sommerfeltia

8

R.H. Økland

A phytoecological study of the mire Northern
Kisselbergmosen, SE. Norway. I. Introduction,
flora, vegetation and ecological conditions.

1989

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A part of the mire complex N. Kisselbergmosen, termed the special area, is subjected to a detailed investigation of hydrotopography, species distributions, and ecological conditions. Species occurrences and distributions are related to four main complex-gradients; (1) the mire expanse - mire margin gradient, (2) the nutrient gradient, (3) the gradient in depth to the water table, and (4) a peat productivity gradient. The former two are termed broad-scale, the latter fine-scale gradients.

A hydrotopographical mapping was made, including establishment of a detailed map of mire features and subfeatures, and construction of a map showing the topography of the water table. Two or three synsegments and seven catchments make up the special area. Broad-scale distributions of species were mapped in a contiguous 4x4 m grid, resulting in a classification of species to nine D-groups. Six zones reflecting variation along gradients (1) and (2) were discerned. The concepts of mineral soil water limit and fen plant limit were discussed by reference to hydrotopography, species distributions, and chemical composition of peat along transects.

Fine-scale patterns were studied by use of 800 randomly placed plots, analyzed with respect to vegetational composition and provided with measurements of depth to the water table. Fluctuations of depth to the water table in the period 1980-82 was related to climate. Particular emphasis was put on studying parameters of the cumulative distribution functions of depth to the water table; between-year variation, interdependence, and estimation from few observations. Species were classified to seven W-groups according to relationships with the water table, and five series were considered along this gradient. The vegetation was classified into 32 site-types by a reticulate division of the ecological space spanned by the four gradients. These site-types were described by use of 654 randomly and 765 subjectively selected plots. The site-types were compared to main types of other works, and successional relationships of site-types were inferred from observed transitions and ecological measurements. Mechanisms responsible for vegetational variation along the four gradients are thoroughly discussed.

Keywords: Bog, Depth to water table, Distribution, Fen plant limit, Gradient, Hydromorphology, Mire, Site-type.

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INTRODUCTION

The vegetation and ecological relationships of Fennoscandian mires have partly been approached by monographic treatments of intensively studied mires or parts of mires (e.g., C. Malmström 1923, Osvald 1923, Booberg 1930, Sjörs 1948, Malmer 1962a, Mörnjö 1969), and partly by monographs treating mire vegetation within a region (e.g., Sjörs 1948, Ruuhijärvi 1960, Persson 1961, Eurola 1962, Sonesson 1970a, Fransson 1972). The basis of these works is a subjective classification of vegetation into a large number of categories by the methodologies of the Northern European tradition (cf. Whittaker 1962, Trass & Malmer 1978, Økland & Bendiksen 1985), and detailed mapping of species distributions at various scales. During the last two decades, emphasis has changed from monographic treatments of many aspects relating to restricted areas to in-depth treatments of single problems (e.g., Malmer & Nihlgård 1980, Rydin 1985, 1986, Wallén *et al.* 1988). This is in accordance with general international publishing practice in ecology today. However, the synthetic perspective of a monograph should still make monographic treatment attractive as it enables a potentially fruitful interaction between different investigations carried out simultaneously within one region. Since the last Fennoscandian monographs appeared, significant developments have been made in the fields of mire hydrology, mire chemistry, and in the methodology for analysis of vegetational data. Furthermore, there appears to be an unbridged gap between the traditional methods of subjective classification as the basis for ecological interpretation, and more recently developed multivariate methods based on randomized sampling.

One of the fundamental tenets of modern mire ecology; the existence of three main vegetational and ecological gradient pairs (ecoclines in the terminology of Whittaker (1967)) in northern mires, originated in the subjective classificatory period (cf. Sjörs 1948, 1950, Malmer 1962a). Although each of the three ecoclines; the nutrient (poor-rich) gradient, the mire expanse - mire margin gradient, and the gradient in depth to the water table, are well-documented, the assumption of a set of three gradients as sufficient to explain most of the variability in boreal mire has not been properly tested.

The existence of a discontinuity in the nutrient gradient, the mineral soil water limit (Thunmark 1940), and a corresponding discontinuity in the parallel vegetational gradient, the fen plant limit (Sjörs 1947), have been vigorously debated (e.g., Sjörs 1948, Witting 1948, Du Rietz 1954, Malmer 1962a). It is now generally accepted that the mineral soil water limit cannot be characterized satisfactorily by single chemical or physical parameters (Malmer 1962a, Tolonen & Seppänen 1976, Tolonen & Hosiainluoma 1978), but the use of multivariate characteristics for characterization appears more promising (Tolonen & Hosiainluoma 1978). The usefulness of the fen plant concept is still under debate (cf. Müller 1976).

The ecological basis of the mire expanse - mire margin gradient still remains obscure (Sjörs 1948, Malmer 1962a, Damman & Dowhan 1981).

Water table fluctuations in mires are treated in several recent papers, and the major spatial and temporal patterns of variation are well known (Malmer 1962a, Johansson 1974, Wildi 1977, Ivanov 1981). There is, however, an apparent lack of large sets of observations relating to a long observation period (cf. Clymo 1984), and detailed studies of species responses to water table fluctuations are still needed.

This series, of which the present paper is the first, discusses the boreal, poor mire, Northern Kisselbergmosen, SE Norway. The main aim of the series is to approach the vegetation and ecological conditions of the mire by an integrated methodology, where

traditional (subjective) and modern (multivariate) methods are applied in parallel. This should aid interpretation, be fruitful to the understanding of critical problems, and facilitate comparison and evaluation of the two methodological strategies.

The aims of this paper are (1) to describe the special area at Northern Kisselbergmosen hydrotopographically; (2) to map broad-scale distributions of species, and discuss the ecological basis for the patterns observed; (3) to analyze the chemical and physical composition of peat with reference to the "mineral soil water limit" and "fen plant limit" concepts; (4) to monitor fluctuations in depth to the water table for three consecutive years, and address local and climatic causes of the fluctuations as well as the distribution of plant species along the gradient in depth to the water table, (5) to provide a reference classification of the vegetation by a method comparable to traditional methods, and (6) to discuss the relationships between vegetation types and ecological gradients. The second paper in this series. (Økland 1990a) is devoted to a comparison between the subjective classification and ordinations by detrended correspondence analysis. The third, and final, paper (Økland 1990b) employs niche metrics to the vegetational data sets from the special area. Regional aspects are treated in two separate papers, one dealing with hydromorphology of mires and phytogeography (Økland 1989) and one dealing with vegetation (Økland 1990c).

THE INVESTIGATION AREA

The investigation area is situated in Rødenes parish, Østfold county, close to the Swedish border (Fig. 1). The special area considered in this study comprises the southern half of the Northern Kisselbergmosen mire complex (cf. Fig. 2), an area of approximately 30 ha within the altitudinal interval 290-305 m. The UTM grid reference is PM 50, 13-14.

Fig. 1. Map of Norway showing the position of N. Kisselbergmosen (dot). Based on map 1:10.000.000. Permission No. 79/87 Statens Kartverk.

GEOLOGY AND GEOMORPHOLOGY

The area belongs to the southeast Norwegian Precambrian, the Romerike grey gneisses. These grey gneisses are mostly steeply dipping and have a SSE-NNW to S-N strike (Ofte Dahl 1980). A comprehensive account of the geomorphology of inner Østfold and adjacent part of Akershus, is given by Økland (1989). The investigation area is situated on the Rødenesfjellet plateau, falling off gently to the east and cut off to the west by a steep edge running in the NW-SE direction. Although fringed at its margins by deep, narrow valleys, the topography of the Rødenesfjellet plateau is remarkably smooth. The investigation area is situated above the upper coastal line (cf. Undås 1952). The bedrock is covered with morainic deposits only in areas sheltered from ice movement (Holmsen 1951).

CLIMATE

Temperature. Based on material from nearby meteorological stations, maps for monthly mean temperatures reduced to sea level (Laaksonen 1979a), and estimates of the vertical temperature gradient (Laaksonen 1976), Økland (1989: Fig. 2) has estimated the local variation in some temperature parameters in inner Østfold and adjacent part of Akershus. The values for the investigation area is: January mean temperature -5.9°C , July mean temperature 15.5°C , and annual mean temperature 3.9°C . The length of the growing season with a basal temperature 5°C is estimated to be 168 days by use of data from Laaksonen (1979b). Similarly, the effective temperature sum is calculated as 1070 day-degree-units by Økland (1989).

Precipitation. Økland (1989) used data from nearby meteorological stations, and considerations of the influence of altitude and local topography on precipitation (cf. Sjørs 1948, Førland 1979, Krohn & Hardeng 1981) to estimate precipitation normals 1901-60 for inner Østfold and adjacent part of Akershus. The estimated annual precipitation normal for the western part of the Rødenesfjellet plateau is ca. 850 mm, decreasing in all directions.

Humidity. Two indices of humidity were calculated by Økland (1989) on the basis of the temperature and precipitation estimates; Tamm's index of humidity (Tamm 1954, 1959), $H = \text{ca. } 510$ (strongly humid), and Malmström's moisture index (V. Malmström 1969), $MI = \text{ca. } 2.5$. As with precipitation, these humidity indices reach local maxima at the Rødenesfjellet plateau.

Snow cover. The area has a stable snow cover, lasting for about 130 days; from the beginning of December to the middle of April (Norske Meteorologiske Institutt 1949).

THE SURROUNDING VEGETATION

The special study area is surrounded by low hills and knolls with shallow soil; the most drought-exposed sites are dominated by xeric pine forests (the terminology follows Økland & Bendiksen 1985) with a sparse field layer and a bottom layer with a prominence of *Cladonia* subg. *Cladina* spp. On somewhat deeper soil, an open subxeric pine forest with

a dominance of *Calluna vulgaris*, *Vaccinium myrtillus*, and *V. vitis-idaea*, locally also *Empetrum nigrum*, occurs. The bottom layer is dominated by *Cladonia* subg. *Cladina* spp., *Dicranum polysetum*, *D. scoparium*, and *Pleurozium schreberi*. A seasonally hygrophilous variant often developed in slight depressions is characterized by a prominence of *Salix aurita* and *Sphagnum capillifolium*. The sparsely occurring broad slopes with an easterly or northerly aspect contain standith submesic spruce forests, often with some scattered pines. The field layer is dominated by *Vaccinium myrtillus*, the bottom layer by *Dicranum majus*, *D. scoparium*, *Hylocomium splendens*, *Pleurozium schreberi*, and *Ptilium crista-castrensis*. Seasonally hygrophilous variants dominated by *Sphagnum girgensohnii* and *S. russowii* occur in depressions.

FLORISTIC PHYTOGEOGRAPHY

The phytogeography of the mire flora of inner Østfold and adjacent part of Akershus is treated in detail by Økland (1989). Økland (1989) characterized the western part of Rødnesfjellet as an area where western and northern phytogeographical elements meet, and attributed this to the combination of a humid climate with high elevation (relatively short summers). Eastern species occur, but southern species are few.

Four out of the five phytogeographic elements proposed by Bendiksen & Halvorsen (1981) for a division of the southern Norwegian flora (later amended by Økland & Bendiksen (1985) and Økland (1989)), are represented in the special area. The western element contains five species, two in group W3 - slightly western species (*Erica tetralix*, *Odontoschisma sphagni*) and three in group W4 - widespread species with a western tendency (*Sphagnum molle*, *Bazzania trilobata*, *Cladonia floerkeana*). The southern element contains two regionally widespread species in group S3 - slightly southern species (*Myrica g.*, *Rhynchospora alba*) as well as several regionally widespread species in group S4 - widespread species with a southern tendency. No southeastern species occur. The eastern element contains five species, four in group E1 - eastern species (*Carex globularis*, *Ledum palustre*, *Splachnum luteum*, *S. rubrum*) and one in group E2 - slightly eastern species (*Scheuchzeria palustris*). The northern element contains nine species, three in group N2 - boreal-alpine species (*Cetraria delisei*, *Micarea turfosa*, *Ochrolechia frigida*) and six in group N3 - hemiboreal-alpine species (*Betula nana*, *Carex magellanica*, *Sphagnum centrale*, *S. lindbergii*, *Cladonia bellidiflora*, *C. subfucata*). The investigation area is situated in the southern boreal zone (cf. Dahl *et al.* 1986, Økland 1989).

Fig. 2. Map of the Rødnesfjellet plateau showing the immediate surroundings of N. Kisselbergmosen. Based on economic maps CWX 037038-20 and CWX 039040-20. Main road is indicated by double line, minor road by broken line. Lakes are demarcated by continuous line and densely spaced dots, mires by broken line and less dense spacing of dots. The special area of N. Kisselbergmosen is surrounded by a thick, continuous line. A UTM grid with a mesh width of 2 km is indicated.

HUMAN INFLUENCE

With some minor exceptions, Northern Kisselbergmosen bears no signs of human influence. These exceptions are a couple of ditches in the southeastern, far southern, and northern parts (only the first is bordering on the special area), remnants of an old timber track in the lagg along the western margin of the mire, and some logging in the surrounding forests, though not within 200 m off the limit onto mineral soil. Northern Kisselbergmosen is protected as a Mire Nature Reserve.

MATERIALS AND METHODS

INTRODUCTION

The field work was carried out during the years 1976-1983. Processing of data was done on the Digital DEC-10 and VAX 8650/INGER computers, USE, Univ. of Oslo. The terminology of mire hydrology and hydromorphology follows Økland (1989).

The reference grid

In order to provide a means for exact mapping and localization, a reference grid with cells 40 x 40 m was superimposed upon a map of the special area (Fig. 3). The grid was marked by pegs on the mire surface after exact surveying. Positions relative to the reference grid are given by six digits, e.g., 078 116. The third and sixth digit indicate tenth of the cell, thus giving a resolving power of 4 m.

Recognized gradients and scales of investigation

There is a general agreement in the mire literature that three local complex-gradients (cf. Økland & Bendiksen 1985, Økland 1989) are important in the differentiation of boreal mire vegetation (Sjörs 1947, 1948, 1950, Du Rietz 1949, 1954, Malmer 1962a, 1986, Fransson 1972, Horton *et al.* 1979, Vitt & Slack 1984, Økland 1989): (1) the mire expanse-mire margin gradient, (2) the nutrient (ombrotrophic-minerotrophic, poor-rich) gradient, and (3) the gradient in depth to the water table. (4) Malmer (1962a) implicitly suggests a fourth vegetational gradient (coenocline; Whittaker 1960, 1967), separating strongly peat-producing ("progressive") *Sphagnum*-rich vegetation from slightly peat-producing ("regressive") vegetation dominated by hepatics, lichens, or devoid of a bottom layer. The underlying ecological basis for this coenocline is not clear. This gradient has previously been connected with the cyclic regeneration theory (cf. Økland 1989 for further discussions), but there is nothing to prevent its recognition independent of any theory of mire processes. This provisional gradient has been taken into consideration in this study as the fourth gradient. Økland (1989) recognizes five size levels of mire components. In order of decreasing size, there are (1) mire complex, (2) mire synsegments, (3) mire segments, (4) mire features, and (5) mire subfeatures. The four gradients can be classified according to the size levels on which they operate: the mire expanse-mire margin gradient on the mire segment level, the nutrient gradient on the mire segment to mire feature level, and the gradient in depth to the water table and the gradient in peat productivity at the mire subfeature level. Thus two groups of gradients can be recognized according to the scales on which they operate.

Recognition of patterns in vegetation must be based on observations in plots, the size of which must be a compromise between representativity and homogeneity. In this study, two different plots sizes or recording scales have been chosen: 16 m² for *broad-scale patterns* (the mire expanse - mire margin and nutrient gradients) and 0.25 m² for *fine-scale patterns* (all gradients, but particularly addressing the depth to the water table and peat productivity gradients).

Fig. 3. Map of the special area on N. Kisselbergmosen with the reference grid system and the positions of the 800 random samples. Sample plots providing 3-year and 2-year measurements of distance to water level are indicated by large and small dots, respectively.

BROAD-SCALE PATTERNS: SPECIES DISTRIBUTIONS AND ECOLOGICAL CONDITIONS

Methods of hydromorphological mapping

A hydromorphological mapping was done (1) to give a hydromorphological background description of the special area, and (2) as an aid to interpretation of broad-scale vegetational patterns.

The distribution of mire subfeatures and mire features, as well as the limit between mire margin and mire expanse, was mapped in 1982. The three subfeature categories; hummock, lawn, and carpet, were defined according to Sjörs (1948), Malmer (1962a), and Økland (1989). The limit between mire margin and mire expanse was based on the more or less complementary limits of D-group (distributional groups, based on distribution in the special area) 2 and 5 species on one hand, and 3, 6 and 8 on the other (cf. p. 56). Particular attention was put on *Scirpus cespitosus*, *Sphagnum rubellum*, and *S. tenellum* as indicators of the mire expanse, and *Vaccinium vitis-idaea* as an indicator of the mire margin. A map of the topography of the ground water table at 13 May 1982 was also constructed. This map is based on measurements of the position of the water table relative to the bottom layer surface (pp. 21) at 555 points distributed all over the special area. At each point, the absolute level of a marker at the bottom layer surface was established by levelling relative to a fixed point in the mire margin (top of boulder at position 089 015, just at the interface between the steel rod marking the boundary of the Nature Reserve and the boulder surface). The accuracy of the levellings was checked to be ± 5 cm by cross-levelling. The absolute level of the fixed point was set equal to 1200 cm.

Mapping of species distributions in the special area

In 1982, several species apparently responding to the mire expanse-mire margin and nutrient gradients were thoroughly mapped by recording presence/absence in all 16 m² squares of the special area as given by six digit grid references. On the basis of the recorded distributional patterns, all species observed in the special area were subjectively classified to broad-scale distributional groups (D-group). The term zone is used in a geographical meaning, to include those parts of the investigation area, characterized by presence of species of a particular subset of the D-groups.

Hydrological criteria on the mineral soil water limit

The mineral soil water limit concept was introduced by Thunmark (1940, 1942), who gave the following definition: "... the highest level to which the mineral soil water reaches, or is able to influence the site" (Thunmark 1942: 15, translated). Inspection of the curvature of contour lines at maximum water table is the least objectionable way to assess this limit (Malmer 1962a, Ivanov 1981). At maximum water table, the obstacles to surface water flow are minimal (Sjörs 1948, Rycroft *et al.* 1975a, 1975b, Ivanov 1981), and water from the mineral soil will reach the potential limit for lateral transgression on the mire (Malmer 1962a). The map of the topography of the ground water table (cf. Fig. 7) represents the compensation level (cf. p. 22). The curvatures of contour lines at the compensation level and at maximum water table are closely similar (Malmer 1962a, Ivanov 1981), thus

allowing an optimal interpretation of the mineral soil water limit from the map.

Analysis of chemical and physical properties of peat along transects

The analysis of chemical and physical properties of peat was done (1) to investigate whether the zones defined by broad-scale patterns of plant distributions could be referred to a nutrient gradient as expressed by properties of the peat, and (2) to characterize the mineral soil water limit by properties of the peat.

Sampling. Five transects (broad belts) at right angles to zonal limits were demarcated in the field. Sampling of peat was restricted to mud-bottoms, with sampling points spaced 5 to 25 m along the transects (Fig. 4), for the following reasons: (1) The seasonal variability of constituents in peat is considerably lower than in mire water (Malmer 1962b, Boatman *et al.* 1975). (2) Restriction to one relative level reduces effects of the strong vertical variation in peat properties (Malmer 1962b, Damman 1978, 1986, Damman & Dowhan 1981, Clymo 1983) to a minimum. (3) Mud-bottoms have virtually no vegetation, thus reducing the effects of temporal variation in peat properties caused by vegetation processes (cf. Damman 1978, 1986). Volumetric sampling of peat from 5-15 cm below the peat surface was effected at 15 October 1981 by a 0.772 dm³ steel corer with a lower cutting edge. After superfluous water had run off, the samples were transferred to polyethylene bags and stored at 3-6 °C until analysis.

Choice of parameters. As the purpose of this part of the study was to approach the chemical and physical basis of broad-scale patterns of distribution, analysis was restricted to inclusion of parameters that had shown to correlate well with the nutrient gradient in previous studies (Malmer 1962a, Sonesson 1970b, Pakarinen & Tolonen 1977).

pH was determined by a glass electrode inserted directly into the fresh peat. Ten measurements were made for each sample, and their mean calculated. The within-sample range of values rarely exceeded 0.20 pH-units.

Ash content. Ca. 50 g fresh peat were dried at 110°C to constant weight (at least 48 hours). 1 g dry peat was treated in a muffle furnace at 550°C for 16 hours before calculation of ash content.

Exchangeable cations. 25 g fresh peat were extracted with 0.150 dm³ 1 M NH₄Ac (pH adjusted to 7.0), shaken for two hours, and filtered. Exchangeable H⁺ was calculated after measurement of pH in filtrates and comparison with smoothened curves for titration of the NH₄Ac solution with 0.1 M HCl (Brown 1943, Malmer & Sjörs 1955). Exchangeable Na⁺, K⁺, Ca²⁺, and Mg²⁺ in the filtrates were measured by a Varian Techtron atomic adsorption spectrophotometer at Institute of Biology, Dept. of Marine Chemistry, Univ. of Oslo. Concentrations of exchangeable cations are given as mmol (dm³ fresh peat)⁻¹.

Base saturation was calculated as percentage metallic cations out of the total amount of extracted cations.

Statistical analysis

All chemical and physical parameters approached normal distributions, as assessed visually. This was due to the small among-sample variation along the nutrient gradient. Pearson's product-moment correlation coefficients (Sokal & Rohlf 1981) were calculated for all pairs of parameters. Their significance probabilities are in accordance with Owen (1962). One-sided T-tests were applied to assess the significance of differences in each parameter between zones.

Fig. 4. Positions of transects T1-T5 for sampling of mud-bottom peat.

PCA ordination

PCA ordination (e.g., Orlóci 1978, ter Braak & Prentice 1988) was applied to the matrix of 8 chemical or physical parameters in 74 peat samples. The CANOCO program (ter Braak 1987) was run on a correlation matrix, with euclidean distance biplot scaling of axes. Pearson's product-moment correlation coefficients between sample scores and parameter values, and between sample scores and zone, were calculated for the first four PCA axes.

FINE-SCALE PATTERNS: SPECIES DISTRIBUTIONS AND ECOLOGICAL CONDITIONS

The random sampling design and the R data set

To avoid subjective bias, random sampling design (cf. Greig-Smith 1964) was used for the study of fine-scale patterns. A total of 800 sample plots, each 0.25 m², were distributed on the special area (Fig. 3) by taking six-digit sequences of random numbers in Owen (1962) as positions relative to the reference grid. These positions were taken as the SW corners of the sample plots. Thus the minimum spacing between sample plots was 4 m. The set of 800 random sample plots analyzed with respect to vegetational composition in 1981 constitute the R data set.

The subjective sampling design and the S data set

In order to assess the relative merits of the random sampling design and traditional Fennoscandian subjective sampling procedures (Du Rietz 1921, 1932, Nordhagen 1943; for mire vegetation see Sjörs 1948, Persson 1961, Malmer 1962a, Svensson 1965, Sonesson 1970a, Fransson 1972), a second data set was sampled independent of the R set. According to Fennoscandian mire tradition, a system for classification of vegetation into types (site-types, cf. p. 24) was constructed prior to sampling. Series of 5 sample plots, each 0.25 m² and classified to the same site-type, were placed within stands no more than 400 m². Sample plots were selected to fulfil two criteria (Sjörs 1948, Fransson 1972): (1) as high within-sample plot homogeneity as possible, and (2) as high within-sample plot series variation as possible (without exceeding the limits of the site-type). In particular, it was attempted at representing as many of the species occurring in the site-type in this stand as possible. A sample plot was considered homogeneous if all of it fell within one site-type. In practice, the demands for homogeneity were weakened so as to allow inclusion of sample plots with 95 percent of their area within one site-type. A total of 153 stands with 765 sample plots make up the S data set. The vegetation of these plots was analyzed in 1982.

Quantification of species amounts

For all sample plots of the R and S data sets, percentage cover of all species except trees and larger shrubs (> 80 cm) was recorded. The following scale was used: 1, 2, 3, 5, 7, 10, 12, 15, 17, 20, 22, 25, 30, 35, ..., 100. For sample plots with individuals of *Betula*

pubescens, *Picea abies*, and *Pinus sylvestris* higher than 80 cm, cover was recorded in a square 2 x 2 m plot with the 0.25 m plot in the centre. This was done (1) to increase the accuracy of cover estimation, and (2) because large species influence the vegetation over a larger area by their more extensive rooting systems and by shading.

Recording and estimation of fluctuations in depth to the water table

Depth from the surface of the bottom layer to the water table was recorded during the ice-free periods of 1980, 1981, and 1982.

Climatic background information. As the weather is of fundamental importance for water table fluctuations in mires (Malmer 1962a, Johansson 1974, Wildi 1977, Ivanov 1981), climatic data for the full period of measurement were collected.

Temperature. Daily mean temperatures from the meteorological station 0284 Høland-Kollerud some 20 km off N. Kisselbergmosen were used (Norske Meteorologiske Institutt, unpubl.). Assuming a vertical temperature gradient of 0.4-0.6°C per 100 m (Laaksonen 1976), these figures represent a mean overestimation of temperatures at N. Kisselbergmosen amounting to 0.8°C.

Precipitation. Total daily precipitation on N. Kisselbergmosen was recorded by a rain gauge, Feuss type 94, in position 11 10 on the mire expanse. The accuracy of recordings from such a free-standing gauge with small diameter, as well as the comparability with standard meteorological measurements, can be questioned. Records from Høland-Kollerud (The Norwegian Meteorological Institute, unpubl.) have also been taken into account.

Field methods. All of the 800 sample plots of the R data set had a pit, 7 cm across, for recording water table. Pits were localized just outside the sample plots, in places representative for the vertical position of the plots. A small marker was used to indicate the level of the bottom layer surface. The position of this marker was adjusted each spring to avoid effects of differential vertical growth between sample plots.

Sample plots violating one of the following four criteria were omitted from water table measurements: (1) Cover of the bottom layer less than 25 %. (2) Representative for one vertical level; not spanning a vertical range larger than 10 cm. (3) Accessible (applies to two sample plots in the erosion area). (4) Peat depth sufficient to allow a free water table also during dry periods.

A total of 699 sample plots satisfying these criteria were included in further recording. Three different recording periods were used (cf. Fig. 3). (1) *Three years* ($n = 79$). Position of the water table measured each eighth day (on average) during the 1980 growing season (from 1 May 1980 to 22 October 1980), each tenth day during the 1981 growing season (from 13 April 1981 to 14 November 1981), and each tenth day during the 1982 growing season (from 29 April 1982 to 16 November 1982). (2) *Two years* ($n = 202$). As (1), but no measurements in 1982. (3) *Two occasions* ($n = 699$). Only measurements on 13 May 1982 and 14 July 1982. Measurements were always completed within three hours (at 13 May 1982 and 14 July 1982 within 15 hours). When possible, readings were made after at least 24 hours without precipitation.

Cumulative probability distribution functions. For the 79 sample plots provided with three-year measurements, depth to the water table was treated as a function of time, $w_k(t)$. Change in depth to the water table between measurements was assumed to be linear. For each plot and year, duration of water cover at vertical levels spaced 2 cm, was calculated as the number of days with a water table above the specified level. Furthermore, the cumulative probability distribution function for each plot k and year y , was calculated as

$$P_{ky}(w_x) = \text{Prob}(w_k(t) > w_x)$$

Positive w_x values indicate water tables *below* the bottom layer surface. Average cumulative probability distribution functions $P_3(w)$, were prepared for each sample plot k as

$$P_{k3}(w_x) = 1/3 \sum_{y=1980}^{1982} P_{ky}(w_x).$$

The following characteristic levels were identified on all average cumulative probability distribution functions: (1) $P_{100,3}$ - minimum water level, (2) $P_{90,3}$ - lower decile, (3) $P_{50,3}$ - median water level, (4) $P_{10,3}$ - upper decile, (5) $P_{0,3}$ - maximum water level, (6) K_3 - compensation level (Malmer 1962a), i.e. the most frequently encountered water level, the inflexion points of the average cumulative probability distribution functions, (7) R_3 - range ($P_{0,3} - P_{100,3}$).

Correspondingly, two-year average cumulative probability distribution functions, $P_{k2}(w_x)$, were prepared, and characteristic levels $P_{100,2}$, $P_{90,2}$, $P_{50,2}$, $P_{10,2}$, $P_{0,2}$, K_2 , and R_2 identified.

Correlation coefficients between characteristic levels. For the 79 sample plots providing three-year measurements, Pearson's product-moment correlation coefficients between characteristic levels (1) - (7) were calculated.

Estimation of three-year characteristic levels. In order to take full advantage of the R data set, characteristic levels of three-year average cumulative probability distribution functions were estimated from two-year characteristic levels, and two observations. The regularity of the shapes of average cumulative probability distribution functions made such estimation possible (cf. Wildi 1977). A comparison of measurements at the two occasions with the average cumulative probability distribution functions for the 79 sample plots, showed the 13 May 1982 observations to have an average characteristic level of $P_{50,3}$ (range $P_{14,3} - P_{61,3}$), and the 14 July 1982 observations to average $P_{90,3}$ (range $P_{85,3} - P_{93,3}$). Several possible estimators for three year characteristic levels were tested for expectation and variance by use of the 79 sample plots providing three-year measurements. The sets of unbiased estimators with the lowest variances, based on two-years, and two observations, respectively, are denoted P^* and P^* .

Modelling climatic control of fluctuations in depth to the water table. The mean depth to the water table, V_i , at each time measurements were made (a total of 58 times), was calculated for the 79 sample plots providing three-year measurements. Missing observations due to ice in spring were corrected for by weighting by mean median depth to water table for the sample plots included. Change in mean depth to the water table from time i to time $(i + 1)$ was denoted Δ_i .

Daily change in this period was denoted Δ_i/d .

Simple modelling of the effects of different climatic (and other) parameters on fluctuations of the water table, was effected by forward selection multiple regression (Sokal & Rohlf 1981) by the SPSS procedure NEW REGRESSION (Nie *et al.* 1975, Hull & Nie 1981). Hydrological models were not taken into account. Two separate runs were made: (1) with Δ_i as the dependent variable, and (2) with Δ_i/d as the dependent variable. The following independent variables were included (asterisk denotes a variable that is included in run (2) as daily mean): (1*) P_i - precipitation on Northern Kisselbergmosen from time i to time $(i + 1)$, (2) POS_i - average characteristic level at time i , (3*) WN_i - water need in the period from i to $(i + 1)$, calculated according to V. Malmström (1969) by use of daily mean temperature data from the meteorological station Høland-Kollerud, corrected for

differences in altitude according to Laaksonen (1976), (4) T_i - mean temperature from time i to time $(i + 1)$, data as above, (5) $P2_i$ - precipitation i on Northern Kisselbergmosen during the last 48 hours before measurement at time $(i + 1)$.

Species responses to the gradient in depth to the water table

The 699 sample plots provided with measurements of the distance to the water level, were grouped into intervals according to median distance to water level, $P_{50,3}$ or estimates of this characteristic level, $P^*_{50,3}$ or $P^{**}_{50,3}$. Each interval spanned 2 cm vertically, and was denoted by the lowermost level included (interval 2 means $P_{50,3} = 1-2$). For each species i and interval j , the importance I_{ij} was calculated according to the formula

$$I_{ij} = \frac{c_{ij} \ln(1+d_{ij})}{\ln 101}$$

where c_{ij} is the constancy of species i in interval j , and d_{ij} is the mean percentage cover. Only intervals containing ten or more samples were considered. Intervals 28 and 30 were lumped to satisfy this criterion, and was denoted interval 29.

CLASSIFICATION OF VEGETATION

Terminology and basic assumptions

Terminology of gradients follows Whittaker (1967) (also see Økland & Bendiksen 1985). Single environmental gradients, changing more or less parallel in space, form *complex-gradients* (Whittaker 1956). The directions of variation (Sjörs 1947, 1948) in vegetation are termed *coenoclines* (Whittaker 1960). Together coenoclines and the underlying complex-gradients constitute *ecoclines* (Whittaker 1960).

The nature of vegetational variation along continuous complex-gradients has been strongly debated (see, for instance, general reviews by Whittaker (1962) and McIntosh (1967), and the review of Fennoscandian forest and alpine vegetation by Økland & Bendiksen (1985)). In the mire part of vegetation science, this debate calmed down early. Since the theoretical work of Tuomikoski (1942), the continuous variation of mire vegetation along continuous complex-gradients has been repeatedly emphasized (e.g., Sjörs 1948, Malmer 1962a, Fransson 1972, Horton *et al.* 1979). Furthermore, the major ecoclines have been considered as well-known (cf. p. 15). Vegetational continuum, the acceptance of three ecoclines as the most important (p. 15), and the inclusion of a fourth coenocline representing peat productivity (p. 15) are the basic assumptions of classification in this work.

The direct gradient approach

Principles. The direct gradient approach to classification (Økland & Bendiksen 1985, also see Whittaker 1967, 1978) is well-suited for continuously varying vegetation where the

ecoclines are considered as known. The task then reduces to a description of the vegetation along the recognized coenoclines. Furthermore, this multidimensional pattern has to be converted into discrete units by dividing the gradient axes, thus providing a reticulate, non-hierarchic classification (Tuomikoski 1942, Webb 1954).

Direct gradient approaches in studies of Fennoscandian mire vegetation. The pioneering thoughts of Tuomikoski (1942) actually introduced the direct gradient approach to classification to Fennoscandian mire ecology. His ideas of a multidimensional network of continuous variation, and non-hierarchic systems based on division of gradients were followed by several authors. Swedish mire scientists combined the traditional unit of vegetation, the association (Du Rietz 1936, Nordhagen 1943), with Tuomikoski's approach by defining associations each corresponding to a specified interval along each of the gradients considered (e.g., Sjörs 1947, 1948, Persson 1961, Malmer 1962a, Svensson 1965, Sonesson 1970a, Fransson 1972). The Finnish tradition of classification of mire vegetation pioneered by Cajander (1913) has also shown some tendencies to more clear-cut representation of gradient relationships (cf. Ruuhijärvi 1960, Euroala 1962).

The direct gradient approach to classification of mire vegetation on N. Kisselbergmosen. Four main gradients (cf. p. 15) were considered for the study of species distributions. Species responses to these four gradients and the analysis of correlated environmental gradients, was taken as the bases of division of the gradient axes. This division thus was based on local criteria, and strictly applicable to the investigation area only.

The units distinguished comprised one specified interval along each of the four gradients, and represented a joint classification of vegetation and the underlying complex-gradients. As the units represented a division of ecoclines, they were termed *site-types* (Cajander 1926, Kalela 1954, Økland & Bendiksen 1985). All site-types corresponding to one zone along the nutrient gradient make up a *zonation*, while all site-types corresponding to one step along the gradient in depth to the water table constitute a *series* (cf. Malmer 1962a). Separate series and zonations were considered for mire expanse and mire margin site-types. The series of mire expanse site-types were divided into *subseries* along the peat productivity gradient.

Abbreviations referring to the classification system are explained on pp. 85-86, cf. also Fig. 66.

Description of site-types: material and presentation

Description of the site-types was based upon a material consisting of the S-data set (765 sample plots in 153 stands) and the 654 sample plots of the R data set homogeneous with respect to site type; a total of 1419 sample plots.

One vegetation table was compiled for each site-type. Separate columns are shown for each stand of the S-set, for all R-set sample plots originating from the same zone, and for the whole site-type. For each column and species, constancy percentage (Dahl 1957, Trass & Malmer 1978) and mean percentage cover were given. Survey tables were compiled for each series.

Vegetation complexes

An attempt was made to differentiate vegetation complexes in the E1 and E2 zones of the special area in accordance with Osvald (1923). As pointed out by Malmer (1962a), Osvald's

bog complexes are relevant for sites with slight influence by fen water (corresponding to the E2 zone), too. The frequency of sample plots of the R data set in each site-type in each area was taken as the basis for discerning such complexes. The seven complex types discerned by Osvald (1923) relevant to the special area are: (1) *The regeneration complex*. High importance of the PL and PH site-types, RH present, hollows frequently with pools. (2) *The pool complex*. Higher areal importance of pools. (3) *The marginal complex*. Hummocks dominating, PL occurring with low areal importance. (4) *The heath-like marginal complex*. Hummocks totally dominating. High importance of RH site-types. (5) *The stagnation complex*. High importance of PH, RH, and RC site-types. Lawns unimportant. (6) *The Rhynchospora-rich regeneration complex*. High importance of RL (dominated by *Sphagnum tenellum*) and PH, partly also RH and RC site-types. (7) *The erosion complex*. Characterized by severe erosion.

Transitions between site-types and inference of successional relationships

Transitions between site-types were recorded in the field. The inference of successional relationships from observed transitions was based on (1) stratigraphy of the upper few cm of the peat, (2) observations of horizontal transgression of the vegetation on either side of a vegetational transition, and (3) observations of the vitality of species of contrasting ecology growing together.

NOMENCLATURE AND TAXONOMIC NOTES

The nomenclature of vascular plants follows Flora Europaea (Tutin *et al.* 1964, 1968, 1972, 1976, 1980, Moore 1982). *Empetrum nigrum* L. thus includes *E. hermaphroditum* Hagerup. Only dioecious flowers have been observed on *Empetrum* in the investigation area, indicating that all material probably belongs to *E. nigrum* L. ssp. *nigrum*. *Vaccinium oxycoccos* coll. includes *V. microcarpum* (Rupr.) Schmalh. and *V. oxycoccos* (Hill) A. Gray. Mosses and *Sphagnum* L. follow Corley *et al.* (1981), so that *Polytrichum strictum* Brid. is recognized at specific level. *Pohlia sphagnicola* (B., S. & G.) Broth. is not accepted, and reduced to synonymy with *P. nutans* (Hedw.) Lindb. (cf. Nyholm 1958).

Hepatics follow Grolle (1976), except that the orthography *Calypogeja* is used, in accordance with Stotler (1982). Macrolichens follow Krog *et al.* (1980), except for *Cladonia pyxidata* (L.) Hoffm. which is used in a collective sense, also including the *C. chlorophaea* and *C. grayi* aggregates. *Icmadophila ericetorum* (L.) Zahlbr. and *Ochrolechia frigida* (Sw.) Lynge follow Poelt (1969), *Micarea turfosa* (Massal.) Du Rietz follows Poelt & Vezda (1977).

RESULTS

BROAD-SCALE PATTERNS: SPECIES DISTRIBUTIONS AND ECOLOGICAL CONDITIONS

Hydromorphology

The description of the hydromorphology of the special area is based on the map of microfeatures, pools, and marginal forest segments (Fig. 5), an aerial photo (Fig. 6), and the map showing the topography of the ground water table (Fig. 7).

To the east (pos. 12-15 07-12), there was a typical multilaterally sloping kermi raised bog synsegment. The mire features (kermis and lawn-dominated hollows) showed distinct orientation around the highest point. The topography of the ground water table (Fig. 7) showed that the larger part of this synsegment received ombrogenous water only. The hummock level dominated towards the periphery of the open, slightly domed bog plain. To the south and east, a more or less continuous marginal forest segment was present, separated from the mineral soil by a narrow lagg zone (1-5 m). The lagg was replaced by floating carpets along the margin of the tarn Kisselbergmosetjern. A steep edge, 0.5-1.2 m high, separated the marginal forests from the floating carpets. Runoff from the lake was through a ditch, indicating that the steep edge might owe its origin to an artificial lowering of the water table, probably more than 25 years ago. This multilaterally sloping kermi raised bog synsegment fell steeply off towards the north.

From the border onto mineral soil in the S (pos. 08 01) and SW (pos. 07 02-04) two soligenous fen soaks spread out on the mire. Farthest SW they were separated by a small, hummock-dominated segment on an indistinct watershed, but at pos. 09-10 05-07 they were only indistinctly separated. The soaks partly drained into Kisselbergmosetjern, partly ran northwards to lake Svartekulpa as a narrow, lawn-dominated depression (pos. 13-14 16-17), and partly spread diffusely out on the mire at pos. 09-10 09-19 (visible as a marked concavity on the 920 and 930 contours in Fig. 7).

A broad soligenous fen soak from the mineral soil in SW (pos. 05 06) ran the length of the western margin of the mire as a 30-80 m broad soak, dominated by carpets and lawns. At pos. 05-06 08-12, the soak spread diffusely out on the mire. A hummock-dominated, partly forested segment occurred at pos. 05 07 between the fen soak and the lagg.

In the wide, open central part of the special area, kermis and hollows were distinctly orientated perpendicular to the slope. Farthest south, between the western fen soak and the two southern soaks, this central part had the appearance of a unilaterally sloping kermi raised bog. A distinct watershed ran the length of the bog plain segment from the border onto mineral soil (pos. 06 05) to pos. 08 10. This segment was distinctly domed, dominated by hummocks farthest SW, and with an increasing areal importance of lawn-dominated hollows towards NE. Where the western fen soak spread out, the surface immediately lost its domed profile, wet and large hollows abounded, and many hollow-pools occurred. North of pos. 05-07 14 the area was strongly eroded, and the segment had assumed the character of a unilaterally sloping plane transitional mire. The orientation of mire features was less distinct as the erosion had affected all microfeatures. Extensive mud-bottoms were connected by diffuse, confluent water-tracks, ending in deep erosional gullies and eventually forming brooklets. This area had a large catchment (cf. Fig. 7). Domed, hummock-dominated and,

Fig. 5. Map of N. Kisselbergmosen showing distribution of mire features, mire margin segments, and pools. Based on field investigations 1982.

Fig. 6. N. Kisselbergmosen. Aerial photo by Fjellanger Widerøe A/S, published with permission.

Fig. 7. Map of N. Kisselbergmosen showing the topography of the ground water table 1982 05 13. Contour interval 10 cm. Additional contours (broken lines) with interval 5 cm. Thick lines indicate 50 cm intervals. Levels are relative to a fixed point in the mire margin (set to 1200 cm).

in part, sparsely forested areas occurred SW of the Svartekulpa tarn.

Fen soaks spread from the border onto mineral soil at pos. 07 18 eastwards, in the direction of Svartekulpa, and northwards. Forested, often slightly domed miniature segments occurred several places between the 1-5 m broad, relatively dry lagg and the open mire expanse. The special area may be divided into seven catchment areas: (1) the fen soaks in S and SE and the southern part of the multilaterally sloping kermi raised bog synsegment; draining into Kisselbergmosetjern, (2) the fen soak running along the western margin; draining out of the mire at pos. 01 15, (3) the area N of the small forested area at pos. 03 13; draining into a small tarn NW of pos. 02 19, (4) the central parts of the special area; draining through the brooklets at pos 05 19, (5) the northern half of the multilaterally sloping kermi raised bog synsegment, the fen soak S of Svartekulpa, and adjacent parts of the mire to the west; draining into Svartekulpa from S, (6) the diffuse fen soak spreading out on the mire at pos. 09-10 08-09 (indistinctly separated from (4) and (5)), including the areas further north and the fen soak from pos. 07 18; draining into Svartekulpa from W, and (7) the northernmost parts of the mire, pos. 07-08 20-21; draining out of the mire farthest north.

Two or three synsegments may be separated in the special area, the multilaterally sloping kermi raised bog and the large, central synsegment including transitions from unilaterally sloping kermi raised bog to unilaterally sloping plane transitional mire (could be considered as two synsegments).

Fig. 7 may be used to demonstrate several issues discussed by Økland (1989): (1) The kermi raised bog synsegments developed on the watersheds; the only sites sufficiently sheltered from strong influence of soligenous water supply. A levelled transect across the kermi raised bog synsegments shows the surface to be distinctly domed. (2) Forested bog segments developed where the slope was high (and the water table consequently low for most of the growing-season), or where the catchment area was small (on watersheds). (3) Plane transitional mires developed where the catchment was large, but sheltered from the direct influence of distinct fen soaks and large amounts of soligenous water. A levelled transect across the unilaterally sloping plane transitional mire synsegment shows the plane or slightly concave shape of the surface. The eroded area apparently had distinct kermis and hollows orientated perpendicular to the slope before the onset of erosion. Remnants of kermis were visible as a regular arrangement of isolated hummocks. (4) Hollow-pools apparently formed in areas with low slope and ample water supply. Thus hollows were absent from watersheds and occurred abundantly in nearby level sites just below a relatively steep slope.

Species distributions in the special area

Nine broad-scale distributional groups were recognized. Tab. 1 gives a survey of the affiliation of all recognized taxa.

D-group 1. Species classified to this group occurred all over the special area; in the forested marginal areas and the central, open parts. There was some within-group variation, from species with slight preference for the peripheral, forested parts (denoted *) to those with distribution skewed towards the open, central parts (denoted §). These extremes were transitory to D-groups 3 and 2, respectively. The following 20 species were assigned to this group:

§*Calluna vulgaris*
Empetrum nigrum

Tab. 1. Species occurring in the special area and their abundance in each of the zones. E - mire expanse, M - mire margin. 1, 2, and 3 - zones along the supposed nutrient gradient. D - distributional group No. O - a + indicate presence in at least one of the 800 random samples. S - a + indicate presence in at least one of the 765 subjective samples. Distributional groups as explained in the text. Abundances: + - occasional (one or a few records), 1 - rare, 2 - frequent, 3 - dominant or important.

Nr. Species name	O	S	E1	E2	E3	M1	M2	M3	U	Nr. Species name	O	S	E1	E2	E3	M1	M2	M3	U	
001 <i>Betula pubescens</i> Ehrh.	++		+	+	+	1	2	2	3	003 <i>Pinus sylvestris</i> L.	++		1	1	1	3	3	2	3(-1)	
002 <i>Picea abies</i> (L.) Karsten	++		+	+	+	1	1	1	3	012 <i>Salix aurita</i> L.	++						1	2	6	
004 <i>Andromeda polifolia</i> L.	+	+	3	3	3	1	1	1	2	013 <i>S. repens</i> L.	-	+					+	+	9	
005 <i>Betula nana</i> L.	-	+	+	+	+	1	1	1	3	014 <i>Sorbus aucuparia</i> L.	-	+					+	+	-	
- <i>B. nana x pubescens</i>	-	+	+	+	+				-	015 <i>Vaccinium microcarpum</i>									-	
006 <i>Calluna vulgaris</i> (L.) Hull	++		3	3	2	2	2	2	1	(Rupr.) Schmalh.	++		2	1	1	+	+	+	2	
007 <i>Empetrum nigrum</i> L.	++		2	2	2	2	2	2	1	016 <i>V. myrtillus</i> L.	++		+	+	+	3	3	2	3	
008 <i>Erica tetralix</i> L.	++			3	3				5	017 <i>V. oxycoccus</i> (Hill) A. Gray	++		3	3	3	2	2	2	1	
009 <i>Frangula alnus</i> Miller	++								8	018 <i>V. uliginosum</i> L.	++		+	+	+	3	3	3	1	
010 <i>Juniperus communis</i> L.	-	+							9	019 <i>V. vitis-idaea</i> L.	++					3	3	2	3	
011 <i>Myrica gale</i> L.	++			3					7	025 <i>Orthilia secunda</i> (L.) House	-	+							8	
020 <i>Dactylorhiza maculata</i> (L.) Soó	-	+							8	026 <i>Potentilla erecta</i> (L.) Rauschel	-	+					1		8	
021 <i>Oxera anglica</i> Hudson	++		2	2	2				2	027 <i>Rubus chamaemorus</i> L.	++		3	3	2	3	3	2	1	
022 <i>D. anglica x rotundifolia</i>	++		1	1	1				2	028 <i>Trientalis europaea</i> L.	-	+							8	
023 <i>D. rotundifolia</i> L.	++		3	3	3	1	+	+	2(-1)	Trin.	-	+						+	9	
024 <i>Melampyrum pratense</i> L.	++					1	2		6	037 <i>Eriophorum angustifolium</i>	++			2			2		7	
029 <i>Carex curta</i> Good.	+	+							8	Honckeney	++								1	
030 <i>C. echinata</i> Murray	-	+							2	038 <i>E. vaginatum</i> L.	++			3	3	3	3	2	1	
031 <i>C. globularis</i> L.	++						3	2	6	- <i>Juncus filiformis</i> L.	-	+							-	
032 <i>C. lasiocarpa</i> Ehrh.	++			2				1	7	039 <i>Molinia caerulea</i> (L.) Moench	++							1	8	
033 <i>C. limosa</i> L.	++			2	2				5	040 <i>Phragmites australis</i> Steudel	-	+		1				+	7	
- <i>C. magellanica</i> Lam.	-	+							+	041 <i>Rhynchospora alba</i> (L.) Vahl	++			3	3	2			2	
- <i>C. nigra</i> (L.) Reichard	-	+							6	042 <i>Scheuchzeria palustris</i> L.	++				2	2			5	
034 <i>C. pauciflora</i> Lightf.	++			2	2				5(-4)	043 <i>Scirpus cespitosus</i> L.	++		3	3	3				2	
035 <i>C. rostrata</i> Stokes	++				3				7	055 <i>D. uncinatus</i> (Hedw.) Warnst.	-	+						+	-	
036 <i>Deschampsia flexuosa</i> (L.) Trin.	-	+							+	056 <i>Hylocomium splendens</i> (Hedw.) B. S. & G.	++						+	+	3	
044 <i>Aulacomnium palustre</i> (Hedw.) Schwaegr.	++		1	1	2	2	2	2	1	057 <i>Plagiothecium laetum</i> B. S. & G.	++			+	+	+			-	
- <i>Brachythecium reflexum</i> (Stärke) B. S. & G.	-	+							+	058 <i>Pleurozium schreberi</i> (Brid.) Mitt.	++		1	1	+	2	2	+	1(-3)	
045 <i>Calliergon stramineum</i> (Brid.) Kindb.	++							2	7	059 <i>Pohlia nutans</i> (Hedw.) Lindb.	++		1	1	1	2	1	1	1	
046 <i>Ceratodon purpureus</i> (Hedw.) Brid.	++								-	060 <i>Polytrichum commune</i> Hedw.	-	+					1	1	6	
047 <i>Dicranella cerviculata</i> (Hedw.) Schimp.	-	+		1					5	061 <i>Polytrichum strictum</i> Brid.	++		1	1	1	2	2	1	1	
048 <i>Dicranum affine</i> Funck	++		1	1	+				2	- <i>Ptilium crista-castrensis</i> (Hedw.) de not.	-	+				+	+	-	-	
049 <i>D. ruscocens</i> Sm.	++			+	+				-	- <i>Plachnum ampullaceum</i> Hedw.	-	+	+	+	+	+	+	-	-	
050 <i>D. teloneum</i> Kindb.	++			1	1				2(-1)	- <i>S. luteum</i>	-	+					+	+	-	
051 <i>D. majus</i> Sm.	++			+	+				+	- <i>S. rubrum</i>	-	+	+	+	+	+	+	+	-	
052 <i>D. polysetum</i> Sw.	++		1	+	+		1	+	1	- <i>S. sphaericum</i> Hedw.	-	+	+	+	+	+	+	+	-	
053 <i>D. scoparium</i> Hedw.	++		1	+	+	1	1	+	1	062 <i>Tetraphis pellucida</i> Hedw.	-	+							-	
054 <i>Drepanocladus fluitans</i> (Hedw.) Warnst.	++			+	+				4	070 <i>S. girgensohnii</i> Russ.	-	+						+	8	
063 <i>Sparganium angustifolium</i> (Russ.) C. Jens.	++		+	+	+	2	2	3	3	071 <i>S. lindbergii</i>	++			1	+				+	5
064 <i>S. balticum</i> (Russ.) C. Jens.	++		3	3	3				2	072 <i>S. magellanicum</i> Brid.	++		2	3	3	3	3	3	1	1
065 <i>S. capillifolium</i> (Ehrh.) Hedw.	++		+	+	+	2	2	1	3	073 <i>S. majus</i> (Russow) C. Jens.	++			2	3				5	
- <i>S. centrale</i> C. Jens.	++								8	074 <i>S. molle</i> Sull.	-	+		1	+				5	
066 <i>S. compactum</i> DC.	++			2	1				8	075 <i>S. papillosum</i> Lindb.	++			2	3				+	5
067 <i>S. cuspidatum</i> Hoffm.	++		3	3	2				5	076 <i>S. rubellum</i> Wils.	++		3	3	3	1	+	+	2	
068 <i>S. tallax</i> (Klinggr.) Klinggr.	++				1				2	077 <i>S. rubellum</i> Wils., pale form	-	+	1	1					2	
069 <i>S. ruscum</i> (Schimp.) Klinggr.	++		3	3	2	2	2	1	1	078 <i>S. russowii</i> Warnst.	++						2	2	6	
080 <i>Barbilophozia attenuata</i> (Mart.) Loeske	++								-	079 <i>S. tenellum</i> (Brid.) Bory	++		3	3	3				+	2
081 <i>Bazzania trilobata</i> (L.) S. Gray	-	+		+	+				-	088 <i>Cladodiella fluitans</i> (Nees) Jørg.	++		3	3	2					2
082 <i>Calypogeja integristipula</i> Stepp.	+	+							-	089 <i>Gymnocolea inflata</i> (Huds.) Dum.	++		2	2	2					2
083 <i>C. muellerana</i> (Schiffn.) K. Mull.	-	+							-	090 <i>Kurzia pauciflora</i> (Dicks.) Grolle	++		2	2	2	+	+	+	2	
084 <i>C. neesiana</i> (Mass. & Carest.) K. Mull.	++		1	1	+	2	1	+	1	091 <i>Lophozia ventricosa</i> (Dicks.) Dum.	++		+	+			+	+	-	
085 <i>C. sphagnicola</i> (H. Arn. & J. Perss.) Warnst. & Loeske	++		2	2	2	1	+	+	2(-1)	092 <i>Mylia anomala</i> (Hook.) S. Gray	++		2	2	2	1	+	+	2	
086 <i>Cephalozia</i> (Dum.) Dum. spp.	++		2	2	2	2	1	1	1	093 <i>Odontoschisma sphagni</i> (Dicks.) Dum.	++		+	+	+				2	
087 <i>Cephalozia</i> (Spruce) Schiffn. spp.	++		1	1	+	+			2(-1)	094 <i>Ptilidium ciliare</i> (L.) Hampe	++		+	+	+	+	+	+	2	
096 <i>Cetraria gelisei</i> (Schaer.) Nyl.	-	+	1	1					2	095 <i>Riccardia latifrons</i> (Lindb.) Lindb.	++		1	1					2	
097 <i>C. ericetorum</i> Opiz.	++		1	1	+				2	113 <i>C. aurcata</i> (Fuds.) Schrad.	-	+							3	
098 <i>C. islanica</i> (L.) Ach.	++		1	1	+				2	114 <i>C. gracilis</i> (L.) Willd.	++		+	+					-	
099 <i>C. pinastri</i> (Scop.) S. F. Gray	-	+		+	+				-	115 <i>C. mitis</i> Sandst.	++		1	1					2	
100 <i>Cladonia arbuscula</i> (Wallr.) Rabenh.	++		2	2	+				2	116 <i>C. pleurota</i> (Flörke) Schaer.	++		+	1					2	
101 <i>C. bacillaris</i> (Ach.) Nyl.	++			+	+				2	117 <i>C. pyxidata</i> (L.) Hoffm. coll.	++		2	2	1	1	1	1	1	
102 <i>C. bellioflora</i> (Ach.) Schaer.	-	+							-	118 <i>C. rangiferina</i> (L.) Wigg.	++		3	3	1	1	1	+	1	
103 <i>C. carneola</i> (Fr.) Fr.	++		+	+	+				-	119 <i>C. squamosa</i> (Scop.) Hoffm.	++		3	3	1	+			2	
104 <i>C. canotae</i> (Ach.) Schear.	++			+	+				-	120 <i>C. stellaris</i> (Opiz.) Pouz. & Vězda	++		2	2	1				2	
105 <i>C. coniocraea</i> (Flörke) Spreng.	++		+	+	+				1	121 <i>C. subfurcata</i> (Nyl.) Arn.	-	+	+	+					2	
106 <i>C. cornuta</i> (L.) Hoffm.	-	+							-	122 <i>C. sulphurina</i> (Michx.) Fr.	++		1	1			+	+	2	
107 <i>C. crispata</i> (Ach.) Flot.	-	+							-	123 <i>C. uncialis</i> (L.) Wigg.	++		1	1					2	
108 <i>C. cyanipes</i> (Sommerf.) Nyl.	++			1	1				2	124 <i>Hypogymnia physodes</i> (L.) Nyl.	++		+	+					-	
109 <i>C. deformis</i> auct non Hoffm.	-	+							-	125 <i>Imadophila ericetorum</i> (L.) Du Rietz	-	+	1	1					2	
110 <i>C. digitata</i> (L.) Hoffm.	++			+	+				-	126 <i>Micarea turfosa</i> (Massal.) Rietz	-	+		+					-	
111 <i>C. rimbiata</i> (L.) Fr.	++		1	1	+	2	1	+	1	127 <i>Ochrolechia frigida</i> (Sw.) Lynge	++		1	1					2	
112 <i>C. floerkeana</i> (Fr.) Flörke	++		+	+	+				2											

§ *Vaccinium oxycoccos*
Rubus chamaemorus
Eriophorum vaginatum
 * *Aulacomnium palustre*
 * *Dicranum polysetum*
D. scoparium
 * *Pleurozium schreberi*
 * *Pohlia nutans*
 * *Polytrichum strictum*
 § *Sphagnum fuscum*
S. magellanicum
Calypogeja neesiana
Cephalozia spp.
Ptilidium ciliare
Cladonia coniocraea
C. fimbriata
 § *C. pyxidata* coll.
C. rangiferina

D-group 2. The species making up this group occurred all over the central, open areas, but typically did not enter the *Pinus sylvestris*-dominated marginal forests. The distributional patterns of D-group 2 and D-group 3 species were complementary. Nearly perfect complementarity was shown by the two hummock-inhabiting D-group 2 species *Scirpus cespitosus* and *Sphagnum rubellum* on one hand, and *Vaccinium vitis-idaea* (Fig. 10) on the other. Scattered occurrences also in the marginal forested areas (transition to D-group 3) were observed for species marked §. The following 38 taxa were classified in this group:

§ *Andromeda polifolia*
Vaccinium microcarpum
Drosera anglica
D. anglica x *rotundifolia*
 § *D. rotundifolia*
Rhynchospora alba
Scirpus cespitosus
 § *Dicranum leioneuron*
D. undulatum
Sphagnum balticum
S. cuspidatum
S. rubellum
S. tenellum
 § *Calypogeja sphagnicola*
 § *Cephaloziella* spp.
Cladopodiella fluitans
Gymnocolea inflata
Kurzia pauciflora
 § *Mylia anomala*
Odontoschisma sphagni (Fig. 27)
Riccardia latifrons
Cetraria delisei (Fig. 27)
C. ericetorum

C. islandica
Cladonia arbuscula
C. bacillaris
C. cyanipes
C. floerkeana
C. mitis (Fig. 27)
C. pleurota
C. squamosa
C. stellaris
C. subfurcata (Fig. 27)
 §*C. sulphurina*
C. uncialis
Icmadophila ericetorum
Ochrolechia frigida

D-group 3. The species classified to this group showed a concentration to the peripheral parts of the mire, with *Pinus sylvestris* forest. *Vaccinium vitis-idaea* (Fig. 10) showed the most typical D-group 3 distribution. *Vaccinium myrtillus* (Fig. 8) and *V. uliginosum* (Fig. 9) both had scattered occurrences in the open, central parts of the special area. Species even more frequent in the central areas (transitions to D-group 1) are denoted by *. The following 11 species were classified in this group:

**Betula pubescens*
Picea abies
 **Pinus sylvestris*
 **Betula nana* (Fig. 27)
Vaccinium myrtillus (Fig. 8)
V. uliginosum (Fig. 9)
V. vitis-idaea (Fig. 10)
Hylocomium splendens
 **Sphagnum angustifolium*
S. capillifolium (Fig. 11)
Cladonia furcata

D-group 4. This group only comprised one species, *Drepanocladus fluitans*. The distribution of this species is characterized by its restriction to the wettest part of the special area, distinctly influenced by soaks from areas near the border onto mineral soil. Furthermore, it showed no preference for central or peripheral parts of the area.

D-group 5. Species classified to this group were restricted to the more or less distinct, open, central fen soaks or areas where fen soaks spread out on the mire (cf. p. 26). The widest distribution of D-group 5 species was shown by *Sphagnum papillosum* (Fig. 20). Though less abundant, *Carex pauciflora* (Fig. 14) and *Erica tetralix* largely had a similar distributions. The remaining species had still more restricted distributions. Four species; *Carex limosa*, *Scheuchzeria palustris*, *Sphagnum lindbergii*, and *S. majus*, were restricted to the central, wetter parts of fen soaks (compare Figs 5 and 6). *Sphagnum compactum* and *S. molle* were restricted to the distal (bogward) side of the the large, western and southern fen soaks. Species denoted § were also noted in more peripheral sites, and were transitory to D-group 4. The following 10 species were classified in this group:

Erica tetralix (Fig. 12)

Fig. 8. The distribution of *Vaccinium myrtillus*.

Fig. 9. The distribution of *Vaccinium uliginosum*.

Fig. 10. The distribution of *Vaccinium vitis-idaea*.

Fig. 11. The distribution of *Sphagnum capillifolium*.

Fig. 12. The distribution of *Erica tetralix*.

Fig. 13. The distribution of *Carex limosa*.

Fig. 14. The distribution of *Carex pauciflora*.

Fig. 15. The distribution of *Scheuchzeria palustris*.

Fig. 16. The distribution of *Sphagnum compactum*.

Fig. 17. The distribution of *Sphagnum lindbergii*.

Fig. 18. The distribution of *Sphagnum majus*.

Fig. 19. The distribution of *Sphagnum molle*.

Fig. 20. The distribution of *Sphagnum papillosum*.

Fig. 21. The distribution of *Carex globularis*.

Fig. 22. The distribution of *Myrica gale*.

Fig. 23. The distribution of *Carex lasiocarpa*.

Fig. 24. The distribution of *Carex rostrata*.

Fig. 25. The distribution of *Eriophorum angustifolium*.

Fig. 26. The distribution of *Dactylorhiza maculata* (open triangles), *Carex curta* (filled triangles), *C. magellanica* (open squares), and *Phragmites australis* (filled squares).

Fig. 27. The distribution of *Betula nana* (circles), *B. nana* x *pubescens* (dots), *Bazzania trilobata* (open triangles), *Odontoschisma sphagni* (filled triangles), *Cladonia mitis* (open squares), *C. subfurcata* (filled squares), and *Cetraria delisei* (rotated triangle).

Fig. 28. The distribution of *Splachnum ampullaceum* (squares), *S. luteum* (circles), and *S. sphaericum* (triangles).

Carex limosa (Fig. 13)
 §*C. pauciflora* (Fig. 14)
Scheuchzeria palustris (Fig. 15)
Dicranella cerviculata
Sphagnum compactum (Fig. 16)
S. lindbergii (Fig. 17)
S. majus (Fig. 18)
S. molle (Fig. 19)
S. papillosum (Fig. 20)

D-group-6. Species in this group occurred in the peripheral parts of the special area, near the border onto mineral soil, in sites seemingly influenced by fen soaks. *Carex globularis* (Fig. 20) had the widest distribution encountered in this group. The following 6 species were included:

Salix aurita
Melampyrum pratense
Carex globularis (Fig. 21)
C. nigra
Polytrichum commune
Sphagnum russowii

D-group 7. Only species that occurred in the central parts of fen soaks and in peripheral areas distinctly influenced by water from the mineral soil, were classified to this group. A § indicates preference for the open, central parts, while an * indicates preference for peripheral areas, the latter transitional to D-group 8. The following 7 species were classified in this group:

Myrica gale (Fig. 22)
Carex lasiocarpa (Fig. 23)
 §*C. rostrata* (Fig. 24)
Eriophorum angustifolium (Fig. 25)
 §*Phragmites australis* (Fig. 26)
 **Calliargon stramineum*
 **Sphagnum fallax*

D-group 8. As D-group 7, but restricted to the peripheral, forested areas. The following 10 species were classified in this group:

Frangula alnus
Dactylorhiza maculata (Fig. 26)
Orthilia secunda
Potentilla erecta
Trientalis europaea
Carex curta (Fig. 26)
C. echinata
Molinia caerulea
Sphagnum centrale
S. girgensohnii

D-group 9. The three species classified to this group were restricted to shallow peat near the border onto mineral soil:

Juniperus communis
Salix repens
Deschampsia flexuosa

Some species were not possible to assign to particular distributional groups, in most cases because of sparse occurrence (examples in Figs 26-28).

Zones: definition and interpretation

Definition of zones

The division of species into D-groups according to broad-scale patterns could be interpreted as a response to two gradients: (1) the mire expanse - mire margin gradient, and (2) the nutrient (poor-rich) gradient.

(1) *The mire expanse - mire margin gradient.* The classification into D-groups suggested a division of the special area into two main categories along this gradient. The open, central parts of the special area were characterized by the presence of species of D-groups 2 and 5, while the peripheral, wooded parts contained members of D-groups, 3, 6, and 8. It was possible to divide the special area into two zones, the mire expanse (E-zone), and the mire margin (M-zone) by use of species in D-groups 2 and 3 (Fig. 29). The complementary distributions of the mire expanse species *Scirpus cespitosus* and *Sphagnum rubellum*, and the mire margin species *Vaccinium vitis-idaea* turned out to be the most operational criterion for this limit.

(2) *The nutrient (poor-rich) gradient.* Based on the distributional patterns; three zones (parallel divisions of the mire expanse and the mire margin) could be discerned: (a) Some areas in the middle, wetter parts of broad fen soaks on the mire expanse, and in wet laggs close to the border onto mineral soil, characterized by the presence of species in D-groups 7 and 8. These species neither occurred in the marginal parts of these soaks nor in smaller or less distinct soaks. Such areas made up zone 3. (b) The species of D-groups 4, 5 and 6 also had restricted distributions. The areas characterized by the presence of species in D-group 4-6 and absence of D-group 7 and 8 species, constituted zone 2. (c) Areas not containing species of any of the D-groups 4-9 constituted zone 1.

Zones along the two gradients were combined to give a total of six zones; E1, E2, and E3 on the mire expanse, and M1, M2, and M3 in the mire margin (Fig. 29). Distributions of D-groups 1-8 are related to the zones as follows:

D-group 1 - E1, E2, E3, M1, M2, M3
 D-group 2 - E1, E2, E3
 D-group 3 - M1, M2, M3
 D-group 4 - E2, E3, M2, M3
 D-group 5 - E2, E3
 D-group 6 - M2, M3
 D-group 7 - E3, M3
 D-group 8 - M3

Tab. 1 shows the frequency of all recorded species in each zone.

Fig. 29. Division of the special area into zones according to large-scale species distributions: mire margin - dotted (small dots), mire expanse - without dots, zone 1 - without hatching, zone 2 - hatched, isolated occurrences of zone indicators - medium sized dots. zone 3 - densely hatched, isolated occurrences of zone indicators - large dots.

Hydrological interpretation of zones

A comparison of Figs. 5, 7, and 29 gave good reasons to assume correspondence between the E1 - E2 zonal limit and the limit for influence of water that might come into contact with mineral soil. The four larger E1 areas in Fig. 29 were all characterized by convex contour lines. The three unilaterally sloping (westernmost) of these areas had distinct fen soaks at their flanks and were sheltered from influence by mineral soil water from above by large, hummock-dominated areas. These extensive deposits of highly humified hummock peat acted as dams for the water, effectively channelling surface water into the lateral fen soaks. Even in situations with maximal horizontal flow-rates, this shielding was probably sufficient for the E1 areas to remain truly ombrogenous. The peak of the water table in the multilaterally sloping kermi raised bog confirmed the ombrogenous status of this synsegment. The spread of the fen soaks out on the mire (p. 26, Fig. 6) was closely paralleled by concave (or straight) contours (Fig. 7), and the dominance of carpets and lawns (Fig. 5), further amplifying the interpretation to the E1-E2 limit as a reasonable approximation to the mineral soil water limit.

The fen plant limit and distribution of fen plants

From the hydrological assessment it was clear that species characteristic of zones 2 and 3 acted as fen plants at N. Kisselbergmosen. The species of D-groups 4,5, and 6 showed the least restricted distribution, and, taken together, appeared roughly to coincide with the areas on the fen side of the mineral soil water limit (Figs. 1-7, 29). When the hydrological interpretation was compared with the detailed maps of species' distributions, some deviant patterns occurred. These deviations were of two kinds.

(1) Disjunct occurrences in areas where the occurrence of mineral soil water was unlikely for hydrological reasons. Examples are: (a) *Erica tetralix* in pos. 113-114 110-112, (b) the same in pos. 095 206 (Fig. 12), (c) *Carex pauciflora* in pos. 084 074, (d) the same in pos. 144-151 080-082 (Fig. 14), (e) *Carex rostrata* in pos. 111 035 (Fig. 24), (f) *Sphagnum papillosum* in pos. 129 083, and (g) the same in pos. 127 143 (Fig. 20).

(2) Areas without fen plants, but nevertheless influenced by mineral soil water. The most typical examples are the least distinct (and driest) fen soaks (cf. Figs 5-7), containing scattered fen plants. Examples of such soaks are (a) pos. 07 07-10, (b) pos. 10 08, (c) pos. 09 12-15, and (d) pos. 13 12-14.

Chemical and physical properties of peat along transects

Zonational relationships of transects

The five transects each consisted of 10 to 21 peat samples.

Transect 1 (10 samples). From the central parts of the E1 zone at pos. 11 12, the transect ran across the broad, diffuse fen soak at pos. 09-10 10-11 into the E1 zone further SW (Figs 4 and 29). Samples 1-3 and 9-10 were from E1, 4-8 from E2.

Transect 2 (10 samples). A short transect in the broad fen soak close to the western border of the mire (Fig. 4) that ran from the E2 zone (samples 1-5) into the E3 zone (samples 6-10). At this site, the E3 zone was characterized by presence of *Carex rostrata*, *Eriophorum angustifolium*, and *Myrica gale*.

Transect 3 (17 samples) ran from the E1 zone of the unilaterally sloping kermi raised

Tab. 2. PCA ordination of peat samples. Eigenvalues of axes, correlations of sample scores with zones 1-3, and loadings of chemical parameters (correlations of chemical parameters with axes). Significance of correlation coefficients according to Owen (1962).

PCA axis	1		2		3		4	
	r	P	r	P	r	P	r	P
eigenvalue	.335		.187		.147		.112	
zone	.541	<.001	-.002	n.s.	.260	<.025	.032	n.s.
ASH	.284	<.010	-.103	n.s.	.230	<.025	.443	<.001
pH	.371	<.001	.085	n.s.	-.155	<.100	-.290	<.010
H	-.420	<.001	.125	n.s.	-.300	<.005	.088	n.s.
NA	-.188	<.010	.239	<.025	.345	<.005	-.575	<.001
K	-.265	<.010	-.067	n.s.	.578	<.001	.180	<.100
CA	.176	<.100	.559	<.001	-.140	n.s.	.178	<.100
MG	-.200	<.050	.537	<.001	.084	n.s.	.229	<.050
BS	.411	<.001	.210	<.050	.305	<.005	.067	n.s.

bog part of the central synsegment at pos. 09 09 (samples 1-5) westwards across a diffuse fen soak with *Carex pauciflora* and *Sphagnum papillosum* (*Erica tetralix* occurred somewhat further south). Samples 6-8 were taken from the E2 zone. At pos. ca. 070 090, the transect traversed a small area without E2 indicators (samples 9-12) before ending in the E2 zone of the western fen soak (samples 13-17).

Transect 4 (16 samples) ran in a south-easterly direction from the unilaterally sloping kermi raised bog (samples 1-4 in the E1 zone) across a diffuse fen soak with scattered *Carex pauciflora* and *Sphagnum papillosum* (samples 5-7 in the E2 zone), through a small E1 zone (samples 8-9), and into the broad soak from the south. Samples 10-11 originated from the E2 zone of this soak, samples 12-16 from the E3 zone characterized by the presence of *Eriophorum angustifolium*.

Transect 5 (21 samples) started between samples 1 of each of the transects 3 and 4 (samples 1-3 from the E1 zone), and ran eastwards to the multilaterally sloping kermi raised bog synsegment. The transect ran across the broad fen soak N of Kisselbergmøsetjern, with a central, *Carex rostrata*-dominated E3 zone (samples 9-12), bordered by E2 zones (samples 4-8, 13-15). Samples 16-21 were from the E1 zone of the multilaterally sloping kermi raised bog expanse segment.

Correlation between chemical and physical parameters

The only high value of r in the correlation matrix (Fig. 30) was observed between exchangeable H^+ and the derived parameter base saturation ($r = -0.816$, $P < 0.001$). Base saturation was primarily influenced by H^+ concentrations because of their more than tenfold higher values than total exchangeable cations (Tab. 3). A group of significantly positively correlated parameters contained pH, ash content, base saturation, and exchangeable Ca^{2+} . H^+ was negatively correlated with this group. Exchangeable Mg^{2+} was positively correlated with Ca^{2+} , but negatively correlated with ash content and pH. Exchangeable K^+ and Na^+ showed no correlations at the $P < 0.005$ level.

	Ash	pH	H	Na	K	Ca	Mg	% B
Ash		<.025	<.001	-	-	<.1	<.025	<.01
pH	0.272		<.005	-	<.05	<.005	<.025	<.001
H	-0.402	-0.330		<.05	<.1	-	<.005	<.001
Na	-0.104	-0.092	0.213		<.01	-	<.05	-
K	-0.009	-0.204	0.192	0.270		<.01	<.1	<.1
Ca	0.179	0.313	-0.028	0.029	-0.288		<.005	<.025
Mg	-0.254	-0.248	0.314	0.211	0.180	0.334		-
% B	0.313	0.441	-0.816	-0.047	-0.160	0.258	0.019	

Fig. 30. Peat chemistry; Pearson product-moment correlation coefficients (lower left) and their significance probabilities (upper right), based on 74 peat samples.

Fig. 31. Principal component analysis (PCA) of the 8 chemical parameters in the 74 peat samples. Axes 1 and 2.

PCA ordination

A summary of the PCA ordination of the eight chemical and physical parameters is given in Tab. 2.

PCA 1. The first PCA axis accounted for 33.5 % of the variance of the correlation matrix. High loadings on this axis as reflected by correlations with the sample scores, were obtained for base saturation ($r = 0.411$, $P < 0.001$) and pH ($r = 0.371$, $P < 0.001$), low loadings for exchangeable H^+ ($r = -0.420$, $P < 0.001$); a relatively high value also for ash content ($r = 0.284$, $P < 0.01$). The first PCA axis thus reflected the grouping of strongly correlated parameters also evident from Fig. 30, but partly excluded Ca^{2+} from this group (Fig. 31). Zone (from which the samples originated) was strongly correlated with sample scores along PCA 1 ($r = 0.541$, $P < 0.001$). Thus the zonal origin of sample plots explained the variation along PCA 1 better than did any single chemical or physical parameter. The division into zones can consequently be explained by a set of 3-4 peat parameters.

PCA 2. The second PCA axis accounted for 18.7 % of the variance. High loadings and highly significant correlations with this axis were only obtained by Ca^{2+} and Mg^{2+} (Fig. 31, Tab. 2). Zonal relationships of the samples were not correlated with this axis.

PCA 3. The third PCA axis accounted for 14.7 % of the variance. Exchangeable K^+ obtained high loading ($r = 0.578$, $P < 0.001$), but relatively high (positive and negative

Fig. 32. Principal component analysis (PCA) of the 8 chemical parameters in the 74 peat samples. Axes 1 and 3.

Tab. 3. Ash content, pH, percentage base saturation, and extractable cations (in mmol/dm³) in peat samples from mud bottoms in zones E1, E2, and E3. Median values and standard deviations are given. Differences of the zone means are tested for statistical significance by Student's T-test (Sverdrup 1973). T-values and significance probability levels according to Owen (1962) are given. p_1 refers to the two-tailed, p_2 to the one-tailed test.

Parameter	Zone	n	$\bar{x}$	s	Zone	T	p_1	p_2
Ash content (%)	E1	29	2.5	1.0	E1-E2 E2-E3	0.37 5.67	- <.001	- <.001
	E2	30	2.6	0.7				
	E3	13	4.9	2.1				
pH	E1	29	3.30	0.12	E1-E2 E2-E3	3.29 1.62	<.0025 -	<.001 <.1
	E2	31	3.40	0.10				
	E3	14	3.45	0.12				
H	E1	29	67	17	E1-E2 E2-E3	2.25 1.31	<.05 -	<.025 <.1
	E2	31	56	21				
	E3	14	48	12				
Na	E1	29	0.84	0.12	E1-E2 E2-E3	0.31 0.02	- -	- -
	E2	30	0.83	0.13				
	E3	14	0.83	0.15				
K	E1	29	0.21	0.09	E1-E2 E2-E3	0.15 0.06	- -	- -
	E2	31	0.21	0.12				
	E3	14	0.21	0.08				
Ca	E1	29	0.98	0.23	E1-E2 E2-E3	3.15 0.91	<.005 -	<.0025 -
	E2	31	1.20	0.30				
	E3	14	1.11	0.24				
Mg	E1	27	1.60	0.23	E1-E2 E2-E3	0.71 1.48	- -	- -
	E2	27	1.56	0.22				
	E3	14	1.46	0.20				
% base sat.	E1	27	9.1	2.3	E1-E2 E2-E3	2.85 1.41	<.01 -	<.005 <.1
	E2	26	10.9	2.4				
	E3	14	12.0	3.8				

loadings were also obtained by Na⁺, base saturation, and H⁺, to a lesser extent also by ash content (Fig. 32, Tab. 2). Zone was slightly correlated with PCA 3 ($r = 0.260$, $P < 0.025$), as expected from the correlations between PCA 3 and each of H⁺ and base saturation.

PCA 4. Accounting for only 11.2 % of the variance and uncorrelated with zone, this axis reflected residual variance in single parameters.

Correspondence between the zonal division and chemical and physical parameters

Tab. 3 shows the statistical tests of differences between the pairs of zones, each parameter taken separately. Four parameters showed significant differences between E1 and E2; pH

Figs 33-35. Variation in peat chemistry along Transect T1. Fig. 33. Ca. Fig. 34. pH. Fig. 35. Ash content.

($P < 0.001$), exchangeable Ca^{2+} ($P < 0.0025$), base saturation ($P < 0.005$), and exchangeable H^+ ($P < 0.025$). However, for all these parameters the mean for one zone was within one S.D. off the mean of the other zone, indicating that no single parameter enabled reliable prediction of zone from the chemical data. Between E2 and E3, only ash content was significantly different at levels below $P = 0.10$ ($P < 0.001$). However, the T value of this test was the highest encountered (Tab. 3). Values of Ca^{2+} , pH, and ash content, the three parameters which showed the greatest between-zone differences, were plotted against transect positions (Figs 33-47).

Transect 1. All three parameters increased from E1 to E2 (Figs 33-35). The increase was particularly strong from sample 3 to sample 4 (pH and Ca^{2+}). The pattern was not consistent, sample 1 showed higher Ca^{2+} concentration than sample 7, while the minimum of Ca^{2+} was observed in sample 8.

Transect 2. pH differed consistently between zones; on the average pH was higher by about 0.1 unit in zone E3 than in zone E2 (Fig. 37). Ca^{2+} showed no clear trend, while ash content was higher in E3.

Transect 3. The diffuse E2 zone at samples 6-8 was not, except for slightly higher pH values (cf. Fig. 40), reflected in the three parameters. Ash content decreased slightly from sample 8 to the E1 zone (samples 9-12). pH and ash content increased at the transition to the broad fen soak (samples 13-17).

Transect 4. Ca^{2+} , to a lesser degree also pH, increased from the E1 zone (samples 1-4) to the diffuse fen soak (samples 5-7). Ca^{2+} decreased markedly at the transition to the next E1 zone, then increased again in the E2 zone (samples 10-11), but decreased strongly on the transition to the E3 zone (Fig. 42). pH showed no consistent variation along this transect (Fig. 43). Ash content did not respond to the E1-E2 transitions, but increased strongly from E2 to E3 (between samples 11 and 12).

Transect 5. With one exception (the high value for sample 4), pH increased from zone E1 via E2 to E3, and decreased again towards the E1 zone of the kermi raised bog

Figs 36-38. Variation in peat chemistry along Transect T2. Fig. 36. Ca. Fig. 37. pH. Fig. 38. Ash content.

plain (Fig. 46). Ash content reached a maximum in the E3 sample 9, and otherwise showed no trends. Ca^{2+} increased along the transect, the highest values were noted for the E1 zone farthest east (Fig. 45).

Summary of trends

There was a considerable local variation in chemical and physical properties of peat, as seen from the variation of three parameters along transects (Figs 33-47). However, most zonal transitions were reflected in at least one parameter although not always the same. There was a tendency for pH to monitor E1-E2 transitions the best, while ash content best separated zones E2 and E3. Diffuse fen soaks with few and scattered E2 indicators appeared to be more poorly characterized by the parameters studied than were the main E2 water-tracks. The characterization of zones by peat properties was strongly improved when multidimensional trends were considered (e.g., by PCA) rather than single parameters. One group of correlated parameters, including base saturation (and the strongly correlated exchangeable H^+), pH, and ash content, appeared to give the optimal characterization of zones by peat properties.

Figs 39-41. Variation in peat chemistry along Transect T3. Fig. 39. Ca. Fig. 40. pH. Fig. 41. Ash content.

FINE-SCALE PATTERNS: SPECIES DISTRIBUTIONS AND ECOLOGICAL CONDITIONS

Fluctuations in depth to the water table

Climate in the observation period

Monthly mean temperature and total precipitation for the nearby meteorological station Høland-Kollerud 1980-82 are shown in Tab. 4; daily precipitation in the special area as well as total precipitation between successive water table recordings are shown in Figs 48, 51 and 54; while temperature means for the same periods at Høland-Kollerud are given in Figs 49, 52, and 55.

1980. The temperature was above normal in May, June, and September, while October was colder than normal. A warm period occurred from May 19 to June 3. Precipitation was higher than normal for all months except July (96 per cent of normal). The total precipitation of the ice-free season (May to October) was 147 per cent of normal. Particularly high precipitation occurred in June (123 mm, 189 per cent of normal) and October (153 mm, 195 per cent of normal). The longest rain-free periods lasted for eight days. The highest precipitation in one day was noted on August 4 (43.5 mm).

1981. May was considerably warmer than normal, while June was colder. Mean temperatures of the two months differed only slightly. Apart from a relatively warm September, temperatures differed but slightly from normals. May precipitation was close

Figs 42-44. Variation in peat chemistry along Transect T4. Fig. 42. Ca. Fig. 43. pH. Fig. 44. Ash content.

Tab. 4. Monthly and annual mean temperature (T) and monthly and annual total precipitation at the meteorological station 0284 Høland-Kollerud (Akershus, Aurskog-Høland, S. Høland, 139 m), relative to normals 1931-60. Data from The Norwegian Meteorological Institute, unpubl.

Period of observation		Monthly												Annual	M-O
		J	F	M	A	M	J	J	A	S	O	N	D		
T	Normal	- 6.8	- 6.4	- 2.2	3.2	9.2	13.3	15.8	14.4	9.9	4.9	0.1	- 3.4	4.3	11.3
	1980 mean	- 9.5	-10.8	- 4.6	3.7	10.2	14.9	15.6	14.0	11.0	3.2	- 3.4	- 1.7	3.5	11.5
	1981 mean	- 5.3	- 6.1	- 3.6	3.1	11.0	12.0	15.1	13.8	11.3	4.3	- 0.3	-13.1	3.5	11.3
	1982 mean	-13.3	- 3.8	0.9	4.2	8.8	12.8	16.7	15.4	11.1	5.9	2.6	- 1.8	5.0	11.8
P	Normal	52	37	27	46	45	65	80	84	78	78	78	70	740	430
	1980 total	20	28	28	10	55	123	77	135	87	153	47	56	819	630
	1981 total	22	22	70	6	53	115	145	7	75	115	125	25	780	510
	1982 total	23	36	76	27	88	42	41	80	109	82	152	100	856	442

Figs 45-47. Variation in peat chemistry along Transect T5. Fig. 45. Ca. Fig. 46. pH. Fig. 47. Ash content.

to normal, while June and July were extremely rainy (177 and 181 per cent of normals, respectively). However, the mire received less than 20 mm of precipitation from July 29 to August 22, and virtually no precipitation from August 23 to the reading of depths to the water table on September 18. The last half of September was rainy, and precipitation remained high for the rest of the autumn. Maximum precipitation in one day was recorded on October 4; 51.9 mm.

1982. May was cold and rainy (88 mm, 196 per cent of normal). Mean June temperature was also below normal, but a warm, dry period occurred at the May-June transition. An exceptionally long, warm period lasted for one month (July 8 to August 8). The first days of August had daily maxima well above 30°C, while daily means above 20°C were recorded for nine successive days. The last half of August was cool, but temperatures were above normal (by more than 1°C) for the rest of the year. The warm period in July was accompanied by a period of negligible precipitation. Precipitation was 65 per cent of normal in June, only 51 per cent in July. Except for the 7 mm falling on the mire July 15-16, no precipitation occurred from July 7 to August 12. For the rest of the ice-free season, precipitation was close to normals, and evenly distributed.

Variation in mean depth to the water table in the observation period

Only the mean course of depths to the water table for 79 sample plots is shown (Figs 50, 53, 56). Although some between-sample plot variation occurred (as described in a later section, cf. pp. 73), the seasonal variation of the mean was highly representative for all

Figs 48-50. Fluctuations in climate and mean depth to the water in the 79 three-year observation points during the growing season of 1980. Fig. 48. Daily total precipitation on N. Kisselbergmosen. Means for the periods between each water table recording are indicated. Fig. 49. Daily mean temperatures at the meteorological station Høland-Kollerud (data from The Norwegian Meteorological Institute, unpubl.). Means for the periods between each water table recording are indicated. Fig. 50. Mean depth to the water table (as measured from the surface of the bottom layer) in the 79 three-year observation points.

sample plots. A close correspondence between the mean distance to the water table and climate was demonstrated by Figs 48-56.

1980. By May 1 most hollows were ice-free (or some ice remained 10-20 cm below the actual water table). No ice was observed in hummocks after May 13. The mean depth to the water table increased 6 cm until the reading on May 20; mainly due to low precipitation. For the rest of the season the depth to the water table mainly remained low, as expected from the high and frequent precipitation. The annual maximum mean depth to the water table occurred on June 18 (17 cm), while local maxima occurred after dry, warm

Figs 51-53. Fluctuations in climate and mean depth to the water table in the 79 three-year observation points during the growing season of 1981. Fig. 51. Daily total precipitation on N. Kisselbergmosen. Means for the periods between each water table recording are indicated. Fig. 52. Daily mean temperatures at the meteorological station Høland-Kollerud (data from The Norwegian Meteorological Institute, unpubl.). Means for the periods between each water table recording are indicated. Fig. 53. Mean depth to the water table (as measured from the surface of the bottom layer) in the 79 three-year observation points.

periods of one week's duration (readings on July 12 and August 2). Addition of 40-50 mm of precipitation within one week always seemed to rise the water table to about the same level (mean distance to the water table 8-9 cm). This level was rarely exceeded. In the autumn after long periods of heavy rain, exceptionally low depths to the water table were noted (5.5 cm on September 14 after three days with heavy rain, 4 cm on October

Figs 54-56. Fluctuations in climate and mean depth to the water table in the 79 three-year observation points during the growing season of 1982. Fig. 54. Daily total precipitation on N. Kisselbergmosen. Means for the periods between each water table recording are indicated. Fig. 55. Daily mean temperatures at the meteorological station Høland-Kollerud (data from The Norwegian Meteorological Institute, unpubl.). Means for the periods between each water table recording are indicated. Fig. 56. Mean depth to the water table (as measured from the surface of the bottom layer) in the 79 three-year observation points.

18 after a long, rainy and cool period). However, these low depths to the water table did not last for more than a couple of days in the absence of further addition of rain. The hollows froze about October 30, the hummocks some 1-2 weeks later. The annual mean range of depths to the water table was 13 cm.

1981. Some hollows had thawed already by April 13. The warm and dry middle of

May caused rapid melting of most of the remaining ice, but ice was still observed in some large hummocks on June 8. The depth to the water table increased only slightly. The cool and rainy months to follow resulted in an almost constant depth to the water table close to 10 cm until the reading on July 25. Apart from a slight decrease in the middle of August, the depth to the water table increased steadily until the maximum, 24 cm, was recorded on September 18. During the initial stages of a dry period, the daily increase of depth to the water table was higher than during later stages (cf. Fig. 52). Addition of 60 mm of precipitation within a one-week period caused a 17 cm decrease in the mean depth to the water table, while the addition of 85 mm the next ten days only caused a 0.5 cm further decrease. In spite of 51.9 mm rain two days before the recording on October 5, the minimum depth of 1980 was not reached (difference between annual minima 2 cm). The hollows froze November 3 and were covered with snow, but ice and snow thawed later on. Not until the last week of November did the mire freeze permanently. The annual mean range of depth to the water table was 18 cm.

1982. Due to the warm March and April, large parts of the mire had thawed by mid-April, and almost no site was frozen on April 29. Ice was not observed in hummocks after May 7. The cool and wet first half of May kept mean depths to the water table low (about 9 cm) until the reading on May 23. The following warm and dry period caused the depths to the water table to increase to 24 cm within a three-week period. The addition of 12 mm of precipitation (but maintenance of a cool weather) during the next week caused a 1.5 cm decrease in the depth, while the 39 mm the following 12 days resulted in a decrease to 13 cm. The long drought period of July and the first week of August caused a dramatic increase in the depth to the water table. The increase was rapid at first, then slowed down (in spite of increasing mean temperatures), but accelerated again as a response to the unusually warm first week of August. The three-year maximum depth to the water table, 37 cm, was noted on August 8. Addition of 25 mm of precipitation the next ten days caused a 7 cm decrease of depth to the water table. Precipitation remained above normals and temperature was low for the rest of the month, but the 9 cm level was not re-established until September 26 after a long, rainy period. Thereafter, depths to the water table remained low. The mire did not freeze permanently until the end of November or the beginning of December. The annual mean range of depths to the water table was 29 cm, the three-year range was 33.5 cm.

Cumulative probability distribution functions

Variation between years. Fig. 57 shows the one-year cumulative probability distribution functions for depth to the water table for four sample plots. The variation between sample plots was insignificant as the four graphs in Fig. 57 representing the same year largely follow each other closely. The variation between years was, however, considerable. P_0 (maximum water table; minimum depth to the water table) and P_{10} did not differ by more than 2 cm between the years. The differences between years increased towards higher cumulative probabilities, but were still relatively small for P_{30} . Maximum depth to the water table (minimum water table; P_{100}) differed by ca. 20 cm between the driest and the wettest year (1982 and 1980, respectively). All graphs showed a distinct inflexion point, the compensation point, around P_{30} . This was less pronounced on the 1982 curves because of shorter duration of low depths to the water table.

Three-year cumulative probability distribution functions differed only to a minor extent between sample plots (Figs 57, 58). They all showed a sigmoid shape with a distinct compensation point at about $P_{30,3}$. There was some tendency for the lowermost curves in Fig. 58 to have higher slopes at given P , at least for $x < 10$ and $x > 90$. The slopes of the

Tab. 5. Unbiased estimators for characteristic levels of cumulative distributions of distance to the water table 1980-82. $\hat{X}$ - estimators based on observations during two years (1980-81), X^* - estimators based on two observations (1980 05 13 and 1980 07 14).

Estimated parameter	$\hat{X}$		X^*	
	Formula	Var.	Formula	Var.
$P_{100,3}$	$\hat{P}_{100,3} = P_{100,2} - 13$	3.18	$P_{100,3}^* = o(07\ 14) - 15$	3.28
$P_{90,3}$	$\hat{P}_{90,3} = P_{90,2} - 6$	1.30	$P_{90,3}^* = o(07\ 14) - 1$	1.46
$P_{50,3}$	$\hat{P}_{50,3} = P_{50,2} - 1$	0.63	$P_{50,3}^* = o(05\ 13) - 1$	1.03
$P_{10,3}$	$\hat{P}_{10,3} = P_{10,2}$	0.63	$P_{10,3}^* = o(05\ 13) + 2$	1.02
$P_{0,3}$	$\hat{P}_{0,3} = P_{0,2}$	0.10	$P_{0,3}^* = o(05\ 13) + 6$	1.64
K_3	$\hat{K}_3 = K_2^*$	0.54	$K_3^* = o(05\ 13)$	0.96
R_3	$\hat{R}_3 = \hat{P}_{0,3} - \hat{P}_{100,3}$	3.28	$R_3^* = P_{0,3}^* - P_{100,3}^*$	3.67

slightly peat-producing lawn sample plots 149, 196, 211, and 238 are higher than the strongly peat-producing lawn sample plot 081 for $x < 20$.

Seasonal variation between lawn sample plots differing with respect to peat productivity

The course of the depth to the water table in 1981 for 35 sample plots classified as lawns (cf. p. 85) is shown in Figs 59-62. As evident from Tab. 16, means for all characteristic levels were lower at the lower than at the upper lawn level (also compare Figs 59-60 and Figs 61-62). Visually inspected, the course of the water table did not differ much between the strongly and the slightly peat-producing sites. A very slight tendency for stronger reactions, that is, steeper curves in the same time interval, may be noted for the slightly peat-producing sites (Fig. 60 vs Fig. 59, Fig. 62 vs Fig. 61). However, by taking zonal relationships into account it appeared that this tendency was fully explained as a difference between zones E1 and E2 (stronger reactions in E1). The combinations of zone E1 and high peat productivity, and E2 and low peat productivity, were rare in the material.

Fig. 57. Duration of depth (from the surface of the bottom layer) to the water table in four sample plots during the growing seasons 1980 (unbroken line), 1981 (long dashes), and 1982 (short dashes). Depth to the water table, x , is given as ordinate. Abscissa indicate cumulative probability distribution functions, $P_y(x)$. Cumulative duration curves 1980-82 are indicated by unbroken line. Sample plots: 070 - E1 zone, low hummock (the E1RL1 site-type), 111 and 149 E1 zone, low lawn (the E1RL1 site-type), 391 - M1 zone, hummock (the M1H site-type).

Tab. 6. Modelling fluctuations in mean distance to the water table by means of stepwise inclusion multiple regression. DV - dependent variable. IV - independent variable, in order of entrance, C - constant. Mult R - multiple regression coefficient. T - T-value for inclusion of variable. P - significance of T. a - coefficient of variable in regression equation.

DV	IV	Mult R	T	P	a
	P	0.679	-6.83	<0.001	-0.134
	POS-1	0.809	-7.11	<0.001	-0.096
	P2	0.841	-5.07	<0.001	-0.360
	WN	0.860	3.36	<0.002	0.283
	C				4.216
/d	P/d	0.677	-6.81	<0.001	-1.420
	POS-1	0.815	-7.03	<0.001	-0.102
	WN/d	0.837	3.54	<0.001	3.567
	P2	0.858	-3.41	<0.002	-0.428
	C				3.404

Correlation between characteristic levels

The correlations between the seven characteristic levels (Fig. 63) amplified some of the qualitative statements above. The most highly correlated characteristic levels were those describing the situation in wet periods (P_0 , P_{10} , P_{50} , and K), making up a group of variables so highly correlated that each could be almost exactly predicted from any of the others. P_{90} was highly correlated with P_{50} , while P_{100} was less strongly correlated with any other variable, than any combination of P_0 , P_{10} , P_{50} , P_{90} , and K . In general, correlations were highest between adjacent characteristic levels along the sequence P_0 , P_{10} , K , P_{50} , P_{90} , and P_{100} . The three-year range of depths to the water table was but slightly correlated with P_0 , P_{10} , K , and P_{50} , although there was a low, positive correlation. This indicated increasing range with increasing median depth to the water table, that is, increasing range from carpets, via lawns, to hummocks. The higher correlation of R with P_{100} than with any other variable indicated that the range was primarily determined by the maximum depth to the water table.

The distribution of R in the special area is shown in Fig. 64. By comparison with Figs 5 and 7 and the hydromorphological description, the following trends became apparent:

Fig. 58. Duration of depth (from the surface of the bottom layer) to the water table for some selected sample plots. Cumulative duration curves 1980-82. 305, 389, 415 - E1 zone, high hummock (the E1PHu site-type); 070, 094 - E1 zone, low hummock (the E1PHl site-type); 125 - E2 zone, low hummock (the E2PHl site-type); 196, 238 E1 zone, upper lawn (the E1RLu site-type); 111, 149 - E1 zone, low lawn (the E1RLl site-type); 081 E2 zone, low lawn (the E2PLl site-type); 014, 015, 391 - M1 zone, hummock (the M1H site-type); 001 - M3 zone, hummock (the M3H site-type).

Fig. 59. Fluctuations in depth to the water table during the growing season of 1981 for ten sample plots from the EPLI series. Broken line - the E1PLI site-type (E2 zone), continuous line - E2PLI site-type (E2 zone).

1) the highest values of R were encountered in the marginal forests, (2) higher values were noted for wide, continuous hummock areas bordering on the marginal forests or situated in steeper slopes (notably in the eastern parts of the special area), (3) higher values were noted for hummocks than for adjacent hollows, although the difference was mostly small (mean value 0.4 cm), and (4) lower values were noted for E2 and E3 than for the E1 zone; the broad, distinct fen soaks having lower values for R than the indistinct soaks, again having lower values than larger raised bog segments.

The value of $P_{50,3}$ corresponding to $P_0 = 0$ generally was within $6 < P_{50,3} < 10$, with an estimated mean value of $P_{50,3} = 8$ (Fig. 65). Similarly, $P_{50,3} = 4$ corresponded to an

Fig. 60. Fluctuations in depth to the water table during the growing season of 1981 for ten sample plots from the ERLI series. Broken line, short dashes - the E1RLI site-type (E1 zone), Broken line, long dashes - the E1RLI site-type (E2 zone). continuous line - E2RLI site-type (E2 zone).

expected value of $P_{10,3} = 0$.

Estimation of characteristic levels

Unbiased estimators for characteristic levels based on two-year observations (X^*) and two observations (X') are given in Tab. 6. It may be noted that $P_{0,3}$, $P_{10,3}$, $P_{50,3}$, and K_3 could be estimated for two-year observations to within one cm off the true value. These variables, as well as $P_{90,3}$, could be estimated from two single observations with a variance below 2 cm. Variances of R_3^* , R_3' , $P_{100,3}^*$, and $P_{100,3}'$ were in the range 3-4 cm, indicating that relatively large uncertainty was associated with estimation of these variables, even when two-year observation records were available.

Fig. 61. Fluctuations in depth to the water table during the growing season of 1981 for ten sample plots from the EPLu series. Broken line - the E1PLu site-type (E2 zone), continuous line - E2PLu site-type (E2 zone).

Modelling climatic control of fluctuations in depth to the water table

The apparently close relationship between climate and mean depth to the water table emerging from Figs 48-56 was substantiated by multiple regression (Tab. 5). Regardless of choice of dependent variable (Δ_i - change in mean distance to the water table from time i to time $(i+1)$ or Δ/d - daily change in this period), a set of four significant independent variables yielded a multiple correlation of $= 0.860$! Precipitation was the single variable that best explained the change in mean depth to the water table ($r = 0.679$, $P < 0.001$), but average cumulative probability at time i (a measure related to the mean depth to the water table at this time), contributed strongly to increase r . This substantiated the observation that the mean difference in depth to the water table between two successive readings was not only influenced by precipitation, but that a given amount of precipitation had strikingly different effects depending on whether the depth to the water table was high or low. The

Fig. 62. Fluctuations in depth to the water table during the growing season of 1981 for ten sample plots from the ERLu series. Broken line, short dashes - the E1RLu site-type (E1 zone), Broken line, long dashes - the E1RLu site-type (E2 zone). continuous line - E2RLu site-type (E2 zone).

higher the initial depth to the water table, the more strongly did depth decrease by addition of a specified amount of precipitation. The other significant variables were P2, precipitation during the last 48 hours before the readings, and WN, the water need during the period before reading. Mean temperature was strongly correlated with water need, and thus not significant. The inclusion of P2 and WN as significant variables had the following implications: (1) Temperature differences had roughly the same influence on distance to the water table as the distribution of precipitation in the period immediately before water table readings. (2) The mire responded rapidly to addition of precipitation. This second point was probably related to response at very low mean depths to the water table (mean depth below ca. 9 cm), when surface runoff caused a rapid increase in depth to the water table to the

	$P_{100,3}$	$P_{90,3}$	$P_{50,3}$	$P_{10,3}$	$P_{0,3}$	R_3	K_3
$P_{100,3}$		<.001	<.001	<.001	<.001	<.001	<.001
$P_{90,3}$	0.931		<.001	<.001	<.001	<.001	<.001
$P_{50,3}$	0.888	0.972		<.001	<.001	<.005	<.001
$P_{10,3}$	0.864	0.954	0.993		<.001	<.010	<.001
$P_{0,3}$	0.833	0.934	0.973	0.980		<.050	<.001
R_3	0.716	0.515	0.338	0.291	0.227		<.005
K_3	0.881	0.967	0.997	0.993	0.980	0.352	

Fig. 63. Pearson's product-moment correlation coefficients (lower left) and their significance probabilities (upper right) between characteristic levels (fractiles) of curves for duration of water level at specified depths below the surface of the bottom layer 1980-82.

9-10 cm level within a couple of days after addition of further precipitation. The importance of the P_2 parameter probably increases when the water table is above the compensation point.

Distribution of species according to depth to the water table

Tab. 7 shows the relationship of the 55 most frequent species (occurring in 20 or more of the sample plots of the R data set) to depth to the water table. According to distribution on 2 cm intervals along the gradient, species have been classified to seven W-groups.

W-group 1 consisted of seven species, preferring sites with water at or above the bottom layer for at least half the ice-free period (optimum outside the sampled portion of the gradient). All these species were restricted to sites that were at some time covered by water ($P_{50,3} > 8$):

Drosera anglica
Rhynchospora alba
Scheuchzeria palustris
Sphagnum compactum
S. cuspidatum
S. majus
Gymnocolea inflata

W-group 2. These species had optimum near $P_{50,3} = 4$, thus preferring sites that were inundated for at least a tenth of the ice-free period. A marked frequency-limit was noted at $P_{50,3} = 8$, indicating a strong preference for sites inundated at least some times during the year. The following five taxa were classified to this group:

Drosera anglica x rotundifolia

Fig. 64. Distribution of R_3 and R_4 on N. Kisselbergmosen. Large figures indicate M zones, small figures E zones. Hummock sites in the E zones are indicated by underlining. Zone 2 is indicated by small ring, zone 3 by large ring.

Fig. 65. Relations between $P_{50,2}$ and $P_{50,3}$ and x ; $P_x = 0$. The regression of x on P_{50} is $x = 3.63 P_{50} + 29.4$, $r = -0.712$, $n = 102$. Both regressions are significant at the $P < 0.001$ level.

Sphagnum papillosum
S. tenellum
Cladopodiella fluitans
Ochrolechia frigida

W-group 3. The species in this group spanned the whole gradient, but had a distinct optimum below the limit for occasional inundation. Four species were classified in this group:

Andromeda polifolia
Sphagnum balticum
S. magellanicum
Cladonia squamosa

W-group 4 comprised eight species, like the *W-group 3* species spanning the whole or a larger part of the gradient, but unlike this group having optima at or below $P_{50,3} = 8$ and consequently preferring sites that were not inundated:

Erica tetralix
Myrica gale
Carex pauciflora

Tab. 7. Distribution of species according to distance from the surface of the bottom layer to the median ground water table. W - grouping of species according to relationship to the water table. Tabulated values are I for each species in each interval. MDWT - median distance to the water table. CPWB - estimated cumulative probability of water at or above the bottom layer surface.

W	MDWK (cm)	0 2 4 6 8 10 12 14 16 18 20 22 24 26 29															
		.50	.30	.10	.04	.01	0	0	0	0	0	0	0	0	0	0	0
1	<i>Drosera anglica</i>	19	20	10	8	4	3	0	0			0					
	<i>Rhynchospora alba</i>	45	38	36	25	8	6		1								
	<i>Scheuchzeria palustris</i>	5	2	1	1	1	1										
	<i>Sphagnum compactum</i>	10	5	5	1	0											
	<i>S. cuspidatum</i>	46	48	22	9	3	3										
	<i>S. majus</i>	24	15	6	2	5	0										
	<i>Gymnocolea inflata</i>	15	15	10	4	0	1										
2	<i>Drosera anglica</i> x <i>rotundif.</i>	3	2	2	2	0	1		0								
	<i>Sphagnum papillosum</i>	19	26	18	25	23	9	5	3	2	0	0					
	<i>S. tenellum</i>	66	68	78	65	42	30	9	1		1						
	<i>Cladopodiella fluitans</i>	49	53	58	50	39	23	10	11	1	2		0		1		
	<i>Ochrolechia frigida</i>		0	1	1		1										
3	<i>Andromeda polifolia</i>	14	23	30	29	29	23	23	20	18	18	10	7	9	8	11	
	<i>Sphagnum balticum</i>	43	59	60	58	57	47	34	21	10	13	6	5	4		2	
	<i>S. magellanicum</i>	14	24	31	44	42	33	22	20	16	30	24	6	5	16	7	
	<i>Cladonia squamosa</i>	2	7	12	6	7	12	5	3		2	4	1		1	1	
4	<i>Erica tetralix</i>		1	1	2	2	1	7	4	0	2	3					
	<i>Myrica gale</i>		1	2	3	3	2	2		2	3	3					
	<i>Carex pauciflora</i>			0	2	3	1	5	1	1		3					
	<i>Scirpus cespitosus</i>	3	14	19	20	35	31	33	15	15	12	11	7	6	3	2	
	<i>Sphagnum rubellum</i>	10	17	41	53	62	66	73	63	57	52	46	39	40	34	24	
	<i>Calypogeia sphagnicola</i>		2	3	10	14	16	15	11	5	7	4	10	8	5	8	
	<i>Cephalozia</i> spp.	9	23	33	37	32	34	26	25	23	23	15	13	13	11	13	
	<i>Kurzia pauciflora</i>	2	6	15	30	38	45	45	35	23	21	13	12	10	10	13	
5	<i>Calluna vulgaris</i>	2	6	25	33	47	59	66	74	70	73	73	75	75	72	78	
	<i>Vaccinium uliginosum</i>				1	1	4	3	4	10	9	9	8	13	9	5	
	<i>Rubus chamaemorus</i>	1	3	6	17	18	25	28	35	29	34	30	26	33	33	39	
	<i>Aulacomnium palustre</i>			0	0	1	2	3	1	2	4	2		2	3	2	
	<i>Sphagnum angustifolium</i>				0	2	4	3	5	22	19	14	6	6	12	1	
	<i>Polytrichum strictum</i>				1	0	0		2	4	0	4	3	1			
	<i>Cephaloziella</i> spp.			0	0	2	1	2	1	1	0		2	1	3	1	
	<i>Mylia anomala</i>	2	5	15	21	27	34	43	38	36	33	21	31	30		29	
	<i>Cetraria islandica</i>				1	2	2	0	3		2	1	2	1			
	<i>Cladonia arbuscula</i>		0				0	2	1	1	1		1		3	1	
	<i>C. rangiferina</i>			2	4	3	24	32	34	39	41	36	51	43	35	48	
	6	<i>Betula pubescens</i>			0	1	1	0	4	2		0	4	1	4		1
<i>Picea abies</i>							0		1	1	1	1	2	2	1	2	
<i>Pinus sylvestris</i>				1	2	8	9	12	24	34	36	38	42	49	56	52	
<i>Empetrum nigrum</i>						2	3	5	11	17	16	14	17	28	41	27	
<i>Vaccinium myrtillus</i>							2		2	1	3	6	6	11	6	3	
<i>V. vitis-idaea</i>							1	0	5	9	5	11	6	8	4	16	
<i>Carex globularis</i>							1		0					1	2	2	
<i>Dicranum polysetum</i>								0	1	1	1	1		2	3		
<i>D. scoparium</i>						0	0		1	0	1	1	3	2		1	
<i>Pleurozium schreberi</i>						2	1	5	11	15	15	27	25	32	43	41	
<i>Pohlia nutans</i>				0		0	0	2	5	8	8	8	3	8	15	11	
<i>Sphagnum capillifolium</i>									4	1	1	2	6		1	6	
<i>S. fuscum</i>				0	5	16	20	41	59	59	57	64	65	71	66	78	
<i>Calypogeia neesiana</i>							1	0	1	4	2	2	1	6	2	4	
<i>Cladonia fimbriata</i>					0	2	2	3	4	4	4	7	7		3	4	
<i>C. pyxidata</i> coll.					0			0	1	2	2	3	2		1	1	
<i>C. stellaris</i>			0	0	1	0	0	2	1	3	4	9	5		4		
7	<i>Vaccinium oxycoccos</i> coll.	13	21	24	24	24	23	30	35	38	29	34	39	33	42	42	
	<i>Drosera rotundifolia</i>	7	11	14	14	14	14	12	11	9	10	6	7	8	8	6	
	<i>Eriophorum vaginatum</i>	41	48	55	57	58	59	56	60	56	59	52	54	52	50	48	
Number of sample plots		21	47	86	83	73	63	42	55	42	50	37	31	25	14	17	
Expected cumulative probability of water cover at the surface of the bottom layer		50	30	10	4	1	0	0	0	0	0	0	0	0	0	0	

Scirpus cespitosus
Sphagnum rubellum
Calypogeja sphagnicola
Cephalozia spp.
Kurzia pauciflora

W-group 5. The species in this group showed a clear preference for high depths to the water table, with a distinct frequency limit about $P_{50,3} = 8-10$, thus showing susceptibility towards inundation. The following 11 species were classified in this group:

Calluna vulgaris
Vaccinium uliginosum
Rubus chamaemorus
Aulacomnium palustre
Polytrichum strictum
Sphagnum angustifolium
Cephaloziella spp.
Mylia anomala
Cetraria islandica
Cladonia arbuscula
C. rangiferina

W-group 6. Like *W-group 5*, but with a distinct frequency limit at $P_{50,3} = 14$, thus showing preference for well-aerated peat. The following 17 species were classified to this group:

Betula pubescens
Picea abies
Pinus sylvestris
Empetrum nigrum
Vaccinium myrtillus
V. vitis-idaea
Carex globularis
Dicranum polysetum
D. scoparium
Pleurozium schreberi
Pohlia nutans
Sphagnum capillifolium
S. fuscum
Calypogeja neesiana
Cladonia fimbriata
C. pyxidata coll.
C. stellaris

W-group 7 contained three taxa, apparently indifferent with respect to this gradient:

Vaccinium oxycoccos coll.
Drosera rotundifolia
Eriophorum vaginatum

Area covered by bare peat in relation to depth to the water table

Area covered by bare peat varied along the gradient in depth to the water table (Tab. 8). Highest importance of bare peat was observed at low median distance to the water table. Lowest importance was noted at 4-6 cm, and in the interval 16-24 cm, while local maxima were noted at 12 cm and at 26-29 cm.

CLASSIFICATION OF VEGETATION

The classification system

Thirty-two site-types were recognized in the special area (Fig. 66). Naming of site-types was by combination of gradient segment designations (Fig. 66), defined as follows:

(1) *The mire expanse - mire margin gradient*. This gradient was divided into two segments, *E* (mire expanse) and *M* (mire margin), by the criteria given on p. 56.

(2) *The nutrient (poor-rich) gradient*. This gradient was divided into three zones; broad-scale geographical phenomena defined by species distributions (p. 56). However, in zones 2 and 3, zonal indicators were locally absent from the 0.25 m² sample plots. A zonation was defined as all site-types that had a floristic composition of sample plots characteristic to one particular zone. Thus three zonations, 1, 2, and 3, could be discerned along the poor-rich coenocline by the presence or absence of zonal indicators (cf. p. 56).

(3) *The gradient in depth to the water table*. Based on the division of species into W-groups (pp. 80-84, cf. Tab. 7), this gradient was divided into five segments. Each segment corresponds to one or a part of one mire subfeature, as characterized by floristic criteria. These five segments or relative levels were carpet (*C*), lower lawn (*Ll*), upper lawn (*Lu*), lower hummock (*Hl*), and upper hummock (*Hu*). In the mire margin only the lower and upper hummock levels occurred. Floristic criteria on limits were as follows: (a) *The C-Ll limit*. Dominance of sphagna in W-group 1 indicated the C, dominance of W-group 2 sphagna the Ll level. (b) *The Ll-Lu limit*. Occurrence of *Sphagnum cuspidatum* and dominance of the W-group 1 vascular plants (*Drosera anglica* and *Rhynchospora alba*) indicated Ll; frequent or even dominant position of W-group 4 species suggested Lu. (c) *The Lu-Hl limit*. With the exception of scattered individuals of *Cladopodiella fluitans*,

		Subseries									
		P			R						
Series	E1Hu	E1PHu	E2PHu	E3PHu	E1RHu	E2RHu		M1Hu	M2Hu	M3Hu	MHu
	E1L	E1PH1	E2PH1	E3PH1	E1RH1	E2RH1				M3H1	MM1
	ELu	E1PLu	E2PLu	E3PLu	E1RLu	E2RLu	E3RLu				
	EL1	E1PL1	E2PL1	E3PL1	E1RL1	E2RL1	E3RL1				
	EC	E1PC	E2PC	E3PC	E1RC	E2RC	E3RC				
	E1	E2	E3	E1	E2	E3	M1	M2	M3		
Zonations											

Fig. 66. The classification system adopted in the present study. Site-type designations are indicated within boxes. Empty boxes indicate combinations not met within the investigated area.

Tab. 8. Percentage of the surface of the bottom layer in sample plots from the mire expanse (the R data set) occupied by bare peat, as a function of median depth to the water table.

Water table	n	x	+ S.D.
0	21	22	+ 24
2	47	18	+ 22
4	87	8	+ 12
6	82	9	+ 15
8	73	12	+ 17
10	58	13	+ 15
12	40	15	+ 18
14	52	14	+ 17
16	32	8	+ 15
18	40	12	+ 15
20	29	13	+ 16
22	23	13	+ 17
24	20	10	+ 17
26	10	16	+ 15
29	12	14	+ 20

W-group 2 species were absent from H1. *Calluna vulgaris* had a distinct frequency limit here (dominates in H1, in Lu only young colonists and dying relicts), *Sphagnum fuscum* and *Cladonia rangiferina* were virtually absent from Lu. (d) The H1-Hu limit corresponded to the coincident reciprocal frequency limits of *Scirpus cespitosus* and *Empetrum nigrum*. In the mire margin presence of *Sphagnum fallax* indicated the H1 series.

(4) *The gradient in peat productivity.* Two segments were recognized, according to assumed peat-producing ability of the bottom layer dominants. Strongly peat-producing vegetation (P; progressive) was indicated by the dominance of *Sphagnum fuscum*, *S. magellanicum*, *S. papillosum*, and *S. rubellum*; or *S. balticum*, *S. cuspidatum*, and *S. majus* virtually devoid of intermingled hepatics. Positively differentiating criteria for slightly peat-producing (R; regressive) vegetation were the high importance of lichens and prominence of hepatics and *Sphagnum tenellum*.

		Subseries											
		P					R						
Series	PH	21.1/5.0 (67)	16.5/6.4 (2)	(0)	22.4/6.8 (39)	19.0 (1)		22.3/6.4 (46)	20.1/5.7 (8)	15.8/5.1 (6)		PH	
	HH	14.8/4.5 (92)	12.4/3.9 (17)	9.3/2.5 (3)	13.4/3.7 (52)	15.2/3.6 (5)				12.3/5.9 (4)		HH	
	HL	9.3/2.2 (4)	7.7/2.5 (32)	10.0/4.3 (9)	7.0/2.1 (39)	5.8/2.2 (11)	(0)						
	FL	5.5/0.6 (4)	5.8/2.6 (17)	7.6/3.9 (5)	4.6/1.9 (67)	4.8/2.4 (37)	4.2/1.5 (4)						
	P	2.0/0.0 (2)	1.9/3.6 (9)	1.5/2.1 (2)	1.8/1.4 (6)	2.0/1.9 (9)	1.0 (1)						
		F1	F2	E3	E1	E2	E3		H1	H2	H3		
Zonations													

Fig. 67. Estimated depth to the water table and standard deviation of the same for each of the site-types. Number of observations in brackets.

Tab. 9. The vegetation of the E1PC site-type.

Sample set No.	S1	S2	S3	S4	S	O	
Number of samples	5	5	5	5	20	2	22
Zone	E1	E1	E2	E2		E2	
<i>Anaromeda polifolia</i>	100- 1	100- 2	40- 1	80- 2	80- 1	+	82- 1
<i>Vaccinium oxycoccos</i> coll.	80- 1	60- 1	60- 1	100- 1	75- 1	+	73- 1
<i>Drosera anglica</i>	100- 1	100- 2	80- 1	100- 1	95- 2	+	96- 2
<i>Eriophorum vaginatum</i>	60- 2	100- 2	20- 3	100- 2	70- 2	+	73- 2
<i>Rhynchospora alba</i>	100- 3	100-12	100- 3	100- 9	100- 7	+	100- 7
<i>Sphagnum balticum</i>	100- 2	100- 4	60- 8	100- 2	90- 3	+	91- 4
<i>S. cuspidatum</i>	100-91	100-92	100-95	100-97	100-94	+	100-92
<i>S. magellanicum</i>	40- 1	40- 1	80- 1	20- 1	45- 1	+	45- 1
<i>S. tenellum</i>	20- 1	80- 2	20- 1	60- 4	45- 2	+	50- 2
<i>Cephalozia</i> spp.	20- 1	20- 1	-	40- 1	20- 1	+	23- 1
<i>Cladopodiella fluitans</i>	100- 9	100- 5	40- 2	100- 2	85- 5	+	86- 5

Additional species (with constancy below 10):

Drosera anglica x *rotundifolia* 5-1 (S1: 20-1; S: 5-1), *D. rotundifolia* 9-1 (S1: 20-1; S: 5-1, O: +).

Sphagnum rubellum 9-1 (S1: 40-1; S: 10-1).

Calypogeja sphagnicola 5-1 (S1: 20-1; S: 5-1), *Gymnocolea inflata* 9-6 (O: +).

The mire expanse carpet series

The E1PC site-type

The floristic composition of this site-type is shown in Tab. 9. The constant species are *Andromeda polifolia*, *Drosera anglica*, *Rhynchospora alba*, *Sphagnum balticum*, *S. cuspidatum*, and *Cladopodiella fluitans*. The only dominant is *Sphagnum cuspidatum*.

The mean number of species per sample plot is 12, while the total number in the 22 sample plots is 16. Physiognomically the site-type is characterized as a continuous carpet of *Sphagnum cuspidatum* with a sparse cover of vascular plants.

The site-type covers less than 0.5 per cent of the special area, confined to the central parts of larger hollows. It is quantitatively more important in the E2 than in the E1 zone. E1 occurrences have only been encountered as small segments in larger hollows close to the E2 transition at pos. 09 07-10.

The variation of the site-type is negligible.

The E2PC site-type

The floristic composition of this site-type is shown in Tab. 10. The constant and only dominant species are *Sphagnum cuspidatum* and *S. majus* (except for the occasional dominance of *S. lindbergii*).

The mean number of species per sample plot is 11, while the total number in the 37 sample plots is 24. This site-type is characterized by having an often floating continuous carpet of *Sphagnum* and a field layer with graminids in variable density.

The estimated area of this site-type is 2 per cent. It occurs in wet parts of the fen

Tab. 10. The vegetation of the E2PC site-type.

Sample set No.	S1	S2	S3	S4	S5	O1	O2	S	O	
Number of samples	5	5	5	5	5	11	1	25	12	37
Zone	E2	E2	E2	E2	E2	E2	E3			
<i>Anemone pulsatilla</i>	60- 1	40- 1	40- 2	20- 1	20- 1	64- 2	-	36- 1	58- 2	43- 1
<i>Vaccinium oxycoccos</i> coll.	100- 1	20- 1	40- 1	60- 1	20- 1	64- 2	-	48- 1	58- 2	51- 1
<i>Prosera anglica</i>	80- 1	100- 1	60- 1	80- 1	60- 1	64- 1	+	76- 1	67- 2	73- 1
<i>Carex limosa</i>	-	-	20-10	80- 7	60- 6	36- 2	-	32- 7	33- 2	32- 5
<i>Eriophorum vaginatum</i>	40- 2	100- 4	80- 2	-	60- 1	55- 4	-	56- 3	50- 4	54- 3
<i>Rhynchospora alba</i>	60- 1	100- 5	40- 5	80- 2	100- 6	73- 5	+	76- 4	75- 5	76- 4
<i>Scheuchzeria palustris</i>	80- 2	-	20- 3	60- 4	80- 6	27-10	-	48- 4	25-20	41- 6
<i>Sphagnum balticum</i>	20- 1	20- 2	80- 5	80- 7	-	55- 6	-	40- 6	50- 6	43- 5
<i>S. compactum</i>	80- 2	20- 1	-	-	-	-	-	20- 2	-	14- 2
<i>S. cuspidatum</i>	100-17	100-19	100-66	100-30	100-17	100-44	+	100-32	100-47	100-37
<i>S. lindbergii</i>	80-16	-	-	-	-	-	-	16-16	-	11-16
<i>S. magellanicum</i>	100- 3	-	40- 1	60- 2	40- 3	73- 2	-	48- 2	67- 2	54- 2
<i>S. majus</i>	100-53	100-79	40-68	100-63	100-71	64-52	+	88-67	67-49	81-62
<i>S. papillosum</i>	100-12	20- 1	60- 1	20- 4	60- 1	73-10	+	52- 6	75- 9	59- 7
<i>S. tenellum</i>	20- 1	-	40- 2	-	20- 1	36- 3	-	16- 1	33- 1	22- 2
<i>Cladopodiella fluitans</i>	100- 2	100- 3	80- 2	20- 1	60- 1	64- 6	+	72- 2	67- 6	70- 3

Additional species (with constancy below 10):

Prosera anglica x *rotundifolia* 3-1 (S1: 20-1; S: 4-1), *D. rotundifolia* 5-1 (O1: 18-1; O: 17-1).

Scirpus cespitosus 3-2 (S4: 20-2; S: 4-2).

Drepanocladus fluitans 3-2 (O1: 9-2; O: 8-2).

Sphagnum rubellum 8-1 (S3: 20-2, O1: 18-1; S: 4-2, O: 17-1).

Calypogeja sphagnicola 5-1 (S4: 20-1, O1: 9-1; S: 4-1, O: 8-1), *Cephalozia* spp. 5-3 (O1: 18-3; O: 17-3), *Mytilia anomala* 3-1 (O1: 9-1; O: 8-1).

soaks; particularly frequent in the western soak (pos. 04-05 09-11) and the erosion area. Large stands are also encountered at pos. 08-09 16-18.

Some variation occurs with respect to dominance relationships in the bottom layer. *Sphagnum majus* and *S. cuspidatum* often co-dominate, with *S. majus* as the quantitatively most important species. In two or three sites, *S. lindbergii* dominates over 0.1-0.5 m². There is considerable variation in presence and relative amounts of the four common graminids.

The E3PC site-type

The floristic composition of this site-type is shown in Tab. 11. The constant (and only dominant ones) species are *Sphagnum cuspidatum* and *S. majus*.

The mean number of species per sample plot is 9, while the total number in the 27 sample plots is 21.

Physiognomically this site-type is characterized by having a floating continuous *Sphagnum* carpet with graminids.

The site-type covers less than 0.5 per cent of the special area, and occurs in wet parts of most E3 areas.

Variation occurs with respect to dominance relationships of *Sphagnum cuspidatum* and *S. majus*, as well as the relative importance of the six common graminid species. Stands almost devoid of a field layer occur (e.g., S1 in Tab. 11).

The E1RC site-type

The floristic composition of this site-type is shown in Tab. 12. No constants occur, and *Cladopodiella fluitans* and *Sphagnum cuspidatum* are the only dominants.

Tab. 11. The vegetation of the E3PC site-type.

Sample set No.	S1	S2	S3	S4	S5	S	O	
Number of samples	5	5	5	5	5	25	2	27
Zone	E3	E3	E3	E3	E3			
<i>Andromeda polifolia</i>	80- 1	100- 1	100- 1	20- 1	80- 1	76- 1	+	78- 1
<i>Myrica gale</i>	80- 2	-	100- 4	-	-	36- 3	-	33- 3
<i>Vaccinium oxycoccos</i> coll.	60- 1	60- 1	60- 1	20- 1	100- 1	60- 1	+	63- 1
<i>Drosera anglica</i>	100- 1	100- 1	100- 1	40- 1	40- 1	76- 1	+	74- 1
<i>Carex limosa</i>	-	100- 5	-	-	20- 7	24- 6	+	26- 5
<i>C. rostrata</i>	-	-	-	100- 2	100- 3	40- 2	+	41- 2
<i>Eriophorum angustifolium</i>	-	100- 6	20- 1	-	-	24- 5	+	26- 5
<i>E. vaginatum</i>	100- 2	40- 1	60- 1	-	100- 2	60- 2	+	63- 2
<i>Rhynchospora alba</i>	60- 2	100- 2	100- 7	-	60- 3	64- 4	+	63- 4
<i>Scheuchzeria palustris</i>	-	100- 5	60- 5	100- 6	60-10	64- 6	+	63- 6
<i>Sphagnum balticum</i>	-	20- 1	40- 1	60- 3	80- 4	40- 3	+	41- 3
<i>S. cuspidatum</i>	100-69	100-46	80-53	100-47	60-75	88-57	+	89-54
<i>S. magellanicum</i>	40- 1	20- 1	20- 1	60- 1	80- 5	44- 2	+	44- 2
<i>S. majus</i>	100-30	100-54	80-71	100-50	100-46	96-49	+	96-50
<i>S. papillosum</i>	60- 2	40- 1	40- 1	80- 1	40- 3	52- 1	+	56- 1
<i>S. tenellum</i>	20- 1	-	100- 1	-	60- 1	36- 1	+	37- 1
<i>Cladopodiella fluitans</i>	100- 2	60- 1	80- 2	20- 1	80- 3	68- 2	+	70- 2

Additional species (with constancy below 10):

Erica tetralix 4-2 (S1: 20-2; S: 4-2).

Drepanocladus fluitans 4-1 (S4: 20-1; S: 4-1).

Sphagnum rubellum 7-1 (S5: 20-1; S: 4-1, O: +).

Gymnocolea inflata 7-1 (S1: 20-1, S3: 20-1; S: 8-1).

The mean number of species per sample plot is 7, while the total number in the 42 sample plots is 20.

The site-type comprises mud-bottoms with no or a discontinuous bottom layer. Hepatics are more prominent than *Sphagnum* spp. Vascular plants occur, mostly as stunted individuals with distinct signs of low vitality.

The estimated area of this site-type is 3 per cent. It occurs in the central parts of all fen soaks, and is more common in the E2 than in the E1 zone. In the latter it occurs in the central part of the larger hollows.

The variation is considerable. Some sample plots completely lack vegetation. More common is the scattered occurrence of small *Sphagnum cuspidatum* carpets, more or less densely set with *Cladopodiella fluitans* and *Sphagnum tenellum*, in a mosaic with bare peat. The bryophytes often grow horizontally, and are covered with algae to variable extents. Small scattered tussocks of dwarf shrubs and graminids occur, and form templates for a prolific growth of *Cladopodiella fluitans*.

The E2RC site-type

The floristic composition of this site-type is shown in Tab. 13. The constants are *Drosera anglica*, *Rhynchospora alba*, *Sphagnum cuspidatum*, and *Cladopodiella fluitans*. Dominants are *Sphagnum compactum*, *S. cuspidatum*, and *Cladopodiella fluitans*.

The mean number of species per sample plot is 10, while the total number in the 36 sample plots is 28.

Tab. 12. The vegetation of the EIRC site-type.

Sample plot No.	S1	S2	S3	S4	O1	O2	S	O	
Number of samples	5	5	5	5	7	15	20	22	42
Zone	E1	E1	E2	E2	E1	E2			
<i>Andromeda polifolia</i>	60- 1	100- 1	100- 1	40- 1	57- 2	47- 1	75- 1	50- 1	62- 1
<i>Vaccinium oxycoccos</i> coll.	80- 1	80- 1	40- 1	60- 1	43- 1	40- 1	65- 1	41- 1	52- 1
<i>Drosera anglica</i>	60- 1	100- 3	100- 2	20- 1	57- 1	27- 1	70- 2	36- 1	52- 2
<i>D. rotundifolia</i>	-	-	-	-	43- 1	27- 1	-	32- 1	17- 1
<i>Eriophorum vaginatum</i>	20- 1	60- 4	80- 2	80- 2	57- 6	53- 3	60- 2	55- 4	57- 3
<i>Rhynchospora alba</i>	100- 2	100- 7	100- 5	80- 2	57- 7	33- 9	95- 4	41- 8	67- 5
<i>Sphagnum balticum</i>	60- 1	100- 2	80- 2	60- 1	57- 6	33- 9	75- 2	41- 8	57- 4
<i>S. cuspidatum</i>	80- 4	100-19	100-21	100- 4	71-25	60-25	95-12	64-25	79-18
<i>S. magellanicum</i>	-	-	-	-	14- 1	20- 2	-	18- 2	10- 2
<i>S. rubellum</i>	-	-	20- 1	-	14- 2	13- 1	5- 1	14- 1	10- 1
<i>S. tenellum</i>	80- 1	100- 1	100- 5	40- 3	71-11	53- 9	80- 3	59-10	69- 6
<i>Cephalozia</i> spp.	20- 7	100- 1	-	-	-	40- 3	30- 2	27- 3	29- 3
<i>Cladopodiella fluitans</i>	100-47	100-45	100-15	80-11	57-12	40- 8	95-31	45-10	69-24
<i>Gymnocolea inflata</i>	-	-	-	-	29- 4	13- 6	-	18- 5	10- 5
<i>Mylia anomala</i>	20- 1	-	20- 1	-	14- 1	7- 1	10- 1	9- 1	10- 1

Additional species (with constancy below 10):

Calluna vulgaris 7-1 (O2: 20-1; O: 14-1).

Drosera anglica x *rotundifolia* 2-1 (O1: 14-1; O: 5-1).

Scirpus cespitosus 5-1 (O2: 13-1; O: 9-1).

Calypogeia sphagnicola 5-1 (O2: 13-1; O: 9-1), *Kurzia pauciflora* 5-1 (O1: 14-1, O2: 7-1; O: 9-1).

Cladonia squamosa 7-2 (S4: 20-1, O2: 13-2; S: 5-1, O: 9-2).

The site-type appears as patches of *Sphagnum* spp., often strongly intermingled with hepatics, in a matrix of bare peat. The sparse field layer of low vitality is mainly concentrated to the patches where a bottom layer is present.

The estimated area covered by this site-type is 2.5 per cent. It is common in the central, wetter parts of the fen soaks and in the erosion area.

The one extreme encountered within this site-type, comprises stands almost devoid of vegetation (S3 in Tab. 13). Such sites covers considerable areas in the erosion area where the otherwise rare species *Dicranella cerviculata* and *Cladonia pleurota* were observed growing directly on bare peat. The typical variant of this site-type includes *Sphagnum cuspidatum* and *S. compactum* as the prominent species. *Cladopodiella fluitans*

		Subseries									
		P			R						
Series	EHu	5+10	1+ 5	1+ 2	15+19	5+ 7		26+29	25+27	13+23	MHu
	EH1	5+ 7	2+ 3	1+ 2	27+18	27+22				1+ 2	MH1
	ELu	1+ 3	1+ 3	1+ 2	11+12	3+ 5	0+ 0				
	EL1	0+ 0	3+10	0+ 0	14+19	10+16	1+ 3				
	EC	1+ 3	3+ 9	1+ 5	66+37	44+36	48+37				
		E1	E2	E3	E1	E2	E3	M1	M2	M3	
Zonations											

Fig. 68. Mean cover of bare peat and standard deviation of the same for each of the site-types. Based on visual estimates in all sample plots classified to site-type (the R and S data sets).

Tab. 13. The vegetation of the E2RC site-type.

Sample set No.	S1	S2	S3	S4	O1	O2	S	O	
Number of samples	5	5	5	5	15	1	20	16	36
Zone	E2	E2	E2	E2	E2	E3			
<i>Andromeda polifolia</i>	60- 1	100- 1	20- 1	80- 1	93- 1	+	65- 1	94- 1	78- 1
<i>Vaccinium oxycoccos</i> coll.	60- 1	80- 1	40- 1	100- 1	87- 1	+	70- 1	88- 1	78- 1
<i>Drosera anglica</i>	100- 1	100- 2	40- 2	80- 4	80- 2	+	80- 2	81- 2	80- 2
<i>D. rotundifolia</i>	-	-	-	-	27- 1	+	-	31- 1	14- 1
<i>Eriophorum vaginatum</i>	-	100- 3	-	60- 6	60- 5	+	40- 4	63- 6	50- 5
<i>Rhynchospora alba</i>	100- 1	100- 8	60- 1	100- 3	80- 7	+	90- 3	81- 7	86- 5
<i>Scheuchzeria palustris</i>	-	-	-	40- 1	13- 5	+	10- 1	19- 3	14- 2
<i>Sphagnum balticum</i>	-	80- 1	40- 1	40- 1	73- 8	+	40- 1	75- 7	56- 5
<i>S. compactum</i>	100-36	100-25	-	100-10	27- 4	-	75-24	25- 4	53-20
<i>S. cuspidatum</i>	100- 5	100-23	80- 1	80-38	93-26	+	90-16	94-25	92-20
<i>S. magellanicum</i>	-	-	-	20- 1	33- 3	-	5- 1	31- 3	17- 3
<i>S. majus</i>	60- 1	-	40- 4	20-12	67- 8	+	30- 4	69- 8	47- 7
<i>S. papillosum</i>	80- 2	-	-	-	60- 2	-	20- 2	56- 2	36- 2
<i>S. rubellum</i>	-	-	-	-	27- 1	-	-	25- 1	11- 1
<i>S. tenellum</i>	100- 4	100- 1	20- 1	60- 2	80- 9	+	70- 2	81- 8	75- 5
<i>Cephalozia</i> spp.	-	-	40- 1	20- 2	40- 3	+	15- 1	44- 2	28- 2
<i>Cladopodiella fluitans</i>	100-47	100-34	40- 2	100-36	93-10	+	85-35	94- 9	89-23
<i>Gymnocolea inflata</i>	-	-	-	20-12	47- 8	+	5-12	50- 9	25- 9

Additional species (with constancy below 10):

Calluna vulgaris 3-1 (S3: 20-1; S: 5-1).

Drosera anglica x *rotundifolia* 8-1 (O1: 20-1; O: 19-1).

Carex limosa 8-1 (S3: 60-4; S: 15-4), *Scirpus cespitosus* 3-1 (O1: 7-1; O: 6-1).

Dicranella cerviculata 3-3 (S3: 20-1; S: 5-3).

Calypogeja sphagnicola 6-1 (O1: 13-1; O: 13-1), *Kurzia pauciflora* 3-1 (O1: 7-1; O: 6-1), *Mylia anomala* 8-1 (S4: 20-1, O1: 13-1; S: 5-1, O: 13-1).

Cladonia pleurota 3-1 (S3: 20-1; S: 5-1), *C. squamosa* 6-1 (S3: 20-2, O1: 7-1; S: 5-1, O: 6-1).

mostly occurs as the dominant hepatic, but *Gymnocolea inflata* occasionally dominates, particularly in the presence of *Sphagnum compactum*.

The E3RC site-type

The floristic composition of this site-type is shown in Tab. 14. The constants are *Rhynchospora alba*, *Sphagnum cuspidatum*, *S. tenellum*, and *Cladopodiella fluitans*. The main dominant is *Cladopodiella fluitans*, occasional dominants are *Sphagnum compactum*, *S. majus*, and *Gymnocolea inflata*.

The mean number of species per sample plot is 10, while the total number in the 21 sample plots is 22.

The site-type includes mud-bottoms dominated by patches of *Cladopodiella fluitans*, growing on bare peat or among *Sphagnum* spp. of low vitality. The field layer is mostly sparse, with variable vitality.

The site-type covers small areas in the wetter parts of the E3 zone. There is only small variation within the site-type, mainly relating to the occasional dominance of *Gymnocolea inflata* over *Cladopodiella fluitans*, the relative importance of *Sphagnum* spp., and presence of the six graminid species (cf. Tab. 14).

Tab. 14. The vegetation of the E3RC site-type.

Sample set No.	S1	S2	S3	S4	S	O	
Number of samples	5	5	5	5	20	1	21
Zone	E3	E3	E3	E3			
<i>Anaromeda polifolia</i>	80- 1	60- 1	60- 1	80- 1	70- 1	+	71- 1
<i>Myrica gale</i>	80- 6	-	40- 1	-	30- 4	-	29- 4
<i>Vaccinium oxycoccos</i> coll.	60- 1	60- 1	20- 1	60- 1	50- 1	+	52- 1
<i>Drosera anglica</i>	100- 2	60- 1	60- 1	80- 1	75- 1	+	76- 1
<i>Carex limosa</i>	-	20- 2	-	40- 2	15- 2	-	14- 2
<i>C. rostrata</i>	-	-	40- 2	100- 3	35- 2	-	33- 2
<i>Eriophorum angustifolium</i>	20- 7	80- 6	40- 5	-	35- 6	+	38- 7
<i>E. vaginatum</i>	40- 2	40- 4	-	100- 2	45- 2	+	48- 4
<i>Rhynchospora alba</i>	100- 2	60- 1	100- 2	100- 1	90- 2	-	90- 2
<i>Scneuchzeria palustris</i>	60- 2	20- 1	20- 1	20- 7	30- 2	-	29- 2
<i>Sphagnum balticum</i>	40- 1	-	-	80- 1	30- 1	+	33- 2
<i>S. compactum</i>	100-18	40- 2	60- 1	20-75	55-16	+	57-15
<i>S. cuspidatum</i>	80- 3	100- 3	100- 5	80- 3	90- 3	+	90- 3
<i>S. majus</i>	40- 6	80- 8	20- 1	60- 9	50- 7	+	52-13
<i>S. papillosum</i>	60- 2	40- 1	20- 1	-	30- 1	+	33- 1
<i>S. tenellum</i>	100- 5	80- 1	100- 1	100- 3	95- 3	+	95- 3
<i>Cephalozia</i> spp.	-	-	-	60- 2	15- 2	-	14- 2
<i>Cladopodiella fluitans</i>	100-52	100-26	100-18	80-14	95-28	+	95-27
<i>Gymnocolea inflata</i>	40-16	-	60-46	-	25-34	+	29-30

Additional species (with constancy below 10):

Sphagnum magellanicum 5-1 (O: +).

Mylia anomala 5-1 (S4: 20-1; S: 5-1).

Cladonia squamosa 5-1 (S4: 20-1; S: 5-1).

Survey of the mire expanse carpet series

A survey of the mire expanse carpet series is given in Tab. 15. The physiognomy is strikingly different between the subseries; the P subseries has a closed *Sphagnum* carpet, the R subseries is mud-bottoms with patches of hepatics and *Sphagnum* spp. in a matrix of bare peat (cf. Fig. 68). Graminids are by far the most important taxocene in the field layer, but in most plots they occur as scattered individuals only.

Floristically, the series is characterized by the presence (or dominance) of the seven species of group 1 in Tab. 15, all reaching high importance throughout the zones and subseries. *Sphagnum cuspidatum* is present in almost every sample plot. The P subseries is characterized by an unbroken carpet of *Sphagnum cuspidatum* or *S. majus*, and by the frequent presence of the group 4-5 species *S. magellanicum* and *S. papillosum*, while the R subseries is characterized by dominance of *Cladopodiella fluitans* (rarely *Sphagnum compactum* or *Gymnocolea inflata*) and the presence of group 6 species. The frequent, but scattered occurrence of species with optima in the L1 and Lu series, e.g., *Drosera rotundifolia*, *Scirpus cespitosus*, *Cephalozia* spp., *Mylia anomala*, and *Cladonia squamosa*, is characteristic of the R subseries. The zonations differ by the zonal indicator species of groups 2, 5 and 7 (for E2), and 3 (for E3). Quantitatively as well as qualitatively, the E2 and E3 site-types of the P subseries are better characterized by zonal indicators than the R subseries. Apart from *Cephalozia* spp., no species show marked decline from

Tab. 15. Survey of the EPC series.

Subseries	P			R		
Zonation	E1	E2	E3	E1	E2	E3
Site-type	E1PC	E2PC	E3PC	E1RC	E2RC	E3RC
Number of sample plots	22	37	27	42	36	21
<i>Andromeda polifolia</i>	82- 1	43- 1	78- 1	62- 1	78- 1	71- 1
<i>Vaccinium oxycoccos</i> coll.	73- 1	51- 1	63- 1	52- 1	78- 1	52- 1
<i>Drosera anglica</i>	96- 2	73- 1	74- 1	52- 2	80- 2	76- 1
<i>Eriophorum vaginatum</i>	73- 2	54- 3	63- 2	57- 3	50- 5	48- 4
<i>Rhynchospora alba</i>	100- 7	76- 4	63- 4	67- 5	86- 5	90- 2
<i>Sphagnum balticum</i>	91- 4	43- 5	41- 3	57- 4	56- 5	33- 2
<i>S. cuspidatum</i>	100-92	100-37	89-54	79-18	92-20	90- 3
<i>Carex limosa</i>	-	32- 5	26- 5	-	8- 1	14- 1
<i>Myrica gale</i>	-	-	33- 3	-	-	29- 4
<i>Carex rostrata</i>	-	-	41- 2	-	-	33- 2
<i>Eriophorum angustifolium</i>	-	-	26- 5	-	-	38- 7
<i>Sphagnum magellanicum</i>	45- 1	54- 2	44- 2	10- 2	17- 3	5- 1
<i>Scheuchzeria palustris</i>	-	41- 6	63- 6	-	14- 2	29- 2
<i>Sphagnum majus</i>	-	81-62	96-50	-	47- 7	52-13
<i>S. papillosum</i>	-	59- 7	56- 1	-	36- 2	33- 1
<i>Sphagnum tenellum</i>	50- 2	22- 2	37- 1	69- 6	95- 5	95- 3
<i>Cephalozia</i> spp.	23- 1	5- 3	-	29- 3	28- 2	14- 2
<i>Cladopodiella fluitans</i>	86- 5	70- 3	70- 2	69-24	89-23	95-27
<i>Gymnocolea inflata</i>	9- 6	-	7- 1	10- 5	25- 9	29-30
<i>Sphagnum compactum</i>	-	14- 2	-	-	53-20	57-15

the E1 to the E3 zonation.

The EC series makes up ca. 8 per cent of the special area. The highest areal importance of carpets and mud-bottoms is in fen soaks and in the erosion area (cf. Fig. 5), where such vegetation occupies the wettest parts. In the E1 zone the carpet series is quantitatively less important, mostly restricted to large hollows bordering on fen soaks.

Carpets occupy sites with site-type means for median depth to the water table in the range 1.0-2.0 cm (Tab. 16, Fig. 67), indicating that the bottom layer is inundated for 25-40 per cent of the ice-free season. Maximum water tables are 3-6 cm above the bottom layer surface (Tab. 17). The slight difference between subseries indicated in Tabs I-15 and 16 is probably an effect of the sparse material (compare with Fig. 67). This series is inundated after heavy rain. The average distance to the compensation level is 0 cm. In periods of strong drought, the carpet sphagna mostly dry out very quickly (as compared to the P lawn and hummock series), except for very large and wet hollows. On 8 August 1982 the mudbottoms all over the special area were covered by a paper-like film of dried-out algae. In many places, this film broke up into a polygonal pattern.

Tab. 16. Median water-table (P_{50}) of the subseries. Only samples providing measurements for 2 or three years are included. The statistics tabulated are based upon $P_{50,3}$ or $\hat{P}_{50,3}$. n - number of samples.

Subseries	n	$x_{\min}$	$\bar{x} - SD$	$\bar{x}$	$\bar{x} + SD$	$x_{\max}$
EPHu	21	13	15.8	19.8	23.8	29
ERHu	7	11	12.2	18.0	23.8	25
EPH1	30	8	9.4	14.4	19.4	25
ERH1	15	8	8.5	13.1	17.7	23
EPLu	7	5	4.8	7.4	10.0	11
ERLu	13	4	3.7	6.8	9.9	12
EPL1	16	2	3.7	5.8	7.9	9
ERL1	35	2	3.1	4.9	6.7	9
EPC	2	-1		0.0		1
ERC	3	0		1.7		4
MHu	22	10	15.8	21.0	26.3	32

Tab. 17. Maximum water-table (P_0) of the subseries. Only samples providing measurements for 2 or 3 years are included. The statistics tabulated are based upon $P_{0,3}$ or $\hat{P}_{0,3}$. n - number of samples.

Subseries	n	$x_{\min}$	$\bar{x} - SD$	$\bar{x}$	$\bar{x} + SD$	$x_{\max}$
EPHu	21	4	6.7	10.5	14.3	17
ERHu	7	2	3.1	9.3	15.5	16
EPH1	30	0	1.2	5.8	10.4	15
ERH1	15	-1	0.9	5.2	9.5	14
EPLu	7	-3	-2.5	0.1	2.7	5
ERLu	13	-2	-1.8	0.1	2.0	4
EPL1	16	-4	-3.3	-1.6	0.1	1
ERL1	35	-4	-3.6	-1.8	0.0	2
EPC	2	-6		-5.0		-4
ERC	3	-4		-3.7		-3
MHu	22	2	5.9	11.9	17.9	16

Tab. 18. The vegetation of the E1PL1 site-type.

Sample set No.	S1	S2	S3	S4	S	O	
Number of sample plots	5	5	5	5	20	4	24
Zone	E1	E1	E2	E2			
<i>Andromeda polifolia</i>	100- 3	100- 2	100- 2	60- 1	90- 2	100- 3	92- 3
<i>Vaccinium oxycoccos</i> coll.	100- 1	60- 2	100- 3	100- 1	90- 2	100- 2	92- 2
<i>Drosera anglica</i>	100- 3	100- 1	100- 1	20- 1	80- 2	100- 2	83- 2
<i>D. anglica</i> x <i>rotundifolia</i>	20- 1	-	40- 1	-	15- 1	-	13- 1
<i>D. rotundifolia</i>	80- 2	60- 1	100- 1	40- 1	70- 1	100- 1	75- 1
<i>Rubus chamaemorus</i>	40- 1	60- 1	40- 1	-	35- 1	25- 1	33- 1
<i>Eriophorum vaginatum</i>	100- 6	100-17	100- 3	100-15	100-10	100- 9	100-10
<i>Rhynchospora alba</i>	100- 7	-	100-19	20- 3	55-12	100-22	63-15
<i>Scirpus cespitosus</i>	40- 1	-	-	-	10- 1	50- 2	17- 2
<i>Sphagnum balticum</i>	100-44	100-14	20- 5	100-71	80-41	100-15	83-36
<i>S. cuspidatum</i>	-	100- 3	80- 2	40-10	55- 4	50-13	54- 5
<i>S. magellanicum</i>	60- 1	100- 5	100-87	100-12	90-29	100-35	92-30
<i>S. rubellum</i>	100-45	100-78	80- 7	100-12	95-37	75-39	92-37
<i>S. tenellum</i>	100- 8	-	80- 5	80- 2	65- 5	100-12	71- 7
<i>Calypogeja sphagnicola</i>	40- 1	60- 1	60- 1	20- 1	45- 1	25- 1	42- 1
<i>Cephalozia</i> spp.	100- 2	20- 1	-	-	30- 2	75- 2	38- 2
<i>Cladopodiella fluitans</i>	100-13	100- 2	100- 2	100- 1	100- 4	100- 6	100- 4
<i>Kurzia pauciflora</i>	20- 2	20- 1	-	-	10- 2	75- 3	21- 3
<i>Mylia anomala</i>	80- 2	60- 1	-	20- 1	40- 2	75- 1	46- 2

Additional species (with constancy below 10):

Calluna vulgaris 8-2 (O: 50-2).

The mire expanse lower lawn series

The E1PL1 site-type

The floristic composition of this site-type is shown in Tab. 18. The constant species are *Andromeda polifolia*, *Vaccinium oxycoccos* coll., *Drosera anglica*, *Eriophorum vaginatum*, *Sphagnum balticum*, *S. magellanicum*, *S. rubellum*, and *Cladopodiella fluitans*. The field layer is occasionally dominated by *Eriophorum vaginatum* and *Rhynchospora alba*. Dominants of roughly equal total importance in the bottom layer are *Sphagnum balticum*, *S. magellanicum*, and *S. rubellum*.

The mean number of species per sample plot is 12, while the total number in the 24 sample plots is 20.

Physiognomically the site-type is characterized by dominance of graminids; tussocks of *Eriophorum vaginatum* with more or less dense stands of *Rhynchospora alba* in between. Other vascular plants only occur as scattered individuals. The bottom layer is a closed *Sphagnum* lawn with frequent occurrences of *Cladopodiella fluitans*, while other hepatics are unimportant.

The site-type covers about 0.5 per cent of the special area, mostly along the margins of larger hollows in the E1-E2 transition on the N and NE sides of the unilaterally sloping kermi raised bog area.

The variation within this site-type is small. The local frequency of *Rhynchospora alba* is variable (cf. Tab. 18), so is also the dominance relationships of the three major

Tab. 19. The vegetation of the E2PL1 site-type.

Sample set No.	S1	S2	S3	S4	S5	S	O	
Number of sample plots	5	5	5	5	5	25	18	43
Zone	E2	E2	E2	E2	E2			
<i>Andromeda polifolia</i>	100- 1	80- 1	100- 1	100- 2	100- 2	96- 2	94- 3	95- 2
<i>Vaccinium oxycoccos</i> coll.	100- 1	100- 1	100- 1	100- 1	100- 1	100- 1	83- 2	93- 1
<i>Drosera anglica</i>	100- 2	80- 1	100- 1	100- 2	100- 2	96- 2	94- 2	95- 2
<i>D. anglica</i> x <i>rotundifolia</i>	20- 1	40- 1	-	-	-	12- 1	17- 1	14- 1
<i>D. rotundifolia</i>	100- 1	100- 1	100- 1	80- 1	100- 1	96- 1	94- 1	95- 1
<i>Rubus chamaemorus</i>	40- 1	20- 1	60- 1	20- 1	-	28- 1	39- 1	33- 1
<i>Eriophorum vaginatum</i>	100- 4	100-11	100-12	100- 6	100-13	100- 9	94-11	98-10
<i>Rhynchospora alba</i>	60- 2	20- 1	80- 3	40-28	100- 3	60- 6	89-11	72- 9
<i>Scheuchzeria palustris</i>	40- 2	-	-	20- 4	60- 7	24- 5	22- 6	23- 5
<i>Scirpus cespitosus</i>	-	-	-	60- 1	-	12- 1	17- 1	14- 1
<i>Sphagnum balticum</i>	80- 6	80- 3	60- 4	100-36	80- 4	80-12	100-26	88-18
<i>S. compactum</i>	20- 2	-	20- 2	-	-	8- 2	11- 3	10- 3
<i>S. cuspidatum</i>	40- 1	20- 1	60- 2	80-22	60- 2	52- 8	50- 4	51- 6
<i>S. magellanicum</i>	100-16	100-39	100-51	100-12	100-28	100-29	94-13	98-23
<i>S. majus</i>	60- 6	20- 1	-	-	100- 6	36- 6	39- 5	37- 6
<i>S. papillosum</i>	100-47	100-50	100-40	100-10	100-54	100-40	94-28	98-35
<i>S. rubellum</i>	100-12	80- 2	40- 2	80-19	60- 2	72- 8	89-15	79-11
<i>S. tenellum</i>	100- 7	100- 7	100- 5	100- 8	80- 8	96- 7	83-11	91- 9
<i>Calypogeja sphagnicola</i>	40- 1	20- 1	100- 1	60- 1	-	44- 1	44- 2	44- 1
<i>Cephalozia</i> spp.	-	-	-	40- 2	20- 1	12- 1	39- 2	23- 2
<i>Cladopodiella fluitans</i>	100- 4	100- 4	100- 4	100- 4	80- 2	96- 4	100- 8	98- 6
<i>Kurzia pauciflora</i>	-	-	20- 1	20- 2	-	8- 2	33- 3	19- 3
<i>Mylia anomala</i>	-	-	-	60- 1	-	12- 1	33- 1	21- 1

Additional species (with constancy below 10):

Calluna vulgaris 7-1 (O: 17-1).

Carex lasiocarpa 9-1 (S4: 40-16, S5: 40-9; S: 16-13).

Sphagnum lindbergii 5-9 (S1: 20-15; S: 4-15, O: 6-2), *S. molle* (S1: 20-20; S: 4-20).

Gymnocolea inflata 9-2 (S4: 20-2, S5: 20-1; S: 8-2, O: 11-1).

Sphagnum spp.

The E2PL1 site-type

The floristic composition of this site-type is shown in Tab. 19. The constant species are *Andromeda polifolia*, *Vaccinium oxycoccos* coll., *Drosera anglica*, *D. rotundifolia*, *Eriophorum vaginatum*, *Sphagnum balticum*, *S. magellanicum*, *S. papillosum*, *S. tenellum*, and *Cladopodiella fluitans*. Dominants in the bottom layer are *Sphagnum balticum*, *S. magellanicum*, and *S. papillosum*.

The mean number of species per sample plot is 14, while the total number in the 43 sample plots is 28.

Physiognomically, this site-type is characterized by extensive lawns dominated by species of *Sphagnum* sect. *Sphagnum*; *S. magellanicum* and *S. papillosum*, mostly intermixed with *S. balticum*, *S. rubellum*, and *S. tenellum*, and including *Cladopodiella fluitans* as a frequent species. *Eriophorum vaginatum* tussocks rise above the *Sphagnum* lawn. The dwarf shrubs and *Drosera* spp. occur frequently, but in small quantities. Graminids dominate the field layer, but with the exception of *Eriophorum vaginatum* they are normally quantitatively unimportant.

Tab. 20. The vegetation of the E3PL1 site-type.

Sample set No.	S1	S2	S3	S4	S5	S	O	
Number of sample plots	5	5	5	5	5	25	5	30
Zone	E3	E3	E3	E3	E3			
<i>Andromeda polifolia</i>	100- 5	80- 1	100- 1	60- 5	100- 1	88- 3	100- 2	90- 3
<i>Erica tetralix</i>	-	-	-	-	40- 1	8- 1	10- 1	13- 1
<i>Myrica gale</i>	100- 5	100- 2	80- 9	-	60- 4	68- 5	20- 3	60- 5
<i>Vaccinium oxycoccos</i> coll.	100- 1	100- 1	100- 2	40- 3	100- 1	88- 2	80- 1	87- 2
<i>Drosera anglica</i>	80- 1	100- 1	100- 1	60- 3	100- 1	88- 1	100- 1	90- 1
<i>D. anglica</i> x <i>rotundifolia</i>	-	-	40- 1	-	-	8- 1	20- 1	10- 1
<i>D. rotundifolia</i>	40- 1	80- 1	60- 1	60- 1	100- 1	68- 1	80- 1	70- 1
<i>Rubus chamaemorus</i>	-	-	-	-	-	-	60- 1	10- 1
<i>Carex limosa</i>	-	-	-	60- 1	-	12- 1	-	10- 1
<i>C. rostrata</i>	-	-	-	-	40- 2	8- 2	60- 2	17- 2
<i>Eriophorum angustifolium</i>	40- 2	-	100- 2	60- 3	40- 2	48- 2	-	40- 2
<i>E. vaginatum</i>	80- 5	80- 1	100- 9	60- 5	60- 1	76- 5	80-22	77- 8
<i>Rhynchospora alba</i>	100- 9	40- 1	-	40- 3	100- 5	56- 6	80- 5	60- 6
<i>Scheuchzeria palustris</i>	80- 2	100- 6	-	60-10	80- 1	64- 5	20- 4	57- 5
<i>Sphagnum balticum</i>	100- 9	100- 9	20- 1	100-10	100- 2	84-10	100- 4	87- 9
<i>S. compactum</i>	-	-	40- 1	-	20- 1	12- 1	-	10- 1
<i>S. cuspidatum</i>	-	40- 2	-	100- 2	-	28- 2	20- 3	27- 2
<i>S. magellanicum</i>	80- 4	100-12	20- 1	100-24	100-19	80-15	100-22	83-17
<i>S. majus</i>	-	40- 4	80- 3	100- 7	-	44- 5	20- 5	40- 5
<i>S. papillosum</i>	100-68	100-46	100-78	100-36	100-69	100-59	100-51	100-58
<i>S. rubellum</i>	80- 8	100- 9	20- 1	80- 9	80- 6	72- 8	100- 4	77- 7
<i>S. tenellum</i>	100-14	100- 6	100-14	100- 2	100- 5	100- 8	80-17	97-10
<i>Calypogeja sphagnicola</i>	60- 1	-	40- 1	60- 1	60- 1	44- 1	-	37- 1
<i>Cladopodiella fluitans</i>	100- 3	100- 1	100- 6	100- 5	100- 4	100- 4	100- 4	100- 4

Additional species (with constancy below 10):

Carex lasiocarpa 7-2 (S3: 20-2; S: 4-2, O: 20-1), *C. pauciflora* 3-1 (S3: 20-1; S: 4-1).

Sphagnum fallax 7-38 (S2: 40-38; S: 8-38), *S. fuscum* 3-1 (S2: 20-1; S: 4-1), *S. lindbergii* 3-1 (S1: 20-1; S: 4-1), *S. molle* 3-12 (S3: 20-12; S: 4-12).

Cephalozia spp. 7-2 (S3: 20-1; S4: 20-2; S: 8-2), *Kurzia pauciflora* 3-1 (S4: 20-1; S: 4-1).

The estimated area covered by this site-type is 3 per cent. It is particularly important in the southern and western fen soaks where it often covers large areas in the wetter parts (cf. Fig. 5).

The variation in the composition of the field layer is small; *Rhynchospora alba* rarely occurs as a dominant (S4 in Tab. 18). Variation in the bottom layer is mainly with respect to dominance relationships among *Sphagnum*. *S. papillosum* is the dominant of four S-sets and the O-set, in the latter and in S4 *S. balticum* is co-dominant. *S. magellanicum* is the dominant of three, *S. cuspidatum* and *S. rubellum* the dominant of one S-set each. The S4 set deviates by including the upper lawn species *Scirpus cespitosus* and the carpet species *Rhynchospora alba* and *Sphagnum cuspidatum*. This set originates from a stand where the L1 series occupies a narrow border between C and Lu, with considerable overlap in species distributions.

The E3PL1 site-type

The floristic composition of this site-type is shown in Tab. 20. Constant species are *Andromeda polifolia*, *Vaccinium oxycoccos* coll., *Drosera anglica*, *Sphagnum balticum*, *S.*

magellanicum, *S. papillosum*, *S. tenellum*, and *Cladopodiella fluitans*. The major dominant of the bottom layer is *Sphagnum papillosum*, minor dominants are *S. magellanicum* and *S. tenellum*.

The mean number of species per sample plot is 14, while the total number in the 30 sample plots is 32.

The light green, swelling *Sphagnum papillosum* carpets give this site-type a characteristic appearance. The field layer is often relatively dense; graminids dominate, shrubs (*Myrica gale* in particular) are not unimportant, while herbs are sparse.

The estimated area of this site-type is 1 per cent. It occurs in the wetter parts of most E3 areas. The variation within the site-type is mostly with respect to the species composition of the field layer. *Myrica gale* and all graminids except *Eriophorum vaginatum* have a patchy distribution, and seemingly occur in random combinations within the five S-sets. Occasional dominance of *Eriophorum vaginatum* tussocks (the O-set) grossly influences the appearance of the vegetation. Some variation in dominance relationships of the bottom layer is observed; *Sphagnum papillosum* may be replaced by *S. magellanicum* as the main dominant (e.g., S4 in Tab. 20).

Calypogeja sphagnicola occurs frequently in this site-type, creeping over the *Sphagnum capitula*. This species seemingly prefers growing on *Sphagnum sect. Sphagnum* individuals.

The E1RL1 site-type

The floristic composition of this site-type is shown in Tab. 21. The constant species are *Andromeda polifolia*, *Vaccinium oxycoccos* coll., *Drosera anglica*, *D. rotundifolia*, *Eriophorum vaginatum*, *Rhynchospora alba*, *Sphagnum balticum*, *S. tenellum*, *Cephalozia* spp., and *Cladopodiella fluitans*. The dominant in the field layer is *Rhynchospora alba*, while the bottom layer is dominated by *Sphagnum tenellum*, more occasionally by *S. balticum*, *Cladopodiella fluitans* or *Gymnocolea inflata*.

The mean number of species per sample plot is 15, while the total number in the 100 sample plots is 38.

The field layer is characterized by the dominance of *Rhynchospora alba*, which often forms dense, light green stands (e.g., S5 and S6 in Tab. 21), and by the constant presence of *Eriophorum vaginatum*. Dwarf shrubs occur regularly. Stunted and dead individuals of *Calluna vulgaris* are often present. The bottom layer is yellowish green owing to the dominance of *Sphagnum tenellum*, but the *Sphagnum* lawns are mostly broken by bare peat flecks, often partly covered by hepatics. Lichens occur more occasionally on elevated segments (e.g., around *Eriophorum vaginatum* tussock bases). The total number of lichen species in the site-type is high. The site-type covers ca. 11 per cent of the special area, equal parts on the E1 and E2 zones. It is common all over the mire expanse except for the western and southern fen soaks.

The field layer is remarkably invariant. The bottom layer, however, shows considerable variation with respect to total cover, the occurrence of bare peat (Fig. 68), microtopography (small tussocks and interspaces), and thus to occurrence and dominance relationships. *Sphagnum tenellum*, the most important species, reaches dominance in the majority of sample plots. In some sites with sparse cover of *Eriophorum vaginatum* it almost reaches total dominance (S6). *Cladopodiella fluitans* and *Gymnocolea inflata* mostly prefer bare peat, while *Cephalozia* spp. may dominate small elevated areas. *Cladonia squamosa* (and other lichen species) preferably grows on small, elevated bare peat flecks, frequently around *Calluna vulgaris* bases.

Tab. 21. The vegetation of the E1RL1 site-type.

Sample set No.	S1	S2	S3	S4	S5	S6	O1	O2	S	O
Number of samples	5	5	5	5	5	5	38	32	30	70
Zone	E1	E1	E1	E1	E2	E2	E1	E2		100
<i>Andromeda polifolia</i>	100- 4	100- 3	100- 3	100- 2	100- 4	100- 5	100- 3	97- 3	100- 4	99- 3
<i>Calluna vulgaris</i>	40- 1	-	80- 4	20- 2	80- 3	60- 2	79- 4	59- 4	47- 3	70- 4
<i>Vaccinium oxycoccus</i> coll.	100- 1	100- 1	100- 2	100- 1	100- 1	100- 2	100- 2	97- 2	100- 1	99- 2
<i>Drosera anglica</i>	80- 1	100- 1	100- 1	80- 1	80- 1	60- 1	92- 1	78- 1	83- 1	86- 1
<i>D. anglica x rotundifolia</i>	-	-	-	-	-	-	18- 1	13- 1	-	16- 1
<i>D. rotundifolia</i>	100- 1	60- 1	100- 1	60- 1	100- 1	60- 1	97- 1	91- 1	80- 1	94- 1
<i>Rubus chamaemorus</i>	-	-	-	-	-	-	24- 1	6- 2	-	16- 1
<i>Eriophorum vaginatum</i>	100- 3	100- 3	100- 3	100- 4	100- 2	100- 2	100-10	97- 8	100- 3	99- 9
<i>Rhynchospora alba</i>	100-17	100-19	100-19	100-16	100-39	100-40	68-10	94-13	100-25	80-12
<i>Scirpus cespitosus</i>	40- 2	-	80- 1	40- 3	60- 1	80- 2	61- 2	69- 2	50- 2	64- 2
<i>Sphagnum balticum</i>	100-14	100-11	100- 8	80- 5	100- 4	80- 2	97-17	100-15	93- 8	99-16
<i>S. cuspidatum</i>	40-11	40- 9	40-21	-	-	40- 6	16- 9	44- 6	27-12	29- 7
<i>S. magellanicum</i>	40- 2	20- 1	40- 1	-	40- 1	60- 1	50- 4	69- 4	33- 1	59- 4
<i>S. rubellum</i>	100- 1	80- 1	80- 2	40- 1	40- 1	20- 1	92- 6	75- 3	60- 1	84- 5
<i>S. tenellum</i>	100-65	100-71	100-52	100-57	100-69	100-84	100-40	100-44	100-66	100-42
<i>Cephalozia</i> spp.	100- 3	80- 1	100- 3	60- 2	100- 2	100- 1	92- 7	78- 8	90- 2	86- 7
<i>Cladopodiella fluitans</i>	100-19	100- 5	100- 9	100- 9	100- 4	100- 4	100-13	100-12	100- 8	100-12
<i>Gymnocolea inflata</i>	-	60-17	20- 1	100-16	100-11	100- 8	21- 6	44- 8	63-12	31- 7
<i>Kurzia pauciflora</i>	20- 2	-	60- 1	-	20- 1	-	50- 5	44- 5	17- 1	47- 5
<i>Mylia anomala</i>	60- 1	20- 1	100- 1	40- 2	-	40- 1	79- 3	53- 2	43- 1	67- 3
<i>Cladonia squamosa</i>	80- 2	-	100- 7	60- 1	80- 6	40- 1	42- 5	47- 5	60- 4	44- 5

Additional species (with constancy below 10):

Pinus sylvestris 2-2 (O1: 3-3; O2: 3-1; O: 3-2).*Empetrum nigrum* 1-7 (O2: 3-7; O: 1-7).*Carex pauciflora* 1-1 (O2: 3-1; O: 1-1).*Sphagnum fuscum* 1-2 (O2: 3-2; O: 1-2).*Calypogeja sphagnicola* 8-2 (S3: 20-1, O1: 11-3, O2: 9-1; S: 3-1, O: 10-2), *Cephalozia* spp. 2-1 (S3: 20-1, O2: 3-1; S: 3-1; O: 1-1), *Odontoschisma sphagni* 2-2 (O1: 3-2; O2: 3-2; O: 3-2).*Cetraria delisei* 1-7 (S4: 20-7; S: 3-7), *C. islandica* 1-7 (S5: 20-7; S: 3-7), *C. mitis* 2-1 (S5: 20-1, O1: 3-1; S: 3-1, O: 1-1), *C. pleurota* 1-1 (O2: 3-1; O: 1-1), *C. pyxidata* coll. 1-1 (3-1; O: 1-1), *C. rangiferina* 6-2 (O1: 13-2, O2: 3-1; O: 9-2), *C. stellaris* 1-2 (O1: 3-2; O: 1-2), *C. uncialis* 4-5 (S4: 20-10, S5: 20-7, S6: 20-5, O2: 3-1; S: 10-7, O: 1-1), *Micarea turfosa* 2-5 (O2: 6-5; O: 3-5), *Ochrolechia frigida* 7-2 (S3: 20-2, S4: 20-1, S5: 20-4, S6: 20-1, O1: 3-5, O2: 6-1; S: 13-2, O: 4-2).

The E2RL1 site-type

The floristic composition of this site-type is shown in Tab. 22. The constant species are *Andromeda polifolia*, *Vaccinium oxycoccus* coll., *Drosera anglica*, *D. rotundifolia*, *Eriophorum vaginatum*, *Rhynchospora alba*, *Sphagnum balticum*, *S. tenellum*; and *Cladopodiella fluitans*. The only dominant in the field layer is *Rhynchospora alba*. The dominant in the bottom layer is *Sphagnum tenellum*; more occasionally *S. balticum*, *S. compactum*, and *Cladopodiella fluitans* reach dominance.

The mean number of species per sample plot is 16, while the total number in the 60 sample plots is 36.

The field layer is mostly dominated by graminids; *Rhynchospora alba* may form dense stands. Dwarf shrubs are also frequent. The almost closed bottom layer is mostly dominated by light-coloured *Sphagnum* spp., but with locally high importance of hepatics. With the exception of *Cladonia squamosa*, lichens are almost absent. The estimated area covered by this site-type is 6 per cent. It is mostly confined to the wetter parts of the more diffuse fen soaks. The highest areal importance of this site-type is observed in the broad fen soak south of the erosion area.

Variation in the field layer is mostly with respect to quantity of *Rhynchospora alba*. The bottom layer shows a pattern of variation similar to the E1RL1 site-type, and a similar microtopographic differentiation. This differentiation is often due to *Eriophorum vaginatum*

Tab. 22. The vegetation of the E2RL1 site-type.

Sample set No.	S1	S2	S3	S4	S	O	
Number of samples	5	5	5	5	20	40	60
Zone	E2	E2	E2	E2			
<i>Andromeda polifolia</i>	100- 6	100- 1	100- 2	100- 6	100- 4	100- 3	100- 3
<i>Calluna vulgaris</i>	80- 2	-	20- 1	80- 2	45- 1	45- 6	45- 4
<i>Erica tetralix</i>	-	20- 2	20-12	20-12	15- 9	8- 2	10- 6
<i>Vaccinium oxycoccus</i> coll.	100- 1	100- 1	100- 2	100- 2	100- 2	100- 2	100- 2
<i>Drosera anglica</i>	80- 1	80- 2	100- 1	60- 1	80- 1	93- 1	89- 1
<i>D. anglica</i> x <i>rotundifolia</i>	20- 1	20- 1	-	-	10- 1	18- 1	15- 1
<i>D. rotundifolia</i>	80- 1	60- 1	100- 1	100- 1	85- 1	88- 1	87- 1
<i>Eriophorum vaginatum</i>	100- 2	100-10	100- 9	100- 4	100- 6	88-11	92- 9
<i>Rhynchospora alba</i>	100-37	80- 4	100-26	100-37	95-27	93-11	94-16
<i>Scirpus cespitosus</i>	60- 2	20- 1	20- 3	80- 3	45- 2	40- 2	42- 2
<i>Sphagnum balticum</i>	100-17	20- 1	80- 2	80-10	70- 9	98-13	88-12
<i>S. compactum</i>	-	80- 9	60-21	-	35-14	25-22	28-19
<i>S. cuspidatum</i>	-	20- 1	60- 3	-	20- 3	60- 5	47- 4
<i>S. magellanicum</i>	20- 1	-	40- 1	40- 3	25- 2	85- 5	65- 4
<i>S. majus</i>	-	-	-	20- 5	5- 5	38- 3	27- 4
<i>S. papillosum</i>	100- 1	20- 1	100- 3	60- 2	70- 2	70- 4	70- 3
<i>S. rubellum</i>	60- 2	-	60- 2	60- 1	45- 2	78- 5	67- 4
<i>S. tenellum</i>	100-71	100-66	100-52	100-67	100-64	100-38	100-47
<i>Calypogeja sphagnicola</i>	-	-	20- 1	-	5- 1	25- 2	18- 2
<i>Cephalozia</i> spp.	60- 1	-	40- 2	60- 5	40- 3	70- 8	60- 7
<i>Cladopodiella fluitans</i>	100- 6	100- 8	100-11	100- 7	100- 8	100-13	100-11
<i>Gymnocolea inflata</i>	80- 5	80- 2	20-17	100- 7	70- 6	35- 7	47- 7
<i>Kurzia pauciflora</i>	-	20- 1	40- 1	-	15- 1	38- 4	30- 4
<i>Mylia anomala</i>	20- 1	-	20- 1	10- 1	15- 1	45- 1	35- 1
<i>Cladonia squamosa</i>	20- 1	20- 1	20- 4	80- 2	35- 2	30- 9	32- 7

Additional species (with constancy below 10):

Rubus chamaemorus 7-1 (S3: 20-1; S: 5-1, O: 8-1).

Carex limosa 2-1 (O: 3-1), *C. pauciflora* 2-1 (O: 3-1), *Scheuchzeria palustris* 4-2 (S4: 20-2; S: 5-2, O: 3-1).

Sphagnum molle 5-47 (S2: 40-48, S3: 20-45; S: 15-47).

Cephaloziella spp. 2-1 (O: 3-1).

Cladonia floerkeana 2-1 (O: 3-1), *C. pleurota* 3-1 (O: 5-1), *C. oxidata* coll. 2-1 (S3: 20-1; S: 5-1), *C. rangiferina* 2-1 (S1: 20-1; S: 5-1), *Ochrolechia frigida* 5-2 (S3: 20-2, S4: 20-1; S: 10-2, O: 3-1).

tussocks, apparently sinking into the surrounding *Sphagnum tenellum* lawn. *Cladonia squamosa* has been observed to prefer growing on the bases of such tussocks, sometimes associated with *Ochrolechia frigida*. The occasional dominance of *Sphagnum molle* and *S. compactum* in level segments, often slightly elevated relative to the surroundings, should be noted. The dense patches dominated by these species remained moist long after the surroundings had dried out completely (1982 observations).

A peculiar feature often noted is the killing of patches of sphagna, most often *S. tenellum*, in late summer, associated with occurrence of the fungus *Tephroclybe palustris*.

Tab. 23. The vegetation of the E3RL1 site-type

Sample set No.	S1	S2	S3	S4	S	O	
Number of samples	5	5	5	5	20	4	24
Zone	E3	E3	E3	E3			
<i>Andromeda polifolia</i>	100- 2	100- 1	100- 2	80- 3	95- 2	100- 3	96- 2
<i>Erica tetralix</i>	60- 1	-	-	60- 2	30- 2	50- 2	33- 2
<i>Myrica gale</i>	100-13	20-15	-	100- 5	55-10	100- 5	63- 9
<i>Vaccinium oxycoccos</i> coll.	100- 2	100- 2	100- 2	60- 1	90- 2	100- 3	92- 2
<i>Drosera anglica</i>	80- 3	60- 2	60- 1	100- 2	75- 2	50- 2	71- 2
<i>D. rotundifolia</i>	20- 1	20- 1	60- 1	40- 1	35- 1	100- 1	46- 1
<i>Carex lasiocarpa</i>	-	60- 2	-	-	15- 2	-	13- 2
<i>C. rostrata</i>	-	-	100- 3	40- 2	35- 3	-	29- 3
<i>Eriophorum angustifolium</i>	40- 4	80- 4	-	60- 4	45- 4	-	38- 4
<i>E. vaginatum</i>	100- 2	100-12	100-10	100- 2	100- 6	100-17	100- 8
<i>Rhynchospora alba</i>	100-13	-	80- 9	80- 8	65-10	75- 8	67-10
<i>Scheuchzeria palustris</i>	20- 7	-	-	40- 2	15- 4	50- 3	21- 4
<i>Scirpus cespitosus</i>	40- 1	20- 4	40- 1	-	25- 2	-	21- 2
<i>Sphagnum balticum</i>	80- 1	20- 2	100- 6	40- 4	60- 4	100-19	67- 8
<i>S. compactum</i>	40- 5	60-41	20- 1	80-29	50-25	25- 3	46-23
<i>S. cuspidatum</i>	-	40- 4	-	20- 3	15- 3	-	13- 3
<i>S. magellanicum</i>	100- 3	20- 1	80- 3	60- 1	65- 2	100- 3	71- 2
<i>S. majus</i>	-	60- 3	-	-	15- 3	25- 1	17- 3
<i>S. molle</i>	40-48	20-40	20-17	-	20-38	-	17-38
<i>S. papillosum</i>	20- 2	100- 1	40- 2	80- 2	60- 1	100- 9	67- 3
<i>S. rubellum</i>	40- 2	20- 1	100- 1	20- 1	45- 1	100- 2	54- 1
<i>S. tenellum</i>	100-66	100-61	100-84	100-70	100-70	100-60	100-68
<i>Cladopodiella fluitans</i>	100-14	100- 2	100- 5	100- 5	100- 6	100- 5	100- 6
<i>Gymnocolea inflata</i>	20- 1	-	-	40- 2	15- 1	25-25	17- 7

Additional species (with constancy below 10):

Drosera anglica x *rotundifolia* 8-1 (S1: 20-1; S: 5-1, O: 25-1).

Cephalozia spp. 4-1 (S2: 20-1; S: 5-1).

The E3RL1 site-type

The floristic composition of this site-type is shown in Tab. 23. The constants are *Andromeda polifolia*, *Vaccinium oxycoccos* coll., *Eriophorum vaginatum*, *Sphagnum tenellum*, and *Cladopodiella fluitans*. Dominants are rarely encountered in the field layer. *Sphagnum tenellum* always dominates the bottom layer, sometimes together with *S. compactum* and *S. molle*, or *S. balticum*.

The mean number of species per sample plot is 13, while the total number in the 24 sample plots is 26.

This site-type has a light green colour, due to the dominance of *Sphagnum tenellum*. The *Sphagnum* lawn is mostly unbroken. Shrubs, particularly *Myrica gale*, are relatively important. Graminids, notably *Eriophorum vaginatum* and *Rhynchospora alba*, are also important, and this taxocene is the dominant in the field layer.

The E3RL1 site-type covers ca. 0.5 per cent of the special area, and is mostly restricted to the E3 areas outside the western fen soak.

There is some variation in the field layer with respect to the presence of zonal indicators in various combinations, and to the amounts of *Myrica gale*, *Eriophorum*

Tab. 24. Survey of the EL1 series.

Subseries	P			R		
	E1	E2	E3	E1	E2	E3
Zonation	E1PL1	E2PL1	E3PL1	E1RL1	E2RL1	E3RL1
Number of sample plots	24	43	30	100	60	24
<i>Andromeda polifolia</i>	92- 3	95- 2	90- 3	99- 3	100- 3	96- 2
<i>Vaccinium oxycoccos</i> coll.	92- 2	93- 1	87- 2	99- 2	100- 2	92- 2
<i>Drosera anglica</i>	83- 2	95- 2	90- 1	85- 1	89- 1	71- 2
<i>D. rotundifolia</i>	75- 1	95- 1	70- 1	90- 1	87- 1	46- 1
<i>Eriophorum vaginatum</i>	100-10	98-10	77- 8	99- 7	92- 9	100- 8
<i>Rhynchospora alba</i>	63-15	72- 9	60- 6	86-17	94-16	67-10
<i>Sphagnum balticum</i>	83-36	88-18	87- 9	97-14	53-12	67- 8
<i>S. cuspidatum</i>	54- 5	51- 6	27- 2	28- 9	47- 4	13- 3
<i>Cephalozia</i> spp.	38- 2	23- 2	7- 2	87- 5	60- 7	4- 1
<i>Cladopodiella fluitans</i>	100- 4	98- 6	100- 4	100-11	100-11	100- 6
<i>Kurzia pauciflora</i>	21- 3	19- 3	3- 1	38- 4	30- 4	-
<i>Mylia anomala</i>	46- 2	21- 1	-	59- 2	35- 1	-
<i>Erica tetralix</i>	-	-	13- 1	-	10- 6	33- 2
<i>Carex limosa</i>	-	9- 1	10- 1	-	2- 1	-
<i>Myrica gale</i>	-	-	60- 5	-	-	63- 9
<i>Carex lasiocarpa</i>	-	-	7- 2	-	-	13- 2
<i>C. rostrata</i>	-	-	17- 2	-	-	29- 3
<i>Eriophorum angustifolium</i>	-	-	40- 2	-	-	38- 4
<i>Sphagnum magellanicum</i>	92-30	98-23	83-17	51- 3	65- 4	71- 2
<i>S. rubellum</i>	92-37	79-11	77- 7	78- 4	67- 4	54- 1
<i>Calypogeja sphagnicola</i>	42- 1	44- 1	37- 1	8- 2	18- 2	-
<i>Scheuchzeria palustris</i>	-	23- 5	57- 5	-	4- 2	21- 4
<i>Sphagnum majus</i>	-	37- 6	40- 5	-	27- 4	17- 3
<i>S. papillosum</i>	-	98-35	100-58	-	70- 3	67- 3
<i>Calluna vulgaris</i>	8- 2	7- 1	-	63- 4	100- 4	-
<i>Scirpus cespitosus</i>	17- 2	14- 1	-	60- 2	42- 2	21- 2
<i>Sphagnum tenellum</i>	71- 7	91- 9	97-10	100-49	100-47	100-68
<i>Gymnocolea inflata</i>	-	9- 2	-	41- 9	47- 7	17- 7
<i>Cladonia squamosa</i>	-	-	-	49- 5	32- 7	-
<i>Ocnrolechia frigida</i>	-	-	-	7- 2	5- 2	-
<i>Sphagnum compactum</i>	-	10- 3	10- 1	-	28-19	46-23
<i>S. molle</i>	-	2-20	3-12	-	5-47	17-38

vaginatum, and *Rhynchospora alba*. Except for the variable amounts of the non-constant dominants, there is little variation in the composition of the bottom layer. Hepatics are quantitatively unimportant, while lichens are lacking.

Survey of the mire expanse lower lawn series

A survey of the mire expanse lower lawn series is given in Tab. 24. The physiognomy of the series is somewhat variable. Graminids dominate in the field layer, *Eriophorum vaginatum* tussocks often give rise to a marked microtopographic variation. *Rhynchospora alba* is the common dominant of the interspaces, and of level stands. *Sphagnum* spp. dominate in both subseries. *S. magellanicum* and *S. papillosum* give the P subseries a

swelling appearance. The bottom layer of the R subseries often has a mosaic-like appearance, with irregularly alternating patches of bare peat, hepatics, and some lichen species, intermixed with *Sphagnum* lawns (cf. Fig. 69).

Floristically the series is characterized by the presence of the twelve species of group 1 in Tab. 23. As noted above, the subseries differ slightly in physiognomy. The P subseries is characterized by an unbroken *Sphagnum* lawn dominated by *S. rubellum* (E1PL1), *S. magellanicum*, and *S. papillosum* (E2PL1, E3PL1). The occurrence of *Calypogeja sphagnicola* creeping over the *Sphagnum* capitula is typical for the P subseries. The R subseries is partly characterized by a broken bottom layer, and partly by the occurrence of species of groups 6 and 7. The prominence of *Sphagnum tenellum*, *S. compactum*, *S. molle*, several hepatic species and occasionally also lichens, should be noted. The R subseries, particularly the E1RL1 and E2RL1 site-types, frequently contains *Calluna vulgaris* and *Scirpus cespitosus* of low vitality; species with optima in series at higher relative levels. The zonations differ by the zonal indicator species of group 2, 5 and 7 (for E2) and 3 (for E3). *Rhynchospora alba* and all species with preference for the R subseries except the *Sphagnum* spp. decrease from E1 to E3. The strongest decline is observed for the lichens. The areal importance of bare peat decreases from E1 to E3 (Fig. 68).

The E1L series is important throughout the special area, having a total estimated area of ca. 22 per cent. The R subseries is the most important, covering ca. 18 per cent. The relative importance of the R relative to the P subseries decreases from a factor of twenty in the E1 zonation to factors of two and one in E2 and E3, respectively.

Site-types of the P subseries (in particular stands dominated by *Sphagnum magellanicum* and *S. papillosum*), may differ from the R subseries by properties of substrate firmness. The substrate of the R subseries is mostly a firm humified peat, densely interwoven by roots, particularly of *Calluna vulgaris*. The P subseries is sometimes developed as floating carpets (quagmire) on slightly humified peat.

Site-types of the lower lawn series have average median distances to the water table in the range 4.2-7.6 cm (Tab. 16, Fig. 67). The site-types are always inundated in periods of low depth to the water table, and the compensation level is 1-3 cm below the surface of the bottom layer. There is a significant difference between the subseries with respect to mean median depth to the water table; increasing from 0.9 cm in the E1 zonation to 1.0 in E2 and 3.4 in E3. The subseries often appear to segregate locally; P vegetation in larger hollows, R vegetation in smaller hollows outside distinct water tracks. This should indicate a relationship between subseries and range of the depth to the water table. The material available on water table fluctuations does not, however, support this.

The mire expanse upper lawn series

The E1PLu site-type

The floristic composition of this site-type is shown in Tab. 25. The constant species are *Andromeda polifolia*, *Vaccinium oxycoccos* coll., *Drosera rotundifolia*, *Eriophorum vaginatum*, *Scirpus cespitosus*, *Sphagnum balticum*, *S. magellanicum*, *S. rubellum*, *S. tenellum*, *Cladopodiella fluitans*, and *Mylia anomala*. The field layer is dominated by *Eriophorum vaginatum*, often forming large tussocks. Dominants in the bottom layer are *Sphagnum balticum*, *S. magellanicum*, and, above all, *S. rubellum*.

The mean number of species per sample plot is 15, while the total number in the 26 sample plots is 27.

The dominance of *Eriophorum vaginatum* and the high importance of *Scirpus*

Tab. 25. The vegetation of the E1PLu site-type.

Sample plot No.	S1	S2	S3	S4	O1	O2	S	O	
Number of sample plots	5	5	5	5	1	5	20	6	26
Zone	E1	E1	E2	E2	E1	E2			
<i>Andromeda polifolia</i>	100- 5	100- 2	100- 3	100- 2	+	100- 2	100- 3	100- 2	100- 3
<i>Calluna vulgaris</i>	80- 3	100- 2	60- 2	20- 1	+	60- 8	65- 2	67-10	66- 4
<i>Vaccinium oxycoccos</i> coll.	100- 1	100- 2	100- 2	100- 2	+	100- 3	100- 2	100- 2	100- 2
<i>Drosera anglica</i>	100- 1	40- 1	80- 1	40- 1	-	40- 1	65- 1	33- 1	58- 1
<i>D. rotundifolia</i>	100- 1	100- 1	100- 1	100- 1	+	100- 1	100- 1	100- 1	100- 1
<i>Rubus chamaemorus</i>	20- 2	20- 1	20- 1	20- 1	+	80- 5	20- 1	83- 5	35- 3
<i>Eriophorum vaginatum</i>	100-17	100-10	100- 9	100-29	+	100-25	100-16	100-22	100-17
<i>Rhynchospora alba</i>	60- 1	60- 2	80- 1	-	-	-	50- 1	-	38- 1
<i>Scirpus cespitosus</i>	100- 5	100- 4	100- 8	60- 1	+	100- 3	90- 5	100- 3	92- 4
<i>Sphagnum balticum</i>	100- 7	80-12	80- 3	100-18	+	100-21	90-10	100-27	92-13
<i>S. magellanicum</i>	100-24	20- 1	80-38	100-17	+	100-31	75-24	100-26	81-25
<i>S. rubellum</i>	100-56	100-74	100-63	100-58	+	100-37	100-63	100-35	100-57
<i>S. tenellum</i>	100- 4	100- 5	80- 1	80- 5	+	60- 1	90- 4	67- 3	85- 4
<i>Calypogeja sphagnicola</i>	60- 1	60- 1	40- 1	40- 1	+	100- 1	50- 1	100- 1	62- 1
<i>Cephalozia</i> spp.	60- 2	100- 7	80- 2	60- 2	+	60- 3	75- 3	67- 3	73- 3
<i>Cladopodiella fluitans</i>	100- 5	100- 4	100- 4	100- 6	+	100- 1	100- 5	100- 1	100- 4
<i>Kurzia pauciflora</i>	80- 6	100- 4	60- 1	60- 3	+	80- 6	75- 4	83- 6	77- 5
<i>Mylia anomala</i>	80- 3	100- 2	80- 1	60- 2	+	100- 3	80- 2	100- 2	85- 2

Additional species (with constancy below 10):

Pinus sylvestris 4-1 (S2: 20-1; S: 5-1).

Empetrum nigrum 4-1 (O2: 20-1; O: 17-1), *Vaccinium uliginosum* 4-2 (O2: 20-2; O: 17-2).

Drosera anglica x *rotundifolia* 4-1 (S1: 20-1; S: 5-1).

Sphagnum fuscum 8-3 (S1: 20-2, S2: 20-3; S: 10-3).

Gymnocolea inflata 4-1 (S2: 20-1; S: 5-1).

Cetraria ericetorum 4-1 (S2: 20-1; S: 5-1), *Cladonia rangiferina* 8-1 (S2: 20-1, S3: 20-1; S: 10-1), *C. squamosa* 4-1 (S2: 20-1; S: 5-1).

cespitosus give the field layer a characteristic physiognomy. The bottom layer has an unbroken *Sphagnum* lawn in which the prominence of red sphagna is typical. Hepatics occur on and between the *Sphagnum* individuals, but do not form patches larger than a few sq. cm.

The site-type covers an estimated area of 1 per cent, mostly in the E2 zone in the marginal drier parts of diffuse fen soaks.

The variation within this site-type is negligible.

The E2PLu site-type

The floristic composition of this site-type is shown in Tab. 26. The constant species are *Andromeda polifolia*, *Vaccinium oxycoccos* coll., *Drosera rotundifolia*, *Eriophorum vaginatum*, *Sphagnum balticum*, *S. magellanicum*, *S. papillosum*, *S. rubellum*, *S. tenellum*, and *Cladopodiella fluitans*. The only dominant in the field layer is *Eriophorum vaginatum*. Dominants in the bottom layer are *Sphagnum balticum*, *S. magellanicum*, *S. papillosum*, and *S. rubellum*.

The mean number of species per sample plot is 15, while the total number in the 57 sample plots is 30.

Graminids, notably the tussock-former *Eriophorum vaginatum*, to a lesser extent also *Scirpus cespitosus* and *Carex pauciflora*, give the site-type its appearance. The bottom layer is characterized by the dominance shared between four *Sphagnum* species, two red, one

Tab. 26. The vegetation of the E2PLu site-type.

Sample set No.	S1	S2	S3	S4	S5	O1	O2	S	O	
Number of sample plots	5	5	5	5	5	31	1	25	32	57
Zone	E2	E2	E2	E2	E2	E2	E3			
<i>Andromeda polifolia</i>	100- 6	100- 2	100- 2	100- 2	100- 5	97- 2	+	100- 3	97- 3	98- 3
<i>Calluna vulgaris</i>	-	-	-	-	-	61- 5	+	-	63- 5	35- 5
<i>Erica tetralix</i>	-	60- 5	-	80- 7	-	13- 8	-	28- 6	13- 8	20- 7
<i>Vaccinium oxycoccos</i> coll.	100- 3	100- 2	100- 2	100- 6	100- 2	100- 3	+	100- 3	100- 3	100- 3
<i>Drosera anglica</i>	20- 1	-	20- 1	-	20- 1	16- 1	-	12- 1	16- 1	14- 1
<i>D. rotundifolia</i>	100- 2	100- 1	100- 1	100- 1	100- 1	100- 1	+	100- 1	100- 1	100- 1
<i>Rubus chamaemorus</i>	100- 4	80- 4	100- 1	40- 1	40- 2	58- 5	+	72- 2	59- 4	65- 3
<i>Carex pauciflora</i>	-	40-16	20- 4	20-22	20- 3	19- 3	-	20-12	19- 3	19- 7
<i>Eriophorum vaginatum</i>	100-26	100-17	100-18	100-19	100-20	100-22	+	100-10	100-22	100-21
<i>Rhynchospora alba</i>	-	-	40- 1	20- 1	20- 2	19- 2	-	16- 1	19- 2	18- 2
<i>Scirpus cespitosus</i>	-	40- 6	60- 8	80- 2	80-10	87-10	+	52- 6	88-10	72- 8
<i>Sphagnum balticum</i>	100-10	80-14	60-15	100- 7	100-14	100-19	+	88-12	100-20	95-17
<i>S. magellanicum</i>	100- 4	100-45	60-27	100-33	100-20	97-26	+	92-26	97-26	95-26
<i>S. papillosum</i>	100-17	80-28	100-54	20-10	100-18	97-17	+	80-28	97-17	90-22
<i>S. rubellum</i>	100-65	100-15	80-20	100-44	80-44	100-21	+	92-38	100-21	97-28
<i>S. tenellum</i>	100- 2	80- 7	60- 6	40- 2	100- 4	87- 9	-	76- 4	84- 9	81- 7
<i>Calypogeja sphagnicola</i>	100- 4	100- 2	100- 1	100- 2	100- 1	61- 1	-	100- 2	59- 1	77- 2
<i>Cephalozia</i> spp.	40- 2	-	-	40- 1	60- 6	45- 4	-	28- 3	44- 4	37- 4
<i>Cladopodiella fluitans</i>	100- 5	100- 3	100- 2	100- 5	100- 4	100- 7	+	100- 4	100- 7	100- 6
<i>Kurzia pauciflora</i>	80- 4	40- 1	20- 1	40- 4	60- 4	65- 5	-	48- 3	63- 5	56- 4
<i>Mylia anomala</i>	80- 1	40- 1	40- 1	60- 3	60- 1	61- 2	+	56- 2	63- 2	60- 2

Additional species (with constancy below 10):

Pinus sylvestris 5-3 (S4: 20-1, O1: 6-4; S: 4-1, O: 6-4).

Drosera anglica x *rotundifolia* 5-1 (O1: 10-1; O: 9-1).

Scheuchzeria palustris 4-2 (S4: 20-2, S5: 20-1; S: 8-2).

Aulacomnium palustre 2-3 (O1: 3-3; O: 3-3), *Polytrichum strictum* 2-1 (O1: 3-1; O: 3-1).

Sphagnum cuspidatum 7-2 (S2: 20-1, O1: 10-2; S: 4-1, O: 9-2), *S. fuscum* 9-3 (S4: 40-7, O1: 10-1; S: 8-7, O: 9-1), *S. majus* 7-1 (O1: 13-1; O: 13-1).

Gymnocolea inflata 4-3 (O1: 6-3; O: 6-3).

golden, and one green. Hepatics occur among the sphagna, mostly scattered and not forming patches. *Cladopodiella fluitans* is constant and abundantly present, but always occurs as single shoots or few shoots together.

The site-type covers an estimated area of 5 per cent, mainly concentrated to the lawn-dominated southern and western fen soaks.

The field layer shows some variation as *Erica tetralix*, *Carex pauciflora*, and *Scirpus cespitosus* vary strongly in their occurrence and abundance. The relative importance of the dominating *Sphagnum* spp. also varies. *Sphagnum magellanicum* (S2), *S. papillosum* (S3), and *S. rubellum* (S1, S4, S5) are the important dominants, while *S. balticum* is present with high frequency in most plots. Some variation also occurs with respect to the importance of hepatics. Sample plots dominated by *S. rubellum* show a considerable increase in quantities of *Cephalozia* spp., *Kurzia pauciflora*, and *Mylia anomala*, as compared to plots dominated by *Sphagnum magellanicum* and *S. papillosum*. The higher importance of hepatics in the O-set is likely to be due to lower sample plot homogeneity. In one plot, hepatics were observed to invade a depression caused by trampling.

The E3PLu site-type

The floristic composition of this site-type is shown in Tab. 27. The constant species are *Andromeda polifolia*, *Vaccinium oxycoccos* coll., *Drosera rotundifolia*, *Eriophorum vaginatum*, *Sphagnum balticum*, *S. magellanicum*, *S. papillosum*, *S. rubellum*, and

Tab. 27. The vegetation of the E3PLu site-type.

Sample set No.	S1	S2	S3	S4	S5	S6	S	O	
Number of sample plots	5	5	5	5	5	5	30	9	39
Zone	E3	E3	E3	E3	E3	E3			
<i>Betula pubescens</i>	20- 1	-	-	-	-	20- 2	7- 2	22- 3	10- 3
<i>Pinus sylvestris</i>	-	-	-	-	-	40- 1	7- 1	33- 2	13- 2
<i>Andromeda polifolia</i>	100- 7	100- 4	100- 8	80- 2	80- 2	100- 3	93- 5	100- 2	95- 5
<i>Calluna vulgaris</i>	-	40- 2	-	-	-	-	7- 2	44- 1	15- 1
<i>Erica tetralix</i>	20- 4	100-15	20-12	20-15	60-10	-	37-12	44-11	39-12
<i>Myrica gale</i>	100-10	100-11	100- 9	-	100- 8	-	67-10	89- 8	72-10
<i>Vaccinium oxycoccos</i> coll.	100- 5	100- 9	100- 6	100- 3	100- 5	100- 3	100- 5	100- 5	100- 5
<i>Drosera anglica</i>	20- 1	-	-	-	60- 1	-	13- 1	-	10- 1
<i>D. rotundifolia</i>	100- 1	100- 1	80- 1	100- 2	100- 1	100- 2	97- 1	78- 1	92- 1
<i>Rubus chamaemorus</i>	-	60- 1	20- 2	40- 1	-	-	20- 1	33- 3	23- 2
<i>Carex lasiocarpa</i>	-	-	20- 1	-	-	100- 3	20- 3	11- 2	18- 3
<i>C. pauciflora</i>	-	20-10	40- 3	20-12	20-17	80- 4	30- 7	22- 1	28- 6
<i>C. rostrata</i>	-	-	-	100- 2	20- 1	-	20- 2	-	15- 2
<i>Eriophorum angustifolium</i>	-	20- 1	20- 1	-	40- 5	40- 1	20- 2	33- 4	23- 3
<i>E. vaginatum</i>	100-28	100-16	100-28	100-20	100-10	100-11	100-19	100-18	100-19
<i>Scirpus cespitosus</i>	40- 1	80-10	60-15	80- 3	60- 1	80-20	67- 8	44- 2	62- 7
<i>Sphagnum balticum</i>	100-22	100- 9	80-16	100-12	100- 8	100-24	97-15	78-24	92-17
<i>S. magellanicum</i>	80- 3	100-32	100-27	100-43	100-20	100-23	97-25	100-35	97-28
<i>S. papillosum</i>	100-39	100-23	60-37	80-14	100-48	100-41	90-34	89-19	90-31
<i>S. rubellum</i>	100-27	100-27	100-25	100-27	100-13	40- 6	90-23	100-15	93-21
<i>S. tenellum</i>	100- 8	80- 3	60-12	60- 3	80- 9	40- 7	70- 7	33-15	62- 8
<i>Calypogeja sphagnicola</i>	60- 2	100- 2	100- 1	80- 1	60- 1	100- 1	83- 2	56- 2	77- 2
<i>Cephalozia</i> spp.	40- 1	20- 1	-	-	-	-	10- 1	11- 1	10- 1
<i>Cladopodiella fluitans</i>	100- 3	100- 6	100- 2	100- 3	100- 2	100- 6	100- 4	89- 3	97- 4
<i>Kurzia pauciflora</i>	40- 2	40- 3	60- 2	80- 3	20- 1	20- 1	43- 2	11- 1	36- 2
<i>Mylia anomala</i>	60- 1	60- 2	80- 2	80- 2	-	40- 2	53- 2	22- 2	46- 2

Additional species (with constancy below 10):

Vaccinium uliginosum 8-4 (O: 33-4).

Carex curta 3-1 (O: 11-1), *Phragmites australis* 8-5 (S2: 20-10, S4: 40-3; S: 10-5), *Rhynchospora alba* 3-1 (S1: 20-1; S: 3-1), *Scheuchzeria palustris* 8-3 (S1: 40-4, S5: 20-2; S: 10-3).

Aulacomnium palustre 5-1 (O: 22-1), *Pohlia nutans* 3-4 (O: 11-4).

Sphagnum angustifolium 5-6 (O: 22-6), *S. cuspidatum* 3-4 (O: 11-1), *S. fallax* 5-16 (O: 22-16), *S. lindbergii* 3-2 (S1: 20-2; S: 3-2).

Cladonia rangiferina 3-1 (O: 11-1).

Cladopodiella fluitans, *Eriophorum vaginatum*, sometimes also *Erica tetralix* and *Myrica gale*, dominate the field layer. *Sphagnum balticum*, *S. magellanicum*, *S. papillosum*, *S. rubellum*, and *S. tenellum*, are dominants in the bottom layer.

The mean number of species per sample plot is 15, while the total number in the 39 sample plots is 38.

Dwarf shrubs and graminids both reach dominance, and together make up a densely stocked field layer. *Andromeda polifolia*, *Erica tetralix*, and *Vaccinium oxycoccos* are close to their optima. Like the E2PLu site-type, the bottom layer is characterized by shared dominance of differently coloured *Sphagnum* spp. Hepatics occur, but except for *Cladopodiella fluitans* and *Calypogeja sphagnicola*, in small quantities.

The site-type covers an estimated area of 1.5 per cent, and is among the quantitatively most important site-types of the E3 areas in the southern and western fen soaks.

There is a considerable variation in the dominance (and presence) relationships of the field layer: *Erica tetralix*, *Myrica gale*, *Carex pauciflora*, and *Scirpus cespitosus* may all occur as dominants, with strong impact on the appearance of the vegetation. Variation

Tab. 28. The vegetation of the E1RLu site-type.

Sample set No.	S1	S2	S3	S4	S5	O1	O2	S	O	
Number of sample plots	5	5	5	5	5	31	8	25	39	64
Zone	E1	E1	E1	E2	E2	E1	E2			
<i>Andromeda polifolia</i>	100- 5	100- 2	100- 2	100- 2	100- 7	100- 2	100- 3	100- 4	100- 2	100- 3
<i>Calluna vulgaris</i>	100- 2	100- 9	100- 6	100- 9	100- 5	97-11	88- 9	100- 6	95-11	98- 9
<i>Vaccinium oxycoccos</i> coll.	100- 2	100- 1	100- 3	100- 3	100- 2	100- 2	100- 2	100- 2	100- 2	100- 2
<i>Drosera anglica</i>	60- 1	20- 1	20- 1	-	-	16- 1	13- 1	20- 1	15- 1	17- 1
<i>D. rotundifolia</i>	80- 2	80- 1	80- 1	100- 1	60- 1	90- 1	75- 1	80- 1	87- 1	84- 1
<i>Rubus chamaemorus</i>	60- 1	60- 1	20- 1	40- 4	40- 1	74- 2	88- 2	44- 1	77- 2	64- 2
<i>Eriophorum vaginatum</i>	100- 6	100- 8	100- 8	100- 6	100-12	100-12	100-11	100- 8	100-12	100-11
<i>Rhynchospora alba</i>	80- 2	-	-	-	20- 4	6- 1	-	20- 2	5- 1	11- 2
<i>Scirpus cespitosus</i>	100- 9	100- 1	100- 3	100-13	100-17	94- 4	88- 5	100- 9	92- 4	95- 6
<i>Sphagnum balticum</i>	60- 2	100- 3	40- 7	100-12	60- 4	87-15	100-23	72- 6	90-17	83-13
<i>S. magellanicum</i>	20- 2	20- 1	-	100- 1	80- 1	29- 1	88- 2	44- 1	41- 2	42- 2
<i>S. rubellum</i>	100- 3	80- 1	100- 3	100- 2	100- 1	100- 9	88- 9	96- 2	97- 9	97- 6
<i>S. tenellum</i>	100-73	100-16	100-58	100-53	100-66	97-34	100-26	100-53	97-33	98-41
<i>Calypogeja sphagnicola</i>	-	-	20- 1	-	-	39- 2	50- 2	4- 1	41- 2	27- 2
<i>Cephalozia</i> spp.	100- 8	100-12	100- 8	100- 5	100- 8	100-10	88-10	100- 8	97-10	98- 9
<i>Cladopodiella fluitans</i>	100-20	100- 3	100-12	100- 8	100- 5	97-11	100-14	100-10	97-11	98-11
<i>Kurzia pauciflora</i>	60- 2	100- 3	80- 4	100- 2	20- 2	77-10	75-10	72- 3	77-10	75- 7
<i>Mylia anomala</i>	100- 2	100- 3	100- 2	100- 2	100- 1	94- 4	100- 3	100- 2	95- 3	97- 3
<i>Cladonia rangiferina</i>	20- 1	80- 1	80- 1	20-10	20- 1	19- 5	25- 7	44- 2	21- 5	30- 3
<i>C. squamosa</i>	100- 1	100-17	100- 3	80- 5	100- 6	61- 7	63- 3	96- 7	62- 6	75- 6
<i>C. uncialis</i>	20-12	40-12	60- 2	20-20	-	6- 1	-	28- 9	5- 1	14- 8
<i>Ochrolechia frigida</i>	20- 1	60- 3	-	20- 3	40- 3	6- 4	-	28- 2	5- 4	14- 3

Additional species (with constancy below 10):

Empetrum nigrum 3-1 (O1: 6-1; O: 5-1).

Drosera anglica x *rotundifolia* 2-1 (O1: 3-1; O: 3-1).

Sphagnum cuspidatum 6-4 (O1: 10-4, O2: 13-3; O: 10-4), *S. fuscum* 5-1 (S3: 20-1, O1: 6-1; S: 4-1, O: 5-1).

Cephalozia spp. 6-1 (S2: 20-1, S4: 20-1, O1: 3-1; S: 8-1, O: 3-1), *Gymnocolea inflata* 9-3 (S3: 20-2, S5: 80-4, O2: 13-1; S: 20-4, O: 3-1), *Riccardia latifrons* 5-1 (S2: 20-1, O1: 3-1, O2: 13-1; S: 4-1, O: 5-1).

Cetraria delisei 6-25 (S2: 40-44, S3: 40- 6; S: 16-25), *C. ericetorum* 6-25 (S2: 20-55, S3: 20-7, O1: 3-7; S: 8-31, O: 3-7), *C. islandica* 6-7 (S2: 20-7, S3: 20-2, O1: 3-10; S: 8-5, O: 3-10), *Cladonia arbuscula* 2-1 (S1: 20-1; S: 4-1), *C. fimbriata* 3-1 (O1: 6-1; O: 5-1), *C. mitis* 2-12 (S3: 20-12; S: 4-12), *C. pyxidata* coll. 3-1 (S2: 20-1, O1: 3-1; S: 4-1, O: 3-1), *C. stellaris* 2-1 (O1: 3-1; O: 3-1), *C. subfurcata* 2-20 (S3: 20-20; S: 4-20).

of the bottom layer only occurs with respect to relative dominance of *Sphagnum* spp.

The E1RLu site-type

The floristic composition of this site-type is shown in Tab. 28. The constant species are *Andromeda polifolia*, *Calluna vulgaris*, *Vaccinium oxycoccos* coll., *Drosera rotundifolia*, *Eriophorum vaginatum*, *Scirpus cespitosus*, *Sphagnum balticum*, *S. rubellum*, *S. tenellum*, *Cephalozia* spp., *Cladopodiella fluitans*, and *Mylia anomala*. The field layer is mostly not dominated by any single species, occasional dominants are *Eriophorum vaginatum* and *Scirpus cespitosus*. The main dominants of the bottom layer are *Sphagnum tenellum* and *S. balticum*.

The mean number of species per sample plot is 16, while the total number in the 64 sample plots is 37.

The site-type has a characteristic physiognomy. *Calluna vulgaris*, mostly shoots with low vitality (low leaf-to-stem weight ratio), attains high importance. *Eriophorum vaginatum* and *Scirpus cespitosus* form tussocks, and contribute to a considerable variation in microtopography within the site-type. The bottom layer has a highly variable physiognomy, ranging from a prominence of *Sphagnum tenellum* to dominance, at least locally, of dark-

coloured hepatics. Lichens occur with moderate abundance, but a high number of species have been recorded from the site-type.

The estimated area covered by this site-type is 6 per cent, of which 5 per cent in the E1 zone. This site-type is the dominant vegetation in small, relatively dry hollows of the central parts of the true bog areas (in particular the unilaterally sloping kermi raised bog and at pos. 08-10 12-14 outside the fen soak).

The variation is mostly with respect to the bottom layer, although the microtopography is affected by the importance of tussock-forming graminids. Bare peat occurs occasionally, and then occupies the lowermost, often waterfilled depressions (Fig. 68). More common is the dominance of *Sphagnum tenellum*, alone or with variable quantities of *S. balticum*, in the interspaces. The lichen species prefer growing on the bases of tussocks. *Cetraria delisei*, *C. ericetorum*, and *Cladonia uncialis* have been observed in several sample plots, often as dominants, and always exhibit radial growth from elevated graminid tussocks or *Calluna vulgaris* bases. Dead *Calluna* stems may serve as templates for growth of *Ochrolechia frigida*. *Cladonia squamosa* also prefers elevated sites, but shows preference for elevated sites with bare peat. Blackening of the basal parts and ultimately the death of podetia has been observed in *Cladonia rangiferina* stands towards low median depth to the water table. Considerable variation exists with respect to dominance of hepatics. Patches up to 25 x 25 cm totally dominated by *Cephalozia* spp., *Cladopodiella fluitans*, and *Kurzia pauciflora*, mostly in combination, occur frequently.

The E2RLu site-type

The floristic composition of this site-type is shown in Tab. 29. The constant species are *Andromeda polifolia*, *Vaccinium oxycoccos* coll., *Drosera rotundifolia*, *Eriophorum vaginatum*, *Scirpus cespitosus*, *Sphagnum balticum*, *S. magellanicum*, *S. rubellum*, *S. tenellum*, and *Cladopodiella fluitans*. The field layer is dominated by *Eriophorum vaginatum*. The bottom layer is dominated by *Sphagnum tenellum* with *S. balticum* as a less important co-dominant.

The mean number of species per sample plot is 15, while the total number in the 31 sample plots is 32.

The site-type is characterized by dominance of graminid tussocks (*Eriophorum vaginatum* and *Scirpus cespitosus*) in the field layer, promoting variation in microtopography. The bottom layer is dominated by lightcoloured *Sphagnum* spp., with high amounts of intermixed hepatics. Smaller patches are dominated by hepatics, particularly around tussock bases. Lichens play a minor role.

The area of this site-type is estimated to be 2 per cent. The site-type appears as a minor constituent of lawns in the E2 zone, most commonly in the southern fen soak and SW and S of the erosion area.

The variation in the field layer is small, restricted to the variable dominance-relationships of graminids. There seems to be some negative correlation between the cover of *Eriophorum vaginatum* and *Scirpus cespitosus* in 0.25 m² sample plots (cf. Tab. 29). The variation in the bottom layer mainly occurs at a fine scale (variation in microtopography and frequency of patches dominated by hepatics). This variation is almost not reflected by the data sets. The O-set contains several sample plots with dominance of hepatics (*Cephalozia* spp. and *Cladopodiella fluitans*).

The E3RLu site-type

The floristic composition of this site-type is shown in Tab. 30. The constant species are

Tab. 29. The vegetation of the E2RLu site-type.

Sample set No.	S1	S2	S3	S4	S	O	
Number of sample plots	5	5	5	5	20	11	31
Zone	E2	E2	E2	E2			
<i>Andromeda polifolia</i>	100- 7	100- 2	100- 2	100- 6	100- 4	100- 3	100- 4
<i>Calluna vulgaris</i>	40- 1	20- 1	40- 1	80- 6	45- 3	64- 8	52- 5
<i>Erica tetralix</i>	-	100- 1	-	40-16	35- 5	27- 3	32- 4
<i>Vaccinium oxycoccos</i> coll.	100- 5	100- 3	100- 2	100- 2	100- 3	100- 3	100- 3
<i>Drosera anglica</i>	-	-	-	40- 1	10- 1	18- 1	13- 1
<i>D. rotundifolia</i>	100- 1	60- 1	80- 1	100- 1	85- 1	91- 1	87- 1
<i>Rubus chamaemorus</i>	20- 1	40- 2	60- 1	-	30- 1	64- 5	42- 5
<i>Carex pauciflora</i>	-	40- 2	20- 1	-	15- 1	45- 2	26- 2
<i>Eriophorum vaginatum</i>	100-27	100-22	100-10	100- 8	100-17	100-14	100-16
<i>Rhynchospora alba</i>	-	40- 3	20- 1	20- 1	20- 2	18- 3	19- 2
<i>Scirpus cespitosus</i>	60- 2	80-11	100- 8	100-11	85- 9	82-11	84-10
<i>Sphagnum balticum</i>	100-18	80-10	100-21	100- 6	95-14	100-15	97-14
<i>S. cuspidatum</i>	-	20- 1	20- 1	20- 1	15- 1	-	10- 1
<i>S. magellanicum</i>	100- 2	60- 2	100- 3	60- 2	80- 2	91- 6	84- 3
<i>S. papillosum</i>	100- 2	60- 2	100- 2	40- 3	75- 2	64- 7	71- 4
<i>S. rubellum</i>	100- 2	60- 1	100- 2	100- 2	90- 2	91- 5	90- 3
<i>S. tenellum</i>	100-70	100-82	100-69	100-61	100-71	100-41	100-60
<i>Calypogeja sphagnicola</i>	40- 1	-	40- 2	20- 1	25- 1	36- 1	29- 1
<i>Cephalozia</i> spp.	100- 3	20- 2	20- 2	100- 8	60- 5	73-10	65- 7
<i>Cladopodiella fluitans</i>	100- 6	100- 4	100- 3	100- 6	100- 5	100-16	100- 9
<i>Gymnocolea inflata</i>	-	40- 1	-	60- 3	25- 2	9-15	19- 4
<i>Kurzia pauciflora</i>	40- 2	-	80- 1	20- 1	35- 1	64- 7	45- 4
<i>Mylia anomala</i>	100- 1	20- 1	20- 1	100- 1	60- 1	64- 2	61- 1
<i>Cladonia squamosa</i>	-	-	-	80- 6	20- 6	36- 2	26- 4

Additional species (with constancy below 10):

Drosera anglica x *rotundifolia* 3-1 (O: 9-1).

Scheuchzeria palustris 3-3 (S4: 20-3; S: 5-3).

Dicranum leioneuron 3-1 (S4: 20-1; S: 5-1).

Sphagnum compactum 3-1 (S2: 20-1; S: 5-1), *S. fuscum* 3-1 (O: 9-1).

Cephaloziella spp. 3-1 (O: 9-1).

Cladonia rangiferina 3-1 (S4: 20-1; S: 5-1), *Ochrolechia frigida* 3-10 (S4: 20-10; S: 5-10).

Andromeda polifolia, *Vaccinium oxycoccos* coll., *Eriophorum vaginatum*, *Sphagnum balticum*, *S. tenellum*, and *Cladopodiella fluitans*. The field layer is dominated by *Eriophorum vaginatum*, while *Sphagnum tenellum* is the only dominant in the bottom layer.

The mean number of species per sample plot is 13, while the total number in the 20 sample plots is 27.

Graminids are the quantitatively most important taxocene in the field layer, but there is no differentiation into tussocks and interspaces. The dwarf shrubs *Erica tetralix* and *Myrica gale* occasionally have high abundance. The bottom layer is a homogeneous *Sphagnum tenellum* lawn. Hepatics are almost absent.

This site-type was not represented in the O-set, and only occurs as small segments

Tab. 30. The vegetation of the E3RLu site-type.

Sample set No.	S1	S2	S3	S4	S
Number of sample plots	5	5	5	5	20
Zone	E3	E3	E3	E3	
<i>Andromeda polifolia</i>	100- 2	100- 3	100- 2	100- 2	100- 2
<i>Calluna vulgaris</i>	-	20- 1	-	20- 1	10- 1
<i>Erica tetralix</i>	100- 4	20- 1	-	100- 4	55- 4
<i>Myrica gale</i>	100- 9	80- 5	-	80- 5	65- 7
<i>Vaccinium oxycoccos</i> coll.	100- 3	100- 3	100- 4	100- 1	100- 3
<i>Drosera rotundifolia</i>	80- 1	40- 1	80- 1	60- 1	65- 1
<i>Rubus chamaemorus</i>	40- 1	40- 1	20- 1	-	25- 1
<i>Carex pauciflora</i>	40- 2	20- 5	20- 1	-	20- 1
<i>C. rostrata</i>	-	-	100- 5	60- 4	40- 4
<i>Eriophorum angustifolium</i>	-	40- 3	-	100- 4	35- 4
<i>E. vaginatum</i>	100-17	100-21	100-14	100- 4	100-14
<i>Rhynchospora alba</i>	20- 2	-	-	60- 1	20- 2
<i>Scirpus cespitosus</i>	100- 6	40-13	100- 3	80- 2	80- 5
<i>Sphagnum balticum</i>	80- 1	60-14	100-11	100- 2	85- 7
<i>S. magellanicum</i>	80- 3	80- 2	100- 3	60- 2	80- 3
<i>S. majus</i>	-	40- 5	-	-	10- 5
<i>S. papillosum</i>	40- 1	100- 3	80- 3	80- 5	75- 3
<i>S. rubellum</i>	-	100- 1	100- 2	80- 3	70- 2
<i>S. tenellum</i>	100-95	100-79	100-80	100-91	100-86
<i>Cladopodiella fluitans</i>	100- 3	100- 2	100- 3	80- 3	95- 3
<i>Kurzia pauciflora</i>	-	20- 1	20- 1	20- 2	15- 1
<i>Mylia anomala</i>	-	-	-	40- 1	10- 1

Additional species (with constancy below 10):

Drosera anglica 5-1 (S4: 20-1).

Scheuchzeria palustris 5-1 (S4: 5-1).

Calypogeja sphagnicola 5-1 (S4: 20-1), *Cephalozia* spp. 5-1 (S4: 20-1), *Gymnocolea inflata* 5-17 (S2: 20-17).

(rarely above 2-3 m²) scattered in E3 areas.

With the exception of the variable dominance relationships in the field layer, this site-type is uniform throughout the material.

Survey of the mire expanse upper lawn series

A survey of the mire expanse upper lawn series is given in Tab. 31. The physiognomy of the series is, with the exception of the E1RLu (and some variants of the E2RLu) site-types, remarkably homogeneous throughout the zonations and subseries. Graminids, *Eriophorum vaginatum* and *Scirpus cespitosus*, dominate in the field layer. Dwarf shrubs (different species in different site-types) may also become dominant and contribute to the physiognomy of the field layer. *Sphagnum* spp. dominate in both subseries. The prominence of

Tab. 31. Survey of the ELu series.

Subseries	P			R		
Zonation	E1	E2	E3	E1	E2	E3
Site-type	E1PLu	E2PLu	E3PLu	E1RLu	E2RLu	E3RLu
Number of sample plots	26	57	39	64	31	20
<i>Andromeda polifolia</i>	100- 3	98- 3	95- 5	100- 3	100- 4	100- 2
<i>Calluna vulgaris</i>	66- 4	35- 5	15- 1	98- 9	52- 5	10- 1
<i>Vaccinium oxycoccos</i> coll.	100- 2	100- 3	100- 5	100- 2	100- 3	100- 3
<i>Drosera anglica</i>	58- 1	14- 1	10- 1	17- 1	13- 1	5- 1
<i>D. rotundifolia</i>	100- 1	100- 1	92- 1	84- 1	87- 1	65- 1
<i>Rubus chamaemorus</i>	35- 3	65- 3	23- 2	64- 2	42- 3	25- 1
<i>Eriophorum vaginatum</i>	100-17	100-21	100-19	100-11	100-16	100-14
<i>Scirpus cespitosus</i>	92- 4	72- 8	62- 7	95- 6	84-10	80- 5
<i>Sphagnum balticum</i>	92-13	95-17	92-17	83-13	97-14	85- 7
<i>Cephalozia</i> spp.	73- 3	37- 4	10- 1	98- 9	65- 7	5- 1
<i>Cladopodiella fluitans</i>	100- 4	100- 6	97- 4	98-11	100- 9	95- 3
<i>Kurzia pauciflora</i>	77- 5	56- 4	36- 2	75- 7	45- 4	15- 1
<i>Mylia anomala</i>	85- 2	60- 2	46- 2	97- 3	61- 1	10- 1
<i>Erica tetralix</i>	-	20- 7	39-12	-	32- 4	55- 4
<i>Carex pauciflora</i>	-	19- 7	28- 6	-	26- 2	20- 2
<i>Carex lasiocarpa</i>	-	-	18- 3	-	-	-
<i>C. rostrata</i>	-	-	15- 2	-	-	40- 4
<i>Eriophorum angustifolium</i>	-	-	23- 3	-	-	35- 4
<i>Sphagnum magellanicum</i>	81-25	95-26	97-28	42- 2	84- 3	80- 3
<i>S. rubellum</i>	100-57	97-28	93-21	97- 6	90- 3	70- 2
<i>Calypogeja sphagnicola</i>	62- 1	77- 2	77- 2	27- 2	29- 1	5- 1
<i>Sphagnum papillosum</i>	-	90-22	90-31	-	71- 4	75- 3
<i>Sphagnum tenellum</i>	85- 4	81- 7	62- 8	98-41	100-60	100-86
<i>Cladonia rangiferina</i>	8- 1	-	3- 1	30- 3	3- 1	-
<i>C. squamosa</i>	4- 1	-	-	75- 6	26- 4	-
<i>C. uncialis</i>	-	-	-	14- 8	-	-
<i>Ocnrolechia frigida</i>	-	-	-	24- 3	3-10	-

red sphagna or shared dominance between red, yellow and green species is typical of the P subseries. The R subseries is yellow-green by the dominance of *Sphagnum tenellum*, but the E1RLu (and to some extent also E2RLu) has a distinct microtopographic variation and a differentiation of dark patches of lichens, hepatics or bare peat in mosaic with *Sphagnum tenellum*. Bare peat only rarely occurs outside the E1RLu site-type (cf. Fig. 68). The upper lawn series is characterized by the presence of the thirteen species in group 1 in Tab. 31. The subseries differ in physiognomy (in particular the E1RLu series is characterized by the high importance of *Calluna vulgaris*, hepatics, and lichens). The P subseries is characterized by an unbroken *Sphagnum* lawn with prominent *Sphagnum magellanicum*, *S. rubellum*, and *S. papillosum* (not in the E1 zonation). *Calypogeja sphagnicola* growing over the *Sphagnum* capitula is a typical feature of the P subseries. Many hepatics, e.g., the four species of group 1 in Tab. 31, are common in the P subseries, but never form extensive stands there. The L1 species *Drosera anglica* is not uncommon in this subseries. *Sphagnum tenellum* is most characteristic of the R subseries. Hepatics (and, more rarely, lichens) may form pure patches in the E1RLu and E2RLu site-types. The most important lichen species is *Cladonia squamosa*. The zonations differ by the zonal indicators of groups 2 and 5 (for E2) and 3 (for E3). Hepatics decrease from the E1 to the E3 zonation, a trend even more distinct

for the lichen species of group 6. The relative importance of *Sphagnum tenellum* increases from the E1RLu to the E3RLu site-types.

The ELu series occurs all over the special area, having a total estimated area of 15 per cent. The subseries do not differ with respect to areal importance. The relative areal importance of the subseries is almost equal in the E2 zonation, while in the E1 zonation R dominates over P by a factor of six and in the E3 zonation the R subseries is only present as small fragments.

The P subseries is less quagmire-like than in the EL1 series. The substrate of the R subseries is always firm, in the E1RLu site-type with a prominence of *Calluna* roots. The site-types of this series have means for median depth to the water table ranging from 5.8 to 10.0 cm (Tab. 16, Fig. 67). About one half of the ELu sample plots are inundated at minimum depth to the water table (Tab. 17), but this series has the water table within 3-6 cm off the bottom layer surface every wet period. The mean minimum depth to the water table does not differ between the subseries, as does the mean of median distances (0.6 cm higher depth in the P subseries, cf. Tab. 16). There is no significant variation between zonations.

The upper lawn series is particularly common in small hollows (where it defines the wet extreme), and often occurs away from the water tracks. In large hollows the Lu series may be absent or restricted to a narrow border between the EL1 and EH1 series, where species typical for each of these series broadly overlap.

In the ERLu subseries, *Sphagnum tenellum* mostly dries out in a few days in the absence of precipitation. *Drosera rotundifolia* seems to avoid *Sphagnum tenellum* lawns, but occurs in ELu in patches dominated by hepatics and other *Sphagnum* spp. The loose growth form of *S. tenellum* must be responsible for the rapid desiccation. This is likely to make *Sphagnum tenellum* an unfavourable substrate for the growth of *Drosera rotundifolia* and perhaps other species as well.

The mire expanse lower hummock series

The E1PH1 site-type

The floristic composition of this site-type is shown in Tab. 32. The constant species are *Andromeda polifolia*, *Calluna vulgaris*, *Vaccinium oxycoccos* coll., *Drosera rotundifolia*, *Rubus chamaemorus*, *Eriophorum vaginatum*, *Scirpus cespitosus*, *Sphagnum fuscum*, *S. rubellum*, *Cephalozia* spp., and *Mylium anomala*. This site-type is dominated by *Calluna vulgaris* in the field layer, locally with *Eriophorum vaginatum* as a codominant. Dominants in the bottom layer are *Sphagnum rubellum*, *S. fuscum*, and *S. magellanicum*.

The mean number of species per sample plot is 15, while the total number in the 117 sample plots is 47.

Physiognomically the site-type is characterized by the dominance of *Calluna vulgaris*. The bottom layer is a continuous cover of dark and red *Sphagnum* spp.

The site-type covers extensive areas both in the E1 and the E2 zones. The estimated area is 14 per cent of the special area. It is the dominant hummock vegetation type of both of the E1 and E2 zones.

The densities of *Calluna vulgaris* and *Eriophorum vaginatum* are variable (Tab. 32). There is considerable variation with respect to dominance relationships in the bottom layer. *Sphagnum rubellum* is the most important dominant, closely followed by *S. fuscum*. The two species often occur intermixed, but there is some tendency for *S. rubellum* to prefer small hummock areas and to occur close to the border onto hollows. *S. fuscum* is the

Tab. 32. The vegetation of the E1PH1 site-type.

Sample set No.	S1	S2	S3	S4	S5	O1	O2	O3	S	O
Number of sample plots	5	5	5	5	5	70	20	2	25	92
Zone	E1	E1	E1	E2	E2	E1	E2	E3		
<i>Pinus sylvestris</i>	60- 1	60- 6	-	20- 1	80- 6	56- 4	50- 5	+	44- 4	54- 4
<i>Andromeda polifolia</i>	100- 1	80- 1	100- 2	100- 2	100- 5	84- 1	90- 2	+	96- 2	86- 2
<i>Calluna vulgaris</i>	100-17	100-46	100-17	100-26	100-26	100-32	100-27	+	100-26	100-31
<i>Empetrum nigrum</i>	20- 1	40- 1	20- 2	40- 1	-	19- 1	15- 1	-	24- 1	17- 1
<i>Vaccinium oxycoccos</i> coll.	100- 2	100- 2	100- 2	100- 1	100- 1	100- 3	100- 3	+	100- 2	100- 3
<i>Drosera rotundifolia</i>	100- 1	100- 1	100- 2	100- 1	100- 1	89- 1	70- 1	+	100- 1	85- 1
<i>Rubus chamaemorus</i>	100- 8	60- 2	60- 3	100- 8	60- 4	80- 5	90- 4	+	80- 6	83- 5
<i>Eriophorum vaginatum</i>	100-12	100-15	100-12	100- 5	100-14	100-11	100-17	+	100-11	100-12
<i>Scirpus cespitosus</i>	80- 3	40- 2	100- 5	100- 2	20- 2	86- 5	85- 6	+	68- 3	86- 5
<i>Sphagnum balticum</i>	80-13	60- 1	60- 1	40- 1	80- 4	66- 8	75-15	+	72- 6	68-10
<i>S. fuscum</i>	100- 5	100-36	100-43	100-47	40-53	84-35	70-31	+	88-39	80-35
<i>S. magellanicum</i>	80-10	40- 8	-	60- 3	100-50	36- 6	50-15	+	56-23	40- 9
<i>S. rubellum</i>	100-68	100-55	100-45	100-36	100-16	99-42	95-32	+	100-44	98-40
<i>S. tenellum</i>	-	-	20- 1	-	-	14- 2	20- 2	-	4- 1	15- 2
<i>Calypogeja sphagnicola</i>	60- 1	100- 1	80- 1	40- 1	60- 2	64- 1	65- 1	+	68- 1	64- 1
<i>Cephalozia</i> spp.	100- 3	80- 1	100- 6	100- 2	60- 1	86- 3	75- 4	+	88- 3	83- 3
<i>Cladopodiella fluitans</i>	40- 2	-	20- 2	-	-	21- 1	45- 2	-	12- 2	26- 2
<i>Kurzia pauciflora</i>	100- 9	100- 1	100- 4	100- 4	60- 2	81- 4	60- 8	+	92- 4	76- 5
<i>Mylia anomala</i>	100- 3	100- 4	100- 4	100- 3	80- 2	99- 5	90- 5	+	96- 3	97- 5
<i>Cladonia rangiferina</i>	100- 2	40- 1	80- 3	100- 1	40- 2	59- 7	45- 7	+	72- 2	55- 7
<i>C. squamosa</i>	60- 1	-	-	20- 1	-	16- 1	5- 1	-	16- 1	13- 1

Additional species (with constancy below 10):

Betula pubescens 9-3 (S1: 20-1, S2: 40-1, S3: 20-1, S4: 20-1, S5:20-15, O1: 4-1, O2: 5-3; S: 24-3, O: 4-2), *Picea abies* 1-1 (O1: 1-1; O: 1-1).*Vaccinium myrtillus* 1-2 (O1: 1-2; O: 1-2), *V. uliginosum* 3-2 (O1: 4-2; O: 3-2), *V. vitis-idaea* 2-1 (O1: 3-1; O: 2-1).*Drosera anglica* 2-1 (O1: 1-1, O2: 5-1; O: 2-1), *D. anglica* x *rotundifolia* 1-1 (O1: 1-1; O: 1-1).*Aulacomnium palustre* 2-2 (O2: 10-2; O: 2-2), *Dicranum leioneuron* 5-2 (S2: 20-4, O1: 6-1, O2: 5-2; S: 4-4, O: 5-1), *D. polysetum* 1-1 (O2: 5-1; O: 1-1), *Pleurozium schreberi* 9-4 (S2: 20-1, S4: 20-1, O1: 9-4, O2: 15-4; S: 8-1, O: 10-4), *Pohlia nutans* 7-2 (S2: 20-1, S4: 20-1, O1: 3-1, O2: 15-4, O3: +; S: 8-1, O: 7-2), *Polytrichum strictum* 1-1 (O2: 5-1; O: 1-1).*Sphagnum angustifolium* 7-14 (S2: 20-2, O1: 7-4, O2: 10-48; S: 4-2, O: 8-16), *S. capillifolium* 1-2 (O1: 1-2; O: 1-2), *S. cf. subtile* 3-32 (S4: 60-42, O1: 1-1; S: 12-42, O: 1-1).*Calypogeja neesiana* 1-1 (O3: +; O: 1-1), *Cephaloziella* spp. 7-1 (S4: 20-1, S5: 20-1, O1: 7-1, O2: 5-1; S: 8-1, O: 7-1), *Lophozia ventricosa* 1-1 (O2: 5-1; O: 1-1), *Ptilidium ciliare* 1-1 (O1: 1-1; O: 1-1), *Riccardia latifrons* 1-2 (O1: 1-2; O: 1-2).*Cetraria islandica* 6-2 (S3: 20-1, S4: 20-1, O1: 6-3, O2: 5-2; S: 8-1, O: 5-3), *Cladonia arbuscula* 3-1 (S4: 20-1, O1: 4-1; S: 4-1, O: 3-1), *C. fimbriata* 7-1 (S1: 20-1, O1: 7-1, O2: 10-1; S: 4-1, O: 8-1), *C. pyxidata* coll. 1-1 (S1: 20-1; S: 4-1), *C. stellaris* 4-1 (S4: 40-1, O1: 4-1; S: 8-1, O: 3-1), *C. uncialis* 1-1 (O1: 1-1; O: 1-1).

common dominant where continuous hummocks cover larger areas, and where the upper hummock series is present as well. *S. magellanicum* is not infrequently encountered as a dominant in this site-type in the E2 zone (e.g., S5 in Tab. 32), particularly in the isolated hummocks along the eastern margin of the western fen soak (pos. 05-06 08-11). The rare *Dicranum leioneuron* has its optimum in this site-type. Hepatics and lichens are unimportant, but occasionally, *Mylia anomala* has been observed to invade footprint depressions.

The E2PH1 site-type

The floristic composition of this site-type is shown in Tab. 32. The constant species are *Andromeda polifolia*, *Calluna vulgaris*, *Vaccinium oxycoccos* coll., *Drosera rotundifolia*, *Eriophorum vaginatum*, *Sphagnum balticum*, *S. rubellum*, and *Mylia anomala*. Dominants in the field layer are *Calluna vulgaris* and *Eriophorum vaginatum*. The bottom layer is dominated by *Sphagnum rubellum*, *S. fuscum*, and *S. magellanicum*.

Tab. 33. The vegetation of the E2PHI site-type.

Sample set No.	S1	S2	S3	S4	S5	O1	O2	S	O	
Number of sample plots	5	5	5	5	5	16	2	25	18	43
Zone	E2	E2	E2	E2	E2	E2	E3			
<i>Pinus sylvestris</i>	-	-	100- 2	80- 1	-	25- 3	-	36- 2	22- 3	30- 2
<i>Andromeda polifolia</i>	100- 4	80- 1	100- 1	100- 1	100- 2	88- 2	+	96- 2	89- 2	93- 2
<i>Calluna vulgaris</i>	100-20	100-25	100-22	100-21	100-18	94-17	+	100-21	94-17	98-19
<i>Erica tetralix</i>	-	60- 2	40- 6	40- 7	80-12	31-11	+	44- 7	33- 9	39- 8
<i>Vaccinium oxycoccos</i> coll.	100- 1	100- 3	100- 1	100- 2	100- 3	94- 3	+	100- 2	94- 3	98- 2
<i>Drosera rotundifolia</i>	100- 1	100- 1	100- 1	100- 1	100- 1	88- 1	+	100- 1	89- 1	95- 1
<i>Rubus chamaemorus</i>	80- 2	60- 2	80- 3	80- 3	20- 1	81- 5	-	64- 2	72- 5	67- 3
<i>Carex pauciflora</i>	80- 8	40- 2	40- 2	100- 5	60- 6	75- 1	+	64- 5	78- 2	70- 4
<i>Eriophorum vaginatum</i>	100-15	100-16	100-26	100-18	100- 8	100-20	+	100-17	100-20	100-18
<i>Scirpus cespitosus</i>	100-15	60- 1	40- 1	60- 2	100- 3	88- 8	+	72- 6	89- 9	79- 7
<i>Sphagnum balticum</i>	100- 2	40- 1	100- 8	100- 5	100- 2	94-12	+	88- 4	94-11	91- 6
<i>S. fuscum</i>	60-20	100-24	60-23	80-75	40-31	63-24	+	68-36	67-23	68-31
<i>S. magellanicum</i>	100-25	40- 5	100-34	80-14	60-31	75-16	+	76-24	78-17	77-21
<i>S. papillosum</i>	60- 2	-	40-16	-	-	38- 8	+	20- 7	39- 7	28- 7
<i>S. rubellum</i>	100-49	100-64	100-26	100-19	100-60	100-43	+	100-44	100-43	100-44
<i>Calypogeja sphagnicola</i>	40- 1	100- 2	100- 2	80- 2	40- 1	69- 2	+	72- 1	72- 2	72- 1
<i>Cephalozia</i> spp.	80- 2	20- 1	40- 1	80- 1	60- 1	75- 3	+	56- 1	78- 3	65- 2
<i>Cladopodiella fluitans</i>	60- 2	20- 1	40- 1	40- 1	40- 2	50- 2	+	36- 1	56- 3	44- 2
<i>Kurzia pauciflora</i>	80- 3	80- 1	80- 1	80- 3	40- 1	88- 4	+	72- 2	83- 4	77- 3
<i>Mylia anomala</i>	100- 1	100- 5	100- 3	80- 3	100- 3	94- 6	+	96- 3	94- 6	95- 4
<i>Cladonia rangiferina</i>	60- 1	40- 1	100- 1	20- 4	-	13- 7	-	44- 1	11- 7	30- 2

Additional species (with constancy below 10):

Betula pubescens 2-1 (S4: 20-1; S: 4-1).

Empetrum nigrum 5-1 (S4: 20-1, O1: 6-1; S: 4-1, O: 6-1).

Drosera anglica 2-1 (O1: 6-1; O: 6-1), *Trientalis europaea* 2-2 (S5: 20-2; S: 4-2).

Scheuchzeria palustris 2-1 (O2: +; O: 6-1).

Dicranum affine 2-12 (S5: 20-12; S: 4-12), *D. leioneuron* 2-4 (S5: 20-4; S: 4-4), *Pleurozium schreberi* 2-1 (S5: 20-1; S: 4-1), *Pohlia nutans* 2-1 (S2: 20-1; S: 4-1), *Polytrichum strictum* 2-2 (O1: 6-2; O: 6-2).

Sphagnum tenellum 9-2 (O1: 13-2, O2: +; O: 22-2).

Cephalozia spp. 2-1 (S2: 20-1; S: 4-1), *Odontoschisma sphagni* 2-1 (S5: 20-1; S: 4-1).

Cladonia arbuscula 2-1 (S3: 20-1; S: 4-1), *Cladonia pyxidata* coll. 7-1 (S3: 20-1, S4: 20-1, O1: 6-1; S: 8-1, O: 6-1), *C. squamosa* 7-2 (S1: 40-1, O1: 6-3; S: 8-1, O: 6-3).

The mean number of species per sample plot is 16, while the total number in the 43 sample plots is 37.

The physiognomy of the field layer is characterized by a dense cover of dwarf shrubs and graminids. The bottom layer has a continuous cover of *Sphagnum*. Hepatics and lichens occur, but are quantitatively unimportant.

The estimated area of this site-type is 3 per cent. It occurs in fen soaks in unorientated hummocks between the water tracks and the border onto the E1 zone (usually with *Carex pauciflora* as the E2 indicator), or on the long hummock banks (kermi-string transitions), orientated at right angles to the slope (e.g., in pos. 05-07 11-14).

Some variation occurs with respect to dominance relationships. *Erica tetralix* may reach high importance (S4 and O1 in Tab. 33), but is always subordinate to *Calluna vulgaris*. *Sphagnum rubellum* is the most important of the dominants in the bottom layer, but *S. fuscum* (S4) or *S. magellanicum* (S3) prevail locally.

The E3PHI site-type

The floristic composition of this site-type is shown in Tab. 34. The constant species are

Tab. 34. The vegetation of the E3PH1 site-type.

Sample set No.	S1	S2	S3	S4	S	O	
Number of sample plots	5	5	5	5	20	3	23
Zone	E3	E3	E3	E3			
<i>Betula pubescens</i>	-	40- 1	40- 1	20- 3	25- 1	-	22- 1
<i>Pinus sylvestris</i>	-	40- 1	60- 1	40- 4	35- 3	33- 1	35- 3
<i>Andromeda polifolia</i>	80- 1	100- 1	20- 1	100- 1	75- 1	67- 2	74- 1
<i>Calluna vulgaris</i>	100-19	100-17	80-19	100-23	95-19	100-16	96-19
<i>Erica tetralix</i>	-	100-12	100-23	20- 1	55-16	-	48-16
<i>Myrica gale</i>	-	100-14	100- 6	-	50-10	67- 1	52- 9
<i>Vaccinium oxycoccos</i> coll.	100- 3	100- 3	100-10	100- 3	100- 5	100- 4	100- 5
<i>Drosera rotundifolia</i>	100- 1	100- 2	80- 1	100- 1	95- 1	100- 1	96- 1
<i>Rubus chamaemorus</i>	80- 6	-	-	20- 1	25- 5	67- 7	30- 5
<i>Carex pauciflora</i>	40-12	40-14	40-21	40- 7	40-13	-	35-13
<i>C. rostrata</i>	100- 1	-	20- 1	80- 2	50- 2	33- 2	48- 2
<i>Eriophorum angustifolium</i>	-	-	80- 1	-	20- 1	-	17- 1
<i>E. vaginatum</i>	100-21	100-18	100-19	100-17	100-19	100-18	100-19
<i>Scirpus cespitosus</i>	40-17	20- 1	40- 5	100- 9	50- 9	33- 1	48- 8
<i>Aulacomnium palustre</i>	-	-	-	20- 2	5- 2	67- 4	13- 3
<i>Calliergon stramineum</i>	-	40- 1	-	-	10- 1	33- 1	13- 1
<i>Pohlia nutans</i>	20- 1	20- 3	-	-	10- 2	33- 5	13- 3
<i>Sphagnum angustifolium</i>	20- 1	-	-	20-10	10- 6	67- 3	17- 5
<i>S. balticum</i>	100- 9	60- 1	100- 4	100- 9	90- 6	100-22	91- 8
<i>S. fuscum</i>	40-21	60-23	20-17	40-19	40-21	33- 5	39-19
<i>S. magellanicum</i>	100-37	60-73	100-25	100-22	90-35	100-38	91-35
<i>S. papillosum</i>	20- 1	-	-	60- 2	20- 2	33-30	22- 8
<i>S. rubellum</i>	100-36	100-32	100-48	100-45	100-44	100-17	100-41
<i>Calypogeja sphagnicola</i>	100- 1	40- 1	100- 1	80- 2	80- 1	100- 2	83- 1
<i>Cephalozia</i> spp.	20- 7	-	20- 1	40- 1	20- 3	33- 1	22- 3
<i>Cladopodiella fluitans</i>	100- 3	60- 1	60- 1	60- 3	70- 2	100- 6	74- 3
<i>Kurzia pauciflora</i>	80- 3	40- 2	20- 1	60- 2	50- 2	33- 7	48- 3
<i>Mylia anomala</i>	100- 3	60- 5	80- 2	80- 3	80- 3	67- 2	78- 3

Additional species (with constancy below 10):

Vaccinium uliginosum 4-7 (O: 33-7).

Phragmites australis 4-7 (S1: 20-7; S: 5-7), *Scheuchzeria palustris* 4-1 (S4: 20-1; S: 5-1).

Pleurozium schreberi 4-2 (O: 33-2), *Polytrichum strictum* 9-2 (S1: 20-3; S: 5-3; O: 33-2).

Sphagnum tenellum 4-1 (O: 33-1).

Odontoschisma sphagni 4-1 (S4: 20-1; S: 5-1).

Cladonia rangiferina 9-2 (S2: 40-2; S: 10-2).

Calluna vulgaris, *Vaccinium oxycoccos* coll., *Drosera rotundifolia*, *Eriophorum vaginatum*, *Sphagnum balticum*, *S. magellanicum*, *S. rubellum*, and *Calypogeja sphagnicola*. Dominants in the field layer are *Calluna vulgaris*, *Erica tetralix*, *Carex pauciflora*, and *Eriophorum vaginatum*. *Mylia anomala* has also been recorded as a dominant. The bottom layer is dominated by *Sphagnum rubellum*, *S. magellanicum*, and *S. fuscum*, in some sample plots also by *S. balticum* and *S. papillosum*.

The mean number of species per sample plot is 15, while the total number in the

Tab. 35. The vegetation of the E1RHL site-type.

Sample set No.	S1	S2	S3	S4	S5	S6	S7	O1	O2	S	O	
Number of sample plots	5	5	5	5	5	5	5	47	4	35	51	86
Zone	E1	E1	E1	E1	E2	E2	E2	E1	E2			
<i>Pinus sylvestris</i>	-	20- 1	40- 4	20- 1	20- 2	-	20- 1	60- 3	25- 4	17- 2	57- 3	40- 3
<i>Andromeda polifolia</i>	60- 2	100- 2	80- 2	100- 2	100- 2	100- 8	100- 3	89- 2	100- 3	91- 3	90- 2	90- 2
<i>Calluna vulgaris</i>	60-24	100-16	100-13	100-20	100-23	100-19	100-22	100-29	100-32	94-20	100-29	98-25
<i>Vaccinium oxycoccos</i> coll.	60- 1	100- 1	100- 3	100- 2	100- 1	100- 2	100- 2	98- 2	100- 1	94- 2	98- 2	96- 2
<i>Drosera rotundifolia</i>	60- 1	80- 1	80- 1	80- 1	40- 1	100- 1	40- 1	89- 1	100- 1	74- 1	90- 1	83- 1
<i>Rubus chamaemorus</i>	60- 1	100- 3	80- 1	100- 7	20- 7	20- 1	100-11	83- 4	100- 6	69- 4	84- 4	77- 4
<i>Eriophorum vaginatum</i>	60-10	100- 9	100-12	100- 5	60- 2	100- 9	100-12	100-12	100-18	89- 8	100-12	95-10
<i>Scirpus cespitosus</i>	20- 1	40- 1	40- 3	100- 2	80- 3	80- 1	60- 1	85- 4	75- 5	60- 2	84- 4	74- 3
<i>Sphagnum balticum</i>	60- 1	80- 3	20- 2	-	80- 1	80- 2	80- 5	57- 4	100- 3	57- 2	61- 4	59- 3
<i>S. fuscum</i>	60- 1	20- 5	80- 6	80- 2	20- 1	80- 2	100- 2	70- 8	50- 9	63- 3	69- 8	67- 6
<i>S. magellanicum</i>	40- 2	-	-	-	40- 2	20- 1	20- 1	21- 4	50- 1	17- 2	24- 4	21- 3
<i>S. rubellum</i>	80- 1	80- 2	100- 3	100- 1	80- 1	100- 6	80- 9	100- 8	100-12	89- 3	100- 9	96- 7
<i>S. tenellum</i>	20- 1	20- 1	-	-	20- 1	-	-	15- 1	25- 1	9- 1	16- 1	13- 1
<i>Calypogeja sphagnicola</i>	20- 1	20- 1	60- 2	20- 1	20- 1	80- 1	40- 1	55- 2	75- 1	37- 1	57- 2	49- 2
<i>Cephalozia</i> spp.	100- 9	100- 5	100- 7	100- 3	100- 3	100-10	100- 5	98- 6	100- 5	100- 6	98- 6	99- 6
<i>Cephalozia</i> spp.	40- 1	40- 1	40- 1	20- 1	40- 1	60- 1	60- 1	19- 1	25- 1	43- 1	20- 1	29- 1
<i>Cladopodiella fluitans</i>	20- 5	20- 1	-	-	60- 1	40- 2	20- 1	36- 3	100- 2	23- 2	41- 3	34- 3
<i>Kurzia pauciflora</i>	100-17	80-33	100-29	100-30	100- 6	100-14	80-10	91-18	100- 8	91-20	92-17	92-18
<i>Mylia anomala</i>	100- 8	100- 4	100-15	100-11	80- 4	100- 9	100- 7	100- 9	100-14	97- 8	100- 9	99- 9
<i>Cetraria ericetorum</i>	20- 3	40- 6	20- 7	60- 7	40-10	-	60- 9	-	-	34- 7	-	13- 7
<i>Cladonia arbuscula</i>	-	-	20- 4	60-21	20-15	-	40-35	6- 1	-	20-22	6- 1	10-14
<i>C. fimbriata</i>	60- 1	20- 3	-	-	20- 1	-	-	28- 1	75- 2	14- 1	31- 1	24- 1
<i>C. pyxidata</i> coll.	20- 1	20- 2	60- 2	40-13	60- 1	20- 1	80- 2	6- 1	-	43- 2	6- 3	21- 2
<i>C. rangiferina</i>	100-18	100-36	100-28	100- 3	40- 1	100-38	100-28	70-22	50- 3	91-24	69-21	78-22
<i>C. squamosa</i>	100- 4	100- 4	-	80- 2	100-32	100- 5	80- 2	38- 2	75- 2	80- 9	41- 2	57- 6

Additional species (with constancy below 10):

Betula pubescens 4-2 (S5: 20-3, O1: 4-1; S: 3-3, O: 4-1).

Empetrum nigrum 7-1 (S7: 40-1, O1: 9-1; S: 6-1, O: 8-1).

Drosera anglica 1-1 (O1: 2-1; O: 2-1).

Dicranum fuscescens 1-1 (O1: 2-1; O: 2-1), *D. polysetum* 1-1 (O1: 2-1; O: 2-1), *Pleurozium schreberi* 1-15 (O1: 2-15; O: 2-15).

Sphagnum cuspidatum 1-1 (S1: 20-1; S: 3-1).

Gymnocloa inflata 1-1 (S5: 20-1; S: 3-1), *Riccardia latifrons* 5-2 (S1: 20-1, S7: 20-3, O1: 4-1; S: 6-2, O: 4-1).

Cetraria delisei 1-10 (S2: 20-10; S: 3-10), *C. islandica* 9-12 (S2: 20-3, S3: 40-15, S7: 60-17, O1: 4-3; S: 17-15, O: 4-3), *C. pinastri* 1-1 (S5: 20-1; S: 3-1), *Cladonia bacillaris* 2-1 (S2: 20-1, O1: 2-1; S: 3-1, O: 2-1), *C. cornuta* 1-1 (O1: 2-1; O: 2-1), *C. floerkeana* 5-11 (S5: 80-11; S: 11-11), *C. pleurota* 5-2 (S5: 80-2; S: 11-2), *C. stellaris* 9-6 (S4: 20-15, S6: 20-7, O1: 11-4, O2: 25-2; S: 6-11, O: 12-4), *C. sulphurina* 5-1 (S2: 40-1, O1: 4-1; S: 6-1, O: 4-1), *C. uncialis* 4-2 (S3: 40-3, O1: 2-1; S: 6-3, O: 2-1), *Hypogymnia physodes* 4-1 (S2: 20-1, O1: 2-1, O2: 25-1; S: 3-1, O: 4-1), *Imadophila ericetorum* 2-1 (S4: 20-1, S5: 20-1; S: 6-1), *Ochrolechia frigida* 6-6 (S2: 20-2, S5: 60-6, S6: 20-10; S: 14-6).

23 sample plots is 36.

The field layer is dominated by dwarf shrubs, but with a high importance of graminids. The bottom layer is dominated by red sphagna, making a closed mat. Hepatics only occur as scattered individuals.

The estimated area covered by this site-type is less than 0.5 per cent. It mostly occurs as scattered, isolated hummocks in the E3 zone.

There is considerable variation in the field layer with respect to dominants other than *Calluna vulgaris* and *Eriophorum vaginatum*. S2 in Tab. 34 is a stand where all site-type dominants reach dominance, the sample plots represent different combinations of dominant species. Some sample plots reach a total cover in the field layer of more than 80 per cent (e.g., in S3). In such plots the bottom layer is mostly reduced with respect to cover and vitality. There is some variation with respect to relative dominance of *Sphagnum rubellum* and *S. magellanicum*. Other *Sphagnum* spp. rarely occur as dominants.

The E1RHL site-type

The floristic composition of this site-type is shown in Tab. 35. The constant species are

Andromeda polifolia, *Calluna vulgaris*, *Vaccinium oxycoccos* coll., *Drosera rotundifolia*, *Sphagnum rubellum*, *Cephalozia* spp., *Kurzia pauciflora*, and *Mylia anomala*. *Calluna vulgaris*, occasionally also *Eriophorum vaginatum*, is the dominant in the field layer. *Cladonia rangiferina*, *Kurzia pauciflora*, and *Mylia anomala* are the main dominants of the bottom layer.

The mean number of species per sample plot is 16, while the total number in the 86 sample plots is 47.

The physiognomy of the field layer is dominated by *Calluna vulgaris*, while herbs (*Drosera rotundifolia* and *Rubus chamaemorus*) and graminids mostly play subordinate roles. The physiognomy of the bottom layer is variable, but commonly this layer includes light patches dominated by lichens and dark patches dominated by hepatics, apparently arranged randomly in a mosaic with the E1PH1 site-type (and with frequent transitions). Patch size varies from few sq. cm to 1 m² for lichen-dominated, to 0.25 m² for hepatic-dominated vegetation. Patches devoid of a bottom layer, or with dead sphagna, hepatics or lichens, often covered by algae, have high areal importance (Fig. 69). Algae invade after hepatics have weakened the dominant *Sphagnum* spp.

The estimated area covered by this site-type is 8 per cent. It is most common in the E1 zone, notably in the two kermi raised bog segments, where it is one of the quantitatively most important site-types.

There is little variation in the field layer. However, no site-type shows larger variation in the bottom layer. Three species have been recorded as dominating more than half the area of a sample plot; *Cladonia rangiferina* (13 plots), *Kurzia pauciflora* (3), and *Cladonia arbuscula* (2). The number of dominants (percentage cover 15) recorded is ten, listed in order of decreasing number of sample plots in which they dominate: *Kurzia pauciflora* (39 plots), *Cladonia rangiferina* (31), *Mylia anomala* (17), *Cephalozia* spp. (8), *Cladonia squamosa* (5), *Cetraria islandica* and *Cladonia arbuscula* (3), *Cladonia floerkeana* (2), and *Cetraria ericetorum* and *Cladonia pyxidata* coll. (1).

Some observations relating to preferences of individual species should be noted. *Mylia anomala* always grows over dead or dying *Sphagnum fuscum*. In the P subseries *Mylia* occurs as scattered individuals among the *Sphagnum* plants; in the R subseries *Mylia* forms dense patches overtopping dead *Sphagnum fuscum*. The other hepatics (the most important is *Kurzia pauciflora*) mostly form thick, appressed mats overlying *Sphagnum* peat. Long before the time the hepatics reach optimal development, all *Sphagnum* is dead. *Riccardia latifrons* typically prefers such hepatic mats. Several of the small *Cladonia* spp. (9 species recorded) seem to prefer growing on bare peat areas, *Eriophorum vaginatum* bases, debris, and litter.

The E2RHI site-type

The floristic composition of this site-type is shown in Tab. 36. The constant species are *Andromeda polifolia*, *Calluna vulgaris*, *Erica tetralix*, *Vaccinium oxycoccos* coll., *Drosera rotundifolia*, *Eriophorum vaginatum*, *Scirpus cespitosus*, *Sphagnum rubellum*, *Cephalozia* spp., *Kurzia pauciflora*, *Mylia anomala*, and *Cladonia rangiferina*. The main dominant in the field layer is *Calluna vulgaris*, but *Erica tetralix*, *Rubus chamaemorus*, and *Eriophorum vaginatum* also sometimes reach dominance. *Cladonia rangiferina*, *Kurzia pauciflora*, and *Mylia anomala* are bottom layer dominants.

The mean number of species per sample plot is 17, while the total number in the 25 sample plots is 34.

Dwarf shrubs, in combination with or rarely replaced by graminids, give the site-type its physiognomy. The occasional dominance of *Rubus chamaemorus* (S3 in Tab. 36), should

Tab. 36. The vegetation of the E2RH1 site-type.

Sample set No.	S1	S2	S3	S4	S	O	
Number of sample plots	5	5	5	5	20	5	25
Zone	E2	E2	E2	E2			
<i>Pinus sylvestris</i>	-	-	-	40- 1	10- 1	20- 1	12- 1
<i>Andromeda polifolia</i>	80- 1	100- 1	100- 2	60- 1	85- 1	100- 1	88- 1
<i>Calluna vulgaris</i>	100-15	100-25	100-18	100-23	100-20	100-21	100-20
<i>Erica tetralix</i>	100- 4	100-11	100-10	100-14	100-10	40-10	88-10
<i>Vaccinium oxycoccus</i> coll.	100- 2	100- 6	100- 1	100- 1	100- 3	100- 2	100- 3
<i>Drosera rotundifolia</i>	80- 1	100- 1	80- 1	80- 1	85- 1	80- 1	84- 1
<i>Rubus chamaemorus</i>	20- 1	60-11	100-19	100- 6	70-11	60- 2	68- 9
<i>Carex pauciflora</i>	-	-	-	-	-	60- 5	12- 5
<i>Eriophorum vaginatum</i>	100-26	100-10	100- 4	80- 3	95-11	100-18	96-12
<i>Scirpus cespitosus</i>	80- 2	100- 1	80- 1	100- 2	90- 2	80- 3	88- 2
<i>Sphagnum balticum</i>	20- 1	80- 5	100- 2	80- 3	70- 3	100- 9	76- 4
<i>S. fuscum</i>	60- 4	40- 4	20- 2	80- 2	50- 3	80- 9	56- 4
<i>S. magellanicum</i>	20- 1	40- 2	60- 1	40- 1	40- 1	100- 3	52- 2
<i>S. rubellum</i>	100- 5	100- 9	100- 2	100- 2	100- 5	100-13	100- 7
<i>Calypogeja sphagnicola</i>	60- 2	100- 1	60- 1	20- 1	60- 2	40- 3	56- 2
<i>Cephalozia</i> spp.	100- 6	100- 5	100-10	100- 2	100- 6	100- 8	100- 6
<i>Cephaloziella</i> spp.	-	20- 1	-	40- 2	15- 1	-	12- 1
<i>Cladopodiella fluitans</i>	80- 1	60- 1	40- 1	40- 2	55- 1	60- 1	56- 1
<i>Kurzia pauciflora</i>	80-17	100- 6	100-11	80-16	90-12	100-15	92-13
<i>Mylia anomala</i>	100- 5	100-30	100- 4	100- 9	100-12	100- 9	100-11
<i>Cladonia fimbriata</i>	40- 1	60- 5	20- 1	-	30- 3	20- 1	28- 3
<i>C. pyxidata</i> coll.	60- 2	-	40- 1	60- 1	40- 1	20- 1	36- 1
<i>C. rangiferina</i>	100-55	100-19	100-29	100-22	100-31	60-14	92-28
<i>C. squamosa</i>	60- 1	-	80- 2	-	35- 1	20- 7	32- 2

Additional species (with constancy below 10):

Betula pubescens 4-1 (O: 20-1).

Empetrum nigrum 4-1 (S4: 20-1; S: 5-1).

Sphagnum papillosum 4-1 (O: 20-1), *S. tenellum* 8-2 (S2: 20-1; S: 5-1, O: 20-3).

Calypogeja neesiana 4-1 (S1: 20-1; S: 5-1), *Odontoschisma sphagni* 4-1 (O: 20-1).

Cladonia arbuscula 4-1 (S1: 20-1; S: 5-1), *C. bacillaris* 4-1 (S4: 20-1; S: 5-1), *C. uncialis* 4-1 (S1: 20-1; S: 5-1), *Ochrolechia frigida* 4-1 (S3: 20-1; S: 5-1).

be noted. The patchy bottom layer, with a mosaic of hepatics, lichens, sites devoid of vegetation (for example due to dwarf shrub shade or litter), etc., is like the E1RH1 site-type (cf. Fig. 68).

This site-type covers less than 1 per cent of the special area, and occurs as a rare constituent of hummock areas in the E2 zone.

There is some variation with respect to dominance relationships in the field layer, but *Erica tetralix* almost always occurs as an important species. *Rubus chamaemorus* and *Eriophorum vaginatum* dominate one S-set each apparently without affecting the composition of the rest of the vegetation. The variation in the bottom layer is not different from the E1RH1 site-type, except that dominance is restricted to four species and that the number of small lichen species is negligible. A negative relationship is noted between the importance of *Erica tetralix* and the development of the bottom layer vegetation. When the

Tab. 37. Survey of the EH1 series.

Subseries	P			R	
Zonation	E1	E2	E3	E1	E2
Site-type	ElPH1	E2PH1	E3PH1	ElRH1	E2RH1
Number of sample plots	117	43	23	86	25
<i>Pinus sylvestris</i>	51- 4	30- 2	35- 3	40- 3	12- 1
<i>Andromeda polifolia</i>	89- 2	93- 2	74- 1	90- 2	88- 1
<i>Calluna vulgaris</i>	100-30	98-19	96-19	98-25	100-20
<i>Vaccinium oxycoccus</i> coll.	100- 3	98- 2	100- 5	96- 2	100- 3
<i>Drosera rotundifolia</i>	88- 1	95- 1	96- 1	83- 1	84- 1
<i>Rubus chamaemorus</i>	82- 5	67- 3	30- 5	77- 4	68- 9
<i>Eriophorum vaginatum</i>	100-12	100-18	100-19	95-10	96-12
<i>Scirpus cespitosus</i>	82- 4	79- 7	48- 8	74- 3	88- 2
<i>Sphagnum balticum</i>	69- 9	91- 6	91- 8	59- 3	76- 4
<i>Calypogeja sphagnicola</i>	65- 1	72- 1	83- 1	49- 2	56- 2
<i>Cephalozia</i> spp.	84- 3	65- 2	22- 3	99- 6	100- 6
<i>Cladopodiella fluitans</i>	23- 2	44- 2	74- 3	34- 3	56- 1
<i>Erica tetralix</i>	-	39- 8	48-16	-	88-10
<i>Carex pauciflora</i>	-	70- 4	35-13	-	12- 5
<i>Myrica gale</i>	-	-	52- 9	-	-
<i>Carex rostrata</i>	-	-	48- 2	-	-
<i>Eriophorum angustifolium</i>	-	-	17- 1	-	-
<i>Sphagnum fuscum</i>	82-36	68-31	39-19	67- 6	56- 4
<i>S. magellanicum</i>	44-13	77-21	91-35	21- 3	52- 2
<i>S. rubellum</i>	99-41	100-44	100-41	96- 7	100- 7
<i>Sphagnum papillosum</i>	-	28- 7	22- 8	-	4- 1
<i>Kurzia pauciflora</i>	79- 5	77- 3	48- 3	92-18	92-13
<i>Mylia anomala</i>	97- 4	95- 4	78- 3	99- 9	100-11
<i>Cladonia fimbriata</i>	7- 1	-	-	24- 1	28- 3
<i>C. pyxidata</i> coll.	1- 1	7- 1	-	21- 2	36- 1
<i>C. rangiferina</i>	59- 6	30- 2	9- 2	78-22	92-28
<i>C. squamosa</i>	14- 1	7- 2	-	57- 6	32- 2

density of *Erica* is high (as in S4), the bottom layer is often devoid of vegetation or only a crisp, dry film of hepatics with a scorched appearance occurs.

Survey of the mire expanse lower hummock series

A survey of the mire expanse lower hummock series is given in Tab. 37. The field layer is dominated by dwarf shrubs, with graminids as a subordinate, but significant element. The bottom layer is variable between subseries, in the P subseries it is continuous, with red and brown sphagna, in the R subseries it is mostly a mosaic of light patches dominated by lichens and dark patches dominated by hepatics.

The lower hummock series is characterized floristically by the presence of the twelve species in group 1 in Tab. 37. The subseries differ with respect to the physiognomy of the bottom layer, reflected in the dominance of *Sphagnum* spp. (group 4) in the P subseries,

the dominance of hepatics and lichens (group 6) in the R subseries, and the high areal importance of bare peat in the latter (Fig. 68). Transitions between the subseries, represented by hepatics or lichens overtopping the sphagna, are extremely common. The zonations differ slightly, as very few zonal indicators enter hummocks. Species groups 2 and 5 indicate the E2, group 3 the E3 zonation. There are small differences between the zonations with respect to dominance relationships. In the P subseries, *Sphagnum rubellum* maintains the position as the main dominant throughout the zonations. *S. fuscum* decreases while *S. magellanicum* increases from E1 to E3.

Covering ca. 25 per cent of the special area, this is the quantitatively most important series. The importance of the P subseries is twice that of the R subseries. The R subseries covers small areas outside the E1 zone.

Site-type means for median depth to the water table lie in the range 9.3-15.2 cm (Fig. 67). Inundation of the bottom layer occurs only exceptionally (cf. Tab. 17), while mean minimum depth to the water table is ca. 5.5 cm. There are considerable differences between the subseries, the mean median depth of P sample plots being 1.3 cm higher than R plots. In the P subseries, site-type means for median depth to the water table decreases from 14.8 cm in the E1PHI to 12.4 in the E2PHI, and 9.3 in the E3PHI site-type. The increase in depth to the water table from E1RHI to E2RHI must be an artifact, caused by the sparse material from the latter. The trend of decreasing depth to the water table with increasing nutrient availability has two causes: (1) the reduced height of hummocks from E1 to E3, and (2) the carpet and lawn preference of all zonal indicators, rendering the higher hummocks in the E2 and, even more, the E3 zones devoid of such species (and thus, by definition, classified to the E1HI site-types).

Inverse relationships are observed between (1) litter cover and the development of the bottom layer, (2) the cover of dwarf shrubs and the development of the bottom layer, and (3) the vitality of *Sphagnum* and the cover of hepatics.

The mire expanse upper hummock series

The E1PHu site-type

The floristic composition of this site-type is shown in Tab. 38. The constant species are *Pinus sylvestris*, *Calluna vulgaris*, *Empetrum nigrum*, *Vaccinium oxycoccos* coll., *Rubus chamaemorus*, *Eriophorum vaginatum*, *Sphagnum fuscum*, *S. rubellum*, *Cephalozia* spp., and *Mylia anomala*. The field layer is dominated by *Calluna vulgaris*, the bottom layer by *S. fuscum* with *S. magellanicum* and *S. rubellum* as subordinate dominants.

The mean number of species per sample plot is 15, while the total number in the 98 sample plots is 44.

The site-type has a uniform physiognomy, scattered small pines occur in a field layer dominated by dwarf shrubs (particularly *Calluna vulgaris*), and a dark bottom layer with *Sphagnum fuscum* as the major species. Hepatics and lichens have no importance.

The site-type covers 10 per cent of the special area. It occurs all over the E1 zone and has particularly high areal importance in the extensive hummock-dominated areas to the east (e.g., pos. 13-14 10-11 and 11-12 11-14).

There is but minor variation within this site-type, mainly relating to the occurrence, or dominance, of *Sphagnum magellanicum* and *S. rubellum*. A couple of sample plots with co-dominance of *S. angustifolium* mediate the transition to the M1Hu site-type. *S. balticum* occurs as scattered, single individuals among other sphagna. *Pohlia nutans* is common as single plants in the *Sphagnum* mat.

Tab. 38. The vegetation of the E1PHu site-type.

Sample set No.	S1	S2	S3	S4	S5	S6	O1	O2	S	O
Number of sample plots	5	5	5	5	5	5	65	3	30	68
Zone	E1	E1	E1	E2	E2	E2	E1	E2		
<i>Pinus sylvestris</i>	80- 3	80- 3	80-14	60- 7	80- 5	60- 2	83- 6	100- 2	73- 6	84- 6
<i>Andromeda polifolia</i>	80- 1	80- 1	-	80- 1	100- 1	40- 1	63- 2	100- 1	63- 1	65- 2
<i>Calluna vulgaris</i>	100- 9	100-34	100-36	100-39	100-30	100-29	100-38	100-35	100-30	100-38
<i>Empetrum nigrum</i>	100- 4	80- 4	100- 5	80- 3	100- 2	60- 2	83- 4	100- 2	87- 3	84- 3
<i>Vaccinium oxycoccus</i> coll.	100- 4	100- 3	100- 5	100- 8	100- 3	100- 2	98- 5	100- 4	100- 4	99- 5
<i>Drosera rotundifolia</i>	100- 3	100- 1	60- 2	100- 1	80- 1	80- 1	63- 1	100- 1	87- 2	64- 1
<i>Rubus chamaemorus</i>	100- 3	60- 1	100-15	100- 8	40- 1	100- 6	91- 6	100- 9	83- 7	91- 6
<i>Eriophorum vaginatum</i>	100- 8	100- 5	80- 1	100- 2	100-15	100- 7	100- 9	100-10	97- 7	100- 9
<i>Pleurozium schreberi</i>	-	-	40- 1	-	-	40- 2	55- 4	-	13- 1	53- 4
<i>Pohlia nutans</i>	-	-	100- 3	20- 1	-	-	45- 2	33- 2	20- 3	44- 2
<i>Sphagnum angustifolium</i>	-	-	-	-	-	-	14-14	33-22	-	15-15
<i>S. balticum</i>	-	-	-	-	60- 2	60- 3	29- 2	33- 1	20- 3	29- 2
<i>S. tuscum</i>	100-60	100-70	100-74	100-74	60-46	80-49	98-52	100-50	90-64	99-52
<i>S. magellanicum</i>	-	-	100-13	80-15	80-44	40-29	34-18	67-10	50-24	35-17
<i>S. rubellum</i>	100-30	100-23	-	80- 6	100-27	100-24	94-16	100-19	80-23	94-16
<i>Calypogeja neesiana</i>	-	-	20- 1	40- 1	20- 1	20- 1	17- 2	-	17- 1	16- 2
<i>C. sphagnicola</i>	100- 3	80- 2	80- 1	40- 1	60- 1	80- 2	49- 1	67- 1	73- 2	50- 1
<i>Cephalozia</i> spp.	80- 4	80- 1	80- 3	60- 1	60- 1	60- 1	92- 2	67- 2	70- 2	91- 2
<i>Kurzia pauciflora</i>	60- 4	60- 1	-	20- 1	40- 2	40- 1	57- 2	33- 5	37- 2	56- 2
<i>Mylia anomala</i>	100- 5	100- 3	100- 3	100- 2	100- 2	100- 3	97- 4	67- 4	100- 3	96- 4
<i>Cladonia fimbriata</i>	-	-	-	-	20- 1	-	17- 1	-	3- 1	16- 1
<i>C. rangiferina</i>	100- 2	40- 7	40- 1	60- 1	100- 3	60- 1	66- 6	67-11	67- 2	66- 7

Additional species (with constancy below 10):

Betula pubescens 5-3 (S6: 40-2, O1: 5-3; S: 7-2, O: 4-3), *Picea abies* 5-1 (O1: 8-1; O: 7-1).

Vaccinium myrtillus 5-1 (S3: 20-1, O1: 6-1; S: 3-1, O: 6-1), *V. vitis-idaea* 2-1 (O1: 3-1; O: 3-1).

Scirpus cespitosus 5-1 (O1: 8-1; O: 7-1).

Aulacomnium palustre 8-2 (S4: 40-3, O1: 9-1; S: 7-3, O: 9-1), *Dicranum affine* 2-2 (S4: 20-1, O1: 2-3; S: 3-1, O: 1-3), *D. leiocneuron* 2-2 (O1: 3-2; O: 3-2), *D. majus* 1-1 (O1: 2-1; O: 1-1), *D. polysetum* 9-1 (S6: 20-1, O1: 12-1; S: 3-1, O: 12-1), *D. scoparium* 6-1 (S6: 40-1, O1: 6-1; S: 7-1, O: 6-1), *Polytrichum strictum* 9-13 (S3: 40-20, O1: 11-11; S: 7-20, O: 10-11).

Sphagnum capillifolium 1-70 (S6: 20-70; S: 3-70), *S. cf. subtile* 1-4 (S2: 20-4; S: 3-4).

Cephalozia spp. 4-1 (S1: 20-1, O1: 5-1; S: 3-1, O: 4-1), *Cladopodiella fluitans* 1-1 (O1: 2-1; O: 1-1), *Ptilidium ciliare* 1-1 (S6: 20-1; S: 3-1).

Cetraria islandica 2-10 (O1: 2-2, O2: 33-17; O: 3-10), *Cladonia arbuscula* 2-2 (S5: 20-1, O2: 33-3; S: 3-1, O: 1-3), *C. coniocraea* 1-1 (O1: 2-1; O: 1-1), *C. pyxidata* coll. 2-2 (O1: 2-2; O: 3-2), *C. squamosa* 1-1 (O1: 2-1; O: 1-1), *C. stellaris* 7-3 (S1: 20-1, S2: 20-1, S6: 20-1, O1: 5-3, O2: 33-5; S: 10-1, O: 6-4), *C. sulphurina* 2-1 (O1: 3-1; O: 3-1).

The E2PHu site-type

The floristic composition of this site-type is shown in Tab. 39. The constant species are *Andromeda polifolia*, *Calluna vulgaris*, *Vaccinium oxycoccus* coll., *Drosera rotundifolia*, *Rubus chamaemorus*, *Eriophorum vaginatum*, *Sphagnum fuscum*, *S. rubellum*, and *Mylia anomala*. The field layer is dominated by *Calluna vulgaris* and *Eriophorum vaginatum*. *Sphagnum fuscum* is the most important dominant in the bottom layer, followed by *S. magellanicum* and *S. rubellum*.

The mean number of species per sample plot is 15, while the total number in the 27 sample plots is 30.

The physiognomy of this site-type is uniform; a dense field layer dominated by *Calluna vulgaris*, and with high importance of the graminid *Eriophorum vaginatum* and the herb *Rubus chamaemorus* overlies a continuous *Sphagnum* carpet.

The site-type covers less than 0.5 per cent of the special area, restricted to interior parts of the larger hummock areas in the E2 zone, most frequent in pos. 04-06 09-12. The variation within this site-type is negligible.

Tab. 39. The vegetation of the E2PHu site-type.

Sample set No.	S1	S2	S3	S4	S5	S	O	
Number of sample plots	5	5	5	5	5	25	2	27
Zone	E2	E2	E2	E2	E2			
<i>Betula pubescens</i>	-	-	20- 1	40- 1	-	12- 1	-	11- 1
<i>Pinus sylvestris</i>	40- 2	60- 5	80- 4	20- 5	20- 1	44- 3	+	44- 3
<i>Andromeda polifolia</i>	80- 1	100- 2	60- 1	100- 1	100- 2	88- 2	+	89- 2
<i>Calluna vulgaris</i>	100-45	100-34	100-30	100-38	100-27	100-35	+	100-34
<i>Empetrum nigrum</i>	40- 2	60- 1	40- 1	20- 2	80- 1	48- 1	+	52- 1
<i>Erica tetralix</i>	40- 1	80-10	100- 3	100- 6	60- 3	76- 5	+	74- 5
<i>Vaccinium oxycoccus</i> coll.	100- 2	100- 2	100- 2	100- 6	100- 4	100- 3	+	100- 3
<i>Drosera rotundifolia</i>	80- 1	100- 1	80- 1	80- 2	100- 1	88- 1	+	89- 1
<i>Rubus chamaemorus</i>	80- 2	80- 4	80- 5	80-10	100-16	84- 8	+	82- 8
<i>Carex pauciflora</i>	100- 1	20- 1	-	20-10	60- 3	40- 3	+	44- 3
<i>Eriophorum vaginatum</i>	100-11	100-23	100-14	100-15	100- 9	100-14	+	100-14
<i>Pohlia nutans</i>	-	-	-	40- 1	40- 2	16- 2	-	15- 2
<i>Sphagnum balticum</i>	40- 1	60- 2	100- 4	80- 2	60- 2	68- 2	+	67- 2
<i>S. fuscum</i>	100-69	40-58	80-64	100-51	100-71	84-63	+	85-60
<i>S. magellanicum</i>	80- 7	100-38	100-15	80-14	40-31	80-20	+	78-21
<i>S. rubellum</i>	100-15	100-17	100-22	100-19	100- 6	100-16	+	100-16
<i>Calypogeja sphagnicola</i>	20- 1	80- 1	80- 1	80- 1	20- 1	56- 1	+	59- 1
<i>Cephalozia</i> spp.	60- 1	40- 1	80- 1	100- 1	80- 3	72- 1	+	74- 1
<i>kurzia pauciflora</i>	20- 1	60- 2	40- 1	60- 3	20- 4	40- 2	+	44- 2
<i>Mylia anomala</i>	100- 2	80- 2	80- 6	80- 5	100- 4	88- 4	+	89- 4
<i>Cladonia rangiferina</i>	40- 4	80- 4	60- 1	40- 2	20- 1	48- 3	-	44- 3

Additional species (with constancy below 10):

Scirpus cespitosus 7-1 (S1: 20-1, S3: 20-1; S: 8-1).

Aulacomnium palustre 4-1 (O: +), *Ceratodon purpureus* 4-1 (S5: 20-1; S: 4-1), *Dicranum affine* 4-1 (S5: 4-1; S: 4-1), *Pleurozium schreberi* 7-1 (S4: 40-1; S: 8-1), *Polytrichum strictum* 4-1 (S5: 20-1; S: 4-1).

Sphagnum cf. *subtile* 4-1 (S2: 20-1; S: 4-1).

Calypogeja neesiana 7-1 (S4: 20-1, S5: 20-1; S: 8-1), *Cephaloziella* spp. 4-1 (S2: 20-1; S: 4-1).

Cladonia stellaris 4-1 (S3: 20-1; S: 4-1).

The E3PHu site-type

The floristic composition of this site-type is shown in Tab. 40. The constant species are *Calluna vulgaris*, *Vaccinium oxycoccus* coll., *Eriophorum vaginatum*, *Sphagnum magellanicum*, and *Mylia anomala*. Dominants in the field layer are *Calluna vulgaris*, *Myrica gale*, and *Eriophorum vaginatum*. Dominants in the bottom layer are *Sphagnum magellanicum*, *S. rubellum*, *S. fuscum*, *Polytrichum strictum*, and *Pleurozium schreberi*.

The mean number of species per sample plot is 16, while the total number in the 10 sample plots is 34.

Dwarf shrubs strongly dominate in the field layer. The bottom layer is dominated by *Sphagnum* spp., often with co-dominance of *Polytrichum strictum*. Abundance of ants is frequent in hummocks dominated by the latter.

This site-type occurs as scattered, isolated hummocks in the E3 zone of the western fen soak.

Tab. 40. The vegetation of the E3PHu site-type.

Sample set No.	S1	S2	
Number of sample plots	5	5	
Zone	E3	E3	
<i>Betula pubescens</i>	-	60- 5	30- 5
<i>Pinus sylvestris</i>	-	100- 2	50- 2
<i>Andromeda polifolia</i>	20- 2	60- 2	40- 2
<i>Calluna vulgaris</i>	100-16	100-23	100-20
<i>Empetrum nigrum</i>	40-12	60- 2	50- 6
<i>Myrica gale</i>	20-22	100-20	60-20
<i>Vaccinium oxycoccos</i> coll.	100- 8	80- 3	90- 6
<i>V. uliginosum</i>	20- 2	20- 4	20- 3
<i>Drosera rotundifolia</i>	80- 1	80- 1	80- 1
<i>Rubus chamaemorus</i>	100- 6	60- 1	80- 4
<i>Carex lasiocarpa</i>	40- 1	-	20- 1
<i>C. pauciflora</i>	-	20- 1	10- 1
<i>Eriophorum vaginatum</i>	100-12	100-15	100-14
<i>Phragmites communis</i>	20- 1	-	10- 1
<i>Scirpus cespitosus</i>	20- 1	-	10- 1
<i>Aulacomnium palustre</i>	40- 3	-	20- 3
<i>Calliergon stramineum</i>	80- 2	-	40- 2
<i>Pleurozium schreberi</i>	20-45	20- 1	20-23
<i>Pohlia nutans</i>	60- 6	-	30- 6
<i>Polytrichum strictum</i>	100-42	-	50-42
<i>Sphagnum angustifolium</i>	100- 4	-	50- 4
<i>S. balticum</i>	20- 1	20- 1	20- 1
<i>S. capillifolium</i>	20- 7	20- 5	20- 6
<i>S. fuscum</i>	60- 7	100-20	80-15
<i>S. magellanicum</i>	100-27	100-57	100-42
<i>S. papillosum</i>	40- 1	-	20- 1
<i>S. rubellum</i>	60-40	100-14	80-24
<i>Calypogeja sphagnicola</i>	60- 1	60- 1	60- 1
<i>Cephalozia</i> spp.	40- 1	60- 1	50- 1
<i>Cladopodiella fluitans</i>	20- 1	20- 1	20- 1
<i>Kurzia pauciflora</i>	20- 1	40- 1	30- 1
<i>Lophozia ventricosa</i>	20- 1	-	10- 1
<i>Mylia anomala</i>	100- 2	80- 3	90- 2
<i>Cladonia rangiferina</i>	-	60- 1	30- 1

The variation within the site-type is small due to its low areal importance. The two S-sets represent variants with, and without, co-dominance of *Polytrichum strictum*.

The E1RHu site-type

The floristic composition of this site-type is shown in Tab. 41. The constants are *Calluna*

Tab. 41. The vegetation of the EIRN site-type.

Sample set No.	S1	S2	S3	S4	S5	S6	S7	S8	O1	O2	S	O	
Number of sample plots	5	5	5	5	5	5	5	5	33	7	40	40	80
Zone	E1	E1	E1	E1	E2	E2	E2	E2	E1	E2			
<i>Pinus sylvestris</i>	60- 2	100- 7	80- 2	60- 2	80- 8	80- 8	40- 2	60- 5	88- 9	100- 8	70- 4	90- 8	80- 6
<i>Andromeda polifolia</i>	80- 6	40- 4	80- 1	100- 3	40- 1	60- 1	100- 2	80- 1	73- 3	57- 1	73- 3	70- 2	71- 3
<i>Calluna vulgaris</i>	100- 9	80-29	100-25	80-21	100-30	100-16	100-33	100-43	100-37	100-49	95-26	100-39	98-33
<i>Empetrum nigrum</i>	100- 2	100-23	80- 3	60- 8	40- 2	100-11	100- 8	100- 2	79- 5	86- 5	85- 8	80- 5	83- 7
<i>Vaccinium oxycoccus</i> coll.	100- 1	80- 2	100- 2	60- 1	80- 2	80- 2	80- 2	100- 3	100- 5	86- 6	85- 2	98- 5	91- 4
<i>Drosera rotundifolia</i>	-	40- 1	40- 1	-	-	20- 1	20- 1	-	36- 1	29- 1	15- 1	35- 1	25- 1
<i>Rubus chamaemorus</i>	100- 6	80- 1	100- 3	100- 3	60- 3	40- 2	60- 3	100- 4	82- 4	86- 3	80- 3	83- 4	81- 4
<i>Eriophorum vaginatum</i>	80- 7	100-12	100- 4	100- 2	80-10	100-19	80- 2	100- 4	100-13	86-20	93- 8	98-14	95-11
<i>Dicranum scoparium</i>	-	40- 2	-	20- 1	-	40- 3	20- 2	40- 6	15- 1	14- 1	20- 3	15- 1	18- 2
<i>Pleurozium schreberi</i>	-	40- 5	-	60- 2	-	60- 2	40- 2	80- 6	79- 6	43-13	35- 3	73- 7	54- 6
<i>Pohlia nutans</i>	-	20- 1	-	-	-	20- 1	20- 1	20- 1	21- 3	43- 1	10- 1	25- 2	18- 2
<i>Sphagnum fuscum</i>	80- 1	80- 3	80- 5	40-10	60- 1	20- 5	-	80- 5	79-10	86-10	55- 4	80-10	68- 7
<i>S. magellanicum</i>	-	-	20- 1	-	-	-	20- 1	40- 2	12- 4	14- 1	10- 1	11- 3	11- 2
<i>S. rubellum</i>	40- 1	40- 1	80- 2	40- 2	40- 1	-	-	40- 2	73- 5	86- 1	35- 2	75- 4	55- 3
<i>Calypogeja neesiana</i>	-	-	-	-	20- 1	80- 2	-	-	33- 1	14- 1	13- 2	30- 1	21- 1
<i>C. sphagnicola</i>	20- 1	20- 1	40- 1	-	-	20- 1	-	-	33- 1	43- 1	13- 1	35- 1	24- 1
<i>Cephalozia</i> spp.	80- 1	60- 1	80- 2	60- 2	80- 2	40- 2	60- 2	80- 1	82- 2	86- 1	68- 2	83- 2	75- 2
<i>Cephalozia</i> spp.	20- 1	20- 1	20- 1	20- 1	-	40- 2	60- 1	20- 1	15- 1	-	25- 1	13- 1	19- 1
<i>Kurzia peuciflora</i>	60- 1	60- 3	40- 5	40- 1	20- 1	20- 1	40- 3	20- 2	42- 5	14- 1	38- 2	38- 4	38- 3
<i>Mylia anomala</i>	80- 2	80- 6	80- 4	40- 2	80- 1	-	60- 2	80- 1	85- 4	57- 4	68- 2	80- 4	74- 3
<i>Cetraria islandica</i>	-	20- 1	-	20-20	20- 1	-	60-19	-	6-19	14-40	15-13	8-26	12-18
<i>Cladonia arbuscula</i>	-	60-25	60-32	60-10	40- 4	40-12	20- 1	80-23	12- 2	14-17	45-18	13- 5	29-14
<i>C. fimbriata</i>	60- 1	20- 1	40- 1	20- 1	-	-	60- 2	20- 1	45- 2	29- 2	27- 1	43- 2	35- 2
<i>C. pyxidata</i> coll.	100- 3	60-11	80- 2	100- 1	100- 2	100- 3	100- 3	100- 3	20- 2	18- 1	-	90- 3	15- 1
<i>C. rangiferina</i>	100-78	100-31	100-54	100-40	100-67	100-46	100-37	100-53	97-32	86-27	100-51	95-31	98-41
<i>C. squamosa</i>	20- 1	-	60- 5	60- 1	20- 4	20- 2	80- 4	-	9- 1	14- 7	33- 3	10- 3	21- 3
<i>C. stellaris</i>	60-20	40-26	100- 9	80-54	40-35	40- 8	20-80	20-75	30-10	14-17	50-31	27-11	39-24
<i>C. sulphurina</i>	40- 1	-	40- 1	-	40- 1	-	20- 1	-	3- 1	-	18- 1	2- 1	10- 1

Additional species (with constancy below 10):

Betula pubescens 6-2 (S5: 60-3, O1: 3-1, O2: 14-1; S: 8-3, O: 5-1), *Picea abies* 3-1 (O1: 6-1; O: 5-1).*Vaccinium myrtillus* 4-1 (S6: 20-1, O1: 6-2; S: 3-1, O: 5-2), *V. uliginosum* 1-1 (O1: 3-1; O: 3-1), *V. vitis-idaea* 1-1 (S4: 20-1; S: 3-1).*Scirpus cespitosus* 3-1 (O1: 3-1, O2: 14-1; O: 5-1).*Ceratodon purpureus* 1-1 (S4: 20-1; S: 3-1), *Dicranum affine* 1-12 (S7: 20-12; S: 3-12), *D. fuscescens* 1-1 (S6: 20-1; S: 3-1), *D. leconteuron* 3-6 (S6: 20-10, O1: 3-1; S: 3-10, O: 3-1), *D. majus* 1-2 (S6: 20-2; S: 3-2), *D. polysetum* 4-2 (S6: 20-1, O1: 3-1, O2: 14-2; S: 3-1, O: 5-2), *Plagiothecium laetum* 3-1 (S6: 20-1, O1: 3-1; S: 3-1, O: 3-1), *Polytrichum strictum* 3-8 (S8: 20-1, O1: 3-15; S: 3-1, O: 3-15).*Sphagnum angustifolium* 4-22 (O1: 6-31, O2: 14-3; O: 8-22), *S. balticum* 7-2 (S8: 20-1, O1: 12-2; S: 3-1, O: 10-2), *S. capillifolium* 1-1 (S2: 20-1; S: 3-1).*Barbilophozia attenuata* 3-3 (O1: 3-2, O2: 14-4; O: 5-3), *Bazzania trilobata* 1-30 (S5: 20-30; S: 3-30), *Cladopodiella fluitans* 1-1 (S6: 20-1; S: 3-1), *Lophozia ventricosa* 1-1 (S4: 20-1; S: 3-1), *Ptilidium ciliare* 6-9 (S2: 20-10, S6: 20-35, S8: 20-1, O1: 3-1, O2: 14-3; S: 8-15, O: 5-2), *Riccardia latifrons* 1-1 (O1: 3-1; O: 3-1).*Cladonia bacillaris* 4-2 (S4: 40-2, S7: 20-3; S: 8-2), *C. carneola* 4-1 (S3: 20-1, S7: 40-1; S: 8-1), *C. cenotea* 1-1 (S5: 20-1; S: 3-1), *C. coniocraea* 3-1 (S3: 20-1, S5: 20-1; S: 5-1), *C. cornuta* 3-1 (S3: 20-1, S6: 20-1; S: 5-1), *C. cyanipes* 9-1 (S4: 40-1, S5: 20-1, S6: 40-1, S8: 20-1, O1: 3-1; S: 15-1, O: 3-1), *C. deformis* 5-4 (S1: 40-2, S7: 40-6; S: 10-4), *C. digitata* 1-1 (S6: 20-1; S: 3-1), *C. floerkeana* 3-1 (S7: 20-1, O2: 14-1; S: 3-1, O: 3-1), *C. gracilis* 1-1 (S7: 20-1; S: 3-1), *C. pleurota* 1-1 (S7: 20-1; S: 3-1), *C. uncialis* 3-1 (S6: 20-1, S8: 20-1; S: 5-1), *Hypogymnia physodes* 1-1 (S8: 20-1; S: 3-1), *Imadophila ericetorum* 1-1 (S7: 20-1; S: 3-1).

vulgaris, *Empetrum nigrum*, *Vaccinium oxycoccus* coll., *Rubus chamaemorus*, *Eriophorum vaginatum*, and *Cladonia rangiferina*. The field layer is dominated by *Calluna vulgaris*. More occasionally, *Empetrum nigrum* and *Eriophorum vaginatum* reach dominance. The bottom layer is dominated by *Cladonia rangiferina*, more rarely by *C. stellaris*, *C. arbuscula*, and *Cetraria islandica*.

The mean number of species per sample plot is 15, while the total number in the 80 sample plots is 65.

The site-type is physiognomically distinct with a field layer dominated by dwarf shrubs (and occasionally also by *Eriophorum vaginatum*) and a bottom layer almost totally covered by lichens.

The estimated area covered by this site-type is 6 per cent. It is most frequent in the two kermi raised bog synsegments, often dominating near the centres of large, hummock-dominated areas.

Tab. 42. The vegetation of the E2RHu site-type.

Sample set No.	S1	S2	S3	S	O	
Number of sample plots	5	5	5	15	1	16
Zone	E2	E2	E2			
<i>Betula pubescens</i>	-	40- 4	-	-	-	-
<i>Pinus sylvestris</i>	-	80- 3	20- 7	33- 4	+	38- 4
<i>Andromeda polifolia</i>	80- 1	100- 1	100- 1	93- 1	+	94- 1
<i>Calluna vulgaris</i>	100-25	100-35	100-35	100-32	+	100-31
<i>Empetrum nigrum</i>	-	60- 2	40- 2	33- 2	-	31- 2
<i>Erica tetralix</i>	100- 6	100- 8	100- 6	100- 7	+	100- 7
<i>Vaccinium oxycoccos</i> coll.	100- 2	100- 2	100- 2	100- 2	+	100- 2
<i>Drosera rotundifolia</i>	40- 1	-	60- 1	33- 1	-	31- 1
<i>Rubus chamaemorus</i>	20- 1	40- 4	100- 2	53- 3	-	50- 3
<i>Eriophorum vaginatum</i>	100-19	100-13	100-18	100-17	+	100-18
<i>Scirpus cespitosus</i>	20- 1	-	40- 1	20- 1	-	19- 1
<i>Pleurozium schreberi</i>	-	40- 7	20- 1	20- 5	-	19- 5
<i>Sphagnum balticum</i>	40- 1	40- 1	-	27- 1	-	25- 1
<i>S. fuscum</i>	100- 3	-	100-12	67- 7	+	69- 7
<i>S. rubellum</i>	100- 2	60- 6	100- 4	87- 3	+	88- 3
<i>Calypogeja neesiana</i>	40- 2	80- 1	20- 1	47- 1	-	44- 1
<i>C. sphagnicola</i>	80- 1	-	20- 1	33- 1	-	31- 1
<i>Cephalozia</i> spp.	100- 2	100- 2	100- 2	100- 2	+	100- 2
<i>Kurzia pauciflora</i>	40- 2	20- 1	60- 1	40- 1	-	38- 1
<i>Mylia anomala</i>	100- 5	100- 2	80- 9	93- 5	-	88- 5
<i>Cladonia arbuscula</i>	-	40-23	-	13-23	-	13-23
<i>C. pyxidata</i> coll.	60- 2	80- 2	40- 2	60- 2	+	63- 2
<i>C. rangiferina</i>	100-60	100-57	100-76	100-64	+	100-65
<i>C. stellaris</i>	20-55	40- 6	-	20-22	-	19-22

Additional species (With constancy below 10):

Vaccinium myrtillus 6-2 (S2: 20-2; S: 7-2).

Dicranum affine 6-3 (S1: 20-3; S: 7-3), *D. fuscescens* 6-7 (S2: 20-7; S: 7-7), *D. scoparium* 6-2 (S2: 20-2; S: 7-2), *Pohlia nutans* 6-1 (S2: 20-1; S: 7-1).

Sphagnum magellanicum 6-1 (S1: 20-1; S: 7-1), *S. papillosum* 6-1 (O: +).

Ptilidium ciliare 6-10 (S1: 20-10; S: 7.10).

Cladonia digitata 6-1 (S1: 20-1; S: 7-1), *C. fimbriata* 6-1 (S3: 20-1; S: 7-1), *C. squamosa* 6-1 (S2: 20-1; S: 7-1), *C. uncialis* 6-1 (S1: 20-1; S: 7-1).

The variation within this site-type is not large. Apart from vicariant dominance relationships, the composition of the field layer is uniform. The field layer is mostly relatively open, but some plots are almost devoid of vegetation in the bottom layer owing to shade and litter from unusually dense *Calluna vulgaris* stands (Fig. 68). The field layer of dense *Cladonia* stands is sparse; all vascular plants appear to regenerate poorly in a closed lichen mat. Similarly, the bottom layer is poorly developed around exceptionally large *Eriophorum vaginatum* tussocks. *Sphagnum fuscum* mats in all stages towards complete overgrowth by

lichens have been observed. Secondary *Sphagnum fuscum* hummocks sometimes arise from *Cladina* mats. The top of the decaying *Sphagnum* mat (after being overtopped by lichens) is often a substrate for *Calypogeja neesiana* and *Cephalozia* spp. Such a lower bottom layer is most frequently developed underneath *Cladonia stellaris*. *Pleurozium schreberi* is common on dry debris under *Cladonia stellaris*. *Calypogeja neesiana* occurs with highest frequency in shaded fissures in the peat, on the bases of *Eriophorum vaginatum*, and in similar sites. The decaying bases of dead *Eriophorum vaginatum* are often inhabited by small *Cladonia* spp.; *C. bacillaris*, *C. cenotea*, and *C. cyanipes* have been observed to spread from such sites onto the neighbouring peat. A deviant variant is often met with in depressions near the centres of large, high hummocks. Although situated at lower relative levels than the surroundings, the species composition of the vegetation unequivocally points in the direction of the upper hummock series (presence of *Empetrum nigrum*, absence of *Scirpus cespitosus*, etc.). This variant often shows reduced vitality of lichens and exposition of bare peat, often inhabited by *Dicranum affine*, *D. scoparium*, *Cephaloziella* spp., and *Ptilidium ciliare*. The only liverworts observed as dominants in this site-type are *Bazzania trilobata*, *Mylia anomala*, and *Ptilidium ciliare*.

The E2RHu site-type

The floristic composition of this site-type is shown in Tab. 42. The constant species are *Andromeda polifolia*, *Calluna vulgaris*, *Erica tetralix*, *Vaccinium oxycoccos* coll., *Eriophorum vaginatum*, *Sphagnum rubellum*, *Cephalozia* spp., *Mylia anomala*, and *Cladonia rangiferina*. The field layer is dominated by *Calluna vulgaris* and *Eriophorum vaginatum*. The bottom layer is dominated by *Cladonia rangiferina*, rarely replaced by *C. arbuscula* or *C. stellaris*.

The mean number of species per sample plot is 14, while the total number in the 16 sample plots is 36.

The field layer is dominated by dwarf shrubs and the graminid, *Eriophorum vaginatum*. The bottom layer is dominated by lichens. Hepatics play a minor role.

The site-type covers a negligible area. Small, isolated stands occur in larger hummock areas in the E2 zone, most frequently along the eastern margin of the western fen soak (pos. 05-06 08-12).

The within site-type variation is negligible, apart from the vicariance of three *Cladonia* spp. as bottom layer dominants. Deviant variants are encountered in the erosion area (not analyzed). The thin, crisp, dry and paperlike surface film is a preferred substrate of small *Cladonia* spp., particularly *C. floerkeana* and *C. pleurota*.

Survey of the mire expanse upper hummock series

A survey of the mire expanse upper hummock series is given in Tab. 43. The field layer is dominated by dwarf shrubs, with graminids as a subdominant taxocene. The bottom layer is a more or less continuous *Cladonia* mat.

The upper hummock series is characterized floristically by the presence of the fourteen species in group 1 in Tab. 43. The subseries differ with respect to the dominant taxocene in the bottom layer. Hepatics occur in both subseries, mostly without preference for one subseries to the other. Exceptions are *Calypogeja sphagnicola*, preferring living *Sphagnum* as its substrate, and *C. neesiana* and *Ptilidium ciliare*, preferring the R subseries. Preference for the P subseries is shown by several group 1 species in Tab. 43; *Drosera rotundifolia*, *Polytrichum strictum* and *Sphagnum balticum*. Transitions between subseries occur frequently. The *Sphagnum fuscum* mats of the P subseries apparently maintain a high

Tab. 43. Survey of the EHu series.

Subseries	P			R	
	E1	E2	E3	E1	E2
Zonation	ElPHu	E2PHu	E3PHu	ElRHu	E2RHu
Site-type	ElPHu	E2PHu	E3PHu	ElRHu	E2RHu
Number of sample plots	98	27	10	80	16
<i>Pinus sylvestris</i>	81- 6	44- 3	50- 2	80- 6	38- 4
<i>Andromeda polifolia</i>	64- 2	89- 2	40- 2	71- 3	84- 1
<i>Calluna vulgaris</i>	100-35	100-34	100-20	98-33	100-31
<i>Empetrum nigrum</i>	85- 3	52- 1	50- 6	83- 7	31- 2
<i>Vaccinium oxycoccos</i> coll.	99- 5	100- 3	90- 6	91- 4	100- 2
<i>Drosera rotundifolia</i>	71- 1	89- 1	80- 1	25- 1	31- 1
<i>Rubus chamaemorus</i>	88- 6	82- 8	80- 4	81- 4	50- 3
<i>Eriophorum vaginatum</i>	99- 8	100-14	100-14	95-11	100-18
<i>Pleurozium schreberi</i>	40- 4	7- 1	20-13	54- 6	19- 5
<i>Polytrichum strictum</i>	9-13	4- 1	50-42	3- 8	-
<i>Sphagnum balticum</i>	26- 2	67- 2	20- 1	7- 2	25- 1
<i>Cephalozia</i> spp.	85- 2	74- 1	50- 1	75- 2	100- 2
<i>Kurzia pauciflora</i>	50- 2	44- 2	30- 1	38- 3	38- 1
<i>Mylia anomala</i>	97- 4	89- 4	90- 2	74- 3	88- 5
<i>Erica tetralix</i>	-	74- 5	40- 2	-	100- 7
<i>Carex pauciflora</i>	-	44- 3	10- 1	-	-
<i>Myrica gale</i>	-	-	60-20	-	-
<i>Carex lasiocarpa</i>	-	-	20- 1	-	-
<i>Calliergon stramineum</i>	-	-	40- 2	-	-
<i>Pohlia nutans</i>	37- 2	15- 2	30- 6	18- 2	6- 1
<i>Sphagnum fuscum</i>	96-56	85-60	80-15	68- 7	69- 7
<i>S. magellanicum</i>	40-20	78-21	100-42	54- 2	44- 2
<i>S. rubellum</i>	90-18	100-16	80-24	55- 3	88- 3
<i>Calypogeja sphagnicola</i>	57- 1	59- 1	60- 1	24- 1	31- 1
<i>Calypogeja neesiana</i>	16- 2	7- 1	-	21- 1	44- 1
<i>Ptilidium ciliare</i>	1- 1	-	-	6- 9	6-10
<i>Cladonia arbuscula</i>	2- 2	-	-	29-14	12-23
<i>C. fimbriata</i>	12- 1	-	-	35- 2	6- 1
<i>C. pyxidata</i> coll.	2- 2	-	-	53- 3	62- 2
<i>C. rangiferina</i>	66- 5	44- 3	30- 1	98-41	100-65
<i>C. squamosa</i>	1- 1	-	-	21- 3	6- 1
<i>C. stellaris</i>	7- 3	4- 1	-	39-24	19-22

vitality until the lichen cover closes above the capitula. Transitional stands with a double bottom layer, a lower dominated by *Sphagnum fuscum*, and an upper dominated by *Cladonia rangiferina*, are common. Observations indicate that a closed *Sphagnum fuscum* mat will be adversely affected, and may eventually disappear, as a consequence of the increasing shade and loss of needles from a growing pine. There are smaller differences between zonations than within any other series. Species of group 2 indicate the E2, group 3 the E3 zonation. The zonal indicators occur in this series at the very limit of their amplitude, and in small quantities. The high importance of *Erica tetralix* in the E2 zonation

is caused by the absence of other zonal indicators (except some occurrences of *Carex pauciflora*), and thus does not indicate some general preference for this series.

The series covers ca. 17 per cent of the special area, almost totally restricted to the E1 zonation. The areal importance of E1PHu is twice that of E1RHu.

Reliable data for depth to the water table are only available for the E1 zonation. From the small set of sample plots with 2-3 years of water table recordings, means of median depth to the water table appear to be less in the R, than in the P subseries. The opposite trends are indicated in the larger set of estimated parameters (Fig. 67). The large vertical span of the median distances within this series (and hence the large standard deviations (cf. Fig. 67, Tab. 17), make the differences between subseries insignificant. Median depth to the water table ranges from 11 cm to more than 30 cm. There is no variability in the material that appears possible to correlate with this variation in depth to the water table. The occurrence of typical EHu vegetation at lower relative levels and hence at lower depth to the water table in the interior of large hummocks, is previously commented upon. Inundation of the bottom layer never occurs in the upper hummock series. The overlap of the upper and lower hummock series with respect to median depth to the water table, is not greater than between any other pair of series.

Tab. 44. The vegetation of the M3H1 site-type.

Sample set No.	S1	S2	S3	S4	S5	S6	S	O	
Number of samples	5	5	5	5	5	5	30	4	34
Zone	M3	M3	M3	M3	M3	M3			
<i>Betula pubescens</i>	-	60- 1	60- 8	60-16	60- 2	20- 1	43- 6	75-17	47- 8
<i>Pinus sylvestris</i>	20-30	100-15	20- 3	-	60- 4	40- 4	40-11	50- 6	47-10
<i>Andromeda polifolia</i>	100- 4	60- 4	60- 1	60-10	20- 3	60- 6	60- 5	50- 1	57- 5
<i>Myrica gale</i>	100-36	100-31	100-14	100-44	100-22	80-19	97-28	100-33	97-29
<i>Vaccinium oxycoccos</i> coll.	100- 7	100- 6	100- 2	100- 5	100- 4	100-11	100- 6	100- 2	100- 5
<i>V. uliginosum</i>	80-11	80-13	100-30	100- 5	100-11	100- 7	93-13	100-16	94-13
<i>Rubus chamaemorus</i>	100- 5	100- 1	100-16	80- 2	80- 5	100- 1	93- 5	50- 6	88- 5
<i>Carex lasiocarpa</i>	-	60- 1	-	80- 2	60- 1	-	33- 1	25- 1	32- 1
<i>C. pauciflora</i>	-	-	-	-	80- 2	-	13- 2	25- 1	15- 2
<i>C. rostrata</i>	-	-	-	-	-	60- 7	10- 7	-	9- 7
<i>Eriophorum angustifolium</i>	20- 2	-	60- 1	-	-	-	13- 2	25- 2	15- 2
<i>E. vaginatum</i>	80- 4	100- 3	100- 6	80- 6	100-32	80-35	90-14	100-14	91-14
<i>Molinia caerulea</i>	60- 1	40- 1	-	40- 2	80-23	60-17	47-11	25- 2	44-10
<i>Aulacomnium palustre</i>	-	-	20- 2	-	-	-	3- 2	75- 1	12- 1
<i>Calliergon stramineum</i>	20- 1	100- 2	80- 3	80- 2	20- 1	80- 2	63- 2	-	56- 2
<i>Sphagnum angustifolium</i>	20- 1	40- 9	40-14	100-25	-	100-47	50-27	100-10	56-23
<i>S. fallax</i>	100-93	100-80	100-81	100-50	100-86	80-21	97-70	100-61	97-69
<i>S. magellanicum</i>	40-12	100-14	20-45	80-12	40-17	20- 1	50-15	75- 2	53-13
<i>S. russowii</i>	20- 2	-	-	80-17	-	20-50	20-20	50- 2	24-16

Additional species (with constancy below 10):

Calluna vulgaris 6-2 (S3: 20-1; S: 3-1, O: 25-3), *Erica tetralix* 9-19 (O: 75-10), *Salix aurita* 3-17 (O: 25-17).

Drosera rotundifolia 6-1 (S2: 20-1, S4: 20-1; S: 7-1), *Trientalis europaea* 3-1 (S6: 20-1; S: 3-1).

Carex echinata 9-3 (S1: 20-1, S4: 20-7, S6: 20-1; S: 10-3), *C. globularis* 9-3 (S3: 60-1; S: 10-1), *C. rostrata* 9-7 (S6: 60-7; S: 10-7), *Phragmites australis* 6-2 (S4: 40-2; S: 7-2).

Drepanocladus fluitans 3-7 (S6: 20-7; S: 3-7), *Pohlia nutans* 6-2 (O: 6-2), *Polytrichum strictum* 50-41 (O: 50-41).

Sphagnum papillosum 3-1 (O: 25-1), *S. rubellum* 3.5 (O: 25-5).

The mire margin lower hummock series

The only site-type in this series is the M3H1 site-type. The floristic composition is shown in Tab. 44. The constant species are *Myrica gale*, *Vaccinium oxycoccos* coll., *V. uliginosum*, *Rubus chamaemorus*, *Eriophorum vaginatum*, and *Sphagnum fallax*. A tree layer dominated by *Pinus sylvestris* is occasionally present. *Myrica gale* makes up a dense shrub layer, overlying a field layer dominated by *Vaccinium uliginosum*, *Eriophorum vaginatum*, and *Molinia caerulea*. The bottom layer is dominated by *Sphagnum angustifolium*, *S. fallax* (main dominant), *S. magellanicum*, and *S. russowii*, making up a closed, level mat.

The mean number of species per sample plot is 11, while the total number in the 34 sample plots is 33.

The estimated area of this site-type is ca. 0.5 per cent. It is restricted to the wetter parts of the lagg, adjacent to the border onto mineral soil.

The variation within this site-type is negligible.

The mean of median distances to the water table is 12.3 cm, corresponding to the EH1 series (Fig. 67).

The mire margin upper hummock series

The M1Hu site-type

The floristic composition of this site-type is shown in Tab. 45. The constant species are *Pinus sylvestris*, *Vaccinium oxycoccos* coll., *Eriophorum vaginatum*, and *Pleurozium schreberi*. *Pinus sylvestris* dominates the tree/shrub layer. The main dominants in the field layer are *Calluna vulgaris*, *Vaccinium uliginosum*, *V. myrtillus*, and *V. vitis-idaea*, but *Eriophorum vaginatum*, *Rubus chamaemorus*, and *Empetrum nigrum* have also been recorded as dominants in some sample plots. Dominants in the bottom layer are *Sphagnum fuscum*, *S. capillifolium*, *S. magellanicum*, *Cladonia rangiferina*, *Pleurozium schreberi*, and *Polytrichum strictum*.

The mean number of species per sample plot is 14, while the total number in the 86 sample plots is 50.

The site-type is a low-grown pine-forest (tree height 4-8 m) with frequent gaps. The field layer is mostly dominated by dwarf shrubs, but may locally be open or have dominance of *Eriophorum vaginatum* tussocks. The bottom layer is a mosaic of *Sphagnum* patches (mostly monospecific stands less than 0.25 m²), patches dominated by mosses or lichens, and patches without vegetation (mostly in the interspaces).

The estimated area covered by this site-type is 8 per cent. It is the only site-type of the M1 zone, the distribution of which is shown in Fig. 29.

Dominance relationships of the field layer are strongly variable; mostly many species co-occur and form dense stands. *Calluna vulgaris* and *Empetrum nigrum*, partly also *Eriophorum vaginatum* and *Rubus chamaemorus*, seemingly avoid the densest *Vaccinium* stands. The mosaic pattern in the bottom layer is to some extent dependent on the field layer. *Pleurozium schreberi* is the only species thriving beneath strongly litter-forming *Vaccinium* and *Pinus* stands. *Sphagnum* spp. dominate in open areas, particularly in clearings both in the tree and field layers. *S. fuscum*, making loose or dense cushions in the more open parts of the M1 zone, is most frequent near the border to the E1 zone. When *Drosera rotundifolia*, *Calypogeja sphagnicola*, and *Mylia anomala* occur in the mire margin, they are almost always associated with *Sphagnum fuscum*. This may be due to the dense growth of *S. fuscum* giving relatively stable moisture conditions. *Sphagnum*

Tab. 45. The vegetation of the M1Hu site-type.

Sample set No.	S1	S2	S3	S4	S5	S6	S7	S	O	
Number of samples	5	5	5	5	5	5	5	35	51	86
Zone	M1	M1	M1	M1	M1	M1	M1			
<i>Betula pubescens</i>	-	-	-	40-11	20-1	20-1	-	11-6	12-5	12-5
<i>Picea abies</i>	-	40-2	40-1	-	-	60-3	-	20-2	10-5	14-3
<i>Pinus sylvestris</i>	100-28	100-13	100-12	100-9	100-9	100-15	80-6	97-14	98-20	98-18
<i>Andromeda polifolia</i>	20-1	40-1	40-3	20-2	20-1	40-2	20-2	29-2	39-2	35-2
<i>Calluna vulgaris</i>	40-12	40-2	100-25	40-18	100-13	80-30	60-25	66-20	82-29	76-26
<i>Empetrum nigrum</i>	80-2	-	100-2	20-22	40-3	80-17	80-4	57-6	69-7	64-7
<i>Vaccinium myrtillus</i>	100-21	100-24	100-4	40-10	100-26	100-12	80-9	89-16	41-9	60-13
<i>V. oxycoccos coll.</i>	100-3	100-3	100-11	100-7	60-6	100-6	100-9	94-6	88-5	91-5
<i>V. uliginosum</i>	20-50	100-21	20-12	100-19	80-20	-	60-19	54-21	45-21	49-21
<i>V. vitis-idaea</i>	100-12	100-12	40-12	80-5	100-8	40-2	60-13	74-9	65-12	69-11
<i>Drosera rotundifolia</i>	-	-	20-1	20-1	-	-	-	6-1	16-1	12-1
<i>Rubus chamaemorus</i>	100-18	-	60-2	80-9	100-11	100-3	100-12	91-10	73-6	80-8
<i>Eriophorum vaginatum</i>	100-3	100-2	100-11	80-14	100-4	100-6	100-2	97-6	96-13	96-10
<i>Aulacomnium palustre</i>	-	20-2	-	80-3	20-2	-	60-4	26-3	22-2	24-2
<i>Dicranum polysetum</i>	20-1	60-5	40-2	20-2	40-1	-	-	26-2	8-1	15-2
<i>Pleurozium schreberi</i>	80-7	80-11	80-21	40-9	100-14	100-6	100-3	83-10	88-13	86-12
<i>Pohlia nutans</i>	40-2	60-3	20-7	80-2	60-4	40-9	100-2	57-3	61-2	59-2
<i>Polytrichum strictum</i>	-	40-9	-	80-14	20-22	20-90	80-2	34-16	12-3	21-12
<i>Sphagnum angustifolium</i>	-	-	20-1	100-23	-	-	60-46	26-28	31-34	29-31
<i>S. capillifolium</i>	60-85	40-61	40-51	-	20-85	80-25	-	34-55	25-19	29-36
<i>S. fuscum</i>	20-70	20-80	60-56	60-32	60-39	60-12	100-33	54-39	63-18	59-26
<i>S. magellanicum</i>	20-7	-	-	100-20	20-50	20-2	60-21	31-20	24-16	27-18
<i>S. rubellum</i>	-	-	20-1	-	-	-	-	3-1	18-5	12-5
<i>Calypogeja neesiana</i>	40-1	40-3	20-1	20-1	-	60-3	-	26-2	33-1	30-1
<i>C. sphagnicola</i>	-	-	20-1	-	20-3	-	40-1	11-2	22-1	17-1
<i>Cephalozia spp.</i>	20-5	-	20-1	60-1	-	60-1	40-1	29-1	57-1	39-1
<i>Mylia anomala</i>	20-3	-	40-3	20-1	40-2	60-1	60-1	34-2	33-3	33-2
<i>Cladonia fimbriata</i>	20-1	-	-	20-1	20-1	20-1	20-1	14-2	20-2	17-2
<i>C. rangiferina</i>	-	20-15	60-28	20-60	40-24	40-12	10-75	29-30	41-9	35-16

Additional species (with constancy below 10):

Dicranum scoparium 8-1 (S1: 20-1, S5: 20-1; S: 6-1, O: 10-1), *Hylocomium splendens* 2-30 (S2: 40-30; S: 6-30), *Plagiotneccium laetum* 1-1 (O: 2-1), *Tetraphis pellucida* 2-1 (O: 4-1).

Calypogeja integristipula 1-1 (O: 2-1), *C. muellerana* 1-1 (O: 2-1), *Cephaloziella spp.* 5-1 (S7: 20-1; S: 3-1, O: 6-1), *Kurzia pauciflora* 2-1 (O: 4-1), *Ptilidium ciliare* 1-12 (O: 2-12).

Cladonia arbuscula 3-2 (O: 6-2), *C. bellidiflora* 1-1 (O: 2-1), *C. carneola* 1-2 (O: 2-2), *C. cenotea* 1-1 (O: 2-1), *C. coniocraea* 2-1 (S7: 20-1; S: 3-1, O: 2-1), *C. cornuta* 2-1 (O: 4-1), *C. crispata* 1-1 (O: 2-1), *C. digitata* 1-1 (O: 2-1), *C. furcata* 1-3 (S2: 20-3; S: 3-3), *C. pyxidata* coll. 9-1 (S5: 20-1, S6: 80-1; S: 14-1, O: 6-1), *C. squamosa* 2-6 (O: 4-6), *C. sulphurina* 5-1 (O: 8-1).

capillifolium occurs locally, and makes large, domed hummocks with a loose packing of capitula (at least when compared to *S. fuscum*). The *S. capillifolium* hummocks are mostly completely devoid of other mosses or liverworts.

The M2Hu site-type

The floristic composition of this site-type is shown in Tab. 46. The constant species are *Pinus sylvestris*, *Vaccinium vitis-idaea*, and *Carex globularis*. *Betula pubescens* and *Pinus sylvestris*, rarely *Picea abies*, dominate in the tree layer. Dominants in the field layer are *Vaccinium myrtillus*, *V. uliginosum*, *V. vitis-idaea*, and *Calluna vulgaris*. Dominants in the bottom layer are *Sphagnum capillifolium*, *S. russowii*, *S. angustifolium*, *S. fuscum*, *S. magellanicum*, and *Pleurozium schreberi*.

The mean number of species per sample plot is 13, while the total number in the 34 sample plots is 43.

The site-type is a pine or a mixed pine-birch forest. The field layer is densely

Tab. 46. The vegetation of the M2Hu site-type.

Sample set No.	S1	S2	S3	S4	S	O	
Number of samples	5	5	5	5	20	14	34
Zone	M2	M2	M2	M2			
<i>Betula pubescens</i>	80-13	60- 1	60-16	-	50-10	36-32	44-17
<i>Picea abies</i>	80- 8	40-15	80- 2	-	50- 7	29- 4	41- 6
<i>Pinus sylvestris</i>	100-12	100-26	100-12	100-13	100-16	79-20	91-17
<i>Andromeda polifolia</i>	-	40- 1	40- 2	20- 1	25- 1	29- 2	26- 1
<i>Calluna vulgaris</i>	60-19	60- 3	40-24	100-18	65-15	57-15	62-15
<i>Empetrum nigrum</i>	40- 2	20-10	-	40- 3	25- 4	43- 5	32- 5
<i>Vaccinium myrtillus</i>	100-38	80-20	100-30	20-10	75-29	71-24	74-27
<i>V. oxycoccus</i> coll.	40-10	80- 2	40- 2	60- 7	55- 5	50- 5	53- 5
<i>V. uliginosum</i>	40- 4	100-30	100-30	40- 4	70-23	64-23	68-23
<i>V. vitis-idaea</i>	100-11	100-10	100- 9	100-11	100-10	86-16	94-12
<i>Melampyrum pratense</i>	40- 2	-	40- 1	-	20- 1	36- 1	26- 1
<i>Rubus chamaemorus</i>	100- 9	20- 2	-	80- 4	50- 6	29- 7	41- 6
<i>Carex globularis</i>	100- 6	100- 3	100- 4	100- 4	100- 4	86- 3	94- 4
<i>Eriophorum vaginatum</i>	80- 4	60- 1	60- 8	100- 9	75- 6	64-14	71- 9
<i>Aulacomnium palustre</i>	40- 2	20- 2	100- 3	80-13	60- 6	64- 2	62- 4
<i>Dicranum polysetum</i>	20-10	40- 7	40- 1	20- 1	30- 5	36- 6	32- 5
<i>Pleurozium schreberi</i>	80-15	80-17	60- 1	100- 9	80-11	71-25	76-16
<i>Pohlia nutans</i>	20- 1	-	20- 1	60- 4	25- 3	21- 2	24- 3
<i>Sphagnum angustifolium</i>	40- 2	40-34	80-30	60-23	55-24	50-37	53-29
<i>S. capillifolium</i>	40-83	60-44	40-28	40-41	45-48	21-47	35-48
<i>S. fuscum</i>	-	-	-	80-30	20-30	14-24	18-28
<i>S. magellanicum</i>	60-31	40-12	20- 4	40- 4	40-16	21- 3	32-12
<i>S. russowii</i>	20- 2	40-31	80-46	-	35-35	21-17	29-30
<i>Calypogeja neesiana</i>	20- 3	-	-	40- 3	15- 3	21- 1	17- 2
<i>Cephalozia</i> spp.	40- 1	-	-	20- 1	15- 1	7- 1	12- 1
<i>Mylia anomala</i>	-	-	-	40- 2	10- 2	14- 2	12- 2
<i>Cladonia fimbriata</i>	20- 1	-	-	-	5- 1	21- 1	12- 1
<i>C. rangiferina</i>	-	20-15	-	-	5-15	21-13	12-14

Additional species (with constancy below 10):

Betula nana 9-9 (S1: 60-9; S: 15-9), *Erica tetralix* 3-1 (O: 7-1), *Salix aurita* 3-35 (S3: 20-35; S: 5-35), *S. repens* 3-3- (S2: 20-3; S: 5-3).

Drosera rotundifolia 3-2 (S4: 20-2; S: 5-2).

Dicranum scoparium 3-1 (O: 7-1), *Hylocomium splendens* 6-3 (S2: 20-1; S: 5-1, O: 7-4), *Polytrichum commune* 3-7 (S2: 20-7; S: 5-7), *P. strictum* 3-12 (S1: 20-12; S: 5-12).

Sphagnum rubellum 3-4 (O: 7-4).

Calypogeja muelleriana 3-2 (O: 7-2), *Kurzia pauciflora* 6-1 (S4: 20-1; S: 5-1; O: 7-1), *Ptilidium ciliare* 3-5 (S2: 20-5; S: 5-5).

Cladonia coniocraea 3-3 (S4: 20-3; S: 5-3), *C. furcata* 3-1 (S2: 20-1; S: 5-1).

dominated by dwarf shrubs. As in the M1Hu site-type, the bottom layer is patchy; a mosaic of *Sphagnum* spp. (five species), mosses, and patches covered by litter.

The estimated area covered by this site-type is 2 per cent, its distribution is shown in Fig. 29. It occurs in the parts of the marginal forest slightly influenced by minerogenous water, in dry lags at the water divides, and even on shallow peat islands surrounded by the E2 zone (pos. 11 07).

Tab. 47. The vegetation of the M3Hu site-type.

Sample set No.	S1	S2	S3	S4	S5	S	O	
Number of samples	5	5	5	5	5	25	11	36
Zone	M3	M3	M3	M3	M3			
<i>Betula pubescens</i>	60- 9	40-21	40- 9	60- 3	80-12	56-10	27- 7	47- 9
<i>Picea abies</i>	-	20- 1	40- 2	60- 6	40- 3	32- 3	9- 5	25- 3
<i>Pinus sylvestris</i>	20- 7	100- 7	20- 7	40-25	40- 3	44- 9	55-10	47- 9
<i>Andromeda polifolia</i>	60- 6	20- 3	100- 1	-	-	36- 3	64- 1	44- 2
<i>Calluna vulgaris</i>	100- 8	80-12	80-26	-	20- 4	56-14	64-32	58-20
<i>Empetrum nigrum</i>	-	20- 1	60- 1	-	-	16- 1	36- 4	22- 3
<i>Myrica gale</i>	100-22	40-40	80-12	100-33	80- 6	80-21	64-38	75-25
<i>Salix aurita</i>	-	-	60-22	-	40- 4	20-15	-	14-15
<i>Vaccinium myrtillus</i>	20- 5	100-12	100- 4	100- 8	100- 8	84- 8	55- 8	75- 8
<i>V. oxycoccus</i> coll.	100- 6	80- 2	100-16	60- 6	100- 1	88- 7	82- 3	86- 6
<i>V. uliginosum</i>	100-33	100-20	100-20	60- 4	100-25	92-22	55-18	83-21
<i>V. vitis-idaea</i>	40- 2	100- 5	60- 3	100- 4	100- 6	80- 5	64- 5	75- 5
<i>Dactylorhiza maculata</i>	-	20- 1	-	-	60- 3	16- 3	18- 1	17- 2
<i>Melampyrum pratense</i>	-	80- 1	60- 2	20- 1	100- 2	52- 2	-	36- 2
<i>Rubus chamaemorus</i>	100-20	80- 5	100- 5	100- 3	20- 7	80- 8	73- 5	78- 7
<i>Trientalis europaea</i>	20-10	20- 1	60- 3	20- 1	100- 4	44- 4	9- 2	33- 4
<i>Carex echinata</i>	-	-	40- 3	-	40- 6	16- 4	-	11- 4
<i>C. globularis</i>	40- 2	100- 5	40- 1	100-11	80- 2	72- 5	-	50- 5
<i>Eriophorum angustifolium</i>	80- 2	-	-	-	-	16- 2	9- 1	14- 2
<i>E. vaginatum</i>	100- 6	100- 3	100- 6	60- 7	20- 1	76- 5	82-11	78- 7
<i>Molinia caerulea</i>	20-20	20- 7	40-14	60-26	100- 5	48-13	27- 6	42-11
<i>Aulacomnium palustre</i>	40- 3	80- 2	60- 9	20- 4	80- 1	56- 3	82- 2	64- 3
<i>Calliergon stramineum</i>	80- 4	80- 1	60- 5	80- 2	20- 1	64- 3	36- 2	56- 3
<i>Dicranum polysetum</i>	-	-	20- 2	20- 1	20- 1	12- 1	18- 1	14- 1
<i>Pleurozium schreberi</i>	20- 1	-	80- 2	20-15	20- 3	28- 4	55- 7	36- 5
<i>Pohlia nutans</i>	-	-	-	-	-	-	36- 1	11- 1
<i>Polytrichum commune</i>	-	100-20	-	-	40- 4	28-16	-	19-16
<i>Sphagnum angustifolium</i>	100-67	100-44	100-28	80- 3	100-50	96-40	73-11	89-33
<i>S. magellanicum</i>	80-16	100-21	80-38	80-33	80- 5	84-23	73-25	81-24
<i>S. russowii</i>	60- 1	100- 9	80-12	100-42	100-34	88-22	36-47	72-26
<i>Cephalozia</i> spp.	20- 1	-	40- 1	-	-	12- 1	9- 1	11- 1

Additional species (with constancy below 10):

Betula nana 3-10 (S4: 20-10; S: 4-10), *Erica tetralix* 3-3 (O: 9-3), *Frangula alnus* 3-22 (S2: 20-22; S: 4-22), *Juniperus communis* 3-7 (S5: 20-7; S: 4-7).

Drosera rotundifolia 3-1 (S3: 20-1; S: 4-1), *Orthilia secunda* 6-1 (S5_ 40-2; S: 8-2), *Potentilla erecta* 6-11 (S3: 20-17, S5: 20-5; S: 8-11).

Carex lasiocarpa 8-2 (S1: 20-1, S3: 40-3; S: 12-2), *C. pauciflora* 3-1 (S3: 20-1; S: 4-1), *Deschampsia flexuosa* 6-1 (S2: 40-1; S: 8-1).

Dicranum scoparium 3-10 (O: 9-10), *Drepanocladus uncinatus* 3-1 (S3: 20-1; S: 4-1), *Hylocomium splendens* 3-1 (S3: 20-1; S: 4-1), *Polytrichum strictum* 8-20 (S1: 20-30, S3: 20-30; S: 8-30, O: 9-1).

Sphagnum balticum 3-3 (O: 9-3), *S. capillifolium* 6-75 (O: 18-75), *S. fallax* 8-8 (S1: 60-8; S: 12-8), *S. fuscum* 3-1 (O: 9-1), *S. papillosum* 3-1 (O: 9-1), *S. rubellum* 8-2 (O: 27-2).

Calypogeja neesiana 6-1 (S1: 20-1; S3: 20-1; S: 8-1), *C. sphagnicola* 8-2 (O: 27-2), *Cephaloziella* spp. 3-1 (O: 9-1), *Cladopodiella fluitans* 6-1 (O: 18-1), *Lophozia ventricosa* 3-4 (O: 9-4), *Ptilidium ciliare* 3-1 (O: 9-1).

Cladonia rangiferina 3-5 (O: 9-5).

The pattern of variation within this site-type closely corresponds to the M1Hu site-type.

Tab. 48. Survey of the MHu series.

Zonation	M1	M2	M3
Site-type	M1Hu	M2Hu	M3Hu
Number of sample plots	86	34	36
<i>Betula pubescens</i>	12- 5	44-17	47- 9
<i>Picea abies</i>	14- 3	41- 6	25- 3
<i>Pinus sylvestris</i>	98-18	91-17	47- 9
<i>Andromeda polifolia</i>	35- 2	26- 1	44- 2
<i>Calluna vulgaris</i>	76-26	62-15	58-20
<i>Empetrum nigrum</i>	64- 7	32- 5	22- 3
<i>Vaccinium myrtillus</i>	60-13	74-27	75- 8
<i>V. oxycoccus</i> coll.	91- 5	53- 5	86- 6
<i>V. uliginosum</i>	49-21	68-23	83-21
<i>V. vitis-idaea</i>	69-11	94-12	75- 5
<i>Rubus chamaemorus</i>	80- 6	41- 6	78- 7
<i>Eriophorum vaginatum</i>	96-10	71- 9	78- 7
<i>Aulacomnium palustre</i>	24- 2	62- 4	64- 3
<i>Dicranum polysetum</i>	15- 2	32- 5	14- 1
<i>Pleurozium schreberi</i>	86-12	76-16	36- 5
<i>Pohlia nutans</i>	59- 2	24- 3	11- 1
<i>Polytrichum strictum</i>	21-12	3-12	8-20
<i>Sphagnum angustifolium</i>	29-31	53-29	89-33
<i>S. capillifolium</i>	29-36	35-48	6-75
<i>S. fuscum</i>	59-26	18-28	3- 1
<i>S. magellanicum</i>	27-18	32-12	81-24
<i>Calypogeja neesiana</i>	30- 1	17- 2	6- 1
<i>Cephalozia</i> spp.	39- 1	12- 1	11- 1
<i>Mylia anomala</i>	33- 2	12- 2	-
<i>Cladonia fimbriata</i>	17- 2	12- 1	-
<i>C. rangiferina</i>	35-16	12-14	3- 5
<i>Melampyrum pratense</i>	-	26- 1	36- 2
<i>Carex globularis</i>	-	94- 4	50- 5
<i>Polytrichum commune</i>	-	3- 7	19-16
<i>Sphagnum russowii</i>	-	29-30	72-26
<i>Myrica gale</i>	-	-	75-25
<i>Dactylorhiza maculata</i>	-	-	17- 2
<i>Trientalis europaea</i>	-	-	33- 4
<i>Carex echinata</i>	-	-	11- 4
<i>Eriophorum angustifolium</i>	-	-	14- 2
<i>Molinia caerulea</i>	-	-	42-11
<i>Calliergon stramineum</i>	-	-	56- 3

The M3Hu site-type

The floristic composition of this site-type is shown in Tab. 47. The constant species are *Vaccinium oxycoccus* coll., *V. uliginosum*, *Sphagnum angustifolium*, and *S. magellanicum*. The tree layer is occasionally dominated by *Betula pubescens* and *Pinus sylvestris*. Dominants in the field/shrub layer are *Myrica gale*, *Vaccinium uliginosum*, *Salix aurita*,

Calluna vulgaris, and, occasionally, *Molinia caerulea*. The bottom layer is dominated by *Sphagnum angustifolium*, *S. russowii*, *S. magellanicum*, and *Pleurozium schreberi*.

The mean number of species per sample plot is 16, while the total number in the 36 sample plots is 58.

The site-type is mostly devoid of a tree layer. Instead, a low-grown shrub layer dominated by *Myrica gale* and *Salix aurita* is present. A field layer dominated by dwarf shrubs mostly occurs. The bottom layer mostly has a closed mat of *Sphagnum* spp.

The estimated area covered by this site-type is ca. 2 per cent. Being the dominant site-type of the M3 zone, its distribution is shown in Fig. 29.

The bottom layer is mostly uniformly covered by *Sphagnum*, *S. angustifolium* is the most important dominant, often co-occurring with *S. magellanicum*. *S. russowii* prefers the areas close to the border onto mineral soil. The upper layers have a strongly variable physiognomy. The tree layer is open, or more often, is reduced to single, widely spaced trees. The shrub and field layers are well developed, with an upper stratum of *Myrica gale* and a lower dominated by *Vaccinium uliginosum*. The high number of variants dominated by other species, and the many combinations of dominants occurring, are apparent from Tab. 47. There is a prominent element in this site-type of species with their main habitat on mineral soil, while mire expanse species are rare. The dominant *Sphagnum* species appear to be a poor substrate for hepatics, while mosses occur frequently. *Aulacomnium palustre* most frequently occurs with *Sphagnum angustifolium*.

Survey of the mire margin upper hummock series

A survey of the mire margin upper hummock series is given in Tab. 48. This series mostly has a tree layer dominated by *Pinus sylvestris*. The dense field layer is dominated by dwarf shrubs. The bottom layer is mostly a mosaic with patches dominated by mosses, lichens, and *Sphagnum*, as well as patches without vegetation (cf. Fig. 68). More rarely (the M3Hu site-type) the bottom layer is a continuous *Sphagnum* mat.

The mire margin upper hummock series is characterized by the presence of the twenty-six species in group 1 in Tab. 48. The M1Hu and M2Hu site-types are similar with respect to physiognomy and species composition; the species of group 2 distinguish the M2Hu site-type. The M3Hu site-type, however, differs with respect to physiognomy (poorly developed tree layer, presence of a shrub layer, continuous *Sphagnum* mat), and by the presence of group 3 species. Several species common or dominant in the M1Hu and M2Hu site-types are unimportant in M3Hu, e.g., *Vaccinium myrtillus*, *V. vitis-idaea*, *Pleurozium schreberi*, *Sphagnum capillifolium*, *S. fuscum*, and the hepatics.

The series covers ca. 12 per cent of the special area. The median depth to the water table spans a wide range; from 8 to above 32 cm, closely corresponding to the range of the EHu series (Fig. 67, Tab. 16). The MHu series is never subjected to inundation. The mean median depth to the water table decreases from the M1 to the M3 zonation (Fig. 67). The annual range of depth to the water table is higher in the mire margin than in the mire expanse hummocks.

Vegetation complexes

Four vegetation complexes, defined by the relative frequency of site-types, were identified

Fig. 69. Vegetation complexes in the special area, according to Osvald (1923).

in the E1 and E2 zones (Fig. 69). Transitions were frequent.

(1) *The marginal complex.* Continuous hummock-dominated areas (mostly the E1PHu and E1PHl site-types) occurred in the peripheral parts of the E1 zone (cf. Fig. 5). In particular, the marginal complex played an important part in the sloping, northeastern part of the special area. Small hollows with the E1PLu or E1RLu site-types occurred sparsely. Transitions to the "heath-like marginal complex" were observed, but the low importance of the E1RH site-types suggested that this complex-type was not represented.

(2) *The fen regeneration complex.* A regeneration complex was only observed in the E2 zone, and restricted to the central parts of the western, southeastern, and northern fen soaks, and the E2 zone north of the central, unilaterally sloping kermi raised bog synsegment. This fen regeneration complex was characterized by high importance of the E2PLl and E2PLu site-types and relatively high importance of the E1PHl and E2PHl site-types, while the R subseries played a minor role.

(3) *The Rhynchospora-rich regeneration complex.* The lower part of the central, unilaterally sloping kermi raised bog, the multilaterally sloping kermi raised bog, and the peripheral parts of the E2 fen soaks may be classified in this complex-type. Hollows and hummocks occupied approximately equal areas; the hollows were dominated by the RLl (and RLu) site-types, the hummocks by the E1PHl and E1PHu site-types, but with a prominent element of the E1RH site-types. RC site-types occurred sparsely. The relative importance of PL site-types increased gradually towards the central parts of the fen soaks, indicating the transition to the fen regeneration complex. Towards the upper and peripheral parts of the bog segments, the E1PLl site-type was replaced by E1RLu, mediating the transition to the marginal complex. Locally high importance of RH vegetation and high areal cover of RL site-types with sparse cover of *Sphagnum tenellum* suggested transitions to the stagnation complex. A typical stagnation complex did, however, not occur in the special area.

(4) *The erosion complex.* The northernmost part of the unilaterally sloping plane transitional mire synsegment was the only erosion complex occurring in the special area. Eroded peat prevailed in former hollows, with isolated hummocks or kermis occurring in between.

Transitions between site-types and successional relationships

The observed and suggested transitions between site-types of the E1 and E2 zones are shown in Figs 70 and 71.

The E1 zone, the marginal complex. Apart from the infrequent overgrowth of the E1PHu site-types by lichens (E1RHu), transitions between site-types apparently were rare in this complex.

The E1 zone, the Rhynchospora-rich regeneration complex. Transitions between site-types, both horizontally and vertically, were frequent. The most frequent transitions were the overgrowth of PH sites by lichens and hepatics, although secondary development of *Sphagnum* spp. in RH sites was also noted. The importance of bare peat was particularly high in the EHl series (Fig. 68), apparently because of occasional dying of dominant hepatics. In the EHu series lichens appeared to invade such patches rapidly. Frequent transitions of the *Cladina*-dominated E1RHu stands into the E1RHl site-types by gradual disappearance of vascular plants towards lower levels, and eventual dying of the dominant lichen and/or overgrowth by *Sphagnum tenellum* or hepatics, were noted, particularly in smaller hummocks and in marginal parts of larger hummocks. This downward succession was also evident from the relatively frequent relict occurrences of *Empetrum nigrum* and

Fig. 70. Transitions between site-types and inferred successional relationships, the E1 zone. Thick arrow - frequent transition, thin arrow - observed transition, broken arrow - suggested not observed transition. Major dominance types are boxed. Numbers refer to number of sample plots of the R data set in each subseries.

Cladonia rangiferina on slightly elevated tussocks among patches dominated by *Sphagnum tenellum* and hepatics. Patches dominated by hepatics similarly appeared able to remain for some time while invaded by progressively more hydrophilous species (RH1 - RLu(- RL1) transitions), although more often overgrown by *Sphagnum tenellum*. Emergence of E1PH1 hummock segments dominated by *Sphagnum rubellum* from the E1RLu site-type was observed at some occasions. The carpets generally gave a regressive impression; the *Sphagnum cuspidatum* carpets were often heavily infested by hepatics and algae. In the E1RC site-type, the mean cover of bare peat was above 50 per cent (Fig. 68).

The E2 zone, the Rhynchospora-rich regeneration complex. Patterns of transitions resembled those of the E1 zone, but with some differences. The E2RLu and E2RL1 site-types occurred along with the E1RLu and E2RL1 site-types in the hollows. The areal importance of the E2PL site-types was variable, but mostly low. Hepatics played a minor role, as did the EHu site-types. Transitions between the P and R lawn and carpet subseries were frequent, and succession apparently proceeded in both directions. The expansion of PC vegetation over mud-bottoms was not observed. The relationships of the R site-types of the various series could not be decided from field observations (cf. Fig. 71).

The E2 zone, the fen regeneration complex. A tendency for vertical transgression, PC - PL1 - PLu - PH1 was noted. At each level, transitions to the R site-types was noted, but the R site-types mostly played a quantitatively unimportant role. The stability of the P site-types (the frequency of transitions) could not be decided from field observations.

The E2 zone, the erosion complex. The strong tendency to erosion at all levels below

Fig. 71. Transitions between site types and inferred successional relationships, the E2 zone. Thick arrow frequent transition, thin arrow - observed transition, broken arrow - suggested not observed transition. Major dominance types are boxed. Numbers refer to number of sample plots of the R data set in each subseries, in the E1 and E2 zonations, respectively.

the maximum water table was observed in several periods with heavy rain. In places with high water flow-rates, isolated hummocks with strongly eroded marginal (and lower) parts were observed. Redistribution of eroded peat occurred close to the outlet of the erosion brooklet.

The relationship of the subseries to depth to the water table. All series except Hu showed lower average median depth to the water table in the R as compared to the P subseries (Tab. 16, Fig. 67). The material from the Hu series was less conclusive, but might indicate higher depth for the R subseries (Fig. 67). The difference in depth to the water table between site-types differing only with respect to subseries, amounted to 1-3 cm in the Ll, Lu, and Hl series.

The frequent occurrence in the R subseries of individuals with low vitality, characteristic for higher relative levels, while the converse was observed in the P subseries (cf. Tabs 15, 24, 31, 37, 43), indicated that these occurrences might be of a relict nature, due to successional transitions in regressive and progressive directions, respectively.

DISCUSSION

COMPARISON WITH OTHER INVESTIGATIONS

The four-gradient representation of the vegetation of the special area (Fig. 66) was taken as a local reference frame (Økland & Bendiksen 1985), presumably representing the most important local ecoclines in corresponding vegetation all over SE. Fennoscandia, the area used for comparison. Ecologically corresponding vegetation types (cf. Økland & Bendiksen 1985) of the more important works, representing the major approaches to classification, were displayed in the four-gradient reference frame or some reduced version.

Swedish approaches

(1) *Osvald (1923)*. The classification of mire vegetation on Komosse is performed according to the tradition of the early Uppsala school (Du Rietz *et al.* 1918, 1920, Du Rietz 1921). The association concept is narrow, and a multitude of such units is described. With the exceptions of some deviant and rare associations, their positions with respect to the gradient reference frame can be identified. One association often spans a wide range along the nutrient gradient. Ecological correspondence between the associations of Osvald (1923) and the site-types described from the special area is shown in Figs. 72, 73.

(2) *Sjörs (1948)* classifies the vegetation on Skattlösbergs Stormosse into associations of intermediate rank. He does not pay attention to the peat productivity gradient above the carpet level. Correspondence between his associations and the site-types in the reference frame of the three remaining gradients is easily established (Fig. 74). Sjörs does not separate upper and lower hummocks, mostly not even upper and lower lawns.

(3) *Du Rietz (1949, also see Waldheim & Weimarck 1943, Waldheim 1944, Weimarck 1944)* gives an outline of a system proposed to be applicable to the classification of Swedish mire vegetation. The fundamental division is between the bog and fen formations (Ombrophagnetea and Sphagno-Drepanocladetea; Du Rietz 1954). Bog subformations and alliances are separated along regional gradients. Within each alliance, two associations, corresponding to hollow and hummock, respectively, are separated. Subassociations are delimited to include variation along the depth to the water table and peat productivity gradients. All vegetation of zones 2 and 3 correspond to the extremely poor fens, Euapiculation, of this system. No further division of this alliance is, however, suggested.

(4) *Malmer (1962a)*. The fundamental unit in the classification of vegetation on Åkhultmyra, the small association, closely corresponds to Sjörs' association. However, Malmer also takes what is here included as the peat productivity gradient into account. Small associations are divided into variants, representing upper and lower levels of hummocks and lawns. A series comprises all small associations with the same position along the hummock-lawn-carpet and peat productivity coenoclines. The concepts zone and zonation in this paper are in accordance with Malmer (cf. p. 24, 56). The close correspondence between Malmer's mire expanse vegetation units and the site-types is evident from Fig. 75. The M1Hu site-types corresponds to Malmer's "Wooded bog vegetation", the other site-types of the M zones apparently correspond to the "*Vaccinium-Sphagnum parvifolium* small association".

(5) *Svensson (1965)* applies Malmer's (1962a) system to the vegetation of Store Mos-

	P		
	1	2	3
III	52. <i>Calluna vulgaris</i> - <i>Sphagnum magellanicum</i> -Ass.; <i>Empetrum</i> -Var. 53. <i>Calluna vulgaris</i> - <i>Sphagnum fuscum</i> -Ass. 56. <i>Calluna vulgaris</i> - <i>Sphagnum imbricatum</i> -Ass. 57. <i>Empetrum nigrum</i> - <i>Sphagnum fuscum</i> -Ass.	52. <i>Calluna vulgaris</i> - <i>Sphagnum magellanicum</i> -Ass.; <i>Narthecium ossifragum</i> -Var.; <i>Carex pauciflora</i> -Var.	52. <i>Calluna vulgaris</i> - <i>Sphagnum magellanicum</i> -Ass.; <i>Eriophorum polystachyum</i> -Var.
III	52. <i>Calluna vulgaris</i> - <i>Sphagnum magellanicum</i> -Ass.; <i>Erica</i> -Var.		
III	140. <i>Eriophorum vaginatum</i> - <i>Sphagnum magellanicum</i> -Ass. p.p.	113. <i>Narthecium ossifragum</i> - <i>Sphagnum papillosum</i> -Ass. 129. <i>Carex pauciflora</i> - <i>Sphagnum papillosum</i> -Ass. 141. <i>Eriophorum vaginatum</i> - <i>Sphagnum papillosum</i> -Ass. 140. <i>Eriophorum vaginatum</i> - <i>Sphagnum magellanicum</i> -Ass. p.p.	58. <i>Erica tetralix</i> - <i>Sphagnum papillosum</i> -Ass. 133. <i>Carex rostrata</i> - <i>Sphagnum papillosum</i> -Ass. 151. <i>Scirpus austriacus</i> - <i>Sphagnum papillosum</i> -Ass.
III		109. <i>Drosera longifolia</i> - <i>rotundifolia</i> - <i>Sphagnum magellanicum</i> -Ass. 140. <i>Eriophorum vaginatum</i> - <i>Sphagnum magellanicum</i> -Ass. p.p.	137. <i>Eriophorum polystachyum</i> - <i>Sphagnum papillosum</i> -Ass.
		148. <i>Rhynchospora alba</i> - <i>Sphagnum papillosum</i> -Ass.	
III	Reine <i>Sphagnum</i> -Gesellschaften 131. <i>Carex limosa</i> - <i>Sphagnum cuspidatum</i> -Ass.	149. <i>Scheuchzeria palustris</i> - <i>Eriophorum vaginatum</i> -Ass.	130. <i>Carex rostrata</i> - <i>Sphagnum cuspidatum</i> -Ass. 131. <i>Carex rostrata</i> - <i>Sphagnum Dusenii</i> -Ass. 136. <i>Eriophorum polystachyum</i> - <i>Sphagnum cuspidatum</i> -Ass. 138. <i>Eriophorum vaginatum</i> - <i>Sphagnum cuspidatum</i> -Ass.

Fig. 72. Comparison of the classification system adopted in this work with types of Osvald (1923). The mire expanse.

se, but terms his units associations. The correspondence of Svensson's mire expanse associations and variants and the site-types of this paper is shown in Fig. 76. The "*Vaccinium-Sphagnum parvifolium* small association" also includes the MIHu site-type.

(6) *Fransson* (1972) discerns associations, subassociations, variants, and facies. His associations mainly separate variation along the nutrient, hummock-lawn-carpet, and mire expanse-mire margin gradients. A finer division of hummocks and lawns, and the recognition of the peat productivity gradient is achieved at the level of subassociation or at lower levels. Correspondence between *Fransson*'s vegetation units and the site-types is shown in Figs. 77 and 78.

Finnish approaches

The regional surveys of Finnish mire vegetation (*Ruuhijärvi* 1960, *Eurola* 1962) are based on the Finnish approach to classification developed by *Cajander* (1913). The fundamental unit is the site-type, representing a joint classification of the site and its vegetation (*Cajander* 1926). Site-types are aggregated into the four site-type groups "Weissmoor", "Reisermoor", "Braunmoor", and "Bruchmoor". The "Weissmoor" group corresponds to ombrotrophic and poor minerotrophic mire expanse carpets and lawns, while almost all of

R		
1	2	3
34. <i>Andromeda polifolia</i> - <i>Cladonia rangiferina</i> - <i>silvatica</i> -Ass. 35. <i>Calluna vulgaris</i> - <i>Cladonia rangiferina</i> - <i>silvatica</i> -Ass.; <i>Empetrum nigrum</i> -Var. 36. <i>Empetrum nigrum</i> - <i>Cladonia rangiferina</i> -Ass. 39. <i>Empetrum nigrum</i> -Ass. 44. <i>Calluna vulgaris</i> - <i>Grimmia hypnoides</i> -Ass. 45. <i>Calluna vulgaris</i> - <i>Hylocomium parietinum</i> -Ass. 162. <i>Cladonia rangiferina</i> -Ass. 163. <i>Grimmia hypnoides</i> -Ass.	46. <i>Empetrum nigrum</i> - <i>Hylocomium parietinum</i> - <i>proliferum</i> -Ass. 37. <i>Erica tetralix</i> - <i>Cladonia</i> -Ass. p.p.	
35. <i>Calluna vulgaris</i> - <i>Cladonia rangiferina</i> - <i>silvatica</i> -Ass.; <i>Erica</i> -Var. 37. <i>Erica tetralix</i> - <i>Cladonia</i> -Ass. p.p.	71. <i>Narthecium</i> -Ass.	
54. <i>Calluna vulgaris</i> - <i>Sphagnum tenellum</i> -Ass. 58. <i>Erica tetralix</i> - <i>Sphagnum tenellum</i> -Ass. 152. <i>Scirpus austriacus</i> - <i>Sphagnum tenellum</i> -Ass.		
150. <i>Scirpus austriacus</i> - <i>Sphagnum cuspidatum</i> -Ass. p.p.		
147. <i>Rhynchospora alba</i> - <i>Sphagnum tenellum</i> -Ass.		
Sphagnia-Gesellschaften: Mischungen <i>Sphagnum Jungermania</i> , <i>Sphagnum-Zygozonium</i> , <i>Sphagnum-Jungermania-Zygozonium</i> : Algen-Gesellschaften	77. <i>Carex limosa</i> -Ass. 80. <i>Carex rostrata</i> -Ass. 81. <i>Eriophorum polystachyum</i> -Ass. 104. <i>Carex limosa</i> - <i>Jungermania inflata</i> -Ass. 105. <i>Carex rostrata</i> - <i>Jungermania inflata</i> -Ass.	
84. <i>Rhynchospora alba</i> -Ass.		

the mire expanse and mire margin hummock site-types in the special area have their counterparts among the "Reisermoor". Transitions to "Bruchmoor" "Waldweissmoor", and "Anmoorige Heidewälder" are observed in the M2 and M3 zones. With few exceptions, the peat productivity gradient is not easily traced in the studies mentioned. The nutrient gradient is often not clearly indicated. The considerable differentiation of mire margins in Finland

	1	2	3
MHu	31. <i>Pinus silvestris</i> - <i>Calluna vulgaris</i> - <i>Sphagnum angustifolium</i> -Ass. 14. <i>Betula alba</i> - <i>Oxycoccus quadripetalus</i> - <i>Sphagnum angustifolium</i> -Ass. 16. <i>Betula alba</i> - <i>Rubus chamaemorus</i> -Ass.	17. <i>Betula alba</i> - <i>Eriophorum vaginatum</i> - <i>Rubus chamaemorus</i> -Ass. 55. <i>Calluna vulgaris</i> - <i>Sphagnum angustifolium</i> -Ass.	
MHI			13. <i>Betula alba</i> - <i>Calluna vulgaris</i> - <i>Sphagnum acutifolium</i> -Ass. 15. <i>Betula alba</i> - <i>Vaginatum uliginosum</i> - <i>Sphagnum angustifolium</i> -Ass. 59. <i>Oxycoccus quadripetalus</i> - <i>Sphagnum</i> -Ass. 74. <i>Carex Goodenowii</i> -Ass.

Fig. 73. Comparison of the classification system adopted in this work with types of Osvald (1923). The mire margin.

	E			M		
	1	2	3	1	2	3
EHu	Calluna-Cladonia-Sphagnum fuscum-ass.			Pinus-Vaccinium-mosseass.	Pinus-Carex globularis-Sphagnum parvifolium-ass.	
EHI		Scirpus caespitosus-Carex pauciflora-Sphagnum tenellum-papillosum-ass.	Scirpus caespitosus-Molinia-Sphagnum papillosum-ass.	Betula-Eriophorum vaginatum-Carex pauciflora-fusca-Sphagnum parvifolium-ass.		
ELu	Eriophorum vaginatum-Scirpus caespitosus-Sphagnum rubellum-balticum-cuspidatum-ass.					
ELI		Carex rostrata-pauciflora-Sphagnum papillosum-ass.				
EPC	Scheuchzeria-Rhynchospora alba-Carex limosa-Sphagnum cuspidatum-Dusenii-ass.	Carex rostrata-limosa-Sphagnum apiculatum-pulchrum-ass.				
ERC	Scheuchzeria-Rhynchospora alba-Carex limosa-lösbotten-höljeass.	Carex limosa-chordorrhizalivida-lösbottenass.				

Fig. 74. Comparison of the classification system adopted in this work with types of Sjörs (1948).

makes correspondence to the special area hard to establish. Figs 79 and 80 show the correspondence between site-types and variants in the systems of Ruuhijärvi (1960) and Eurola (1962), and site-types in the special area.

The Braun-Blanquet approach

The only recent regional surveys of mire vegetation applicable to parts of SE. Fennoscandia using the full hierarchy of the Braun-Blanquet approach (cf. Westhoff & van der Maarel 1978), are the contributions by Dierssen (1982) and Dierssen & Reichelt (1988). The range of vegetational (and environmental) variation encountered in the special area falls into two classes. Class Oxycocco-Sphagnetalia comprises the EHu, EHI, ELu, and MHu series, while ELI, EC, and MHI are included in class Scheuchzerio-Caricetalia nigrae. The former is divided into three orders. The Empetro-Sphagnetalia fusci comprises all mire expanse and mire margin hummock vegetation, classified in the association Empetro-Sphagnetum fusci. The ELu vegetation is divided on Sphagnetalia magellanici and Oxycocco-Ericetalia tetralicis; the limits between orders mainly set by regional criteria. Within class Scheuchzerio-Caricetalia nigrae, the M3HI corresponds to order Caricetalia nigrae, association Caricetum nigrae, part of the E3 site-types to order Caricetalia lasiocarpae, and the remain-

	P			R		
	1	2	3	1	2	3
EHu	Eriophorum vaginatum-Sphagnum rubellum small ass. Empetrum nigrum var.	Narthecium ossifragum-Sphagnum rubellum small ass. Empetrum nigrum var.	Eriophorum angustifolium-Sphagnum rubellum small ass. Empetrum nigrum var.	Eriophorum vaginatum-Cladonia small ass.		Eriophorum angustifolium-Cladonia small ass.
EHl	Eriophorum vaginatum-Sphagnum rubellum small ass. Trichophorum caespitosum var.	Narthecium ossifragum-Sphagnum rubellum small ass. Trichophorum caespitosum var.	Eriophorum angustifolium-Sphagnum rubellum small ass. Trichophorum caespitosum var.			
ELu	Eriophorum vaginatum-Sphagnum magellanicum small ass. Trichophorum caespitosum var.	Narthecium ossifragum-Sphagnum magellanicum small ass. Trichophorum caespitosum var.	Eriophorum angustifolium-Sphagnum magellanicum small ass.	Eriophorum vaginatum-Sphagnum tenellum small ass. Trichophorum caespitosum var.	Narthecium ossifragum-Sphagnum tenellum small ass. Trichophorum caespitosum var.	Eriophorum angustifolium-Sphagnum tenellum small ass. Trichophorum caespitosum var.
ELl	Eriophorum vaginatum-Sphagnum magellanicum small ass. Drosera anglica var.	Narthecium ossifragum-Sphagnum magellanicum small ass. Drosera anglica var.	Eriophorum angustifolium-Sphagnum magellanicum small ass. Drosera anglica var.	Eriophorum vaginatum-Sphagnum tenellum small ass. Drosera intermedia var.	Narthecium ossifragum-Sphagnum tenellum small ass. Drosera intermedia var.	Eriophorum angustifolium-Sphagnum tenellum small ass. Drosera intermedia var.
EC	Eriophorum vaginatum-Sphagnum cuspidatum small ass.		Eriophorum angustifolium-Sphagnum cuspidatum small ass.	Eriophorum vaginatum-Cladopodia fluitans small ass.	Rhynchospora fusca-Sphagnum auriculatum small ass.	Eriophorum angustifolium-Sphagnum auriculatum small ass.

Fig. 75. Comparison of the classification system adopted in this work with types of Malmer (1962a). The mire expanse.

ning mire expanse site-types to order Scheuchzerietalia palustris, alliance Rhynchosporion albae. In this alliance, some of the EPC vegetation is classified to Caricetum limosae, the remainder to Sphagno tenelli-Rhynchosporietum albae. The separation of communities of rank below the association is mainly by dominance of single species. Correspondence between site-types and units in this system can therefore in general not be established. The system does not provide clear-cut divisions along any of the four gradients here considered. Improvements of phytosociological classifications to give better ecological separation of types are proposed by Malmer (1968).

BROAD-SCALE PATTERNS: THE NUTRIENT GRADIENT

Hydrological characterization of the mineral soil water limit

Five problems relating to hydrological characterization of the mineral soil water limit can be identified in the special area.

(1) *Temporal variation.* The mineral soil water limit moves temporarily over the mire surface. When the water table drops slightly below the compensation level, the horizontal flow-rates are strongly reduced (Jørgensen 1929, Malmer 1962a, cf. also Johansson 1974, Ivanov 1981). Then the lateral transgression of mineral soil water is strongly restricted

	P			R		
	1	2	3	1	2	3
EHu	Eriophorum vaginatum-Sphagnum rubellum-ass. Bipetrum nigrum-var.		Carex lasiocarpa-Sphagnum rubellum-ass.	Eriophorum vaginatum-Cladonia rangiferina-ass.		
EHL						
ELu	Eriophorum vaginatum-Sphagnum magellanicum-ass.	Scheuchzeria palustris-Sphagnum papillosum-ass.	Menyanthes trifoliata-Sphagnum papillosum-ass.	Eriophorum vaginatum-Sphagnum tenellum-ass.		
ELl						
EC	Eriophorum vaginatum-Sphagnum cuspidatum-ass.	Scheuchzeria palustris-Sphagnum dusenii-ass.	Menyanthes trifoliata-Sphagnum apiculatum-ass.	Eriophorum vaginatum-Sphagnum cuspidatum-Cladopodiella fluitans-ass.	Scheuchzeria palustris-Sphagnum auriculatum-ass.	Menyanthes trifoliata-Sphagnum inundatum-ass.

Fig. 76. Comparison of the classification system adopted in this work with types of Svensson (1965) The mire expanse.

(Malmer 1962a). The temporal variation of mean depth to the water table in the special area indicates that the mineral soil water limit is very rarely reached by mineral soil water. In 1980 and 1981 the highest water tables were reached in the autumn. In 1982 the water table never reached the highest levels from the previous years, and this year the absolute mineral soil water limit was probably not influenced by mineral soil water at any occasion. In the special area, the mineral soil water limit is probably most often reached just before the mire freeze. Malmer (1962a) describes a different situation at Åkhultmyra, where the mineral soil water limit is reached in the spring. This difference is due to the small catchment of all lags and fen soaks at N. Kisselbergmosen; higher water tables in spring than in autumn are typical for mires with large catchment and large amounts of snow in winter (Damman 1977, 1986).

(2) *Spatial variation.* The temporal variation of the mineral soil water limit has a counterpart in spatial variation on the mire. In drier periods when lateral movement of water is negligible the mineral soil water limit moves towards the fen (Malmer 1962a), leaving functionally ombrotrophic sites behind (Elveland 1976). This variation can be conceived as a gradient running from the mineral soil water limit to the wet, central parts of the fen soak continuously influenced by mineral soil water. The E2 and E3 zones take contrasting positions along this gradient, as evident from a comparison of Figs 7 and 29 with respect to the western, broad fen soak.

(3) *Vertical variation.* The curvature of water level contours precludes mineral soil water to be transported horizontally beyond the mineral soil water limit. However, when lateral transgression of ombrotrophic peat over a minerotrophic substrate takes place, the

	P			R		
	1	2	3	1	2	3
EHu	Calluno-fuscetum Sphagnum fuscum- fac. <u>p.p.</u>	Calluno-straminetum ----- Trichophoro-papillosetum Rhynchosporo-papillosetum Menyantho-dusenietum <u>p.p.</u>		Calluno-fuscetum Cladina-fac. <u>p.p.</u>	Sphagnetum compacti	
EHl	Calluno-fuscetum Sphagnum fuscum- fac. <u>p.p.</u> S. magellanicum- fac. S. rubellum-fac.			Calluno-fuscetum Cladina-fac. <u>p.p.</u> Levermoss-fac.		
ELu	Rubello-tenel- letum magellanicetosum			Rubello-tenel- letum tenelletosum		
ELl	Cuspidatetum dusenietosum övrig Cuspidate- tum-vegetation			Cuspidatetum tenelletosum		
EC				Cuspidatetum zyggonietosum	Menyantho-dusenietum <u>p.p.</u>	

Fig. 77. Comparison of the classification system adopted in this work with types of Fransson (1972). The mire expanse.

	1	2	3
MHu	Vaccinietum uli- ginosi	Caricetum globularis	
MHl			Paucifloro-par- vifolietum paucifloretosum

Fig. 78. Comparison of the classification system adopted in this work with types of Fransson (1972). The mire margin.

	P			R		
	1	2	3	1	2	3
EHu	Calluna-Sphagnum fuscum-Rm. P.P. Empetrum-Sphagnum fuscum-Rm. Andromeda-Vaccinium-Sphagnum fuscum-Rm.			Calluna-Sphagnum fuscum Rm. P.P.		
EHI		Kurzhalmige Wm-Rm. Eigentliche Wm-Rm.				
ELu	Ombrotrophe Kurz- halmige Wm.	Rimpiartige Sphagnum balti- cum-Wm.			Sphagnum compactum-Wm.	
	Eriophorum vaginatum- Sphagnum balticum-Schlenken	Kurzhalmige Sphagnum pa- pillosum Wm.				
ELI	Scheuchzeria palustris- Sphagnum balticum-Schlen- ken	Rimpiartige Sphagnum pa- pillosum-Wm. Scheuchzeria-Sphagnum balti- cum-Rimpiwm. Seggenreiche Sphagnum papillo- sum-Wm.		Moosarme Schlen- kenwm.		Drepanocladus fluitans-Rimpiwm. Oligotrophe moosarme Rimpiwm. (Rhyn- chospora alba-Rimpiwm.)
EC		Sphagnum Dusenii-Rimpiwm.				

Fig. 79. Comparison of the classification system adopted in this work with types of Ruuhijärvi (1960). The mire expanse.

situation is more complex. A site not at present directly influenced by mineral soil water may have contact with the minerotrophic peat below through upward capillary movement of water (Eurola 1962). This capillary zone may reach a 50 cm vertical extent (Granlund 1932). As the unilaterally sloping, ombrogenous parts of the special area have developed on soligenous peat (Økland 1989), such a vertical variation cannot be precluded in E1 areas close to the zonal divides.

(4) *Fen windows* (Witting 1947, Sjörs 1950, Du Rietz 1954, Siegel & Glaser 1987) are caused by upwelling of minerogenous water from below a bog. Such an upwelling may add to the strong increase in wetness at pos. 06-09 11 in the special area (Fig. 5), coinciding with an abrupt increase of the slope of the water table (Fig. 7). The influence by mineral soil water is, however, also evident from the curvature of contour lines alone.

(5) *Straight contour lines*. In unilaterally sloping mire areas the exact position of the mineral soil water limit can not be decided when the transition from concave to convex contours is mediated by a straight segment (Malmer 1962a, cf. also Sjörs 1948, Du Rietz 1949, Damman 1986). Then the limit must be conceived as two currents running parallel to each other (Malmer 1962a). In the special area, this situation is common. Some aid to the establishment of the limit can be obtained by considering the distribution of hydromorphological features and subfeatures.

Theoretically, Thunmark's (1940) definition of the mineral soil water limit (cf. p. 17) seems clear cut. However, from the discussion of temporal and vertical variation (points (1) and (3) above) it appears that the dynamic nature of the limit, at least in actively developing unilaterally sloping raised bogs, precludes the concept of the limit as a sharp

	P			R		
	1	2	3	1	2	3
EHu	Calluna-Sphagnum fuscum-Cladonia-Rm.; Flechten- und Lebermoosarme Var. Eig. Empetrum-Sphagnum fuscum-Rm.: beinahe baumlos	Sphagnum papillosum-Wald-Wm.; Bultenhorizont, p.p.		Calluna-Sphagnum fuscum-Cladonia-Rm.; Flechtenreiche Var.: Lebermoosreiche Var.		
EH1	Andromeda-Sphagnum fuscum-Wm.					
ELu	Sphagnum rubellum-Wm. Sphagnum balticum-Wm.	Sphagnum papillosum-Wald-Wm.; Teppichhorizont p.p.; Minerotrophe kurzhalbige Wm. Eig. Sphagnum papillosum-Wm. p.p.	Sphagnum papillosum-Wald-Wm.	Sphagnum tenellum-Wm.	Sphagnum compactum-Wm.	
EL1	Scheuchzeria-Sphagnum balticum-Wm. Sphagnum cuspidatum-Wm. p.p.	Eig. Sphagnum papillosum-Wm. p.p. Sphagnum papillosum-reiche Grosseggen-Wm. Rimpiartige Sphagnum balticum-Wm.				Rimpi-Wm.
EC	Sphagnum cuspidatum-Wm. Sphagnum Dusenii-Wm.	Eig. Grosseggen-Wm.	Torfschlamm-Wm.			

Fig. 80. Comparison of the classification system adopted in this work with types of Eurola (1962). The mire expanse.

border. Furthermore, problems (4) and (5) confound the practical application of Thunmark's definition to the extent that exact hydrological determination of the mineral soil water limit becomes impossible. Accepting the inexactness of the limit, the best approach to a hydrological determination is by detailed mapping of the topography of the maximum water table, aided by taking the distribution of fine-scale hydromorphological mire components into account.

Correlations between chemical parameters

The analysis of peat samples points to the existence of one factor complex strongly correlated with the differentiation into zones. This complex, consisting of pH, ash content, base saturation, and H, with Ca as a less well correlated parameter, conforms very well to the nutrient factor complex identified in previous investigations (Gorham 1953, Sjörs 1961, Malmer 1962a, Sonesson 1970b, Wildi 1977). pH, H and base saturation are logically correlated, and act as an integration of several chemical parameters (metallic cations, etc.). pH correlates particularly well with the zonal gradient in the poorer end, while ash content differentiates better in the richer end. Ash content reflects the relative amounts of minerogenous water, as most of the ash is insoluble SiO₂ brought from the mineral soil (Malmer 1962a, Sonesson 1970b).

The only study providing chemical analysis of comparable peat samples (cf. criteria for comparability on p. 18) is Malmer (1962a). His values for pH in ombrogenous areas

are similar to mine, but at Åkhultmyra pH rises more rapidly by minerogenous water supply. The ash content varies in a similar manner at Åkhultmyra; values in E1 and E2 zones correspond to the *Eriophorum vaginatum* and *Narthecium ossifragum* zones, while the increase from E2 to E3 is paralleled by the transition from *Narthecium ossifragum* to *Eriophorum angustifolium* zones.

The small variation along the zonal gradient in the special area, also within the minerogenous zones, suggests that both of the E2 and E3 zones correspond to extremely poor fen in the system of Du Rietz (1949; cf. Waldheim & Weimarck 1943, Waldheim 1944).

The second PCA axis, with high loadings for Mg, partly also Ca, is not related to the nutrient gradient. These two bivalent ions are relatively strongly bound to the peat colloids (cf. Brehm 1968, Damman 1986), none of them show any concentration to upper peat strata (Damman 1978, Damman & Dowham 1981), nor appear to be in short supply for the vegetation (Damman 1986).

The observed Ca and Mg values are less than half of those given by Malmer (1962a) from Åkhultmyra. The correlation of the mineral soil water limit with a Ca concentration of 3.0 mmol dm⁻³ fresh peat at Åkhultmyra does not apply to the special area where all Ca values measured are below 2.0. Furthermore, the value of the Ca/Mg ratio is 0.7-0.8 along the entire zonal gradient in the special area; these are typical bog values at Åkhultmyra. However, Vorren (1979b) reported even lower values from mesotrophic sites at Færdesmyra, N. Norway.

K and Na, mobile monovalent ions with strong concentrations to the uppermost peat stratum (Damman 1978, 1986), obtain high loadings on the third PCA axis. These ions show individualistic behaviour. K concentrations are often lowered near the peat surface in the growing season (Anschtütz & Gessner 1954, Malmer & Sjörs 1955, Malmer 1962b, Damman 1978) due to active uptake in plants (Goodman & Perkins 1968a, 1968b, Damman 1978, Damman & Dowham 1981). Na is transported upwards with capillary water, and by evaporation of water accumulating in the upper stratum (Damman 1978, 1986).

The observed Na values are twice those given by Malmer (1962a), while the K values are considerably lower than values from Åkhultmyra.

Characterization of the mineral soil water limit by chemical and physical properties of the peat

The inability of single chemical and physical parameters (of peat or mire water) to be useful for characterization of the mineral soil water limit has also been demonstrated by Malmer (1962a), Sonesson (1970b), Tolonen and Seppänen (1976), and Tolonen and Hosiaislouma (1978). As in this study, Tolonen and Hosiaislouma (1978) observe a strongly improved ability to characterize the limit when invoking multivariate trends instead of single parameters.

Four problems relating to the characterization of the mineral soil water limit by constituents of the peat can be identified with reference to the special area.

(1) *Large local variation* in peat parameters, also demonstrated by Malmer (1962a) and Damman (1978). The local variation in peat is greater than in mire water (Malmer 1962a).

(2) *Small difference between precipitation water and mineral soil water* is likely to confound the tracing of minerogenous water by chemical means in areas with archaean bedrock and small catchments. The investigation area fully conforms to this description. This may explain the comparable values for ash content and the far lower pH and Ca

values in the special area as compared with Åkhultmyra (Malmer 1962a).

(3) *The temporal and spatial variation of the mineral soil water limit* (cf. p. 143-144). At the mineral soil water limit, minerogenous water is added so rarely and in so small amounts that it hardly affects the chemical composition of the peat. Furthermore, the mineral soil water limit is always reached by minerogeneous water after heavy rain, when the minerogeneous character of this water is lost by dilution with rain water. The effect of (2) is amplified by (3), and may be the main reason for the minor difference between E1 and E2 in the absence of distinct fen soaks beyond the E1-E2 limit (as is the situation in most transects).

(4) *Differential flow-rates*. In transects across zonal limits, the water flow-rate gradient runs parallel to the nutrient gradient. At any time, higher flow-rates are expected to occur in areas with concave contours, than in areas with convex contours because of the larger catchment area of the former. This higher flow-rate inevitable implies an improved nutrient supply to the minerogeneous part of the transect, and amplifies the chemical difference at the mineral soil water limit. Thus in transect 1 in the special area, running across a broad, wet fen soak, the clear increase in pH, Ca, and ash content is probably because of this combined effect. This also explains the mineral soil water limit being less well characterized in terms of peat composition in transects across indistinct fen soaks (e.g. T3 and T4).

Higher flow-rates imply better nutrition regardless of the origin of the water (Malmer 1962b, 1986, Damman 1978, Damman & Dowhan 1981), in turn resulting in increased growth-rates of the vegetation (Malmer 1962b, Sonesson et al. 1980, Clymo & Hayward 1982). The increasing flow-rates from the upper to the lower part of a unilaterally sloping mire surface, both in ombrogenous and minerogenous mire areas, strongly confounds the characterization of the mineral soil water limit by peat properties (Müller 1965, 1976, Aletsee 1967). No difference was observed between transects up and downslope in the special area (T3 vs T2, T4 vs T5), probably because of the small distance between transects. Damman (1986), however, suggests that the nutrient supply may increase by a factor of up to twenty down an ombrogenous slope. Lindsay *et al.* (1985) suggest volume of water transported per unit time to be conceived as a direction of variation in addition to the gradients normally considered.

The points discussed above, in particular point (4), make it impossible, even within a small area like the special area, to characterize the mineral soil water limit unambiguously by properties of the peat or mire water (cf. also Malmer 1962a). Furthermore, it is clear from the present study that the hydrological approach to the mineral soil water limit has fewer shortcomings than the approach by peat properties. The latter will probably give unambiguous contributions to assessment of the limit only in the case of fen windows (an example is given by Witting 1948, cf. also p. 146).

The fen plant limit

Although the correspondence between the hydrological mineral soil water limit and the floristical fen plant limit is relatively good in the special area, numerous examples of discrepancies occur. Eight different explanations may apply to deviations of the fen plant limit from the mineral soil water limit, the first six relevant to occurrences of fen plant on ombrogenous peat.

(1) *Relicts* (Sjörs 1947, Aletsee 1967). Vascular plants in bogs and extremely poor fens mostly reproduce vegetatively (Backéus 1985). Establishment from spores is assumed to be rare in bryophytes in these habitats as well (Boatman & Lark 1971, Clymo & Duckett

1986). There are good reasons to ascribe this to the higher demands for establishment than for maintenance (Summerfield 1972, 1973, Harper 1977). The longevity of individuals of many bog plants, combined with their ability to clonal growth (Backéus 1985), enables a well-established stand to be maintained vegetatively for a long time (even hundreds of years) after the site has crossed the mineral soil water limit (Chapman 1964). Such relicts are often sterile (Du Rietz 1954), and show reduced vitality of vegetative shoots; examples are given by Olausson (1957), Boatman (1961), and Chapman (1964). The most typical relict occurrence in the special area is the occurrence of *Carex pauciflora* in the middle of the largest ombrotrophic area (example (c) at p. 58). Relict occurrences of this species are often noted by other authors (e.g., Ruuhijärvi 1960). The two occurrences of *Erica tetralix* and *Sphagnum papillosum* slightly on the bogward side of the mineral soil water limit (examples (a), (b), (f) and (g) at p. 58) may have similar explanations.

(2) *Different nutrition of plants at a site* (Ackenheil 1944, Du Rietz 1954). The bottom layer is exclusively fed by precipitation, lateral flow of water, and by capillarity. As soon as a site has crossed the mineral soil water limit and the acrotelm entirely consists of peat formed by ombrotrophic nutrition, access to minerogenous water is cut off. On the contrary, vascular plants show considerable variation in root depths (Metsävainio 1931, Du Rietz 1954, Björkback 1965), thereby allowing for the possibility that plants growing together may have fundamentally different nutrition. Several fen plants, e.g. *Carex rostrata* (Metsävainio 1931, Malmer 1962a) and *Eriophorum angustifolium* (Goodman 1963, 1968) have living roots penetrating to more than 1.0 m into the peat. This explains the occurrence of *Carex rostrata* in otherwise typical E1 vegetation (example (e) at p. 58). Towards the border onto mineral soil these species are likely to obtain nutrients directly from the mineral soil below (this may explain the scattered occurrences of *Carex rostrata* and *Eriophorum angustifolium* in otherwise poorer vegetation near the border onto mineral soil). Towards the alpine zones, the shallow peat deposits often render the separation of bog and fen impossible (cf. Sonesson 1970a).

(3) *Spatio-temporal dynamics* (Aletsee 1967). As the mineral soil water limit is neither constant in space nor in time, a dynamic fen plant limit is expected. Repeated colonization and die-backs result in the typically unsharp limit documented in this study.

(4) *Response to differential flow-rates*. Differential flow-rates result in variable nutrient availability within an ombrogenous area (p. 149). Müller (1973, 1976) suggests that some species, limnobionts, among them *Carex limosa* and *Scheuchzeria palustris*, are able to establish and grow under ombrogenous conditions given high flow-rates and thus optimal nutrition. In the special area, these two species, as well as the similarly distributed carpet species *Sphagnum lindbergii* and *S. majus*, do not occur in the E1 zone. This is most probably due to the absence of large, wet hollows downslope in the ombrogenous parts of the special areas as all these species have been observed in certainly ombrotrophic sites in inner Østfold (Økland 1989, and unpubl.). This absence of suitable conditions for carpet species in ombrogenous sites is also reflected in the almost absence of the E1PC and E1PLI site-types from the E1 zone (cf. pp. 87, 95-96). Increased flow rates do not only imply improved nutrient availability, but also better oxygenation (Havas 1961, Aletsee 1967, Armstrong & Boatman (1967), and removal of toxic metabolites by oxidation (Rutter 1955, Gore & Urquhart 1966, Crawford 1983).

(5) *Response to nutrient enrichment by animals* (Aletsee 1967, Müller 1973, 1976). Müller (1976) coins the term coprobiont for species occurring in ombrogenous areas that are actually dependent on nutrient enrichment by animals. In the special area, the *Splachnum* spp. on elk's faeces are typical examples (cf. Fig. 28).

(6) *Response to differential peat mineralization rates* (Aletsee 1967, Müller 1965, 1976). Stagnant peat growth leads to increased mineralization of peat and accumulation of

nutrients in the superficial peat layers (Damman 1978, Damman & Dowhan 1981). Such stagnant peat is frequently encountered in eroded areas, in the mire margin, and on the mire expanse of bogs with cessation of vertical height growth (Damman 1978). Müller (1976) terms species restricted to marginal (but ombrogenous) parts of bogs kremnobionts, and mentions many of the typical mire marginal species (D-group 3) in the special area as belonging to this group. He further maintains that the kremnobionts are less demanding than the limnobionts, and that the habitat of the limnobionts is included in that of the kremnobionts. This investigation shows the carpet species of D-group 5 and the mire margin species of D-group 3 to have mutually exclusive distributional patterns. Furthermore, no species of the mire margin appears to enter the eroded areas. The concept of kremnobionts thus does not improve the understanding of the fen plant concept in this area, and appears to rest on a confounding of the mire expanse - mire margin and nutrient gradients. The conditions responsible for the differentiation along the mire expanse - mire margin gradient are discussed on pp. 152-153.

(7) *Local vertical variation in peat.* Hummocks and adjacent hollows differ strongly with respect to pH, nutrient concentrations, water availability, etc. (Malmer 1962a, Damman 1978, cf. p. 155). Hummocks are situated above the maximum water level, and are therefore excluded from nutrient addition by surface flow. The majority of fen plants are restricted to carpets and lawns (Økland 1990a, 1990b). Thus, at a fine scale, an "upper fen plant limit" (Malmer 1962a) often occurs on the hummocks. This is reflected by (a) the frequent occurrence of *Sphagnum papillosum* in the lawns of less distinct fen soaks, while the adjacent hummocks lack fen plants, (b) the larger difference in mean median distance to the water table from carpet to hummock in the E1 than in the E2 zonation, and (c), the increasing frequency of sample plots in the E2 zone without fen plants from carpet to hummock. Northwards, this differentiation is carried to the extreme in stable mixed mires with large, ombrogenous kermis separating minerogenous rimpis (Ruuhijärvi 1960, Næss 1969, 1970).

(8) *Absence by chance factors.* Random factors associated with the spatio-temporal dynamics of populations may be responsible for the occasional absence of fen plants from fen sites close to the mineral soil water limit (compare point (3) above).

The fen plant limit is not sharp in the investigation area, except where the bog slope meets the lagg. An indistinct fen plant limit associated with a diffuse mineral soil water limit is noted by Sjörs (1948), Malmer (1962a), and Fransson (1972), inter alia. Contrasting opinions are expressed on the importance of the fen plant limit; from Du Rietz (1949, 1954) considering this limit a main border in mire vegetation, to Müller's (1973, 1976) characterization of the limit as a rather senseless concept.

In the special area, the nutrient gradient is a continuous response to the gradual fading of mineral soil water supply from fen soak to bog. By detailed hydrological mapping it is possible to distinguish a mineral soil water limit; conceivable as a zone, not a sharp limit. Even though this limit is confounded by variation along other gradients (water flow-rates, mineralization rates), it is clearly reflected in more species with nearly coincident distributional limits towards the bog. Thus the concepts of fen plant and fen plant limit are useful if they are based on detailed hydrological determination of the mineral soil water limit (cf. Malmer 1962a). The opposite procedure, to approach the (sharper) mineral soil water limit by the (more diffuse) fen plant limit should be avoided due to the many pitfalls (the eight points above, in addition to the problems involved in hydrological assessment of the mineral soil water limit).

BROAD-SCALE PATTERNS: THE MIRE EXPANSE - MIRE MARGIN GRADIENT

The mire expanse-mire margin transition in the special area is characterized by a gradual increase in height and density of *Pinus sylvestris*, accompanied by large shifts in the species composition of the field and bottom layers. *Pinus sylvestris* has a horizontal rooting system with mycorrhizae (Melin 1917, Metsävainio 1931, Sjörs 1948), and is vulnerable to waterlogging (Sjörs 1948, Crawford 1983). The following differences between the EHu and MHu series explain the restriction of pine trees to the latter: (1) the higher range of depths to the water table in M than in E (mean median depths to the water table are similar), and the associated higher maximum depths, and (2), the restriction of M zones to sites with a small catchment, strong slope, or both, giving shelter from surface water flow or providing good run off conditions (Sjörs 1948, Ivanov 1981, Økland 1989). Furthermore, the increasing areal importance of *Pinus* bog forests towards less humid climates accords with the above observations (cf. Økland 1989).

The gradual transition in the tree layer is followed by gradual transitions in the field and bottom layers. The following conditions may be responsible for the transitions: (1) The aeration of the surface peat (as for *Pinus*; Sjörs 1948, 1950). (2) The shade (and litter) from *Pinus* (Sjörs 1948, Elveland 1976). (3) The lower amplitude of microclimatic variation in the mire margin (Firbas 1931, Dierssen 1982, Rydin 1984). (4) The lower peat depth (Heikurainen 1953, Ruuhijärvi 1960, Elveland 1976). (5) Chemical differences related to stagnation of peat growth and subsequent increase in mineralization of the surface peat (Valmari 1956, Malmer 1962a, 1986, Damman 1978, Damman & Dowhan 1981). (6) Higher interspecific competition in the mire margin (Sjörs 1948).

Point (6) has to be a secondary effect of some primary factor increasing favourability for plant growth in the mire margin, and will not be further considered here (see Økland 1990b). Point (3) is strongly correlated with (2), and point (4) with (1) by promoting subsurface run-off. The importance of (5) has been repeatedly emphasized (see references above). However, Malmer (1962a) presents closely similar values of K, Na, Ca, and Mg in the wooded bog (corresponding to the M1 zone) and in the *Eriophorum vaginatum* zone (corresponding to E1), and Damman (1978) shows higher Ca, P, and N, but lower K in a similar comparison of bog areas. The latter may be explained by increased mineralization following stagnant peat growth (Damman 1978, Damman & Dowhan 1981). Point (5) is at odds with the currently held view that K is the restricting nutrient for ombrotrophically growing plants (cf. Malmer 1962b, 1986, Goodman & Perkins 1968a, 1968b, Damman 1986). However, this point may be applicable to the M2 and M3 zones. The available material is too sparse to allow further speculations. The first two points; the hydrological conditions and the shade produced by the tree layer, together appear to be responsible for the differentiation into E1 and M1 zones. The better aeration of the surface peat is important for the mycorrhizal *Vaccinium* spp. (Metsävainio 1931, Sjörs 1948, 1950) and *Empetrum nigrum* (Bell & Tallis 1973, 1974), while the photophilous *Calluna vulgaris* prefers gaps. Several species with optimum in mire expanse habitats are restricted to *Sphagnum fuscum* patches when they occur in the M zones, e.g., *Andromeda polifolia*, *Drosera rotundifolia*, *Calypogeja sphagnicola*, *Kurzia pauciflora*, and *Mylia anomala*. *Sphagnum fuscum* has a far better water-holding capacity than the co-occurring species owing to the shoot arrangement (Vitt *et al.* 1975, Silvola & Aaltonen 1984, Rydin 1985, Wallén *et al.* 1988), and is photophilous (cf. Hayward & Clymo 1983). The combination of high demands for moisture, high radiation, and small amounts of deposited litter appear to restrict these species from the dense *Pinus* and *Vaccinium* stands (where the bottom layer is poorly developed). The relative importance of light and peat aeration thus appears

to be variable among the species, with light (and litter) being the most important factor for the bottom layer and the smaller plants of the field layer, aeration the more important for the dominant dwarf-shrubs.

FINE-SCALE PATTERNS: THE GRADIENT IN DEPTH TO THE WATER TABLE

Seasonal and local variation

The overall shapes of one and three year cumulative probability distribution functions for depth to the water table are invariant over the special area. The sigmoid curves closely resemble curves described from other mires (Malmer 1962a, Johansson 1974, Wildi 1977). Curve shapes differ more strongly between years than between site-types, indicating the greater importance of climatic factors than peat properties for the seasonal variation in depth to the water table. The existence of a distinct compensation level (cf. Conway 1949, Rutter 1955, Malmer 1962a, Wildi 1977, Boatman 1983) depends on an adjustment between addition and run-off of water (Malmer 1962a) so that extreme levels are of short duration (Damman & Dowhan 1981). This investigation confirms the observation of Malmer (1962a) that a distinct level occurs, to which the water table rises every time a certain, high amount of precipitation is added. This level is close to the upper decile of the cumulative distribution, ca. 2 cm below the minimum depth to the water table. The minimum depth is only reached after extreme rain, not even necessarily once a year. The curves (for different years and sites) are closely similar in their upper part, the variation between years is mostly with respect to the duration of high distances to the water table. The occurrence of highly asymmetric curves in 1982 (extended duration of high distances) depends on extreme drought; Johansson (1974) observed similar curves during four consecutive years of study on Komosse, S. Sweden. Drought periods like that occurring in 1982 rarely occur more often than once in twenty years, so that the maximum depth to the water table this year is probably close to the absolute maximum.

The simple modelling of climatic influence on variation in depth to the water table gives good insights into the relative importance of different factors on water table fluctuations. Amount of precipitation is by far the most decisive factor, as suggested by Malmer (1962a, 1986), Damman & Dowhan (1981), Boatman (1983), and Lindholm & Markkula (1984). The next important factor is position of the water table at the start of a time interval. The operation of these two factors can only be understood by simultaneous consideration. The response of a dip well to addition of an amount of water is determined by the active porosity of the peat, that is, the relative volume of unfilled pores in its immediate surroundings (Sjörs 1948, Boelter 1964, 1969, Ivanov 1981, Clymo 1983); the higher active porosity, the lower response.

The active porosity decreases with increasing degree of humification, that is from carpet to hummock, and with increasing peat depth. Similar responses are predicted by removal of water, e.g., by evaporation (see the references quoted above). This explains the following observations : (1) The higher range of depths to the water table in mire expanse hummocks in a hummock-dominated than in a mixed hummock-hollow area. (2) The higher range of depths to the water table in mire margin than in mire expanse sites. (3) The stronger decrease in depth to the water table by addition of a specified amount of precipitation, the higher the initial depth to the water table (also observed by Malmer (1962a) and Lindholm & Markkula (1984)). The response function of a peat profile with

a specified depth to the water table to addition of water is described by the coefficient of magazination (Johansson 1974) or the layer coefficient (Ivanov 1981); both expressing vertical variation of active porosity of the peat.

Precipitation the two days before recording the depth to the water table is strongly correlated with run-off (cf. Johansson 1974), thus reducing the effect of large amounts of precipitation at mean depths to the water table below the compensation level. The low importance of water need (an expression of evaporation) must be due to the relatively low amplitude of daily mean temperatures during the ice-free season. Effects of this factor is observed at large depths to the water table. Increased temperatures explain the acceleration of rates of increase in depth to the water table observed in dry periods in 1981 and 1982. Similar observations are made by Malmer (1962a).

In spite of the very high multiple correlation coefficient, the linear regression model does not correspond to the mathematical model for water exchange in mires developed by Ivanov (1981); who gives the following relationship between P, E (evaporation), R (run-off), L (the layer coefficient, a function of cumulative probability, P), and W (change in water storage) within a specified time interval:

$$W = P - E - R$$

As

$$W = L_p$$

we obtain the equation

$$1 = L_p^{-1} (P - E - R),$$

indicating that the position of the water table is acting to determine the amplitude of the reaction by its direct effect on E, and R. As L_p for a large mire area (as, for instance, the special area) is a most complex function, the available data from the special area could not be fitted into Ivanov's model without further work on peat porosity. Nevertheless, the simple model used was able to demonstrate the relative importance of the parameters in Ivanov's model.

Estimation of characteristic levels of cumulative probability distribution functions

The similarity of the shapes of one year cumulative probability distribution functions for $P < 0.75$, the high correlation of P_0 , P_{10} , K , and P_{50} (partly also P_{90}), and the low variance of the estimators for these characteristic levels based on one or two observations, indicate that (1) if the one year cumulative probability distribution for a site is known, one observation at median or lower distance to the water table is sufficient for a reliable estimate of the four characteristic levels mentioned, and (2) one observation at relatively high water table is sufficient for a reliable ordering of sites according to median or minimum distance to the water table (as done by Vitt & Slack 1984, Kenkel 1987, Wallén *et al.* 1988). The absolute maximum depth to the water table (and hence the range) can hardly ever be exactly defined, and cannot be reliably estimated from few observations as argued by Wildi (1977). The low correlation between maximum depth and the other characteristic levels points to the importance of long-term recording if reliable cumulative distribution functions are required (cf. Malmer 1962a, Ivanov 1981).

Relationship of the series to depth to the water table

Characterization of limits between series

The existence of an upper hummock level situated well above the maximum water table, conforms with results obtained by Malmer (1962a) for the *Empetrum nigrum* variants of the *Sphagnum rubellum* series. The considerable decrease in mean median depth to the water table in the EHu series from the E1 to the E2 zone also accords with Malmer's (1962a) results. This is likely to be due to the higher porosity, and hence a higher ability for capillary rise of water in the E1 zone (Malmer 1962a).

The occurrence of the EHI series from just above the maximum water table also accords with Malmer (1962a). Occasionally, the ice level in spring is above the Lu/HI level (cf. Osvald 1923, Malmer 1962a, Damman & Dowhan 1981). The position of the limit, relative to the water table, was not specifically determined. Comparison of values for minimum distance to the water table in the Lu and HI series suggests that this limit between series is situated at 1-3 cm minimum distance, while Malmer (1962a) found a close correspondence between the *Calluna* limit and the maximum water table.

The ELu series is situated close to the minimum depth to the water table, slightly above the *Trichophorum cespitosum* variants of the *Sphagnum magellanicum-papillosum* and *S. tenellum* series (Malmer 1962a). This series is characterized by inundation of the root layer after moderate rainfall and by aerated peat most of the season (cf. Sjörs 1948, Malmer 1962a).

The bottom layer of the ELI series is covered by water for ca. 10% of the season and is thus inundated after every moderate rainfall and with considerable duration of an inundated root layer (cf. Malmer 1962a).

The EC series is approximately level with the compensation level (cf. Malmer 1962a). This investigation does not suggest considerably lower range of depths to the water table in the C than in the LI series, as expected from the often quoted quagmire-like nature of the carpets (Sjörs 1948, Malmer 1962a). This partly results from the rareness of floating carpets in the special area (restricted to a few large hollows far north in the area), rendering the material from the EC series less representative, and from the occurrence of non-floating carpet vegetation (the EPC site-types).

Chemical parameters correlated with the gradient in depth to the water table

Obviously, the water table gradient gives rise to variable aeration and firmness of the peat (Sjörs 1948, Malmer 1962a). Less obvious correlated parameters are:

(1) *Redox potential*. A close correspondence between permanent waterlogging and reducing conditions is demonstrated by Malmer (1962a), Persson (1962), and Boatman (1983). Malmer (1962a) demonstrates a high variance of redox potentials in each series, but with a marked trend towards higher redox potentials in hummocks.

(2) *pH* decreases from hollow to hummock by up to 1 unit (Malmer 1962a, Vitt *et al.* 1975, Pakarinen 1979).

(3) *Nutrient availability* is often considered to decrease from hollow to hummock (Malmer 1962a, Johnson 1977a, Pakarinen 1979). However, Damman (1978) shows that this relationship is more complex: Fe, Al, and Zn accumulates in the zone of periodic inundation, Mn and K reach highest values in hummocks, while most of the remaining cations reach higher values in hollows or show no significant difference.

The intensity of disturbance along the gradient in depth to the water table

The pattern of variation in area covered by bare peat (Tab. 8, Fig. 68) must result from variable intensity of destabilizing factors (local catastrophic events) along the gradient in depth to the water table and/or differential vulnerability of different taxocenes to such events. Two features are particularly emphasized: (1) the increasing areal importance of bare peat from upper lawns to carpets, and (2) the high areal importance of bare peat at the level of the EHI series.

Local catastrophic events in hollows. Bare peat appears locally as a result of several processes.

(1) *Water erosion.* The likelihood of water erosion increases with increasing length of the inundated period (Sjörs 1947, Foster *et al.* 1983). The erosive power of water is particularly high at high water tables (Backéus 1985), as demonstrated by Osvald (1923), Vorren (1979), and Økland (1989). The somewhat more strongly fluctuating water tables in the E1 than in the E2 zone may, in part, explain the higher areal importance of bare peat in hollows in the former. In carpets, or in lower lawns after long periods of inundation, erosion of *Sphagnum* mats may be brought about by redistribution of floating shoots (Aartolahti 1965, Boatman & Tomlinson 1977, Boatman 1983). Variable intensity of water erosion is probably the most important single factor for the explanation of the pattern of bare peat distribution in hollows.

(2) *Ice erosion.* The ice level extends vertically to the Lu-HI limit, or occasionally slightly higher (this paper, also see Osvald 1923, Malmer 1962a, Damman & Dowhan 1981). The mechanism is described in detail by Auer (1920), Ruuhijärvi (1960), and Økland (1989). Ice erosion is considered most severe in carpets (Malmer 1962a).

(3) *Methane release.* Methane produced by catotelmic peat decomposition has a low solubility in water and is therefore lost from the peat surface as gas bubbles (Clymo 1984). The gas bubbles repeatedly follow the same lines of weakness in the peat, and are normally released at the locally lowest situated parts of the mire surface. They also include catotelmic peat remnants that by redistribution on the peat surface near the orifice may impose a constant risk of burial upon the bottom layer residents (Gams & Ruoff 1929, Aario 1932, Aartolahti 1965).

(4) *Corrosive oxidation* of wet surfaces (Sjörs 1961, 1965).

(5) *Drought.* Lawns (and carpets) dry out rapidly in periods with warm weather and low precipitation (pp. 93, 112).

(6) *Parasitism by fungi.* The observed necrotic *Sphagnum* patches associated with the occurrence of the fungus *Tephrocye palustris* is due to parasitism (Redhead 1981).

(7) *Trampling by birds and moose* (Pakarinen 1978). Variable intensities of water (and ice) erosion are probably the most important single factors affecting the pattern of bare peat distribution in hollows.

Local catastrophic events in hummocks. Water and ice do not affect the bottom layer of hummocks directly. The most important agents bringing about the occurrence of bare peat are:

(1) *Fluctuations in the environment*, in particular drought (cf. Osvald 1923, Vitt *et al.* 1975). Drought selectively affects the different taxonomic groups. Hepatics are probably more strongly vulnerable to long periods of drought than are *Sphagnum*, and obviously more vulnerable to drought than lichens (cf. Clausen 1952, Kappen 1973, Ahti 1977, Proctor 1982). The humid climate in the investigation area is favourable to hepatics, making this group able to undergo ecesis on intact *Sphagnum* peat and even dominate patches in the EHI series. However, drought selectively kills hepatics, leaving patches of bare peat covered with a crisp surface. The lower area covered by bare peat in the EHu series is

likely to be due to the dominant position of lichens there.

Other kinds of destabilizing factors occur, but have minor importance. Worthy of mention are (2) *wind and frost action* (Osvald 1923, Eurola 1968, Sonesson 1970b), (3) *trampling by large animals* (Schmeidl 1977, Pakarinen 1978), and (4) *destruction by ants* (Booberg 1930, Fransson 1972), and (5) *destruction by honey buzzards* (Malmer 1962a).

The vascular plants

The distribution of vascular plant species in the special area according to distance to the water table demonstrates distinct upper and lower limits along this gradient. In both cases, these sets of limits can be interpreted as responses to external factors.

Lower limits. *Empetrum nigrum*, restricted to well-aerated sites, is strongly sensitive to waterlogging (Bell & Tallis 1974). Similar observations exist for *Calluna vulgaris* (Bannister 1964a, Wallén 1987), but its tolerance to low distances to the water table is obviously higher in this case. *Erica tetralix*, *Rubus chamaemorus*, *Carex pauciflora*, and *Scirpus cespitosus*, all having a marked lower frequency limit at the Lu-L1 transition, have a demonstrated moderate tolerance for intermittent waterlogging (cf. Sjörs 1948, Malmer 1962a, Bannister 1964a). These species all possess mycorrhizae, lack root aerenchyma, or both (Metsävainio 1931, Sjörs 1950, Malmer 1962a, Bannister 1966, Clymo & Hayward 1982).

Upper limits. The coincident upper limits of *Drosera anglica*, *Rhynchospora alba*, and *Scheuchzeria palustris* (at the L1-Lu transition) indicate susceptibility to drying-up (Sjörs 1948, Malmer 1962a). These species have optima in carpets, have deep roots with aerenchyma, and lack mycorrhizae (Metsävainio 1931, Sjörs 1950). That the upper limits of *Erica tetralix*, *Carex pauciflora*, and *Scirpus cespitosus* are due to drought sensibility is demonstrated by Bannister (1964b) and Boatman & Armstrong (1968).

The most important ecological borderline affecting vascular plants appears not to be the upper limit of inundation, the *Calluna* limit, as maintained by Du Rietz (1949), Malmer (1962a, 1986), and Fransson (1972), nor the limit between carpets and lawns (Sjörs 1948). Instead, the Lu-L1 limit, corresponding to the limit of frequent inundation (after moderate rain) should be emphasized. This is the marked frequency limit of a large number of species, and corresponds to the shift from dominance of species with mycorrhizae (and mostly without aerenchyma) to species without mycorrhizae, but possessing aerenchyma. The adaptive significance of root aerenchyma in permanently water-logged sites is the oxidation of toxic substances by diffusion of O₂ from the roots into the surrounding reducing environment (Armstrong & Boatman 1967, Bell & Tallis 1973, Boatman 1983, Crawford 1983).

The bottom layer

The sequence of drying up of the bottom layer during prolonged periods without precipitation demonstrated during the summer of 1982; first RLu and RL1 (*Sphagnum tenellum*), then *S. cuspidatum* carpets followed by PLu and PL1, and, lastly, hummocks, supports the view of Rydin (1985) and Andrus (1986) that the hollows are drier than the hummocks, seen from the point of view of the *Sphagnum* spp. The dryness of the habitat is a function of the active porosity of the peat (cf. p. 153), as resulting from differential abilities of *Sphagnum* spp. with contrasting morphologies to capillary rise of water (Overbeck & Happach 1957, Clymo & Hayward 1982, Rydin 1985).

The upper limits of the *Sphagnum* spp. towards the hummocks are often sharper than the lower limits, a feature particularly pronounced in the two species that most easily dry

out; *S. tenellum* and *S. cuspidatum* (Tab. 7). No species shows such sharp lower limits. This is in accordance with the current view that the upper limit of *Sphagnum* spp. is set by physiological tolerance, while the lower limit is set by interspecific competition as mediated by length growth rate or production (Clymo & Reddaway 1971, Rydin & McDonald 1985, Andrus 1986, Rydin 1986). The rationale behind this view and its implications is explained in detail and elaborated further by Økland (1990b). The reasons for the zonation of lichens and hepatics, and the complex interrelationships of species along the gradient in depth to the water table, are also discussed further by Økland (1990b).

The importance of variable intensity of destabilizing factors along the gradient in depth to the water table for relations between taxonomic groups and small-scale successions in the bottom layer is also discussed by Økland (1990b).

Relationship of the subseries to depth to the water table

The observed differences between subseries with respect to median depth to the water table are consistent with the view of Malmer (1962a) that this differentiation is not due to differences in water table conditions. On the contrary, these differences may be explained by invoking successional relationships between site-types (Malmer 1962a). The areal importance of the subseries, as indicated by the classification into vegetation complexes, shows strong correlation with the broad-scale variation in water supply. I will consider these aspects in turn, starting with the differentiation of subseries.

The carpet series. In this study, no consistent difference in depth to the water table was observed between the subseries. This contrasts with the observations of Malmer (1962a) on Åkhultmyra where mud-bottoms tend to occur at lower relative levels than carpets, and the suggestion of Dierssen (1982) that carpets dominated by hepatics experience more fluctuating water tables and more severe summer drought than *Sphagnum*-dominated carpets. The complex mechanisms involved in development of mud-bottoms from carpets are discussed by Økland (1989).

The lawn series. The RL1 and RLu subseries occur at slightly lower mean median depths to the water table, compared to the PL1 and PLu subseries. This suggests that Malmer's (1962a) statement that these vegetation types do not differ with respect to depth to the water table is in need of amplification. According to Malmer (1962a), cf. also p. 156, the RL1 subseries is strongly exposed to ice pressure and erosion due to the firm substrate and the occurrence in sites with higher range of water table fluctuations. This study does not show any such differences between the subseries unrelated to zone (cf. p. 73), and indicates that the fine-scale differentiation of lawns into subseries is primarily a consequence of biological interactions of species, as suggested by Malmer (1962a). The occurrence of relicts of lower series in the P subseries, and of higher series in the R subseries, suggests that the species, at least the vascular plants, have more restrictive demands for establishment than for maintenance. The biological aspects of differentiation into subseries are further discussed by Økland (1990b).

The hummock series. The differences between the PHu and RHu, as well as the PH1 and RH1 subseries with respect to median depth to the water table are small relative to the variation within subseries. This accords well with the observations in this, as well as other studies (Osvald 1923, Sjörs 1948, Foster 1984, Foster & Glaser 1986) that reciprocal transitions between the hummock subseries occur frequently.

Relationship of the vegetation complexes to depth to the water table

The *marginal complex* is restricted to water divides and sites sheltered from influence of soligenous water, and occupies the parts of the E1 zones with the highest range of water tables. High distance to the water table over large areas is necessary for the development of the marginal complex (cf. Osvald 1923, Malmer 1962a).

The *fen regeneration complex* and the *Rhynchospora-rich regeneration complex* show characteristic, reciprocal distributions in the special area (Fig. 69, pp. 136). The differentiation of the complexes can only be resolved by considering the differences in vegetation and ecological conditions between them. Vegetational differences include: (1) The dominance of PL site-types in the fen regeneration complex and RL site-types in the *Rhynchospora-rich* regeneration complex. (2) The lower importance of hummocks, in particular the RH subseries, in the fen regeneration complex. (3) The strongly lowered importance of hepatics in the R subseries towards the E2 zone, combined with increased relative importance of *Sphagnum tenellum* in the RL site-types (Tabs 24 and 31). (4) The strong decrease in areal importance of bare peat spots in the RL site-types towards the E2 zone. The most striking difference in ecological conditions relates to water supply and water flow-rates (cf. p. 149). This is shown in the areal importance of carpets; much higher in the fen soaks and areas with regeneration complex (compare Figs 5 and 69). The distribution of *Sphagnum compactum* and *S. molle* on one hand, and *Carex limosa*, *Scheuchzeria palustris*, *Sphagnum lindbergii*, and *S. majus* on the other, show distinct affinities to the *Rhynchospora-rich* regeneration complex and the fen regeneration complex parts of the E2 zone, respectively.

It has previously been shown that high water flow-rates are associated with a better nutrient supply (p. 149) and a less variable range of the water table, at least along the western fen soak (Fig. 64). This lends some support to the view of Fransson (1972) that mire surfaces with an abundance of *Rhynchospora alba* and *Sphagnum tenellum* (the E1RL1 and E2RL1 site-types) depend on periodically strong variability of the water supply; abundant supply in spring (and autumn), and desiccation, at least in some summers. The common opinion that *Sphagnum compactum* and *S. molle* depend on strongly fluctuating water tables (Waldheim 1944, Ruuhijärvi 1960, Fransson 1972) further accords very well with the almost total restriction of these species to those parts of the E2 zone with the *Rhynchospora-rich* regeneration complex (p. 33). The fluctuation of depth to the water table in the RL and PL subseries does not, at a first glance, lend support to this explanation (pp. 73, 158), but when taking broad-scale variation into account, the agreement is better. It has been shown that the tendencies for stronger water table fluctuations, stronger response to a given amount of precipitation, and a more firm peat, are more pronounced in the E1 than in the E2 zone (p. 73). Thus it is most likely that the differentiation of the fen regeneration complex is due to differences in water supply. The vegetational differences may be brought about by the differential frequency of catastrophic events in different water regimes, as discussed on pp. 156-157. Support for this comes from the fact that the occurrence of a regeneration complex in true ombrogenous sites in other mires (Osvald 1923, Du Rietz & Nannfeldt 1925, Malmer 1962a) appears to be closely connected with wet parts of large bogs, often the distal areas with ample water supply and small water table fluctuations (cf. Osvald 1923, Damman 1986). Thus the clear-cut separation of the two complex types along the nutrient gradient is a result of the coincidence of the water flow-rate and nutrient gradients in the special area. Such a coincidence is expected in areas where strong soligenous water supply restricts bog development (Økland 1989).

The *erosion complex*. The erosion complex apparently has developed in an area with abundance of carpets (and pools?). This is suggested from the low abundance of hummocks

in, and south of, the erosion area (Fig. 5), and the apparent expansion of the erosion area into the very wet areas to the southeast. The pathway leading to erosion is described by Økland (1989) as "erosion by oversaturation".

Successional relationships in the two regeneration complexes

The observed transitions within hummocks of the *Rhynchospora*-rich regeneration complex are consistent with the short-cycle regeneration of hummocks (Økland 1989), well documented by stratigraphic evidence (Tolonen 1971, 1980). Apparently this takes place all over the area where E1RH site-types are quantitatively important. Furthermore, the relative sparsity of observed hummock-hollow transitions in the R subseries outside small, isolated hummocks or along margins of larger hummocks (cf. Malmer 1962a), lends support to rejection of the theory of cyclic regeneration (von Post & Sernander 1910, Osvald 1923) as a general explanation for bog regeneration (Malmer 1962a, Backéus 1972, Barber 1981, Wallén *et al.* 1988, Økland 1989). This is also supported by the apparent stability of mudbottoms. The biological mechanisms involved in short-cycle regeneration of hummocks are discussed by Økland (1989, 1990b), pointing to the importance of hepatics for vegetation dynamics. The suggestion of Osvald (1923) that the *Rhynchospora*-rich regeneration complex develops from the stagnation complex apparently does not hold true for the special area. As the RL subseries overlies firm peat with an abundance of intervoven roots, regressive development from hummocks is more likely than progressive development from mud-bottoms. This is supported by observations in the field (pp. 103, 112), and accords with the theory of regressive development of bog patterns (Aartolahti 1965, Økland 1989). In contrast to the general opinion that *Sphagnum tenellum* represents a regressive stage in mire development, Fransson (1972) considers that bogs dominated by the *Rhynchospora*-rich regeneration complex are strongly regenerative. This should be tested by growth measurements.

The fen regeneration complex in the E2 zone of the special area differs from that described from bogs by Osvald (1923) and Malmer (1962a) by the overriding importance of the P subseries. The small area covered by RH and RL subseries is an indication that bog growth takes place by a process mainly involving P vegetation, and that differential growth rates at different relative levels alone controls development. Ample water supply and high water flow-rates increase oxygenation of the acrotelm, enhance the nutrient supply (cf. p. 149) and promote production (Malmer 1962b, Sonesson *et al.* 1980, Clymo & Hayward 1982). However, the relative decomposition rates are probably increased even more, as these productive sites rest on more shallow peat (Damman 1979, Økland 1989). High decomposition rates, particularly at sites with high median depth to the water table may account for the frequent levelling out of the surface in the fen regeneration complex in the special area. In contrast, the hydrological conditions of the *Rhynchospora*-rich regeneration complex must result in much lower decomposition rates, strongly disfavours species adapted to high growth rates under permanently good water supply such as *Sphagnum magellanicum* and *S. papillosum* (cf. Pedersen 1975, Gaberšček & Martinčič 1988, Wallén *et al.* 1988) while favouring *S. tenellum*. The strongly contrasting quantitative importance of hepatics in the two complex types suggests that this group plays an important role in the dynamics (cf. also Økland 1989). This will be further discussed by the treatment of regional variation in vegetation (Økland 1990c). The biological mechanisms involved are further discussed by Økland (1990b).

The transitions involved in successions in mires occur on a very fine scale (Tolonen 1971, Schmeidl 1977, Barber 1981). The only way to establish the extent and rate of

successional transitions is by long-term studies in permanent plots (Du Rietz 1932, Schmeidl 1977, Rydin 1986).

THE POSITION OF NORTHERN KISSELBERGMOSEN RELATIVE TO REGIONAL VARIATION

The position of the vegetation of the special area will be treated briefly by comparison with other studies. Økland (1990c) treats regional variation in SE. Fennoscandian mire vegetation in detail.

Fen plants

The group of species characterizing the E2 zone in the special area contains species frequently entering bogs in SW. Sweden (*Erica tetralix*, *Sphagnum papillosum*) or in the north (*Carex limosa*, *Scheuchzeria palustris*, *Sphagnum lindbergii*, *S. majus*, and *Drepanocladus fluitans*), cf. Sjörs (1948), Olausson (1957), Malmer (1962a), and Fransson (1972). The species-poor flora of the bog areas (actually a southeastern trait, cf. Økland 1989), is caused by the small catchment of the bog segments, the sparsity of the carpet level, and the corresponding absence of the northern limnominerobiontic fen plants (cf. Müller 1976). The presence of *Odontoschisma sphagni* in bogs is a southwestern trait.

Vegetation

Carpets. The species-poor bog carpets accord well with the southern to southeastern types (cf. Malmer 1962a). The rich water supply and partly high water flow rates of the E2 and E3 zones give these site-types a prominent northern impression.

Lawns. The vegetation of bog lawns, dominated by the E1RL site-types (and characterized by the *Rhynchospora*-rich regeneration complex) has a humid, but species-poor tendency. Vegetation of this kind, with low importance of the P subseries and high importance of *Sphagnum tenellum*, appears to have an optimum in the humid part of the Southern Boreal zone, as judged from records in Fransson (1972). The E2 and partly also E3 zones show a high importance of suboceanic, partly also southwestern species; *Erica tetralix*, *Sphagnum compactum*, *S. molle*, and presence of *Odontoschisma sphagni*. Northern lichens are also prominent in the lawns. The importance of water table fluctuations for the suboceanic species composition of lawns is discussed by Waldheim (1944) and Malmer (1962a).

Hummocks. The high importance of hepatics and lichens is a feature of humid areas (Økland 1989). The vegetation of the E1PH subseries comes close to the Rubello-fuscion regional subformation (Du Rietz 1949) or the Skagershultmosse type (Waldheim & Weimarck 1943), characterizing hummocks in an intermediate position along a SW - NE regional gradient. The dominance of *Sphagnum fuscum* in the Hu series, and the shared dominance between *S. fuscum* and *S. rubellum* as a prominent species in the E2 and E3 zones is a southwestern trait.

Mire margin hummocks. The extremely sparse occurrence of *Betula nana* and *Ledum palustre* indicates affinity to the south-western regional subformation, "The *Ledum*-free

Parvifolion" of Du Rietz (1949). The fact that these species do occur indicate an intermediate position relative to regional variation in SE Fennoscandia. A northeastern feature of the M2 zone is the prominence of *Carex globularis*.

Assessment. The vegetation of the special area shows a high importance of features characteristic of mires in humid, southern boreal areas within the range of western, suboceanic species like *Erica tetralix*. The phytogeographic affinity of the mire flora and its local distribution is, however, also a result of the local hydrological conditions. A full understanding of the relationships between local and regional variation is not possible except by an integrated approach involving the effect of climatic factors on mire hydrology and species performance on both geographic scales.

CONCLUSION

This study shows that on the local scale of one mire complex, the variation in vegetation and ecological conditions can be conceived as four local complex-gradients. Furthermore, it is shown that these four gradients operate on different scales, and that the entangling of the complex pattern of variation benefits from allowing for more spatial scales to be considered within one sampling design. In this respect, it should be emphasized that the broad-scale gradients; nutrient availability and mire margin-mire expanse, are easily recognizable also in the small sample plots, but that the fine-scale gradients; depth to water table and peat productivity, are impossible to recognize in larger plots. This points to the importance of proper choice of scale for the resolving power of any ecological analysis (Birks 1986, Økland 1989). Furthermore, the poor knowledge of dynamic relationships of mire vegetation, and the obscure basis of the peat productivity gradient strongly suggest that much important information may be achieved by including smaller scales than used here (0.25 m²). Dynamics in vegetation primarily occurs at very small scales (cf. Kimmel 1962, Rydin 1986, van Tooren *et al.* 1987).

Several of the observations described in this study are explicable by the results of comparative physiological studies. Additional phenomena, so far poorly understood, will probably only be possible to approach the experimental way.

The four gradients recognized in this study are selected on the basis of accumulated knowledge, from more than fifty years of intensive descriptive investigations. A more detailed and less biased insight into the relationships between these gradients, and between mire vegetation and ecological conditions in general, must take advantage of the potential provided by robust numerical techniques (Gauch 1982, Minchin 1987, ter Braak 1988, Peet *et al.* 1988). A re-evaluation and amplification of the results in this paper by the ordination method DCA and the techniques of canonical correspondence analysis (cf. ter Braak 1987, ter Braak & Prentice 1988) will be presented in two forthcoming papers (Økland 1990a, 1990b).

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