Long-Term Effects of Water Level Drawdown on the Vegetation of Drained Pine Mires in Southern Finland

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Summary

1. The effect of water level drawdown after drainage of mires for forestry was studied by comparing the vegetation on undrained pine-mire sites with that of sites drained 3–55 years earlier. The plant communities were analysed with respect to the following environmental variables: drainage age, total nutrient contents of surface peat, and tree stand characteristics. Canonical correspondence analysis was used to relate the environmental variables to data on the botanical composition of vegetation .

2. Two main gradients were found in the data. The first ordination axis clearly relates to a gradient in forest vegetation succession and the second axis to a gradient in peat nutrient level and pH.

3. The secondary succession towards forest vegetation started soon after drainage and proceeded most rapidly in the most nutrient-rich site types. This led to a more uniform vegetation composition between the site types.

4. Original mire species reacted differently to the changing post-drainage environment. Tall sedges (*Carex lasiocarpa*, *C. rostrata*) disappeared soon after drainage. The coverages of the mire dwarf shrubs gradually decreased with increasing tree stand volumes; *Betula nana* appears to have been the most sensitive species. The coverages of the *Sphagna* studied appear to have decreased in response to increasing tree stand shading in the order: *S. fuscum* > *S. recurvum* complex > *S. magellanicum* > *S. russowii.*

5. The development towards forest vegetation on mires may diminish the regional (gamma-) diversity on forest-dominated landscapes, even if the species (alpha-) diversity on individual sites is little affected.

6. Long-term vegetation changes after artificial water level drawdown, emphasized in this study, can be used to mimic the effects of the predicted global climatic warming on mire vegetation.

Key-words: biodiversity, canonical correspondence analysis, forest drainage, global warming, vegetation succession.

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Introduction

Ecologically, a mire can be defined as an ecosystem with a high water level, as a result of which the organic matter produced is, to a considerable extent, deposited as peat. The actual rates of carbon accumulation on virgin mires in Finland vary from 5 g m^{-2} a^{-1} on wet minerotrophic sites to 30 g m^{-2} a^{-1} on drier ombrotrophic mires (Tolonen *et al.* 1992, 1994).

In Finland, drainage of mires for forestry has been very extensive. The practice started at the beginning of this century and there are now over $5{\cdot}5 \times 10^6$ ha of mires and paludified upland forests drained for forestry purposes (Aarne 1992). The effect of forest drainage on the carbon stores in peat has aroused much interest lately (Armentano & Menges 1986; Cannell, Dewar & Pyatt 1993; Laine *et al.* 1994).

Drainage causes an immediate drawdown of the water level (e.g. Heikurainen, Kenttämies & Laine 1978), and the minerotrophic waters important for the nutrition of hollow-dwelling plant species are diverted by the ditches. Thus, the hydrogeochemistry of sites that were originally different is made more uniform. On natural sedge-pine fens, the water level is near the mire surface, whereas on drained sites the median water levels have been found to vary by between 25 and 60 cm during the growing season (Laine & Vanha-Majamaa 1992).

After drawdown of the water level, subsidence of the mire surface takes place, caused at first by the removal of water leading to a physical collapse and compression of the peat. The thickness of the aerated surface peat layer increases and the organic matter is increasingly exposed to efficient aerobic microbial activity. The loss of carbon and release of nutrient ions from the organic matrix are increased to levels exceeding those before drainage (e.g. Lieffers 1988; Freeman, Lock & Reynolds 1993). The amount of subsidence measured in Finnish conditions has varied between 7 and 70 cm depending on the site type and its wetness, the thickness of the peat layer and the effectiveness and duration of drainage (Lukkala 1949; Laine *et al.* 1994).

The oxidation of the inorganic (e.g. Fe, S, and Al) complexes and organic compounds (de Vries & Breeuwsma 1987) increases the acidity of the aerated surface peat, especially in the nutrient-rich sites, and, as a consequence, the original differences between sites diminish (Lukkala 1929).

A rapid increase in tree growth takes place soon after drainage. On nutrient-poor sites, the maximum growth levels are reached later than on nutrient-rich sites (e.g. Seppälä 1969). In the poorest ombrotrophic site types, the increase in tree growth may be insignificant (Vasander 1982). The increasing uptake of mineralized nutrients by the tree stands may diminish their availability to the lower vegetation layers, even if the total amounts in the surface peat do not appear to decrease after drainage (Laiho & Laine 1992, 1994).

With the changing growth substrate and tree layer, the composition of lower vegetation layers also changes drastically after drainage. The plant species living on wet surfaces are the first to disappear while hummock-dwelling species (e.g. dwarf shrubs) may even benefit from drainage (Sarasto 1961; Eurola, Hicks & Kaakinen 1984). The number of plant species is highest some years after drainage when representatives of three groups of plants are found on the sites: original mire species, colonists and forest species (Vasander 1987). With the increase in shading caused by the growing tree layer, mire dwarf shrubs are gradually replaced by typical forest floor species (Laine & Vanha-Majamaa 1992). The change in species composition is fastest on more nutrient-rich site types (Sarasto 1961; Pienimäki 1982) which are usually also wet in the natural state (e.g. Hotanen & Vasander 1992).

Previous studies of the effects of forest drainage on vegetation have concentrated on the species composition changes only (e.g. Sarasto 1961; Pienimäki 1982). The present study is the first to apply direct multivariate methods to analyse the changes in composition together with the changing environment after forest drainage, in a range of sites forming a drainage-age continuum from undrained to fairly old drained areas, and which covers a fairly large range of nutrient level. The aim of the study was to analyse the effect of water level drawdown caused by forest drainage on the vegetation of the sedge and cottongrass pine-mire continuum. The results are based on the assumption that drained sites belonging to the same original site type were similar before drainage. The secondary succession following drainage, studied here, will be used to discuss the long-term vegetation change after possible drying of peatlands due to climatic warming.

Material and methods

MATERIAL

The material consists of mires, both undrained and drained, which belong to the following site types in the Finnish classification system (e.g. Cajander 1913; Laine & Vasander 1990): herb-rich sedge birch-pine fen (RhSR; site type names and abbreviations according to Laine & Vasander 1990), tall-sedge pine fen (VSR), cottongrass–sedge pine fen (TSR), low-sedge**Sphagnum papillosum*-pine fen (LkR) and cottongrass-pine bog (TR). These site types form a continuum from mesotrophy (RhSR) to oligotrophy and, ultimately, ombrotrophy (TR). The selection of the material and the criteria for determination of the original, pre-drainage site types are described in detail by Laiho & Laine (1994). Altogether, measurements were made at 82 sample plots on 43 mires during the summers from 1987 to 1989. The oldest drainage areas sampled had been drained 55 years earlier.

The mires studied are located in central Finland, in a region between 61°35'–62°05'N and 23°50'–24°55'E. The area is part of the southern boreal coniferous forest zone (Ahti, Hämet-Ahti & Jalas 1968) and the eccentric raised bog region in central Finland (Ruuhijärvi 1982, 1983). The elevation of the sites varies between 105 and 170 m a.s.l. The mean annual temperature in the region is +3 °C and that of July is +16 °C. The mean annual temperature sum (accumulated mean daily temperatures $\geq +5$ °C) varies between 1150 and 1250 degree days. The annual precipitation is *c.* 650 mm, of which *c.* 240 mm is snowfall.

FIELD MEASUREMENTS

To standardize hydrological conditions on drained sites, the sample plots (10 × 30 m) were placed along contour ditches, the longer side of the plot parallel to the ditch.

The cover of each plant species present was determined using cover classes 1, 2, 4, 8, 16, 32 and 64%. Species with a cover of less than 1% were assigned to the 1% class. Species with a cover of 50% or more were assigned to the 64% class. Rather wide classes were used because vegetation was mapped in the area of the whole sample plot, and because rather crude cover classifications have been found to result in interpretations similar to more refined ones in numerical analyses (e.g. Hotanen 1990). In some analyses, summed cover values of different plant species have been used. Thus, these values do not always indicate real cover; e.g. a cover sum of 2% may result from two species with real cover of less than 1%. Plant nomenclature follows Moore (1982) for vascular plants, Koponen, Isoviita & Lammes (1977) for bryophytes and Ahti (1993) for lichens. *Sphagnum angustifolium* and

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* i.e. dwarf sedge

S. fallax were determined as *S. recurvum* complex (e.g. Flatberg 1992). This was done because the species are difficult to separate from each other in the field, especially on drained mires, without checking with hand-lens or microscope. On our large sample plots this would not have been feasible.

Some of the sampling sites had been fertilized to increase forest growth. Sometimes this could be confirmed by checking documents retained by the local District Forestry Board. Otherwise, the sites were classified as 'fertilized' if there were visible signs of fertilization such as empty fertilizer bags, or abundant occurrences of plant species that grow in these site types only after fertilization (especially *Epilobium angustifolium*; e.g. Päivänen & Seppälä 1968), or if the tree stand showed a clear growth response. In uncertain cases, the sites were classified as 'possibly fertilized'.

The diameter at 1·3 m above ground was measured (± 1 cm) for all trees with a diameter $\geq$ 5 cm. For stand volume calculations, 10 sample trees were chosen on each plot with systematic random sampling, and measured for bark thickness, diameter at 6 m above ground, and height.

Three points for peat sampling were chosen, as equally spaced as possible, *c.* 5 m from the ditch, at the level of the lawn community (intermediate between dry hummock and wet flark levels: see Eurola *et al.* 1984) to avoid possible variation caused by microtopography. Undisturbed samples (746 cm^3) were taken from four depths: 0–10, 10–20, 25–35, and 50–60 cm. The zero-level was taken as the upper level of the rooting zone, which often corresponds to the lower level of the living moss layer. The samples were stored frozen until further treatment. Only the 0–10 and 10–20 cm samples will be referred to in this article.

PRELIMINARY TREATMENT OF THE DATA

The degree of humification (von Post scale 1–10; presented e.g. by Clymo 1983) was determined for fresh peat samples. The samples were then dried at 105 °C to constant mass, weighed for bulk density calculations, and ground through a 2-mm sieve. Roots with diameter $\geq$ 1 cm, if present, were removed before grinding. For each sample plot, the samples from all three sample points representing the same depths were combined and mixed thoroughly for chemical analyses.

Total element concentrations (P, K, Ca, Mg, Mn, Fe, Al, Cu, Zn, Mo, Cd, Cr, Pb) in the peat samples were measured with an atomic emission spectrometer (vacuum ICP emission spectrophotometer, ARL 3580 OES, Fison* Instruments, Valencia CA) after HNO_3-H_2SO_4-$HClO_4$-digestion, except for N, C and H which were measured with a gas chromatograph (CHN-600, Leco corp., St Joseph, MI). Peat pH was measured from a soil–0·01 M $CaCl_2$ (1:2·5 v/v) suspension. Ash content (loss-on-ignition) was determined by ashing to constant mass at 550 °C. The effect of drainage on peat nutrient concentrations is reported separately (Laiho & Laine 1992, 1994) and in future papers.

Stem volumes and stem numbers (ha^{-1}) were computed separately for pine, spruce and birch on each sample plot, using software created at the Finnish Forest Research Institute.

Because of the clustered distribution in relation to drainage age, we divided the material into four 'drainage age' classes according to time elapsed since drainage: undrained plots, plots drained 1–20 years, 21–40 years, and 41–55 years before sampling.

NUMERICAL METHODS

Laine & Vanha-Majamaa (1992) have recently reviewed the three principal methods used in studying vegetation changes following drainage. The approach of applying numerical methods to study plant communities on natural mires and on the successional communities of the same site types after drainage was adopted in this study.

Canonical correspondence analysis (CCA) (ter Braak 1986, 1987) was used in the analyses of the plant community data, since it allows environmental information to be combined with the plant community data (Jongman, ter Braak & van Tongeren 1987). The use of the technique and its qualifications are explained in detail by ter Braak (1986, 1987, 1988, 1990).

In the analyses, 21 of the 31 measured environmental variables were removed to diminish the problem of multicollinearity (on *a priori* basis) and the species data were not transformed. Plant species present on one sample plot only were removed, together with tree species. All species found on the plots are given in the Appendix. The ordination axes were scaled so that the species scores are weighted mean sample scores. For the figures, the biplot scores of the environmental variables were multiplied by 2. As can be seen in the Appendix, the number of plant species was considerable. In order to make the species–environment biplot clearer, many species not having any indicator value concerning drainage succession or nutrient level differences (on *a priori* basis), were omitted.

The inverse of the Simpson diversity measure (Hill 1973), as described by ter Braak (1990), was used to study the effect of drainage age on the species diversity of the sites. This measures the alpha-diversity of the sites. When discussing the species change in the whole data, we used the concepts beta- and gamma-diversity (*sensu* Whittaker 1972).

Results

GENERAL FEATURES OF THE SITES

The standard deviations of the nutrient contents in the surface peat of individual site types are very large (Table 1; see also Laiho & Laine 1992, 1994). There was a trend,

Table 1. Mean values (with standard deviations) of selected environmental variables used in the CCA analysis, grouped according to site type and drainage-age class. Soil variables are mean values for the 0-20 cm layer. RhSR = herb-rich sedge-birch-pine fen, VSR = tall-sedge pine fen, TSR = cottongrass-sedge- pine fen, LkR = low-sedge-*Sphagnum papillosum*-pine fen and TR = cottongrass-pine bog (Laine & Vasander 1990). The volume-based nutrient amounts can be converted to gravimetric concentrations (mg g^{-1}) by dividing by 200 × bulk density)

	Undrained		Time elapsed since drainage (years)					
			1–20		21–40		41–55	
RhSR								
Total N (kg ha^{-1})	3320		4150	(640)	4520	(1110)	3870	(1110)
Total Ca (kg ha^{-1})	696		1220	(490)	850	(276)	516	(164)
Total Fe (kg ha^{-1})	3960		1620	(980)	1290	(390)	732	(274)
Total Zn (kg ha^{-1})	5		3	(1)	4	(2)	4	(1)
C(%)	47·6		46·2	(3·3)	50·2	(1·9)	49·2	(1·6)
pH in CaCl$_2$	3·7		3·6	(0·3)	3·3	(0·2)	2·9	(0·2)
Tree stand volume (m^3 ha^{-1})	5		81	(49)	164	(67)	214	(27)
Birch volume (m^3 ha^{-1})	1		55	(39)	79	(43)	45	(25)
Peat bulk density (g cm^{-3})	0·086		0·131	(0·033)	0·117	(0·017)	0·110	(0·013)
Number of sites	1		4		7		3	
VSR								
Total N (kg ha^{-1})	2810	(2990)	2950	(800)	3990	(1110)	3690	(1160)
Total Ca (kg ha^{-1})	604	(426)	614	(112)	560	(170)	552	(158)
Total Fe (kg ha^{-1})	1180	(1240)	494	(344)	932	(370)	598	(514)
Total Zn (kg ha^{-1})	4	(2)	4	(1)	4	(3)	5	(1)
C(%)	47·6	(3·6)	48·8	(2·3)	48·7	(3·0)	51·2	(2·1)
pH in CaCl$_2$	3·8	(0·5)	3·1	(0·1)	3·1	(0·2)	2·9	(0·2)
Tree stand volume (m^3 ha^{-1})	14	(11)	66	(40)	121	(37)	168	(58)
Birch volume (m^3 ha^{-1})	1	(1)	21	(25)	36	(37)	32	(32)
Peat bulk density (g cm^{-3})	0·075	(0·046)	0·099	(0·025)	0·111	(0·020)	0·120	(0·025)
Number of sites	2		10		7		11	
TSR								
Total N (kg ha^{-1})	968	(694)	1970	(600)	2550	(1750)	2600	(860)
Total Ca (kg ha^{-1})	290	(100)	398	(142)	574	(426)	374	(94)
Total Fe (kg ha^{-1})	164	(118)	248	(66)	360	(250)	378	(212)
Total Zn (kg ha^{-1})	4	(1)	5	(1)	3	(2)	4	(1)
C(%)	45·8	(0·9)	48·0	(0·5)	46·7	(3·1)	48·5	(2·7)
pH in CaCl$_2$	3·1	(0·1)	3·0	(0·2)	3·0	(0·2)	2·9	(0·2)
Tree stand volume (m^3 ha^{-1})	9	(3)	40	(23)	82	(29)	128	(28)
Birch volume (m^3 ha^{-1})	1	(1)	<1	(<1)	4	(7)	12	(14)
Peat bulk density (g cm^{-3})	0·047	(0·008)	0·078	(0·003)	0·088	(0·029)	0·101	(0·023)
Number of sites	3		4		3		8	
LkR + TR								
Total N (kg ha^{-1})	782	(92)	1270	(360)	1100	(310)	1720	(130)
Total Ca (kg ha^{-1})	258	(30)	298	(70)	364	(82)	348	(76)
Total Fe (kg ha^{-1})	126	(20)	154	(48)	132	(22)	190	(30)
Total Zn (kg ha^{-1})	5	(1)	5	(2)	7	(3)	8	(5)
C(%)	45·8	(0·6)	46·5	(1·5)	46·7	(1·8)	47·8	(1·4)
pH in CaCl$_2$	2·9	(0·1)	2·8	(0·1)	2·8	(0·1)	2·8	(0·1)
Tree stand volume (m^3 ha^{-1})	24	(13)	40	(25)	38	(13)	114	(48)
Birch volume (m^3 ha^{-1})	0	(0)	<1	(1)	<1	(<1)	1	(1)
Peat bulk density (g cm^{-3})	0·055	(0·002)	0·065	(0·006)	0·067	(0·008)	0·085	(0·007)
Number of sites	3		7		5		4	

however, for the total amounts of nutrients in the 0–20 cm surface peat layer to decrease gradually from the mesotrophic RhSR sites to oligo-ombrotrophic LkR + TR sites. On the RhSR sites the nutrient pools (except for N) appeared to decrease towards the oldest drainage-age class but, in the data from other site types, the trend may even be reversed (Table 1). Drainage clearly increased the acidity of the surface peat in the more nutrient-rich site types much more than in the nutrient-poor types. In the oldest drainage-age class, all the site types showed the same average pH (Table 1). Also, bulk densities of the peat increased after drainage.

The tree stands before drainage were very sparse in all the site types. The development of the stand volumes was fastest on the nutrient-rich sites (RhSR, VSR) and the volumes in the oldest age class were highest in these site types (Table 1, Fig. 1).

ORDINATION OF PLANT COMMUNITIES

The eigenvalues from the canonical correspondence analyses are fairly low (Table 2), which is common

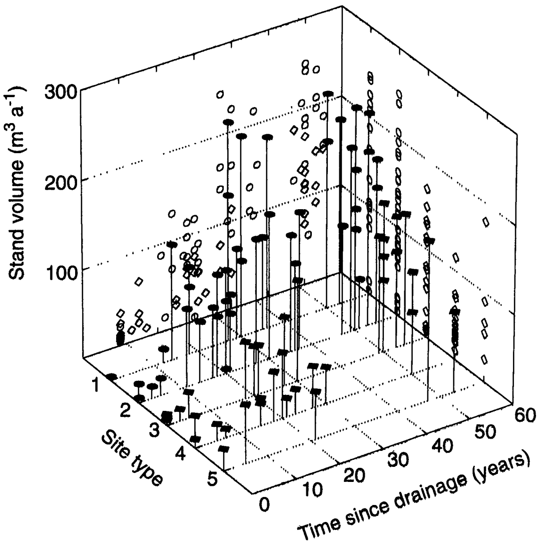

Fig. 1. Distribution of the stand volumes in the data for different site types along the drainage-age gradient. Site type codes: 1, herb-rich sedge birch-pine fen (RhSR); 2, tall-sedge pine fen (VSR); 3, cottongrass-sedge pine fen (TSR); 4 = low-sedge *Sphagnum papillosum* pine fen (LkR); 5, = cottongrass pine bog (TR). Circles, meso-oligotrophic sites (RhSR, VSR); diamonds, oligo-ombrotrophic sites (TSR, LkR, TR).

Table 2. Eigenvalues and species–environment correlations from the CCA analysis

	Axis 1	Axis 2	Axis 3
Eigenvalue	0·365	0·257	0·134
Correlation	0·912	0·909	0·784

in ecological applications (ter Braak 1988). The species– environment correlations that measure the strength of relation between species and environment, on the other hand, are rather high (Table 2). The two first ordination axes explain 56·6% of the variance in the species– environment ordination biplot.

The first ordination axis forms a clear 'forest vegetation succession' gradient, which correlates positively with such environmental variables as drainage age (years since drainage, Age), tree stand volumes (Vtot, VBet) and carbon content of the organic matter (C), which is a measure of the degree of post-drainage decomposition of the surface peat. The second axis is a nutrient-pH gradient which has rather high intraset correlations with total amounts of N, Ca, Fe and pH (Table 3).

Table 3. Intraset correlations in CCA for the first two axes. Environmental variables as in Fig. 2

	Axis 1	Axis 2
Drainage age	0·680	–0·244
VTot	0·860	0·044
VBet	0·613	0·505
C	0·536	0·179
N	0·469	0·496
Ca	0·208	0·694
Fe	0·027	0·753
Zn	–0·239	0·782
pH	0·043	–0·314

The sites are located along a drainage-age gradient from left to right in the ordination biplot and form a trophic gradient directed towards the top of the diagram (Fig. 2). The sites belonging to the mesotrophic (RhSR) and meso-oligotrophic (VSR) site types are rather clearly separated from the more nutrient-poor site types.

Because sample scores are weighted averages of species scores, the arrows graphically fitted in the data for individual site types depict the change in the vegetation after drainage. It is clear that the change was relatively greater in the more nutrient-rich site types (RhSR, VSR), as shown by the lengths of the arrows (Fig. 2). The older drained sites belonging to different site types are nearer each other in the ordination diagram than the undrained and younger drained sites (Fig. 2).

There was a clear change in vegetation along the drainage-age gradient (Fig. 3). The mesotrophic species of virgin RhSR sites (e.g. *Sphagnum subsecundum*, *Potentilla palustris*) were replaced by species of mesic forests (e.g. *Trientalis europaea*, *Dryopteris carthusiana*, *Rubus idaeus*). Similarly, the oligotrophic species (e.g. *Sphagnum papillosum*, *Carex lasiocarpa*, *C. rostrata*) were replaced by forest species, such as *Pleurozium schreberi*, *Melampyrum pratense*, *Vaccinium myrtillus* and *V. vitis-idaea*. The comparison of Figs 2 and 3 shows that the change in species composition was smaller in the oligo-ombrotrophic site types (LkR, TR).

The species diversity on the sites changed along the drainage-age gradient. The diversity values are highest for the fairly young drained sites and gradually decrease with increasing drainage age (Fig. 4). The effect of fertilization on diversity differed in different site types. On mesotrophic (RhSR) sites, diversity decreased along the age gradient faster on fertilized sites. In oligo-ombrotophic site types fertilization increased diversity (Fig. 4).

SPECIES RESPONSE TO WATER LEVEL DRAWDOWN

The cover of the dwarf shrubs increased after drainage (Fig. 5). *Betula nana* began to decrease 20–30 years after drainage, especially in the meso-oligotrophic site-type group, because of the increasing tree stand volumes. *Ledum palustre* and *Vaccinium vitis-idaea* were affected to a lesser degree by the increasing stand volumes and the highest cover of *V. myrtillus* were found under the highest stand volumes in the oldest drained sites. The increasing stand volumes appeared to diminish the dwarf shrub cover in the following order: *B. nana*, *L. palustre*, *V. vitis-idaea* and *V. myrtillus* (Fig. 5). The highest cover of the dwarf shrubs (especially *V. myrtillus*) was recorded from sites with lowest pH-values.

Herbs were found only with low cover on the more nutrient-rich sites (RhSR, VSR, Appendix). The cover of the mesotrophic mire species (e.g. *Potentilla palustris*,

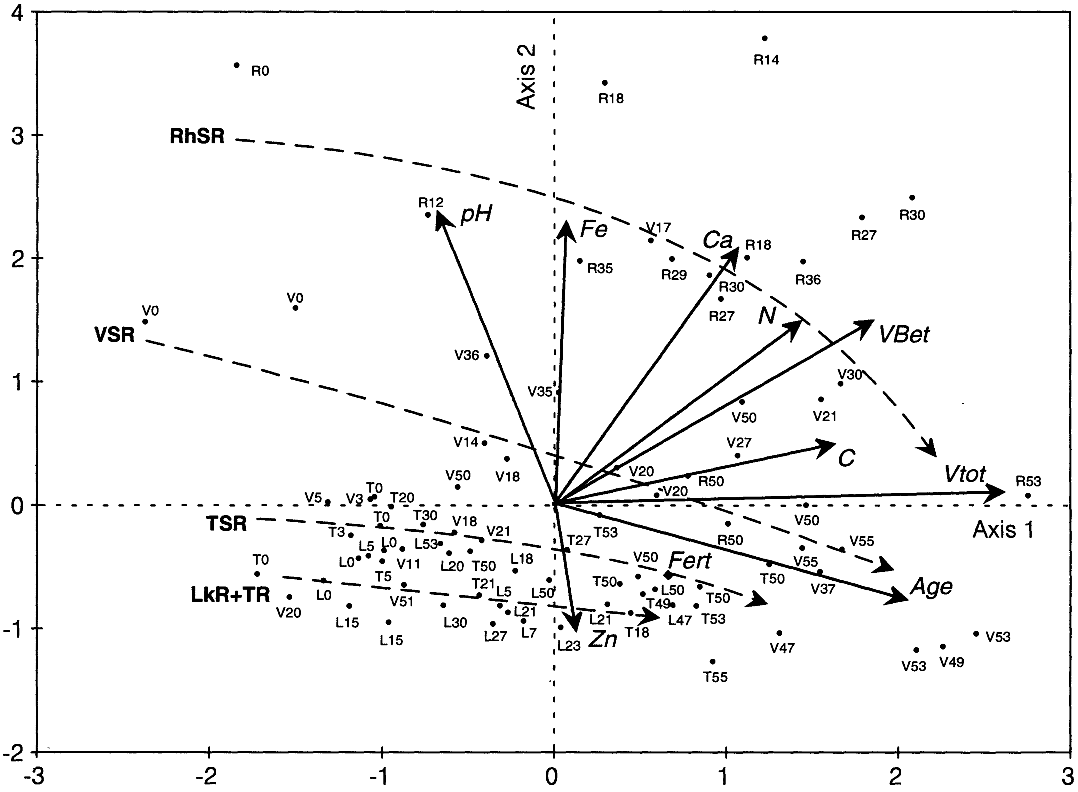

Fig. 2. CCA site–environment biplot. Abbreviations in sample plot names: R = RhSR (for site type names, see Fig. 1), V = VSR, T = TSR, L = LkR and TR; number = drainage age (years since drainage). The environmental variables are: *Age* , drainage age; *Vtot*, total tree stand volume; *VBet,* volume of birches; *pH,* peat pH; *C*, total peat carbon content; *N,* total nitrogen content, *Ca,* total calcium content; *Fe*, total iron content; *Zn*, total zinc content; *Fert*, fertilization. Arrows (dotted lines) added in the diagram show the extent of the vegetation succession in the data for each site type.

Viola palustris) decreased after drainage but these species still occurred sporadically on sites drained 30 to 40 years previously (Appendix, Fig. 6). The cover of the mesic forest herbs (e.g. *Dryopteris carthusiana*, *Trientalis europaea*) clearly increased with increasing drainage-age. Both of the above mentioned herb groups were found with similar cover on sites drained 20–30 years earlier (Fig. 6).

The tall sedges (*Carex lasiocarpa*, *C. rostrata*) disappeared soon after drainage. On drained sites, they were found only under the lowest *Betula nana* cover and tree stand volume (Fig. 7).

The cover of the forest moss species and *Sphagnum russowii* increased after drainage (Fig. 8). The spreading of *Pleurozium schreberi* on the fertilized sites was especially fast. *Sphagnum recurvum* complex and *S. magellanicum* were clearly influenced by tree stand volumes, *S. russowii* to a lesser extent. *Sphagnum fuscum* persisted on the older drained sites if the stand volumes did not exceed 50 $m^3 ha^{-1}$. The cover of the *Sphagna* appeared to decrease in response to increasing tree stand shading in the order: *S. fuscum* > *S. recurvum* complex > *S. magellanicum* > *S. russowii* (Fig. 8).

Discussion

METHODOLOGICAL CONSIDERATIONS

The underlying assumption in this study is that sites belonging to the same site types were originally similar and that their post-drainage development has proceeded similarly. Therefore, the trends in the data with varying drainage ages should show the effects of water level drawdown.

The variation in nutrient contents of the surface peat layer of undrained sites belonging to the same site types has been shown to be considerable (Westman 1981). As nutrient status, together with hydrology, largely determines the vegetation composition (Pakarinen & Ruuhijärvi 1978; Laine & Vanha-Majamaa 1992), it is evident that the variation in vegetation within a site-type class may also be rather large (e.g. Heikurainen 1953). Thus, the assumption in our approach may be questioned. Nonetheless, in view of the extent of our data, we consider the post-drainage changes in vegetation we have outlined to be reliable. The vegetation composition on our natural sites (Appendix) conforms to the species lists given by Ruuhijärvi (1960) and Eurola (1962) for natural mire sites belonging to the same types. Also, the trends in vegetation changes after drainage conform to those described by Pienimäki (1982) from permanent plots and by Sarasto (1961) from a data set gathered on drainage-age continua from various site types.

As the sample plots were located close to the ditches, their water table levels were deeper than average on the sites. Consequently, the effects of drainage may have been more pronounced, which is also shown in higher-than-average tree stand volumes (cf. Keltikangas *et al.* 1986).

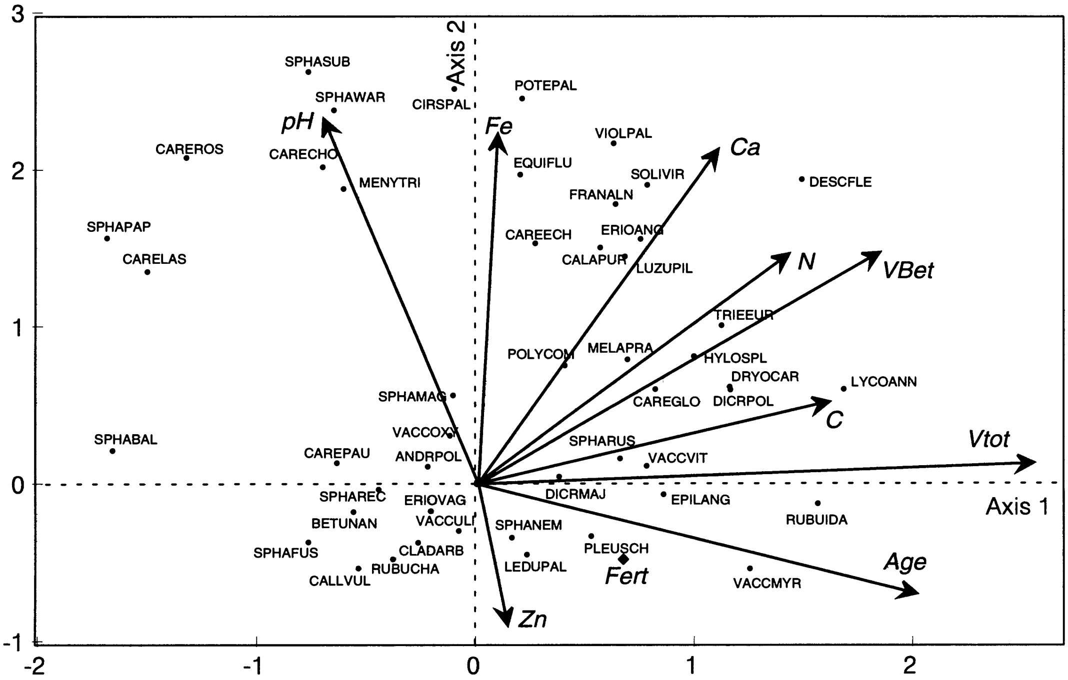

Fig. 3. CCA species–environment biplot. Plant species: andrpol, *Andromeda polifolia*; betunan, *Betula nana*; calapur, *Calamagrostis purpurea*; callvul, *Calluna vulgaris*; carecho, *Carex chordorrhiza*; careech, *C. echinata*; careglo, *C. globularis*; carelas, *C. lasiocarpa*; carepau, *C. pauciflora*; careros, *C. rostrata*; cirspal, *Cirsium palustre*; cladarb, *Cladina arbuscula*; descfle, *Deschampsia flexuosa*; dicrmaj, *Dicranum majus*; dicrpol, *D. polysetum*; dryocar, *Dryopteris carthusiana*; epilang, *Epilobium angustifolium*; erioang, *Eriophorum angustifolium*; eriovag, *E. vaginatum*; equiflu, *Equisetum fluviatile*; franaln, *Frangula alnus*; hylospl, *Hylocomium splendens*; ledupal, *Ledum palustre*; luzupil, *Luzula pilosa*; lycoann, *Lycopodium annotinum*; melapra, *Melampyrum pratense*; menytri, *Menyanthes trifoliata*; pleusch, *Pleurozium schreberi*; polycom, *Polytrichum commune*; potepal, *Potentilla palustris*; rubucha, *Rubus chamaemorus*; rubuida, *R. idaeus*; solivir, *Solidago virgaurea*; sphabal, *Sphagnum balticum*; sphafus, *S. fuscum*; sphamag, *S. magellanicum*; sphanem, *S. nemoreum*; sphapap, *S. papillosum*; spharec, *S. recurvum* complex (*S. angustifolium*, *S. fallax*); spharus, *S. russowii*; sphasub, *S. subsecundum*; sphawar, *S. warnstorfii*; trieeur, *Trientalis europaea*; vaccmyr, *Vaccinium myrtillus*; vaccoxy, *V. oxycoccos*; vacculi, *V. uliginosum*; vaccvit, *V. vitis-idaea*; violpal, *Viola palustris*. Environmental variables as in Fig. 2.

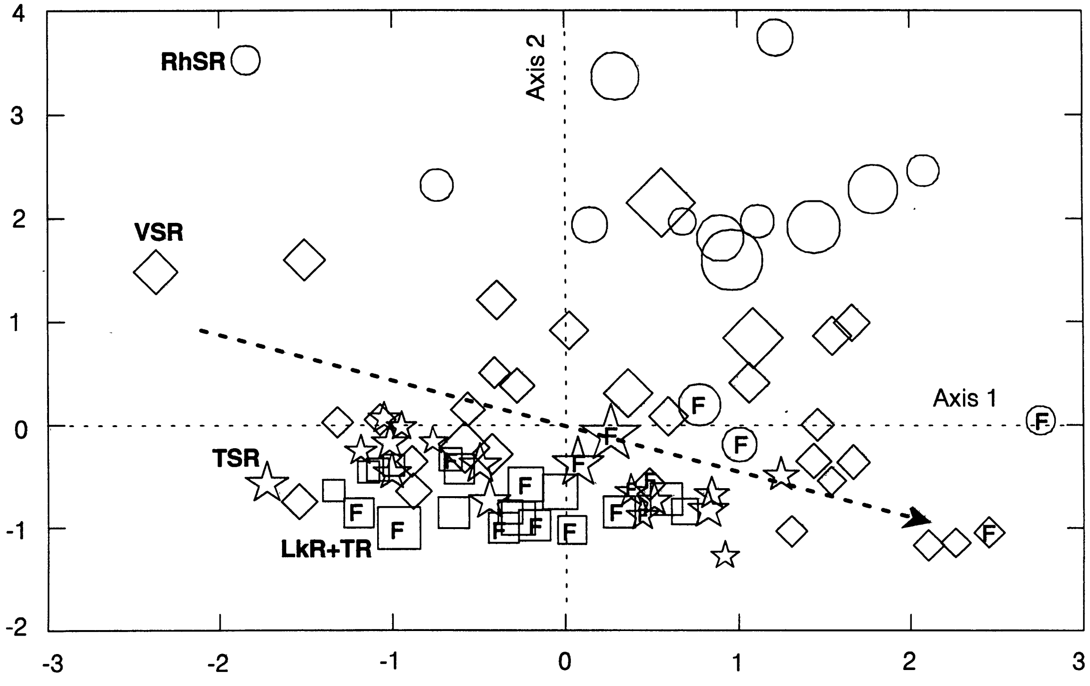

Fig. 4. Effect of drainage age, as depicted by the Age-vector (Fig. 2) and its extension (dotted line), on the species diversity (inverse of the Simpson diversity measure) on the sample sites. RhSR, circles; VSR, diamonds; TSR, stars; LkR + TR, squares. The width of the symbol represents the square root of the species diversity value, and shows the relative level of species richness. The sites marked with F have been fertilized.

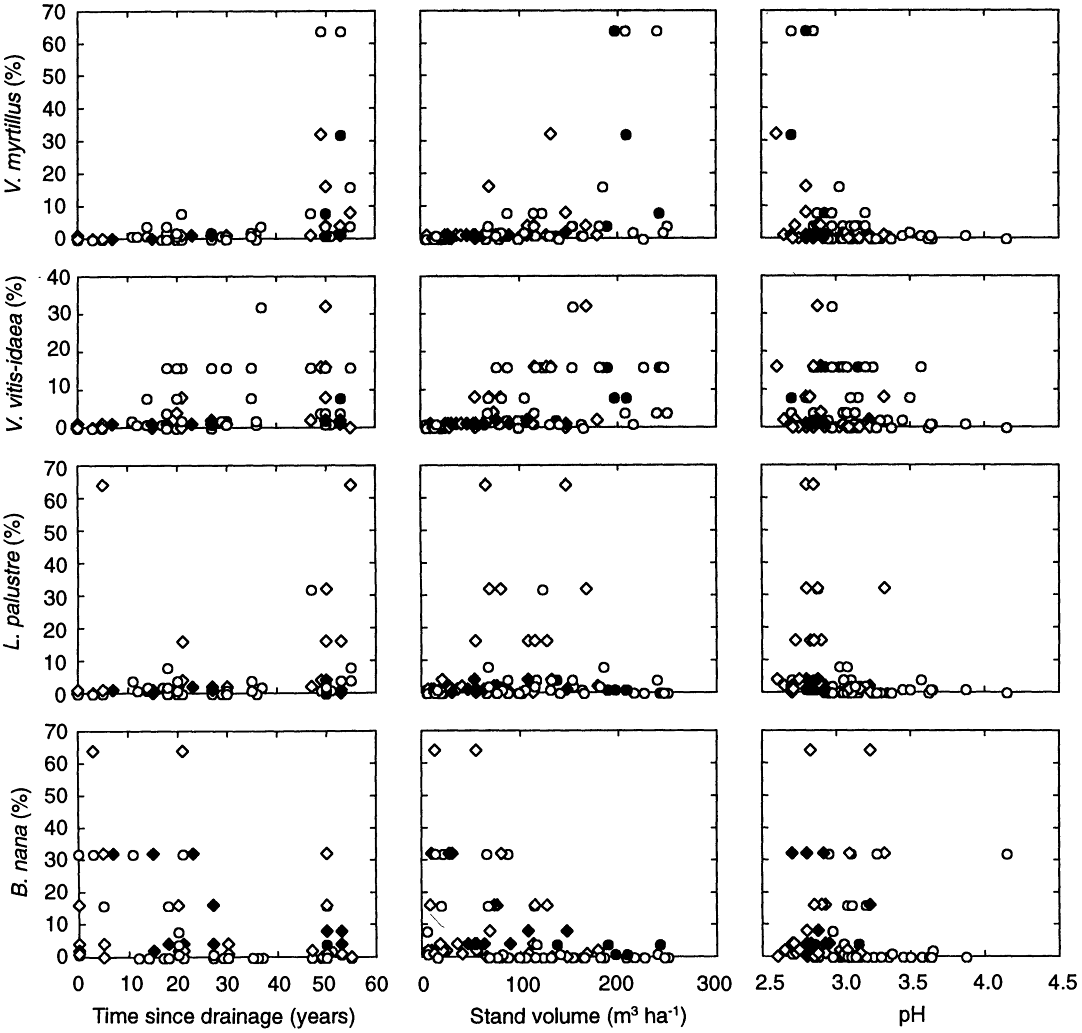

Fig. 5. Distributions of selected dwarf shrub species (*Betula nana*, *Ledum palustre*, *Vaccinium vitis-idaea*, *V. myrtillus*) in relation to drainage age, tree stand volume and surface peat pH($CaCl_2$). Circles = meso-oligotrophic sites (RhSR, VSR), diamonds = oligo-ombrotrophic sites (TSR, LkR, TR). Filled symbols denote fertilized sites.

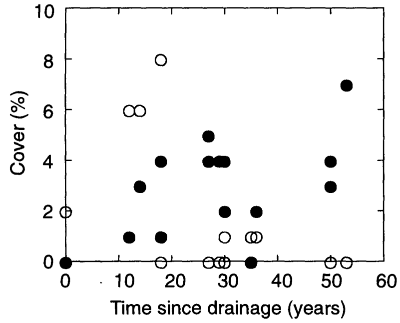

Fig. 6. Distributions of the summed cover of herbs of mesotrophic mire (*Cirsium palustre*, *Galium palustre*, *Peucedanum palustre*, *Potentilla erecta*, *P. palustris*, *Viola palustris*: open symbols) and mesic forest (*Dryopteris carthusiana*, *Luzula pilosa*, *Lycopodium annotinum*, *L. clavatum*, *Melampyrum sylvaticum*, *Pyrola rotundifolia*, *Trientalis europaea*: filled symbols) along the drainage-age gradient. Material from mesotrophic (RhSR) sites only.

In exploratory ecological studies such as this, interpretation of the effects of individual environmental variables is always hampered by the multicollinearity problem, as discussed by Laine & Vanha-Majamaa (1992). Therefore, on the basis of preliminary analyses of the data, only 10 of the measured 31 environmental variables were included in the final analyses. The effects of these variables also include the effects of those variables that were excluded from the analyses but which correlate with them. Thus, phosphorus, for instance, is included in the

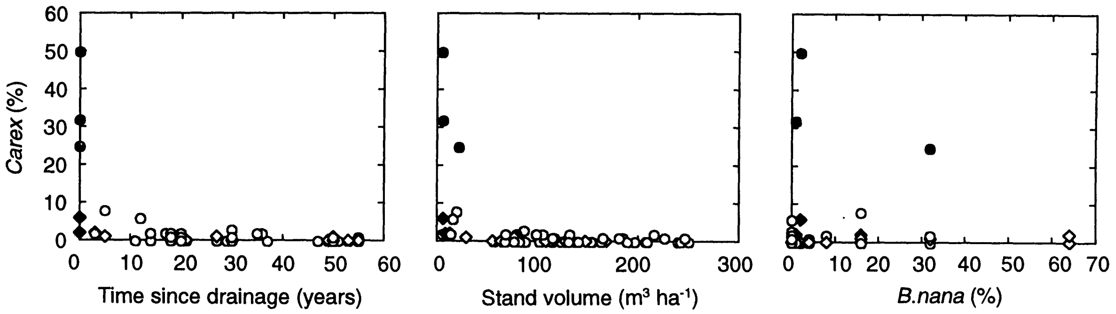

Fig. 7. Distribution of tall sedge species *Carex rostrata* and *C. lasiocarpa* in relation to drainage age, tree stand volume and *Betula nana* cover. Filled symbols denote undrained sites. Material from RhSR, VSR and TSR sites. Circles, meso-oligo trophic sites (RhSR, VSR); diamonds, oligotrophic sites (TSR).

effect of nitrogen; magnesium and most of the micronutrients (e.g. Mn, Cu, Cr) are included in the effect of calcium; and bulk density and degree of humification (von Post) are included in the effect of carbon content.

FOREST DRAINAGE, VEGETATION SUCCESSION AND SPECIES DIVERSITY

The ordination of vegetation on undrained mires is governed by gradients in (i) hydrological conditions and (ii) nutrient level (e.g. Pakarinen & Ruuhijärvi 1978). After drainage, the hydrological conditions become more uniform and, consequently, the influence of the tree stand, which depends on nutrient level, gradually becomes dominating. This is shown by the intraset correlations (Table 3): that between the tree stand volume and the first ordination axis, interpreted as the forest vegetation succession gradient, being clearly the highest. Similarly, in a data from drainage areas of the same age (*c.* 25 years), Laine & Vanha-Majamaa (1992) found only one major gradient which correlated with both nutrients and tree stand characteristics: during a certain period of time, the growth rate, which depended on nutrient level, resulted in higher stand volumes on more nutrient-rich sites. In the present study, the longer drainage age continuum (0–55 years) produced a tree-stand gradient within each nutrient-level, class (site type), allowing a separate nutrient gradient to appear in the ordination.

Both the forest vegetation succession and nutrient – pH gradients influence the species diversity distribution. The calculated alpha-diversity (*sensu* Whittaker 1972) was higher on meso-oligotrophic sites (RhSR, VSR) than on oligo-ombrotrophic sites (TSR, LkR, TR) both in natural conditions and after drainage (Fig. 4). Similarly, Vasander (1987) found the diversity to be highest on wet and nutrient-rich natural sites. This was mainly due to considerable microhabitat variation caused by water flow and flark–hummock topography, giving horizontal and vertical variation in the nutrient and moisture regimes.

The diversity within each site type was found to be highest in the middle of the drainage-age gradient (Fig. 4), when many of the original mire species grew alongside the colonizing forest species (Fig. 3). On meso-oligo-trophic sites, some ruderal species (e.g. *Deschampsia cespitosa, Galeopsis speciosa*) also occurred at that stage, whereas nutrient-poor site types were colonized by fewer species during secondary succession, as also reported by Grime (1979). The decrease in diversity towards the oldest drained sites was greater on meso-oligotrophic sites, where the tree stand had developed faster. Fertilization still accelerated the forest vegetation succession and decrease of diversity on these sites. On the oligo-ombrotrophic sites, on the other hand, fertilization increased diversity as has also been noted before (Vasander 1984).

When studying different plant communities on a single bog, Vasander (1984) noted that the total diversity of the mire decreased from natural sites to drained and fertilized sites. This reflects a general trend in disturbed ecosystems: biomass, production and dominance increase while diversity decreases (e.g. Bakelaar & Odum 1978). Also, in the present material, the beta-diversities describing the differences between plant communities (site types) decreased as the hydrological conditions became more uniform after drainage. This is shown in Fig. 2 as a smaller dispersion between the older drained sites representing different site types.

The effect of long-term water level drawdown on regional total (gamma-) diversity may be inferred to be negative. Mire species are gradually substituted by forest species which already dominate in the surrounding forests.

SPECIES RESPONSES

The change in hydrological conditions leads first to a decrease in *Sphagna* which, according to During (1979), belong to 'perennial stayers'. This gives free space for other bryophytes to establish from spores: first the colonists and then forest floor species, which also belong to the 'perennial stayers' group. The latter may already exist on drier hummocks in the natural state and then spread after drainage.

Seed banks are often important to upland vegetation communities in determining the field layer composition after disturbance (e.g. Kiirikki 1993). On mires, they probably play a minor role, because the species established after drainage rarely exist on natural mires or existed there only at the beginning of the mire succession thousands of years ago. Clonal growth may play an important role in the vegetation dynamics of developing communities.

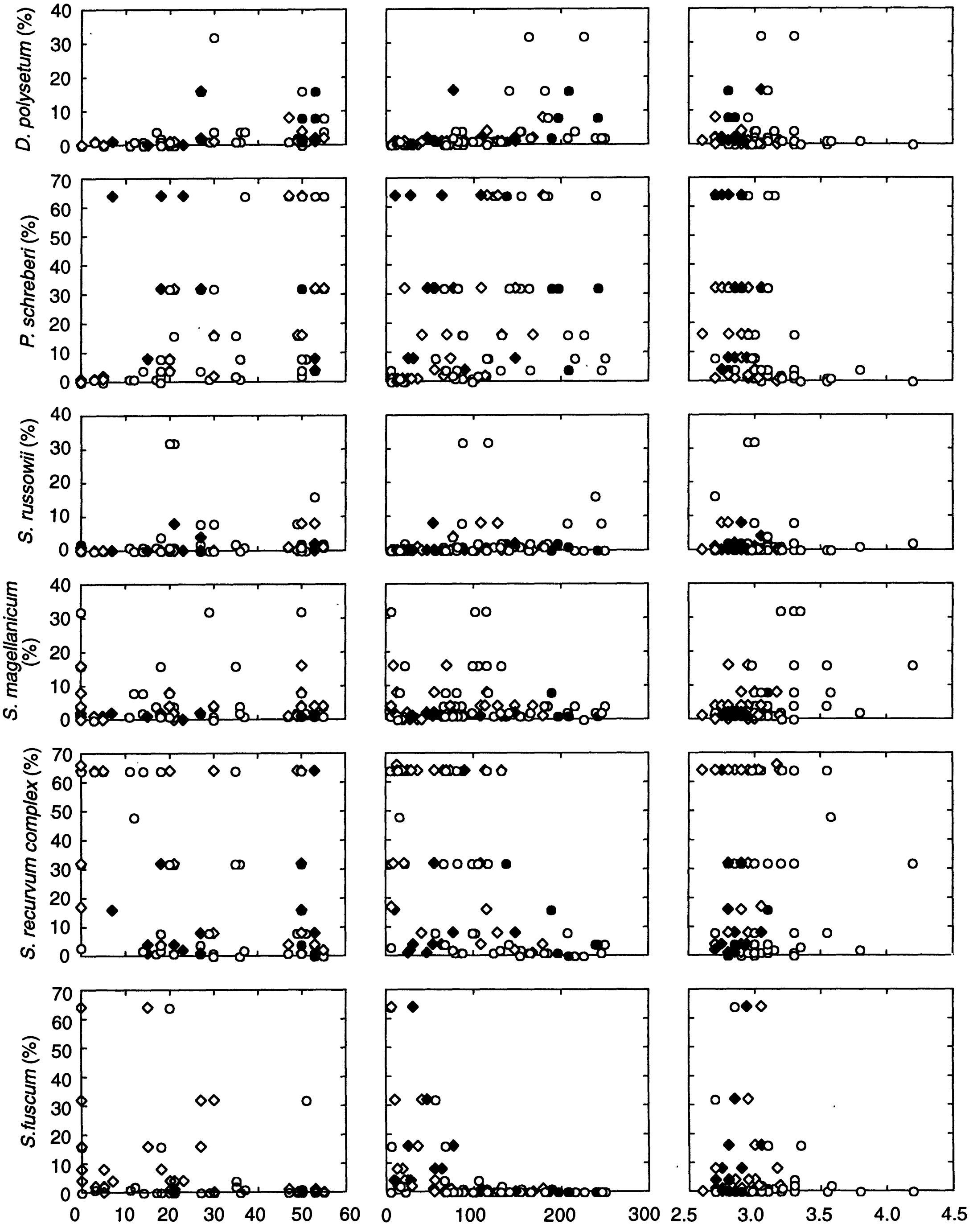

Fig. 8. Distributions of selected moss species (*Sphagnum fuscum, S. recurvum* complex, *S. magellanicum, S. russowii, Pleurozium schreberi, Dicranum polysetum*) in relation to drainage age, tree stand volume and surface peat pH($CaCl_2$). Circles, meso-oligotrophic sites (RhSR, VSR); diamonds, oligo-ombrotrophic sites (TSR, LkR, TR). Filled symbols denote fertilized sites.

Seed dispersal by animals may also be an important factor. For example, we often found that *Trientalis europaea* had become established on moose dung. In Finland, moose often graze on drained peatlands (Heikkilä & Härkönen 1993). As they eat *Vaccinium myrtillus*, herbs and grasses during summer and autumn (Cederlund *et al.* 1980; Hjeljord, Hövik & Pedersen 1990), it is possible that they also spread seeds of these species. The changing microclimatic conditions also affect the abundance relationships in successional plant communities (Busby, Bliss & Hamilton 1978).

The gradual replacement of mire dwarf shrubs (*Betula nana, Ledum palustre*) by forest species (*Vaccinium myrtillus, V. vitis-idaea*) is most probably explained by the effect of shading and competition from the tree stands (Fig. 5). *V. myrtillus*, which was not found on the sites before drainage, was the last to arrive: high cover being achieved only some 50 years after drainage. This may have been due to the slow spreading of the species or to its weak competitive ability in the sparse tree stands in comparison with other dwarf shrub species. The rhizome growth rate of *V. myrtillus* is slower than that of e.g. *V. vitis-idaea* (Flower- Ellis 1971; Tolvanen 1994). *V. myrtillus* is the only one of these species that does not appear to react to shading by tree stands over 200 m^3 ha^{-1} (Fig. 5). In this material, the differences in the responses of *V. myrtillus* and *V. vitis-idaea* to shading are quite clear, which slightly contradicts the results of Laine & Vanha-Majamaa (1992) from younger drained sites.

The fast disappearance of sedges after drainage may be due to (i) changed hydrological conditions (water level drawdown, cutting off the moving ground water and nutrients) or (ii) increased competition from other species. Tree stand development towards canopy closure was so slow (Fig. 1) that it can hardly have been the main reason. Increase in *Betula nana* cover, on the other hand, took place so fast (Fig. 5) as potentially to cause the suppression of sedges. The effect of the changed geohydrology, however, cannot be ruled out, because many sedges are inefficient in cycling nutrients internally and are thus dependant on the nutrients in the moving water (Bernard & Hankinson 1979).

The *Sphagna* are gradually replaced by forest mosses, especially by *Pleurozium schreberi*. Many of the *Sphagnum* species, however, maintained their positions almost unchanged for a long time after water level drawdown and some species (e.g. *S. russowii*) clearly increased on the sites after drainage (see also Sarasto 1961). The occurrence of *S. russowii* may often have been overlooked because, under tree stands, it often totally lacks red colouring.

Most of the *S. recurvum* complex on the older drained sites belongs to the species *S. angustifolium* (Sarasto 1961), even though on undrained oligo- and mesotrophic sites, *S. fallax* mostly dominates (*S. apiculatum* in Ruuhijärvi 1960 and Eurola 1962; Flatberg 1991). The occurrence of *S. flexuosum* on these sites is also probable, but the two other European species in this complex, *S. brevifolium* and *S. isoviitae*, recognized recently by Flatberg (1991, 1992), are scarce on sites of the type studied. Since *S. angustifolium* is the only species in the *S. recurvum* complex which can thrive in the hummock conditions (Eurola *et al.* 1984; Table 3) that prevail on drained sites, the separation of individual species from each other might still have increased the separation between undrained and drained minerotrophic sites in the ordination diagrams.

The typical forest species, such as *Pleurozium schreberi* and *Vaccinium myrtillus*, achieved highest cover on sites with the lowest pH values in the surface peat. This is due to the fact that these species were most abundant on the oldest drained sites where, on an average, post-drainage acidification of the aerated surface peat had proceeded furthest (Table 1). These species were apparently not sensitive to low soil pH (Figs 5 and 8).

Besides increasing the availability of nutrients in the soil, fertilization may have had an indirect effect on understorey vegetation through increasing the tree stand biomass, especially needles (Finér 1991). The addition of large quantities of soluble nutrients may also have had a direct toxic effect on some species. The rapid disappearance of *Sphagna*, together with the simultaneous increase of *Pleurozium schreberi* on some oligo-ombrotrophic sites (Fig. 8), may be the outcome of such a phenomenon (Heikurainen & Veijola 1971; Vasander, Kuusipalo & Lindholm 1993). The occurrence of mesic forest herbs such as *Dryopteris carthusiana* and *Trientalis europaea* on VSR sites (Appendix) may also be attributed to the fertilization effect. *Epilobium angustifolium* is generally considered to be a coloniser after fertilization on nutrient-poor sites (e.g. Päivänen & Seppälä 1968) and was used in the present study as an indicator when assigning sites to the 'fertilized' group. *E. angustifolium* is thus located near the centroid of the fertilization effect (*Fert*) in Fig. 3.

SPECIES CHANGE AND SEQUESTRATION OF CO$_2$

Sedges and *Sphagna* are the most important species groups sequestering carbon in natural mires. The cover of these groups decreased rapidly after drainage, especially in the more nutrient-rich site types (RhSR, VSR; Appendix). Simultaneously, the tree stand biomass and net primary production increased. The net primary production of the developing tree stand may have become even higher than that of the original mire vegetation (Reinikainen, Vasander & Lindholm 1984).

The decrease and gradual disappearance of *Sphagna* may finally end the upward growth of the mire surface. However, the accumulation of carbon through the root systems may continue for a long time, because less than 20% of the peat volume is filled with organic matter (average bulk densities 0·05– 0·13 g cm^{-3}, Table 1; density of solids 1·4–1·6 g cm^{-3}, Puustjärvi 1970). Theoretically, the amount of organic matter in the root zone may increase up to 4-fold until the air space becomes too small (5–10%, as discussed by Paavilainen 1967) for the roots to function. How the carbon balance of a mire ecosystem is affected by forest drainage is, however, determined to a high degree by the change in the rate of decomposition, as discussed in Immirzi, Maltby & Clymo (1992) and Cannell *et al.* (1993).

It has been predicted that the influence of climatic warming on peatlands will be largely indirect, caused by the alterations (drawdown) in the water table level (Gorham 1991; Malmer 1992) Effects of water level drawdown after drainage of peatlands for forestry can thus be regarded as a simulation of these indirect climatic change effects.

Our results suggest that a stable, long-term water level drawdown of 30–50 cm, which is common in forest drainage areas, leads to a forest vegetation succession and, consequently, to a changed carbon sequestration regime. Accumulation may either increase or decrease, depending on the nutrient level and geographical location of the site (Laine *et al.* 1994). If the water level drawdown is smaller and less stable, it is possible that originally wet, minerotrophic mires may start an accelerated development towards ombrotrophic hummock vegetation and higher rates of carbon sequestration. Studies to determine the critical water level drawdown which leads to forest vegetation instead of ombrotrophic mire succession have already been started within the research programme 'Carbon Balance of Peatlands and Global Climatic Change', which is part of the Finnish Research Programme on Climate Change (Laine & Päivänen 1992).

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References

Aarne, M. (ed.) (1992) Yearbook of forest statistics 1990–91. *Folia Forestalia*, **790**, 1–281.

Ahti, T. (1993) Names in current use in the *Cladoniaceae* (lichen-forming ascomycetes) in the ranks of genus to variety. *Regnum Vegetabile*, **128**, 58–106.

Ahti, T., Hämet-Ahti, L. & Jalas, J. (1968) Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici*, **5**, 169–211.

Armentano, T.V. & Menges, E.S. (1986) Patterns of change in the carbon balance of organic soil-wetlands of the temperate zone. *Journal of Ecology*, **74**, 755–774.

Bakelaar, R.G. & Odum, E.P. (1978) Community and population level responses to fertilization in an old-field ecosystem. *Ecology*, **59**, 660–665.

Bernard, J.M. & Hankinson, G. (1979) Seasonal changes in standing crop, primary production, and nutrient levels in a *Carex rostrata* wetland. *Oikos*, **32**, 328–336.

Busby, J.R., Bliss, L.C. & Hamilton, C.D. (1978) Microclimate control of growth rates and habitats of the boreal forest mosses, *Tomentypnum nitens* and *Hylocomium splendens*. *Ecological Monographs*, **48**, 95–110.

Cajander, A.K. (1913) Studien über die Moore Finnlands. *Acta Forestalia Fennica*, **2**, 1–208.

Cannell, M.G.R., Dewar, R.C. & Pyatt, D.G. (1993) Conifer plantations on drained peatlands in Britain: a net gain or loss of carbon? *Forestry*, **66**, 353–369.

Cederlund, G., Ljunqvist, H., Markgren, G. & Stålfelt, F. (1980) Foods of moose and roe-deer at Grimsö in Central Sweden – results of rumen content analyses. *Swedish Wildlife Research*, **11**, 169–247.

Clymo, R.S. (1983) Peat. *Ecosystems of the world 4A. Mires: Swamp, Bog, Fen and Moor. General Studies* (ed. A.J.P. Gore), pp. 159–224. Elsevier, Amsterdam.

de Vries, W. & Breeuwsma, A. (1987) The relation between soil acidification and element cycling. *Water, Air, and Soil Pollution*, **35**, 293–310.

During, H.J. (1979) Life strategies of Bryophytes: a preliminary review. *Lindbergia*, **5**, 2–18.

Eurola, S. (1962) Über die regionale Einteilung der südfinnischen Moore. *Annales Botanici Societatis 'Vanamo'*, **33**, 1–243.

Eurola, S., Hicks, S. & Kaakinen, E. (1984) Key to Finnish mire types. *European Mires* (ed. P.D. Moore), pp. 11–117. Academic Press, London.

Finér, L. (1991) Effect of fertilization on dry mass accumulation and nutrient cycling in Scots pine on an ombrotrophic bog. *Acta Forestalia Fennica*, **223**, 1–42.

Flatberg, K.I. (1991) The European taxa in the *Sphagnum recurvum* complex. 2. Amended descriptions of *Sphagnum brevifolium* and *S. fallax*. *Lindbergia*, **17**, 96–110.

Flatberg, K.I. (1992) The European taxa in the *Sphagnum recurvum* complex. 1. *Sphagnum isoviitae sp. nov. Journal of Bryology*, **17**, 1–13.

Flower-Ellis, J.G.K. (1971) *Age structure and dynamics in stands of bilberry (*Vaccinium myrtillus *L.)*. Department of Forest Ecology and Forest Soils, Royal College of Forestry, Sweden, Research Notes 9, Uppsala.

Freeman, C., Lock, M.A. & Reynolds, B. (1993) Climatic change and the release of immobilized nutrients from Welsh riparian wetland soils. *Ecological Engineering* **2**, 367–373.

Gorham, E. (1991) Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecological Applications*, **1**, 182–195.

Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*. John Wiley, Chichester.

Heikkilä, R. & Härkönen, S. (1993) Moose (*Alces alces* L.) browsing in young Scots pine stands in relation to the characteristics of their winter habitats. *Silva Fennica*, **27**, 127–143.

Heikurainen, L. (1953) Die kiefernbewachsenen eutrophen Moore Nordfinnlands. Eine Moortypenstudie aus dem Gebiet des Kivalo-Höhenzuges. *Annales Botanici Societatis 'Vanamo'*, **26**, 1–189.

Heikurainen, L. & Veijola, P. (1971) Lannoituksen ja sarkaleveyden vaikutus rämeen uudistumiseen ja taimien kasvuun (Summary: Effect of fertilization and ditch spacing on regeneration and seedling growth in pine swamps). *Acta Forestalia Fennica*, **114**, 1–19.

Heikurainen, L., Kenttämies, K. & Laine, J. (1978) The environmental effects of forest drainage. *Suo*, **29**, 49–58.

Hill, M.O. (1973) Diversity and evenness: a unifying notation and its consequences. *Ecology*, **54**, 427–432.

Hjeljord, O., Hövik, N. & Pedersen, H.B. (1990) Choice of feeding sites by moose during summer, the influence of forest structure and plant phenology. *Holarctic Ecology*, **13**, 281–292.

Hotanen, J.-P. (1990) Esimerkki pseudolajien runsauskynnysten muuntelun vaikutuksesta TWINSPAN-luokittelussa (Summary: The effect of pseudospecies cut level settings on the results of TWINSPAN classification). *Suo*, **41**, 43–53.

Hotanen, J.-P. & Vasander, H. (1992) Eteläsuomalaisten metsäojitettujen turvemaiden kasvillisuuden numeerinen ryhmittely (Summary: Post-drainage development of vegetation in southern Finnish peatlands studied by numerical analysis). *Suo*, **43**, 1–10.

Immirzi, C.P., Maltby, E. & Clymo, R.S. (1992) *The Global Status of Peatlands and their Role in Carbon Cycling*. A report for Friends of the Earth by the Wetland ecosystems research group, Department of Geography, University of Exeter. Friends of the Earth, London.

Jongman, R., ter Braak, C. & van Tongeren, O. (1987) *Data Analysis in Community and Landscape Ecology*. Pudoc, Wageningen.

Keltikangas, M., Laine, J., Puttonen, P. & Seppälä, K. (1986) Vuosina 1930–1978 metsäojitetut suot: ojitusalueiden inventoinnin tuloksia (Summary: Peatlands drained for forestry during 1930–1978: results from field surveys of drained areas). *Acta Forestalia Fennica*, **193**, 1–94.

Kiirikki, M. (1993) Seed bank and vegetation succession in abandoned fields in Karkali Nature Reserve, southern Finland. *Annales Botanici Fennici*, **30**, 139–152.

Koponen, T., Isoviita, P. & Lammes, T. (1977) The bryophytes of Finland: An annotated checklist. *Flora Fennica*, **6**, 1–77.

Laiho, R. & Laine, J. (1992) Potassium stores in peatlands drained for forestry. *Proceedings of the 9th International Peat Congress Uppsala, Sweden* 1, pp. 158–169. International Peat Society, Helsinki.

Laiho, R. & Laine, J. (1994) Nitrogen and phosphorus stores in peatlands drained for forestry in Finland. *Scandinavian Journal of Forest Research*, **9**, 251–260.

Laine, J. & Päivänen, J. (1992) Carbon balance of peatlands and global climatic change: summary. *The Finnish Research Programme on Climate Change. Progress Report* (eds M. Kanninen & P. Anttila), pp. 189–192. Publications of the Academy of Finland 3, Helsinki.

Laine, J. & Vanha-Majamaa, I. (1992) Vegetation ecology along a trophic gradient on drained pine mires in southern Finland. *Annales Botanici Fennici*, **29**, 213–233.

Laine, J. & Vasander, H. (1990) *Suotyypit*. Kirjayhtymä, Helsinki.

Laine, J., Minkkinen, K., Puhalainen, A. & Jauhiainen, S. (1994) Effect of forest drainage on the carbon balance of peatland ecosystems. *The Finnish Research Programme on Climate Change. Second Progress Report* (eds M. Kanninen & P. Heikinheimo), pp. 303–308. Publications of the Academy of Finland 1, Helsinki.

Lieffers, V.J. (1988) Sphagnum and cellulose decomposition in drained and natural areas of an Alberta peatland. *Canadian Journal of Soil Science*, **68**, 755–761.

Lukkala, O.J. (1929) Über den Aziditätsgrad der Moore und die Wirkung der Entwässerung auf denselben. *Communicationes ex Instituto Quaestionum Forestalium Finlandiae*, **13**, 1–24.

Lukkala, O.J. (1949) Soiden turvekerroksen painuminen ojituksen vaikutuksesta (Referat: Über die Setzung des Moortorfes als Folge der Entwässerung). *Communicationes Instituti Forestalis Fenniae*, **37**, 1–67.

Malmer, N. (1992) Peat accumulation and the global carbon cycle. *Catena Supplement*, **22**, 97–110.

Moore, D.M. (1982) *Flora Europaea Check-list and Chromosome Index.* Cambridge University Press, Cambridge.

Paavilainen, E. (1967) Männyn juuriston suhteesta turpeen ilmatilaan (Summary: Relationships between the root system of Scots pine and the air content of peat). *Communicationes Instituti Forestalis Fenniae*, **63**(6), 1–21.

Päivänen, J. & Seppälä, K. (1968) Hajalannoituksen vaikutus lyhytkortisen nevan pintakasvillisuuteen (Summary: Effect of broadcast fertilizer on the ground vegetation of a low sedge swamp). *Suo*, **19**, 51–56.

Pakarinen, P. & Ruuhijärvi, R. (1978) Ordination of northern Finnish peatland vegetation with factor analysis and reciprocal averaging. *Annales Botanici Fennici*, **15**, 147–157.

Pienimäki, T. (1982) Kasvillisuuden ojituksenjälkeinen kehitys eräillä suotyypeillä Pohjois-Pohjanmaalla (Summary: Development of vegetation on some drained mire site types in North-Ostrobothnia). *Suo*, **33**, 113–123.

Puustjärvi, V. (1970) Degree of decomposition. *Peat & Plant News,* **3**, 48–52.

Reinikainen, A., Vasander, H. & Lindholm, T. (1984) Plant biomass and primary production of southern boreal mire-ecosystems in Finland. *Proceedings of the 7th International Peat Congress Dublin, Ireland* 4, pp. 1–20. Irish National Peat Committee, Dublin.

Ruuhijärvi, R. (1960) Über die regionale Einteilung der nordfinnischen Moore. *Annales Botanici Societatis 'Vanamo'*, **31**, 1–360, Vanamo, Helsinki

Ruuhijärvi, R. (1982) Mire complex types in Finland. *Peatlands and their Utilization in Finland* (ed. J. Laine), pp. 24–28. Finnish Peatland Society, Helsinki.

Ruuhijärvi, R. (1983) The Finnish mire types and their distribution. *Ecosystems of the World. 4 B. Mires: Swamp, Bog, Fen and Moor. Regional studies* (ed. A.J.P. Gore), pp. 47–67. Elsevier, Amsterdam.

Sarasto, J. (1961) Über die Klassifizierung der für Walderziehung entwässerten Moore. *Acta Forestalia Fennica*, **74**(5), 1–57.

Seppälä, K. (1969) Kuusen ja männyn kasvun kehitys ojitetuilla turvemailla (Summary: Post-drainage growth rate of Norway spruce and Scots pine on peat). *Acta Forestalia Fennica*, **93**, 1–89.

ter Braak, C.J.F. (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology*, **67**, 1167–1179.

ter Braak, C.J.F. (1987) *CANOCO – a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal component analysis and redundancy analysis (version 2.0).* TNO Institute of Applied Computer Science, Wageningen.

ter Braak, C.J.F. (1988) CANOCO: an extension of DECORANA to analyze species – environment relationships. *Vegetatio*, **75**, 159–160.

ter Braak, C.J.F. (1990) *Update notes: CANOCO version 3.10.* Agricultural Mathematics Group, Wageningen.

Tolonen, K., Vasander, H., Damman, A.W.H. & Clymo, R.S. (1992) Preliminary estimate of long-term carbon accumulation and loss in 25 boreal peatlands. *Suo*, **43**, 277–280.

Tolonen, K., Turunen, J., Vasander, H. & Jungner, H. (1994). Rate of carbon accumulation in boreal mires. *The Finnish Research Programme on Climate Change. Second Progress Report* (eds M. Kanninen & P. Heikinheimo), pp. 297–302. Publications of the Academy of Finland 1, Helsinki.

Tolvanen, A. (1994) Differences in recovery between a deciduous and an evergreen Ericaceous clonal dwarf shrub after simulated above-ground herbivory and below-ground damage. *Canadian Journal of Botany*, **72**, 853–859.

Vasander, H. (1982) Plant biomass and production in virgin, drained and fertilized sites in a raised bog in southern Finland. *Annales Botanici Fennici*, **19**, 103–125.

Vasander, H. (1984) Effect of forest amelioration on diversity in an ombrotophic bog. *Annales Botanici Fennici*, **21**, 7–15.

Vasander, H. (1987) Diversity of understorey biomass in virgin and in drained and fertilized southern boreal mires in eastern Fennoskandia. *Annales Botanici Fennici*, **24**, 137–153.

Vasander, H., Kuusipalo, J. & Lindholm, T. (1993) Vegetation changes after drainage and fertilization in pine mires. *Suo*, **44**, 1–9.

Westman, C.J. (1981) Fertility of surface peat in relation to the site type and potential stand growth. *Acta Forestalia Fennica*, **172**, 1–77.

Whittaker, R.H. (1972) Evolution and measurement of species diversity. *Taxon*, **21**, 213–251.

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Appendix

The median cover and frequency of the plant species in this study. The sites have been divided into four drainage-age groups (years since drainage). See Table 1 for site type abbreviations and names.

	RhSR			
	Years since drainage			
	Undrained $n = 1$	1-20 $n = 4$	21-40 $n = 7$	41-55 $n = 3$
Alnus incana	– (–)	+ (1)	– (–)	– (–)
Betula pubescens	– (–)	3 (4)	1 (6)	2 (3)
Frangula alnus	1 (1)	+ (1)	+ (2)	– (–)
Juniperus communis	– (–)	+ (1)	+ (1)	– (–)
Picea abies	1 (1)	24 (4)	4 (7)	4 (3)
Pinus sylvestris	1 (1)	1 (3)	+ (3)	– (–)
Salix. caprea	– (–)	+ (1)	– (–)	– (–)
S. cinerea	– (–)	+ (1)	+ (3)	+ (1)
S. myrtilloides	1 (–)	– (–)	+ (1)	– (–)
S. phylicifolia	8 (–)	1 (2)	+ (1)	– (–)
S. repens	– (–)	+ (1)	– (–)	– (–)
Sorbus aucuparia	– (–)	1 (2)	+ (3)	1 (3)
Andromeda polifolia	1 (1)	2 (4)	1 (5)	1 (2)
Betula nana	2 (1)	– (–)	– (–)	4 (3)
Empetrum nigrum	1 (1)	+ (1)	1 (5)	4 (3)
Ledum palustre	1 (1)	1 (2)	+ (2)	1 (2)
Vaccinium myrtillus	– (–)	1 (3)	1 (6)	8 (3)
V. oxycoccos	2 (1)	3 (4)	1 (6)	1 (2)
V. uliginosum	2 (1)	2 (4)	1 (5)	1 (3)
V. vitis-idaea	1 (1)	1 (3)	2 (6)	16 (3)
Carex canescens	– (–)	– (–)	+ (1)	– (–)
C. cespitosa	– (–)	1 (2)	+ (3)	– (–)
C. chordorrhiza	2 (1)	+ (1)	+ (2)	– (–)
C. dioica	– (–)	– (–)	+ (1)	– (–)
C. echinata	1 (1)	+ (1)	+ (3)	– (–)
C. globularis	– (–)	– (–)	+ (1)	– (–)
C. lasiocarpa	16 (1)	1 (2)	+ (3)	– (–)
C. magellanica	1 (1)	1 (2)	1 (4)	+ (1)
C. nigra	– (–)	– (–)	+ (2)	+ (1)
C. pauciflora	– (–)	+ (1)	+ (3)	– (–)
C. rostrata	32 (1)	1 (2)	+ (5)	– (–)
C. vaginata	– (–)	– (–)	– (–)	+ (1)
Agrostis canina	– (–)	1 (3)	+ (1)	– (–)
A. stolonifera	1 (1)	– (–)	– (–)	– (–)
Calamagrostis purpurea	1 (1)	+ (3)	+ (4)	– (3)
Deschampsia cespitosa	– (–)	+ (1)	+ (1)	– (–)
D. flexuosa	– (–)	+ (1)	+ (1)	– (–)
Eriophorum angustifolium	– (–)	1 (2)	1 (5)	– (–)
E. vaginatum	– (–)	3 (4)	1 (6)	8 (3)
Milium effusum	– (–)	+ (1)	– (–)	1 (2)
Molinia coerulea	– (–)	+ (1)	– (–)	– (–)
Trichophorum alpinum	– (–)	+ (1)	– (–)	– (–)
Cirsium palustre	– (–)	1 (2)	– (–)	– (–)
Corallorhiza trifida	– (–)	+ (1)	– (–)	– (–)
Dactylorhiza incarnata	1 (1)	– (–)	– (–)	– (–)
D. maculata	– (–)	1 (2)	+ (2)	– (–)
Drosera rotundifolia	1 (1)	– (–)	+ (1)	– (–)
Dryopteris carthusiana	– (–)	1 (2)	1 (5)	2 (3)
Epilobium angustifolium	– (–)	– (–)	+ (1)	1 (2)
Equisetum fluviatile	2 (1)	1 (2)	+ (2)	– (–)
Galeopsis speciosa	– (–)	+ (1)	– (–)	– (–)
Galium palustre	– (–)	+ (1)	– (–)	– (–)
Goodyera repens	– (–)	– (–)	+ (2)	– (–)
Luzula pilosa	– (–)	+ (1)	+ (2)	– (–)
Lycopodium annotinum	– (–)	– (–)	+ (1)	– (–)
L. clavatum	– (–)	– (–)	+ (1)	+ (1)
Lysimachia thyrsiflora	– (–)	+ (1)	– (–)	– (–)
L. vulgaris	– (–)	+ (1)	– (–)	– (–)
Melampyrum pratense	– (–)	1 (2)	1 (6)	– (–)

Appendix (*Continued*)

	RhSR			
	Years since drainage			
	Undrained *n* = 1	1–20 *n* = 4	21–40 *n* = 7	41–55 *n* = 3
Melampyrum sylvaticum	– (–)	– (–)	+ (1)	– (–)
Menyanthes trifoliata	8 (1)	1 (3)	+ (2)	– (–)
Moneses uniflora	– (–)	+ (1)	– (–)	– (–)
Peucedanum palustre	– (–)	+ (1)	– (–)	– (–)
Potentilla erecta	– (–)	1 (2)	+ (1)	– (–)
P. palustris	2 (1)	2 (3)	1 (4)	– (–)
Pyrola rotundifolia	– (–)	– (–)	+ (1)	– (–)
Rubus arcticus	– (–)	+ (1)	– (–)	– (–)
R. chamaemorus	– (–)	– (–)	+ (2)	1 (3)
R. idaeus	– (–)	– (–)	– (–)	1 (3)
Rumex acetosella	– (–)	+ (1)	– (–)	+ (1)
Scutellaria galericulata	– (–)	+ (1)	– (–)	– (–)
Solidago virgaurea	– (–)	+ (1)	+ (1)	– (–)
Trientalis europaea	– (–)	1 (2)	1 (6)	2 (3)
Viola palustris	– (–)	2 (3)	+ (1)	– (–)
Sphagnum centrale	1 (1)	– (–)	– (–)	– (–)
S. compactum	– (–)	+ (1)	– (–)	– (–)
S. fuscum	– (–)	+ (1)	+ (1)	+ (1)
S. girgensohnii	– (–)	– (–)	+ (1)	– (–)
S. magellanicum	4 (1)	5 (4)	4 (6)	1 (3)
S. nemoreum	– (–)	+ (1)	+ (1)	– (–)
S. papillosum	1 (1)	+ (1)	– (–)	– (–)
S. recurvum complex	64 (1)	5 (4)	1 (5)	4 (2)
S. russowii	– (–)	1 (2)	2 (4)	+ (1)
S. subsecundum	1 (1)	1 (2)	– (–)	– (–)
S. teres	1 (1)	– (–)	– (–)	– (–)
S. warnstorfii	– (–)	1 (2)	– (–)	– (–)
S. wulfianum	1 (1)	– (–)	– (–)	– (–)
Aulacomnium palustre	1 (1)	1 (4)	+ (3)	– (–)
Brachythecium complex	– (–)	1 (2)	1 (4)	+ (1)
Dicranum majus	– (–)	+ (1)	– (–)	– (–)
D. polysetum	– (–)	1 (4)	2 (7)	8 (3)
D. scoparium	– (–)	1 (2)	+ (3)	– (–)
Hylocomium splendens	1 (1)	+ (1)	1 (5)	1 (2)
Plagiothecium complex	– (–)	+ (1)	– (–)	– (–)
Pleurozium schreberi	1 (1)	2 (3)	4 (7)	32 (3)
Pohlia nutans	– (–)	1 (2)	– (–)	– (–)
Polytrichum commune	1 (1)	1 (2)	1 (5)	+ (1)
P. juniperinum	– (–)	– (–)	+ (1)	– (–)
P. strictum	1 (1)	2 (4)	1 (5)	+ (1)
Cladina arbuscula	– (–)	– (–)	+ (1)	– (–)
C. rangiferina	– (–)	1 (3)	+ (1)	– (–)
C. stellaris	– (–)	+ (1)	– (–)	– (–)
Cladonia spp.	– (–)	1 (2)	+ (6)	– (3)

	VSR			
	Undrained *n* = 2	1–20 *n* = 10	21–40 *n* = 7	41–55 *n* = 11
Betula pendula	– (–)	– (–)	– (–)	+ (1)
B. pubescens	1 (2)	1 (10)	1 (7)	1 (10)
Frangula alnus	– (–)	+ (1)	+ (1)	– (–)
Picea abies	1 (1)	2 (10)	2 (6)	1 (10)
Pinus sylvestris	3 (2)	1 (8)	+ (2)	+ (4)
Salix aurita	– (–)	+ (1)	– (–)	– (–)
S. cinerea	– (–)	+ (2)	+ (3)	– (–)
S. myrtilloides	1 (1)	+ (3)	+ (1)	– (–)
S. phylicifolia	– (–)	+ (1)	+ (1)	– (–)
S. repens	– (–)	– (–)	+ (1)	– (–)
Sorbus aucuparia	1 (1)	+ (2)	+ (2)	+ (1)

Appendix (*Continued*)

	VSR			
	Undrained *n* = 1	1–20 *n* = 4	21–40 *n* = 7	41–55 *n* = 3
Andromeda polifolia	2 (2)	1 (9)	1 (5)	1 (6)
Betula nana	17 (2)	6 (7)	+ (2)	+ (5)
Calluna vulgaris	1 (1)	+ (2)	– (–)	+ (1)
Empetrum nigrum	2 (2)	2 (7)	1 (4)	1 (6)
Ledum palustre	– (–)	2 (7)	+ (3)	2 (10)
Rubus idaeus	– (–)	– (–)	– (–)	+ (1)
Vaccinium microcarpum	1 (2)	+ (3)	– (–)	– (–)
V. myrtillus	– (–)	1 (6)	1 (4)	8 (11)
V. oxycoccos	2 (2)	2 (10)	2 (6)	1 (6)
V. uliginosum	1 (2)	4 (9)	+ (3)	1 (9)
V. vitis-idaea	– (–)	3 (7)	2 (7)	4 (11)
Carex cespitosa	– (–)	+ (4)	+ (1)	+ (1)
C. chordorrhiza	1 (1)	+ (1)	– (–)	– (–)
C. echinata	– (–)	– (–)	+ (1)	+ (1)
C. globularis	– (–)	+ (2)	– (–)	+ (5)
C. lasiocarpa	24 (2)	+ (4)	+ (2)	+ (1)
C. magellanica	– (–)	+ (2)	+ (3)	+ (2)
C. nigra	– (–)	+ (1)	– (–)	– (–)
C. pauciflora	1 (1)	+ (3)	+ (3)	+ (2)
C. rostrata	4 (1)	+ (4)	+ (2)	+ (1)
Calamagrostis canescens	1 (1)	– (–)	– (–)	+ (1)
C. purpurea	– (–)	+ (1)	+ (1)	+ (1)
Deschampsia cespitosa	– (–)	– (–)	+ (2)	– (–)
D. flexuosa	– (–)	+ (1)	– (–)	– (–)
Eriophorum angustifolium	1 (1)	+ (1)	+ (1)	+ (2)
E. vaginatum	5 (2)	4 (9)	8 (6)	3 (11)
Juncus filiformis	– (–)	– (–)	– (–)	+ (1)
Milium effusum	– (–)	+ (1)	– (–)	– (–)
Scheuchzeria palustris	1 (1)	– (–)	– (–)	– (–)
Trichophorum cespitosum	1 (1)	+ (1)	– (–)	+ (1)
Dactylorhiza maculata	– (–)	+ (2)	+ (3)	– (–)
Drosera rotundifolia	1 (2)	+ (1)	+ (1)	– (–)
Dryopteris carthusiana	– (–)	+ (2)	+ (2)	+ (2)
Epilobium angustifolium	– (–)	– (–)	– (–)	+ (1)
Equisetum fluviatile	– (–)	+ (2)	– (–)	+ (1)
E. sylvaticum	– (–)	– (–)	– (–)	+ (1)
Goodyera repens	– (–)	– (–)	– (–)	+ (1)
Luzula pilosa	– (–)	+ (2)	+ (1)	– (–)
Lycopodium annotinum	– (–)	– (–)	– (–)	+ (1)
Melampyrum pratense	– (–)	1 (6)	1 (5)	+ (5)
Menyanthes trifoliata	– (–)	+ (2)	+ (2)	– (–)
Potentilla palustris	1 (1)	– (–)	– (–)	– (–)
Rubus chamaemorus	4 (1)	1 (6)	+ (2)	1 (7)
Solidago virgaurea	– (–)	– (–)	+ (1)	– (–)
Trientalis europaea	1 (1)	– (–)	+ (2)	+ (2)
Viola palustris	– (–)	– (–)	+ (1)	– (–)
Sphagnum balticum	16 (1)	+ (1)	– (–)	– (–)
S. fuscum	8 (1)	1 (5)	+ (3)	+ (2)
S. girgensohnii	– (–)	– (–)	– (–)	+ (1)
S. jensenii	1 (1)	– (–)	– (–)	– (–)
S. magellanicum	24 (2)	1 (9)	2 (7)	2 (11)
S. nemoreum	– (–)	+ (2)	+ (1)	– (–)
S. papillosum	1 (1)	– (–)	– (–)	– (–)
S. recurvum complex	18 (2)	48 (10)	4 (7)	4 (10)
S. riparium	– (–)	+ (1)	– (–)	– (–)
S. rubellum	– (–)	+ (1)	– (–)	– (–)
S. russowii	1 (1)	+ (4)	1 (4)	1 (9)
Aulacomnium palustre	1 (1)	1 (7)	1 (5)	+ (4)
Brachythecium complex	– (–)	+ (1)	– (–)	+ (1)
Calliergon stramineum	1 (1)	– (–)	– (–)	– (–)
Dicranum majus	– (–)	– (–)	+ (1)	– (–)
D. polysetum	– (–)	1 (5)	1 (6)	2 (11)

Appendix (*Continued*)

	VSR			
	Years since drainage			
	Undrained *n* = 1	1-20 *n* = 4	21-40 *n* = 7	41-55 *n* = 3
Dicranum scoparium	– (–)	– (–)	– (–)	+ (4)
D. undulatum	– (–)	+ (1)	– (–)	– (–)
Hepatica spp.	– (–)	+ (2)	+ (1)	– (–)
Hylocomium splendens	– (–)	+ (1)	+ (3)	+ (4)
Plagiothecium complex	– (–)	+ (1)	– (–)	– (–)
Pleurozium schreberi	– (–)	4 (9)	32 (7)	32 (11)
Pohlia nutans	1 (1)	+ (3)	– (–)	+ (1)
Polytrichum commune	– (–)	+ (2)	2 (4)	+ (5)
P. strictum	3 (2)	2 (9)	1 (7)	1 (10)
Cladina arbuscula	1 (1)	+ (4)	+ (1)	+ (2)
C. rangiferina	1 (1)	1 (5)	+ (2)	1 (7)
C. stellaris	1 (1)	– (–)	+ (1)	– (–)
Cladonia spp.	– (–)	+ (3)	– (–)	+ (3)

	TSR			
	Undrained *n* = 3	1–20 *n* = 4	21–40 *n* = 3	41–55 *n* = 8
Betula pendula	– (–)	– (–)	– (–)	+ (1)
B. pubescens	+ (1)	+ (1)	1 (2)	1 (8)
Picea abies	1 (3)	1 (2)	1 (3)	1 (7)
Pinus sylvestris	2 (3)	1 (4)	1 (3)	+ (2)
Salix myrtilloides	– (–)	+ (1)	– (–)	– (–)
Sorbus aucuparia	– (–)	– (–)	– (–)	+ (1)
Andromeda polifolia	2 (3)	2 (4)	2 (3)	1 (8)
Betula nana	2 (3)	18 (4)	16 (3)	5 (6)
Calluna vulgaris	– (–)	– (–)	– (–)	+ (1)
Empetrum nigrum	16 (2)	4 (3)	8 (3)	1 (7)
Ledum palustre	1 (2)	1 (2)	2 (2)	16 (8)
Vaccinium microcarpum	1 (2)	– (–)	– (–)	+ (1)
V. myrtillus	+ (1)	+ (1)	1 (3)	3 (8)
V. oxycoccos	1 (3)	2 (4)	2 (3)	1 (7)
V. uliginosum	1 (3)	9 (4)	1 (3)	2 (7)
V. vitis–idaea	– (–)	+ (1)	2 (3)	5 (7)
Carex lasiocarpa	1 (2)	1 (2)	+ (1)	– (–)
C. magellanica	– (–)	1 (2)	+ (1)	+ (1)
C. pauciflora	4 (3)	1 (2)	– (–)	+ (1)
C. rostrata	2 (3)	+ (1)	– (–)	+ (1)
Eriophorum vaginatum	35 (3)	16 (4)	8 (3)	3 (8)
Scheuchzeria palustris	+ (1)	– (–)	– (–)	– (–)
Drosera rotundifolia	1 (3)	+ (1)	– (–)	– (–)
Dryopteris carthusiana	– (–)	+ (1)	– (–)	+ (2)
Epilobium angustifolium	– (–)	– (–)	– (–)	+ (1)
Melampyrum pratense	– (–)	– (–)	1 (2)	+ (1)
Menyanthes trifoliata	+ (1)	– (–)	– (–)	– (–)
Rubus chamaemorus	2 (3)	1 (3)	4 (3)	1 (4)
Trientalis europaea	– (–)	– (–)	– (–)	+ (1)
Sphagnum balticum	4 (2)	+ (1)	– (–)	– (–)
S. fuscum	8 (3)	3 (4)	+ (1)	+ (1)
S. magellanicum	8 (3)	1 (4)	2 (3)	4 (8)
S. majus	+ (1)	– (–)	– (–)	– (–)
S. nemoreum	– (–)	– (–)	+ (1)	+ (3)
S. recurvum complex	32 (3)	64 (4)	32 (3)	8 (8)
S. rubellum	– (–)	+ (1)	+ (1)	+ (1)
S. russowii	– (–)	– (–)	+ (1)	1 (5)
Aulacomnium palustre	1 (2)	1 (4)	+ (1)	+ (3)
Brachythecium complex	– (–)	– (–)	– (–)	+ (1)
Dicranum polysetum	– (–)	1 (3)	1 (3)	1 (7)
D. scoparium	– (–)	– (–)	– (–)	+ (1)

Appendix (*Continued*)

	LkR + LTR			
	Years since drainage			
	Undrained *n* = 1	1–20 *n* = 4	21–40 *n* = 7	41–55 *n* = 3
Dicranum undulatum	+ (1)	– (–)	– (–)	– (–)
Hepatica spp.	– (–)	+ (1)	– (–)	– (–)
Pleurozium schreberi	1 (2)	3 (4)	32 (3)	24 (8)
Pohlia nutans	+ (1)	+ (1)	– (–)	– (–)
Polytrichum commune	– (–)	– (–)	– (–)	+ (3)
P. strictum	1 (3)	4 (3)	1 (3)	1 (8)
Cladina arbuscula	+ (1)	1 (3)	1 (2)	+ (3)
C. rangiferina	– (–)	1 (4)	1 (2)	1 (7)
C. stellaris	– (–)	– (–)	– (–)	+ (2)
Cladonia spp.	+ (1)	1 (2)	1 (2)	– (–)

	LkR + TR			
	Undrained *n* = 3	1–20 *n* = 7	21–40 *n* = 5	41–55 *n* = 4
Betula pubescens	+ (1)	1 (6)	1 (5)	1 (4)
Picea abies	+ (1)	1 (4)	1 (4)	1 (4)
Pinus sylvestris	1 (3)	1 (7)	1 (5)	1 (2)
Sorbus aucuparia	– (–)	– (–)	– (–)	+ (1)
Andromeda polifolia	1 (3)	1 (7)	1 (5)	1 (4)
Betula nana	2 (3)	4 (6)	4 (5)	6 (4)
Calluna vulgaris	– (–)	+ (3)	+ (2)	– (–)
Empetrum nigrum	4 (3)	8 (7)	4 (5)	6 (4)
Ledum palustre	1 (3)	1 (6)	2 (5)	9 (3)
Vaccinium microcarpum	– (–)	1 (4)	1 (3)	+ (1)
V. myrtillus	1 (2)	+ (2)	1 (4)	3 (4)
V. oxycoccos	– (–)	1 (7)	1 (4)	2 (4)
V. uliginosum	2 (3)	2 (6)	4 (5)	5 (4)
V. vitis–idaea	1 (2)	1 (5)	1 (4)	5 (4)
Carex cespitosa	– (–)	+ (1)	– (–)	– (–)
C. globularis	– (–)	+ (1)	– (–)	1 (2)
C. magellanica	– (–)	– (–)	+ (2)	– (–)
C. pauciflora	– (–)	– (–)	+ (1)	– (–)
Eriophorum vaginatum	8 (3)	16 (7)	8 (5)	6 (4)
Drosera rotundifolia	– (–)	– (–)	+ (1)	– (–)
Dryopteris carthusiana	– (–)	– (–)	+ (1)	– (–)
Epilobium angustifolium	– (–)	+ (1)	+ (1)	– (–)
Melampyrum pratense	– (–)	– (–)	– (–)	+ (1)
Rubus chamaemorus	2 (3)	2 (6)	4 (5)	6 (4)
Trientalis europaea	– (–)	– (–)	– (–)	+ (1)
Sphagnum balticum	+ (1)	+ (1)	– (–)	– (–)
S. fuscum	16 (3)	8 (6)	4 (5)	+ (1)
S. magellanicum	1 (2)	1 (6)	+ (2)	5 (4)
S. nemoreum	– (–)	+ (1)	1 (3)	– (–)
S. recurvum complex	64 (3)	32 (7)	4 (5)	40 (4)
S. rubellum	– (–)	+ (2)	+ (2)	– (–)
S. russowii	+ (1)	– (–)	+ (1)	+ (1)
Aulacomnium palustre	+ (1)	1 (7)	1 (4)	1 (2)
Dicranum polysetum	– (–)	+ (2)	1 (4)	3 (4)
D. scoparium	– (–)	+ (1)	+ (1)	– (–)
D. undulatum	– (–)	+ (1)	– (–)	– (–)
Hepatica spp.	– (–)	– (–)	+ (1)	– (–)
Pleurozium schreberi	1 (3)	8 (7)	32 (5)	40 (4)
Pohlia nutans	– (–)	+ (2)	+ (1)	+ (1)
Polytrichum strictum	1 (3)	4 (7)	1 (4)	1 (3)
Cladina arbuscula	+ (1)	1 (4)	1 (5)	1 (2)
C. rangiferina	+ (1)	1 (5)	1 (4)	1 (2)
C. stellaris	+ (1)	+ (1)	+ (1)	– (–)
Cladonia spp.	– (–)	+ (3)	1 (3)	+ (1)