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Stability of the water regime forms a vegetation gradient in minerotrophic mire expanse vegetation of a boreal aapa mire

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Mire surface levels reflecting the water table depth are known to be an important vegetation gradient in boreal peatlands. We classified the vegetation by TWINSPAN, interpreted the vegetation gradients by ordination (Non-metric Multidimensional Scaling) and analysed the peat thickness for the TWINSPAN communities and species (Indicator Species Analysis) from small-sized sample plots over extremely thin-peated to medium thick-peated, minerotrophic mire expanse vegetation from an aapa-mire complex Hirvisuo, Northern Ostrobothnia, Finland. The TWINSPAN communities and the ordination-result could be interpreted in relation to the mire surface levels and additionally in relation to the stability of the water regime on the basis of water level measurements made from the same habitat types in an earlier research. Peat thickness correlated with the stability of the water regime so that communities with an unstable water regime on sand were thin-peated (0–30 cm), while communities with a stable water regime were more thick-peated. We conclude here that the mire-ecological water-table gradient was dissected into two vegetation gradients in Hirvisuo: the gradient formed by mire surface levels reflecting the mean water table level and the stability of the water regime, which represents a gradient of local importance over boreal Fennoscandia. Peat procuding ability of the bottom layer in mires seems to be much dependent on it.

Key words: ecology, numerical analysis, ordination, peat, TWINSPAN, vegetation classification

Introduction

Peatlands in general are characterised by small water level fluctuations when compared with other wetlands of the world, and the relatively stable water regime is also a condition for the undisturbed growth of peat (Keddy 2000). Wheeler and Proctor (2000) claim that there has been little attempt to classify mires quantitatively into "wetness types" in northwestern Europe, but

Økland *et al*. (2001) present almost an opposite opinion concerning Scandinavia. Havas (1961) showed that in boreal, sloping lawn fens of northeastern and eastern Finland there are several plant communities with a pronounced unstable water regime, alongside with plant communities with an ordinary relatively stable water regime of mires. Havas (1961) also stressed the ecological significance of this division of communities in sloping lawn fens. Ruuhijärvi (1960) briefly mentioned the exceptional unstability of the water regime of a lawn fen (*Trichophorum–Sphagnum compactum*) and a flark fen (*Eriophorum angustifolium*) community of aapa mires. Later Reinikainen *et al*. (1984) briefly touched the topic in connection with a curious type of flood of a small kettle-hole mire in southern Finland and Heikkilä and Lindholm (1988) discussed the significance of seasonal drought for the occurrence of rare *Sphagnum molle* in poor fens in western Finland. Laitinen (1990, *see* also Laitinen *et al*. 2005a) preliminary suggested the occurrence of the stability of the water regime as a general vegetation gradient in various mire surface levels, but the concept was not based on measurements. Recently Laitinen *et al*. (2008) demonstrated with measurements the presence of the water level fluctuation gradient within flat peatlands and from flat peatlands to flat *aro* wetlands (Laitinen *et al*. 2005b) in Northern Ostrobothnia. Abovementioned measuring sites were mainly in aapa mires. Numerical analyses of boreal Fennoscandian mire vegetation from geographical data (Pakarinen & Ruuhijärvi 1978, Vorren *et al*. 1999) or from single mire complexes (Singsaas 1989, Moen 1990, Økland 1989, 1990) stressed major gradients, but not additional directions of variation, such as the seasonality of the water regime in boreal peatlands.

Minerotrophic mire expanse (mire inherent, mire centre) vegetation with a peat layer of medium thickness (1–3 m) is typical of fully developed, relatively flat aapa mires like Hirvisuo (Hänninen 1988, Laitinen *et al*. 2005a); mire expanse vegetation is characterised by the lack of floristic mire margin features i.e. surface water influence (*Sumpfigkeit*), ground water influence (*Quelligkeit*) and features of hummock-level mire margin vegetation (*Bruchmoorigkeit*) (Tuomikoski 1942, 1955, Ruuhijärvi 1960, Eurola 1969, Eurola & Kaakinen 1977, 1978, Eurola *et al*. 1984, 1995). In slope mires the peat layer is typically highly humified (Auer 1922) and thin, the steeper the slope the thinner the peat (Huttunen 1987). Flat aapa mires, however, also have extremely thin-peated mire-complex parts with genuine mire expanse vegetation on sandy substratum. This is the case in Hirvisuo mire complex (*see* Laitinen *et al*. 2005a).

The aims of this research were to study (1) whether the stability of the water regime, which was assessed by direct water level measurements over some peatland habitat types by Laitinen *et al*. (2008), is revealed as a vegetation gradient by numerical classification and ordination in the mire expanse vegetation of an aapa mire complex, and (2) whether this direction of variation is reflected in peat thickness ranges of species and communities. The significance of the stability of the water regime as a general vegetation gradient and its relation to mire surface levels in boreal mires, are discussed. Interwoven factors are briefly discussed.

Material and methods

Study area

Hirvisuo (Fig. 1) is an extensive lowland (about 120 m a.s.l.) mire complex (4400 hectares) bordering on the Gulf of Bothnia in north-central Finland. The area belongs to the middle boreal zone (Hämet-Ahti 1981). The mean annual temperature is +1 to +2 °C (Alalammi 1987). The climate is humid: annual precipitation is 600 mm, evapotranspiration 250–300 mm and annual flow 300–350 mm (Karlsson 1986). The precipitation and evaporation are nearly equal in the early growing season (in cultivated areas), from the snow melt into the end of July (Alalammi 1987).

The bedrock consists of granitic veins in basement gneiss (Simonen 1987). Cover moraine with some drumlins prevails. The Hirvisuo complex is a flat or slightly convex plateau, from which the mire waters flow in almost all directions. The southern part of Hirvisuo lies on a sandy terrace with a glaciofluvial formation south of the study area, here peat layer is thin (30–60 cm) to extremely thin (0–30 cm). Central

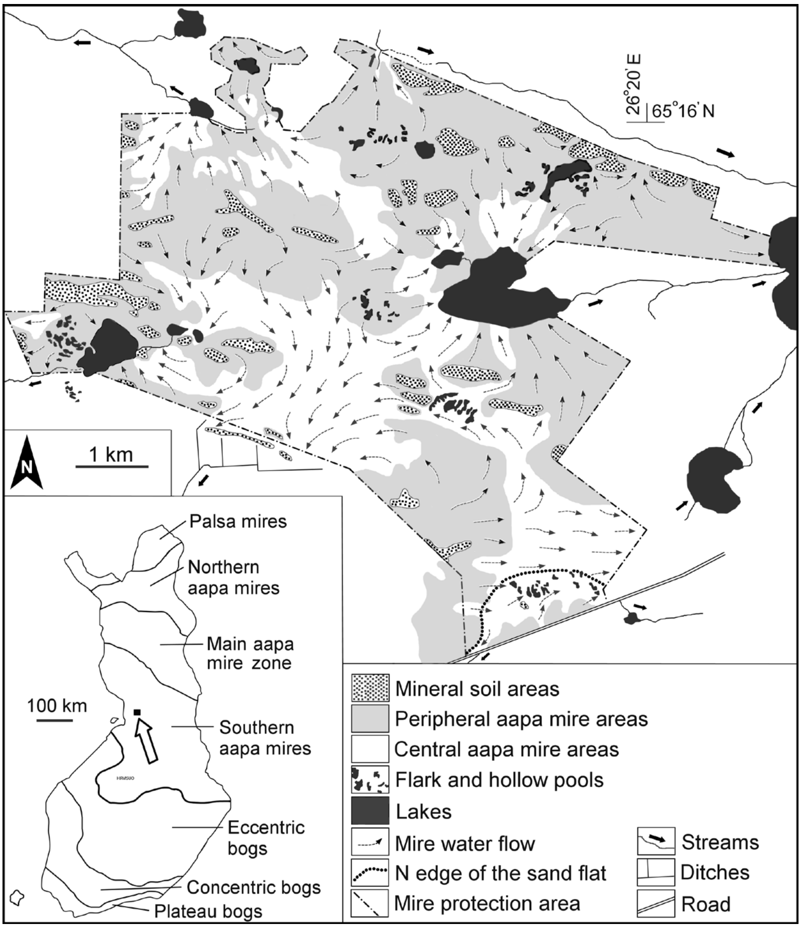


Fig. 1. Location and general features of the study area. The larger map shows the study area with its division to central aapa mire areas and peripheral aapa mire areas according to Laitinen *et al.* (2005a). The area in the south delineated by a dashed line is a thin-peated area on sand flat. The inset map shows the location of the Hirvisuo mire complex and the regional mire zones of Finland according to Ruuhijärvi and Hosiaisluoma (1988).

aapa mire areas — areas which receive water from peripheral aapa mire areas and transport it from the mire complex (Laitinen *et al.* 2005a) — are oligotrophic and partly mesotrophic flark fens with or without strings. Peripheral aapa mire areas — areas which yield water to central aapa mire areas (Laitinen *et al.* 2005a) — are lawn fens (short- or tall sedge fens and corresponding treed fens) or unpatterned or patterned bogs. Next to unsorted mineral soil of the mire margin, there occurs *Carex globularis* pine mires. The area is nearly in virgin state, but traces of previous forestry are present. Large mire areas outside the study area are deeply drained.

Vegetation sampling and peat thickness measurements

A total of 243 small-scale sample plots of 0.25 m^2 were studied in a vegetation survey during summers 1984, 1985 and 2001. Coverages of plants in plots were estimated by eye. Most of the sample plots are in the thin-peated sand flat in the southern part of the study area (Fig. 1); plots in central and northern parts of Hirvisuo form a smaller part of the material. The plots were placed subjectively on the basis of: (1) they represent poor (up to mesotrophic) minerotrophic mire expanse vegetation according to vegetational criteria (by Eurola *et al.* 1984, 1995), (2) they are homogenous in relation to mire surface levels, and (3) they represent both the sites, which were preliminary regarded by us as sites with an unstable water regime according to the concept of Havas (1961) — severe seasonal drought of the peat is typical — and sites which were regarded by us as sites with an ordinary, relatively stable water regime of mires. Communities within the first kind of sites are called here unstable (hereinafter UNST) communities and communities within the latter kind of sites are called here stable (hereinafter STABLE) communities. So our concept of hydrologically unstable mire plant communities was originally based on fragmented information in various studies (Auer 1922, Jalas 1953, Ruuhijärvi 1960, Havas 1961, Eurola 1962, Fransson 1972, Dierssen 1982, Heikkilä & Lindholm 1988) and our own observations without measurements proper. Sample plots were placed on stands of various sizes. The vegetation of aapa-mire strings and their narrow joints, however, were omitted. Within treed fens (combination types, Eurola *et al*. 1984), the sampling was performed on hydrologically homogenous treeless subareas. The mosaic structures on a smaller scale, for instance the patches at the same hydrological surface with dense *Rhynchospora fusca* stands and patches without it, were included in same sample plots so that they represent their estimated proportions in the terrain.

A 1.5-m-long metallic rod was used to measure the peat thickness at 232 sample plots. This method tends to give slightly too high values in thin-peated sandy sites, because the rod easily extends down into the sand. Thin-peated sites are overrepresented to study how the typical mire-expanse species and communities can occur on thin peat.

The nomenclature of vascular plants follows Hämet-Ahti *et al*. (1998), that of mosses Ulvinen *et al*. (2002). *Sphagnum balticum*, *S. annulatum* (incl. *S. jensenii*) and *S. majus* are treated as *Sphagnum balticum* aggr. and *Sphagnum angustifolium* and *S. fallax* as *Sphagnum angustifolium* aggr. The nomenclature of lichens follows Vitikainen *et al*. (1997). Main mire vegetation units and mire site types were used after Eurola *et al*. (1984, 1995) with minor terminological changes.

Data analyses

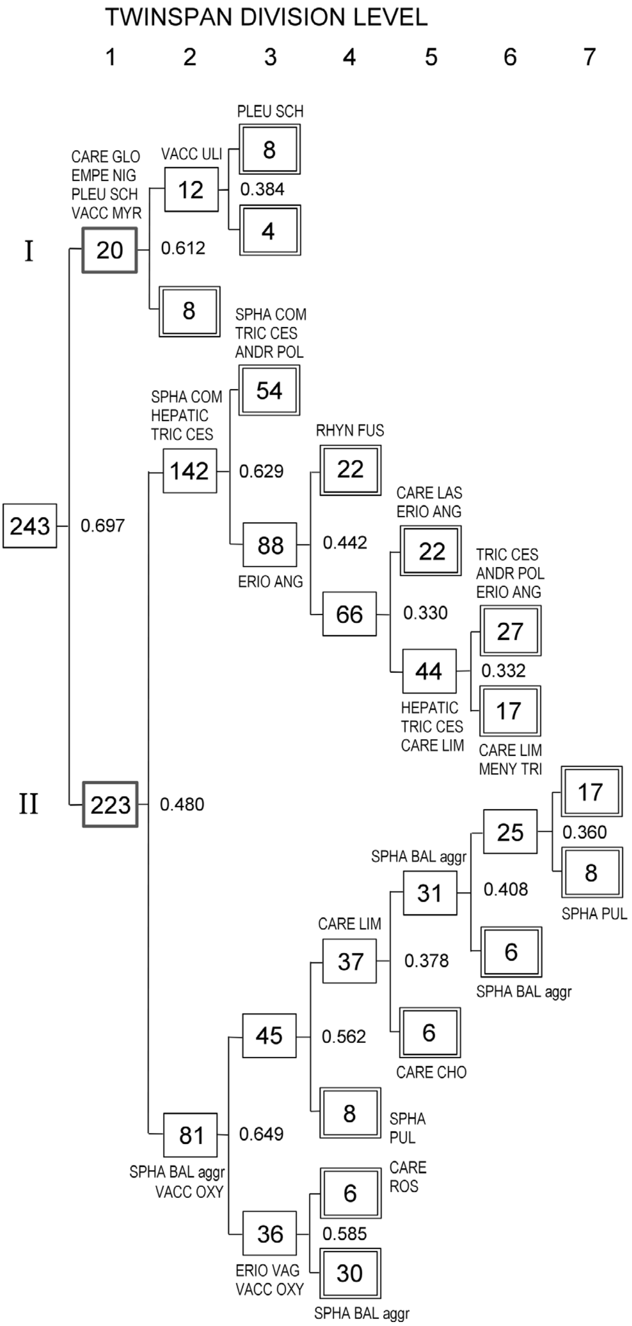
Data analyses were performed using the program package PC-ORD ver. 4.33. The communities for the ecological scrutiny were those resulting from TWINSPAN classification. The pseudospecies cut levels were 1, 2, 5, 10 and 20. Minimum group size to be divided was set at 3, seven levels of division were allowed. The communities used in the analyses represent the second to seventh division levels of TWINSPAN. Nonmetric Multidimensional Scaling (NMS) of plots and species were crried out to interpret vegetational gradients. The autopilot mode of PC-ORD was used to make multiple runs, to choose the best solution at each dimensionality and to test for significance. Dissimilarity measure was Sørensen, a.k.a. Steinhaus. For the Monte Carlo test, the number of runs in real data was 40 and in randomised data 50. In the run of autopilot, mean stress in relation to dimensionalities were in 1D 47.65, 2D 25.75, 3D 17.58 and 4D 13.86. We selected a 3-dimensional solution as the programme recommended, and starting coordinates were taken from the file computed. The final stress for this solution was 17.26 (p = 0.0196) and final instability 0.00069. The number of iterations was 400. We used varimax-unrotated scores for graphs. Species groups of NMS ordination were formed subjectively directly on the basis of the graph as Slack and Hallinbäck (1992). The groups were used for characterising the communities and their ecology.

Indicator Species Analysis (Dufrêne & Legendre 1997) was used for analysing the prevalence of taxa in TWINSPAN community groups interpreted as representing primarily the unstable water regime or primarily stable water regime. The indicator values of the taxa for four peat-thickness classes (0–20 cm, 21–40 cm, 41–60 cm, over 60 cm) were also studied with Dufrêne and Legendre's (1997) method to evaluate the relation between stability of the water regime and peat thickness within species. The significance of observed maximum indicator value for species was calculated using the Monte Carlo test with 1000 permutations.

Results

Classification and ordination of the vegetation

Two TWINSPAN main groups (Fig. 2 and Appendix) represented hummock-level mire expanse (*Reisermoor*) vegetation accompanied by paludified heath forests (communities 1–3)



COMMUNITY	WATER REGIME		
	Stability	Mire surface level	
		3-div.	4-div.
1. Vaccinium uliginosum - Ledum - Pleurozium	ST	Hum	Hum
2. Vaccinium uliginosum - Sphagnum russowii - S. angustifolium	ST	Hum	Hum
3. Calluna vulgaris	UNST	Hum	Hum
4. Trichophorum cespitosum - Sphagnum compactum	UNST	Int	Lawn
5. Rhynchospora fusca	UNST	Flark	Mud
6. Eriophorum angustifolium - Carex lasiocarpa	UNST	Flark	Mud
7. Rhynchospora alba - Trichophorum cespitosum - Eriophorum angustifolium - Hepaticae	UNST	Flark	Mud
8. Carex limosa - Hepaticae	ST	Flark	Mud
9. Carex limosa - Menyanthes - Utricularia intermedia	ST	Flark	Mud
10. Carex limosa - Menyanthes - Sphagnum pulchrum	ST	Flark	Carp
11. Carex limosa - Scheuchzeria - Sphagnum balticum aggr.	ST	Flark	Carp
12. Carex chordorrhiza - Carex limosa - Menyanthes	ST	Flark	Mud (Carp)
13. Eriophorum angustifolium - Sphagnum pulchrum	ST	Flark	Carp
14. Carex rostrata - Menyanthes - Sphagnum angustifolium aggr.	ST	Int	Lawn-Carp
15. Eriophorum vaginatum - Carex lasiocarpa - Sphagnum papillosum	ST	Int	Lawn-Carp

Fig. 2. Classification of the vegetation (TWINSPAN communities) with the mire surface level for each community applied by Eurola *et al.* (1984, 1995) ('3-div') and by Sjörs (1948) ('4-div'), and the stability of the water regime applied by Laitinen *et al.* (2008). Communities are marked in the dendrogram with a double square with the number of plots inside them. Eigenvalues for each division are marked as are the indicator species by each TWINSPAN division. The main division includes (I) hummock-level mire-expanse vegetation (*Reisermoore*) to paludified heath forests, and (II) intermediate- to flark-level mire expanse fens (*Weismoore*).

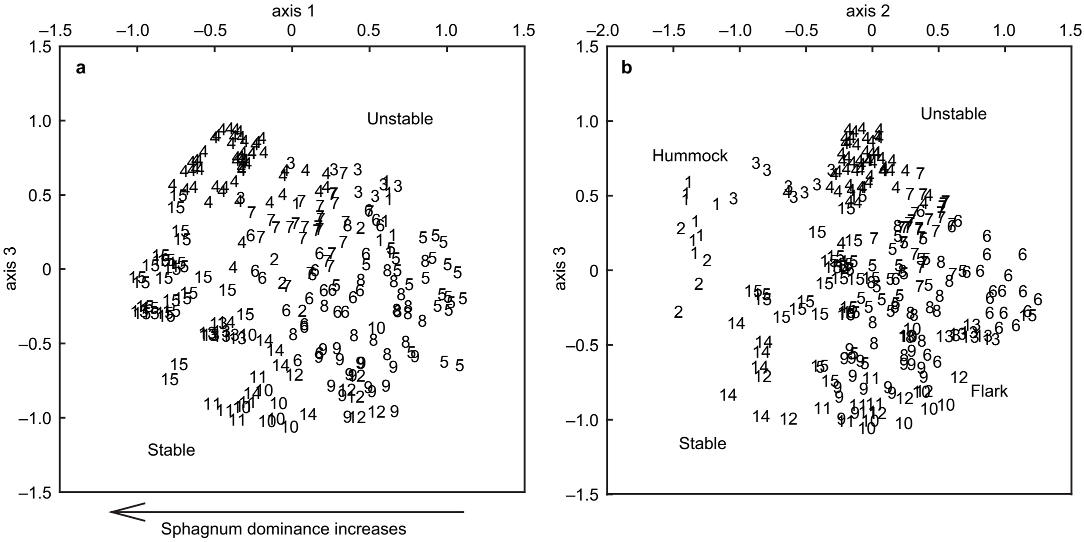


Fig. 3. NMS ordination of the sample plots for (**a**) axes 1 and 3, and (**b**) 2 and 3. Variation from highly *Sphagnum* dominated sites to sites with small *Sphagnum* coverage, the mire surface level i.e., the hummock-to-flark gradient and the stability of water regime (stable to unstable) are shown in the figure. Community types: 1 = *Vaccinium uliginosum–Ledum palustre–Pleurozium schreberi*, 2 = *Vaccinium uliginosum-Sphagnum russowii–Sphagnum angustifolium*, 3 = *Calluna vulgaris*, 4 = *Trichophorum cespitosum–Sphagnum compactum*, 5 = *Rhynchospora fusca*, 6 = *Eriophorum angustifolium–Carex lasiocarpa*, 7 = *Rhynchospora alba-Trichophorum cespitosum–Eriophorum angustifolium–Hepaticae*, 8 = *Carex limosa*–Hepaticae, 9 = *Carex limosa-Menyanthes trifoliata–Utricularia intermedia*, 10 = *Carex limosa–Menyanthes trifoliata–Sphagnum pulchrum*, 11 = *Carex limosa–Scheuchzeria palustris–Sphagnum balticum* aggr., 12 = *Carex chordorrhiza–Carex limosa–Menyanthes trifoliata*, 13 = *Eriophorum angustifolium–Sphagnum pulchrum*, 14 = *Carex rostrata–Menyanthes trifoliata-Sphagnum angustifolium* aggr., 15 = *Eriophorum vaginatum–Carex lasiocarpa–Sphagnum papillosum*.

and flark or intermediate level mire expanse fen-bog (*Weissmoor*) vegetation (communities 4–15). The main group division thus essentially corresponds to the Finnish division of the main mire vegetation units (Eurola *et al*. 1984, 1995). Most communities were slightly narrower units than the Finnish mire-site types, but community 15 is wider, containing 3 closely related mire-site types. The communities could be interpreted in relation to mire surface levels and in relation to the stability of the water regime by Laitinen *et al*. (2008) (Fig. 2 and Appendix). Community types 3–5 in Fig. 2 were exactly the same community types (although not the same localities) as the ones which were called habitats with considerable water level fluctuations according to water level measurements by Laitinen *et al*. (2008). Community types 9, 11 and partly 15 represented habitats with slightly fluctuating water level *sensu* Laitinen *et al*. (2008). The rest of the TWINSPAN communities could be placed either into the ST or UNST community group by comparing the species composition of each community to the species composition of the communities studied by Laitinen *et al*. (2008). Axis 1 in NMS ordination (Fig. 3a) represents the variation from strongly *Sphagnum* dominated sites to sites with small *Sphagnum* coverage. The mire surface levels i.e., the hummock–flark gradient and the stability of water regime can be interpreted from the ordination (Fig. 3b).

Species groups (Fig. 4) elucidate well the species composition of TWINSPAN communities and the relationship of the mire surface levels and the stability of water regime (Fig. 3b). Group 2 emphasises the close ecological relationship (e.g. occurrence on sand and the unstable water regime) of *Trichophorum cespitosum–Sphagnum compactum* community and the *Calluna* community. Flark level species were divided into the group with unstable water regime (group 3) and stable water regime (group 4). The groups

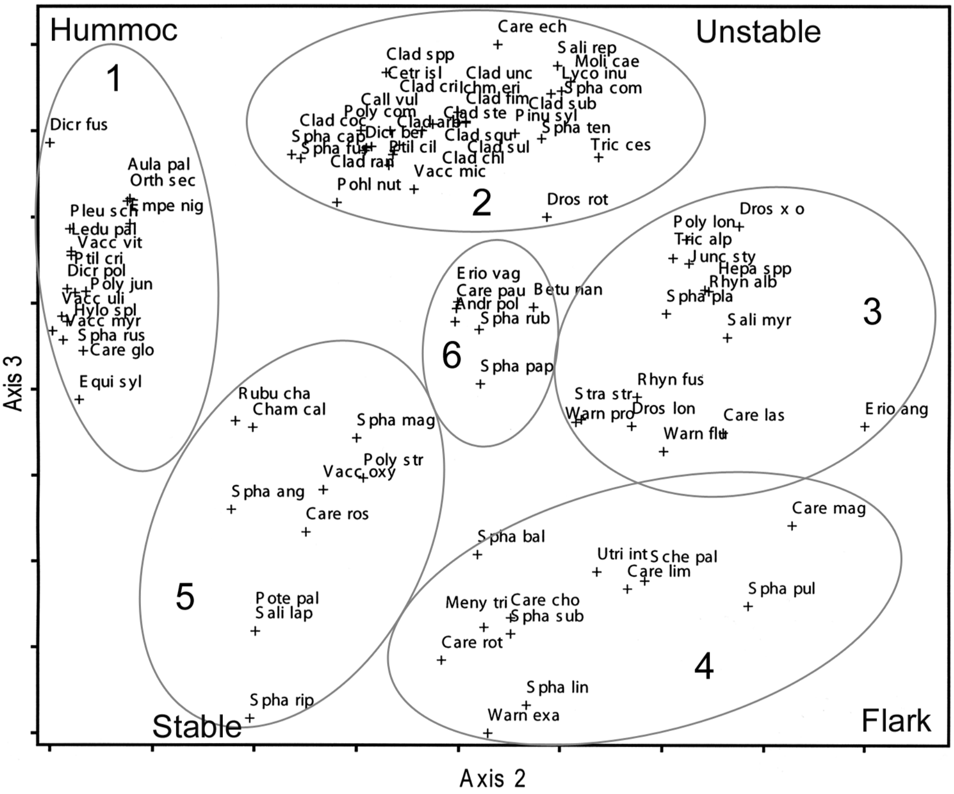


Fig. 4. NMS ordination of the species (with subjective species grouping) for axes 2 and 3. The mire surface level i.e., the hummock to flark gradient and the stability of the water regime (stable to unstable) are shown as in Fig. 3b. 1 = *Vaccinium uliginosum* group, 2 = *Cladonia–Sphagnum compactum* group, 3 = *Rhynchospora fusca* group, 4 = *Carex limosa* group, 5 = *Carex rostrata* group, 6 = *Sphagnum papillosum* group.

are not as compact as group 2. Group 6 is in an intermediate position in relation to the mire surface levels and the stability of water regime. Typical mire margin species occur only within group 1 (*Equisetum sylvaticum*, *Carex globularis*) and group 5 (*Sphagnum riparium*, *Salix lapponum*, *Potentilla palustris*). These species indicate hummock-level mire margin vegetation (*Bruchmoorigkeit*) or surface water influence (*Sumpfigkeit*). The position of those species (Fig. 4) weakly refers to possible stable water regime of corresponding main mire vegetation units (*Bruchmoore*, *Sumpf* wetlands, Laitinen *et al.* 2005b).

Communities not dominated by *Sphagnum* include (1) mud bottom communities, (2) the *Calluna* community (community 3), and (3) the *Vaccinium uliginosum–Ledum–Pleurozium* community (community 1) (Fig. 3a). These communities evidently indicate a reduced state of peat growth; hummock-level communities 1 and 3 occur on sand substratum like several mud bottom communities. *Trichophorum cespitosum-Sphagnum compactum* community (community 4) is the only *Sphagnum* dominated UNST community. It is a typical lawn community. ST community group contains several *Sphagnum* dominated communities ranging from carpet communities to a hummock level community (community 2).

Indicator species analyses for UNST *vs.* ST community groups and for four peat-thickness classes

The species which had a high indicator value (Table 1) with respect to UNST communities

Table 1. Indicator species analysis for UNST *vs.* ST community groups and for four peat thickness classes.

	Communities			Peat thickness (cm)				
	3–7	1,2, 8–15	*P*	0–20	21–40	41–60	> 60	*P*
Trichophorum cespitosum	62	2	0.001	35	19	5	1	0.001
Hepaticae spp.	53	11	0.001	13	23	20	7	0.267
Sphagnum compactum	52	0	0.001	36	9	1	2	0.001
Eriophorum angustifolium	44	13	0.003	3	37	31	1	0.003
Calluna vulgaris	25	0	0.001	31	5	0	0	0.001
Sphagnum tenellum	22	1	0.001	16	4	1	1	0.012
Rhynchospora fusca	18	0	0.001	1	5	12	0	0.010
Rhynchospora alba	18	1	0.013	0	12	12	0	0.130
Vaccinium microcarpum	17	2	0.005	12	9	0	1	0.053
Drosera longifolia	16	5	0.048	3	3	18	4	0.003
Drosera rotundifolia	13	5	0.215	12	3	0	5	0.046
Molinia caerulea	8	0	0.002	5	4	0	0	0.176
Salix repens	7	0	0.010	16	0	0	0	0.001
Sphagnum platyphyllum	7	0	0.090	1	3	3	0	0.812
Juncus stygius	6	0	0.012	0	10	0	0	0.003
Pinus sylvestris	6	0	0.044	6	1	0	0	0.071
Cladina rangiferina	5	0	0.025	7	0	0	0	0.024
Sphagnum fuscum	5	0	0.045	1	6	0	0	0.049
Sphagnum capillifolium	5	1	0.315	13	2	0	0	0.003
Lycopodiella inundata	4	0	0.060	5	1	0	0	0.066
Cetraria islandica	4	0	0.065	4	1	0	0	0.123
Dicranum bergeri	4	0	0.065	10	0	0	0	0.003
Cladonia squamosa	4	0	0.073	7	0	0	0	0.025
Cladonia chlorophaea aggr.	3	0	0.108	8	0	0	0	0.010
Drosera longifolia × *rotundifolia*	3	0	0.120	0	5	0	0	0.051
Polytrichum commune	3	1	0.517	15	0	0	0	0.002
Cladina stellaris	2	0	0.227	4	0	0	0	0.157
Cladonia crispata	2	0	0.237	3	0	0	0	0.213
Cladonia coccifera aggr.	2	0	0.476	4	0	0	0	0.065
Trichophorum alpinum	2	0	0.495	0	3	0	0	0.274
Cladonia subfurcata	2	0	0.497	2	0	0	0	0.478
Cladonia uncialis	2	0	0.497	2	0	0	0	0.478
Cladonia spp.	2	0	0.500	4	0	0	0	0.080
Cladina arbuscula	2	0	0.513	4	0	0	0	0.074
Ptilidium ciliare	2	0	0.527	4	0	0	0	0.067
Carex echinata	1	0	1.000	0	1	0	0	1.000
Cladonia fimbriata	1	0	1.000	2	0	0	0	0.388
Cladonia sulphurina	1	0	1.000	2	0	0	0	0.388
Icmadophila ericetorum	1	0	1.000	0	1	0	0	1.000
Polytrichastrum longisetum	1	0	1.000	0	1	0	0	1.000
Salix myrtilloides	1	0	1.000	0	1	0	0	1.000
Andromeda polifolia	29	29	1.000	21	17	5	17	0.502
Carex lasiocarpa	9	9	0.993	0	6	16	4	0.024
Pohlia nutans	1	1	1.000	4	0	0	0	0.086
Warnstorfia procera	0	0	1.000	0	0	0	2	0.383
Sphagnum rubellum	0	1	0.892	0	0	1	1	0.899
Straminergon stramineum	0	1	0.740	0	1	1	1	0.984
Equisetum sylvaticum	0	1	0.479	2	0	0	0	0.362
Hylocomium splendens	0	1	0.478	0	1	0	0	1.000
Sphagnum lindbergii	0	1	0.467	0	0	0	1	0.639
Dicranum fuscescens	0	1	0.462	0	1	0	0	1.000
Potentilla palustris	0	1	0.455	0	0	0	1	0.672
Salix lapponum	0	1	0.455	0	0	0	1	0.672

continued

Table 1. Continued.

	Communities			Peat thickness (cm)				
	3–7	1,2, 8–15	*P*	0–20	21–40	41–60	> 60	*P*
Orthilia secunda	0	1	0.443	2	0	0	0	0.362
Warnstorfia exannulata	0	2	0.466	0	0	0	3	0.243
Polytrichum strictum	0	2	0.218	0	0	1	0	0.668
Polytrichum juniperinum	0	2	0.202	1	0	0	0	0.690
Carex rotundata	0	2	0.189	0	0	0	3	0.153
Chamaedaphne calyculata	0	2	0.182	0	0	0	1	0.640
Sphagnum riparium	0	3	0.092	0	0	0	3	0.146
Aulacomnium palustre	0	3	0.087	4	0	0	0	0.105
Ptilium crista-castrensis	0	4	0.048	0	2	0	0	0.400
Dicranum polysetum	0	4	0.043	0	4	0	0	0.164
Sphagnum russowii	0	5	0.102	8	2	0	0	0.031
Sphagnum magellanicum	0	5	0.004	0	0	0	5	0.095
Utricularia intermedia	2	6	0.158	0	0	18	3	0.001
Carex magellanica	0	7	0.002	2	2	0	0	0.824
Warnstorfia fluitans	0	8	0.028	0	0	4	2	0.563
Sphagnum subsecundum	0	8	0.001	0	0	1	9	0.007
Empetrum nigrum	1	9	0.078	5	10	0	0	0.038
Carex globularis	1	10	0.063	15	3	0	0	0.004
Pleurozium schreberi	0	10	0.008	8	6	0	0	0.087
Vaccinium myrtillus	0	11	0.002	7	5	0	0	0.093
Vaccinium vitis-idaea	0	11	0.001	6	4	0	0	0.111
Ledum palustre	0	12	0.001	5	6	0	0	0.184
Betula nana	9	13	0.552	12	7	0	4	0.199
Carex chordorrhiza	1	13	0.037	0	1	7	11	0.047
Carex rostrata	0	13	0.001	0	1	2	5	0.260
Vaccinium uliginosum	0	14	0.002	12	4	0	0	0.011
Sphagnum pulchrum	0	16	0.001	1	2	1	6	0.181
Carex pauciflora	2	17	0.003	4	3	0	8	0.180
Rubus chamaemorus	0	17	0.001	2	0	0	13	0.012
Eriophorum vaginatum	8	23	0.028	0	5	6	18	0.033
Sphagnum angustifolium aggr.	0	24	0.001	1	0	0	13	0.008
Sphagnum papillosum	0	28	0.001	0	1	4	26	0.001
Menyanthes trifoliata	1	34	0.001	0	0	10	33	0.001
Vaccinium oxycoccos	1	35	0.001	1	1	1	29	0.001
Scheuchzeria palustris	0	35	0.001	0	0	11	25	0.001
Sphagnum balticum aggr.	1	42	0.001	0	1	1	49	0.001
Carex limosa	2	44	0.001	0	0	33	30	0.001
Number of plots	133	110		49	80	35	68	

(3–7) had generally high indicator values with respect to lowest peat-thickness classes (1–20 cm, 21–40 cm and partly 41–60 cm) and the species which had high indicator values with respect to ST communities (1, 2, 8–15) had high indicator values with respect to the thickest peat class (over 60 cm). Species, which best indicate unstable water regime are either preferably lawn species (*Trichophorum cespitosum*, *Sphagnum compactum*) or preferably mud-bottom taxa (*Hepaticae* spp., *Eriophorum angustifolium*, *Rhynchospora fusca*). The best indicators of a stable water regime are either mud bottom-carpet taxa (*Carex limosa*, *Scheuchzeria palustris*, *Menyanthes trifoliata*) or carpet-lawn taxa (*Vaccinium oxycoccos*, *Sphagnum papillosum*, *Sphagnum angustifolium* aggr.). Species occurring on the thin-peated sand flat form a gradient (Fig. 5) in relation to peat thickness (according to lower quartiles of boxplots).

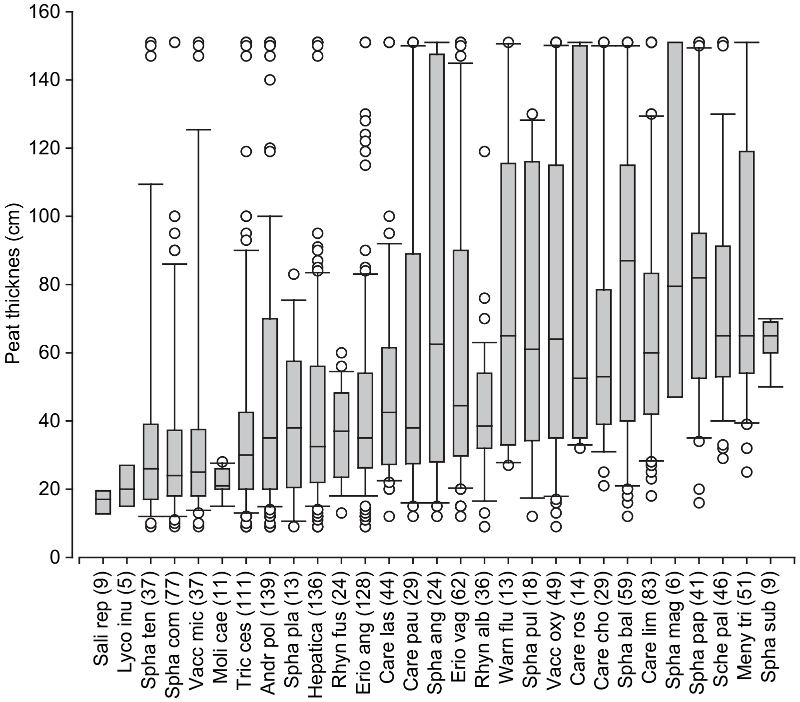


Fig. 5. Peat thickness variation for selected vascular plant and moss species (*n* in parentheses).

Peat thickness variation within communities

Communities differed in relation to peat thickness. UNST communities were more thin-peated than ST communities (Fig. 6). Communities form a gradient from UNST to ST along increasing peat thickness (Fig. 7). Thin-peated communities on till (communities 2 and 13) and seemingly continuously dry (ST) community 1 (*Vaccinium uliginosum–Ledum–Pleurozium* community) on sand form an exception from the gradient in relation to the stability of water regime.

Discussion

Stability of the water regime was found to be an important vegetation gradient independent of mire surface levels in relatively thin-peated mire expanse vegetation of the boreal aapa mire complex. There are at least two reasons why this gradient has not been recognised in other numerical mire vegetation studies of boreal Fennoscandian regions (Pakarinen & Ruuhijärvi 1978, Singsaas 1989, Økland 1989, 1990, Moen 1990, Vorren *et al.* 1999). The ecological range with respect to two major gradients, the poor-rich and the mire margin-mire expanse gradients, is very narrow in Hirvisuo material. So there is more "capacity" in the ordination to reveal the variation outside these major directions of variation. The third gradient is "water table" according to the central paradigm in Scandinavian (and Finnish) mire ecology (Økland *et al.* 2001). In fact the ordination of Hirvisuo vegetation divided "water table" (*see* also Økland 1992) into two independent vegetation gradients: the mire surface levels (Sjörs 1948, Ruuhijärvi 1960, Eurola *et al.* 1984, 1995), which roughly reflect the mean water table level (Laitinen *et al.* 2008) and stability of the water regime, which may be regarded as a reflection of both the fluctuation of the water table and the moisture of the surface peat (water table–soil moisture complex gradient, Wheeler 1999).

The other reason, why stability of the water regime was recognised as an independent gradient is due to the peculiar habitat range within mire expanse vegetation in the mire complex Hirvisuo. Corresponding hydrologically unstable vegetation (at least *Trichophoro–Sphagnetum*

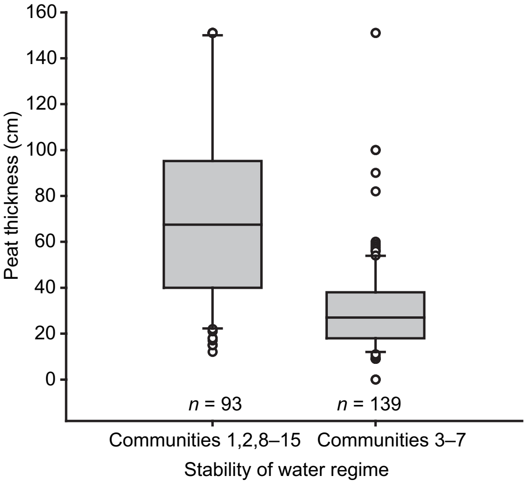


Fig. 6. Peat thickness variation within preferably hydrologically stable (ST) communities (1, 2, 8–15) and within preferably hydrologically unstable (UNST) communities (3–7). For the classification of communities *see* Fig. 2.

compacti Waren 1926 emend.) occurs at certain sites in most of Norway (Dierssen & Dierssen 1978), in Sweden (Fransson 1972) and in large areas of Finland (Ruuhijärvi 1960, Havas 1961) and instability of the water regime within this habitat is well-known (e.g. Ruuhijärvi 1960, Havas 1961, Fransson 1972). Ordination studies in Fennoscandia (Singsaas 1989, Moen 1990, Økland 1989, 1990) do not simply include these kind of mire habitats. In larger regional data sets the stability of water regime may be concealed by more important directions of variation (Pakarinen & Ruuhijärvi 1978) or the material is composed solely of lowland vegetation without e.g. steep sloping fens on higher elevations (Vorren *et al*.1999). So this extreme end of the water regime seems to be lacking in modern Fennoscandian vegetation gradient studies, although the phenomenon in itself — the occurrence of certain habitats with a considerably unstable water regime — has been well known for a long time in Fennoscandia. Thus stability of the water regime may be regarded as an independent vegetation gradient in mires of boreal Fennoscandia provided that the survey is extended to a very large range of mire vegetation, including steep sloping fens (Havas 1961) and thin-peated mires on sand (Laitinen *et al*. 2005a). Accordingly, the stability of water regime may be regarded as a

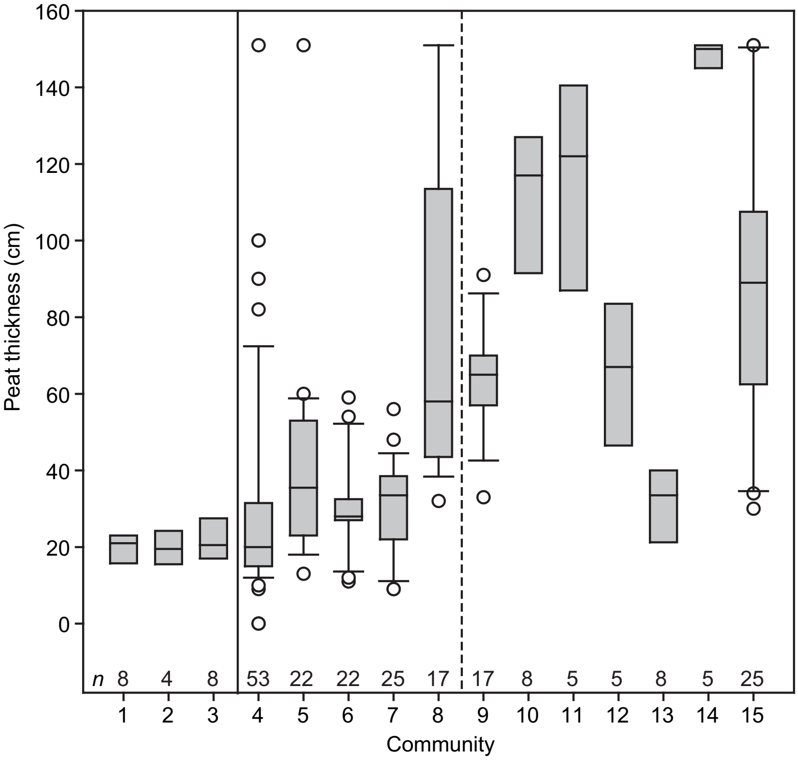


Fig. 7. Peat-thickness variation within individual communities. The grouping of communities by TWINSPAN division. For the classification of communities *see* Fig. 2.

vegetation gradient of local importance in boreal Fennoscandia by the gradient-importance categories of Økland *et al*. (2001).

The relationship of the stability of water regime and peat-thickness is complicated and the result of the present study represents a special case (Laitinen *et al*. 2005a): on flat, well-permeable sand, the indicator species of "normal" stable water regimes and corresponding communities do not occur until the peat thickness exceeds 30–40 cm. Furthermore, mire sites with extremely thin peat layers on sand are characterised by species and communities belonging to a hydrologically unstable group. This is not, however, a general pattern in mires because, for instance, in thick-peated raised bogs the hollows dry out considerably during dry periods (e.g. Rydin 1985). Thus very thick-peated sites also include vegetation that belongs to hydrologically unstable group. Raised bog centres even have much in common with hydrologically unstable, thin-peated parts of aapa mires (Laitinen *et al*. 2005a).

The fact that the species in Hirvisuo form a gradient with respect to their occurrence on extremely thin peat layer on sand evidently indicates their tolerance to dry conditions. Severe seasonal drought is typical of mire sites with permeable mineral soil beneath the very thin peat layer (Heikkilä & Lindholm 1988). Drought and its effects or more generally the moisture of the surface peat are hardly satisfactorily reflected in the division to mire surface levels with 3 to 4 categories, but e.g. typical hummock level (with *Sphagnum fuscum*, Rydin 1985) is continuously moist whereas flark level may be seasonally dry at its very surface. Stability of the water regime as a vegetation gradient evidently reflects the tolerance of peatland plants to drought (although other factors may be involved), while the mire surface levels may rather reflect the tolerance of plants to oxygen-poor conditions and their cation exchange-capacity (Eurola *et al*. 1984).

Occurrence of communities with unstable water regimes on thin peat layers in Hirvisuo indicates a stagnant state in peat growth, which is also evident on the highly humified peat at such sites (e.g. Huttunen 1987). Fransson (1972) relates the unstable water regime to the regressive developmental stage of mires, represented by e.g. the occurrence of *Cladopodiella fluitans*, *Gymnocolea inflata* and *Cladonia squamosa* and the *Sphagnetum compacti* association. *Sphagnum majus*, *S. fuscum*, *S. magellanicum* and *S. papillosum*, instead, represent progressive species (Fransson 1972). Økland (1989, 1990) suggests the peat productivity gradient (coenocline associated with the peat producing ability of the bottom layer, Økland 1990), but does not suggest any environmental factors as a reason for this. The strongly peat producing species of Økland (1990) and progressive species of Fransson (1972) correspond quite well to species that do not abundantly occur on the extremely thin-peated sand flat of Hirvisuo and the weakly peat producing species of Økland (1989, 1990) and regressive species of Fransson (1972) correspond well to species which occur on the extremely thin-peated sand flat of Hirvisuo. Peat thickness in general, however, does not directly indicate the net peat accumulation rate; the age of the basal peat should be known to make comparisons. So, with caution, the peat productivity gradient of Økland (1989, 1990) may be regarded as a gradient much dependent on stability of the water regime.

Natural disturbance (Keddy 2000) is strongly linked with the unstable water regime in mires. This is evident when viewing mud bottoms where the water-table fluctuation does not seem large in all the cases, but the surface may seem dry. This is evident e.g. for the *Rhynchospora fusca* community (a rarish aapa mire community concentrated to the southern aapa mire zone in Finland, Lahti *et al*. 1995): in central Europe the ecology of *Rhynchospora fusca* has been described in terms of a periodically disturbance-dependent rare species, which occurs only on sites in established communities (wet heathlands) characterised by disturbance of a fluctuating water table (Kesel & Urban 1999).

We conclude here that this investigation supports the view of Økland (1989, 1990) and Økland *et al*. (2001) that a gradient reference frame including more than the three traditional gradients is necessary to describe the main local variation in Fennoscandian mires. The stability of the water regime is in certain environments and mire complexes the fourth, local gradient and variation in peat producing ability of the vegetation may probably be regarded as its consequence. In the coastal half of the southern aapa mire zone of Finland — where large flat sand areas and even *aro* wetlands (Laitinen *et al*. 2005b) occur — the importance of the stability of the water regime seems moderate to considerable. Due to the complex nature of the "stability of the water regime" (water table fluctuations, moisture changes of the surface peat, forces that retain water), its components require measurement investigations in order to better understand water ecology of the mire surface at different communities and sites.

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Appendix. Site characteristics and mean percentage cover of plant species in communities. Communities: 1 = *Vaccinium uliginosum–Ledum palustre–Pleurozium schreberi*, 2 = *Vaccinium uliginosum–Sphagnum russowii–Sphagnum angustifolium*, 3 = *Calluna vulgaris*, 4 = *Trichophorum cespitosum–Sphagnum compactum*, 5 = *Rhynchospora fusca*, 6 = *Eriophorum angustifolium–Carex lasiocarpa*, 7 = *Rhynchospora alba–Trichophorum cespitosum–Eriophorum angustifolium*–Hepaticae, 8 = *Carex limosa*–Hepaticae, 9 = *Carex limosa–Menyanthes trifoliata–Utricularia intermedia*, 10 = *Carex limosa–Menyanthes trifoliata–Sphagnum pulchrum*, 11 = *Carex limosa–Scheuchzeria palustris–Sphagnum balticum* aggr., 12 = *Carex chordorrhiza–Carex limosa–Menyanthes trifoliata*, 13 = *Eriophorum angustifolium–Sphagnum pulchrum*, 14 = *Carex rostrata–Menyanthes trifoliata–Sphagnum angustifolium* aggr., 15 = *Eriophorum vaginatum–Carex lasiocarpa–Sphagnum papillosum*. Corresponding Finnish heath forest site types indicated according to Kalela (1961) and mire site types by Eurola *et al*. (1984, 1995): sEVT = paludified *Empetrum–Vitis-idaea* heath forest site type, KgR = thin-peated pine mire, Ol/Me = oligo/mesotrophic, KaN = *Sphagnum compactum* fen and *Sphagnum papillosum* fen, RuRiN = mud bottom flark fen, SphRiN = *Sphagnum* flark fen, VSN = ordinary tall-sedge fen, LkN = low sedge fen. Site characteristics: Hum = hummock level, Int = intermediate level, ST/UNST = stable/unstable, Per/Cent = peripheral aapa mire areas/central aapa mire areas. The frequencies of taxa in each community are indicated as follows: boldface, frequency > 66.7%; underlined, frequency 33.3%–66.7%; regular text, frequency < 33.3%.

Community number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Number of plots	8	4	8	54	22	22	27	17	17	8	6	6	8	6	30
Site type	sEVT	KgR	KgR	OlKaN (MeKaN)	MeRuRiN	OlRuRiN (MeRuRiN)	OlRuRiN (MeRuRiN)	OlRuRiN	MeRuRiN (OlRuRiN)	OlSphRiN	OlSphRiN	OlRuRiN	OlVSN (unusual case)	OlVSN	OlKaN OlKaSN OlLkN
Site characteristics															
Mire surface level															
3-division	Hum	Hum	Hum	Int	Flark	Flark	Flark	Flark	Flark	Flark	Flark	Flark	Flark	Int	Int
4-division	Hum	Hum	Hum	Lawn	Mud	Mud	Mud	Mud	Mud	Carpet	Carpet	Mud	Carpet	Lawn carpet	Lawn carpet
Stability of water regime	ST	ST	UNST	UNST	UNST	UNST	UNST	ST	ST	ST	ST	ST	ST	ST	ST
Mineral soil	Sand	Till	Sand	Sand	Sand	Sand	Sand	(Sand)					Till		
Position in aapa complex	Per	Per	Per	Per	Cent	Cent	Cent	Cent	Cent	Cent	Cent	Cent	Cent	Per	Per
Species	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D
Equisetum sylvaticum	–	0.1	–	–	–	–	–	–	–	–	–	–	–	–	–
Ptilium crista-castrensis	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hylocomium splendens	0.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Dicranum polysetum	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Dicranum fuscescens	0.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Orthilia secunda	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Polytrichum juniperinum	+	0.1	–	–	–	–	–	–	–	–	–	–	–	–	–
Aulacomnium palustre	3	0.1	–	–	–	–	–	–	–	–	–	–	–	–	–
Vaccinium vitis-idaea	**5**	**2**	+	–	–	–	–	–	–	–	–	–	–	–	–
Vaccinium uliginosum	**21**	**34**	0.1	+	–	–	–	–	–	–	–	–	+	–	+
Vaccinium myrtillus	**4**	**9**	0.2	–	–	–	–	–	–	–	–	–	–	–	–
Ledum palustre	**14**	**4**	0.3	–	–	–	–	–	–	–	–	–	+	–	+
Pleurozium schreberi	**68**	**4**	1	+	–	–	–	–	–	–	–	–	–	–	–
Empetrum nigrum	**8**	**9**	**4**	+	–	+	–	–	–	–	–	–	–	–	+
Sphagnum russowii	2	**51**	1	+	–	–	–	–	–	–	–	–	+	–	–
Carex globularis	**1**	**3**	**0.2**	+	–	–	–	–	–	–	–	–	–	–	–
Sphagnum capillifolium	6	–	**9**	1	–	–	–	–	–	–	–	–	–	–	–

Phagnum fuscum	–	6	**49**	1	–	–	–	–	–	–	–	–	–	–	–
Cladonia stellaris	–	–	0.1	0.2	–	–	–	–	–	–	–	–	–	–	–
Cladonia chlorophaea	–	–	0.3	+	–	–	–	–	–	–	–	–	–	–	–
Dicranum bergeri	–	–	1	+	–	–	–	–	–	–	–	–	–	–	–
Cladonia arbuscula	–	–	0.1	–	–	–	–	–	–	–	–	–	–	–	–
Ptilidium ciliare	–	–	6	–	–	–	–	–	–	–	–	–	–	–	–
Icmadophila ericetorum	–	–	0.1	–	–	–	–	–	–	–	–	–	–	–	–
Cladonia squamosa	–	–	0.4	0.1	–	–	–	–	–	–	–	–	–	–	–
Cladonia rangiferina	–	–	1	0.2	–	–	–	–	–	–	–	–	–	–	–
Cladonia spp.	–	–	+	+	–	–	–	–	–	–	–	–	–	–	–
Cladonia uncialis	–	–	0.3	0.3	–	–	–	–	–	–	–	–	–	–	–
Cladonia crispata	–	–	1	0.1	–	–	–	–	–	–	–	–	–	–	–
Calluna vulgaris	1	–	**52**	4	–	–	–	–	–	–	–	–	–	–	–
Polytrichum commune	+	**6**	1	1	–	–	–	–	–	–	–	–	–	–	–
Pohlia nutans	+	–	+	+	–	–	–	–	–	–	–	–	–	–	+
Vaccinium microcarpum	+	0.1	**0.4**	0.1	–	+	–	–	–	–	–	–	–	–	0.1
Cladonia subfurcata	–	–	0.1	0.2	–	–	–	–	–	–	–	–	–	–	–
Cetraria islandica	–	–	0.1	0.1	–	–	–	–	–	–	–	–	–	–	–
Pinus sylvestris	–	–	+	+	–	–	–	–	–	–	–	–	–	–	+
Drosera rotundifolia	+	–	0.1	0.1	+	+	0.1	–	+	+	–	–	–	–	0.1
Andromeda polifolia	1	1	**1**	**1**	+	1	**0.3**	+	0.1	0.1	+	+	**0.5**	**2**	**2**
Betula nana	0.3	–	–	0.2	+	–	0.2	+	0.1	–	–	+	**0.4**	–	0.3
Sphagnum tenellum	–	–	–	4	–	–	–	–	–	–	–	–	–	–	1
Cladonia sulphurina	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Cladonia fimbriata	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Cladonia coccifera	–	–	–	0.2	–	–	–	–	–	–	–	–	–	–	–
Sphagnum compactum	–	–	–	**79**	0.1	0.2	1	0.1	–	–	–	–	–	–	5
Molinia caerulea	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Carex echinata	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Lycopodiella inundata	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–
Salix repens	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
Trichophorum cespitosum	–	–	4	**19**	0.3	1	**16**	1	+	0.4	–	–	–	–	4
Sphagnum platyphyllum	–	–	–	–	0.1	+	0.2	+	+	–	–	–	–	–	–
Drosera longifolia	–	–	–	+	0.3	0.1	0.1	0.1	0.2	–	0.1	–	–	–	–
Eriophorum angustifolium	–	–	–	0.2	**1**	**24**	**7**	**2**	1	**1**	**0.2**	**2**	**26**	–	0.2
Polytrichastrum longisetum	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–
Drosera longifolia × *rotundifolia*	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–
Trichophorum alpinum	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–
Rhynchospora fusca	–	–	–	–	25	–	+	–	–	–	–	–	–	–	–
Rhynchospora alba	–	–	–	+	0.4	+	8	1	+	1	–	–	–	–	–
Juncus stygius	–	–	–	–	+	–	0.1	–	–	–	–	–	–	–	–
Salix myrtilloides	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–
Hepaticae spp.	–	–	**2**	2	**5**	**10**	**41**	**32**	**0.4**	3	+	–	–	–	+
Carex lasiocarpa	–	–	–	+	1	7	1	–	1	–	–	0.2		–	8

continued

Appendix. Continued.

Community number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Warnstorfia procera	–	–	–	–	–	–	+	–	+	–	–	–	–	–	–
Carex limosa	–	–	–	+	**0.4**	1	1	**8**	**11**	**5**	**7**	**7**	–	–	+
Utricularia intermedia	–	–	–	–	+	+	–	+	0.2	–	–	–	–	–	–
Menyanthes trifoliata	–	–	–	–	1	+	+	1	**4**	**4**	+	**7**	–	7	–
Scheuchzeria palustris	–	–	–	+	–	0.1	0.2	4	**2**	3	**6**	2	–	–	1
Warnstorfia exannulata	–	–	–	–	+	–	–	–	1	–	–	–	–	–	–
Sphagnum subsecundum	–	–	–	–	–	–	–	+	0.5	–	–	–	–	–	–
Sphagnum pulchrum	–	–	–	–	–	–	–	0.1	0.1	**85**	–	–	**96**	–	–
Sphagnum lindbergii	–	–	–	–	–	–	–	–	–	–	5	–	–	–	–
Potentilla palustris	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–
Carex magellanica	–	–	–	–	–	–	–	–	–	–	–	–	6	–	+
Salix lapponum	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–
Sphagnum riparium	–	–	–	–	–	–	–	–	–	–	–	16	–	27	–
Carex chordorrhiza	–	–	–	–	0.3	+	0.3	–	0.5	–	1	**10**	–	**5**	–
Warnstorfia fluitans	–	–	–	+	–	+	+	0.3	0.1	–	+	–	+	–	+
Straminergon stramineum	–	–	–	–	–	+	–	–	+	–	–	–	–	–	+
Sphagnum balticum	–	–	–	1	–	3	–	+	0.1	**1**	**93**	–	1	–	**22**
Carex rotundata	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1
Polytrichum strictum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+
Sphagnum papillosum	–	–	–	2	–	–	–	–	0.1	0.1	0.1	–	–	–	**58**
Sphagnum magellanicum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.3
Carex rostrata	–	–	–	0.1	–	–	–	–	–	–	–	+	0.2	**9**	1
Chamaedaphne calyculata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+
Carex pauciflora	–	–	–	2	–	–	–	–	–	–	–	–	1	–	**6**
Vaccinium oxycoccos	–	0.1	–	+	+	+	+	–	–	+	0.1	0.3	0.1	**4**	**0.5**
Sphagnum rubellum	–	–	–	+	–	–	–	–	–	–	–	–	–	–	0.1
Eriophorum vaginatum	–	–	1	4	–	–	0.4	+	–	+	–	–	0.3	0.2	13
Sphagnum angustifolium aggr.	–	**30**	–	+	–	+	–	–	–	–	1	18	±	73	11
Rubus chamaemorus	–	3	+	+	–	–	–	–	–	–	–	–	–	+	1