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Vegetation succession and diversity on Teuravuoma experimental drainage area in northern Finland

Kasvillisuuden sukkessio ja monimuotoisuus Teuravuoman koeojitusalueella Pohjois-Suomessa

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This case study deals with the effects of forest drainage on six mire site types represented by 33 permanent sample plots within a Finnish aapa mire complex located in north boreal vegetation zone. We analysed the main compositional gradients, the abundances of plant species and the diversity of vegetation. The vegetation descriptions were made about at the time of drainage in 1933 and after that in 1943, 1950 and 1994. The forest drainage emphasized the importance of *spruce mire* and *hummock-level bog* influences (mire margin and mire expanse effects respectively) in controlling the structure of plant communities. The change of plant community was greatest on fertile mire site types, also spruce mire influence promoted the secondary succession. As expected, the shallow-rooted and/or demanding flark-level vascular plants and (eutrophic) fen mosses had not been able to adapt to the ground water level drawdown. At first, after drainage, species number, Shannon's H' and Simpson's D increased: many mire species of hummock and intermediate level microsites had increased while also pioneer and forest species had colonized the plots. By 1994, however, as the mire species were decreasing these measures had turned to decline except on the (most) infertile site types. Pielou's J' and the evenness based on D reacted vaguely, decreasing a little, though, from 1933 to 1994. Thus, in such cases the dominance in the vegetation had increased. The beta-diversity describing here the differences between plant communities (or site types) decreased along with the hydrological conditions becoming more uniform after drainage.

Key words: aapa mire, compositional gradients, fen, FUPGMA classification, GNMDS ordination, peatland vegetation

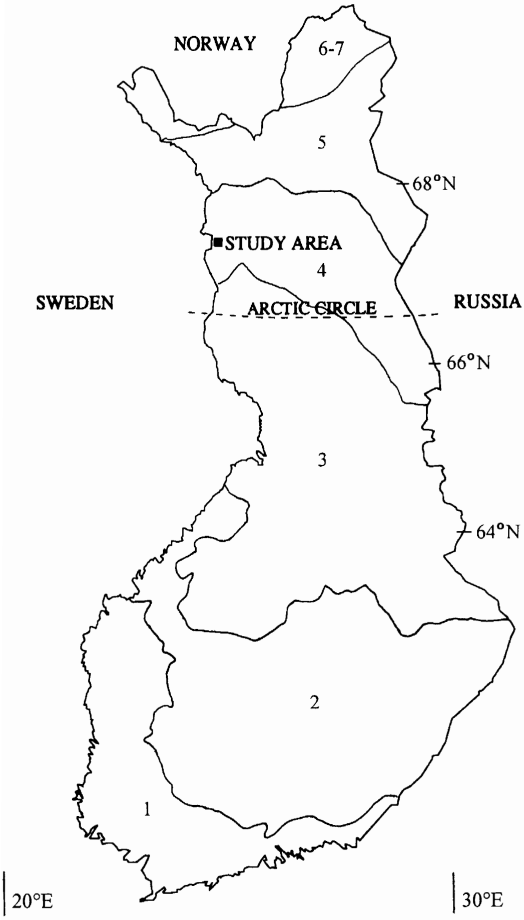


Fig. 1. Situation of the study area and the Finnish mire vegetation zones (Atlas of Finland 1988): 1 = Concentric bogs, 2 = Eccentric bogs and *Sphagnum fuscum* bogs, 3 = Southern aapa mires (Pohjanmaa-type), 4 = Main aapa mires (Peräpohjola-type), 5 = Northern aapa mires (Forest-Lapland-type), 6–7 = Palsa mires and orohemiarctic mires in Fjeld Lapland.

Kuva 1. Tutkimusalueen sijainti ja Suomen suokasvillisuusvyöhykkeet (Atlas of Finland 1988). 1 = Kilpikeitaat eli konsentriset kermikeitaat, 2 = Viettokeitaat eli eksentriset kermikeitaat ja rahkakeitaat eli Sphagnum fuscum -keitaat 3 = Pohjanmaan aapasuot, 4 = Peräpohjolan aapasuot, 5 = Metsälapin aapasuot, 6–7 = Tunturi-Lapin palsa- ja paljakkasuot.

INTRODUCTION

In Finland, the current knowledge of the vegetation succession induced after forest drainage has been largely based on Sarasto's (1952, 1957, 1961) studies (see also Keltikangas 1945 and references therein). In some later works (e.g. Laine et al. 1995) further knowledge is obtained and some of these results are based on observations from permanent sample plots (e.g. Mannerkoski 1976, Pienimäki 1982, Reinikainen 1984, Silfverberg 1991). The studies by Melin (1917), Holmen (1964) and Platonov (1976) present results concerning secondary succession on corresponding latitudes outside Finland.

About a half of the over 5 million ha which have been drained for forestry in Finland is located in the aapamire zone (zones 3–5, Fig. 1) of which about 0.8 million ha is situated north of 66°N (Sevola 1996). However, very little is known about the structure of the vegetation or about how the secondary succession proceeds on mires after drainage in the aapamire zone. There are some publications dealing with these aspects in southern aapa mires (Pohjanmaa-type) (e.g. Pienimäki 1982, Aapala & Kokko 1988).

The use of multivariate methods in 1970s (e.g. Pakarinen 1976) initiated a new phase also in the research of plant communities on drained peatlands (Mannerkoski 1979, Kuusipalo & Vuorinen 1981). Starr (1984) and Kurimo and Uski (1988) applied numerical methods when investigating the plant communities of both pristine mires and of the corresponding site types undergoing succession after drainage. This approach was applied also by Hotanen and Vasander (1992) on Sarasto's (1961) material. In South Finland Laine & Vanha-Majamaa (1992) and Laine et al. (1995) have studied the relation between environmental factors and the vegetation on drained pine mires of different drainage age and of varying nutrient level as well as the relation of these to the vegetation of corresponding pristine mires. The studies of Reinikainen (1988), Laine (1989), Hotanen & Nousiainen (1990), Hotanen (1991) and Eurola et al. (1995) deal with the main stress on the ecological and compositional gradients caused by drainage as well as on the problems of classifying drained peatlands. With the exeption of Paalamo (1996) no investigations are known in which the main compositional gradients are examined using observations in the same place before and after drainage. In her study the drainage effect has lasted for a short time, only 5 years.

There are some studies on the variation of the vegetational diversity on drained peatlands. Sarasto (1952, 1961) examined the variation in species number. Vasander (1984, 1987a, 1987b) has studied the effects of drainage and fertilization on the alpha- diversity indices of the field and bottom layers as well as on the relationships between the indices and the aboveground biomass of the vegetation (see also Vasander et al. 1997). Conclusions concerning the changes in beta-diversity between plant communities (or site types) can be drawn by the studies of Hotanen & Vasander (1992), Laine et al. (1995) and Vasander et al. (1997).

The aim of this case study was to examine the effects of drainage on (1) the main compositional gradients, on (2) the abundance of plant species and on (3) the diversity of vegetation on the permanent sample plots of an experimental drainage area in the main aapamire zone (Peräpohjola-type). So far, these are apparently the northernmost vegetation observations in the world reported from drained peatlands. The material of this study consists of six mire site types, the main emphasis, however, being put upon the eutrophic pine fen (LR) site type as it was the original site type on most plots (21 of 33). As is the case on most eutrophic mire sites as well as on *Sphagnum fuscum* -hummocky and flark rich mire site types the final stage of the secondary succession (the so called transformed or climax stage of a drained mire site type) of LR is unclear (cf. Laine 1989).

MATERIAL AND METHODS

Study area and sample plots

The study area is situated in the main aapamire zone (Peräpohjola type) in the northern boreal vegetation zone in Finland (Atlas of Finland 1988, Fig. 1). The sample plots are located on the experimental drainage area of the Teuravuoma mire in the commune of Kolari. The mean altitude in the area is about 150 m a.s.l., the mean annual precipitation is 500–550 mm, the thermal growing period is 125–130 days, and the effective temperature sum about 800 d.d. with the threshold value + 5°C (Atlas of Finland 1987).

The sample plots were established in 1932–1933. This involved draining, description of the site types and measurement of the tree stand. The sample plots were classified (by Ilmari Paasio) as: LR = eutrophic pine fen (plots 1a–b, 9a–c, 14a–b, 15a–f, 16a–d, 17, 18, 30a–b, 31c), LK = eutrophic spruce fen (28a–b), RhK = herb-grass spruce mire (28c, 29, 31a–b), MkK = *Equisetum sylvaticum* spruce mire (10a–b), Rä = *Sphagnum fuscum* spruce-pine mire (11a–b), RaSR = rahka-hummocky (*S. fuscum*) oligotrophic tall-sedge pine fen (with features of VaPsR = dwarf-shrubby *Carex globularis* pine mire) (12) (Cajander 1913, Eurola et al. 1994).

Until 1989 the drainage efficiency had been rather weak. In that year the drainage was improved by cleaning the old ditches and digging complementary ditches. Before that the distance between the ditches varied between 100 and 140m on the LR plots. On the LK and RhK plots the distance was 100m. However, most sample plots have been located next to the ditches, only a part (15b,e,28b,30b,31b) farther away (Hökkä 1992). The plots 10a–b (MkK), 11a–b (Rä) and 12 (RaSR) were located outside the drainage area with regular ditch intervals, next to either a drainage ditch (MkK) or a trap ditch (Rä, RaSR). In the beginning of the 1970s improvement of the ditches was performed in the neighbourhood of the sample plots which to some extent has improved the drainage conditions.

In connection with the establishment the tree stands were treated with different cutting methods (Hökkä 1992). Afterwards, as the need arised, thinnings have been made and the natural drain cut in connection with tree stand measurements. On some plots the storms in the 1980s caused wind damage. The stands on 10a–b were felled to seed-tree position in 1989.

Field work

The first vegetation descriptions were made in June–July 1933 (by I. Paasio), 1943 and 1950 (by A. Välivuori) applying Norrlin's density-abundance scale which earlier was widely used in Finland. The scale is based on the average distances between individual plant shoots or between bottom layer patches of each species: continuous 10 (the degree of mixture of other species 1–4), 9 (4–6), 8 (6–7.5); abundant 7 (average spacing of shoots/patches 2.5–15 cm), 6 (15–50 cm), 5 (0.5–1 m); scattered 4 (1–2 m), 3 (2–5 m); scanty 2 (5–10 m), 1 (> 10 m); sporadic 1– (e.g. Ilvessalo 1932, see also Pakarinen 1984). For the sake of comparison the same method was used on 8–13 August 1994. On the plots 14a–b, 17, 18, 31c (LR) and 31b (RhK) the vegetation was described in 1933 and 1994.

In earlier field notes abundances had occasionally been marked as e.g. 3–4. In such cases the mean was used in calculations. When considering the size of the plots (1a–b, 9a–c, 16a–d = 40 m × 50 m; 10a–b = 25 × 50; 11a–b, 29, 30a–b = 30 × 40; 12 = 30 × 50; 14a–b, 15a–f, 17, 18 = 30 × 66; 28a–c, 31a–c = 25 × 40) and due to interpretation difficulties the values 1 and 1– were combined. In 1994 two observers (the authors Hotanen and Nousiainen) estimated the abundance of every species on each sample plot independently and in the case of different opinions the final abundance was decided as a compromise (*not* as a mean).

The accuracy of determination between different sampling occasions was standardized by marking the moss genera labelled with question marks in old papers (uncertain determinations) with the same code (e.g. *Hepaticae spp.*). Some species had been estimated as groups (*Vaccinium oxycoccos and V. microcarpum, Cladina arbuscula and C. rangiferina*) throughout the follow-up period. For vascular plants the nomenclature is according to Hämet-Ahti et al. (1998), for bryophytes to Eurola et al. (1990) (*Dicranum bergerii* according to Eurola et al. 1994) and for lichens to Vitikainen et al. (1997).

In 1994 the thickness of the peat was measured in the middle and in every corner of each sample plot, on intermediate (lawn) levels of the mire. The sample plot mean was calculated from these measurements. The peat depth was reported also in 1932 but the exact probing points are not known. The degree of humification of the peat (layer 5–10 cm) was estimated in 1994 using the method of von Post (1922) (Table 1).

The stand characteristics have been measured repeatedly since establishment, so far the latest measurements are from 1989. Hökkä (1992) has examined the growth- and yield values of most LR stands of this study more closely.

Data analysis

The compositional trends of the variation of the vegetation were detected by global nonmetric multidimensional scaling (GNMDS) using DECODA software (Minchin 1991). GNMDS was applied to a matrix of Bray-Curtis (alias Czekanowski or Sørensen) coefficient (Faith et al. 1987). This matrix of dissimilarities between the sample plots was calculated from abundance values of species. GNMDS was performed for the 1933 and 1994 materials separately and for the combined data of 1933, 1943, 1950 and 1994.

In GNMDS, solutions of 1–4 dimensions were calculated and ten starting configurations in each number of dimensions were used. All possible pairs of ordination configurations were compared using the method of Procrustean analysis (Schönemann & Carrol 1970). A Monte Carlo approach (in DECODA) was used to test the significance of the maximum correlation for environmental variables through the configuration.

Two dimensions were needed for the separate 1933 and 1994 ordinations. Correspondingly three dimensions were needed in the combined (1933, 1943, 1950, 1994) ordination. The stress values were as follows: for the 1933 material ID (one dimensional solution) = 0.21, 2D = 0.09 (3D = 0.07, 4D = 0.05); for the 1994 material ID = 0.23, 2D = 0.11 (3D = 0.06, 4D = 0.04); and for the combined material 1D = 0.29, 2D = 0.17, 3D = 0.09 (4D = 0.07).

In Procrustean analysis the minimum stress configurations of the two dimensional solutions were all identical as well as the configurations of the three dimensional solution in combined ordination.

To elucidate vegetation relations between the sample plots the FUPGMA (flexible unweighted pair-group method using arithmetic averages) classification (Belbin 1994) was performed separately for the 1933 and 1994 materials. The recommended Bray-Curtis coefficient was used as an association measure (Belbin 1994). This was calculated from the abundance values of species. In preanalyses the same classification was also made for the material from 1943 and 1950.

In addition to species number, the Shannon's (H'), Simpson's (D) and Pielou's (J') diversity indices (Pielou 1966, Whittaker 1972, Peet 1974) were calculated for the sample plots for which four separate vegetation descriptions were available. From Simpson's index an evenness measure ((1/Simpson's index)/ species number) was calculated with the DIVER programme (Finnish Forest Research Institute 1989). The variation of the indices between the sampling occasions was tested in the LR material applying the SPSS-X MANOVA procedure (SPSS-X User's Guide 1988).

RESULTS

Compositional gradients – ordination

In 1933 the main compositional gradient (coenocline) primarily showed variation in trophic status: the plots of fertile mire site types (LR, LK, RhK) obtained low scores and the more infertile plots (MkK, RaSR, Rä) high scores along GNMDS1 (Fig. 2). Variation in moisture was also connected to this gradient because the fertile plots had been wetter than the infertile ones. Especially the LK plots had been wet; e.g. *Carex chordorrhiza* and *Carex limosa* had been dominant on them. Fen species, e.g. *Equisetum fluviatile*, were found also on the infertile plots (App. 1). On the 2nd axis the pine mires were separated from the spruce mires. Thus, this gradient mainly represented hummock-level bog influence–spruce mire influence reflecting mire expanse (mire inherent) and mire margin (supplementary nutrient) effects.

The drainage/water level drawdown had affected the gradient structure so that in 1994 the hummock-level bog influence and spruce mire influence was the main compositional gradient

Table 1. Some stand and peat characteristics (means, standard deviations) of the study sites in 1932 (above) and 1994 (below). G = stand basal area, G_{spruce} = basal area of *Picea abies*, V = stand volume, Iv = stand volume increment, Yv = total yield of the stand, Bet% = *Betula pubescens* percentage of the stand volume, H, v.Post = degree of humification, von $Post_{1-10}$ (5–10 cm). LR = eutrophic pine fen, LK = eutrophic spruce fen, RhK = herb-grass spruce mire, MkK = *Equisetum sylvaticum* spruce mire, Rä = *Sphagnum fuscum* spruce-pine mire, RaSR = rahka-hummocky *(Sphagnum fuscum)* oligotrophic tall-sedge fen.

Taulukko 1. Näytealojen metsikkötunnuksia (keskiarvot ja -hajonnat) suotyypeittäin vuosina 1932 (yläp.) ja 1994 (alap.). G = puuston pohjapinta-ala, G_{spruce} = kuusen (Picea abies) pohjapinta-ala, V = metsikön tilavuus, Iv = tilavuuskasvu, Yv = kokonaistuotos, Bet% = hieskoivun (Betula pubescens) osuus kokonaistilavuudesta, H,v.Post = turpeen maatumisaste (5–10 cm). LR = lettoräme, LK = lettokorpi, RhK = ruohokorpi, MkK = metsäkortekorpi, Rä = rääseikkö, RaSR = rahkainen sararäme.

Mire site type	n	G $m^2 ha^{-1}$	G_{spruce} $m^2 ha^{-1}$	V $m^3 ha^{-1}$	Iv $m^3 ha^{-1} a^{-1}$	Yv $m^3 ha^{-1}$	Bet%	H,v.Post 5–10 cm	Peat depth, cm
LR	22	4.9 ± 1.4	–	17.9 ± 5.4	0.4 ± 0.2	17.9 ± 5.4	2.7 ± 3.3[2]	–	112 ± 41
		13.3 ± 4.2	–	66.6 ± 27.0	1.9 ± 1.2[1]	125.0 ± 46.0[2]	11.1 ± 12.3	5.5 ± 0.7	110 ± 42
LK	2	1.9 ± 0.6	0.0 ± 0.0	6.3 ± 2.4	0.2 ± 0.0	6.3 ± 2.4	62.9 ± 21.8	–	100 ± 28
		11.7 ± 5.2	0.3 ± 0.1	53.6 ± 29.8	1.9 ± 0.4	71.8 ± 32.2	33.5 ± 9.1	5.5 ± 0.7	83 ± 25
RhK	4	9.2 ± 2.4	0.4 ± 0.2	36.8 ± 10.9	0.7 ± 0.1	36.8 ± 10.9	36.1 ± 14.4	–	48 ± 25
		22.2 ± 5.1	2.9 ± 0.7	121.7 ± 38.1	2.1 ± 0.9	168.5 ± 23.3	47.2 ± 13.1	7.0 ± 0.0	45 ± 15
MkK	2	16.0 ± 0.1	10.2 ± 0.0	73.9 ± 3.6	1.2 ± 0.0	73.9 ± 3.6	38.0 ± 3.9	–	55 ± 7
		5.6 ± 2.0	4.7 ± 0.6	37.4 ± 12.4	–	214.2 ± 13.9	15.0 ± 21.0	7.0 ± 0.0	33 ± 4
Rä	2	3.0 ± 0.6	–	10.6 ± 2.0	0.3 ± 0.1	10.6 ± 2.0	–	–	–
		7.0 ± 1.3	–	27.1 ± 10.6	0.4 ± 0.3	33.1 ± 13.2	–	3.5 ± 0.7	43 ± 11
RaSR	1	1.7	–	5.7	0.2	5.7	–	–	90
		–	–	–	–	–	–	5.0	75

[1] n = 19

[2] n = 20

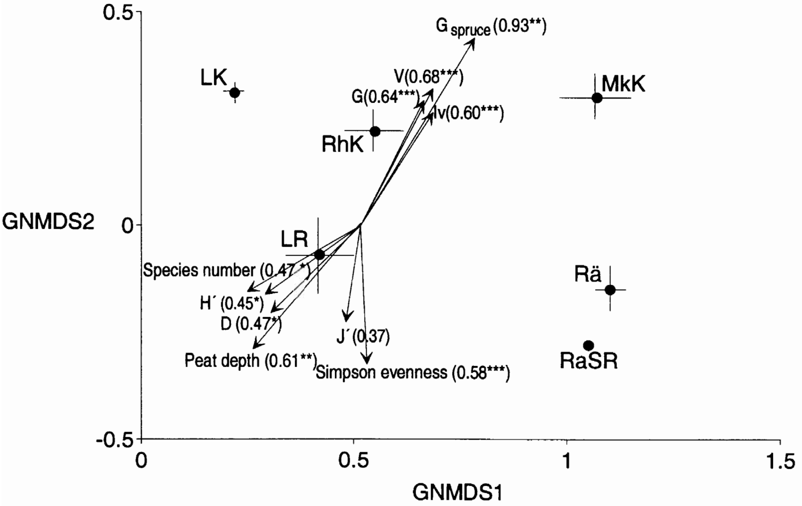


Fig. 2. GNMDS ordination of the undrained sample plots in 1933 (the centroids and S.D.). The maximum correlations between the ordination space and the external variables are presented. For the abbreviations, see material and methods and Table 1.

Kuva 2. Ojittamattomien koealojen GNMDS-ordinaatio, aineisto vuodelta 1933 (suotyyppiä edustavien alojen sentroidit ja keskihajonnat). Ulkoisten muuttujien ja ordinaatioavaruuden väliset maksimikorrelaatiot esitetty nuolin. Lyhenteet, ks. Taulukko 1 ja aineisto ja menetelmät.

while the trophic status together with soil moisture form the secondary gradient (Fig. 3). Especially the vegetation in LR and LK had become poorer after drainage and the dispersion of the sample plots had diminished along this gradient when compared to the situation in 1933.

The vectors expressing monotonic trends between the ordination space and the number of species, H' and D increased in the direction of more eutrophic types, especially the LR type (Fig. 2). Generally speaking Pielou's J' (which actually is evenness based on H') and Simpson evenness increased from spruce mires towards pine mires. In the material from 1994 (Fig. 3) the diversity indices still increased in the direction of the trophic gradient (see also Fig. 9), but the correlation between Simpson's evenness and the ordination space was low.

There was a high correlation between the degree of humification of the peat and the ordination space (Fig. 3). The degree of humification was highest in RhK and lowest in Rä (Table 1). From 1932 to 1994 the thickness of the peat layers had decreased a little but for instance on the LR plots only slightly (Table 1).

By means of combined ordination of different sampling occasions it was detected that the changes of the plant communities were greatest in the fertile mire site types (LR, LK, RhK) whereas in the infertile types (RaSR, Rä) the changes were small (Fig. 4). Also in the MkK type the changes have been remarkable. The only relevant thing which was revealed on the 3rd axis was that the cutting of the MkK stands to seed tree position in 1989 may have influenced the direction of the trajectory (displaying the progress of succession) at the third dimension. For this reason the 3rd axis is not presented. As a consequence of the cuttings certain species, e.g. *Carex globularis, Epilobium angustifolium, Poaceae*, have most likely benefited from the increased light conditions after 1989. Their success may also have to some degree affected the location of the MkK plots in Fig. 3.

Classification

In the numerical classification of the plant communities from 1933 the sample plots formed logical groups in accordance with the different mire site types. The plot LR31c was an exception as it was located in the RhK type group (Fig. 5a). This plot is located in the neighbourhood of the RhK type plots. For instance *Pyrola rotundifolia, Sphagnum girgensohnii, Sphagnum centrale* and *Calliergon cordifolium* which were found on the plot LR31c are indicator species of spruce mire influence (and RhK type features). On the RhK type plots there occured features of the LK and RhSK (mesotrophic tall-sedge birch fen) types. On the pristine LK type plots there occurred features of KoL (eutrophic birch fen) (e.g. *Scorpidium vernicosum*).

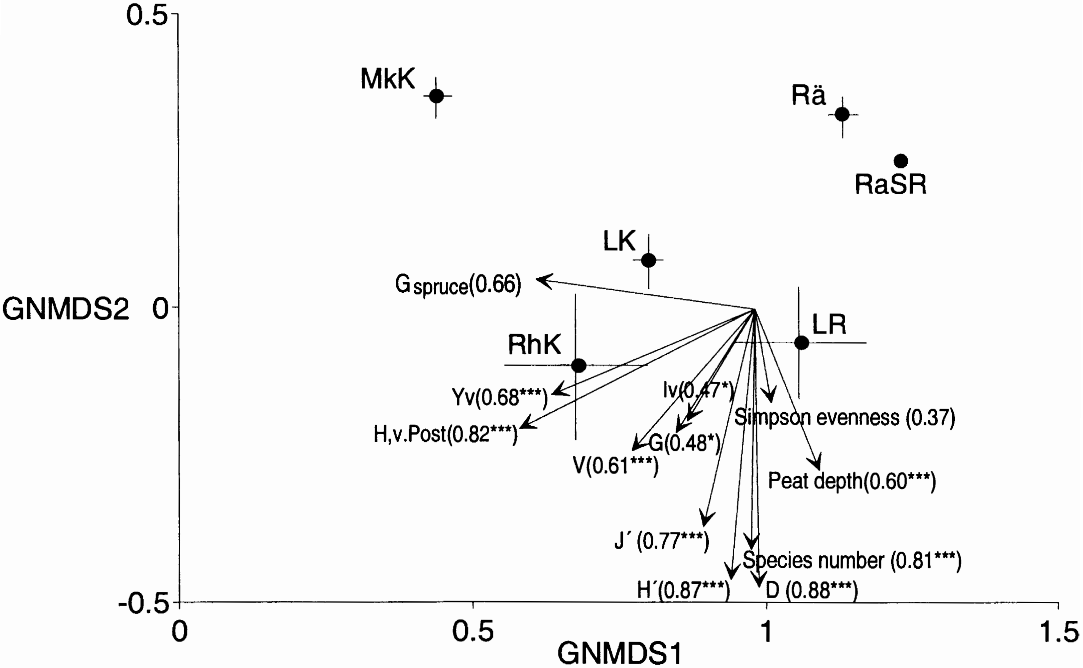


Fig. 3. GNMDS ordination of the drained sample plots in 1994. Explanations as in Fig. 2.

Kuva 3. Ojitettujen koealojen GNMDS-ordinaatio, aineisto vuodelta 1994. Selitykset, ks. Kuva 2 ja Taulukko 1.

In the 1994 classification the plots LR1a–b, LR17 and LR18 had moved to the group with characteristics of fertile spruce mires (Fig. 5b). Together with the pine mire species on these plots there was — irrespective of the thick peat layer (220–130 cm) — a moderate abundance of forest vegetation that reflects spruce mire influence. The most prominent ones were *Gymnocarpium dryopteris, Geranium sylvaticum, Trientalis europaea, Solidago virgaurea, Epilobium angustifolium, Hylocomium splendens.* Species indicating surface-water influence as. *Calamagrostis canescens, Calamagrostis purpurea, Calamagrostis stricta* and *Carex canescens* were also fairly abundant. Despite the drainage, surface-water influence was evident on almost all the sample plots.

The total yields of the tree stands on the above mentioned LR plots with spruce mire influence were high: on the plots LR1a–b 151–179 m^3/ha and on plot LR17 even 226m^3/ha (cf. Table 1). Because of especially storm damage there are no yield values from the plot LR18 but the former yield was about the same as on plot LR17 (Hökkä, pers. comm.). The groups confronted to different silvicultural treatments of the stands (Hökkä 1992) did not manifest themselves in the numerical classifications, neither in the preanalyses of the material from 1943 and 1950. Consequently other factors have determined the structure of the vegetation. After 50 years of drainage there is no effect that can be observed on the total yield of the different cuttings methods which were applied at either the time of drainage or ten years later (Hökkä 1992).

Species abundances

The average abundances of plant species in 1933 and 1994 are presented by site types in Appendix 1. Diagrams of variation in abundance (Fig. 6) have been presented only for the LR type because it is the most numerous of the sample plots.

After drainage, there was an increase of woody plants, as dwarf shrubs and willows (Fig. 6, App. 1). However, many light demanding pine mire- and fen dwarf shrubs, for instance *Andromeda polifolia, Betula nana* and *Vaccinium oxycoccos and*

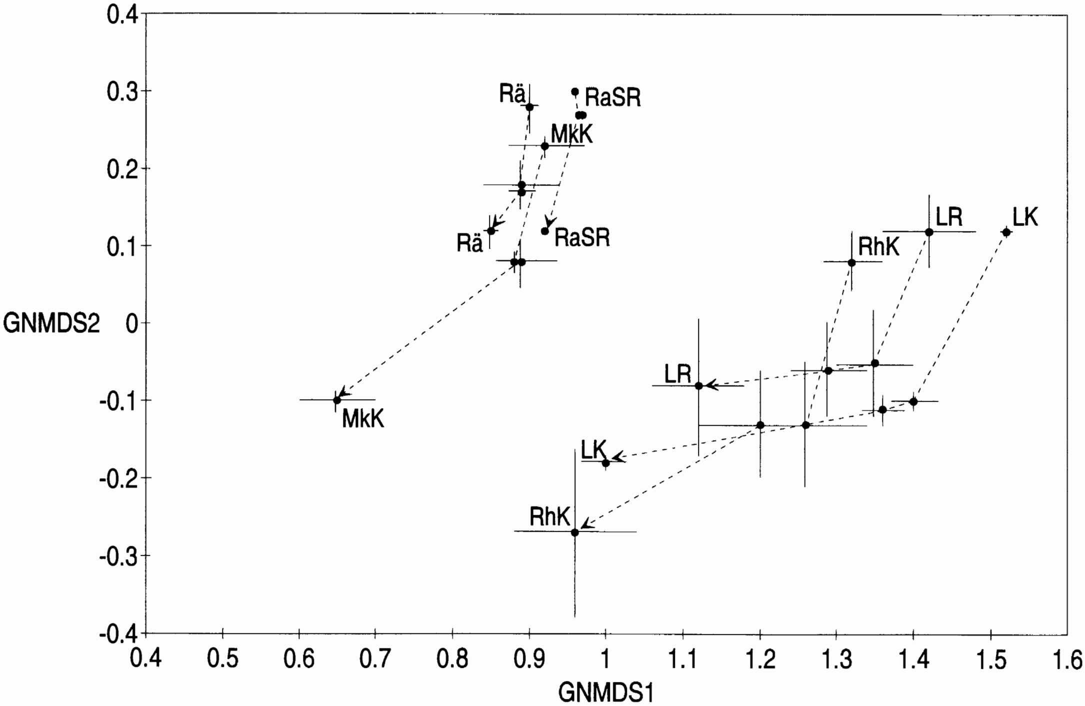


Fig. 4. GNMDS ordination of the sample plots for the 1933, 1943, 1950 and 1994 materials (dimensions 1–2). The centroids and S.D. are presented. For the abbreviations, see text.

Kuva 4. Eri havaintokertojen (vuodet 1933, 1943, 1950, 1994) GNMDS-koealaordinaatio (akselit 1–2) (suotyyppien sentroidit ja keskihajonnat). Lyhenteet, ks. teksti.

V. microcarpum, had decreased in the stocked spruce mire types (RhK, MkK) being in 1994 scantier than in 1933. Also on the LR (Fig. 6) and LK plots *A. polifolia* has begun to decline. The abundance of *Juniperus communis* has remained almost unchanged.

After the year 1950 *Vaccinium myrtillus* began to appear on the LR plots (Fig. 6). It occurred on the MkK and Rä plots already in their pristine state and by 1943 it had colonized the RhK plots. *V. myrtillus* has not yet occurred on the LK and RaSR plots. *Vaccinium vitis-idaea* had become more abundant in all types except for the RhK and MkK types where it by 1994 had become scantier.

Carex lasiocarpa which thrives on intermediate and flark levels as well as *Carex chordorrhiza* and *Carex limosa* which grow on flark levels had decreased strongly (Fig. 6, App. 1). On the LK and RhK plots they did not occur anymore in 1994. *Carex rostrata*, which grows on intermediate and flark levels, had at first increased a little but then decreased. Even as late as in 1994 it grew on more LR sample plots than in 1933; on the RhK and LK plots, however, it was not found anymore.

Carex magellanica and *Carex canescens* which are species that indicate among other things influence of surface water had become more abundant. In 1994 *C. magellanica* seemed to be clearly declining on many sample plots, evidently due to the recent more effective drainage. The hummock- and intermediate-level species *Carex dioica* has increased after the initial phases of succession. On the RhK plots also these three species had begun to decline.

After the drainage *Eriophorum angustifolium* had appeared onto most of the LR plots. Only recently it has started to decrease (Fig. 6). The variation in abundance and frequency of some other species, e.g. *Trichophorum alpinum, Trichophorum cespitosum* was analogous. The hummock-level species *Eriophorum vaginatum* resists the

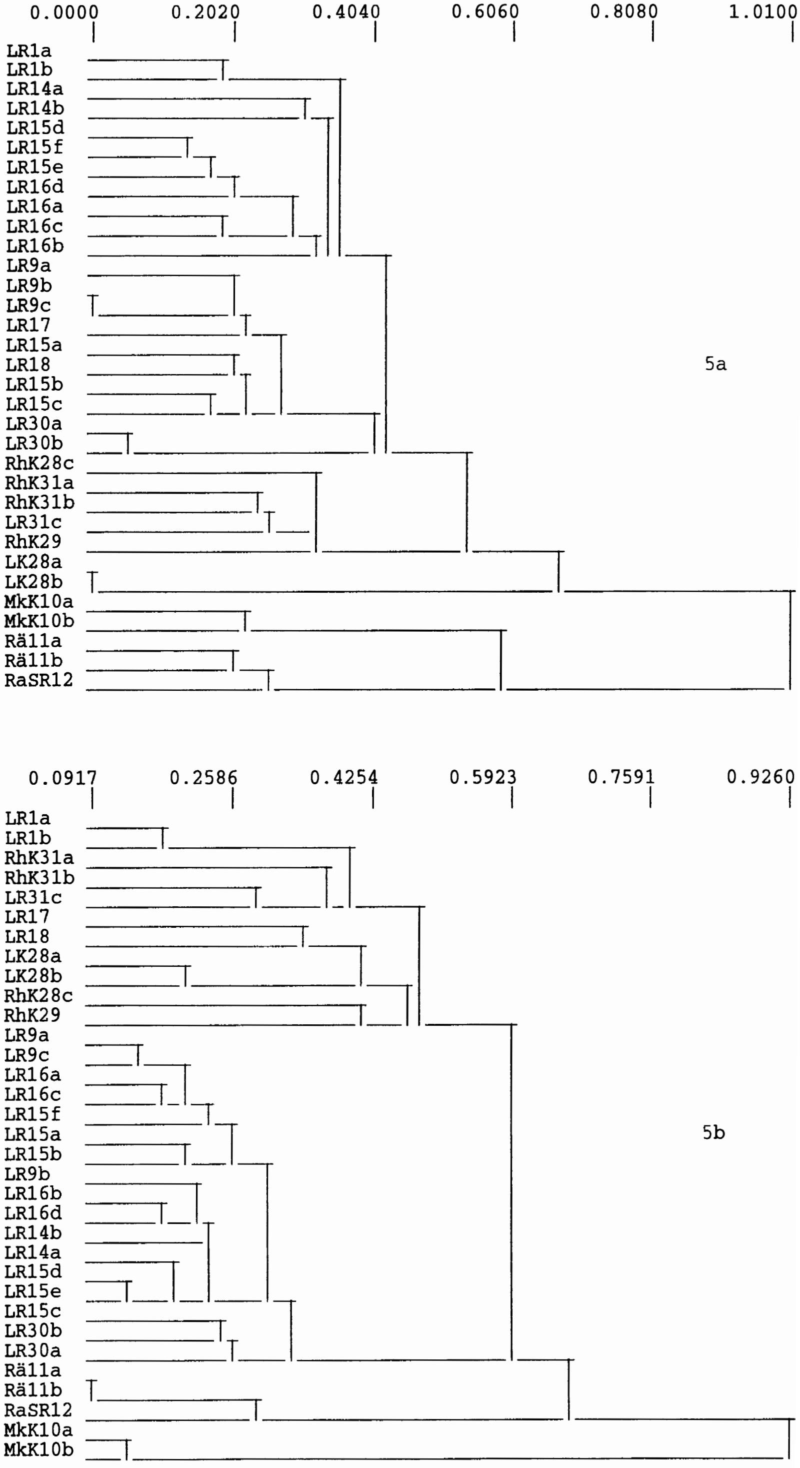
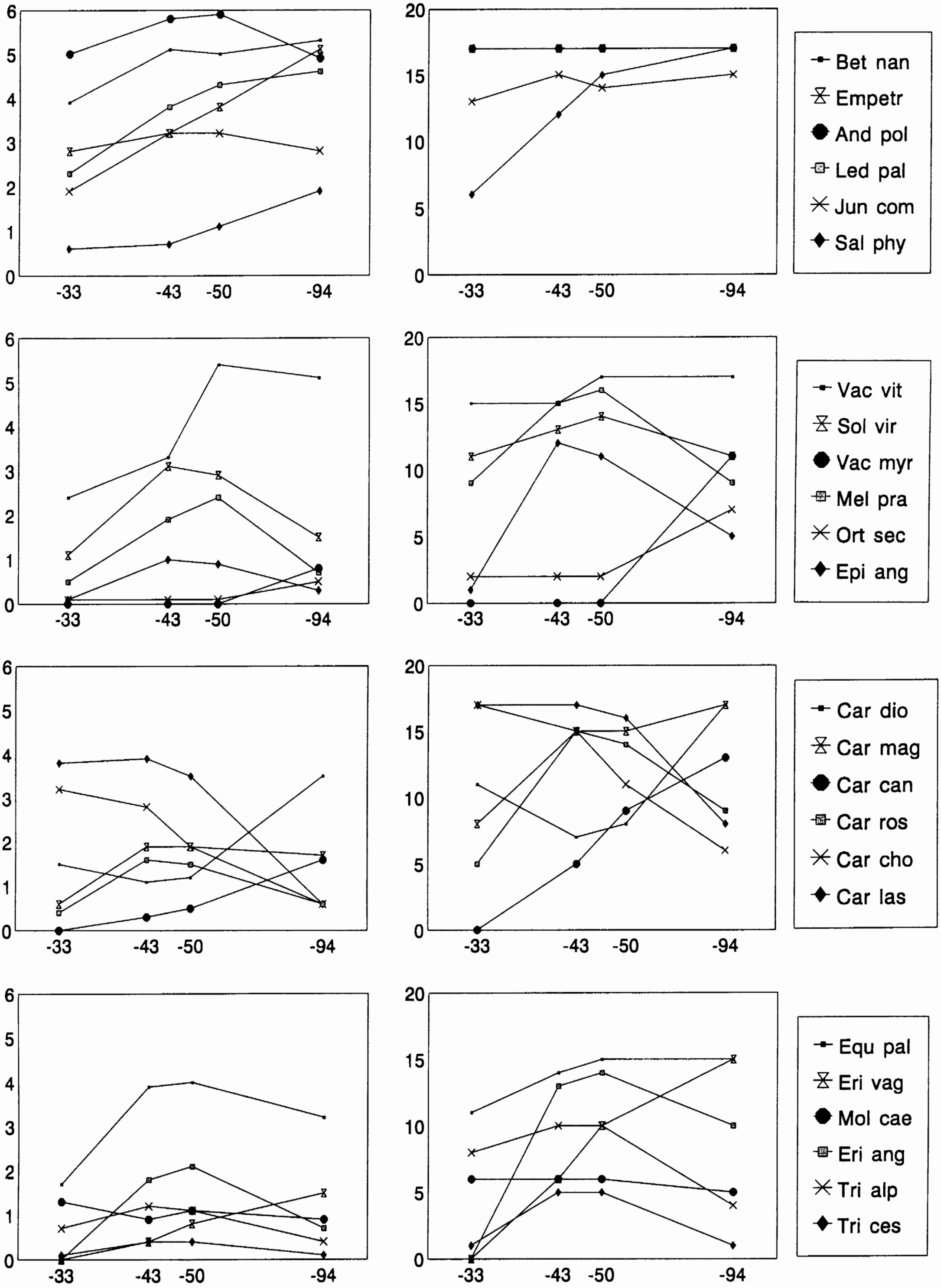


Fig. 5a–b. Agglomerative hierarchical clustering (FUPGMA) of the undrained sample plots in 1933 (5a) and of the drained sample plots in 1994 (5b).

Kuva 5a–b. Ojittamattomien (aineisto vuodelta 1933) (5a) ja ojitettujen koealojen (aineisto vuodelta 1994) (5b) kokoavat, hierarkkiset luokittelut (FUPGMA).

drainage well so except for the MkK type where it had slightly increased. By the latest sampling event *E. vaginatum* had appeared on almost all the LR plots although it is nowhere very abun-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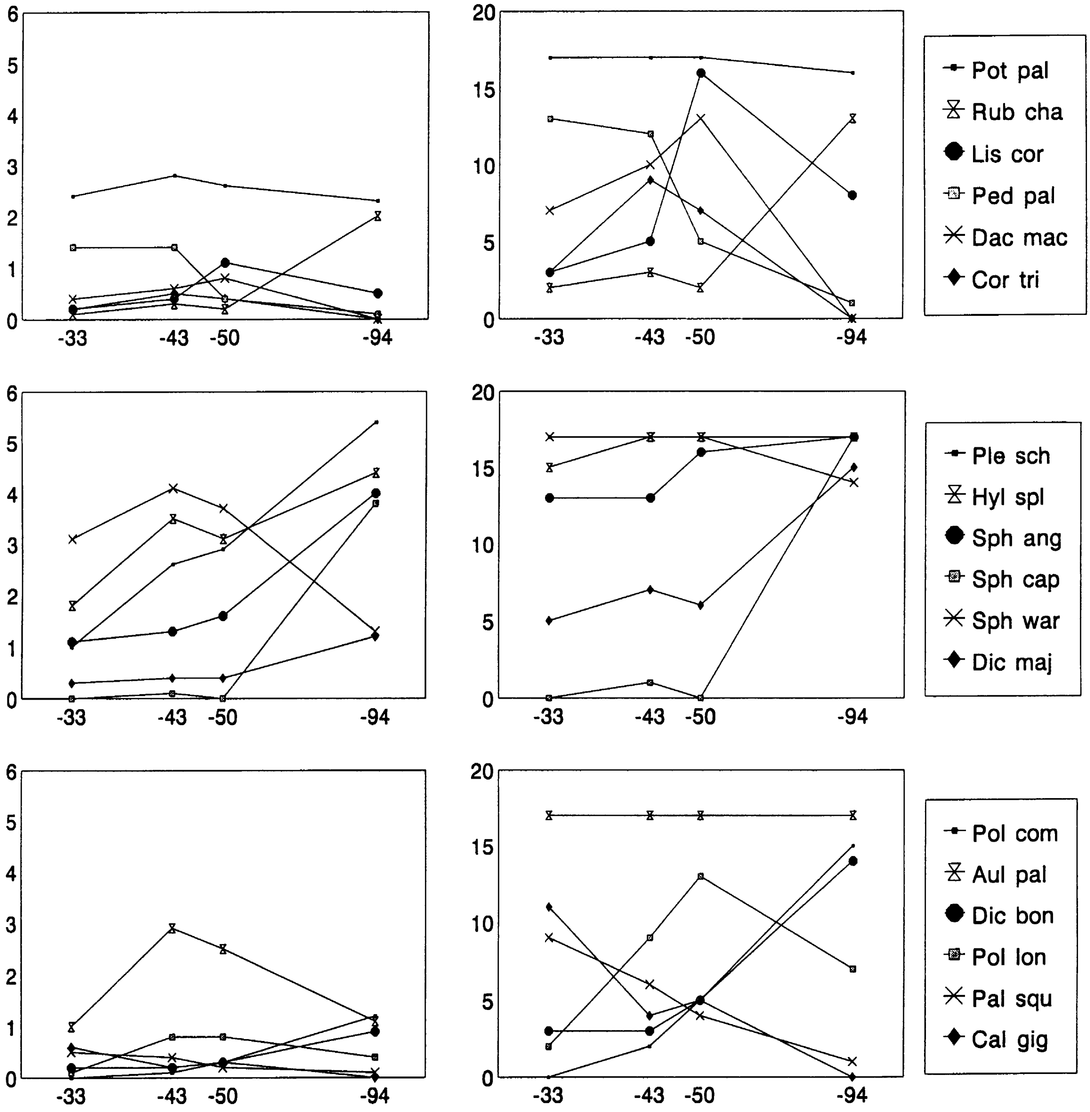

Fig. 6 (Left and above). Average Norrlin's density-abundances (left) and frequencies (the number of sample plots on which the species occurred) (right) of some selected species in different sampling occasions in the eutrophic pine fen (LR) material. Only the plots with a complete set of vegetation data from all the sampling occasions are included (n = 17).

Kuva 6 (Vasemmalla ja yllhällä). Muutamien valittujen lajien keskimääräiset Norrlin-runsaudet (vasemmalla) ja frekvenssit (alojen lukumäärä, joilla laji esiintyi) (oikealla) eri havaintokerroilla lettorämeaineistossa. Mukana ovat ne LR-alat, joilta kasvillisuuskuvaukset ovat kaikilta havaintokerroilta (n = 17).

dant.

The moderately deep-rooted intermediate-level species *Molinia caerulea* grew only on the LR plots where hardly no changes in its abundance has taken place. Many other graminoids, e.g. the *Calamagrostis* species had become more abundant (App. 1).

Also some orchids and some other herb species, as *Melampyrum pratense, Epilobium angustifolium* and *Solidago virgaurea* have at some stage after drainage been more abundant or frequent than at the first or last observation occasion (Fig. 6). Of the orchids *Corallorrhiza trifida* which grows on intermediate and flark levels and the chiefly intermediate-level species *Dactylorhiza maculata* do not occur on the sample plots anymore. Also *Listera cordata* which thrives on hummock and intermediate levels had clearly begun to become scantier. The shallow-rooted *Pedicularis palustris* which indicates surface water influence is an example of a species which has decreased during the whole observation period. In 1994 *Drosera rotundifolia* occurred on only two LR plots. *Equisetum fluviatile* was still abundant on the LR plots but on the spruce mire plots it had almost disappeared. The deep-rooted *Potentilla palustris* had begun to decline slightly.

The deep-rooted hummock-level species *Rubus chamaemorus*, which efficiently propagates vegetatively, and the forest species *Trientalis europaea* and *Orthilia secunda* had increased together with many other forest species (App. 1). *Rubus arcticus* and *Rubus saxatilis* had formed hybridies on the Teuravuoma drainage area.

Pleurozium schreberi, Hylocomium splendens, Dicranum majus and e.g. *Pohlia nutans, Brachythecium spp.* and *Plagiothecium spp.* as well as many mire mosses of hummock and intermediate levels, such as *Sphagnum angustifolium, Sphagnum capillifolium, Sphagnum magellanicum, Dicranum bonjeanii, Polytrichum commune* and *Polytrichum strictum,* had become more abundant.

Sphagnum warnstorfii which is common and abundant on pristine LR mires had clearly began to decline. The hummock and intermediate level species *Aulacomnium palustre* and the intermediate-level species *Polytrichastrum longisetum* had increased temporarily. The demanding *Tomentypnum nitens* had disappeared from many of the LR plots and from all RhK plots, on which it originally occurred. It is a sign of a long lasting not too efficient drainage that the moderately hydrophilous *Sphagnum subsecundum* occurred on nine of the LR plots, although dilapidated, whereas the intermediate-level species *Sphagnum squarrosum* which was found on seven LR plots is an indicator of surface water influence.

As expected, the demanding flark-level mosses, many of which indicate influence of surface water or ground water, were not able to adapt to the conditions after drainage. For instance *Calliergon giganteum* and *Paludella squarrosa* had immediately started to decrease. *Meesia triquetra, Scorpidium revolvens* and *Warnstorfia exannulata* were not found in 1994 anymore (App. 1). On the contrary *Limprichtia intermedia* which thrives on intermediate levels still occurred on 11 of the LR plots. *Calliergon cordifolium* and *Pseudobryum cinclidioides* had disappeared totally.

On the LR plots the reindeer lichens (*Cladina arbuscula* and *C. rangiferina*) had become slightly scantier while cup lichens (*Cladonia spp.)* had become more frequent and abundant. In 1994 *Peltigera aphthosa* occurred only on one LR plot. It seems to be sensitive to drainage succession (see also Reinikainen 1984).

The succession towards vegetation typical for hummock level and forest is illustrated merely by the species number representing different mire surface levels and ecological groups. For example on the LR and RhK plots the number of hummock level species has increased while the number of intermediate and particularly flark level species has decreased. However, in the field layer the number of intermediate level species has remained almost unchanged (Fig. 7). The species that reflect spruce mire influence had increased in many plant groups as well as the species that reflect hummock-level bog influence, especially in the group of mosses (Fig. 8). The number of poor and rich fen species had decreased.

Diversity indices

The number of species as well as Simpson's (D) and Shannon's (H') indices, which correlated strongly with the number of species ($r = 0.94–0.99^{***}$ in different years), and also partly Pielou's (J') index, were higher in the fertile types than in the infertile types (Fig. 9). Because of their wide wet surfaces in their pristine state, the LK plots were poor in species number: there were almost no hummock level species and where fen species dominated the bottom layer was very scanty.

After the drainage species number, D and H'

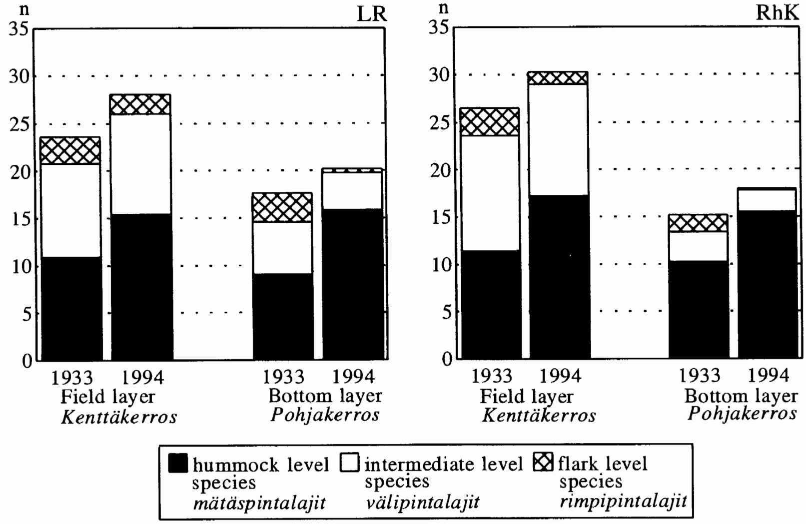

Fig. 7. Average number of species representing different mire surface levels (Eurola et al. 1994) in eutrophic pine fen (LR, n = 22) and in herb-grass spruce mire (RhK, n = 4) in 1933 and 1994.

Kuva 7. Eri kosteustasoja edustavien lajien (Eurola et al. 1994) keskimääräinen lajilukumäärä lettorämeellä (LR, n = 22) ja ruohokorvessa (RhK) vuosina 1933 ja 1994.

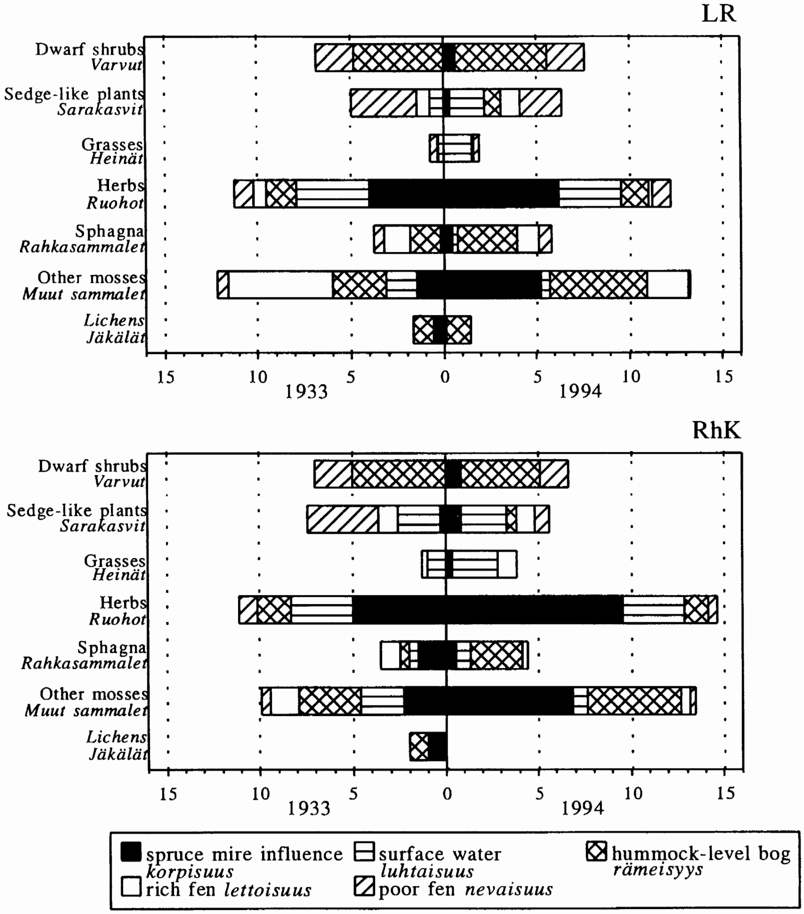

Fig. 8. Average number of species representing different ecological plant groups (Eurola et al. 1994) in eutrophic pine fen (LR) and in herb-grass spruce mire (RhK) in 1933 and 1994.

Kuva 8. Eri ekologisia ryhmiä edustavien lajien (Eurola et al. 1994) keskimääräinen lajilukumäärä lettorämeellä (LR) ja ruohokorvessa (RhK) vuosina 1933 ja 1994.

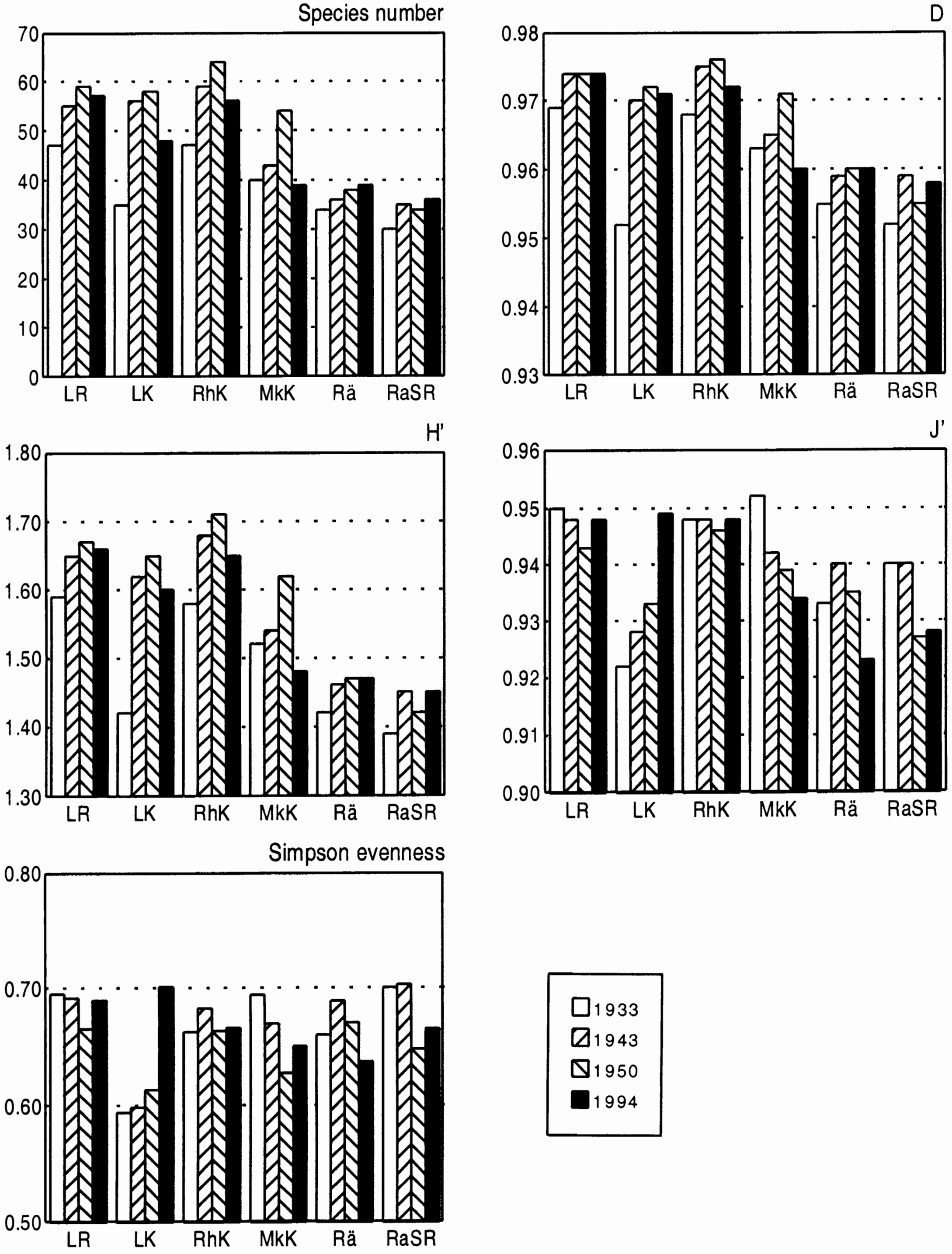

Fig. 9. Diversity and evenness indices by mire site types in different sampling years. All species included. For the species abbreviations, see Appendix 1.

Kuva 9. Diversiteetti- ja tasaisuustunnuksia suotyypeittäin eri havaintokerroilla. Kaikki lajit mukana. Lajilyhenteet, ks. Liite 1.

at first increased (Fig. 9). For instance in that part of the material from the LR plots for which statistical testing was possible, the increase was highly significant (Table 2). In addition to the many mire species of hummock and intermediate level microsites that had increased there also occurred pioneer and forest species which had colonized these plots.

By 1994, as the mire species were decreasing the diversity indices had turned to decline also, except on the Rä and RaSR plots. There the species number in the bottom layer still was higher than at the previous sampling occasions. The turn to decline had been faster in the spruce mire types than in the LR type - after the initial increase.

Pielou's J', which moderately correlated with species number ($r = 0.37–0.62^{**}$), and the evenness calculated from Simpson's D ($r = -0.04–0.24$) behaved a bit vaguely. In most cases they seemed to decline a little from 1933 to 1994. Thus, the species dominance had increased. In the LR material J' and D evenness decreased from 1943 to 1950 and after that increased so that the difference between 1933 and 1994 was not significant (Table 2). The LK plots were an exception because the species were very unevenly distributed at the moment of drainage.

DISCUSSION

Compositional gradients

In a systematic or random sampling of the mire surface the main compositional gradients of pristine boreal mire vegetation generally reflect (1) the mire margin (supplementary nutrient) versus mire expanse (mire inherent) effects (e.g. Pakarinen & Ruuhijärvi 1978, Hotanen & Nousiainen 1990, Økland 1990a), (2) variation in moisture (e.g. Pakarinen 1985, cf. Økland 1990a) (3) variation in nutrient status (e.g. Jeglum 1991). However, the main compositional gradients (coenoclines, ordination axes) represent ecological complex factors (Pakarinen 1985, Økland 1990a, cf. Økland 1992).

The reciprocal order and clarity of the main coenoclines depend on the nature of the region under examination: geobotanical location, size, etc. Also the methods used in the study have their own effect (cf. e.g. Pakarinen 1976, Pakarinen & Ruuhijärvi 1978, Pakarinen 1985, Økland 1990b). In the materials limited by mire site types one or two gradients may well represent the whole variation (Heikkilä 1987, Laine & Vanha-Majamaa 1992).

In the materials of drained peatlands the complexity of the main coenoclines must be emphasized because the variations in succession age introduce additional features to the analyses (e.g. Reinikainen 1988, Hotanen 1991, Laine & Vanha-Majamaa 1992). It is even more complicated to connect the interpretation of the main gradients with the ordination axes in the follow-up ordinations, where for example as many as three dimensions are needed.

The analyses of this study corroborate the hypotheses and observations that forest drainage accentuates the significance of the mire margin and mire expanse effects (which in this case were spruce mire and hummock-level bog influences respectively) in controlling the structure of plant communities on drained peatlands — instead of trophic status and soil moisture (Eurola et al.

Table 2. The statistical differences (Sig. of F) of diversity indices between sampling years in eutrophic pine fen (LR) material (n = 17), cf. Fig. 9.

Taulukko 2. Lajilukumäärän ja diversiteetti-indeksien tilastolliset erot (F-arvon merkitsevyys p) havaintovuosien välillä lettorämaineistoissa (LR) (n = 17), vrt. Kuva 9.

	1933 vs 1943	1943 vs 1950	1950 vs 1994	1933 vs 1994	1943 vs 1994
Species number	.000	.058	.441	.000	.365
D	.000	.503	.897	.000	.586
H'	.000	.235	.687	.000	.512
J'	.117	.000	.029	.305	.940
Simpson evenness	.755	.000	.039	.716	.903

1995). Drainage decreases the variation in soil moisture and nutrient status. This is connected with the drying and increase in acidity of the peat substrate, and subsequently with the exchange capacity controlling the nutrient supply of the plants (Puustjärvi 1968). When, as a result of drainage, the water volume decreases and the acidity increases (Vahtera 1955), a species able to utilize a higher exchange capacity than species thriving on wet substrates will increase it's abundance.

The spruce mire influence is a silviculturally important feature as it contributes to the succession (Reinikainen 1989). The hummock-level bog influence resists drainage well (Reinikainen 1989), and on fen-like mires the dwarf shrub vegetation generally increases (e.g. Pienimäki 1982, Silfverberg & Hotanen 1989). Poor or rich fen influence (Eurola et al. 1984) loses its importance when drying, although it leaves its typical mark on the drained peatland vegetation for a long time (Reinikainen 1988, Laine 1989). Thus, the variation between hummock-level bog influence and spruce mire influence (or between mire expanse and mire margin) generally becomes a primary factor in the data collected from drained mires. Effective drainage mostly disconnects surface- and ground-water influence. The mire margin effects are remarkable sources of diversity (Eurola et al. 1994, Korpela & Reinikainen 1996).

From a hydrological point of view drainage generally transforms the substrate into a site resembling the conditions of the hummock level (Eurola & Holappa 1984). In Teuravuoma many intermediate level species, e.g. *Sphagnum warnstorfii*, and even some deep-rooted intermediate- and flark-level species, e.g. *Potentilla palustris* and *Menyanthes trifoliata* (Metsävainio 1931), occurred commonly still in 1994. The reasons for this are the humid climate prevailing on the site and the long period of fairly weak drainage efficiency connected with the flat topography. However, according to Hökkä (1992) the development of the forest stands have been at least satisfactory.

In the drainage succession the secondary decrease of the original trophy level as discussed above may prevail for a reasonably long time. Many drained mires have originally been wet with poor or rich fen influence; the majority of these are presently in the transforming drained mire phase or in other words moderately young objects (Tomppo & Henttonen 1996). It remains to be seen, what the result will be in the long run with the mineralization of the peat (cf. Melin 1917). From a nutritional point of view the favourable consequences of drainage are that the aerobic surface of the peat becomes larger which increases the decomposition of organic material and accelerates the nutrient accumulation and cycle in aerobic layer (e.g. Paavilainen & Päivänen 1995).

In addition to proportions of flark levels also the degree of spruce mire influence may vary in eutrophic pine fens (Heikurainen 1954, 1958). The large variation in total yield of the LR stands is partly caused by this (Table 1). According to Hökkä (1992) the variation in proportion of flark levels has also affected the variation in yield values between the LR sample plots. Probably there was most flark levels on the plots 15d–e, 16d (Hökkä 1992) and on 14a–b, but in the numerical classifications these plots did not discern properly (Fig. 5a). This could partly be caused by Norrlin's coarse field method.

The drainage has probably changed the water flows so that four LR plots (1a–b,17,18) have turned to a state with quite strong spruce mire influence. Apparently, surface-water flows have brought nutrients onto these plots too, especially onto plots LR17 and LR18, because many swamp species that demand a surface water supply still occurred abundantly on them. On the basis of the vegetation in 1933 on these plots one could not detect anything divergent from the other LR plots which could have predicted the present development. The example of these plots emphasize the importance of the actual vegetation in the classification of drained peatlands (also Silfverberg 1991). Moreover, the importance will be still more accentuated in the future, since the era of initial ditchings has nearly ended and we must operate with vegetation which has been affected by drainage for an ever longer time; there is also the increasingly important influence from silvicultural measures which add — partly unknown — aspects.

In a traditional sense the sample plots were in the transforming phase of drained mires (Sarasto 1961). The RhK and MkK plots and those LR plots with a clear spruce mire influence were the farthest advanced in their secondary succession. They were near the transformed drained mire (final III) phase. Spruce mire influence promotes the 'ideal' drainage succession (Holmen 1964, Reinikainen 1989). The abundance of many mire plants on the MkK plots is probably a consequence of the removal (in 1989) of a large number of trees that had evaporated considerable amounts of soil water.

Because of the climatic factors in north Finland one cannot make as strict requirements about the proportion of forest vegetation for the transformed drained mire phase (Sarasto 1961, cf. Laine 1989) as in south Finland. Also, it is evident that the drainage succession in the north is slower than in the south. It is too early to draw any final conclusions about what directions the future succession will take on the Teuravuoma LR plots since the secondary succession still is incomplete. The present vegetation, however, indicates a development to some form of herb-rich type (Rhtkg) (cf. Heikurainen 1958, Laine 1989).

Species responses

After drainage the increase of mire dwarf shrubs happens chiefly by spreading through vegetative propagation to the dried intermediate and flark levels (e.g. Pienimäki 1982). According to Laine et al. (1995) clonal growth may play an important role in the vegetation dynamics of developing communities. The mire dwarf shrubs survive for a long time on drained peatlands (Holmen 1964, Reinikainen 1984). In addition to drainage degree, the shading and competition control the composition of understorey vegetation. Later the mire dwarf shrubs decline and the forest species gain ground. On fen-like drained mires *Vaccinium myrtillus* colonizes and increases slowly (also Sarasto 1961). This may be due to the slow spreading of the species or to its weak competitive ability in the sparse tree stands in comparison to other dwarf shrub species; also the rhizome growth rate of *V. myrtillus* is slower than that of e.g. *Vaccinium vitis-idaea* (Laine et al. 1995 and references therein).

The temporary increase of some species is worth noticing. The strength and length of increase depend, among other things, on the hydrophilic status, on the exchange capacity and on the depth of roots of the plant species. The drying of wet and moist surfaces has offered for example *Eriophorum angustifolium, Melampyrum pratense, Listera cordata* and *Epilobium angustifolium* space for germinating and growth. According to the studies of Sarasto (1961), Mannerkoski (1976) and Laine et al. (1995) it can be noticed that on many minerotrophic composite mire site types *Eriophorum angustifolium* and *M. pratense* have been more abundant in the recently drained and transforming drained phase than in the pristine state or the transformed drained phase. On a drained mesotrophic tall-sedge pine fen studied by Reinikainen (1984) *L. cordata* had occurred for a part of the study period.

The well-known pioneer species *Epilobium angustifolium* which is nitrogen and light demanding occurs usually scattered on drained pine mires as is the case on Teuravuoma (Sarasto 1961, Reinikainen 1984, Laine et al. 1995). On infertile drained areas the species is generally a sign that the site has been fertilized (Päivänen & Seppälä 1968). On minerotrophic pine fens studied by Laine et al. (1995) it seemed to increase slightly with the drainage age. Increase followed by subsequent decrease like on Teuravuoma has not been substantiated from pine mires. The decrease may be a consequence of competition from the other species because the light conditions on the LR plots were rather good despite the good development of the stands. In the drainage succession of spruce mires *E. angustifolium* has after a slight increase decreased when the tree stands close up (Sarasto 1961).

Equisetum palustre is able to adapt to the drainage for quite a long period and it may even slightly benefit at the beginning of drainage if the water table level is suitable (Huttunen 1969), in the transformed drained mire phase, however, it disappears (Sarasto 1961). Also *Trichophorum alpinum* and *T. cespitosum* benefit from the environmental change in the early phases of succession (also Aapala & Kokko 1988). They are able to resist large changes in moisture (Laitinen 1990).

The species of hummock and intermediate levels, *Moneses uniflora* which indicates spruce mire influence, was common on the LR plots in 1933 compared to for instance the material from LR types collected by Ruuhijärvi (1960). Although the frequence of *M. uniflora* had decreased (App. 1), it had found new growth space on the former wet surface occurring quite abundant on some sample plots in 1994.

The increase of grasses is an indication that sufficient light, growth space and mineral nitrogen is available, as well as influence of surface water for some species (Holmen 1964, Platonov 1976). The nitrogen content of the surface peat layer from some of the Teuravuoma LR plots have been analysed in the 1940's and 1980's. The total nitrogen content ($N_{tot}\%$) has varied between 2.28–2.34 (Heikki Veijalainen, pers. comm.).

Contrary to almost all earlier observations (cf. Reinikainen 1984) *Carex rostrata* became temporarily more common after the drainage. The increase may have been enabled by the drying of wet surfaces so that there still has been water enough for the roots. According to Saarinen et al. (1994) the living roots of *C. rostrata* can extend much deeper than earlier observed (Metsävainio 1931), to a depth of even 2.3 m. It may also be that the species has propagated vegetatively but has not been as tall or fertile as earlier. Mannerkoski (1976) noticed that *Carex lasiocarpa* increased temporarily after drainage (also Kurimo & Uski 1988), while the observations of Sarasto (1961) and Laine et al. (1995) rather indicate a rectilinear decrease. Their observations were not from permanent sample plots and the first drainage phase contained sample plots of various ages. In Teuravuoma the species has started to decline clearly after 1950.

Carex canescens and *Carex magellanica* tolerate drainage quite well and they may increase at the beginning of secondary succession (Sarasto 1961, Mannerkoski 1976). In the humid conditions of Teuravuoma with a supply of surface water flow also they have increased during almost the whole follow-up period. For *Carex dioica*, a very weakly hydrophilous species with deep roots (Metsävainio 1931, Lumiala 1944) the moisture conditions have obviously been good for a long time at Teuravuoma. It has been observed that on drained areas in south and middle Finland it decreases slowly in secondary succession (Aapala & Kokko 1988). The sedges are inefficient in cycling nutrients internally and thus nutrition from moving water ensures their success (Bernard & Hankinson 1979). The population biological characters of many species are still insufficiently known, although their ecology on pristine mires is known in outline.

Apparently the peat in the LR plots has not been acid enough for *Eriophorum vaginatum* to form typical tussocks (e.g. Kuusipalo & Vuorinen 1981) although the moisture and light conditions would have been favourable (cf. Laine & Vanha-Majamaa 1992). The acidity (pH) of the LR plots from where nitrogen was analysed varied between 4.99 and 5.48 (Heikki Veijalainen, pers. comm.). Instead, on the infertile RaSR plots with more acid surface peat *E. vaginatum* was abundant.

For some species the ditches or the ditch soils may have worked as primary germination beds, from which new species then have spread to the sample plots. The size and functioning of seed banks on drained mires are so far not well known (Heikkilä & Lindholm 1995, Jauhiainen 1998). According to Laine et al. (1995) the seed banks probably play a minor role on drained peatlands compared to upland vegetation communities in determining the field layer composition after disturbance.

As predicted the demanding flark-level mosses (Lumiala 1944) and many eutrophic vascular plants as well as species regarded as weak competitors had disappeared or declined most (e.g. *Tofieldia pusilla*, *Selaginella selaginoides*, *Pedicularis palustris*, *Drosera rotundifolia*). Instead ombro-oligotrophic *Sphagna* of hummock and intermediate levels with their good capillary characters (see also Holmen 1964, Platonov 1976, Reinikainen 1984, Rydin 1986, Laine et al. 1995) had increased in the changed moisture conditions. Also *Polytrichum* (see Huttunen 1969, Pienimäki 1982), the colonists (e.g. *Pohlia nutans*) (During 1979) and forest mosses had benefited from the changed substrate. In many mire site types studied by Sarasto (1961) *Aulacomnium palustre* reacted in the same way as in this study (also Laine et al. 1995).

Many species 'behaved very consistently'; for instance both *Sphagnum warnstorfii* and *Dicranum bonjeanii* are (meso)-eutrophic species, but the former represents the intermediate level and the latter (hummock-) intermediate level (Eurola et al. 1994). *S. warnstorfii* had begun to decrease, but *D. bonjeanii* had so far increased. It is necessary to follow the secondary succession from now on to see how strong the effect of intensified drainage is on the composition of vegetation in these arctic conditions.

Diversity

Species richness, Simpson's D and Shannon's H' are generally higher in eutrophic and meso-eutrophic sites (e.g. RhK, LK, LR) than in oligotrophic (e.g. MkK, Rä, RaSR) or ombrotrophic sites both on pristine mires and on drained peatlands (Sarasto 1961, Holmen 1964, Vasander 1987b). In most cases many ecological gradients affect simultaneously on fertile peatlands and generally considerable microhabitat variation caused by water flow and flark-hummock microtopography gives horizontal and vertical variation in the nutrient and moisture regimes (Eurola et al. 1984, Vasander 1987b, Laine et al. 1995).

The succession after ditching which can be divided into two overlapping phases the drainage- and the forest succession (Reinikainen 1984), temporarily increases the alpha-diversity, though not always significantly (Vasander et al. 1997). According to Sarasto (1952, 1961) species richness after drainage reaches its maximum earlier on nutrient-rich types than on nutrient-poor types, and the increase in species number is the higher the richer in species the mire site type has originally been. Correspondingly the number of mire species later declines the faster the more fertile the site type is; this is also connected to the fast development of the tree stands through competition and shading on the fertile substrate (Vasander 1990, Laine et al. 1995). However, when comparing different nutrient status levels with each others, the rules should be standardized by main type group and by proportions of different microhabitats, as original moisture level.

After drainage the alpha-diversity on the different surface levels (flark, intermediate, hummock) can vary (increase/decrease) in different ways depending on the original mire site type and on the moisture levels of different mire surfaces or microhabitats as well as on fertilization (Vasander 1984, 1987a,b). Also the field- and bottom layer can behave in different ways. According to Vasander (1990) after forest amelioration, species richness and H' usually decrease in the field layer, but were more likely to increase in the bottom layer. In Teuravuoma the total species number (Fig. 9), the species number of the field- and bottom layers as well as the corresponding D and H' were in most cases still slightly higher in 1994 than in 1933 (Hotanen 1998).

Pielou's J' (= H' based evenness) and Simpson evenness reacted a bit vaguely, but as an overall trend seemed to be declining with time. In that case it is connected with the increase in species dominance which reflects a general trend in disturbed ecosystems (Grime 1979). Because many alpha-diversity indices are determined both by species richness and by abundance relationships their use should be applied with certain reservations. They are suitable for the comparison between communities, but rather weakly for the description of communities.

Drainage diminishes the separation between the species composition of the site types, i.e. the beta-diversities describing the differences between plant communities decrease as the hydrological conditions become more uniform after drainage (Hotanen & Vasander 1992, Laine et al. 1995). This is also shown in the ordinations as a smaller dispersion between the drained sites than between the undrained sites. However, as pointed out by Vasander et al. (1997), if only a part of a peatland is drained, the invading forest vegetation may even increase the beta-diversity within the peatland.

The development towards forest vegetation (via intermediate- and hummock-level species and communities) on drained mires may diminish the regional gamma-diversity, even if the alpha-diversity on individual plots and sites may not be much affected (Reinikainen 1984, Vasander 1984, Laine et al. 1995). There are no species known to be dependent on drained mires (Vasander et al. 1997). Mire species of which a part may be quite rare in a certain region are gradually substituted by forest species which already dominate in the surrounding forests.

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TIIVISTELMÄ

Kasvillisuuden sukkessio ja monimuotoisuus Teuravuoman koeojitusalueella Pohjois-Suomessa

Tutkimuksen tarkoitus oli tarkastella metsäojituksen vaikutuksia pysyvillä koealoilla (1) kasvillisuuden päävaihtelusuuntiin, (2) kasvilajien runsauksiin ja (3) kasvillisuuden diversiteettitunnuksiin. Aapasuovyöhykkeeltä on hyvin vähän tietoja ojituksen aiheuttamasta sekundaarisukkessiosta tai ojitusalueiden kasvillisuuden rakenteesta. Mukana oli kuusi eri suotyyppiä (Taulukko 1), mutta pääpaino on koealamäärältään selvästi lukuisimmalla, lettorämeellä (LR).

Koealat oli perustettu (mm. ojitus) vuosien 1932–1933 aikana. Vuonna 1989 tehtiin kunnostusojitus. Kasvillisuuskuvaukset on suoritettu vuosina 1933, 1943, 1950 ja 1994 käyttäen Norrlinin runsausasteikkoa (Ilvessalo 1932). Kasvillisuuden päävaihtelusuunnat analysoitiin GNMDS-ordinaatiolla (Minchin 1991). Koealojen kasvillisuussuhteiden selvittämiseksi suoritettiin myös FUPGMA-luokittelu (Belbin 1994). Aloille laskettiin lajilukumäärän lisäksi Shannonin (H'), Simpsonin (D) ja Pieloun (J') diversiteetti-indeksit sekä Simpsonin indeksiin perustuva tasaisuustunnus ((1/D)/lajilukumäärä).

Pysyviin koealoihin perustuvat analyysit tukivat hypoteesia siitä, että metsäojitus korostaa reuna- ja keskustavaikutuksen (tässä tapauksessa lähinnä korpisuuden ja rämeisyyden) merkitystä kasviyhteisöjen koostumusta määräävänä tekijänä (Kuvat 2 ja 3) (Eurola et al. 1995). Tämä on seurausta mm. ojituksen aiheuttamasta kosteus- ja ravinnevaihtelun pienentymisestä. Kun vesitilavuus pienenee ja happamuus kasvaa (Vahtera 1955), kasvupaikalla runsastuu laji, jonka vaihtokapasiteetti (Puustjärvi 1968) on kosteammalla alustalla viihtyvän lajin kapasiteettia korkeampi. Kasviyhteisön muutos oli suurin viljavilla suotyypeillä (LR,

LK, RhK) kun taas karummilla tyypeillä (RaSR, Rä) muutos on ollut vähäistä (Kuva 4). Myös MkK:ssa muutos oli huomattava. Korpisuus edistääkin ojitussukkessiota (Holmen 1964, Reinikainen 1989).

Sekä märkäpintojen osuus että korpisuuden aste voi lettorämeillä vaihdella (Heikurainen 1954). Suuri puuston kokonaistuotoksen hajonta viittaa myös tähän (Taulukko 1). On ennenaikaista sanoa lopullista Teuravuoman LR-alojen tulevasta yleisimmästä muuttumistuloksesta, sillä sukkessio on kesken. Tämänhetkinen kasvillisuus viittaa ruohoturvekankaiden (Rhtkg) ryhmään (vrt. Heikurainen 1958, Laine 1989). Neljä LR-alaa oli muuttunut varsin korpisiksi (Kuva 5b), myös monet luhtalajit kasvoivat niillä runsaina. Luonnontilassa ei voinut havaita ko. aloilla muista LR-aloista poikkeavaa (Kuva 5a), jonka perusteella tulevaa kehitystä olisi voinut ennustaa. Esimerkki korostaa aktuaalisen kasvillisuuden merkitystä ojitusalueiden luokittelussa. Merkitys kasvaa tulevaisuudessa, sillä uudisojitus on lähes loppunut, ja joudutaan operoimaan yhä kauemmin ojituksenalaisena olleen kasvillisuuden kanssa, johon metsänhoidolliset toimenpiteet tuovat osin tuntematonta lisäväriä.

Useimmat mätäspinta- ja monet välipintalajit olivat vielä vuonna 1994 runsaampia kuin vuonna 1933. Osaksi syinä ovat pohjoisen humidi ilmasto ja pitkään jatkunut suhteellisen tehoton ojitus. Metsiköiden kehitys on kuitenkin ollut hyvä (Hökkä 1992). Varvut ja pajut olivat yleensä runsastuneet ojituksen jälkeen. Kuitenkin monet runsaassa valossa viihtyvät räme- ja nevavarvut, mm. suokukka (*Andromeda polifolia*) ja vaivaiskoivu (*Betula nana)* olivat vuonna 1994 puustoisissa korvissa (RhK, MkK) jo niukempia kuin koetta perustettaessa (liite 1). Suokukka oli alkanut niukentua myös LR:llä (Kuva 6). Suovarpujen runsastuminen johtuu pääasiassa varpukloonien kasvullisesta leviämisestä (Pienimäki 1982, Laine ym. 1995). Myöhemmin suovarvut taantuvat ja metsävarvut valtaavat alaa.

Rimpipintojen juurtosara (*Carex chordorrhiza*) ja mutasara (*C. limosa*) olivat vähentyneet voimakkaasti. Riippasara (*C. magellanica*) ja harmaasara (*C. canescens*), jotka sietävät ojitusta melko hyvin (Sarasto 1961, Mannerkoski 1976), olivat Teuravuoman humideissa oloissa (myös liikkuvia pintavesiä) runsastuneet kuten myös syväjuurinen ja heikosti hydrofiilinen äimäsara (*C. dioica*) (Lumiala 1944). RhK:ssa nämäkin lajit olivat alkaneet jo vähentyä. Pullosara (*C. rostrata*) oli tilapäisesti yleistynyt. Vielä vuonna 1994 lajia oli useammalla LR-alalla kuin vuonna 1933, sen sijaan RhK:ssa ja LK:ssa sitä ei enää tavattu. Märkäpintojen kuivuminen siten, että vettä on kuitenkin ollut riittävästi juurten käytettävänä, lienee mahdollistanut runsastumisen. Pullosaran elävät juuret voivat ulottua aiemmin havaittua (Metsävainio 1931) syvemmälle, jopa 2.3 m:iin (Saarinen ym. 1994). Voi olla niin, että laji on vegetatiivisesti lisääntynyt, mutta ei ole ollut yhtä kookas tai fertiili kuin ennen.

Ojituksen jälkeen luhtavilla (*Eriophorum angustifolium*) oli ilmestynyt useimmille LR-koealoille. Laji on niukentunut vasta viime aikoina. Vastaavantapainen oli esim. villapääluikan (*Trichophorum alpinum*) ja tupasluikan (*T. cespitosum*) runsausvaihtelu (myös Aapala & Kokko 1988). Mätäspinnan tupasvilla (*E. vaginatum*) kestää hyvin ojitusta ja se oli hieman runsastunut lähes kaikilla koealoilla MkK:a lukuunottamatta. Muutamat kämmekkälajit kuten jotkut muut ruoholajit, esim. kangasmaitikka (*Melampyrum pratense*) ja maitohorsma (*Epilobium angustifolium*) olivat väliaikaisesti runsastuneet. Kämmekkälajeista mm. harajuuri (*Corallorrhiza trifida*) ei enää esiinny koealoilla.

Esimerkki koko ajan vähentyneestä lajista on luhtaisuutta osoittava, matalajuurinen luhtakuusio (*Pedicularis palustris*). Kohtalaisen syväjuurinen välipintalaji siniheinä (*Molinia caerulea*) kasvoi vain LR:llä, jossa sen runsaudessa ei ollut tapahtunut muutoksia. Monet muut heinät, esim. kastikat (*Calamagrostis*) olivat runsastuneet, mikä on osoitus valoisuudesta ja runsaasta typestä sekä osalla lajeista myös luhtaisuudesta (Holmen 1964, Platonov 1976). Tehokkaasti vegetatiivisesti lisääntyvä syväjuurinen mätäslaji suomuurain (*Rubus chamaemorus*) oli monien metsälajien ohella runsastunut.

Metsäsammalet kuin myös useat mätäs- ja välipintojen suosammalet, esim. jokasuon- (*Sphagnum angustifolium*) ja kangasrahkasammal (*S. capillifolium*), lettokynsisammal (*Dicranum bonjeanii*), korpi- (*Polytrichum commune*) ja rämekarhunsammal (*P. strictum*) olivat runsastuneet. Heterahkasammal (*S. warnstorfii*) oli jo selvästi alkanut niukentua. Märkäpintojen vaateliaat suosammalet, joista monet osoittavat usein myös luhtaisuutta ja/tai lähteisyyttä, eivät odotetusti ole kestäneet ojitusta; esim. hetekuirisammal (*Calliergon giganteum*) ja rassisammal (*Paludella squarrosa*).

Ojituksen jälkeen lajilukumäärä sekä siihen positiivisessa korrelaatiossa olleet D ja H' (r = 0.94–0.99***) aluksi kasvoivat (Kuva 9). Koealoilla olleen suolajiston ja monien suokasvien runsastumisen lisäksi paikalle oli kolonisoitunut pioneeri/metsälajistoa. Suolajien vähentyessä em. tunnukset olivat vuoteen 1994 mennessä kääntyneet laskuun, ei kuitenkaan Rä:ssä ja RaSR:llä. Tämä johtui niiden pohjakerroksesta, jossa lajimäärä oli edelleen suurempi kuin aiemmilla havaintokerroilla (Hotanen 1998). Lajilukumäärä, H' ja D olivat nousun jälkeen kääntyneet laskuun kaikilla korpityypeillä lettorämettä nopeammin.

Lajimäärän maksimi ojitussukkessiossa saavutetaan viljavilla suotyypeillä yleensä aikaisemmin kuin karuilla tyypeillä. Lajimäärän nousu on myös sitä suurempi mitä runsaslajisempi suotyyppi on alunperin ollut (Sarasto 1952, 1961). Myöhemmin varsinkin suolajien määrä laskee sitä nopeammin mitä ravinteisempi suo on, mikä on yhteydessä myös puuston nopeaan kehitykseen (kilpailu, varjostus) (Vasander 1990, Laine ym. 1995). Perussääntö ojitusalueiden kasvillisuuden kehittymisessä on ollut: mitä viljavampi ja kosteampi kasvupaikka, sitä nopeampi sekundaarisukkessio (Sarasto 1961). Verrattaessa eri ravinteisuustasoja toisiinsa säännöt tulisi kuitenkin vakioida päätyyppiryhmällä ja suon eri pintojen osuuksilla (alkuperäisellä kosteusasteella).

Kohtalaisessa korrelaatiossa lajilukumäärään nähden (r = 0.37–0.62**) oleva J' sekä D:n perusteella laskettu tasaisuus (r = – 0.04–0.24) vaihtelivat hieman epämääräisesti, mutta useimmissa tapauksissa ne näyttivät vähän laskeneen verrattaessa esim. vuosia 1933 ja 1994 (Kuva 9, Taulukko 2). Lajiston dominanssi oli siten lisääntynyt. LK-alat olivat poikkeus, sillä laajan märkäpinnan vuoksi lajisto oli vuonna 1933 hyvin epätasaisesti jakautunut: dominantteja nevalajeja ja harvakseltaan muita, etenkin pohjakerroslajeja. Ojitus vähensi tyyppien välistä beta-diversiteettiä hydrologisten olosuhteiden muututtua yhtenäisemmiksi (Kuvat 2 ja 3) (myös Hotanen & Vasander 1992, Laine ym. 1995). Kehitys kohti metsäkasviyhteisöjä voi pienentää alueellista gamma-diversiteettiä, sillä suolajit, joista osa voi olla harvinaisia, korvautuvat ympäröivissä metsissä jo esiintyvillä lajeilla (Vasander ym. 1997).

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Appendix 1. Species frequencies and average Norrlin's density-abundances (mean) in different mire site types in 1933 and 1994.

Liite 1. Lajien frekvenssit ja keskimääräiset Norrlin-runsaudet suotyypeittäin vuosina 1933 ja 1994.

	LR (n = 22)		LK (n = 2)		RhK (n = 4)		MkK (n = 2)		Rä (n = 2)		RaSR (n = 1)	
	1933	1994	1933	1994	1933	1994	1933	1994	1933	1994	1933	1994
Alnus incana	(7) 0.4	(7) 0.5	–	–	–	–	–	–	–	–	–	–
Betula pubescens	(20) 1.1	(22) 3.2	(2) 1.5	(2) 4.0	(4) 1.6	(4) 2.8	(2) 1.5	(2) 4.0	(1) 0.5	(1) 0.5	–	1.0
Picea abies	(19) 0.9	(22) 2.0	(2) 1.0	(2) 3.0	(4) 1.0	(4) 3.3	(2) 2.0	(2) 3.5	(2) 1.3	(2) 4.0	1.5	3.0
Pinus sylvestris	(22) 1.6	(22) 3.6	(2) 1.0	(2) 3.5	(4) 1.1	(4) 2.0	–	–	(2) 1.3	(2) 3.5	1.5	4.0
Sorbus aucuparia	(8) 0.4	(14) 0.7	–	–	(2) 0.5	(3) 1.3	–	–	–	–	–	–
Betula nana x pubescens	(7) 0.3	(2) 0.2	(2) 1.0	–	–	–	–	–	–	–	–	–
Juniperus communis	(18) 1.9	(19) 2.7	–	–	(2) 0.5	(2) 0.5	–	–	–	–	–	–
Salix lapponum	(17) 1.0	(21) 2.1	–	(2) 1.0	(4) 2.4	(4) 2.3		(1) 0.5	(1) 0.5	–	–	–
Salix myrtilloides	(18) 1.4	(20) 2.7	–	(1) 0.5	(4) 1.3	(3) 1.3	(1) 0.5	(1) 0.5	–	–	1.0	3.0
Salix phylicifolia	(8) 0.6	(22) 1.9	–	–	(2) 0.5	(3) 0.8	–	(1) 0.5	(2) 2.0	(2) 3.0	–	–
Andromeda polifolia	(22) 5.0	(22) 4.6	(2) 5.0	(2) 4.0	(4) 3.3	(4) 1.8	(1) 1.0	–	(2) 3.0	(2) 4.5	4.0	6.0
Betula nana	(22) 3.9	(21) 4.9	(2) 2.0	(2) 2.5	(4) 1.3	(2) 0.5	(2) 1.0	–	(2) 4.0	(2) 6.0	3.0	6.0
Calluna vulgaris	–	–	–	–	–	–	–	–	(2) 1.5	(2) 1.0	2.0	5.0
Empetrum	(22) 2.9	(22) 4.7	–	(2) 2.5	(4) 2.0	(3) 1.5	(2) 2.0	–	(2) 4.0	(2) 5.5	6.0	7.0
Ledum palustre	(21) 2.1	(22) 4.5	–	(2) 1.0	(4) 2.3	(4) 3.0	(2) 2.5	–	(2) 3.0	(2) 6.0	3.0	6.0
Vaccinium myrtillus	–	(13) 0.7	–	–	–	(3) 1.3	(2) 2.5	(2) 4.5	(2) 1.5	(2) 4.5	–	–
Vaccinium oxycoccos and V. microcarpum	(22) 3.8	(22) 5.1	(2) 4.0	(2) 5.5	(4) 3.3	(2) 1.0	(2) 2.5	–	(2) 4.5	(2) 6.5	5.0	6.0
Vaccinium uliginosum	(21) 3.3	(22) 5.1	–	(2) 2.5	(4) 2.8	(4) 3.3	(2) 2.0	–	(2) 5.0	(2) 6.5	6.0	6.0
Vaccinium vitis–idaea	(20) 2.4	(22) 4.9	–	(2) 2.5	(4) 3.0	(4) 5.0	(2) 4.0	(2) 4.5	(2) 4.5	(2) 6.0	4.0	5.0
Carex brunnescens	–	(2) 0.1	–	–	–	(1) 0.3	–	–	–	–	–	–
Carex canescens	–	(15) 1.5	–	(2) 4.5	(1) 0.3	(4) 2.0	(2) 2.0	(2) 5.5	–	(1) 0.5	–	1.0
Carex cespitosa	(3) 0.2	(6) 0.3	–	–	(4) 1.5	(2) 1.3	–	–	–	–	–	–
Carex chordorrhiza	(22) 3.4	(7) 0.6	(2) 6.0	–	(4) 2.8	–	(1) 1.0	–	–	–	–	–
Carex dioica	(14) 1.5	(22) 3.4	–	(2) 1.5	(4) 1.0	(4) 1.8	–	–	–	–	–	–
Carex disperma	–	–	–	–	–	–	(1) 0.5	–	–	–	–	–
Carex echinata	–	–	–	–	–	–	–	(1) 0.5	–	–	–	–
Carex globularis	–	(3) 0.3	–	–	–	(2) 0.8	(2) 2.5	(2) 4.5	(2) 5.8	(2) 6.0	4.0	2.0
Carex lasiocarpa	(22) 3.8	(11) 0.7	(2) 2.0	–	(4) 1.8	–	–	–	–	–	–	–
Carex limosa	(14) 1.7	(1) 0.1	(2) 6.0	–	(1) 0.5	–	–	–	–	–	–	–
Carex loliacea	–	–	–	–	–	–	(2) 1.5	–	–	–	–	–
Carex magellanica	(12) 0.7	(21) 1.8	(2) 4.0	(2) 4.0	(4) 2.5	(4) 1.8	(2) 2.0	(2) 2.0	–	–	–	1.0
Carex pauciflora	–	–	–	–	–	–	–	–	–	–	–	3.0
Carex rostrata	(7) 0.4	(13) 0.7	(2) 1.0	–	(4) 1.3	–	–	–	–	–	–	–
Carex vaginata	(1) 0.1	(2) 0.1	–	–	(1) 0.3	–	–	(1) 1.0	–	–	–	–
Eriophorum angustifolium	(1) 0.1	(14) 1.0	(2) 2.0	(2) 3.0	(2) 0.5	(3) 1.3	–	–	–	–	–	–
Eriophorum gracile	–	–	(2) 1.0	–	–	–	–	–	–	–	–	–
Eriophorum latifolium	(1) 0.1	–	–	–	–	–	–	–	–	–	–	–
Eriophorum russeolum	–	(1) 0.1	–	–	–	–	–	–	–	–	–	–
Eriophorum vaginatum	–	(19) 1.5	–	(2) 1.0	–	(2) 0.5	–	–	(1) 0.5	(2) 1.5	3.0	6.0
Trichophorum alpinum	(9) 0.6	(5) 0.4	–	–	–	–	–	–	–	–	–	–
Trichophorum cespitosum	(1) 0.1	(2) 0.2	–	–	–	–	–	–	–	–	–	1.0
Agrostis canina	(1) 0.1	–	–	–	–	–	–	–	–	–	–	–
Agrostis capillaris	–	–	–	–	–	–	–	(2) 1.0	–	–	–	–
Calamagrostis canescens	(1) 0.1	(7) 0.5	–	–	(1) 0.8	(2) 2.0	–	–	–	–	–	–
Calamagrostis purpurea	(5) 0.3	(17) 1.7	–	(2) 3.5	(2) 2.6	(4) 4.0	–	(2) 2.0	–	(1) 0.5	–	–
Calamagrostis stricta	–	(7) 0.5	–	(2) 3.0	(1) 0.8	(3) 2.0	–	(2) 2.5	–	–	–	–
Deschampsia cespitosa	–	(1) 0.1	–	–	–	–	–	(1) 0.5	–	–	–	–
Deschampsia flexuosa	–	–	–	–	–	(1) 0.3	–	–	–	–	–	–
Festuca ovina	(1) 0.1	(2) 0.1	–	–	–	–	–	–	–	–	–	–
Festuca rubra	–	–	–	–	–	(1) 0.3	–	–	–	–	–	–
Molinia caerulea	(8) 1.3	(7) 1.1	–	–	–	–	–	–	–	–	–	–
Poa alpigena	–	(5) 0.3	–	(2) 1.0	(1) 0.3	(4) 1.8	–	–	–	–	–	–

Continued ...

Appendix 1. Continues.

Liite 1. Jatkuu.

	LR (n = 22)		LK (n = 2)		RhK (n = 4)		MkK (n = 2)		Rä (n = 2)		RaSR (n = 1)	
	1933	1994	1933	1994	1933	1994	1933	1994	1933	1994	1933	1994
Cerastium fontanum	–	(2) 0.1	–	–	–	(2) 0.5	–	(2) 1.0	–	–	–	–
Corallorhiza trifida	(3) 0.1	–	–	–	–	–	–	–	–	–	–	–
Dactylorhiza maculata	(7) 0.3	–	–	–	(2) 0.5	–	–	–	–	–	–	–
Drosera rotundifolia	(17) 1.0	(2) 0.1	–	–	–	–	–	–	–	–	3.0	–
Dryopteris carthusiana	(3) 0.1	–	–	–	–	(1) 0.3	–	–	–	–	–	–
Ebilobium angustifolium	(1) 0.1	(7) 0.5	–	(2) 1.0	(2) 0.5	(4) 2.8	–	(2) 3.5	–	–	–	–
Epilobium palustre	(1) 0.1	(4) 0.2	–	–	(3) 1.5	(2) 0.5	–	(2) 1.0	–	–	–	–
Equisetum fluviatile	(22) 5.0	(21) 3.0	(2) 5.0	–	(4) 6.0	(3) 1.0	(2) 4.3	–	(1) 1.0	–	2.0	–
Equisetum palustre	(14) 1.6	(19) 2.8	–	–	–	(2) 1.3	–	–	(1) 0.5	(2) 1.0	3.0	1.0
Equisetum sylvaticum	–	–	–	–	–	(1) 1.8	(2) 5.5	(2) 7.0	(2) 4.0	(2) 6.0	2.0	1.0
Filipendula ulmaria	(1) 0.1	(1) 0.1	–	–	–	–	–	–	–	–	–	–
Galium uliginosum	(3) 0.1	(1) 0.1	–	–	(2) 0.5	–	–	–	–	–	–	–
Geranium sylvaticum	(6) 0.6	(6) 0.5	–	–	(2) 0.5	(1) 0.3	–	–	–	–	–	–
Goodyera repens	–	(1) 0.1	–	–	–	–	–	–	–	–	–	–
Gymnocarpium dryopteris	–	(4) 0.4	–	–	–	(1) 0.5	–	–	–	–	–	–
Hieracium sp.	–	–	–	(1) 0.5	–	(1) 0.3	–	–	–	–	–	–
Huperzia selago	–	(4) 0.2	–	–	–	–	–	–	–	–	–	–
Juncus filiformis	–	(1) 0.1	–	–	–	–	–	–	–	–	–	–
Juncus stygius	(1) 0.1	(2) 0.1	–	–	–	–	–	–	–	–	–	–
Linnaea borealis	(3) 0.1	(4) 0.3	–	–	(1) 0.3	(2) 0.5	–	–	–	–	–	–
Listera cordata	(3) 0.1	(9) 0.5	–	–	–	–	(1) 0.5	–	–	–	–	–
Luzula multiflora	–	(2) 0.1	–	–	–	(1) 0.3	–	–	–	–	–	–
Luzula sudetica	–	(3) 0.1	–	(2) 1.0	–	–	–	–	–	–	–	–
Lycopodium annotinum	–	(6) 0.4	–	(1) 1.5	–	(2) 1.8	(1) 0.5	–	–	–	–	–
Maianthemum bifolium	(1) 0.1	(2) 0.1	–	–	–	(3) 1.0	–	–	–	–	–	–
Melampyrum pratense	(14) 0.7	(13) 0.9	(2) 1.0	(2) 2.0	(4) 1.3	(2) 0.8	–	–	(1) 0.5	–	–	2.0
Menyanthes trifoliata	(22) 4.7	(20) 3.0	(2) 5.0	(1) 1.5	(4) 5.6	(2) 0.8	–	–	–	–	–	–
Moneses uniflora	(17) 0.9	(12) 1.1	–	(2) 1.0	(2) 0.5	(1) 0.3	–	–	–	–	–	–
Orthilia secunda	(2) 0.1	(10) 0.5	–	–	(1) 0.3	(1) 0.8	(1) 0.5	(2) 1.0	(2) 1.0	(2) 3.5	–	–
Parnassia palustris	(3) 0.1	–	–	–	–	–	–	–	–	–	–	–
Pedicularis palustris	(17) 1.4	(1) 0.1	(2) 1.0	–	–	–	–	–	–	–	–	–
Potentilla palustris	(21) 2.3	(19) 2.3	(2) 4.0	(2) 3.0	(4) 4.0	(4) 3.5	(1) 1.0	(1) 1.5	–	–	–	–
Pyrola minor	–	(8) 0.6	(2) 1.0	(1) 1.0	(1) 0.3	(2) 1.0	(1) 0.5	–	–	–	–	–
Pyrola rotundifolia	(4) 0.2	–	–	–	(2) 0.5	–	–	–	–	–	–	–
Ranunculus lapponicus	–	–	–	–	–	–	(1) 0.5	–	–	–	–	–
Ribes rubrum	–	–	–	–	–	(1) 0.3	–	–	–	–	–	–
Rubus arcticus	(3) 0.1	(12) 1.1	–	–	(2) 0.5	(3) 1.5	–	–	–	–	–	–
R. arcticus x saxatilis	–	(9) 0.8	–	–	–	(3) 1.0	–	–	–	–	–	–
Rubus chamaemorus	(4) 0.2	(17) 2.2	–	(2) 5.0	(3) 1.3	(3) 4.0	(2) 5.3	(2) 6.0	(2) 5.0	(2) 6.0	6.0	7.0
Rubus saxatilis	(12) 1.2	(5) 0.3	–	–	(1) 0.3	(2) 1.5	–	–	–	–	–	–
Rumex acetosa	–	(3) 0.1	–	–	–	–	–	–	–	–	–	–
Selaginella selaginoides	(9) 0.5	(2) 0.1	–	–	–	–	–	–	–	–	–	–
Solidago virgaurea	(15) 1.0	(15) 1.5	–	(1) 0.5	(2) 0.5	(3) 1.8	–	–	–	–	–	–
Stellaria graminea	–	(1) 0.1	–	–	–	–	–	–	–	–	–	–
Stellaria longifolia	–	(2) 0.1	–	–	–	(2) 0.5	–	–	–	–	–	–
Tofieldia pusilla	(6) 0.4	–	–	–	–	–	–	–	–	–	–	–
Trientalis europaea	(15) 1.0	(19) 3.0	–	(2) 2.0	(2) 0.5	(4) 3.8	–	–	–	(1) 0.5	–	–
Sphagnum angustifolium	(18) 1.0	(22) 3.9	(2) 1.0	(2) 5.0	(2) 1.3	(4) 2.3	(2) 1.0	(2) 4.0	(2) 2.0	(2) 2.0	1.0	4.0
Sphagnum capillifolium	(2) 0.1	(22) 3.5	–	(2) 1.5	–	(3) 1.0	–	(1) 0.5	(1) 0.5	(2) 3.5	1.0	4.0
Sphagnum centrale	(2) 0.1	–	–	–	(2) 0.5	–	(2) 1.0	–	–	–	–	–
Sphagnum contortum	(2) 0.1	–	–	–	–	–	–	–	–	–	–	–
Sphagnum fuscum	(2) 0.1	(3) 0.1	–	–	–	–	–	–	(2) 5.0	(2) 4.0	5.0	5.0
Sphagnum girgensohnii	(1) 0.1	(8) 0.4	–	(1) 0.5	(4) 1.3	(2) 0.5	(2) 2.0	(2) 2.0	–	–	–	–
Sphagnum lindbergii	–	–	–	–	–	–	–	–	–	–	1.0	–
Sphagnum magellanicum	(12) 0.5	(15) 1.0	–	–	–	(2) 0.5	–	(1) 0.5	–	–	–	–
Sphagnum papillosum	(10) 0.5	(15) 0.9	–	–	–	–	–	–	–	–	–	–
Sphagnum riparium	–	–	–	–	–	–	(2) 1.0	(1) 0.5	–	–	–	–
Sphagnum russowii	(1) 0.1	(8) 0.5	–	–	–	(2) 0.5	(1) 0.5	(2) 4.0	–	(1) 0.5	–	–

Continued ...

Appendix 1. Continues.

Liite 1. Jatkuu.

	LR (n = 22)		LK (n = 2)		RhK (n = 4)		MkK (n = 2)		Rä (n = 2)		RaSR (n = 1)	
	1933	1994	1933	1994	1933	1994	1933	1994	1933	1994	1933	1994
Sphagnum squarrosum	–	(7) 0.3	–	(2) 1.0	(2) 0.5	(3) 0.8	(2) 1.0	(2) 1.0	–	–	–	–
Sphagnum subsecundum	(7) 0.3	(9) 0.4	(2) 1.0	–	–	–	–	–	–	–	–	–
Sphagnum teres	(2) 0.1	–	(2) 1.0	–	–	–	–	–	–	–	–	–
Sphagnum warnstorfii	(22) 2.9	(17) 1.3	(2) 1.0	–	(4) 1.3	(1) 0.3	–	–	–	–	–	–
Aulacomnium palustre	(22) 1.0	(22) 1.0	(2) 1.0	(2) 1.0	(4) 1.0	(4) 1.5	(2) 1.0	(1) 0.5	(2) 1.0	(2) 1.0	1.0	1.0
Brachythecium spp.	–	(11) 0.6	–	(2) 1.0	–	(3) 2.0	–	(2) 1.0	–	–	–	–
Bryales spp.	(2) 0.1	(10) 0.5	–	(1) 0.5	–	(2) 0.5	–	(1) 0.5	–	–	–	–
Bryum pseudotriquetrum	(3) 0.1	–	–	–	–	–	–	–	–	–	–	–
Calliergon cordifolium	(1) 0.1	–	(2) 1.0	–	(4) 1.3	–	(2) 1.0	–	–	–	–	–
Calliergon giganteum	(13) 0.6	–	–	–	(1) 0.3	–	–	–	–	–	–	–
Calliergon richardsonii	(1) 0.1	–	–	–	–	–	–	–	–	–	–	–
Calliergon stramineum	(6) 0.3	–	(2) 1.0	–	–	–	(1) 0.5	(2) 1.0	–	–	–	–
Campylium stellatum	(17) 0.8	(4) 0.2	–	–	–	–	–	–	–	–	–	–
Cinclidium stygium	(8) 0.4	–	–	–	–	–	–	–	–	–	–	–
Dicranum angustum	(2) 0.1	–	–	–	–	–	–	–	–	–	–	–
Dicranum bergeri	(12) 0.5	(20) 0.9	–	(1) 0.5	(2) 0.5	(1) 0.3	–	–	(1) 0.5	(2) 1.0	1.0	1.0
Dicranum bonjeanii	(5) 0.2	(17) 0.8	–	(2) 1.0	–	(2) 0.5	–	–	–	–	–	–
Dicranum fuscescens	(1) 0.1	(8) 0.4	–	–	–	(1) 0.3	–	–	–	(2) 1.0	–	–
Dicranum majus	(6) 0.3	(19) 1.2	–	(2) 1.0	(1) 0.3	(4) 1.5	(2) 1.0	(2) 2.0	(1) 0.5	–	–	–
Dicranum polysetum	–	(5) 0.2	–	(1) 0.5	–	(1) 0.3	–	(2) 1.0	–	(1) 0.5	–	–
Dicranum scoparium	–	(2) 0.1	–	–	(1) 0.3	(2) 0.5	(1) 0.5	(2) 1.0	–	–	–	–
Fissidens adianthoides	–	(1) 0.1	–	–	–	–	–	–	–	–	–	–
Helodium blandowii	(5) 0.2	(1) 0.1	(2) 1.0	(1) 0.5	(1) 0.3	(1) 0.3	(1) 0.5	–	–	–	–	–
Hepaticae spp.	(2) 0.1	(22) 1.1	–	(2) 1.0	–	(4) 1.0	–	(2) 1.0	(1) 0.5	(2) 1.0	–	1.0
Hylocomium splendens	(20) 1.6	(22) 4.5	(2) 1.0	(2) 3.5	(4) 1.0	(4) 5.3	(2) 1.5	(2) 3.5	(1) 0.5	(2) 1.0	–	–
Limprichtia intermedia	(18) 0.8	(11) 0.5	–	–	–	–	–	–	–	–	–	–
Limprichtia revolvens	(7) 0.3	–	–	–	–	–	–	–	–	–	–	–
Loeskypnum badium	(2) 0.1	(1) 0.1	–	–	–	–	–	–	–	–	–	–
Meesia triquetra	(17) 0.8	–	(2) 1.0	–	(1) 0.3	–	–	–	–	–	–	–
Mylia anomala	–	(1) 0.1	–	–	–	–	–	–	(2) 1.0	(2) 1.0	1.0	1.0
Paludella squarrosa	(11) 0.5	(1) 0.1	–	–	–	–	–	–	–	–	–	–
Paraleucobryum longifolium	(1) 0.1	–	–	–	–	–	–	–	–	–	–	–
Plagiothecium spp.	–	(6) 0.3	–	(1) 0.5	–	(4) 2.0	–	(2) 2.0	–	–	–	–
Pleurozium schreberi	(22) 1.0	(22) 5.3	(2) 1.0	(2) 5.5	(4) 1.0	(4) 4.0	(2) 1.0	(2) 2.0	(2) 1.5	(2) 7.0	2.0	6.0
Pohlia nutans	–	(20) 0.9	–	(2) 1.0	–	(4) 1.0	–	(2) 1.0	–	(2) 1.0	–	1.0
Polytrichastrum longisetum	(2) 0.1	(9) 0.4	–	(1) 0.5	–	(2) 0.5	(1) 0.5	–	(1) 0.5	–	–	–
Polytrichum commune	–	(19) 1.2	–	(2) 1.5	–	(3) 0.8	(2) 1.0	(2) 1.0	(1) 0.5	(2) 1.0	–	1.0
Polytrichum juniperinum	–	(9) 0.4	–	–	–	(3) 0.8	–	–	–	(1) 0.5	–	–
Polytrichum strictum	(7) 0.3	(22) 1.6	(2) 1.0	(2) 3.5	(2) 0.5	(4) 1.0	–	–	(2) 1.0	(2) 1.0	1.0	1.0
Polytrichum swartzii	–	–	(2) 1.0	–	–	–	–	–	–	–	–	–
Pseudobryum cinclidioides	(3) 0.1	–	–	–	(3) 0.8	–	(1) 0.5	–	–	–	–	–
Ptilidium ciliare	–	(4) 0.2	–	–	(2) 0.5	–	–	–	–	–	–	–
Ptilium crista-castrensis	(4) 0.2	–	–	–	(2) 0.5	(1) 0.3	–	–	–	–	–	–
Rhizomnium pseudopunctatum	(3) 0.1	–	–	–	(2) 0.5	–	(2) 1.0	–	–	–	–	–
Sanionia uncinata	–	–	–	(1) 0.5	–	–	–	–	–	–	–	–
Scorpidium scorpioides	(1) 0.1	–	–	–	–	–	–	–	–	–	–	–
Scorpidium vernicosum	(6) 0.3	–	(2) 1.0	–	–	–	–	–	–	–	–	–
Tomentypnum nitens	(22) 1.1	(13) 0.6	–	–	(3) 0.8	–	–	–	–	–	–	–
Warnstorfia exannulata	(5) 0.3	–	–	–	–	–	–	–	–	–	–	–
Warnstorfia fluitans	(13) 0.6	(3) 0.1	(2) 1.0	(2) 1.0	(2) 0.5	(1) 0.3	(2) 1.0	(2) 1.0	–	–	–	1.0
Cetraria islandica	–	–	–	–	–	–	–	–	(1) 0.5	–	–	–
Cladina rangiferina and C. arbuscula	(20) 0.9	(15) 0.7	–	(1) 0.5	(4) 1.0	–	–	–	(2) 1.0	(2) 1.0	1.0	1.0
Cladina stellaris	(2) 0.1	(2) 0.1	–	–	–	–	–	–	(1) 0.5	–	1.0	–

Continued ...

Appendix 1. Continues.

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	LR (n = 22)		LK (n = 2)		RhK (n = 4)		MkK (n = 2)		Rä (n = 2)		RaSR (n = 1)	
	1933	1994	1933	1994	1933	1994	1933	1994	1933	1994	1933	1994
Cladonia spp.	(1) 0.1	(11) 0.5	–	–	–	–	(1) 0.5	–	(1) 0.5	(2) 1.0	1.0	1.0
Nephroma arcticum	–	–	–	–	–	–	(1) 0.5	–	(2) 1.0	(2) 1.0	–	–
Peltigera aphthosa	(14) 0.6	(1) 0.1	–	–	(4) 1.0	–	(2) 1.0	(1) 0.5	(2) 1.0	(1) 0.5	–	–
Peltigera sp.	–	(1) 0.1	–	(1) 0.5	–	–	(1) 0.5	–	(1) 0.5	(2) 1.0	–	–
Stereocaulon sp.	(2) 0.1	–	–	–	–	–	–	–	–	–	–	–