Regional variation in SE Fennoscandian mire vegetation

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The distribution in bogs is outlined for all species occurring in bogs only in part of their SE Fennoscandian area. The patterns displayed by these species are diverse, and different explanations are applicable to different patterns. Regional variation in SE Fennoscandian bog and extremely poor fen vegetation is described, based on all available published material. Carpets, lawns, and hummocks are considered separately. Four regional vegetational gradients are identified: (1) W-E, (2) S-N, (3) SW-NE, and (4) NW-SE. These are related to different underlying climatic gradients: (1) humidity (precipitation surplus), (2) temperature, (3) and (4) combinations of humidity and temperature. Effects of climatic gradients on the ground water regime are outlined. The decisive factor for the SW-NE gradient is probably frequency of ground water table fluctuations, the NW-SE gradient is likely to be caused by differences in water supply and ground water flow rates. The main gradient of carpets is S-N (SE-NW), of lawns SW-NE (W-E), and of hummocks partly SW-NE, partly S-N. The effects of the underlying ecological factors on the different plant groups are discussed in order to explain the patterns of regional variation in vegetation.

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Introduction

Regional aspects of Fennoscandian mire vegetation have been approached by relating local types to types described in other works (Sjörs 1948; Malmer 1962a; Svensson 1965), by mapping the distribution of floristically defined vegetation types (Ruuhiäärvi 1960; Erola 1962; Fransson 1972), and by mapping individual species distributions (Økland 1989a). Even though the main gradients in Fennoscandian mires, both on a local and on a regional scale, are well-known (cf. Sjörs 1948, 1950, 1983; Malmer 1962a; Fransson 1972; Økland & Bendiksen 1985; Økland 1989a,b, 1990a), an approach to regional variation by means of variation along gradients has not been attempted. No survey of mire vegetation exists for more than a part of one of the Fennoscandian countries, except for the work by Økland (1989a) treating species distribution and hydromorphology of mires.

The regional fen plant problem, i.e. the problem that many species are confined to fens in part of their area (cf. Aletsee 1967) is not sufficiently understood. This applies to conceptual as well as descriptive aspects of the problem, as discussed by Malmer (1962a), Aletsee (1967), Fransson (1972), Müller (1973, 1976), and Moen (1983). The aims of this study are to provide a survey of regional variation in SE Fennoscandian mire vegetation by a gradient approach, and to discuss the regional fen plant problem on the basis of this approach.

Materials, methods, and the study area

Materials and delimitation of the study area.

All available published data from SE Fennoscandia satisfying the various criteria given below, were included. The study area shown in Fig. 1 comprised SE Norway, S Sweden, and Finland from the boreonemoral to the middle boreal zone. The upper limit of the middle boreal zone was defined in accordance with Økland & Bendiksen (1985) to correspond to the upper (northern)
Fen plants and vegetation

Fen plants

A fen plant (Sjörs 1947, 1948; cf. also Ackenheil 1944; Du Rietz 1949) is a species that, in a given region or at a given site, is restricted to areas regularly influenced by minerogenous water. Because of differing opinions on the classification of species as fen plants, even within restricted areas, the authors' opinions on bog (ombrotrophic) occurrences of species in their respective investigation areas, are given. Uncertainty, by the original author, or by myself, is specified in each case.

Vegetation: terminology

As the basis for a reference framework for local complex gradients (Økland & Bendiksen 1985) in vegetation and ecological conditions (terminology of gradients in accordance with Whittaker (1967)), the four-gradient representation of Økland (1989b) was used. The num-

Fig. 1. Position of study areas of investigations providing the material used for description of regional variation in mire vegetation and distribution of fen plants. Numbers refer to Tab. 1.
Tab. 1. Investigations used for description of SE Fennoscandian distribution of fen plants and bog and extremely poor fen vegetation (*). Numbers refer to Fig. 1.

| Nr. | Veg. an. | Reference | Geographic position |
|-----|----------|-----------|---------------------|
| 1   |          | Waldheim 1939, Waldheim & Weimarck 1943 | S: Skåne NW |
| 2   |          | Olausson 1957 | S: Halland: Roshultsmyren |
| 3   |          | Osvald 1923 | S: Småland + Västergötland: Komosse |
| 4   |          | Svensson 1965 | S: Småland: Store Mosse |
| 5   |          | Witting 1947, 1948, Du Rietz 1950a | S: Västergötland: Blångsmossen |
| 6   |          | Waldheim 1939, Waldheim & Weimarck 1943 | S: Skåne NE |
| 7   |          | Malmer 1962a | S: Småland: Åkultmyren |
| 8   |          | Økland 1989a, 1989b | N: Östfold: N. Kissenbergmossen |
| 9   |          | Fransson 1972 | S: Värmland SW |
| 10  |          | Fransson 1972 | N: Hedmark: Rønnásmyra |
| 11  |          | Korso 1980 | S: Närke + Värmland + Västmanland: Örebro län |
| 12  |          | Waldheim 1944, Backéus 1984 | S: Småland: Breesfallsmossen |
| 13  |          | Du Rietz 1950b | S: Dalarna: Skattlösbergs Stormosse |
| 14  |          | Sjörs 1948, Backéus 1985 | S: Jämtland: Långan |
| 15  |          | Sjörs 1947 | S: Jämtland: Rörvattnet |
| 16  |          | Fransson 1963 | S: Jämtland: Älgfloarna |
| 17  |          | Björkbäck 1965 | S: Västmanland: Gavelmossen + Bredmossen |
| 18  |          | Sjörs 1948 | S: Gästrikland: Österfarnebo; Karinmossen |
| 19  |          | Sjörs 1948 | S: Gästrikland: Hedesunda; Jordbärsmyren |
| 20  |          | Sjörs 1948 | S: Uppland: Ryggmossen |
| 21  |          | Du Rietz & Nannfeldt 1925, Du Rietz 1950c | S: Uppland: Bälinge; Stormosens |
| 22  |          | Eriksson 1912 | S: Angermanland + Västerbotten (SW) + Åsele Lappmark (SE) + Lycksele Lappmark (SE) |
| 23  |          | Melin 1917 | S: Västerbotten: Degero Stormyr |
| 24  |          | Malmström 1923 | a) SF: Schärensfinnland |
| 25  |          | Eurola 1962 | b) SF: Küstengebiet v. Südfinnland |
| 26  |          | Ruuhijärvi 1960 | c) SF: Satakunta + Süd-Pohjanmaa |
|     |          |             | d) SF: Seenfinnland |

The following gradients (with segmentation relevant to this study indicated in brackets) were considered (cf. Økland 1989b):

1. **The poor – rich gradient** (divided into zonations, of which two were included; ombrotrophic (1), and extremely poor minerotrophic, slightly influenced by mineral soil water (2)).

2. **The gradient in depth to the water table** (divided into five series; carpet (C), lower lawn (LI), upper lawn (Lu), lower hummock (HI), and upper hummock (Hu); the two lawn series and the two hummock series were often considered collectively).

3. **The coenoclone associated with peat-producing ability of the vegetation** (divided into two subseries; strongly peat-producing or progressive (P) and slightly peat-producing or regressive (R)).

The number of gradients was reduced to three as variation along the mire expanse – mire margin gradient was avoided. A reticulate classification was performed by dividing each gradient into a specified number of segments. Every combination of such segments was considered a site-type.

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3. **The coenoclone associated with peat-producing ability of the vegetation** (divided into two subseries; strongly peat-producing or progressive (P) and slightly peat-producing or regressive (R)). Positions along the mire expanse – mire margin gradient have been referred to as E (mire expanse) and M (mire margin), when necessary. Site types were denoted by combinations of gradient and segment designations.

This local reference framework was used as a basis for the recognition of ecologically corresponding vegetation types in different regions (Økland & Bendiksen 1985), see Økland (1989b: Tabs 71-79).

**Vegetation: regional variation**

The criteria for inclusion of published material in the regional vegetation survey were: (1) Vegetation types including richer vegetation than corresponding to zonation 2 (extremely poor minerotrophic, slightly influenced by minerogenous water) were avoided. (2) The vegetation type could be classified as carpet, lawn or hummock. (3) The vegetation type was represented by five or more sample plots. (4) The sample plots were referable to a restricted geographic region. (5) Sample plots should ideally not be larger than 1 m². (6) Thorough treatment of the bottom layer (Finnish material mostly not satisfying this criterion).

Each vegetation type satisfying these criteria made up...
Tab. 2. Distribution of regional fen plants in SE Fennoscandia, based on published data (cf. Tab. 1). ? – doubtful ombrotrophy expressed by the original author. (?) – doubtful ombrotrophy expressed by the present author. s – exceptionally occurring in ombrotrophic sites. r – relict. Arrows are used to indicate direction of regionally increasing frequency of ombrotrophic occurrence. + – ombrotrophic occurrence. – – minerotrophic occurrence. Column 9a refers to Økland 1989b, 9b refers to Økland 1989a, column 15 includes data from Sjörs 1950.

| Mire No. | 1  | 2  | 3  | 4  | 5  | 6  | 7  | 8   | 9a | 9b | 10 | 11 | 12 | 13 | 14 | 15  | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 |
|----------|----|----|----|----|----|----|----|-----|----|----|----|----|----|----|----|-----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| Erica tetralix     | ++++ |    |    |    |    |    |    |      |    |    |    |    |    |    |    |      |    |    |    |    |    |    |    |    |    |    |    |    |
| Myrica gale      | − | s | ? | − | (s) | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| Drosera anglica   | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + |
| D. intermedia    | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + |
| Narthecium ossifragum | − | r | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| Carex limosa   | − | ? | − | + | + | + | + | + | + | + | + | s | − | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + |
| C. pauciflora | − | r | ? | − | r | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| Erichthanthum angustifolium | − | s | r | s | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| Rhynchospora alba | + | + | + | + | + | + | + | + | + | + | s | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| Scheuchzeria palustris | ? | − | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + |
| Scirpus cespitosus | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + |
| Drepanocladus fluitans | ? | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| Sphagnum compactum | (+) (? | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| S. imbricatum      | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + |
| S. lindbergii     | − | − | − | − | s | + | s | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + |
| S. majus          | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| S. molle          | (+) | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − | − |
| S. papillosum     | − | s | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + |

one column of a vegetation table. One table was made for each of carpets, lawns and hummocks.

All species except the occasional ones (subjectively judged) were included. For each species, constancy class 1-5 (Dahl 1957:53) and characteristic degree of cover with respect to the Hult-Sernander-Du Rietz cover-abundance scale (Du Rietz 1921) (calculated by conversion of cover values into mid-points of cover classes according to Persson (1961), or by conversion of mean percentage cover into this scale) were calculated.

Vegetation complexes

A qualitative account of the distribution of vegetation complexes of bogs (according to Osvald (1923), cf. Økland (1989b)), was given.

Climate

For the areas investigated in the included published accounts, two climatic parameters were estimated; Tamm's index of humidity, H (Tamm 1954, 1959) and effective temperature sum (ETS) with basal temperature 5°C (Laaksonen 1979b), cf. Fig. 2. Tamm's H was calculated from the formula given by Tamm (1959). For Sweden, Tamm's H was extracted from the map in Tamm (1959). The considerable local variation in precipitation (mostly not reflected in the sources available) gives rise to a high statistical error.
Fig. 3. Approximate distributional limits of thirteen species in bogs in SE Fennoscandia based on published material. Distributional limits (towards southeast) in Finland for *Sphagnum lindbergii* and *S. majus* are not drawn in.

in Tamm's H. Deviations of ± 100 mm may be expected in single estimates, somewhat less in estimates along continuous borderlines. In this context, the effect of basing estimates upon different normal periods (1931–60 for Norway, 1921–50 for Sweden and Finland), is negligible.

ETS was read from a map of ETS values reduced to sea level in Laaksonen (1979b), and corrected for altitude. Monthly mean temperatures were taken from maps in Laaksonen (1979a), corrected for altitude in accordance with Laaksonen (1976).

**Nomenclature**

The nomenclature of vascular plants follows Flora Europaea (cf. Moore 1982). Mosses and *Sphagnum* follow Corley et al. (1981) except that *Pohlia sphagnicola* (B., S. & G.) Broth. is reduced to synonymy with *P. nutans* (Hedw.) Lindb. (cf. Nyholm 1958). *Sphagnum imbricatum* refers to *Sphagnum imbricatum* Hornsch. ex Russ. ssp. *austrinii* (Sull.) Flatb. (cf. Flatberg 1984). Hepatics follow Grolle (1976), except that the spelling *Calypogeja* is used, in accordance with Stotler (1982). Macro-
lichens follow Krog et al. (1969), Icmadophila ericetorum (L.) Zahlbr. and Ochrolechia frigida (Sw.) Lyne follow Poelt (1969).

Results

Fen plants

The distribution of all species occurring in truly ombrotrophic sites only in part of their SE Fennoscandian area, is shown in Tab. 2 (cf. Figs 1, 2). These species fall into four groups.

(1) Species not growing in bogs except possibly as relics. Three of the species, Narthecium ossifragum, Carex pauciflora, and Sphagnum molle, belong to this group. A possible relict occurrence of Narthecium at Komosse is mentioned by Osvald (1923), but Malmer (1962a) expresses doubt regarding the ombrotrophy of this site. The absence of this species from ombrotrophic parts of Roshultmyren (Olausson 1957) supports the view that Narthecium is a fen plant all over SE Fennoscandia where it occurs. Contrasting opinions have been expressed on the relationship of Carex pauciflora to the mineral soil water limit (e.g. Eurola 1962; Dierssen 1982). All available evidence (cf. Sjörs 1948, 1950; Malmer 1962a; Svensson 1965; Backéus 1985; Ökland 1989b), points to Carex pauciflora as the most frequently occurring and the most tolerant relict among the fen plants, but establishment of the species in ombrotrophic sites has not been demonstrated. Waldheim (1939) claims Sphagnum molle to occur in bogs in SW Götaland, and Flatberg & Moen (1972) mention possible bog sites in Norway. None of these records have been confirmed by hydrological data.

(2) Species occurring in ombrotrophic sites in the south-western part of their area. Nine species show this pattern (Fig. 3). The most restricted distribution in bogs is shown by Eriophorum angustifolium, occurring in a few bogs in south-westernmost Sweden, mostly as sterile relics (Olausson 1957; Svensson 1965). Myrica gale even occurs on bogs in W Dalslan (Sjörs 1953), and is not infrequent in bogs in SW Götaland (Olausson 1957). Erica tetralix (and the other species of this group) is frequent to abundant on the bog expanse in SW Götaland (Osvald 1923; Olausson 1957). The northern limit of Erica tetralix in bogs is in Vestfjella, inner Østfold (Økland 1989a). Drosera intermedia shows a wider distribution in bogs towards SE Sweden, but is not recorded in bogs north of Store Mosse (Svensson 1965). Sphagnum imbricatum ssp. austini has a distribution not very different from Erica tetralix in bogs (cf. Flatberg 1986). A much wider distribution in bogs is shown by Sphagnum papillosum. It appears to have a southern or south-western distribution of ombrotrophic occurrences, extending northwards to SW. Värmland (Fransson 1972), a few sites in Bergslagen (Sjörs 1948), and is absent from SE Sweden (cf. Du Rietz 1950c), but has a few occurrences in wet sites in some south-western Finnish bogs (Aartolahti 1965, Tolonen & Hosiaislouma 1978). The remaining three species show some differences in their distribution in bogs. Scirpus cespitosus is absent from bogs in SE Värmland (Fransson 1972), and, like Rhynchospora alba and Drosera anglica, from SE and E Sweden. The northward extension of the three species in bogs in Sweden is not known exactly, but Scirpus cespitosus apparently shows no limit in its bog occurrences (cf. Sjörs 1947). Rhynchospora alba may be restricted to fens in the middle boreal zone (Eurola & Vorren 1980; Sjörs 1983; Moen 1987). All species show an increase towards the southwest of Finland (Eurola 1962). Rhynchospora alba is the most, and Drosera anglica the least restricted of the three species in Finland (Eurola 1962).

(3) Species occurring in ombrotrophic sites in the northern part of their area. Five species, all having an optimum in carpets, are classified to this group: Carex limosa, Scheuchzeria palustris, Drepanocladus fluitans, Sphagnum lindbergii, and S. majus. The three first mentioned species occur in bogs all over S Finland (Eurola 1962; Tolonen & Hosiaislouma 1978) while the two Sphagnum species have a southern and a southeastern limit, respectively (Eurola 1962). In Sweden and Norway, all species apparently occur in bogs throughout the southern boreal zone (cf. Tab. 2). From data of Fransson (1972) and Backéus (1984), Sphagnum lindbergii appears more restricted than S. majus (reaching Blångmossen; Witting 1947), again more restricted than Carex limosa and Scheuchzeria palustris, occurring on Komosse, Blångmossen, Brealfallsmossen and with a wider distribution, in SW Värmland (Osvald 1923; Du Rietz 1950a,b; Fransson 1972). Scheuchzeria palustris extends further south (Du Rietz & Nannfeldt 1925; Sjörs 1948). According to Malmer (1962a), also Drepanocladus fluitans occurs on SW Swedish bogs.

(4) Deviant species: Sphagnum compactum. No reliable records of this species from bogs in SW and S Sweden exist (claimed to occur in bogs by Waldheim (1939) and Olausson (1957)), nor from SW Värmland (Fransson 1972; Sjörs 1948). It occurs in bogs in N Jämtland (Sjörs 1947), and is frequent in bogs in N Finland (Ruuhijärvi 1960; Tolonen & Hosiaislouma 1978), with reduced frequency southwards (Eurola 1962).

Vegetation

Carpets

Tabs 3 and 4 show the regional variation of carpet vegetation.

Dominance relationships. The field layer is mostly sparse, but is occasionally more dense towards the east (mostly transitional types to lawns). In the P subseries, Sphagnum cuspidatum dominates in bogs in the BN zone, northwards gradually giving way to Sphagnum majus. In the MB zone Sphagnum cuspidatum hardly
occurs as a dominant (Ruuhijärvi 1960; Vorren 1979a,c). In sites slightly influenced by mineral soil water, S. majus occurs as a dominant farther south, although rarely in the less humid, southeastern parts of S Sweden (Malmer 1962a) and S Finland (Eurola 1962). In these areas, carpets become rare, and transitions to lawns, dominated by S. balticum, take over. Note the shared dominance of S. cuspidatum and S. balticum in the “Sphagnum cuspidatum-Weissmoore”, of Eurola (1962; columns 21 and 22 in Tab. 3). From the MB zone, Sphagnum lindbergii is a frequent dominant in carpets (cf. Sjörs 1949; Ruuhijärvi 1960; Sonesson 1970a). Data from Finland excluded (incomplete with respect to hepatics), the amount of hepatics in the R subseries (mud-bottoms) appears to increase towards the west (and south?).

Floristic variation. A south-western distribution in the carpet series of bogs and extremely poor fens in the area studied is shown by Drosera intermedia, Rhynchospora fusca, and Sphagnum auriculatum. These are southern species in Fennoscandia (e.g. Økland 1989a), but in southeastern parts of Sweden and towards their northern limits they are restricted to richer sites. A similar distribution is shown by Rhynchospora alba, but this species is more southern due to less strong demands in the southeast. The southern distribution of Sphagnum cuspidatum is previously noted.

A prominent northern element includes the five species Carex limosa, Scheuchzeria palustris, Drepanocladus fluitans, Sphagnum lindbergii, and S. majus, common or dominant both in fens and bogs N of the limes norrländicus and in Finland (p. 00). Further south, they are restricted to large, wet hollows in N Götaland (Sjörs 1953; Malmer 1965) and to fens (Svensson 1965). In S Småland, these species do not reach the mineral soil water limit (Malmer 1962a). A northeastern element is represented by Eriophorum medium and E. russeolum (N Finland). Sphagnum annulatum occurs in carpets farther west, but is then probably more demanding.

Relative importance of the subseries. In Sweden and adjacent parts of Norway, the P subseries reaches the greatest areal importance in the Bergslagen area (Sjörs 1948; Fransson 1972), that is in the SB zone. From there, Sphagnum-dominated carpets decrease strongly northwards and westwards, and are gradually replaced by mud-bottoms (Økland 1989a). From the SB-MB
Tab. 4. Material used for the survey of regional variation of the vegetation of the carpet series. Column Nos refer to Tab. 3. Reference refers to Tab. 1.

| Column No. | Reference [Author (No. of Tab. 1): Tab. No.: Sample plot Nos] | Type name | Site-type affiliation | Sample size |
|------------|------------------------------------------------------------|----------|----------------------|-------------|
| 1          | Svensson 1965 (4): Tab. 2 | Eriophorum vaginatum-Sphagnum cuspidatum-Cladopodiella fluitans-ass. | E1RC | 25 0.25 |
| 2          | Tab. 2 | Scheuchzeria palustris-Sphagnum auriculatum-ass. | E2(-3)RC | 16 0.25 |
| 3          | Tab. 3 | Eriophorum vaginatum-Sphagnum cuspidatum-ass. | E1PC | 25 0.25 |
| 4          | Tab. 3 | Scheuchzeria palustris-Sphagnum dusenii-ass. | E2(-3)PC | 12 0.25 |
| 5          | Malmer 1962a (8): Tab. A4 | Eriophorum vaginatum-Sphagnum cuspidatum-ass. | E1RC | 30 0.25 |
| 6          | Tab. A4 | as above, Drosera intermedia var. | E1RC | 11 0.25 |
| 7          | Tab. A3 | Rhynchospora fusca-Sphagnum auriculatum small ass. | E2RC | 24 0.25 |
| 8          | Tab. B3 | Eriophorum vaginatum-Sphagnum cuspidatum small ass. | E1PC | 31 0.25 |
| 9          | Økland 1989b (9): Tab. 9 | The E1PC site-type | E1PC | 22 0.25 |
| 10         | Tab. 10 | The E2PC site-type | E2PC | 37 0.25 |
| 11         | Tab. 12 | The E1RC site-type | E1RC | 42 0.25 |
| 12         | Tab. 13 | The E2RC site-type | E2RC | 36 0.25 |
| 13         | Fransson 1972 (10): Tab. 3: A–E, J | Cuspidacetum dusenietaosum p.p. + Övrig Cuspidacetum-vegetation | E1PC | 39 0.25 |
| 14         | Korsmo 1980 (11): Tab. 3 | Cuspidacetum zygodonietosum | E1PC | 10 0.25 |
| 15         | Tab. 3 | Cuspidacetum majusetosum | E1PC | 15 0.25 |
| 16         | Sjörs 1948 (14): Tab. D | Scheuchzeria-Rhynchospora alba-Carex limosa-Sphagnum cuspidatum-duseni-ass. | E1-2PC | 21 0.25 |
| 17         | Tab. E | Scheuchzeria-Rhynchospora alba-Carex limosa-lösbotten-höljeass. | E1-2RC | 35 0.25 |
| 18         | Backéus 1985 (14): Tab. 5A | Cuspidacetum cusenietaosum | E1PC | 10 0.25 |
| 19         | Eurola 1962 (25a): Tab. 25:1–4 | Sphagnum cuspidatum-Wm | E1PC | 4 1 |
| 20         | Tab. 24:2–8 | Sphagnum dusenietaosum-Wm. | E1(-3)PC | 7 1 |
| 21         | Tab. 25:5–23 | Sphagnum cuspidatum-Wm. | E1(-2)PC | 19 1 |
| 22         | Tab. 25:24–33 | Sphagnum cuspidatum-Wm. | E1PC | 10 1 |
| 23         | Ruuhijärvi 1960 (26c): Tab. 12 | Sphagnum dusenII-Rimpiv. | E1(-3)PC | 35 1 |
| 24         | (26c): Tab. 15: 1–16 | Oligotrope Rhynchospora alba-Rimpiv. | E2-3RC | 16 1 |
| 25         | (26d): Tab. 13 | Sphagnum-Rimpiv. | E2-3PC | 17 1 |

limit mud-bottoms are more common than *Sphagnum* carpets (Sjörs 1948, 1950, 1965). The strong increase of mud-bottoms towards the west is shown by Økland (1989a), as his “borderline 3”, closely coinciding with isolines for humidity. The great importance of mud-bottoms in SW Sweden is demonstrated by Osvald (1923, 1930). Towards the southeast the *Sphagnum* carpets are gradually replaced by lawns, while mud bottoms are lacking altogether (Sjörs 1948; Du Rietz 1950c). In the moderately humid parts of Skåne and Småland, both subseries occur (Malmer 1962a; Svensson 1965). In Finland, mud-bottoms (“Torfschlammm-Weissmoore" sensu Eurola 1962) increase in areal importance with increasing humidity to a maximum in Satakunta (Aario 1932, 1933; Eurola 1962). Furthermore, the importance of mud-bottoms increases northwards (Ruuhi járv 1960). In the less humid central Finland, even *Sphagnum*-dominated carpets disappear, as the mires are too dry because of high evapotranspiration and small size of mire complexes due to broken topography (Eurola 1962).

**Lawn**

Tabs 5 and 6 show the regional variation in lawn vegetation.

**Dominance relationships.** The field layer shows variable combinations of dominants. In the P subseries of the bottom layer, dominance by *Sphagnum papillosum* (in ombrotrophic sites) and *S. magellanicum* are distinctly south-western traits (Osvald 1923; Waldheim & Weimarck 1943; Du Rietz 1950a; Malmer 1962a; Sonesson 1967). In Bergslagen *Sphagnum magellanicum* is a subordinate element except in a few larger hollows (Sjörs 1948), and the species is extremely rare in the bog expanse vegetation of Ryggmossen (Du Rietz 1950c). In the superhumid south-western parts of Sweden, *Sphagnum papillosum* replaces *S. magellanicum* as the domi-
nant species even in bogs (Olausson 1957). The distribution of S. papillosum in extremely poor fens spans most of the studied area, except for a slightly southern tendency (cf. Ruuhijärvi 1960). Sphagnum rubellum has a less distinct southwestern distributional tendency as a dominant, even occurring as a dominant in the PLu subseries far into E Sweden (Sjörs 1948; Backéus 1984) and the least humid parts of Finland (Eurola 1962; cf. Tab. 5). Sphagnum balticum replaces S. magellanicum as the dominant in bogs and fens slightly influenced by mineral soil water (Tab. 5), and dominates totally in Finland, E Sweden (Du Rietz 1950b,c; Rydin 1986) and in N Sweden (Fransson 1963; Sonesson 1970a). Its tendency is distinctly northeastern.

In the R subseries, Sphagnum tenellum plays a prominent part in the southwestern parts, while S. compactum reaches dominance in the north (Ruuhijärvi 1960) and the west (Sonesson 1967; Fransson 1972). The importance of heathies in this subseries increases considerably towards the west, see Tab. 5.

Floristic variation. The series shows a prominent position for species with southwestern (to western) distribution in the area. Such species are Erica tetralix, Drosera intermedia, Narthecium ossifragum, Sphagnum molle, Odontoschisma sphagni, and Cornicularia aculeata. The most western species do not avoid high altitudes (cf. Økland 1989a). Calluna vulgaris and other hummock relicts (cf. Økland 1989b), as well as the southern species Drosera anglica and Rhynchospora alba, also show a south-western distributional tendency in lawns in the area (apparent from Tab. 5). These are typical examples of the more south-western distribution of southern species in lawns than in carpets. Correspondingly, some northern carpet species (notably Carex limosa, Schewchzeria palustris, Sphagnum annulatum and S. lindbergii) show a northeastern distribution in lawns (Tab. 5). Northeastern species are Eriophorum medium and E. russeolum. Northern species in lawns are Betula nana (Sjörs 1948; Fransson 1972), Vaccinium microcarpum, Pilidium ciliare (Sjörs 1947; Eurola & Vorren 1980), Cetraria delisei (Fransson 1972; Økland 1989a), and Cladonia subfurfurata (Hasselrot 1953; Økland 1989a). A strong tendency for hummock species like Chamaedaphne calyculata, Empetrum nigrum s.l., Ledum palustre, Vaccinium uliginosum, Sphagnum angustifolia, and S. fuscum, to enter lawns in the less humid eastern (northeastern) parts of Finland is apparent from Tab. 5.

Relative importance of the subseries. A southern or western tendency of the R subseries is often emphasized (e.g. Waldheim 1944; Malmer 1962a). Details of the distribution are as follows. The RLI subseries shows a strongly western distribution. Vegetation of this kind is described from N Finland (parts of the “Sphagnum compactum-Weissmoore” of Ruuhijärvi 1960). In the MB zone of N Sweden, the R subseries is dominant in the lower lawn series (cf. Sjörs 1947; Fransson 1963; Björkback 1965; Sonesson 1970a). In Bergslagen (the SB zone), vegetation of the RLI type is extremely rare (Sjörs 1947; Fransson 1972; Backéus 1985), but increases westwards to be the dominant vegetation type of smaller (or all) hollows in the humid upland areas around limes norrlandicus, close to the national border (Fransson 1972; Økland 1989b). Vegetation of this kind also occurs south of limes norrlandicus, but from the descriptions and area valuations of Olausson (1923), Olausson (1957), Malmer (1965), and Svensson (1965), it always appears to be a subordinate element in the superhumid south-western areas, despite the opposite opinion expressed by Waldheim (1944) and Fransson (1972). Considerably higher importance is noted in the less humid upland mire Åkultmyren (Malmer 1962a). Vegetation corresponding to the RLu subseries occurs all over Sweden up to the middle boreal zone (Fransson 1972), but with low importance in the least humid eastern areas (Du Rietz 1950c; Fransson 1972). In S Finland RLu vegetation (“Sphagnum tenellum-Weissmoore” of Eurola 1962) is restricted to the southwestern, humid parts of coastal S Finland (Eurola 1962), and in Estland Sphagnum tenellum increases northwesternwards with increasing humidity (Paasio 1939). Vegetation of the P subseries occurs all over the studied area, but plays a minor role in middle boreal bogs (Sjörs 1947, 1963), at least outside Finland (cf. Ruuhijärvi 1960). Higher importance of Sphagnum magellanicum and S. papillosum than S. tenellum even in bogs are noted for the southwestern parts of Sweden (Olausson 1923; Olausson 1957; Malmer 1962a; Svensson 1965). It appears that the P subseries gives way to the R subseries towards the west and north.

Hummocks

Tabs 7 and 8 show the regional variation in hummock vegetation.

Dominance relationships. The field layer shows considerable variation in dominance relationships of the dwarf shrubs. Erica tetralix and to a much lesser degree, Calluna vulgaris, have a southwestern distribution as dominants. Empetrum nigrum ssp. nigrum and ssp. hermaphroditum replace each other from south to north (Ruuhijärvi 1960, Eurola 1962). Betula nana may occur as a dominant in the SB and MB zones, while Rubus chamaemorus increases to dominance northeastwards; Chamaedaphne calyculata, Ledum palustre, and Vaccinium uliginosum eastwards.

In the bottom layer, the major dominants of the P subseries replace each other along a SW-NE gradient. In SW Sweden, Sphagnum magellanicum and S. rubellum share dominance in the PHI subseries, without any consistent geographical pattern of variation in bogs (Tab. 7). In the PHu subseries, Sphagnum rubellum, S. imbricatum, and S. fuscum may dominate. The latter shows a considerable northward increase (compare Waldheim & Weimarck 1943; Malmer 1962a; Olausson 1923; Svensson 1965). Sphagnum magellanicum is rare.
as a dominant in vegetation corresponding to the EIPHI site-type at N. Kisselbergmosen (Økland 1989b: Tab. 31), distinctly southwestern in SW Värmland (Fransson 1972) and Örebro län (Backéus 1984), and is absent further north (cf. Sjörs 1948; Korstro 1980) and east (Tab. 7). Sphagnum rubellum is the dominant species in the PH series, and is reduced to a subordinate species further north and east (Prándose 1989b: Tab. 31; Backéus 1972, 1984; Fransson 1972). In this zone, Sphagnum fuscum is the only dominant in the PH series. Within short distances, S. fuscum gains dominance in PH series, while S. rubellum is reduced to a subordinate species (Backéus 1984; cf. also Sjörs 1948; Du Rietz 1950b, c; Eurola 1962).

From Tab. 7, it appears that the importance of hepatics increases westwards, (material from Finland dis-
from most areas, but very few investigations of such
vegetation have been conducted. From the material of
Nord. Flora (Malmer 1962a).

In Finland, the maximum im-
portance of hepatics is reached in the southwestern areas
(Paasio 1933; Eurola 1962). Dominance relationships
among the lichen species cannot be deduced from the
available data.

Floristic variation. Racomitrium lanuginosum is a west-
ern species in hummocks, occurring in SW Sweden (Os-
vald 1923; Malmer 1962a), Dalsland (Fransson 1972),
Östfold (Moen 1970), and W Jämtland (Sjörs 1947,
Tab. 6. Material used for the survey of regional variation in the vegetation of the lawn series. Column Nos refer to Tab. 5.

| Column Reference [Author (No. of Tab. No. 1): Tab. No.: Sample plot Nos.] | Type name | Site-type affiliation | Sample No. | Sample size |
|---|---|---|---|---|
| 1 | Osvald 1923 (3): | 54. Calluna vulgaris-Sphagnum tenellum-ass. | E1RLu | 11 |
| 2 | | 140. Erica intermedia-Sphagnum magellanicum-ass. | E1(-2)PLu | 31 |
| 3 | | 147. Rhynchospora alba-Sphagnum tenellum-ass. | E1RLu | 5 |
| 4 | Svensson 1965 (4): | Eriophorum vaginatum-Sphagnum magellanicum-ass. | E1PLI (-u) | 26 |
| 5 | Malmer 1962a (8): | Narthecium ossifragum-Sphagnum magellanicum small ass., Drosera anglica var. | E2PLI | 11 |
| 6 | | as above, Trichophorum caespitosum var. | E2PLu | 20 |
| 7 | | Eriophorum vaginatum-Sphagnum magellanicum small ass., Drosera anglica var. | E1PLI | 25 |
| 8 | | as above, Trichophorum caespitosum var. | E1FLu | 38 |
| 9 | | Narthecium ossifragum-Sphagnum tenellum small ass., Drosera intermedia var. | E2RLI | 16 |
| 10 | | as above, Trichophorum caespitosum var. | E2RLu | 31 |
| 11 | | Eriophorum vaginatum-Sphagnum tenellum small ass., Drosera intermedia var. | E1RLu | 13 |
| 12 | Økland 1989b (9): | as above, Trichophorum caespitosum var. | E1RLu | 13 |
| 13 | | The E1PLI site-type | E1PLI | 24 |
| 14 | | The E2PLI site-type | E2PLI | 43 |
| 15 | | The E1RLI site-type | E1RLI | 100 |
| 16 | | The E2RLI site-type | E2RLI | 60 |
| 17 | | The E1PLu site-type | E1PLu | 26 |
| 18 | | The E2PLu site-type | E2PLu | 57 |
| 19 | | The E1RLu site-type | E1RLu | 64 |
| 20 | | The E2RLu site-type | E2RLu | 31 |
| 21 | Fransson 1972 (10): | Cuspidatetum dusenietosum, Sphagnum magellanicum-facies | E1PLI | 5 |
| 22 | | Cuspidatetum tenelletosum | E1RLI | 14 |
| 23 | | Rubello-tenelletosum magellanicetosum | E1PLu | 10 |
| 24 | | Rubello-tenelletosum tenelletosum | E1RLI | 25 |
| 25 | | Sphagnetum compacti | E2(-3)RL | 6 |
| 26 | Korsho 1980 (11): | Cuspidatetum tenelletosum | E1RLI | 20 |
| 27 | | Rubello-tenelletosum tenelletosum | E1RLu | 15 |
| 28 | | Rubello-tenelletosum + Sphagnetum compactum | E1FLu | 15 |
| 29 | | Rubello-tenelletosum + Sphagnetum compactum p.p. | E1PL | 10 |
| 30 | Sjörs 1948 (14): | Eriophorum vaginatum-Scirpus caespitosus-Sphagnum rubellum-balticum-cuspidalum-ass., as above | E1(-2)L | 23 |
| 31 | | Eriophorum vaginatum-Scirpus caespitosus-Sphagnum rubellum-balticum-cuspidalum-ass. | E1(-2)RL | 36 |
| 32 | | Scirpus caespitosus-Carex pauciflora-Sphagnum tenellum-papillosum-ass. | E2PL | 13 |
| 33 | | Cuspidatetum tenelletosum | E1-2RLI | 10 |
| 34 | | Scirpus caespitosus-Sphagnum compactum-tenelletosum-ass. | E2RL | 36 |
| 35 | Backéus 1985 (14): | Scirpus caespitosus-Sphagnum compactum-tenelletosum-ass. | E1RLu | 6 |
| 36 | | Scirpus-Carex pauciflora-Sphagnum compactum-tenelletosum-ass. | E2(-3)RLu | 7 |
| 37 | Fransson1963 (16): | Extremfattigkär fastmattor | E2RLu | 5 |
| 38 | | Exig. Sphagnum papillosum-Wm. | E2(-3)PL | 4 |
| 39 | | Sphagnetum tenellum-Wm. | E1(-2)PL | 5 |
| 40 | | Sphagnum balicum-Wm. | E1PLu | 8 |
| 41 | | Sphagnum balicum-Wm. | E1PLu | 9 |
| 42 | | Sphagnum rubellum-Wm. | E1-2PLu | 5 |
| 43 | | Scheuchzeria-Sphagnum balicum-Wm. | E1(-2)PL | 5 |
| 44 | | Sphagnum balicum-Wm. | E1(-2)PL | 14 |
| 45 | | Sphagnum rubellum-Wm. | E1-2PLu | 6 |
| 46 | | Exig. Sphagnum papillosum-Wm. | E1(-2)PL | 7 |
| 47 | | Exig. Sphagnum papillosum-Wm. | E1(-2)PL | 6 |
| 48 | | Exig. Sphagnum papillosum-Wm. | E1(-2)PL | 15 |
| 49 | Ruohijärvi 1960 (26a): | Kurzhalmige Sphagnum | E1(-2)PL | 15 |
| 50 | | Kurzhalmige Sphagnum papillosum-Wm. | E2(-3)PL | 50 |
| 51 | | Kurzhalmige Sphagnum papillosum-Wm. | E2(-3)PL | 30 |
| 52 | | Kurzhalmige Sphagnum papillosum-Wm. | E2(-3)PL | 30 |
| 53 | | Exig. Sphagnum papillosum-Wm. | E2(-3)PL | 35 |
| 54 | | Exig. Sphagnum papillosum-Wm. | E2(-3)PL | 26 |
The areal importance of the vegetation complexes in vegetation. The distribution of creasing importance of PHu series and with an increasing importance of trees on bogs (cf. Økland 1989a and Tab. 7).

The pool complex. The distribution of hollow-pools is western and northern in the area (Økland 1989a), hollow-pools are rare south of limes norrlandicus (Osvald 1923; Sjörs 1953, 1983), but strongly increasing northwards (Lundqvist 1951; Sjörs 1965) and towards more humid areas (Sjörs 1948; Fransson 1972; Økland 1989a).

The erosion complex is a humid feature, as shown by Økland (1989a). Descriptions are given from SW Sweden (Osvald 1923, 1930, Mörnsjö 1971), Østfold (Moen 1970, Økland 1989a), and Dalarna and W Jämtland (Sjörs 1948, 1950).

The regeneration complex, characterized by prominence of the PLI vegetation, increases in its importance in bogs eastwards. In Finland this is the dominant complex-type along with the marginal complex. Osvald (1930) considers this to be the dominant complex type in E Sweden, e.g. in the Rygmgossen. He describes its importance as gradually decreasing westwards, but in Kosmosse (Osvald 1923), Akhultmyren (Malmer 1962a), Skagershultmossen (Osvald 1923), as well as in Bergslagen (cf. Sjörs 1948) and SW Värmland (cf. Fransson 1972), this is a dominant complex type.

The stagnation complex is absent from areas with low humidity, that is all of Finland and E Sweden (Osvald 1923). From data available, it appears that the stagnation complex is southwestern in the area, dominating in the SW Swedish upland areas (Osvald 1923, 1930), and extending eastwards to the uplands of S Småland (cf. Malmer 1962a), northwards to Dalsland (Sjörs 1953), perhaps to southern Østfold (atypical representatives of this type, pers. obs.).

The Rhychospora-rich regeneration complex is characterized by prominence of the RLI subseries, showing a western distribution with an indicated optimum in the area around the limes norrlandicus (p. 293, cf. also Økland 1989b).

Discussion

Identification of regional gradients in flora and vegetation

Four gradients in flora and vegetation (coenoclines according to Whittaker (1956, 1967)) can be identified.

(1) W-E (or slightly NW-SE) variation: for example, (i) the distribution of Sphagnum compactum, S. pulchrum and, to some degree, S. molle, western or northwestern species without a pronounced upper limit east of the Scandes, (ii) the western distribution of Racemortium.
lanuginosum in hummocks, (iii) the increasing quantitative importance of hepatics and lichens in hummocks (the RH subseries) westwards, (iv) the distribution of the RL subseries, (v) the distribution of mud-bottoms (more NW-SE trend), (vi) the appearance of Chamaedaphne calyculata and Ledum palustre and increase of Vaccinium uliginosum on the mire expanses eastwards, and (vii) the occasional descendance of these and other species (notably Sphagnum angustifolium and S. fuscum) in lawns towards the east.

(2) S-N variation: for example, (i) the distribution of Rhynchospora spp., Drosera spp., Sphagnum cupdia-
tum, and several other southern species, (ii) the southern limit of several northern carpet plants in bogs (the

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limnominerobionts of Müller 1973, 1976), (iii) the areal importance of carpets in bogs, (iv) the shift in dominance between closely related taxa in Vaccinium and Emperotum, and (v) the increasing frequency of Rubus chamaemorus, Emperotum nigrum s.l., and northern lichens and hepatics in lawns and carpets.

(3) SW-NE variation: for example, (i) the replacement series Sphagnum papillosum – S. magellanicum – S. rubellum – S. balticum as dominants of bog lawns, (ii) the replacement series Sphagnum magellanicum – S. rubellum – S. fuscum as dominants of bog hummocks, (iii) the regional shift of each of these species to occupy lower relative levels (as compared to the Calluna limit, cf. Du Rietz 1949, Malmer 1962a) from SW to NE, (iv)

![Table Image]
the distribution of Sphagnum tenellum as a dominant species in the RL subseries, (v) the regional distribution of several western fen plants with an upper limit (e.g. Erica tetralix, cf. Økland 1989a), (vi) the distribution of several western and southern species in fens, and (vii) the distribution of the northeastern species, e.g. Pin-
Ecological factors and hydromorphological variation correlated with regional gradients in flora and vegetation

The four component gradients are correlated with regional variation in climatic parameters, strongly influencing the hydrology of mires at all size levels (Økland 1989a). I will consider these four gradient complexes in turn.

The W-E variation

This direction of variation is related to the humidity of the climate (cf. Fig. 2; Økland 1989a), influencing vegetation directly and indirectly.

Increasing humidity leads to increasing leakage of minerals. The monovalent ions N, K, and P are relocated to the mire surface by capillary flow of water (Brehm 1968; Damman 1986), a process strongly counteracted by leaching in humid areas (Damman 1986).

Humidity, or more precisely, the precipitation surplus, is the most important single parameter affecting the seasonal variation in depth to the water table (Økland 1989b, and references quoted therein). Water supply increases towards more humid areas (as well as northwards, owing to late spring, increasing amounts of snow, etc. (cf. Sjörs 1948; Økland 1989a)). This affects the annual range of depth to the water table, strongly increasing towards less humid areas. This is apparent from a comparison of range estimates in normal years; 10–15 cm in oceanic, strongly humid areas (Green & Pearson 1968; Damman & Dowhan 1981), 20–25 cm in humid areas (Malmer 1962a; Johansson 1974; Økland 1989b), and close to 50 cm in warm, continental areas (Clymo 1984), where the input to the catotelm, the permanently waterlogged lower peat stratum, is lower. The aeration of the peat favours development of hummocks and development of forested bogs (Glaser & Janssens 1986; Økland 1989a,b). Furthermore, good aeration favours an oxidising environment, and a lower pH (Sparling 1967; Sonesson 1970b).

The zone of water-table fluctuations, comprising lawns and partly also carpets (cf. Malmer 1962a; Økland 1989b), shows a strong accumulation of several metallic cations, including Pb, Zn, and Al (Damman 1978, 1986). The gradual attenuation of this zone towards more humid areas may lead to increasing concentrations of these ions there.

Peat depths of bogs increase with increasing humidity (Clymo 1984; Økland 1989a, and references quoted therein). The catotelmic decomposition of peat increases accordingly, and thereby also the amounts of methane gas produced by the breakdown process (Clymo 1984). Methane gas bubbles are released to the surface through pores in the peat, the release mostly follows the same routes, causing redistribution of extruded peat near the orifices of the pores (cf. Gams & Ruoff 1929; Aario 1932; Aartolahti 1965).

The geographic patterns of occurrence of severe erosion in SE Fennoscandia and its causes are treated by Økland (1989a), who demonstrates a limit for the frequent occurrence of erosion in bogs and slightly minerotrophic mires strongly correlated with humidity (the borderline (3) of Økland (1989a)). This limit also defines the transition from the dominance of plateau raised bogs and kermi raised bogs to plane transitional mires. Two mechanisms by which erosion occur are suggested by Olausson (1957) and Økland (1989a); erosion by oversaturation and erosion by stagnation. The erosive power of water is strongest when the water table is close to the surface of the bottom layer. Thus the probability of erosion decreases with decreasing duration of water cover at the level of the bottom layer surface (Sjörs 1947; Foster et al. 1983), that is, from carpet to lawns. Above the limit between the lower and upper lawn series, the bottom layer is rarely covered with water (Økland 1989b), and in N Kisselbergmosen (situated in a moderately humid area), patches of bare, eroded peat rarely occurs. Erosive action of water is particularly important at extremely high water tables (Backéus 1985), as demonstrated by Osvald (1923) and Vorren (1979c). Furthermore, the erosive power of water is highest at high water through-flow rates, as shown by Aario (1932).

The S-N variation

This direction of variation is correlated with temperature parameters, as shown for the zonal gradient by Tuukanen (1980) and Økland & Bendiksøn (1985), and exemplified by the effective temperature sum (cf. Økland 1989a).

Temperature has important effects on the water table and on water supply. Lower temperature leads to increased snow accumulation, later snow-melt in spring, higher surface runoff rates, and high water tables far into summer (Sjörs 1947, 1948; Økland 1989a). Low temperatures lead to increased solubility of oxygen (Sjörs 1961) and in turn to a surplus of oxygenated melt water in spring that favours surface corrosion (Sjörs 1961, 1983), and thus, erosion. Økland (1989a) found the lower limit of sharply demarcated kermis, his borderline (1), and thus the lower limit of kermi raised bogs, to be almost perfectly correlated with the effective temperature sum. This limit is actually the southern and lower limit of important regelation effects (Aario 1932; Eurola 1962; Økland 1989a). The impact of regelation increases strongly northwards (Tanttu 1915; Auer 1920; Ruuhijärvi 1960; Sjörs 1983), leading to an increased kermi-hollow differential and a stabilization of depressions (Sjörs 1947). The effects of ice pressure and ice erosion are strongest in carpets, and decrease towards lawns (Malmer 1962a; Økland 1989b). Regelation occurs in autumn and spring. Aartolahti (1965) describes how small tussocks are elevated by frost upheaval in the autumn, and how they sink in spring as the ice thaws, leaving a small ring of bare peat behind around the tussock.
The crests of hummocks are more strongly exposed to wind and frost northwards (Ruuhiälärvi 1960; Eurola 1968; Sonesson 1969), the ecological conditions approaching those of the xeric alpine crags without a stable snow cover in winter (cf. Nordhagen 1943; Dahl 1957; Sonesson 1970a). Snow-free hummocks in winter due to wind action have also been demonstrated for more southern areas, e.g. at Komosse (Osvald 1923).

The SW-NE variation

This direction of variation is a result of the W-E and S-N directions, but also shows some unique features. Most important is the pattern of water table fluctuations in lawns. In the southwest, high precipitation and high evapotranspiration contribute to a strong, periodic fluctuation of the water table, with remoistening after each period of heavy rain (Malmer 1962a; Økland 1989b). In particular, the lower lawn series is exposed to variable water tables, as the water table rises to the level of the bottom layer or 1–2 cm within during each moist period (Økland 1989b). Northeastwards, low precipitation and low evapotranspiration result in a more smooth path of the depth to the water table curves throughout the growing season (cf. Malmer 1986). The number of occasions with water tables close to the maximum also increases southwestwards.

The NW-SE variation

This direction of variation is accompanied by increasing water supply and increasing ground water flow rates (Økland 1989a). Water supply is the determinant of more important hydrological borders of SE Fennoscandian mires, as studied in detail by Økland (1989a). The most important of these is his borderline (2), the limit for soligenous water supply. Soligenous water supply is favoured by high humidity (Sjörs 1948), low temperatures, large amounts of snow, late springs and large amounts of melting water far into the summer (Ruuhiälärvi 1983; Eurola & Holappa 1985). This borderline is most strongly influenced by humidity in oceanic areas, approaching the E-W direction of variation, and by temperature in continental areas, there aligning more to the S-N direction. The presence of soligenous water is a necessary condition for development of unilaterally sloping bogs (Sjörs 1948). As the volume of seepage water conveyed through each point along the lower perimeter of a unilaterally sloping bog is far higher than in a multilaterally sloping bog of comparable size (cf. Damman 1986), this limit marks a fundamental limit also in bogs. The limit of dominance of sloping fens over bogs (borderline 4) of Økland (1989a) follows his borderline (2), but is displaced towards west and north.

All features encouraged by high humidity (the E-W gradients) as well as all features promoted by low temperatures (the S-N gradients) show an increase along this gradient. In particular, this applies to erosion in a wide sense, as promoted both by water supply and by regelation.

Regional variation within each series

Factors limiting distribution of the individual species or phytogeographical elements are discussed, among others, by Økland (1989a), and mostly will not be considered here.

Carpets

The main vegetational gradient in carpets is S-N, or slightly displaced in the SE-NW direction. This is in accordance with the need for permanently high water tables for the development of bog carpets (Sjörs 1948). Sjörs (1948) showed a considerable decline in the areal importance of carpets when moving out of the region of unilaterally sloping bogs. It is generally assumed that vascular plants of carpets are sensitive to drying-out (Sjörs 1948; Økland 1989a), thus offering an explanation for the restriction of limnominerobionts to fens in the southernmost part of their area.

The displacement of the southern Sphagnum cuspidatum by the northern S. majus may be explained by differences in desiccation tolerances (higher in the former) and growth rates under permanent water supply (higher in the latter), as S. majus replaces S. cuspidatum when moving from bog to poor fen also south of the occurrence of S. majus in bogs (cf. Malmer 1962a; Svensson 1965; Økland 1989b). The absence of S. cuspidatum from suitable microsites (carpets susceptible to drying-up) in N Finland does not fit into this explanation (Eurola, pers. comm.)

Lawns

The decisive factor in giving the main regional gradient in lawn vegetation a SW-NE, and partly a W-E direction, is the pattern of water table fluctuations. The more strongly fluctuating water tables in bogs than in fens (Malmer 1962a; Økland 1989b) exclude the southern species from bogs in the southeastern, least humid areas, giving a distinct SW-NE gradient in bog lawns. The variation is restricted to the western and northern areas, while an impoverishment gradient runs from NW to SE in the direction of reduced water supply. Very similar trends in phytogeographic variation within a smaller area, are reported by Økland (1989a). The higher proportion of western, suboceanic species in lawns than in carpets and hummocks, particularly in the lower lawn series (Malmer 1962a, Økland 1989b), and the fact that such species are almost restricted to this series near their eastern limit, suggest that this species group prefers strong, periodic fluctuations of the water table. The decisive factor may be the frequent occurrence of reducing conditions, coupled with waterlogging (Malmer 1962a;Persson 1962; Boatman 1983). The associated accumulation of metallic cations (Økland 1989b, cf. p. 00) may be toxic to many species (as shown for Eupatorium nigrum by Bell & Tallis (1974), and for Calluna vulgaris by Bannister (1964)). The western lawn spe-
cies, *Erica tetralix*, is more tolerant in this respect (Bannister 1964).

For species of the bottom layer, the lawns make up a potentially very dry biotope, probably drier than the hummocks (Malmer 1962a; Rydin 1985; Andrus 1986; Økland 1989b). High decomposition rates in the water-air interface give rise to a strongly humified peat with small pores and tightly bound water (Andrus 1986; supported by observations by Økland (1989b)). When the water table is lowered, the lawns dry out. The typical lawn species, *Sphagnum tenellum* and *S. balticum*, share with *S. fallax* a low desiccation resistance, and a high desiccation tolerance (Wagner & Titus 1984; Rydin 1985; Andrus 1986). Desiccation resistance, or ability to capillary rise of water depends on the arrangement of pendant branches and leaves (Clymo & Hayward 1982; Rydin 1985). The reciprocal distribution of *Sphagnum tenellum* and *S. balticum* may be explained by (1) the poorer capacity of water transport in the former (Rydin 1985), due to the lack of differentiated hanging branches and the spreading, ovate leaves, and (2) the higher water content needed for net photosynthesis in *S. tenellum* (Rydin & McDonald 1985b). Furthermore, the periodic drought increases the danger of periodic temperature limitation of photosynthesis (Rydin 1984).

No species are likely to demand strongly fluctuating water tables, the decisive factor for the dominating lawn species appears to be the ability to endure such conditions (cf. Sjörs 1948).

Hummocks

As the water table never reaches the surface of the hummock bottom layer, the pattern of water table fluctuations plays a less important role for the regional variation in vegetation. The seasonal variation in depth to the water table influences the hummocks indirectly by its effects on water availability. Higher water availability in humid areas, combined with higher growth rates in the favourable temperature climate of the south, is likely to be the reason for the SW-NE direction of variation among the bottom layer dominants. *Sphagnum magellanicum* and *S. rubellum* have higher growth rates than *S. fuscum* at lower relative levels in the same climate (Rydin & McDonald 1985a; Wallén et al. 1988), a fact easily explaining replacement along the regional moisture gradient. Furthermore, the superior ability of *Sphagnum fuscum* for capillary rise of water (Silvola & Aaltonen 1984; Rydin 1985) makes this species the only dominant of hummocks in continental areas. Structural properties are decisive in this respect (Hayward & Clymo 1983).

A peculiar distribution in hummocks is shown by *Sphagnum balticum*, being relatively frequent in hummocks in moderately humid areas, decreasing both towards the southwest and towards the east. The upper limit of this species is set by water transport ability (desiccation resistance), as demonstrated by Rydin (1985). Commensalism with *S. fuscum* enables *S. balti-

cum to grow in hummocks in the intermediate area; surrounded by *S. fuscum* the species gets sufficient moisture to keep pace with the upward growth of the *S. fuscum* sward. However, in the southwest *S. fuscum* is reduced to a minor component of tall hummocks, too dry for *S. balticum*, while the competitive species *S. rubellum* and *S. magellanicum*, with their looser growth form, partly outcompete *S. balticum* and partly fail to give *S. balticum* sufficient water supply. Far east, the longer drought periods are likely to exclude *S. balticum* from hummocks.

The increasing density of dwarf shrubs on the hummocks, and the increasing quantity of pine eastwards are due to the higher range of depths to the water table (Eurola 1962; Malmer 1962a; Økland 1989b).

A conspicuous S-N direction of variation is associated with the coincidence of two factors northwards; (1) the increased height of hummocks, and (2) the increasing wind action. Thus a prominent element of chionopho-bous species like *Cetraria cucullata*, *C. nivalis*, and *Ochrolechia frigida* occurs in hummocks from the MB zone and increases its importance northwards and towards higher altitudes (Ruuhiäärvi 1960; Hämet-Ahti 1963; Sonesson 1970a), partly also eastwards (Sonesson 1970a). The northward decrease of *Calluna vulgaris* in mires (while it still occurs on mineral soil) has been associated with low tolerance to permafrost (Ruuhiäärvi 1960).

Regional aspects of the differentiation into subseries

In all series, the presence of the R subseries of slightly peat-producing vegetation shows a W-E tendency, with a NW-SE deflection particularly apparent in carpets. The favouring of slightly peat-producing vegetation by high humidity is due to a complex set of factors. The increasing effect of water erosion from lawns to carpets in bogs explains the higher quantitative importance of the R subseries (mud-bottoms) in carpets at any geographic site, and is also responsible for the higher vegetation cover in RL than in RC. The higher importance of regelation processes in carpets explains the NW deflection of the mud-bottom importance gradient. Both the P and the R subseries (and all transitions and intermediates) occur in all series all over SE Fennoscan-dia. As shown by Malmer (1962a) and Økland (1989b) differences along local gradients cannot explain the P-R differentiation. The geographic differentiation therefore must be ascribed to increased probability of substitution of the P by the R type of vegetation along the gradient. I will examine this hypothesis, series by series.

Carpets

The increasing probability of erosion westwards and of regelation effects northwards is apparent from p. 301. This promotes development of mud-bottom patches. Furthermore, very wet conditions are suboptimal for *Sphagnum*, as assumed by von Post & Sernander
(1910), Osvald (1923), Aario (1932), and Boatman (1983). Apart from the abiotic factors, this is due to competition from algae. Sjörs (1961, 1963, 1965) suggests that active algal growth restricts the growth of *Sphagnum*, and considers the competitive ability of algae to increase with increasing humidity. Support for the importance of this factor, and its increased action west- and northwards comes from experimental studies: dominant bog hollow algae endure variable temperatures, low pH and desiccation (Hosiaisluoma 1975), and the algal growth potential for two most important species of green algae is higher in bogs than in poor fens (Tolonen & Hosiaisluoma 1978). The northward increasing algal production due to better oxygenation of meltwater is considered as an important factor for the northwestern distribution of hollow-pools (Økland 1989a).

**Lawns**

On a local scale, strongly peat-producing lawns dominated by *Sphagnum magellanicum, S. papillosum, S. rubellum*, or even *S. balticum*, is favoured by less fluctuating water-tables, e.g. by a slight influence of mineral soil water (Økland 1989b). These species appear to be favoured by somewhat better aeration of the peat, promoting decomposition (Økland 1989b). *Sphagnum magellanicum* and *S. papillosum* prefer sites where good water supply ensures high growth rates (Pedersen 1975; Gabersčik & Martinčič 1988; Wallén et al. 1988). *Sphagnum papillosum* shows a considerable loss of nutrients after remoistening (Gabersčik & Martinčič 1988).

On the other hand, *Sphagnum auriculatum, S. compactum, S. molle*, and *S. tenellum* are locally slightly favoured by the strongly fluctuating water tables of southwestern lawns with slight or none (in the case of *S. tenellum*) supply of mineral soil water (Malmer 1962a; Økland 1989b). Dynamic and structural properties explain the increase of the RL subseries towards the southwest and the west. The probability of local catastrophic events increases with increasing humidity (p. 303). The slightly peat-producing Sphagna are pioneer species with a well documented ability to colonize bare patches, patches dominated by heathers (Økland 1989b, 1990b), periodically dry mud flats dominated by *Zygodonum ericetorum* (Osvald 1923), and bare, slimy peat produced by burning (Ratcliffe & Walker 1958). The westward increase in the amounts of heaths suggests a higher tolerance of the R Sphagna to overgrowth by heathers. Økland (1990b) assumes that *Sphagnum tenellum* is a less suitable substrate for the poikilohydric heathers than most other *Sphagnum* species because of its very low desiccation resistance, among the lowest among the common Sphagna (Rydin 1985; Rydin & McDonald 1985b). The very dense cushions of *Sphagnum compactum* and *S. molle* may be disadvantageous because of the danger of burial. The desiccation tolerances of *Sphagnum balticum, S. compactum, S. molle*, and *S. tenellum* are high, they even occur in xeric and sub-xeric heaths (Clymo & Hayward 1982; pers. obs. in humid W Norway).

Økland (1990a,b), analyzing the puzzling problem of the inclusion of the habitat niche of *S. tenellum* within that of *S. balticum* (at a local scale, i.e., within one mire; Rydin 1985, 1986; Økland 1989b), shows that the two species separate well along the coenocline associated with peat-producing ability of the vegetation; from patches dominated by heathers, via dominance by *S. tenellum*, to *S. balticum*, the locally most common of the P species. Furthermore, he interpolates these observations as indicating a successional relationship, with the direction of the succession frequently reversed by local catastrophic events. This then explains the observation of Rydin (1986) that *S. balticum* replaces *S. tenellum* without any abiotic factors involved (or, more correctly, any influence by abiotic factors during the replacement phase), and amplifies the explanation of Rydin (1986, 1987) that the differentiation of the two species is due to priority of colonization.

**Hummocks**

The increasing quantitative importance of hepatics and lichens towards more humid areas, and the increasing importance of the so-called short-cycle regeneration of hummocks (Økland 1989a), is explained in detail by Økland (1989a). The assimilation rate of lichens increases with increasing thallus moisture content (Kershaw & Rouse 1971; Kershaw 1972), and lichens dry out very rapidly (Blum 1973). This explains the much lower annual production rates measured by Vasander (1981) in Finland than by Prince (1974) in humid Scotland. Lichens apparently do not easily invade a hummock dominated by healthy *Sphagnum*, because of lower growth rates. However, the physical and chemical conditions produced by *Sphagnum* appear to promote growth of leafy heaptics (Clymo & Hayward 1982). Hepatics are ectohydric and poikilohydric (Buch 1947; Hosokawa et al. 1964). Their distribution and local abundance are governed by the microclimate (Buch 1947; During 1979). Mire heaptics are considered to have a low drought tolerance (Clausen 1952; Proctor 1982). This explains the increase of this group westwards. The growth rate of *Sphagnum fuscum* declines strongly with increasing admixture of *Mylia anomala* (Pakarinen 1978). Thus, the increasing importance of heaptics towards more humid climates increases the probability of reducing the growth rates of the dominating *Sphagnum* spp. below that of the lichens of *Cladonia* subg. *Cladina*. Similarly, the northward increase of chionophobous lichens is due to an increasing probability of wind abrasion of hummock crests, desiccatiing or killing the *Sphagnum* spp. and laying the hummocks open for invasion by lichens.
Regional aspects of the differentiation into vegetation complexes

The differentiation of vegetation along regional gradients also explains the reason for the optimum areas of particular vegetation complexes sensu Osvald (1923). The pool, erosion and marginal complexes require the development of particular hydromorphological mire component types, as discussed by Økland (1989a).

The regeneration complex, with a prominent position of the PLI subseries, declines towards more humid climates because of the increasing probability of catastrophic events in the zone of water table fluctuations. Furthermore, the lower water supply to bogs in the southwest (Økland 1989a) favours a fluctuating water table (cf. also Økland 1989b).

The stagnation complex is favoured by a warm, humid climate. In early phases of bog development this combination favours production. In later phases, when the critical profile is reached (cf. Økland 1989a), humidity favours erosion of hollows and invasion of hummocks by hepatics and lichens, giving the characteristic mosaic of mud-bottoms and R hummocks. The cessation of peat productivity leads to increased water tables and decreasing decomposition, and erosion by stagnation.

The Rhynchospora-rich regeneration complex is most prominent in the zone immediately north of the domain of the stagnation complex. The lower humidity may partly explain its distribution; the associated, more moderate intensity of the erosive forces promotes recolonization of mud-bottom flecks by Sphagnum tenellum. Farther north, more abundant water supply of bogs promotes the development of carpets and the regeneration complex. The stagnation complex may be rare in this northern area due to lower temperatures, lower evapotranspiration, higher surface water flow-rates, and erosion by oversaturation before stagnation is achieved (Økland 1989a).

The regional fen plant problem

The numerous hypotheses proposed to explain the restriction of some plant species to bogs in part of their area, will be evaluated with reference to the material presented from SE Fennoscandia.

(1) Variable genetic constitution throughout their range (Gorham 1956; Aletsee 1967). The presence of a separate bog taxon, Sphagnum imbricatum ssp. austinii, has been demonstrated to account for the distribution of Sphagnum imbricatum in bogs (Flatberg 1984, 1986).

(2) Species become more demanding towards their distributional limit, and are generally better suited for conditions (along local and regional gradients) in the central part of their area, thus such ecological shifts towards range margins are frequently observed in mires (Kotilainen 1951; Glaser & Foster 1984; Økland 1989a) and other habitats (e.g. Pesola 1928; Du Rietz 1954; Gjærevol 1966; Hengeveld & Haeck 1981). This improvement of conditions towards the central parts of the range may be mediated by superior competitive ability (Aletsee 1967; Økland 1989a). The group (2) species of regional fen plants mostly conforms to a pattern of regular thinning out towards range limits, and thus, of congruent distribution in bogs and overall distribution. This is typical in Erica tetralix, Drosera intermedia, the northern limits of Rhynchospora alba and Drosera anglica, and the southern limits of the group (3) species without restriction to humid, W Finnish bogs. The wide-spread species Scirpus cespitosus and Eriophorum angustifolium and the southeastern limits of bog occurrences of Rhynchospora alba, Drosera anglica, Sphagnum magus etc. violate this pattern. Apparently, this hypothesis may be a partial explanation, applicable to several species.

(3) Distribution of habitable sites (Müller 1973, 1976; Malmer 1986). The southwestern bog species do not, generally, have specific demands that are not satisfied outside their range in bogs. Exceptions may be related to the demands for particular hydrological regimes. The increasing danger of severe drought may restrict Scirpus cespitosus, Rhynchospora alba, and Drosera anglica to fens beyond their southeastern limits for bog occurrences. The restriction of the northern bog species (termed linnobions by Müller (1973, 1976)) to carpets, and the established relationship between the distribution of carpets and water supply (p. 303), explain the distribution of such species. This gains support from the coincidence of distributional limits with the limit of unilaterally sloping bogs, and the restriction of these species to large, wet hollows in the downslope, wetter parts of large bogs at their southernmost outpost localities (cf. Osvald 1923; Du Rietz 1950a).

(4) Variable chemical composition of the precipitation, giving a higher nutrient addition to bogs in oceanic areas (Ackenhel 1944; Witting 1948; Olausson 1957). A corollary of this hypothesis is the expectation of a mineral soil water limit that is well-defined in chemical terms over wide geographical areas. Suggested parameters for characterization are Ca-concentration and the Ca/Mg ratio of mire water (Witting 1948), but neither these nor others show geographically consistent patterns of variation (compare data of Witting 1948, 1949; Malmer 1962a; Sonesson 1970b; Wildi 1977; Tolonen & Hosiaisluoma 1978; Vorren 1979a,b, and Økland 1989b). Thus this hypothesis is now abandoned as a general explanation (Aletsee 1967; Müller 1976; Dierssen 1982; Malmer 1986).

The only species possible to fit into this pattern are some western species (Erica tetralix and perhaps Myrica gale, but neither Drosera intermedia as suggested by Aletsee (1967), cf. Fig. 3, nor Eriophorum angustifolium). Even for these species, the hypothesis is only acceptable as part of the explanation, for three reasons: (a) The constituents of precipitation differing most between oceanic and continental areas, Na, Mg, Cl, and S,
partly also N, are not considered to restrict plant growth in bogs (Malmer 1962b; Damman 1978, 1986), (b) the lack of congruence between different parameters (Aletsee 1967), and (c) the general adaptation of western heath plants to poor, leached sites gives support to hypotheses (2), (3), or (5) rather than this one.

(5) Geographical variation in bog hydrology. Several mechanisms have been put forward: (a) Increasing precipitation towards more humid climates leads to increasing surface water flow rates and better nutrition, thus stimulating minerotrophic conditions (Aletsee 1967; Müller 1976; Lindsay et al. 1985). Müller (1973) points to the improved nutrient availability when oxygen supply is improved by lateral water movement. Ölausson (1957) points to the occurrences of Eriophorum angustifolium downslope in unilaterally sloping bogs in the west, where the water throughflow rates are high. (b) The importance of high, relatively constant water tables for the occurrence of species like Eriophorum angustifolium, Narthecium ossifragum, and Rhynchospora alba in bogs (Malmer 1986). This hypothesis comes close to hypothesis (3) here. (c) The higher mineralization rate in southwestern bogs (Aletsee 1967; Dierssen 1982). The high humidity of the southwest leads to high water tables, disfavouring decomposition. However, stagnation acts the opposite way, by reducing input to the acrotelm. By erosion, water tables are lowered sufficiently much to give considerably increased remineralization rates. No evidence points to the restriction of the species in question to eroded bogs.

(6) Higher pH in humid areas due to waterlogged peat (Pearsall & Lind 1941). No evidence points to particular importance of pH as an independent factor.

(7) Geographic variation in Al sensitivity (Sparling 1967); rejected by Damman (1980).

(8) Historical reasons can be rejected as the area of species in fens exceeds that in bogs (Aletsee 1967).

(9) Anthropogenic influence, such as burning of heaths (Olausson 1957) do not seem likely to affect species distributions.

Assessment. Hypotheses (1), (4), and (5) may apply to special cases, but the general pattern of fen plant regionality in SE Fennoscandia must be ascribed to the general trend of species being more demanding near their distributional limits, in combination with the distribution of habitable sites. As the effects of these two mechanisms can only be separated in a few cases, these two hypotheses can be combined into an explanation valid for most of the species with restricted distribution in bogs. The distribution of Eriophorum angustifolium in bogs still cannot be explained satisfactorily.

General discussion and conclusions

This study shows that most of the variation in SE Fennoscandian mire vegetation is a response to two main regional gradients: the W-E gradient in humidity, and a N-S gradient in temperature factors. These gradients act through a set of complex mechanisms to produce a regional variation in the mire habitat. In bogs and slightly minerogenous fens this regional variation is mainly related to the depth to the water table, its characteristic levels and seasonal course, and the danger of water erosion and intensity of regelation processes. This affects the distribution of species (Ökland 1989a), the relative competitive abilities of different species in different habitats (Ökland 1990b), and the stability of the habitat. With very few exceptions, the vegetational variation can be fully explained as responses to these factors.

It is commonly assumed that the main regional gradient in SE Fennoscandian vegetation runs from SW to NE (Malmer 1986). At a first glance, this seems to be at odds with the results presented here. The apparent disparity is due to several reasons: (1) The main gradient in phytogeographical change in this area runs from the southern and western, to the northern and eastern species, gradually replacing each other from SW to NE (Malmer 1986; Ökland 1989a). (2) The water supply, the main single factor affecting the hydrology and hydromorphology of mires in this area, increases from SE to NW, creating a stronger diversity of mire habitats in the west and north (Ökland 1989a). (3) The southeastern phytogeographic element does not contain species of bogs and poor mires (Ökland 1989a). (4) Consequently, the southeastern mires, poor in species, have not attracted much interest, and are underrepresented in the vegetation material from the area. (5) The long axis of the investigated area runs in a SW-NE direction. (6) Both the W-E and S-N directions of variation vary in a SW-NE direction.

According to this study, the SW-NE gradient is merely a result of two strong, more or less independent gradients. Only in lawns is the SW-NE variation prominent, due to a complex gradient in water table fluctuation characteristics. The variation in carpet and hummock vegetation (partly also the lawn vegetation) cannot be understood fully in ecological terms unless the W-E and N-S gradients are considered separately. The concept of the SW-NE gradient as a result of two separate trends gains further support from regional studies within parts of SE Fennoscandia. Studies in S Swedish mire vegetation emphasize the W-E axis and humidity as the most important eccline (Walheim 1944; Du Rietz 1949; Malmer 1962a), while Finnish studies emphasize S-N variation (Ruuhiäärvi 1960; Eurola & Ruuhijärvi 1961; Eurola 1962).

The existence of a major, SW-NE gradient in mire vegetation is also the basis of the regional subformations of bogs discerned by Du Rietz (1949), see also Waldheim & Weimarck (1943), with the Rubellion subformation (the Komosse type of bogs) in SW Götaland, the Rubello-fusicion (the Skagershultmosse type) in a zone north and east of the latter, and the Eufuscion (the Ryggmoss type) in E Sweden and Finland (Fig. 1). The
The present study points to the conceptual advantages of separating the humidity-oceanicity factor complex from the temperature complex, as strongly recommended by Ahti et al. (1968), and practiced in regional mire studies by Vorren (1979a, 1979c) and Eurola & Vorren (1980). The concepts of regional subformations of Du Rietz (1949) should be replaced by a framework of types allowing for recognition of variation along both main regional gradients.

This study has confirmed the importance of the ecological law of plant distribution (Boyko 1947; Walter & Walter 1953; Peet 1978; Økland & Bendiksen 1985): a plant species will occupy sites with similar habitat conditions in different regions, thus tending to have their local distributions displaced against the xeric (hummock) end of the depth to the water table gradient in the more humid area. This is excellently shown by the dominant Sphagnum spp., S. fuscum, S. magellanicum, and S. rubellum, regardless of distributional tendency, and by several dwarf shrubs.

The present study shows that understanding of regional variation in mire vegetation benefits strongly from two aspects: (1) the classification of local ecoclines into a reticulate local reference frame, making recognition of ecologically corresponding vegetation types in different regions possible (Økland & Bendiksen 1985), and (2) a detailed knowledge of the distribution of hydromorphological mire component types (Økland 1989a), phytogeographic relationships (Hultén 1950, 1971; Økland 1989a), and climatically induced changes in ecological conditions. An integrated approach to regional variation is thus strongly recommended.

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References

Aario, L. 1932. Pflanzentopographische und paläogeographische Mooruntersuchungen in N-Satakunta. – Fennia 55: 1: 1-179.
- 1933. Pohjoisatakantalaisen kermikeidastypin luonne ja levineisyys. – Fennia 59: 3: 1-52 (Deutsches Referat: Die Verbreitung der Kermihochmoore von N-Satakunta und darauf einwirkende Faktoren).
Aartolahti, T. 1965. Overflächenformen von Hochmosen und ihre Entwicklung in Südwest-Häme und Nord-Satakunta. – Fennia 93: 1: 1-268.
Achenheil, H. V. 1944. Zur Hauptgliederung der südwestdeutschen Moorvegetation. – Medd Tëmatal. Stn Ägård 2: 1-40.
Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968. Vegetation zones and their sections in northwestern Europe. – Ann. bot. fenn. 5: 169-211.
Aletsee, L. 1967. Begriffliche und floristische Grundlagen zu einer pflanzengeographischen Analyse der europäischen Regenwassertorstande. – Beitr. Biol. Pfl. 43: 117-283.
Andrus, R. E. 1986. Some aspects of Sphagnum ecology. – Can. J. Bot. 64: 416-426.
Angervo, J. M. 1960. The yearly precipitation (mm) 1921-50. – In: Aario, L. (ed.), Atlas of Finland. Otava, Helsinki, map 5: 10.

Auer, V. 1920. Über die Entstehung der Strände auf den Torfmooren. – Acta for. fenn. 12: 2: 1-145.
Backéus, I. 1972. Bog vegetation re-mapped after sixty years. Studies on Skagershultsmossen, central Sweden. – Ökos 23: 384-393.
- 1983. Hedley, Cornicularia aculeata, på mossar. – Svensk bot. Tidskr. 77: 27-28.
- 1984. Myrar i Örebro län. – Svensk bot. Tidskr. 78: 21-44.
- 1985. Aboveground production and growth dynamics of vascular bog plants in Central Sweden. – Acta phytogeogr. suer. 74: 1-98.
Bannister, P. 1964a. The water relations of certain heath plants with reference to their ecological amplitude. II. Field studies. – J. Ecol. 52: 481-497.
Bell, J. N. B. & Tallis, J. H. 1974. The response of Empetrum nigrum L. to different mire water regimes, with special reference to Wybunbury Moss, Cheshire and Featherbed Moss, Derbyshire. – J. Ecol. 62: 75-95.
Björkbäck, F. 1965. Northern mires. Algfloarna, a mixed mire complex in Jämmtland. – Acta phytogeogr. suer. 50: 188-192.
Blum, O. B. 1973. Water relaions. – In: Ahmadjian, V. & Hale, M. E. (eds), The lichens. Academic Press, New York London, pp. 381-400.
Boatman, D. J. 1983. The Silver Flowe national reserve, Galloway, Scotland. – J. Biogeogr. 10: 163-274.
Boyko, H. 1947. On the role of plants as quantitative climate indicators and the geoeocological law of distribution. – J. Ecol. 35: 138-157.
Brehm, K. 1968. Die Bedeutung des Kationenaustausches für den Kationengehalt lebender Sphagnum. – Plantas 79: 324-345.
Bruun, I. 1967. Standard normals 1931-60 of the air temperature in Norway. – Norske meteorologiske Inst., Oslo.
Buch, H. 1947. Über die Wasser- und Mineralstoffversorgung der Moose I, II. – Soc. scient. fenn. Commentnes biol. 9: 16: 1-44 + 20: 1-49.
Clausen, E. 1952. Hepatics and humidity. – Dansk bot. Ark. 15: 1: 1-80.
Clymo, R. S. 1984. The limits to peat bog growth. – Phil. Trans. r. Soc. Lond. B 303: 605-654.
- & Hayward, P. M. 1982. The ecology of Sphagnum. – In: Smith, A. J. E. (ed.), Bryophyte ecology. Chapman and Hall, London, pp. 229-289.
Corley, M. F. V., Crudwell, A. C. Düll, R., Hill, M. O. & Smith, A. J. E. 1981. Mosses of Europe and the Azores; an annotated list of species, with synonyms from the recent literature. – J. Bryol. 11: 609-689.
Dahl, E. 1957. Rondane: Mountain vegetation in South Norway and its relation to the environment. – Skr. norske Vidensk.-Akad. Oslo mat.-naturvid. Klasse 1956: 3: 1-374.
Damman, A. W. H. 1978. Distribution and movement of elements in ombrotrophic peat bogs. – Ökos 30: 480-495.
- 1980. Ecological and floristic trends in ombrotrophic peat bogs of Eastern North America. – Coll. phytosoc. 7: 61-77.
- 1986. Hydrology, development, and biogeochemistry of ombrogenous peat bogs with special reference to nutrient conditions in a western Newfoundland bog. – Can. J. Bot. 64: 384-394.
- & Dowhan, J. J. 1981. Vegetation and habitat conditions in Western Head Bog, a southern Nova Scotia plateau bog. – Can. J. Bot. 59: 1343-1359.
Dierssen, K. 1982. Die wichtigsten Pflanzen-gesellschaften der Moore des östlichen Deutschland. – Beitr. Biol. Pfl. 43: 1-145.
- & Hoehne-Herzog, i. 1950. Vegetation and habitat conditions in the Billingen-Falbygden district in Västergötland (Southwestern Sweden). – Seventh int. bot. Congr. Stockholm 1950 Excursion Guides A II b 1: 1-54.
- 1950b. Phytogeographical mire excursion to Northeastern Småland and Östergötland. - Seventh int. bot. Congr. Stockholm 1950 Excursion Guides A II b 2: 1-22.
- 1950c. Phytogeographical excursion to the Ryggmossen mire near Uppsala. - Seventh int. bot. Congr. Stockholm 1950 Excursion Guides A II b 3: 1-24.
- 1954. Die Mineralbodenwasserzeigergruppe als Grundlage einer natürlichen Zweigliederung der nord- und mitteleuropäischen Moore. - Vegetatio 5-6: 571-585.
- & Nannfeldt, J. A. 1925. Ryggmossen and Stigebo Rödmosse, die letzten lebenden Hochmoore der Gegend von Uppsala. - Svenska växtsociol. Sällsk. Handl. 3: 1-21.
During, H. J. 1979. Life strategies of bryophytes: a preliminary survey. - Lindbergia 5: 2-18.
Eurola, S. 1962. Über die regionale Einteilung der südfinnischen Moore. - Annls bot. Soc. zool.bot. fenn. Vanamo 33: 2: 1-243.
- 1968. Über die Ökologie der nordfinnischen Moorvegetation im Herbst, Winter und Frühling. - Annls bot. fenn. 5: 83-97.
- & Holappa, K. 1985. The Finnish mire type system. - Aquilo Ser. bot. 21: 101-110.
- & Ruuhiävji, R. 1961. Über die regionale Einteilung der finnischen Moore. - Archiv Soc. zool. bot. fenn. Vanamo 16: Suppl. 1: 43-53.
- & Vormen, K.-D. 1980. Mire zones and sections in North Fennoscandia. - Aquilo Ser. bot. 17: 39-56.
Flatberg, K. I. 1984. A taxonomic revision of the Sphagnum imbricatum complex. - K. norske Vidensk. Selsk. Skr. 1984: 3: 1-80.
- 1986. Taxonomy, morphovariation, distribution and ecology of the Sphagnum imbricatum complex with main reference to Norway. - Gunneria 54: 1-118.
- & Moen, A. 1972. Sphagnum angermanicum og S. molle in Norge. - K. norske Vidensk. Selsk. Skr. 1972: 3: 1-15.
Foster, D. R., King, G. A., Glaser, P. H. & Wright, H. E. 1983. Origin of string patterns in boreal peatlands. - Nature 306: 256-258.
Fransson, S. 1963. Myrvegetation vid Rörvattenån i nordvästra Jämtland. - Svensk bot. Tidskr. 57: 283-332.
- 1972. Myrvegetation i sydvästra Värmland. - Acta phytogeogr. suec. 57: 1-133.
Gaberskij, A. & Martinčič, A. 1988. Seasonal dynamics of net photosynthesis and productivity of Sphagnum papillosum. - Lindbergia 13: 105-110.
Gams, H. & Ruoff, S. 1929. Geschichte, Aufbau und Pflanzendecke des Zehlaubruches. Monographie eines wachsen den Hochmoore in Ostpreussen. - Schr. phys. ökon. Ges. Königsberg Pr. 66: 1: 1-192.
Gjæreøvoll, O. 1966. Vegetasjonen i sørøg i Nord-Ostledalen. - Annls bot. fenn. 24: 187-187.
Glaser, P. H. & Foster, D. R. 1984. The vascular flora of raised bogs in southeastern Labrador and its phytogeographic significance. - Can. J. Bot. 62: 1361-1364.
- & Janssens, J. A. 1986. Raised bogs in eastern North America: transitions in landforms and gross stratigraphy. - Can. J. Bot. 64: 395-415.
Gottham, E. 1956. The ionic composition of some bog and fen waters in the English Lake District. - J. Ecol. 44: 142-152.
Green, B. H. & Pearson, M. C. 1968. The ecology of Wyburnbury Moss, Cheshire. I. The present vegetation and some physical, chemical and historical factors controlling its nature and distribution. - J. Ecol. 56: 245-267.
Grolle, R. 1976. Verzeichnis der Lebermoose Europas und benachbarter Gebiete. - Feddes Reprium 87: 171-279.
Håmed-Ahti, L. 1963. Zonation of the mountain birch forest in northernmost Fennoscandia. - Annls bot. Soc. zool. bot. fenn. Vanamo 34: 4: 1-127.
Hasselrot, T. 1953. Nordliga laver i Syd- och Mellansverige. - Acta phytogeogr. suec. 33: 1-200.
Hayward, P. M. & Clymo, R. S. 1983. The growth of Sphagnum: experiments on, and simulation of, some effects of light flux and water table depth. - J. Ecol. 71: 845-863.
Hengeveld, R. & Haeck, J. 1981. The distribution of abundance. II. Models and implications. - Proc. k. ned. Akad. Wetensch. Ser. C 84: 257-284.
Hosiaiumo, V. 1975. Muddy peat algae of Finnish raised bogs. - Annls bot. fenn. 12: 63-73.
Hosokawa, T., Odani, N. & Tagawa, H. 1964. Causality of distribution of corticolous species in forests with special reference to the physio-ecological approach. - Bryologist 67: 396-411.
Hultén, E. 1950. Atlas över växtarnas utbredning i Norden. - Generalstabens litografiska anstalt, Stockholm.
- 1971. Atlas över växtarnas utbredning i Norden, ed. 2. - Generalstabens litografiska anstalt, Stockholm.
Johansson, J. 1974. Hydrologiska undersökningar inom morgkomplexet Komosse. - K. tekn. Högsk. Lantmäteri Inst. Kulturtek. Rapp. 3: 17: 1-161.
Kershaw, K. A. 1972. The relationship between moisture content and net assimilation rate of lichen thalli and its ecolog ical significance. - Can. J. Bot. 50: 543-555.
- & Rouse, W. R. 1971. Studies on lichen-dominated systems. II. The growth pattern of Cladonia alpestris and Cladonia rangiferina. - Can. J. Bot. 49: 1401-1410.
Kolkki, O. 1980. Mean annual temperature (°C) 1921-50. - In: Aario, L. (ed.), Atlas of Finland. Otava, Helsinki, map 5: 1.
Korsoo, M. 1980. Myrvegetasjonen på Rønnsåmyra, Grue kommune, Hedmark. - Cand. real. Thesis, Univ. Troms heim. (Unpubl.).
Kotilainen, M. J. 1951. Über die Verbreitung der meso eutrophen Moorpflanzen in Nordfinland. - Finska M osskultfören. vetensk. Skr. 19: 1-162.
Krog, H., Øst hagen, H. & Tønsberg, T. 1980. Lavflora. Norske busk- og bladlav. - Universitetsforlaget, Oslo.
Laaksonen, K. 1976. The dependence of mean air temperatures upon latitude and altitude in Fennoscandia (1921-1950). - Annls Acad. scient. fenn. Ser A 3 Geol.-Geogr. 119: 1-19.
- 1979a. Areal distribution of monthly mean air temperatures in Fennoscandia (1921-1950). - Fennia 157: 1: 89-124.
- 1979b. Effective temperature sums and durations of the vegetative period in Fennoscandia (1921-1950). - Fennia 157: 2: 171-197.
Lindsay, R. A., Riggall, J. & Burd, P. 1985. The use of smallscale surface patterns in the classification of British peatlands. - Aquilo Ser. bot. 21: 69-79.
Lundqvist, G. 1951. Beskrivning till Jordartskarta över Kopparbergs län. - Sver. geol. Unders. Ser. Ca. Avh. Upps. 21: 1-213.
Malmer, N. 1962a. Studies on mire vegetation in the Archaean area of Southwestern Götaland (South Sweden). I. Vegetation and habitat conditions on the Åkhult mire. - Opera bot. 7: 1: 1-322.
- 1962b. Studies on mire vegetation in the Archaean area of Southwestern Götaland (South Sweden). II. Distribution and seasonal variation in elementary constituents on some mire sites. - Opera bot. 7: 2: 1-67.
- 1965. The southern mires. - Acta phytogeogr. suec. 50: 149-158.
- 1986. Vegetational gradients in relation to environmental conditions in northwestern European mires. - Can. J. Bot. 64: 375-383.
Melin, E. 1917. Studier över de norrländska myrmarkernas vegetation. - Norrl. Handbblkt 7: 1-426.
Moen, A. 1970. Myrundersaker i Østfold. Akershus, Oslo og Hedmark. Rapport i forbindelse med Naturvernrådets landsplan for myrreserver og IBB-CT-Telmæs myrundersaker i Norge. - Univ. Tromsdalen, K. norske Vidensk. Selsk. Mus., Tromsheim. (Copied).
- 1983. Myrundersaker i Sør-Trøndelag og Hedmark i for-
Svensson, G. 1965. Vegetationsundersökningar på Store mosse. Bot. Notiser 118: 49–86.

Tamm, O. F. S. 1954. Till frågan om bestämning av klimatets humiditetsgrad i Sverige. K. Lantbr.-Akad. Tidskr. 93: 105–122.

– 1959. Studier över klimatets humiditet i Sverige. – K. Skogshögsk. Skr. 32: 1–48.

Tanttu, A. 1915. Über die Entstehung der Bulten und Stränge der Moore. – Acta fo. fenn. 4: 1: 1–24.

Tolonen, K. & Hosiaisluoma, V. 1978. Chemical properties of surface water in Finnish ombrotrophic mire complexes with special reference to algal growth. – Annls bot. fenn. 15: 55–72.

Tuhkanen, S. 1980. Climatic parameters and indices in plant geography. – Acta phytogeogr. suiec. 67: 1–105.

Vasander, H. 1981. The length growth rate, biomass, and production of Cladonia arbuscula and Cladonia rangiferina in a raised bog in southern Finland. – Annls bot. fenn. 18: 237–243.

Vorren, K. D. 1979a. Myrinventeringer i Nordland, Trons og Finnmark sommeren 1976, i forbindelse med den norske myrreservatplanen. – Tromura Naturvit. 3: 1–116.

– 1979b. Vegetational investigations of a pals bogs in Northern Norway. – Tromura Naturvit. 5: 1–182.

– 1979c. Die Moorvegetation in Namdalen, Mittel-Norwegen. Eine Untersuchung mit besonderer Berücksichtigung des oceanischen Gradienten der südborealen Hochmoorvegetation. – Tromura Naturvit. 8: 1–102.

Wagner, D. J. & Titus, J. E. 1984. Comparative desiccation tolerance of two Sphagnum mosses. – Oecologia (Berlin) 62: 182–187.

Waldheim, S. 1939. Bidrag till Skånes flora. 4. Sphagnum-floran i nordöstra Skåne. – Bot. Notiser 1939: 757–772.

– 1944. Die Torfmoosvegetation der Provinz Närke. – Lunds Univ. Årsskr. N. F. Avd. 2 40: 6: 1–89.

& Weimarck, H. 1943. Bidrag till Skånes flora. 18. Skånes myrtyper. – Bot. Notiser 1943: 1–40.

Wallén, B., Falkengren-Gruner, U. & Malmer, N. 1988. Biomass, productivity and relative rate of photosynthesis of Sphagnum at different water levels on a South Swedish peat bog. – Holarct. Ecol. 11: 70–76.

Walter, H. & Walter, E. 1953. Einige allgemeine Ergebnisse unserer Forschungsreise nach Südwestafrika 1952/53: Das Gesetz der relativen Standortskonstanz; das Wesen der Pflanzengemeinschaften. – Ber. dt. bot. Ges. 66: 228–236.

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. – Ecol. Monogr. 26: 1–80.

– 1967. Gradient analysis of vegetation. – Biol. Rev. Camb. phil. Soc. 42: 207–264.

Wildi, O. 1977. Beschreibung exzentrischer Hochmoore mit Hilfe quantitativer Methoden. – Veröff. geobot. Inst. eidg. tech. Hochsch. Rübel Zürich 60: 1–128.

Witting, M. 1947. Katjonsbestämningar i myrvatten. – Bot. Notiser 1947: 287–304.

– 1948. Preliminär meddelande om fortsatta katjons-be-stämningar i myrvatten sommaren 1947. – Svensk bot. Tidskr. 42: 116–134.

– 1949. Kalciumhalten in einige nordöstra myrvatten. – Svensk bot. Tidskr. 43: 715–739.