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A numerical analysis of mire margin forest vegetation in South and Central Finland

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The ecological structure of boreal mire margin vegetation (paludified forests, mire margin forests and forested pine and spruce mires) in South and Central Finland was examined using ordination (DCA) and classification (TWINSPAN) techniques on the vegetation data of 92 sample plots from the 8th National Forest Inventory (1985–86). The first DCA axis was interpreted as respond to a complex-gradient of nutrient availability on the basis of site classification, species composition and correlation with all measured tree stand variables. According to the distribution of species ecological groups along DCA1 axis the mire margin/mire expanse gradient was one of the main factors determining this nutrient availability. The second axis was interpreted in terms of paludification on the basis of species composition, site classification and its correlation with peat depth. Seven clusters resulted from a TWINSPAN classification of the vegetation data. These could be arranged into a sequence along the nutrient availability gradient by their species composition: three clusters represented ombro-oligotrophic, three clusters meso-oligotrophic and one cluster mesotrophic vegetation. The clusters corresponded only weakly to the traditional Finnish forest and mire site types as determined in the field.

Key words: boreal forest, boreal mire, ecological gradient, forest site types, mire site types

INTRODUCTION

Classification of boreal mires in Finland has traditionally followed the ecological site type principle proposed by Cajander (1913). As species distributions are determined by environmental factors, units (‘types’) at all hierachical levels, i.e., mire complex types (e.g. Ruuhijärvi 1982, Påhlsson 1994), site type groups (bogs, fens and swamps, see Heikurainen & Pakarinen 1982), site types (Eurola *et al.* 1984), and subtypes characterised by Eurola and Kaakinen (1979) and Eurola *et al.* (1994) can be placed in an environmental space defined by physical and chemical environmental factors.

Knowledge of the ecological indicator value of species has accumulated by autecological studies (e.g. Kotilainen 1927, Pankakoski 1939), studies of site quality (e.g. Lumiala 1945, Reinikainen *et al.* 1984) and description of vegetation types (e.g. Paasio 1933, 1941, Tuomikoski 1942, Ruuhijärvi 1960, Havas 1961, Eurola 1962). More recently, species, site types or mire complex types have been related to environmental factors by use of numerical classification and ordination techniques (e.g. Pakarinen & Ruuhijärvi 1978, Pakarinen 1979, 1982, Økland 1990ab, Jeglum 1991).

A distinction between mire expanse and mire margin vegetation was made already in early mire vegetation studies (Lumiala 1937, Sjörs 1948). Later on, the mire expanse and mire margin gradient has been confirmed as one of the main ecological gradients in mire vegetation in the Nordic countries (Eurola & Holappa 1985, Malmer 1985). In this study the Finnish definition (Eurola & Kaakinen 1979) of the mire margin concept is used. There is a difference to the Scandinavian interpretation (Sjörs 1983, Økland 1989, 1990c) according to which also marginal pine forests of bogs despite being ombrotrophic are included in mire margin sites. According to Finnish environmental characterisations mire margin vegetation occurs often on sites with a thin peat layer (Ilvessalo 1956, Ruuhijärvi 1960, Eurola 1962) that receive a supplementary input of mineral nutrients from surrounding mineral soil (Heikurainen 1954, Eurola & Holappa 1985). The importance of this external nutrient flow is strongly related to topography and slope (Backman 1919, Lukkala 1929) and the inflow of oxygen-rich surface or spring water (e.g. Havas 1961, Persson 1961, Eurola & Kaakinen 1979). Mire expanse vegetation, in contrast, is often characterised by thick peat, by high and slowly moving watertable and by lacking external nutrient flow (Eurola & Kaakinen 1979).

Mire margin vegetation typically occurs in a zone between proper upland vegetation and mire expanse vegetation. The sites include 1) paludified forests (= paludified mineral soil forests), 2) mire margin forests and 3) forested pine and spruce mires (Lumiala 1937, Tuomikoski 1942). Descriptions of the flora and vegetation of forested mire margins have appeared in several regional studies (e.g. Cajander 1913, 1926, Kujala 1921, Auer 1922, Aario 1932, Paasio 1933, Ruuhijärvi 1960, Eurola 1962, Tolonen 1967). Rather few special studies, however, have been made on the community structure, ecology and classification of mire margin forest and forested pine and spruce mire sites and vegetation (Lumiala 1937, Tuomikoski 1942, Heikurainen 1954, Nurminen 1964, Hotanen 1989, Hotanen & Nousiainen 1990, Tolvanen 1994). Paludified forests have typically remained without detailed vegetation studies or classification supported by investigations, they have merely been mentioned in early typological studies (e.g. Cajander 1909, 1913, 1926, Kujala 1921, Kalela 1962).

Because of their potential productivity, the mire margin forests and forested pine and spruce mires have been drained to a large extent (Heikurainen 1971, Gustavsen & Päivänen 1986). The area of these undrained mire margin sites in 1985–86 according to the data of permanent sample plots of the 8th National Forest Inventory (8th NFI) was half of what it was in the early 1950's according to data from the 3rd NFI (Ilvessalo 1956, 1957).

Our study was motivated by the lack of coherence between different descriptions of forested mire margin vegetation and by the assumed relative importance of these communities as sources of biodiversity. The aims were (1) to explore the structure of the vegetation of forested mire margins located in South and Central Finland, using systematically sampled data and ordination and classification techniques, and (2) to compare the traditional Finnish site type classification and the results of the numerical analyses.

MATERIAL AND METHODS

Sample plots and study area

We used the vegetation and tree stand data of the permanent plots collected during the eighth National Forest Inventory (8th NFI). In 1985–86, 3 009 permanent plots covering the entire forestry land (forests and mires, see Aarne 1995) area of Finland (Reinikainen 1990) were established for monitoring tree vitality (Jukola-Sulonen *et al.* 1990), ground vegetation (Tonteri *et al.* 1990), and deposition (Ruhling *et al.* 1987). Circular plots were placed systematically: four circular plots in one cluster (a sample plot tract) in each 16 × 16 km grid square in Southern and Central Finland (S of 66°N; 2 618 plots) (see Salemaa *et al.* 1991). On each of the circular plots (300 m^2) there were three to six vegetation sample quadrates (2 m^2).

In this study, only plots that satisfied the following criteria were included: 1) location S of the 66th latitude, 2) classified as paludified forest site types, mire margin forest site types, or forested pine and spruce mire site types, 3) each plot classified to one site type, 4) four vegetation sample quadrates on the plot, 5) site not drained, 6) tree stand untreated at least two years before inventory. Altogether, 92 plots fulfilled all criteria.

Biogeographically, the area (Fig. 1) investigated extends from the northernmost border of the hemiboreal zone to the southern parts of the northern subzone of the boreal zone (according to Ahti *et al.* 1968). The study area comprise three subzones of forest vegetation (coast-Finland, South-Finland and West-Central-East-Finland, Kalela 1961) and the border between the zones of raised bogs and aapa-fens runs through the area (Ruuhijärvi 1982).

The mean annual temperature (for the period 1961–80) within the study area ranges from +1 to +5°C; the temperature sum (threshold +5°C) from 850 to 1 350 degree days (Heino & Hellsten 1983); the mean annual precipitation from 500 to 600 mm; the duration of the growing season from 135 to 180 days; Conrad's continentality index from 24 to 34; and Thornthwaite's index of humidity from 20 to 50 (Tuhkanen 1980).

The traditional Finnish forest type approach of Cajander (Cajander 1926, Frey 1973) was used in classification of the 92 plots on site type classes. Paludified forest site types are classified in accordance with Kalela (1973). Mire site types are classified in accordance with Heikurainen and Pakarinen (1982). For each site type, fertility classes I (richest)–VI (poorest) according to the six-scale system of Huikari (1974) describe the forest production potential of site types (Table 1).

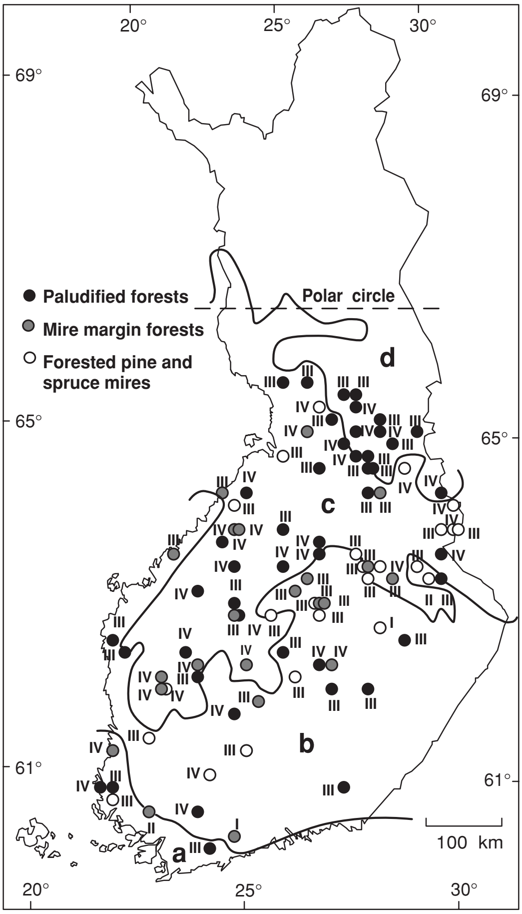

Fig. 1. Distribution of the 92 sample plots. The vegetation zones are: a = hemiboreal zone and b = southern, c = middle, and d = northern boreal subzones of boreal zone (Ahti *et al.* 1968). The fertility classes (I–IV) (Huikari 1974) of the sites are indicated.

Field work and vegetation survey

The vegetation survey of the plots was carried out by a biologist member of each inventory crew. The data were collected in 1985–86 by 12 crews.

Four 2 m^2 sample quadrates placed systematically along a line passing through the centre of the plot in a S–N direction were used for description of the field and bottom layer vegetation. Percentage cover was estimated for vascular plants (tree and shrub specimens lower than 50 cm included), bryophytes and terricolous lichens. The nomenclature follows Hämet-Ahti *et al.* (1986) for vascular plants, Koponen *et al.* (1977) for bryophytes and Santesson (1993) for lichens. Vascular plants were determined to species. Mosses were identified to species except for the genera *Brachythecium, Plagiothecium* and the family *Mniaceae*, in which only the genera *Plagiomnium* and *Rhizomnium* were separated. Hepatics were treated collectively. *Sphagna* and lichens (*Cladonia*) were identified to species level in the field without subsequent microscopic checking. The 12 biologists who carried out the survey attended a training course before the field work began and the inter-observer variation in species cover estimation was determined in a study afterwards (see Tonteri 1990). Inter-observer variation in ability to recognise taxa was not checked.

The canopy cover of trees (> 1.5 m high) and shrubs (0.5–1.5 m high) was recorded for all species in 300 m^2 sample plot. Total basal area was estimated using three telascope observations. Determination of the mean diameter was based on a tree tally. By coring of one representative dominant canopy tree, stand age and dominant height (site index H_{100} = height of dominant trees at 100 year age) were approximated. The dominant tree species was defined as the one with largest volume in the dominant canopy layer. Peat depth was recorded as the mean of four measurements in each of the 2 m^2 vegetation.

Data analysis and ecological interpretation

The mean percentage cover for each species was calculated from the four surveyed quadrates on each plot. Species present in only one or two plots as well as the taxa not determined to species level were excluded from numerical analyses, leaving 88 plant species (from the total of 135 species, see Appendix) in 92 sample plots.

The main compositional gradients in vegetation were extracted by detrended correspondence analysis (DCA; Hill & Gauch 1980). DCA was carried out with the CANOCO program, using detrending by segments (Ter Braak 1987). After testing first the default option the use of 15 segments gave the most interpretable configuration of ordination for 92 sample plots. No rescaling of the axes and no transformation options except that the down-weighting option for rare species was used (see Økland 1990c). Biplot scores for regional variables (temperature sum, latitude, longitude) and the measured site variables (peat depth, tree cover, shrub cover) and tree stand variables (basal area, mean diameter at breast height (= DBH), dominant height and stand age) were obtained.

The vegetation data was classified numerically by TWINSPAN (two-way indicator species analysis; Hill 1979). TWINSPAN was applied using default options for minimum group size (5), maximum number of indicator species (7), and pseudo-species cut levels (0, 2, 5, 10, 20 cover %). Three levels of division were used.

Spearman correlation coefficients between DCA axes (plot scores) and explanatory variables were calculated (cf. Sokal & Rohlf 1981). Analysis of variance (ANOVA) was used to test TWINSPAN clusters for environmental differences.

In the ecological interpretation of the results the indicator values of forest and mire plants were used, according to several earlier Finnish studies and mainly synthesised by Eurola *et al*. (1984, 1994) for mires and by Kalela (1973) for forests, respectively. The grouping of species into different ecological groups (see Fig. 2) was carried out on the basis of the same lists.

RESULTS

DCA ordination and ecological interpretation

In the DCA ordination of 92 sample plots and 88 species, the eigenvalue of the first axis was 0.49, and the eigenvalues of axes two to four were distinctly lower (0.22, 0.20, 0.14). The gradient length along the DCA axis 1 was 4.2 *S.D.*-units and the gradient lengths along axis two to four were 3.2, 3.3 and 2.5 *S.D.*-units, respectively. For the two-axis solution axes 1 and 2 was chosen on the basis of interpretation (Figs. 2 and 3).

In the species ordination space (Fig. 2), ombro-oligotrophic species typical of bogs (e.g. *Vaccinium uliginosum, Ledum palustre, Betula nana, Eriophorum vaginatum, Vaccinium microcarpum, Sphagnum russowii, S. angustifolium, S. nemoreum*) and also xeric forest species (e.g. *Cladonia* spp., *Empetrum nigrum, Calluna vulgaris*) obtained high DCA1 scores and the more mesotrophic spruce mire species (e.g. *Equisetum sylvaticum, Sphagnum girgensohnii, S. squarrosum*) and herb rich forest species (e.g. *Athyrium filix-femina, Oxalis acetosella, Maianthemum bifolium*) obtained low scores along

Table 1. The studied site types and their Finnish abbreviations within 1) paludified upland forests according to Kalela (1973), 2) mire margin forests and (3) forested pine and spruce mires according to Heikurainen and Pakarinen (1982) and fertility classes of the site types according to Huikari (1974).

Site types	Abbrev.	Fertility classes
1. Paludified forests		
Paludified *Empetrum–Vaccinium* type	sEVT	IV
Paludified *Vaccinium* type	sVT	IV
Paludified *Vaccinium–Myrtillus* type	sVMT	III,IV
Paludified *Myrtillus* type	sMT	III,IV
Paludified *Deschampsia–Myrtillus* type	sDeMT	III
2. Mire margin forests		
Paludified pine forest	KgR	IV
Oligo-mesotrophic paludified spruce forest	KgK	II,III
Eutrophic paludified hardwood-spruce forest	LhK	I
3. Forested pine and spruce mires		
Rubus chamaemorus-spruce swamp (mire)	MrK	IV
Spruce-pine swamp (mire)	KR	III,IV
Vaccinium myrtillus-spruce swamp (mire)	MK	III
Equisetum sylvaticum-spruce swamp (mire)	MkK	III
Herbrich hardwood-spruce swamp (mire)	RhK	II

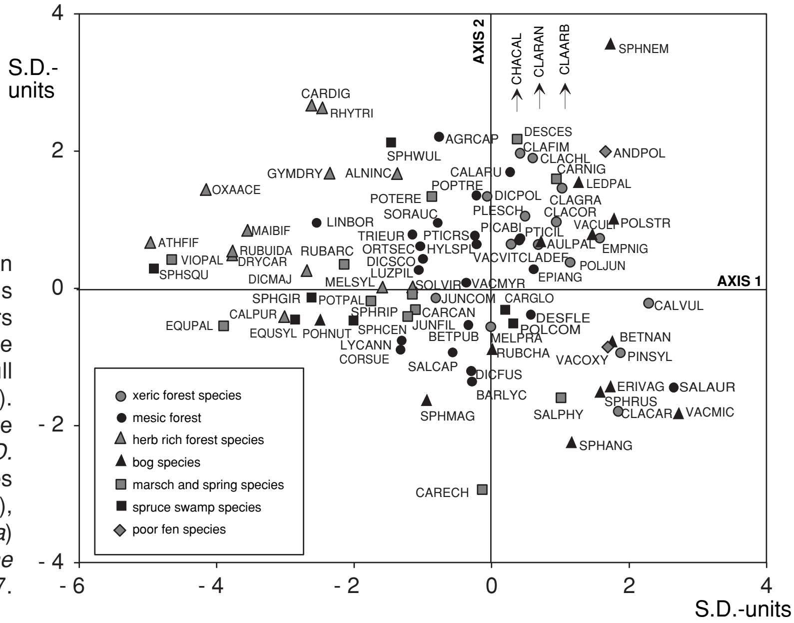

Fig. 2. DCA species ordination for axes 1 and 2. Species names are the first three letters of the genus and the first three letters of the species (for full species names see Appendix). Species ecological groups are presented. On axis 2 the *S.D.* values of the outlying species CLAARB (*Cladonia arbuscula*), CLARAN (*Cladonia rangiferina*) and CHACAL (*Chamaedaphne calyculata)* are 6.8, 5.5 and 4.7.

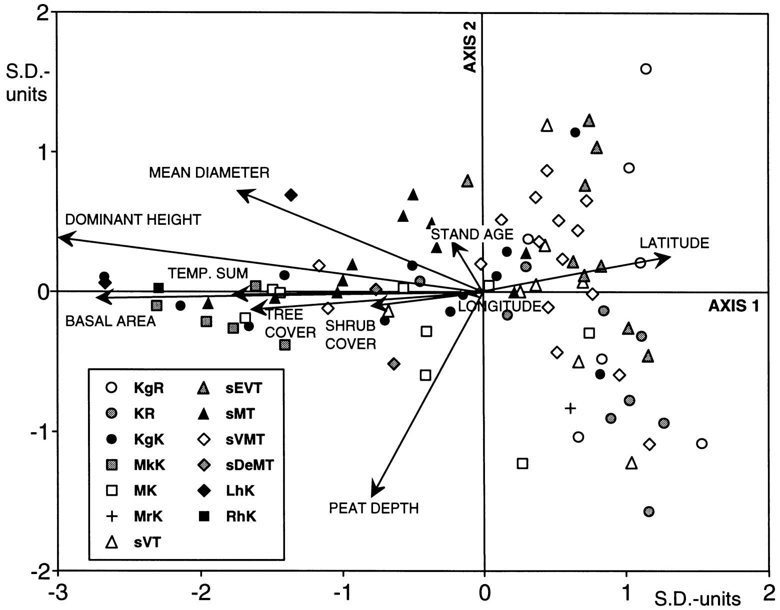

Fig. 3. DCA ordination of the 92 sample plots for axes 1 and 2 with the vectors of passive explanatory variables.

DCA1. The optima of constant species typical of oligotrophic and meso-oligotrophic forests (*Vaccinium vitis-idaea, V. myrtillus Pleurozium schreberi, Dicranum polysetum, Hylocomium splendens*) were in the centrum of the ordination space. *Carex globularis* and *Polytrichum commune*, the constant species for paludification, were also centrally placed. In the sample plot ordination space (Fig. 3), the bog and xeric forest site types (KR, KgR and sEVT, see Table 1) obtained correspondingly high DCA1 scores and the mesic and herb-rich forested spruce mire and forest site types (LhK, RhK, MkK, KgK, MK, sMT, see Table 1) obtained low scores along DCA1. Along the mid-point of DCA1, plots from a wide variety of oligotrophic pine and spruce mire types and paludified forest types occurred intermixed.

The first DCA axis was significantly correlated and rather parallel with all the measured variables connected with tree stand productivity (basal area, dominant height, mean diameter, see Fig. 3 and Table 2). The significant negative correlation of DCA1 with temperature sum and the significant positive correlation with latitude is likely to reflect intercorrelations with the tree stand variables indicating forest production (fertility gradient) and geographical variables (climatic gradient). Significant correlations occurred between dominant height and temperature sum and between dominant height and latitude (Table 3). Most fertile site types (LhK and RhK, fertility classes I and II) were absent from the northern third of the study area. Most commonly recorded fertility classes, III and IV, were equally frequent in each of the northern, middle and southern third of the study area (see Fig. 1).

Variation in vegetation along the second axis was related only to the peat depth variable (Table 2). Most of the mire expanse species (bogs and poor fens species like, *Sphagnum russowii, S. angustifolium, S. magellanicum, Vaccinium oxycoccus,* in Fig. 2) and also the spruce mire species had low scores along this axis while most of the xeric (e.g. *Cladonia* species) and mesic forest species (e.g. *Oxalis acetosella, Rhytidiadelphus triquetrus, Carex digitata*) obtained high scores. In the sample plot ordination space (Fig. 3) mires like spruce-pine mires (KR) and *Vaccinium myrtillus*-spruce mires (MK) had low scores along this axis and paludified xeric and mesic forests (sEVT, sVMT, sMT, see Table 1 for abbreviations) obtained high scores correspondingly. Less fertile site types and bog species had wide amplitudes along this axis. Variation along DCA1 was lower in plots with low DCA1 scores. The significant negative correlation between stand age and the third axis and between temperature sum and the third axis revealed significant intercorrelation with these variables (– 0.39***, Table 3).

The ecological species groups (xeric, mesic and herb-rich forest, bog, spruce swamp and poor fen species) were fairly well separated in the species ordination, axes 1 and 2, except marsh and spring water species, which were evenly distributed on the ordination space Fig. 2.

TWINSPAN classification

The TWINSPAN classification of the 92 sample plots separated one cluster with six plots (cluster G) from the remaining 86 plots at the first dichotomy. *Dryopteris carthusiana* and *Oxalis acetosella* were indicator species for cluster G. Several mesotrophic herbs otherwise rare in the data with few species in common with the other clusters, occurred in this cluster (see Fig. 4, Table 4 and Appendix).

The first division of the remaining 86 plots separated ombro-oligotrophic pine mire type (KR and KgR) and xeric forest type (sEVT and most of the sVMT) plots (left, $n = 44$) from the oligo-mesotrophic spruce mire (MK, MkK and KgK) and mesic forest type (sMT and the remaining sVMT and sVT) plots (right, $n = 42$). The ombro-oligotrophic group had bog species and xeric forest species as preferentials

Table 2. Spearman rank correlations between DCA scores and 1) tree stand, 2) site quality and 3) geographical variables. *** = $P \leq 0.001$, ** = $0.001 < P \leq 0.010$, * = $0.010 < P \leq 0.050$.

DCA axis	1	2	3	4
1. Basal area	– 0.46***	– 0.13	0.05	– 0.01
1. Dominant height	– 0.57***	0.01	0.08	0.05
1. Mean DBH	– 0.26**	0.04	0.06	0.15
1. Stand age	0.09	– 0.05	0.40***	– 0.01
2. Tree cover	– 0.30**	– 0.15	– 0.07	0.03
2. Shrub cover	– 0.09	0.02	– 0.11	0.16
2. Peat depth	– 0.04	– 0.50***	– 0.01	– 0.20
3. Temperature sum	– 0.35**	– 0.05	– 0.40***	– 0.03
3. Latitude	0.27**	0.08	0.30**	0.09
3. Longitude	– 0.04	– 0.03	0.35**	0.01

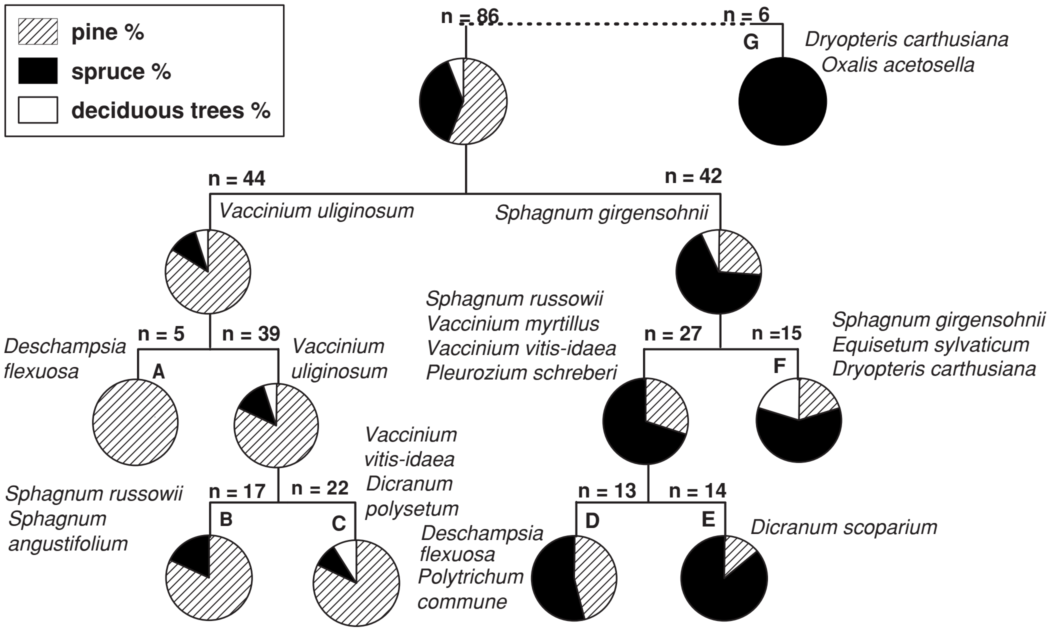

Fig. 4. TWINSPAN- clustering dendrogram for the 92 sample plots. Indicator species for each division level and each final vegetation cluster are included. Pies describe the percentage of sample plots with different tree species domination on each division level and in each final vegetation cluster.

and *Vaccinium uliginosum* as indicator, the oligo-mesotrophic group was indicated by the presence of *Sphagnum girgensohnii,* and had meso-oligotrophic mire margin species and constant species of mesic forests as preferentials. Thus the first division of the 86 plots appeared to represent a division between ombro-oligotrophy and meso-oligotrophy.

The second division of the ombro-oligotrophic group (on the left, $n = 44$) resulted in the separation of a final cluster A, which contained paludified xeric forest (sVT, sEVT) and mire margin forest (KgR) plots, indicated by *Deschampsia flexuosa* and characterized by several pioneer species (Fig. 4, Table 4 and Appendix). The rest of the plots ($n = 39$) which, according to their preferential species, had a more boggy character, were further divided to form clusters B ($n = 17$) and C ($n = 22$). Cluster B was indicated by *Sphagnum russowii* and *S. angustifolium,*

Table 3. Correlations between 1) tree stand, 2) site quality and 3) geographical variables.*** = $P \leq 0.001$, ** = $0.001 < P \leq 0.010$, * = $0.010 < P \leq 0.050$.

	1	2	3	4	5	6	7	8	9
1. Basal area (1)									
2. Dominant height (1)	0.65***								
3. Mean DBH (1)	0.46***	0.61***							
4. Stand age (1)	0.35***	0.39***	0.46***						
5. Tree cover (2)	0.36***	0.12	0.02	−0.02					
6. Shrub cover (2)	−0.29**	−0.12	−0.28**	−0.22*	0.09				
7. Peat depth (2)	−0.02	−0.15	−0.21*	−0.03	0.05	−0.04			
8. Temperature sum (3)	0.12	0.26*	0.07	−0.39 ***	0.16	0.07	0.08		
9. Latitude (3)	−0.21*	−0.29**	−0.08	0.29**	−0.17	−0.01	−0.09	−0.91***	
10. Longitude (3)	0.11	0.07	0.04	0.33**	−0.06	0.15	0.07	−0.56***	0.54***

and had many bog species as preferentials and consisted mainly of plots representing mire site types. Cluster C was indicated by *Vaccinium vitis-idaea* and *Dicranum polysetum* and contained most of the northern paludified forest site type (sEVT and sVMT) plots (Fig. 4, Table 4 and Appendix).

The second division of the meso-oligotrophic group (on the right, *n* = 42) resulted in a separation of a final cluster F (*n* = 15). Cluster F was indicated by the slightly mesotrophic species *Sphagnum girgensohnii, Equisetum sylvaticum* and *Dryopteris carthusiana* and preferred by other meso-oligotrophic mire margin species as well. This cluster mainly consisted of plots assumed to be the most fertile among the remaining 86 plots not in G; the ordinary spruce-hardwood mire site types (MK, MkK and KgK) and mesic paludified forest site types (sMT, sDeMT). The remaining set of plots (*n* = 27), indicated by *Sphagnum russowii, Vaccinium myrtillus, Vaccinium vitis-idaea* and *Pleurozium schreberi* were divided once more to form final clusters D (*n* = 13) and E (*n* = 4). Cluster D had *Deschampsia flexuosa* and *Polytrichum commune* as indicators. Cluster E was indicated by *Dicranum scoparium* with some oligotrophic mire margin species as preferentials. Cluster E was dominated by mire type plots while cluster D with forest type plots (Fig. 4, Table 4 and Appendix).

Table 4. Distribution of 1) paludified forest, 2) mire margin forest and 3) forested pine and spruce mire site types within 7 TWINSPAN vegetation clusters (A–G). The amount of each site type in each cluster and total (*n*) are presented.

Site types	Fertility classes	TWINSPAN-clusters							
		A	B	C	D	E	F	G	*n*
1. sEVT	IV	1	2	6					9
1. sVT	IV	3	1	1	3				8
1. sVMT	III,IV		3	9	2	2			16
1. sMT	III,IV				3	3	5		11
1. sDeMT	III				1		1		2
2. KgR	IV	1	5	3					9
2. KgK	II,III				2	5	3	1	11
2. LhK	I							2	2
3. MrK	IV		1						1
3. KR	III,IV		5	2	1				8
3. MK	III			1	1	4	3		9
3. MkK	III						3	2	5
3. RhK	II							1	1
n		5	17	22	13	14	15	6	92

Ecological interpretation of TWINSPAN clusters

The dominant tree species on each division level and in each final vegetation cluster is included in Fig. 4. The main division between ombro-oligotrophic and meso-oligotrophic groups separated the Scots pine-dominated stands (group *n* = 44) from the Norway spruce-dominated stands (group *n* = 42). Tree species composition also clearly differed between clusters at lower TWINSPAN division levels. The tree cover was significantly higher in the Norway spruce-dominated meso-oligotrophic group (clusters D, E, F and G) than in the Scots pine-dominated ombro-oligotrophic group (clusters A, B and C). The oligotrophic boggy cluster B differed significantly from the meso-oligotrophic mire margin clusters E and F (see Table 5).

The stand productivity variables, basal area and dominant height, differed strongly between clusters (Table 5). In the ombro-oligotrophic group the values for these variables were lower than in the meso-oligotrophic group. The basal area was significantly higher in the most spruce dominated clusters E and G. The oligotrophic cluster A differed clearly from all the other clusters with lower values for the tree stand variables, i.e. including the stands with the lowest tree stand age.

Clusters A, C and D which included most of the paludified forests had the lowest mean peat depths while cluster B with higher prominence of bog species and the spruce mire cluster G had the highest.

There was a significant difference in temperature sum between the clusters, reflecting distributional differences along the S–N-gradient. Clusters B and C, which contained most of the northern forest (sEVT and sVMT) plots, and clusters F and G, made up extremes with respect to temperature sums.

Parity of TWINSPAN clusters and conventional site classification

All final TWINSPAN clusters with more than 10 sample plots (clusters B–F) included plots classified into four or more site types. Plots classified as mire and forest site types were included in all clusters A–F, while cluster G contained mire sites only. All plots of the KgR (oligotrophic mire) and sEVT (xeric forest) types were classified to the ombro-oligotrophic main group (clusters A–C) and all plots of the KgK (oligo-mesotrophic mire) and sMT (mesic forest) types were classified to the meso-(oligo)trophic main group (clusters D–G). Most of the paludified forest types were divided into several clusters, sVT and sVMT were both distributed on all clusters A–E. The mire types KgK and MK had the widest distribution between clusters D and G and between clusters C and F. KR plots concentrated in cluster B but were also found in clusters C and D.

DISCUSSION

Results of ordination and clustering

The fertility gradient that strongly dominates the pattern of boreal forest and mire vegetation in Finland (e.g. Eurola *et al*. 1984, Kuusipalo 1985, Lahti & Väisänen 1987, Tonteri *et al*. 1990) was also apparent in this analysis of mire margin influenced forested sites. The mire sites and paludified forest sites seemingly make up a continuum along the main ordination axes. The assumed gradient mire margin/mire expanse was parallel with the fertility gradient, apparently making up one complex gradient. The analysis failed to separate these two gradients because the indicators of margin influence in mire sites are mesotrophic forest and wetland species. The indicators of mire expanse, on the other hand, partly belong to the xeric forest species (e.g. Eurola *et al*. 1994). The secondary gradient (second axis) was interpreted as a paludification gradient. In Pakarinen's (1982) Bray-Curtis-ordination of South Finnish mire and forest types the most dominant gradient was the paludification gradient, which was shortened in our study by not including unpaludified forest sites.

A distinct regional variation was evident, but the site type distribution in our material was too uneven for a thorough analysis in this respect due to a relatively low number of plots. The forest types have parallel regional variants in the vegetation (climatic)

Table 5. Mean values (± *S.E.)* of 1) tree stand 2) site quality and 3)geographical variables in the final TWINSPAN-vegetation clusters (A–G). For each variable TWINSPAN-clusters with different letters are significantly different ($P < 0.05$).

	TWINSPAN-clusters							
Variables	A	B	C	D	E	F	G	*F*-values
1. Basal area (m^2/ha)	5.4 b	11.4 a	16.9 a	20 a	27.6 abc	21.8 ab	28.7 abc	9.88 ***
	(1.4)	(2.2)	(1.7)	(1.8)	(2.2)	(2.2)	(2.6)	
1. Dominant height (m)	5.9	9.2	13.3 a	14.5 ab	16.3 ab	17.9 abc	19.8 ab	13.0 ***
	(10.3)	(12.3)	(6.3)	(10.5)	(9.5)	(10.8)	(15.7)	
1. Mean DBH (cm)	9.0	10.6	12.8	13.5	15.2	13.3	18.2 ab	1.7
	(1.0)	(1.4)	(1.3)	(1.8)	(1.8)	(1.3)	(1.4)	
1. Stand age (years)	21.8 b	82.1 a	105.5 a	88.7 a	125.7 a	82.3 a	90.0 a	3.1 **
	(2.2)	(16.0)	(11.0)	(14.0)	(16.7)	(7.7)	(10.0)	
2. Tree cover (%)	38.3	28.8	36.6	40.3	51.7 b	48.7 b	52.1	2.8 *
	(5.1)	(5.1)	(4.4)	(5.7)	(5.1)	(3.9)	(8.3	
2. Shrub cover (%)	8.8	5.6	7.6	5.8	2.6	9.5	6.2	1.2
	(1.9)	(1.5)	(2.0)	(1.1)	(0.5)	(3.0)	(1.9)	
2. Peat depth (dm)	0.5 b	2.7 a	1.3	1.4	2.6	1.7	3.2	2.1*
	(0.2)	(0.6)	(0.3)	(0.3)	(0.7)	(0.4)	(1.6)	
3. Temp. sum (dd)	1142	1022	1016	1093	1056	1185 bc	1145	5.6 ***
	(5.3)	(2.6)	(1.6)	(3.2)	(2.9)	(3.1)	(4.0)	
Number of plots	5	17	22	13	14	15	6	

subzones (Kalela 1960). No analogous system exist for mire site types or paludified forest site types.

The rather poor agreement between the TWINSPAN clusters and the site types determined in the field was not surprising (see Hotanen & Nousiainen 1990). There may be at least three different reasons for this: 1) the relatively high floristic similarity between different site types in the Finnish classification system, e.g., between forested mires and paludified forests, 2) continuity of the vegetation along the main gradient and, in particular, effect*s* of the other subsidiary complex gradients on the cluster formation in TWINSPAN, and 3) errors in the field determination of site types (see Hotanen 1989, Hotanen & Nousiainen 1990).

Data quality and sources of error

The number of mire margin plots included in this study was relatively small. Due to systematic sampling the types are represented in the material according to their frequency in Finland. This inevitably causes poor or inadequate representation of the variation in mire margin vegetation; ecologically and floristically distinct types are represented by few sample plots and the relationships between these types and the rest of the data set is not adequately described (e.g. Økland 1990c). This is one reason why the few most fertile plots separated at the first division level in TWINSPAN.

The size and number of sample squares per plot was largely decided upon by practical considerations. The total area of 4×2 m^2 squares was the same on all plots but this may not have been enough to include all the potential species and produce reliable mean coverage values (Trass & Malmer 1978, Pakarinen 1984, Økland 1990c).

The vegetation data was collected by 12 different persons and the inter-observer difference in coverage values varied between 15–40% depending on the plant species (Tonteri 1990). This range does, however, appear moderate when considering cover estimations in general (e.g. Bråkenhielm & Qinghong 1995). Jukola-Sulonen and Salemaa (1985) noted that high coverage values tended to be underestimated and the low coverage values overestimated. With the methods used, the quality of the data was sufficient for revealing the gradients (see also Hotanen 1990).

CONCLUSIONS

In this first, as far as we know, simultaneous ordination of mire and paludified forest types, the similarity in the vegetation of mire and paludified upland forest habitats was clearly revealed by the numerical analysis. The difficulties in the field determination of site types studied are well-known (Hotanen 1989). In practice, characteristics of the site such as peat depth and peat morphology are used in addition to vegetation and tree stand structure when site types are determinated. Thus, there seems to be a discrepancy between usage and the site-type principle (Eurola *et al.* 1984) in establishment of typology in the studied forest and mire sites. Instead of a revision of the classification we first suggest more extensive use of gradient analyses and non-classifying methods (Lahti 1994ab).

This study demonstrates the high floristic diversity of mire margin vegetation. High species richness results from the mixing of mire and forest species and the occurrence of special mire margin features, such as spring, flooding and marsh, whereby species richness is added through associations with the forest and bog species groups. These sites represent an ecological edge effect (Tolvanen 1994). In Finland where the mire margin sites have decreased after intensive forest drainage also this kind of — still pristine — rather trivial mire margin sites should be studied in more detail. Being still more common than the boreal mire margin types with the highest alpha diversity, i.e. the most fertile hardwood-spruce mire site types, for instance, (Eurola *et al.* 1991, Forestry Environment Guide 1993, Heikkilä 1994) the recent remnants of forested mire margin types in southern Finland should be protected against further amelioration activities.

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APPENDIX

Field and ground layer vegetation in seven TWINSPAN-clusters (A–G). Mean cover percentage value of each species in each cluster (+ < 0.1%) are presented. Total number of species was 135. The amount of sample plots in each cluster = (*n*).

	TWINSPAN-clusters						
	A (*n* = 5)	**B** (*n* = 17)	**C** (*n* = 22)	**D** (*n* = 13)	**E** (*n* = 14)	**F** (*n* = 15)	**G** (*n* = 6)
Field layer							
Trees and shrubs:							
Salix aurita	0.1	1.3	+	–	–	–	–
Salix phylicifolia	–	–	+	–	–	–	–
Pinus sylvestris	+	0.1	+	0.1	–	+	–
Betula pubescens	0.1	0.1	0.1	0.1	+	0.2	+
Picea abies	0.5	0.2	0.1	0.2	0.1	0.1	0.1
Sorbus aucuparia	0.4	+	0.1	0.1	+	+	0.2
Salix caprea	–	0.1	0.2	–	+	0.1	0.1
Juniperus communis	–	+	+	0.1	–	+	–
Populus tremula	0.1	–	–	+	–	+	–
Alnus incana	–	–	+	–	–	+	+
Rubus idaeus	–	–	–	–	–	+	+
Dwarf-shrubs:							
Betula nana	–	0.8	–	–	–	–	–
Vaccinium microcarpum	–	+	+	–	–	–	–
Arctostaphylos uva–ursi	–	–	+	–	–	–	–
Andromeda polifolia	–	0.3	0.1	–	–	–	–
Vaccinium oxycoccus	–	0.1	+	+	–	–	–
Chamaedaphne calyculata	–	0.3	+	–	0.1	–	–
Empetrum nigrum	4.0	4.1	5.4	0.9	0.3	–	–
Calluna vulgaris	2.9	6.9	0.9	+	–	0.1	–
Ledum palustre	–	2.3	8.9	+	–	0.1	–
Vaccinium uliginosom	0.3	7.8	10.1	+	–	0.4	–
Vaccinium vitis-idaea	6.5	2.5	11.7	10.7	4.4	2.6	3.3
Vaccinium myrtillus	2.0	7.0	11.3	16.5	28.0	10.4	3.0
Graminoids:							
Calamagrostis epigejos	1.4	–	–	–	–	–	–
Festuca ovina	0.1	–	–	–	–	–	–
Eriophorum vaginatum	–	0.3	–	–	–	–	–
Eriophorum angustifolium	–	–	+	–	–	–	–
Carex nigra	–	+	0.1	+	–	–	–
Carex globularis	2.0	3.6	2.7	2.6	5.0	2.0	1.0
Deschampsia flexuosa	13.1	0.2	1.0	5.8	0.1	0.4	0.1
Luzula pilosa	0.2	–	+	0.1	+	0.1	0.1
Calamagrostis arundinacea	0.1	+	0.1	+	+	0.1	+
Carex echinata	–	–	+	+	–	–	–
Juncus filiformis	–	–	+	0.2	–	–	–
Agrostis capillaris	–	–	+	+	–	+	–

(continues)

	TWINSPAN-clusters						
	A (*n* = 5)	**B** (*n* = 17)	**C** (*n* = 22)	**D** (*n* = 13)	**E** (*n* = 14)	**F** (*n* = 15)	**G** (*n* = 6)
Carex canescens	–	–	+	+	–	–	+
Deschampsia cespitosa	–	–	0.3	+	–	+	0.1
Calamagrostis purpurea	–	–	0.1	–	–	1.6	0.3
Calamagrostis canescens	–	–	–	–	–	+	–
Carex digitata	–	–	–	–	–	+	0.1
Melica nutans	–	–	–	–	–	–	0.1
Carex lasiocarpa	–	–	–	–	–	–	+
Carex rostrata	–	–	–	–	–	–	+
Herbs:							
Potentilla erecta	0.1	–	–	–	–	+	–
Melampyrum pratense	0.1	+	+	0.1	0.1	+	–
Epilobium angustifolium	0.2	–	0.2	0.1	–	+	0.1
Solidago virgaurea	0.3	+	–	0.1	–	0.4	0.1
Rubus chamaemorus	–	1.5	1.4	+	4.3	+	0.6
Equisetum sylvaticum	–	+	0.8	0.2	1.8	6.1	9.1
Trientalis europea	+	+	0.4	0.7	+	0.3	0.7
Linnaea borealis	0.1	+	–	0.3	+	0.1	1.7
Cornus suecica	–	+	0.1	0.3	–	0.4	–
Goodyera repens	–	–	+	–	–	–	–
Epilobium palustre	–	–	–	+	–	–	–
Lycopodium annotinum	–	–	+	+	+	+	–
Melampyrum sylvaticum	–	–	–	–	+	0.1	–
Listera cordata	–	–	–	+	–	+	–
Orthilia secunda	0.1	+	0.3	0.2	+	0.1	0.7
Rubus arcticus	–	–	0.1	+	–	0.1	0.1
Gymnocarpium dryopteris	–	–	+	–	+	1.3	2.7
Dryopteris carthusiana	–	–	–	–	0.4	0.3	4.5
Oxalis acetosella	–	–	–	+	–	0.1	4.0
Maianthemum bifolium	–	–	+	0.1	0.1	0.5	3.8
Equisetum palustre	–	–	+	–	–	–	0.9
Dryopteris expansa	–	–	–	1.1	–	–	0.2
Potentilla palustris	–	–	–	0.2	–	–	0.1
Thelypteris phegopteris	–	–	–	0.2	–	–	–
Lysimachia vulgaris	–	–	–	–	–	+	–
Viola palustris	–	–	–	–	–	–	0.6
Athyrium filix-femina	–	–	–	–	–	–	1.8
Rubus saxatilis	–	–	–	–	–	–	0.4
Anemone nemorosa	–	–	–	–	–	–	0.3
Cirsium helenioides	–	–	–	–	–	–	0.1
Equisetum arvense	–	–	–	–	–	–	+
Equisetum pratense	–	–	–	–	–	–	+
Geranium sylvaticum	–	–	–	–	–	–	+
Geum rivale	–	–	–	–	–	–	+
Ranunculus repens	–	–	–	–	–	–	+
Stellaria palustris	–	–	–	–	–	–	+
Ground layer							
Sphagnum mosses:							
Sphagnum nemoreum	5.0	4.4	3.5	–	0.1	+	–
Sphagnum russowii	–	25.1	5.0	5.7	5.4	+	–
Sphagnum magellanicum	–	0.1	+	–	1.0	+	–
Sphagnum angustifolium	7.4	34.0	8.0	8.0	8.1	3.1	1.5
Sphagnum girgensohnii	0.2	+	4.0	15.8	24.5	42.1	48.5
Sphagnum compactum	–	0.1	–	0.3	–	–	–
Sphagnum centrale	–	–	–	0.5	0.4	–	1.7
Sphagnum wulfianum	–	–	+	–	–	–	+
Sphagnum fallax	–	–	–	1.2	–	–	–
Sphagnum riparium	–	–	–	0.7	–	–	–
Sphagnum squarrosum	–	–	–	–	–	0.1	1.0
Sphagnum teres	–	–	–	–	–	+	–
Other mosses:							
Polytrichum strictum	2.0	0.7	0.1	+	+	–	–
Polytrichum juniperinum	3.4	+	0.1	0.1	+	–	–
Dicranum drummondii	–	+	–	–	–	–	–
Ptilidium pulcherrimum	–	0.1	–	–	–	–	–
Dicranum fuscescens	–	–	+	–	+	+	–
Aulacomnium palustre	1.1	0.8	0.2	0.3	0.1	0.2	0.3
Pleurozium schreberi	31.8	15.7	29.0	23.0	22.7	8.6	2.9
Polytrichum commune	24.2	10.4	6.9	20.7	3.8	7.7	0.4
Hylocomium splendens	1.7	0.6	5.0	3.3	9.1	3.0	2.4
Dicranum polysetum	3.3	0.2	1.1	0.5	1.5	1.6	0.3
Dicranum scoparium	0.5	+	0.2	0.2	2.0	0.4	0.2
Hepaticae spp.	–	0.1	+	+	0.1	+	0.1

(continues)

	TWINSPAN-clusters						
	A (*n* = 5)	**B** (*n* = 17)	**C** (*n* = 22)	**D** (*n* = 13)	**E** (*n* = 14)	**F** (*n* = 15)	**G** (*n* = 6)
Barbilophozia lycopodioides	–	0.1	–	–	–	+	0.1
Pohlia nutans	+	+	+	+	+	+	0.4
Ptilidium ciliare	+	–	+	+	+	–	–
Ptilium crista-castrensis	–	–	+	+	1.0	0.2	–
Mnium spp.	–	–	+	–	–	+	0.2
Calliergon stramineum	–	–	+	0.1	–	–	–
Barbilophozia barbata	–	–	–	–	+	–	–
Atrichum undulatum	–	–	–	–	–	+	–
Blepharostoma trichophyllum	–	–	–	–	–	+	–
Rhodobryum roseum	–	–	–	–	–	+	–
Brachythecium spp.	–	–	+	+	+	0.2	3.0
Dicranum majus	–	–	+	0.1	1.6	0.5	2.6
Rhizomnium spp.	–	–	+	–	–	–	+
Plagiomnium spp.	–	–	–	+	–	–	+
Rhytidiadelphus triquetrus	–	–	–	–	+	+	0.2
Plagiochila asplenioides	–	–	–	–	–	–	+
Lichens:							
Cladonia botrytes	+	–	–	–	–	–	–
Cladonia crispata	+	–	–	–	–	–	–
Cladonia gracilis	0.1	–	+	–	–	–	–
Cladonia stellaris	0.1	–	0.2	–	–	–	–
Cladonia cariosa	+	+	+	–	–	–	–
Cladonia cornuta	2.0	+	–	–	–	+	–
Cladonia arbuscula	0.1	1.1	0.3	–	+	–	–
Cladonia rangiferina	0.3	1.1	0.6	0.1	0.1	+	–
Cladonia fimbriata	+	+	–	–	–	+	–
Cladonia deformis	+	+	+	–	–	+	–
Cladonia chlorophaea	+	–	+	–	–	+	–
Cladonia furcata	–	–	–	–	–	+	–
Peltigera aphthosa	–	+	–	–	–	–	–