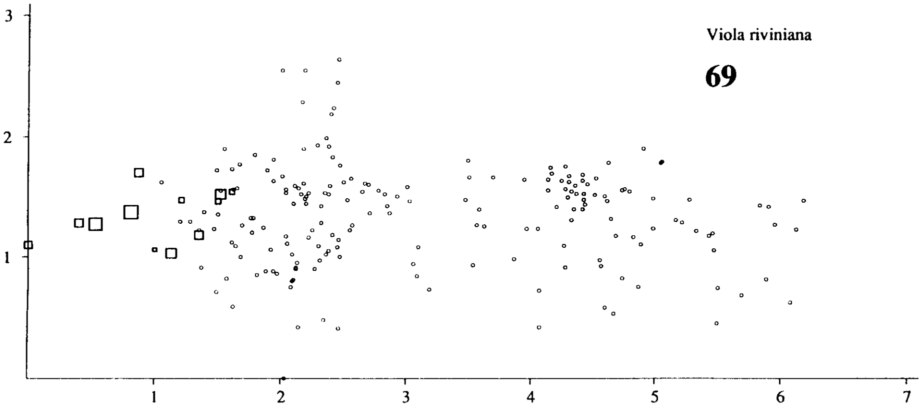


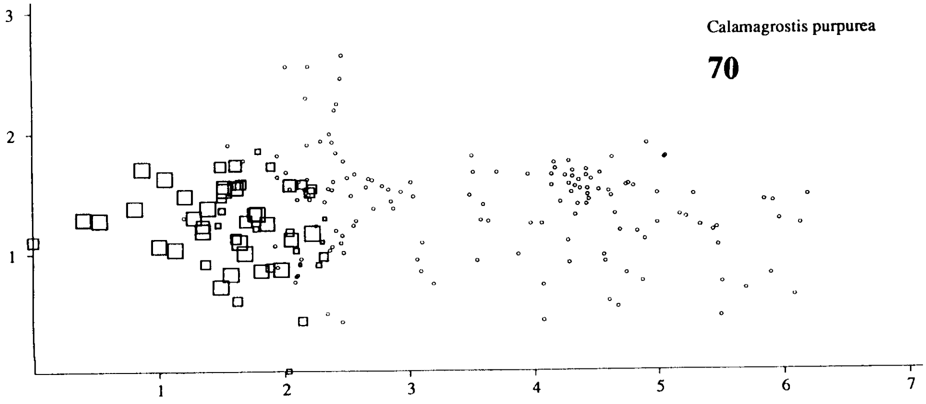




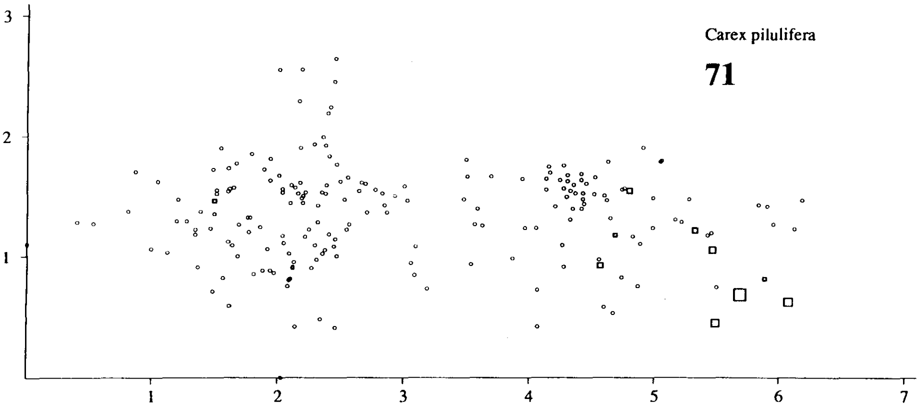
Figs 65-67. DCA of the ME 200 data set, axes 1 and 2. Frequency in subplots for each species in the meso sample plots plotted on to the meso sample plot positions. Scaling of axes in S.D. units. Small circle - absent. Square - present; area of square proportional to frequency in subplots. Fig. 65. *Rubus saxatilis*. Fig. 66. *Solidago virgaurea*. Fig. 67. *Thelypteris phegopteris*.

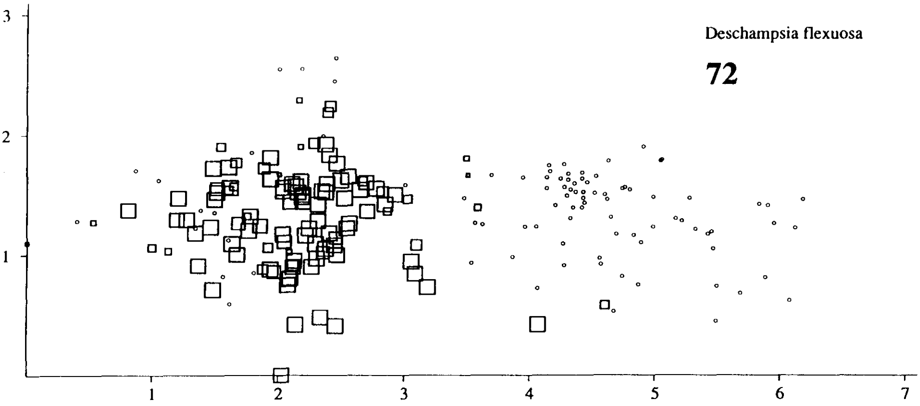


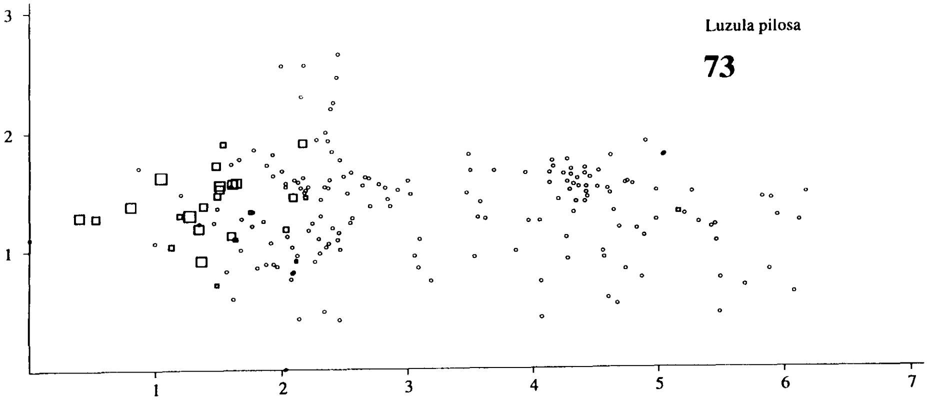




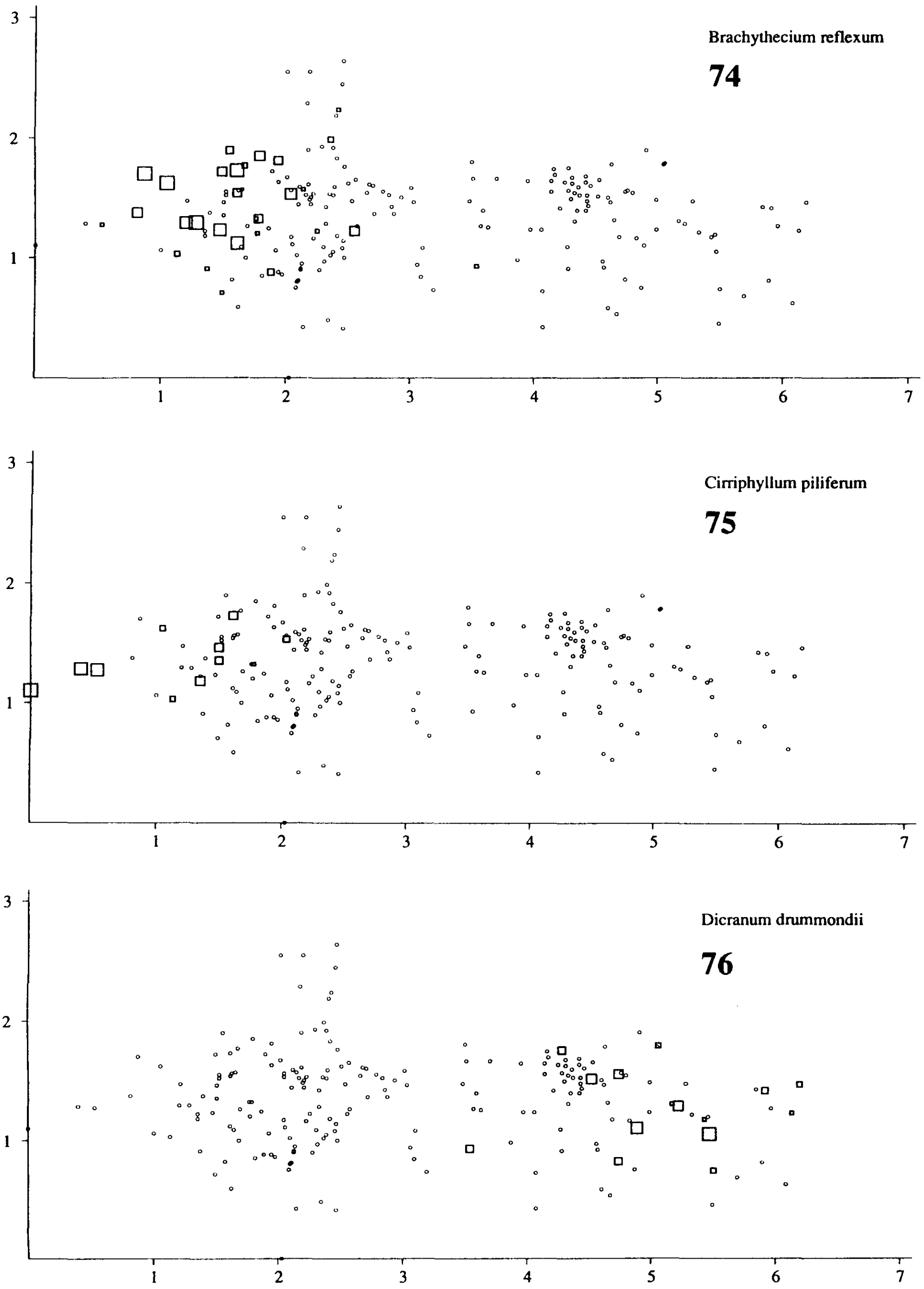
Figs 68-70. DCA of the ME 200 data set, axes 1 and 2. Frequency in subplots for each species in the meso sample plots plotted on to the meso sample plot positions. Scaling of axes in S.D. units. Small circle - absent. Square - present; area of square proportional to frequency in subplots. Fig. 68. *Trientalis europaea*. Fig. 69. *Viola riviniana*. Fig. 70. *Calamagrostis purpurea*.



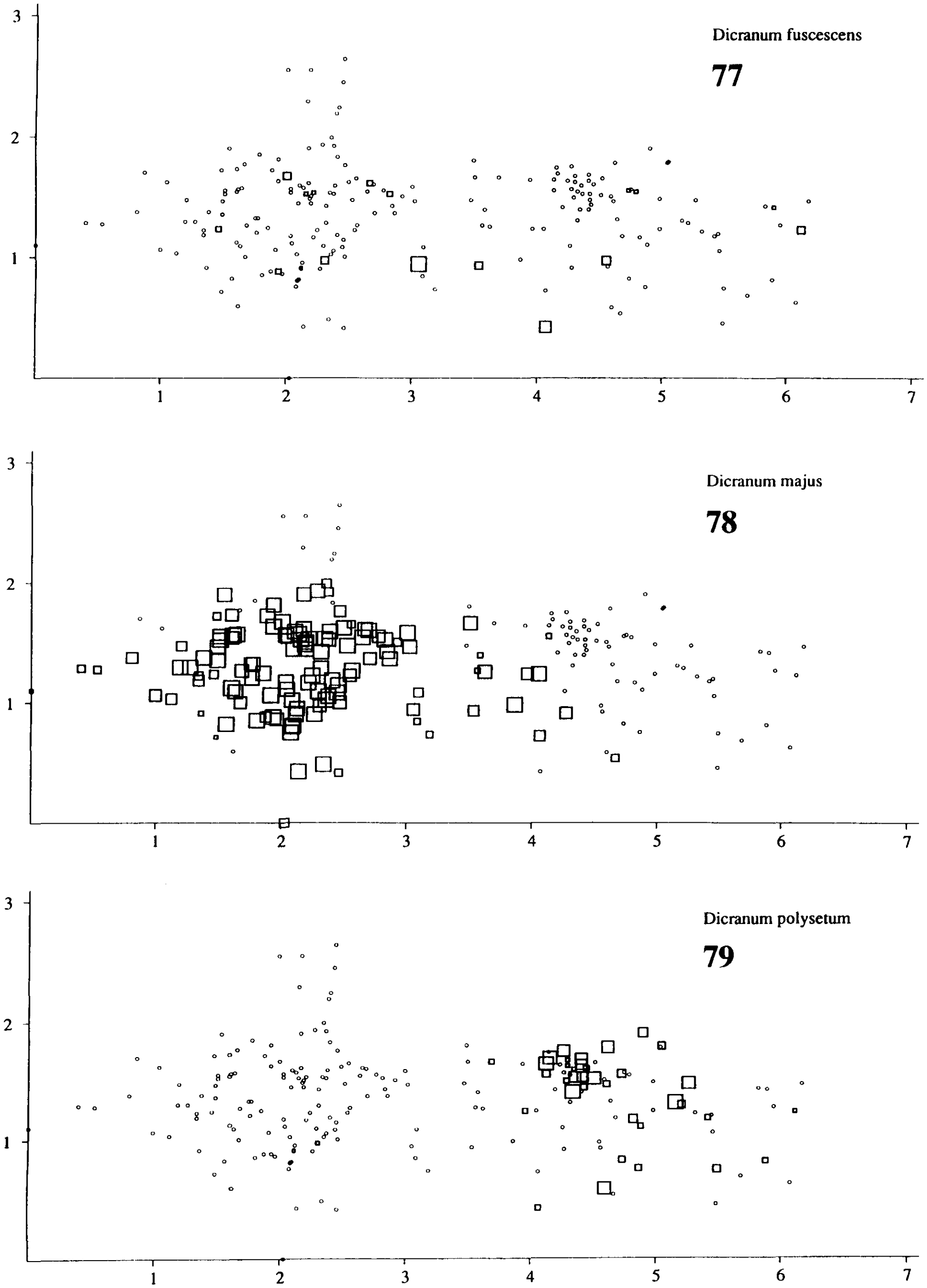




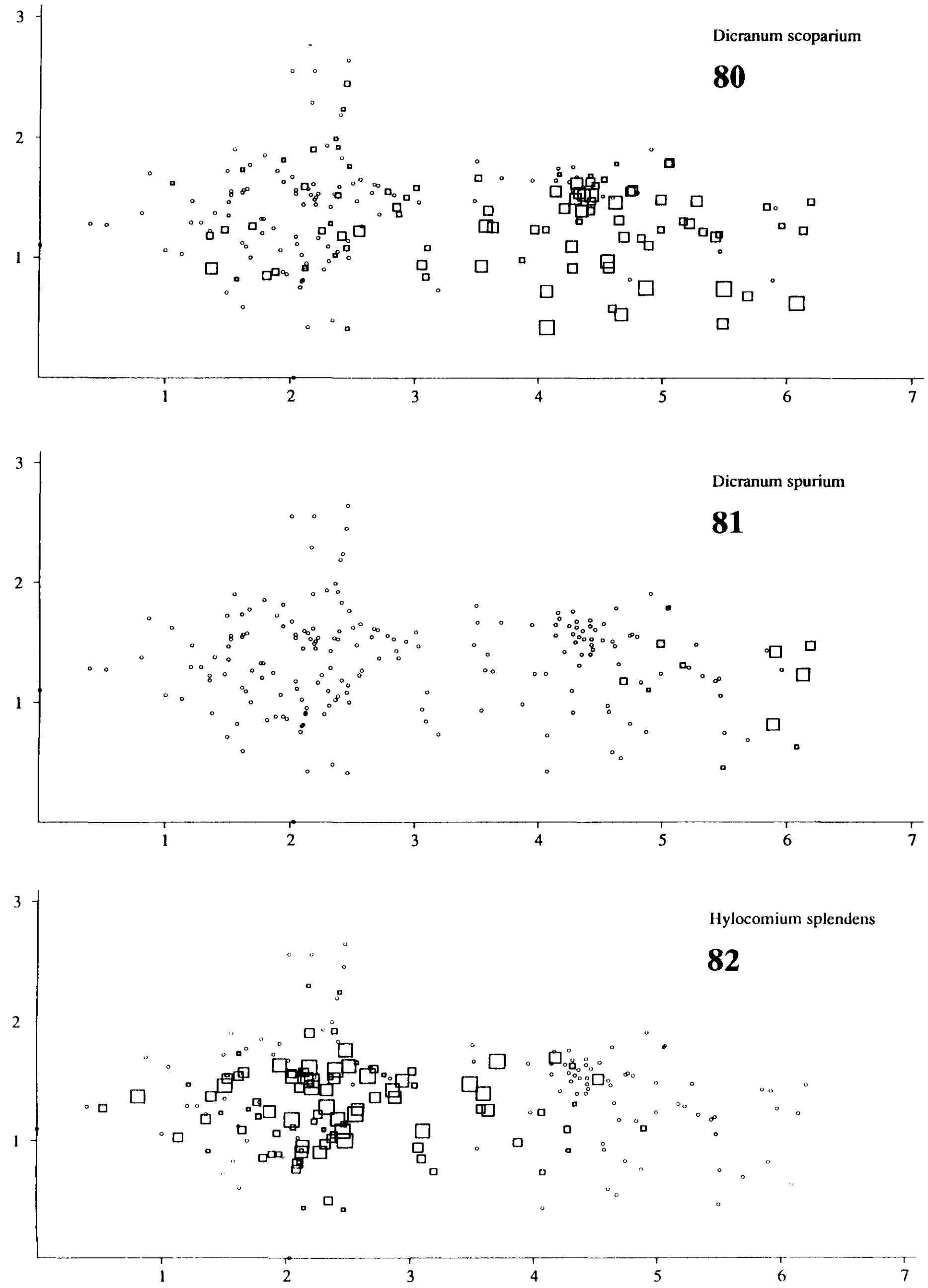
Figs 71-73. DCA of the ME 200 data set, axes 1 and 2. Frequency in subplots for each species in the meso sample plots plotted on to the meso sample plot positions. Scaling of axes in S.D. units. Small circle - absent. Square - present; area of square proportional to frequency in subplots. Fig. 71. *Carex pilulifera*. Fig. 72. *Deschampsia flexuosa*. Fig. 73. *Luzula pilosa*.



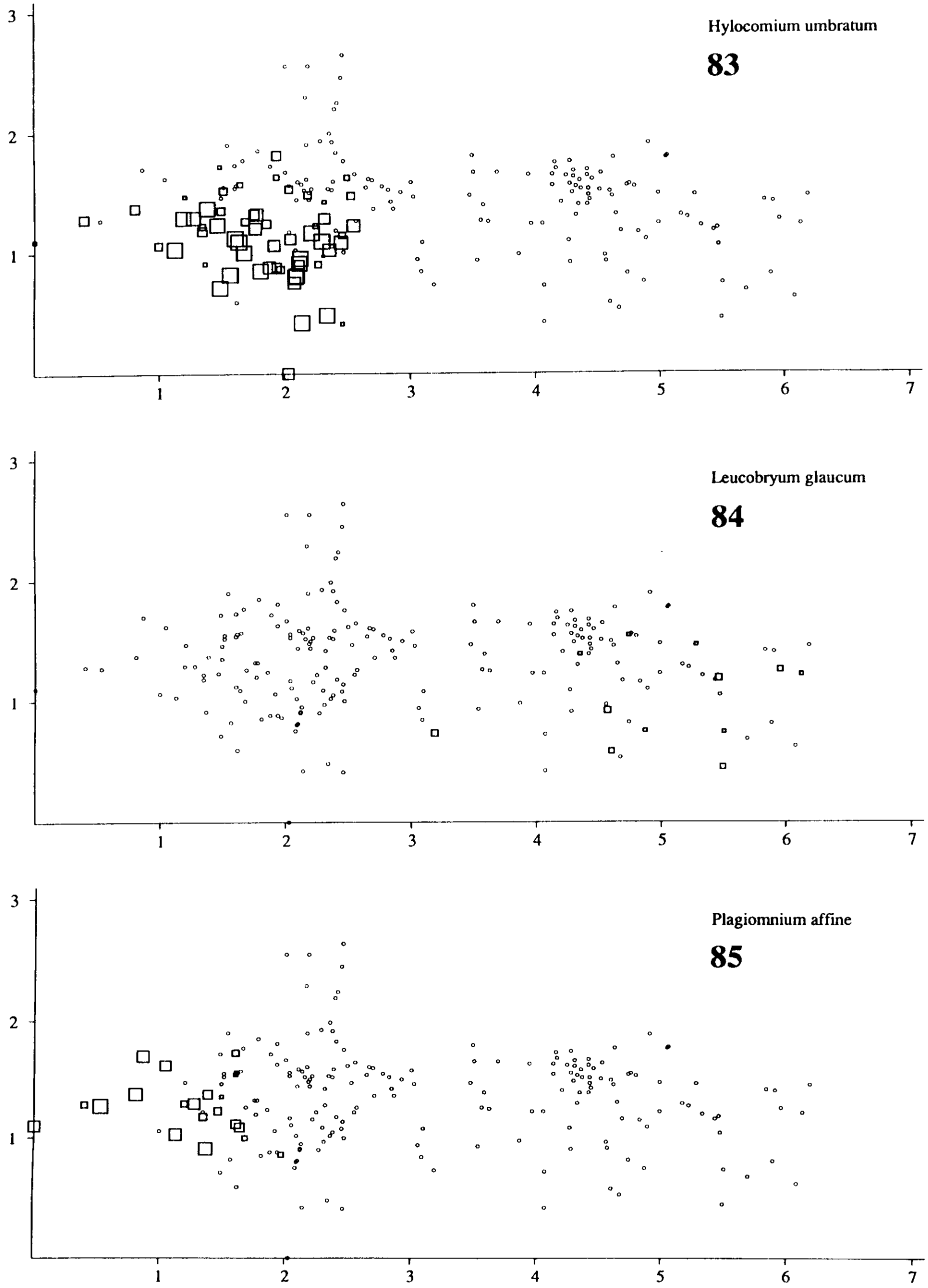
Figs 74-76. DCA of the ME 200 data set, axes 1 and 2. Frequency in subplots for each species in the meso sample plots plotted on to the meso sample plot positions. Scaling of axes in S.D. units. Small circle - absent. Square - present; area of square proportional to frequency in subplots. Fig. 74. *Brachythecium reflexum*. Fig. 75. *Cirriphyllum piliferum*. Fig. 76. *Dicranum drummondii*.



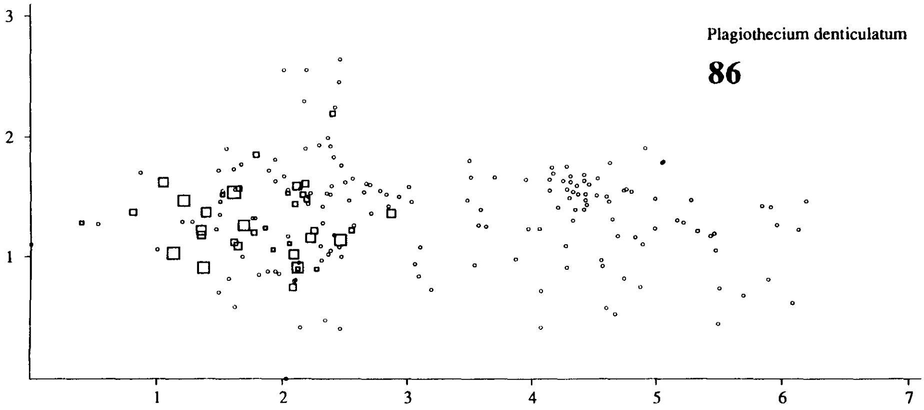
Figs 77-79. DCA of the ME 200 data set, axes 1 and 2. Frequency in subplots for each species in the meso sample plots plotted on to the meso sample plot positions. Scaling of axes in S.D. units. Small circle - absent. Square - present; area of square proportional to frequency in subplots. Fig. 77. *Dicranum fuscescens*. Fig. 78. *Dicranum majus*. Fig. 79. *Dicranum polysetum*.

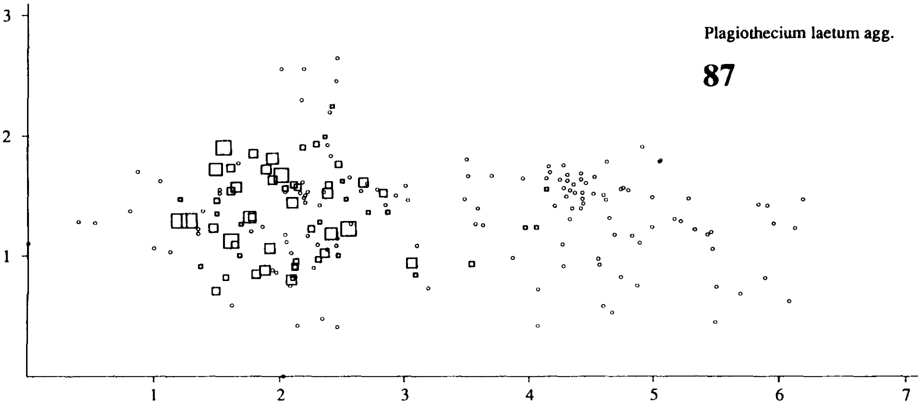


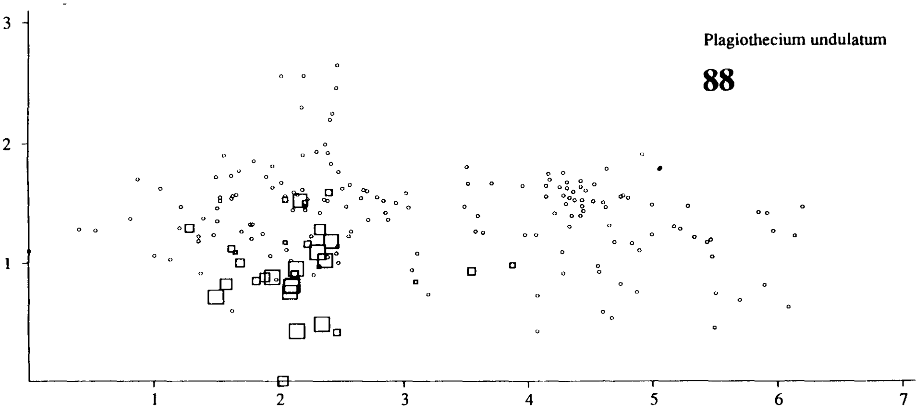
Figs 80-82. DCA of the ME 200 data set, axes 1 and 2. Frequency in subplots for each species in the meso sample plots plotted on to the meso sample plot positions. Scaling of axes in S.D. units. Small circle - absent. Square - present; area of square proportional to frequency in subplots. Fig. 80. *Dicranum scoparium*. Fig. 81. *Dicranum spurium*. Fig. 82. *Hylocomium splendens*.



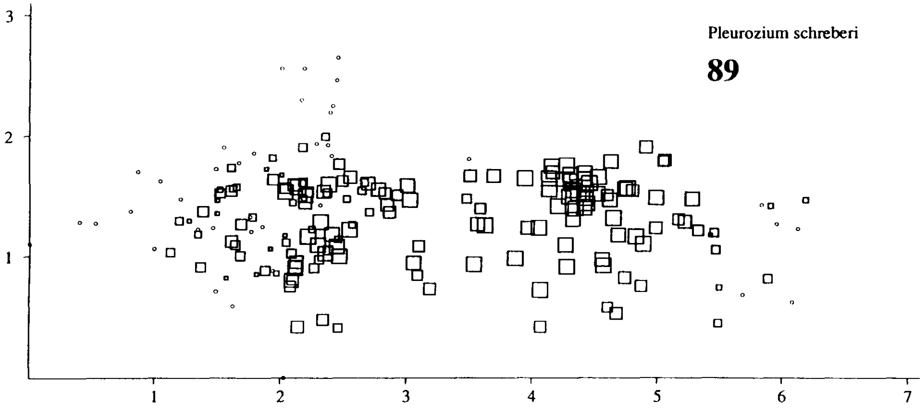
Figs 83-85. DCA of the ME 200 data set, axes 1 and 2. Frequency in subplots for each species in the meso sample plots plotted on to the meso sample plot positions. Scaling of axes in S.D. units. Small circle - absent. Square - present; area of square proportional to frequency in subplots. Fig. 83. *Hylocomium umbratum.* Fig. 84. *Leucobryum glaucum.* Fig. 85. *Plagiomnium affine.*

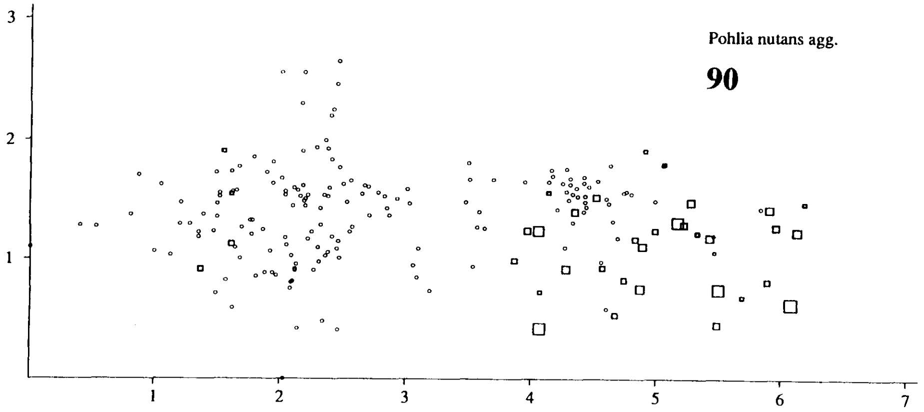


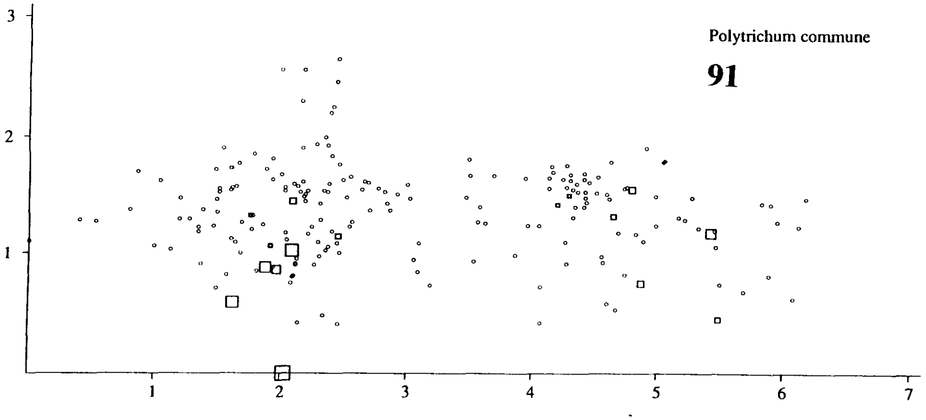




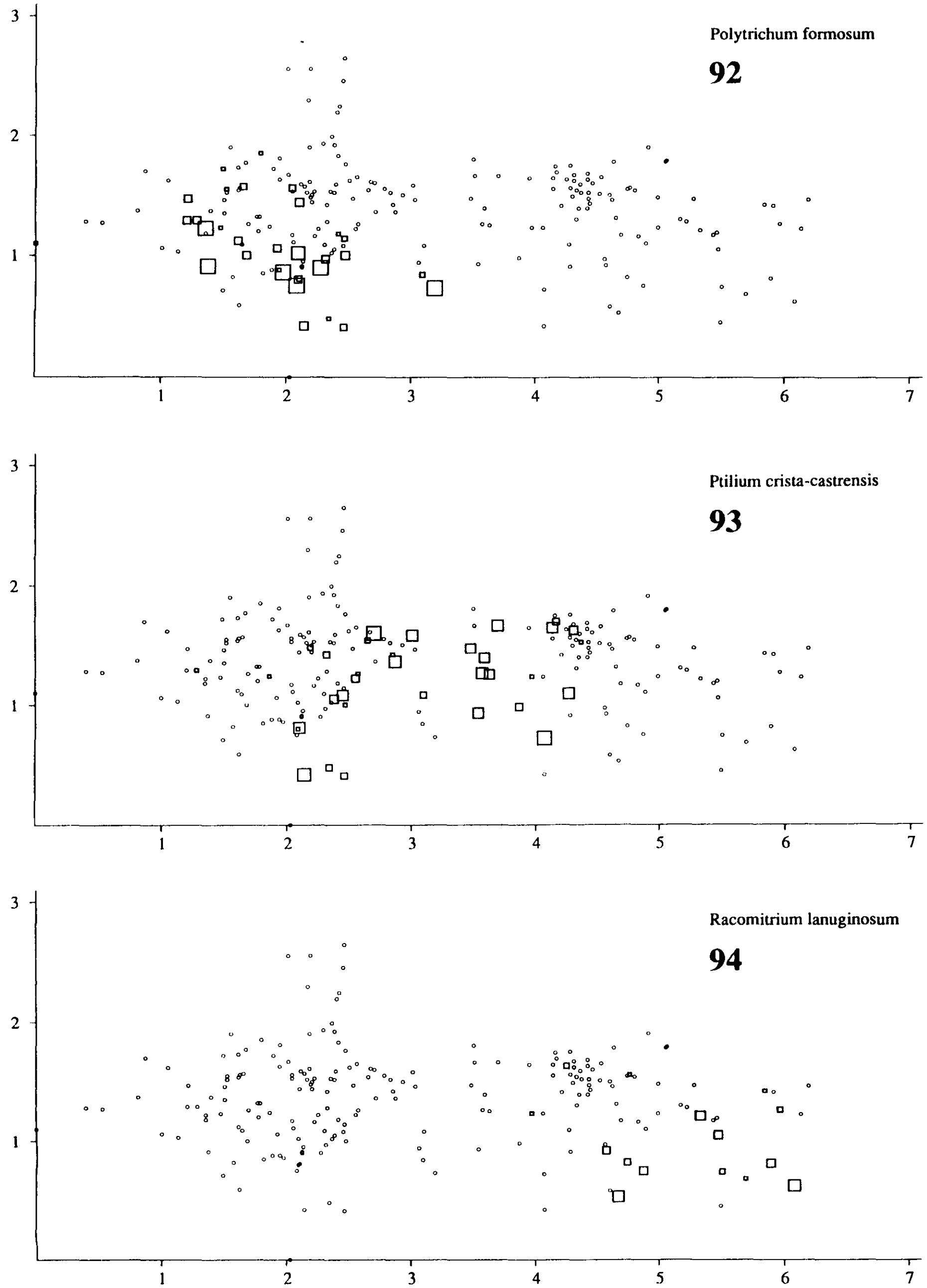
Figs 86-88. DCA of the ME 200 data set, axes 1 and 2. Frequency in subplots for each species in the meso sample plots plotted on to the meso sample plot positions. Scaling of axes in S.D. units. Small circle - absent. Square - present; area of square proportional to frequency in subplots. Fig. 86. *Plagiothecium denticulatum.* Fig. 87. *Plagiothecium laetum* agg. Fig. 88. *Plagiothecium undulatum.*



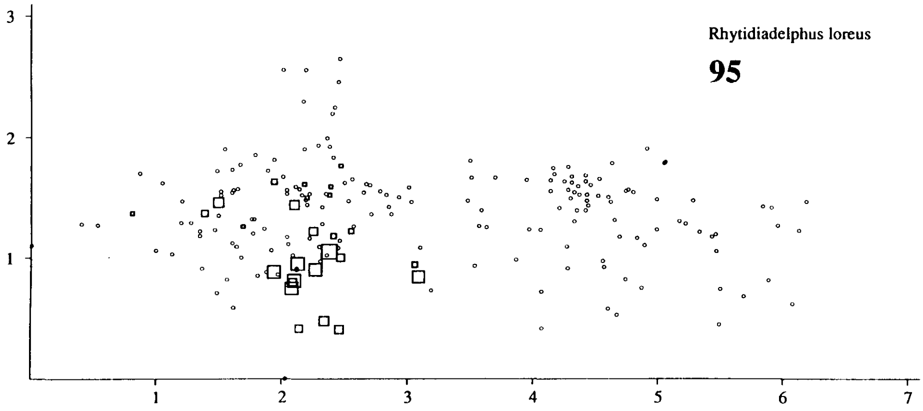


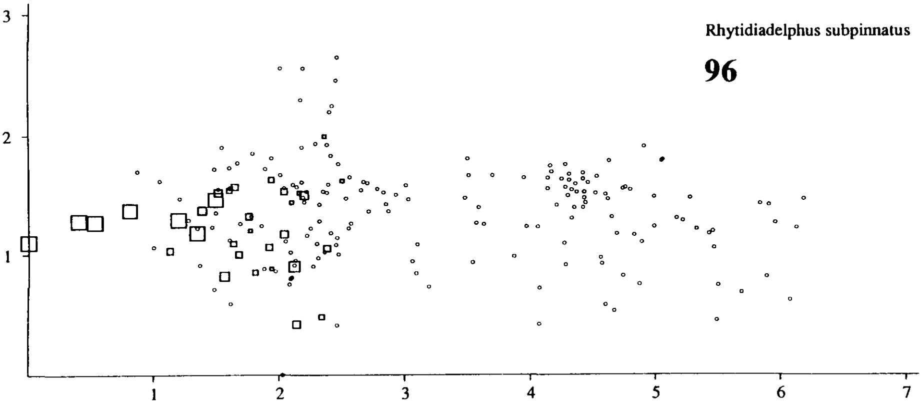


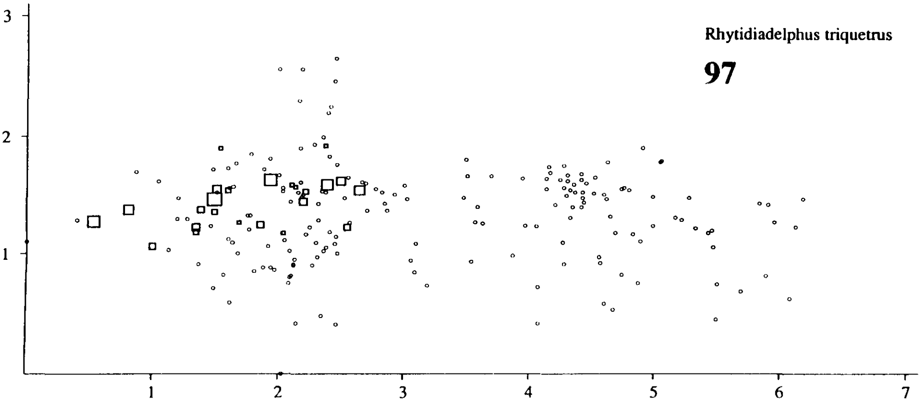
Figs 89-91. DCA of the ME 200 data set, axes 1 and 2. Frequency in subplots for each species in the meso sample plots plotted on to the meso sample plot positions. Scaling of axes in S.D. units. Small circle - absent. Square - present; area of square proportional to frequency in subplots. Fig. 89. *Pleurozium schreberi*. Fig. 90. *Pohlia nutans* agg. Fig. 91. *Polytrichum commune*.



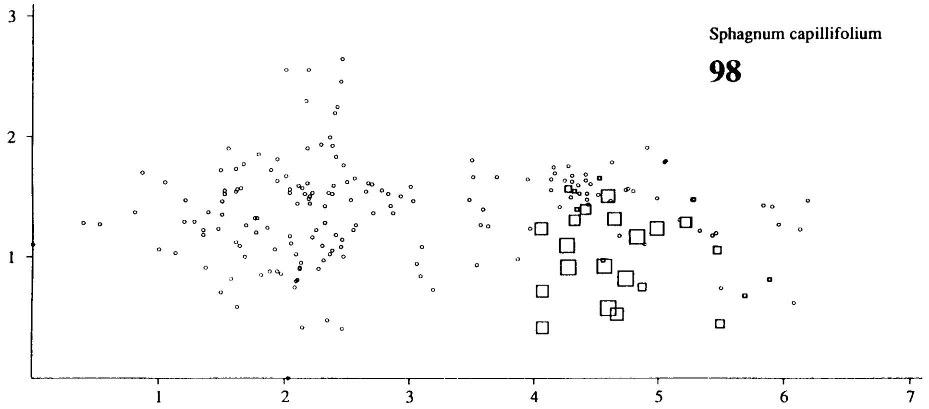
Figs 92-94. DCA of the ME 200 data set, axes 1 and 2. Frequency in subplots for each species in the meso sample plots plotted on to the meso sample plot positions. Scaling of axes in S.D. units. Small circle - absent. Square - present; area of square proportional to frequency in subplots. Fig. 92. *Polytrichum formosum*. Fig. 93. *Ptilium crista-castrensis*. Fig. 94. *Racomitrium lanuginosum*.

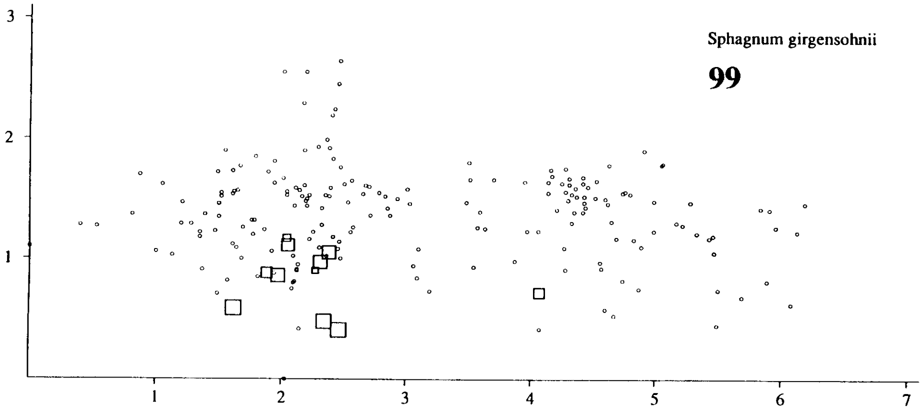


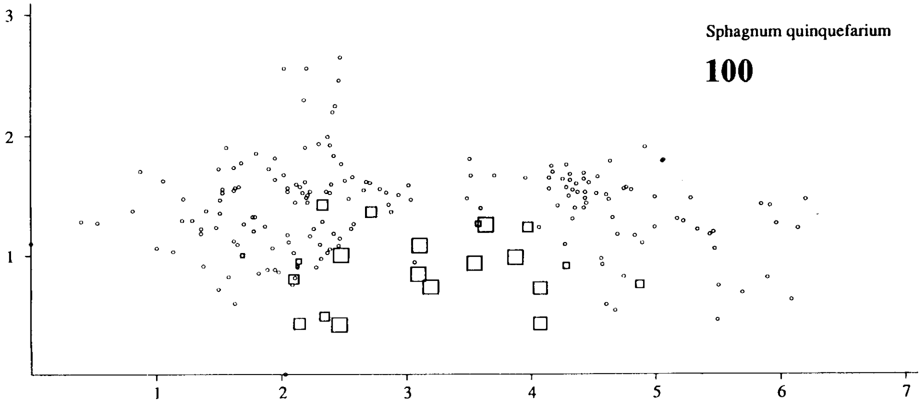




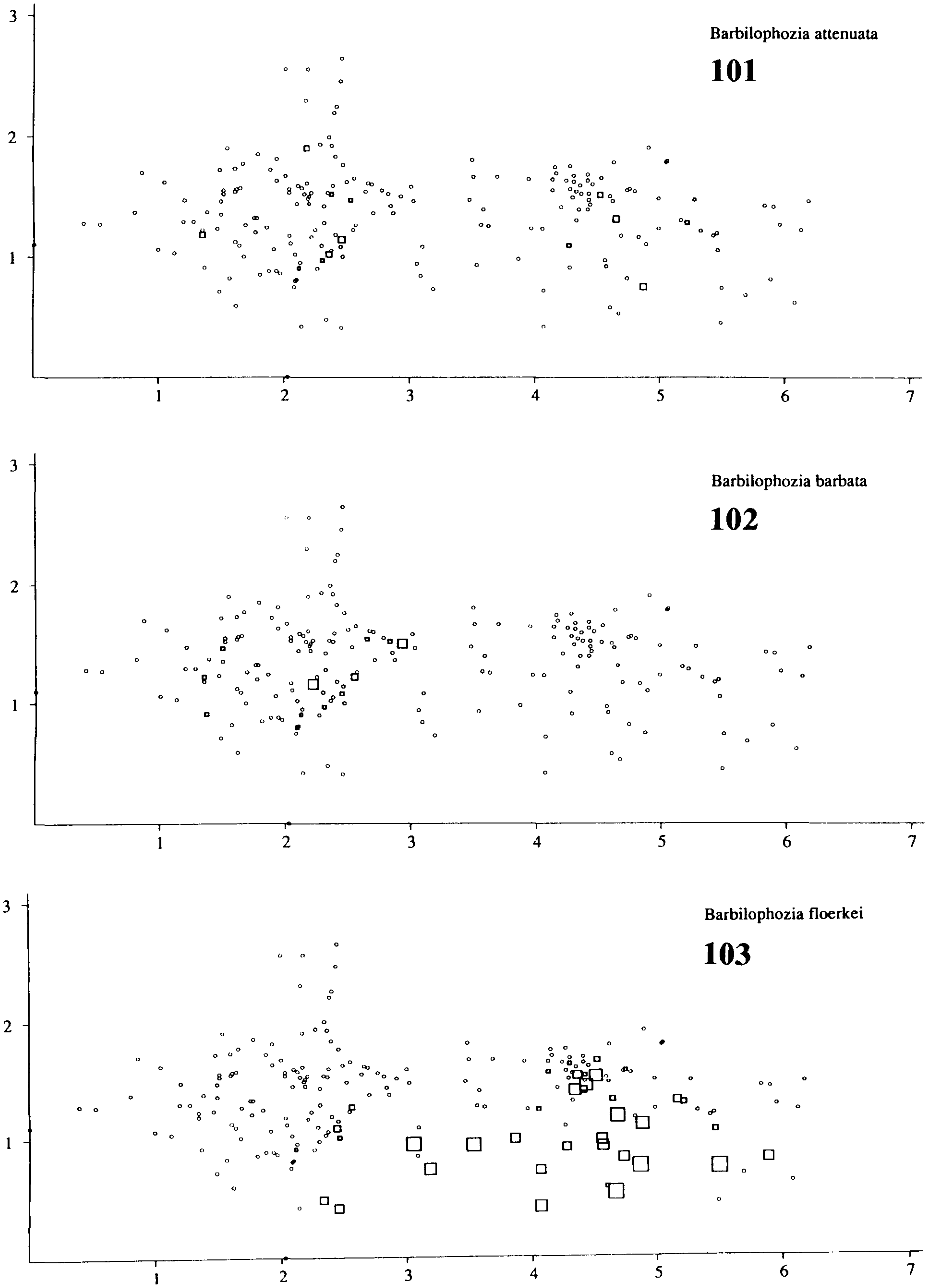
Figs 95-97. DCA of the ME 200 data set, axes 1 and 2. Frequency in subplots for each species in the meso sample plots plotted on to the meso sample plot positions. Scaling of axes in S.D. units. Small circle - absent. Square - present; area of square proportional to frequency in subplots. Fig. 95. *Rhytidiadelphus loreus*. Fig. 96. *Rhytidiadelphus subpinnatus* agg. Fig. 97. *Rhytidiadelphus triquetrus*.



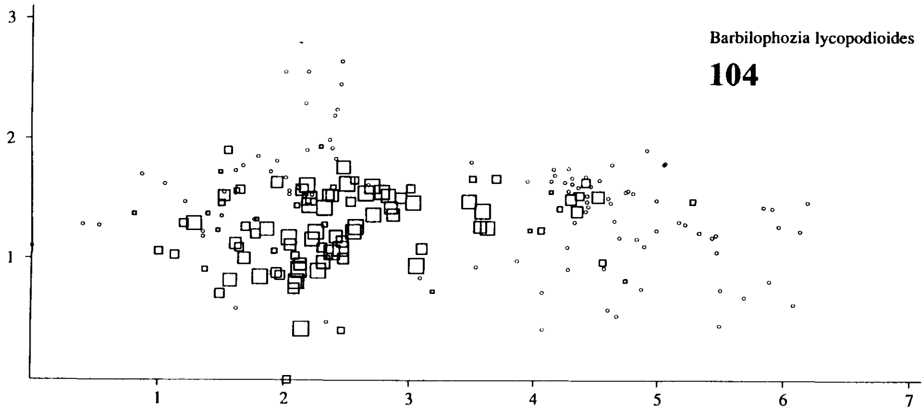


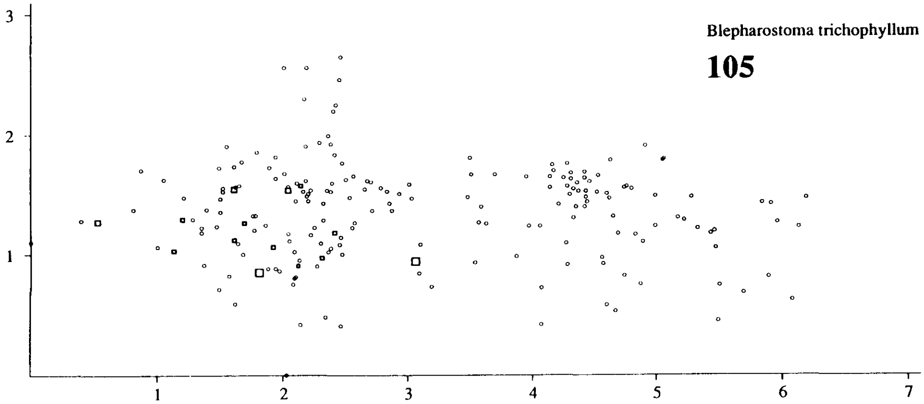


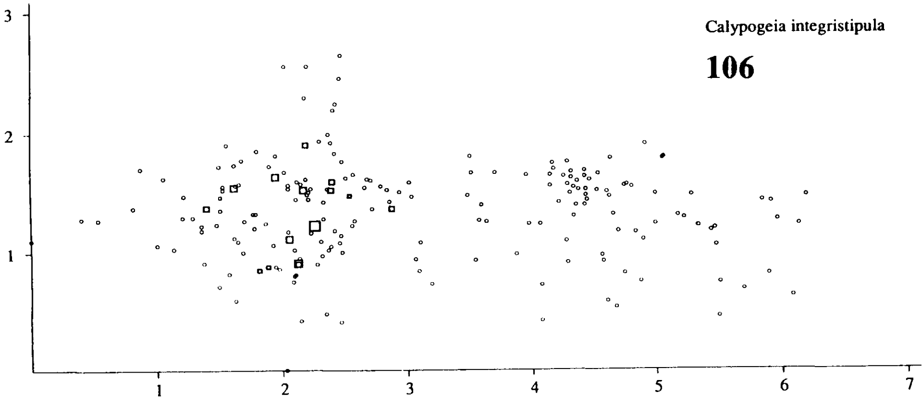
Figs 98-100. DCA of the ME 200 data set, axes 1 and 2. Frequency in subplots for each species in the meso sample plots plotted on to the meso sample plot positions. Scaling of axes in S.D. units. Small circle - absent. Square - present; area of square proportional to frequency in subplots. Fig. 98. *Sphagnum capillifolium*. Fig. 99. *Sphagnum girgensohnii*. Fig. 100. *Sphagnum quinquefarium*.



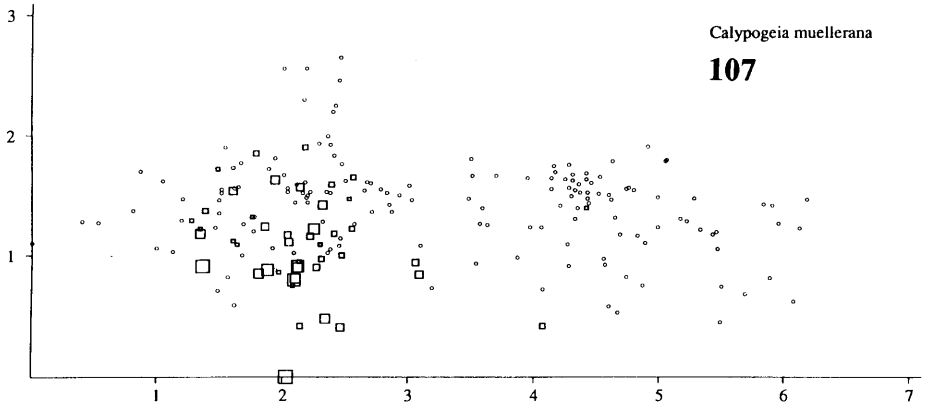
Figs 101-103. DCA of the ME 200 data set, axes 1 and 2. Frequency in subplots for each species in the meso sample plots plotted on to the meso sample plot positions. Scaling of axes in S.D. units. Small circle - absent. Square - present; area of square proportional to frequency in subplots. Fig. 101. *Barbilophozia attenuata*. Fig. 102. *Barbilophozia barbata*. Fig. 103. *Barbilophozia floerkei*.

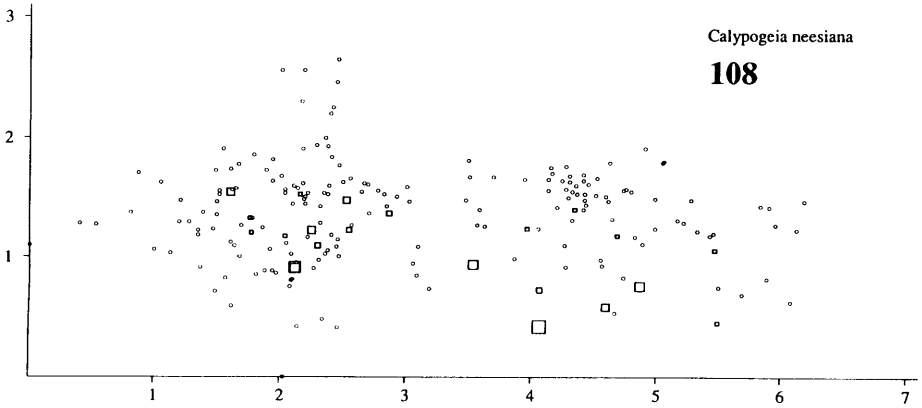


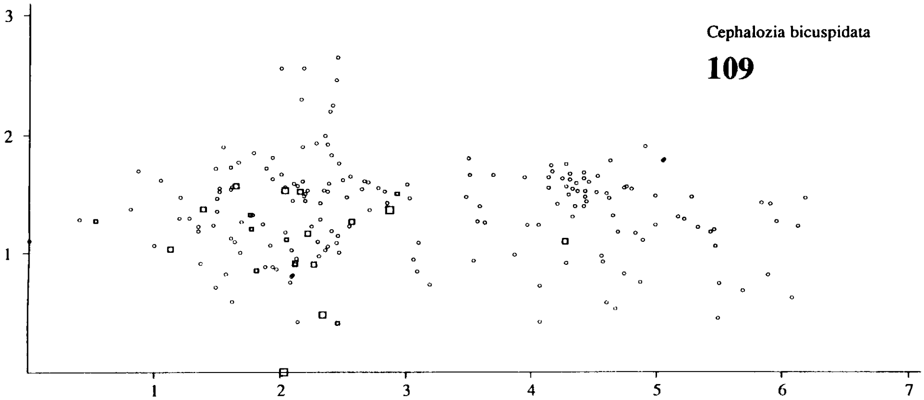




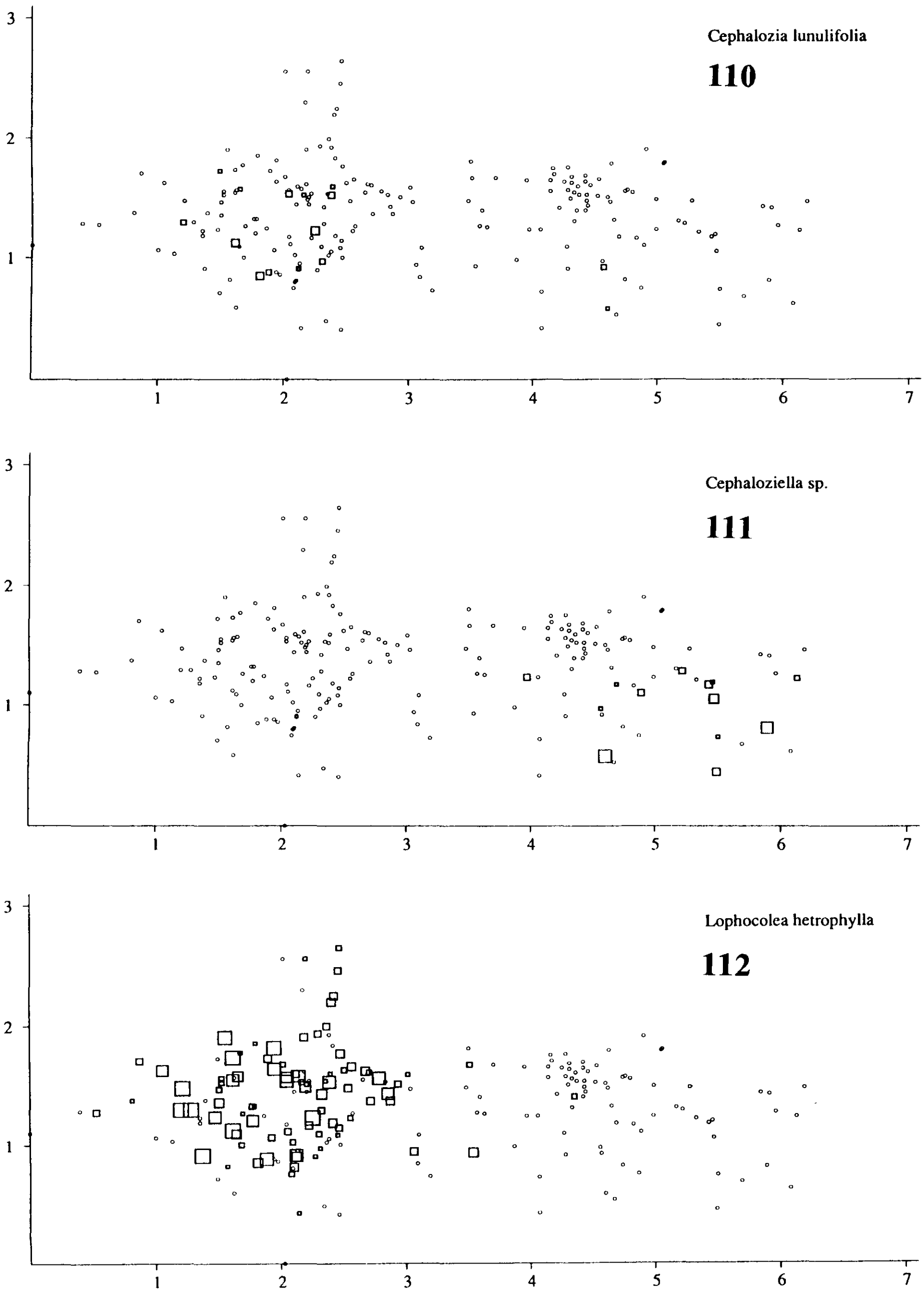
Figs 104-106. DCA of the ME 200 data set, axes 1 and 2. Frequency in subplots for each species in the meso sample plots plotted on to the meso sample plot positions. Scaling of axes in S.D. units. Small circle - absent. Square - present; area of square proportional to frequency in subplots. Fig. 104. *Barbilophozia lycopodioides*. Fig. 105. *Blepharostoma trichophyllum*. Fig. 106. *Calypogeia integristipula*.



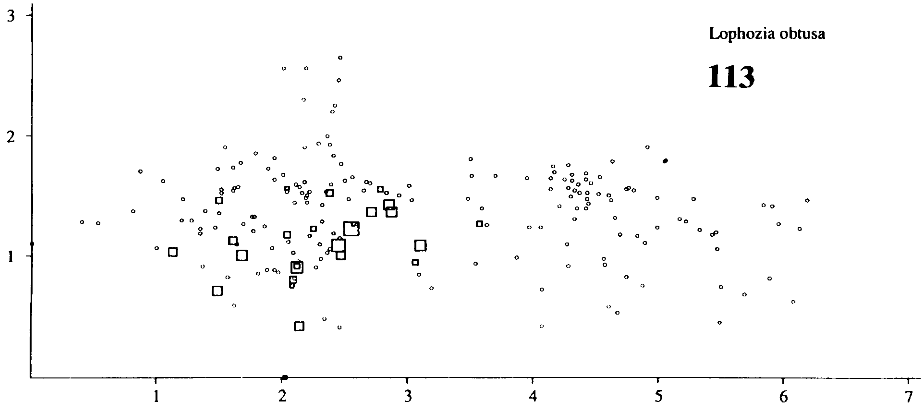


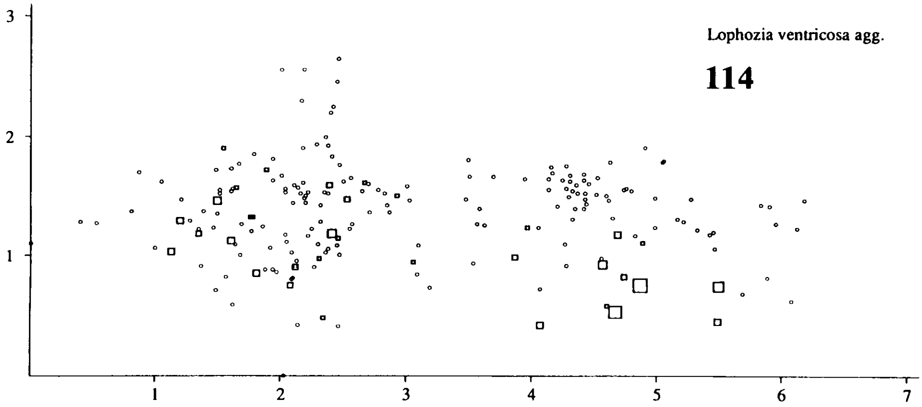


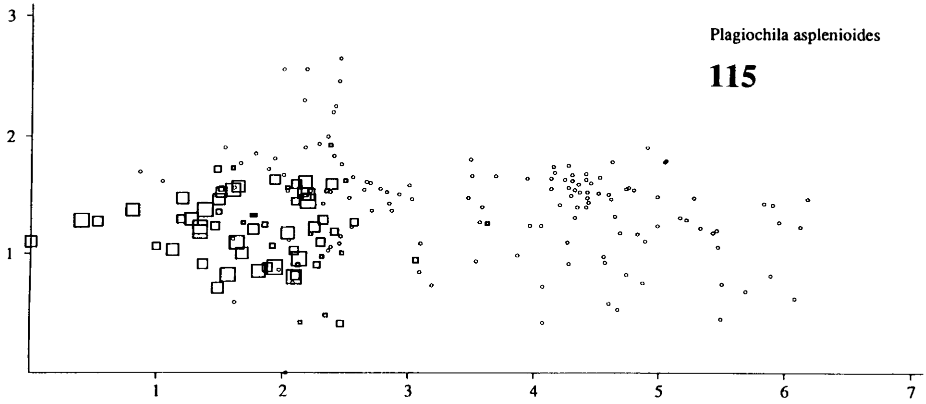
Figs 107-109. DCA of the ME 200 data set, axes 1 and 2. Frequency in subplots for each species in the meso sample plots plotted on to the meso sample plot positions. Scaling of axes in S.D. units. Small circle - absent. Square - present; area of square proportional to frequency in subplots. Fig. 107. *Calypogeia muellerana*. Fig. 108. *Calypogeia neesiana*. Fig. 109. *Cephalozia bicuspidata*.



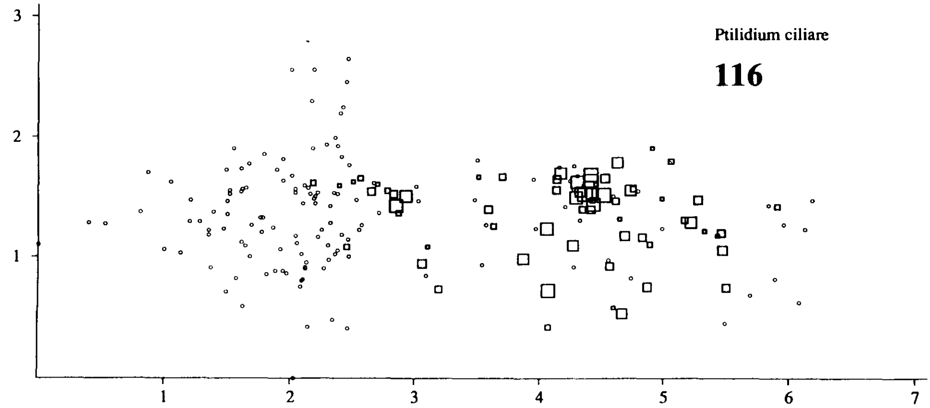
Figs 110-112. DCA of the ME 200 data set, axes 1 and 2. Frequency in subplots for each species in the meso sample plots plotted on to the meso sample plot positions. Scaling of axes in S.D. units. Small circle - absent. Square - present; area of square proportional to frequency in subplots. Fig. 110. *Cephalozia lunulifolia.* Fig. 111. *Cephaloziella* spp. Fig. 112. *Lophocolea heterophylla.*

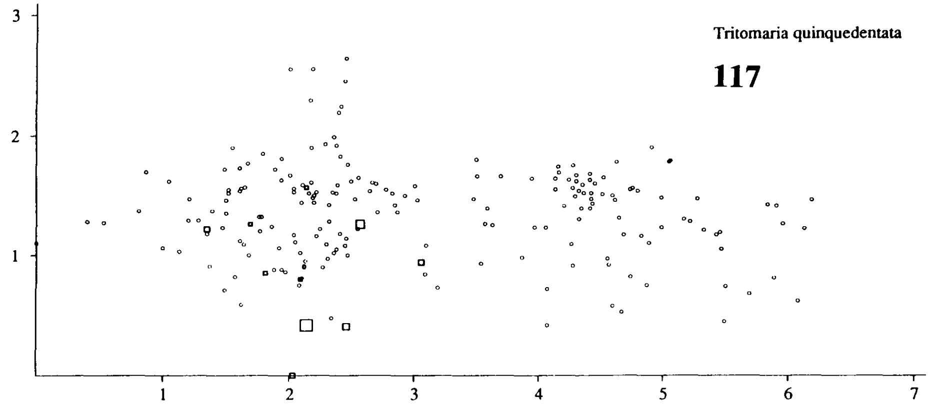


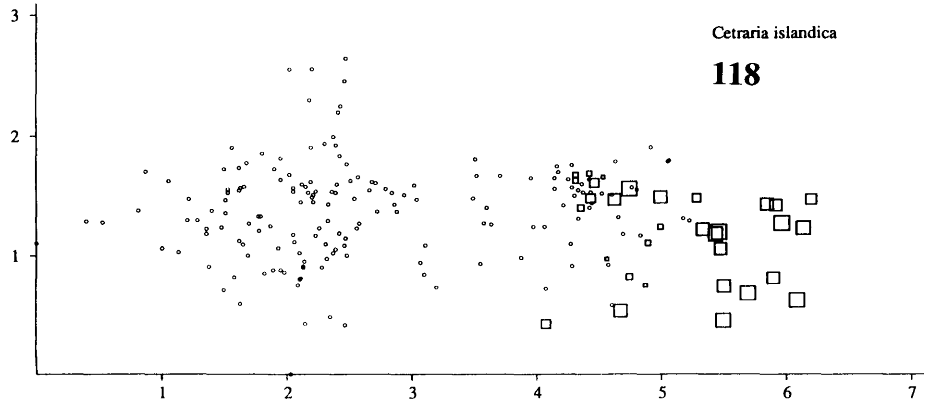




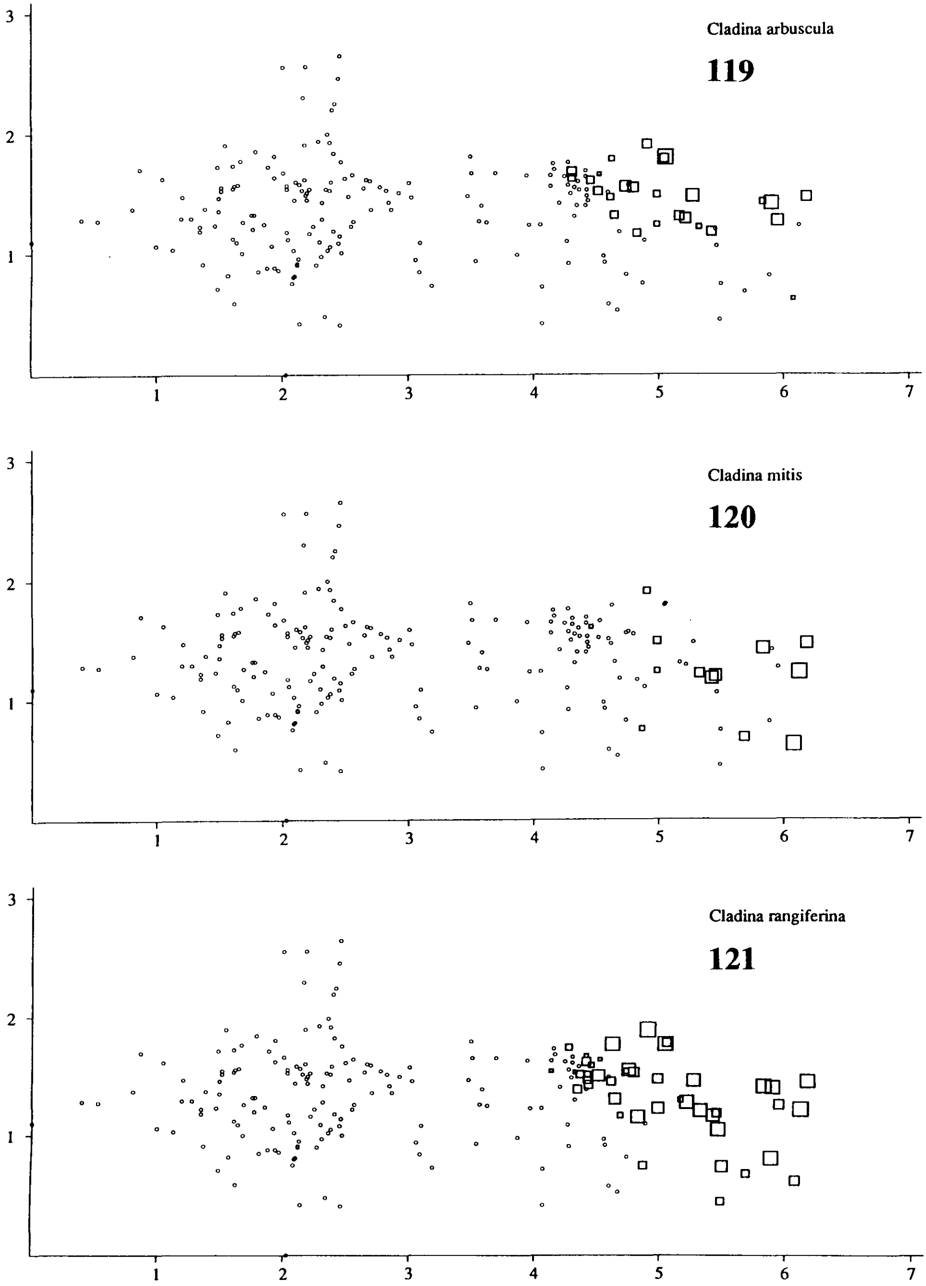
Figs 113-115. DCA of the ME 200 data set, axes 1 and 2. Frequency in subplots for each species in the meso sample plots plotted on to the meso sample plot positions. Scaling of axes in S.D. units. Small circle - absent. Square - present; area of square proportional to frequency in subplots. Fig. 113. *Lophozia obtusa*. Fig. 114. *Lophozia ventricosa* agg. Fig. 115. *Plagiochila asplenioides*.



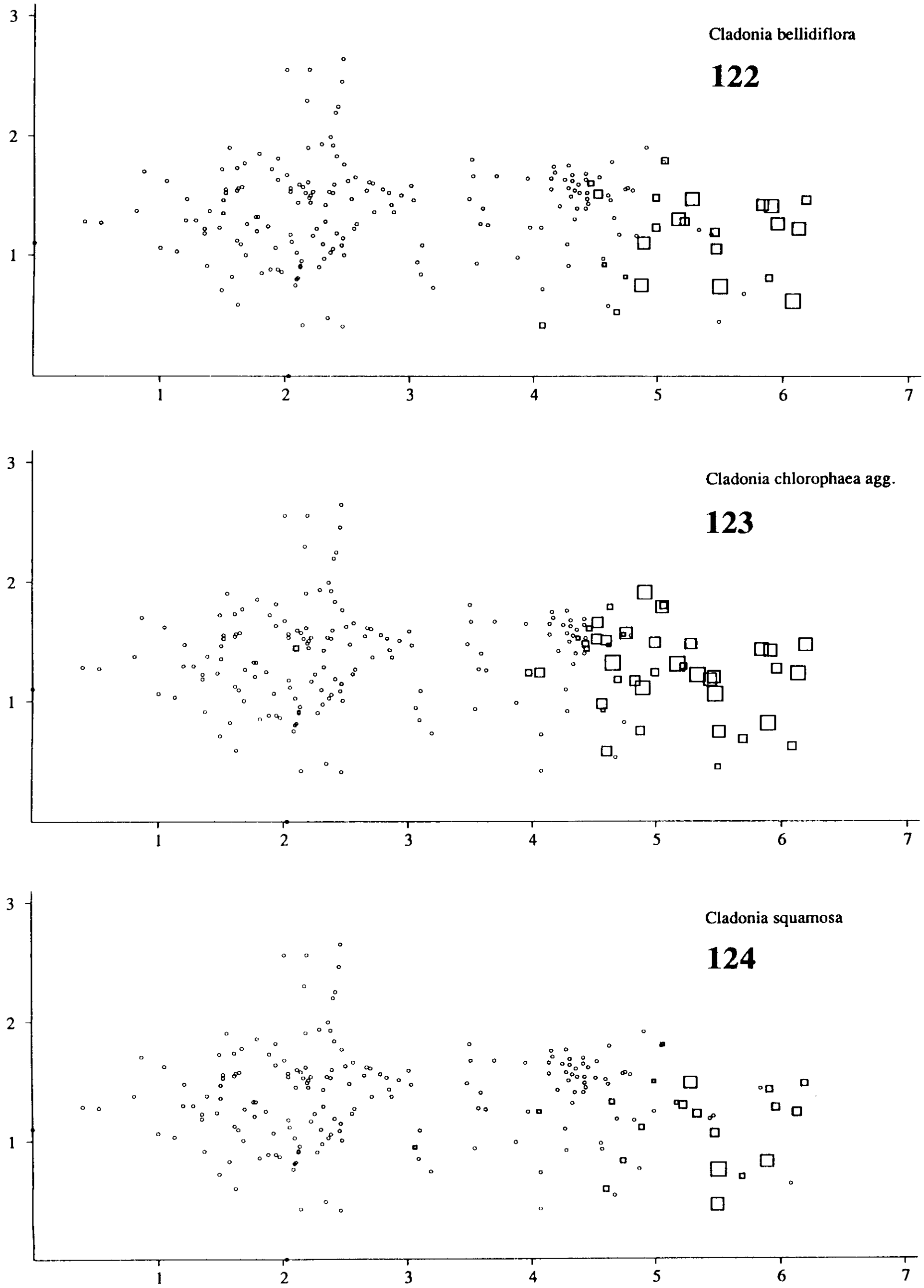




Figs 116-118. DCA of the ME 200 data set, axes 1 and 2. Frequency in subplots for each species in the meso sample plots plotted on to the meso sample plot positions. Scaling of axes in S.D. units. Small circle - absent. Square - present; area of square proportional to frequency in subplots. Fig. 116. *Ptilidium ciliare*. Fig. 117. *Tritomaria quinquedentata*. Fig. 118. *Cetraria islandica*.



Figs 119-121. DCA of the ME 200 data set, axes 1 and 2. Frequency in subplots for each species in the meso sample plots plotted on to the meso sample plot positions. Scaling of axes in S.D. units. Small circle - absent. Square - present; area of square proportional to frequency in subplots. Fig. 119. *Cladina arbuscula*. Fig. 120. *Cladina mitis*. Fig. 121. *Cladina rangiferina*.



Figs 122-124. DCA of the ME 200 data set, axes 1 and 2. Frequency in subplots for each species in the meso sample plots plotted on to the meso sample plot positions. Scaling of axes in S.D. units. Small circle - absent. Square - present; area of square proportional to frequency in subplots. Fig. 122. *Cladonia bellidiflora*. Fig. 123. *Cladonia chlorophaea* agg. Fig. 124. *Cladonia squamosa*.

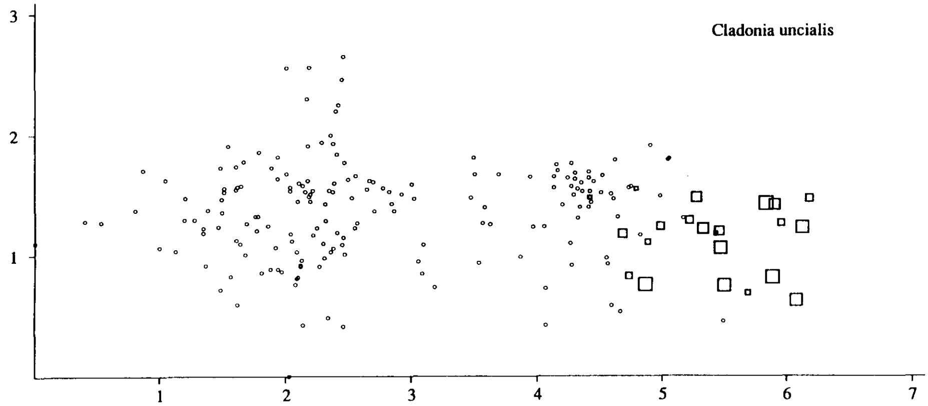


Fig. 125. DCA of the ME 200 data set, axes 1 and 2. Frequency in subplots for *Cladonia uncialis* in the meso sample plots plotted on to the meso sample plot positions. Scaling of axes in S.D. units. Small circle - absent. Square - present; area of square proportional to frequency in subplots.

occurred in plots with low DCA 2 scores. *Melampyrum pratense* (Fig. 61) and *Ptilidium aquilinum* (Fig. 64) preferred plots with high DCA 2 scores.

In the bottom layer, key species (constant and with generally high frequency in subplot and high cover) were few. Lichens (alternative dominants, *Cladina arbuscula* (Fig. 119), *C. rangiferina* (Fig. 121), *Cladonia chlorophaea agg.* (Fig. 123), and *C. uncialis* (Fig. 125), all constants, as well as *Cetraria islandica* (Fig. 118) and *Cladina mitis* (Fig. 120)), dominated at DCA 1 > ca. 4.5. Only three bryophytes appeared as constants: *Pleurozium schreberi* (Fig. 89) was constantly present (in almost all meso subplots) in the range 2.1-5.3 along DCA 1; DCA 2 > 0.8. *Dicranum majus* (Fig. 78) was constant and omnipresent in the range 1.4-3.0. The only constant hepatic, *Plagiochila asplenioides* (Fig. 115) had the optimum range 0.4-2.0. Several other bryophytes occurred as dominants, but did not reach constancy in 1 m^2 plots.

The bottom layer displayed several patterns of potential interest:

(1) Almost all of the species characterized as occasional within their range (frequency 1 in range) were hepatics.

(2) As compared to vascular plants with similar total frequency, species of the bottom layer tended to have lower constancy within their range. In addition to the main constants, there were many non-constant, alternative dominants at each point along the axes.

(3) Several important genera showed segregation of species along DCA axes, DCA 1 or DCA 2. Examples are: *Dicranum*; in order of increasing DCA 1 species scores, *D. majus*, (*D. fuscescens*), *D. scoparium*, *D. polysetum*, *D. drummondii* and *D. spurium*. *Plagiothecium*; no segregation along DCA 1, in order of increasing DCA 2 species scores: *P. undulatum*, *P. denticulatum* and *P. laetum* agg. *Rhytidiadelphus*; indistinct segregation along DCA 1, in order of increasing DCA 2 species scores: *R. loreus*, *R. subpinnatus* and *R. triquetrus*. *Sphagnum*; in order of increasing DCA 1 species scores: *S. girgensohnii*, *S. quinquefarium* and *S. capillifolium* (optimal ranges almost completely separated, cf. Tab. 14). *Barbilophozia*; segregating along both axes, in order of increasing DCA 1 (and decreasing DCA 2) species

scores: *B. barbata*, *B. lycopodioides*, *B. attenuata* and *B. floerkei*. *Calypogeia*, segregating along both axes: *C. muellerana* (and the rare *C. azurea*) low DCA 1 score, low DCA 2 score, *C. integristipula* low DCA 1 score, high DCA 2 score, *C. neesiana* relatively high DCA 1 score, low DCA 2 score, and the rare *C. sphagnicola* high DCA 1 score and low DCA 2 score. The lichen species show a lower degree of segregation.

ORDINATION OF THE MESO SAMPLE PLOTS: SUBSETS A AND B

Subsets A and B were ordinated separately to test whether the ordination of the ME 200 data had actually summarized the main coenoclines in each subset, considered separately. Correlation coefficients between corresponding axes of subset and ME 200 ordinations were 0.9707 and 0.9656 for DCA 1 of Subset A and B, respectively, and 0.6219 and 0.8772 for DCA 2. Clearly, the variation expressed along DCA 1 and DCA 2 in the ordination of ME 200 reappeared on the first two axes of the separate ordinations. Thus the ordination of the ME 200 data set was considered to summarize main gradient relationships of the subsets as well. Further interpretation of the subset ordinations was therefore not performed.

ORDINATION OF THE MESO SAMPLE PLOTS: SEPARATE LAYERS

Characteristics of the DCA ordination of the MEV 200 and MEB 200 data sets are given in Tab. 8. The ordinations of the field and bottom layers will be described and interpreted separately, with reference to the DCA ordination of the ME 200 data set. Axis n of the three ordinations are referred to as DCA n (full species composition), DCAV n (field layer) and DCAB n (bottom layer).

The field layer

The first axis was 5.34 S.D. units long (0.86 times the length of the corresponding axis, DCA 1, in the ordination of the full species composition), and had an eigenvalue of 0.63 (Tab. 8). The correlation between this axis and DCA 1 was 0.9613 (Tab. 15), and the environmental variables most strongly correlated with DCAV 1 and DCA 1 were the same (compare Tabs 8 and 15). Highest correlations were noted for MA Ter ($r = 0.7873$), MA S d ($r = -0.7060$), pH_{CaCl2} ($r = -0.6567$), and N ($r = 0.6520$). Most of the correlations were slightly lower for DCAV 1 than for DCA 1. Exceptions were N, the two pH variables, and LI. The lower end of the axis was defined by sample plots 153 and 53 (Fig. 126), the upper end by plots 63 and 179 (as with DCA 1). Compared to DCA 1 (Fig. 10), the separation of sample plots was better in the left half of the ordination diagram (site-types 5.2-6). The overall correspondence between the axes was very good from 0.0-4.0 S.D ($r = 0.9690$, $P < 0.0001$ in Subset A, see Tab. 16), thus the correlations between DCAV 1 and environmental variables in Subset A differed but slightly from those of DCA 1 (compare Tabs 11 and 17). The separation from

Tab. 15. Pearson's product-moment correlation coefficients between meso sample plot scores relative to axes of the separate DCA ordinations of layers (DCAV - vascular plants, DCAB - bryophytes and lichens), the axes of the DCA ordination (DCA n) of the full species composition, and the 33 environmental variables (r), with significance probabilities (P). Correlations significant at level $P < 0.0001$ in bold face. n.s. - significance probability less than 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 3.

Variable	DCAV 1		DCAV 2		DCAV 3		DCAV 4		DCAB 1		DCAB 2		DCAB 3		DCAB 4	
	r	P	r	P	r	P	r	P	r	P	r	P	r	P	r	P
DCA 1	**.9613**	**.0000**	.2554	.0003	.1487	.0356	**.4693**	**.0000**	**.9772**	**.0000**	-.1419	.0451	-.0572	n.s.	.1263	.0747
DCA 2	-.0131	n.s.	**-.3033**	**.0000**	**-.3866**	**.0000**	.1479	.0366	-.0980	n.s.	**.8069**	**.0000**	.1830	.0095	.2069	.0033
DCA 3	-.0907	n.s.	-.0785	n.s.	.1457	.0395	**-.4446**	**.0000**	-.1446	.0411	.1730	.0143	**.4365**	**.0000**	**-.3871**	**.0000**
DCA 4	.2155	.0022	**-.3121**	**.0000**	.2214	.0016	**.3739**	**.0000**	.0957	.n.s.	-.1099	n.s.	.1154	n.s.	.0153	n.s.
01 MA Slo	**-.5554**	**.0000**	-.0676	n.s.	-.0412	n.s.	**-.4486**	**.0000**	**-.5959**	**.0000**	-.0693	n.s.	.0784	n.s.	-.1708	.0156
02 MA Asf	-.1297	.0672	-.1433	.0430	.2539	.0003	-.1738	.0138	-.2195	.0018	-.0741	n.s.	.0125	n.s.	-.1925	.0063
03 MA Ter	**.7873**	**.0000**	.0902	n.s.	.0528	n.s.	.2530	.0003	**.7835**	**.0000**	.0066	n.s.	.0076	n.s.	.1567	.0267
04 MA Une	**-.3346**	**.0000**	-.0322	n.s.	-.1407	.0469	-.2762	.0001	**-.3012**	**.0000**	-.0098	n.s.	-.0469	n.s.	-.1339	.0587
05 MA S d	**-.7060**	**.0000**	-.1345	.0575	-.1243	.0794	-.1542	.0293	**-.7285**	**.0000**	.2144	.0023	.1765	.0124	.0231	n.s.
06 MA Rel	**-.3730**	**.0000**	-.2418	.0006	-.1669	.0181	-.2787	.0001	**-.3826**	**.0000**	**.2971**	**.0000**	.1535	.0300	.0972	n.s.
07 MA Can	**-.3379**	**.0000**	-.2416	.0006	-.1917	.0065	-.1201	.0903	**-.3891**	**.0000**	**.4311**	**.0000**	.2723	.0001	.0579	n.s.
08 ME Slo	**-.4003**	**.0000**	-.0954	n.s.	.0140	n.s.	**-.2922**	**.0000**	**-.4055**	**.0000**	-.0841	n.s.	.1628	.0213	-.1897	.0071
09 ME Asf	-.1539	.0296	-.0171	n.s.	.0798	n.s.	-.1321	.0623	-.1950	.0057	-.0624	n.s.	.0276	n.s.	.2698	.0001
10 ME Une	-.2105	.0028	-.2122	.0026	.0900	n.s.	-.1935	.0060	**-.3034**	**.0000**	.0822	n.s.	-.0615	n.s.	-.0450	n.s.
11 ME Con	-.0862	n.s.	.1302	.0661	-.1210	.0878	-.0829	n.s.	-.0613	n.s.	.0166	n.s.	.0166	n.s.	.0080	n.s.
12 ME Smi	-.0736	n.s.	**-.3073**	**.0000**	.1564	.0270	.1629	.0212	-.1818	.0100	.2387	.0007	.0013	n.s.	.0734	n.s.
13 ME Sme	-.2470	.0004	**-.3572**	**.0000**	.0877	n.s.	.0820	n.s.	**.3771**	**.0000**	**.3146**	**.0000**	.0360	n.s.	.1377	.0518
14 ME Sma	**-.3529**	**.0000**	**-.3458**	**.0000**	.0198	n.s.	.0816	n.s.	**-.4435**	**.0000**	**.2965**	**.0000**	.0927	n.s.	.1264	.0745
15 ME Lit	**-.3205**	**.0000**	-.2086	.0030	-.1708	.0156	-.1994	.0046	**-.3752**	**.0000**	**.3441**	**.0000**	.2237	.0014	.0421	n.s.
16 ME Rel	**-.4981**	**.0000**	-.1744	.0135	-.2096	.0029	**-.3400**	**.0000**	**-.5027**	**.0000**	.2488	.0004	.0823	n.s.	.0433	n.s.
17 Mois	-.1551	.0283	.2294	.0011	.1224	.0843	.0538	n.s.	-.0069	n.s.	**-.5366**	**.0000**	-.0157	n.s.	-.1286	.0696
18 LI	**.5917**	**.0000**	-.1929	.0062	**.4206**	**.0000**	**.3577**	**.0000**	**.4271**	**.0000**	.0542	n.s.	.0519	n.s.	.1024	n.s.
19 pH_{H_2O}	**-.5916**	**.0000**	-.0001	n.s.	-.2777	.0001	-.1465	.0384	**-.5015**	**.0000**	-.2630	.0002	-.0347	n.s.	-.1660	.0188
20 pH_{CaCl_2}	**-.6567**	**.0000**	-.0328	n.s.	**-.3198**	**.0000**	-.1912	.0067	**-.5871**	**.0000**	-.1186	.0945	-.0099	n.s.	-.1310	.0645
21 Ca	**-.3903**	**.0000**	-.1684	.0172	**-.3008**	**.0000**	-.2503	.0003	**-.4235**	**.0000**	.2574	.0002	.0875	n.s.	-.1113	n.s.
22 Mg	**-.2857**	**.0000**	-.1675	.0177	-.2388	.0007	-.2002	.0045	**-.3485**	**.0000**	.2636	.0002	.0722	n.s.	-.0572	n.s.
23 Na	-.1580	.0255	-.0608	n.s.	-.1728	.0144	-.0748	n.s.	-.1778	.0118	-.0032	n.s.	.1160	n.s.	-.0704	n.s.
24 K	**-.3588**	**.0000**	-.1478	.0367	-.2184	.0019	**-.2881**	**.0000**	**-.4141**	**.0000**	.1624	.0216	.0259	n.s.	-.1381	.0512
25 H	**.3568**	**.0000**	.1207	.0886	.2486	.0004	.2247	.0014	**.3981**	**.0000**	-.2685	.0001	.0395	n.s.	.1013	n.s.
26 N	**-.6520**	**.0000**	.1645	.0199	**-.3781**	**.0000**	**-.2962**	**.0000**	**-.4976**	**.0000**	-.0749	n.s.	.1019	n.s.	-.0527	n.s.
27 P-AL	-.2384	.0007	-.0441	n.s.	-.1439	.0420	-.2117	.0026	**-.2896**	**.0000**	.2726	.0001	.1033	n.s.	.0333	n.s.
28 Al	-.1179	.0964	.2108	.0027	-.0112	n.s.	-.1062	n.s.	.0169	n.s.	**-.4277**	**.0000**	-.2292	.0011	-.1515	.0322
29 Fe	**.4039**	**.0593**	.1402	.0476	.0876	.2173	-.0773	n.s.	.1188	.0937	-.2763	.0001	-.1296	.0673	-.0909	n.s.
30 Mn	**-.4345**	**.0000**	-.0283	n.s.	**-.3519**	**.0000**	**-.3952**	**.0000**	**-.4177**	**.0000**	.1094	n.s.	-.1060	n.s.	-.1742	.0136
31 Zn	-.1046	n.s.	.0500	n.s.	-.1714	.0152	-.2043	.0037	-.1036	n.s.	.1281	.0708	-.1878	.0078	-.0916	n.s.
32 P	-.0016	n.s.	-.0414	n.s.	.0053	n.s.	-.2212	.0016	-.0686	n.s.	.2082	.0031	-.0836	n.s.	-.0394	n.s.
33 S	-.2422	.0006	.0225	n.s.	-.2341	.0008	**-.2895**	**.0000**	-.2044	.0037	.0265	n.s.	.1770	.0122	-.1666	.0184

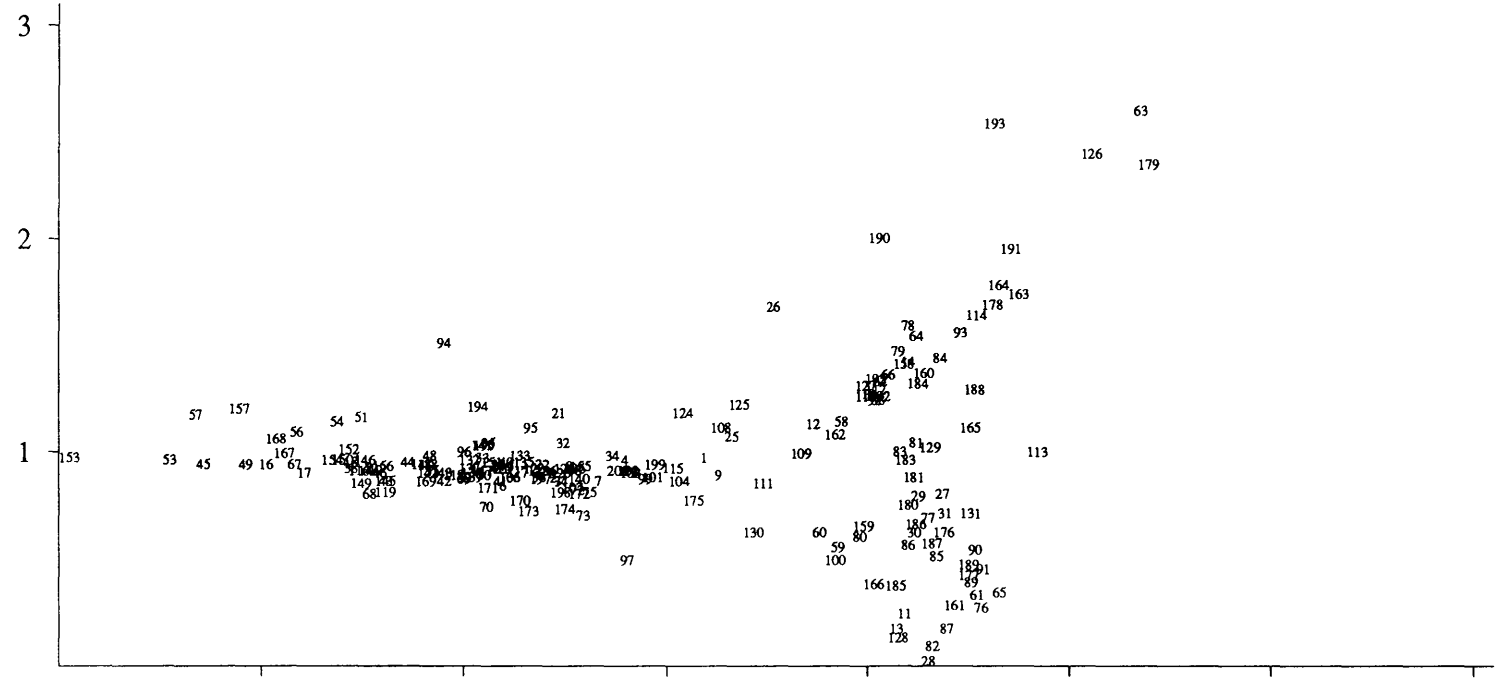


Fig. 126. DCA ordination of the MEV 200 data set (vascular plants only), axes 1 and 2. Meso sample plot numbers plotted onto the sample plot positions. Axes scaled in S.D. units.

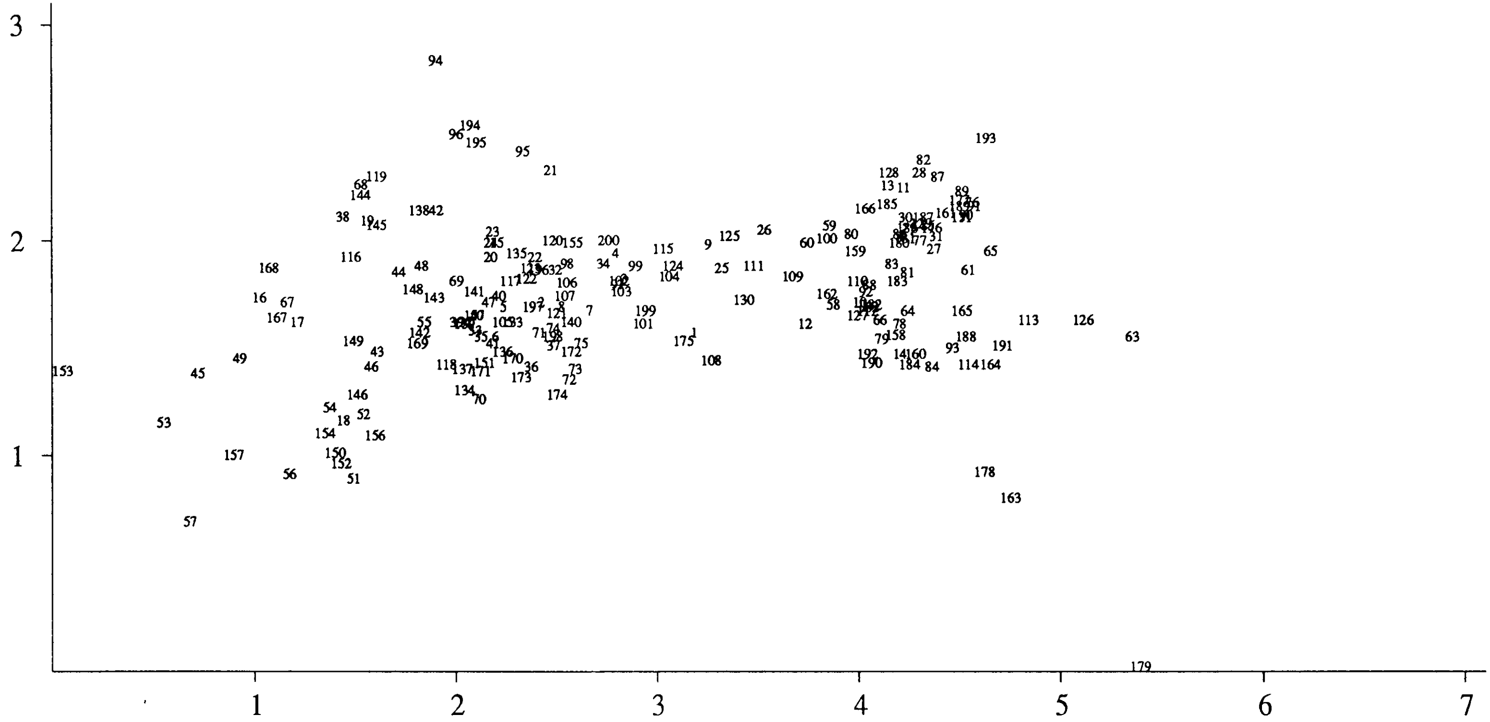


Fig. 127. DCA ordination of the MEV 200 data set (vascular plants only), axes 1 and 3. Meso sample plot numbers plotted onto the sample plot positions. Axes scaled in S.D. units.

Tab. 16. Pearson's product-moment correlation coefficients between meso sample plot scores relative to axes of the separate DCA ordinations of layers (DCAV - vascular plants, DCAB - bryophytes and lichens), and the axes of the DCA ordination (DCA n) of the full species composition (r), with significance probabilities (P). Correlations are given for all sample plots (Subsets A+B; n = 200), for plots with DCA 1 < 3.3 (Subset A; n = 121) and for sample plots with DCA 1 > 3.3 (Subset B; n = 79). Correlations significant at level P < 0.0001 in bold face. n.s. - significance probability less than 0.1.

Subset	A+B		A		B	
	r	P	r	P	r	P
DCA 1 - DCAV 1	**.9613**	**.0000**	**.9690**	**.0000**	**.5610**	**.0000**
DCA 1 - DCAB 1	**.9772**	**.0000**	**.8439**	**.0000**	**.9670**	**.0000**
DCA 2 - DCAB 2	**.8069**	**.0000**	**.8105**	**.0000**	**.8239**	**.0000**
DCAV 1 - DCAB 1	**.9026**	**.0000**	**.7403**	**.0000**	.4087	.0002

4.0-5.3 S.D. along DCAV 1 was considerably lower than along DCA 1, and the correspondence between sample plot positions was also lower (r = 0.5610, P < 0.0001; cf. Tab. 16). The correlations between DCAV 1 and environmental variables in Subset B were generally low; none was significant at the P < 0.0001 level. Highest correlations were noted for MA Slo (r = -0.3356, P = 0.0025) and MA Ter (r = 0.3346, P = 0.0026). Among the other variables correlated with DCA 1 at the P < 0.0001 level; ME Une, ME Sma, LI and N were not significantly correlated with DCAV 1, while the correlations of DCAV 1 with ME Smi, ME Sme and MA Ter were significant at 0.002 < P < 0.1. The low correlation coefficients between DCAV 1 and environmental variables in Subset B might be due to the low number of vascular plants in many Subset B sample plots (cf. pp. 81-89; Fig. 38).

The second axis (2.57 S.D. units, eigenvalue 0.22), showed almost no separation of sample plots for 0 < DCAV 1 < 3.3, while the sample plots spread like a fan from DCAV 1 = 3.3 to the right end of Fig. 126. The extremes of DCA 2 were defined by sample plots 28 and 87 (lower end) and 193, 126, 63 and 179 (upper end). DCAV 2 did not correspond to any of the DCA axes (Tab. 15). The only environmental variables correlated with DCA 2 at significance level P < 0.0001 were the group of soil depth variables, the highest correlation coefficient shown by ME Sme (r = -0.3572). This indicated a separation of sample plots at high DCA(V) 1 values in response to soil depth, higher soil depths at low DCAV 2 positions.

The third axis (2.82 S.D. units, eigenvalue 0.14), showed the strongest separation of sample plots for 0.5 < DCAV 1 < 2.6. The lowest positions were obtained by sample plots 57, 56, and 74, the highest by plots 94 and 21 (Fig. 127). Thus this axis separated the plots of the northeast-facing, rather cool slopes of Transects 1 and 8 (with high importance of suboceanic species) from the drier slopes, often with a more thermophilous vegetation. This is clearly shown by the species ordination; the lowest species scores were obtained by *Lathyrus montanus*, *Acer platanoides*, *Melampyrum sylvaticum*, and *Carex digitata*, the highest by *Molinia caerulea*, *Listera cordata*, *Cornus suecica* and *Blechnum spicant*. DCAV 3 was

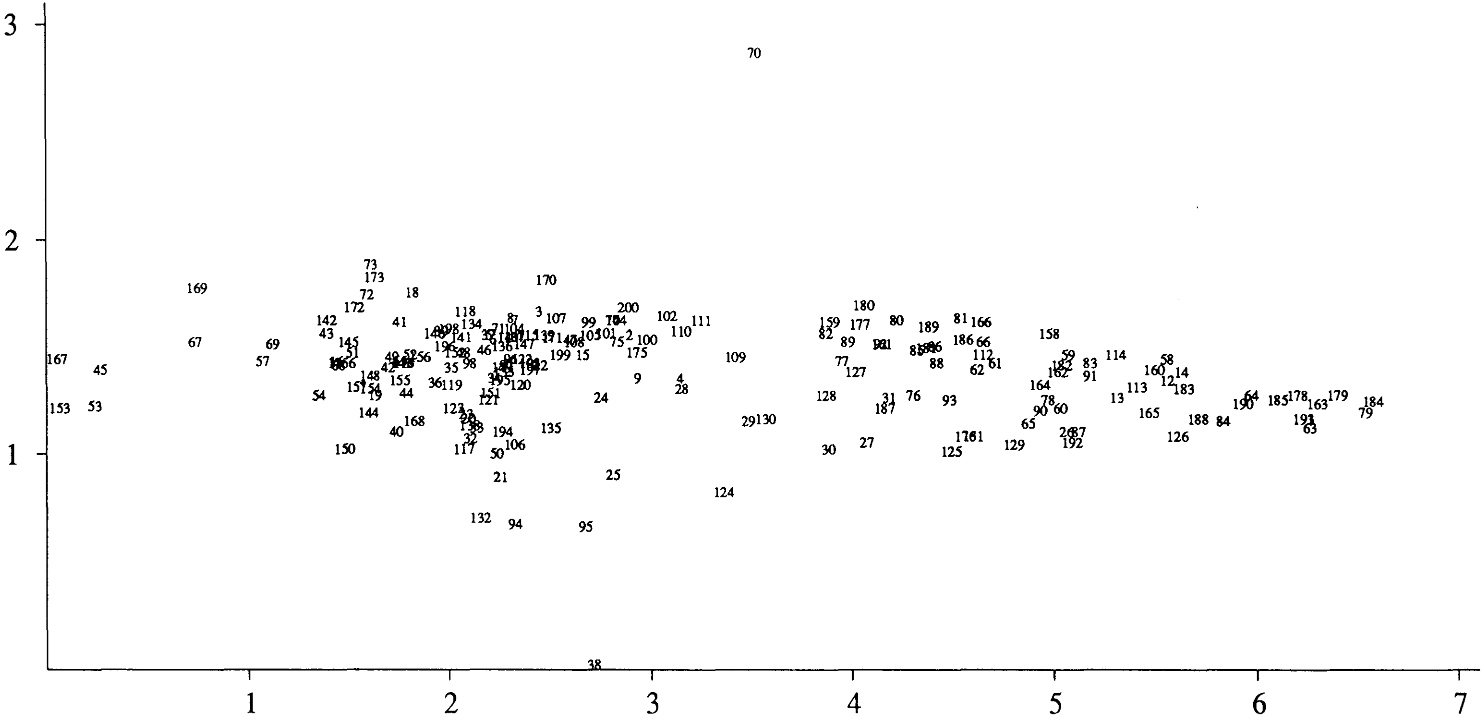


Fig. 128. DCA ordination of the MEB 200 data set (cryptogams only), axes 1 and 2. Meso sample plot numbers plotted onto the sample plot positions. Axes scaled in S.D. units.

significantly correlated with DCA 2, but the correlation coefficient was relatively low (r = -0.3866). Environmental variables most strongly correlated with DCAV 3 were LI (r = 0.4206), N (r = -0.3781), and Mn (r = 0.3519), all among variables with high correlations with DCAV 1.

The fourth axis was correlated with DCA 1, DCA 3, and DCA 4, and with many of the same environmental variables as were DCAV 3. This axis was not considered interpretable.

The bottom layer

The first axis in the ordination of the bottom layer had a gradient length of 6.53 S.D. units and an eigenvalue of 0.78 (Tab. 8). The lowest positions were obtained by sample plots 167, 153, 53, 45, 67 and 169 (with 1.0 < DCA 1 < 2.0), the highest positions by plots 184, 79 and 179. The main features of separation of sample plots along the axis (cf. Fig. 128) did not differ markedly from DCA 1, although the two main clusters of sample plots along DCA 1 (site-types 5.1-5.3 to the left and site-types 2-3 to the right) were stretched along DCAB 1. DCAB 1 was correlated with DCA 1 with r = 0.9772; sightly lower correlations were found for Subset A than for Subset B (Tab. 16). MA Ter and MA S d were the most strongly correlated environmental variables. No other variable showed r > 0.6. Correlations between DCAB 1 and environmental variables for Subset A were lower than the corresponding correlations with DCA 1 (Tab. 17), but all correlations with DCA 1 significant at P < 0.0001 maintained this significance level also with DCAB 1. This was also true for Subset B; correlations between environmental variables and DCAB 1 differed but slightly from those with DCA 1 (Tab. 17). The slightly higher correlations of moisture and Al with DCAB 1 than with DCA 1 in Subset B was probably due to the expression of some of the vegetational variability expressed along DCA 2 along DCAB 1. This gained support from the correlation between DCA 2 and DCAB 1 sample scores for Subset B, being r = -0.2325, P = 0.0392.

The second axis had a gradient length of 2.85 and an eigenvalue of 0.29. Two sample plots, strongly separated from the rest (plot 38 at DCAB 2 = 0, plot 70 at the opposite end), defined the axis end-points. Both of these were extremely poor in species. The rest of the sample plots were placed within an interval of 1.2 S.D. units along DCAB 2. The correlation with DCA 2 was high; r = 0.8069, and the correspondence between DCAB 2 and DCA 2 was maintained for both subsets. The environmental variables most strongly correlated with DCAB 2 were Mois (r = -0.5366), MA Can (r = 0.4311) and Al (r = -0.4277), as with DCA 2.

The third axis (gradient length 3.54 S.D., eigenvalue 0.23) was correlated with DCA 3 (r = 0.4365), but did not show any correlations with environmental variables significant at P < 0.0001.

The fourth axis (2.45 S.D. units, eigenvalue 0.17) was also correlated with DCA 3, and had no correlation with environmental variables significant at P < 0.0001.

The first axes of the ordinations of vascular plants and cryptograms separately, were strongly correlated (r = 0.9026, P < 0.0001, cf. Tab. 16). The correspondence was good in Subset A (r = 0.7403, P < 0.0001), moderate in Subset B (r = 0.4087, P = 0.0002).

Tab. 17. Pearson's product-moment correlation coefficients between meso sample plot scores relative to the first axis of the separate DCA ordinations of layers (DCAV - vascular plants, DCAB - bryophytes and lichens) and the 33 environmental variables (r), with significance probabilities (P). Correlations are given for all sample plots (Subsets A+B; n = 200), for plots with DCA 1 < 3.3 (Subset A; n = 121) and for sample plots with DCA 1 > 3.3 (Subset B; n = 79). Correlations significant at level P < 0.0001 in bold face. n.s. - significance probability less than 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 3.

Variable	DCAV 1						DCAB 1					
Subset	A+B		A		B		A+B		A		B	
	r	P	r	P	r	P	r	P	r	P	r	P
01 MA Slo	**-.5554**	**.0000**	.0369	n.s.	-.3356	.0025	**-.5959**	**.0000**	-.0450	n.s.	-.3724	.0007
02 MA Asf	-.1297	.0672	-.0717	n.s.	-.0650	n.s.	-.2195	.0018	-.1004	n.s.	-.3717	.0007
03 MA Ter	**.7873**	**.0000**	.3348	.0002	.3346	.0026	**.7835**	**.0000**	.2449	.0068	**.4847**	**.0000**
04 MA Une	**-.3346**	**.0000**	-.1064	n.s.	-.0925	n.s.	**-.3012**	**.0000**	-.0448	n.s.	-.0315	n.s.
05 MA S d	**-.7060**	**.0000**	-.2323	.0104	-.1845	n.s.	**-.7285**	**.0000**	-.2993	.0009	-.4344	.0001
06 MA Bas	**-.3730**	**.0000**	-.1426	n.s.	-.2161	.0557	**-.3826**	**.0000**	-.0746	n.s.	-.3628	.0010
07 MA Can	**-.3379**	**.0000**	.0635	n.s.	-.2260	.0452	**-.3891**	**.0000**	-.0166	n.s.	-.3237	.0036
08 ME Slo	**-.4003**	**.0000**	.0327	n.s.	-.2493	.0267	**-.4055**	**.0000**	.0429	n.s.	-.2005	.0765
09 ME Asf	-.1539	.0296	.0107	n.s.	-.1327	n.s.	-.1950	.0057	-.0605	n.s.	-.1331	n.s.
10 ME Une	-.2105	.0028	.1023	n.s.	-.2288	.0425	**-.3034**	**.0000**	.0399	n.s.	**-.4544**	**.0000**
11 ME Con	-.0862	n.s.	.0038	n.s.	-.1395	n.s.	-.0613	n.s.	-.0100	n.s.	.0372	n.s.
12 ME Smi	-.0736	n.s.	-.0313	n.s.	-.2014	.0751	-.1818	.0100	.0037	n.s.	**-.6229**	**.0000**
13 ME Sme	-.2470	.0004	-.0713	n.s.	-.2115	.0613	**.3771**	**.0000**	-.1299	n.s.	**-.6184**	**.0000**
14 ME Sma	**-.3529**	**.0000**	-.1667	.0676	-.1005	n.s.	**-.4435**	**.0000**	-.1521	.0958	**-.5474**	**.0000**
15 ME Lit	**-.3205**	**.0000**	-.0047	n.s.	-.1258	n.s.	**-.3752**	**.0000**	-.1090	n.s.	-.2833	.0114
16 ME Bas	**-.4981**	**.0000**	-.1216	n.s.	-.1727	n.s.	**-.5027**	**.0000**	-.1218	n.s.	-.2352	.0369
17 Mois	-.1551	.0283	-.2814	.0018	.0607	n.s.	-.0069	n.s.	-.1117	n.s.	.4002	.0003
18 LI	**.5917**	**.0000**	**.6699**	**.0000**	.0607	n.s.	**.4271**	**.0000**	**.5384**	**.0000**	**-.6349**	**.0000**
19 pH_{H2O}	**-.5916**	**.0000**	**-.6482**	**.0000**	-.0627	n.s.	**-.5015**	**.0000**	**-.5215**	**.0000**	-.0676	n.s.
20 pH_{CaCl2}	**-.6567**	**.0000**	**-.6785**	**.0000**	-.1307	n.s.	**-.5871**	**.0000**	**-.5898**	**.0000**	-.2427	.0312
21 Ca	**-.3903**	**.0000**	-.2947	.0010	-.2117	.0611	**-.4235**	**.0000**	**-.3672**	**.0000**	-.3052	.0062
22 Mg	**-.2857**	**.0000**	-.1859	.0412	-.1505	n.s.	**-.3485**	**.0000**	-.2762	.0022	-.3182	.0043
23 Na	-.1580	.0255	-.2368	.0089	-.1574	n.s.	-.1778	.0118	-.2358	.0092	-.2116	.0613
24 K	**-.3588**	**.0000**	-.0750	n.s.	-.1864	.0999	**-.4141**	**.0000**	-.1126	n.s.	-.3330	.0027
25 H	**.3568**	**.0000**	.2528	.0052	.2189	.0526	**.3981**	**.0000**	**.4080**	**.0000**	.3131	.0050
26 N	**-.6520**	**.0000**	**-.6902**	**.0000**	.1373	n.s.	**-.4976**	**.0000**	**-.5597**	**.0000**	**.5024**	**.0000**
27 P-AL	-.2384	.0007	-.0519	n.s.	-.2145	.0577	**-.2896**	**.0000**	-.2017	.0265	-.2152	.0568
28 Al	-.1179	.0964	-.1761	.0534	.0067	n.s.	.0169	n.s.	.0088	n.s.	.3679	.0009
29 Fe	**.4039**	**.0593**	.1390	n.s.	.0486	n.s.	.1188	.0937	.2206	.0265	-.2152	.0568
30 Mn	**-.4345**	**.0000**	-.2967	.0010	-.2304	.0411	**-.4177**	**.0000**	-.2526	.0052	-.3128	.0050
31 Zn	-.1046	n.s.	.0587	n.s.	-.1856	n.s.	-.1036	n.s.	.0401	n.s.	-.0580	n.s.
32 P	-.0016	n.s.	**.3799**	**.0000**	-.2634	.0190	-.0686	n.s.	.3090	.0006	-.2416	.0320
33 S	-.2422	.0006	-.1039	n.s.	-.2212	.0501	-.2044	.0037	-.0017	n.s.	-.1240	n.s.

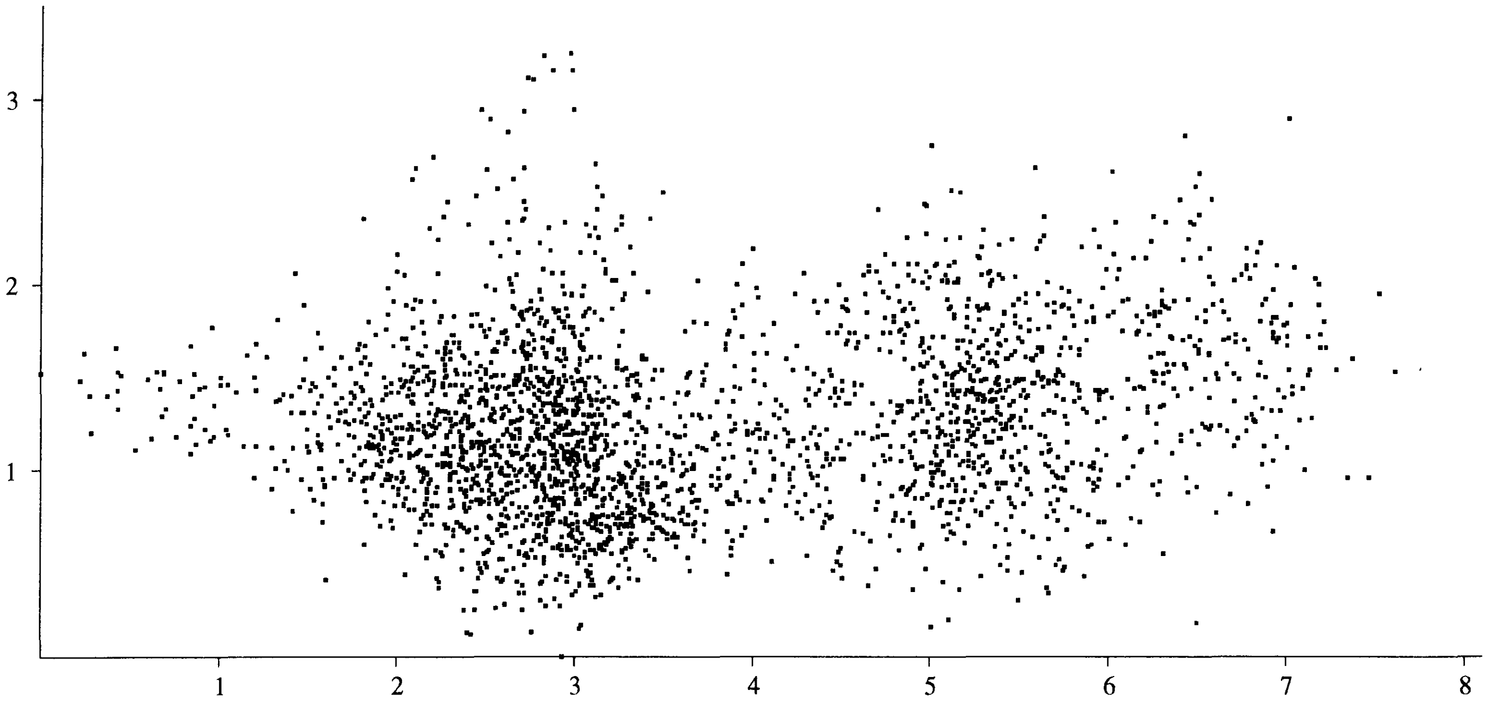


Fig. 129. DCA ordination of the MES 3200 data set (meso subplots), axes 1 and 2. Axes scaled in S.D. units.

Tab. 18. Pearson's product-moment correlation coefficients between mean scores for meso sample plots relative to axes of the DCA ordination of 3198 meso subplots (DCAS) and the axes of the DCA ordination of 400 micro sample plots (DCAM), and the DCA ordination (DCA n) of the full species composition, and the 33 environmental variables (r), with significance probabilities (P). Correlations significant at level P < 0.0001 in bold face. n.s. - significance probability less than 0.1. Numbers and abbreviations for names of environmental variables in accordance with Tab. 3.

Variable	DCAS 1		DCAS 2		DCAS 3		DCAS 4		DCAM 1		DCAM 2		DCAM 3		DCAM 4	
	r	P	r	P	r	P	r	P	r	P	r	P	r	P	r	P
DCA 1	**.9993**	**.0000**	-.2139	.0024	.2489	.0004	-.2294	.0011	**.9784**	**.0000**	-.0838	n.s.	**.6444**	**.0000**	-.0636	n.s.
DCA 2	.2139	.0024	**-.8624**	**.0000**	-.0038	n.s.	-.2126	.0025	-.0509	n.s.	.1689	.0168	.2239	.0014	**.4888**	**.0000**
DCA 3	-.1085	n.s.	.0038	n.s.	**-.5745**	**.0000**	**.5723**	**.0000**	-.1450	.0405	-.0264	n.s.	**-.4702**	**.0000**	**.2432**	**.0000**
DCA 4	.1141	n.s.	-.2126	.0025	**.7735**	**.0000**	**.4223**	**.0000**	.1334	.0597	**-.4691**	**.0000**	.2288	.0011	-.0755	n.s.
01 MA Slo	**-.5739**	**.0000**	.0059	n.s.	**-.4485**	**.0000**	-.0916	n.s.	**-.5758**	**.0000**	.0817	n.s.	**-.6219**	**.0000**	-.0652	n.s.
02 MA Asf	-.1856	.0085	-.1054	n.s.	-.2514	.0003	.0935	n.s.	-.2013	.0043	-.0177	n.s.	**-.3282**	**.0000**	-.1282	.0703
03 MA Ter	**.8019**	**.0000**	-.0540	n.s.	.1695	.0164	-.1096	n.s.	**.7920**	**.0000**	.0212	n.s.	**.4600**	**.0000**	.0374	n.s.
04 MA Une	**-.3191**	**.0000**	.0802	n.s.	**-.2913**	**.0000**	.0631	n.s.	**-.3273**	**.0000**	.1188	.0937	**-.3285**	**.0000**	.1048	n.s.
05 MA S d	**-.7261**	**.0000**	.1888	.0074	-.0066	n.s.	.1961	.0054	**-.7182**	**.0000**	.0061	n.s.	**-.3067**	**.0000**	.-1434	.0428
06 MA Bas	**-.4036**	**.0000**	**.3990**	**.0000**	-.0285	n.s.	.2734	.0001	**-.4213**	**.0000**	.1251	n.s.	-.2566	.0002	.2247	.0014
07 MA Can	**-.3702**	**.0000**	**.4303**	**.0000**	.1200	.0905	**.2996**	**.0000**	**-.3795**	**.0000**	.0491	n.s.	-.1961	.0054	**.3479**	**.0000**
08 ME Slo	**-.3999**	**.0000**	-.0839	n.s.	**-.3435**	**.0000**	.1429	.0435	**-.4096**	**.0000**	-.0552	n.s.	**-.5091**	**.0000**	-.0446	n.s.
09 ME Asf	-.1757	.0128	-.0430	n.s.	-.2214	.0016	.0727	n.s.	-.2054	.0035	.0056	n.s.	-.2350	.0008	.0155	n.s.
10 ME Une	-.2737	.0001	.1464	.0385	-.1798	.0109	.0554	n.s.	-.2751	.0001	.0038	n.s.	-.2633	.0002	-.0286	n.s.
11 ME Con	-.0628	n.s.	.0295	.0661	-.0764	n.s.	-.0424	n.s.	-.0423	n.s.	.0592	n.s.	-.0101	n.s.	.0409	n.s.
12 ME Smi	-.1619	.0220	.1718	.0150	.2327	.0009	.1622	.0218	-.1341	.0504	-.1561	.0273	.0297	n.s.	.1184	.0950
13 ME Sme	**-.3521**	**.0000**	**.3005**	**.0000**	**.3025**	**.0000**	.1478	.0378	**-.3175**	**.0000**	-.0407	n.s.	-.0033	n.s.	.1502	.0337
14 ME Sma	**-.4379**	**.0000**	**.2894**	**.0000**	.2381	.0007	.1673	.0179	**-.3985**	**.0000**	-.0143	n.s.	-.0613	n.s.	.1201	.0028
15 ME Lit	**-.3603**	**.0000**	**.3999**	**.0000**	.0516	n.s.	**.2910**	**.0000**	**-.3636**	**.0000**	.0978	n.s.	-.2165	.0021	.2673	.0001
16 ME Bas	**-.5195**	**.0000**	**.3893**	**.0000**	-.1184	.0949	.2176	.0020	**-.5363**	**.0000**	.1458	.0394	**-.3128**	**.0000**	.1979	.0050
17 Mois	-.0661	n.s.	**-.5497**	**.0000**	-.1944	.0058	-.1956	.0055	-.0763	n.s.	-.1435	.0426	-.1176	.0978	-.1612	.0026
18 LI	**.5010**	**.0000**	.0029	n.s.	.1932	.0061	-.0940	n.s.	**.4888**	**.0000**	-.1621	.0219	**.2917**	**.0000**	-.0213	n.s.
19 $\mathrm{pH}_{\mathrm{H20}}$	**-.5581**	**.0000**	-.1735	.0140	-.0713	n.s.	.1652	.0194	**-.5516**	**.0000**	-.0626	n.s.	-.2771	.0001	-.1610	.0228
20 $\mathrm{pH}_{\mathrm{CaCl2}}$	**-.6323**	**.0000**	-.0529	n.s.	-.1182	.0955	.2038	.0038	**-.6227**	**.0000**	.0173	n.s.	**-.3076**	**.0000**	-.1004	.1572
21 Ca	**-.4168**	**.0000**	**.3591**	**.0000**	-.1296	.0673	.2001	.0045	**-.4327**	**.0000**	.2046	.0037	-.2557	.0003	.1912	.0067
22 Mg	**-.3282**	**.0000**	**.3478**	**.0000**	-.0677	n.s.	.1566	.0268	**-.3463**	**.0000**	.1559	.0275	-.2249	.0014	.1974	.0051
23 Na	-.1731	.0142	.0567	n.s.	-.0683	n.s.	.0940	n.s.	-.1881	.0076	.0299	n.s.	-.1584	.0251	.0444	n.s.
24 K	**-.3966**	**.0000**	**.2926**	**.0000**	-.1928	.0062	.1132	n.s.	**-.4146**	**.0000**	.2000	.0045	**-.3523**	**.0000**	.1216	.0863
25 H	**.3836**	**.0000**	**-.3510**	**.0000**	.1482	.0363	-.1694	.0165	**.3904**	**.0000**	-.2467	.0004	.1680	.0174	-.1144	n.s.
26 N	**-.5595**	**.0000**	-.0800	n.s.	-.2135	.0024	-.1282	.0704	**-.5511**	**.0000**	.0309	n.s.	**-.3313**	**.0000**	.0430	n.s.
27 P-AL	-.2408	.0006	.2572	.0002	-.1915	.0066	.0794	n.s.	-.2450	.0005	.1334	.0596	-.2189	.0018	.2727	.0001
28 Al	-.0428	n.s.	**-.3828**	**.0000**	-.2292	.0011	-.1739	.0138	-.0284	n.s.	-.0302	n.s.	-.1117	n.s.	**-.3457**	**.0000**
29 Fe	.0973	n.s.	-.2218	.0016	-.1211	.0876	-.0704	n.s.	.1114	n.s.	-.1035	n.s.	-.0567	n.s.	-.1462	.0388
30 Mn	**-.4316**	**.0000**	.2459	.0004	**-.3220**	**.0000**	.1108	n.s.	**-.4315**	**.0000**	.2781	.0001	**-.3567**	**.0000**	-.0076	n.s.
31 Zn	-.0948	n.s.	.2409	.0006	**-.3118**	**.0000**	-.0877	n.s.	-.1063	n.s.	**.3109**	**.0000**	-.1642	.0202	-.0180	n.s.
32 P	-.0255	n.s.	**.2946**	**.0000**	-.2807	.0001	-.1309	.0647	-.0455	n.s.	**.3086**	**.0000**	-.1836	.0093	.0874	n.s.
33 S	-.2236	.0015	.1529	.0306	**-.2933**	**.0000**	.0254	n.s.	-.2237	.0015	.2000	.0015	-.2307	.0010	-.0990	n.s.

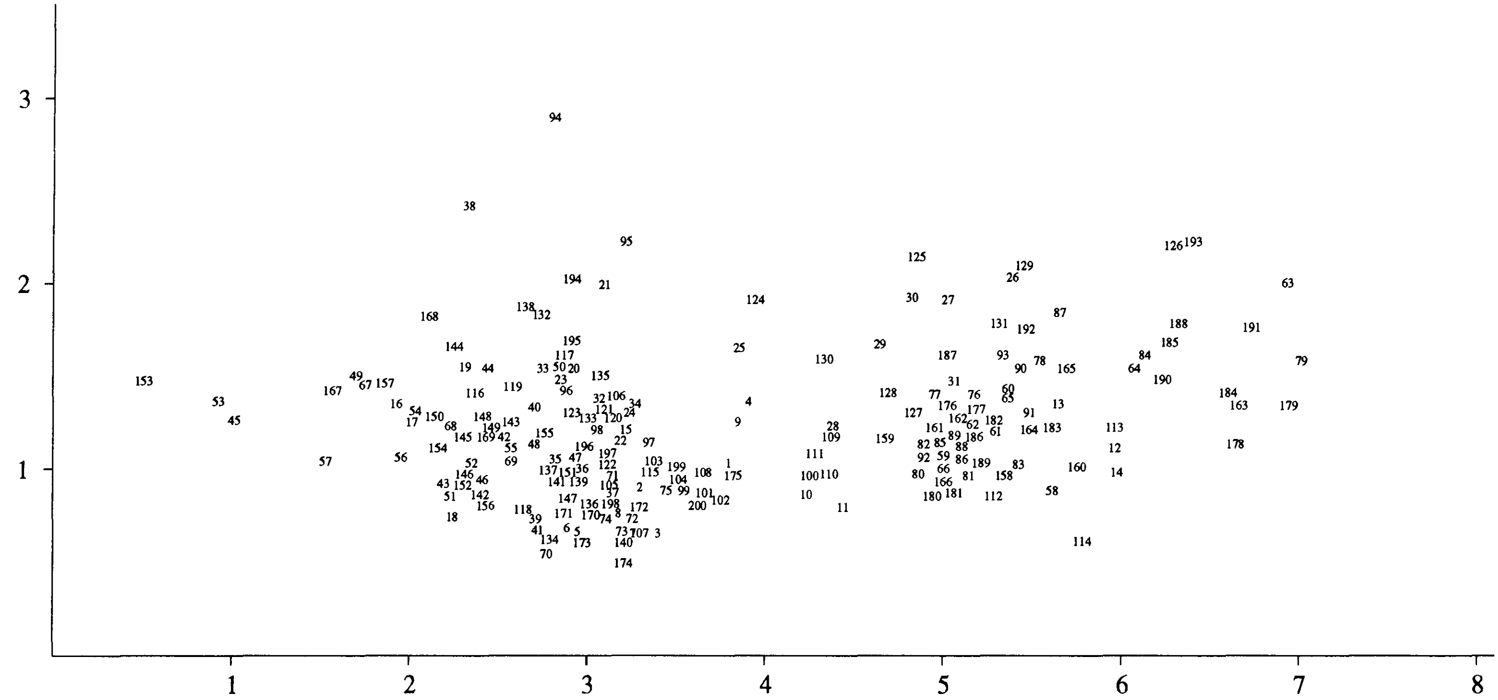


Fig. 130. DCA ordination of the MES 3200 data set (meso subplots), axes 1 and 2. Meso plot numbers plotted onto the mean subplot score within each meso plot. Axes scaled in S.D. units.

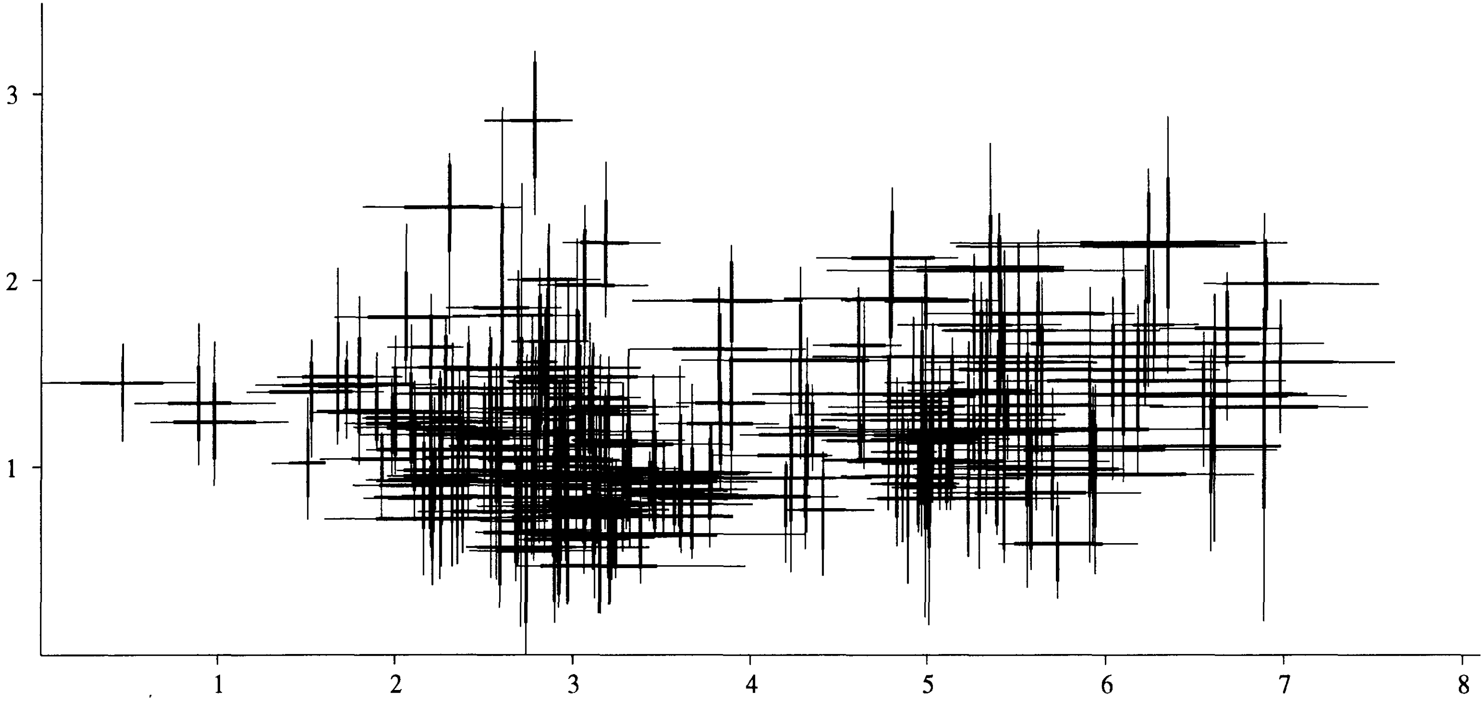


Fig. 131. DCA ordination of the MES 3200 data set (meso subplots), axes 1 and 2. For each meso sample plot, bars are given to indicate the range of variation and standard deviation of subplot scores along each axis. The cross of bars indicate the mean subplot score for each meso subplot. Axes scaled in S.D. units.

ORDINATION OF THE MESO SUBPLOTS

Characteristics of the ordination and correlation with axes of the meso sample plot ordination

Characteristics of the ordination of 3198 meso subplots are given in Tab. 8. The scattering of meso subplots along the first two axes is shown in Fig. 129. The first axis had a gradient length of 7.62 S.D. units, while the eigenvalue was 0.72. This axis was perfectly correlated with DCA 1 (the correlation between mean meso subplot score, DCAS 1, and DCA 1 was r = 0.9993!, see Tab. 18 and Fig. 130).

The second axis (gradient length 3.23 S.D., eigenvalue 0.26) was correlated with DCA 2 (r = 0.8624). The most strongly correlated environmental variable was Mois (r = -0.5497), while other variables mostly showed lower correlations than with respect to DCA 2.

The third axis was correlated with DCA 3 (r = -0.5745) and DCA 4 (r = 0.7735), the environmental variable most strongly correlated with DCAS 3 was MA Slo (r = -0.4485). The fourth axis also most strongly correlated with DCA 3 (r = 0.5723), but mostly showed low correlations with environmental variables.

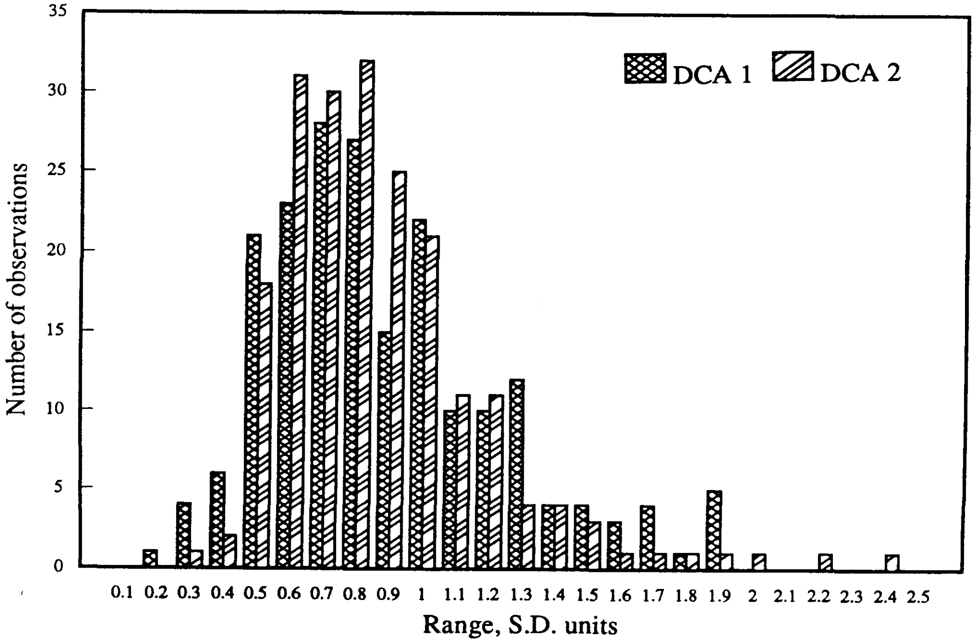


Fig. 132. Frequency distribution for within meso plot range of meso subplot scores; axes 1 and 2 of the DCA ordination of the MES 3200 data set.

Within meso sample plot variation in meso subplot scores

Fig. 131 shows the range of variation and the standard deviation of meso subplot scores within each meso sample plot. The within meso plot variation was limited, as substantiated by the frequency distribution of within meso plot range of meso subplot scores (Fig. 132). The range of variation was almost similar for both DCAS 1 and DCAS 2; 0.844 ± 0.361 S.D. and 0.818 ± 0.318 S.D. units, respectively. The largest range of subplot scores (DCAS n-R) along DCA 1 were noted by sample plots with high DCA 1 scores, in order of decreasing range: 193 (range 1.89 S.D.), 12 (1.87 S.D.), 14 (1.84 S.D.), 26 (1.78 S.D.), 128 (1.66 S.D.), 190 (1.64 S.D.), 72 (1.62 S.D.), 126 (1.59 S.D.), and 178 (1.54 S.D.). Along DCAS 2 the following meso plots showed the largest range of subplot scores: 155 (2.37 S.D.), 179 (2.18 S.D.), 138 (1.92 S.D.), 47 (1.82 S.D.), 170 (1.72 S.D.), 164 (1.67 S.D.), and 135 (1.52 S.D.).

The mean number of species per subplot had the same relationship to DCAS scores as N-TOT to DCA (cf. Tab. 12). The influence of meso subplots poor in species on the within meso plot spread of subplot scores was addressed by calculation of correlation coefficients between DCAS 1-SD (the standard deviation of within mesoplot DCAS 1 scores), DCAS 2-SD (the same, for DCAS 2), N-MEAN (mean number of species per meso subplot) and N-MIN (minimum number of species observed in any of the meso subplots). The spread of subplot scores along the two DCAS axes (DCAS 1-SD and DCAS 2-SD) were positively correlated ($r = 0.3739$, $P < 0.0001$). The spread along both axes was correlated with species number, more strongly so with minimum than with mean number of species (DCAS 1-SD and N-MIN, $r = -0.2942$, $P < 0.0001$; DCAS 2-SD and N-MIN, $r = -0.3280$, $P < 0.0001$; DCAS 1-SD and N-MEAN, $r = -0.2535$, $P = 0.0003$; DCAS 2-SD and N-MEAN, $r = -0.2099$, $P = 0.0029$). Most of the sample plots with large DCAS 1-R had mean numbers of species per sample subplot close to the average of 9 (exception: 193, with N-MEAN = 4 and 72 with N-MEAN = 5), while plots with large DCAS 2-R had 3 < N-MEAN < 7, with the exceptions of the environmentally inhomogeneous plots 135 and 138 (N-MEAN = 10, 12), both containing elevated segments within a moist matrix.

ORDINATION OF THE MICRO SAMPLE PLOTS

Characteristics of the ordination of the MI 400 data set are given in Tab. 8. The gradient length of the first axis was 6.99 S.D. units, the eigenvalue was 0.74. The axis was almost perfectly correlated with the first axis of the DCA ordination of meso sample plots ($r = 0.9784$, cf. Tab. 18). Correlated environmental variables were as with DCA 1.

Among the meso plot ordination axes, the second axis of the micro plot ordination, DCAM 2 (gradient length 3.88 S.D., eigenvalue 0.29), was only correlated with DCA 4 ($r = 0.4691$). Only Zn and P were correlated with DCAM 2 at level $P < 0.0001$. The axis did not appear interpretable.

The third axis had a gradient length of 3.55 S.D. units, while the eigenvalue was 0.25. The axis was correlated with DCA 1 ($r = 0.6444$) and DCA 3 ($r = -0.4702$). The environmental variable most strongly correlated with DCAM 3 was MA Slo ($r = -0.6219$) and ME Slo ($r = 0.5091$). The axis did not appear to give any new interpretable information relative to DCAM 1.

The fourth axis (gradient length 3.22 S.D. units, eigenvalue 0.23) was correlated with

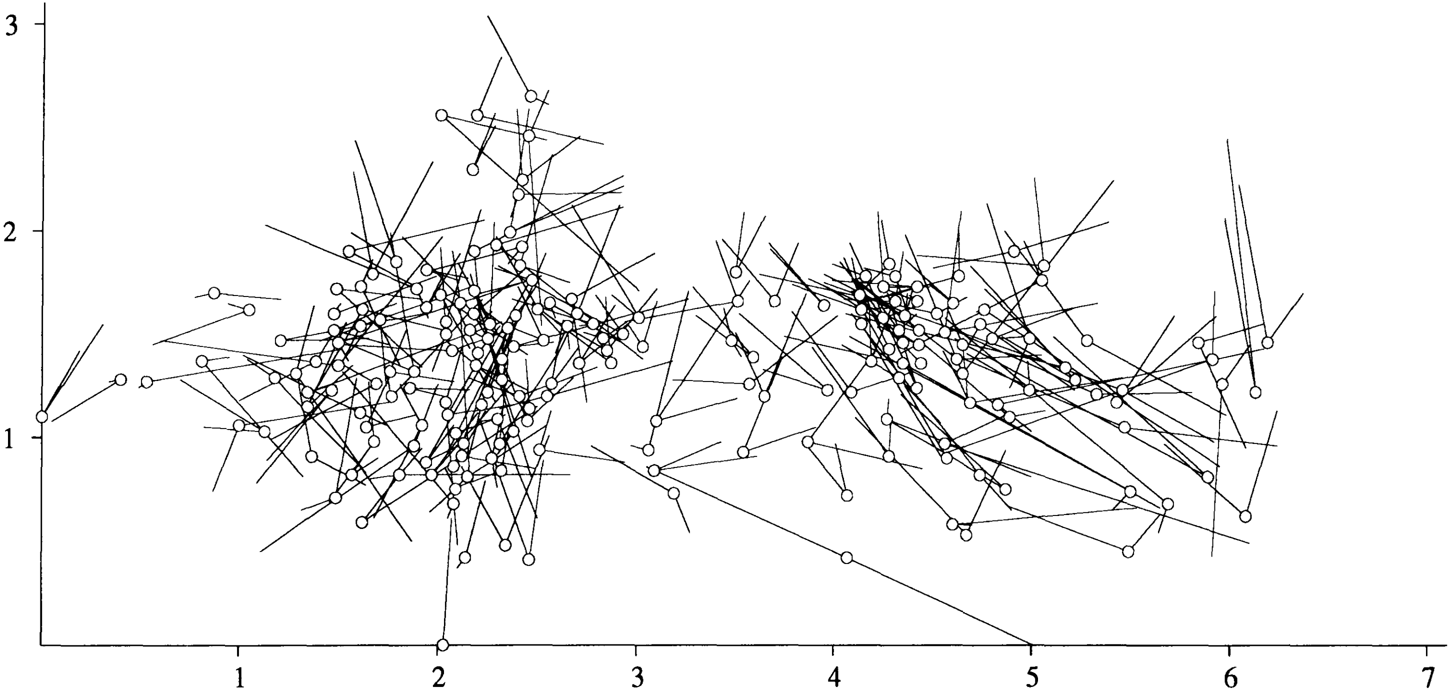


Fig. 133. Passive DCA ordination of the MI 400 data set (micro sample plots) into the ordination of the ME 200 data set. Positions of meso sample plots indicated by circles, positions of corresponding micro sample plots by radiating lines. Axes scaled in S.D. units.

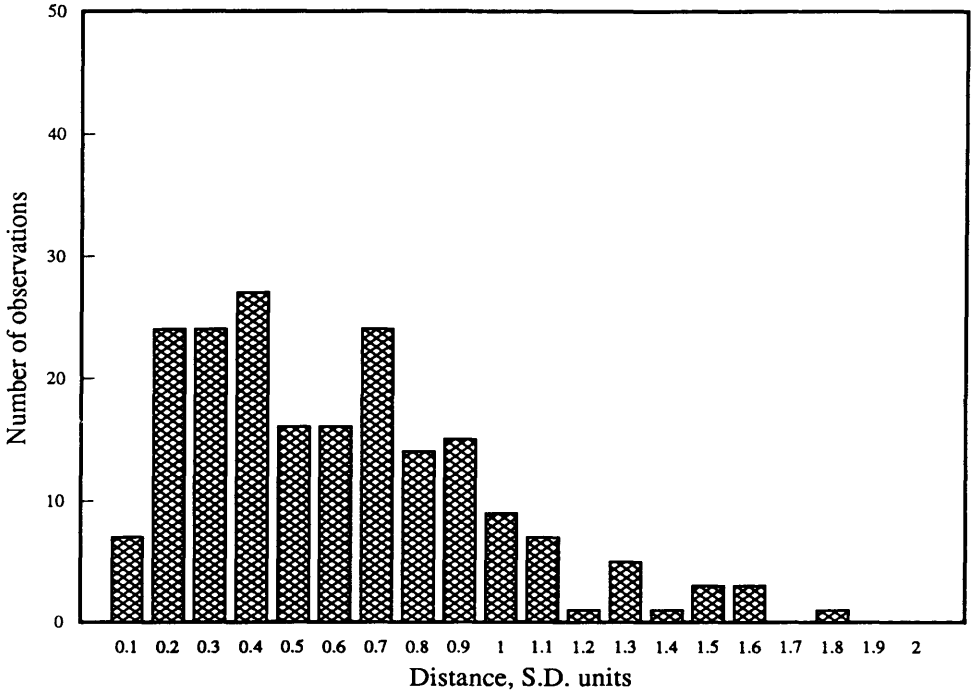


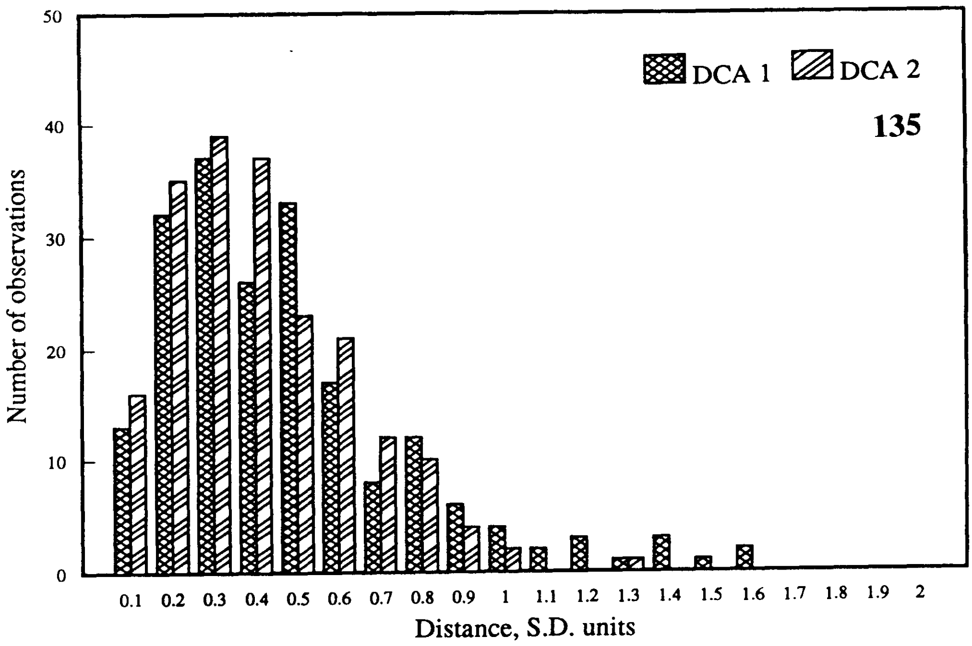
Fig. 134. Passive DCA ordination of the MI 400 data set (micro sample plots) into the ordination of the ME 200 data set. Frequency distribution of distances between corresponding micro sample plots (from the same meso plot) in the space generated by the first two ordination axes.

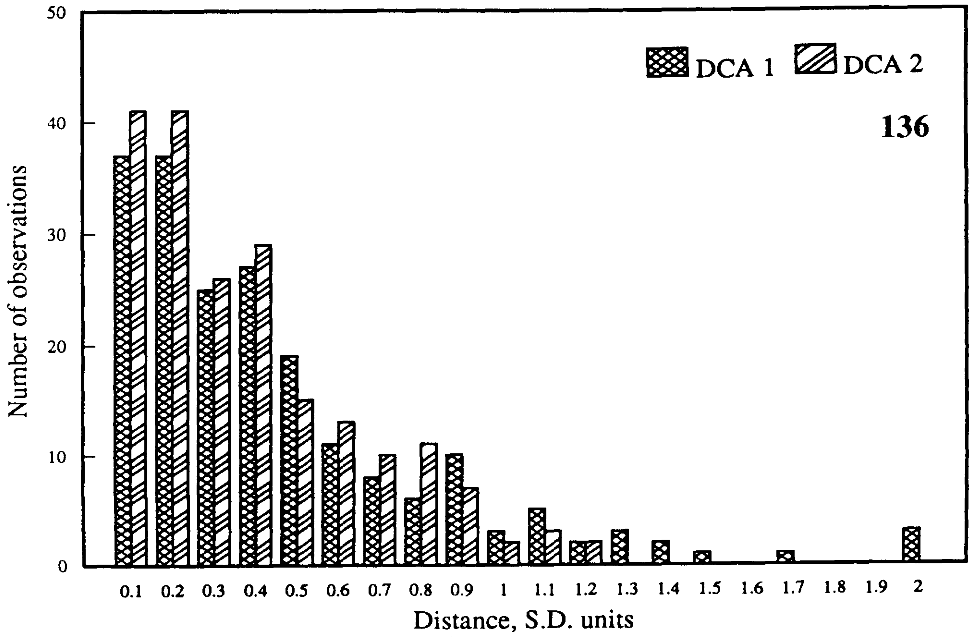
DCA 2 (r = 0.4888), but showed generally low correlations with environmental variables (the highest with Ma Can, r = 0.3479 and Al, r = -0.3457).

PASSIVE ORDINATION OF THE MICRO SAMPLE PLOTS

Fig. 133 shows the passive ordination of micro sample plots in the DCA ordination of meso plots. Several parameters were calculated to describe the deviation of the two corresponding micro sample plots from each other and from the position of the meso plot of which they are parts: DCAP-DIS - the two-dimensional Euclidean distance between corresponding micro sample plots in the DCA 12 ordination space, with two components, DCAP-DI1 - the distance along DCA 1 and DCAP-DI2 - the distance along DCA 2. DCAP-DE1 denotes maximum deviation of any of the corresponding micro sample plots from the meso sample plot score along DCA 1, DCAP-DE2 is the corresponding value for DCA 2.

DCAP-DIS was mostly between 0.2 and 0.8, as shown from Fig. 134. The maximum





Figs 135-136. Passive DCA ordination of the MI 400 data set (micro sample plots) into the ordination of the ME 200 data set. Fig. 135. Frequency distribution of distances between corresponding micro sample plots (from the same meso plot) along each of the first two ordination axes. Fig. 136. Frequency distribution of maximum deviation of a micro sample plot score from the score of the corresponding meso sample plot along each of the first two ordination axes.

was 2.14 S.D. units for sample plot 125, followed by 2.12 S.D. for 185 and 2.07 for 88. All of these meso plots were situated in sharp transitional zones and the DCAP-DIS values therefore reflected abrupt environmental transitions.

DCAP-DI1 and DCAP-DI2 were lower than DCAP-DIS, the frequency of observations decreased from 0.1 S.D. (Fig. 135). Mean values and standard deviations were 0.410 ± 0.380 and 0.331 ± 0.269, respectively. DCAP-DI1 was correlated with DCA 1 ($r = 0.2792$, $P = 0.0001$), indicating increasing between-micro plot separation from more mesic to more xeric sample plots (inverse to the trend in N-TOT, cf. Tab. 12). Highest DCAP-DI1 values were noted for sample plots 185 (1.97 S.D.) and 125 (1.96 S.D.). DCAP-DI2 was generally lower than DCAP-DI1 (Fig. 135), the highest values being 1.14 S.D. (sample plot 17) and 1.13 (sample plot 174). DCAP-DI2 was not correlated with DCA 2 ($r = -0.0455$, n.s.).

DCAP-DE1 and DCAP-DE2 mostly showed similar distributions as DCAP-DI1 and DCAP-DI2 (Fig. 136), although the maximal values were generally lower for DCAP-DEn because the meso plot mostly took an intermediate position. The correlation between DCAP-DE1 and DCA 1 was $r = 0.2650$, $P = 0.0002$, between DCAP-DE2 and DCA 2 was $r = -0.0165$, n.s.

DISCUSSION

ORDINATION METHODS: DCA OR LNMDS?

The present study demonstrates that curvilinear distortion of the underlying gradient structure can also occur in LNMDS ordinations of field data sets (LNMDS 3, axis 2; Fig. 13), despite the use of variants and options found in tests to be among the best available (cf. Faith et al. 1987, Minchin 1987). Curvilinear distortion appears in connection with choice of too high dimensionality, shown by Minchin (1987) occasionally to give distorted ordinations of simulated data sets. The curvilinear LNMDS ordination depicted by R. Økland (1990a: Fig. 117) may also be due to distortion; a 2-dimensional LNMDS was used with an essentially unidimensional data-set. No unambiguous method for *a priori* determination of the appropriate number of dimensions is available (cf. Prentice 1980, Kenkel & Orlóci 1986, Minchin 1987). It is not known whether similar distortions occur with improved MDS variants like HMDS (Faith et al. 1987) and SHS (Belbin 1991).

Distortions also occur with DCA, as exemplified by the axes DCAV 2 (tongue effect; Fig. 126) and DCAB 2 (strongly influenced by outliers; Fig. 128). Distortions in DCA (tongues, instabilities) may have several causes (Minchin 1987, Oksanen 1988, R. Økland 1990a, 1990b, Jackson & Somers 1991). The reason for the appearance of a tongue in the DCAV ordination is not known.

The results of the present study lend support to the view of R. Økland (1990a, 1991) that DCA is superior to LNMDS for general-purpose ordination of data sets with one strongly dominant gradient (length of major gradient (in beta diversity units) more than approximately three times the length of subordinate gradients, cf. R. Økland 1990a). Data sets with one long gradient are common (e.g., R. Økland 1990b, Eilertsen 1991). Higher correlations of the DCA axes with environmental variables may be due to higher single-point stability in DCA (as suggested by R. Økland (1990a)). This may be brought about by higher robustness of sample plot scores that are weighted averages of species scores (in DCA) than sample scores derived from ranked dissimilarities (in LNMDS).

The contrasts between results by tests of DCA and LNMDS on simulated data (e.g., Minchin 1987) and those obtained with field data sets (e.g., in the present study), suggests that the robustness criterion often used in ordination tests by simulated data (e.g., by Minchin 1987) may be inappropriate as there is a great danger that data-sets with unrealistic properties may influence the test results too strongly (R. Økland 1990a, 1990b). Neither will the robustness criterion enable recognition of variation in the success of methods, depending on data-set properties.

The choice of DCA or LNMDS will probably remain a controversial matter (cf. Beals 1984, Kenkel & Orlóci 1986, Minchin 1987, Wartenberg et al. 1987, Peet et al. 1988, R. Økland 1990a). However, the fact that both methods may distort an underlying gradient structure strongly suggests parallel application of the two techniques, as proposed by Kenkel & Orlóci (1986) and supported by R. Økland (1990a, 1990b). Because of the fundamental conceptual differences between the two techniques (cf. Minchin 1987, R. Økland 1990a), congruent configurations (like the DCA and LNMDS 2 ordinations of the ME 200 data set in this study) strongly strengthen the conclusions about major gradients. On the other hand, dissimilar results may aid the discovery of distorted or otherwise suboptimal results with one or both techniques. R. Økland (1990a, 1990b) sums up advantages and disadvantages of DCA and LNMDS. Favourable properties of DCA are the non-linear rescaling of axes (also see Eilertsen et al. 1990, Eilersen 1991, R. Økland 1990d, 1992), its relationship with the correspondence analysis concept (ter Braak 1986, 1987b, Cramer & Hytteborn 1987), and its simultaneous ordination of samples and species. In cases of congruent patterns, DCA is the natural choice for further interpretation and derived analyses. Otherwise, improved gradient interpretation by linear rescaling of each axis individually by rhCCA (Eilertsen et al. 1990, R. Økland 1990a) is recommended.

ENVIRONMENTAL INTERPRETATION OF GRADIENTS IN VEGETATION

Division of the main, broad-scale topographic gradient

The high similarity of the first axes of all ordinations - independent of ordination method and data set - unequivocally points to the existence of one major gradient in the investigated vegetation. Correlations of sample plot positions along this axis with environmental variables indicate that the variation from pine to spruce dominated forests depends primarily on a macro-scale topographic (ridge-slope-valley) gradient, accompanied by different sets of more or less strongly correlated variables in different parts of the gradient. The contrasting patterns of correlations within each of the two subsets (Subset A; spruce forest, and Subset B; pine forest) indicate that, although broad-scale topographic differences may be a primary driving force, different complex-gradients are likely to be responsible for the present vegetational differentiation *within* the pine and spruce forests; topography and soil depth in the pine forest and a nutrient complex-gradient within the spruce forest. We will consider these two ecoclines separately, starting with the pine forests.

Pine forests: the topography-soil depth complex-gradient and its relation to soil moisture deficiency

Firstly, we will consider the main coenocline of the pine forests (Subset B; i.e. the variation in pine forests from the subxeric-submesic transitional site-types of series 4, dominated by ericaceous species, to the xeric, lichen-dominated site-types of series 1). We will also pay some attention to the right-hand end (in the ordinations) of Subset A; occupied by the submesic *Vaccinium myrtillus*-dominated spruce forest (site-types 5.1).

Variation in nutrient content and associated variables along the gradient

Concentrations of most nutrients (E-group 2) in the humus remain unchanged or decrease very slightly along DCA 1 in the pine forest (Subset B). This is in accordance with data presented by other authors; Kielland-Lund (1981) reports a slight increase in Ca between vegetation types along the gradient, Malmström (1963) observes no differences, while Lahti & Väisänen (1987) report a slight decrease in Ca.

The absence of trends in pH along the gradient is in accordance with Aaltonen (1926), Glømme (1928), Malmström (1949, 1963), Söyrinki et al. (1977) and Kielland-Lund (1981), while a slight decrease in pH was noted by Kivenheimo (1947) and Lahti & Väisänen (1987).

Malmström (1949) notes a strong decrease in loss on ignition along the gradient, and attributes this trend to the very thin humus layer in the lichen-rich pine forests, making inclusion of mineral soil particles in the humus samples unavoidable. This explanation applies to the investigation area as well.

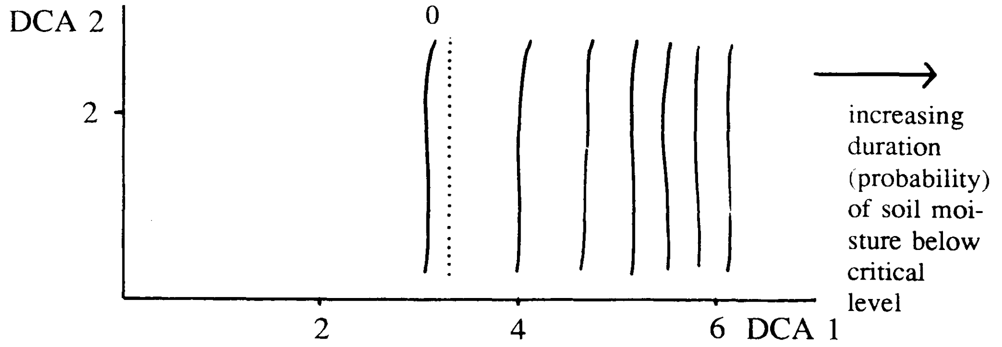
The significant increase in total N (given as percentage of LI) in the investigation area contrasts observations in the literature; no trends are present in the data of Aaltonen (1926) and Malmström (1963), while Dahl et al. (1967), Kielland-Lund (1981) and Lahti & Väisänen (1987) report slightly decreasing N along the gradient. The increased N in the humus layer along a gradient characterized by decreasing productivity (decreasing stand density and decreasing field layer cover) may be due to the high input of long distance airborne N for several decades. This gains support from several recent investigations. While Abrahamsen (1984) maintained that no signs of N saturation were yet observed in Norway, a significant increase in N leachage from coniferous forest soils in Birkenes, Aust-Agder (some 90 km SSW of the study area) occurs from 1985 onwards (Abrahamsen et al. 1990) and increasing N leachage to rivers and inland waters is recorded by Henriksen et al. (1987). Bjørnstad (1991) report an increase in the N content of pine and oak forest soils at Søgne, Vest-Agder, during the last 20 years. The negative correlation between N and Ca in our pine forest subset is also noteworthy.

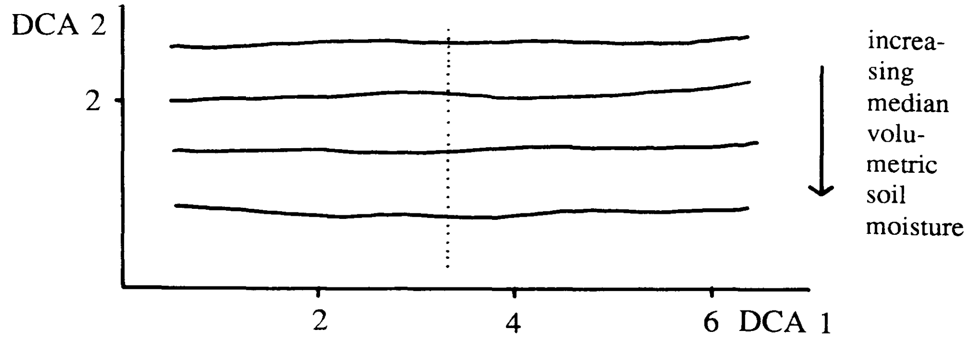
We conclude that variation in nutrient status cannot account for the vegetational variation along the topography-soil depth gradient in the pine forest.

Interpretation of soil moisture measurements and the soil moisture deficiency hypothesis

Soil moisture, as measured in this study, *increase* slightly along the gradient, despite the common interpretation (e.g., Malmström 1949, Kuusipalo 1985, van Cleve & Yarie 1986) of corresponding variation in vegetation and environmental variables as governed primarily by the macro-scale topography which, in turn, determines the broad-scale soil moisture conditions. In order to resolve this apparent paradox, we hypothesize that the direction of isolines for duration of soil moisture in the DCA ordination diagram in this study is dependent on soil moisture level. (Such isolines can be estimated from the cumulative distribution functions for soil moisture in different sample plots during a specified period of time; cf. R. Økland (1989b)). We will discuss this hypothesis in some detail. Bjor (1971) reports strongly contrasting moisture conditions in *Vaccinium myrtillus*-dominated spruce forests (corresponding to site-types 5.1 and 5.2) and lichen-rich pine forests (corresponding to site-types 1 and 2) during a dry period in early summer. While the spruce forest humus maintains a moisture content above field capacity, a drought front rapidly penetrates the humus layer of the pine forest, resulting in moisture levels below the wilting point for an extended period. Apparently, the *Vaccinium myrtillus*-dominated spruce forest experiences extreme drought very rarely or not at all (cf. Bjor 1971), while *the probability and duration of soil moisture deficiency* increases along the main gradient (Fig. 137).

The soil moisture measurements reported in the present study are made on samples collected two or three days after a long, rainy period. They therefore rather represent normal (median) soil moisture, apparently not varying significantly along DCA 1 (the response of vegetation to a gradient in median soil moisture is further discussed on p. 154).





Figs 137-138. The soil moisture deficiency hypothesis and the hypothesized variation in median soil moisture. Hypothetic isolines for characteristic parameters of soil moisture duration curves, provided the hypotheses are correct, are tentatively drawn onto the DCA ordination of the ME 200 data set, axes 1 and 2 (Fig. 10). Fig. 137. Isolines for duration of soil moisture below a certain critical level (e.g., number of days per 10 years with soil moisture below the wilting point), provided the soil moisture deficiency hypothesis adequately explains compositional variation along DCA 1. Fig. 138. Isolines for median volumetric soil moisture content, provided that positions along the fine-scale paludification gradient (responsible for variation along DCA 2) are adequately explained by differences in median soil moisture. Scaling of axes in S.D. units. Limit between Subsets A and B indicated by dotted line.

This interpretation accords well with observations by Malmström (1949), that lichen-dominated pine forest soils may be periodically moist.

On this basis, we forward the hypothesis that the main coenocline in the pine forest is the response to a gradient in soil moisture deficiency, governed primarily by the macro-scale topography. We will refer to this as *the soil moisture deficiency hypothesis.*

Soil depth, slope and unevenness decrease along the gradient, in response to shifts in broad-scale topography. Similar observations are reported by Söyrinki et al. (1977) and Kuusipalo (1985) who note decreasing soil depth (and thickness of the humus layer) along corresponding gradients, and by several authors who report increasing median particle size of the mineral soil (Kivenheimo 1947, Malmström 1963, Urvas & Erviö 1974, Sepponen et al. 1982, Kuusipalo 1985, Sepponen 1985). The probability of drying out is determined by topographic position, soil depth and soil texture (Kuusipalo (1985). Soil moisture determines the productivity of a site (cf. the decrease in tree cover along the gradient), and soil moisture deficiency strongly reduces the rates of decomposition in the soil, in particular the N mineralization rates (Malmström 1926, Glømme 1928, 1932, Hesselman 1937, Johansson 1986). The variation in rate of pedogenic processes along the gradient explains the variation in soil depth, and indicates that soil depth is not the primary cause of the variation in vegetation. This is further supported by the similar vegetation on rock outcrops with shallow soil and on deep glaciofluvial deposits (cf. Kielland-Lund 1981), and by the fact that the vegetation can not be predicted from knowledge of type of superficial deposits (Malmström 1963, Sepponen 1985). The soil moisture deficiency hypothesis is also consistent with the current view that the mor humus has a good ability to magasinize water, although at the same time also highly liable to dry out (Tirén 1934, Wittich 1955, Bjor 1963).

Some authors suggest that the critical factor for plant growth and vegetation differentiation in pine forests is nutrient deficiency, in particular lack of N (cf. Björkman & Lundeberg 1971, T. Moore 1984). Statements in the literature in favour of the whole broad-scale topographic gradient as a "nutrient" gradient are frequent (e.g., Dahl et al. 1967, Kielland-Lund 1981, Kuusipalo 1985, Lahti & Väisänen 1987, Allen & Peet 1990, Carleton 1990, Tonteri et al. 1990b). Such a nutrient deficiency hypothesis is strongly at odds with (1) the observations of negligible variation in cation contents and pH along the topography-soil depth gradient in the pine forest, (2) the absence of growth increase upon N fertilization in poor pine forests (Hesselman 1937, Romell & Malmström 1945, Malmström 1949, Jalkanen 1990), and (3) the *increase* in N along the gradient in the investigation area. The positive response of the *Vaccinium myrtillus*-dominated spruce forests (corresponding to site-types 5.1) to N fertilization (cf. p. 149) and the low probability of moisture deficiency in this type suggest that the change from limitation by soil moisture deficiency to limitation by nutrient deficiency occurs in the transition between spruce and pine forests (Subsets A and B in the present study).

Kuusipalo (1985), supported by Tonteri et al. (1990a), considers the pine and spruce forests to be separated by a main vegetational borderline, a discontinuity not matched by a corresponding discontinuity in environmental factors (cf. also Sarvas 1951, Kuusipalo 1983b, Lahti & Väisänen 1987). As the transect sampling used in this study is expected to represent the different parts of middle slopes more or less in proportion to their areal importance, our data support the existence of a zone of slightly lower point density, although not actually a discontinuity. This transitional zone (series 4 in this work) is ecologically important as it separates vegetation likely to be limited by periodic soil moisture deficiency from vegetation limited by nitrogen availability. Whether this zone is a result of steeper environmental gradients, a result of the shift in dominating tree species, or both, cannot be judged from our material.

The response of vascular plants to soil moisture deficiency

The low β diversity of vascular plants in the pine forests and the low correlation between the first axis of the vascular plant ordination (DCAV 1) with DCA 1 in the ordinations of the full species composition and the bottom layer, apparently indicate that the topography-soil depth complex-gradient in the pine forest primarily affects the bottom layer. However, the compression of the right end of DCAV 1 may result from (1) the low number of vascular plant species in the pine forest, all having wide ecological amplitudes (cf. Eilertsen et al. 1990), (2) the high stochasticity of vascular plant composition in the pine forest plots due to the low species number, and (3) the tendency of the ordination method to put deviating, species-poor sample plots at gradient extremes (cf. T. Økland 1988, R. Økland 1990a, 1990b).

The soil moisture deficiency hypothesis is supported by: (1) The decrease in vascular plant cover (and species number) along DCA 1. (2) The relatively sharp right-hand limits of many vascular plants (e.g., *Maianthemum bifolium* and *Trientalis europaea*) along DCA 1. (3) Observations that species´ limits along the gradient are displaced towards the spruce forest after severe drought. Erkamo (1958) reports strong retreat of spruce from subxeric forests in Finland (corresponding to site-type 3) after the extremely dry summer of 1955, following an almost continuous expansion in the first half of the century. Early development and survival of spruce seedlings is dependent on sufficient soil moisture (Bjor 1963), as demonstrated by the watering experiments of Holmbäck & Malmström (1947). Hiirsalmi (1969) reports a retreat of *Trientalis europaea* from the dry end of its range (pine forests) after severe drought. R. Økland & Bendiksen (1985) report local death of *Calluna vulgaris* in exposed sites (notably sites corresponding to site-type 1) after drought. (4) The response of pine forests to increased ground water tables and irrigation (Sjöström 1936, Hesselman 1937, Holmbäck & Malmström 1947, Malmström 1949): the field layer develops in the direction of the *Vaccinium myrtillus* or *Gymnocarpium dryopteris* types.

Vascular plants along the topography-soil depth complex-gradient: relevance of pattern to process

The more open field layer towards the xeric end of this gradient indicates that vascular plant production is restricted by physiological tolerance to the recurrent episodes of extreme drought. Thus the survival of vascular plants in the xeric site-types is a matter of stress-tolerance (cf. Grime 1979).

In the subxeric and transitional site-types 3-1 to 4-1, however, there are indications of high intensity of interspecific competition in the field layer: (1) a closed field layer, and (2) fine-scale co-occurrence, and often co-dominance, of the dwarf shrubs *Calluna vulgaris*, *Empetrum nigrum*, *Vaccinium myrtillus*, *V. uliginosum* and *V. vitis-idaea*. Kuusipalo (1983b) considers *Vaccinium myrtillus* the structuring species in the field layer of pine forests. Due to its bigger size and easy establishment from seeds (cf. Kujala 1926a), *Vaccinium myrtillus* may be a good-effect as well as a good-response competitor (cf. Hutchings 1986, Goldberg & Landa 1991). However, the result of Karlsson (1987), that only a negligible fraction of fine-scale variation in cover (of the same five species except *Calluna*) in subarctic, N Swedish heath vegetation can be explained by the cover of other dwarf-shrub species, questions the importance of interspecific competition as a structuring factor. Other hypotheses relevant to explain the co-occurrence of these species are:

(1) Differentiation along minor environmental gradients. *Calluna vulgaris* and *Empetrum*

nigrum are generally considered more photophilous than the *Vaccinium* spp. (cf. Kujala 1926a, Beijerinck 1940, Mork 1946). No consistent abundance trends for these species along the between trees - under tree gradient (DCA 2) is, however, documented in this study.

(2) Spatial segregation. Callaghan (1987) suggests segregation of *Vaccinium myrtillus* and *Vaccinium vitis-idaea* by complementary patterns of leaf canopy development and by separation of rooting zones (also see Kujala 1926a). The importance of layering of rooting systems for reduction of root competition has, however, been questioned (Kivenheimo 1947). All ericaceous species have most of their root biomass concentrated to the upper 5 cm of the humus layer (Kivenheimo 1947, Karlsson 1987).

(3) Density-independent reductions by herbivore grazing, considered a more important cause of mortality than competition *per se* by Ericson (1977).

(4) Density-independent mortality caused by unknown factors, senescence of clones, etc.

The relatively low number of seedlings observed in pine forests may indicate that interspecific competition occurs, but is mainly of the pre-emptive type (cf. Werner 1976); i.e., competition for empty space (Yodzis 1986), and competition for space for establishment of tillers etc.

The shift from pine to spruce forest (site-type 4 to 5.1) implies a considerable reduction in dwarf shrub cover (total cover in the field layer is reduced from a mean of 94 % in site-type 4-1 to 63 % in 5.1-1, cf. Tabs. 25 and 27); only *Vaccinium myrtillus* and *V. vitis-idaea* occur regularly in site-types 5.1. The limits of *Calluna vulgaris* and *Empetrum nigrum* are most probably set by shade tolerance, perhaps mediated by competition (Kujala 1926a, Kuusipalo 1985). However, the low total cover in the field layer in most spruce forest plots questions the importance of competition. The reduced quantitative importance of *Vaccinium myrtillus* in site-types 5.1 is probably caused by increasing shade (Kuusipalo 1983b, Sjörs 1989). The limit towards the pine forests for herbs occurring in site-types 5.1 is, however, considered to be set by physiological tolerance (cf. p. 143), not by reduced competition from *Vaccinium myrtillus*.

Kuusipalo (1985) explains the variation along the gradient from xeric pine forests to submesic spruce forests by competition for N versus light, according to Tilman's model (Tilman 1982, 1988). We consider Tilman's model inadequate for understanding variation along this coenocline, for two main reasons: (1) the topography-soil depth gradient is *not* a nutrient gradient as claimed by Kuusipalo, and (2) the shifts in species composition along the gradient appear rather to be set by physiological tolerance in a stressed habitat than by competition (cf. Austin 1990, R. Økland 1992).

The response of bryophytes and lichens to soil moisture deficiency

The hypothesis that the variation in species composition in the bottom layer along the topography-soil depth complex-gradient in the pine forest is indirectly related to soil moisture deficiency through the decreasing cover of (and shelter from direct insolation by) the uppermost layers is motivated by the following observations: (1) one of the variables most strongly correlated with DCA 1 in the pine forest subset is the cover of vascular plants ($r < -0.7$), and (2) the cover of trees also decreases significantly along DCA 1.

Bryophytes and lichens are ectohydric and poikilohydric organisms, depending on the humidity of the surrounding air and on precipitation for their water uptake (Buch 1947, C.O. Tamm 1953, Hosokawa et al. 1964, Busby et al. 1978, Callaghan et al. 1978), as their ability to water uptake directly from the soil is poor (Stålfelt 1937a, C.O. Tamm 1953, L. Anderson

& Bourdeau 1955). The moisture-holding capacity of the bottom layer depends on the cover of the tree and field layers (Bjor 1971). Lichens dominate the more xeric pine forests (site-types 1 and 2), bryophytes the less xeric (site-types 2 to 4). This is in accordance with well-documented physiological differences: lichens are more tolerant to drought (cf. Kappen 1973, Ahti 1977), and have higher endurance of long periods without net production of organic matter (Billings & Mooney 1968). The dominant boreal forest bryophytes, on the other hand, do not tolerate direct insolation. Death after clear-felling is reported by Kujala (1926b), C.O. Tamm (1953), Weetman (1968), Busby et al. (1978) and Ipatov & Tarkhova (1980, 1983), while higher cover of bryophytes in more closed tree stands and under trees is noted by Malmström (1949), Hämet-Ahti (1963), R. Økland & Bendiksen (1985), Lahti & Väisänen (1987), and During & van Tooren (1990). The decisive factor preventing bryophytes from growing in open tree stands without a covering field layer is likely to be the occurrence of extremely high temperatures in warm sunny days (Ipatov & Tarkhova 1980). Bjor (1971) demonstrates extremely high temperatures in moss patches when the bryophytes are so strongly desiccated that no more energy is used for transpiration. Mass loss by respiration at supraoptimal summer temperatures is demonstrated in *Dicranum polysetum* and *Hylocomium splendens* (Stålfelt 1937b, W. Peterson & Mayo 1975, N. Collins 1978, Callaghan et al. 1978, Skre & Oechel 1981). Stålfelt (1937b) and Dilks & Proctor (1974) document recovery times after post-wetting respiration that are dependent of the length of the drought period. Further support for the hypothesis comes from the sharp limit of several species towards more xeric series, e.g. *Dicranum majus* (Fig. 78), *Hylocomium splendens* (Fig. 82), *H. umbratum* (Fig. 83), *Plagiothecium undulatum* (Fig. 88), *Ptilium crista-castrensis* (Fig. 93), *Polytrichum formosum* (Fig. 92), and *Rhytidiadelphus loreus* (Fig. 95). We conclude that the limits of bryophyte species towards the xeric end of their range appear to be set by physiological desiccation tolerance.

Bryophytes and lichens along the topography-soil depth complex-gradient: relevance of pattern to process

Relatively high total cover in several *Cladina*-dominated sample plots indicates competitive interactions. This is in accordance with the view that successions in lichen-dominated vegetation proceed from small species to larger (*Cladina* spp.) by overgrowth and spatial exclusion (Oksanen & Ahti 1982, Oksanen 1983, 1984, 1986). However, the high number of small *Cladonia* spp. in most such plots indicate that these successions are frequently interrupted by disturbance. Lichens are vulnerable to trampling (Kellomäki & Saastamoinen 1975), to the extent that their cover vary with rodent cycles (Ericson 1977). *Cladina* spp. are also vulnerable to other kinds of mechanical damage (Oksanen 1984), wind abration, etc.

The shift in dominance from lichens to mosses near the xeric end of the topography-soil depth gradient, perhaps also the shift in moss dominance from the subxeric to the submesic site-types (from site-type 3 to site-type 5.1), from *Dicranum scoparium*, *D. polysetum* (and *D. drummondii*) via *Pleurozium schreberi* to *Dicranum majus* (and *Hylocomium splendens*) is in accordance with the competitive hierarchy theory (Wilson & Keddy 1986, Keddy 1990, cf. also Carleton 1990). Transplantation experiments by Iparov & Tarkhova (1983) show that lichens thrive in habitats normally occupied by mosses, provided they are shielded from moss overgrowth. Furthermore, *Cladina* lichens have high tolerance to burial in litter (Kauppi 1990). Mosses are competitively superior because of their higher growth rates (Topham 1977, Johnson 1981, Ipatov & Tarkhova 1983) under conditions of adequate water supply.

The following set of factors can be hypothesized to limit bryophytes towards the mesic end of their range in the investigation area: (1) A possible relationship with field layer cover is indicated from the negative relationship between cover in the two layers in the present study. The maximum mean cover in the field layer (site-types 3-1 and 4-1) coincides with the minimum mean cover of bryophytes and a local minimum in the number of bryophyte species per sample plot. (2) The fact that the cover of bryophytes is generally far below 100% is an indication that the interactions between moss shoots may often be interrupted by episodes of density-independent mortality (or constant, high radiation stress). Such interruption will prevent competitive exclusion. (3) Competition among bryophytes, whenever occurring, is mainly for space; competitive effectivity is determined by relative growth rates (Callaghan et al. 1978, Rydin 1986, R. Økland 1990c). There are indications that some species may locally be suppressed towards their mesic limit due to competition for space: (i) The occurrence of *Dicranum fuscescens* and *D. scoparium* (as well as other species characteristic of more xeric sites) mainly on stones covered with shallow soil, stumps, etc. in submesic sites. (ii) The diffuse limits of many species, e.g., *Dicranum scoparium* (Fig. 80) and *D. drummondii* (Fig. 76) towards the mesic end of this gradient; they show a gradual decrease in frequency (compare the sharpness of the xeric limits set by physiological tolerance). Other species, e.g., *Dicranum polysetum* (Fig. 79) and *Sphagnum capillifolium* (Fig. 98), show sharp limits towards more mesic series, but the causes of these limits are not known. The relative importance of competition in subxeric to submesic sites deserves further study.

The increase in number of bryophyte species from site-types 4 to 5.1 may partly be due to a parallel increase in the diversity of microniches with a sufficiently high microclimatic humidity (cf. LaRoi & Stringer 1976, Havas & Kubin 1983), e.g., "pockets" in the forest floor (R. Økland & Bendiksen 1985).

Spruce forests: the complex-gradient in nutrient status

In this section, we consider the main coenocline of the spruce forests (Subset A; i.e. the variation (from high to low DCA 1 scores) from spruce forests dominated by *Vaccinium myrtillus* (site-types 5.1) to types with increasing prominence of low ferns (e.g., *Gymnocarpium dryopteris*) and low herbs (site-type 5.3), to the more luxuriant types of site-type 6, approaching tall herb and tall fern vegetation). The coenocline is accompanied by a strong increase in α diversity (number of vascular plants per meso sample plot and DCA 1 in Subset A has r = -0.8405!).

Variation in environmental variables along the gradient

Topography, soil depth and soil profile type. Variation along this coenocline is associated with topographic shifts, but hardly with soil depth (cf. also T. Økland 1990). The coenoline is associated with a shift from mor (in site-types 5.1 and 5.2) to transitions to mull in site-type 5.3 and mull-like humus in site-type 6. Similar shifts are reported in several treatments of comparable vegetation. The fine fraction of the mineral soil generally increases significantly along comparable coenoclines (Kivenheimo 1947, Kuusipalo 1985, Sepponen 1985).

Slope and aspect favourability. No significant correlations between slope and aspect favourability and position along DCA 1 (and pH and nutrient concentrations) are observed in the spruce forest, although it is generally accepted that the pH and nutrient content is higher on steep, south to west-facing slopes, as reported by Glømme (1928), Rajakorpi (1984), T. Økland (1990) and Heikkinen (1991). The poor representation of southerly to westerly aspects is the likely explanation of the deviant pattern in our material.

Soil moisture. While measured soil moisture increase with increasing nutrient concentrations in Subset A in the present study, T. Økland (1990) observes opposite trends. Apparently, the frequency of moist versus dry sample plots along the nutrient gradient varies from area to area.

Nutrient content and associated variables. LI (negatively correlated), the two pH measurements, and N show the highest correlations with this coenocline in spruce forests in the study area. T. Økland (1990) report strong, negative correlations between LI and pH, and LI and N, in a study of spruce forest vegetation in Rausjømarka, SE Norway, comprising a range of variation corresponding more or less to site-types 5.1-5.3. Strong positive correlations between N (in percentage of LI) and pH are noted by Hesselman (1926, 1937), Malmström (1949) and Kuusipalo (1983a), while strong negative correlations between N and LI are noted by Hesselman (1926), Dahl et al. (1967) and Bergseth (1977).

Systematic trends in pH along comparable coenoclines are reported by Valmari (1921), Aaltonen (1925), Malmström (1949), Dahl et al. (1967), Kielland-Lund (1981), Sepponen (1985) and T. Økland (1990), among others. Base saturation normally follows pH closely (Bergseth 1977, Falkengren-Grerup et al. 1987).

Concentrations of most cations in the humus (E-group 2) are also significantly correlated with DCA 1 (P and Ca most strongly) in the spruce forest (Subset A), but at considerably lower significance levels than pH, N and LI. Kuusipalo (1983a) report Ca to follow pH closely. The data of Dahl et al. (1967) and Kielland-Lund (1981), sampled selectively with respect to a phytosociological classification, indicate similar trends. Studies using a more randomized distribution of samples (e.g., Sepponen 1985, T. Økland 1990) show low to moderate correlations between Ca and pH, as in the present study. T. Økland (1990; cf. also 1988) demonstrates insignificant correlations also between Ca and N. Mg and Mn normally follow Ca closely (cf. T. Økland 1990).

Stand density and associated variables. In most studies, increasing soil nutrient content is coupled with increasing tree layer productivity, increasing stand density (Kuusipalo 1984) and, in turn, increasing litterfall (van Cleve et al. 1983, Kuusipalo 1985, 1988, T. Økland 1990). The low correlation between soil nutrient status and tree stand density in this study is likely to be due to local conditions: (1) low representation of favourable aspects, (2) interference between gradients, and (3) the open tree layer in site-type 6. Furthermore, the low correlation between soil nutrients and stand density may owe its origin to the forest history; a high correlation may be typical of managed stands, while lower correlations may result from the higher importance of random events in unmanaged stands, causing a generally more open canopy (E. Bendiksen, pers. comm.).

We conclude that the variation along the main coenocline in the spruce forest bears a close relationship with variation in the nutrient status of the humus layer.

Factors controlling the nutrient status of the humus layer

The contrasting vegetation on siliceous and calcareous bedrocks leaves no doubt that properties of the parent material control the initial development of vegetation and humus. When the parent material is homogeneous, however, there are no correspondence between nutrients in the humus layer and subsoil chemistry (Malmström 1949, Bergseth 1977, Sepponen 1985). Through its influence on rates of weathering of the parent material, litter decomposition rates (via temperature), etc. (cf. Sirén 1955, Kuuspialo 1985, Sepponen 1985), topography is the major controlling factor in geologically homogeneous areas (Kuusipalo 1985, Sepponen 1985). This holds true on a broad scale, i.e., between spruce and pine forest sites, but also within each of spruce and pine forests. A spruce stand developing on weathering-resistant parent materials will undergo a meiotrophication if not influenced by particularly favourable topographic or other conditions. With increasing age of the stand, acid litter will accumulate, nutrients will leach to the subsoil where they are immobilized, and a bottom layer of increasing thickness, strongly resistant to decomposition (cf. Mikola 1955, Oechel & van Cleve 1986), will develop. Thus heat transfer into the litter layer is strongly reduced and soil decomposition is further retarded (Sirén 1955, van Cleve & Viereck 1981, Oechel & van Cleve 1986). Reduced humus pH during primary and secondary spruce forest successions is documented by Hesselman (1926, 1937), Malmström (1937) and Sirén (1955).

The biological theory of humus formation (Romell 1935), i.e., that the type of humus formed is controlled by properties of the parent material as mediated by biological differences between the soils, is now generally accepted (cf. C.O. Tamm & Hallbäcken 1986, 1988): In a humid climate with siliceous bedrock (as in the study area), the dominant direction of water movement is downwards. Anions of organic acids produced in the humus layer by decomposition of acid litter cause leaching of metallic cations from the upper inorganic layers by chelatization. Insoluble precipitates are formed in the less acid deeper layers, giving rise to the characteristic podzol profile. Only in sites where the topographic conditions give rise to a favourable local temperature climate or special water supply conditions, will the downward transport be counteracted and the nutrient status remain suitable for larger soil-dwelling organisms that are able to bring about the mixing of layers that is necessary to prevent future nutrient leakage. Soil acidity is critical in determining the composition of the soil fauna; fungi dominate in an acid mor type humus, bacteria (and larger invertebrates like earthworms) in a mull type humus (Glømme 1928, Romell 1935). The importance of the soil fauna in decomposer processes is evident from the results of Hesselman (1937), obtaining an increase in soil pH by 0.4 units after addition of earthworms to a mor humus sample. Soil perturbation by small animals causes increased decomposition rates by exposing new litter surfaces to microbial decomposers (Berg 1986). The positive effects of favourable slope and aspect are associated with increasing temperatures and, in turn, more rapid decomposition (Glømme 1932, Sirén 1955). The strong decrease in the present study in loss on ignition with increasing pH and increasing nutrient concentrations in the humus, demonstrates that the rates of decomposition processes, litter degradation and biological mixing of soil layers increase along the gradient (cf. Bonnevie-Svendsen & Gjems 1957, Lindgren 1975, T. Økland 1988, 1990). Thus the exchangeable amounts of most nutrients, *as well as their turnover rates* (rates of mineralization) in the soil, must be expected to increase along this coenocline. Measured soil nutrient concentrations reflect static conditions in the soil at the time of sampling.

Litter is the most important source of most nutrients (C.O. Tamm & Holmen 1967, Staaf 1982, Buldgen et al. 1983, Kubin 1983, cf. also T. Økland 1988, 1990). The increasing rate of mineralization and litter degredation along the gradient is particularly important for the availability of Ca, being a relatively immobile ion due to the low ability of plants to withdraw it before leaves are shed (Staaf 1982, van Cleve et al. 1983). Ca therefore has to be remineralized from litter to be available for further plant growth (Staaf 1982, T. Økland 1988, 1990). Several studies indicate that the Ca content of the litter shed follows the Ca content of the soil (Mork 1942, Staaf 1982, Falkengren-Grerup 1990a, Aamlid et al. 1992), although the universality of such a relationship has been questioned (Johansson 1986). Ca may be involved in a positive feedback mechanism, as experimental investigations indicate that the Ca content of litter is of critical importance for decomposition rates in later phases of decomposition (Johansson 1986).

Hesselman (1926) postulates that Ca might be the primary environmental factor (cf. Fries 1925, Dahl et al. 1967) responsible for the rate of N mineralization in humus. Dahl et al. (1967) interpret correlations between Ca and N content in humus samples from SE Norwegian forests in favour of this hypothesis. Support to the hypothesis is also expressed by Kuusipalo (1983b) and Sepponen (1985). Despite the existence of two sets of observations which at a first glance appear to be at odds with this hypothesis, viz. (1) that the relationship between Ca and N in humus varies strongly from one study site to another (cf. p. 147), and (2) that Ca is not the environmental variable most closely following the poor-rich coenocline (in this and other studies), the hypothesis may still hold. There are three reasons for this: (1) The availability of Ca (e.g., to the decomposers) may be pH-dependent (Sjörs 1967). Soil acidity is known to affect the N mineralization rate significantly; ammonium release from humus reaches optimum at $4.5 < pH < 5.0$ (Hesselman 1926, Glømme 1932), i.e., in site-types 5.2 and 5.3 in the investigation area, while nitrate production reaches optimum at $5.0 < pH < 6.0$. (2) Kubin (1983) observes lower humus total-N in spruce forest sites with high pH than in low-pH sites due to higher nitrification rates in the former; the more easily available nitrate is more rapidly consumed! This explanation may also apply to lack of correlation between Ca and total-N reported by T. Økland (1990). (3) A low proportion of the total N is available to plants (Nömmik 1968, C.O. Tamm & Pettersson 1969), thus total-N may be poorly suited for assessment of available N. Assessment of the relative importance of Ca content and soil acidity for N availability requires studies of ammonium and nitrate mineralization rates within a vegetation ecological framework.

The response of vascular plants to the complex-gradient in nutrient status

The physiological processes responsible for the response of vegetation to soil nutrient status cannot be decided from vegetation-environment correlations alone, because of (1) the high number of single environmental variables making up the complex-gradient, (2) the variable(s) most strongly correlated with the associated coenocline varies from study to study; pH (Sepponen 1985, Tyler 1989), pH and Ca (T. Økland 1988), pH and N (this study), or a larger group of variables, including pH, Ca, Mn etc. (T. Økland 1990), and (3) the potentially weak relationship between total (exchangeable) amounts measured in most studies and (i) the *rate* of mineralization, which is generally considered to be the factor of critical importance to plants (Kubin 1983, van Cleve et al. 1983, Kuusipalo 1984), and (ii) the amounts of the nutrients in forms easily available to plants (cf. Nömmik 1967).

Experimental evidence unequivocally points to N as the factor restricting vascular plant growth in submesic spruce forests of poor as well as richer sites (Hesselman 1937, Malmström 1949, C.O. Tamm & Carbonnier 1961, Mork & Brantseg 1963, Viro 1967, Albrektson et al. 1977, van Cleve et al. 1983, Gerhardt & Kellner 1986, Kukkola & Saramäki 1983). Addition of N in the form of ammonium and/or nitrate always causes a rapidly increased production, vitality and fertility of most species, while the response to K, P, wood ash, etc. is negligible. Addition of Ca has a small, long-term effect (Becker et al. 1992).

The observations of Kubin (1983) that there may be an inverse relationship between pH and total N despite a more rapid N mineralization in the high-pH sites (cf. above), explain why the N contents of leaves and humus are often uncorrelated (Karlsson 1987). As most of the N in the forest ecosystem is immobilized in the mineral soil (Kubin 1983), N in the humus layer (mostly originating from litter) accounts for more than 90 % of the N consumption by trees (C.O. Tamm & Holmen 1967). Thus the decomposition of litter in the humus layer is of critical importance for the vascular plant species composition in (spruce) forests.

The pH-dependence of the ammonium/nitrate mobilization ratio in forest soils (p. 149) suggests that the vegetational response to the nutrient complex-gradient may not only be a response to the *amounts* of available N, but also to the *form* in which N is supplied. A gradient from species preferring ammonium as their N source to species preferring nitrate, running parallel with the poor-rich coenocline, is demonstrated by experiments (Schlenker 1968, Gigon & Rorison 1972, cf. also Ellenberg 1978, T. Økland 1988). However, most species, e.g., *Vaccinium myrtillus* and *V. vitis-idaea*, are able to exploit both sources (Ingestad 1973).

Soil acidity is often claimed to be the most important cause of vascular plant distribution and abundance along the poor-rich coenocline (cf. Sjörs 1967, Falkengren-Grerup 1989b, Tyler 1989). pH is the single environmental parameter that explains the variation along the poor-rich coenocline the best, in other studies as well as in the present study. Soil acidity does not influence plants directly, but has a major controlling role in spruce forests through its influence on (1) the association of cations to ion exchange sites on the humus particles, and hence on the availability of mineral nutrients, (2) the composition of the soil fauna, and (3) the litter decomposition and N mineralization rates, and hence, the availability of N.

Vascular plants along the complex-gradient in nutrient status: relevance of pattern to process

The variation in vascular plant species composition and α diversity along the coenocline (from site-type 5.1 to 5.3) is followed neither by variation in total cover in the field layer nor the tree layer. There are several indications of low competition among established vascular plants along the nutrient gradient:

(1) The very low number of sample plots with field layer cover above 90 %.

(2) The constant stress in spruce forests due to low radiation (cf. Kuusipalo 1987, 1988, Tonteri et al. 1990a). Spruce forest plants are generally shade-tolerant; C-S-strategists in Grime's (1979) terminology (Lindholm & Nummelin 1983).

(3) Increasing concentration of the root biomass to the upper 5 cm of the humus layer with increasing soil fertility (Kivenheimo 1947).

(4) The presence of species typical of poor, *Vaccinium myrtillus*-dominated spruce forests (site-type 5.1) also in richer site-types.

(5) The report by Havas & Kubin (1983) of *positive* associations between most species (except *Vaccinium myrtillus*) in a N Finnish OMT spruce forest (corresponding to site-type 5.2), while negative associations are the expected outcome of interspecific competition.

(6) The conclusion of Oinonen's (1971) detailed studies of clonal development of spruce forest species, that "only very rarely ... conclusive proof has been obtained for the assumption that one individual would suppress another one, or force it out". Oinonen observed a few *Maianthemum bifolium* and *Pteridium aquilinum* clones establishing within older conspecific clones; the younger clones invariably showing signs of reduced vitality.

(7) The observations by Sirén (1955), Bendiksen (1980) and others, that the cover of vascular plants generally decrease during secondary successions in northern spruce forests.

Except for the negative associations between *Vaccinium myrtillus* and several other species observed by Havas & Kubin (1983), well-documented indications of interspecific competition in spruce forest vegetation are few, and point to pre-emptive competition as the only important kind of competition: seedlings are mostly very rarely encountered, as they are generally dependent on open (disturbed) patches as well as favourable moisture conditions for successful establishment (Södergård 1935, Perttula 1941, Hiirsalmi 1969, Oinonen 1969, 1971, Ericson 1977).

Kuusipalo (1985) suggests increasing fine-scale environmental heterogeneity with increasing fertility as a possible cause of increasing α diversity along the nutrient gradient. This hypothesis does not appear to apply to the studied area, as there are no indications of higher within meso plot variation in subplot scores with increasing fertility. However, increased stoniness in richer slopes (also observed in the investigation area) also increases patchiness and reduces vasular plant competition (Kujala 1926a, Hiirsalmi 1969, Tyler 1989). High patchiness due to fine-scale variation in canopy closure (between trees - under tree gradient) has been claimed to favour coexistence of species differing with respect to shade tolerance (Schaetzl et al. 1989). However, the poor differentiation of vascular plants along DCA 2 in this study (significantly correlated with canopy closure) rather support the claim by Jonsson & Esseen (1990), that the importance of canopy gaps and tree uprooting for field layer composition and α diversity is low (cf. also B. Collins & Pickett 1987, 1988, Beatty & Sholes 1988). The gap structure of the tree layer does, however, influence the population dynamics of the field layer species (Sirén 1955, Havas & Kubin 1983, Hytteborn et al. 1987, Jonsson & Esseen 1990), and, hence, their abundance (Tyler 1989). Competition may also be reduced by herbivory (Ericson 1977).

Indications presented above suggest that physiological tolerance (to low nutrient availability, a stress factor in the terminology of R. Økland (1990a)) is the most important structuring factor for the differentiation of the field layer along the nutrient gradient. Fine-scale patchiness and local disturbance may be important additional structuring factors, providing empty space and facilitating establishment from seeds. As with the topography-soil depth complex-gradient in the pine forests, Kuusipalo's (1985) explanation of the poor-rich coenocline as due to light versus N competition appears inconsistent with available evidence.

The response of bryophytes to the complex-gradient in nutrient status

The importance of edaphical site factors for the composition of bryophyte communities is a controversial matter. Kuusipalo (1988; also see Kujala 1926b, Buch 1947, C.O. Tamm 1953, Brown 1982) maintains that their role is insignificant; Carleton (1990), on the other hand, points to the apparent paradox that these predominantly ectohydric plants are the best site *indicators* in his study area. Variation in bryophyte species composition along a complex-gradient in nutrient status is documented by, for instance, Kuusipalo (1985), Carleton (1990) and T. Økland (1990). In the investigation area, the response of the bottom layer (bryophytes) and vascular plants to the complex-gradient in nutrient status run parallel (high correlations between DCA 1, DCAV 1 and DCAB 1 in Subset A), but the correlations of the major environmental factors (notably Ca and Mg, but also pH, N and LI) are lower with the main cryptogamic coenocline (DCAB 1) than with the main vascular plant coenocline in the spruce forest.

Hypotheses relevant to understanding the response of bryophytes to this complex-gradient will be discussed with reference to the results of the present study:

(1) *Nutrient supply determined by the density of the field and tree layers.* Kuusipalo

(1988) suggests that the soil nutrient level influences bryophytes indirectly, through effects on the tree layer. These effects may owe their origins to an increase in (tree and vascular plant) cover alone, through (i) reduced throughfall (cf. p. 156), and thus reduced total nutrient supply, (ii) reduced light, (iii) increased amounts of litter. There is, however, no correlation between tree and field layer cover and position along this coenocline in this investigation; instead the response to fine-scale variation in canopy closure occurs along the independent second axis of the ordinations (cf. p. 154).

(2) *Nutrient supply determined by concentrations of nutrients released from the tree and field layers.* Increased soil nutrient availability may also cause increasing nutrient concentrations in species of the field and tree layers; in living plants, leaf leachates and litter, because of (i) a change of the chemical constitution of each species along the gradient, and/or (ii) a change of the species composition of the upper layers, favouring species with higher nutrient content (Chapin et al. (1987) present this explanation to the slight increase in P content of *Hylocomium splendens* as a response to higher soil concentrations). The opinions on (i) differ between studies. The concentrations of Ca and P in spruce litter are reported to be positively correlated with soil concentrations by Mork (1942), while generally weak relationships are found by Mikola (1955), and no relationship is noted for Ca by Johansson (1986). Aamlid et al. (1992) did, however, find stongly significant correlations between concentrations in spruce needles *in situ* and humus of Ca, N, and Mn, while Mg and K showed inconsistent patterns of variation. We thus conclude that the importance of (i) cannot yet be decided. With respect to (ii), differences in leaf nutrient concentrations, leaf leakage and litter decomposition rates between species are well-documented (cf. Hesselman 1926, Mikola 1955, Sirén 1955, Taylor et al. 1991). Litter nutrient content influences litter degradation; the initial rate of decomposition is dependent on nutrient concentrations in the litter (Berg & Staaf 1980, Berg 1986, Meentemeyer & Berg 1986), while the rate of decomposition in later phases is controlled by the lignin content (Berg 1986), through the dependence on the decomposition rate of lignin itself (Berg et al. 1982, Berg 1984). The lignin content varies considerably between species, being far lower in herb than in needle litter (Mikola 1955). The chemical composition of "throughfall" precipitation also varies with herb species (R. Hutchinson et al. 1986b). Thus the increasing importance of herbs along the nutrient gradient may in part imply increasing availability of nutrients to bryophytes. However, fine-scaled patterns of vascular plant distribution, apparently not reflected in the distribution of bryophytes (pers. obs.), questions the importance of this hypothesis. The hypothesis is further weakened by the relatively favourable litter also of *Vaccinium myrtillus* (Romell 1939, Mikola 1955), the dominant species towards the deficient end of the gradient.

(3) *Nutrient uptake directly from the soil.* Stålfelt (1937a) expermentally demonstrates water (and nutrient) uptake by *Hylocomium splendens* from moist soil both through external capillary movement and internal transport, despite the fact that this species is known to have a poor ability for internal translocation relative to many other mosses (cf. C.O. Tamm 1953, Weetman & Timmer 1967, Skre & Oechel 1979, Skre et al. 1983, Chapin et al. 1987). However, Stålfelt (1937a) doubts whether water uptake from soil actually takes place in *Hylocomium splendens* under natural conditions, but points out that only a small uptake of nutrients from the soil may be of decisive importance for the moss. Uptake from the soil may be greater for species of other genera, e.g., *Brachythecium* and *Plagiothecium*, growing more closely appressed to the substrate. Acrocarpous species with well-developed subterranean organs and internal transport systems, have the soil as their major source of nutrients (cf. Callaghan et al. 1978).

(4) *Nutrient supply dependent on properties of the humus layer other than the nutrient status per se.* The structural properties of the humus layer, including loss on ignition, vary along the nutrient complex-gradient. La Roi & Stringer (1976) group bryophyte species according to their ability to establish and grow on substrates differing with respect to humus content. The increasing proportion of mineral particles in the upper soil layers may improve the bryophytes´ contact with, and nutrient supply from, the mineral soil in several ways: (i) by direct contact between the moss plants and the mineral particles, e.g., by upward capillary water movement, (ii) by increasing supply of mineral particles from soil dust (Steinnes 1989), (iii) by redistribution of mineral particles from the soil due to irregularities in snowmelt (Steinnes 1989) or surface water flow after heavy rain, and (iv) by increasing supply of mineral particles due to the redistribution caused by the soil fauna (cf. Lyford 1964, Troedsson & Lyford 1973).

(5) *Variation in other properties of the humus layer.* The continuous variation in soil textural and other mechanic properties, including loss on ignition, along the nutrient gradient opens for other explanations as well. For instance, the higher earthworm and subterranean ant activity (Lyford 1964, Troedsson & Lyford 1973) in mull soils may reduce substrate stability along the gradient. This may affect bryophytes in several ways. Interspecific differences in mode of attachment to the substrate may be followed by differences in establishment success, ability to maintain viable polulations, and mortality along the gradient; compare the loosely attached pleurocarpous species of poor sites (*Hylocomium* spp., *Pleurozium schreberi*) and the more closely appressed (and firmly attached) *Brachythecium* spp., *Plagiomnium affine*, etc. of richer sites. This hypothesis requires further testing.

(6) *Population effects of changes in litter quality (type) along the gradient.* Litter quality is as important for the bottom layer as litter quantity. For instance, the small, narrow conifer needles easily penetrate the moss layer, while deciduous leaves cover the moss layer and increase mortality, cf. Kujala (1926b), C.O. Tamm (1953), Oechel & van Cleve (1986), and During & Verschuren (1988). There is a strong increase in the importance of broad-leaved herbs, grasses and deciduous trees along the complex-gradient in nutrient status in the investigation area (cf. Tab. 4). Thus the probability of burial may increase along with changes in the frequency distribution of litter sizes along the gradient (cf. LaRoi & Stringer 1976). Such a gradient in probability of burial may contribute to explain the *change* in the species composition if the species occurring in the "rich" end of the gradient have better ability to escape burial. Several observations suggest that this is actually the case. Kujala (1926b), R. Økland & Bendiksen (1985) and T. Økland (1988) observe lower bryophyte cover *and* shifts in the species composition associated with increasing cover of fern debris. Rincon & Grime (1989) demonstrate that bryophyte species in grasslands and deciduous forests, e.g., *Brachythecium* spp., can tolerate higher litter deposition than species of less productive habitats because of much higher ability to uncouple dry weight increase and length growth: by concentrated length increase in autumn when the litterfall is highest, they are more likely to escape burial.

(7) *Increasing grazing pressure and trampling damage in more fertile sites* may be a result of longer residence time of herbivores.

(8) *Forest fires and other broad-scale disturbance events.* Carleton (1990) suggests that the variation in bryophyte species composition may be due to "apparently random events", such as the probability of establishment after fire. However, the scale of variation in soil nutrient status strongly contrasts the more coarse-scaled patterns of forest fires, both in time and in space (cf. Tirén 1934, Zachrisson 1977, Engelmark 1984), weakening the hypothesis

considerably. So does also the fact that no trace of forest fires have been observed in the vicinity of the sample plots in the investigation area.

Assessment. Hypotheses (1) and (8) are consistent neither with the results of the present study nor with cited experimental evidence, and doubt is expressed as to the importance of hypothesis (2). No evidence in support of hypothesis (7) is known. The remaining four hypotheses may all contribute to explain the response of bryophytes to the complex-gradient in nutrient status. The structural change of the humus from mor to mull brings about improved nutrient supply to the bryophytes by several mechanisms (4); one of these is to enhance the possibility of direct uptake of nutrients from the soil (3). In addition, this structural change of the humus as well as the change in canopy species may affect the population biology of different bryophyte species differently (5, 6).

Bryophytes along the complex-gradient in nutrient status: relevance of pattern to process

The lack of a closed bottom layer in non-paludified sites (total cover variable, but usually below 80 %) indicates that density-independent mortality factors (disturbance) may be important, and hence, that interspecific competition plays an inferior part. As with vascular plants, stress because of low radiation and, in patches, low throughfall precipitation (cf. C.O. Tamm 1953, Abolin' 1974), may reduce growth rates, and hence, competition. Hypotheses (5), (6) and (7) above open for the possibility that the intensity of destabilizing factors varies along the gradient. Variation in the intensity of destabilizing factors may (i) reduce interspecific competition, and (ii) cause shifts in the species composition.

Pine and spruce forests: the fine-scale paludification gradient

The high similarity of the second axes of all ordinations - except vascular plants and micro sample plots - shows existence of a secondary coenocline in the investigated area. Correlations of this coenocline with environmental variables indicate response to a complex-gradient consisting of more or less parallel gradients in soil moisture, fine-scale canopy closure (under tree - between trees gradient), soil depth, and exchangeable amounts of Al and Fe. The apparent lack of vascular plant response indicates that the coenocline is a response to environmental variation on fine spatial scales. The low but significant correlation of the third axes of the vascular plant ordination (DCAV 3) with this secondary coenocline (DCA 2) may indicate some relevance of the complex-gradient (or partly correlated gradients) also to vascular plants (cf. pp. 158-159). Sample plot separation along the second axis occurs all along the main gradient, and the correlations between this coenocline and environmental variables do not differ between spruce and pine forests (Subsets A and B). Thus the secondary complex-gradient is independent of all of the broad-scale topographic gradient and its components; the topography-soil depth complex-gradient in the pine forests as well as the complex-gradient in soil nutrient status.

The secondary gradient is associated with shifts in the bottom layer from dominance of *Sphagnum* spp. at high measured soil moisture, via luxuriance of feather mosses and hepatics, to a poorly developed bottom layer. A similar fine-scale coenocline in the bottom layer, often associated with the degree of *paludification* (cf. Kuusipalo 1985), is reported in several treatises of boreal forest vegetation (e.g., Kujala 1926b, Arnborg 1943, Malmström 1949, 1963, Havas & Kubin 1983, Viereck et al. 1983, Taylor et al. 1987, Svensson & Callaghan

1988, Bonan & Korzuhin 1989, T. Økland 1990, Bendiksen & Salvesen 1992).

Median soil moisture and its relationship to fine-scale paludification

Interpretation of the soil moisture measurements in the present study as median soil moisture values (pp. 140-141), motivates an interpretation of the secondary coenocline as a response to normal (median) soil moisture (cf. Fig. 138).

Neither in the present study nor in the study by T. Økland (1990), are macro scale terrain shape or meso scale (1 m^2) concavity correlated with (median) soil moisture. Thus T. Økland (1990) attributes this variation in soil moisture to topographic variation on scales between the macro- and microtopographical. A likely cause of such a relationship is that the water runoff and transpiration rates, the factors responsible for the pattern of variation in median soil moisture reestablishing within a few days after rain (when the soil matrix has been saturated with water) is controlled by variation in topography on this moderately fine scale. In the investigation area, the relevant scales are likely to be within the interval 1-100 m^2. Correlations between soil moisture and microtopography at these scales are often stressed in connection with studies of pit-mound dynamics (e.g., Beatty 1984, Beatty & Stone 1986, Schaetzl et al. 1989, C. Peterson & Pickett 1990).

Just as a permanently high subsoil water table is a necessary condition for mire formation (Sjörs 1948, R. Økland 1989a), long duration of high soil moisture content is a necessary condition for fine-scale paludification to occur (cf. Sjörs 1948, Havas & Kubin 1983, R. Økland 1989a). The conditions favouring mire formation and fine-scale paludification of boreal forests are the same, but the duration of high subsoil water tables required for fine-scale paludification to occur, are considerably less than for mire formation (cf. Malmström 1949). Fine-scale paludification corresponds to minerogenous mire development on previously dry ground, which may be brought about by two main categories of water supply (mire terminology follows R. Økland 1989a); topogenous and soligenous, corresponding to a nearly horizontal and a sloping subsoil water table, respectively. Accordingly, we distinguish topogenous and soligenous fine-scale paludification.

Topogenous fine-scale paludification occurs in small depressions with impeded drainage and stagnant water, over a wide range of climatic conditions. There are few examples of topogenous paludification in the present material (e.g., meso plot Nos 60, 63, 65, 78, 165); all are associated with shallow depressions in nearly horizontal rock outcrops (site-types 1-2, 2-2 and 3-2 only), covered by a very shallow soil layer. Low importance of topogenous water supply is expected in an area with a broken topography (R. Økland 1989a).

Soligenous water supply (and soligenous fine-scale paludification) is favoured by a humid and cold climate (Sjörs 1948, Eurola 1962, R. Økland 1989a); high precipitation ensures high water supply rates and persistently high median soil moisture levels, low temperatures counteract evapotranspiration. Cold winters with late springs and large amounts of snow contribute strongly to keep the soil moisture high, far into the summer. The study area is situated in a region characterized by dominance of sloping (soligenous) fens (R. Økland 1989a, cf. also p. 14). Local factors promoting soligenous water supply (and soligenous fine-scale paludification) are (cf. R. Økland 1989a): (1) gently sloping terrain, (2) large catchment area (Næss 1969), and (3) impenetrable parent material (Malmström 1937) or lower soil layers (Malmström 1931, Foster & Fritz 1987). The opposing signs of the correlations between median soil moisture (and the coenocline) and slope and soil depth (median soil moisture decreases, slope decreases and soil depth increases along DCA 2) is not unexpected in a superhumid climate: in the investigation area, soligenous fine-scale paludification is favoured by frequent flushing of shallow soils on long, gentle slopes by surface water run-off. This kind of flushing (not to be confused with the wet flushing often resulting in fern-dominated vegetation (cf. pp. 162-163)) apparently causes a minor increase in nutrient content and pH in the area. The slightly stronger correlation between slope and the coenocline in the pine forests than in the spruce forests in this study is due to the wider range of slopes encountered in the pine forests (slope significantly correlated also with the main gradient). While pine forests often occur in horizontal terrain, spruce forests are largely restricted to slopes.

Anaerobic conditions due to waterlogging reduce decomposition and mineralization rates (cf. Mikola 1955, Nykvist 1961a, 1961b, van Cleve et al. 1983, van Cleve & Yarie 1986); with a positive correlation between soil moisture and soil depth as the expected outcome. Such a relationship is reported by Malmström (1949), Sirén (1955), Bergeron & Bouchard (1983), Kuusipalo (1985), and Taylor et al. (1987). Differences in prevailing type of fine-scale paludification is probably the reason why the present study does not fit into this picture: soligenous in the investigation area and topogenous in more continental areas, e.g. in N Sweden and N Finland. T. Økland (1990) found no relationship between soil moisture, soil depth and slope in Rausjømarka (T. Økland 1990), as should be expected if both kinds of fine-scale paludification are important. The shallower soil and somewhat more favourable soil nutrient status of paludified than non-paludified sites in the study area indicate that decomposition rates of litter in the soil increase with increasing supply of moving surface water. Removal of litter in episodes of excess precipitation and high surface water flow rates would strengthen the correlation between soil depth and degree of paludification.

Variation in canopy closure along the gradient

Higher median soil moisture between trees than under trees is noted in several studies (e.g., Sirén 1955, R. Anderson et al. 1969, Minckler et al. 1973, Ipatov & Tarkhova 1980, Taylor et al. 1987, Schaetzl et al. 1989, Tonteri et al. 1990a). In the investigation area, median soil moisture and tree stand density, litterfall etc. are negatively correlated, on the macro as well as the meso scale, and more strongly so in the generally more closed spruce forest (Subset A) than in the pine forest. T. Økland (1990) report a strikingly similar pattern of variation in spruce forests.

Several studies point to a potentially high impact of the tree canopy on soil moisture:

(1) *Canopy interception.* The interception of precipitation by a tree canopy is considerable, causing a gradient in throughfall precipitation quantities from a gap to the stem. Throughfall quantity at a point in space depends on tree species, tree height, canopy density etc., and is lower beneath *Picea abies* than beneath *Pinus sylvestris*, *Betula pubescens* and the other tree species dominating in the study area (cf. Lukkala 1942, 1946, Stålfelt 1944, C.O. Tamm 1953, Sirén 1955, Päivänen 1966, Nihlgård 1970, Mahendrappa & Kingston 1982, Rosén & Lundmark-Thelin 1985). Low throughfall quantities imply low snow cover under trees, and, hence, longer duration of thaw (Arnborg 1943, Sirén 1955, Havas & Kubin 1983).

(2) *Interception by litter.* The great amounts of loose litter occurring under dense spruce trees have low moisture retention capacity (cf. Hesselman 1909, 1917, Malmström 1937, T. Økland 1990), and therefore dry out easily.

(3) *Root uptake of water* increases with increasing needle mass (and tree density), due to increasing transpiration (cf. Taylor et al. 1987, Schaetzl et al. 1989, T. Økland 1990).

(4) *Soil transpiration.* By their shading, trees provide shelter for the soil against evaporation (Stålfelt 1944). This process counteracts differences in soil moisture along the gradient from beneath a tree into the open. The correlations reported in this study indicate that this process is considerably less strong than processes (1) to (3) above.

In the investigation area, independent vegetational variation along the canopy closure gradient, i.e., variation not also attributable to fine-scale paludification, appears to be low. Factors that might contribute to a response to the canopy closure gradient, not associated with soil moisture, are:

(1) *Nutrient input.* Monovalent cations are generally more easily leached from leaves than divalent ions (C.O. Tamm 1953). Throughfall chemistry is dependent on the chemical states of substances in living plant tissues and the chemical composition of precipitation. K^+, Mg^{2+} and Ca^{2+} concentrations are generally higher in throughfall than in incident rain (C.O. Tamm 1953, Abrahamsen et al. 1977, Rosén & Lundmark-Thelin 1985). This may in part explain the higher Ca concentrations in humus under trees reported by Kubin (1983), and why the concentrations of these cations are negatively correlated with soil moisture in spruce forest in the investigation area.

(2) *Litterfall* quantities, determining the probability of burial of bryophytes.

(3) *Radiation.* Radiation is strongly reduced under dense canopies. For instance, Havas & Kubin (1983) observed "light" intensities of one third of the values in interspaces in a dense spruce stand in N Finland during June and July.

Regional trends in the correlation between median soil moisture and canopy closure should be established, in order to judge whether the positive correlation observed by T. Økland (1990) and in this study have general validity.

Variation in the content of Al and Fe in the humus along the gradient

Positive correlations between Al and Fe, as well as between each of these ions and (median) soil moisture, are observed in pine as well as spruce forests in the investigation area. Sepponen (1985) and T. Økland (1990) reports similar observations. The leakage of water soluble organic acids (and hence, the chelatized cations Al and Fe) is considerable in dry sites with predominantly downward water transport (cf. p. 148). Accumulation of Al and Fe occurs in paludified sites because leakage is there counteracted by high water supply rates, high median soil moisture contents, and upward capillary water movement by *Sphagnum* spp. (cf. Granlund 1932). Accumulation instead of leaching promotes development of a humus podzol instead of the iron-humus podzol or iron podzol characteristic of non-paludified sites, cf. O. Tamm (1931), Arnborg (1943) and Malmström (1949, 1963). Accumulation of Al, Fe (and Zn) also occurs in periodically water-saturated peat, i.e. in the zone of water table fluctuation in the peat profile (Damman 1978).

The response of bryophytes to the fine-scale paludification gradient

The variation in species composition in the bottom layer along the fine-scale paludification gradient may be due to effects of (median) soil moisture or correlated factors, e.g., canopy closure.

Responses to median soil moisture. The ectohydric *Sphagnum* spp. respond strongly to variation in median soil moisture because of their good ability to capillary uptake of water (Granlund 1932). The length growth of the *Sphagnum* spp. characteristic of paludified sites is limited by moisture supply (e.g., Clymo & Reddaway 1971, Rydin & McDonald 1985, Andrus 1986). The response of ectohydric bryophytes to this gradient may be because the air humidity in moss carpets depends on soil moisture content. This is supported by Pakarinen & Rinne (1979), observing that the productivity of *Pleurozium schreberi* increases with increasing soil moisture in a spruce forest. The maintenance of high soil water contents by the *Sphagnum* spp. is also likely to be the reason for the preference of *Picea abies* seedlings for sample plots with high soil moisture observed in this study and noted by, inter alia, Arnborg (1943).

Responses to canopy closure. The strong decrease in bryophyte cover along this coenocline, and the shifts in species composition near the dry end of the gradient, may be due to any of the three factors varying along the canopy closure gradient (p. 157): (1) reduced light under dense canopies (Stålfelt 1937b, C.O. Tamm 1953, Tarkhova & Ipatov 1975), (2) high litterfall (suggested for some species, e.g., *Dicranum polysetum* and *Hylocomium splendens*, by Tarkhova & Ipatov (1975)), and (3) insufficient water supply (Malmström 1937, Abolin 1974, Busby et al. 1978), resulting in drought stress (Skre et al. 1983, Hytteborn et al. 1987). The relative importance of these factors requires further study.

A well-developed bryophyte layer within or around canopy gaps accentuates the differences in (median) soil moisture along the canopy closure gradient. Feather-mosses (and *Dicranum majus*?) intercept a considerable part of the precipitation (Stålfelt 1937a, Sirén 1955). However, the moss layer also has an insulating effect; causing reduced temperatures and hence, reduced soil transpiration, increased soil moisture, reduced decomposition and reduced nutrient availability (Stålfelt 1937a, Teivainen 1952, Sirén 1955, van Cleve et al. 1983, van Cleve & Yarie 1986, Oechel & van Cleve 1986).

Bryophytes along the fine-scale paludification gradient: relevance of pattern to process

Differentiation of the bottom layer along the fine-scale paludification gradient is likely to be in accordance with the competitive hierarchy theory, just as the differentiation of species along the hummock-hollow gradient in bogs (cf. Rydin & McDonald 1985, Andrus 1986, Rydin 1986, R. Økland 1990c): the paludified habitat is optimal for many species, but slower-growing species are displaced towards drier sites because of too low growth rates to avoid overgrowth by the *Sphagnum* spp. The rarity of a completely closed bottom layer in paludified sites in forests, indicate that competitive exclusion by the *Sphagnum* spp. may frequently be prevented by litter accumulation and other kinds of disturbance, as discussed above.

Interpretation of the third axis of the vascular plant ordination

Optima of species (and sample plots) separate along the third vascular plant ordination axis (DCAV 3), indicating a coenocline from high importance of thermophilous (southern and southeastern) species to high importance of suboceanic (western) species. As no explanatory variables are available to support such an interpretation, no more than speculations can be offered. Altitude (not formally treated as a variable) apparently increases along DCAV 3 (indicated from the joint occurrence of the high-situated plots of transects 1, 7 and 8 towards one end of the axis). An interpretation that also accounts for the slight correlation of DCAV 3 with DCA 2, is that the differentiation is due to thermal differences (and differences in humidity) caused by differences in altitude (cf. R. Økland 1989a). Thus this gradient in vascular plant composition operates on a broad scale; the partial coincidence with the fine-scale paludification gradient reflects the increasing areal importance of soligenous paludification at higher altitudes. A similar coenocline may also be caused by differences in aspect favourability (van Cleve et al. 1983, R. Økland & Bendiksen 1985, Sepponen 1985, Heikkinen 1991). Better representation of slopes facing south and west in our material might have strengthened the differentiation along this coenocline.

Interpretation of micro-scale patterns

The gradients in vegetation and environmental conditions possible to identify in a particular study depend on several factors (e.g., R. Økland 1989a, 1990a, 1990b), among them (1) sample plot size, (2) relative amounts of co-ordinated and unco-ordinated variation in species abundances ("structure" and "noise" in the terminology of Gauch (1982)), and (3) the method for quantification of species abundances.

The variation in species abundances in a data set can be partitioned into between plots and within plot variation, of which only the former can be extracted as gradient structure by numerical techniques (cf. R. Økland 1990a). The smaller the sample plots, the higher a proportion of the total variation is between plots variation (Smith & Urban 1988, R. Økland 1989a), the more homogeneous are the plots (R. Økland 1990a), and the finer are the grains of vegetation patterns and environmental variation that can be separated (Green 1979, Gauch 1982, R. Økland 1989a). This explains the increase in gradient length estimates in DCA with decreasing sample plot sizes in this study (cf. also R. Økland et al. 1990). The lower limit for acceptable sample plot size is set by representativity (R. Økland 1990a): the demand for occurrence of a sufficiently high number of species with sufficiently narrow tolerances, in order for the plot to be adequately placed along the major coenoclines (and for sufficiently precise inference of the environmental conditions at the site from the species composition). The method used for quantification of species abundances is known to have considerable effects on pattern recognition by ordination (cf. Jensén 1978, van der Maarel 1979, R. Økland 1986, T. Økland 1988, Eilertsen et al. 1990). In the following, we will discuss the results obtained by use of different sample plots sizes and abundance scales in the light of the three points mentioned above.

Differences in β diversity between layers

The gradients identified in this study by analysis of meso sample plots reflect variation on different spatial scales; rough estimates for the broad-scale topographical complex-gradients and the fine-scale paludification gradient are 10^2-10^4 m^2 and 10^{-1}-10^1 m^2, respectively. The ß diversity of the bottom layer is higher than field layer ß-diversity along the main gradient(s) (compare gradient length estimates in DCAV and DCAB, cf. Tab. 8). Similar patterns are reported for coniferous forests by McCune & Antos (1981) and R. Økland & Bendiksen (1985), and by R. Økland (1990c) for mires. The more fine-grained variation in composition of the bottom layer as compared to the field layer is due to the smaller size of the cryptogams, and the fact that most cryptogams lack extensive subterranean organs like the roots of the vascular plants. Clonal vascular plants, e.g., *Lycopodium annotinum*, are able to nutrient transport over several decimeters (Headley et al. 1985, Callaghan et al. 1986), thus differing from most bryophytes in ability to integrate over environments (Kujala 1926b, Svensson & Callaghan 1988, Maslov 1989, Palmer & Dixon 1990). More fine-grained patterns of variation in the field layer vegetation than those observed by use of 1 m^2 sample plots in this study, should not be expected to occur. This also explains why the response to the fine-scale paludification gradient is almost only reflected in the composition of the bottom layer.

Interpretation of micro-scale ordinations

There are no indications in this study of additional coenoclines in the bottom layer, in response to more fine-scaled complex-gradients, as evident from the facts that (1) the first four axes of meso sample plot and meso subplot ordinations (DCA and DCAS) are strongly correlated, and (2) only one axis of the ordination of micro sample plots (DCAM) appears interpretable. There may be several reasons for (2):

(i) More fine-grained gradients exist, but lack of available micro-scale environmental variables has made them impossible to discover and/or to interpret. This could be the case for the DCAM ordination, but is not very likely as the ordination of this data set did not even enable recognition of a dominant gradient such as the fine-scale paludification gradient.

(ii) The range of the abundance scale, 16, used for ordination of micro sample plots, is inappropriate. DCA generally performs better with a lower range of the abundance scale when the ß diversity of the material is high (R. Økland 1986), i.e., when the ratio of qualitative to quantitative variation in the data set is high, as in the present case. The better interpretability of the meso subplot ordination (which is based on presence/absence in subplots) than the ordination of micro plots, lends additional support to this view. Weir & Wilson (1987) similarly obtained better species-environment correlations in small sample plots using presence/absence than quantitative data. It is important to note that a reduction of the range of the abundance scale (which is done by weighting, cf. R. Økland 1986) is not equivalent with a reduction in the number of subplots. While a positive effect of the former might be anticipated (in micro sample plot ordination), this is not the case with the latter (cf. p. 165).

(iii) Low representativity of smaller plots (low species number) is not likely to have affected the micro plot and meso subplots ordinations, as the DCAS axes conform to the DCA axes.

(iv) Low areal importance of specific micro niches may prevent representation of end-points of micro-scale coenoclines by a sufficiently high number (or fraction) of plots to allow extraction as ordination axes. This may be the case with "pockets" in the forest floor (cf. R. Økland & Bendiksen 1985), the vegetation of stones, stumps, twigs and other wooden remains, etc.

The causes of within meso plot variation

There existence of considerable micro-scale variation in vegetation is evident from the considerable variation in meso subplot scores within many meso plots (a mean range of 0.8 S.D. units along both DCAS 1 and DCAS 2). This variation may have several causes:

(1) Random variation due to low representativity of the subplots. Meso plot values for (i) range of variation in subplot scores and (ii) minimum number of species in any subplot, are only slightly negatively correlated. This applies to DCAS 1 as well as DCAS 2 (cf. p. 133). The fraction of variation in subplot range possible to explain by species number was only 6 and 4 per cent for the two axes, respectively! The strong congruence of DCA and DCAS axes also contradicts this hypothesis.

(2) Micro-scale variation in environmental factors (scales below 1 m^2) causes a

cryptogamic species response not qualitatively different from the response observed along more broad-scale gradients. This hypothesis is forwarded for a N Swedish boreal birch forest by Svensson & Callaghan (1988), observing that a sample plot size of 0.01 m^2 is not sufficiently fine to detect patterns different from the more broad-scaled patterns. Carleton (1990, cf. also Palmer & Dixon 1990) suggests that broad-scale species responses are actually the results of "more immediate processes which operate at the scale of the within-stand microhabitats". Variation in microtopography, the factor most often mentioned as responsible for micro-scale patterns in forests (Havas & Kubin 1983, Beatty 1984, Schaetzl et al. 1989) may in fact cause micro-scale vegetation shifts corresponding those observed along *all three main complex-gradients*!! Higher risk of desiccation in convex microhabitats (mounds) than in concave pits is documented by Beatty & Stone (1986) and C. Peterson et al. (1990). Micro-scale variation in soil depth often follows microtopography (cf. Svensson & Callaghan 1988). The parallel variation in vegetation might resemble the variation along the topography-soil depth complex-gradient. In more nutrient-rich forests, there is often a mosaic pattern with the more nutrient-demanding species in low-lying and the less demanding species in elevated sites (Kuusipalo 1984). Beatty (1984) and Beatty & Stone (1986) show that there may be considerable variation in pH, Ca and other nutrients with microtopography; the mounds generally being poorer in nutrients than the pits. The fine-scale paludification gradient has previously been connected with fine- (and micro-)scale microtopographic variation (p. 155).

The absence of correlations between the microtopographical indices and the two first ordination axes may be due to (i) general shortcomings of the convexity and unevenness indices, (ii) their use on inappropriate scales, or (iii) the small shifts in vegetation caused by microtopography are masked in trends of microtopographic variation along the major complex-gradients. If vegetation responds to microtopography as hypothesized above, the microtopographic position of each meso subplot and DCAS ordination score should be correlated within each meso subplot. No data are presently available to test whether this is the case.

The observations of Troedsson & C.O. Tamm (1969; cf. also Palmer & Dixon 1990) that the variance of pH, Ca and N (in % of LI) is almost constant on all scales below ca. 1 m^2, point to the existence of environmental heterogeneity on scales down to the size of moss individuals! Considerable variation in several soil properties, both in time and in space, are documented by Hesselman (1937), Troedsson & C.O. Tamm (1969), Beckett & Webster (1971), Troedsson & Lyford (1973), Bringmark (1989) and Nykvist & Skyllberg (1989). Many factors that may contribute to this fine-scale heterogeneity are mentioned; the variation in microtopography, the activity of soil-dwelling animals (ants, earthworms), faeces, root growth and dieback, and the occurrence of stones, stumps, wood pieces and logs. However, neither Troedsson & C.O. Tamm (1969) nor Nykvist & Skyllberg (1989) were able to relate fine-scale variation (on scales from 0.1-1 m^2) in N and pH to variation in microtopography or to variation in vegetation. These topics obviously require further study.

(3) Micro-scale variation in environmental factors that causes a cryptogamic species response qualitatively different from the response observed along broad-scale gradients. We have previously commented on the possible occurrence of micro-niches of too low areal importance to result in interpretable gradient patterns ("pockets", etc.). We are, however, not aware of any documentation of micro-scale vegetation patterns in coniferous forests explained as responses to micro-scale gradients in the environment other than those correlated with microtopograpy (see (2), above).

Different kinds of unpredictable variation ("noise" (Gauch 1982), or "disorderliness" (Fowler 1990)) may also contribute significantly to within meso-plot variation (e.g., in meso subplot ordination scores). Important sources of unpredictability are: (4) fine-scale inter- and intraspecific interactions, (5) fine-scale destabilizing factors (disturbance and fluctuations), causing density-independent mortality (cf. R. Økland 1990a), and (6) other random events.

COMPARISON WITH OTHER STUDIES AND IMPLICATIONS FOR CLASSIFICATION

The existence of one broad-scale coenocline in boreal coniferous forests corresponding to the full range of variation in topographic positions has been appreciated for a long time (cf. Cajander 1909, 1921, Kalela 1961, Whittaker 1956, 1960), and has later been substantiated by studies from different parts of the circumboreal zone using numerical methods; N. America (e.g., Carleton & Maycock 1978, Zoladeski 1988, Allen & Peet 1990, Carleton 1990) as well as N. Europe (Kuusipalo 1985, Milberg 1986, Lahti & Väisänen 1987, Tonteri et al. 1990b). However, the environmental *interpretation* of this coenocline differs strongly between studies; corresponding coenoclines have been referred to as a "fertility gradient" (e.g., Dahl et al. 1967, Kielland-Lund 1981, Kuusipalo 1985, Lahti & Väisänen 1987, Allen & Peet 1990, Carleton 1990, Tonteri et al. 1990b) as well as a "(topographic) moisture (-fertility) gradient" (e.g., Whittaker 1956, Peet 1981, R. Økland & Bendiksen 1985).

We have stressed that the main coenocline in the investigation area is in fact the response to two complex-gradients, both conditioned by topographic variation: a topography-soil depth complex-gradient in the pine forests on rigdes and upper slopes, and a complex-gradient in soil nutrient status in the spruce forests on lower slopes. On more favourable parent materials, however, the occurrence of nutrient-rich soils is independent of topographic position, and no correlation between the two complex-gradients exists (cf. Bjørndalen 1980, Rajakorpi 1984, Heikkinen 1991). Despite the existence of one main *coenocline* on poor parent materials, separation of the two underlying complex-gradients is thus the key to understanding vegetation-environment relationships in the boreal coniferous forest.

The results of the ordination analyses performed in this study do not only support a two-gradient approach to classification of boreal coniferous forest vegetation according to local gradients (R. Økland & Bendiksen 1985 and this study, cf. also the N Swedish forest site-type system by Eneroth (1931, 1934, 1937) and Arnborg (1943, 1964)), but also motivate some modifications of such systems. Site-types 1 to 5.1 make up a series of poor site-types along the topography-soil depth complex-gradient, corresponding to the series along the dryness gradient in the N Swedish forest site-type scheme (cf. Arnborg 1964), and the parallel site-type series on poor ground in the Finnish system of forest site-types (cf. Kalela 1961, Hämet-Ahti 1963, Kalliola 1973). Site-types 5.1-5.3 make up a series of submesic site-types along the complex-gradient in soil nutrient status, corresponding to variation along the nutrient gradient in the N Swedish system of forest site-types.

R. Økland & Bendiksen (1985) also include a mesic series, dominated by tall ferns, along their "topographic moisture" gradient. Fern-dominated vegetation is generally considered to be dependent on wet flushing in the sense of Dahl (1957; also see Samuelsson 1917, Nordhagen 1928, 1943, Malmström 1949, Kielland-Lund 1981 and R. Økland & Bendiksen 1985): water movement parallel with the soil surface or even upwards, counteracting the leaching normally associated with a downward water stream. In the investigation area, transitions to tall fern and herb vegetation (site-type 6) occur on terraces and in groves, obviously dependent on moderate flushing. Nutrient conditions of flushes are normally more favourable than adjacent, non-flushed sites. As fern-dominance is thus dependent on a special set of environmental conditions, flushed sites should not be included in simple two-gradient representations of major vegetational variation.

SOME COMMENTS ON THE FIELD METHODOLOGY IN VEGETATION ECOLOGICAL STUDIES, WITH PARTICULAR EMPHASIS ON MONITORING

Montitoring vegetational changes: choice of strategy

Two contrasting opinions of optimal strategies for monitoring vegetational changes are reflected in recent publications; T. Økland (1990) maintains that "using methods for relating vegetation to the environmental variables on which vegetation is dependent should be considered an important part of all vegetation monitoring programmes ... in order to distinguish between changes caused by man, natural variation in vegetation and changes due to factors intrinsic to the ecosystems", while Wilmann & Engen (1991) hold the opinion that sample plots should *not* be placed along gradients but instead be independent replicates from one vegetation type. They further argue that investigations of environmental factors and vegetation-environment relationships should not be included in the monitoring programmes. Wilmann & Engen (1991) emphasize statistical testing of changes in quantities of single species as the main purpose of vegetation monitoring, while understanding the causes of these changes, if not obvious, should be taken on as separate investigations. T. Økland (1990) consider data analysis by ordination an important part of the monitoring programme, as such methods enable recognition of complex, multi-species trends; resultants of trends in individual species that are mostly not significant. Ordination and related techniques are powerful methods for detection of structure in a species-sample plot data matrix (e.g., ter Braak & Prentice 1988, R. Økland 1990a and references quoted therein). Their efficiency for analysis of temporal trends is well documented (e.g., Grootjans et al. 1991, R.J. Whittaker 1991, Becker et al. 1992). In our opinion, ordination and related techniques are by far superior to single-species tests for early detection of temporal trends, assessment of their significance, and, by inclusion of environmental variables in the monitoring concept, understanding of their causes.

The performance of ordination (and constrained ordination) based on the correspondence analysis concept is best with data sets of high and moderate β diversity (ter Braak & Barendregt 1986, ter Braak & Looman 1986, R. Økland 1990a). Thus the inclusion of variation along gradients is necessary for this tool to be applicable, in monitoring as well as in general-purpose ecological analysis. Other advantages of including β diversity are: (1) one does not have to guess which vegetation type is most likely to respond the first to environmental changes, and (2) temporal trends can be related to variation along local environmental gradients, thus facilitating interpretation of causes of change (meiotrophication giving sample plot displacement along a coenocline associated with variation in soil nutrient status, etc.). Inclusion of variation along gradients does not preclude testing changes in the quantities of single species in relatively homogeneous subsets.

Sampling design

Acceptance of ordination as an important part of data treatment in vegetation monitoring and a necessary link between vegetational and environmental monitoring has implications for the choice of field methodology. The transect sampling method used in the present study is considered superior to the traditional subjective sampling techniques used in vegetation studies, due to the higher objectivity of the results; no single sample plot is placed according to the ecologist's personal preferences. Thus the representativity of observed trends for the studied area is likely to be good. However, the method also has obvious disadvantages:

(1) Common vegetation types (and combinations of environmental conditions), e.g., site-types 3-1, 4-1, 5.1-1 and 5.2-1 in this study, are heavily sampled, while gradient extremes, e.g., site-types 1-2 and 6, are poorly represented in the material. This is problematic when these extremes are represented by so few samples that their variation and relationships to the remaining material are poorly defined (Minchin 1987, R. Økland 1990b).

(2) The low number of transects make many combinations of environmental conditions unrepresented in the material, while there is considerable redundancy in others. In the present study, warm, S and SW-facing slopes are underrepresented while there is considerable redundancy for site-type 5.1.

Both for the purpose of establishing which are the most important complex-gradients affecting the vegetation in a study area and for the purpose of vegetation monitoring, some of the objectivity provided by the transect method should be sacrified in order to obtain a more balanced representation of major combinations of environmental factors, including heavier sampling of gradient extremes. The most favourable compromise is likely to be randomization within selected blocks (R. Økland 1990a), as used in NIJOS' monitoring programme (T. Økland 1990).

Sample plot size

Sample plot size must be selected after consideration of vegetation properties, methods to be used for data treatment, and the desired resolving power (spatial scale on which patterns are to be detected). A practical compromize has to be made between the mutually exclusive demands for homogeneity (the smaller the sample plots, the more homogeneous, the lower is the within-plot variation in species composition and environmental parameters, and the better is the spatial resolving power) and representativity (the larger the sample plots, the higher the number of species per sample plots, and the better is the predictability of coenocline positions from the plots' vegetational composition), cf. R. Økland (1990a).

The partial coincidence of patterns produced by ordinations of meso and micro plots, and the fact that no new, interpretable gradients are detected by use of the smaller plot size are strong indications that sample plots smaller than, say, 0.25 m^2, are not suitable for general-purpose vegetation ecological investigations in forests. Furthermore, the results of this study suggest the use of 1 m^2 as standard sample plot size in general-purpose coniferous forest vegetation studies. The arguments of Wilmann & Engen (1991) in favour of 0.25 m^2 rather than 1 m^2 sample plots rest on different basic opinions on purpose and strategy in vegetation monitoring (cf. p. 163), and will not be discussed further. The fact that the number of species per sample plot is sufficient for representativity of all (or almost all) of the 200 sample plots in this study, indicate that there are no reasons for a further increase in the sample plot size.

This is in accordance with T. Økland (1988) and Rydgren (1989) who consider 25 m^2 too large for recovery of major gradients in forest vegetation.

Quantification of species abundances

Frequency in subplots used for quantification of species abundances often gives interpretable ordination results (e.g., T. Økland 1988, 1990, R. Økland 1990a, Eilertsen 1991). The use of 16 subplots apparently gives an acceptable weighting of quantitative versus qualitative variation with moderate sample plot sizes (cf. R. Økland 1986, 1990a, T. Økland 1988), although it is not known whether this number of subplots is optimal. The use of more subplots, combined with weighting to a lower range (10-25), might result in improved ordinations (in terms of correlations between coenoclines and explanatory variables). Loss of precision in ordination is the likely result of the recommendation of Wilmann & Engen (1991) that the number of subplots should be reduced to four (and the sample plot size reduced to 0.25 m^2).

As discussed by T. Økland (1988), frequency in subplots is recommended to cover estimation due to higher objectivity, exactness, less influence of time of the year the analysis is performed on the results, and, above all, far lower sampling error due to subjectivity in estimations (cf. also Kennedy & Addison 1987, Tonteri 1990) and danger of introduction of systematic errors (Falkengren-Grerup 1990b). Impacts of inter-observer differences on ordination results have been shown to be small in the case of frequency estimations (R.J. Whittaker 1991), but occasionally high in the case of cover estimations (Tonteri 1990). Thus the more time-consuming frequency estimation is considered worthwhile (T. Økland 1988).

STRUCTURING PROCESSES AND THEIR RELEVANCE TO ECOSYSTEM THEORY

Structuring processes in the field layer

The present investigation indicate that vascular plants in the boreal coniferous forest experience high environmental stress; the most important stress factors being recurrent episodes of moisture deficiency (in the pine forests), and low incoming radiation (in the spruce forests). Stress reduces competition (Grime 1973, Fresco 1982) by inhibiting competitively superior species from monopolizing the critical resources (Grime 1979, Pickett 1980). Competitive interactions, e.g., suppression of other species by *Vaccinium myrtillus*, may occur locally, but competition apparently is mostly for empty space. The dynamics in the field layer is poorly known, but destabilizing factors, including those producing gaps in the tree layer, may be important by producing the empty spaces needed for recruitment to the field layer. Thus the field layer may also function in accordance with the patch dynamics or gap dynamics theories of non-equilibrium coexistence (cf. Whittaker & Levin 1977, Pickett & Thompson 1978, Pickett 1980, Chesson & Case 1986, Grubb 1986).

Structuring processes in the bottom layer

The diversity of structuring processes affecting the composition of the bottom layer in the investigated area is appearently higher than in the field layer, as evident from discussions above. Furthermore, they vary in relative importance along the major complex-gradients. R. Økland (1990a, 1990c) distinguish several kinds of structuring processes; their importance to the bottom layer will be discussed in turn:

(1) *Interspecific interactions: competition.* Several authors assume that interspecific competition is generally one of the most significant processes in the boreal forest floor (Kujala 1926b, C.O. Tamm 1953, Kuusipalo 1985, Slack 1990, Vitt 1990). However, this view is neither consistent with the high frequency of naked patches in the forest floor along all major complex-gradients, nor with the high number of species in most sample plots, also plots with high bryophyte cover, in the investigation area. Interspecific competition may be reduced by morphological differences between co-occurring species: the disadvantage of generally lower length growth rates of acrocarpous than pleurocarpous mosses under similar conditions (Pakarinen & Rinne 1979, Kuusipalo 1988) may, for instance, be outweighted by the advantage of the vertical shoot orientation, favouring escape from overgrowth (C.O. Tamm 1953, Pakarinen & Rinne 1979). However, competition may locally be important in patches sheltered from the influence of destabilizing factors. Competition for empty space is important in a patchy environment.

(2) *Interspecific interactions: facilitation.* The high number of bryophyte species co-occurring in the boreal coniferous forest floor indicate that some mechanisms may favour coexistence. Kujala (1926b) mentions the possibility that coexistence of major moss species may be aided by small interspecific differences in growth rates in similar habitats. Coexistence will also be favoured if the improved survival in closed mats resulting from a more favourable microclimate (Callaghan 1987, Hobbs & Pritchard 1987, Scandrett & Gimingham 1989, During 1990) is larger than the decrease in survival resulting from competitive interactions.

(3) *Destabilizing factors; disturbance.* The high areal important of empty space in the bottom layer at most positions along all major gradients, indicate that the intensity (and episodic frequency) of fine-scale disturbance factors (that increase density-dependent mortality and produce empty space; cf. During & van Tooren 1987, van Tooren et al. 1987) is generally sufficiently high to prevent competitive exclusion, except possibly in small, sheltered patches. The most important destabilizing factors are considered to be: (i) litter cover, as demonstrated by several studies (e.g., Kujala 1926a, 1926b, C.O. Tamm 1953, Sydes & Grime 1981, During & Verschuren 1988, During & van Tooren 1990), (ii) tree uprooting and other meso-macro scale disturbance. also acting to increase habitat diversity (Jonsson & Esseen 1990), (iii) grazing by rodents and other herbivores; bryophytes are important parts of the diet of microtine rodents (O. Kalela 1957, O. Kalela et al. 1963, Hansson 1969, 1971, Oechel & Sveinbjörnsson 1978); all species are consumed with the possible exception of some hepatics (O. Kalela et al. 1963), thus rodent grazing may result in more or less density-independent mortality, (iv) trampling; providing open patches in runways etc. (Kellomäki & Saastamoinen 1975, Ericson 1977), (v) manuring and urinating, particularly by large mammals (Frisvoll & Flatberg 1990).

High importance of density-independent mortality factors is in accordance with recent studies of During & ter Horst (1987) and During & van Tooren (1987, 1990), showing high rates of species replacement in the bottom layer, mostly due to local, fine-scale disturbances and re-establishment. Furthermore, these studies indicate that the rate of dynamics in the bottom layer is positively correlated with species richness (During & ter Horst 1987).

(4) *Destabilizing factors: fluctuations.* Environmental fluctuations (e.g., drought and temporary occurrence of very high temperatures) restrict species distributions along gradients by causing local extinctions (cf. p. 143-145). Environmental fluctuations may also promote coexistence by periodic reversal of competitive superiority (G. Hutchinson 1961).

(5) *Stress.* The effects of stress, fluctuations and fine-scale disturbance on the boreal forest floor (in spruce forest exemplified by low incoming radiation, periodic drought, and high litterfall under dense spruce canopies, respectively) can hardly be separated as their intensities vary together along the canopy closure gradient. Stress promotes coexistence by reducing growth rates, and hence, competitive effects.

(6) *Chance.* The high importance of random processes is demonstrated by the often very different species composition in apparently similar, recently created patches favourable for colonization by more ruderal species, e.g., naked humus patches in lichen-dominated vegetation (also see Oksanen 1984, R. Økland 1990c), and mineral soil "pockets" in submesic spruce forest sites (cf. also R. Økland & Bendiksen 1985).

Assessment. Indications from the present study point to the relatively higher importance of fine- (and micro-)scale disturbance than interspecific competition, in accordance with patch dynamics theories of non-equilibrium coexistence (Pickett 1980, During & ter Horst 1987, During & van Tooren 1990). The older view of high stability of the forest floor (cf. Kujala 1926b, Slack 1990, Vitt 1990) is obviously in need of revision, but more studies in this field are urgently needed to gain a proper understanding of the processes.

Relevance to ecosystem theory

The field and bottom layers of the investigation area both appear to be non-equilibrium systems on a fine scale, thus conforming to the patch dynamics or gap dynamics theories. Similar explanations for the dynamics of the tree layer have been generally accepted for a long time (Sernander 1936, Hytteborn et al. 1987, Bonan & Shugart 1989, Leemans 1991). In conclusion, we therefore forward the hypothesis that the main structuring processes are essentially the same in all layers, although operating on different scales and partly through different environmental factors.

The gradient interpretation of the vegetation in the investigation area is relevant to current discussions of vegetation models. The main coenocline is the result of two complex-gradients; along which species responses are mostly set by physiological tolerance. This is accordance with Austin (1990), suggesting that physiological tolerance might be more important as determinant of patterns than hitherto assumed (cf. also R. Økland 1992). Asymmetry of competitive interactions (whenever occurring), with superiority for the species with the highest maximal growth rate (e.g., Grime 1979, Hutchings 1986), leads to competitive hierachies (Wilson & Keddy 1986, Keddy 1990, Goldberg & Landa 1991). Kuusipalo (1985), on the other hand, interprets a coenocline corresponding to the main coenocline in the present study as a light-nutrient competition gradient in accordance with Tilman's (1982, 1988) approach. The present study suggests (1) that such an interpretation is not adequate, in close agreement with results of studies in boreal mires (cf. R. Økland 1992), and (2) that models of resource competition are particularly inadequate for soil-inhabiting cryptogamic species competing for space rather than for resources in short supply.

GENERAL CONCLUSIONS

The identical results obtained by use of parallel DCA and LNMDS ordinations of the vegetation in permanently marked sample plots, provide a firm fundament for monitoring of temporal changes in vegetation and environmental conditions, and for the understanding of possible vertical relationships (soil-bottom layer-field layer-trees, or the opposite). This fundament is further improved by the fact that the major environmental threats (airborne pollutants and climatic change) are expected to lead to vegetational changes corresponding to shifts along the two main ordination axes (cf. Wittig & Werner 1986, Falkengren-Grerup 1990b).

A study like the present should also provide a good starting point for further studies addressing important, still unsolved questions in boreal forest ecology: (1) assessment of the rate of natural, fine- and micro-scale dynamics in the bottom and field layers by observations in the permanent plots, (2) knowledge of the micro-scale spatial variation in disturbance intensity, (3) knowledge of the extent of micro-scale variation in environmental parameters, (4) understanding the extent and causes of micro-scale vegetation patterns, (5) knowledge of the population biology of important species, and its relationship to environmental variation, and (6) assessment of the importance of identified complex-gradients for other organisms (fungi, soil-dwelling animals, herbivores). The regional validity of the hypotheses forwarded in this paper on the basis of one study area, should be tested by studies in other regions.

DESCRIPTION OF SITE-TYPES

INTRODUCTION

Naming of site-types

The site-types were defined and delimited *a priori* by division of the complex-gradients assumed at the start of the study to be the most important (principles of classification are described on pp. 25-27). The fourteen site-types encountered in the investigation area (cf. p. 31) were coded by a number combination, referring to positions along the complex-gradients. The present study has, to a large extent, confirmed the importance of three coenoclines corresponding to the complex-gradients selected *a priori*, although the causal relationships between environmental variation and vegetation response is not always clear.

The soil moisture deficiency hypothesis as explanation to variation along the "topographic moisture gradient", cf. pp. 140-142, suggests that the names xeric (site-type 1), subxeric (site-type 3) and submesic (site-type 5) used by R. Økland & Bendiksen (1985) should be adopted. The mesic series of R. Økland & Bendiksen (1985) (site-type "7" in this work) should, according to discussions on pp. 162-163, not be included as end-point of this gradient, but appears rather to be dependent on flushing. Thus, site-type 6 in this work is termed "slightly flushed". The importance of the "complex-gradient in nutrient status" is confirmed by the analysis, and site-types are named as suggested on p. 26. In accordance with discussions on pp. 154-156, the steps along the "complex-gradient in fine-scale moisture" are termed non-paludified and paludified, respectively.

Comments to descriptions

Site-type descriptions are based on materials from the investigation area only. Standard descriptions, vegetation tables and tables of untransformed environmental parameters (Appendix 4) are given for each site-type. The ecological descriptions are in accordance with conclusions of the discussion.

Comparisons with other authors are restricted to Kielland-Lund (1981) and Fremstad & Elven (1987) from Norway and Kujala (1961) and Kalela (1961) from S and C Finland. Corresponding site-types in R. Økland & Bendiksen (1985) are evident from the site-type names.

DESCRIPTIONS

1-1: The non-paludified xeric site-type

Vegetation. The floristic composition of this site-type is shown in Tab. 19. Constant species were *Pinus sylvestris*, *Calluna vulgaris*, *Vaccinium vitis-idaea*, *Dicranum scoparium*, *Pohlia*

Tab. 19. The vegetation of the 1-1 site-type. Species quantity is given as frequency in subplots. The right column gives mean ± S.D. for explanatory and biotic variables; constancy and mean frequency in subplots for species.

Sample plot	12	14	64	79	114	160	163	178	179	184	188	191	
N-TOT	23	23	18	21	15	10	15	19	15	14	23	21	18.1±4.3
N-VAS	5	4	6	4	3	4	3	4	1	4	5	6	4.1±1.4
N-BOT	18	19	12	17	12	6	12	15	14	10	18	15	14.0±3.8
MA Can (x10)	1	3	3	0	3	3	1	2	0	5	3	0	2.0±1.6
ME Lit (x10)	0	3	7	0	7	8	0	3	0	2	0	0	2.5±3.2
CC	12	22	30	7	65	20	2	2	1	20	17	30	19±18
CD	35	30	40	85	70	10	90	90	30	45	65	35	52±27
Pinus sylvestris	3	5	1	2	1	1	7	7	5	3	4	3	100^{4}
Calluna vulgaris	3	11	15	4	16	9	2	2	.	7	9	16	92^{9}
Vaccinium myrtillus	14	11	8	6	.	2	.	2	.	4	4	5	75^{6}
V. vitis-idaea	9	14	16	2	15	16	6	5	.	15	10	2	92^{10}
Carex pilulifera	.	.	2	.	.	.	.	.	.	.	.	1	17^{2}
Dicranum drummondii	1	.	.	1	2	.	.	3	2	.	2	.	50^{2}
D. fuscescens	.	.	.	4	.	.	.	1	.	.	.	.	17^{3}
D. montanum	1	11	.	.	.	.	.	.	.	.	.	.	17^{6}
D. polysetum	16	12	.	1	4	.	.	.	.	.	4	2	50^{7}
D. scoparium	4	8	4	4	5	4	2	.	3	3	16	.	83^{5}
D. spurium	2	.	.	11	.	1	.	9	6	.	.	10	50^{7}
Leucobryum glaucum	.	1	.	11	.	.	2	.	.	.	1	.	33^{1}
Pleurozium schreberi	9	14	8	.	10	8	.	3	2	.	2	5	75^{7}
Pohlia nutans agg.	9	4	1	5	1	.	3	4	1	.	9	2	83^{4}
Racomitrium lanuginosum	.	.	6	.	.	.	2	.	.	1	2	5	42^{3}
Sphagnum capillifolium	.	1	.	.	.	.	.	.	.	.	.	1	17^{1}
Barbilophozia floerkei	4	.	.	.	.	.	.	.	.	.	16	7	25^{9}
Cephaloziella sp.	.	.	.	2	.	.	.	.	.	.	1	9	25^{4}
Ptilidium ciliare	3	5	1	.	2	.	.	2	.	.	4	.	50^{3}
Cetraria islandica	.	5	11	13	.	.	16	10	8	11	12	10	75^{11}
Cladina arbuscula	6	11	2	.	16	5	9	14	7	3	.	.	75^{8}
C. mitis	.	.	6	16	.	.	.	.	10	11	.	.	33^{11}
C. rangiferina	2	12	12	16	5	15	7	14	14	15	9	14	100^{11}
Cladonia bellidiflora	12	12	.	12	3	.	11	13	5	9	15	3	83^{10}
C. chlorophaea agg.	16	8	15	14	3	11	7	11	12	12	10	15	100^{11}
C. coccifera agg.	5	2	.	.	.	.	.	.	.	.	.	16	25^{8}
C. deformis	5	.	.	.	.	.	.	1	.	.	.	.	17^{3}
C. gracilis	.	2	.	11	.	.	5	.	2	6	1	.	50^{5}
C. squamosa	1	10	4	5	1	.	4	3	3	.	16	11	83^{6}
C. sulphurina	9	2	.	2	.	.	.	.	.	.	.	.	25^{4}
C. uncialis	.	7	8	11	.	.	3	8	4	13	11	13	75^{9}

Additional species (occurring in only 1 sample plot; Plot No.: Frequency in subplots):

Picea abies 64:2, Empetrum nigrum 188:3, Melampyrum pratense 191:1, Luzula pilosa 12:1; Polytrichum juniperinum 178:3, Barbilophozia lycopodioides 14:2, Lophozia ventricosa agg. 188:7, Cladonia cornuta 12:3, Stereocaulon saxatile 114:1.

nutans agg., *Cladina rangiferina*, *Cladonia bellidiflora*, *C. chlorophaea* agg., and *C. squamosa*. Local dominants, often with high subplot frequency, were *Calluna vulgaris* and *Vaccinium vitis-idaea* in the field layer, while *Cetraria islandica*, *Cladina arbuscula*, *C. mitis*, *C. rangiferina*, *Cladonia bellidiflora*, *C. chlorophaea* agg., *C. coccifera* agg., and *C. squamosa* locally reached high subplot frequency in the bottom layer.

The mean number of species per sample plot was 18, while the total number in the 12 sample plots was 45.

The field layer normally had a relatively sparse dwarf shrub cover (below 30 % in all plots except one), that could exceptionally be almost absent (e.g., plot 179). Lichens and naked humus occupied almost the same areas. Bryophytes were quantitatively unimportant.

Environment. The environmental data for this site-type are given in Appendix 4. The site-type mostly occurred on level or elevated sites (rock outrops), with a convex macro-scale topography. Plot 12 was situated on a convex-shaped rock outcrop in a long slope.

Pinus sylvestris was the only dominant in the open, low-stature tree layer. This site-type typically occurred between large pine trees, often in mosaic with site-type 2-1 (or 3-1) occurring under the trees.

The humus layer thickness was variable, often shallow and with considerable mixing of inorganic particles (coarse sand). The organic matter content was between 50 and 90 %. The humus layer was strongly acid; pH_{H2O} = 3.9-4.3, pH_{CaCl2} = 3.1-3.4, with moderate or small amounts of cations and total N (1.39-2.09 % of organic matter).

Variation. Only 9 species occurred in the field layer, and variation was with respect to the relative importance of dominants and the occurrence of occasional species. Plots 163, 178 and 179, with field layer cover of 1-2 % only, were transitional to non-forested rock outcrop vegetation. The variation in the bottom layer was considerable; 12 species had a subplot frequency of 12 or more in at least one plot. With few exceptions, dominance relationships changed throughout each plot; the size of patches dominated by a single species varied from a few cm^2 for the small *Cladonia* spp. to some sq. dm for *Cladina rangiferina* and *Cetraria islandica*. The total cover of the bottom layer showed some relationship to tree density; plot 160 with the lowest cover in the bottom layer was situated underneath a pine tree.

Notes. *Vaccinium myrtillus* individuals were mostly small with reduced vitality. Dead bilberry ramets occurred frequently.

Bryophytes occurred as single individuals within the lichen carpet (e.g., *Pohlia nutans* agg.), or in small, pure carpets intermingled with lichen-dominated patches (e.g., *Dicranum polysetum*, *D. scoparium*, and *D. spurium*). Cracks in the lichen carpet and frequent occurrence of naked soil indicate high death risks and high re-establishment rates of lichens and bryophytes.

Corresponding site-types: Kielland-Lund (1981): Cladonio-Pinetum pp. Elven & Fremstad (1987): A1 (transitions between A1a and A1c). Kujala (1961), Kalela (1961): ClT.

1-2: The paludified xeric site-type

Vegetation. The floristic composition of this site-type is shown in Tab. 20. Constant species were *Pinus sylvestris*, *Vaccinium vitis-idaea*, *Dicranum scoparium*, *Pohlia nutans* agg., *Cladina rangiferina*, *Cladonia chlorophaea* agg. and *C. uncialis*. Occasional local dominants in the field layer with high subplot frequency were *Calluna vulgaris*, *Empetrum nigrum* and *Vaccinium vitis-idaea*. Quantitatively important species in the bottom layer in one or more plots were *Dicranum scoparium*, *Pleurozium schreberi*, *Cladina mitis*, *C. rangiferina*, *C. bellidiflora*, and, notably, *Cetraria islandica*.

The mean number of species per sample plot was 19, while the total number in the 3 sample plots was 33.

The field layer was sparse in two out of three plots while one plot had mixed dwarf

Tab. 20. The vegetation of the 1-2 site-type. For explanation, see Tab. 19.

Sample plot	63	113	193	
N-TOT	17	23	17	19.0±3.4
N-VAS	5	5	6	5.3±0.6
N-BOT	12	18	11	13.7±3.8
MA Can (x10)	1	1	1	1.0±0.0
ME Lit (x10)	1	13	8	7.1±6.2
CC	7	35	7	16±16
CD	85	70	80	78±7
Betula pubescens	.	.	2	33^{2}
Pinus sylvestris	4	7	1	100^{4}
Calluna vulgaris	8	14	.	66^{11}
Empetrum nigrum	.	12	.	33^{12}
Vaccinium myrtillus	.	1	7	67^{4}
V. vitis-idaea	2	15	2	100^{6}
Carex panicea	.	.	7	33^{7}
C. pilulifera	5	.	10	67^{8}
Scirpus cespitosus	5	.	.	33^{5}
Dicranum drummondii	.	7	.	33^{7}
D. polysetum	.	4	.	33^{4}
D. scoparium	14	7	6	100^{9}
D. spurium	1	.	.	33^{1}
Pleurozium schreberi	.	12	.	33^{12}
Pohlia nutans agg.	11	3	1	100^{5}
Racomitrium lanuginosum	10	.	1	66^{6}
Sphagnum capillifolium	.	8	1	67^{5}
S. compactum	.	.	2	33^{2}
Barbilophozia attenuata	.	1	.	33^{1}
B. floerkei	.	2	.	33^{2}
Cephaloziella sp.	.	3	.	33^{3}
Ptilidium ciliare	.	9	.	33^{9}
Cetraria islandica	16	.	16	67^{16}
Cladina arbuscula	1	8	.	67^{5}
C. mitis	15	.	6	67^{11}
C. rangiferina	6	13	4	100^{8}
Cladonia bellidiflora	15	5	.	67^{10}
C. chlorophaea agg.	5	3	5	100^{4}
C. coccifera agg.	8	4	.	67^{6}
C. squamosa	.	4	2	67^{3}
C. sulphurina	.	1	.	33^{1}
C. uncialis	10	4	2	100^{5}

shrub dominance. The bottom layer was mostly well stocked, with equal prominence of mosses and lichens. *Sphagnum* spp. were not prominent in the rather atypical sample plots encountered in the material, but *S. capillifolium*, *S. compactum* and exceptionally also *S. tenellum* (transitions to sloping fens) were all observed as dominants in this site-type.

Environment. The environmental data for this site-type are given in Appendix 4. This site-type mostly occurred on level or elevated sites, often with fine-scale conditions (small cracks in the bedrock, small (diameter < 1 m) depressions) favouring topogenous paludification (plot 63). Site-type 1-2 was also observed in sloping sites with soligenous paludification (slightly sloping terrain in 113 and 193).

Pinus sylvestris was the only dominant in the tree layer. As with site-type 1-1, this site-type typically occurred between large pine trees, often in mosaic with site-types 1-1, 2-1 (and 3-1) and 2-2.

The humus layer was shallow, except below *Sphagnum* where peat could accumulate. Most often, this site-type occurred in mosaic with naked rock. The organic matter content was variable. The humus layer was strongly acid; pH_{H2O} = 4.0-4.1, pH_{CaCl2} = 3.1-3.3, with moderate or small amounts of cations and moderate amounts of total N (1.66-2.27 % of organic matter).

Variation. There was a considerable variation in dominance relationships in the field and bottom layers, not evident from the sparse material. Part of this variation was associated with variation from topogenous to soligenous paludification; *Sphagnum capillifolium* preferring the former, *S. compactum* and *S. tenellum* the latter. There was a continuous variation from transitions to site-type 1-1 (plot 63) via forms with shared dominance of lichens, mosses and *Sphagnum* spp., to soligenous fens on very shallow peat. This variation was associated with variation in topography (watershed area, ground water flow rates, etc.).

Notes. An element of species characteristic of sea-shores with fluctuating water tables and poor fens, e.g., *Carex panicea* and *Scirpus cespitosus*, is notable.

Corresponding site-types: Elven & Fremstad (1987): A1 (close to A1c).

2-1: The non-paludified xeric-subxeric transitional site-type

Vegetation. The floristic composition of the site-type is shown in Tab. 21. Constant species were *Calluna vulgaris*, *Vaccinium vitis-idaea*, *Dicranum scoparium*, *Pleurozium schreberi*, *Ptilidium ciliare*, *Cladonia rangiferina*, and *Cladonia chlorophaea* agg. In addition to *Calluna vulgaris* and *Vaccinium vitis-idaea*, *Empetrum nigrum* locally reached dominance. The quantitatively most important species in the bottom layer were *Dicranum scoparium*, *Pleurozium schreberi*, *Cetraria islandica* and *Cladina rangiferina*.

The mean number of species per sample plot was 17, while the total number in the 13 sample plots was 48.

The field layer was characterized by a moderate dwarf shrub cover, mostly in the range 40-75 %, but both sparsely (10-20 % in plots 183 and 185) and densely covered plots (plot 164) occurred. The total cover in the bottom layer was variable, from very sparse (2 % in plots 162 and 164) to well stocked (90 % in plot 185). On average, less than half the bottom layer was covered with cryptogams. Lichens were quantitatively most important, but bryophytes also dominated small patches.

Environment. The environmental data for this site-type are given in Appendix 4. The site-type occured on elevated (both level and sloping) sites with a convex macro-scale topography. Typically, the soil was shallow to moderately deep.

The open tree layer was dominated by *Pinus sylvestris*. With few exceptions (plots 59 and 61), stand densities were below 50 %. Most sample plots represented interspaces between trees, but some plots had high values of the litter index (plots 59 and 162). Site-type 2-1 often occurred in mosaic with site-type 3-1 (close to trees).

The thickness of the humus layer was variable, from very shallow to ca. 10 cm. Some mixing of inorganic particles occurred (loss on ignition above 70 %). The humus layer was strongly acid; pH_{H2O} = 3.8-4.3, pH_{CaCl2} = 3.0-3.4, with small amounts of cations and a low total N content (1.20-2.05 % of organic matter).

Variation. There was some variation in the relative dominance of dwarf shrub species.

Tab. 21. The vegetation of the 2-1 site-type. For explanation, see Tab. 19.

Sample plot	13	58	59	61	83	84	87	90	93	162	164	183	185	
N-TOT	23	14	15	15	16	19	27	21	12	11	10	17	16	16.6±4.9
N-VAS	5	3	4	6	5	3	5	8	3	3	4	6	4	4.5±1.5
N-BOT	18	11	11	9	11	16	22	13	9	8	6	11	12	12.1±4.4
MA Can (x10)	1	1	8	6	0	5	3	0	1	3	3	0	3	2.6±2.5
ME Lit (x10)	0	2	22	10	0	6	0	0	0	12	7	0	0	4.5±6.7
CC	40	40	60	65	35	40	70	75	65	60	95	10	20	52±24
CD	40	55	12	40	70	45	60	17	15	2	2	60	90	39±2
Picea abies	1	.	.	.	.	.	.	1	.	.	.	.	.	15^{1}
Pinus sylvestris	.	.	.	4	.	1	.	3	.	.	3	4	3	46^{3}
Calluna vulgaris	.	8	1	7	14	9	6	15	16	7	16	7	.	84^{10}
Empetrum nigrum	11	.	.	12	5	.	11	16	.	.	.	4	.	46^{10}
Vaccinium myrtillus	16	15	16	14	16	.	16	16	.	16	.	15	12	66^{15}
V. uliginosum	6	.	8	.	.	.	16	13	.	.	.	.	9	38^{10}
V. vitis-idaea	14	15	16	16	16	15	13	16	16	16	16	9	1	100^{14}
Melampyrum pratense	.	.	.	.	5	.	.	.	1	.	.	5	.	23^{4}
Carex pilulifera	.	.	.	.	.	.	.	1	.	.	2	.	.	15^{2}
Dicranum drummondii	9	.	.	.	6	1	.	.	.	.	.	.	.	23^{5}
D. fuscescens	.	.	.	.	1	.	.	.	5	.	1	.	.	23^{2}
D. polysetum	2	6	2	.	5	2	3	.	.	.	.	.	.	46^{3}
D. scoparium	5	.	3	2	6	7	15	7	12	4	.	7	3	85^{6}
D. spurium	1	.	.	.	.	.	.	3	.	.	.	4	.	23^{3}
Leucobryum glaucum	.	.	.	.	1	.	1	.	.	.	.	.	3	23^{2}
Pleurozium schreberi	16	11	16	16	15	1	9	14	14	14	10	15	5	100^{12}
Pohlia nutans	4	1	.	.	.	4	5	.	.	.	.	.	.	31^{4}
Polytrichum commune	.	.	.	.	.	7	3	.	.	.	3	.	.	23^{4}
Sphagnum capillifolium	.	.	.	1	.	.	4	.	1	.	.	.	.	23^{4}
Barbilophozia floerkei	11	.	.	2	.	.	16	14	8	.	.	.	.	38^{10}
Calypogeia neesiana	.	.	.	.	.	.	6	1	.	.	.	.	.	15^{4}
Cephaloziella spp.	3	.	.	.	.	4	.	1	1	.	.	.	1	38^{2}
Lophozia ventricosa agg.	1	.	.	.	.	.	13	3	.	.	.	.	.	23^{6}
Ptilidium ciliare	2	1	1	5	8	1	5	6	.	2	.	1	4	85^{3}
Cetraria islandica	2	.	6	1	16	14	1	.	1	6	.	11	16	77^{7}
Cladina arbuscula	.	6	4	1	8	6	.	.	.	.	7	3	.	54^{5}
C. mitis	.	3	1	.	.	11	2	.	.	.	.	3	5	38^{6}
C. rangiferina	.	16	2	1	2	11	4	2	.	4	7	7	5	85^{6}
Cladonia bellidiflora	10	.	2	.	.	.	12	.	.	.	.	3	5	38^{6}
C. chlorophaea agg.	14	14	2	8	1	11	5	3	7	3	.	8	11	92^{7}
C. coccifera agg.	1	.	.	.	.	.	7	.	.	.	.	.	.	15^{4}
C. furcata	.	.	.	.	.	1	.	4	.	3	.	.	.	23^{3}
C. squamosa	2	.	.	.	.	.	.	.	.	.	.	1	.	15^{2}
C. sulphurina	7	.	1	.	.	.	.	.	.	.	.	.	.	15^{4}
C. uncialis	2	.	.	.	.	1	12	5	.	1	1	.	6	54^{4}

Additional species (occurring in only 1 sample plot; Plot No.: Frequency in subplots):

Erica tetralix 61:12; Aulacomnium palustre 87:1, Dicranum montanum 58:2, Hylocomium splendens 13:2, Racomitrium heterostichum agg. 90:9, R. lanuginosum 87:5, Sphagnum quinquefarium 87:5, Barbilophozia attenuata 87:1, B. lycopodioides 93;3, Ptilidium pulcherrimum 185;2, Cladonia cornuta 58:1, C. deformis 84:2, C. gracilis 183:1.

The indication from the material that field layer cover was not related to tree layer closure, was not generally valid (own obs.). The bottom layer was strongly variable, depending on the dominance of upper layers. Low cover was observed in plot 164, being almost completely covered by dwarf shrub phytomass, plot 162, and plot 59 situated under a large pine tree.

Pleurozium schreberi was the only prominent species beneath a dense field layer, giving way to dominance of *Cladina* spp. in more open patches. Plots 13 and 87 occurred in slopes (both on the meso and macro scales). Both included *Barbilophozia floerkei* as a prominent species and had high species numbers (23 and 27, respectively). Several species occurring in these plots, e.g., *Leucobryum glaucum, Polytrichum commune, Sphagnum capillifolium,* and *Calypogeia neesiana,* indicated temporarily wetter conditions and a transition to site-type 2-2. Fine-scale patchiness in the bottom layer was a charactetistic feature of this site-type.

Notes. The relatively low cover in the bottom layer indicate high death risks (and/or establishment difficulties) for bryophytes and lichens. This applies to open plots as well as plots with a dense dwarf shrub cover.

Cladonia chlorophaea agg. is the most prominent of the small *Cladonia* spp. in shaded sites and in sites with high litterfall, as evident from its frequent colonization of *Calluna* litter in dense stands.

Corresponding site-types: Kielland-Lund (1981): Transitions between Cladonio-Pinetum, Leucobryo-Pinetum, Barbilophozio-Pinetum and Vaccinio-Pinetum. Elven & Fremstad (1987): A1-A2-A3 transitions. Kujala (1961): ClT-CT transitions. Kalela (1961): ClT-ECT-EVT transitions.

2-2: The paludified xeric-subxeric transitional site-type

Vegetation. The floristic composition of this site-type is shown in Tab. 22. Constant species were *Pinus sylvestris, Calluna vulgaris, Vaccinium myrtillus, Pleurozium schreberi* and *Sphagnum capillifolium.* Dominants with high subplot frequency were *Calluna vulgaris* in the field layer, *Pleurozium schreberi* and *Sphagnum capillifolium* in the bottom layer.

The mean number of species per sample plot was 20, while the total number in the 8 sample plots was 54.

The field layer had a sparse to moderate dwarf shrub cover. The bottom layer was well developed except in the atypical plot 165. *Sphagnum capillifolium* (occasionally *S. compactum* as in plot 126) was always prominent, but mosses were also important. The role of lichens was variable, but *Cetraria islandica* and *Cladina rangiferina* both occasionally reached dominance.

Environment. The environmental data for this site-type are given in Appendix 4. The site-type most frequently occurred on moderately sloping sites with a distinctly convex macro-scale topography, associated with soligenous paludification (plots 126, 129, 131, 190, and 192). Occurrences in small depressions in level terrain with a distinctly convex macro-scale topography, associated with topogenous paludification, were noted in Transects 4 and 6 (plots 60, 78 and 165).

The only dominant in the open tree layer was *Pinus sylvestris.* The site-type mostly occurred in the interspaces between pine trees, in mosaic with site-types 1-1, 2-1, and 3-1.

The humus layer was shallow, except below large *Sphagnum* patches. The organic matter content was above 70 %, highest below *Sphagnum.* The humus layer was strongly acid; pH_{H2O} = 3.8-4.3, pH_{CaCl2} = 3.0-3.4, with small amounts of cations and total N (1.31-2.12 % of organic matter).

Variation. The field layer was mostly dominated by *Calluna vulgaris,* but occasionally the normal subdominants *Vaccinium myrtillus* and *V. vitis-idaea* dominated on the expense of *Calluna* (plots 60 and 192). The bottom layer was strongly variable, with changes in

Tab. 22. The vegetation of the 2-2 site-type. For explanantion, see Tab. 19.

Sample plot	60	78	126	129	131	165	190	192	
N-TOT	15	20	121	20	24	17	24	21	20.3±3.1
N-VAS	4	7	5	6	10	5	7	5	6.1±1.9
N-BOT	11	13	16	14	14	12	17	16	14.1±2.1
MA Can (x10)	3	2	0	0	1	1	0	3	1.2±1.3
ME Lit (x10)	0	9	0	0	0	0	0	2	1.4±3.2
CC	45	17	30	60	65	70	40	22	43±20
CD	45	60	70	75	60	10	75	75	59±22
Picea abies	.	2	1	9	1	.	.	.	50^{3}
Pinus sylvestris	.	5	3	4	3	5	1	4	88^{4}
Sorbus aucuparia	.	1	.	.	.	.	.	2	25^{2}
Calluna vulgaris	1	10	16	15	16	15	12	9	100^{12}
Empetrum nigrum	.	.	.	12	14	8	1	.	50^{9}
Vaccinium myrtillus	16	9	.	15	16	9	3	11	88^{11}
V. uliginosum	5	.	.	.	11	.	.	.	25^{8}
V. vitis-idaea	14	1	.	.	16	16	8	12	75^{11}
Melampyrum pratense	.	3	2	2	2	.	.	.	50^{2}
Carex pilulifera	.	.	4	.	2	.	3	.	38^{3}
Dicranum drummondii	.	.	.	.	.	.	12	4	25^{8}
D. polysetum	.	5	.	.	.	.	.	3	25^{4}
D. scoparium	6	4	8	11	8	3	.	.	75^{7}
Leucobryum glaucum	.	.	2	.	3	.	.	.	25^{3}
Pleurozium schreberi	16	16	4	10	16	10	5	10	100^{11}
Pohlia nutans agg.	.	2	3	2	2	2	.	2	75^{2}
Polytrichum commune	2	.	2	.	.	.	.	.	25^{2}
Racomitrium lanuginosum	.	.	.	9	4	.	5	3	50^{5}
Sphagnum capillifolium	12	15	5	11	14	13	4	16	100^{11}
S. compactum	.	.	8	.	.	.	.	5	25^{7}
Barbilophozia floerkei	2	.	.	16	8	.	2	7	63^{7}
Calypogeia neesiana	.	.	1	.	.	.	1	.	25^{1}
C. sphagnicola	.	.	.	8	5	.	.	.	25^{7}
Cephaloziella sp.	.	.	4	.	.	.	6	.	25^{5}
Lophozia ventricosa agg.	.	.	3	11	5	.	.	2	50^{5}
Ptilidium ciliare	1	4	.	7	4	.	6	.	63^{4}
Cetraria islandica	.	.	15	12	.	2	10	3	63^{8}
Cladina arbuscula	4	4	.	.	.	2	.	.	38^{3}
C. rangiferina	9	12	4	.	.	9	13	.	63^{9}
Cladonia bellidiflora	.	.	.	2	1	4	7	1	63^{3}
C. chlorophaea agg.	16	7	2	.	1	4	16	.	75^{8}
C. furcata	.	.	.	.	.	2	1	.	25^{2}
C. squamosa	2	.	11	.	.	.	5	2	50^{5}
C. uncialis	.	.	.	.	.	4	11	3	38^{6}

Additional species (occurring in only 1 sample plot; Plot No.: Frequency in subplots):

Betula pubescens 131:1, Populus tremula 190:6; Dicranum majus 129:4, D. spurium 126:1, Polytrichum juniperinum 78:11, Sphagnum russowii 129:2, Barbilophozia attenuata 60:3, B. lycopodioides 192:1, Cephalozia loitlesbergeri 131:2, C. lunulifolia 131:2, Gymnocolea inflata 192:1, Lophozia bicrenata 192:2, Mylia taylorii 129:8, Sphenolobus minutus 78:1, Cladina mitis 165:2, Cladonia coccifera agg. 190:1, C. coniocraea agg. 78:5, C. fimbriata 78:5, C. gracilis 190:2, C. sulphurina 126:2.

dominance from *Sphagnum* to mosses, hepatics or lichens within few cm. Part of this variation was associated with variation from topogenous to soligenous paludification. The species composition of plots with topogenous paludification was close to site-type 2-1; dominated by

Pleurozium schreberi, *Sphagnum capillifolium* and *Cladonia rangiferina*. *Cladina arbuscula* only occurred in the three plots with topogenous paludification. Several species were more or less confined to sites with soligenous paludification, e.g., *Leucobryum glaucum*, *Racomitrium lanuginosum*, *Sphagnum compactum*, *Barbilophozia floerkei*, *Calypogeia neesiana*, *C. sphagnicola*, *Cephaloziella* spp., *Gymnocolea inflata*, *Lophozia bicrenata*, *Lophozia ventricosa* agg., *Mylia taylorii* and *Sphenolobus minutus*. Within the soligenously paludified plots, there was a variation from the transitional plots 190 and 192 via plot 131 to plots 126 and 129, associated with increasing (meso and macro scale) slope and increasing importance of species preferring soligenous paludification.

Humus layer pH also appeared to vary according to the kind of paludification; sample plots with topogenous paludification (and stagnant water) consistently had lower pH (pH_{H20} = 3.8-3.9) than the sample plots with moving water (pH_{H20} = 4.0-4.3). Corresponding differences in cation contents were not observed.

Notes. Several species characteristic of more mesic forests reach their absolute limit towards the dry end of the soil moisture deficiency gradient in this site-type, e.g., *Calypogeia neesiana*, *Cephalozia loitlesbergeri* and *C. lunulifolia*.

The occurrence of some western species, e.g., *Racomitrium lanuginosum* and *Mylia taylorii*, should be noted.

Corresponding site-types: Kielland-Lund (1981): Barbilophozio-Pinetum sphagnetosum. Elven & Fremstad (1987): A2-A3 transitions.

3-1: The non-paludified subxeric site-type

Vegetation. The floristic composition of this site-type is shown in Tab. 23. Constant species were *Calluna vulgaris*, *Vaccinium myrtillus*, *V. vitis-idaea* and *Pleurozium schreberi*. The most frequently occurring dominants in the field layer were the three dwarf shrub species listed above; they are also the species normally reaching the highest subplot frequency. *Empetrum nigrum* and *Vaccinium uliginosum* dominated locally. The only dominant in the bottom layer, mostly occurring in all subplots, was *Pleurozium schreberi*.

The mean number of species per sample plot was 11, while the total number in the 21 sample plots only was 40.

The field layer was densely stocked with dwarf shrubs. The bottom layer was variable, if well developed then dominated by mosses, while hepatics and lichens were quantitatively unimportant.

Environment. The environmental data for this site-type are given in Appendix 4. Occurrence of site-type 3-1 was associated with a convex topography, level or slightly to moderately sloping (5-15°).

The tree layer was mostly open and dominated by *Pinus sylvestris*, but occasionally with scattered *Betula pubescens* and *Picea abies* of reduced vitality. The site-type occurred between as well as underneath trees, and in dense as well as open pine stands.

The humus layer was mostly rather thick, often in the range 5-10 cm. The soil was mostly not stony; the median soil depth of (9-)25-50 cm thus reflected the depth to the bedrock. With few exceptions, the organic matter content of humus was high (above 80, in a majority of cases above 90 %). The humus was strongly acid; pH_{H20} = 3.7-4.2, pH_{CaCl2} = 3.0-3.3, with moderate to small amounts of cations and small amounts of total N (1.06-1.75 % of organic matter).

Tab. 23. The vegetation of the 3-1 site-type. For explanation, see Tab. 19.

Sample plot	62	66	81	82	85	86	88	89	91	92	112	158	159	161	166	176	177	181	182	186	189	
N-TOT	10	8	10	7	10	15	18	12	16	15	18	11	5	6	8	7	7	16	13	10	12	11.1±4.0
N-VAS	3	4	4	6	5	6	5	6	6	5	4	4	4	4	4	5	5	7	5	4	5	4.8±1.0
N-BOT	7	4	6	1	5	9	13	6	10	10	14	7	1	2	4	2	2	9	8	6	7	6.3±3.7
MA Can (x10)	3	0	4	2	3	3	3	0	0	3	1	1	8	6	0	5	3	4	2	3	0	2.6±2.1
ME Lit (x10)	9	0	16	10	14	0	0	0	0	1	3	0	8	13	2	13	14	4	2	12	0	5.7±5.9
CC	90	85	85	65	90	50	75	90	60	70	70	85	95	95	85	100	100	85	50	85	85	81±15
CD	40	75	35	30	15	90	40	55	35	7	65	40	2	1	20	1	0	80	10	20	55	34±28
Pinus sylvestris	.	1	.	.	.	.	.	.	2	.	1	4	.	.	.	.	.	1	1	.	.	29^2
Calluna vulgaris	16	16	16	2	7	7	15	16	16	16	13	16	4	4	2	11	15	14	12	12	14	100^{12}
Empetrum nigrum	.	.	7	12	13	8	.	16	16	.	.	.	.	16	.	16	13	5	.	.	16	52^{13}
Vaccinium myrtillus	16	15	16	16	12	16	16	16	16	16	16	16	16	10	16	16	16	16	14	16	16	100^{15}
V. uliginosum	.	.	.	16	.	4	.	16	14	.	.	.	9	.	14	.	16	3	.	16	10	48^{12}
V. vitis-idaea	16	16	16	16	15	16	16	16	12	16	16	16	16	16	16	16	16	16	15	16	16	100^{16}
Melampyrum pratense	.	.	.	6	2	.	5	4	.	5	.	.	.	.	.	.	.	14	2	.	.	33^5
Dicranum polysetum	3	1	10	.	.	9	15	2	.	4	12	10	.	.	10	.	1	1	3	8	8	71^6
D. scoparium	.	.	1	.	9	10	10	9	7	8	.	1	.	.	.	.	.	9	12	12	5	57^8
Pleurozium schreberi	16	16	16	15	15	16	16	16	16	16	16	14	16	13	16	2	7	14	14	15	16	100^{14}
Pohlia nutans agg.	.	.	.	.	.	.	3	.	.	1	3	.	.	.	.	.	.	.	.	.	.	14^2
Sphagnum capillifolium	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	3	.	.	.	.	.	14^2
Barbilophozia floerkei	11	.	.	.	.	5	9	.	1	1	11	.	.	.	.	.	.	1	.	1	.	38^5
B. lycopodioides	.	.	.	.	.	5	9	8	.	1	10	.	.	.	.	.	.	.	.	.	5	29^6
Ptilidium ciliare	12	.	13	.	7	15	3	11	2	4	14	8	.	.	.	.	.	11	3	10	12	67^9
Cetraria islandica	.	2	2	.	.	.	3	.	.	.	.	.	.	.	.	.	.	2	10	.	.	24^4
Cladina arbuscula	.	6	.	.	.	.	.	.	.	.	5	2	.	.	.	.	.	4	3	.	.	24^4
C. rangiferina	5	.	1	.	1	4	5	.	12	1	10	14	.	.	3	.	.	.	5	3	5	62^5
Cladonia chlorophaea agg.	2	.	.	.	.	1	.	.	10	.	7	2	.	.	.	.	.	.	1	.	.	29^4

Additional species (occurring in two sample plots or less; Plot No: Frequency in subplots, Constancy and mean frequency in subplots):

Picea abies 176:1 5^1, Sorbus aucuparia 92:1 5^1, Erica tetralix 86:1 5^1, Monotropa hypopitys 88:1 5^1; Dicranum drumondii 112:7, 166:4 10^6, Dicranum majus 92:2 5^1, Hylocomium splendens 112:8, 181:2 10^5, Leucobryum glaucum 88:1 5^1, Plagiothecium laetum agg. 92:1 5^1, Polytrichum commune 89:1 5^1, Ptilium crista-castrensis 86:1, 181:5 10^3, Racomitrium heterostichum agg. 112:3 5^3, R. lanuginosum 91:1, 161:2 10^2, Barbilophozia attenuata 112:2 5^2, Calypogeia neesiana 88:1 5^1, Lophocolea heterophylla 88:2 5^2, Cladonia bellidiflora 112:5 5^5, C. crispata 91:9 5^9, C. furcata 62:1, 91:1 10^1, C. gracilis 91:3 5^3, C. phyllophora 189:1 5^1.

Variation. Variation in the field layer was with respect to dominance between dwarf shrub species. There was no clear relationship between cover (or dominant species) in the field layer and development of the tree layer. There was considerable variation in the total cover in the bottom layer. Poor bottom layer development (0-2 % cover) was always associated with a dense field layer (95-100 % cover) dominated by *Vaccinium myrtillus*, *V. uliginosum*, and/or *Empetrum nigrum*, typically making up a tall, dense canopy (plots 159, 161, 176 and 177), *and* a position under trees. *Pleurozium schreberi* was the only moss species able to grow under such conditions. With a more open field layer (cover up to 90 %), there did not seem to be any clear relationship between development of the bottom layer and dwarf shrub cover. There was some variation in the relative importance of bottom layer species that occasionally reached high subplot frequency, e.g., *Dicranum polysetum*, *D. scoparium*, *Ptilidium ciliare* and *Cladina rangiferina*. Slight affinity to site-type 3-2 was shown by the sloping plots 88 and 112, and plot 62; all having high subplot frequency of *Barbilophozia floerkei* and *Ptilidium ciliare*, partly also *Barbilophozia lycopodioides*.

Notes. The poverty of species in the bottom layer partly results from the sparsity of lichens, partly from the sparsity of bryophytes associated with spruce forest sites. Low cover in the bottom layer is likely to be caused by the dense field layer, acting to reduce incoming radiation as well as causing a high mortality risk due to large amounts of litter.

Corresponding site-types: Kielland-Lund (1981): Barbilophozio-Pinetum typicum and transitions to Vaccinio-Pinetum. Elven & Fremstad (1987): A3a and transitions to A2. Kujala (1961): CT (and transitions to VT). Kalela (1961): ECT-ECT transitions.

3-2: The paludified subxeric site-type

Vegetation. The floristic composition of the site-type is shown in Tab. 24. Constant species were *Calluna vulgaris*, *Vaccinium myrtillus*, *V. vitis-idaea*, *Pleurozium schreberi* and *Sphagnum capillifolium*. Other species that locally dominated in the field layer (and then reached high subplot frequency) were *Empetrum nigrum*, *Erica tetralix* and *Vaccinium uliginosum*. *Pleurozium schreberi* and *Sphagnum capillifolium* were the quantitatively most important species in the bottom layer, while high subplot frequency (15 or 16) in one or more plots also was obtained by *Calliergon stramineum*, *Dicranum majus*, *D. scoparium* and *Sphagnum quinquefarium*.

The mean number of species per sample plot was 17, while the total number in the 11 plots was 54.

The field layer normally had a dense dwarf shrub cover (≥ 80 % in 8 out of 11 plots). The bottom layer varied from being almost devoid of species (plot 77) to including dense *Sphagnum* tussocks (plot 26). Mosses were prominent while lichens mostly occurred only as scattered *Cladonia* podetia.

Environment. The environmental data for this site-type are given in Appendix 4. With few exceptions, this site-type occurred on moderately sloping ridges with soligenous paludification. One sample plot, No. 65, represented a shallow depression on a level ridge, with topogenous paludification. Two sample plots (77 and 187) were transitional; occurring close to the top of a small hill, and close to a depression in a long slope, respectively.

The open tree layer was dominated by *Pinus sylvestris*, with sparse occurrence of *Betula pubescens*.

Soligenous paludification was associated with shallow soil (maximum soil depths below 40 cm) overlying the bedrock. The humus layer was also mostly shallow; 3-7 cm. Plot 65, with topogenous paludification, had deeper soil. The organic matter content of the humus was normally 97-98 %. The humus layer was strongly acid; pH_{H2O} = 3.9-4.3, pH_{CaCl2} = 3.0-3.4, with moderate amounts of cations, and variable but mostly small to moderate amounts of total N (1.23-2.14 % of organic matter).

Variation. There was some variation in dominance relationships in the field layer, not possible to relate to environmental conditions (including closure of the tree layer). The strongly sloping, shallow-soil plots 26 and 125 included *Trientalis europaea* and *Deschampsia flexuosa*, both characteristic of more mesic sites. There was a considerable variation in the bottom layer; several species occurred as dominants and/or obtained high subplot frequency. The total cover ranged from 5 to 90 %. Poor development of a bottom layer was associated with high dwarf shrub cover (plot 77), or a combination of high dwarf shrub and tree layer cover (plot 76). *Pleurozium schreberi* was the most important species in such species-poor plots. Particularly high number of species in the bottom layer was observed in the open,

Tab. 24. The vegetation of the 3-2 site-type. For explanation, see Tab. 19.

Sample plot	26	27	29	30	31	65	76	77	125	127	187	
N-TOT	22	18	19	23	13	10	13	10	27	17	15	17.0±5.5
N-VAS	7	8	6	7	7	7	7	6	9	4	6	6.7±1.3
N-BOT	15	10	13	16	6	3	6	4	18	13	9	10.3±5.1
MA Can (x10)	0	1	0	2	1	1	5	3	1	1	3	1.6±1.5
ME Lit (x10)	0	0	0	0	9	0	10	0	0	12	6	3.4±4.9
CC	25	85	85	80	85	95	95	100	25	80	70	75±26
CD	90	50	65	60	30	40	15	5	70	80	70	50±27
Picea abies	2	1	1	3	1	.	.	.	9	.	1	64^{3}
Pinus sylvestris	.	3	.	.	2	2	.	1	1	.	.	45^{2}
Sorbus aucuparia	.	.	.	1	.	.	.	.	.	2	.	18^{2}
Calluna vulgaris	11	16	16	14	16	16	4	14	12	16	13	100^{14}
Empetrum nigrum	.	7	.	5	7	16	6	.	2	.	5	64^{8}
Erica tetralix	.	.	.	.	.	16	5	2	.	.	.	27^{8}
Vaccinium myrtillus	3	16	16	16	16	16	16	16	13	16	16	100^{14}
V. uliginosum	.	10	15	16	13	2	13	16	.	.	15	73^{13}
V. vitis-idaea	16	16	14	16	16	16	16	16	13	16	16	100^{16}
Melampyrum pratense	.	1	3	.	.	.	.	.	1	.	.	17^{2}
Trientalis europaea	2	.	.	.	.	.	.	.	4	.	.	18^{3}
Deschampsia flexuosa	5	.	.	.	.	.	.	.	16	.	.	18^{11}
Calliergon stramineum	.	16	12	.	.	.	.	.	.	.	.	18^{14}
Dicranum majus	.	10	16	8	.	.	.	.	.	15	.	36^{12}
D. polysetum	11	.	.	.	.	.	.	.	2	.	.	18^{7}
D. scoparium	4	6	2	10	2	.	4	7	15	3	9	91^{6}
Hylocomium splendens	.	1	5	2	1	.	.	.	.	3	3	55^{3}
Pleurozium schreberi	7	16	16	16	14	9	14	16	9	16	15	100^{13}
Pohlia nutans agg.	.	4	2	1	.	.	.	.	9	7	.	45^{5}
Polytrichum juniperinum	14	.	.	9	.	.	.	.	7	.	.	27^{10}
Ptilium crista-castrensis	.	.	4	14	.	.	.	.	.	.	9	27^{9}
Sphagnum capillifolium	16	16	.	10	8	12	7	.	10	11	15	82^{12}
S. quinquefarium	.	3	16	13	.	.	.	.	12	.	.	35^{11}
Barbilophozia floerkei	1	5	6	6	.	.	3	.	9	1	.	64^{4}
B. lycopodioides	.	.	.	.	.	.	.	2	.	3	.	18^{3}
Calypogeia muellerana	.	.	.	.	.	.	1	.	2	.	.	18^{2}
C. neesiana	4	.	.	2	.	.	.	.	12	.	.	27^{6}
C. sphagnicola	.	5	4	10	1	.	.	.	.	.	2	45^{4}
Lophozia ventricosa agg.	1	.	2	.	.	.	.	.	3	.	.	27^{2}
Ptilidium ciliare	1	.	8	12	.	.	4	.	2	11	8	64^{7}
Cladonia chlorophaea agg.	7	.	.	.	.	7	.	.	.	6	.	27^{7}
C. squamosa	2	.	.	.	.	.	.	.	.	1	.	18^{2}

Additional species (occurring in only 1 sample plot; Plot No.: Frequency in subplots):

Betula pubescens 26:8, Vaccinium oxycoccos 76:3; Aulacomnium palustre 30:1, Dicranum fuscescens 125:9, Drepanocladus uncinatus 31:1, Leucobryum glaucum 26:2, Plagiothecium laetum agg. 127:1, P. undulatum 29:2, Polytrichum commune 77:1, Sphagnum girgensohnii 30:8, S. russowii 30:3, Barbilophozia attenuata 187:1, Cephalozia bicuspidata 187:2, C. lunulifolia 26:1, Cephaloziella spp. 26:12, Cetraria islandica 125:6, Cladonia bellidiflora 125:2, C. coniocraea agg. 127:2, C. deformis 125:4, C. floerkeana 125:2, C. furcata 125:1, C. sulphurina 26:4.

strongly sloping plots 26, 30 and 125. A species-poor bottom layer was also observed in plot 65 with topogenous paludification. Several species were characteristic to sites characterized by soilgenous paludification, e.g., *Calliergon stramineum*, *Leucobryum glaucum*, *Sphagnum quinquefarium*, *Barbilophozia floerkei*, *Calypogeia muellerana*, *C. neesiana*, *C. sphagnicola*, *Cephalozia bicuspidata*, *C. lunulifolia*, *Cephaloziella* spp., *Lophozia ventricosa* agg. and *Ptilidium ciliare*. A high number of small *Cladonia* spp. were observed in plot 125 on exposed peat.

Some variation in humus layer pH was associated with kind of paludification; the lowest pH_{H2O} = 3.9-4.0 was observed in topogenous paludifications and in transitional sites (gentle slopes). The strongly sloping, soligenously paludified plots 26 and 125 had particularly high values of Al (and Fe). The highest values of total N were also observed in these plots.

Notes. Several mire species reach their forest optimum in this site-type; e.g., *Erica tetralix*, *Vaccinium uliginosum*, *Calliergon stramineum* and *Calypogeia sphagnicola*. Absolute limits towards the xeric end of the soil moisture deficiency gradient are reached by several spruce forest species, e.g., *Dicranum majus*, *Ptilium crista-castrensis*, *Plagiothecium laetum* agg., *P. undulatum*, *Sphagnum quinquefarium* and *Calypogeia muellerana*.

Corresponding site-types: Kielland-Lund (1981): Barbilophozio-Pinetum sphagnetosum. Elven & Fremstad (1987): A3a (and transitions to A3c and A3d).

4-1: The non-paludified subxeric-submesic transitional site-type

Vegetation. The floristic composition of this site-type is shown in Tab. 25. Constant species were *Vaccinium myrtillus* and *V. vitis-idaea*. They were also the most common dominants, although *Calluna vulgaris* and *Pteridium aquilinum* also dominated locally. *Empetrum nigrum* and *Deschampsia flexuosa* were also observed with high subplot frequencies. Local dominants or species with high subplot frequency in the bottom layer were *Dicranum majus*, *Hylocomium splendens*, *Pleurozium schreberi* and *Barbilophozia lycopodioides*.

The mean number of species per sample plot was 12, while the total number in the 18 sample plots was 47.

The field layer normally was dense (cover mostly above 80 %) and dominated by dwarf shrubs (notable *Vaccinium myrtillus*), while the bottom layer was poorly developed (cover mostly below 50 %). Lichens were mostly absent; pleurocarpous mosses mostly were more important than acrocarpous mosses, again more important than hepatics.

Environment. The enviromental data for this site-type are given in Appendix 4. The site-type occurred in a wide range of topographic situations, ranging from plane valley sides to ridges and small hilltops. The majority of sample plots were situated in long, gently to moderately sloping valley sides.

The tree layer of site-type 4-1 was mostly well stocked with a mixture of *Pinus sylvestris* and *Picea abies*, among which occasional *Betula pubescens* occurred.

Soil thickness was variable, the pattern of variation related to topography, stone content of soil, etc. The humus layer was mostly relatively thick (5-10 cm), often overlain by a 2-5 cm deep layer of ericaceous litter that easily dried up. The organic content of the humus was high; in sites with a well-developed humus layer not below 94 %. The humus was strongly acid; pH_{H2O} = 3.8-4.2, pH_{CaCl2} = 3.1-3.5. With the exception of plot 80 (having extremely low amounts of most cations), the cation content was moderate. The total N content was low (1.28-1.96 % of organic matter).

Variation. The field layer was mostly not very variable, always dominated by *Vaccinium myrtillus*. Some variation occurred with respect to subordinate dominants, associated with variation from transitions to site-type 3-1 (plots 180 and 128) with prominence of *Vaccinium uliginosum* and *Empetrum nigrum*, to transitions to site-type 5.1 (plots 173, 74,

Tab. 25. The vegetation of the 4-1 site-type. For explanation, see Tab. 19.

Sample plot	4	10	11	74	75	80	99	100	108	109	110	111	128	173	174	175	180	200	
N-TOT	26	9	11	5	14	8	14	13	20	14	12	5	19	7	7	12	11	13	12.2±5.4
N-VAS	6	5	5	5	7	4	6	7	6	6	5	5	4	6	5	4	5	4	5.3±1.0
N-BOT	20	4	6	0	7	4	8	6	14	8	7	0	15	1	2	8	6	9	6.9±5.3
MA Can (x10)	5	3	11	8	4	5	3	2	3	2	3	11	3	13	8	4	5	2	5.3±3.4
ME Lit (x10)	1	4	15	18	9	12	0	8	0	1	0	16	15	21	21	13	3	3	8.8±7.6
CC	50	95	95	90	95	75	90	90	65	100	95	100	85	85	50	90	90	70	84±16
CD	50	15	35	0	20	40	25	15	60	30	90	0	12	0	0	5	20	75	27±27
Picea abies	6	.	1	.	1	.	.	.	.	2	.	1	.	.	.	.	.	.	28^{2}
Sorbus aucuparia	3	1	.	14	7	.	2	3	13	2	.	.	.	8	13	4	.	3	67^{6}
Calluna vulgaris	.	15	.	.	.	4	.	.	11	5	16	.	.	.	.	.	12	.	67^{6}
Empetrum nigrum	.	.	16	.	.	.	.	.	.	.	.	.	6	.	.	.	1	.	17^{8}
Vaccinium myrtillus	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	100^{16}
V. uliginosum	.	.	.	.	.	9	.	10	.	.	.	.	13	.	.	.	11	.	22^{11}
V. vitis-idaea	11	16	16	8	15	15	14	16	13	16	14	16	16	1	6	15	16	5	100^{13}
Maianthemum bifolium	2	.	.	8	1	.	7	.	.	.	.	.	.	2	4	.	.	.	33^{4}
Melampyrum pratense	.	2	6	.	.	.	4	7	.	4	5	1	.	.	.	.	.	.	39^{4}
Pteridium aquilinum	.	.	.	.	16	.	.	.	.	.	.	.	.	16	11	6	.	.	22^{12}
Deschampsia flexuosa	16	.	.	16	14	.	16	1	4	.	3	2	.	.	.	.	.	16	50^{10}
Dicranum majus	10	.	.	.	16	.	11	13	15	2	2	.	10	.	.	16	.	15	56^{11}
D. polysetum	.	.	2	.	.	14	.	.	.	.	.	.	2	.	.	.	13	.	22^{8}
D. scoparium	6	.	.	.	.	.	2	3	2	11	6	.	5	.	2	2	1	4	61^{4}
Hylocomium splendens	7	16	16	.	4	.	1	.	11	5	14	.	.	.	.	4	9	13	61^{9}
Plagiothecium laetum agg.	7	.	.	.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	17^{3}
Pleurozium schreberi	14	6	12	.	12	16	13	10	10	13	8	.	12	.	.	13	12	11	78^{12}
Ptilium crista-castrensis	.	7	9	.	14	8	.	.	10	9	7	.	1	.	.	9	3	1	61^{7}
Sphagnum quinquefarium	.	.	.	.	.	.	.	.	.	2	.	.	7	.	.	.	.	.	11^{5}
Barbilophozia lycopodioides	16	14	5	.	16	.	15	3	11	10	16	.	1	.	.	5	.	11	67^{10}
Calypogeia neesiana	.	.	.	.	.	.	.	.	2	.	.	.	1	.	.	.	.	.	11^{2}
Lophocolea heterophylla	4	.	.	.	2	.	11	2	5	.	.	.	.	1	3	1	.	10	50^{4}
Lophozia obtusa	2	.	.	.	.	.	2	.	7	2	.	.	.	.	.	.	.	7	28^{4}
L. ventricosa agg.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	11^{1}
Ptilidium ciliare	5	.	3	.	1	4	2	1	2	.	4	.	.	.	.	.	9	12	56^{4}

Additional species (occurring in only one sample plot; Plot No: Frequency in subplots):

Pinus sylvestris 100:2, Linnaea borealis 108:2, Trientalis europaea 173:3; Dicranum fuscescens 4:16, Drepanocladus uncinatus 175:2, Plagiothecium denticulatum 108:5, Pohlia nutans agg. 128:3, Racomitrium lanuginosum 128:1, Rhytidiadelphus loreus 4:2, Barbilophozia floerkei 4:14, Blepharostoma trichophyllum 4:4, Calypogeia integristipula 108:2, C. muellerana 4:3, Cephalozia bicuspidata 108:4, Cephaloziella sp. 128:3, Plagiochila asplenioides 4:2, Tritomaria quinquedentata 4:2, Cladonia cenotea 4:5, C. chlorophaea agg. 128:3, C. coniocraea agg. 128:1, C. fimbriata 4:3, C. squamosa 4:1.

174, 75, 200, 108, 175 and 4) with high importance of spruce forest species like *Maianthemum bifolium*, *Pteridium aquilinum*, and to a lesser extent, *Deschampsia flexuosa*.

Variation in the bottom layer was related to cover in both upper layers. Plots 74, 111, 128, 173 and 174 were situated underneath dense spruce crowns. They mostly had a dense field layer, and were almost devoid of a bottom layer. In interspaces between trees, a dense field layer did not necessarily suppress bottom layer development (e.g., plots 11, 99, 109). Variation in the species composition of this site-type was mostly parallel to the variation in the field layer; *Dicranum polysetum* indicated transitions to site-type 3-1; *D. majus*, *Lophocolea heterophylla* and *Lophozia obtusa* indicating affinity to 5.1-1.

Notes. *Vaccinium myrtillus* reaches its quantitative optimum in this site-type. Species characteristic of site-type 5.1-1 (the typical boreal spruce forest species) like *Linnaea borealis*, *Maianthemum bifolium*, *Trientalis europaea*, *Dicranum majus*, *Plagiothecium laetum* agg., *Calypogeia muellerana*, *Cephalozia bicuspidata*, *Lophocolea heterophylla*, *Lophozia obtusa*, and *Tritomaria quinquedentata*, all occur irregularly (and mostly independent of each other) and with distinctly lower subplot frequency than in site-type 5.1-1.

In this site-type, we find the best development of a field layer and the poorest development of a bottom layer among the 14 site-types. The dry, litter-covered forest floor mostly precludes small bryophytes (the "pocket species" of R. Økland & Bendiksen (1985)) from occurring, thus contributing further to a low mean species number in the bottom layer.

Corresponding site-types: Kielland-Lund (1981): Transitions between Barbilophozio-Pinetum typicum and Eu-Piceetum myrtilletosum, Dicranum rugosum variety. Elven & Fremstad (1987): Transitions between A3 (mostly A3a) and A4a. Kujala (1961): Transitions between CT (and VT) and MT. Kalela (1961): Transitions between EVT (and ECT) and VMT.

4-2: The paludified subxeric-submesic transitional site-type

Vegetation. The floristic composition of this site-type is shown in Tab. 26. Constant (and dominant) species were *Vaccinium myrtillus*, *V. vitis-idaea*, *Dicranum majus*, *Pleurozium schreberi*, and *Sphagnum quinquefarium*. Other species occasionally reaching high subplot frequency were *Deschampsia flexuosa*, *Hylocomium splendens* and *Polytrichum formosum*.

The mean number of species per sample plot was 18, while the total number in the 8 sample plots was 46.

The field layer was moderately to well developed; the physiognomically most important species being the dwarf shrub *Vaccinium myrtillus*. The bottom layer was mostly dominated by *Sphagnum quinquefarium*, with a more or less prominent element of mosses.

Environment. The environmental data for this site-type are given in Appendix 4. The site-type occurred on flushed rigdes and convex valley-sides; always associated with slopes with soligenous paludification and shallow soil.

The tree layer was open, with scattered *Pinus sylvestris* and *Picea abies*. The site-type mostly occurred between trees (except plot 199), in mosaic with site-type 4-1 dominating close to trees.

The organic content of the humus was variable, dependent on the soil depth and the extent of mixing of sand particles. Typically, the organic matter content was above 85 %. The humus was strongly acid; pH_{H2O} = 3.9-4.2, pH_{CaCl2} = 3.0-3.4, with moderate or small amounts of cations and total N (1.38-2.09 % of organic matter). High amounts of Al (partly also Fe) were observed in some plots.

Variation. There was some variation in the occurrence of locally common or subdominant species in both the field and bottom layers. Furthermore, variation occurred along two gradients. Plots 199 and 8 represented transitions to site-type 4-1, the former also atypical for site-type 4-2 in the dense tree and field layers. *Sphagnum* spp. had low prominence, and these plots also included species characteristic of spruce needles and twigs in shaded sites, such as *Plagiothecium laetum* agg. and *Lophocolea heterophylla*. The other extreme was indicated by the typical 4-2 sites, dominated by *Sphagnum quinquefarium* and with presence of *Polytrichum formosum* and *Calypogeia muellerana*. There was also some variation from transitions to site-type 3-2 (plots 28 and 130 with high importance of *Vaccinium uliginosum*)

Tab. 26. The vegetation of the 4-2 site-type. For explanation, see Tab. 19.

Sample plot	8	9	24	25	28	124	130	199	
N-TOT	21	14	20	15	17	17	23	14	17.6±3.3
N-VAS	7	5	7	5	7	7	7	6	6.4±0.9
N-BOT	14	9	13	10	10	10	16	8	11.3±2.8
MA Can (x10)	3	2	2	1	3	2	2	3	2.2±0.7
ME Lit (x10)	2	0	2	0	3	0	8	12	3.2±4.2
CC	60	80	60	70	85	50	70	100	72±16
CD	30	85	75	95	65	95	65	15	66±29
Picea abies	1	3	1	.	.	.	1	.	50^{1}
Pinus sylvestris	.	.	.	.	.	4	1	.	25^{3}
Sorbus aucuparia	8	.	13	.	2	.	9	9	63^{8}
Calluna vulgaris	.	.	.	8	1	10	.	3	50^{6}
Vaccinium myrtillus	16	16	16	16	16	16	16	16	100^{16}
V. uliginosum	.	.	.	.	15	.	6	.	25^{11}
V. vitis-idaea	5	16	1	16	16	15	16	15	100^{13}
Maianthemum bifolium	.	3	.	.	6	.	.	.	25^{5}
Melampyrum pratense	.	3	.	.	6	.	.	.	25^{5}
Trientalis europaea	1	.	15	1	.	12	.	.	50^{7}
Deschampsia flexuosa	16	8	16	16	.	16	.	14	75^{14}
Dicranum majus	13	6	12	3	13	3	8	11	100^{9}
D. scoparium	2	2	.	3	8	.	10	.	63^{5}
Hylocomium splendens	9	14	16	5	10	3	.	8	63^{9}
Plagiothecium laetum agg.	7	.	1	1	.	.	2	1	63^{2}
P. undulatum	.	.	.	1	.	.	4	.	25^{3}
Pleurozium schreberi	5	9	16	7	16	9	16	4	100^{10}
Polytrichum formosum	.	.	5	2	.	16	.	.	38^{8}
Ptilium crista-castrensis	.	3	1	.	7	.	8	.	50^{5}
Rhytidiadelphus loreus	1	.	4	10	.	.	.	.	38^{5}
Sphagnum quinquefarium	.	16	16	16	16	16	15	8	88^{15}
Barbilophozia floerkei	.	.	1	.	.	9	13	.	38^{8}
B. lycopodioides	10	8	8	.	14	1	.	14	75^{9}
Calypogeia muellerana	.	.	2	4	.	.	.	.	25^{3}
Lophocolea hererophylla	11	.	.	.	.	.	6	4	38^{7}
Lophozia obtusa	3	8	5	.	.	.	.	6	50^{6}
Plagiochila asplenioides	.	.	1	.	1	.	.	.	25^{1}
Ptilidium ciliare	.	1	.	.	2	3	.	.	38^{2}

Additional species (occurring in only 1 sample plot; Plot No.: Frequency in subplots):

Salix aurita 130:4, Empetrum nigrum 28:16, Linnaea borealis 8:3; Aulacomnium palustre 28:4, Brachythecium populeum 130:2, B. reflexum 130:1, Dicranum drummondii 130:4, D. fuscescens 130:4, Leucobryum glaucum 124:3, Polytrichum juniperinum 124:4, Barbilophozia attenuata 8:1, Calypogeia integristipula 8:2, C. neesiana 130:6, C. sphagnicola 130:1, Cephalozia loitlesbergeri 130:1. C. lunulifolia 8:3, Cladonia cenotea 8:2, C. fimbriata 8:2.

to transitions to site-type 5.1-2 (plots 24 and 199), with occurrences of *Trientalis europaea*, *Polytrichum formosum* and *Rhytidiadelphus loreus*.

Notes. *Sphagnum quinquefarium* reaches its optimum in this site-type. Several species characteristic of spruce forests occur frequently, e.g., *Dicranum majus*. "Pocket species" are infrequent. The occurrence in this site-type of some slightly western (suboceanic) species like *Rhytidiadelphus loreus* and *Plagiothecium undulatum* is typical of humid regions (R. Økland & Bendiksen 1985).

Corresponding site-types: Kielland-Lund (1981): Transitions between Barbilophozio-

Pinetum sphagnetosum and Eu-Piceetum myrtilletosum. Elven & Fremstad (1987): Transitions between A3 and A4a.

5.1-1: The poor non-paludified submesic site-type

Vegetation. The floristic composition of this site-type is shown in Tab. 27. Constant species in the field layer were *Vaccinium myrtillus*, *Maianthemum bifolium* and *Deschampsia flexuosa*. The only constant in the bottom layer was *Dicranum majus*, but three species (*Hylocomium splendens*, *Pleurozium schreberi* and *Lophocolea heterophylla*) all had constancies above 75 %. Several species occurred as local dominants, having high subplot frequency in several sample plots: *Vaccinium vitis-idaea*, *Pteridium aquilinum* and *Trientalis europaea* in the field layer; *Hylocomium umbratum*, *Plagiothecium undulatum*, and, in particular, *Barbilophozia lycopodioides*, in the bottom layer.

The mean number of species per sample plot was 16, while the total number in the 46 sample plots was 73.

Normally, the field layer was well developed, showing mixed dominance of the dwarf shrub *Vaccinium myrtillus* and herbs, also with a prominent element of graminids. The bottom layer was strongly variable (0-95 % cover recorded), with prominence of mosses.

Environment. The environmental data for this site-type are given in Appendix 4. The site-type prevailed on plane and slightly convex valley sides; in gently to strongly sloping terrain.

This site-type was a *Picea abies* forest, mostly with a well-developed tree layer. It covered extensive areas in the lower parts of long slopes, sometimes in mosaic with site-type 5.1-2 in the openings between trees, or in mosaic with site-types 5.2-1 (or, more rarely, 5.2-3 or 5.3). Several other trees occasionally occurred as dominants, e.g., *Pinus sylvestris*, *Betula pubescens*, *Quercus* sp. and *Taxus baccata*. Site-type 5.1-1 was the quantitatively most important spruce forest type in the investigation area.

Soil depth was strongly variable, but often quite low due to high stone content of the soil (cf. the many plots with low minimum but considerable maximum soil depth in Appendix 4. Several plots in Transect 5 did, however, have deep soil. The thickness of the humus layer was variable, but mostly in the range 4-8 cm. The organic matter content was also variable, from about 50 % to 96 %; lowest on shallow soil, highest on deep soil with strong litter accumulation. With few notable exceptions, the humus layer was strongly acid; pH_{H20} = 3.9-4.3, pH_{CaCl2} = 3.1-3.6. The exceptions refer to plots 34 and 155, both with pH_{H20} = 4.5 and pH_{CaCl2} = 3.8. Throughout, the cation content was small or moderate. Total N content was mostly moderate, ranging from 1.42-2.17 % of organic matter (except for two deviant sample plots; No. 22 with 2.90 % N and No. 155 with 2.48 %). Particularly high Al content was recorded in plots 3, 6, 22 and 121.

Variation. The variation in cover and dominance relationships in the field layer was not clearly related to tree layer cover or other environmental variables. The physiognomically important species *Pteridium aquilinum* occurred as a dominant in Transect 5 only. The bottom layer showed dependence on the tree as well as the field layer. Suppression of a bottom layer by the tall, abundantly litter-producing species *Vaccinium myrtillus* and *Pteridium aquilinum* was observed in plots 71 and 169; suppression by a dense *Picea abies* canopy, often with low crown height, was observed in plots 73, 118, 170 and 172. Well developed bottom layers occasionally occurred under a relatively dense crown (plots 36, 101, 120 and 123) and under

Tab. 27. The vegetation of the 5.1-1 site-type. For explanation, see Tab. 19.

Sample plot	1	2	3	5	6	7	15	22	34	36	37	41	70	71	72	73	96	97	98	101	102	103	104	105	107
N-TOT	10	12	14	13	15	17	19	21	18	23	13	11	7	16	13	5	28	19	27	13	16	17	11	11	17
N-VAS	6	5	6	7	7	6	7	7	7	8	8	4	6	8	7	4	10	7	7	6	6	7	4	5	9
N-BOT	4	7	8	6	8	11	12	14	11	15	5	7	1	8	6	1	18	12	20	7	10	10	7	6	8
MA Can (x10)	12	12	2	6	0	3	1	5	13	6	6	5	12	2	12	13	3	7	1	12	12	2	5	6	3
ME Lit (x10)	20	17	1	11	0	3	0	22	19	24	9	19	16	0	14	27	8	15	0	25	18	0	15	16	4
CC	70	70	80	90	70	70	60	65	25	35	70	25	95	95	85	25	80	85	85	60	90	90	40	25	20
CD	15	5	90	80	95	80	90	35	20	90	1	10	1	1	1	0	35	20	50	60	5	30	5	55	20
Picea abies	.	.	1	2	.	.	.	4	10	.	1	.	.	.	.	.	2	.	1	.	1	1	.	.	1
Sorbus aucuparia	.	8	1	4	10	7	4	5	3	9	4	16	8	4	11	3	4	3	.	3	.	2	.	7	3
Vaccinium myrtillus	16	16	16	16	16	16	16	16	15	16	16	16	16	16	16	16	16	.	16	16	16	16	16	16	16
V. vitis-idaea	16	8	16	.	4	15	2	9	12	16	12	.	.	16	16	3	4	13	14	16	16	16	10	.	6
Convallaria majalis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.
Dryopteris expansa agg.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	12	.	.	.	.	.	.	.	.
Gymnocarpium dryopteris	.	.	.	.	.	.	.	.	1	.	.	.	2	.	.	.	.	.	.	.	2	.	.	.	.
Linnaea borealis	.	.	.	1	.	.	.	.	.	7	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.
Lycopodium annotinum	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	12	.	.	.	.	.	.	.	.
Maianthemum bifolium	6	14	7	15	15	13	16	15	7	15	16	16	13	13	9	.	16	16	12	5	8	7	4	16	16
Pteridium aquilinum	.	.	.	.	11	.	.	.	.	9	12	.	16	16	12	14	.	10	3	.	.	.	.	.	8
Trientalis europaea	.	.	.	.	4	.	13	9	.	5	.	.	1	8	.	.	10	3	8	.	.	.	.	.	1
Calamagrostis purpurea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Deschampsia flexuosa	5	16	16	16	16	16	16	16	11	16	16	16	.	.	8	.	16	16	16	9	15	16	6	16	16
Brachythecium reflexum	.	.	.	.	.	.	.	.	.	.	.	5	.	2	1	.	.	.	1	.	.	.	.	.	.
Dicranum majus	13	4	16	16	16	15	16	16	16	16	5	14	.	6	.	.	15	16	16	16	5	16	14	16	9
D. scoparium	.	.	.	.	.	.	2	5	.	.	1	1	.	1	1	.	.	.	3	.	2	.	.	.	1
Hylocomium splendens	2	1	16	14	16	13	15	13	2	10	2	.	.	.	1	.	11	.	5	.	12	10	1	2	13
H. umbratum	.	.	.	.	.	2	12	.	3	.	.	6	.	.	.	.	6	4	2	.	.	.	.	.	.
Plagiothecium denticulatum	.	.	.	.	3	.	.	.	9	2	.	.	.	.	.	.	1	.	3	.	.	.	.	.	.
P. laetum agg.	.	.	.	.	.	1	.	10	.	.	.	9	.	1	1	.	2	1	3	4	.	.	6	.	3
P. undulatum	.	.	.	.	.	.	.	14	.	13	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.
Pleurozium schreberi	15	11	4	11	5	8	15	14	3	1	.	3	.	4	.	.	15	3	3	9	8	3	4	12	8
Polytrichum formosum	.	.	.	.	.	.	.	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ptilium crista-castrensis	.	.	2	.	.	.	8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.
Rhytidiadelphus loreus	.	.	.	.	1	.	.	2	.	.	.	.	.	.	.	.	.	.	5	.	.	.	.	.	1
R. subpinnatus	.	.	.	.	.	1	.	.	.	1	.	.	.	1	.	.	8	.	.	.	.	.	.	.	.
R. triquetrus		.	.	4	7	.	5	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Barbilophozia barbata	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	6	.	.	.	.
B. lycopodioides	15	4	16	16	16	16	16	11	9	1	.	.	.	.	.	.	16	6	16	13	8	16	.	9	12
Calypogeia integristipula	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	2	1	7	.	.	.	.	.	.
C. muellerana	.	2	.	.	.	.	.	2	.	.	.	.	.	.	.	.	6	1	8	.	.	.	.	.	.
C. neesiana	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	6	3	4	.	.	.	.	.	.
Cephalozia bicuspidata	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	1	.	.	.	1	2	.	.	.
Lophocolea heterophylla	.	5	.	.	.	2	1	5	3	2	.	14	.	3	4	2	6	4	15	.	3	.	5	1	5
Lophozia obtusa	.	.	.	.	.	.	11	.	.	.	.	.	.	.	.	.	9	.	2	.	.	1	.	.	.
L. ventricosa agg.	.	.	.	.	.	.	.	5	1	.	.	.	.	.	.	.	2	2	.	.	1	.	1	.	.
Plagiochila asplenioides	.	.	.	16	12	1	.	4	.	7	1	.	.	.	.	.	1	.	8	.	.	4	.	1	.
Ptilidium ciliare	.	2	4	.	2	1	2	.	.	.	.	.	.	.	.	.	.	.	.	4	10	.	.	.	.

Additional species (occurring in four sample plots or less; Plot No: Frequency in subplots, Constancy and mean frequency in subplots):

Pinus sylvestris 1:3, 37:1 4^2, Populus tremula 71:3, 72:1, 141:4 7^3, Vaccinium uliginosum 97:16 2^{16}, Anemone nemorosa 136:3 2^3, Cornus suecica 96:6 2^6, Melampyrum pratense 7:2, 15:1, 107:7, 115:1 9^3, M. sylvaticum 1:1 2^1, Potentilla erecta 137:2 2^2, Solidago virgaurea 122:1, 134:2, 136:2 7^2, Luzula pilosa 5:1, 171:4 4^3; Brachythecium populeum 71:1 2^1, B. salebrosum 72:3 2^3, B. starkei 97:3, 141:1 4^2, Bryhnia novae-angliae 171:1 2 , Cirriphyllum piliferum 141:3 2^3, Dicranum fuscescens 36:1, 101:2, 104:2, 134:4 9^2, Drepanocladus uncinatus 115:5 2^5, Herzogiella striatella 140:2 2^2, Hypnum cupressiforme 169:1 2^1, Polytrichum commune 34:2, 155:1 4^2, Tetraphis pellucida 36:1, 140:2

Tab. 27 (continued).

Sample plot	115	117	118	120	121	122	123	134	136	137	140	141	147	155	169	170	171	172	196	197	198	
N-TOT	24	20	14	16	19	18	20	12	21	20	25	25	22	20	10	8	18	10	17	16	11	16.3±5.3
N-VAS	6	6	8	7	9	8	8	7	12	12	6	9	12	6	7	7	8	8	8	8	7	7.2±1.8
N-BOT	18	14	6	9	10	10	12	5	9	8	19	16	10	14	3	1	10	2	9	8	4	9.0±4.7
MA Can (x10)	1	0	10	3	4	5	5	13	6	6	5	5	5	7	4	12	2	12	3	7	1	6.0±4.1
MA Lit (x10)	1	0	28	20	10	2	16	30	6	13	9	13	11	15	0	24	12	16	14	6	24	12.5±8.9
CC	80	60	15	75	95	75	40	4	35	70	45	80	75	1	85	100	95	80	80	65	45	64±27
CD	75	95	3	90	60	60	85	30	50	2	95	25	25	40	0	1	25	0	35	40	15	39±34
Picea abies	2	.	1	1	3	.	1	1	1	2	.	.	1	.	.	.	6	.	.	.	.	43^{2}
Sorbus aucuparia	1	5	7	5	8	2	5	4	9	7	11	6	13	1	14	8	6	10	4	6	5	91^{6}
Vaccinium myrtillus	16	14	13	16	16	16	16	7	16	16	16	16	16	4	16	16	16	16	16	16	16	98^{15}
V. vitis-idaea	14	.	.	.	13	7	7	.	15	11	16	1	5	3	.	.	.	15	11	11	11	78^{11}
Convallaria majalis	.	.	5	.	.	.	.	.	.	10	.	2	2	.	.	.	.	.	.	.	.	13^{4}
Dryopteris expansa agg.	.	1	.	1	.	.	.	.	.	.	.	1	2	.	.	.	.	.	.	.	.	11^{3}
Gymnocarpium dryopteris	.	.	.	.	.	.	.	2	3	4	.	.	.	.	16	1	.	.	.	.	.	17^{4}
Linnaea borealis	.	.	.	.	2	.	.	.	.	.	.	.	5	.	.	.	.	.	.	.	.	11^{3}
Lycopodium annotinum	.	.	.	.	.	.	.	.	.	.	.	.	7	.	.	.	.	2	6	2	.	13^{5}
Maianthemum bifolium	.	11	16	2	14	16	13	8	10	16	15	16	15	1	16	5	15	6	13	15	11	96^{12}
Pteridium aquilinum	.	.	.	.	.	.	2	.	9	2	.	.	8	.	16	10	16	14	6	9	12	46^{10}
Trientalis europaea	.	1	2	2	3	7	9	.	4	4	2	7	7	2	16	2	1	1	4	5	4	63^{5}
Calamagrostis purpurea	.	.	5	.	1	1	.	.	7	11	.	.	.	.	.	.	.	.	.	.	.	11^{5}
Deschampsia flexuosa	16	16	9	11	16	16	16	1	16	16	16	16	16	6	7	2	2	7	16	16	8	93^{13}
Brachythecium reflexum	6	.	.	.	.	.	.	.	.	.	.	9	.	.	2	.	.	.	.	.	.	15^{4}
Dicranum majus	11	16	14	16	16	15	15	16	16	16	16	7	16	16	.	.	13	.	16	16	14	87^{14}
D. scoparium	8	.	.	1	.	1	.	.	.	.	.	.	3	.	.	.	2	.	.	.	.	30^{2}
Hylocomium splendens	16	5	.	5	1	16	11	.	15	5	16	11	1	3	.	1	6	.	3	10	.	76^{8}
H. umbratum	11	10	.	11	16	8	16	.	.	.	.	4	.	9	.	.	.	.	4	1	.	37^{7}
Plagiothecium denticulatum	2	3	.	.	.	.	.	.	.	.	.	1	4	1	.	.	.	2	2	.	.	26^{3}
P. laetum agg.	16	.	6	5	.	1	2	14	.	2	3	.	3	7	.	.	2	.	.	.	2	50^{5}
P. undulatum	.	15	.	15	16	8	16	.	2	.	3	2	.	.	.	.	.	.	.	.	.	24^{10}
Pleurozium schreberi	16	8	1	15	15	16	12	1	14	8	16	16	11	1	.	.	5	.	2	.	.	80^{8}
Polytrichum formosum	.	16	.	.	.	.	.	.	.	3	.	.	.	4	.	.	.	.	.	.	.	11^{2}
Ptilium crista-castrensis	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	3	.	13^{4}
Rhytidiadelphus loreus	2	11	.	.	.	.	12	.	1	.	1	.	.	.	.	.	.	.	.	.	.	20^{4}
R. subpinnatus	.	.	.	.	.	.	.	.	5	.	.	3	.	3	.	.	.	.	.	.	.	15^{4}
R. triquetrus	3	.	.	.	.	.	.	.	.	.	9	.	1	.	.	.	.	.	.	.	.	15^{4}
Barbilophozia barbata	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	11^{2}
B. lycopodioides	16	8	.	2	6	2	10	.	14	.	2	.	1	2	.	.	.	.	2	16	1	67^{10}
Calypogeia integristipula	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	2	.	.	.	.	13^{3}
C. muellerana	2	1	.	.	1	.	1	.	.	.	2	.	.	.	.	.	2	.	.	5	.	26^{3}
C. neesiana	2	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	13^{3}
Cephalozia bicuspidata	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	11^{2}
Lophocolea heterophylla	2	2	4	.	2	3	1	2	1	8	1	11	4	3	1	.	4	5	8	7	3	78^{4}
Lophozia obtusa	14	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	15^{6}
L. ventricosa agg.	.	2	1	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	20^{2}
Plagiochila asplenioides	.	.	.	.	5	6	15	.	12	1	9	.	6	2	.	.	.	.	4	.	.	41^{6}
Ptilidium ciliare	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	17^{3}

4^{2}, Sphagnum quinquefarium 123:2, 197:8 4^{5}, Barbilophozia attenuata 34:3, 97:1, 120:2, 171:2 9^{2}, B. floerkei 15:3, 103:2, 4^{3}, Blepharostoma trichphyllum 22:1, 141:2, 155:1 7^{1}, Cephalozia lunulifolia 36:1, 98:5, 140:1, 141:3 9^{3}, Diplophyllum taxifolium 98:1, 155:2 4^{2}, Lepidozia reptans 117:2, 140:2, 4^{2}, Lophozia excisa 117:2, 140:2 4^{2}, L. longidens 140:2 2^{2}, Mylia taylorii 98:1 2^{1}, Ptilidium pulcherrimum 70:2, 118:1 4^{2}, Tritomaria quinquedentata 103:5 2^{5}, Cladonia coniocraea agg. 96:1, 98:1, 141:3 7^{2}.

a dense field layer (plots 3, 6 and 115), but in general the bottom layer was better developed between trees than under trees. This direction of variation was mostly in species quantities, but a few species, e.g., *Plagiothecium laetum* agg. (notably *P. laetum* s.str.) and *Lophocolea heterophylla* preferred patches with high litter cover close to spruce trunks.

There was considerable variation according to aspect (probably related to microclimatic humidity, cf. pp. 158-159). In the SE-facing Transect 5, *Pteridium aquilinum* and *Vaccinium myrtillus* dominated, and the bottom layer was mostly poorly developed. The other extreme in this respect were the transitions towards site-type 5.1-2, e.g., plots 117, 123, 96 and 34), confined to northwesterly to northerly slopes with a more open tree layer and promince of shade-tolerant species and species less tolerant to drought, e.g., *Cornus suecica*, *Hylocomium umbratum*, *Plagiothecium undulatum*, *Polytrichum formosum* (mostly on shallow soil overlying large boulder stones or slightly flushed bedrock), *Rhytidiadelphus loreus*, *Barbilophozia lycopodioides*, *Calypogeia neesiana*, *Cephalozia lunulifolia*, *Lophozia obtusa* and *Plagiochila asplenioides*. The commonly occurring mosses *Dicranum majus* and *Hylocomium splendens* showed particular luxuriance in such sites.

Plot 1 was transitional to site-type 4-1, with sparse presence of herbs and *Deschampsia flexuosa* and a species-poor bottom layer with only the trivial species of the site-type present (shared with site-type 4-1). Plots 101 and 102 represented less distinctly transitional sites. The opposite extreme was represented by plots 169, 118, 41 and 155, with occurrence of species characteristic to site-types 5.2-1 and 5.3, e.g., *Gymnocarpium dryopteris* (in plot 169), *Calamagrostis purpurea*, *Brachythecium reflexum* and *Rhytidiadelphus triquetrus*.

Notes. Site-type 5.1-1 is characteristically distinct from site-types 1 to 4 in the presence of several herbs, grasses and bryophytes characteristic to boreal spruce forests, but with absence of edaphically more demanding species. Due to the often uneven surface (among others, caused by stoniness), a variety of microniches occurs. In contrast to site-type 4-1, these microniches are often inhabited by "pocket species", putatively dependent on relatively long duration of the microhabitat, low competitive ability of larger species due to high slope and low light, and sufficient microclimatic humidity. Examples of such pocket species occurring in site-type 5.1-1 are *Herzogiella striatella*, *Tetraphis pellucida*, *Blepharostoma trichophyllum*, *Calypogeia integristipula*, *C. muellerana*, *C. neesiana*, *Cephalozia bicuspidata*, *C. lunulifolia*, *Diplophyllum taxifolium*, *Lepidozia reptans* and *Lophozia longidens*.

Sample plots with exceptionally high pH values were found in mosaic with site-type 5.2-1, thus likely to represent edaphically richer sites that, for some reason, do not possess edaphically more demanding species.

Corresponding site-types: Kielland-Lund (1981): Eu-Piceetum myrtilletosum (*Plagiochila major* variety). Elven & Fremstad (1987): A4ab. Kujala (1961): MT. Kalela (1961): VMT.

5.1-2: The poor paludified submesic site-type

Vegetation. The floristic composition of the site-type is shown in Tab. 28. Constant species were *Picea abies* and *Sorbus aucuparia* (seedlings and saplings), *Vaccinium myrtillus*, *V. vitis-idaea*, *Maianthemum bifolium*, *Trientalis europaea*, *Deschampsia flexuosa*, *Dicranum majus*, *Hylocomium splendens*, *Pleurozium schreberi*, *Barbilophozia lycopodioides* and *Calypogeia muellerana*. The field layer was dominated by *Vaccinium myrtillus* and *Maianthemum bifolium*, *Deschampsia flexuosa*, or both. Dominance relationships in the bottom layer were

Tab. 28. The vegetation of the 5.1-2 site-type. For explanation, see Tab. 19.

Sample plot	20	21	23	32	35	95	106	132	135	
N-TOT	22	26	26	25	28	28	17	24	30	25.1±3.9
N-VAS	8	9	9	11	15	10	9	15	9	10.6±2.7
N-BOT	14	17	17	14	13	18	8	9	21	14.6±4.2
MA Can (x10)	3	4	5	3	3	2	0	3	3	2.9±1.4
ME Lit (x10)	15	9	17	12	0	4	0	9	0	7.4±6.5
CC	25	35	45	95	60	50	20	80	65	53±25
CD	85	95	95	90	70	95	95	55	55	82±16
Betula pubescens	.	6	.	1	2	.	2	.	.	44^{3}
Picea abies	1	6	1	8	1	2	.	6	4	89^{4}
Sorbus aucuparia	10	2	5	3	2	2	3	1	5	100^{4}
Vaccinium myrtillus	16	16	16	16	16	16	16	16	16	100^{16}
V. vitis-idaea	3	16	2	16	12	8	8	16	11	100^{10}
Convallaria majalis	.	.	.	.	1	.	.	1	1	33^{1}
Gymnocarpium dryopteris	.	.	.	.	8	.	.	8	.	22^{8}
Linnaea borealis	2	.	.	.	2	.	.	.	.	22^{2}
Lycopodium annotinum	.	15	2	5	.	16	.	4	.	56^{8}
Maianthemum bifolium	10	11	16	16	15	5	5	16	12	100^{12}
Potentilla erecta	.	.	.	6	7	.	.	.	.	22^{7}
Pteridium aquilinum	.	.	.	.	.	5	10	5	.	33^{7}
Solidago virgaurea	.	.	.	.	3	.	.	2	.	22^{3}
Trientalis europaea	16	6	7	3	8	1	2	7	15	100^{7}
Calamagrostis purpurea	.	.	.	2	4	.	.	16	5	44^{7}
Deschampsia flexuosa	16	16	16	16	16	16	16	12	16	100^{16}
Dicranum majus	16	16	16	16	14	4	15	12	11	100^{14}
Hylocomium splendens	1	5	7	12	15	1	3	.	7	89^{7}
H. umbratum	16	16	16	3	.	1	.	.	1	67^{9}
Plagiothecium laetum agg.	1	.	7	.	.	.	.	.	2	33^{3}
P. undulatum	16	16	16	.	1	3	.	.	1	67^{9}
Pleurozium schreberi	9	9	14	6	1	5	6	2	5	100^{6}
Polytrichum formosum	2	1	4	16	.	3	.	16	4	78^{5}
Ptilium crista-castrensis	9	3	1	.	.	3	5	.	.	56^{4}
Rhytidiadelphus loreus	12	6	4	11	.	5	16	.	.	67^{9}
R. subpinnatus	.	2	.	.	4	.	3	.	.	33^{3}
Sphagnum girgensohnii	.	15	.	3	4	16	13	13	13	78^{11}
S. quinquefarium	.	6	7	.	.	16	.	.	.	33^{10}
Barbilophozia barbata	.	.	1	.	.	.	.	.	1	22^{1}
B. floerkei	.	4	.	.	.	5	.	.	.	22^{5}
B. lycopodioides	16	.	12	16	16	3	16	6	12	89^{13}
Calypogeia azurea	1	1	.	.	.	2	.	.	2	44^{2}
C. muellerana	6	6	11	3	3	4	.	1	2	78^{5}
Cephalozia bicuspidata	.	3	.	2	.	1	.	.	.	33^{2}
Diplophyllum taxifolium	.	.	.	7	2	.	.	.	.	22^{5}
Lophocolea heterophylla	5	.	.	1	.	.	.	.	1	33^{2}
Lophozia obtusa	.	.	3	.	3	.	.	.	.	22^{3}
L. ventricosa agg.	.	1	.	.	.	.	.	.	1	22^{1}
Plagiochila asplenioides	5	1	15	3	11	3	.	.	1	78^{6}
Tritomaria quinquedentata	.	.	.	1	.	.	3	.	.	22^{2}

Additional species (occurring in only 1 sample plot; Plot No.: Frequency in subplots):

Frangula alnus 132:10; Comus suecica 95:9, Dryopteris expansa agg. 23:1, Luzula pilosa 5:1, Melampyrum pratense 106:1, Rubus saxatilis 132:4; Dicranum fuscescens 135:4, D. polysetum 135:1, D. scoparium 95:1, Plagiomnium affine 132:2, Plagiothecium denticulatum 32:1, Polytrichum commune 132:5, Rhytidiadelphus triquetrus 35:1, Tetraphis pellucida 135:1, Barbilophozia attenuata 135:1, Blepharostoma trichophyllum 135:1, Calypogeia neesiana 35:1, Cephalozia lunulifolia 135:2, Lophocolea bidentata 23:8, Cladonia digitata 135:1.

variable; the most frequently occurring dominants were *Dicranum majus*, *Hylocomium umbratum*, *Plagiothecium undulatum*, *Sphagnum girgensohnii* and *S. quinquefarium*. Other species occasionally having high subplot frequency were *Polytrichum formosum*, *Rhytidiadelphus loreus* and *Plagiochila asplenioides*.

The mean number of species per sample plot was 25, while the total number in the 9 sample plots was 60.

The field layer was dominated by the dwarf shrub *Vaccinium myrtillus*, with relatively high quantitative importance of herbs and graminids. Mosses or *Sphagnum* spp. dominated the more or less continuous bottom layer.

Environment. The environmental data for this site-type are given in Appendix 4. The site-type was confined to valley sides with plane or concave macro-scale topography, moderate to strong slope (15-30°) and soligenous paludification.

The tree layer was open or moderately dense, stocked with *Picea abies* and, more rarely, including single *Betula pubescens* trees. Site-type 5.1-2 often occured in mosaic with 5.1-1 (and, locally, with 5.2-1 and 5.2-2).

Due to the stoniness, soil depth showed considerable fine-scale variability; most plots showed low minimum soil depth and high maximum soil depth. The thickness of the humus layer was variable, and its organic content 50-90 %. The humus layer was acid; pH_{H2O} = 4.1-4.4 (4.8 in plot 132), pH_{CaCl2} = 3.2-3.6 (3.8 in plot 132), with low to moderate amounts of cations, except for relatively high figures for Al. The N content was moderate; 1.77-2.48 % of organic matter.

Variation. The site-type was relatively homogeneous, bound to soligenously paludified slopes with spruce forest. Variation in dominance relationships in the field layer was apparently not related to environmental conditions. The bottom layer showed considerable variation; from dominance of *Sphagnum girgensohnii* in the most strongly paludified sites (plots 21 and 95) via plots with dominance shared between *Sphagnum* and other bryophytes, to plots without *Sphagnum*, but still with dominance of the characteristic shade- and humidity-preferring species *Hylocomium umbratum*, *Plagiothecium undulatum* and *Barbilophozia lycopodioides* (plot 20). In addition to this continuous intergradation with site-type 5.1-1, 5.1-2 also intergraded with 5.2-2. Plot 132 (the one with the high pH values) was situated at the bottom of a long slope, containing *Gymnocarpium dryopteris* and *Calamagrostis purpurea*, thus indicating a transition to 5.2-2. Its occurrence in mosaic with richer types further motivates the high pH values.

Notes. The poor, paludified spruce forest is the optimum of several, more or less western species, e.g., *Cornus suecica*, *Plagiothecium undulatum*, *Rhytidiadelphus loreus*, *Calypogeia azurea* and *C. muellerana*. Furthermore, several widely distributed species reach their quantitative optimum here (shared with 5.2-2), e.g., *Hylocomium umbratum*, *Sphagnum girgensohnii*, *Lophocolea bidentata*, *Lophozia obtusa* and *Tritomaria quinquedentata*. The hepatics grow among the mosses on the ground. "Pockets" are not as frequent as in 5.1-1, as the good moisture supply gives rise to higher growth rates of bryophytes, and thus more rapid revegetation of naked patches.

Corresponding site-types: Kielland-Lund (1981): Eu-Piceetum myrtilletosum (*Plagiochila major* variety). Elven & Fremstad (1987): A4b. Kalela (1961): VMT.

5.2-1: The slightly rich non-paludified submesic site-type

Vegetation. The floristic composition of this site-type is shown in Tab. 32. Constant species were *Sorbus aucuparia* (seedlings and saplings), *Vaccinium myrtillus*, *Maianthemum bifolium*, *Trientalis europaea* and *Dicranum majus*. Other species with high subplot frequency in several plots, occasionally reaching local dominance, were *Dryopteris expansa* agg., *Gymnocarpium dryopteris*, *Calamagrostis purpurea* and *Deschampsia flexuosa*; in the bottom layer *Hylocomium umbratum*, *Plagiothecium undulatum* and *Barbilophozia lycopodioides*.

The mean number of species per sample plot was 23, while the total number in the 25 sample plots was 83.

Dominance in the field layer was shared between the dwarf shrub *Vaccinium myrtillus*, herbs (including low ferns) and graminids (often as a prominent element). Total cover varied, but was mostly above 50 %. The variable bottom layer (range of total cover 1-95 %) was dominated by mosses (acrocarpous and pleurocarpous).

Environment. The environmental data for this site-type are given in Appendix 4. The site-type mostly occurred in the lower parts of long valley sides with plane or concave macro-scale topography. Occurrences in concave terrain were mostly associated with long slopes or particularly broken terrain where site conditions were controlled by factors operating on broader scales.

The tree layer was mostly a dense *Picea abies* forest, not rarely with interspersed deciduous trees.

Soil depth was strongly variable on a fine scale due to the frequent occurrence of this site-type in stony terrain. Low minimum and high maximum soil depths were frequently encountered. The thickness of the humus layer was variable, as was its organic content (range 13-95 %, most measurements within 40-70 %). The humus was acid; pH_{H20} = 4.0-4.6, pH_{CaCl2} = 3.2-3.9, with variable but mostly moderate cation amounts. Particularly high Al contents were measured in plots 17 and 150. Total N content was moderate, but variable (1.56-3.54 % of organic matter).

Variation. The field layer showed some variation in cover. This was weakly related to the density of the tree layer. The highest cover, 100 %, was recorded in the open plot 44, while values below 50 % were mostly recorded beneath dense tree stands. The effects on the species composition were apparently only quantitative. There was some variation in the bottom layer, possible to relate to cover of the upper layers. High cover in the bottom layer was promoted by an open tree stand (plots 17, 40, 119) and/or an open field layer. Suppression of a bottom layer by a dense tree layer was observed in plots 18, 43, 142 and 145; by a dense field layer in plots 142 and 144. Species preferring shaded sites, i.e., close to tree bases, were *Brachythecium reflexum*, *Plagiothecium laetum* agg. and *Lophocolea heterophylla*. Sample plots 18 and 69 represented the extremes of this site-type with respect to tree density and microclimatic dryness, respectively. Species characteristic of sample plots transitional to site-type 5.2-2; i.e., *Hylocomium umbratum*, *Plagiothecium undulatum*, *Rhytidiadelphus loreus*, *Calypogeia muellerana* and *Plagiochila asplenioides*, seemingly preferred more open sites.

There was a considerable variation in dominance relationships in the bottom layer, apparently not possible to relate to environmental variation.

Some variation occurred in the presence of edaphically more demanding species (differential species for 5.2-1 against 5.1-1); *Anemone nemorosa*, *Dryopteris expansa* agg., *Gymnocarpium dryopteris*, *Oxalis acetosella*, *Thelypteris phegopteris*, *Calamagrostis purpurea*, *Milium effusum*, *Brachythecium reflexum*, *B. starkei*, *Plagiomnium affine*, *Plagiothecium*

Tab. 29. The vegetation of the 5.2-1 site-type. For explanation, see Tab. 19.

Sample plot	17	18	19	39	40	42	43	47	48	50	68	69	119	139	142	143	144	145	148	150	151	156	168	195	
N-TOT	32	24	22	22	20	22	26	13	21	18	23	19	29	21	21	23	19	21	27	23	26	26	37	27	23.4±4.9
N-VAS	18	12	12	8	9	10	14	9	12	9	10	12	10	10	11	13	11	12	11	14	13	12	18	10	11.7±2.5
N-BOT	14	12	10	14	11	12	12	4	9	9	13	7	19	11	10	10	8	9	16	9	13	14	19	17	11.8±3.6
MA Can (x10)	0	10	5	5	5	7	9	5	3	7	7	4	5	5	7	9	0	6	3	7	4	5	7	2	5.3±2.5
ME Lit (x10)	0	23	19	19	12	16	27	18	2	17	17	15	7	0	25	12	0	16	0	17	19	15	6	0	12.6±8.6
CC	60	30	40	75	20	80	45	90	45	20	30	70	40	70	90	80	100	35	90	35	70	45	30	85	57±25
CD	85	22	85	75	95	45	5	20	20	15	15	1	95	25	10	30	20	5	40	30	30	45	55	35	38±29
Picea abies	1	.	.	.	2	3	.	.	.	.	.	.	.	.	.	3	.	.	1	2	.	1	.	.	29^{2}
Sorbus aucuparia	6	6	2	10	6	7	16	14	10	5	8	11	5	9	16	10	5	7	4	6	10	15	6	3	100^{8}
Vaccinium myrtillus	13	10	16	16	16	16	16	16	16	16	8	16	16	16	16	16	5	16	16	16	16	16	7	16	100^{14}
V. vitis-idaea	.	.	.	.	2	.	.	9	.	2	.	5	.	5	.	4	.	.	.	1	14	1	.	10	42^{5}
Anemone nemorosa	4	.	2	.	1	.	3	.	1	.	1	.	.	.	.	1	.	7	3	11	1	.	1	.	50^{3}
Convallaria majalis	7	6	1	2	.	.	.	.	.	.	.	.	2	2	.	.	.	.	.	9	.	.	.	.	29^{4}
Dryopteris expansa agg.	13	.	5	.	.	16	3	.	6	.	16	4	12	.	1	6	16	14	4	1	.	.	4	13	67^{8}
Gymnocarpium dryopteris	14	14	4	.	.	2	10	.	.	3	3	.	3	3	2	4	1	1	4	11	.	9	16	.	71^{6}
Huperzia selago	.	.	2	.	.	.	.	.	.	.	10	.	7	.	.	.	.	.	.	.	2	.	5	.	21^{5}
Linnaea borealis	.	.	.	.	.	.	.	3	.	.	.	2	.	.	.	.	.	.	.	.	5	.	.	.	13^{3}
Lycopodium annotinum	.	.	5	.	.	.	.	8	7	.	.	8	3	.	.	.	3	7	4	.	.	.	.	8	38^{6}
Maianthemum bifolium	16	16	13	15	16	16	13	14	16	14	11	10	1	16	16	16	16	16	13	12	15	16	12	16	100^{14}
Melampyrum sylvaticum	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	1	.	.	13^{2}
Oxalis acetosella	10	.	.	.	.	.	6	.	.	.	4	.	.	.	4	1	1	2	.	2	2	6	15	.	46^{5}
Pteridium aquilinum	.	.	.	9	.	2	6	.	4	.	.	15	.	9	1	2	.	4	.	.	.	.	.	5	42^{6}
Solidago virgaurea	.	4	.	2	.	.	.	.	1	2	.	.	.	.	3	.	.	.	.	5	2	9	2	.	38^{3}
Thelypteris phegopteris	.	.	4	.	.	.	.	.	.	.	.	3	.	.	.	.	.	4	.	.	.	.	12	.	17^{6}
Trientalis europaea	8	1	11	12	6	5	3	7	4	7	.	3	3	10	8	4	16	7	.	3	9	.	2	9	88^{7}
Calamagrostis purpurea	14	.	16	.	.	2	8	6	14	2	2	2	14	6	10	16	16	3	15	11	.	7	6	.	79^{9}
Deschampsia flexousa	16	5	.	16	16	16	16	3	14	2	16	.	.	16	16	16	16	.	16	.	15	4	15	8	79^{13}
Luzula pilosa	9	2	.	.	.	.	4	.	.	.	.	.	.	.	.	.	1	.	1	.	4	6	7	.	33^{4}
Milium effusum	4	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	13^{4}
Brachythecium reflexum	13	4	.	.	.	1	6	.	.	.	10	7	.	1	12	5	1	.	.	.	.	.	1	.	46^{6}
B. starkei	10	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	.	14	.	17^{7}
Cirriphyllum piliferum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	1	.	4	.	.	.	.	.	.	13^{3}
Dicranum fuscescens	.	.	.	.	2	.	.	1	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	13^{2}
D. majus	16	13	15	16	16	14	4	16	15	15	5	.	16	16	10	13	1	16	14	5	16	16	2	15	96^{12}
D. scoparium	.	.	1	.	.	.	.	.	.	.	3	.	5	.	1	.	.	.	.	.	.	.	9	2	25^{4}
Hylocomium splendens	.	.	.	13	2	2	.	.	10	.	1	.	4	5	1	.	.	.	4	.	6	7	1	1	54^{4}
H. umbratum	13	.	16	2	6	10	1	.	5	.	15	.	16	.	.	11	16	4	16	3	.	2	1	16	71^{9}
Plagiomnium affine	9	.	.	.	.	.	.	.	.	.	4	.	.	.	3	.	.	1	6	.	.	.	12	.	25^{6}
Plagiothecium denticulatum	.	.	.	.	.	2	.	.	1	6	.	2	.	.	.	.	.	.	4	6	2	2	9	8	42^{4}
P. laetum agg.	16	15	2	5	.	.	11	.	.	.	5	5	5	3	4	4	4	1	3	.	8	7	1	3	75^{6}
P. undulatum	5	.	9	.	16	.	.	.	.	.	.	.	4	.	.	.	16	.	1	.	.	.	.	3	29^{8}
Pleurozium schreberi	1	.	1	8	.	.	.	8	.	6	.	.	1	16	4	4	.	1	6	.	3	3	6	12	63^{5}
Polytrichum formosum	4	.	.	.	1	.	1	.	.	12	1	1	.	.	.	.	.	.	.	15	5	3	16	.	42^{4}
Rhytidiadelphus loreus	.	.	.	2	11	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6	.	.	.	13^{6}
R. subpinnatus	.	.	6	2	1	1	.	.	.	.	.	.	2	.	.	.	.	.	2	.	1	3	.	.	33^{2}
R. triquetrus	.	1	.	10	.	.	.	2	3	.	.	.	.	1	.	.	.	2	.	4	.	.	.	.	29^{3}
Barbilophozia lycopodioides	14	4	12	9	7	6	1	.	13	4	1	.	16	10	.	1	6	.	5	.	2	5	2	16	79^{7}
Calypogeia integristipula	.	.	.	3	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	4	13^{3}
C. muellerana	1	.	.	5	.	.	1	.	4	.	.	2	6	4	.	.	.	.	1	1	.	.	12	10	46^{4}
Cephalozia bicuspidata	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	2	.	2	17^{2}
C. lunulifolia	.	.	.	.	.	.	1	.	.	.	.	.	4	.	.	.	.	.	.	.	.	1	.	1	17^{2}
Lophocolea heterophylla	15	13	1	11	.	9	.	.	.	2	10	1	6	10	15	1	.	6	6	.	.	7	16	11	71^{8}
Lophozia ventricosa agg.	.	1	.	.	.	.	.	.	.	.	.	.	3	.	.	1	.	.	.	.	.	1	.	.	17^{2}
Plagiochila asplenioides	12	.	14	7	16	8	3	.	2	5	5	.	12	.	1	1	9	2	14	14	4	11	7	.	79^{8}
Tritomaria quinquedentata	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	2	.	.	.	.	13^{1}

Additional species (occurring in two sample plots or less; Plot No: Frequency in subplots, Constancy and mean frequency in subplots):

Betula pubescens 48:3 4^{3}, Populus tremula 168:6 4^{6}, Athyrium filix-femina 168:6 4^{6}, Blechnum spicant 69:4, 168:6 8^{5}, Cornus suecica 195:16 4^{16}, Dryopteris filix-mas 17:6 4^{6}, Geranium sylvaticum 43:10 4^{10}, Melampyrum pratense 43^{4} 4^{4}, Potentilla erecta 40:3 4^{3}, Rubus saxatilis 17:3, 150:2 8^{3}, Festuca altissima 17:1, 18:1 8^{1}, Melica nutans 1:3 4^{3}; Brachythecium mildeanum 3 4^{3}, B. rutabulum 18:1, 148:1 8^{1}, B. salebrosum 43:2 4^{2}, Drepanocladus uncinatus 39:1 4^{1}, Hypnum cupressiforme 69:1 4^{1}, Mnium spinosum 18:2 4^{2}, Pohlia nutans agg. 18:1, 168:2 8^{2}, P. commune 50:11, 151:3 8^{7}, Ptilium crista-castrensis 17:1, 48:1 8^{1}, Rhodobryum roseum 50:1 4^{1}, Tetraphis pellucida 195:1 4^{1}, Barbilophozia barbata 150:1, 168:1 8^{1}, Blepharostoma trichophyllum 119:4, 139:1 8^{3}, Calypogeia azurea 42:1, 168:1 8^{1}, C. neesiana 42:1, 195:9 8^{5}, Diplophyllum taxifolium 8^{1}, Gymnocolea inflata 40:2 4^{2}, Lepidozia reptans 168:2 4^{2}, Lophozia obtusa 144:6, 195:2 8^{4}, Plagiochila porelloides 18:1 4^{1}, Ptilidium pulcherrimum 18:3, 43:1 8^{2}, Cladonia chlorophaea agg. 151:2 4^{2}, C. coniocraea agg. 151:1 4^{1}.

denticulatum, *Rhytidiadelphus subpinnatus* s.str. and *Rhytidiadelphus triquetrus*. Examples of plots poor in such species were 5, 47, 139, 151, while plots 17, 150, 168, 68 and 156 were transitional towards site-type 5.3. This variation was partly reflected in pH and cation content.

Notes. The frequency of "pockets" is relatively high, as in site-type 5.1-1 (cf. p. 188).

High mortality rates and establishment problems for bryophytes in the bottom layer (due to low incoming radiation and litter accumulation) are indicated by low total cover, high species diversity, and patchy distribution of most species.

Corresponding site-types: Kielland-Lund (1981): Eu-Piceetum dryopteridetosum. Elven & Fremstad (1987): A5a and transitions to A5b. Kujala (1961): MT-OMT transitions. Kalela (1961): DeMT.

5.2-2: The slightly rich paludified submesic site-type

Vegetation. The floristic composition of this site-type is shown in Tab. 31. Constant species were *Picea abies* and *Sorbus aucuparia* (seedlings and saplings), *Vaccinium myrtillus*, *Gymnocarpium dryopteris*, *Lycopodium annotinum*, *Maianthemum bifolium*, *Calamagrostis purpurea*, *Dicranum majus*, *Hylocomium umbratum*, *Pleurozium schreberi* and *Calypogeia muellerana*. Local dominants, often with high subplot frequency, were *Cornus suecica*, *Blechnum spicant* and *Polytrichum commune* (plot 94) and *Sphagnum girgensohnii* (plot 38).

The mean number of species per sample plot was 24, while the total number in the 6 sample plots was 53.

The field layer had a mixed dominance of dwarf shrubs (*Vaccinium myrtillus*), low ferns, herbs and graminids; normally with total cover above 50 %. The bottom layer was dominated by mosses or *Sphagnum*, with a total cover of 30-70 %.

Environment. The environmental data for this site-type are given in Appendix 4. The site-type occurred on gentle to moderate, concave slopes. Plots 38 and 138 were deviant in this respect, situated in a very gently sloping, strongly paludified depression within a long slope of variable, but mostly considerable steepness. The occurrence of site-type 5.2-2 was always associated with soligenous paludification.

Picea abies was the dominant of an open tree layer, where *Betula pubescens* and *Sorbus aucuparia* also occurred. This site-type occurred in mosaic with site-types 5.2-1 and 5.1-1 on adjacent less concave areas and in directions of higher tree density.

The site-type typically occurred in stony terrain, giving rise to low minimum and high maximum soil depths. Plot 38, situated in the middle of a strongly paludified depression, had a deep peaty soil. The humus layer was mostly 4-8 cm thick, with high organic content (88-95 %). The chemical properties of the humus varied; pH_{H20} = 4.0-5.0, pH_{CaCl2} = 3.2-4.0, with small to moderate amounts of cations (except moderate to high amounts of Al) and total N (1.82-2.40 % of organic matter).

Variation. The low number of sample plots was not sufficient to represent the variation in this rather rare site-type adequately. Representativity was further reduced, as the six plots formed three geographically co-ordinated pairs. Plots 33 and 133 represented transitions to site-type 5.2-1, with low importance of *Sphagnum* spp. (absent from plot 133) and other humidity-preferring bryophytes. Plot 38 represented the wet and rich extreme (pH_{H20} = 5.0); completely dominated by *Sphagnum girgensohnii*, but otherwise poor in bryophyte species. Plot 94 represented an open, humid extreme from a high-situated northeastern slope, with abundance of *Sphagnum* (*S. centrale* and *S. russowii*) and with dominance of slightly western

Tab. 30. The vegetation of the 5.2-2 site-type. For explanation, see Tab. 19.

Sample plot	33	38	94	133	138	194	
N-TOT	25	11	26	25	28	30	24.2±6.7
N-VAS	13	9	14	12	12	14	12.3±1.9
N-BOT	12	2	12	13	16	16	11.8±5.2
MA Can (x10)	2	4	0	2	4	0	2.0±1.8
ME Lit (x10)	1	0	0	1	14	0	2.6±5.6
CC	65	50	60	95	40	80	65±20
CD	70	70	40	0	45	60	48±26
Betula pubescens	1	.	5	2	.	.	50^3
Picea abies	8	6	.	1	2	9	83^5
Sorbus aucuparia	.	2	4	2	4	3	83^3
Vaccinium myrtillus	16	9	16	16	16	16	100^{15}
V. vitis-idaea	14	.	.	16	9	1	67^{10}
Blechnum spicant	.	.	15	.	.	4	33^{10}
Cornus suecica	.	.	14	.	.	13	33^{14}
Gymnocarpium dryopteris	13	16	6	.	13	1	83^{10}
Listera cordata	.	.	9	.	.	1	33^5
Lycopodium annotinum	1	2	3	3	11	7	100^5
Maianthemum bifolium	16	.	3	14	9	11	83^{11}
Potentilla erecta	1	.	.	4	.	.	33^3
Pteridium aquilinum	9	15	.	5	5	.	67^9
Solidago virgaurea	1	.	.	1	.	.	33^1
Thelypteris phegopteris	.	12	2	.	13	.	50^9
Trientalis europaea	.	16	11	.	4	10	67^{10}
Calamagrostis purpurea	13	6	2	16	5	5	100^8
Deschampsia flexuosa	13	.	15	16	7	16	83^{13}
Dicranum majus	14	.	6	15	8	16	83^{12}
Hylocomium splendens	2	.	.	2	3	1	67^2
H. umbratum	8	.	9	16	10	16	83^{12}
Plagiothecium denticulatum	1	.	.	6	.	.	33^4
P. undulatum	.	.	7	3	6	16	67^8
Pleurozium schreberi	4	.	.	16	6	10	83^{12}
Polytrichum commune	.	9	15	.	8	.	50^{11}
Sphagnum girgensohnii	11	16	.	.	8	.	50^{12}
Barbilophozia lycopodioides	9	.	4	14	.	16	67^{11}
Calypogeia integristipula	3	.	.	.	1	.	33^2
C. muellerana	4	.	13	3	9	2	83^6
Cephalozia bicuspidata	1	.	4	2	.	.	50^2
Lophocolea heterophylla	3	.	.	4	12	1	67^5
Lophozia obtusa	.	.	1	.	.	5	33^3
Plagiochila asplenioides	.	.	.	1	6	1	50^3
Tritomaria quinquedentata	.	.	1	.	.	10	33^6

Additional species (occurring in only 1 sample plot; Plot No.: Frequency in subplots):

Anemone nemorosa 33:1, Dryopteris expansa agg. 194:1, Molinia caerulea 94:10; Brachythecium reflexum 138:3, Calliergon stramineum 94:4, Dicranum scoparium 138:3, Drepanocladus uncinatus 138:3, Plagiothecium laetum agg. 138:7, Polytrichum formosum 194:5, Ptilium crista-castrensis 194:12, Rhizomnium punctatum 33:1, Rhytidiadelphus loreus 194:4, R. subpinnatus 194:4, Sphagnum centrale 94:9, S. quinquefarium 194:9, S. russowii 94:13, Barbilophozia barbata 133:7, Calypogeia azurea 133:1, Cephalozia lunulifolia 138:2.

and/or humidity-preferring species like *Blechnum spicant*, *Cornus suecica*, *Listera cordata*, *Polytrichum commune*, and *Calypogeia muellerana*. The poor extreme was represented by plot 194 (pH_{H2O} = 4.0), only containing *Gymnocarpium dryopteris* and *Calamagrostis purpurea* in small amounts, and thus transitional to site-type 5.1-2.

Corresponding site-types: Kielland-Lund (1981): Eu-Piceetum dryopteridetosum (and transitions to Chamaemoro-Piceetum). Elven & Fremstad (1987): A5b.

5.3: The rich submesic site-type

Vegetation. The floristic composition of the site-type is shown in Tab. 31. Constant species were *Sorbus aucuparia* (seedlings and saplings), *Vaccinium myrtillus*, *Anemone nemorosa*, *Gymnocarpium dryopteris*, *Maianthemum bifolium*, *Trientalis europaea*, *Calamagrostis purpurea*, *Deschampsia flexuosa* and *Dicranum majus*. Other species occasionally reaching high subplot frequency (and locally dominating) were *Oxalis acetosella*, *Pteridium aquilinum*, *Festuca altissima*, *Hylocomium umbratum*, *Rhytidiadelphus subpinnatus*, *Lophocolea heterophylla* and *Plagiochila asplenioides*.

The mean number of species per sample plot was 28, while the total number in the 16 sample plots was 69.

The field layer was dominated by low herbs, locally with high importance of graminids, low ferns and dwarf shrubs (*Vaccinium myrtillus*). Total cover in the field layer was variable, but typically about 70 %. The bottom layer was variable, but often patchily developed. Bryophytes, mostly mosses, dominated in the bottom layer.

Environment. The environmental data for this site-type are given in Appendix 4. The site-type typically occurred on moderate to strong slopes, associated with plane (or even convex) macro-scale topography. Occurrence in convex sites was associated with strong slope, occurrence on gentle slopes (plot 44) with concave topography.

The tree layer was variable; mostly an open *Picea abies* forest with single trees of *Betula pubescens*, *Acer platanoides*, *Quercus* spp., *Populus tremula* and *Taxus baccata*.

The site-type mostly occurred close to talus slopes and on very stony sites, thus the soil was shallow. High maximum soil depth occurred on gentle slopes (plot 44) and in less stony sites (plots 16 and 167). The humus layer was thin, mull-like (mostly 1-5 cm), throughout mixed with inorganic particles, and indistinctly separated from the eluviated layer underneath an eluviated layer was occasionally absent). Earthworms were frequently observed. The organic matter content of the humus layer was (10-)25-50(-77) %. The humus was moderately acid; pH_{H20} = 4.0-5.0, pH_{CaCl2} = 3.3-4.2, mostly with moderate to high cation content and rich in total N (2.20-3.82 % of organic matter).

Variation. The site-type showed considerable variation both in the field and the tree layers. Due to the generally higher crowns than in site-types 5.1-1 and 5.2-1, there was a negligible variation in response to upper layers. Most of the variation observed was environmentally uninterpretable; relating to relative amounts and presence of species. However, there was some variation in the importance of edaphically demanding species, possible to relate to variation in pH. The most important species characteristic of site-type 5.3, differentiating against site-type 5.2-1, were *Dryopteris filix-mas*, *Melampyrum sylvaticum*, *Rubus saxatilis*, *Viola riviniana*, *Carex digitata* and *Melica nutans*. These species were most prominent in plot 57, 167, 49 and 157 (pH_{H20} = 4.7-5.0), while the (species-)poor end was represented by plots 44, 46, 55, 56, 116, 146 and 149 (with variable pH).

Some variation occurred in the importance of humidity-demanding species, although paludified sites were not included in the material. Plots 44, 116 and 157 all had prominence of *Hylocomium umbratum*.

Notes. "Pockets" in the surface occur, and contribute to the diversity. In addition, the

Tab. 31. The vegetation of the 5.3 site-type. For explanation, see Tab. 19.

Sample plot	16	44	46	49	51	52	55	56	57	116	146	149	152	154	157	167	
N-TOT	32	26	20	21	35	35	23	26	29	34	25	27	27	32	37	24	28.3±5.3
N-VAS	15	12	14	16	21	17	10	18	16	14	18	12	18	18	20	20	16.2±3.2
N-BOT	17	14	6	5	14	18	13	8	13	20	7	15	9	14	17	4	12.1±5.0
Ma Can (x10)	6	0	6	2	4	1	7	5	5	6	6	2	1	5	5	7	4.2±2.3
ME Lit (x10)	22	0	23	1	6	1	20	21	13	5	19	3	0	1	2	22	9.9±9.5
CC	70	90	70	70	95	95	20	40	80	50	70	25	95	65	80	75	68±24
CD	60	20	60	3	30	10	5	70	20	75	60	10	30	80	60	15	38±27
Acer platanoides	.	.	.	.	.	.	.	.	10	.	.	.	.	.	2	.	13^{6}
Betula pubescens	.	.	.	.	.	.	.	.	.	.	.	.	1	.	3	.	13^{2}
Picea abies	.	2	,	1	3	2	.	.	.	1	.	.	1	2	5	.	50^{2}
Populus tremula	.	.	.	.	5	.	.	5	6	.	.	.	.	.	3	6	31^{5}
Sorbus aucuparia	7	6	12	5	4	8	1	12	9	4	14	12	1	12	6	4	100^{7}
Vaccinium myrtillus	11	14	13	3	16	16	15	10	.	16	15	.	16	16	3	7	88^{12}
V. vitis-idaea	.	1	3	.	6	.	.	.	.	.	13	6	3	3	.	.	44^{5}
Anemone nemorosa	4	.	3	12	15	7	.	11	15	.	9	4	8	14	6	1	81^{8}
Convallaria majalis	4	.	.	3	6	2	.	6	2	.	.	.	8	6	.	2	56^{4}
Dryopteris expansa agg.	4	1	6	4	.	1	.	.	.	16	4	6	.	3	.	2	63^{5}
D. filix-mas	12	.	.	.	.	.	3	.	.	.	.	.	.	.	.	12	19^{9}
Gymnocarpium dryopteris	16	12	.	15	14	4	.	15	15	6	3	7	10	7	16	16	88^{11}
Linnaea borealis	.	.	.	2	8	3	.	.	.	.	.	.	9	8	.	.	31^{6}
Lycopodium annotinum	.	16	.	1	.	.	.	.	.	.	6	.	.	5	.	.	25^{7}
Maianthemum bifolium	13	16	16	15	16	15	7	16	15	11	16	13	16	16	14	13	100^{4}
Melampyrum pratense	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	6	13^{4}
M. sylvaticum	.	.	.	.	6	.	1	3	5	.	1	.	.	2	6	.	44^{3}
Oxalis acetosella	15	.	10	.	1	3	.	2	15	3	13	11	.	9	13	10	75^{9}
Pteridium aquilinum	.	16	.	.	.	11	.	.	.	.	.	.	11	11	.	9	31^{12}
Rubus saxatilis	.	.	6	7	2	1	.	.	.	.	6	3	6	.	3	.	50^{4}
Solidago virgaurea	.	.	4	.	9	4	1	3	.	4	3	.	7	.	.	1	56^{4}
Thelypteris phegopteris	11	.	.	16	.	.	.	.	.	2	.	.	.	.	.	4	25^{8}
Trientalis europaea	9	8	2	1	7	7	2	1	4	12	1	4	7	9	7	9	100^{6}
Viola riviniana	.	.	.	1	2	2	.	2	13	.	.	.	7	.	7	5	50^{5}
Calamagrostis purpurea	.	16	4	15	6	15	13	15	16	7	13	10	14	16	16	16	94^{13}
Deschampsia flexuosa	14	15	16	4	16	5	3	16	15	.	12	11	16	.	3	.	81^{11}
Festuca altissima	16	.	.	.	.	.	.	6	12	6	9	.	.	.	16	5	44^{10}
Luzula pilosa	2	.	6	.	3	.	1	.	7	4	7	.	5	4	2	.	63^{4}
Melica nutans	.	.	.	.	.	.	.	6	14	.	.	.	.	7	1	.	25^{7}
Milium effusum	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	16	13^{10}
Brachythecium reflexum	10	.	.	.	.	5	1	.	7	11	.	.	.	.	2	14	44^{7}
B. starkei	.	3	.	.	.	1	.	.	.	15	.	.	.	.	.	.	19^{6}
Cirriphyllum piliferum	.	.	.	.	5	.	.	.	.	.	.	.	.	.	2	.	13^{4}
Dicranum majus	16	10	16	10	16	12	11	7	9	16	16	12	16	16	8	.	94^{13}
Eurhynchium striatum	4	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	13^{3}
Hylocomium splendens	.	.	.	.	14	6	4	1	13	.	1	1	7	7	6	.	63^{6}
H. umbratum	15	15	.	4	.	.	7	1	6	16	.	4	4	16	16	.	68^{9}
Plagiomnium affine	3	2	1	.	.	1	.	.	12	6	.	.	.	6	10	10	56^{6}
Plagiothecium denticulatum	.	.	.	.	.	11	.	9	3	3	.	8	1	6	10	.	50^{6}
P. laetum agg.	16	1	.	.	2	4	10	1	.	15	.	1	.	.	.	.	50^{6}
P. undulatum	.	5	.	.	.	.	.	.	.	3	.	.	.	.	.	.	13^{4}
Pleurozium schreberi	4	6	3	.	1	8	.	.	.	10	2	8	6	8	5	.	69^{6}
Pohlia nutans agg.	.	.	.	.	.	1	.	.	.	2	.	.	.	.	.	.	13^{2}
Polytrichum formosum	4	4	.	.	.	.	.	4	.	4	1	.	.	.	.	.	31^{3}
Rhizomnium punctatum	4	.	.	.	.	.	.	.	.	2	.	.	.	.	1	.	19^{2}
Rhodobryum roseum	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	8	13^{5}
Rhytidiadelphus loreus	.	.	.	.	7	.	.	.	1	.	.	1	.	3	.	.	25^{3}
R. subpinnatus	16	3	1	.	15	2	3	.	14	.	.	.	4	5	3	.	63^{7}
R. triquetrus	.	.	.	3	14	2	.	.	7	.	5	1	.	3	.	.	44^{5}

Tab. 31 (continued).

Sample plot	16	44	46	49	51	52	55	56	57	116	146	149	152	154	157	167	
Barbilophozia lycopodioides	5	10	2	4	3	.	.	.	1	9	.	5	9	1	5	.	69^5
Blepharostoma trichphyllum	1	.	.	.	.	2	.	.	.	1	.	1	.	.	1	.	31^1
Calypogeia integristipula	.	.	.	.	.	3	.	.	.	.	.	.	.	2	.	.	13^3
C. muellerana	.	.	.	.	.	4	1	.	.	1	.	.	.	2	.	.	25^2
C. neesiana	.	.	.	.	.	4	1	.	.	.	.	.	.	.	.	.	13^3
Cephalozia bicuspidata	.	.	.	.	.	.	1	.	.	.	.	.	.	2	2	.	19^2
C. lunulifolia	2	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	13^3
Lophocolea heterophylla	15	2	.	.	2	10	2	15	1	15	2	1	2	.	.	3	75^6
Lophozia obtusa	.	7	.	.	3	.	.	.	.	4	.	.	.	.	5	.	25^5
L. ventricosa agg.	3	.	.	.	4	.	1	.	.	3	.	.	.	.	3	.	31^3
Plagiochila asplenioides	5	10	.	4	10	14	1	10	12	.	2	1	8	16	16	.	81^8

Additional species (occurring in only 1 sample plot; Plot No.: Frequency in subplots):

Pinus sylvestris 116:1, Vaccinium uliginosum 149:3, Geranium sylvaticum 157:1, Hieracium, Sylvatica-gr. 146:1, Huperzia selago 56:1, Lathyrus montanus 56:1, Paris quadrifolia 167:1, Carex digitata 51:1, C. pilulifera 51:1; Dicranum scoparium 149:3, Herzogiella striatella 16:1, Isopterygium elegans 46:1, Mnium spinosum 57:1, Polytrichum commune 55:1, Tetraphis pellucida 116:5, Sphagnum quinquefarium 44:1, Barbilophozia barbata 51:1, Lepidozia reptans 52:1, Tritomaria quinquedentata 149:1.

high areal importance of litter-covered surfaces provides sites for ecesis of species like *Brachythecium reflexum*, *Plagiothecium* spp. and *Lophocolea heterophylla*.

Corresponding site-types: Kielland-Lund (1981): Melico-Piceetum typicum, typical variety. Elven & Fremstad (1987): B1. Kujala (1961): OMT. Kalela (1961): GOMT.

6: The rich slightly flushed site-type

Vegetation. The floristic composition of the site-type is shown in Tab. 32. Constant species were *Sorbus aucuparia* (seedlings and saplings), *Maianthemum bifolium*, *Solidago virgaurea*, *Trientalis europaea*, *Calamagrostis purpurea*, *Cirriphyllum piliferum* and *Plagiomnium affine*, but the low number of sample plots makes this list in danger of not being representative. Locally dominating species or species with high subplot frequency, were *Vaccinium myrtillus*, *Athyrium filix-femina*, *Gymnocarpium dryopteris*, *Oxalis acetosella* and *Rhytidiadelphus squarrosus* agg.

The mean number of species per sample plot was 36, while the total number in the 5 sample plots was 70.

Environment. The environmental data for this site-type are given in Appendix 4. This site-type was rare in the area, occurring in depressions (plot 45) or concave valley sides, associated with flush effects (all other plots), but devoid of paludification.

The tree layer was open, with a mixture of *Picea abies*, *Alnus incana*, and other deciduous trees. Contact vegetation was mostly site-types 5.3 and 5.2-1.

Soil thickness was variable. The humus was a distinct mull, with an organic matter content below 35 %. The humus was only weakly acid; pH_{H20} = 5.3-5.4, pH_{CaCl2} = 4.6-5.1. Plot 67 was deviant in the low pH (pH_{H20} = 4.3), but shared with the other plots the rather high cation content and had the highest total N content among the 5 sample plots (range 2.44-3.68 %).

Tab. 32. The vegetation of the 6 site-type. For explanation, see Tab. 19.

Sample plot	45	53	54	67	153	
N-TOT	47	37	40	24	34	36.4±8.4
N-VAS	29	29	25	17	26	25.2±4.9
N-BOT	18	8	15	7	8	11.2±5.0
MA Can (x10)	6	2	5	7	2	4.4±2.3
ME Lit (x10)	13	3	14	0	0	6.1±7.0
CC	60	100	80	70	100	82±18
CD	75	30	30	7	40	36±25
Betula pubescens	.	1	5	.	.	40^{3}
Picea abies	1	7	7	.	1	80^{4}
Populus tremula	.	.	3	6	.	40^{5}
Sorbus aucuparia	10	4	8	6	1	100^{6}
Viburnum opulus	.	2	.	.	9	40^{6}
Vaccinium myrtillus	14	.	15	15	.	60^{15}
V. vitis-idaea	2	.	11	.	.	40^{7}
Anemone nemorosa	13	12	10	.	5	80^{10}
Angelica sylvestris	.	1	.	.	3	40^{2}
Athyrium filix-femina	.	15	8	4	16	80^{11}
Convallaria majalis	.	11	.	1	5	60^{6}
Crepis paludosa	12	12	.	.	15	60^{13}
Dactylorhiza fuchsii	1	.	.	.	2	40^{2}
Dryopteris expansa agg.	.	.	1	6	.	40^{4}
Geranium sylvaticum	7	10	2	.	7	80^{7}
Gymnocarpium dryopteris	4	8	12	16	.	80^{10}
Hepatica nobilis	4	7	.	.	5	60^{5}
Linnaea borealis	.	.	3	.	2	40^{3}
Lycopodium annotinum	3	.	.	.	1	40^{2}
Maianthemum bifolium	13	11	14	12	2	100^{10}
Melampyrum sylvaticum	1	.	5	.	.	40^{3}
Oxalis acetosella	9	.	10	9	16	80^{11}
Polygonatum verticillatum	9	8	.	.	11	60^{9}
Pteridium aquilinum	.	16	1	16	3	80^{9}
Rubus saxatilis	2	13	7	.	6	80^{7}
Solidago virgaurea	5	6	8	1	1	100^{4}
Thelypteris phegopteris	13	9	.	4	4	80^{10}
Trientalis europaea	5	2	10	6	3	100^{5}
Valeriana sambucifolia	8	10	.	.	8	60^{9}
Veronica officinalis	6	1	.	.	.	40^{4}
Viola riviniana	11	5	5	.	4	80^{6}
Calamagrostis purpurea	16	15	15	16	9	100^{14}
Carex digitata	.	1	1	.	.	40^{1}
Deschampsia flexuosa	2	.	16	.	1	60^{6}
Luzula pilosa	4	6	6	9	.	80^{6}
Melica nutans	12	1	4	.	9	80^{9}
Brachythecium reflexum	1	.	.	14	.	40^{8}
B. salebrosum	8	.	3	.	.	50^{6}
Cirriphyllum piliferum	11	11	6	2	13	100^{9}
Dicranum majus	4	4	8	.	1	80^{4}
D. scoparium	.	.	3	1	.	40^{2}
Hylocomium splendens	4	.	6	.	.	40^{5}
H. umbratum	.	6	6	.	1	60^{4}
Plagiomnium affine	15	3	4	8	9	100^{8}
Plagiothecium denticulatum	.	1	4	6	.	60^{4}
Rhodobryum roseum	10	12	.	1	6	80^{7}
Rhytidiadelphus subpinnatus	16	16	15	.	16	80^{16}
R. triquetrus	10	.	2	.	.	40^{6}
Lophocolea heterophylla	3	.	.	9	.	40^{6}
Plagiochila asplenioides	7	15	14	.	9	80^{11}

Additional species (occurring in only 1 sample plot; Plot No.: Frequency in subplots):

Dryopteris filix-mas 67:7, Hieracium, Sylvatica-gr. 53:4, H. Vulgata-gr. 45:8, Huperzia selago 45:3, Lathyrus vernus 53:1, Paris quadrifolia 53:7, Pyrola minor 45:14, Milium effusum 67:3; Drepanocladus uncinatus 45:2, Fissidens adianthoides 45:6, Pleurozium schreberi 54:3, Polytrichum formosum 153:1, Rhytidiadelphus squarrosus 45:16, Barbilophozia attenuata 54:2, Blepharostoma trichophyllum 45:2, Calypogeia muellerana 54:6, Cephalozia bicuspidata 45:1, Chiloscyphus polyanthos 45:16, Lophozia ventricosa agg. 54:2, Plagiochila porelloides 45:7.

Variation. The variation within the site-type was not adequately represented by the five sample plots; they could therefore just be considered examples of site-type 6 vegetation. Plot 45 was situated in a depression with seasonal flooding. Plots 53, 54 and 153 occurred in a concave valley-side with a distinct flush, manifest in the luxuriant, species-rich vegetation, dominated by tall herbs and ferns. Plot 67 was poorer in species, and represented the transition to site-type 5.3.

Notes. Site-type 6 as circumscribed here is clearly heterogeneous; but further treatment (or division into several types) was impossible due to sparse representation in the area (and in the material).

ACKNOWLEDGEMENTS

The present study is a result of the projects "The effect of acid precipitation on boreal coniferous forest vegetation: reference area Gjerstad" and "Effects of long-distance airborne pollution on boreal coniferous forest vegetation", grants No. 455.032/87 and 455.032/91 from The Norwegian Research Council for Science and the Humanities. Additional financial support has been obtained from the TOV (Terrestrial monitoring) programme at The Directorate for Nature Management, and from the Botanical Garden and Museum, University of Oslo.

Thanks are due to The Directorate of State Forests, Grenland (and later Sørlandet) district, for kindly putting the log cabin at Svarttjern at our disposal, to Klaus Høiland, Håkon Kvamme and Arne Rørå for participation in field work, to Egil Bendiksen and, in particular, Tonje Økland for stimulating discussions and comments on the manuscript, to colleagues, students and others, too many to mention by their names, who have contributed to discussions and fieldwork companionship. Last, our wives Tonje and Heidi are thanked for patience and support.

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APPENDICES

Appendix 1. Survey of sample plot positions (UTM grid reference) and assignment of meso sample plots to site-types (Class.) and Subset (S). Tr No.- Transect number, MA plot - Macro plot No., l (m) - length along the transect in m (breaking points along the transect given in brackets), Alt. - altitude, ME n plot - number and classification of meso plot. Direction - direction of transect. Meso plots included in the Terrestrial monitoring programme (TOV) of the Directorate for Nature Management are denoted by *.

Tr. No.	MA plot	l (m)	UTM grid ref.	Alt. (m)	ME 1 plot				ME 2 plot			Direction
					No.	Class.		S	No.	Class.	S	
T1	1	10	MK 914 355	350	1	5.1-1	*	A	101	5.1-1	A	190^g
	2	20	MK 914 355	350	2	5.1-1	*	A	102	5.1-1	A	
	3	30	MK 914 355	355	3	5.1-1	*	A	103	5.1-1	A	
	4	60	MK 914 354	360	4	4-1		A	104	5.1-1	A	
	5	70	MK 914 354	360	5	5.1-1	*	A	105	5.1-1	A	
	6	80	MK 914 354	365	6	5.1-1	*	A	106	5.1-2	A	
	7	90	MK 914 354	365	7	5.1-1	*	A	107	5.1-1	A	
	8	110	MK 914 354	375	8	4-2		A	108	4-1	A	
	9	120	MK 914 354	380	9	4-2		A	109	4-1	B	
	10	130	MK 914 354	380	10	4-1		B	110	4-1	B	
	11	140	MK 914 354	385	11	4-1		B	111	4-1	B	
	12	150	MK 914 354	390	12	1-1		B	112	3-1	B	
	13	160	MK 914 354	390	13	2-1		B	113	1-2	B	
	14	170	MK 914 354	395	14	1-1		B	114	1-1	B	200^g
	15	200	MK 914 353	390	15	5.1-1	*	A	115	5.1-1	A	
		(224)										140^g
	16	240	MK 914 353	395	16	5.3	*	A	116	5.3	A	
	17	250	MK 915 352	400	17	5.2-1	*	A	117	5.1-1	A	
	18	260	MK 915 352	400	18	5.2-1	*	A	118	5.1-1	A	
	19	280	MK 915 352	400	19	5.2-1	*	A	119	5.2-1	A	
	20	300	MK 915 352	405	20	5.1-2	*	A	120	5.1-1	A	
		(310)										180^g
	21	320	MK 915 352	405	21	5.1-2	*	A	121	5.1-1	A	
	22	330	MK 915 352	410	22	5.1-1	*	A	122	5.1-1	A	
	23	340	MK 915 352	415	23	5.1-2	*	A	123	5.1-1	A	
	24	370	MK 915 352	425	24	4-2		A	124	4-2	A	
	25	380	MK 915 351	430	25	4-2		A	125	3-2	B	
	26	390	MK 915 351	430	26	3-2		B	126	2-2	B	
	27	400	MK 915 351	435	27	3-2		B	127	3-2	B	
	28	410	MK 915 351	440	28	4-2		B	128	4-1	B	
	29	420	MK 915 351	440	29	3-2		B	129	2-2	B	
	30	430	MK 915 351	445	30	3-2		B	130	4-2	B	
	31	450	MK 915 351	450	31	3-2		B	131	2-2	B	

Appendix 1 (continued).

Tr. No.	MA plot	l (m)	UTM grid ref.	Alt. (m)	ME 1 plot No.	Class.	S	ME 2 plot No.	Class.	S	Direction
T2	32	0	MK 913 353	350	32	5.1-2	* A	132	5.1-2	A	150^{g}
	33	10	MK 913 353	355	33	5.2-2	* A	133	5.2-2	A	
	34	30	MK 913 353	360	34	5.1-1	* A	134	5.1-1	A	
	35	50	MK 913 353	370	35	5.1-2	* A	135	5.1-2	A	
	36	60	MK 913 353	370	36	5.1-1	* A	136	5.1-1	A	
	37	70	MK 913 353	370	37	5.1-1	* A	137	5.1-1	A	
	38	90	MK 913 353	375	38	5.2-2	* A	138	5.2-2	A	
	39	110	MK 913 353	380	39	5.2-1	* A	139	5.2-1	A	
	40	120	MK 913 353	385	40	5.2-1	* A	140	5.1-1	A	
	41	130	MK 913 353	385	41	5.1-1	* A	141	5.1-1	A	
	42	140	MK 913 353	390	42	5.2-1	* A	142	5.2-1	A	
	43	150	MK 914 352	390	43	5.2-1	* A	143	5.2-1	A	
	44	160	MK 914 352	395	44	5.3	* A	144	5.2-1	A	
T3	45	0	MK 911 353	355	45	6	A	145	5.2-1	A	110^{g}
	46	10	MK 911 353	360	46	5.3	* A	146	5.3	A	
	47	20	MK 911 353	360	47	5.2-1	* A	147	5.1-1	A	
	48	30	MK 911 353	360	48	5.2-1	* A	148	5.2-1	A	
	49	50	MK 912 353	360	49	5.3	* A	149	5.3	A	
	50	60	MK 912 353	365	50	5.2-1	* A	150	5.2-1	A	
	51	70	MK 912 353	365	51	5.3	* A	151	5.2-1	A	
	52	80	MK 912 353	365	52	5.3	* A	152	5.3	A	
	53	90	MK 912 353	365	53	6	A	153	6	A	
	54	100	MK 912 353	370	54	6	A	154	5.3	A	
	55	120	MK 912 353	380	55	5.3	* A	155	5.1-1	A	
	56	130	MK 912 353	385	56	5.3	* A	156	5.2-1	A	
	57	150	MK 912 353	395	57	5.3	* A	157	5.3	* A	
T4	58	0	MK 909 352	365	58	2-1	B	158	3-1	B	270^{g}
	59	10	MK 909 352	365	59	2-1	B	159	3-1	B	
	60	20	MK 908 352	365	60	2-2	B	160	1-1	B	
	61	30	MK 908 352	365	61	2-1	B	161	3-1	B	
	62	40	MK 908 352	365	62	3-1	B	162	2-1	B	
	63	50	MK 908 352	365	63	1-2	B	163	1-1	B	
	64	60	MK 908 352	365	64	1-1	B	164	2-1	B	
	65	70	MK 908 352	365	65	3-2	B	165	3-2	B	
	66	90	MK 908 351	365	66	3-1	B	166	3-1	B	
T5	67	0	MK 902 352	395	67	6	A	167	5.3	A	320^{g}
	68	10	MK 901 352	400	68	5.2-1	* A	168	5.2-1	A	360^{g}
	69	20	MK 901 352	405	69	5.2-1	* A	169	5.1-1	A	
	70	30	MK 901 352	405	70	5.1-1	* A	170	5.1-1	A	
	71	40	MK 901 352	410	71	5.1-1	* A	171	5.1-1	A	
	72	50	MK 901 352	410	72	5.1-1	* A	172	5.1-1	A	

Appendix 1 (continued).

Tr. No.	MA plot	l (m)	UTM grid ref.	Alt. (m)	ME 1 plot			ME 2 plot			Direction
					No.	Class.	S	No.	Class.	S	
T5	73	60	MK 901 352	410	73	5.1-1	* A	173	4-1	A	
		(70)									275^g
	74	80	MK 901 352	415	74	4-1	A	174	4-1	A	
	75	90	MK 901 352	415	75	4-1	A	175	4-1	A	
	76	110	MK 901 352	420	76	3-2	B	176	3-1	B	
	77	120	MK 900 352	420	77	3-2	B	177	3-1	B	
T6	78	0	MK 899 352	425	78	2-2	B	178	1-1	B	380^g
	79	20	MK 898 353	425	79	1-1	B	179	1-1	B	
	80	30	MK 898 353	425	80	4-1	B	180	4-1	B	
	81	50	MK 898 353	425	81	3-1	B	181	3-1	B	
	82	60	MK 898 353	425	82	3-1	B	182	3-1	B	
		(66)									45^g
	83	70	MK 898 353	425	83	2-1	B	183	2-1	B	
	84	80	MK 898 353	425	84	2-1	B	184	1-1	B	
	85	90	MK 898 353	425	85	2-1	B	185	2-1	B	
	86	110	MK 899 354	425	86	3-1	B	186	3-1	B	
T7	87	10	MK 892 356	430	87	2-1	B	187	3-2	B	300^g
	88	20	MK 892 356	435	88	3-1	B	188	1-1	B	270^g
	89	30	MK 892 356	435	89	3-1	B	189	3-1	B	
	90	40	MK 891 356	435	90	2-1	B	190	2-2	B	
	91	50	MK 891 356	435	91	3-1	B	191	1-1	B	
	92	70	MK 891 356	440	92	3-1	B	192	2-2	B	
	93	80	MK 891 356	440	93	2-1	B	193	1-2	B	
T8	94	0	MK 889 356	435	94	5.2-2	* A	194	5.2-2	A	250^g
	95	10	MK 889 356	440	95	5.1-2	* A	195	5.2-1	A	
	96	20	MK 889 356	445	96	5.1-1	* A	196	5.1-1	A	
	97	30	MK 889 356	450	97	5.1-1	* A	197	5.1-1	A	
	98	40	MK 889 356	455	98	5.1-1	* A	198	5.1-1	A	
	99	70	MK 889 356	470	99	4-1	A	199	4-2	A	
	100	80	MK 889 356	475	100	4.1	B	200	4.1	A	

Appendix 2. Tree stand data. All trees rooted within the 64 m^2 plot surrounding the 16 m^2 macro plot are included. Tree numbers in accordance with Appendix 3. MA plot - Macro plot No., Site qual. - Site quality (H_{40}), Sp. - Tree species (B - Betula spp., Q - Quercus spp., Pa - Picea abies, Ps - Pinus sylvestris, Pt - Populus tremula, Sa - Sorbus aucuparia, Tb - Taxus baccata), Soc. Stat. - Social status (4 - standard, 3 - dominator, 2 - codomaniator, 1 - dominated, 0 - subdued, x - free-standing), SP - stem perimeter at breast height (mm), H - height (dm), HC -height to the crown (dm), CC - crown cover (%), Dam. - mechanical and biotic damage; the two most important damaging agents listed in order of decreasing importance (1 - broken top, 2 - as 1, new top regenerated, 3 - sry top, 4 - as 3, new top regenerated, 5 - insect damage, 6 - physical damage, 7 - stem cleft).

MA plot	Site qual.	Tree No.	Sp.	Soc. Stat.	SP	H	HC	CC	Dam.	Tree No.	Sp.	Soc. Stat.	SP	H	HC	CC	Dam.
1	G13	01	Ps	1	1258	92	60	30	3	04	Pa	3	1100	189	27	90	2
		02	Pa	0	237	58	4	35		05	Pa	0	668	138	38	75	
		03	Pa	2	797	162	36	85	2								
2	G13	01	Pa	0	223	46	17	45		05	Pa	0	98	21	14	30	
		02	Pa	0	295	69	12	70		06	Pa	0	511	95	12	80	
		03	Ps	2	1299	163	59	65	7	07	B	1	353	91	49	40	
		04	Pa	0	262	33	18	25	1	08	B	0	214	48	32	30	
3	G13	01	Pa	1	312	90	7	65		05	Pa	0	114	21	9	10	
		02	Pa	2	655	155	29	75	67	06	Sa	0	310	34	20	15	1
		03	Pa	3	891	195	36	80		07	Pa	0	121	29	21	20	
		04	Pa	1	454	118	32	60		08	Pa	3	1007	186	26	50	2
4	G13	01	Pa	1	551	111	18	65	7	04	Pa	3	1200	204	48	75	
		02	Pa	1	477	117	23	65	2	05	Pa	0	255	62	42	20	4
		03	Pa	2	686	144	54	45	2								
5	G13	01	Pa	3	866	176	67	40		05	Ps	4	1217	233	73	50	
		02	Sa	0	425	74	32	35		06	Pa	0	302	71	41	30	
		03	Pa	1	574	120	49	75		07	Pa	1	500	111	25	45	7
		04	Pa	3	1002	203	27	45		08	Pa	0	174	32	14	40	
6	G13	01	Pa	0	312	74	12	50		02	Pa	2	617	134	16	60	7
7	G13	01	Pa	3	626	157	18	70		04	Pa	3	864	193	41	70	
		02	Pa	1	458	104	35	45		05	Pa	3	1012	194	54	75	2
		03	Pa	0	238	56	23	35	1	06	Sa	0	421	90	21	35	
8	G7	01	Pa	1	578	124	13	60		04	Pa	0	178	37	11	35	
		02	Pa	0	102	25	7	40		05	Pa	0	306	53	13	45	
		03	Pa	0	333	64	9	40	7								
9	G7	01	Pa	1	521	79	15	30		04	Pa	0	379	64	24	45	6
		02	Ps	1	366	94	50	25	7	05	Ps	3	1133	147	44	40	7
		03	Pa	0	113	27	2	40									
10	G7	01	Pa	1	446	80	16	50		04	Ps	0	52	21	3	15	
		02	Ps	3	1088	134	64	55		05	Pa	1	269	65	3	60	
		03	Ps	0	152	57	22	25									
11	F6	01	Ps	3	1207	142	35	55		04	Ps	0	676	56	37	60	1
		02	Pa	0	71	21	3	75		05	Pt	0	75	27	13	10	
		03	Ps	3	88	139	59	60		06	Pa	0	233	46	3	60	

Appendix 2 (continued).

MA plot	Site qual.	Tree No.	Sp.	Soc. Stat.	SP	H	HC	CC	Dam.	Tree No.	Sp.	Soc. Stat.	SP	H	HC	CC	Dam.
11		07	Pa	0	122	28	4	45		08	Pa	0	187	45	2	55	
12	F6	01	Ps	3	759	126	33	65		02	Pa	0	74	20	3	75	7
13	F5	01	Ps	3	1087	117	35	45		03	Ps	0	123	33	6	20	7
		02	Ps	2	418	95	33	60									
14	F5	01	B	0	47	21	1	45		02	Ps	2	995	92	63	50	
15	G12	01	Pa	1	613	132	22	60	7	02	Pa	2	644	144	21	55	7
16	G16	01	Pa	3	1739	282	39	75									
17	G14	01	Pa	3	1841	261	22	85	2	02	Pa	0	331	67	12	45	7
18	G13	01	Pa	1	896	193	32	50	6	04	Tb	0	993	43	1	55	76
		02	Pa	2	1142	232	35	75	2	05	Pa	3	1847	301	29	70	
		03	Pa	0	302	84	38	35		06	Pa	0	613	184	18	55	
19	G20	01	Pa	0	240	24	16	50	1	04	Pa	0	241	54	8	50	7
		02	Pa	3	1521	290	41	75		05	Pa	0	600	128	39	50	7
		03	Pa	1	887	176	26	55	26	06	Pa	0	574	125	19	55	2
20	G15	01	Pa	0	86	25	9	40		03	Pa	0	107	32	3	55	
		02	Pa	3	1317	230	62	45		04	Pa	0	83	25	3	50	
21	G14	01	Pa	0	181	29	8	65		04	Sa	0	413	76	41	16	66
		02	Tb	0	637	53	16	30	2	05	Pa	2	723	147	44	60	2
		03	Pa	3	1083	200	12	60	2	06	Pa	0	327	59	15	45	7
22	G14	01	Tb	0	325	28	1	30	72	05	Sa	0	252	66	52	25	67
		02	B	2	757	177	54	80	7	06	Pa	3	1006	197	26	80	
		03	Pa	1	563	123	26	40	26	07	Pa	3	1043	201	20	65	
		04	B	1	583	133	48	55	6								
23	G13	01	B	0	291	83	38	60	2	04	Pa	2	661	158	25	80	
		02	B	1	345	119	34	15		05	Pa	0	178	34	27	5	
		03	B	1	369	104	16	85		06	B	2	438	132	46	80	
24	G8	01	Pa	x	174	33	7	40		02	B	x	373	59	37	70	62
25	G8	01	B	x	144	59	4	75	2								
26	F10	01	Ps	0	192	32	8	40	72								
27	F10	01	Ps	2	783	102	34	40	2	04	Ps	2	611	106	32	60	2
		02	Ps	0	302	53	6	35		05	Ps	1	506	83	26	55	7
		03	Ps	0	261	34	13	35	7								
28	F10	01	B	0	44	24	2	50	7	03	B	0	280	69	4	45	
		02	Ps	3	1774	143	26	40									
29	F9	01	B	0	69	26	4	35	7	03	Ps	3	2162	132	43	75	36
		02	B	0	47	20	3	20	7								
30	F9	01	Pa	0	217	31	5	30	7	06	Pa	0	240	38	22	35	2
		02	Pa	1	438	51	12	70	27	07	Pa	1	372	53	11	60	2
		03	Pa	2	442	65	10	65	2	08	Pa	0	491	48	20	45	7
		04	Sa	2	261	67	28	60	7	09	B		376	54	1	65	26
		05	Sa	1	388	57	19	45	62								

Appendix 2 (continued).

MA plot	Site qual.	Tree No.	Sp.	Soc. Stat.	SP	H	HC	CC	Dam.	Tree No.	Sp.	Soc. Stat.	SP	H	HC	CC	Dam.
31	F7	01	Ps	2	437	87	26	40		03	B	2	477	88	20	60	7
		02	Ps	0	148	30	11	25	71								
32	G15	01	Pa	3	1316	202	25	65		02	Pa	3	990	213	26	55	7
		02	Pa	0	473	85	18	30	6								
33	G15	01	(=32-03)							04	Pa	0	172	41	17	30	
		02	Pa	0	303	87	18	35		05	B	0	52	22	10	25	2
		03	Pa	0	543	114	39	45	6	06	Pa	3	1598	246	44	55	
34	G14	01	Pa	1	678	145	11	65	27	06	Pa	2	501	168	35	60	
		02	Pa	1	564	134	16	60		07	Pa	3	897	199	37	85	7
		03	Pa	0	108	21	13	15		08	Pa	3	888	198	46	75	
		04	Pa	3	990	213	30	65	2	09	B	1	546	137	28	55	27
35	G12	01	B	0	347	99	36	85	7	03	Pa	2	874	179	17	75	2
		02	Pa	1	448	118	17	60	27	04	Pa	3	1170	194	18	80	7
36	G12	01	Pa	1	584	159	27	80	2	07	Pa	1	647	144	20	60	2
		02	Ps	3	1424	252	100	45		08	Pa	2	851	186	57	55	
		03	Pa	0	148	38	24	15	16	09	Pa	0	217	21	15	25	16
		04	Pa	0	78	20	13	20	6	10	B	0	457	91	43	40	67
		05	Pa	0	102	23	9	35		11	B	0	345	75	22	35	62
		06	Pa	0	136	35	15	25	67								
37	G12	01	B	3	730	164	72	65	72	06	B	1	320	114	48	45	
		02	Pa	3	1159	183	18	75	2	07	B	1	379	107	40	60	
		03	Sa	0	279	73	24	50		08	Pa	0	282	71	12	35	7
		04	Pt	1	325	124	46	30	7	09	B	0	412	80	22	75	62
		05	Pa	1	570	113	17	50	7								
38	G13	01	B	2	785	146	56	65	7	06	Pa	0	160	34	20	20	
		02	Pa	0	361	84	21	50		07	Pa	0	309	89	32	40	7
		03	Pa	0	404	77	30	15	62	08	B	1	379	107	42	60	6
		04	B	0	325	75	43	30	6	09	Pa	3	653	177	29	60	7
		05	B	2	566	134	50	75	67	10	B	2	532	148	72	80	
39	G12	01	Pa	2	704	149	27	75	2	04	Pa	0	377	91	20	65	
		02	Pa	0	88	22	11	30		05	Q	1	756	125	31	70	7
		03	B	1	368	94	43	70		06	Ps	3	1423	188	91	65	2
40	G12	01	Pa	2	847	142	24	60	2	06	Pa	0	270	64	19	35	6
		02	Sa	0	233	72	43	15	7	07	Pa	1	525	128	36	55	6
		03	Pa	0	112	20	11	25		08	Pa	2	732	162	34	65	27
		04	Pa	3	932	202	29	65		09	Pa	2	808	166	34	60	
		05	Ps	2	722	170	77	40									
41	G12	01	Pa	1	497	90	41	50	62	07	B	2	518	169	89	55	7
		02	Pa	1	518	137	42	65	7	08	Sa	1	558	123	58	40	67
		03	Pa	2	622	165	93	35		09	Pa	0	179	44	27	20	7
		04	Pa	3	977	193	46	70		10	Pa	0	194	34	14	25	2
		05	Pa	0	262	68	27	45		11	Pa	3	1076	175	34	35	
		06	Pa	1	447	115	26	40	7								

Appendix 2 (continued).

MA plot	Site qual.	Tree No.	Sp.	Soc. Stat.	SP	H	HC	CC	Dam.	Tree No.	Sp.	Soc. Stat.	SP	H	HC	CC	Dam.
42	G13	01	Pa	3	1105	199	25	90	2	04	Pa	3	1092	213	36	80	
		02	Pa	1	560	127	23	45	2	05	Pa	3	1037	199	37	75	2
		03	Sa	1	649	128	67	45	27	06	B	2	741	157	77	70	
43	G13	01	Pa	3	1170	214	31	85	2	04	Pa	2	986	180	27	75	26
		02	Pa	0	376	103	27	45		05	Pa	3	1162	209	29	70	2
		03	Pa	2	900	193	34	70									
45	G17	01	B	0	273	85	22	25	7	08	Pa	0	142	32	20	20	
		02	Pt	1	451	142	80	35	7	09	Pa	0	131	33	15	25	7
		03	Pa	1	657	132	31	45	2	10	Pa	0	184	38	14	30	62
		04	Pa	0	79	25	14	15		11	Sa	0	85	32	13	40	6
		05	B	0	294	95	48	50	2	12	B	0	103	28	7	30	6
		06	Pa	1	736	115	22	60	1	13	Pa	0	127	24	14	30	
		07	B	0	402	34	23	10	2								
46	G16	01	Pa	1	416	112	16	65		03	Pa	3	1298	220	36	65	
		02	Pa	3	1278	235	36	60									
47	G15	01	Pa	3	1304	208	51	50	2	03	Pa	2	1008	188	61	55	26
		02	Pa	3	1145	200	32	60	6	04	B	0	90	34	11	25	2
48	G14	01	Pa	0	198	43	5	75		10	Pa	0	142	40	8	35	
		02	B	0	107	51	15	50		11	B	0	178	51	20	40	7
		03	B	0	135	57	14	65	7	12	Pa	0	244	54	9	55	
		04	Pa	0	274	72	11	50		13	Pa	0	192	54	9	50	
		05	B	0	75	33	5	30	6	14	Pa	0	140	33	12	50	6
		06	B	0	133	44	14	35		15	Pa	1	550	124	14	80	
		07	Pa	0	180	38	8	65		16	Pa	3	972	171	29	75	2
		08	Pa	0	109	32	8	60		17	Pa	0	115	31	9	40	6
		09	Pa	0	210	50	9	65									
49	G14	01	Pa	0	312	71	11	70		07	B	0	190	52	6	10	6
		02	Pa	0	272	73	13	70		08	B	0	131	21	9	10	6
		03	Pa	3	1187	210	20	55	2	09	Pa	0	187	41	10	40	
		04	Pa	0	225	50	7	65		10	Tb	0	326	38	15	50	27
		05	Pa	0	128	29	9	40		11	Sa	0	269	74	53	35	76
		06	Pa	0	103	29	8	45		12	Sa	0	483	52	0	30	26
50	G14	01	Pa	2	913	197	72	50		04	Sa	0	337	56	33	5	66
		02	B	1	604	140	59	70		05	Pa	3	963	211	24	75	
		03	Pa	1	727	131	16	75									
51	G14	01	Pa	0	116	28	5	45		02	Pa	2	944	174	37	60	6
52	G14	01	B	0	74	39	7	60		04	Pa	0	454	54	17	35	1
		02	B	0	128	40	5	40	6	05	Pa	3	1230	206	23	65	26
		03	B	0	181	69	18	60									
53	G14	01	(=52-05)							02	Pa	2	971	186	34	40	27
54	G14	01	Pt	0	186	76	26	20	6	03	Pa	0	762	146	29	65	1
		02	Pa	3	1243	236	62	80	2	04	Pa	1	566	127	17	70	

Appendix 2 (continued).

MA plot	Site qual.	Tree No.	Sp.	Soc. Stat.	SP	H	HC	CC	Dam.	Tree No.	Sp.	Soc. Stat.	SP	H	HC	CC	Dam.
54		05	B	0	350	22	5	45	62								
55	G14	01	Pt	2	646	167	76	65	7	06	B	0	597	87	36	75	2
		02	Pt	2	527	160	86	55		07	Pa	0	338	89	27	40	27
		03	Sa	0	170	74	26	35	7	08	Pa	0	206	56	20	35	
		04	Sa	0	269	82	37	25	7	09	Pa	2	943	161	18	55	76
		05	B	1	349	113	63	70		10	Pa	0	462	90	23	60	2
56	G14	01	Pa	2	1139	167	35	55	62	03	Pa	1	886	149	47	55	2
		02	Pa	3	1098	201	29	65	26								
57	G14	01	Pa	2	860	182	3	50	62	04	Pa	0	291	52	11	50	
		02	Pa	3	1733	238	32	65	2	05	Sa	0	212	70	39	15	7
		03	Pa	0	344	83	20	70		06	Pa	0	372	88	12	55	
58	F7	01	Ps	3	912	134	39	45	2	02	Ps	0	268	53	10	35	
59	F7	01	Ps	2	919	125	68	30		07	Ps	2	804	123	38	45	27
		02	Ps	3	1161	153	64	45		08	Ps	0	118	27	14	25	
		03	Ps	0	445	83	35	40	2	09	Ps	3	746	142	46	50	
		04	Ps	0	309	42	18	30	12	10	Ps	0	237	59	15	35	2
		05	Ps	3	1006	148	78	40		11	Ps	0	67	28	13	10	
		06	Ps	0	512	81	27	45		12	Ps	0	129	35	10	25	
60	F7	01	Ps	3	1013	169	48	70	2	03	Ps	2	841	125	49	30	
		02	Ps	2	978	116	39	40	2								
61	F7	01	Ps	0	431	42	27	35	1	04	Ps	2	1091	118	47	40	
		02	Ps	0	440	71	49	15	2	05	Ps	0	190	44	15	25	
		03	B	0	80	33	6	35	7								
62	F7	01	Ps	3	1003	135	36	45		02	Ps	2	884	123	28	30	
63	F7	01	Ps	3	912	130	54	35	2	03	Ps	0	262	46	26	25	7
		02	Ps	1	262	46	26	25	7								
64	F5	01	Ps	3	986	123	59	25									
65	F5	01	Ps	x	220	37	16	30		03	B	x	317	45	23	50	7
		02	B	0	138	21	7	40	7								
66	F5	01	Ps	0	91	25	6	25	7	03	B	x	119	49	6	50	
		02	Ps	0	59	24	7	20									
67	G15	01	Pa	0	128	26	11	35	7	06	Pa	0	468	125	27	35	
		02	Pa	0	176	38	5	40		07	B	0	339	107	15	75	7
		03	Pa	0	207	47	9	45		08	Pa	3	1499	298	42	70	
		04	Pa	0	105	23	8	50	6	09	Pa	0	214	41	17	40	7
		05	Pt	3	1526	236	83	70		10	Sa	1	607	171	84	55	6
68	G14	01	(=67-10)							04	Pa	0	762	137	21	50	6
		02	(=67-09)							05	Pa	3	1396	259	59	65	26
		03	Pa	2	957	177	19	75	7								
69	G12	01	Pa	0	134	30	3	75		03	B	0	89	44	12	30	
		02	B	1	449	119	28	65	7	04	Pa	0	98	21	10	30	7

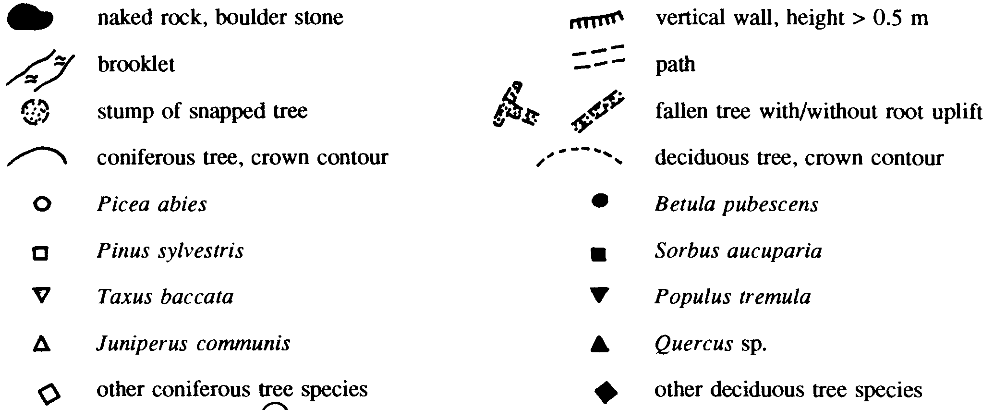
Appendix 2 (continued).

MA plot	Site qual.	Tree No.	Sp.	Soc. Stat.	SP	H	HC	CC	Dam.	Tree No.	Sp.	Soc. Stat.	SP	H	HC	CC	Dam.
69		05	Pa	3	1232	213	44	55									
70	G11	01	Sa	1	673	121	35	70	77	05	Q	3	1438	197	61	90	72
		02	Pa	0	286	64	15	50		06	Pa	0	180	45	8	45	67
		03	Pa	0	399	47	10	65	6	07	Pa	0	102	26	9	30	6
		04	Pa	0	312	37	14	75	67	08	Sa	2	753	139	74	65	62
71	G11	01	Sa	1	520	108	54	45	26	04	Sa	2	638	130	71	70	76
		02	Sa	1	468	101	69	15	27	05	Tb	0	274	27	20	35	1
		03	Sa	1	408	98	63	10	2	06	Sa	0	524	78	17	10	66
72	G11	01	Pa	0	279	65	12	65	6	06	Pa	0	308	61	13	55	
		02	Sa	1	485	96	21	60	7	07	(=71-06)						
		03	Pa	0	204	44	9	45	7	08	Pa	2	847	143	18	85	2
		04	Sa	0	316	60	21	5	6	09	Sa	0	298	42	19	5	66
		05	Pa	0	155	30	8	40		10	B	3	1148	160	57	80	7
73	G11	01	Sa	0	362	72	27	15	66	04	Pt	3	1525	192	91	90	
		02	Pa	3	917	193	13	85		05	Pa	0	819	87	25	35	67
		03	B	0	169	41	22	20									
74	G10	01	Pt	3	1377	169	110	75	1	07	Pa	3	1002	195	32	65	
		02	Pa	3	1083	192	28	75	6	08	Pa	2	689	148	46	55	7
		03	Pa	2	894	165	32	85	2	09	Pt	3	1246	174	107	70	2
		04	Pa	3	1023	196	34	80		10	Sa	1	573	121	93	25	7
		05	Pa	0	328	75	22	60		11	Pa	0	686	138	31	30	27
		06	Pa	3	654	177	67	55	7								
75	F10	01	Sa	1	552	71	24	45	3	04	Pa	0	494	81	25	55	
		02	Ps	0	171	53	24	40		05	Ps	3	1231	176	25	55	
		03	Ps	3	937	168	55	50									
76	F6	01	Ps	1	580	76	17	60	2	05	Ps	3	469	89	32	40	7
		02	Ps	3	606	101	39	55	27	06	Ps	0	279	47	13	45	2
		03	Ps	0	159	37	6	30		07	Ps	0	128	24	9	45	
		04	Ps	3	485	94	31	45		08	Ps	2	478	87	31	50	
77	F6	01	Ps	x	217	49	9	20		04	Ps	3	1002	105	29	55	
		02	Ps	1	419	74	23	45		05	Ps	x	658	77	25	50	2
		03	Ps	0	179	25	9	40	3								
78	F7	01	Pa	x	266	73	3	85	7	06	B	0	65	29	7	30	
		02	B	x	194	61	4	40		07	B	0	83	39	16	40	
		03	B	x	99	34	2	25		08	B	x	109	43	6	25	
		04	Pa	x	139	36	6	65		09	B	x	82	30	10	55	
		05	B	x	177	57	23	45		10	Ps	x	82	30	10	55	
80	F8	01	Ps	1	820	118	37	55	61	04	Ps	2	1070	142	65	70	
		02	Ps	3	1024	158	51	70	36	05	Ps	2	806	129	47	50	2
		03	Ps	0	1029	73	35	45	3								
81	F8	01	Ps	2	811	138	73	35		04	Ps	2	1084	133	44	70	2
		02	Ps	0	453	79	38	25	4	05	Ps	3	853	133	44	70	2
		03	Ps	3	764	161	82	70		06	Ps	0	321	44	32	15	3
82	F8	01	Ps	3	1127	143	44	20	2	02	Ps	3	932	157	56	35	

Appendix 2 (continued).

MA plot	Site qual.	Tree No.	Sp.	Soc. Stat.	SP	H	HC	CC	Dam.	Tree No.	Sp.	Soc. Stat.	SP	H	HC	CC	Dam.
83	F7	01	Ps	0	143	34	11	30		03	Ps	3	1065	141	41	35	2
		02	Ps	0	231	60	16	35	4	04	Ps	1	534	99	22	65	7
84	F7	01	Ps	3	1165	157	39	60		02	B	0	570	62	30	70	
85	F7	01	Ps	x	473	71	12	70									
86	F8	01	Ps	0	269	75	13	40		03	Ps	3	1347	163	44	40	
		02	Ps	2	963	138	44	20	2	04	B	0	152	54	4	40	
87	F6	01	B	x	127	36	4	60		03	Ps	1	504	84	40	40	
		02	Ps	3	874	112	32	65									
88	F6	01	B	2	587	98	1	75		02	Ps	3	793	122	20	60	
89	F6	01	Ps	3	809	145	34	50	27								
90	F6	01	B	x	115	28	5	75		02	Ps	x	66	20	8	30	
92	F5	01	Ps	0	278	42	19	50		05	Ps	3	979	110	45	45	2
		02	B	0	198	36	16	45	2	06	Ps	0	76	21	12	25	
		03	B	0	112	43	15	55		07	Ps	0	162	37	18	20	
		04	B	0	70	36	4	40		08	Ps	3	671	120	40	45	7
93	F5	01	Ps	0	693	53	23	35		03	Ps	1	532	89	41	45	2
		02	Ps	2	832	93	28	40	7								
94	G9	01	Pa	x	170	36	14	35		04	Pa	0	321	64	18	65	
		02	Pa	x	108	29	2	40		05	B	1	771	111	47	80	2
		03	B	0	80	36	17	35									
95	G9	01	Pa	2	1066	159	28	75	2	04	B	x	160	31	8	40	
		02	Sa	0	217	31	9	40		05	Pa	0	193	40	14	35	
		03	Pa	x	160	31	8	40		06	B	x	303	68	40	40	
96	G9	01	Pa	3	989	180	19	90		05	Pa	0	188	36	8	55	
		02	Pa	0	135	29	2	55		06	Pa	2	559	119	26	40	27
		03	Pa	0	90	22	7	40		07	Pa	0	111	22	10	35	
		04	B	1	447	97	11	45									
97	G9	01	Sa	0	394	77	28	50	2	07	Sa	0	280	77	23	15	
		02	B	2	515	110	41	70		08	Sa	0	148	49	25	10	
		03	B	0	97	32	12	20		09	Pa	2	644	131	22	60	2
		04	Pa	0	162	41	14	35		10	Pa	0	97	25	16	35	
		05	Pa	0	193	53	9	65		11	Pa	0	193	53	9	65	
		06	B	3	575	138	43	70		12	Pa	3	568	139	23	70	7
98	G9	01	Sa	1	390	75	38	35	2	03	Pa	3	840	146	15	90	2
		02	Pa	3	736	165	28	70									
99	G7	01	Pa	x	781	126	17	85	2	03	Pa	0	282	69	26	30	
		02	Pa	3	1070	175	25	65	2	04	Pa	0	426	63	10	55	2
100	G7	01	Pa	2	732	106	21	75	2	05	B	x	102	34	14	55	
		02	B	1	492	75	25	30		06	Pa	0	114	34	26	15	
		03	B	x	157	45	12	60		07	Pa	3	886	124	16	80	
		04	Pa	1	229	51	7	40									

Appendix 3. Sketch maps of 16 m^2 macro sample plot (inner square, bold contour) and the 64 m^2 plot surrounding the macro sample plot (outer square, bold contour). Positions of meso sample plots (1 m^2) indicated by squares with thin contour. Macro sample plots orientated along the transect (see Appendix 1). Positions of trees (height > 2.0 m) indicated by large circle enclosing a species-specific symbol. Position of sapling (0.8 m < height < 2.0 m) indicated by the species-specific symbol only. Tree numbers refer to Appendix 2.
Legend to symbols:



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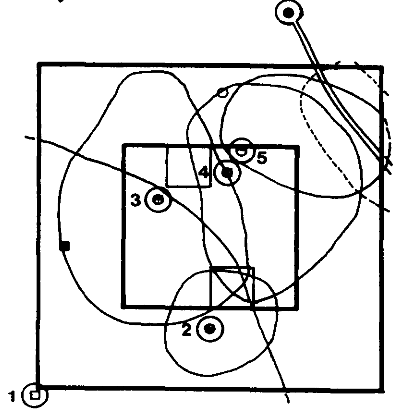

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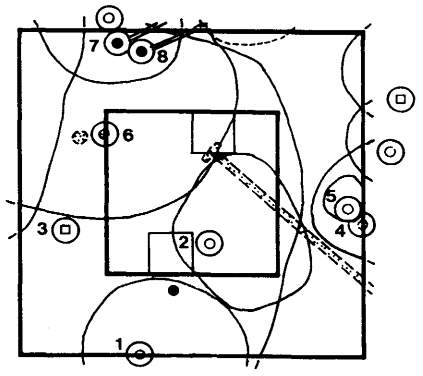

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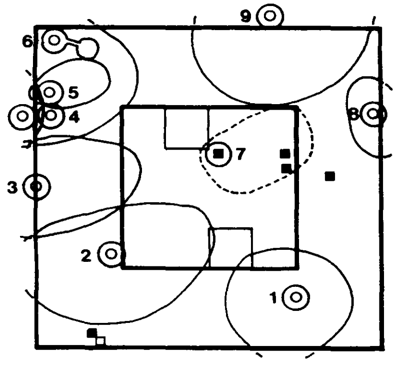

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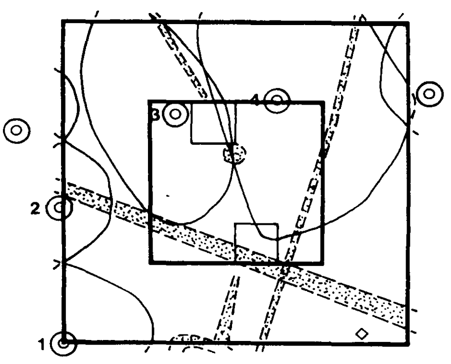

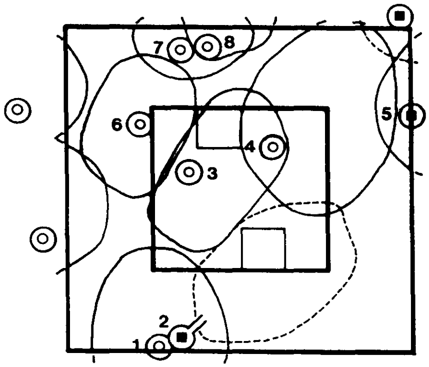

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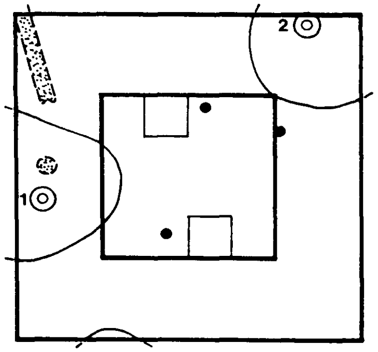

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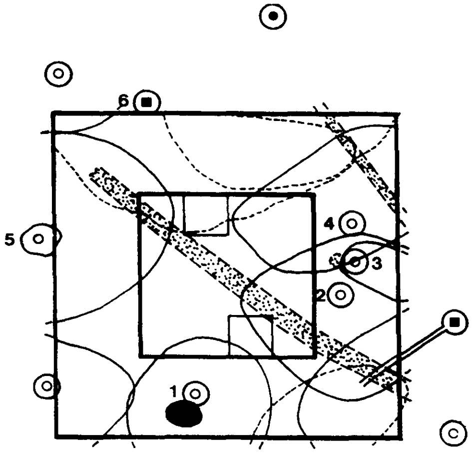

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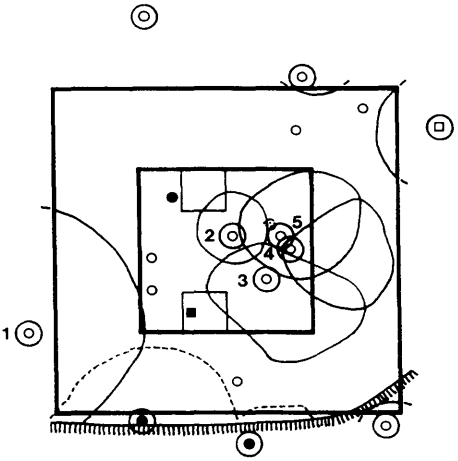

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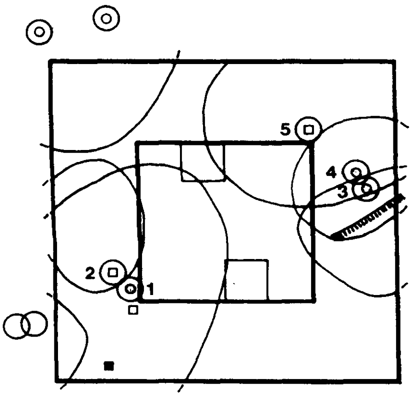

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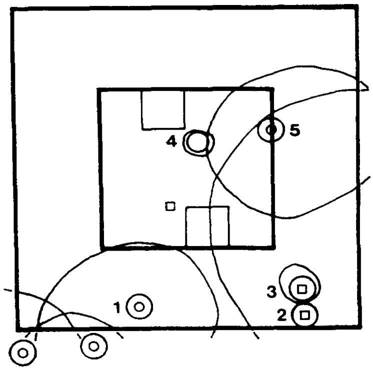

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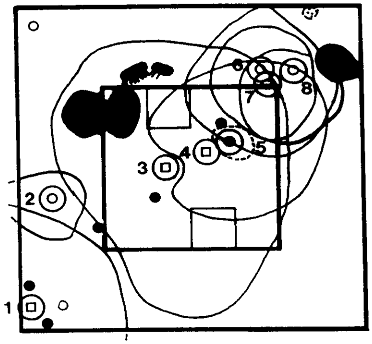

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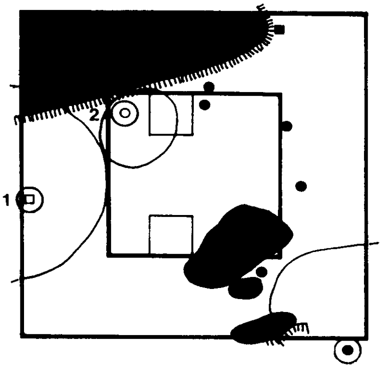

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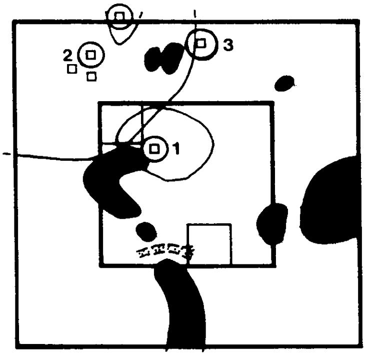

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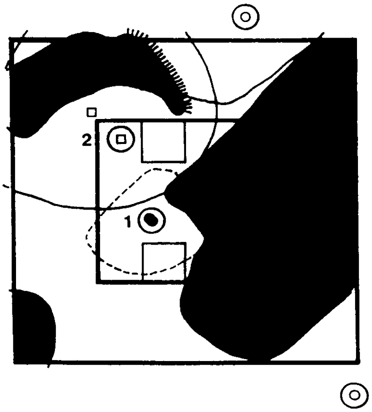

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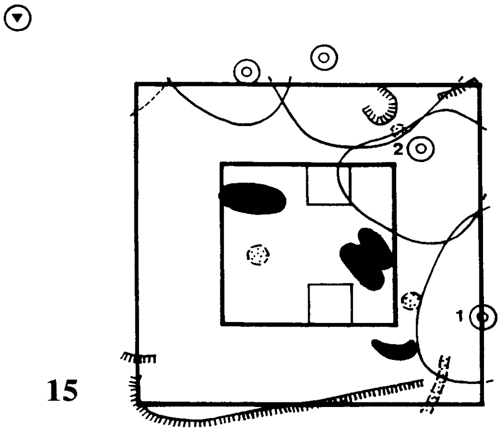

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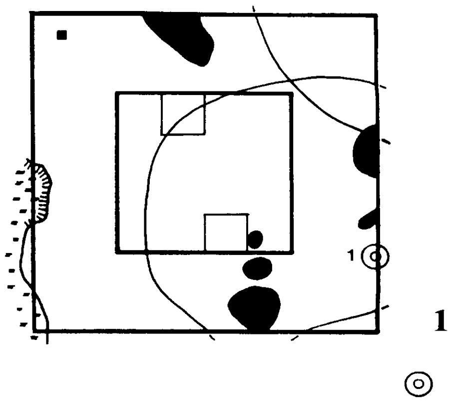

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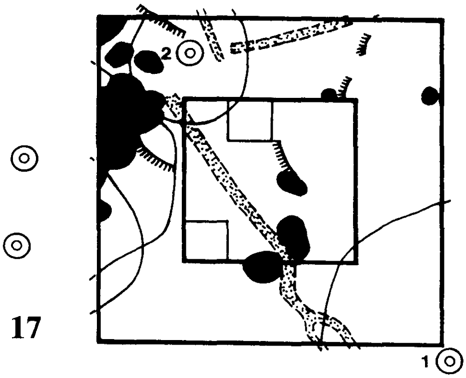

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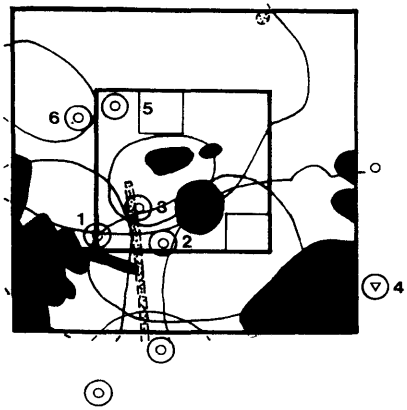

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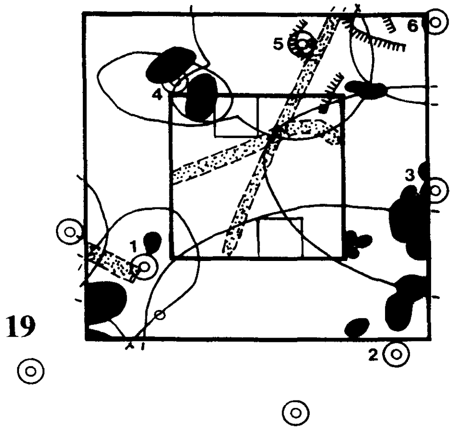

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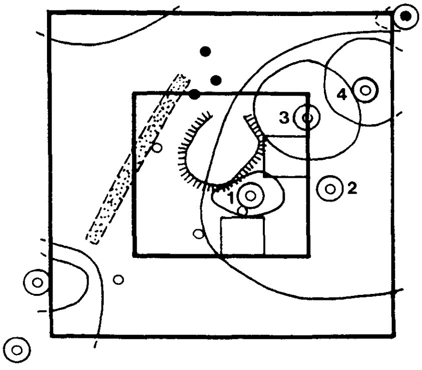

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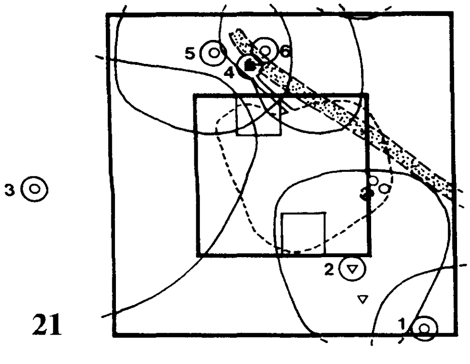

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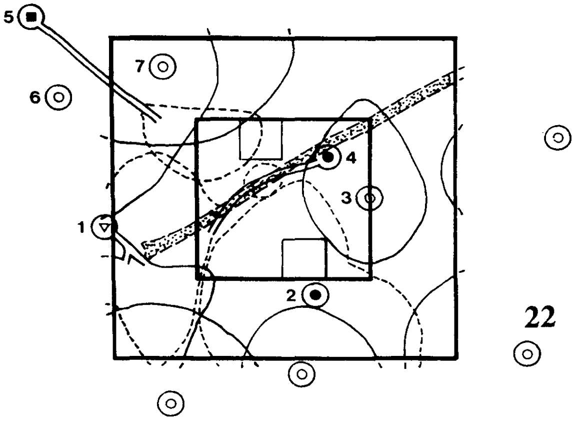

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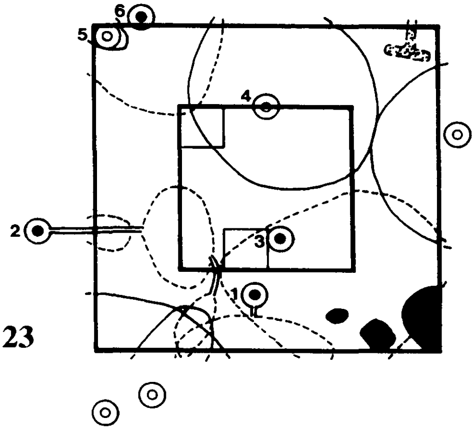

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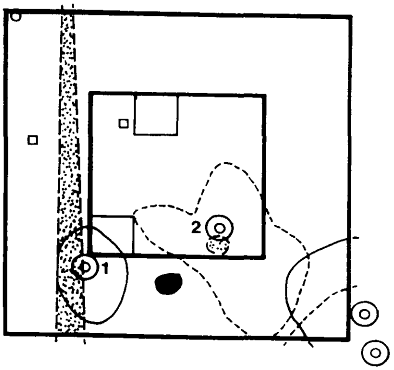

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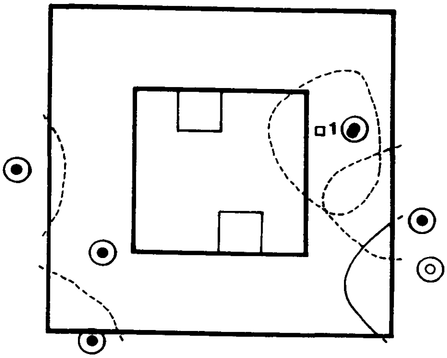

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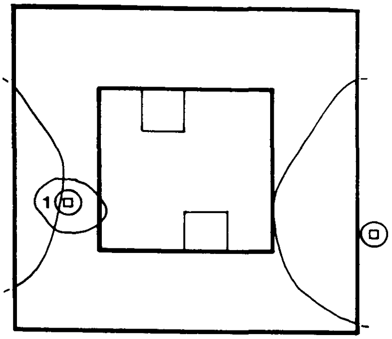

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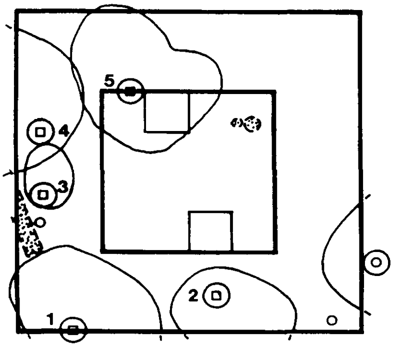

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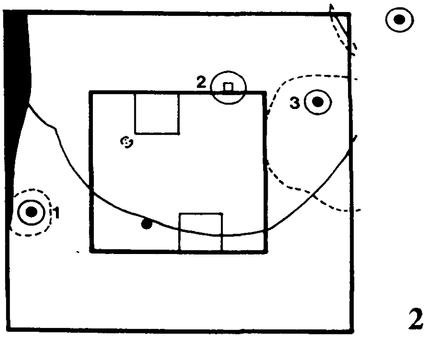

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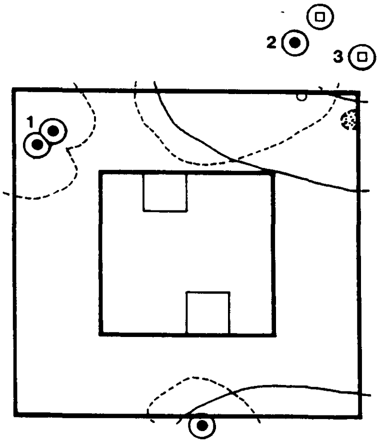

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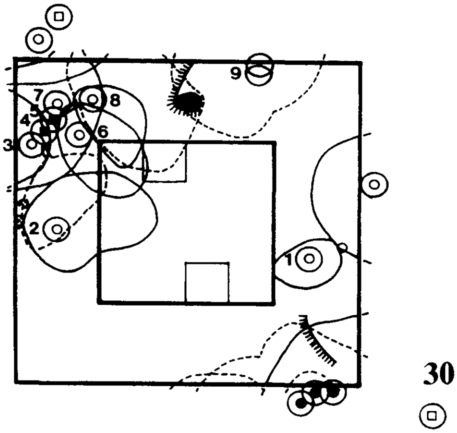

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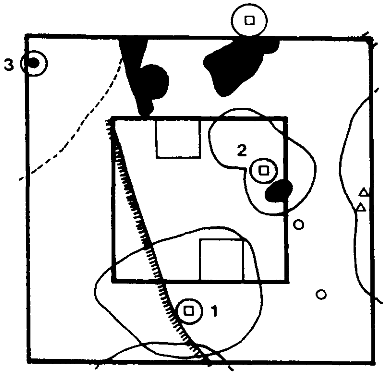

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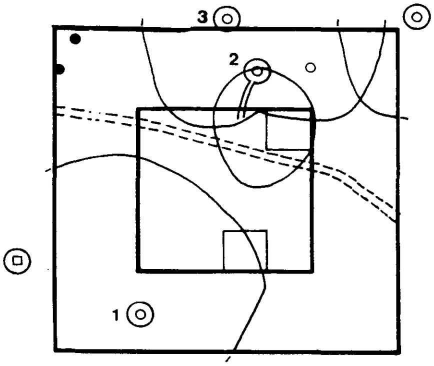

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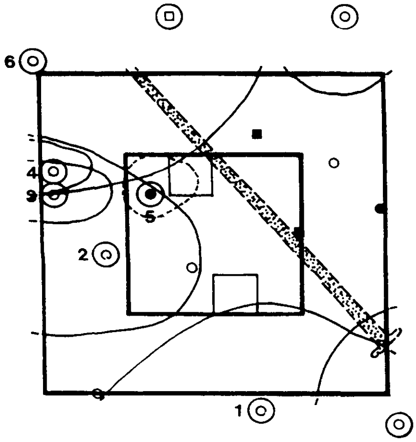

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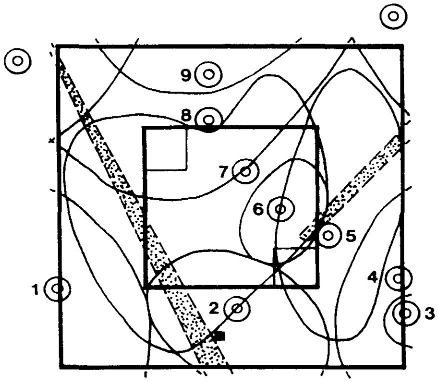

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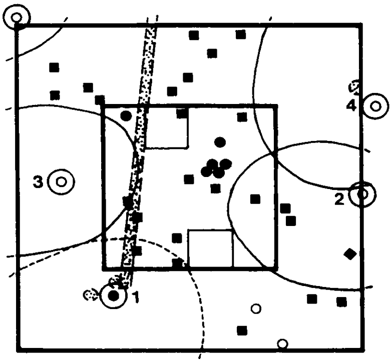

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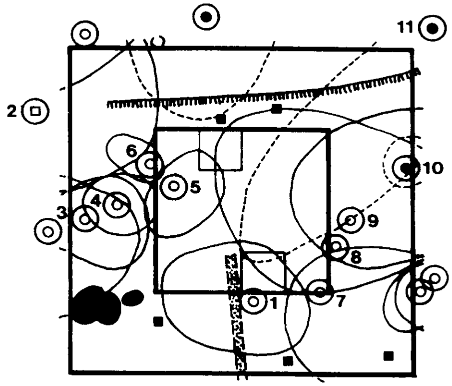

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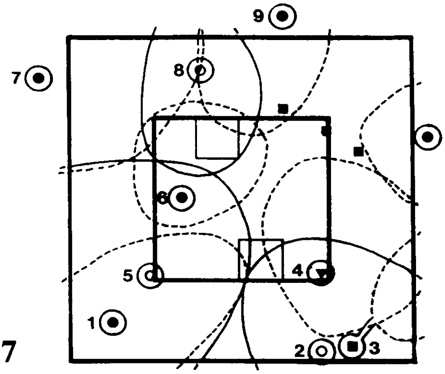

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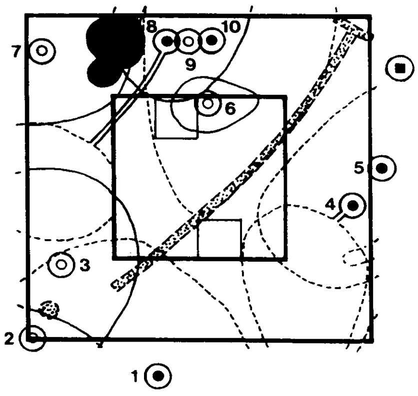

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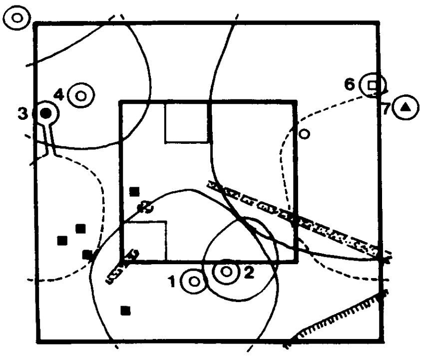

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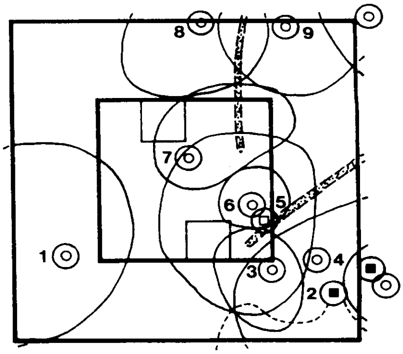

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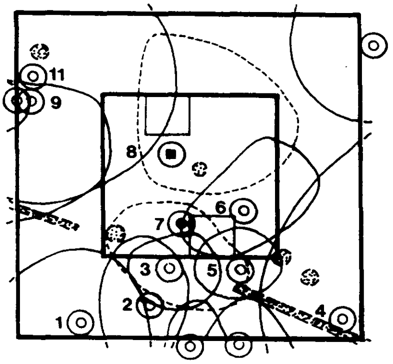

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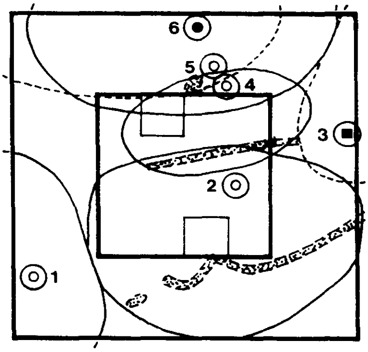

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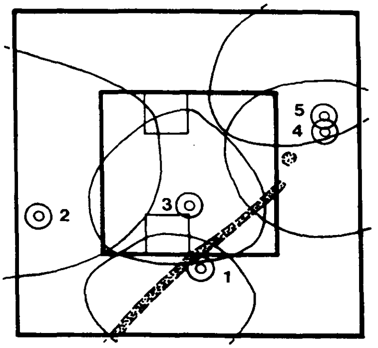

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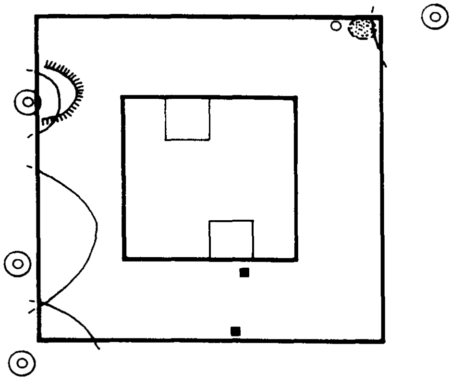

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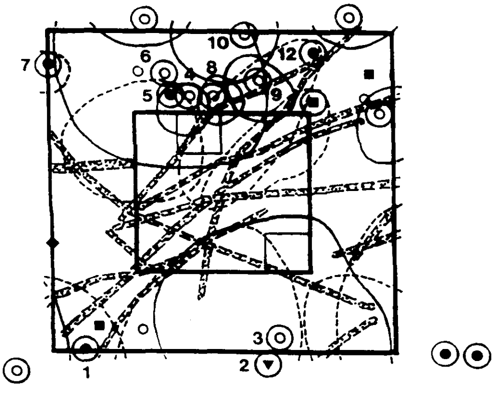

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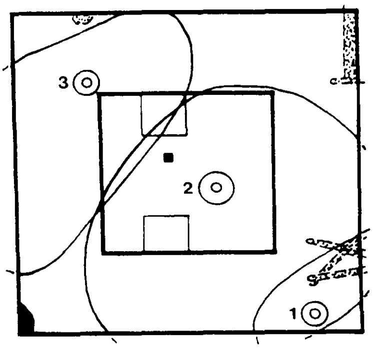

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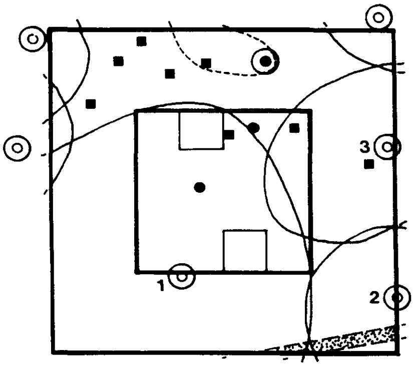

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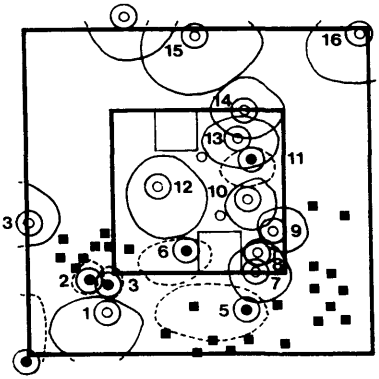

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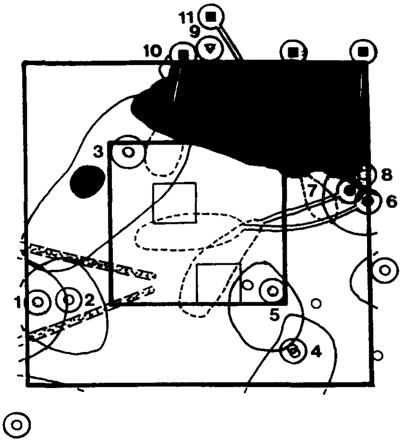

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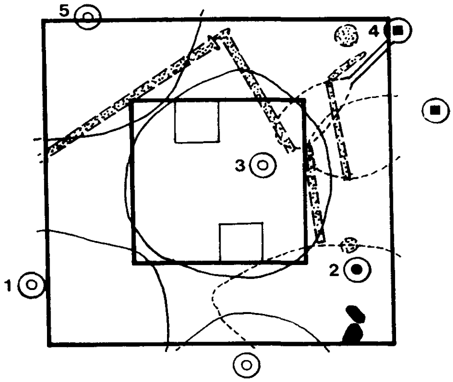

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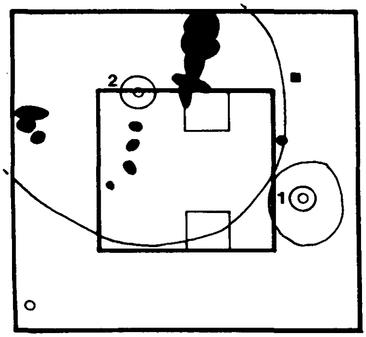

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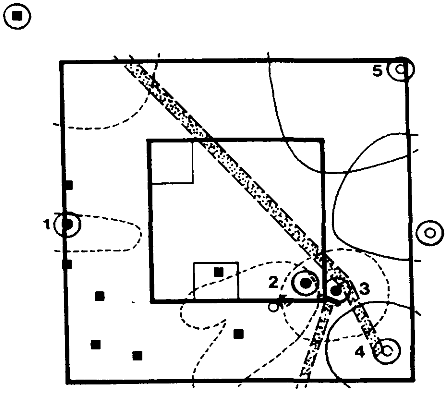

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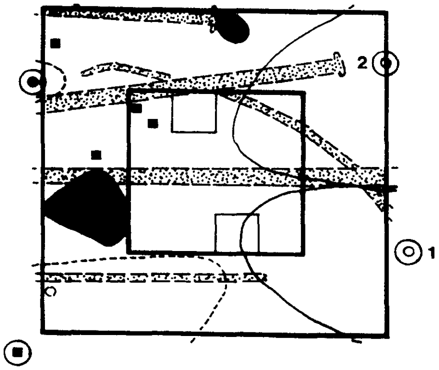

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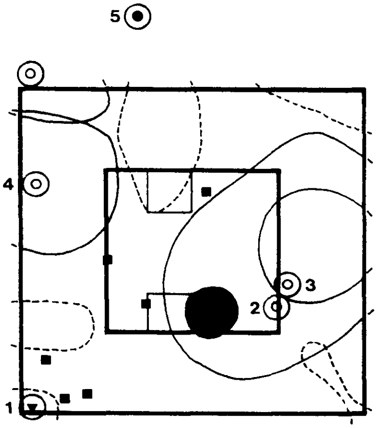

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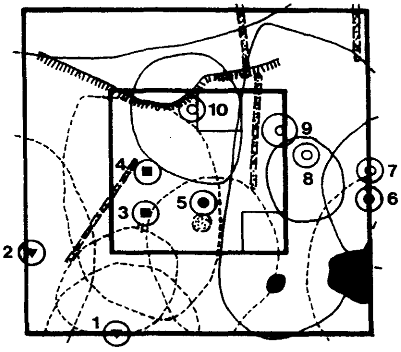

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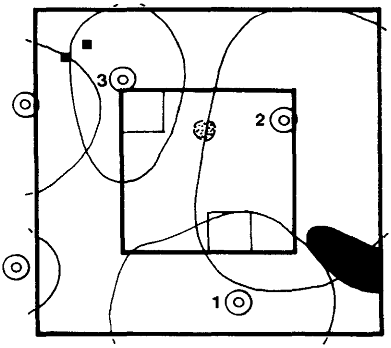

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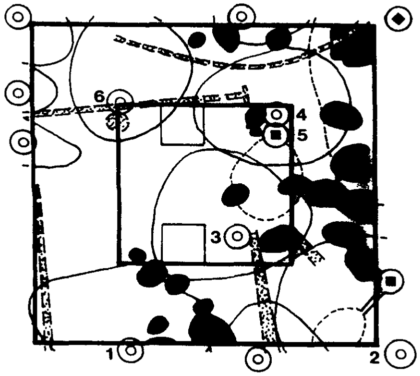

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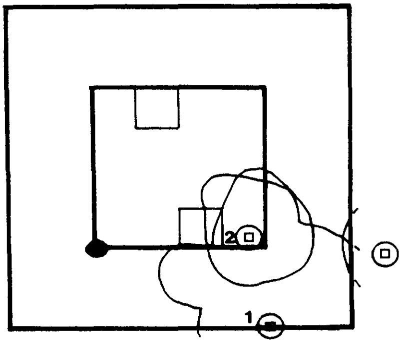

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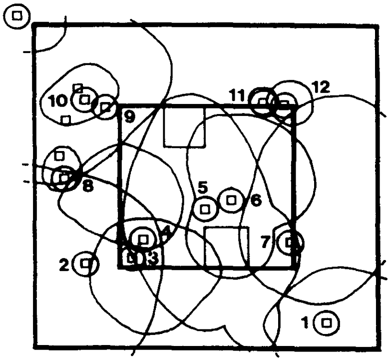

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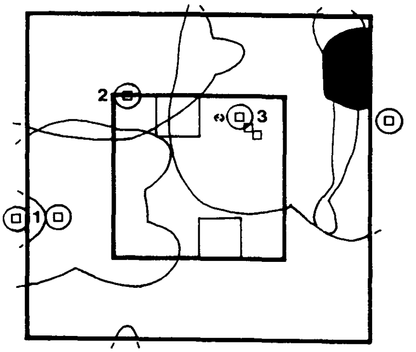

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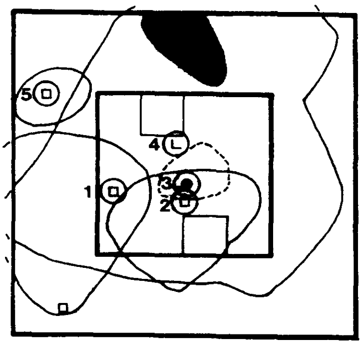

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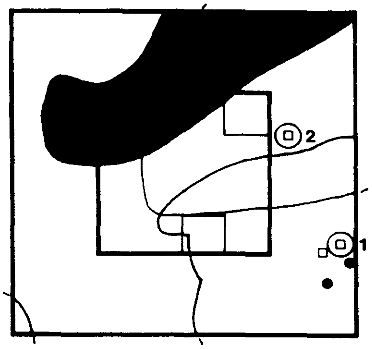

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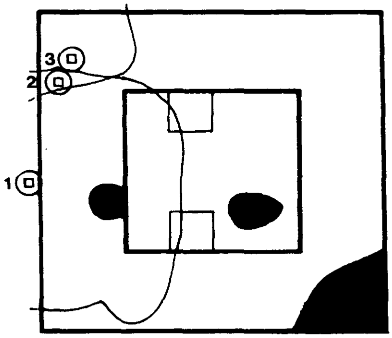

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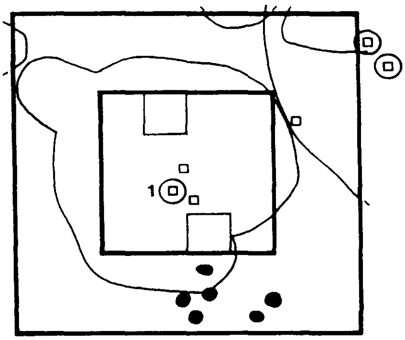

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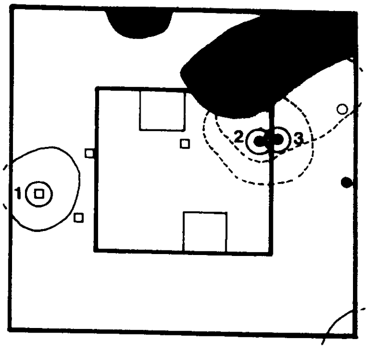

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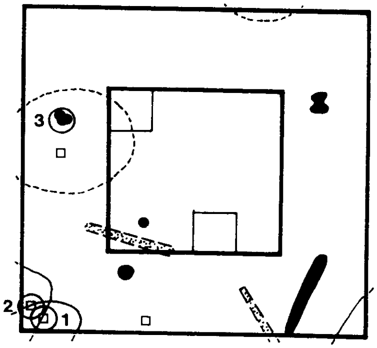

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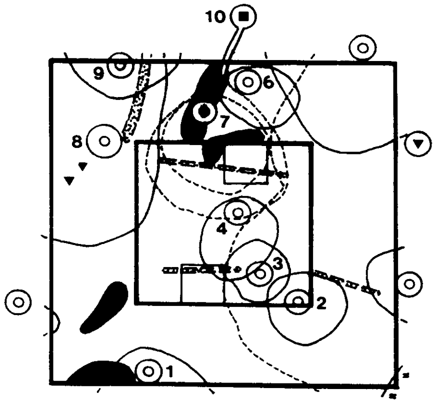

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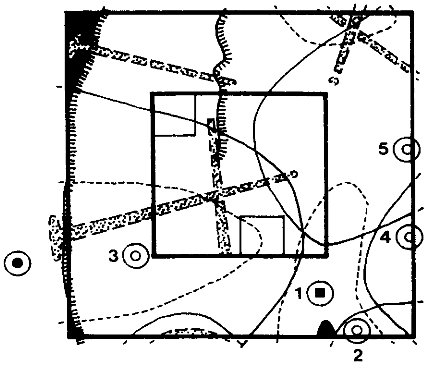

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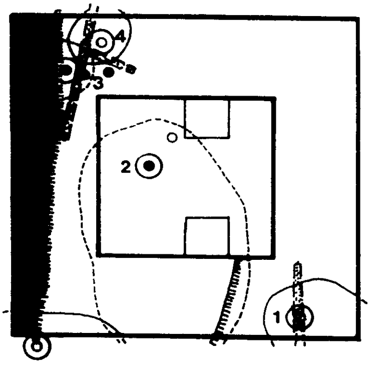

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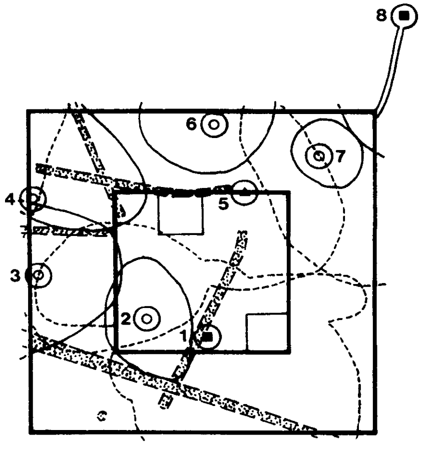

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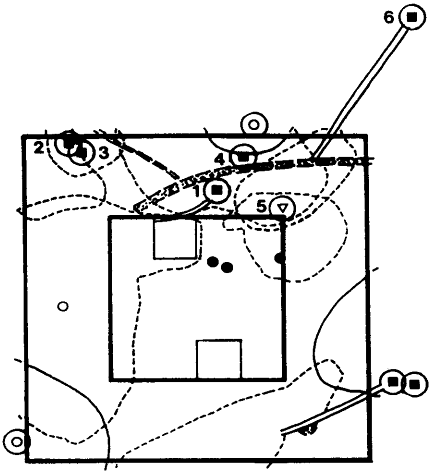

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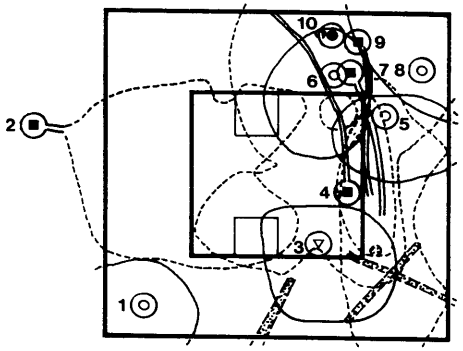

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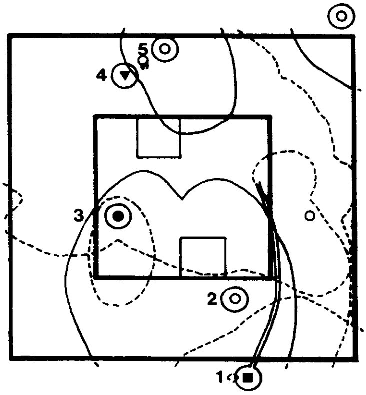

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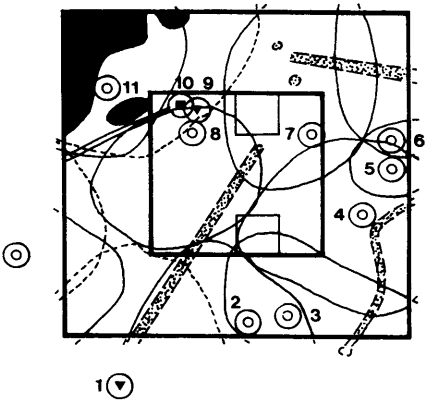

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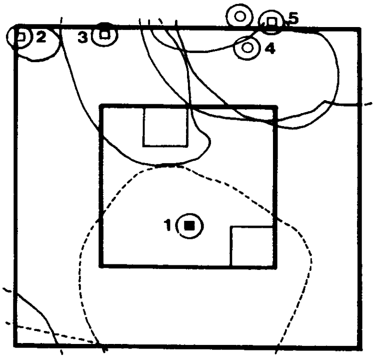

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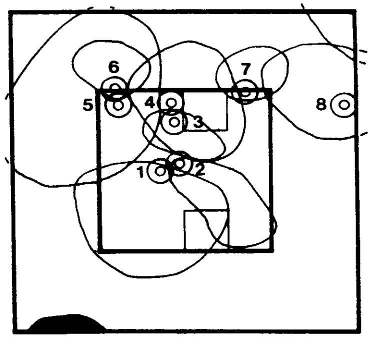

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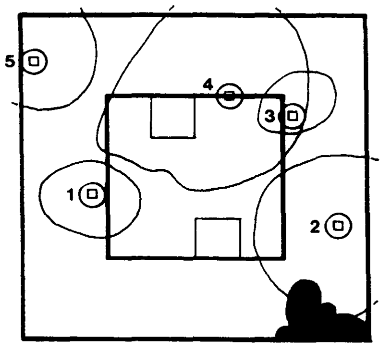

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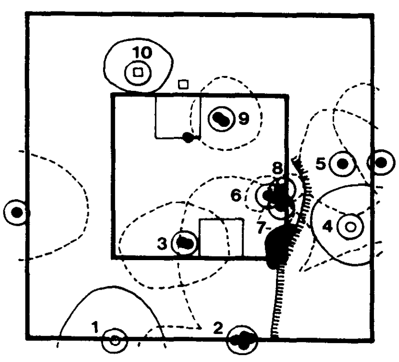

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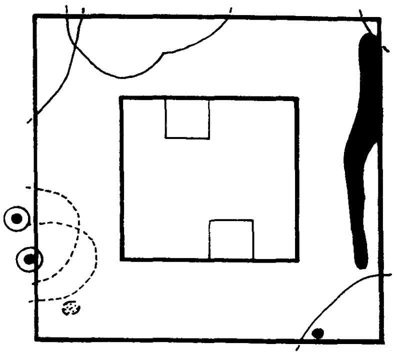

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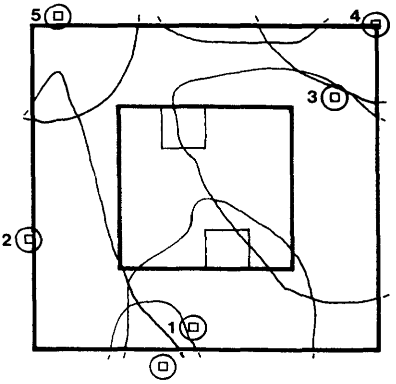

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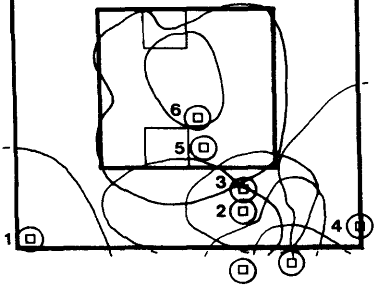

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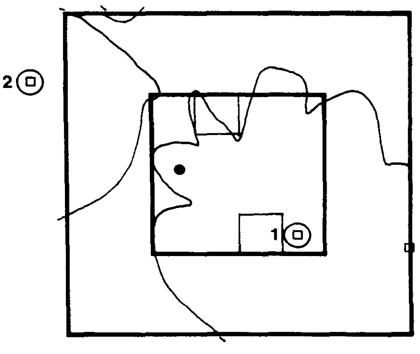

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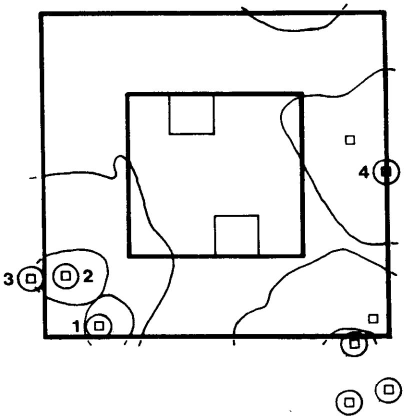

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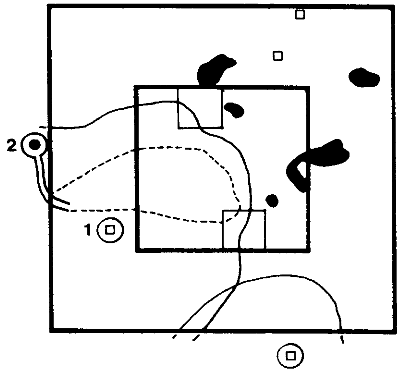

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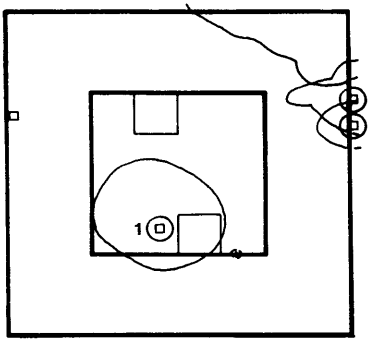

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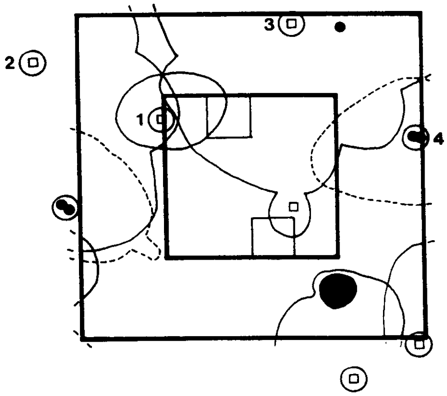

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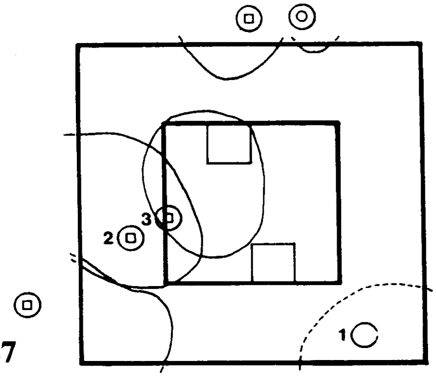

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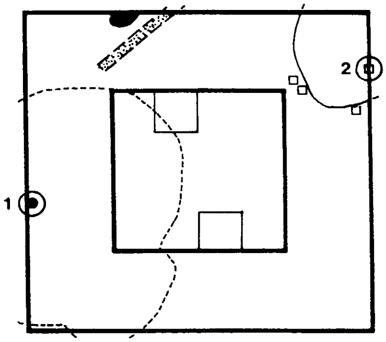

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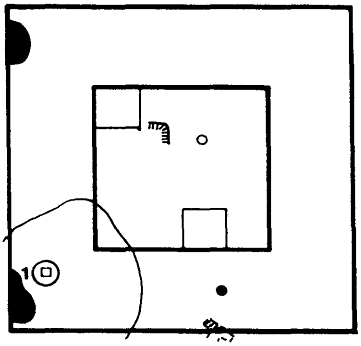

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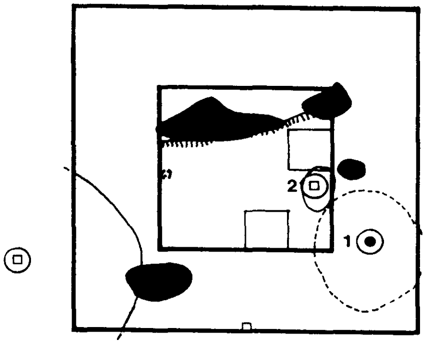

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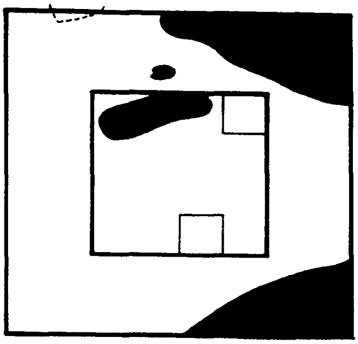

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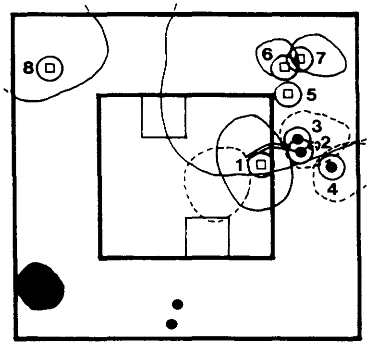

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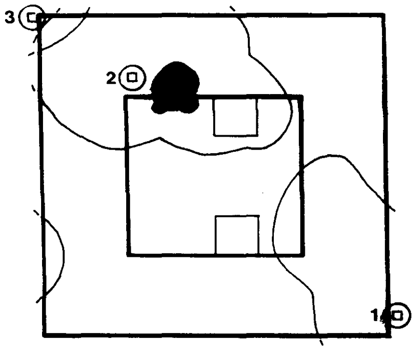

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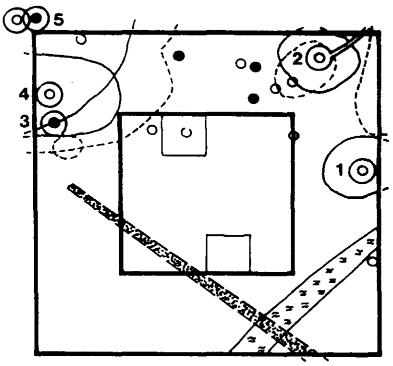

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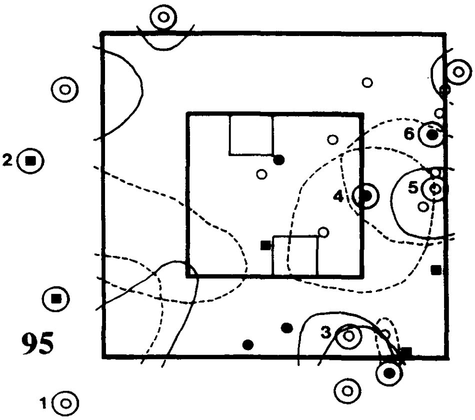

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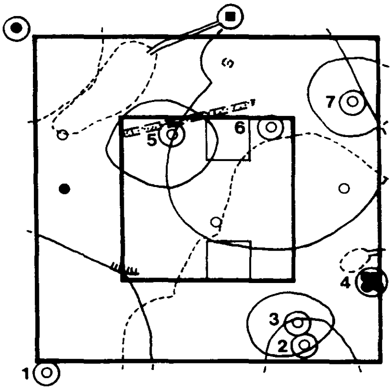

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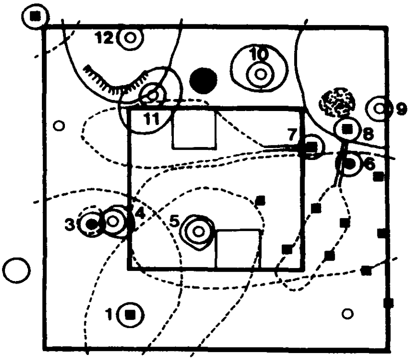

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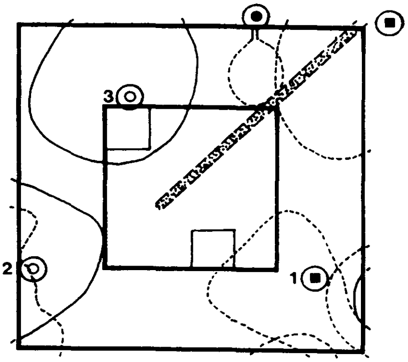

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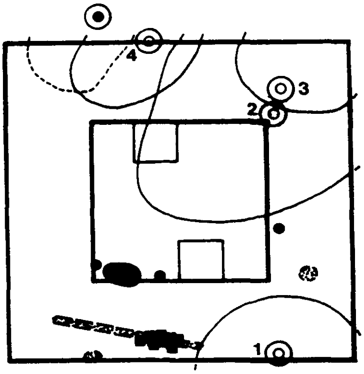

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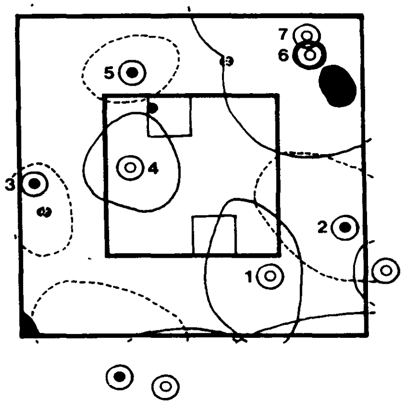

100

Appendix 4. Untransformed values for the 33 measured environmental variables in the 200 meso sample plots. ST - site type. NO - meso sample plot number. 01-33 - numbers of environmental variables in accordance with Tab. 3 (p. 00); 01 - MA Slo; 02 - MA Asf; 03 - MA Ter; 04 - MA Une; 05 - MA S d; 06 - MA Bas; 07 - MA Can; 08 - ME Slo; 09 - ME Asf; 10 - ME Une; 11 - ME Con; 12 - ME Smi; 13 - ME Sme; 14 - ME Sma; 15 - ME Lit; 16 ME Bas; 17 - Mois; 18 - LI; 19 - pH_{H_2O}; 20 - pH_{CaCl_2}; 21 - Ca; 22 - Mg; 23 - Na; 24 - K; 25 - H; 26 - N; 27 - P-AL; 28 - Al; 29 - Fe; 30 - Mn; 31 - Zn; 32 - P; 33 - S.

ST	NO	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
1-1	12	17	130	3	4	1	1.0	0.11	13	165	2.0	1.5	1	5	9	0.00	6	39	76	4.3	3.4	2571	255	364	666	29	1.68	127	581	34	106	86	92	102
1-1	14	4	154	5	1	1	2.0	0.28	12	140	1.8	1.2	2	7	19	0.35	6	48	88	4.2	3.4	3456	373	288	761	48	1.83	125	179	14	142	101	115	68
1-1	64	3	126	5	1	1	1.0	0.29	5	165	0.6	-0.5	6	15	37	1.06	8	31	87	4.0	3.1	2501	356	230	319	96	1.39	96	77	9	23	21	20	14
1-1	79	7	69	5	1	1	0.5	0.00	9	25	1.3	0.7	1	3	8	0.00	5	39	75	4.0	3.2	1574	139	182	346	97	2.09	134	232	20	39	51	87	59
1-1	114	4	154	5	1	1	2.0	0.28	6	100	2.7	3.3	1	14	23	1.10	5	33	86	3.9	3.0	3500	382	356	764	46	1.60	85	185	16	147	105	121	69
1-1	160	5	136	5	1	1	3.5	0.32	3	145	1.4	-0.6	1	25	40	1.18	11	38	72	3.9	3.0	3208	418	183	311	121	1.44	84	103	11	27	31	25	17
1-1	163	2	89	5	1	1	2.0	0.11	7	25	1.0	-0.8	1	2	3	0.03	8	38	66	4.0	3.1	2178	329	210	552	152	1.87	103	120	26	18	23	20	17
1-1	178	2	121	5	1	1	0.0	0.22	10	195	1.5	1.1	0	3	7	0.29	4	49	55	4.0	3.3	2720	324	255	759	102	2.09	160	376	49	100	76	109	85
1-1	179	7	69	5	1	1	0.5	0.00	10	85	0.8	0.2	1	3	18	0.00	7	45	85	3.9	3.1	1565	167	93	282	109	1.73	103	168	26	56	67	78	37
1-1	184	4	6	4	1	1	1.5	0.47	7	65	1.3	0.7	0	2	8	0.20	5	40	79	3.9	3.1	1132	121	78	208	130	2.01	152	37	18	10	30	46	25
1-1	188	13	155	4	1	1	2.0	0.26	18	155	1.3	-1.8	2	3	6	0.04	9	33	81	4.0	3.3	509	53	48	53	111	1.96	149	93	15	11	20	27	15
1-1	191	2	71	4	2	1	0.0	0.00	16	170	2.5	1.8	2	6	14	0.00	1	50	87	4.2	3.4	1392	163	190	332	125	1.97	84	334	28	18	54	29	56
1-2	63	2	89	5	1	1	2.0	0.11	2	85	1.2	0.4	0	3	13	0.05	7	33	53	4.0	3.1	1164	219	147	367	116	1.90	92	188	34	8	17	9	17
1-2	113	17	134	5	1	1	1.5	0.13	9	165	2.5	0.7	0	9	23	2.64	5	31	95	4.1	3.3	3254	364	276	723	95	1.66	93	171	17	115	58	104	74
1-2	193	9	149	4	1	1	1.0	0.12	14	160	1.2	0.3	2	6	7	1.23	7	44	47	4.1	3.2	318	44	44	84	205	2.27	118	458	128	6	17	11	30
2-1	13	17	134	5	1	1	1.5	0.13	35	145	3.5	1.4	3	6	26	0.00	5	39	87	4.2	3.3	1776	222	119	672	59	2.02	95	891	34	72	72	47	71
2-1	58	6	108	4	1	1	1.5	0.06	18	110	3.4	-3.8	7	30	36	0.25	8	38	73	4.0	3.2	3878	462	288	656	116	1.20	106	55	7	18	29	29	22
2-1	59	2	84	5	1	1	7.0	0.81	6	60	2.3	-1.4	8	20	31	7.82	17	34	92	4.0	3.1	2411	306	201	645	88	1.33	73	40	5	12	17	20	14
2-1	61	1	153	5	1	1	3.5	0.55	7	135	2.1	-2.3	3	10	31	1.66	11	29	95	3.8	3.0	1913	315	148	544	84	1.42	87	40	7	8	19	20	14
2-1	83	1	101	4	1	1	2.5	0.04	0	100	1.9	0.7	7	8	36	0.00	12	42	72	3.8	3.0	2315	372	257	688	125	1.87	119	367	77	41	119	113	77
2-1	84	4	6	4	1	1	1.5	0.47	7	65	1.6	-0.3	1	15	37	0.73	7	44	72	4.0	3.2	399	76	32	212	137	1.91	153	191	18	4	35	46	17
2-1	87	14	159	4	1	1	2.5	0.25	33	160	1.9	1.4	2	4	49	0.00	9	54	88	4.3	3.4	1569	235	248	622	166	1.85	111	1245	89	49	55	48	75
2-1	90	8	151	4	2	1	1.0	0.02	8	135	1.5	-0.1	3	5	19	0.00	4	34	94	3.9	3.2	2255	295	236	569	118	1.58	75	370	42	49	72	44	73
2-1	93	9	149	4	1	1	1.0	0.12	11	145	2.1	2.2	8	17	23	0.00	11	38	87	4.0	3.3	358	33	29	89	143	1.81	112	222	39	7	15	7	18
2-1	162	3	161	5	1	1	2.5	0.29	25	175	5.0	-6.9	0	13	36	2.41	6	30	96	3.9	3.0	2466	349	202	573	74	1.47	93	39	6	15	18	22	18
2-1	164	3	126	5	1	1	1.0	0.29	12	55	2.3	1.0	12	32	52	0.92	7	28	81	3.9	3.0	1984	360	235	458	112	1.59	79	105	9	7	21	16	16

Appendix 4 (continued).

ST	NO	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
2-1	183	1	101	4	1	1	2.5	0.04	9	175	1.3	1.2	1	2	17	0.00	10	50	87	4.0	3.2	493	53	11	67	82	1.71	195	51	16	13	21	31	8
2-1	185	8	82	5	1	1	1.5	0.25	3	55	0.8	-0.2	3	7	10	0.00	8	34	72	3.9	3.2	935	85	42	98	108	2.05	127	138	40	22	28	29	22
2-2	60	5	136	5	1	1	3.5	0.32	11	200	2.6	1.3	2	20	30	0.00	12	32	74	3.8	3.0	2177	343	235	490	145	1.31	85	152	12	5	23	19	18
2-2	78	2	121	5	1	1	0.0	0.22	7	115	4.3	4.2	2	5	20	1.48	4	38	94	3.9	3.1	598	76	49	167	90	1.93	138	116	17	31	26	46	18
2-2	126	22	102	4	1	1	1.0	0.00	23	107	1.9	0.1	2	4	11	0.00	6	44	76	4.0	3.1	929	199	114	537	166	2.12	109	219	26	12	12	13	17
2-2	129	13	143	4	1	1	2.0	0.00	27	155	1.1	0.2	2	6	9	0.00	5	59	91	4.3	3.4	2197	243	303	634	137	1.66	75	230	16	20	18	11	20
2-2	131	12	195	4	4	1	1.5	0.12	11	150	2.6	1.3	2	6	22	0.00	8	45	72	4.2	3.3	1979	214	379	557	142	1.84	71	313	15	17	18	10	24
2-2	165	0	100	4	1	1	0.5	0.12	10	95	3.2	-4.3	1	20	39	0.00	3	44	91	3.9	3.0	1916	408	252	433	122	1.79	80	104	10	9	29	19	18
2-2	190	8	151	4	2	1	1.0	0.02	5	165	3.1	-1.3	1	15	30	0.00	4	39	92	4.0	3.2	1046	126	103	179	114	1.56	81	175	16	10	44	20	33
2-2	192	8	151	4	1	1	1.5	0.26	13	155	1.5	0.6	2	6	14	0.27	9	49	88	4.1	3.3	574	50	57	115	139	1.70	85	296	39	7	17	19	20
3-1	62	3	161	5	1	1	2.5	0.29	3	155	3.5	-5.5	24	35	40	1.45	7	31	96	3.9	3.0	2348	340	169	594	92	1.55	75	35	5	10	19	20	17
3-1	66	7	9	4	1	1	0.5	0.03	0	100	1.5	0.2	7	20	35	0.00	6	29	95	4.1	3.3	3056	384	377	752	70	1.62	94	40	3	15	28	24	21
3-1	81	11	142	4	1	1	5.5	0.42	14	105	3.1	2.2	16	42	57	3.83	21	26	77	3.9	3.2	1913	255	194	335	101	1.29	120	129	27	25	49	65	47
3-1	82	3	95	4	1	2	2.5	0.17	0	100	4.0	-3.2	39	49	53	1.81	8	28	97	3.9	3.3	3740	500	264	615	69	1.42	135	56	17	101	59	102	48
3-1	85	8	82	5	1	1	1.5	0.25	4	185	2.0	-0.5	23	35	70	2.90	5	32	97	3.9	3.2	527	98	59	254	101	1.46	186	287	68	7	22	37	35
3-1	86	17	191	4	2	2	3.5	0.28	22	145	2.0	1.2	8	11	16	0.04	12	30	76	4.0	3.2	672	58	27	149	107	1.47	118	118	36	14	22	24	14
3-1	88	13	155	4	1	1	2.0	0.26	14	115	3.1	-4.7	14	28	47	0.00	8	40	90	4.0	3.3	1686	189	144	458	109	1.61	123	51	19	23	60	55	47
3-1	89	6	148	4	1	1	2.5	0.02	11	155	1.4	-1.7	14	28	54	0.00	7	32	95	3.9	3.2	1130	149	70	246	98	1.33	115	32	13	16	26	27	24
3-1	91	2	71	4	2	1	0.0	0.00	6	15	2.1	0.0	13	44	61	0.00	1	33	97	3.9	3.1	872	103	64	166	114	1.54	67	91	14	4	31	8	22
3-1	92	8	151	4	1	1	1.5	0.26	11	120	1.8	2.1	7	14	27	0.06	6	33	93	3.9	3.2	395	41	17	97	110	1.75	108	68	16	6	24	8	12
3-1	112	17	130	3	4	1	1.0	0.11	3	95	1.8	1.8	6	24	38	0.35	5	34	94	4.0	3.2	2882	438	251	1057	57	1.47	118	88	17	178	88	106	81
3-1	158	6	108	4	1	1	1.5	0.06	4	175	2.2	1.9	20	32	51	0.00	11	35	80	3.8	3.1	2477	405	224	761	94	1.50	89	71	10	9	29	22	19
3-1	159	2	84	5	1	1	7.0	0.81	7	55	3.3	-1.0	12	41	59	1.13	14	20	83	3.9	3.1	2306	323	216	575	114	1.33	78	90	8	8	21	19	16
3-1	161	1	153	5	1	1	3.5	0.55	20	5	5.9	-0.3	19	42	59	2.67	11	21	95	3.8	3.0	2437	378	207	534	90	1.22	70	47	26	7	16	7	18
3-1	166	7	9	4	1	1	0.5	0.03	10	55	3.5	-0.7	19	31	35	0.19	5	31	97	4.1	3.2	3736	408	355	660	75	1.65	98	22	2	17	22	19	24
3-1	176	14	168	4	1	1	4.0	0.50	12	145	2.9	-1.8	25	46	59	2.48	14	31	98	4.2	3.2	2279	381	318	673	93	1.06	97	66	24	50	41	82	70
3-1	177	6	172	5	1	2	1.5	0.32	6	185	3.5	-0.5	21	37	57	3.07	5	23	97	3.9	3.1	807	135	45	299	97	1.49	124	29	11	12	28	22	22
3-1	181	11	142	4	1	1	5.5	0.42	9	155	3.6	4.8	28	44	54	0.56	16	30	96	3.7	3.0	464	73	22	115	100	1.18	103	38	17	7	19	22	12
3-1	182	3	95	4	1	2	2.5	0.17	10	145	1.5	-0.2	2	9	18	0.17	9	46	84	3.9	3.1	2184	295	113	477	105	1.58	116	189	33	78	73	94	42
3-1	186	17	191	4	2	2	3.5	0.28	3	185	2.3	-2.8	7	45	62	2.30	14	24	89	3.8	3.2	2040	281	207	423	115	1.63	77	230	38	34	53	68	57
3-1	189	6	148	4	1	1	2.5	0.02	15	25	7.0	-8.3	4	17	35	0.00	6	38	95	4.0	3.3	1096	147	51	330	91	1.44	169	26	13	27	26	37	23

Appendix 4 (continued).

ST	NO	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
3-2	26	22	102	4	1	1	1.0	0.00	28	135	2.1	3.3	3	6	9	0.00	3	52	76	4.2	3.3	2518	240	432	637	181	2.14	113	1089	92	60	60	33	99
3-2	27	12	136	4	1	1	2.5	0.11	18	160	1.8	-1.2	5	12	23	0.00	9	56	93	4.3	3.4	4257	468	534	782	146	1.35	88	109	23	44	22	23	31
3-2	29	13	143	4	1	1	2.0	0.00	13	150	2.5	-2.4	13	17	27	0.00	5	39	97	4.2	3.4	3234	345	337	755	69	1.63	124	61	5	60	15	27	18
3-2	30	19	178	4	1	1	2.5	0.15	19	180	2.0	-2.4	6	13	17	0.00	9	57	97	4.3	3.4	3232	336	504	797	79	1.57	95	109	20	37	18	23	28
3-2	31	12	195	4	4	1	1.5	0.12	17	170	2.6	-0.3	7	25	35	1.39	8	35	98	4.3	3.3	3646	470	413	718	72	1.23	102	18	3	22	21	23	25
3-2	65	0	100	4	1	1	0.5	0.12	7	115	2.3	1.9	30	44	63	0.00	5	23	97	4.0	3.0	2586	599	287	654	136	1.31	68	35	6	5	27	15	15
3-2	76	14	168	4	1	1	4.0	0.50	21	185	2.7	-0.4	1	20	31	1.76	10	32	97	4.3	3.2	1847	275	244	379	96	1.28	103	108	27	74	41	65	46
3-2	77	6	172	5	1	2	1.5	0.32	11	105	2.7	-4.2	10	28	38	0.00	5	26	97	3.9	3.0	1745	363	162	482	101	1.34	104	70	19	27	56	66	40
3-2	125	31	102	4	1	1	0.0	0.07	33	125	1.4	0.2	4	7	9	0.00	2	60	64	4.1	3.1	1116	226	273	569	175	2.13	122	944	75	53	64	125	66
3-2	127	12	136	4	1	1	2.5	0.11	20	125	2.8	-2.6	15	22	23	2.40	10	38	97	4.2	3.4	3337	381	345	759	99	1.68	123	26	5	76	17	27	23
3-2	187	14	159	4	1	1	2.5	0.25	3	20	2.8	-1.7	4	22	32	0.82	7	25	97	3.9	3.2	1000	103	71	125	109	1.32	124	43	16	11	25	27	23
4-1	4	27	70	3	2	2	2.0	0.47	23	75	6.7	-2.3	2	4	18	0.08	14	42	85	3.9	3.1	2578	318	108	849	72	1.67	141	167	36	86	76	134	73
4-1	10	14	127	2	1	2	3.0	0.27	13	135	3.2	0.7	15	27	47	0.42	12	22	95	4.0	3.4	4443	507	304	930	39	1.46	189	74	12	174	87	166	87
4-1	11	17	147	2	1	2	3.0	1.07	18	170	3.3	-0.5	11	36	52	3.25	7	30	97	4.2	3.4	4288	558	317	1032	78	1.42	186	64	11	138	66	151	91
4-1	74	15	133	2	1	3	10.5	0.75	14	145	1.9	1.2	45	90	96	5.32	27	30	96	4.0	3.4	3428	266	225	542	64	1.68	103	82	16	64	51	76	257
4-1	75	18	170	3	2	2	4.0	0.35	23	185	1.7	-1.1	50	58	91	1.42	14	33	96	3.9	3.2	1968	290	139	379	89	1.63	146	40	15	22	44	68	41
4-1	80	4	12	5	1	1	4.5	0.48	10	25	1.3	1.2	8	19	28	2.16	13	22	96	3.8	3.1	444	62	19	49	89	1.47	114	37	15	8	15	19	10
4-1	99	20	179	3	1	2	0.5	0.28	23	165	2.8	1.4	9	31	44	0.00	4	25	88	4.1	3.4	3747	274	252	608	76	1.89	137	59	10	238	56	107	58
4-1	100	6	188	3	1	1	2.5	0.20	13	185	1.4	1.9	8	11	24	1.31	10	29	95	4.1	3.3	2764	407	147	813	111	1.78	168	59	17	124	78	141	56
4-1	108	28	141	3	2	2	0.5	0.27	15	145	5.3	-2.8	3	12	52	0.01	8	35	87	3.9	3.2	3527	386	292	889	58	1.37	113	139	17	77	104	128	74
4-1	109	27	164	3	4	2	2.5	0.22	29	185	3.7	4.1	10	16	32	0.11	10	23	94	3.9	3.2	3183	527	371	1007	67	1.28	159	143	23	82	94	139	83
4-1	110	14	127	2	1	2	3.0	0.27	10	165	1.6	0.7	5	34	49	0.00	8	27	95	3.9	3.1	2841	610	324	1007	79	1.45	158	171	25	82	131	156	98
4-1	111	17	147	2	1	2	3.0	1.07	20	145	4.4	7.3	3	16	29	3.78	6	23	96	4.1	3.4	4305	474	343	989	74	1.69	166	59	8	241	73	188	94
4-1	128	16	147	4	1	1	1.0	0.32	27	155	4.4	-4.2	5	32	52	3.38	3	44	97	4.2	3.4	3209	303	306	485	67	1.70	103	39	6	66	14	21	12
4-1	173	11	118	2	1	3	4.0	1.33	10	135	2.2	1.1	49	62	86	7.13	16	28	94	4.2	3.5	1811	207	100	418	60	1.96	105	12	7	28	64	46	32
4-1	174	15	133	2	1	3	10.5	0.75	18	155	2.2	-0.7	12	24	84	7.01	25	22	96	4.1	3.5	3762	368	225	655	56	1.56	94	27	9	106	63	89	63
4-1	175	18	170	3	2	2	4.0	0.35	19	185	2.1	-1.9	20	46	67	2.64	16	21	97	3.9	3.1	1301	197	66	468	96	1.57	124	34	13	30	31	54	29
4-1	180	4	12	5	1	1	4.5	0.48	5	35	1.0	1.3	5	24	30	0.30	14	19	96	3.8	3.1	1632	260	150	410	114	1.45	156	98	32	35	53	92	52
4-1	200	6	188	3	1	1	2.5	0.20	7	165	1.5	-0.9	10	24	54	0.34	10	34	95	3.9	3.2	1996	241	126	663	112	1.62	148	249	28	114	56	100	44
4-2	8	28	141	3	2	2	0.5	0.27	27	135	5.1	-0.2	12	26	30	0.17	10	42	90	4.1	3.4	3818	450	329	891	27	1.88	145	72	11	257	145	155	87
4-2	9	27	164	3	4	2	2.5	0.22	22	165	3.4	-0.8	2	18	28	0.00	10	31	87	3.9	3.0	1619	357	202	1130	141	1.40	116	653	124	35	82	119	82

Appendix 4 (continued).

ST	NO	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
4-2	24	18	107	3	1	1	0.5	0.20	28	115	1.4	2.4	4	7	13	0.26	4	55	86	4.2	3.4	807	121	120	458	120	1.53	99	684	39	41	32	39	46
4-2	25	31	102	4	1	1	0.0	0.07	35	105	2.6	2.3	3	12	17	0.00	2	43	57	4.1	3.3	2836	482	401	805	202	2.09	175	400	106	209	72	113	89
4-2	28	16	147	4	1	1	1.0	0.32	16	150	3.1	-3.4	12	27	36	0.35	3	37	97	4.1	3.4	3801	412	320	807	68	1.65	124	49	7	66	17	27	24
4-2	124	18	107	3	1	1	0.5	0.20	32	105	1.4	-2.0	9	9	10	0.00	2	45	61	4.2	3.4	1882	262	211	886	136	2.15	136	798	49	95	67	99	82
4-2	130	19	178	4	1	1	2.5	0.15	16	110	3.4	2.8	6	16	36	1.11	14	35	97	4.1	3.2	3010	390	239	792	92	1.38	98	24	6	23	16	24	16
4-2	199	20	179	3	1	2	0.5	0.28	40	185	2.7	1.3	6	13	34	2.15	5	23	93	4.0	3.3	3135	298	262	702	106	1.66	172	133	29	174	53	146	71
5.1-1	1	28	85	2	1	3	3.5	1.21	22	185	4.8	-2.6	9	27	37	6.01	11	28	90	4.0	3.3	3471	397	168	957	74	1.45	102	74	22	183	78	109	72
5.1-1	2	23	109	2	1	3	3.0	1.21	20	135	2.1	-0.3	5	25	51	4.63	11	20	91	4.0	3.2	2764	453	150	961	58	1.53	121	88	25	112	63	128	61
5.1-1	3	19	109	2	2	2	2.5	0.24	17	125	2.3	-1.4	5	22	38	0.06	13	35	84	4.0	3.2	1070	373	110	838	155	1.46	107	1208	42	46	56	73	63
5.1-1	5	14	112	2	2	2	5.5	0.58	20	125	1.9	0.6	2	22	49	1.97	23	36	55	4.1	3.3	3642	413	92	1072	31	2.08	130	177	69	201	60	132	77
5.1-1	6	26	131	3	2	2	0.5	0.02	20	115	2.8	-2.4	3	29	35	0.00	7	28	51	4.0	3.1	1142	331	213	1025	121	1.95	112	813	156	61	75	79	103
5.1-1	7	17	124	3	2	2	4.0	0.33	13	135	2.2	-0.3	2	16	36	0.35	15	29	59	4.1	3.3	3964	400	208	1079	76	1.72	89	97	27	194	80	99	77
5.1-1	15	11	192	2	2	2	2.5	0.08	9	180	1.9	-0.5	7	16	47	0.00	13	52	73	4.0	3.2	3316	456	268	755	70	1.86	125	160	27	67	141	118	77
5.1-1	22	22	129	3	1	2	6.5	0.49	18	165	3.8	2.8	6	7	7	8.26	23	37	61	4.2	3.4	2345	257	181	806	140	2.90	134	759	51	98	70	75	67
5.1-1	34	31	106	3	4	1	6.0	1.31	26	105	7.3	10.8	0	5	18	5.89	17	26	91	4.5	3.8	4764	357	156	853	48	2.00	121	13	1	107	22	23	24
5.1-1	36	18	119	1	2	2	4.5	0.64	16	145	5.4	-5.5	8	26	32	10.10	16	27	57	4.1	3.4	3729	362	81	1062	59	1.89	134	25	12	55	21	37	19
5.1-1	37	13	152	3	2	1	5.5	0.64	7	185	2.0	0.9	2	20	46	1.45	17	31	83	4.4	3.7	4629	464	159	828	38	1.90	121	7	1	86	35	31	19
5.1-1	41	11	126	3	1	2	7.0	0.51	4	155	1.3	-0.3	5	37	55	5.94	29	29	88	4.0	3.3	3632	338	204	774	67	1.70	100	14	5	49	22	26	19
5.1-1	70	7	84	2	1	3	3.5	1.23	14	85	2.0	0.9	10	50	88	4.08	12	30	76	4.0	3.3	3464	382	247	661	94	1.94	131	28	7	13	9	25	17
5.1-1	71	10	77	2	2	3	3.5	0.16	18	105	1.3	0.5	10	50	80	0.00	14	41	81	4.0	3.2	4013	490	369	652	90	1.84	136	42	5	9	11	33	21
5.1-1	72	13	135	2	1	3	2.0	1.18	14	125	2.4	2.5	40	72	84	3.15	14	46	96	4.2	3.6	4870	703	334	783	55	2.05	167	6	1	24	16	30	18
5.1-1	73	11	118	2	1	3	4.0	1.33	21	125	2.3	0.6	1	25	74	14.17	14	16	96	4.2	3.5	3401	429	163	662	47	1.96	136	14	1	32	24	28	15
5.1-1	96	28	170	2	2	2	2.0	0.32	36	145	3.0	-1.3	7	18	35	1.32	8	39	80	4.1	3.3	579	65	35	161	132	2.03	101	240	24	8	23	15	19
5.1-1	97	18	182	3	2	2	2.5	0.72	32	175	2.8	0.7	10	49	63	3.67	10	40	83	4.1	3.4	2446	305	147	443	81	1.85	157	35	23	45	55	60	45
5.1-1	98	21	195	2	2	2	2.0	0.11	34	175	4.9	2.5	7	20	47	0.00	8	40	94	4.1	3.3	869	82	56	159	70	1.81	139	27	33	12	34	27	19
5.1-1	101	28	85	2	1	3	3.5	1.21	12	105	2.7	2.3	0	17	31	10.57	7	27	94	3.9	3.2	3216	323	127	994	72	1.42	90	137	36	154	77	105	78
5.1-1	102	23	109	2	1	3	3.0	1.21	24	125	3.0	-2.3	11	28	47	4.82	11	37	85	4.0	3.2	2376	544	132	1171	54	1.55	153	99	31	137	101	167	60
5.1-1	103	19	109	2	2	2	2.5	0.24	10	105	3.0	2.8	5	25	60	0.00	13	30	81	4.0	3.2	3163	463	151	937	51	1.56	117	167	27	225	75	126	67
5.1-1	104	27	70	3	2	2	2.0	0.47	21	55	2.7	-1.5	0	18	50	3.55	13	21	81	3.9	3.2	3476	356	96	773	47	1.47	122	93	29	198	77	115	57
5.1-1	105	14	112	2	2	2	5.5	0.58	16	115	3.2	0.2	1	24	78	3.69	18	24	79	3.9	3.2	3734	321	154	806	55	1.66	82	104	25	250	82	94	86
5.1-1	107	17	124	3	2	2	4.0	0.33	10	85	2.6	2.8	5	21	38	0.51	17	28	67	4.2	3.6	4306	453	293	1150	6	1.70	105	83	26	281	89	126	105
5.1-1	115	11	192	2	2	2	2.5	0.08	12	175	2.7	4.3	23	52	73	0.14	12	30	86	3.9	3.1	2285	481	271	753	44	1.69	111	138	29	89	134	106	81

Appendix 4 (continued).

ST	NO	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
5.1-1	117	35	148	4	3	1	3.5	0.02	43	190	3.5	5.9	4	6	8	0.00	17	50	53	4.2	3.4	2068	335	130	915	78	2.17	208	277	62	249	62	147	96
5.1-1	118	14	124	2	3	2	7.0	0.99	16	95	1.4	-1.8	8	16	53	15.82	18	36	84	4.2	3.6	3951	297	211	690	10	1.92	94	53	10	450	70	93	80
5.1-1	120	16	131	2	4	2	1.5	0.33	22	95	2.7	1.5	5	13	18	6.29	9	31	93	4.0	3.3	2845	242	160	578	84	1.82	93	132	14	139	56	77	50
5.1-1	121	33	106	1	2	2	3.0	0.42	30	85	3.9	-0.5	7	13	20	1.64	13	53	91	4.3	3.5	2264	290	308	842	105	2.02	110	810	45	82	47	55	85
5.1-1	122	22	129	3	1	2	6.5	0.49	7	155	1.7	1.3	8	10	15	0.17	20	39	94	4.3	3.5	1931	218	245	766	84	1.88	128	436	29	65	54	80	60
5.1-1	123	26	130	3	2	2	4.5	0.47	20	150	2.7	-0.3	3	10	12	3.96	22	57	87	4.2	3.4	2688	241	308	703	90	2.06	115	491	23	100	58	82	69
5.1-1	134	31	106	3	4	1	6.0	1.31	29	145	3.9	-3.8	1	4	32	18.05	16	24	78	4.2	3.5	4088	284	89	868	86	1.99	119	18	4	110	23	32	22
5.1-1	136	18	119	1	2	2	4.5	0.64	16	95	3.4	2.5	5	9	22	0.85	22	38	79	4.2	3.4	2611	341	131	898	122	1.65	107	162	9	42	20	19	.16
5.1-1	137	13	152	3	2	1	5.5	0.64	22	165	2.8	4.4	9	17	49	2.78	17	44	83	4.2	3.4	3480	458	192	826	62	1.62	145	19	4	51	34	37	21
5.1-1	140	17	118	1	2	2	4.5	0.46	30	145	4.1	-0.7	2	3	10	1.46	21	42	82	4.2	3.4	3147	369	197	691	54	1.87	135	27	6	88	20	32	22
5.1-1	141	11	126	3	1	2	7.0	0.51	8	75	2.1	-0.8	2	39	60	2.61	26	35	58	4.1	3.4	3549	384	128	665	46	1.55	151	16	7	56	24	35	19
5.1-1	147	21	102	2	2	2	5.0	0.50	27	95	3.3	-0.2	9	24	39	2.01	19	42	89	3.9	3.1	4220	395	98	203	86	2.10	91	18	6	8	27	23	11
5.1-1	155	34	153	3	4	2	4.5	0.70	22	145	3.3	-0.8	1	2	5	3.63	20	25	64	4.5	3.8	4745	334	232	783	20	2.48	202	17	8	84	25	48	30
5.1-1	169	29	107	3	2	3	3.0	0.40	32	115	2.5	2.3	40	64	91	0.03	9	33	68	4.1	3.4	4976	575	362	869	65	2.02	162	21	6	40	13	43	24
5.1-1	170	7	84	2	1	3	3.5	1.23	10	105	2.0	-0.9	30	67	83	9.77	11	33	96	4.1	3.3	3623	427	229	796	64	1.88	135	12	2	15	9	31	17
5.1-1	171	10	77	2	2	3	3.5	0.16	11	45	2.7	1.0	40	65	87	2.43	15	46	81	4.1	3.5	4752	619	387	721	76	1.91	160	18	2	12	12	41	22
5.1-1	172	13	135	2	1	3	2.0	1.18	7	125	2.0	-0.4	34	44	84	4.02	15	31	96	4.1	3.3	4050	765	337	767	65	1.87	145	11	2	10	28	29	19
5.1-1	196	28	170	2	2	2	2.0	0.32	23	195	3.4	1.3	7	33	60	2.90	9	23	69	4.0	3.3	645	62	37	85	139	1.93	90	188	25	9	22	16	19
5.1-1	197	18	182	3	2	2	2.5	0.72	21	175	2.5	-0.2	8	34	72	0.81	11	34	83	4.0	3.3	656	53	17	113	95	2.07	133	25	29	11	25	11	8
5.1-1	198	21	195	2	2	2	2.0	0.11	32	185	3.5	0.1	2	23	44	9.58	4	29	75	3.9	3.1	903	70	52	230	100	1.74	112	39	43	20	20	20	24
5.1-2	20	16	131	2	4	2	1.5	0.33	30	125	2.5	0.3	4	7	20	3.41	11	63	72	4.1	3.4	1537	187	135	474	75	1.98	121	393	31	88	31	47	36
5.1-2	21	33	106	1	2	2	3.0	0.42	19	125	3.2	-1.3	5	10	37	1.33	8	44	58	4.2	3.3	1297	277	152	727	142	0.77	150	732	99	99	90	118	66
5.1-2	23	26	130	3	2	2	4.5	0.47	25	125	1.5	0.0	6	8	9	4.23	22	48	78	4.3	3.5	3761	299	346	899	97	2.13	141	454	21	152	67	102	84
5.1-2	32	24	128	1	1	2	2.0	0.31	28	165	5.6	1.8	2	9	27	2.21	7	28	70	4.4	3.5	1836	278	147	723	155	2.26	107	337	7	20	17	13	26
5.1-2	35	24	134	2	1	2	3.5	0.25	26	195	8.3	6.4	2	25	32	0.00	12	47	85	4.4	3.4	1475	278	160	862	160	2.02	111	402	15	18	15	12	20
5.1-2	95	24	189	1	2	2	1.0	0.24	21	195	3.7	-1.5	2	14	57	0.49	6	56	91	4.3	3.6	425	31	35	185	144	2.05	86	480	20	4	16	5	13
5.1-2	106	26	131	3	2	2	0.5	0.02	16	145	2.8	-0.4	1	20	80	0.00	7	39	78	4.1	3.3	3172	333	403	1041	52	1.77	118	127	26	73	65	146	99
5.1-2	132	24	128	1	1	2	2.0	0.31	10	155	1.6	-1.3	0	32	46	1.48	9	34	88	4.8	3.8	498	110	139	606	168	2.43	55	442	3	7	8	3	26
5.1-2	135	24	134	2	1	2	3.5	0.25	21	125	5.8	-3.5	2	6	37	0.00	10	41	63	4.1	3.2	2236	360	171	1097	99	1.82	132	57	16	30	16	38	21
5.2-1	17	35	148	4	3	1	3.5	0.02	21	180	2.7	3.3	2	17	42	0.00	15	39	40	4.0	3.3	2369	597	631	955	68	2.82	120	2945	85	254	120	319	90
5.2-1	18	14	124	2	3	2	7.0	0.99	16	175	1.6	-0.2	4	10	90	8.69	15	24	53	4.4	3.9	7778	509	347	1291	67	2.94	179	51	2	1347	119	151	121
5.2-1	19	33	199	2	3	2	4.0	0.47	31	190	3.1	-3.3	6	17	73	5.41	16	43	77	4.1	3.4	2527	254	165	592	55	1.63	82	70	18	215	48	60	52

Appendix 4 (continued).

ST	NO	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
5.2-1	39	22	130	3	2	1	3.0	0.49	25	125	6.6	-1.8	2	21	35	5.49	14	35	63	4.0	3.2	2754	369	84	692	127	1.56	131	38	14	24	28	27	13
5.2-1	40	17	118	1	2	2	4.5	0.46	12	185	1.1	-1.1	3	20	42	2.47	20	40	85	4.1	3.3	2331	305	194	707	105	1.95	95	156	15	29	21	21	23
5.2-1	42	10	137	2	1	3	5.0	0.65	4	135	4.4	2.1	3	43	48	3.78	17	38	56	4.2	3.5	3737	467	199	1028	42	2.18	162	20	5	63	31	41	27
5.2-1	43	16	129	2	1	3	7.0	0.85	28	155	4.0	3.8	0	43	60	14.33	20	31	47	4.3	3.7	5357	429	138	685	26	1.97	158	15	9	111	28	38	21
5.2-1	47	21	102	2	2	2	5.0	0.50	16	125	3.3	-2.5	22	16	53	5.15	16	38	50	4.2	3.3	4293	431	92	462	81	2.28	120	144	12	24	22	28	20
5.2-1	48	15	161	2	1	3	1.0	0.29	15	175	4.2	-1.3	27	49	55	0.20	13	40	48	4.2	3.3	5010	480	100	517	65	2.50	165	29	6	25	31	41	17
5.2-1	50	33	126	2	4	2	5.0	0.74	30	105	2.2	3.8	0	14	38	4.24	20	25	51	4.2	3.4	3621	323	216	710	69	2.46	135	45	8	45	27	43	29
5.2-1	68	19	134	2	1	3	4.5	0.66	14	135	3.5	0.1	1	7	15	4.45	13	49	79	4.3	3.4	2694	357	189	554	69	2.25	165	47	4	29	23	42	18
5.2-1	69	29	107	3	2	3	3.0	0.40	40	135	5.5	-6.2	10	35	65	3.58	10	40	87	4.2	3.4	4844	526	327	637	64	2.13	173	14	2	30	24	35	18
5.2-1	119	33	199	2	3	2	4.0	0.47	34	180	3.0	-2.6	5	14	57	0.92	14	39	55	4.2	3.4	2630	312	187	1581	98	2.02	126	114	29	157	52	94	72
5.2-1	139	22	130	3	2	1	3.0	0.49	24	55	4.1	1.2	18	45	83	0.00	14	49	63	4.1	3.3	1715	225	102	589	91	1.70	114	43	17	13	21	17	17
5.2-1	142	10	137	2	1	3	5.0	0.65	6	145	1.7	-1.1	13	39	46	11.59	20	34	54	4.1	3.4	3028	374	184	948	47	1.75	157	26	13	32	28	37	26
5.2-1	143	16	129	2	1	3	7.0	0.85	5	175	2.4	1.9	8	39	58	2.41	20	31	49	4.3	3.7	4758	565	237	949	23	2.37	198	16	6	130	33	56	29
5.2-1	144	7	158	1	2	2	2.5	0.00	7	115	2.7	-3.0	2	22	100	0.00	11	57	60	4.0	3.3	3121	433	180	520	75	2.60	183	50	10	30	40	53	22
5.2-1	145	13	197	0	1	3	3.0	0.59	20	185	1.9	0.2	22	56	80	4.01	14	32	41	4.3	3.6	7997	455	128	5351	46	3.01	138	24	7	49	24	32	29
5.2-1	148	15	161	2	1	3	1.0	0.29	14	135	1.4	1.2	12	52	74	0.00	10	52	56	4.1	3.2	4824	427	79	500	60	2.54	148	29	7	20	47	45	16
5.2-1	150	33	126	2	4	2	5.0	0.74	25	155	3.8	-1.4	8	25	59	4.39	17	24	13	4.6	3.8	2501	229	173	764	121	3.08	195	1218	241	534	60	23	143
5.2-1	151	28	140	3	4	2	1.5	0.39	36	105	8.0	1.7	0	6	15	5.63	8	32	33	4.5	3.9	5038	505	304	1046	15	3.54	188	55	22	502	102	138	123
5.2-1	156	30	163	2	2	2	7.5	0.50	26	165	2.5	0.2	1	4	21	3.64	21	56	55	4.5	3.8	6164	415	274	875	193	2.36	155	20	2	92	29	42	27
5.2-1	168	19	134	2	1	3	4.5	0.66	29	100	1.6	-0.7	6	16	40	0.88	10	39	50	4.2	3.5	2824	380	297	575	89	2.68	157	91	12	24	20	24	24
5.2-1	195	24	189	1	2	2	1.0	0.24	28	165	4.5	0.2	9	25	60	0.00	8	40	95	4.0	3.3	4304	544	330	664	85	1.80	136	62	29	36	65	102	78
5.2-2	33	21	115	1	1	3	2.0	0.15	22	115	2.3	1.7	4	36	59	0.07	12	38	90	4.9	3.9	356	78	84	478	153	2.37	51	450	1	7	4	1	20
5.2-2	38	2	75	0	1	3	3.5	0.43	4	75	1.6	1.3	39	62	100	0.00	16	73	94	5.0	4.0	2698	244	325	424	207	1.71	68	587	71	6	6	1	18
5.2-2	94	19	198	1	1	3	0.5	0.02	20	185	2.0	0.8	8	43	74	0.00	5	62	92	4.5	3.8	796	76	100	127	139	1.82	58	640	13	11	14	4	31
5.2-2	133	21	115	1	1	3	2.0	0.15	16	115	1.1	-0.1	1	13	71	0.10	11	39	88	4.9	3.9	463	89	71	525	142	2.40	52	419	1	14	6	2	19
5.2-2	138	2	75	0	1	3	3.5	0.43	14	145	4.2	-1.6	7	35	56	3.01	18	53	95	4.5	3.6	1320	180	221	806	201	1.82	48	539	40	16	11	1	23
5.2-2	194	19	198	1	1	3	0.5	0.02	24	180	3.6	1.2	9	21	88	0.00	4	54	95	4.0	3.2	550	78	32	82	118	1.97	97	133	11	6	33	17	13
5.3	16	34	195	2	3	2	3.5	0.56	33	185	4.1	3.3	3	14	100	8.10	14	34	73	4.0	3.4	3731	601	270	983	131	2.20	137	101	30	193	102	141	89
5.3	44	7	158	1	2	2	2.5	0.00	4	45	3.4	-0.7	10	63	83	0.00	16	50	56	4.1	3.3	2538	398	132	517	72	2.61	197	43	14	27	29	52	23
5.3	46	23	128	3	1	2	4.0	0.64	28	165	1.8	1.4	1	28	39	9.10	11	38	40	4.2	3.5	5396	383	133	384	112	2.34	106	58	20	43	20	18	23
5.3	49	18	165	2	4	2	2.0	0.16	15	155	1.3	-0.5	10	16	27	0.11	7	40	70	5.0	4.1	582	99	124	356	162	2.77	67	394	1	21	9	6	30

Appendix 4 (continued).

ST	NO	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
5.3	51	28	140	3	4	2	1.5	0.39	20	95	1.8	-0.4	5	17	33	0.84	10	40	29	4.4	3.6	3375	502	255	991	39	2.40	132	139	21	132	101	125	128
5.3	52	22	14	3	2	2	1.5	0.10	30	125	5.3	-1.4	5	16	29	0.05	8	34	15	4.9	4.1	3942	440	378	849	40	2.83	204	507	33	586	125	66	184
5.3	55	34	153	3	4	2	4.5	0.70	30	165	2.9	-1.7	2	9	17	6.30	21	35	77	4.6	4.0	6087	493	241	856	8	2.27	194	8	0	135	38	47	32
5.3	56	30	163	2	2	2	7.5	0.50	23	145	5.5	8.4	10	26	47	7.06	20	38	38	4.7	3.9	3830	394	258	1082	50	3.08	167	151	5	157	23	18	37
5.3	57	28	136	2	4	2	3.5	0.48	22	125	2.4	0.3	5	20	53	2.76	14	30	24	4.6	3.9	11298	956	757	2268	108	3.54	152	996	33	313	62	12	119
5.3	116	34	195	2	3	2	3.5	0.56	32	165	3.3	-1.2	4	9	21	0.62	15	42	38	4.3	3.6	2870	483	147	1074	145	2.56	187	208	48	277	72	117	83
5.3	146	23	128	3	1	2	4.0	0.64	24	135	2.2	-0.6	7	17	38	5.38	15	32	35	4.3	3.6	4336	314	99	674	64	2.56	124	422	78	213	72	40	66
5.3	149	18	165	2	4	2	2.0	0.16	24	115	2.6	0.3	5	11	15	0.40	14	31	43	5.0	4.1	995	152	168	460	130	2.99	87	464	5	28	7	7	40
5.3	152	22	14	3	2	2	1.5	0.10	32	185	4.5	1.5	9	21	65	0.00	8	33	10	5.0	4.2	2849	346	383	996	82	3.82	186	1255	49	539	78	20	235
5.3	154	13	130	1	1	3	5.0	0.50	16	115	2.4	-0.4	3	28	67	0.09	14	44	25	5.0	4.2	6245	469	332	1020	12	2.85	112	157	32	365	92	36	149
5.3	157	28	136	2	4	2	3.5	0.48	31	125	5.7	-1.0	0	7	22	0.25	14	32	21	4.8	4.2	27226	2808	1303	3779	19	2.95	157	390	14	952	110	14	138
5.3	167	25	100	2	1	3	3.5	0.73	18	125	2.9	-1.4	0	25	90	7.99	13	42	50	4.6	3.9	5306	648	278	1007	39	2.84	201	14	2	123	36	42	24
6	45	13	197	0	1	3	3.0	0.59	15	185	2.0	-0.7	22	52	76	2.78	13	33	26	5.4	5.1	12148	467	187	379	0	2.67	93	1205	0	415	19	4	81
6	53	12	130	1	1	3	2.0	0.17	10	125	1.8	-0.8	25	52	66	0.41	12	61	23	5.3	4.7	7678	486	276	643	13	2.44	89	413	9	436	249	9	111
6	54	13	130	1	1	3	5.0	0.50	20	160	7.9	2.6	1	15	43	3.06	14	46	18	5.3	4.6	8264	540	323	747	34	3.15	118	281	17	399	51	17	140
6	67	25	100	2	1	3	3.5	0.73	20	100	1.8	0.5	23	41	46	0.00	10	41	32	4.3	3.7	5427	830	467	1291	112	3.68	251	35	10	79	35	57	38
6	153	12	130	1	1	3	2.0	0.17	10	95	1.1	-0.4	9	19	41	0.00	12	46	27	5.3	4.7	4023	270	147	382	13	3.01	94	350	4	297	26	8	68

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