Multidimensional Site Description of Peatlands Drained for Forestry

Juha-Pekka Hotanen

Hotanen, J.-P. 2003. Multidimensional site description of peatlands drained for forestry. Silva Fennica 37(1): 55–93.

Sites (n = 119) on drained mires located in the southern aapa mire zone in Finland were analysed by multivariate techniques. The compositional trends of the understorey vegetation were analysed by means of hybrid multidimensional scaling (HMDS). In addition to field classification, two-way indicator species analysis (TWINSPAN) and flexible unweighted paired group arithmetic average (FUPGMA) classifications were used.

The 1st HMDS dimension primarily reflected variation along a gradient from spruce mire influence to hummock-level bog influence. Variation in nutrient status was also connected to this gradient. Factors underlying the 2nd dimension were variation in nutrient status and drainage succession (moisture). Some sample plots representing herb-rich or *Molinia*-rich types were separated along the 3rd dimension. The variation in understorey vegetation (i.e. the ordination space) showed high maximum correlation with stand volume r = 0.81, mean annual stand volume increment r = 0.76, and post-drainage dominant height r = 0.75. The covariation between the vegetation and peat bulk density in both the 0–10 and 10–20 cm peat layers was also strong: r = 0.55 and r = 0.80. The correlations for $H_{v.Post}$ were 0.64 and 0.81, respectively. Of the total macronutrient concentrations, phosphorus (r = 0.73, r = 0.75) and nitrogen (r = 0.59, r = 0.64) were the most strongly correlated with species composition. The environmental sample variables were also presented by the vegetation units of numerical classification. Most of the recorded variables, including nutrient amounts (kg ha^{-1}), were examined in site quality (fertility) classes by succession phases as well. Border variants or transitional forms of the site types were common. Additional vegetation criteria (e.g. surface-water influence) more closely defined the ecology of the site. In addition to the site quality classes, a considerable amount of information about the tree stands, vegetation diversity and peat properties was associated with the separation of the succession phases, i.e. in this study transforming (phase II) vs. transformed (final phase III) sites. In conclusion, the actual vegetation appeared to well reflect various aspects of the ecological conditions, even in labile communities of commercial forests on drained peatlands.

Keywords classification, diversity, macronutrients, ordination, peat properties, site index, vegetation

Author´s address Finnish Forest Research Institute, Joensuu Research Centre, P.O.Box 68, FIN-80101 Joensuu, Finland
Fax 013-2514567 **E-mail** juha-pekka.hotanen@metla.fi

Received 19 April 2002 **Accepted** 20 November 2002

1 Introduction

In Finland, the underlying principles used in the classification of drained mires originate from Cajander's (1911, 1913, 1949) doctrine. As a result, the classification has primarily been based on the understorey vegetation (Keltikangas 1945 and references therein, Lukkala and Kotilainen 1951, Huikari 1952, Sarasto 1961a,b, Huikari et al. 1964, Heikurainen 1986, Laine and Vasander 1990). The post-drainage succession, initiated by the lowering of the water level, has been divided into three phases (Sarasto 1961a,b, Heikurainen and Pakarinen 1982). The classification of recently drained mires and transforming drained mires (phases I and II; Finnish abbreviations oj and mu, respectively) is based on the original mire site types. The relatively stable climax plant communities that develop on older drainage areas are traditionally classified into four (to six) transformed site types (phase III; tkg; Lukkala and Kotilainen 1951, Sarasto 1961a,b, Huikari et al. 1964, Heikurainen and Pakarinen 1982). About 60% of the ca 5 million ha of peatland that have been drained for forestry in Finland represent the second phase, and 27% represent the third phase (Metsätilastollinen vuosikirja 2001, cf. Hökkä et al. 2002).

Determination of the original mire site types on drained peatlands is regarded as problematic, especially in the later phases of secondary succession (Laine 1989, Hotanen and Nousiainen 1990). The borders between the successional phases are diffuse (Pienimäki 1982, Reinikainen 1988, Laine 1989, Saarinen and Hotanen 2000). According to Laine (1989), the classification system could be made more operational by allocating the drained mire sites already in the successional phases to the corresponding drained peatland forest site types. Seven peatland forest site types have been distinguished by Laine, and adopted for use by e.g. Laine and Vasander (1990) and Paavilainen and Päivänen (1995).

The post-drainage succession of many mire site types is still insufficiently known, especially in the aapa mire zone (Pienimäki 1982, Pakarinen 1994, Hotanen et al. 1999). Moreover, a large number of factors can cause variation in the drained mire vegetation and, subsequently, make the prediction of the correct transformed type more difficult: fertilization (e.g. Päivänen and Seppälä 1968, Vasander et al. 1988, Silfverberg and Hotanen 1989, Finér and Brække 1991); tree stand properties such as development class, density, species and former fellings (Reinikainen 1984a, Laine and Vanha-Majamaa 1992, Laine et al. 1995); regressive secondary succession (Kuusipalo and Vuorinen 1981); stratification of the surface peat (Laine 1989); variation and change in climatic conditions as well as prolonged mineralization of the peat (Melin 1917, Keltikangas 1945, Neshatayev 1989); and atmospheric deposition (Silfverberg 1991).

The drainage of pristine mires ceased in Finland during the late 1990's and the ditched area is no longer increasing. As a result, we have to deal with vegetation that has been affected by drainage for an ever-increasing period of time, and which displays additional variation in the peatland environment – caused by the above-mentioned factors. Considering the great variation in the ecological conditions on drained peatlands derived from the numerous mire site types, and additional variation in different climatic areas and variation in silvicultural history, it is clear that our current knowledge of drained mire vegetation and its relation to different external factors is insufficient.

The site classification used in forestry is primarily based on determination of the potential capacity of the site to produce stemwood (Huikari 1952, Heikurainen 1973, 1979). Information about the different factors affecting stand yield capacity is also required – especially from the peatland classification (Reinikainen 1983, 1984a, 1989). This is related to the fact that the variation on peatlands occurs along a larger number of ecological gradients than that in mineral soil forests, and therefore a large set of control measures of the growth factors are needed.

The increasing importance of forest planning has resulted in a need to improve the integration of peatland classification with growth and yield models (e.g. Gustavsen et al. 1998, Hökkä and Penttilä 1999). Developing a system that describes site quality by means of continuous variables instead of categorical ones would permit more efficient use of site quality in growth modelling (Ojansuu 1996, Hökkä 1997, Hökkä and Penttilä 1999). However, the use of site index methods on peatlands is problematic because a wide range of labile variables affect the state of the generally uneven-aged and heterogeneous tree stand (cf. Penttilä 1984, Gustavsen 1996, Hökkä and Penttilä 1999). Determination of the taxatorical importance of different site and vegetation classes requires further examination (Laine and Starr 1979, Hökkä 1994, Gustavsen et al. 1998).

The development of multivariate methods has enabled effective analysis of compositional (vegetational) and ecological gradients in connection with more detailed analyses of the relationships between vegetation and environmental factors on drained mires (e.g. Mannerkoski 1979, Westman 1987, Reinikainen 1988, Nieminen and Pätilä 1990, Laine and Vanha-Majamaa 1992, Eurola et al. 1995, Laine et al. 1995, Vasander et al. 1997, Hotanen et al. 1999). The vegetation gradients are also important from the point of view of the mire site typology used in forestry, because they are connected to the site productivity (Heikurainen 1979, Reinikainen 1989).

Among the factors determining vegetation-based peatland site type classification, the nutrient reserves in the substrate are crucial for peatland forestry (Kaunisto and Paavilainen 1988, Paavilainen and Päivänen 1995). The possibility of using peat and nutrient variables in the classification of drained mires has been discussed (e.g. Vahtera 1955, Kaunisto 1983, Westman 1987, Kaunisto and Paavilainen 1988, Laiho 1994). However, more surveys of the nutrient status and reserves of drainage areas of varying age, different mire site type and phytogeographical region are needed before a consistent classification of this kind is available (Kaunisto and Paavilainen 1988, Laiho and Laine 1994, Westman 1994). As a basis for this, there is an urgent need for confirmation of the ecological background for the classification (Reinikainen 1988, Laine and Vanha-Majamaa 1992).

The aim of this study is to describe the site in a multi-dimensional manner, i.e. 1) to analyse the main compositional gradients, 2) to elucidate the relationships between the vegetation and environment, 3) to classify the sites in different ways, 4) to examine the variation in both vegetation and environmental sample variables between (and within) vegetation units in a systematic sample taken from a random area entity, and 5) to compile additional information on the average nutrient reserves in the surface peat in drained peatland forests in eastern Finland. This study, primarily an explorative one, is also intended as an ecological background analysis for follow-up studies.

2 Material and Methods

2.1 Study Area and Sampling

The study area, comprising the former Nurmes and Lieksa forestry management districts of the Forest and Park Service, lies in the south-eastern part of the southern aapa mire zone in Finland (Fig. 1). The mean altitude in the area is about 180 m a.s.l. (Sevola 1983), annual mean precipitation 550–600 mm, length of the thermal growing period 145–150 days, and effective temperature sum about 1000–1100 d.d. (threshold +5 °C)

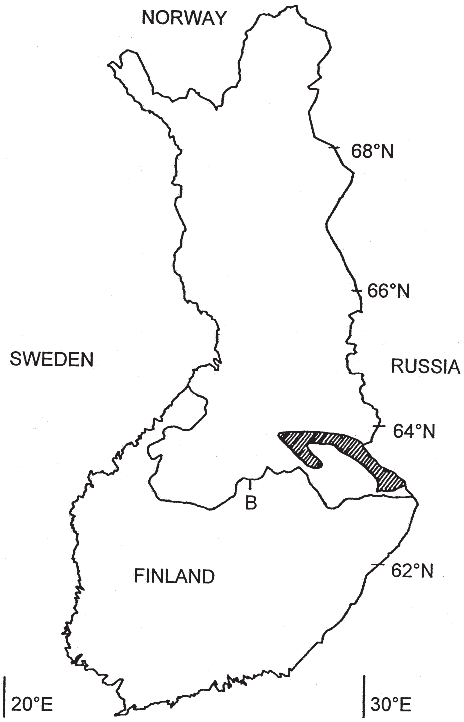


Fig. 1. Location of the study area and the border (B) between eccentric bogs and the southern aapa mire zone (Atlas of Finland 1988).

Table 1. Parameters for the drained mire sites. For the site types, see Fig. 3. Site quality class: II = herb-rich, III = *V. myrtillus* and tall-sedge, IV = *V. vitis-idaea* and small-sedge, V = cottongrass and dwarf-shrub, VI = *S. fuscum* mires. Peat type: S = *Sphagnum*, C = *Carex*, L = woody. Tree species %: Psy = *Pinus sylvestris*, Pab = *Picea abies*, dec = deciduous trees.

Sample plot no.	Site type	TWINSPAN group	FUPGMA group	Site quality class	Peat type		Tree-species dominance % (V)			Drainage year	Fertilization
					0–10	10–20cm	Psy	Pab	dec		
2901	RamTRmu	1	7	V	S	S	97	0	3	1967	
2902	RamTRmu	1	7	V	S	S	96	0	3	1967	
3232	RamTRmu	1	7	V	S	S	100	0	0	1970, -87	1972 (PKCa)
3233	RamTRmu	1	7	V	S	S	100	0	0	1970, -87	1972 (PKCa)
2903	RamTRmu	1	7	V	S	S	100	0	0	1967	
3292	RamTRmur	1	7	V	S	S	100	0	0	1965, -83	1974 (NP)
3293	RamTRmur	1	7	V	S	S	100	0	0	1965, -83	1974 (NP)
3181	TRmu	1	4	V	S	S	100	0	0	1967 ?	1980 (NPK)
3392	RamTRmu	1	7	V	S	S	100	0	0	1972, -83	1973 (K), -74 (Ca)
2913	TRmu	1	4	V	S	S	96	4	0	1968, -84	1983 (NPK)
3393	Vatkg	1	4	V	LS	S	100	0	0	1972, -83	1973 (K), -74 (Ca)
3402	Vatkg	1	4	V	LS	S	100	0	0	1958	
3261	RiVSRmu	2	7	IV	CS	SC	100	0	0	1972, -86	
3401	TSRmu	2	7	IV	CS	CS	100	0	0	1958	
2911	TRmu	2	7	V	S	S	100	0	0	1968, -84	1983 (NPK)
2912	TRmu	2	7	V	S	S	99	0	1	1968, -84	1983 (NPK)
3003	TRmu	2	1	V	S	S	100	0	0	1965	1968 (N), -90 (NPK)
3121	TRmu	2	7	V	S	S	100	0	0	1971 ?	1972 (PK), -74 (N)
3122	TRmu	2	7	V	S	S	100	0	0	1971 ?	1972 (PK), -74 (N)
3123	RamTRmu	2	7	V	S	S	100	0	0	1971 ?	1972 (PK), -74 (N)
3192	TRmu	2	7	V	S	S	100	0	0	1957, -80	
3202	RamTRmur	2	7	V	S	S	82	0	18	1966 ?	1967 (PK), -82 (NPK)
3203	TRmur	2	7	V	S	S	100	0	0	1966 ?	1967 (PK), -82 (NPK)
3251	TRmur+	2	7	V	S	S	100	0	0	1967 ?	1969 (NP)
3252	RaRmur	2	7	VI	S	S	100	0	0	1967 ?	1969 (NP)
3253	RamTmur	2	7	V	S	S	100	0	0	1967 ?	1969 (NP)
3291	TRmur	2	7	V	S	S	100	0	0	1965, -83	1974 (NP)
3193	LiRiTSRmu	2	7	IV	LCS	CS	95	0	5	1957, -80	
2853	PsRmu-	3	1	IV	LS	CS	100	0	0	1969, -84	1983 (NPK)
2871	PtkgI	3	4	IV	CLS	LCS	99	1	0	1959	
2873	PtkgI	3	4	IV	CLS	CS	94	5	0	1959	
2891	Vatkg+	3	4	V	S	S	93	7	0	1972	1973 (PK)
2892	Vatkg+	3	4	V	S	S	92	8	0	1972	1973 (PK)
2893	Vatkg+	3	4	V	LS	S	100	0	0	1972	1973 (PK)
2952	Vatkg	3	4	V	S	S	100	0	0	1970, -82	1971 (PK), -87 (NPK)
2953	Vatkg	3	4	V	S	S	99	1	0	1970, -82	1971 (PK), -87 (NPK)
2981	PtkgI	3	4	IV	LS	CLS	100	0	0	?	
3182	Vatkg	3	4	V	S	S	100	0	0	1967 ?	1980 (NPK)
3183	Vatkg+	3	4	V	LS	S	99	1	0	1967 ?	1980 (NPK)
3231	Vatkg	3	4	V	S	LS	100	0	0	1970, -87	1972 (PKCa)
3391	Vatkg	3	4	V	LS	LS	100	0	0	1972, -83	1973 (K), -74 (Ca)
2872	PtkgI	3	4	IV	LS		90	7	3	1959	
2951	PtkgI	3	4	IV	LS	CS	99	1	0	1970, -82	1971 (PK), -87 (NPK)
2982	KgRmu	3	1	IV	LS	CLS	89	10	1	?	
2983	PtkgI+	3	4	IV	LS	CLS	97	0	3	?	
3041	KRmu	3	1	IV	LS	LS	92	0	7	1975	1980 (PK)
3042	PtkgI+	3	3	IV	LS		96	3	0	1975	1980 (PK)
3043	PtkgI+	3	1	IV	LS		76	4	20	1975	1980 (PK)
3081	PtkgII	3	1	IV	LS	SC	91	0	9	1968, -80	1970 (PK), -83 (NPK)
3082	PtkgII	3	1	IV	LS	SC	83	1	16	1968, -80	1970 (PK), -83 (NPK)
3083	PtkgII	3	1	IV	LS	SC	78	0	22	1968, -80	1970 (PK), -83 (NPK)
3162	KRmu	3	1	IV	LS	LS	53	37	10	1975	?
3163	PKmu	3	1	IV	LS	LS	24	47	29	1975	?
3191	PtkgI	3	4	IV	LCS	LSC	99	0	1	1957, -80	
3242	PtkgII	3	4	IV	LS	CS	100	0	0	1968	
3243	PtkgII	3	1	IV	LS	CS	89	0	11	1968	
3262	KRmu	3	1	IV	LS	CLS	63	31	6	1972, -86	
3263	KRmu	3	1	IV	LS	LCS	63	30	6	1972, -86	
3273	PtkgI	3	4	IV			100	0	0	1964, -82	1971 (K), -73 (Ca)
3403	KRmu	3	1	IV	CLS	CLS	100	0	0	1958	

3421	KRmu	3	1	IV	CSL		13	87	0	1977	
3422	KRmu	3	1	IV	CSL	LC	45	55	0	1977	
3423	KRmu	3	1	IV	CSL	LC	12	88	0	1977	
3441	PtkgI	3	4	IV	CLS		92	2	6	1966, -86	
3442	PtkgI	3	4	IV	SLC	LSC	91	2	7	1966, -86	
3443	PtkgI+	3	4	IV	CSL	CSL	96	4	1	1966, -86	

2852	PsRmu	4	1	IV	CLS	CS	100	0	0	1969, -84	1983 (NPK)
2881	KRmu-	4	1	IV	LS	LS	100	0	0	1966, -80	1968 (PK), -83 (NPK)
2882	KRmu-	4	1	IV	LS	LS	100	0	0	1966, -80	1968 (PK), -83 (NPK)
2883	KRmu-	4	1	IV	LS	LS	100	0	0	1966, -80	1968 (PK), -83 (NPK)
2941	KgRmu	4	1	IV	LS		93	0	7	1979	1966 (PK), -82 (NPK)
2943	KgRmu	4	1	IV	LS		100	0	0	1979	1966 (PK), -82 (NPK)
3001	KgRmu	4	1	IV	LS	LS	91	9	0	1965	1968 (N), -90 (NPK)
3032	KgRmu	4	4	IV	LS		100	0	0	1972	1974 (PK), -89 (NPK)
3033	KgRmu	4	4	IV	LS		100	0	0	1972	1974 (PK), -89 (NPK)
3091	KgRmu	4	1	IV	LS	SL	98	2	0	1952	1967 (PK), -88 (NPK)
3092	PsRmur	4	1	IV	LS	CLS	96	0	4	1952	1967 (PK), -88 (NPK)
3271	PtkgI	4	1	IV	LS		88	2	10	1964, -82	1971 (K), -73 (Ca)
3272	KgRmu	4	1	IV	LS		94	0	6	1964, -82	1971 (K), -73 (Ca)
2851	PsRmu	4	1	IV	CS	CS	92	0	8	1969, -84	1983 (NPK)
2991	PsRmur	4	2	IV	CS	CS	100	0	0	1966, -85	1968 (PK), -83 (NPK)
2992	PsRmur	4	7	IV	S	CS	99	0	1	1966, -85	1968 (PK), -83 (NPK)
2993	PsRmur	4	2	IV	CS	SC	97	2	1	1966, -85	1968 (PK), -83 (NPK)
3002	TRmu+	4	1	V	S	S	94	0	6	1965	1968 (N), -90 (NPK)
3031	KgRmu	4	1	IV	LS		100	0	0	1972	1974 (PK), -89 (NPK)
3093	PsRmur	4	2	IV	LS	CLS	99	0	1	1952	1967 (PK), -88 (NPK)
3113	KRmur	4	1	IV	LS	LS	93	3	4	1979	1989 (NPK)
3201	KRmu-	4	1	IV	CS	CS	88	0	12	1966 ?	1967 (PK, -82 (NPK)
3481	KRmu	4	1	IV	CLS	SCL	82	4	14	1966	1982 (NPK)

2832	MolKnVSRmu	5	2	IV	LSC	SC	80	7	14	1954, -68	1975 (PK)
3483	LuKnVSRmur	5	2	III	LCS	SLC	84	3	13	1966	1982 (NPK)
2833	MolKnPtkgII	5	2	IV	LSC	SC	67	2	30	1954, -68	1975 (PK)
3482	KnLuRhSRmur	5	2	II	LSC	SLC	83	3	13	1966	1982 (NPK)

3241	MtkgII	6	3	III	CLS	LCS	77	1	22	1968	
2942	KgRmu	6	1	IV	LS		81	5	14	1979	1966 (PK), -82 (NPK)
3461	PtkgI+	6	3	IV	LS	LCS	93	6	1	?	1986 (NPK)
3462	PtkgI+	6	3	IV	LS		88	5	7	?	1986 (NPK)
3463	PtkgI+	6	3	IV	LS		93	1	6	?	1986 (NPK)
2831	PKmu	6	1	IV	LS	S	60	26	14	1954, -68	1975 (PK)
3111	PKmu	6	1	IV	LS	SL	64	25	11	1979	1989 (NPK)
3112	PKmur	6	1	IV	LS	CLS	83	6	11	1979	1989 (NPK)
3372	MtkgIr	6	1	III	SL	LC	25	59	17	1970, -81	1974 (NP)

2922	MtkgI	7	3	III	SL	SL	44	50	6	1968 ?	1967 (PK), -83 (NPK)
3052	MtkgI	7	3	III	SL	CSL	0	100	0	1969, -78	1972 (PK)
2921	MtkgI	7	3	III	SL	SL	32	68	0	1968 ?	1967 (PK), -83 (NPK)
2923	MtkgI	7	3	III	SL	SL	0	98	2	1968 ?	1967 (PK), -83 (NPK)
3161	MtkgI	7	3	III	LS	SL	3	81	16	1975	?
3491	MtkgI	7	3	III	SL	SL	17	79	3	1963	1975 (PK)
3492	MtkgI	7	3	III	SL	SL	31	52	17	1963	1975 (PK)
3493	MtkgI	7	3	III	SL		0	92	8	1963	1975 (PK)

3371	MtkgIr	8	5	III	SL	SLC	19	53	28	1970, -81	1974 (NP)
3373	LuMtkgIr	8	5	III	CSL	SLC	48	15	37	1970, -81	1974 (NP)
2841	MkKmur	8	5	III	CSL	CSL	1	34	66	1957	1967 (PK), -79 (NPK)
2842	MkKmur	8	5	III	CSL	CSL	0	62	38	1957	1967 (PK), -79 (NPK)
2843	LuMkKmur	8	5	III	CSL		9	13	78	1957	1967 (PK), -79 (NPK)
3053	LuMkKmu	8	5	III	CSL	CSL	0	72	27	1969, -78	1972 (PK)
3171	RhKmu	8	5	II	CL	CL	49	27	24	1967 ?	1968 (PK), -80 (NPK)

3172	RhKmu	9	6	II	SLC	LC	39	19	43	1967 ?	1968 (PK), -80 (NPK)
3173	Rhtkg-	9	6	II	CL	CL	0	58	42	1967 ?	1968 (PK), -80 (NPK)

(Atlas of Finland 1987). The sites within the area are mainly relatively poor peat (and till) soils (Atlas of Finland 1990, Hotanen and Nousiainen 1990).

The permanent sample plots of the study (n = 119) were located in 40 systematically distributed units (tracts) of the 7th National Forest Inventory (Valtakunnan metsien... 1977, Sevola 1983). The distance between individual tracts was 4 km, and between individual plots (three in each tract) was 40 m. The first three numbers in the plot code refer to tract (Table 1). The plots were established in 1981 according to the guidelines of Gustavsen et al. (1988). In 1991 the plots were linked to the SINKA system (Permanent Forest Inventory Growth plots for peatlands; Penttilä and Honkanen 1986). The size of the circular plots was adjusted according to the stand density in order to have at least (about) 35 trees on each plot.

The successional phases were classified in the field according to Sarasto (1961a,b) and Heikurainen and Pakarinen (1982). In 1991, all the plots represented either transforming (phase II; mu) or transformed drained mires (phase III; tkg). If regressive development had occurred in the succession, this was expressed using the symbol r (mur, tkgr; Table 1). The original mire site type in the mu phase was determined according to Laine and Vasander (1990). The tkg phases were allocated to drained peatland forest site types in accordance with Laine and Vasander (1990). Border variants or transitional types (more fertile + / infertile –) of the site types were identified on the basis of the site fertility characteristics of the vegetation. The additional qualifiers, Kn = spruce mire influence, Lu = surface-water influence, Mol = abundant occurrence of *Molinia caerulea*, Ram = rahka-hummocky (less than 75% coverage of *Sphagnum fuscum*), and Ri = flark-rich (Huikari 1952, Huikari et al. 1964, Eurola et al. 1984), were used to describe the site in more detail (Table 1). Furthermore, the site quality class (Huikari et al. 1964, Huikari 1974) of the plots was determined according to the actual vegetation.

Information about ditching and fertilization was obtained from the Nurmes and Lieksa offices of the Forest and Park Service. The (improvement) ditching and fertilization years of some of the plots were uncertain and labelled with question marks (Table 1).

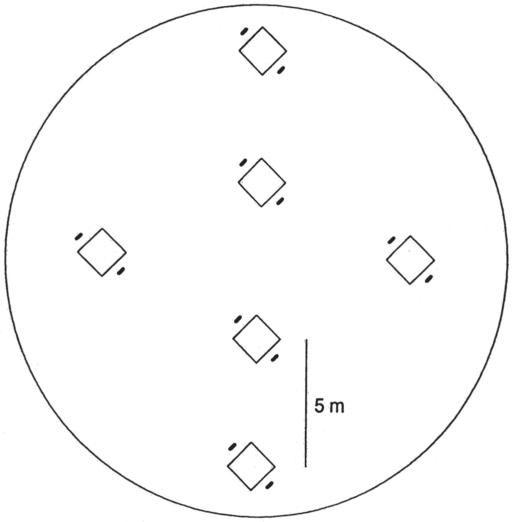


Fig. 2. Location of the vegetation quadrats and the peat sampling points on the sample plots.

2.2 Vegetation Analysis

The vegetation descriptions were made in June–August, 1991. The coverage of the field and bottom layer species was estimated in six quadrats (2 m^2) located systematically on the plots (Fig. 2) using the scale 0.1, 0.2, 0.5, 1, 2, 3, 5, 7, 10, 15, 20, 25...90, 93, 95, 97, 98, 99 and 100%. If an obstacle (stump, large tree, ditch, ditch spoil) occurred in a quadrat, the quadrat was moved to the nearest normal mire surface and a note of this made on the cover drawing of the plot. Shrubs and tree seedlings less than 0.5 m high were included in the field layer. Other shrubs and tree seedlings up to 1.5 m high (genuine shrub species without an upper limit) were included in the shrub layer and estimated for the whole sample plot. Plotwise mean coverages of the individual plant species were calculated. If a species occurred in both the field and shrub layer, the two coverage values were summed. The nomenclature follows Hämet-Ahti et al. (1998) for vascular plants, Eurola et al. (1994) for bryophytes, and Vitikainen et al. (1997) for lichens.

2.3 Recording of Environmental Variables

The tree stands on the plots were measured in 1981, 1986 and 1991 according to the guidelines of Gustavsen et al. (1988) and Penttilä and Honkanen (1986). The basic stand characteristics were calculated using the KPL programme package (Heinonen 1994). A site index, H40dr (Gustavsen 1996), was also calculated. H40dr is the post-drainage dominant height value 40 years after drainage. The post-drainage dominant height is defined as the difference between the current dominant height and the dominant height at the time of drainage. The latter was estimated using Equation 4 of Gustavsen (1996).

The peat depth was measured down to a maximum depth of 1.5 m at a point next to each vegetation quadrat. The mean value was calculated for the plot. Peat was systematically sampled from twelve points adjacent to each vegetation quadrat (Fig. 2), using an auger with cutting edge 4.0 × 6.2 cm. Separate samples were collected for the 0–10 and 10–20 cm depth intervals; the latter omitted if the peat was less than 20 cm thick. If a loose raw humus layer, consisting of litter and especially *Pleurozium schreberi*, was present on the peat surface, it was removed before measuring and sampling the peat layers (Kaunisto and Paavilainen 1988). The sub-samples from the twelve points were combined by layers and kept frozen until analysis.

The peat type was determined macroscopically from the thawed peat samples (Laine and Vasander 1986) (Table 1). The humification degree was assessed by the method of von Post (1922). These determinations were made by the author on anonymised samples and controlled by a second person.

The peat samples were dried at 40 °C to constant weight and weighed. pH was determined from a soil-water suspension (1:2 volume ratio). The peat samples were then dried at 105 °C for dry mass determination and weighed for bulk density calculation. Total nitrogen was analyzed by the Kjeldahl method, and phosphorus spectrophotometrically after dry digestion (550 °C) and extraction with HCl (Halonen et al. 1983). The concentrations of the other macronutrients were determined by inductively couple plasma atomic emission spectrometry (ICP/AES) after wet digestion with HNO_3/H_2O_2. The quality of the analyses was checked by performing parallel determinations on a subset of the samples. The nutrient stores (kg ha^{-1}) were calculated for the 0–10 and 10–20 cm peat layers.

2.4 Data Analysis

The compositional gradients of the vegetation were identified by hybrid multidimensional scaling (HMDS) using DECODA software (version 2.04; Minchin 1991). HMDS was applied to a matrix of the Bray-Curtis coefficient (Faith et al. 1987). This matrix of dissimilarities between sample plots was calculated from $\log_{10}$ transformed abundance values of the species. Default options were used throughout. Thus, the dissimilarity threshold for hybrid scaling was 0.8. In HMDS ordination, solutions of 1–4 dimensions were calculated and ten starting configurations were used in each number of dimensions. The HMDS dimensions were scaled to half-change units. All possible pairs of ordination configurations in the same number of dimensions were compared using the method of Procrustean analysis (Schönemann and Carrol 1970).

In HMDS, three dimensions were needed for proper interpretation of the variation in vegetation. The minimum stress values were 1D = 0.272, 2D = 0.149, 3D = 0.109 (4D = 0.091). The minimum stress was effectively achieved from all 10 starts in the three-dimensional solution. In Procrustean analysis these 10 minimum stress configurations were all identical. Interpretation was determined to this solution.

In DECODA, vector fitting option was applied. This option calculates, for each variable in the second set, a vector or direction through the configuration, along which the scores of the sites (or species) have maximum correlation with that variable (Minchin 1991). Vector fitting allows the identification of variables which display significant monotonic trends across an ordination. A Monte Carlo approach (in DECODA) was used to test the significance of the maximum correlation for environmental variables through the configuration.

TWINSPAN (two-way indicator species analysis; Hill 1979) and FUPGMA (flexible unweighted paired group arithmetic average; Belbin 1994) classifications were carried out on the material. Octave scaling was used as the abundance threshold values of pseudo-species in TWINSPAN (e.g. van der Maarel 1979). Four maximum levels of division were applied, and default options were used in all other cases. The recommended Bray-Curtis coefficient was used as association measure in FUPGMA (Belbin 1994). All species were included in the numerical analyses.

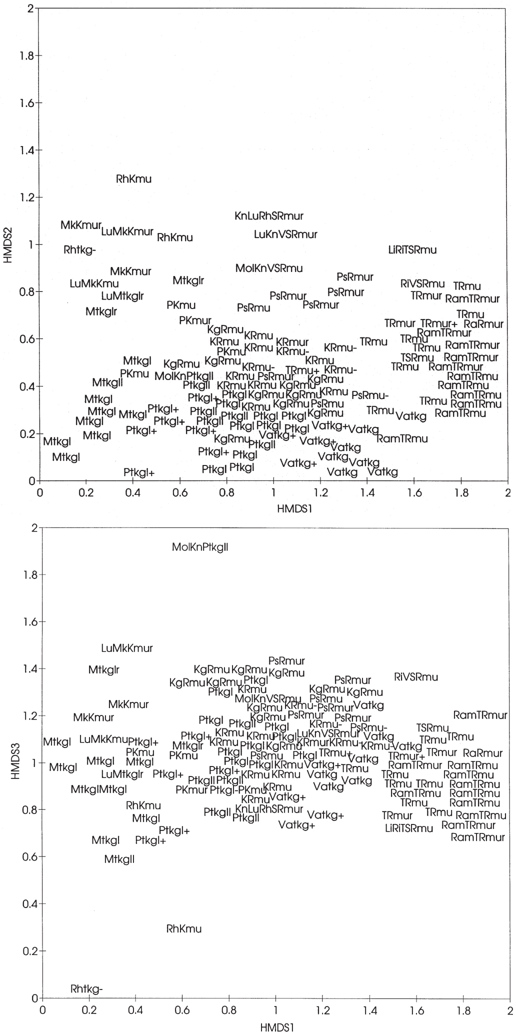
The number of species (species richness), and Shannon's (H') and Pielou's (J') diversity indices (Pielou 1966, Peet 1974) were calculated for the individual plots in order to describe different features of the alpha diversity. H' contains elements both of species richness and evenness, and J' is actually H' based evenness. One-way analysis of variance (ONEWAY) was performed to investigate the variation of the environmental sample variables between numerical vegetation units. Two-way analysis (MANOVA) was applied to test the variables between site quality classes by succession phases (SPSS-X User's Guide 1988). Since the dependent variables were characterized by high variation within the groups, and the variances were in general not homogeneous, a $\log_{10}$ transformation was performed (except for pH) prior to the analyses.

3 Results

3.1 Ordination

3.1.1 Major Compositional Gradients

In the 1st dimension the spruce mires were separated from the pine mires; the plots of MkKmu and RhKmu, as well as the transformed sites of spruce mire origin (in this case MtkgI and Rhtkg-), obtained low scores, whereas the plots of ombrotrophic pine bogs, e.g. RamTRmu, obtained high scores along HMDS1 (Fig. 3). The pine mires of spruce mire influence (KgRmu, KRmu, PsRmu) were located in the middle parts of this dimension. Also the fertility series (Mtkg-Ptkg-Vatkg) of transformed sites (except Rhtkg) appeared to run parallel with the 1st axis.



RhK = Herb-rich hardwood-spruce swamp, MkK = *E. sylvaticum* spruce swamp, PK = *V. vitis-idaea* spruce swamp, KR = Spruce-pine swamp, KgR = Paludified pine forest, PsR = *C. globularis* pine swamp, RhSR = Herb-rich sedge birch-pine fen, VSR = Tall-sedge pine fen, TSR = Cottongrass-sedge pine fen, TR = Cottongrass pine bog, RaR = *S. fuscum* pine bog

Rhtkg = Herb-rich transformed type, MtkgI = *V. myrtillus* transformed type I, MtkgII = *V. myrtillus* transformed type II, PtkgI = *V. vitis-idaea* transformed type I, PtkgII = *V. vitis-idaea* transformed type II, Vatkg = Dwarf-shrub transformed type

mu = transforming type, r = regressive development, Kn = spruce mire influence, Lu = surface-water influence, Ram = rahka-hummocky (*S. fuscum*), Mol = abundant occurrence of *Molinia caerulea*, Ri = flark-rich, Li = slightly, +- = border variant of the site type (more fertile/infertile)

Fig. 3. HMDS ordination of the sample plots. Above: Axes 1 and 2. Below: Axes 1 and 3.

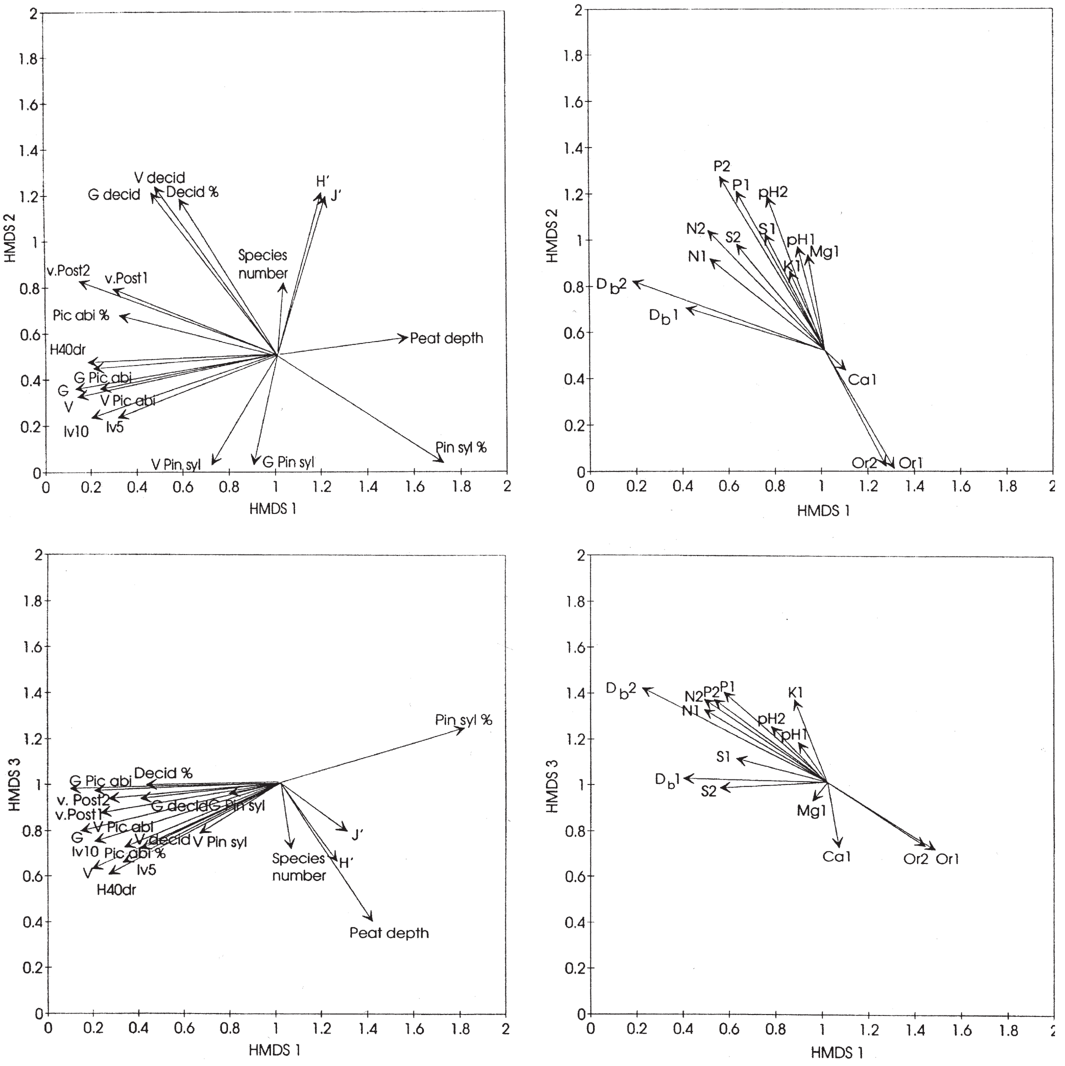


Fig 4. Vectors expressing maximum correlations between the HMDS ordination space and the environmental sample variables. Only significant ($p<0.05$) variables are presented (cf. Table 2). Above: Axes 1 and 2. Below: Axes 1 and 3.

The factors most strongly correlated with the 2nd HMDS dimension were variation in drainage succession phase (moisture) and nutrient status (cf. Fig. 4). For instance, the regressive sample plots (mur, tkgr), and the sample plots of surface-water influence (Lu) and the flark-rich (Ri) plots, were separated on the 2nd axis (Fig. 3).

The RhKmu, Rhtkg- and regressive MkK sites shared a considerable part of the species pool, and were not separated from each other until the 3rd dimension (Fig. 3). On the RhK plots there were also slight fen-like features (of herb-rich sedge hardwood-spruce fen, RhSK), e.g. *Menyanthes trifoliata*, *Potentilla palustris* and *Carex rostrata* (App. 1). One of the plots with an abundant occurrence of *Molinia caerulea* was also discerned along this dimension, but in the opposite direction due to its special species composition.

Table 2. Maximum correlations between the sample variables and the three-dimensional HMDS ordination space. Numbers 1 (0–10 cm) and 2 (10–20 cm) connected with the variable name refer to the peat layer. Nutrients as concentrations (mg g^{-1}) ($p<0.001$ denoted as 0.000).

		n	max r	p
Iv10	mean annual stand volume increment (1981–1991)	115	0.76	0.000
Iv5	mean annual stand volume increment (1986–1991)	115	0.69	0.000
H40dr	post-drainage dominant height (site index)	113	0.75	0.000
G	stand basal area	119	0.80	0.000
V	stand volume	119	0.81	0.000
G Pin syl	basal area of *Pinus sylvestris*	114	0.44	0.000
V Pin syl	volume of *Pinus sylvestris*	114	0.49	0.000
Pin syl %	dominance of *Pinus sylvestris* (V Pin syl/V)	119	0.77	0.000
G Pic abi	basal area of *Picea abies*	60	0.71	0.000
V Pic abi	volume of *Picea abies*	60	0.71	0.000
Pic abi %	dominance of *Picea abies* (V Pic abi/V)	119	0.63	0.000
G decid	basal area of deciduous trees	70	0.76	0.000
V decid	volume of deciduous trees	70	0.79	0.000
Decid %	dominance of deciduous trees (V decid/V)	119	0.71	0.000
Species number		119	0.36	0.000
H’	Shannon’s diversity index	119	0.65	0.000
J’	Pielou’s diversity index	119	0.59	0.000
Adr	drainage age	113	0.23	0.070
Peat depth		119	0.61	0.000
v. Post1	humification degree (von Post H_{1-10})	118	0.64	0.000
v. Post2		101	0.81	0.000
D_b1	bulk density	118	0.55	0.000
D_b2		101	0.80	0.000
Or1	organic matter (%)	118	0.69	0.000
Or2		101	0.61	0.000
pH1		118	0.39	0.000
pH2		101	0.49	0.000
N1		118	0.59	0.000
N2		101	0.64	0.000
P1		118	0.73	0.000
P2		101	0.75	0.000
K1		118	0.44	0.000
K2		96	0.18	0.330
Ca1		118	0.25	0.040
Ca2		101	0.28	0.080
Mg1		118	0.36	0.000
Mg2		101	0.20	0.260
S1		118	0.52	0.000
S2		101	0.51	0.000

3.1.2 Correlation between Vegetation and Sample Variables

The variation in vegetation showed high maximum correlations with the stand characteristics (Table 2). The vectors expressing e.g. stand volume (V), stand basal area (G) and site index (H40dr), mainly ran from pine mires towards spruce mires (Fig. 4). The mean annual stand volume increment for the period 1981–91 (Iv10) showed somewhat higher covariation with the vegetation than the mean increment for the five-year-period before sampling (Iv5). The variables describing the quantity of deciduous trees pointed towards MkK and herb-rich types (cf. Table 1), whereas the dominance of *Pinus sylvestris* increased in almost the opposite direction (Fig. 4).

The alpha diversity variables increased principally along the second gradient (Fig. 4). However, the correlation of the species number within the ordination space was not the same order of magnitude as the correlations of H' and J' (Table 2).

Drainage age was weakly correlated with variation in the ordination space, partly because the material only consisted of the transforming (phase II; mu) and transformed sites (final phase III; tkg), and even regressive stages of these forms (Table 2). The peat thickness increased from spruce mires to pine bogs.

The correlations between the vegetation and humification degrees of the peat (particularly of the deeper 10–20 cm peat layer) in terms of the von Post value or bulk density were strong (Table 2). These two measures behaved in almost the same way (Fig. 4); the Pearson correlation coefficients between these two variables were as high as $r = 0.78$, $p < 0.001$ (0–10 cm) and $r = 0.80$, $p < 0.001$ (10–20 cm).

Of the total macronutrient concentrations in the peat (mg g^{-1}), phosphorus (P) was the most strongly correlated with the variation in the vegetation (Table 2). The covariation between vegetation and nitrogen (N) was stronger for the 10–20 cm peat layer than for the 0–10 cm layer. The correlation between pH and the vegetation was not very strong but consistent.

The correlation between the ordination space and the potassium (K) concentration of the deeper peat layer was very weak. In five cases the K concentration of the deeper peat layer was below the analytical determination limit, 0.08 mg g^{-1}. The trend for calcium (Ca) was also weak. The organic matter content (%) of the peat increased in an opposite direction to the most important nutrient vectors.

It appears from the nutrient vectors that both the 1st and 2nd dimensions were connected to fertility. The 3rd compositional dimension was indeterminate in terms of the environmental variables measured. As presented above, however, this dimension arose as a result of distinct variation in vegetation between some of the sample plots.

3.2 Classification

3.2.1 Numerical Units and Site Types

The sample plots classified as the same type in the field were sometimes placed in different clusters by the numerical techniques. Conversely, there was a range of different original mire site types and actual types in the same numerical clusters (Table 1, Figs 5 and 6). Border variants or transitional forms of the site types were common (Table 1, Fig. 3).

TWINSPAN Groups 1 and 2 mainly contained ombrotrophic types of Site quality class V. Three oligotrophic (IV) sample plots of the composite site types with *Sphagnum fuscum* were also included in Group 2 (Table 1, App. 1). Minerotrophic vegetation was only scantily present on these plots. Group 7 in the FUPGMA classification corresponded to TWINSPAN Groups 1 and 2 (Fig. 6). *Picea abies* saplings occurred on almost all of the plots in the present study, however, the lowest number was present in infertile TWINSPAN Groups 1 and 2 (App. 1).

TWINSPAN Groups 3 and 4 mainly contained peatlands of Site quality class IV. In Group 3, however, there were nine plots determined as Vatkg (Class V) in the field (Table 1). Group 3 mainly consisted of transformed (tkg) sites, whereas Group 4 consisted of transforming (mu) sites. Mire species were the most important indicator species for Group 4, separating it from Group 3 (Fig. 5). In the FUPGMA classification, the same plots were found in Groups 1 and 4,

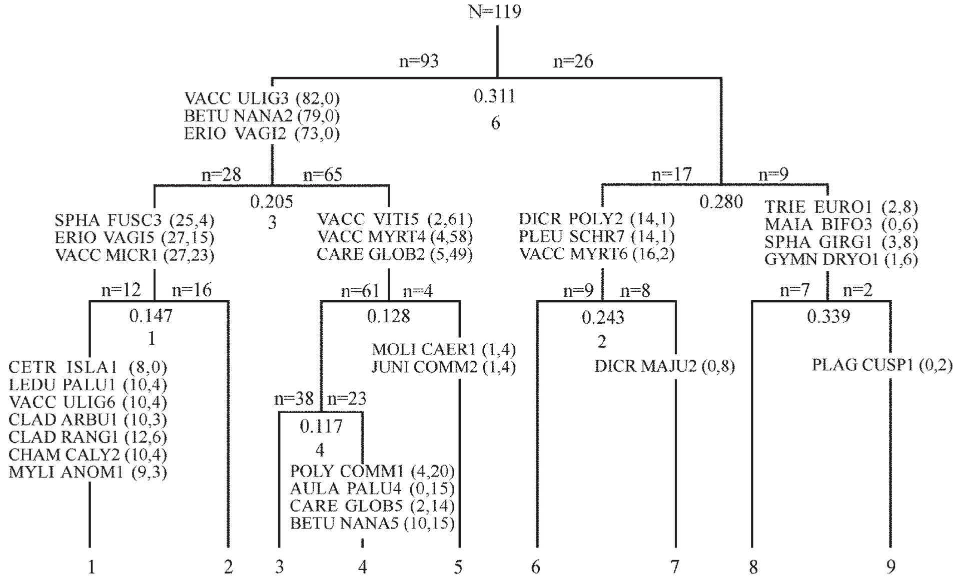


Fig. 5. Divisive hierarchical classification (TWINSPAN) of the drained mire sites (cf. Table 1). The most important indicator species are denoted using abbreviations, e.g. VACC ULIG = *Vaccinium uliginosum* (cf. App. 1). Octave scaling (number after the species abbreviation) was used for the indicator species abundances as follows: 1 = +, 2 = 0.5–1%, 3 = 1–2%, 4 = 2–4%, 5 = 4–8%, 6 = 8–16%, 7 = 16–32%, 8 = 32–64%, 9 > 64%. Numbers in parentheses give the frequencies of the species in the left and and right clusters, respectively. The number of borderline cases is indicated at divisions.

with some exceptions (Fig. 6). The relatively homogeneous FUPGMA Class 4 almost exclusively contained tkg sites, as well as both Vatkg (V) and Ptkg (IV).

It appears from the sorted TWINSPAN table (App. 1) that *S. fuscum* still occurred, although relatively sparsely, on most of the plots classified as Vatkg in Group 3. *Hylocomium splendens* occurred on most of the remaining plots classified as Ptkg (or sites developing most likely into Ptkg). There were also differences in the abundance relationships of some common species, e.g. *Eriophorum vaginatum*, *Cladina arbuscula*, *C. rangiferina*, between the two subroups of Group 3 (App. 1). The differences in the abundances of *Vaccinium myrtillus* and *Carex globularis* were relatively small between these two subgroups.

Sites classified to PtkgII in the field were not distinguished in the numerical analyses from PtkgI, or from the sites most likely developing into PtkgI. The *Carex* peat constituent of the deeper peat layer in the PtkgII plots indicated origin from the minerotrophic composite type. Possibly some other sample plots (e.g. 3442) would have been PtkgII rather than PtkgI on the basis of the composition of their surface peat (Table 1).

Sample plots in TWINSPAN Group 5 were of pine fen (VSR, RhSR) origin with abundant *Molinia* (Mol) or with surface-water influence (Lu) (e.g. *Salix myrtilloides*, *S. phylicifolia*, *Festuca rubra*, *Carex magellanica*) and spruce mire influence (Kn) (e.g. *Juniperus communis*, *Picea abies*, *C. globularis*, *Trientalis europaea*). In FUPGMA the plots were located in Group 2, which also contained three regressive plots of *C. globularis* pine swamp (PsRmur). However, Group 2 seemed to be heterogeneous (Fig. 6).

The sites in TWINSPAN Class 7 represented a more advanced stage in secondary succession than the sites in Class 6. The indicator species separating these groups was *Dicranum majus* with a coverage of >0.5% (Fig. 5). *H. splendens* and *Plagiothecium laetum* were also more abundant in Group 7. Plots in Group 6 were pine-dominated (with one exception), whereas in Group 7 they were spruce-dominated (Table 1). There were also some pine mire dwarf shrubs on the plots in Class 6 (App. 1). The vegetation in Class 6 corresponded to luxuriant Ptkg or poor Mtkg, or to sites that were most likely developing into them. The plots in Group 7 represented typical *V. myrtillus* tkg sites (MtkgI). Thus, there were differences in light conditions, in the hummock-level bog – spruce mire influence and in the moisture conditions between these groups. FUPGMA Group 3, which however contained only tkg sites, mainly corresponded to these groups. The only MtkgII plot in this material was located in TWINSPAN Group 6 (and in FUPGMA 3).

TWINSPAN Groups 8 and 9 (FUPGMA Groups 5 and 6) were fairly luxuriant, with many herb and grass species (App. 1). Most of the plots in TWINSPAN Group 8 were regressive, i.e. re-paludified.

3.2.2 Numerical Units and Sample Variables

TWINSPAN Groups 1 and 2 were characterized by low stand volume increment (Iv10), ranging from 1.8 to 2.1 m^3 ha^{-1} a^{-1} on the average, and consequently a low H40dr of about 11 m (Fig. 7) (cf. also FUPGMA 7). Iv10 varied more clearly than H40dr between TWINSPAN Clusters 3–5. Iv10 was larger in Group 3 than in Groups 4 and 5, which contained transforming and regressive transforming sites. The values of H40dr were relatively equal in TWINSPAN Groups 6 and 7. The variation in Iv10 was considerable in Group 7. Regressive development on most of the plots in Group 8 was reflected e.g. in the site indices (Iv10, H40dr).

The alpha diversity in TWINSPAN Groups 1 and 2, which mainly contained ombrotrophic sites, was moderate (Fig. 8). There were various ecological influences on the sites of TWINSPAN Group 5, which was also reflected as a relatively high number of species. The species number was the highest in herb-rich types of TWINSPAN Group 9.

According to the F-values, H' and J' clearly differed between the FUPGMA classes (Fig. 8). The indices were low, indicating increasing species

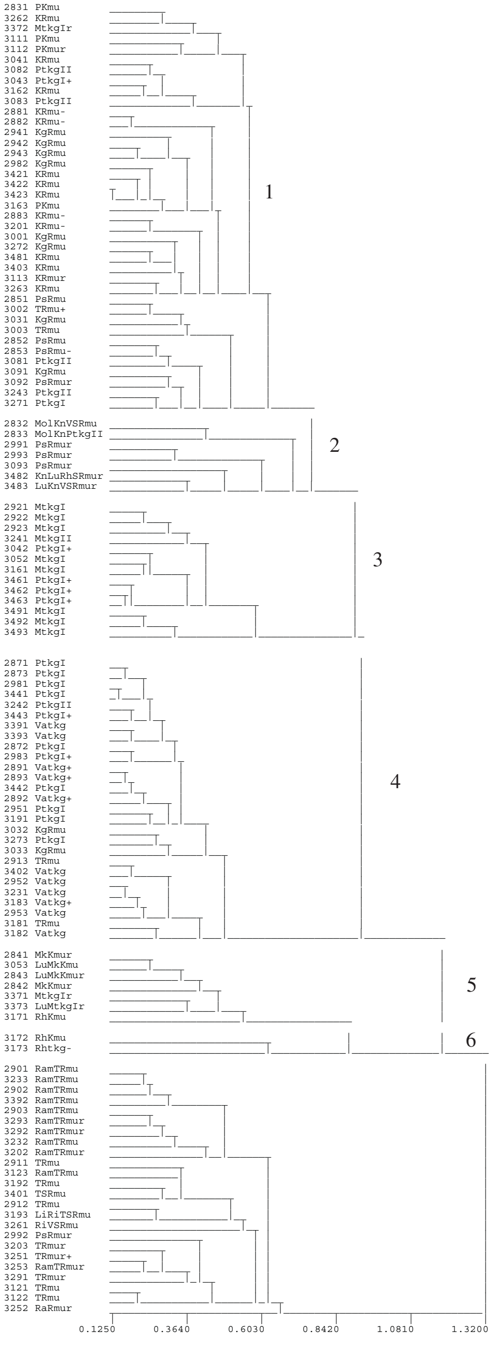


Fig. 6. Agglomerative hierarchical clustering (FUPGMA) of the drained mire sites (cf. Table 1).

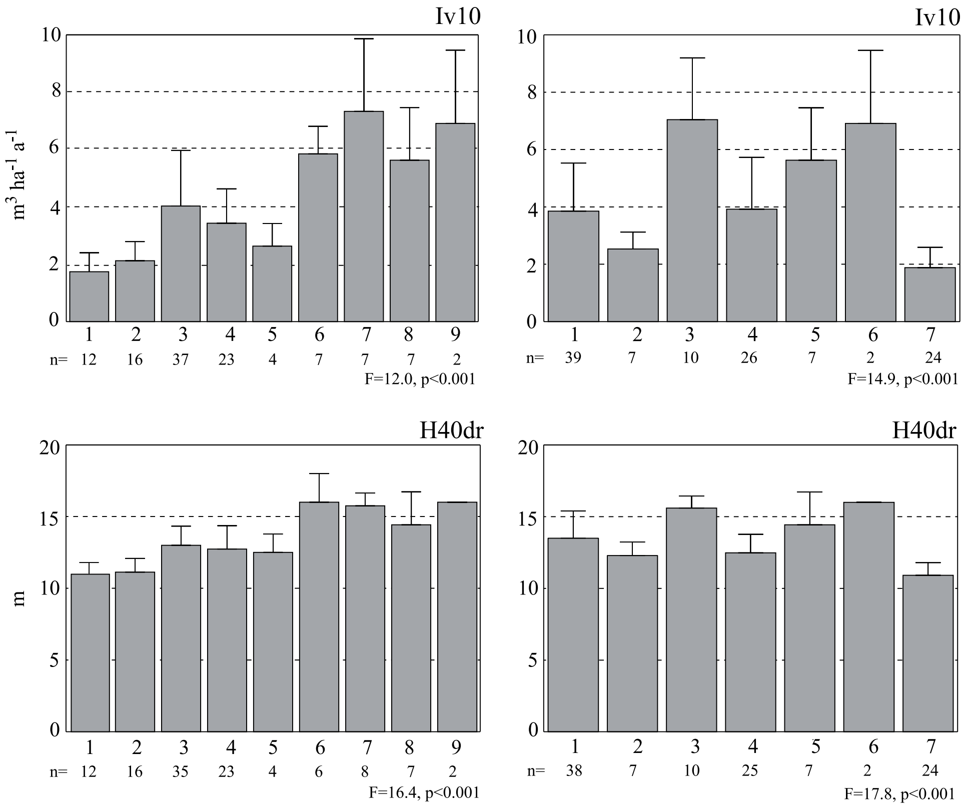


Fig. 7. Mean annual stand volume increment (Iv10) and post-drainage dominant height (H40dr) in TWINSPAN (left) and FUPGMA (right) groups (means, standard deviations). Significance of one-way analysis of variance is shown.

dominance, in Classes 3 and 4, which contained transformed sites.

TWINSPAN Groups 1 and 2 were also characterized by the clearly thickest peat layer, although it was measured down to a maximum depth of 1.5 m (Fig. 9). The humification degree of the peat was low in these Groups 1 and 2.

The organic matter content was low in the surface peat in Group 5 (Fig. 9), which presumably reflected the additions of suspended mineral colloids with moving water. The high bulk density value (and low organic matter content) of the deeper peat layer in TWINSPAN Group 8 most probably indicated the same: there was surface-water influence on many of the plots also in Group 8 (Table 1); as indicated, e.g., by *Salix phylicifolia*, *Calamagrostis purpurea* and *Carex canescens* (App. 1).

Most of the nutrient concentrations were low in TWINSPAN Groups 1 and 2 (Fig. 10). For example, the average N concentration of the surface peat in Group 1 was about 1% (10 mg g^{-1}). The average N concentration was highest in Group 5, where it was as much as 2.54% in the deeper peat layer.

The P and K concentrations of the peat were lower in Group 3 than in Groups 4 and 5. The values of most of the peat and nutrient variables, were relatively equal in TWINSPAN Groups 6 and 7. The P concentration was high in clusters 8 and 9, but e.g. the K concentration varied considerably (Fig. 10).

Degree of humification, pH value and the N and S concentrations were generally higher in the deeper peat layer, whereas the concentrations of P, K, Ca and Mg were usually higher in the surface layer (Figs 9 and 10).

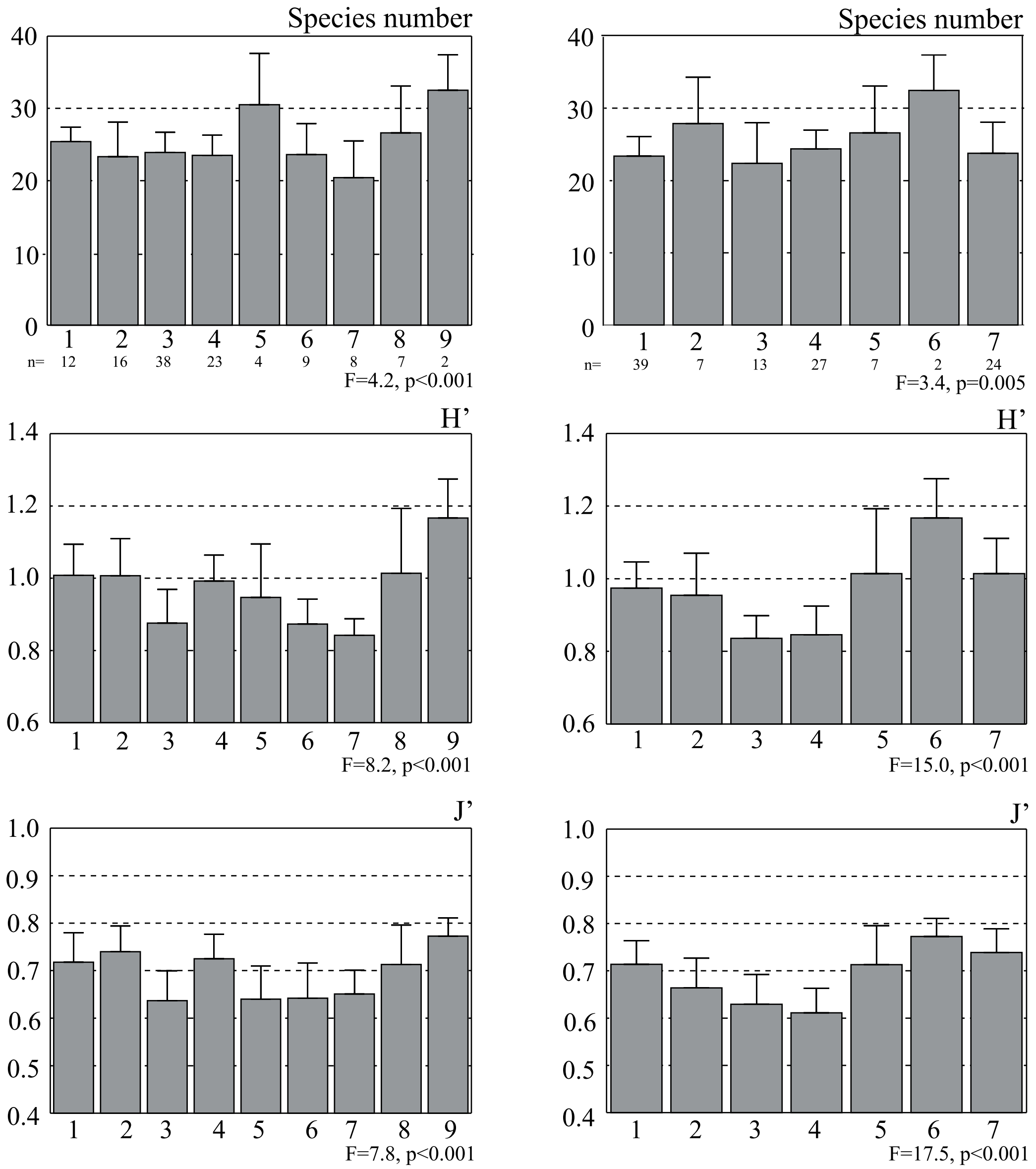


Fig. 8. Species number, Shannon's (H') and Pielou's (J') diversity indices in TWINSPAN (left) and FUPGMA (right) groups (means, standard deviations). Significance of one-way analysis of variance is shown.

3.2.3 Sample Variables by Site Quality Class and Succession Phase

In general, there were clear differences in the average values of the mean annual stand volume increment (Iv10), the post-drainage dominant height (H40dr) and the stand volume (V) between the site quality (fertility) classes. Both Iv10 and H40dr in Classes II and III were relatively close to each other (there were few observations from Class II). The values were higher on transformed (tkg) sites than on transforming (mu) sites (Fig. 11, Table 5).

The alpha diversity was the highest on herb-rich

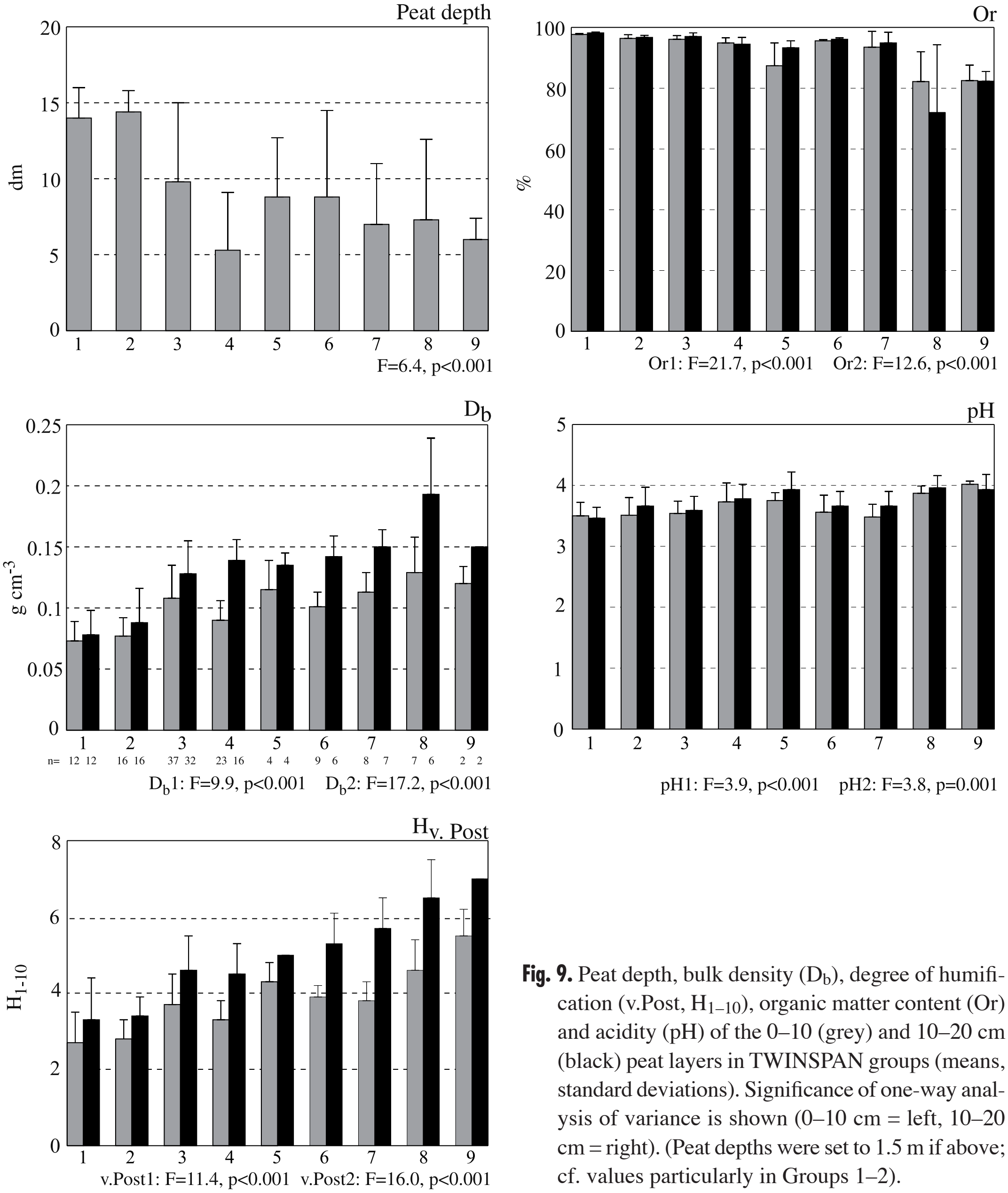


Fig. 9. Peat depth, bulk density (D_b), degree of humification (v.Post, H_{1-10}), organic matter content (Or) and acidity (pH) of the 0–10 (grey) and 10–20 cm (black) peat layers in TWINSPAN groups (means, standard deviations). Significance of one-way analysis of variance is shown (0–10 cm = left, 10–20 cm = right). (Peat depths were set to 1.5 m if above; cf. values particularly in Groups 1–2).

(II) sites while the differences between the other classes were small (Fig. 12). Higher index values were generally observed for the mu sites than for the tkg sites. However, the average number of species on the oligotrophic sites (IV) was almost the same between the succession phases, and at the infertile end (V) the value for the tkg sites even exceeded that of the mu sites.

The clearest differences in the average values of the bulk density and the von Post humification degree with respect to adjacent fertility classes were between the oligotrophic (IV) and ombro-

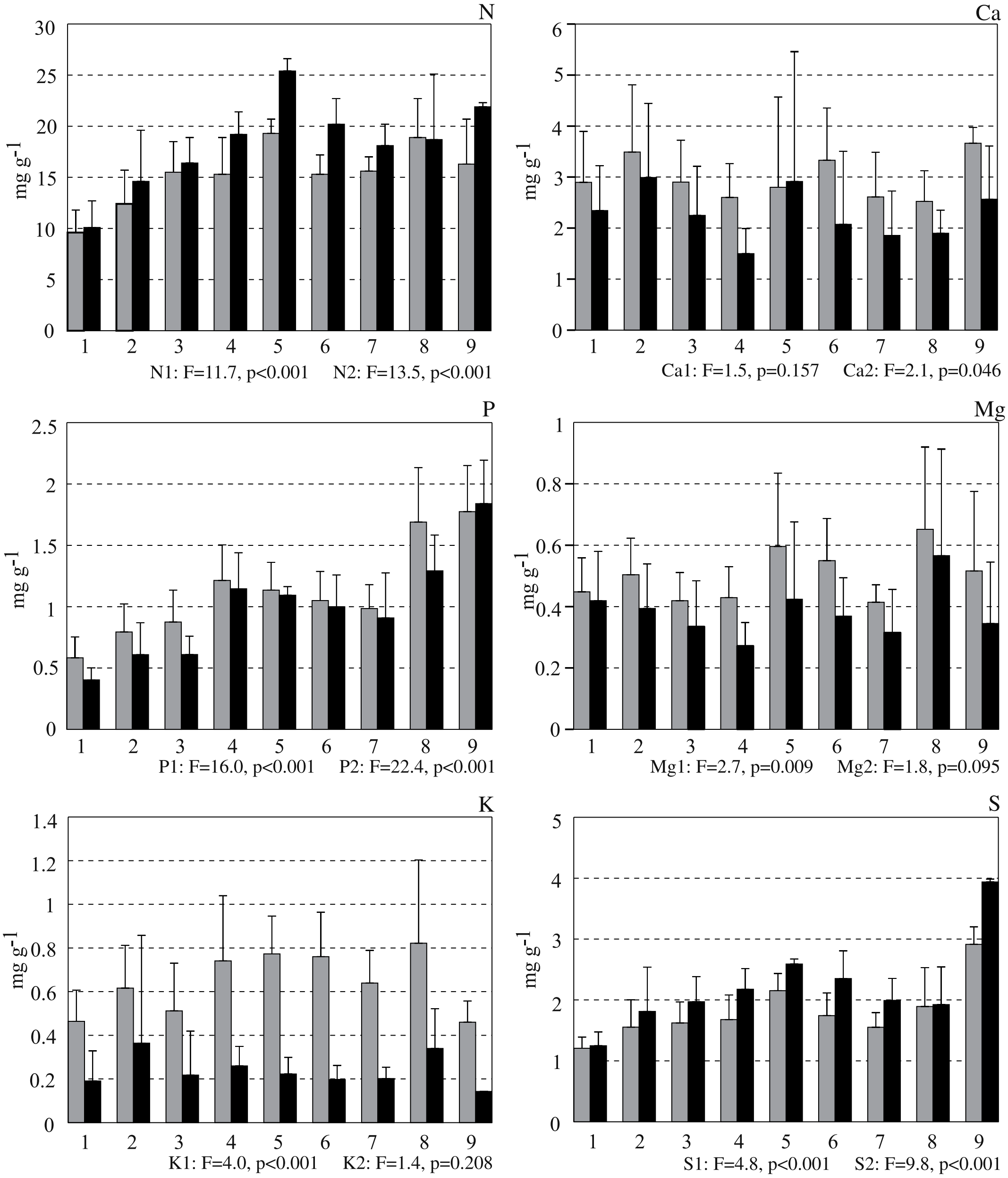


Fig. 10. Concentrations of total nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg) and sulphur (S) in the 0–10 (grey) and 10–20 cm (black) peat layers in TWINSPAN groups (means, standard deviations). Significance of one-way analysis of variance is shown (0–10 cm = left, 10–20 cm = right).

trophic (V) sites (Table 3). The values appeared to be generally slightly higher on the tkg sites than on the mu sites (Table 3), even though the differences were not in general statistically significant (Table 5). Among the mu sites in Site quality class III, there were sample plots with surface-water influence, and the bulk density of the deeper peat layer was high. In the deeper layer the peat pH

Table 3. The mean values (and standard deviations) of bulk density (D_b) and degree of humification ($H_{v.Post}$) in the 0–10 and 10–20 cm peat layers by site quality class and succession phase.

Site quality class	D_b, g cm^{-3} mu	tkg	$H_{v.Post}$ mu	tkg	n mu	tkg
II 0–10	0.127 (0.047)	0.130	5.0 (1.0)	6.0	3	1
10–20	0.147 (0.015)	0.150	6.3 (1.2)	7.0	3	1
III	0.116 (0.023)	0.113 (0.014)	4.0 (0.0)	4.0 (0.6)	5	12
	0.205 (0.056)	0.152 (0.015)	6.5 (1.3)	5.6 (0.7)	4	11
IV	0.099 (0.026)	0.110 (0.021)	3.5 (0.6)	4.0 (0.8)	40	22
	0.132 (0.022)	0.143 (0.015)	4.7 (0.7)	5.1 (0.5)	32	15
V	0.073 (0.015)	0.094 (0.016)	2.7 (0.6)	3.3 (0.5)	23	11
	0.085 (0.030)	0.098 (0.021)	3.2 (0.6)	3.8 (1.1)	23	11

was somewhat lower on the tkg sites than on the mu sites (Tables 4 and 5).

Nutrient amounts combine the ‘characteristics’ of bulk density and nutrient concentrations. The average amount of N was clearly the lowest in the ombrotrophic site types (V), about 1950–2550 kg ha^{-1} for the peat layers combined (0–20 cm) (there were 17 thin-peated cases from which only surface-layer samples could be taken). The corresponding values for herb-rich sites (II) were 5050–6450 kg ha^{-1}. The differences between the succession phases were small. On nutrient-poor sites there was slightly more N in the tkg phase than in the mu phase (Fig. 13, Table 4).

The average amount of P in the 0–20 cm layer varied between 95–470 kg ha^{-1} among site quality classes. The P concentration was to some extent lower on the tkg sites than on mu sites (Tables 4 and 5). No clear differences in the amounts of P were found between succession phases. In particular, this was the case on ombro-oligotrophic sites (Fig. 13).

The largest amounts of K were found in Site quality class III, at an average of about 110–180 kg ha^{-1}. The amount of 180 kg of K obtained in the mu phase was due to only a few high values, and the within-site variation was large. The average K amount in Class V varied about 50–70 kg ha^{-1}. There was slightly less K on the tkg sites than on the mu sites. This appeared more clearly when expressed as concentrations than expressed as amounts (Fig. 13, Tables 4 and 5).

The average amount of Ca varied from 400–550 kg on the ombrotrophic sites to 730–900 kg ha^{-1} on the herb-rich sites (Fig. 13). In Site quality classes IV–V there seemed to be slightly more Ca in the tkg phase than in the mu phase, while on the more fertile sites the situation was reversed by relationships in the 10–20 cm peat layer (Fig. 13, Table 4). However, the within-class variation was large.

The amount of Mg was the highest (even about 250 kg ha^{-1}) on the mu sites in Fertility class III, but this was primarily due to a few high values. On the other sites the average amount of Mg varied between 65 and 125 kg ha^{-1}. There seemed to be slightly more Mg on the mu sites than on the tkg sites, while on the infertile sites the values were of the same order of magnitude (Fig. 13, Table 4).

The average amount of S varied from 240–290 kg ha^{-1} in Class V to 800–950 kg ha^{-1} in Class II (Fig. 13). In site quality classes III–IV there was almost the same amount of S, about 470–500 kg ha^{-1}. No significant differences were found between the succession phases (Fig. 13, Tables 4 and 5).

4 Discussion

4.1 Methodological Aspects

The problem with the use of ordination and classification methods in ecology is the selection of appropriate strategies from an increasing range of choices (e.g. Belbin and McDonald 1993, Belbin

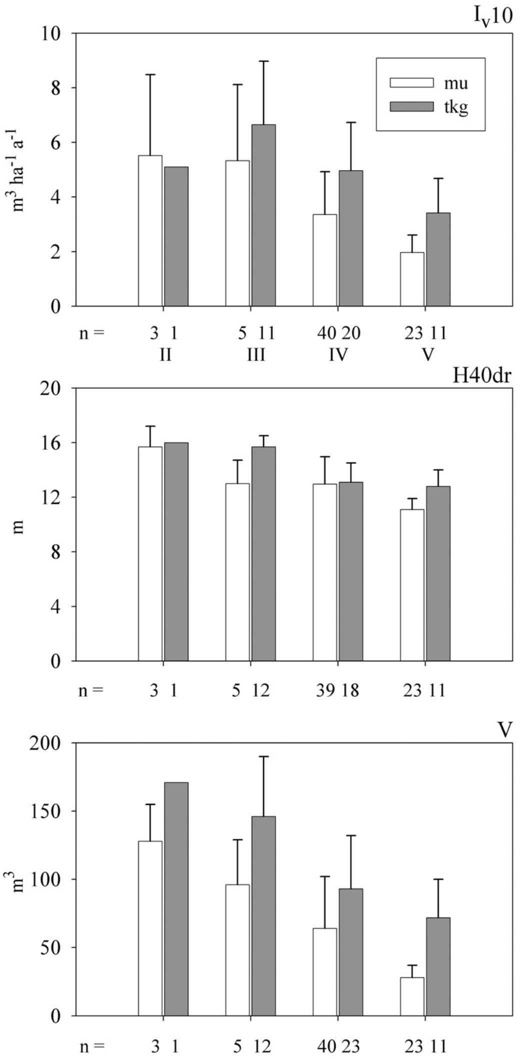


Fig. 11. Mean annual stand volume increment (Iv10), post-drainage dominant height (H40dr) and stand volume (V) by secondary succession phase (mu, tkg) and site quality class (II–V) (means, standard deviations). mu = transforming, tkg = transformed sites. II = herb-rich, III = *V. myrtillus* and tall-sedge, IV = *V. vitis-idaea* and small-sedge, V = cottongrass and dwarf-shrub mires.

1994, Økland, R. 1996). The parallel use of different multivariate approaches is generally useful because the results are frequently complementary (e.g. Wiegleb 1989, Økland 1990a, Belbin and McDonald 1993, Økland et al. 2001).

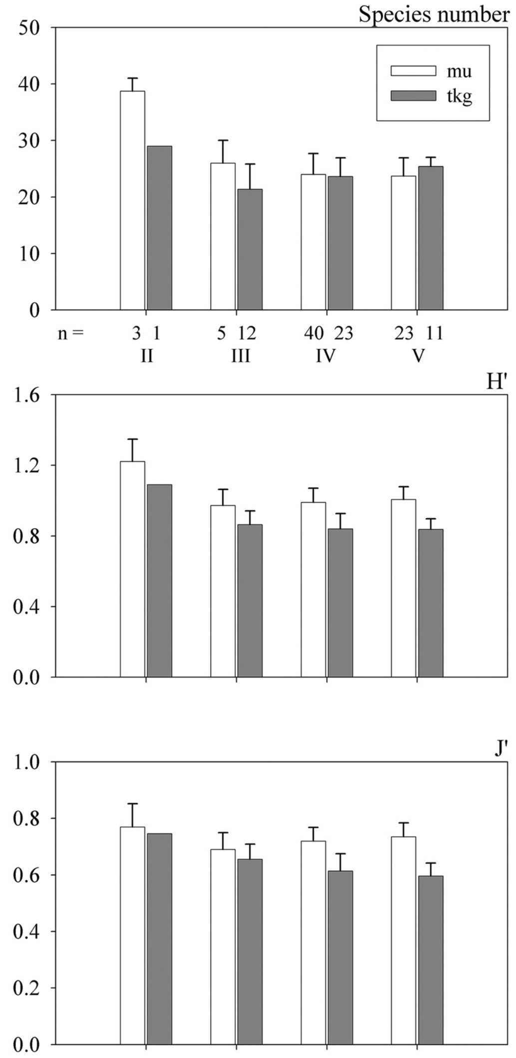


Fig. 12. Species number, and Shannon's (H') and Pielou's (J') diversity indices by succession phase (mu, tkg) and site quality class (II–V) (means, standard deviations).

On the basis of Minchin's (1987) simulations, nonmetric multidimensional scaling (NMDS) is recommended as a robust technique for indirect ordination. According to Minchin (1991), hybrid MDS (HMDS), which was applied in the present study, performs even somewhat better than global (G) or local (L)NMDS. Hybrid MDS, which unites the techniques of metric and nonmetric

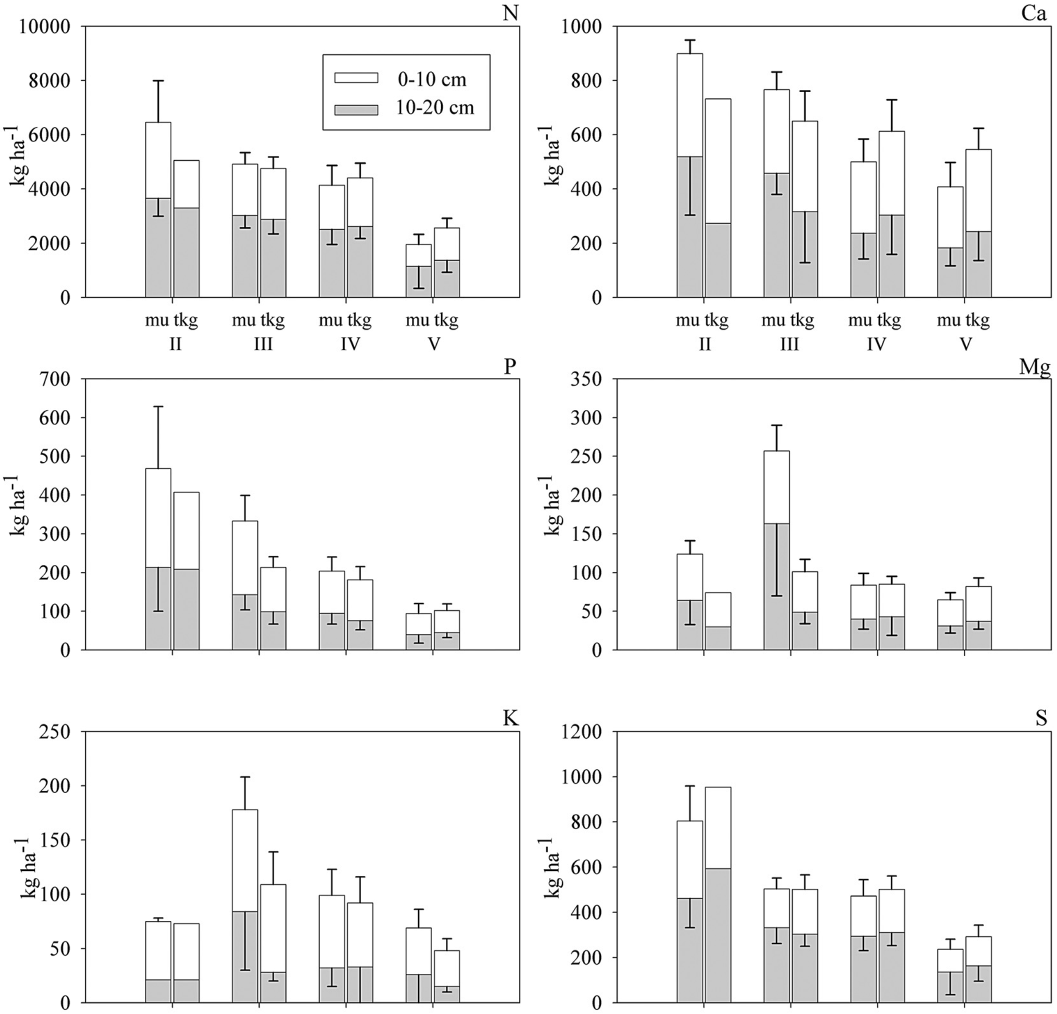


Fig. 13. Total amounts of macronutrient in the 0–10 and 10–20 cm peat layers by succession phase (mu, tkg) and site quality class (II–V) (means, standard deviations).

scaling, is therefore preferable (Belbin 1994). For most purposes the results from e.g. GNMDS or LNMDS are adequate (Minchin 1991, Økland, T. 1996; see also Hotanen 1994 for preanalyses of the present material).

According to the ordination diagrams and FUPGMA classification, there appeared to be mode structures (Dale 1995) in the material. However, the clusters are likely to have been the result of sampling effects (Belbin and McDonald 1993, Dale 1995). Random or systematic sampling over an area produces a material in which the combinations of environmental variables with greatest areal importance recur as clusters in the ordination space (cf. Økland 1990a). However, this could be the very feature that researchers are frequently seeking, i.e. frequent plant communities, and the kind of variation in the environmental variables which they contain.

The low number of observations in some categories, and the possible occurrence of spatial autocorrelation (sample plots that are close

Table 4. The mean values (and standard deviations) of pH and macronutrient concentrations (mg g^{-1}) in the 0–10 and 10–20 cm peat layers by site quality class and succession phase.

Site quality class	pH		N		P	
	mu	tkg	mu	tkg	mu	tkg
II 0–10	3.91 (0.26)	3.98	21.35 (3.39)	13.13	1.90 (0.57)	1.51
10–20	4.11 (0.08)	3.75	24.79 (2.90)	22.14	1.63 (0.55)	1.59
III	3.84 (0.08)	3.57 (0.23)	16.64 (1.71)	16.50 (2.42)	1.64 (0.34)	1.01 (0.21)
	4.09 (0.12)	3.70 (0.22)	16.05 (6.00)	18.93 (2.54)	1.28 (0.10)	0.90 (0.30)
IV	3.68 (0.27)	3.50 (0.26)	15.81 (3.52)	16.20 (2.24)	1.11 (0.29)	0.97 (0.27)
	3.69 (0.25)	3.67 (0.26)	19.09 (2.91)	18.21 (2.55)	0.97 (0.33)	0.67 (0.19)
V	3.49 (0.27)	3.57 (0.13)	10.55 (2.74)	12.48 (2.02)	0.73 (0.25)	0.60 (0.09)
	3.60 (0.26)	3.48 (0.21)	12.19 (4.32)	13.71 (2.36)	0.53 (0.22)	0.48 (0.09)
	K		Ca		Mg	
II	0.47 (0.17)	0.39	3.35 (1.38)	3.45	0.55 (0.27)	0.33
	0.16_a	0.14	3.67 (1.96)	1.83	0.46 (0.26)	0.20
III	0.84 (0.27)	0.73 (0.26)	2.79 (0.84)	2.97 (1.00)	0.81 (0.13)	0.47 (0.13)
	0.39 (0.17)	0.19 (0.05)	2.49 (1.22)	2.10 (1.19)	0.76 (0.26)	0.33 (0.12)
IV	0.70 (0.28)	0.56 (0.22)	2.70 (0.81)	2.86 (0.93)	0.45 (0.12)	0.39 (0.09)
	0.24_b (0.11)	0.24_c (0.26)	1.90 (0.97)	2.19 (1.21)	0.31 (0.11)	0.31 (0.21)
V	0.58 (0.18)	0.36 (0.12)	3.17 (1.33)	3.22 (0.52)	0.48 (0.12)	0.48 (0.09)
	0.33 (0.42)	0.15_d (0.05)	2.39 (1.21)	2.46 (0.83)	0.39 (0.16)	0.38 (0.09)
	a:n=1, b:n=31, c:n=14, d:n=10					
	S					
II	2.66 (0.53)	2.71				
	3.11 (0.70)	3.97				
III	1.51 (0.32)	1.73 (0.46)				
	1.74 (0.58)	2.00 (0.32)				
IV	1.75 (0.35)	1.72 (0.31)				
	2.24 (0.35)	2.17 (0.40)				
V	1.36 (0.40)	1.34 (0.34)				
	1.49 (0.61)	1.62 (0.38)				

together tend to be more similar than plots further apart) resulting from systematic cluster sampling (Legendre and Legendre 1998) precluded further testing of relationships among clusters. The variation in the individual tracts, however, might have been large. For instance, the succession phase varied within 12 tracts and the site quality class in 9 tracts out of 40 (at least one plot differed from the two others), irrespective of the site type, additional criteria or border variants.

The TWINSPAN and FUPGMA classifications showed obvious similarities, thus verifying the results. Both methods appeared to classify relatively well the different succession phases; FUPGMA perhaps better than TWINSPAN. In the comparisons made by Belbin and McDonald (1993), FUPGMA provided a better recovery of true cluster structure than TWINSPAN. This is expected, because TWINSPAN does not strictly seek a cluster form. For example, FUPGMA pays better attention to a (similar) abundance distribution of species than TWINSPAN. This was reflected e.g. in the high F values of indices H' and J', which are determined by both species number and abundance relationships, between the FUPGMA clusters.

Table 5. Significance (F, p<0.001 denoted as 0.000) of two-way analysis of variance for selected variables (cf. Figs. 11–13, Tables 3–4) sq = site quality class, dp = drainage (succession) phase, sq by dp = interaction.

	I_{v10}	H_{40dr}	Species number	H'	J'
sq	11.8 0.000	11.8 0.000	5.9 0.001	7.6 0.000	2.8 0.041
dp	4.7 0.032	5.9 0.017	4.8 0.031	26.0 0.000	18.0 0.000
sq by dp	0.5 0.710	3.5 0.018	3.8 0.012	0.6 0.603	3.9 0.011
	D_b	H, $_{v.Post}$	pH	N, mg g^{-1}	N, kg ha^{-1}
0–10 cm					
sq	11.6 0.000	19.7 0.000	3.6 0.016	24.6 0.000	19.9 0.000
dp	2.1 0.147	4.7 0.032	0.8 0.381	1.1 0.292	0.1 0.713
sq by dp	1.4 0.253	1.4 0.249	2.4 0.068	3.4 0.021	2.2 0.091
10–20 cm					
sq	35.0 0.000	45.3 0.000	7.5 0.000	21.4 0.000	35.0 0.000
dp	0.0 0.925	0.8 0.366	7.1 0.009	0.5 0.490	0.2 0.643
sq by dp	3.0 0.036	2.1 0.112	2.1 0.111	1.8 0.146	1.2 0.311
	P, mg g^{-1}	P, kg ha^{-1}	K, mg g^{-1}	K, kg ha^{-1}	Ca, mg g^{-1}
0–10 cm					
sq	32.4 0.000	39.3 0.000	8.6 0.000	24.6 0.000	1.5 0.216
dp	7.4 0.008	1.2 0.277	4.3 0.040	1.5 0.227	0.4 0.547
sq by dp	1.8 0.153	2.3 0.082	1.2 0.302	0.2 0.877	0.0 0.995
10–20 cm					
sq	25.6 0.000	37.0 0.000	1.1 0.337	8.9 0.000	1.5 0.218
dp	3.0 0.085	0.3 0.585	3.0 0.090	2.1 0.152	0.8 0.376
sq by dp	1.5 0.214	2.4 0.072	0.8 0.524	1.6 0.206	0.9 0.471
	Ca, kg ha^{-1}	Mg, mg g^{-1}	Mg, kg ha^{-1}	S, mg g^{-1}	S, kg ha^{-1}
0–10 cm					
sq	3.0 0.036	9.1 0.000	14.4 0.000	13.7 0.000	16.7 0.000
dp	2.5 0.118	9.2 0.003	2.6 0.112	0.2 0.641	1.4 0.243
sq by dp	0.8 0.519	4.6 0.005	7.5 0.000	0.4 0.791	0.3 0.817
10–20 cm					
sq	6.7 0.000	6.4 0.001	19.5 0.000	23.0 0.000	40.3 0.000
dp	1.0 0.331	8.7 0.004	10.4 0.002	2.7 0.105	1.3 0.260
sq by dp	3.3 0.024	4.2 0.008	10.7 0.000	1.2 0.323	1.2 0.330

According to Dale (1995), TWINSPAN may better reflect what ecologists are intuitively seeking than alternative variance minimization methods, because it is primarily based on a method that identifies gradients (ordination). Furthermore, TWINSPAN incorporates characterization through indicator species. We are often more interested in these differentiating species than in the existence of clusters *per se* (Dale 1995). The table sorting procedure in TWINSPAN is useful, as well as informative (cf. App. 1).

The numerical methods were used in this study as tools for summarising relationships. An element of subjectivity – in addition to the selection of method – is invoked by setting the programme options, as well as in the final compilation of the results (Oksanen 1984, Kuusipalo 1985). As pointed out by Oksanen (1984), the classifier must be responsible for his results, he cannot hide behind 'objective' methods. The optimal level of classification, the number of clusters and the details affecting the desirable locations of boundaries, are then controlled by the ecologist (Kuusipalo 1985, Jeglum 1991).

4.2 Vegetation Gradients, Diversity

The main compositional gradient primarily displayed variation in spruce mire influence – hummock-level bog influence (Eurola et al. 1984), reflecting supplementary nutrient effects (external supply of nutrients; mire margin of Sjörs 1948) against mire inherent (centre) effects (mire expanse of Sjörs 1948; Eurola et al. 1984), and simultaneously, the variation in fertility.

The main compositional gradients of drained boreal mires generally reflect spruce mire – hummock-level bog influences, the variation in nutrient (trophic) status and the variation in moisture / secondary succession (Reinikainen 1988, Hotanen and Nousiainen 1990, Hotanen and Vasander 1992, Eurola et al. 1995, Paalamo 1996, Hotanen et al. 1999). In general, the gradients are intermixed with each other. Especially the trophic gradient is complex and divergent (see also Pakarinen and Ruuhijärvi 1978, Økland et al. 2001 for pristine mires). In material confined to certain mire types, for example pine mires, the gradient structure may be simpler (e.g. Laine et al. 1995).

Forest drainage, because it results in decreased variation in soil moisture and trophic status (e.g. Vahtera 1955, Eurola and Holappa 1984, Laiho and Laine 1994), emphasizes the importance of spruce mire and hummock-level bog influences in controlling the structure of the plant communities on drained peatlands (Eurola et al. 1995, Hotanen et al. 1999). These influences become stronger against the other gradients (e.g. rich fen, poor fen, surface-water) because they also include, on the one hand, the vegetation of spruce-dominated mineral soil forests and, on the other hand, the vegetation of more infertile pine-dominated mineral soil forests (Eurola et al. 1984, 1994).

In general, effective drainage disconnects the surface-water influence. However, especially in material collected in the aapa mire zone, the surface-water influence is frequently indicated by the vegetation (Pienimäki 1982, Hotanen et al. 1999). As in the present material, there are swamp vascular plant species in the vegetation tables of old drained sites in southern Finland, too (Sarasto 1961a, Laine and Vanha-Majamaa 1992, Laine et al. 1995). Mosses typical of swamps and mires are more sensitive to the water level drawdown. The flows of surface-water have a long-lasting effect on the peat by the mineral material and nutrients that they have transported (Eurola and Holappa 1985, Eurola and Huttunen 1990).

The vegetational alpha diversity was higher on mesotrophic (e.g. RhK, RhSR) than on oligotrophic (e.g. MK, PK, KR, PsR) or ombrotrophic drained sites (e.g. TR) (also Sarasto 1961a, Holmen 1964, Reinikainen 1984b, Vasander 1987, Vasander et al. 1997). This may be due to the many ecological gradients that simultaneously affect(ed) fertile peatlands, resulting in multidimensional variation in the nutrient and moisture regimes that gives room for many species by niche diversification (Eurola et al. 1984, Økland 1990b, Laine et al. 1995).

The alpha diversity increases temporarily during secondary succession (Sarasto 1961a, Reinikainen 1984b, Vasander et al. 1997, Hotanen et al. 1999). This is attributed to the simultaneous occurrence of mire species, colonizing pioneer species and forest species. The alpha diversity is, generally speaking, the highest on transforming sites (Sarasto 1961a, Reinikainen 1984b). Since the present material included no undrained or recently drained mires, and there was a combined moisture – fertility gradient that mainly ran in the same direction, the alpha diversity distinctly increased along this dimension.

On infertile sites, however, the differences in species number between transforming and transformed phases are not clear (Sarasto 1961a, Reinikainen 1984b). This was also evident in this study in Site quality classes IV and V. On these sites the values of H' and J' showed increasing dominance and a clearer shift towards forest vegetation than the number of species.

4.3 Comparison among Classifications

The dispersion of the sample plots, classified as the same type in the field, into several numerical clusters may result for the following reasons: a numerical method and the human eye do not analyse the vegetation in the same way (Jongman et al. 1987), the same original mire site type may diverge into a different result after drainage (Hotanen et al. 1999), and misclassifications. The range of original mire types represented in the same clusters immediately seems to accord with the hypothesis that the post-drainage succession of many mire types leads to relatively uniform types of peatland forest (Sarasto 1961a, Hotanen and Vasander 1992).

Border variants or transitional forms between site types commonly occur on drained mires (also Hotanen and Nousiainen 1990). The understorey vegetation composition overlaps more with neighbouring mire site types on successional sites than on stable ones (Cajander 1949, also Keltikangas 1945). The relationship between vegetation and site factors in the succession communities of drained mires should also be weaker compared to 'climax' forests (e.g. Keltikangas 1945, p. 33–45, 91–107).

Some oligotrophic sites (with *Sphagnum fuscum*) in the transforming phase were not distinguished from ombrotrophic sites in the numerical analyses. The mixing of ombrotrophic and minerotrophic mire vegetation in this area, which is located in the intermediate zone between the middle-boreal (aapa mires) and southern vegetation (eccentric bogs), is evident (Tolonen 1967). The peat surface is often stratified in this border zone. Especially minerotrophic vascular plants, e.g. sedges, may occur on infertile sites if their roots extend into a deeper, more fertile layer. The results of Pakarinen (1976) and Pakarinen and Ruuhijärvi (1978) also suggest that there is frequently no sharp limit between ombrotrophic and minerotrophic vegetation. This limit is supposed to become blurred as a result of factors ranging from small-scale variation, via between-site variation, to regional variation of the peatland environment (cf. Pakarinen 1979, Økland 1989). Moreover, in boreal conditions, the composition of the vegetation of minerotrophic composite pine mires (as in this study) becomes poorer after drainage, at least temporarily (Sarasto 1961a, Eurola et al. 1984, Laine et al. 1995, Hotanen et al. 1999). In general, ombrotrophy becomes more apparent in the soil water chemistry than in the vegetation or peat chemistry (Tolonen 1974, Eurola and Holappa 1984, cf. Damman 1990).

Furthermore, the data set contains many sample plots that originally belonged to the body of pine mires with spruce mire influence, as well as closely related oligotrophic spruce mires. This part of the mire type system is heterogeneous with respect to classification (Hotanen 1989, Nieminen and Pätilä 1990, Korpela 1999). The result of drainage of such sites may vary from poor Ptkg (or even luxuriant Vatkg) to Mtkg (Sarasto 1961a,b, Laine and Vasander 1990, Hotanen and Vasander 1992). Additional impacts such as fertilization further adds complexity to the variation, and the presence of different variants ranging from Vatkg to Mtkg is readily understandable. The under-growth of *Picea abies* on dwarf-shrub pine bogs (IR) (Heikurainen 1959) may sometimes result in their being classified as spruce-pine swamp (KR). However, saplings of *P. abies* are assumed to grow clearly better in KR than in IR.

The results show that distinguishing the PtkgII type from the PtkgI type in the transformed phase (Sarasto 1961a,b) purely on the basis of vegetation is difficult. Information about the peat type and sometimes also about the structure of the tree stand is needed for proper classification (Laine 1989, Laine and Vasander 1990).

The only sample plot classified as a *S. fuscum* pine bog (RaRmur, Site quality class VI) was located among other infertile, often rahka-hummocky cottongrass pine bogs (RamTR, V) in the numerical analyses. RamTR changes gradually into RaR; in fact the former is a precursor of the latter (Tolonen 1967, cf. also 'Bunte Reisermoore' in Eurola 1962).

4.4 Species Appraisal

Being a hummock-level species, *S. fuscum* survives for a long time on well-lit drained pine mires, but in the transformed (tkg) phase it is sparse (cf. e.g. TWINSPAN Group 3) because it does not withstand shading (Sarasto 1961a, Hotanen 2000a). Since old drainage areas on more fertile pine mires with *S. fuscum* on hummocks most probably have a higher stocking and are more shaded than the poorer ones, the differences in the abundance of *S. fuscum* between ombrotrophic and minerotrophic sites especially may, however, persist for a considerable period of time (Sarasto 1961a, Laine et al. 1995).

There are no unambiguous indicator species constant enough in the understorey vegetation between Vatkg and Ptkg. In many cases, as in the present material, it is a question of the abundance relationships of certain common species, e.g. *Eriophorum vaginatum* (Hotanen 2000b), *Cladina* spp., *Cetraria* spp. (Nousiainen 2000a,b) and dwarf shrubs, e.g. *Calluna vulgaris* (Salemaa 2000), between these sites. However, *C. vulgaris* and other pine mire dwarf shrubs may be abundant in Ptkg of KgR origin (Laine and Vasander 1990). There might be also regional differences in both Ptkg and Vatkg with respect to the coverages of *Empetrum* and *Calluna*. Also the ordination diagrams of Laine (1989) and Laine and Vanha-Majamaa (1992) show that the differences between Vatkg and PtkgII of c. 25-year-old drainage areas are diffuse.

Being a hummock-level species, *E. vaginatum* (Eurola et al. 1994) is frequent, although not abundant, even in the tkg phase (Sarasto 1961a, Hotanen 2000b,). Ombrotrophic *E. vaginatum* becomes more abundant on regressive sites of many minerotrophic types, too, changing their overall appearance in a less fertile direction (Kuusipalo and Vuorinen 1981). Thus, *E. vaginatum* is problematic in nutritional site type classification because, in addition to the nutrient status, the amount of light and especially the depth of the water table level strongly affect its abundance (Laine and Vanha-Majamaa 1992, Laine et al. 1995). In any case its high coverage on drained mires is a negative sign in the sense of wood productivity.

Carex globularis occurred on only one plot in TWINSPAN Group 1, and on clearly less than half of the plots in Group 2. In these infertile groups the average bulk density of the surface peat (0–10 cm) was below 0.08 g cm^{-3} (cf. also the transforming (mu) sites in Class V; Table 3). In the material presented by Laine and Vanha-Majamaa (1992), *C. globularis* did not occur on drained pine mires where the bulk density of the surface peat was lower than ca. 0.08 g cm^{-3}. *C. globularis* is scarce on ombrotrophic peatlands (Hotanen 2000c), but is assumed to increase slightly on those sites with a secondary succession caused by humification and an associated fertilization. Being a hummock-level species, *C. globularis*, which also indicates spruce mire influence (Eurola et al. 1984), may temporarily increase in abundance after ditching and subsequently change the overall vegetation appearance of oligo-mesotrophic peatlands (Class III) towards Class IV (Sarasto 1961a,b). On old drainage areas of fen and composite type origin (e.g. PtkgII, MtkgII), *C. globularis* seems so far to be scanty (Sarasto 1961a, Reinikainen 1984b, Laine et al. 1995).

Care should be taken when applying *Vaccinium myrtillus* in the classification of drained mires if the material contains both treeless/composite types and genuine forested types. *V. myrtillus* colonises and increases slowly on former drained sites (Sarasto 1961a, Laine et al. 1995, Laiho 1996). However, on genuine transformed sites its coverage generally increases on moving from pine bogs, through spruce-pine swamps, to oligo-mesotrophic spruce swamps (Sarasto 1961a).

Hylocomium splendens was abundant in MtkgI, and it also occurred in Ptkg although rather scattered (also Reinikainen 1984b, Laine et al. 1995). When the fen influence increases, *H. splendens* appears to decrease; for example, it did not occur on Sarasto's (1961a) Ptkg sites of tall-sedge fen (VSN) origin. *H. splendens* did not grow on Vatkg sites of the present study but it may grow, however, scantily in Vatkg of especially genuine forested pine mires (Sarasto 1961a, Reinikainen 1984b).

In addition to the site fertility, the phase in secondary succession also affects the abundance of *Dicranum majus* (cf. TWINSPAN Groups 6 and 7). *D. majus* is a species of the final phase of drainage succession, and its optimal sites appear to be transformed sites of Site quality class III of spruce-mire origin (Sarasto 1961a, cf. also App. 1). In Ptkg it may occur sparsely, but is very scanty in PtkgII especially; in MtkgII, too, it is not as abundant as in MtkgI (Sarasto 1961a, Laine et al. 1995). Thus, the origin of the site (genuine forested vs. treeless or composite) also affects its abundance. When moderately abundant it is a useful species for distinguishing Site quality class III from Class IV on tkg sites (cf. also Mäkipää 2000 for mineral soils).

Equisetum sylvaticum is most abundant on sites of classes III and II of spruce swamp origin (Sarasto 1961a, Korpela 2000). In the present material it was common (on some plots rather abundant) in moist TWINSPAN Groups 6 and 8, but less abundant in tkg Group 7. It was also abundant on both herb-rich plots (mu and tkg) in

Group 9. Generally speaking, the coverage of this species has been found to decrease in the later succession phases of spruce swamps (Korpela 2000). However, after drainage it may temporarily increase in *V. vitis-idaea* spruce swamps (PK), making the vegetation appearance of the swamp more luxuriant (Sarasto 1961a,b). It also benefits from logging (Korpela 2000). Thus, in the classification of drained mires this species is to some extent problematic. In data from southern Finland, *E. sylvaticum* proved to be the most effective differential species for spruce mires in association analysis (Pakarinen 1982).

4.5 Environmental Differentation of Sites

4.5.1 Tree Stand Parameters

The nine TWINSPAN groups were roughly divided into four levels with respect to the site index (H40dr) values. The situation with respect to the stand volume increment (Iv10) was more variable, and the variation within the groups was also greater. The increment during the last ten growing periods (Iv10) seems more sensitive to e.g. variations in moisture than H40dr, which takes into account the whole development of the standing stock after drainage. The changes in moisture, e.g. regressive development, are then reflected in different classifications of the actual vegetation. In the short term, the stand volume increment reacts faster to environmental changes than the other vegetation. For example, the covariation between the vegetation and the last five increment periods (Iv5) was weaker than the covariation between the vegetation and Iv10. This is expected as the ten-year data are likely to show a clearer relationship just because more of the noise (random variation among years) has been averaged out when the longer time period is concerned.

In several studies the post-drainage stand increment has been found to be related to the original site type (e.g. Laine and Starr 1979, Keltikangas et al. 1986, Hökkä 1997, Gustavsen et al. 1998, Hökkä and Penttilä 1999 and references therein). The increment also appears to correlate strongly with the actual vegetation in ordinary forests on drained peatlands (also Laine and Vanha-Majamaa 1992). However, large variation in different site types is typical of the tree stand characteristics of peatlands (e.g. Hökkä 1997). In addition to the stand development phase (e.g. Keltikangas et al. 1986, Laine 1989), the drainage phase also causes variation in tree growth, as was seen in the present study. The differences in standing volume explain a high proportion of the differences in the increment values, since there is a strong positive correlation between stand increment and volume (e.g. Laine and Starr 1979). In the data of Hökkä and Penttilä (1999) the relative growth rate (RGR) index means also increased over time, which was partly interpreted as an effect of a true increase in the wood production potential of the sites. It will be clear from the foregoing that, as far as stand yield characteristics are concerned, only relatively rough comparisons can be made between the present study and other studies.

The stand volume increments of the different site quality classes corresponded rather well to the values of the comparable peatland forest types in southern Finland, except for the herb-rich type (Rhtkg) (Laine 1989). The increment 7.4 m^3 ha^{-1} a^{-1} reported by Laine for Rhtkg was clearly higher than that obtained in this study for Site quality class II. However, this class contained only a few observations. The volume increments in Class III were approximately equivalent to those for the corresponding spruce mire group reported by Gustavsen et al. (1998), and for MK (III) obtained by Laine and Starr (1979). The values in Vatkg (V) were almost as high as the values for old drainage plots of IR and TR ombrotrophic sites given by Gustavsen et al (1998). According to their study, the growth values of infertile LkN (low-sedge fen) and RaR were even lower than those for the transforming (mu) sites in Class V in this study. The growth values for the mu sites of Class V were equivalent to the figures published by Laine and Starr (1979) for 20- to 30-year-old drained and unfertilized IR.

The average range of H40dr in Site quality class V varied from 11 to almost 13, while in the ombrotrophic group presented by Gustavsen (1996) it was 10–12. The ombrotrophic group of Gustavsen (1996) contains a wider range of mire site types, also including the infertile LkN and RaR. The highest H40dr values presented by Gustavsen (1996) exceeded those of the present material due to the inclusion of fertile mire site types, e.g. LhK (eutrophic paludified hardwood-spruce forest). Otherwise, the values in the comparable groups in these two studies were close to each other. However, the fact that the individual yield groups of Gustavsen contained types of various site quality classes makes comparison difficult. The materials of Gustavsen (1996) and of Gustavsen et al. (1998) were to some extent representative of older drainage areas and more southerly regions than the material of the present study, but they contained no fertilized sites.

4.5.2 Bulk Density and Degree of Humification

The bulk density (D_b) and the degree of humification ($H_{v.Post}$) followed almost the same pattern. D_b correlates strongly with $H_{v.Post}$, especially in *Sphagnum* and woody peat samples regardless of drainage (e.g. Päivänen 1969, Tolonen and Saarenmaa 1979). A strong correlation between vegetation and D_b (Laine and Vanha-Majamaa 1992), and between vegetation and $H_{v.Post}$, has also been reported (Hotanen et al. 1999). These variables increase along both the secondary succession (Laiho and Laine 1994) and along the fertility gradient (Laine and Vanha-Majamaa 1992, Minkkinen and Laine 1998). The degree of humification also increases, as in the present material, along the complex gradient of hummock-level bog – spruce mire influence and fertility (Hotanen et al. 1999).

D_b and $H_{v.Post}$ increased on moving from transforming sites to transformed sites, and from surface peat (0–10 cm) to deeper peat (10–20 cm). Similar results have been found by e.g. Laiho and Laine (1994). The water level drawdown after ditching results in subsidence and compaction of the peat surface, which increases the bulk density of the peat. Subsequently, the accelerated rate of organic matter decomposition and increasing weight of the tree stand further compacts the peat (Minkkinen and Laine 1998, Laiho et al. 1999). The downward compaction of peat is not restricted to drained sites, as described in detail e.g. by Clymo (1983) and Økland and Ohlson (1998).

There are many potential reasons for the stronger covariation between the vegetation and both D_b and $H_{v.Post}$ in the deeper peat layer. After drainage the *Sphagnum* peat of infertile ombrotrophic sites decomposes at a slower rate than the peat of more fertile sites (Vahtera 1955, Laiho et al. 1999). This is clearly shown in TWINSPAN Groups 1–2, where the differences in both D_b and $H_{v.Post}$ between the different peat layers were smaller than those on the more fertile sites (Fig. 9). The thickness of the peat layer may also have an effect; in the study of Minkkinen and Laine (1998), the relative increase in D_b after drainage was greatest in the shallow peat layers (cf. Fig. 9). The total variation in species composition between different site types, i.e. the beta diversity, decreases along with the post-drainage succession (e.g. Vasander et al. 1997). Thus, both the litter and the topmost peat surface are also assumed to be more similar between site types after drainage.

4.5.3 pH and Macronutrients

pH. Although the covariation between pH and the vegetation was not very strong, it was consistent. The pH value generally increases when moving down the peat profile (e.g. Vahtera 1955). On the other hand, pH usually decreases with increasing drainage efficiency and during secondary succession (Lukkala 1929, Vahtera 1955, Laine et al. 1995). This was evident in the present material, especially for the 10–20 cm layer between succession phases. The decrease in the pH of the uppermost peat layer resulting from drainage is also greater in the more fertile site types than in infertile types (Lukkala 1929, Laine et al. 1995). Consequently, the covariation was slightly weaker for the surface peat layer. According to Vahtera (1955), the original acidity ranking of the sites is, however, usually retained during secondary succession (cf. Laine et al. 1995).

Nitrogen and Phosphorus. Past fertilizations may have to some extent influenced the correlations between the vegetation and nutrient concentrations in the present study. However, the fertilized plots were distributed relatively evenly between the different vegetation classes (Table 1). It is also likely that fertilization has an effect on the amounts of nutrient in the surface peat layers, despite leaching and nutrient uptake by the trees. The objective just was to analyse the prevailing conditions in ordinary, commercial forests on drained peatlands, which often contain fertilizations.

Regardless of the fact that a data set from drained mires does not necessarily contain an unambiguous trophic gradient (e.g. Westman 1987), the correlation between the actual vegetation and certain nutrients, e.g. N and P, may be strong, as was observed in the present material. The differences in the N concentration of the peat between the site types was more apparent in the 10–20 cm peat layer than in the surface layer. This is most probably due to the increasing amount of litter derived from the developing tree stand, which decreases the N concentration of the uppermost peat in *Carex*-dominated fertile peat at a faster rate than in *Sphagnum*-dominated infertile peat (Vahtera 1955). Also Laiho et al. (1999) found that the N concentration from the surface layer down to the 10–20 cm layer seemed to increase faster in the meso-oligotrophic sites than in the oligo-ombrotrophic sites. The N concentration generally increases on moving downwards in peat profiles (e.g. Vahtera 1955, Holmen 1964, Laiho et al. 1999), but there are also some opposite observations between e.g. the 0–10 and the 10–20 cm layers (Kaunisto and Paavilainen 1988).

The average amounts of total N in the 0–20 cm peat layer were slightly lower or at the same level as those presented by Kaunisto and Paavilainen (1988) for old transformed areas. In their material the average range for ombrotrophic to herb-rich sites varied between 3000 and 7000 kg ha^{-1}. The value (4300 kg) for the transformed *V. vitis-idaea* spruce swamp (PK) reported by Kaunisto and Paavilainen was equivalent to that of Site quality class IV in the present study. Conversely, the amounts were slightly larger (or at the same level) as those reported by Nieminen and Pätilä (1990) and Laine et al. (1995) for comparable sites. The value (1912 kg) for the dwarf-shrub transforming type (IRmu) in eastern Finland presented by Finér (1991) is almost the same as that obtained here for the mu phase of Class V. In an earlier material from the same research area (Hotanen 1991), the average amounts of N in the sites developing into Vatkg and Ptkg were slightly lower than the values obtained for corresponding sites in this study. The average values for the sites developing into Mtkg were similar in both of these studies.

The observed correlation between the vegetation and P concentration was slightly stronger for the deeper peat layer, which indicates that the intensity of relative surface enrichment (or impoverishment of the deeper layer) of P to some extent differed between the sites (also Laiho et al. 1999). P generally accumulates slightly in the surface peat (e.g. Kaunisto and Paavilainen 1988). In some materials the gravimetric P concentration seems to be relatively even from the 10–20 cm layer to the topmost layer (Laiho et al. 1999).

The average amounts of total P (0–20 cm) in Fertility class II (405–470 kg ha^{-1}) and in the transforming sites of Class III (330 kg) were larger than those reported by Kaunisto and Paavilainen (1988) for comparable fertility classes. In other respects the amounts of P in corresponding classes were close to each other in both of these studies. The value for IRmu reported by Finér (1991) was 105 kg ha^{-1}, while in this study it was 95–102 kg for Class V. In the study of Nieminen and Pätilä (1990), the average P range for ombrotrophic to oligotrophic sites was between 110–220 kg ha^{-1}. In the material of Hotanen (1991), the amount of P was about 80 kg ha^{-1} in Class V, 180 kg in Class IV (here 180–205 kg) and 285 kg in Class III, while in this study it was 210 kg ha^{-1} in the transformed (tkg) Class III on the average.

The nutrient stores in the peat also vary with the secondary succession phase and drainage age (also Laiho and Laine 1994, Westman 1994, Laine et al. 1995). Especially the variations in the amounts of N and P, which are mainly organically bound, are related to the bulk density (Westman 1994). Therefore the amounts of these nutrients may increase along with secondary succession, at least in ombro-oligotrophic sites (cf. Fig. 13, Laiho and Laine 1994, Westman 1994). In the more fertile sites the N and P stores may remain unchanged, even though large amount are bound in the increasing tree stand biomass (Laiho and Laine 1994). This is caused by post-drainage subsidence of the mire surface and consequent compaction, which increases the bulk density and brings new stores from the deeper peat layers (Laiho and Laine 1994). According to Westman (1994), the amounts of N and P in MtkgI at first increased, but subsequently turned to a decrease along with drainage age class. In the study of Laine et al. (1995) this was also the case for N in meso-oligotrophic drained pine mires (RhSR, VSR).

Potassium. The correlation between the vegetation and K concentration of the surface peat (0–10 cm) was also relatively strong. The K concentration of the deeper layer was considerably lower, and there was no correlation with the vegetation. K is a very mobile nutrient (Damman 1978, Kaunisto and Paavilainen 1988, Laiho et al. 1999). The surface enrichment of K is due to effective biological cycling by the developing vegetation after drainage (Laiho 1997). In the drained pine mire material of Laine and Vanha-Majamaa (1992), the correlation between the vegetation and K concentration of the peat (0–20 cm) was at almost same level as the correlations for N and P. Nieminen and Pätilä (1990) found no close connections between the nutrient concentrations and vegetation, possibly due to the small differences between the trophy of the sites and to the fact that the material consisted of all succession phases from pristine pine mires to transformed sites.

The average amounts of K were larger than those presented for old drainage areas by Kaunisto and Paavilainen (1988), or those presented earlier for the same area (Hotanen 1991). Especially the value for the tarnsforming sites in Site quality class III was high (even 180 kg ha^{-1}). This, however, was due to a few high K concentration and bulk density values, most probably caused by the presence of mineral material. The amount of K in the drained pine bog reported by Finér (1991) was 64 kg ha^{-1}, while in Class V in this study it was 50–70 kg. The average range between the different site types reported by Nieminen and Pätilä (1990) was 60–80 kg ha^{-1}.

In general, the concentrations and amounts of K are affected by the secondary succession phase and drainage age, as was evident in the present study: K is assumed to decline when virgin peatland becomes transformed (Kaunisto and Paavilainen 1988). In the study of Laiho et al. (1999), the gravimetric K concentrations dropped soon after drainage, but later on they remained relatively unchanged in spite of increased uptake by the tree stand. The decrease might be due to disturbances in the biological cycle and consequently increased leaching, while the K input in dry and wet deposition was probably the main factor explaining the lack of a reduction in soil K concentrations in older drained sites (Laiho et al. 1999). According to Westman (1994), the amount of K may even turn to a slight increase on some old transformed sites. This might be partly caused by the allocation of K into the fine roots of the developing stands, which is then included in the results of analyses of the surface peat (Westman 1994).

Calcium and Magnesium. There were no clear relationships between the vegetation and the concentrations of Ca and Mg. Kaunisto and Paavilainen (1988) reported a tentative positive trend with the site index in some drained spruce mires, but not in pine mires (cf. however Laine et al. 1995). In the data of Laine and Vanha-Majamaa (1992), the covariation between the vegetation and Ca concentration of the peat was somewhat lower than that for N, P and K. In a material from an old drainage area of spruce swamp (RhK) origin, the Ca concentration was the peat parameter that differed the most significantly between the vegetation groups (Mannerkoski 1979). Generally the concentrations of Ca and Mg appear to decrease from the surface layer down to the 10–20 cm layer (also Laiho et al. 1999), but the situation may also sometimes be the reverse (Kaunisto and Paavilainen 1988). According to Laiho et al. (1999), the concentrations may again increase below the rooting zone (>30 cm).

The differences between transforming and transformed sites in the concentrations and amounts of Ca and Mg were varied. This was also the case for Ca according to Laine et al. (1995). According to Laiho et al. (1999), the gravimetric Ca and Mg concentrations decrease in the rooting zone after drainage. In the present material this was not found between succession phases in nutrient-poor sites. In old drainage areas a considerable amount of Ca and Mg may have been taken up by the tree stand or leached out of the peat (Laiho 1997).

The average amount of total Ca varied less between the site types compared to the data of Kaunisto and Paavilainen (1988). The values for Rhtkg and Mtkg from Vesijako (1500–1800 kg ha^{-1}) clearly exceeded the values of the present material. Otherwise, the amounts in corresponding site types were at almost the same level. In the material of Laine et al. (1995) the average amount of Ca varied between 298 and 1220 kg ha^{-1}. The average range between site types according to Nieminen and Pätilä (1990) was 500–750 kg ha^{-1}, and the amount in the IRmu reported by Finér (1991) was 392 kg ha^{-1} on the average. In the study of Hotanen (1991), the amounts of Ca varied only slightly, between 450 and 520 kg ha^{-1} on the average. However, the within-type variation was large.

The amounts of total Mg in certain Rhtkg and Mtkg reported by Kaunisto and Paavilainen (1988) exceeded the amounts of Mg in the present study (except the transforming III sites). Otherwise, the differences between corresponding site types were small. In the data of Nieminen and Pätilä (1990), the average amounts of Mg varied between 90 and 110 kg ha^{-1}, while in that of Hotanen (1991) between 60 and 80 kg ha^{-1}. Finér (1991) presented a value of 69 kg ha^{-1} for IRmu. On the basis of different reference materials (also e.g. Holmen 1964), there seem to be large regional differences in the amounts of Ca and Mg on minerotrophic mire sites especially, because these nutrients are mainly derived from the surrounding mineral soil or the mineral soil underlying the peat layer.

Sulphur. The total S concentration correlated consistently with the vegetation (also Pätilä and Nieminen 1990), and also increased from the surface layer down to the deeper layer. Similar results have been reported for drained pine bogs and oligotrophic pine mires (Pätilä and Nieminen 1990, Brække and Finér 1991). According to Finér (1991), the average amount of S in the 0–20 cm peat layer in IRmu in eastern Finland was 258 kg ha^{-1}, which is almost the same value as for the transforming (mu) sites of Site quality class V in this study. The values for the ombrotrophic group in the study of Pätilä and Nieminen (1990) were slightly higher, and corresponded well to the transformed sites of Class V in the present material. The average amount of S in the low-sedge pine mires of Pätilä and Nieminen was 429 kg ha^{-1}, while in Class IV of this study about 470–500 kg ha^{-1}.

5 Concluding Remarks and Prospects for Further Research

On the basis of classifications made in the field, numerical community analysis, parallel stand measurements, peat chemical and physical properties, it is concluded that the actual understorey vegetation well reflects various aspects of the ecological conditions, even in labile and disturbed communities of drained peatland forests.

In a representative (systematic or random) sample of drained peatlands, the compositional and ecological gradient structure may be complex due to differences in origin of the site types, successions and other impacts. The trophic gradient is particularly complex, consisting of several single variables that do not vary completely in parallel. In ordinations, the individual nutrient vectors are usually located at angles to each other and to the main compositional gradients. Thus, there is not necessarily an unambiguous trophic gradient.

Border variants or transitional forms of site type are common in the successional communities of drained mires. Consequently, the classification is fine-grained and demanding, often based on the differences in abundance of common species. According to the numerical and field classifications, the borders between *transformed* (tkg) phases are also often diffuse. However, classification is useful for complementing the site description made by ordinations.

The additional criteria indicated by the vegetation, e.g. surface-water influence and *Sphagnum fuscum*-hummocky, more closely define the ecology of the site. These criteria are also useful in the classification of drained peatlands. In addition, the degree of humification ($H_{v.Post}$) (especially of the 10–20 cm peat layer) seems to provide a simple and usable auxiliary variable in the ecological description and classification of drained mires.

There are clear differences in many peat and stand yield characteristics, particularly between ombrotrophic and oligominerotrophic sites, i.e. between site quality classes V and IV. Although the division between Vatkg and Ptkg based on the vegetation is diffuse, there are differences in environmental variables between these transformed sites. For example, the mean annual stand volume increment, degree of humification, concentrations and amounts of N, P, K and S were higher in Ptkg (IV) than in Vatkg (V). However, there are in fact no differences in the alpha diversity between these classes. But, as expected, the alpha diversity on herb-rich sites (II) is high compared to that on the other site types.

In general, the average amounts of nutrients in surface peat (0–20 cm) are at about the same level as those reported earlier for corresponding sites. On fertile sites there is somewhat more P than the values presented in other studies. High amounts of K and Mg in some categories are caused by a few high values. Almost all the sites were fertilized, as is the case for a considerable part of drained mires in Finland. The large within-type variation in nutrient concentrations and amounts is also typical of peatlands.

In addition to the site quality classes, a considerable amount of information about the tree stands, peat properties and vegetational diversity was connected to the separation of the succession phases, in this study transforming (mu) vs transformed (tkg) sites. Thus, distinguishing the succession phases from each other appears to be reasonable by their characteristics. It should also be borne in mind that the possible different assemblage of original mire site types in different succession phases – even of the same quality class – may also have had an effect on the observed differences in environmental sample variables. However, the differences between successional phases reflect the actual ecological situations prevailing in the field. Time since drainage does not well indicate the structure of the understorey vegetation due to variations in drainage efficiency (e.g. regressive succession), and to the fact that the rate of secondary succession is strongly affected by site type fertility, together with the rate of post-drainage stand increment.

On the basis of comparisons between numerical clustering and precise field classification, it appears that the (more or less) subjective field classification might be unnecessarily detailed for classifying drained mires: most probably we can disregard the original mire site types in the transforming phase. Thus, the drained peatland forest types (Laine and Vasander 1990) or the site quality classes (Huikari et al. 1964) with the secondary succession phases, as well as additional criteria, are needed. The peatland forest types and site quality classes with succession phases are usable as a framework for generalization, e.g. when comparing the results between different studies. It is more difficult to compare numerical units directly with the results of other studies. However, the numerical methods bring supplementary objectivity to the classification analyses and to the presentation of the results. They can be used as tools, e.g. in order to pay more attention to certain species and abundance criteria when specifying and identifying more traditional vegetation types.

A need for more accurate descriptions and instructions for the classification of transformed sites is apparent. The vegetation descriptions, notably for the aapa mire zone, are so far insufficient to canonize properly differential plant species for tkg types (cf. also Reinikainen 1994). More attention has to be paid to the indicator value, e.g. abundance criteria, of differentiating species. This especially concerns the indicator species of TWINSPAN: the site discriminants are often constant or dominant species. Some species of this kind (e.g. *Eriophorum vaginatum*, *Carex globularis*, *Vaccinium myrtillus*, *Hylocomium splendens*, *Dicranum majus*) were discussed with respect to suitability for classification. In the future, more emphasis should be paid to the nature of the species response to environmental factor gradients (e.g. Mäkipää 1999).

More information is needed about the consequences of subsidence, compaction and mineralization of peat due to long-lasting drainage on different sites and in different climatological areas. To what extent the original mire site type, together with additional qualifiers, predicts the long-term timber productivity is still a current issue (Hökkä and Penttilä 1999). However, it is obvious that the importance attributed to the original mire site type should be reduced while characteristics of the actual vegetation should be more strongly emphasized in the classification of drained mires. Our knowledge of the relationships between the actual understorey vegetation and site characteristics on old drainage areas is still insufficient. What are the effects of different methods of timber harvesting on the understorey vegetation? The effects of competition between vegetation and tree seedlings after harvesting and stand regeneration are also unknown.

Acknowledgements

I would like to thank Hannu Hökkä and Matti Siipola for providing the tree stand data. Hans Gustavsen gave valuable advice in calculating the tree stand characteristics. Leena Finér and Anki Geddala helped to solve problems in the nutrient analyses. Leena Karvinen completed the tables and figures. Toivo Hamunen helped in the field by taking the peat samples with care. The discussions with Mike Dale, Hannu Nousiainen and Risto Ojansuu have been constructive. Thanks are due to Raisa Mäkipää, Antti Reinikainen and journal referees, Rune H. Økland and Tord Magnusson, for their valuable comments on the manuscript, to Juha Heikkinen and Jaakko Heinonen for statistical advice, and to John Derome for revising the English.

References

Atlas of Finland 1987. Folio 131. Climate. National Board of Survey – Geographical Society of Finland. Helsinki. 32 p.

— 1988. Folio 141–143. Biogeography, nature conservation. National Board of Survey – Geographical Society of Finland. Helsinki. 32 p.

— 1990. Folio 123–126. Geology. National Board of Survey – Geographical Society of Finland. 58 p.

Belbin, L. 1994. PATN (Pattern Analysis Package). Division of Wildlife and Ecology. CSIRO. Australia.

— & McDonald, C. 1993. Comparing three classification strategies for use in ecology. Journal of Vegetation Science 4: 341–348.

Brække, F.H. & Finér, L. 1991. Fertilization effects on surface peat of pine bogs. Scandinavian Journal of Forest Research 6: 433–449.

Cajander, A.K. 1911. Kangasmetsistä turvemaalla. Referat: Über gewöhnliche Waldtypen auf Torfboden. Suomen metsänhoitoyhdistyksen julkaisuja 28: 694–699.

— 1913. Studien über die Moore Finnlands. Acta Forestalia Fennica 2(3). 208 p.

— 1949. Forest types and their significance. Acta Forestalia Fennica 56(5). 71 p.

Clymo, R. 1983. Peat. In: Gore, A.J.P. (ed.). Ecosystems of the world. 4A. Mires: swamp, bog, fen and moor: general studies. Elsevier, Amsterdam. p. 159–224.

Dale, M. 1995. Evaluating classification strategies. Journal of Vegetation Science 6: 437–440.

Damman, A.W.H. 1978. Distribution and movement of elements in ombrotrophic peat bogs. Oikos 30: 480–495.

— 1990. Nutrient status of ombrotrophic peat bogs. Aquilo Serie Botanica 28: 5–14.

Eurola, S. 1962. Über die regionale einteilung der südfinnischen Moore. Annales Botanici Societatis Zoologicae Botanicae Fennicae 'Vanamo' 33(2). 243 p.

— , Hicks, S. & Kaakinen, E. 1984. Key to Finnish mire types. In: Moore, P.D. (ed.), European mires. Academic Press, London. p. 11–117.

— & Holappa, K. 1984. Luonnontilaisten soiden ekologia ja soiden metsäojituskelpoisuus. Metsäntutkimuslaitoksen tiedonantoja 148: 90–108.

— & Holappa, K. 1985. The Finnish mire type system. Aquilo Serie Botanica 21: 101–110.

— & Huttunen, A. 1990. Suoekosysteemin toiminnallinen ryhmitys. Summary: The functional grouping of mire ecosystems and their response to drainage. Suo 41(1): 15–23.

— , Huttunen, A. & Kukko-oja, K. 1994. Suokasvillisuusopas. Oulanka Reports 13. 81 p.

— , Laukkanen, A. & Moilanen, M. 1995. The significance of the original mire site type in the classification of old drainage areas. An example from Muhos, Finland (64°49'N, 26°E). Aquilo Serie Botanica 35: 39–44.

Faith, D.P., Minchin, P.R. & Belbin, L. 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69: 57–68.

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

— & Brække, F.H. 1991. Understorey vegetation on three ombrotrophic pine bogs and the effects of NPK and PK fertilization. Scandinavian Journal of Forest Research 6: 113–128.

Gustavsen, H.G. 1996. Site index model approach for drained peatland forest stands. Suo 47(2): 37–46.

— , Roiko-Jokela, P. & Varmola, MJ. 1988. Kivennäismaiden talousmetsien pysyvät (INKA ja TINKA) kokeet. Suunnitelmat, mittausmenetelmät ja aineiston rakenteet. Metsäntutkimuslaitoksen tiedonantoja 292. 212 p.

— , Heinonen, R., Paavilainen, E. & Reinikainen, A. 1998. Growth and yield models for forest stands on drained peatland sites in southern Finland. Forest Ecology and Management 107: 1–17.

Halonen, O., Tulkki, H. & Derome, J. 1983. Nutrient analysis methods. Metsäntutkimuslaitoksen tiedonantoja 121. 28 p.

Hämet-Ahti, L., Suominen, J., Ulvinen, T. & Uotila, P. (eds.) 1998. Retkeilykasvio. Luonnontieteellinen keskusmuseo, Kasvimuseo. 656 p.

Heikurainen, L. 1959. Tutkimus metsäojitusalueiden tilasta ja puustosta. Referat: Über waldbaulich entwässerte Flächen und ihre Waldbestände in Finnland. Acta Forestalia Fennica 69(1). 279 p.

— 1973. Soiden metsänkasvatuskelpoisuuden laskentamenetelmä. Summary: A method for calculation of the suitability of peatland for forest drainage. Acta Forestalia Fennica 131. 35 p.

— 1979. Peatland classification in Finland and its utilization for forestry. In: Kivinen, E. et al. (eds.). Classification of peat and peatlands. International Peat Society. Helsinki. p. 135–146.

— 1986. Suo-opas. Kirjayhtymä, Helsinki. 51 p.

— & Pakarinen, P. 1982. Mire vegetation and site types. In: Laine, J. (ed.). Peatlands and their utilization in Finland. Finnish Peatland Society. Helsinki. p. 14–23.

Heinonen, J. 1994. Koealojen puu- ja puustotunnusten laskentaohjelma KPL. Käyttöohje. Metsäntutkimuslaitoksen tiedonantoja 504. 80 p.

Hill, M.O. 1979. TWINSPAN-A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell University, Ithaca, New York. 48 p.

Hökkä, H. 1994. Kasvillisuusluokat puuston kasvun kuvaajina ojitetuilla soilla. Abstract: The correlation between botanical site classifications and tree growth on drained peatlands. Metsäntutkimuslaitoksen tiedonantoja 531: 51–55.

— 1997. Models for predicting growth and yield in drained peatland stands in Finland. Metsäntutkimuslaitoksen tiedonantoja 651. The Finnish Forest Research Institute. Research Papers 651. 45+53 p.

— & Penttilä, T. 1999. Modelling the dynamics of wood productivity on drained peatland sites in Finland. Silva Fennica 33(1): 25–39.

— & Kaunisto, S., Korhonen, K., Päivänen, J., Reinikainen, A. & Tomppo, E. 2002. Suomen suometsät 1951–94. Metsätieteen aikakauskirja 2B. 357 p.

Holmen, H. 1964. Forest Ecological Studies on Drained Peat Land in the Province of Uppland, Sweden. Parts I–III. Studia Forestalia Suecica 16. 236 p.

Hotanen, J-P. 1989. Korpirämeet ja karut korvet suomalaisissa suoluokitusjärjestelmissä. Summary: The place of spruce-pine mires and oligotrophic spruce mires in Finnish peatland site type classifications. Suo 40(1): 21–30.

— 1991. Suotyyppijärjestelmän käyttökelpoisuus ja turvekangastyypin ennustettavuus metsäojitetuilla turvemailla. Metsäntutkimuslaitoksen tiedonantoja 383: 23–32.

— 1994. Eräiden ordinaatiomenetelmien vertailua. Abstract: Comparing some indirect ordination methods. Metsäntutkimuslaitoksen tiedonantoja 531: 30–38.

— 2000a. Sphagnum fuscum. Ruskorahkasammal. In: Reinikainen, A. et al. (eds.). Kasvit muuttuvassa metsäluonnossa. Tammi, Helsinki. p. 270–271.

— 2000b. Eriophorum vaginatum. Tupasvilla. In: Reinikainen, A. et al. (eds.). Kasvit muuttuvassa metsäluonnossa. Tammi, Helsinki. p. 170–171.

— 2000c. Carex clobularis. Pallosara. In: Reinikainen, A. et al. (eds.). Kasvit muuttuvassa metsäluonnossa. Tammi, Helsinki. p. 164–165.

— & Nousiainen, H. 1990. Metsä- ja suokasvillisuuden numeerisen ryhmittelyn ja kasvupaikkatyyppien rinnastettavuus. Summary: The parity between the numerical units and site types of forest and mire vegetation. Folia Forestalia 763. 54 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): 1–10.

— , Nousiainen, H. & Paalamo, P. 1999. Vegetation succession and diversity on Teuravuoma experimental drainage area in northern Finland. Suo 50(2): 55–82.

Huikari, O. 1952. Suotyypin määritys maa- ja metsätaloudellista käyttöarvoa silmällä pitäen. Summary: On the determination of mire types, specially considering their drainage value for agriculture and forestry. Silva Fennica 75. 22 p.

— 1974. Site quality estimation on forest land. In:

Heikurainen, L. (ed.), Proceedings of the International Symposium on Forest Drainage, 2nd–6th September 1974. Jyväskylä–Oulu, Finland. p. 15–24.

— , Muotiala, S. & Wäre, M. 1964. Ojitusopas. Kirjayhtymä, Helsinki. 244 p.

Jeglum, J.K. 1991. Definition of trophic classes in wooded peatlands by means of vegetation types and plant indicators. Annales Botanici Fennici 28: 175–192.

Jongman, R., ter Braak, C. & van Tongeren, O. 1987. Data analysis in community and landscape ecology. Pudoc Wageningen. 299 p.

Kaunisto, S. 1983. Puuston typpilannoitustarpeen arvioiminen turvemailla. Metsäntutkimuslaitoksen tiedonantoja 94: 4–19.

— 1988. Metsäojitettujen turvemaiden ravinnevaroista ja niiden riittävyydestä. Summary: On nutrient amounts and their sufficiency for wood production on drained peatlands. Suo 39(1–2): 1–7.

— & Paavilainen, E. 1988. Nutrient stores in old drainage areas and growth of stands. Communicationes Instituti Forestalis Fenniae 145. 39 p.

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. 94 p.

Keltikangas, V. 1945. Ojitettujen soitten viljavuus eli puuntuottokyky metsätyyppiteorian valossa. Summary: The Fertility of Drained Bogs as Shown by their Tree Producting Capacity, Considered in Relation to the Theory of Forest Types. Acta Forestalia Fennica 53(1). 237 p.

Korpela, L. 1999. Diversity of vegetation in pristine and drained forested mire margin communities in Finland. International Peat Journal 9: 94–117.

— 2000. Equisetum sylvaticum. Metsäkorte. In: Reinikainen, A. et al. (eds.). Kasvit muuttuvassa metsäluonnossa. Tammi, Helsinki. p. 191–193.

Kuusipalo, J. 1985. An ecological study of upland forest site classification in southern Finland. Acta Forestalia Fennica 192. 78 p.

— & Vuorinen, J. 1981. Pintakasvillisuuden sukkessiosta vanhalla ojitusalueella Itä-Suomessa. Summary: Vegetation succession on an old, drained peatland area in eastern Finland. Suo 32(3): 61–66.

Laiho, R. 1994. Voitaisiinko soita luokitella pelkkien turpeen ravinnetunnusten perusteella? Abstract: Could we create a peatland classification system based on peat nutrient contents? Metsäntutkimuslaitoksen tiedonantoja 531: 56–61.

— 1996. Changes in understorey biomass and species composition after water level drawdown on pine mires in southern Finland. Suo 47(2): 59–69.

— & Laine, J. 1994. Nitrogen and Phosphorus Stores in Peatlands drained for Forestry in Finland. Scandinavian Journal of Forest Research 9: 251–260.

— , Sallantaus, T. & Laine, J. 1999. The effect of forestry drainage on vertical distribution of major plant nutrients in peat soils. Plant and Soil 207: 169–181.

Laine, J. 1989. Metsäojitettujen soiden luokittelu. Summary: Classification of peatlands drained for forestry. Suo 40(1): 37–51.

— & Starr, M. 1979. An analysis of the post-drainage stand increment in relation to the peatland site type classification. In: Kivinen, E. et al. (eds.). Classification of peat and peatlands. International Peat Society. Helsinki. p. 147–159.

— & Vasander, H. 1986. Turpeiden tuntemus ja luokittelu. Abstract: Classification and properties of peat. Publications from the Department of Peatland Forestry, University of Helsinki 9. 56 p.

— & Vasander, H. 1990. Suotyypit. Kirjayhtymä, Helsinki. 80 p.

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

— , Vasander, H. & Laiho, R. 1995. Long-term effects of water level drawdown on the vegetation of drained pine mires in southern Finland. Journal of Applied Ecology 32: 785–802.

Legendre, P. & Legendre, L. 1998. Numerical ecology, ed. 2. Elsevier. Amsterdam. 853 p.

Lukkala, O. 1929. Über den Aziditätsgrad der Moore und die Wirkung der Entwässerung auf denselben. Communicationes ex Instituto Quaestionum Forestalium Finlandiae 13. 24 p.

— & Kotilainen, M. 1951. Soiden ojituskelpoisuus. Keskusmetsäseura Tapio. Helsinki. 63 p.

Mäkipää, R. 1999. Response patterns of Vaccinium myrtillus and V. vitis-idaea along nutrient gradients in boreal forest. Journal of Vegetation Science 10: 17–26.

— 2000. Dicranum majus. Isokynsisammal. In:

Reinikainen, A. et al. (eds.). Kasvit muuttuvassa metsäluonnossa. Tammi, Helsinki. p. 242–243.

Mannerkoski, H. 1979. Comparison of methods in classification of vegetation on a drained peatland area. In: Kivinen, E. et al. (eds.). Classification of peat and peatlands. International Peat Society. Helsinki. p. 109–120.

Melin, E. 1917. Studier över de norrländska myrmarkernas vegetation med särskild hänsyn till deras skogsvegetation efter torrläggning. Norrländskt Handbibliotek 7. 426 p.

Metsätilastollinen vuosikirja 2001. Finnish Statistical Yearbook of Forestry. Metsäntutkimuslaitos. Finnish Forest Research Institute. SVT. Maa-, metsä- ja kalatalous 2001:52. Agriculture, forestry and fishery. 374 p.

Minchin, P.R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. Vegetatio 69: 89–107.

— 1991. DECODA. Database for Ecological Community Data. Version 2.04. Australian National University.

Minkkinen, K. & Laine, J. 1998. Effect of forest drainage on the peat bulk density of pine mires in Finland. Canadian Journal of Forest Research 28: 178–186.

Neshatayev, V. 1989. Changes in forest types on drained peatlands in North-Western Russia. In: Sjögren, E. (ed.). Forests of the World: diversity and dynamics (Abstracts). Studies in Plant Ecology 18: 189.

Nieminen, M. & Pätilä, A. 1990. Karujen rämeiden luokittelu pintakasvillisuuden ja ravinnetunnusten avulla. Summary: Classification of oligotrophic pine mires on the basis of ground vegetation and fertility parameters. Folia Forestalia 749. 29 p.

Nousiainen, H. 2000a. Cladina. Poronjäkälät. In: Reinikainen, A. et al. (eds.). Kasvit muuttuvassa metsäluonnossa. Tammi, Helsinki. p. 288–290.

— 2000b. Cetraria. Hirvenjäkälät. In: Reinikainen, A. et al. (eds.). Kasvit muuttuvassa metsäluonnossa. Tammi, Helsinki. p. 286–287.

Ojansuu, R. 1996. Kasvupaikan kuvaus metsän kehitystä ennustettaessa. Metsäntutkimuslaitoksen tiedonantoja 589: 120–129.

Økland, R.H. 1989. A phytoecological study of the mire Northern Kisselbergmosen. SE Norway. I. Introduction, flora, vegetation and ecological conditions. Sommerfeltia 8. 172 p.

— 1990a. Vegetation ecology: theory, methods and applications with reference to Fennoscandia. Sommerfeltia Supplement 1. 233 p.

— 1990b. A phytoecological study of the mire Northern Kisselbergmosen. SE Norway. III. Diversity and habitat niche relationships. Nordic Journal of Botany 10: 191–220.

— 1996. Are ordination and constrained ordination alternative or complementary strategies in general ecological studies? Journal of Vegetation Science 7: 289–292.

— & Ohlson, M. 1998. Age-depth relationships in Scandinavian surface peat: a quantitative analysis. Oikos 82: 29–36.

— , Økland, T. & Rydgren, K. 2001. Vegetation-environment relationships of boreal spruce swamp forests in Østmarka Nature Reserve, SE Norway. Sommerfeltia 29. 190 p.

Økland, T. 1996. Vegetation-environment relationships of boreal spruce forest in ten monitoring reference areas in Norway. Sommerfeltia 22. 349 p.

Oksanen, J. 1984. Lichen-rich forests and related communities in Finland: ordination and classification studies. University of Joensuu Publications in Sciences 1. 35 p.

Paalamo, P. 1996. Ojituksen vaikutuksia Nurmes-tutkimusalueella: soiden ekologiset vaihtelusuunnat ja pintakasvillisuus. Lic. Phil. thesis. University of Joensuu, Department of Biology. 77 p.

Paavilainen, E. & Päivänen, J. 1995: Peatland Forestry: ecology and Principles. Springer. Ecological Studies 111. 248 p.

Päivänen, J. 1969. The bulk density of peat and its determination. Silva Fennica 3(1): 1–19.

— & Seppälä, K. 1968. Hajalannoituksen vaikutus lyhytkortisen nevan pintakasvillisuuteen. Summary: Effect of broadcast fertilizer on the ground vegetation of a low sedge swamp. Suo 19(3–4): 51–56.

Pakarinen, P. 1976. Agglomerative clustering and factor analysis of south Finnish mire types. Annales Botanici Fennici 13: 35–41.

— 1979. Ecological indicators and species groups of bryophytes in boreal peatlands. In: Kivinen, E. et al. (eds.). Classification of peat and peatlands. International Peat Society. Helsinki. p. 121–134.

— 1982. Etelä-Suomen suo- ja metsätyyppien numeerisesta luokittelusta. Summary: Numerical classification of South Finnish mire and forest types. Suo 33(4–5): 97–103.

— 1994. Impacts of Drainage on Finnish Peatlands and their Vegetation. International Journal of Ecology and Environmental Sciences 20: 173–183.

— & Ruuhijärvi, R. 1978. Ordination of northern Finnish peatland vegetation with factor analysis and reciprocal averaging. Annales Botanici Fennici 15: 147–157.

Pätilä, A. & Nieminen, M. 1990. Turpeen emäsravinne- ja rikkitase karuilla ojitetuilla rämeillä laskeuma huomioon ottaen. Summary: Base cation nutrients and sulphur status of drained oligotrophic pine mires considering the atmospheric input. Folia Forestalia 759. 16 p.

Peet, R.K. 1974. The measurement of species diversity. Annual Review of Ecology and Systematics 5: 285–307.

Penttilä, T. 1984. Suometsien puustobonitoinnin mahdollisuudet. Metsäntutkimuslaitoksen tiedonantoja 148: 79–89.

— & Honkanen, M. 1986. Suometsien pysyvien kasvukoealojen (SINKA) maastotyöohjeet. Metsäntutkimuslaitoksen tiedonantoja 226. 98 p.

Pielou, E.C. 1966. Shannon's formula as a measure of specific diversity: Its use and misuse. The American Naturalist 100: 463–465.

Pienimäki, T. 1982. Kasvillisuuden ojituksenjälkeinen kehitys eräillä suotyypeillä Pohjois-Pohjanmaalla. Summary: Development of vegetation on some drained mire site types in North-Ostrobotnia. Suo 33(4–5): 113–123.

Reinikainen, A. 1983. Problems concerning the classification of drained peatlands in Finland. Proceedings of the International Symposium on Forest Drainage, Tallin, USSR, Sept. 19th–23rd 1983. International Peat Society. p. 203–215.

— 1984a. Soiden ja metsäojitettujen turvemaiden luokittelun perusteet ja nykyongelmat. Metsäntutkimuslaitoksen tiedonantoja 148: 65–78.

— 1984b. Suotyypit ja ojituksen vaikutus pintakasvillisuuteen. In: Jaakkoinsuon koeojitusalue 75 vuotta. Summary: Jaakkoinsuo experimental drainage area 75 years. Metsäntutkimuslaitoksen tiedonantoja 156: 7–21.

— 1988. Metsäojitettujen soiden kasvupaikkaluokituksen suunnanhakua. Summary: The need of improving the site classification of mires drained for forestry. Suo 39(3): 61–71.

— 1989. Luonnontilaisesta suosta turvekankaaksi. Metsäntutkimuslaitoksen tiedonantoja 337: 15–25.

— 1994. Turvekankaat – kangasmetsäkasvillisuutta turvemaalla? Abstract: The similarity of vegetation on old drained peatlands and upland forest site types. Metsäntutkimuslaitoksen tiedonantoja 531: 11–18.

Saarinen, M. & Hotanen, J-P. 2000. Raakahumuksen ja kasvillisuuden yhteisvaihtelu Pohjois-Hämeen vanhoilla ojitusalueilla. Summary: Covariation between raw humus layer and vegetation on peatlands drained for forestry in western Finland. Suo 51(4): 227–242.

Salemaa, M. 2000. Calluna vulgaris. Kanerva. In: Reinikainen, A. et al. (eds.). Kasvit muuttuvassa metsäluonnossa. Tammi, Helsinki. p. 109–111.

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

— 1961b. Ojitettujen soiden luokittelusta. Summary: How the drained peatlands are classified. Suo 12: 75–77.

Schönemann, P.H. & Carroll, R.M. 1970. Fitting one matrix to another under choice of a central dilation and a rigid motion. Psychometrika 35: 245–255.

Sevola, Y. 1983. Metsähallinnon Nurmeksen hoitoalueen voimaperäinen puunkasvatus: seurantajärjestelmä ja tuloksia. Summary: Intensive timber growing in a state forest district: monitoring system and results. Folia Forestalia 574. 83 p.

Silfverberg, K. & Hotanen, J-P. 1989. Puuntuhkan pitkäaikaisvaikutukset ojitetulla mesotrofisella kalvakkanevalla Pohjois-Pohjanmaalla. Summary: Long-term effects of wood-ash on a drained mesotrophic Sphagnum papillosum fen in Oulu district, Finland. Folia Forestalia 742. 23 p.

Silfverberg, U. 1991. Eteläsuomalaisten korpikoealojen ojituksenjälkeinen kehitys. M.Sc. thesis. University of Helsinki, Department of Peatland Forestry. 75 p.

Sjörs, H. 1948. Myrvegetation i Bergslagen. Acta Phytogeographica Suecica 21. 299 p.

SPSSx User's Guide 1988. SPSS Inc. Chicago. 1072 p.

Tolonen, K. 1967. Über die Entwicklung der Moore im finnischen Nordkarelien. Annales Botanici Fennici 4: 219–416.

— 1974. Suomen keidassuovesien ravinteista. Summary: On the nutrient content of surface water in ombrotophic mire complexes in Finland. Suo 25(3–4): 41–51.

— & Saarenmaa, L. 1979. The relationship of bulk density to three different measures of the degree of peat humification. In: Kivinen, E. et al. (eds.). Classification of peat and peatlands. International Peat Society. Helsinki. p. 227–238.

Vahtera, E. 1955. Metsänkasvatusta varten ojitettujen soitten ravinnepitoisuuksista. Referat: Über die Nährstoffgehalte der für Walderziehung entwässerten Moore. Communicationes Instituti Forestalis Fenniae 45(4): 1–108.

Valtakunnan metsien inventoinnin (VMI 7) kenttätyön ohjeet 1977. Yleinen osa. (Field instructions for the 7th National Forest Inventory of Finland. General part). The Finnish Forest Research Institute, Helsinki. 59 p.

van der Maarel, E. 1979. Transformation of cover abundance values in phytosociology and its effect on community similarity. Vegetatio 39: 97–114.

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

— 1990. Plant biomass, its production and diversity on virgin and drained southern boreal mires. Publications from the Department of Botany, University of Helsinki 18. 16 p.

— , Lindholm, T. & Kaipiainen, H. 1988. Vegetation patterns on a drained and fertilized raised bog in southern Finland. Proceedings of the 8th International Peat Congress, USSR Leningrad August 14–21, 1988. 1: 177–184.

— , Laiho, R. & Laine, J. 1997. Changes in species diversity in peatlands drained for forestry. In: Trettin, C. et al. (eds.). Northern Forested Wetlands: Ecology and Management. Lewis Publishers, Boca Raton, New York, London, Tokyo. p. 109–119.

Vitikainen, O., Ahti, T., Kuusinen, M., Lommi, S. & Ulvinen, T. 1997. Checklist of lichens and allied fungi of Finland. Norrlinia 6: 1–123.

von Post, L. 1922. Sveriges Geologiska Undersöknings torvinventering och några av dess hittills vunna resultat. Sv. Mosskulturföreningens Tidskrift 1. 27 p.

Westman, C.J. 1987. Site classification in estimation of fertilization effects on drained mires. Acta Forestalia Fennica 198. 55 p.

— 1994. Turpeen ravinnemäärät ojitusalueen puuntuotantoa säätelevänä tekijänä. Abstract: Forest production on drained peatlands in relation to the content of nutrients in the surface peat. Metsäntutkimuslaitoksen tiedonantoja 531: 69–73.

Wiegleb, G. 1989. Explanation and prediction in vegetation science. Vegetatio 83: 17–34.

Total of 143 references

Appendix 1. Vegetation on the sample plots by TWINSPAN group. Species abundance is according to octave scaling (see Fig. 5).

	1	2	3	4	5	6	7	8	9
Pinus sylvestris	434344444422	3-2444552343334-	-31---23131212---2-2121-21-1221-3-1311	3333--234--13----13-12-	1---	----1----	--------	-------	--
Vaccinium oxycoccos	11---33--1-1	3-132222332--154	-211-1--1--1-----------11---11--111-1-	---1-11-1-1---11-123211	32-1	--------1	--------	------1	--
Vaccinium microcarpum	211221122111	23111111221131-1	--111----11-1--1-------------1-11--2--	-111-1--------11-11111-	--1-	---------	--------	-------	--
Dactylorhiza maculata	------------	1---------------	--------------------------------------	-----------------------	----	---------	--------	-------	--
Trichophorum cespitosum	------------	3---------------	--------------------------------------	-----------------------	----	---------	--------	-------	--
Carex pauciflora	-----1------	---------------1	--------------------------------------	-----------------------	----	---------	--------	-------	--
Mylia anomala	21342221-1--	---------12----1	--------------------------------------	-----------------------	----	---------	--------	-------	--
Polytrichum strictum	4663525444-2	4514654512411412	2-12---1-2122--3------122--11433--1---	11-311321-1-3-263323251	-2-1	-1-------	1-------	-------	--
Warnstorfia fluitans	------------	----------1-----	--------------------------------------	-----------------------	----	---------	--------	-------	--
Sphagnum rubellum	31--2-1-----	---1-----73-----	-------1------------------------------	-----------------------	----	---------	--------	-------	--
Sphagnum magellanicum	111315432--1	2-4641611-1-3366	12-2-11--12-2-11-2-1-11-2-111--3---13-	-1------------2114-233-	14-1	1-----1--	11--1---	-------	--
Sphagnum fuscum	777788757443	7616-667676697-6	1-1423111--16--1-------2-------2------	-------------------4---	----	---------	--------	-------	--
Sphagnum fallax	------------	---------------1	--------------------------------------	-----------------------	----	---------	--------	-------	--
Sphagnum majus	3----1------	----------------	--------------------------------------	-----------------------	----	---------	--------	-------	--
Sphagnum papillosum	------------	----------1-----	--------------------------------------	-----------------------	----	---------	--------	-------	--
Cladina arbuscula	5244--124112	21--1-----------	--122214-1--1--1-------1--------------	1-----1111--1------1---	----	-----1---	--------	-------	--
Cladonia cenotea	------1-----	----------------	--------------------------------------	-----------------------	----	---------	--------	-------	--
Cetraria islandica	1-12---34131	----------------	---322---1--2-1--------1--------------	-----------------------	----	---------	--------	-------	--
Sphagnum balticum	5----2------	----------------	--------------------------------------	-----------------------	----	---------	--------	-------	--
Calluna vulgaris	-------7-666	777-43-6766573-4	----2--5-6454------------1--34--------	175756--544---1----3-7-	1-1-	-3-------	--------	-------	--
Andromeda polifolia	343252234142	3233311113324411	1231-211111122-1-1-1--111---111111112-	12122221211-1-132241131	12-1	-1------1	--------	-------	--
Eriophorum vaginatum	666667755756	3576788657765756	734463664247314213--5432211212-3211341	5235-34-4-61-665266335-	1411	----11111	----1---	1-----1	--
Carex lasiocarpa	------------	12--------------	--------------------------------------	-----------------------	1-12	---------	--------	-------	--
Cladonia deformis	--11---11--1	----------------	-1----11-1----------------------------	-------1---------------	----	---------	--------	-------	--
Cladonia cornuta	--1-----1--1	----------------	-1-------1----------------------------	-------1---------------	----	---------	--------	-------	--
Salix myrtilloides	------------	----------------	--------------------------------------	-----------------------	-3-3	---------	--------	-------	--
Empetrum nigrum	676646556444	1446541653125453	356444545446454555-4-1-425--1543-41533	4454336464515--1-4135-5	3121	-2121--2-	----1---	-------	--
Betula nana	356573-53635	5656777654665663	6354435455564-542---4-43-31246-5-41332	7565--13445447775876556	5424	---------	1-------	-------	--
Vaccinium uliginosum	776765677466	565532162546-464	56623255466566355535654543435765664425	55664168714464445565665	3312	-2122----	--------	-------	1-
Rubus idaeus	------------	----------------	--------------------------------------	-----------------------	1---	---------	--------	-------	--
Carex chordorrhiza	------------	----------------	--------------------------------------	-----------------------	-1--	---------	--------	-------	--
Dicranum bergeri	-1-1-11---1-	--------114-----	--13541-1------1-------1--------------	--------1--------------	----	---------	--------	-------	--
Cladina rangiferina	415512156155	33-1----1---11--	1434425245114113----1--1-1----32----1-	3--1-11331-12---1-31-1-	----	---------	----1---	-------	--
Pyrola rotundifolia	------------	----------------	--------------------------------------	-----------------------	---1	---------	--------	-------	--
Equisetum fluviatile	------------	----------------	--------------------------------------	-----------------------	---1	---------	--------	-------	--
Sphagnum warnstorfii	------------	----------------	--------------------------------------	-----------------------	---5	---------	--------	-------	--
Festuca rubra	------------	----------------	--------------------------------------	-----------------------	-1-3	---------	--------	-------	--
Chamaedaphne calyculata	333324413321	1--21-411--2-13-	21-333432-314-233312233--2332333433433	4232---221412-21-312-1-	----	--211---1	--------	1------	--
Populus tremula	------------	----------------	------------------------------2-------	-----------------------	----	---------	--------	-------	--
Carex magellanica	------------	----------------	--------------------------------------	------------------1----	-1--	---------	--------	-------	--
Cladonia gracilis	------------	----------------	---------1-----1----------------------	-----------------------	----	---------	--------	-------	--
Ledum palustre	2412315-546-	---1---31-----5-	4554665-4-13564676355665444431535--542	4544-42352355----34-211	---1	-2334--3-	----1---	-------	--
Sphagnum capillifolium	-11----42-51	----2---1----2--	--5-221-15143521-1-----3-4----612225--	--11-1323334---------2-	2-1-	---113---	--------	-------	--
Molinia caerulea	------------	5--------------4	-------------------1------------------	-----------------------	6183	-------1-	1-------	------1	--
Sphagnum angustifolium	656478755445	7777477657986886	655-5511613355-7251314246-647718677643	47678775546475787676756	68-7	263116466	24-11---	233113-	5-
Melampyrum pratense	--------1--1	--11--1-1--11--2	---------------------1----------111-1-	----------------11---11	-1--	-----1--1	-1------	----1--	1-
Aulacomnium palustre	5532512133-3	5566564635643416	12113-12-313-131-2133112-111111111121-	43552154556432554154251	1-11	13321212-	11--1-1-	11--114	4-
Betula pubescens	-3-12-211512	1225-34233122234	344--23544-115444555444124233244466344	14432254324335324314342	1312	133432343	44422242	44324-3	3-
Pleurozium schreberi	786765787888	6876876784774766	89999999899998988787887778985898777998	86687878888888766886788	7677	788786766	78878778	6666676	56
Sphagnum russowii	---1--261---	62--6----4744561	3242-5--3431-6-73636578672417734777453	66666744546356--3758776	7847	161127787	1641313-	--65664	--
Rubus chamaemorus	546666674444	2555766472577765	-336653327644411374626365-5465-423414-	-224--3----1242322-3642	5116	5-6517275	44436-21	253--35	43
Polytrichum juniperinum	------------	-1------1-------	--11-----11--1-----------11-111-1-11-1	----11---1-11----------	----	111-1-1--	1-------	-------	-1
Juniperus communis	------------	61--------------	----------------------------3---------	--1--------------------	7366	3--34----	--------	-------	--
Epilobium angustifolium	------------	--------1------1	3-------1--1--1----11-----------------	1------------4--1------	----	---1-----	1-3-----	------3	-1
Polytrichum commune	------------	5--1------1----3	----------------------------1-6---41--	-4447536-143517581-5616	4-11	-6---1-31	-51--2-2	5565866	1-
Ptilidium ciliare	------------	-----------1----	----------2-----------------1---------	------2----------------	----	--1-1----	1---1---	-------	--
Dicranum polysetum	--1---111112	--1--1--2----1-2	13443315121132411133254214541-11111111	1-1-223216122-3-1-1--11	--1-	645431511	74765355	-111-4-	--

	1	2	3	4	5	6	7	8	9
Salix aurita	------------	----------------	-------------------------------------3	--3-14-224-5-------4---	----	-5355----	--------	-------	--
Brachythecium reflexum	------------	----------------	---------------------------1----------	-----------------------	----	-------1-	--------	-------	--
Dicranum fuscescens	------------	----------------	---1------------------1---------------	-----------------------	----	---------	1-------	-------	--
Vaccinium myrtillus	--3-----5263	5-114-----1-11-1	47766544656468778778677787777654777667	37746764577566--1642676	4324	778887566	88888677	5754274	5-
Carex globularis	--4---------	-4-12---1--4-4--	22---1--4-4-13322364---226-22144424333	61224554654556566476236	24-2	355545235	35553444	-56356-	11
Ptilidium crista-castrensis	------------	----------------	-------11----------------1------------	------121--------------	----	--1------	----1---	-------	-1
Picea abies	----1-1--2-3	3-11322-3--3--33	4333332-4-1114432544432342335515544443	2333223---43-22433-3323	3524	2-3314333	34444334	4434-45	5-
Vaccinium vitis-idaea	--1-----445-	-1-45---4----1--	766757557-5666866655766557476666666666	75666666677766556656645	7564	675447556	55555453	7664654	64
Peltigera aphthosa	------------	----------------	--------------------------1-----------	------------------1----	----	---------	--------	---1---	--
Carex vaginata	------------	----------------	--------------------------------------	----2------------------	-1-3	---------	--------	-------	2-
Alnus incana	------------	3---------------	--------------------------------------	-----------------------	----	---------	--------	-------	4-
Carex rostrata	------------	-------------1-1	------------------------------------1-	-----------------------	----	---------	--------	------1	1-
Salix phylicifolia	------------	---------------5	--------------------------------------	----------------3--3--2	2534	---------	-----4--	2-3-333	5-
Carex nigra	------------	----------------	--------------------------------------	-----------------------	---4	---------	--------	------2	11
Gymnocarpium dryopteris	------------	----------------	--------------------------------------	-----------------------	---2	3--------	--------	-314254	--
Dryopteris carthusiana	------------	---------------2	-------1------------12----------------	1------------3---------	---1	1--1-----	1-1--1--	-121-35	-1
Rubus arcticus	------------	----------------	--------------------------------------	-----------------------	----	---------	--------	------2	--
Potentilla palustris	------------	----------------	--------------------------------------	-----------------------	-1--	---------	--------	------3	2-
Epilobium palustre	------------	----------------	--------------------------------------	-----------------------	----	---------	--------	-------	-1
Cornus suecica	------------	----------------	--------------------------------------	-----------------------	----	---------	--------	----1--	--
Viola palustris	------------	----------------	--------------------------------------	-----------------------	----	---------	--------	----1--	--
Orthilia secunda	------------	----------------	--------------------------------------	-----------------------	-1-2	------1--	1-------	--13--1	14
Trientalis europaea	------------	---------------1	--------------------2----1------------	-----------------------	1234	2--------	1-------	-122224	34
Menyanthes trifoliata	------------	----------------	--------------------------------------	-----------------------	----	---------	--------	------1	3-
Melampyrum sylvaticum	------------	----------------	--------------------------------------	-----------------------	----	---------	--------	-------	-1
Solidago virgaurea	------------	----------------	--------------------------------------	-----------------------	---1	---------	--------	---1-1-	--
Maianthemum bifolium	------------	----------------	--------------------------------------	-----------------------	----	2--------	--------	--34433	-6
Juncus filiformis	------------	----------------	--------------------------------------	-----------------------	----	---------	--------	------1	--
Luzula pilosa	------------	----------------	------------------------------------1-	--1-------------1------	----	---------	-1------	-----12	11
Carex canescens	------------	---------------1	--------------------------------------	-----------------------	----	--------1	--------	11----3	32
Calamagrostis purpurea	------------	----------------	--------------------1-----------------	-----------------------	----	---------	--------	--3-42-	13
Agrostis tenuis	------------	----------------	--------------------------------------	-----------------------	----	---------	--------	------1	-1
Agrostis canina	------------	----------------	--------------------------------------	-----------------------	----	---------	--------	------1	1-
Hepaticae spp	------------	----------------	----------1-----------------1---------	-----------------------	----	---------	--------	11----3	--
Sphagnum centrale	------------	----------------	--------------------------------------	-----------------------	----	---------	--------	-------	4-
Viola epipsila	------------	----------------	--------------------------------------	-----------------------	----	---------	--------	------2	21
Sphagnum fimbriatum	------------	----------------	--------------------------------------	-----------------------	----	---------	--------	-------	-1
Rhamnus frangula	------------	----------------	--------------------------------------	-----------------------	----	---------	--------	-1-----	3-
Polytrichastrum longisetum	------------	----------------	--------------------------------------	-----------------------	----	---------	--------	-1----1	--
Plagiomnium cuspidatum	------------	----------------	--------------------------------------	-----------------------	----	---------	--------	-------	42
Brachythecium starkei	------------	----------------	--------------------------------------	-----------------------	----	--------1	--------	12-----	1-
Sorbus aucuparia	------------	---------------2	-----------------1-2-4----------------	----------1------------	---1	3-331----	4-12----	--45434	--
Linnaea borealis	------------	----------------	--------------------------------------	-----------------------	---2	3---1----	4-------	---2-12	24
Lycopodium annotinum	------------	---------------2	--------------------------------------	-----------------------	----	4--------	1-------	-4----4	--
Equisetum sylvaticum	------------	----------------	----------------1--------1-1---------2	-----------3-----------	----	--331-24-	----21--	--33252	76
Deschampsia flexuosa	------------	----------------	------------------11------------------	------1---------1--2---	---1	---11-1--	-141----	1--2423	21
Sphagnum girgensohnii	------------	----------------	--------------------------------------	-----------------------	----	-----5--8	-------1	7688776	-1
Brachythecium curtum	------------	----------------	--------1-------1211432---------------	-------2-----3---------	----	-2553----	343-----	--23-24	56
Plagiothecium laetum	------------	----------------	--------------1-----1----------1-11---	-----------------------	----	--------1	--211324	14---1-	44
Salix caprea	------------	----------------	-------------------1------------------	-----------------------	----	---22----	--------	-------	--
Goodyera repens	------------	----------------	--------------------------------------	-----------------------	----	---------	----1---	-------	--
Barbilophozia barbata	------------	----------------	--------1-----------1111--------------	-----------------------	----	--11-----	-3--1221	-----2-	--
Plagiothecium sp	------------	----------------	--------------------------------------	-----------------------	----	----1----	--------	-------	--
Dicranum scoparium	------------	----------------	---11---1------1------------1---1-----	--------------1-------1	--1-	111111-11	21311426	111----	-1
Dicranum majus	------------	----------------	------------------11---11--1----1-1---	-----------1----------1	-1--	1-----111	44572634	121--31	--
Hylocomium splendens	------------	----------------	--------------215124---63-11---11--114	-------4---------------	-1--	31221154-	45346886	2--1-2-	14
Plagiothecium denticulatum	------------	----------------	--------------------------------------	-----------------------	----	---------	-----111	-------	--
Pohlia nutans	4-1-111---1-	------1---------	-------------------------1------------	-----------------------	1--1	1---1----	1---1-1-	111----	--