Mires of Finland: Regional and local controls of vegetation, landforms, and long-term dynamics

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In this review I examine the geographical patterns of the Finnish mires and the role of regional and local factors that lead to their spatial differentiation. Finland can be divided into three roughly latitudinal mire zones (from south to north): the raised bog zone, the aapa mire zone, and the palsa mire zone. The development of the raised bogs is linked to the dominance of *Sphagnum*, leading to the growth of a thick peat layer that rises above the level of the mineral soil. The gross morphology of an aapa mire is typically inclined and concave. Here, *Sphagnum* species are less dominant, probably due to spring floods which keep the mire surface minerotrophic. Both raised bogs and aapa mires have typically regularly-patterned microtopography. Seasonal movements of microtopographical features of the aapa mires reflect the morphological dynamism of the mires. Mires are also important sources of information regarding past environmental changes. Their growth pattern is affected by environmental conditions and they respond sensitively to the changes in effective humidity and other climatic variables. Most of the present microtopographical patterns have formed during the last 3,000 years as a response to gradual cooling of climate. Research on Finnish peat deposits has shown, however, that not all peat-stratigraphical changes are caused by past climate variations. They can also be due to the natural growth dynamics of the mires, such as the long-term development towards drier conditions on the surface of the raised bogs, the rhythmic growth pattern of the low hummocks, and the local changes in water table resulting from growth of hummocks and hollows.

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Introduction

Finland is the mire-richest country in Western Europe (Heikurainen 1960). Before the extensive drainage of mires especially during the twentieth century, mires covered 30–35 percent of the Finnish land area. They are still a major landscape-ecological factor, increasing Finland's bio- and geodiversity greatly (Aapala et al. 1998; Vasander 1998). One feature explaining the diversity of mires is the great longitudinal dimension of the country that stretches from the hemiboreal vegetation zone south of 60°N to the subarctic zone in Lapland, north of 70°N. There are major regional differences in the nature of mires in Finland. Apart from the blanket bogs, which are confined to the more oceanic regions (Moore & Bellamy 1974), all major mire types of the boreal zone are found. Raised bogs characterise southern Finland, open aapa mires and sloping fens northern Finland. In the far north of Lapland, palsa mires form the northernmost, periglacial mire complex type (Fig. 1).

The diversity of mire site types reflects the richness of the mire vegetation: their total number is over one hundred (Eurola & Kaakinen 1978; Aapala et al. 1998). Many of them are rare and threatened, largely due to the intensive drainage of the nutrient-rich mire site types for forestry and agriculture. The variation in mire site types is due to numerous edaphic and climatic factors, which can be either of a regional or local nature. Simi-

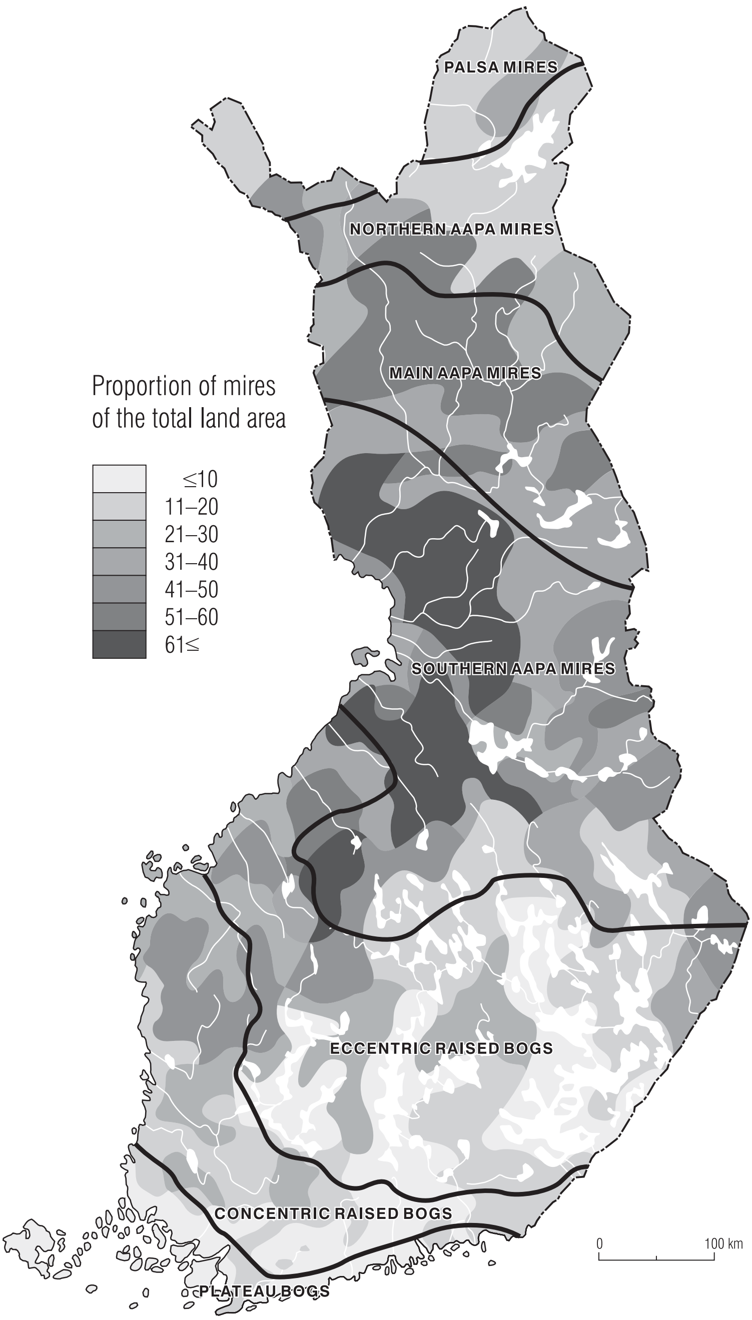

Fig. 1. The geographical division of Finnish mires and the proportion of mires of the land area in different parts of the country (data from Ilvessalo 1960; Ruuhijärvi 1983). The highest proportions are in southern, central, and northern Ostrobothnia and central Lapland. These regions are characterised by large, even peneplains and low evaporation, both important for the initiation and spread of mires. The mire percentages are high also in the subaquatic regions of western Finland, where thick clay deposits smooth the unevenness of the bedrock. The lowest proportions of mires are on the coast of the Gulf of Finland, in the Lake District, and in the far north of Lapland, where small-scale unevenness of the terrain restricts the lateral extension of the mires.

larly, there is considerable diversity in terms of gross morphology, microtopography, and peat stratigraphy between and within each mire complex type and their subtypes.

Regional differences in mires provide the basis for the classification and geographical division of Finnish mires, first suggested by Cajander (1913). His original classification is still valid and widely used in Finland, but the understanding of the environmental factors and processes that lead to the development of different mires increased vastly during the twentieth century. In this article, I describe the basic features of Finnish mires and review the current status of knowledge of their regional and local patterns and processes. Such a comparative geographical approach in mire studies can be of great importance, since regional factors, including climate, geology, and physiography, largely control the development and geographic distribution of mires (Foster & Glaser 1986). Because of the overriding control of climate over the production and decomposition of peat, and because they exhibit vertical and lateral growth, mires also belong to the most dynamic ecosystems in the world. They often respond rapidly to climatic variations and record them as biological, chemical, and physical changes in peat stratigraphy (e.g., Barber 1981; Blackford & Chambers 1991; Chambers et al. 1997). Consequently, I will focus on aspects of stability and change in Finnish mires and on the role of mires in the reconstruction of past environmental conditions.

Mire ecology and mire site types

The most important ecological gradients that affect mire vegetation are pH, nutrient availability, and moisture (Heikurainen 1960; Ruuhijärvi 1983). Variation of these gradients leads to a major ecological division into ombrotrophy and minerotrophy. *Ombrotrophic mires* receive nutrient supply only from the atmosphere and are nutrient-poor and acid (pH usually < 4). Ombrotrophic vegetation dominates the central parts of raised bogs. *Minerotrophic mires* are supplied by minerogenic water flow from the surrounding mineral soils or by ground-water from springs and as seepage through peat, which carries additional nutrients to the mire. Minerotrophic mires can be divided into *oligotrophic, mesotrophic*, and *eutrophic* subtypes according to increasing trophic levels (Ruuhijärvi 1983; Laine & Vasander 1998).

Areas with relatively similar combinations of ecological gradients give rise to ecological niches with typical plant assemblages. These are termed *mire site types* and they form the basis of the ecological classification of Finnish mires (Ruuhijärvi 1983; Laine & Vasander 1998). The four basic mire site type classes in Finland are: (1) *pine fens*, (2) *eutrophic fens*, (3) *spruce swamps*, which are mostly forested mire types, and (4) *open fens* which are treeless. As no two mire plant communities are identical, the mire site type descriptions are abstract simplifications of all the plant communities that belong to the same site type (Heikurainen 1960; Eurola et al. 1982; Laine & Vasander 1998).

Pine fens are forested mire site types. Pine and dwarf shrubs, for example *Betula nana*, *Calluna vulgaris* and *Ledum palustre*, dominate their vegetation. *Rubus chamaemorus* is a characteristic herb. The peat layer is often several metres thick and mostly formed by weakly decomposed *Sphagnum* (*S. magellanicum, S. angustifolium, S. russowii, S. fuscum*) remains with high lignin content.

Eutrophic fens represent the richest mire vegetation in Finland. Their pH and nutrient level are high due to the carbonate content of the soil and bedrock. The most demanding mire species of Finland, such as *Carex dioica, C. flava, Saxifraga hirculus*, and a number of rare mosses, grow on eutrophic fens. Remains of brown mosses and sedges dominate peat stratigraphy. The average depth of the peat layer is circa 150 centimetres (Heikurainen 1960). Because of their strict edaphic requirements, eutrophic fens are confined to few areas in Finland.

Spruce swamps are forested mire site types, usually dominated by dense spruce forests. Other common plants are birch, alder, *Vaccinium myrtillus, V. vitis-idaea*, and several herbs. Tall grasses often characterise the field layer. Peat layers are thin (usually < 100 cm), and the peat is dark, well decomposed, and rich in lignin and tree remains.

Open fens dominate the centres of the ombrotrophic raised bogs and minerotrophic aapa mires. They are mostly treeless and wet mire site types, characterised by *Sphagnum* spp., *Vaccinium oxycoccos, Andromeda polifolia, Eriophorum vaginatum, Carex* spp., and *Tricophorum cespitosa*. Peat is mostly formed by *Sphagnum* spp. and *Carex* spp. The peat layers in the centre of large raised bogs can reach ten metres in depth.

Each main mire site type can be divided further into numerous subtypes depending on the degree of homogeneity required of the mire site types. The number of botanical mire site types is over 100, of which circa 30 are common. That there are more mire site types than forest site types is due to the greater gradient of moisture, greater amplitude in nutrient availability, and also to the broad application of the term *mire* in Finland (Ruuhijärvi 1983; Laine & Vasander 1998).

Mire complex types

On large mires, the combinations of environmental gradients and corresponding mire site types are different in different parts of the mire. Mires are thus formed by a combination of mire site types. Such combinations are termed *mire complexes* (Cajander 1913). The two most common mire complex types in Finland are raised bogs and aapa mires. They differ from each other by various significant morphological, hydrological, trophic, and vegetational characteristics. The palsa mires are a less common but an equally characteristic mire complex type.

Raised bogs

Raised bogs are usually defined on the basis of their gross morphology (*Grossformen* in Aario 1932). The term refers to the profile of the complete mire as defined by precise levellings, usually along the longest diameter of the mire. On raised bogs, the centres of the mires typically rise higher than the level of the surrounding mineral soil. The difference from other mire complex types is not, however, only based on gross morphology, but on several other factors, most of which are superimposed on the morphology. In his original papers about the use of the term *raised bog* (*Hochmoor* in German, *keidassuo* in Finnish), Paasio (1933, 1934) referred exclusively to the mires that are more or less dome-shaped and always rise above the level of the surrounding mineral soil. He thus rejected the definitions based on the trophic status of the mire. On numerous bogs in southern Finland, however, the centre of the bog is not, or is only very slightly, above the level of the mineral soil, but these bogs fulfil all the other criteria of raised bogs, including ombrotrophy. Therefore, such mires can be called *horizontal raised bogs*. Paasio's (1933) list of nutrient-level classes did not include the class 'ombrotrophy'. This may have led to the neglect of trophic status in defining what now are called 'raised bogs'.

The gross morphology of a raised bog can be divided into three gross-morphological parts. The centre, which can rise several metres above the level of the surrounding mineral soil, is termed the *central plateau*. An inclined *marginal slope* surrounds it, and a narrow, minerotrophic *lagg*, which delimits the mire against the mineral soil, encircles the whole of the mire. On the basis of the occurrence and morphology of the central plateau, marginal slope, and lagg, raised bogs can be divided into three gross-morphological types. These are *plateau bogs, concentric bogs*, and *eccentric bogs* (Aario 1932; Paasio 1933; Eurola 1962).

A steep marginal slope and a flat central plateau without higher points or dome-shape characterise *plateau bogs* (Fig. 2A). They correspond with the North-American plateau bogs in their profile, size, and occurrence in relation to the topography of mineral soil (Foster & Glaser 1986). Plateau bogs are mostly found on the fine-sediment plains of the Finnish south coast (Fig. 1) where such mires as Munasuo (in Pyhtää), Punassuo (in Perniö), Maisaarensuo (in Alastaro), and Marjakeidas (in Honkajoki) are good examples of plateau bogs.

Concentric bogs (Fig. 2B) are typically dome-shaped bogs. Their highest point is often close to the centre of the bog, which gives them a symmetrical profile (*symmetrische concentric* in Aartolahti 1965). They are the dominant raised bog type in western Finland (Fig. 1), especially in northern Satakunta and southern Ostrobothnia where they delimit the southern boundary of the aapa mires. Torronsuo in Tammela, which is almost 3,000 hectares in size and the largest raised bog in a natural state in southern Finland, is mostly a concentric raised bog, although this large mire complex includes also other morphological types (Aartolahti 1965).

On *eccentric bogs* (Fig. 2C), the highest point is close to the highest margin of the bog. The bog thus has characteristically an asymmetrical shape (*asymmetriche concentric* in Aartolahti 1965). This is usually due to the uneven, inclined relief of the mineral substratum of the mire (Aartolahti 1965; Ruuhijärvi 1983). Consequently, eccentric bogs are concentrated in areas of uneven topography in eastern and central Finland (Fig. 1). Large, representative eccentric raised bogs are Siikaneva (in Ruovesi), Haapasuo (in Leivonmäki), Kesonsuo and Koivusuo (in Ilomantsi) and Pilvineva (in Veteli).

The development of the gross morphology of a raised bog is a result of continuous accumulation of nutrient-poor *Sphagnum* peat. The growth of the peat deposit means that the bog surface and the water table of the mire rise above the level of the mineral soil, inhibiting the flow of mineral-rich waters from the soils to the centre. Raised bogs have thus been minerotrophic mires until

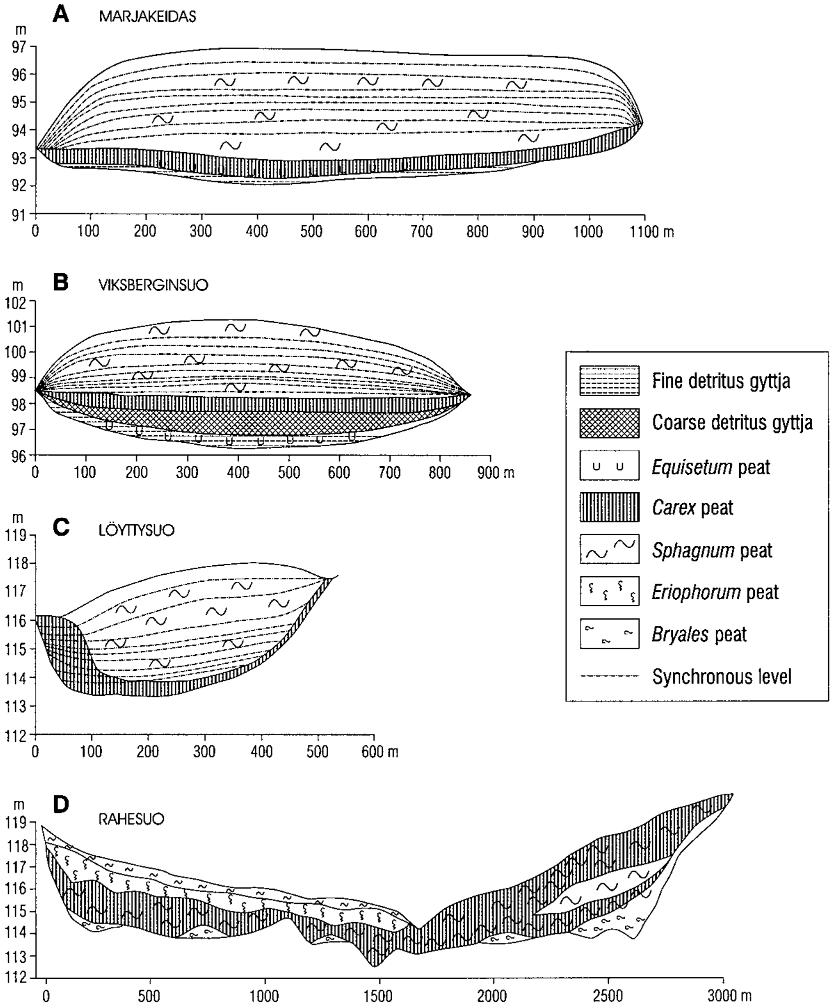

Fig. 2. Differences in gross morphology between different raised bog types (A–C) and an aapa mire (D). (A) A plateau bog; (B) a concentric raised bog; and (C) an eccentric raised bog (all three according to Aartolahti 1965); (D) a typical profile and peat-stratigraphy of an aapa mire (Tolonen 1967).

vertical growth has turned them into ombrotrophy. The development of the gross morphology can be reconstructed by defining synchronous levels in peat stratigraphy in different parts of a raised bog. Earlier, this was carried out by producing pollen diagrams from various parts of the bog and using some synchronous event, often the late-Holocene rise of *Picea* pollen (Aario 1932; Aartolahti 1965). Later, transects of radiocarbon dates have been applied to produce three-dimensional growth models (Korhola et al. 1997). In the future, tephrostratigraphy may provide an even more precise tool for this purpose. These reconstructions indicate that Finland's raised bogs reach their gross morphology during the early stage of their raised bog phase and that the vertical growth of the bog tends to enhance the original gross morphology instead of changing it (Aartolahti 1965; Korhola 1992; Ikonen 1993; Korhola et al. 1997).

As each raised bog undergoes the same main development stages, their general peat stratigraphy is similar. The basal peat varies according the origin of the mire, but is always produced by plants that indicate minerotrophic conditions. The peat often contains remains of trees and large telmatic herbs. Above the basal peat is a layer of *Carex* peat, which also originates during a minerotrophic phase of mire development. This is overlain by often a thick bed of *Sphagnum* peat which reflects the ombrotrophic phase in the mire's history. The shift from the *Carex* to the *Sphagnum* peat layer therefore often – but not always – indicates the initiation of the raised bog phase in mire development. Figures 2A, 2B, and 2C illustrate the standard outlines of peat-stratigraphical patterns of Finnish raised bogs.

Microtopography: hummocks and hollows

In addition to their typical gross morphology, raised bogs are characterised by their *microtopography*, i.e., the patterns of the hummocks and hollows on their surfaces (*Kleinformen* in Aario 1932). *Hummocks* are higher and drier parts of the bog surface, whereas *hollows* are wet depressions. They occur often in regular series located perpendicularly in relation to the inclination and direction of the water flow of the bog. Microtopography is the most conspicuous on the moist and clearly dome-shaped raised bogs, especially on the concentric bogs in northern Satakunta and South Ostrobothnia. There, the hummocks can be 50 to 100 centimetres high and several hundreds of metres long (Aartolahti 1965, 1966). They run parallel to the contours of the bogs and form a distinct rim around the highest point of the mire. Their slopes are usually steeper on the proximal side than on the distal side. On plateau bogs and horizontal bogs, the hummocks are only 10–30 centimetres high and they are either short and discontinuous or form unoriented, low nets on the mire surface (Eurola 1962; Aartolahti 1966; Ruuhijärvi 1983; Tolonen & Seppä 1994). On the south coast of Finland, hummocks and hollows are often the most distinct on hummock–hollow pine bogs, where large hollows separate pine-covered hummocks.

The origin, growth pattern, and stability of the microtopography of the raised bogs have been among the major dilemmas of mire research since the nineteenth century. The earliest theories stressed the transient nature of these landforms. According to the regeneration model, initiated by von Post and Sernander (1910) and further developed by Osvald (1923), hummocks and hollows would be characteristically unstable. The peat accumulation was assumed to be faster on hollows than on hummocks. Therefore, a hollow would eventually rise above the level of the hummock. This development would lead to a cyclic growth pattern where a hollow would turn into a hummock and, eventually, again into a hollow. Investigations of the growth dynamics of *Sphagnum* species in hummocks and hollows would seem to support this model, as measurements show that the *Sphagnum* species of the moist hollows grow faster than the species on dry hummocks and that the annual thickness increment of a living *Sphagnum* cover is also faster in hollows (Lindholm & Vasander 1991). By analysing the peat stratigraphy of open sections, Walker and Walker (1961) showed, however, that on the Irish raised bogs hummocks and hollows are mostly stable landforms. Aartolahti (1965, 1967) made similar conclusions in Finland in his detailed analysis of *Sphagnum* leaves of peat cores from hummocks and hollows in the raised bogs of Southwest Finland. The results (Table 1) show that large hummocks and hollows have been stable and permanent and no cyclic replacement has taken place since their initiation at circa 3000–2000 ^{14}C yrs BP. Tolonen's (1971) detailed peat-stratigraphical investigations of open sections on a raised bog in southern Finland later confirmed this. He stressed that open sections are more reliable in studies of the development of raised bog microtopography and that corings may give false evidence of regeneration.

Thus, there must be a mechanism that compensates the faster thickness increment of the hollows and prevents cyclic regeneration. Apparently, it lies in the distinct floral differences between the hummock and hollow *Sphagnum* species and their biochemical differences. Detailed analyses of *Sphagnum* peat macrostructure indicate that the decomposition of *Sphagnum* species in hollows proceeds more rapidly than their decomposition in hummocks (Johnson et al. 1990). Johnson and Damman (1991) carried out a biological transplantation experiment on raised bogs. They transferred plants of *Sphagnum cuspidatum* (a species that grows on moist hollows) into a hummock and plants of *Sphagnum fuscum* (a species that grows on dry hummocks) into a hollow, and recorded the changes in decomposition degree over time. They observed that *S. fuscum* decomposed significantly more slowly than *S. cuspidatum*, apparently due to biochemical properties that make *S. fuscum* resistant to decomposition processes in general. The results therefore suggest that while the growth of *Sphagnum* species in moist hollows is often faster than the growth of hummock *Sphagnum* species, the greater resistance to decomposition may lead to greater accu-

Table 1. Stability of the microtopography of raised bogs as indicated by microscopic analysis of *Sphagnum* leaves in peat cores from hummocks and hollows – an example from Linturahka, Mellilä, SW Finland. *Sphagnum balticum* and *S. cuspidatum* dominate the hollow since its rapid initiation at circa 3200 ^{14}C yr BP, whereas *S. fuscum* is the dominant species of the hummock (Aartolahti 1967: 77).

	Hummock						Hollow								
Depth (m)	S. fuscum	S. rubellum	S. angustifolium	S. magellanicum	S. papillosum	S. fallax	S. fuscum	S. rubellum	S. angustifolium	S. magellanicum	S. balticum	S. majus	S. cuspidatum	S. fallax	
0.1	92	—	8	—	—	—									
0.2	96	—	3	1	—	—									
0.3	96	2	2	—	—	—	7	6	—	5	79	—	—	—	
0.4	100	—	—	—	—	—	5	—	—	—	36	12	47	—	
0.5	100	—	—	—	—	—	7	—	2	—	68	—	23	—	
0.6	94	—	4	3	—	—	—	—	—	—	15	14	71	—	
0.7	97	—	—	3	—	—	—	—	—	2	26	—	70	—	
0.8	100	—	—	—	—	—	4	—	5	4	84	—	3	—	
0.9	96	—	—	4	—	—	—	—	—	7	62	—	31	—	
1.0	87	—	13	—	—	—	—	—	—	3	11	—	82	—	
1.1	94	—	3	3	—	—	—	1	—	—	12	—	87	—	
1.2	100	—	—	—	—	—	24	—	—	—	13	—	63	—	
1.3	96	—	3	1	—	—	12	—	—	—	10	—	78	—	
1.4	87	2	11	—	—	—	3	3	—	—	7	—	82	—	
1.5	93	4	3	—	—	—	18	—	4	7	3	—	68	—	
1.6	96	—	—	4	—	—	6	—	2	4	12	—	76	—	
1.7	100	—	—	—	—	—	—	4	—	5	71	—	20	—	
1.8	100	—	—	—	—	—	6	7	—	—	87	—	—	—	
1.9	95	1	4	—	—	—	—	2	—	6	91	—	—	—	
2.0	100	—	—	1	—	—	—	—	—	—	93	7	—	—	
2.1	100	—	—	—	—	—	—	—	—	3	11	—	82	—	
2.2	97	—	3	—	—	—	—	2	—	—	7	—	91	—	
2.3	97	—	3	—	—	—	—	—	—	1	9	13	77	—	
2.4	94	—	2	4	—	—	2	—	—	—	64	7	27	—	
2.5	83	1	14	2	—	—	3	12	—	5	80	—	—	—	
2.6	100	—	—	—	—	—	—	5	17	—	78	—	—	—	
2.7	95	—	5	—	—	—	7	3	11	—	82	—	—	—	
2.8	71	—	26	3	—	—	63	—	31	6	—	—	—	—	3170±105
2.9	73	—	25	2	—	—	61	—	36	3	—	—	—	—	^{14}C yr BP
3.0	41	—	47	12	—	—	12	—	84	4	—	—	—	—	
3.1	15	—	39	46	—	—	—	—	81	13	6	—	—	—	
3.2	10	—	88	2	—	—	3	—	89	—	—	—	—	8	
3.3	—	—	19	—	13	68	—	—	17	—	4	—	—	79	
3.4	—		3	—	14	83	—	—	5	—	—	—	—	95	

mulation of peat on hummocks and thus prevent the hollow level from rising above the hummock level (Johnson et al. 1990; Johnson & Damman 1991).

Hypothetically, the inherent decomposition properties of *Sphagnum* species could also cause the development of the microtopographic patterns so that the greater peat production of *S. fuscum* -dominated microsites would give rise to hummocks (Johnson & Damman 1991). There are, however, easily observable features in raised bog microtopography which the decomposition theory alone does not explain. These include the regular patterning of the hummocks and hollows and their perpendicular location in relation to the inclination of the mire surface. A factor that can influence the development of these patterns is flowing water. This is indicated by the fact that the regular, rim-shaped hummock and hollow microtopography develops on a slightly inclined mire surface, and on flat raised bogs it is net-like and less distinct. Once flowing water has initiated the topographical differentiation and led to differences in moisture conditions on the mire surface, the vegetational differences start to develop and the decompositional difference of *Sphagnum* species begins to influence the peat production.

Open water pools, apart from hollows and mud-hollows, are often common on Finland's raised bogs. They are roughly 20 metres in diameter on average, but the largest pools can be up to 200–300 metres long and several metres deep. There are over one thousand pools on Torronsuo (Aartolahti 1965). Dating of the pools' basal peat has shown that the pools are often thousands of years old, but usually younger than the basal peat of the mire. This means that they usually are secondary features on the raised bogs and have developed during the *Sphagnum*-dominated stage of the raised bog from the permanently waterlogged ponds on the mire surface (Aartolahti 1965, 1967). Under such conditions peat accumulation may cease and degradational processes become dominant. Pools are common also elsewhere on the raised bogs. They are believed to be outcomes of the erosion of hollows and the rejoining of several hollows and smaller pools (Foster et al. 1983; Foster & Glaser 1986; Foster et al. 1988).

Aapa mires (Patterned fens)

Aapa mires dominate from central Finland to the northern tree line in Lapland (Fig. 1). Their size varies from small to the largest mire complexes in Finland. In contrast to most of the raised bogs, aapa mires are not convex, but usually concave and inclined in profile (Fig. 2D). Mineral-rich runoff waters can thus reach their centres and aapa mires are minerogenic, apart from their high strings. As aapa mires occur in those parts of Finland where snow depth is considerable and the snow melts rapidly in late spring, spring floods that inundate the mire surface are of great significance for the mires' development and vegetation (Ruuhijärvi 1960).

Aapa mires have a distinct microtopography of higher strings and intermittent lower and moister flarks. These patterns are usually located perpendicularly in relation to the inclination of the aapa mire surface, but they do not form rim-like formations like the hummocks and hollows of the raised bogs. The strings of the aapa mires can be even higher and longer than the hummocks of the raised bogs, being sometimes over a metre in height and several hundreds of metres in length. On strongly inclined aapa mires, the strings are characteristically arch-shaped, their centres pointing in a downhill direction and often damming a large water pool on the uphill side. The string vegetation consists of *Sphagnum* spp., *Calluna vulgaris, Betula nana*, and *Ledum palustre* in the north and, to a lesser extent, of other dwarf shrubs. *Carex* spp., *Eriophorum* spp., and *Sphagnum* spp. dominate the flarks.

The Finnish aapa mires have not been divided into gross-morphological subtypes, but Ruuhijärvi (1960) divided the aapa mire zone into three subzones mainly on vegetational and microtopographical criteria (Fig. 1). In the southern aapa mire zone, *Sphagnum papillosum* -dominated open fens and weakly developed strings and flarks characterise the mires. In the main aapa mire zone, the mires typically have pronounced microtopography, flarks, and long, continuous strings that form regular patterning on the mire surface. In the northern aapa mire zone, microtopography is less regular and the strings form often discontinuous networks (Ruuhijärvi 1960).

The origin of the strings and flarks of the aapa mires is still largely unknown, as is the case with the microtopography of the raised bogs. Several theories have been put forward to explain the origin of these strikingly regular and clear landforms. Moore and Bellamy (1974) and Seppälä and Koutaniemi (1986) reviewed the theories and classified them into three main groups: (1) biological explanations; (2) frost and ice activity theories; and (3) gravity theories. The great variety of proposed theories indicates the difficulty of pointing out one model that would conclusively explain the origin of the microtopography. It is therefore possible that the origin is due to a combination of factors, possibly involving all of the three groups.

Recent work on an aapa mire in Kuusamo, north-eastern Finland, has shed light on the instability of the strings and pools and the importance of various processes causing their movements (Seppälä & Koutaniemi 1986; Koutaniemi 2000). A series of measurements during 21 years shows that the strings are highly unstable landforms, moving downhill, sideways, and even uphill, often 2–5 centimetres but sometimes even up to 50 centimetres in a year (Fig. 3). Seppälä and Koutaniemi (1986) stress the importance of hydrostatic pressure as the cause of the movements. According to Koutaniemi (2000), ice- and frost-related winter processes are of great importance in causing the movements, and an aapa mire in winter behaves like a frozen lake in that the frozen mire surface expands horizontally as the temperature rises. The ice thrust can be one of the causes of the strings' uphill movements (Koutaniemi 2000). This process, however, should cause downhill movement of those strings that are located downhill from the mire centre. It should also affect the flarks of an aapa mire. Hydrostatic water pressure of the flarks is probably the most important cause of the movement in the summer, but some of the summer movements may actually take place in response to the winter movements, i.e., the strings can return downhill after having been pushed uphill during the previous winter (Koutaniemi 2000). All in all, these measurements show the importance of the spring and winter conditions in influencing the microtopography of the aapa mires (Seppälä & Koutaniemi 1986; Koutaniemi 2000), an aspect stressed already by Helaakoski (1912), Tanttu (1915), and Ruuhijärvi (1960).

The *sloping fens*, mostly confined to the hilly regions of Kainuu and eastern Lapland, are a special variant of the aapa mires. They are common in the Kuusamo–Salla and Puolanka–Suomussalmi areas, but there are scattered sloping fens as far as in the Pielisjärvi region in the south (Havas 1961). They are mostly distributed on hill slopes and, because of this, their surface is exceptionally inclined. The altitudinal difference between the upper and lower ends of the mire is usually circa 20 metres, but sometimes up to 200–300 metres (Auer 1922; Havas 1961). Their general form is often oblong and slightly sinuous. The microtopography is weakly developed and the peat layer is usually thinner than on typical aapa mires, being thicker on moister sloping fens (Havas 1961).

The occurrence of the sloping fens depends on a plentiful supply of runoff water. It is often produced, in addition to melting snow, by springs or small aapa mires located at the upper end of the sloping fen. If there is no adequate supply of runoff water to keep the sloping fen's surface wet, the peat layer will become well decomposed and thin, and trees (mostly spruce) will occupy the mire surface (Havas 1961).

The aapa mires of central and northern Lapland are Finland's largest mires. The area of Teuravuoma in Kolari is circa 7,080 hectares. A very large example of the northernmost variant of the aapa mires is Sammuttijänkä in Inari, which has also features of a palsa mire (Ruuhijärvi 1960). In eastern Lapland, there are extensive aapa mires on

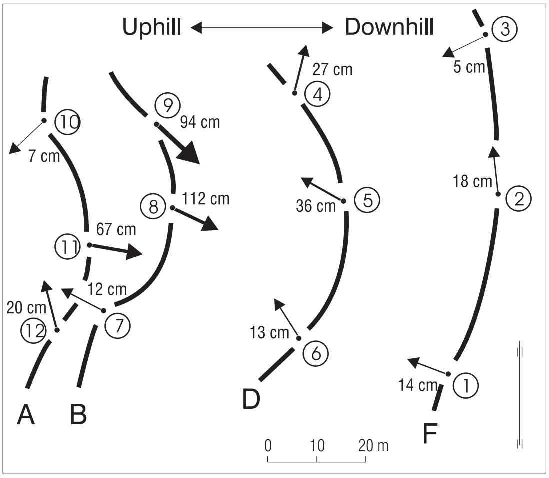

Fig. 3. The movements of the strings on an aapa mire in Kuusamo. The sum vector shows the cumulative movements during the study period 1976–1997 (Koutaniemi 2000: 528).

the lowlands, such as Joutsenaapa in Salla and Sakkala-aapa in Pelkosenniemi, part of which is a raised bog. Large aapa mires dominate also the upper reaches of the Kitinen and Luiro rivers. In this area was located the largest mire of Finland, Posoaapa (in Sodankylä), which the Lokka Reservoir inundated in 1967–1968.

Palsa mires

North of the typical aapa mires is the zone of palsa mires. They can be viewed as the periglacial mire variant in Finland, due to the occurrence of permafrost (Seppälä 1988). Instead of the strings and flarks of the aapa mires, palsa mires are characterised by *palsas*, high peat mounds with permafrost cores. The core is formed of frozen peat or silt with thinner layers of ice and small ice crystals (Seppälä 1988). *Pounus*, small and low (< 50 cm) peat hummocks with a non-permanently frozen core, often surround higher palsas. Vegetation of the palsa mires resembles the plant communities of the flarks of the northern aapa mires. Typical species of the wet surfaces include *Sphagnum lindbergii, Carex vesicaria, C. rotundata*, and *C. rostrata*. The vegetation of the palsas is totally different because of the dryness of their surfaces. Characteristic species are *Betula nana*, *Empetrum nigrum*, *Rubus chamaemorus*, lichens and, on the lower slopes, *Sphagnum fuscum*. Birch and willow are also common (Ruuhijärvi 1960, 1983).

There is considerable variation in palsa morphology. *Dome-shaped palsas* are the most typical morphological palsa type in Fennoscandia. They are usually 0.5–7 metres high and 10–30 metres wide (Åhman 1977; Seppälä 1988). *Plateau palsas* are 1–1.5 metres high, have sharp edges, and a flat central plateau (Sollid & Sørbel 1998). *String-form* palsas are narrow, sinuous ridges with a permafrost core. They resemble the strings of the aapa mires, as they run parallel to the contour of the mire. Elongated string-like palsas that are located parallel to the gradient of the mire are called *ridge-form palsas* (Seppälä 1988) or *esker palsas* (Åhman 1977).

Cold climate and the peat's insulation properties control the initiation and growth of a palsa. On sites where snow accumulation in winter is limited, usually due to wind, the frost penetrates deep in the ground and the summer warmth does not melt it completely. This frozen soil rises above the level of the surrounding soil, leading to an increasingly thin snow cover. This creates small embryonic palsas, which continue their growth as the frozen core attracts water from the surroundings (Åhman 1977; Seppälä 1986, 1988; Matthews et al. 1997). Finally, the palsa may reach a height where tensional cracking begins on the surface peat and the palsa starts to degrade through thermokarstic processes (Seppälä 1986, 1988). A waterlogged rim-ridge rampart remains as evidence of a degraded dome-shaped palsa (Matthews et al. 1997).

Representative and well-known palsa mires in Lapland are located, for example, in Iitto and Markkina in Enontekiö and in Suttisjoki in Inari. Piera-Marin jänkä in the municipalities of Inari and Utsjoki is one of the best-developed palsa mires with tens of high palsas. Pies(järven)jänkä in Inari is a large, legally protected palsa mire.

On the fells of Finnish Lapland, there are typical small alpine or oroarctic mires with very thin and discontinuous peat layers. *Carex* spp. dominate these mires. They are minerotrophic and moist as they receive great amounts of mineral-rich water during the spring snow melt and also during the summer from the melting summer snow beds. Because of their occurrence in the vicinity of springs and in the cation-rich bedrock of northwestern Lapland, they are often botanically eutrophic fens (Ruuhijärvi 1983). In flat depressions, peat layers are thicker (1–2 m) and continuous.

Boundaries of mire complex types: the role of climate

The boundary that separates the raised bog zone and the aapa mire zone is clear and well-established (Fig. 1 & Fig. 4). It was first determined by Cajander (1913) and only minor adjustments have been carried out since then. In the west, the boundary runs southwards along the Suomenselkä watershed, turning to the north-east in the Lake District, and again slightly to the south-east in eastern Finland. These minor wiggles in the boundary probably result from regional climatic differences. The overall location of such a clear boundary between southern and northern Finland reflects the influence of climate on geographical differentation of the mire complex types (Ruuhijärvi 1983). In Figure 4, the boundary is compared against three different climate parameters: duration of thermal winter, mean annual number of days with minimum temperature below –0 degrees centigrade (°C), and annual mean temperature. As all these climate variables are related to winter conditions, the comparison emphasises the importance of frost and snow in influencing the major division of Finland into raised bog and aapa mire zones. The lower summer evaporation and resulting summer moisture surplus may also be important factors that favour the development of aapa mires in the north (Ruuhijärvi 1960, 1983; Solantie 1974).

A straightforward comparison of the boundary and the three climatic variables as in Figure 4 can be misleading, however. The approximate overlap of subjectively selected boundaries is not necessarily a proof of a simple causal relationship between the selected climatic variables and the boundary, especially in a country where most of the temperature-related climatic variables show similar north-to-south gradients. It is therefore possible that no single climatic factor determines the location of the boundary, but it may be formed as a combination of several covariant factors. In this respect, the azonal occurrences of raised bogs and aapa mires far away from their zonal boundaries are of particular significance. There are individual raised bogs in Lapland up to circa 68°N and individual aapa mires in southern Finland (Ruuhijärvi 1960; Atlas of Finland 1988). These occurrences may be linked to non-climatic local conditions that favour the development of regionally exceptional mire complexes.

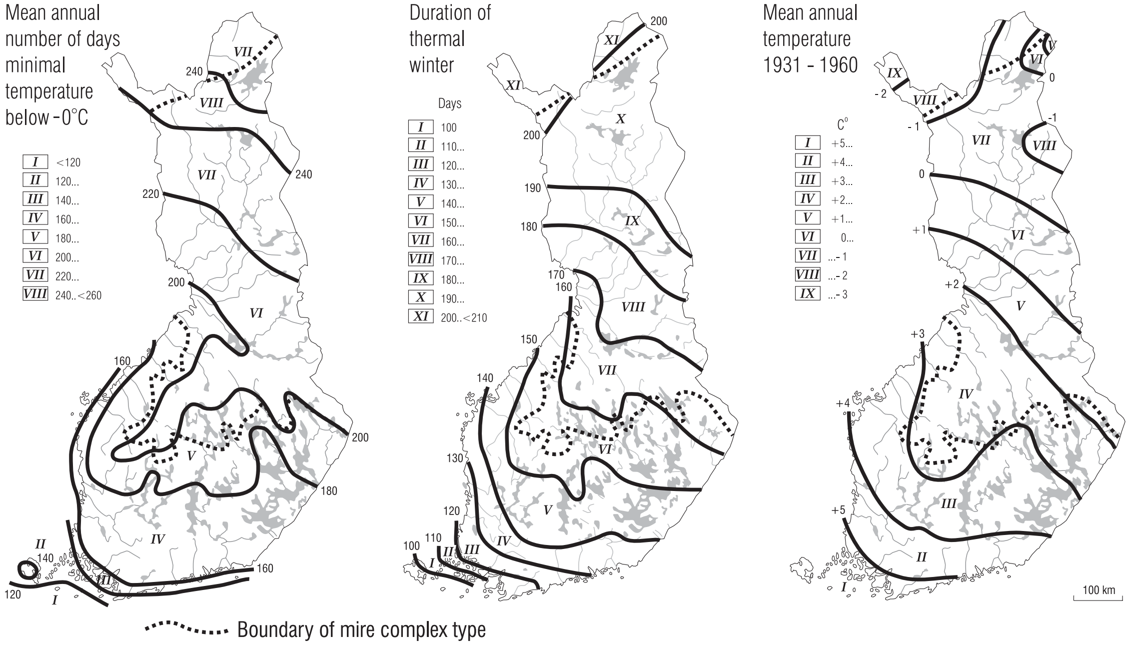

Fig. 4. Boundaries of mire complex types compared against three climate parameters. The climate data are from *Atlas of Finland* (1987).

It is interesting to compare the location of the corresponding boundary and its determinants elsewhere in the boreal zone. In eastern Canada, raised bogs occur on the coastal zone where the climate is comparatively oceanic with less extreme seasonal temperature changes, less precipitation, and less snowfall than further inland (Foster & Glaser 1986). The aapa mire zone (patterned fen zone) is confined to inland where precipitation and snowfall are higher and winters colder because of higher altitude. According to Foster and Glaser (1986), the critical single climatic feature determining the dominant mire complex type is water surplus, especially the higher amount of spring snow melt inland. The surplus of mineral-rich runoff water will support minerotrophic mire vegetation and inhibit the development of raised bogs in a similar way as the margins of raised bogs remain minerotrophic due to the runoff from the surrounding mineral soil. The outlines of this model are consistent with the traditional Finnish view according to which the spring and early summer floods are crucial for the formation of aapa mires. Therefore, the azonal occurrence of individual mire complexes can be explained by local hydrological factors. The aapa mires in southern Finland are often confined to sites with a local source of water surplus, such as an esker or other elevated topographical features in the vicinity of the mire. The raised bogs in Lapland are often located on water divides, riverbanks, lakeshores, and extremely coarse, well-drained soils where the importance of runoff and floodwaters is smaller (Ruuhijärvi 1960, 1983).

The palsa mires in Finland are in northernmost Lapland, north of the –0.5 °C or –1.0 °C annual isotherm (Fig. 4) (Seppälä 1988) and mostly north of the distribution limit of pine. Summer temperatures (July mean temperatures) in the palsa mire region are usually below +12.0 °C. Palsa mires are also common in Finnmarksvidda, northern Norway, where summer temperatures are roughly equal to those in northern Finland and annual precipitation is very low, circa 350–500 millimetres. There are, however, very few palsa mires on the shores of the Barents Sea and northern Norwegian Sea between Hammerfest and Tromsø, despite lower summer temperatures (Åhman 1977; Seppälä 1988; Sollid & Sørbel 1998). This is probably due to the higher precipitation on the coastal area (annual precipitation 500–1,000 mm), since summer moisture decreases the insulation properties of peat and enhances the penetration of summer warmth to the permafrost core of a palsa (Seppälä 1988; Zuidhoff & Kolstrup 2000). Palsa mires are thus mostly continental in their distribution and a climate change towards moister summer conditions may destroy a palsa (Sollid & Sørbel 1998).

Long-term development of the Finnish mires

Mire initiation and peat accumulation

Mires are formed in areas where precipitation is high and evaporation low. A level substrate enables the lateral spread of the mires. The Finnish mires started to develop after the last deglaciation circa 10,000 ^{14}C years ago. The oldest ages recorded from basal peat in Finland are circa 9500 ^{14}C yr BP (Tolonen et al. 1994). In Finland, mire initiation has taken place in three different ways: forest paludification, lake terrestrialisation, and primary mire formation, referring to the spread of mire vegetation on a recently deglaciated soil or one that has emerged from the water as a consequence of post-glacial isostatic land uplift. Locally, river flooding may also have resulted in the initiation of mires.

Studies of basal peats show that primary mire formation and paludification have been the most common mire initiation pathways in Finland (Huikari 1956; Korhola 1990a). Up to 60 percent of the mires have been initiated through primary mire formation in Ostrobothnia where the landscape is flat and post-glacial isostatic land uplift fast (Huikari 1956; Ruuhijärvi 1983). The intensity of paludification is linked to the changes in water table. Climatic change or forest fire may cause a rise of the water table. This, in turn, may lead to paludification, but most of the paludification has happened through a lateral extension of already existing mires (Aario 1932; Lukkala 1933; Korhola 1990a). Lake terrestrialisation was earlier considered the most common form of mire initiation (Heikurainen 1960), but Huikari's (1956) investigations indicated that only 5–10 percent of the Finnish mires have been formed through this process. Later studies suggest, however, that this may be an underestimate, at least in the southern raised bog area, where the proportions of mires with limnic sediment at the bottom are 30–44 percent (Lappalainen & Toivonen 1985; Korhola 1990a). Lake terrestrialisation may have been more common and faster during dry climatic periods when lake levels were low. This may have accelerated the hydroseral succession of lakes (Korhola 1990b; Tikkanen & Korhola 1993).

Lateral growth of the mires was rapid during the earliest post-glacial period when there were large, flat land areas in Finland, suitable for an unrestricted expansion of the mires. The mires may have spread laterally even hundreds of metres in a century (Korhola 1992). Climatic conditions also regulated the spreading rate (Fig. 5). Radiocarbon dating of the paludified mires in southern Finland indicates that the lateral spread was rapid during moist periods (for example at 7000–6000 ^{14}C yr BP and 4000–3000 ^{14}C yr BP), but that during drier times (such as 6000–5000 ^{14}C yr BP) the spread almost ceased (Korhola 1994). These studies show also that during recent millennia very little paludification has occurred in Finland (Korhola 1994). This may not, however, reflect climatic conditions, but results probably from the fact that during the Holocene most of the topographically flat areas have already been paludified and topographical barriers now restrict lateral spread (Ruuhijärvi 1983; Mäkilä 1997; Korhola & Tolonen 1998).

The slow vertical growth of the mires is based on constant peat accumulation. It results from incomplete decomposition of plant litter, so that 5–20 percent of the plant biomass produced on the

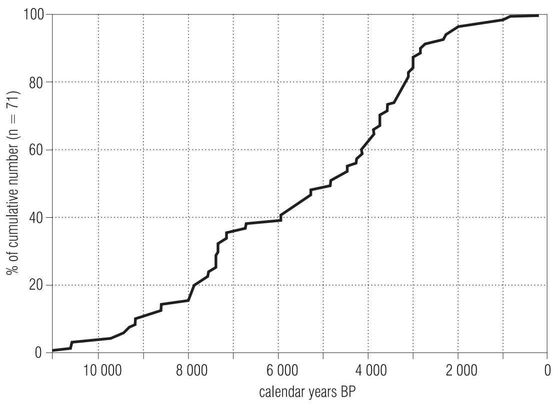

Fig. 5. A cumulative frequency curve of the radiocarbon dates for basal peats from the paludified sites in Finland (Korhola 1994: 54).

mires does not decompose before it accumulates in the anaerobic peat layer of the mire (Clymo 1984; Gorham 1991). Long-term average vertical growth rates have been studied in Finland by means of hundreds of radiocarbon dates. The resulting rates range from 0.2 to over 4.0 millimetres per year, with an average of circa 0.5 mm/year (Tolonen et al. 1994; Korhola & Tolonen 1998). The considerable variation reflects the highly individual growth conditions and peat production on Finnish mires. The rates are generally faster on ombrotrophic raised bogs than on aapa mires. The rates also decrease northwards and with the age of the mires (Tolonen et al. 1994). Consequently, the thickest peat layers in Finland (> 10 m) are found on the raised bogs of southern Finland. They are located in geologically old areas, i.e., in supra-aquatic areas or in areas that have emerged from the Baltic Sea during the early Holocene.

Peat stratigraphy and climate changes

One of the most important applications of peat-stratigraphical studies is their use as archives of past environmental changes. The dynamic relationship between raised bogs and climate, in particular, results from the sensitive balance between the growth of plants (mainly *Sphagnum*), decomposition of peat, the level of the water table, and the thickness of the aerobic layer on top of the mire. The aerobic layer above the water table is termed the *acrotelm* in distinction from the *catotelm*, the anaerobic layer below the water table (Ingram 1978). All biological production and most of the decomposition take place in the acrotelm (Clymo 1984). As this layer is usually only 0–50 centimetres thick, a change of mean water level by only a few centimetres can drastically affect the rate of peat decomposition (Clymo 1984) so that the peat becomes less decomposed as a result of a rise of the water table and more decomposed as a result of its decline. Peat production is thus particularly sensitive to changes in effective humidity, which can vary mainly as a function of temperature, precipitation, or both.

Peat-stratigraphical investigations have had a major role in European climate history research. The classical Blytt–Sernander model of post-glacial climate changes was predominantly based on peat-stratigraphical studies. It influenced strongly the European palaeoclimatological concepts and research during the late nineteenth and early twentieth century (Seppä 1995). It is important to keep in mind, however, that mires are inherently dynamic systems. Their development includes both low-frequency and high-frequency changes caused by local factors that may be independent of climate or other regional environmental changes (e.g., Aario 1932; Aartolahti 1965; Foster & Glaser 1986). It is thus possible that, in the course of its vertical growth, a raised bog develops gradually toward drier surface conditions, even if there is no regional climate change toward dryness. Peat stratigraphy often reflects this natural development. Consequently, changes that reflect deviations from this development, i.e., upcore changes that indicate increasingly moist conditions, may be interpreted as being caused by climate changes (Granlund 1932; Aaby 1976). Corresponding stratigraphical layers are termed *recurrence surfaces* (Granlund 1932).

The best-known recurrence surface in northern Europe that can be linked to climate change is the widespread change from underlying well-decomposed dark peat to overlying less-decomposed lighter peat. The boundary horizon between these two layers is termed SWK (*Swarztorf/Weisstorf Kontakt*) or *Grenzhorizont*, as Weber (1900) first described it in Germany. The Grenzhorizont is usually connected to climate cooling after the Subboreal chronozone at circa 3000–2500 ^{14}C yr BP, and it is associated with the general rejuvenation of the bog, caused by increased water availability on the bog surface (e.g., Svensson 1988). Peat-stratigraphical research in southern Finland (Tolonen 1967, 1973, 1987) has shown that many Finnish raised bogs and aapa mires contain a similar boundary layer, but that the difference between the underlying well-decomposed peat and overlying less-decomposed peat is usually not distinct and sometimes cannot be detected at all. Furthermore, radiocarbon dating of the boundary in Finnish mires does not indicate any precise timing for the change, only that is ranges from circa 5000 to 2500 ^{14}C yr BP even in the relatively small geographical area (circa 100 km^2) of the municipality of Lammi in southern Finland (Tolonen 1987). The diachronity of the Grenzhorizont in Finnish mires suggests that the climate has cooled gradually as well and that the mires have responded to the changing climate individually. Each response has depended on the original individual characteristics of mire hydrology, morphology, and vegetation.

In addition to the Grenzhorizont, the peat stratigraphies of many European mires contain other recurrence surfaces which are identified as sudden changes from more decomposed layers of darker peat to lighter, less-decomposed peat which again can be overlain by a thinner layer of more decomposed peat. Granlund (1932) determined five recurrence surfaces (RYI-V) on Swedish raised bogs. One of these was concurrent with Weber's (1900) classical Grenzhorizont, dating to the first millennium BC. More recurrence surfaces have been reported later (Nilsson 1935; Lundqvist 1962; Svensson 1988) in Fennoscandia, but their link to climate changes is still unclear. Critical questions are the synchronicity of recurrence surfaces on one mire, between the mires, and the precision of chronological control. The dating of peat-stratigraphical changes by means of radiocarbon dating is not always precise enough for comparisons with known climate changes during the late Holocene (Tolonen et al. 1985; Tolonen 1987). Because of its asynchronous nature, it has been impossible to connect the Finnish SWK contact to any recurrence surfaces reported in Sweden (Tolonen 1987). Thus, there is no unambiguous evidence of the occurrence of climatically controlled recurrence surfaces in Finland, despite the long tradition of peat-stratigraphical studies and a large number of detailed peat-stratigraphical analyses.

A further problem complicating the correlation between peat-stratigraphical changes and climate dynamics is the lack of experiments or modern monitoring studies of the influence of rapid climate changes on mire surface and peat. Hence, the influence of high-frequency moist or dry periods on peat stratigraphy is understood inadequately. Investigations of such events might serve to elucidate the origin of the so-called *humification streaks*, common in Finnish raised bogs (Aartolahti 1965; Tolonen 1971). These streaks are usually 2–10 millimetres thick and consist of dark, well-decomposed peat with remains of *Calluna vulgaris*, *Eriophorum vaginatum*, and lichens. They have been studied in detail on Klaukkalan Isosuo, where about 25 dark streaks occur in the peat formed during the last circa 4000 ^{14}C yrs (Fig. 6) (Tolonen 1971). Both a high degree of decomposition of the peat and the peat composition clearly indicate that these streaks are produced by vegetation growing in dry sites on the mire surface. Two theories can be put forward to explain the sudden occurrence of such dry conditions on the mire surface. In boreal peat bogs, thin, dark humification streaks might represent evidence of sudden drying of the mire surface due to an abrupt dry climate period. Alternatively, they may be local features, related to the bog's natural growth rhythm. The latter explanation seems to be true in Finland (Aartolahti 1965; Tolonen 1971), because the lateral extension of these streaks is usually limited and they seem to be fragmentary and asynchronous even in one mire (Fig. 6) (Aartolahti, 1965; Tolonen 1971). Their occurrence seems to be related to the rhythmic changes in *Sphagnum fuscum* growth as the peat above and below is formed by *S. fuscum*. This kind of regen-

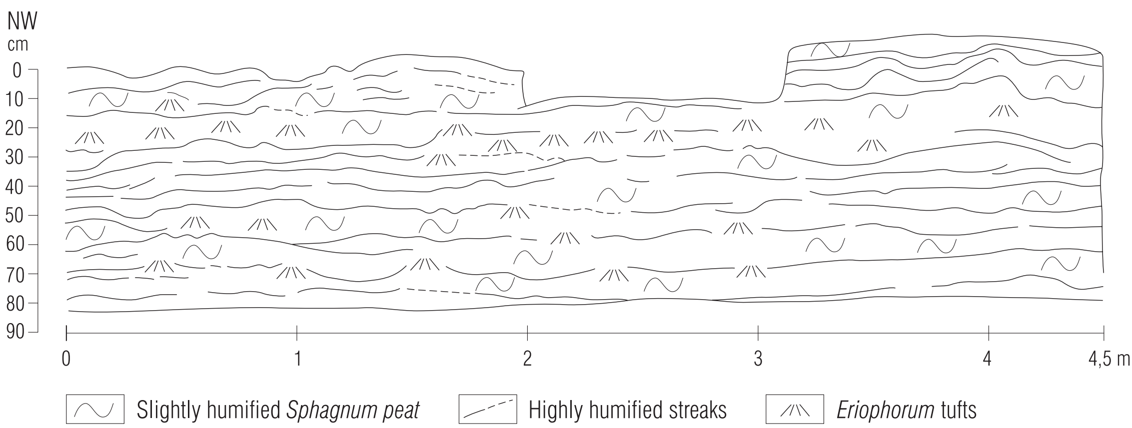

Fig. 6. A schematic picture of the occurrence of dark humification streaks on an open section on Klaukkalan Isosuo, a raised bog in southern Finland (Tolonen 1971: 151).

erative growth pattern can be termed "*fuscum*-regeneration" or "short-cycle regeneration" (Tolonen 1971; Tolonen et al. 1985). In *fuscum*-regeneration, the low *S. fuscum* hummocks grow vertically beyond the moisture range of *S. fuscum* and, e.g., *Calluna vulgaris* and lichens colonize the drying hummock top (Lindholm 1990). The upward growth of the hummock ceases and decomposition and drying lead to the hummock's destruction. The detailed manner in which the streaks are formed is still unclear, however. It is possible that very dry summers and low water tables favour their formation (Tolonen 1971).

The occurrence of the decomposition changes or humification streaks does not bear unambiguous climatic signals in the Finnish raised bogs, but it is probable that the formation of microtopography on raised bogs and aapa mires is connected to mid-to-late Holocene climate changes. Radiocarbon dating of peat from the initiation phase of the raised bog hummock and hollow topography in southern Finland has resulted in ages ranging from 3200 to 2100 ^{14}C yr BP (Aartolahti 1967). Dates of 1940 ± 130, 1050 ± 160, and 1020 ± 120 ^{14}C yr BP have been reported from the basal peats of plateau bog hollows on the Finnish south coast (Tolonen & Seppä 1994). The origin of the hollows on Estonian raised bogs seems to be roughly synchronous with that in Finland (Karofeld 1998). Ages ranging from circa 3000 to 2000 ^{14}C yr BP were obtained for the formation of strings on aapa mires in Kuusamo (Seppälä & Koutaniemi 1988). These were connected to an increasing wetness of the mire surface due to regional climate change. These works suggest that the origin of microtopography of the raised bogs and aapa mires may be a late-Holocene feature, and probably caused by a large-scale cooling of the climate and a related increase in effective humidity. The number of radiocarbon-dated initiations of hummocks and strings is still very low, but it is apparent that the mires of Finland may have been considerably different from the present during the warmer period of the Holocene (circa 7000–5000 ^{14}C yr BP), with generally more decomposed peat, more forest cover and with weakly developed or missing microtopograpical features.

The development of palsa mires may be closely coupled with climate because of their distribution in continental periglacial areas. The initiation of the permafrost core and the initial rise of the palsa can be dated from the contact of hydrophilous and xerophilous peat layers that indicates hydrological change from moist to dry conditions (Vorren 1979; Zuidhoff & Kolstrup 2000). Radiocarbon dating and earlier dating based on pollen-stratigraphical connections from various parts of Fennoscandia have given mainly late-Holocene dates for the initiation of the present palsas. Most of the dates suggest that the palsas were formed during the last 5000 ^{14}C years (Åhman 1977), in step with the gradual cooling of climate in the tree line area (Seppä & Birks 2001). Some palsas are much younger, however. Dating by Vorren (1979) from north Norway showed that some palsas were formed at circa AD 1400–1750, while Zuidhoff and Kolstrup (2000) reported ages as young as AD 1860–1890. The origin of the youngest palsas can therefore be connected to the Little Ice Age cooling, while the reported thermokarstic degradation of some palsas may be due to the rise of annual mean temperatures in the twentieth century (Sollid & Sørbel 1998; Zuidhoff & Kolstrup 2000). To some extent, such a climatic explanation contradicts the cyclic growth model, according to which the initiation and degradation can be natural phases in the life cycle of a palsa (Seppälä 1986, 1988; Matthews et al. 1997) and there is necessarily no connection to climate change. These two models are not exclusive, however, and degradation of a palsa can be due to climate change and/or increasing cracking that results from increased vertical growth. In a case where there is a general synchronous initiation or degradation of palsas of different size in a certain area, there is evidence of a change in climatic conditions (Sollid & Sørbel 1998; Zuidhoff & Kolstrup 2000).

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