Canopy Stratification in Peatland Forests in Finland

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Abundance and species number of the tree and shrub vegetation in different canopy layers were analysed according to site quality class and drainage succession phase on permanent sample plots on spruce mires (n=268) and pine mires (n=628) in the Finnish National Forest Inventory in 1995. The abundances based on the crown coverage were compared with the abundances based on the parallel basal area of the tree stand. The canopy coverages and species number for peatland forests were also compared with those for mineral soil forests on the permanent sample plots (n=1725) in 1995.

In general, effective temperature sum correlated positively, although not very strongly, with the coverages and species number in most of the canopy layers, as well as with the mean range of the diameter distribution. The effects of both site quality class and drainage phase were stronger on pine mires than on spruce mires, most probably due to the longer fertility gradient and large potential free growing space in the former group. On pine mires, drainage increased the abundances and species number in the different canopy layers, as well as the structural inequality of the tree stands. On spruce mires, the increase was principally allocated to the abundances of the dominant and intermediate tree layers. The correlations between the total crown coverage of the tree layers and stand basal area were r=0.45 for spruce mires and r=0.70 for pine mires. Compared to mineral soil forests, in addition to having a higher abundance of *Betula pubescens*, the dominant layer was not as pronounced in peatland forests. On spruce mires, the coverage of the shrub layer on mesotrophic and meso-oligotrophic sites was higher than that in mineral soil forests. The average species number in different canopy layers did not differ significantly between spruce mires and mineral soil forests in corresponding site quality classes. On pine mires, the species number was generally lower (except for the mesotrophic sites) than that in corresponding mineral soil forests.

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1 Introduction

The need for different kinds of descriptions of tree stands has increased especially for assessing and managing biodiversity (e.g. Swindel et al. 1991, Norokorpi et al. 1997, Uuttera et al. 1997, Lähde et al. 1999, Korpela 1999, 2004, Pitkänen 2000, Staudhammer and LeMay 2001). High structural diversity in the tree layer, as well as in the shrub layer, is also considered to provide an opportunity for high diversity among other forest species (Camp 1994, Larsen 1995).

On pristine boreal mires in maritime or semi-maritime climates, the structure of tree stands is uneven-aged with a wide range in tree diameters (e.g. Hörnberg 1995, Päivänen 1999, cf. Lieffers 1986, Groot and Horton 1994). The trees are generally concentrated in the small diameter classes, and the shape of the diameter distribution is usually a reversed J-shape (Heikurainen 1971, Gustavsen and Päivänen 1986, Ågren and Zackrisson 1990). Pristine mire stands represent a dynamic stability with new individuals continually emerging, while others are dying (Päivänen 1999). These are features of a climax forest.

In general, forest management has a tendency to smooth the variation that exists in natural structures, leading to homogenization of the age and size distribution as well as the species composition of the growing stock (Esseen et al. 1992, Larsen 1995). However, the results for drained peatland forests, for example along drainage succession gradients, have varied with respect to stand inequality/diversity (Hökkä and Laine 1988, Uuttera et al. 1996, 1997, Freléchoux et al. 2000, Korpela 2002, Sarkkola et al. 2002, 2003, 2004).

The shape of the diameter distribution has been found to change slowly or sometimes remain unchanged for up to 30–60 years after drainage (Hökkä and Laine 1988, Sarkkola et al. 2002, 2003, cf. Sarkkola et al. 2004, 2005), irrespective of whether silvicultural cuttings are carried out (Hökkä et al. 1991, cf. Sarkkola et al. 2005). This has been explained by the post-drainage regeneration of new seedlings and ingrowth which, in turn, results from the drawdown of the water level and subsequent improvement of the growing conditions (Hökkä and Laine 1988). If the stands

are analysed on the basis of other characteristics, such as growth rate, stand basal area, proportions of different tree species, or the range of the diameter distribution, it is however clear that drainage and other management practices have strongly affected peatland forests (Keltikangas et al. 1986, Uuttera et al. 1997, Hökkä and Penttilä 1999, Hökkä et al. 2002, Sarkkola et al. 2003).

In addition to drainage and extensive fertilization carried out in the 1960–80's (Paavilainen and Päivänen 1995, Metsätilastollinen vuosikirja 2002), the use of different kinds of cutting and soil preparation have also become more and more common in peatland forests (cf. Paavilainen and Päivänen 1995, Hökkä et al. 2002, Penttilä et al. 2002). Despite the fact that our knowledge of the dynamics, structure and productivity of the tree stands on both undrained and drained peatlands has increased considerably over the years (e.g. Gustavsen and Päivänen 1986, Keltikangas et al. 1986, Ågren and Zackrisson 1990, Hökkä et al. 1991, 2002, Groot and Horton 1994, Hörnberg et al. 1995, Norokorpi et al. 1997, Gustavsen et al. 1998, Päivänen 1999, Roy et al. 2000, Jutras et al. 2003), we still have relatively limited information about the structural development of the stands as well as about species abundances and diversity in different canopy layers after water-level drawdown (cf. Korpela 2002, 2004, Sarkkola et al. 2003, 2005). The shrub layer, in particular, has received little attention and, consequently, its structure and variation in different peatland site types are poorly known (Reinikainen 2000a).

In Finland, where almost 6 million ha and nearly 30% of present-day forests are former mires and, in addition, 0.9 mill. ha of pristine mires belong to productive forest land (Hökkä et al. 2002), the question of special character of peatland forests is a central object of interest. One essential feature of peatland forests is the present and continuing rapid change of ecosystem due to the post-drainage succession (Tomppo 1999). Tools for both intensive and extensive description of ecological features associated with peatland forests and, comparisons with dominating mineral soil forests, are needed.

In the 1980's, the possibility of using the Finnish National Forest Inventory (NFI) as an ecological monitoring system was investigated. Over 3000 permanent sample plots, with a wide range

Table 1. Number of permanent sample plots on spruce mires and pine mires in the 1995 inventory by site quality class and drainage succession phase. I=eutrophic, II=herb-rich, III=*Vaccinium myrtillus* and tall-sedge, IV=*Vaccinium vitis-idaea* and small-sedge, V=cottongrass and dwarf-shrub, and VI=*Sphagnum fuscum* mires. lt=undrained, oj=recently drained, mu=transforming drained, tkg=transformed drained mires.

	lt	oj	mu	tkg	Total
Spruce mires, 1995					
I	3	–	1	6	10 (4%)
II	17	2	21	36	76 (28%)
III	28	9	62	58	157 (59%)
IV	6	2	12	5	25 (9%)
Total	54 (20%)	13 (5%)	96 (36%)	105 (39%)	268
Pine mires, 1995					
I	4	3	2	–	9 (1%)
II	7	4	4	4	19 (3%)
III	21	1	31	21	74 (12%)
IV	52	14	134	49	249 (40%)
V	61	41	124	14	240 (38%)
VI	19	15	2	1	37 (6%)
Total	164 (26%)	78 (12%)	297 (47%)	89 (14%)	628

of measurements and observations, were established in addition to the standard forest inventory plot networks (Reinikainen and Nousiainen 1985, 1995, Valtakunnan metsien... 1985–86, Pysyvien koealojen... 1995). In addition to making detailed tree measurements on the permanent plots, there was also an opportunity to test methods simple enough for describing the vertical structure of the stands for use in extensive inventories and mappings. The structure of the stand on these plots was determined in the form of species crown coverages in different canopy layers. Since then, tree crown coverage has become the most important criterion for the world-wide definition of forest (Forest Resources...2000).

The aim of this study was to describe and compare tree and shrub vegetation in different canopy layers in the main groups of peatland site types, site quality classes and post-drainage succession phases on the permanent sample plots in the inventory carried out in 1995. The average structure, described as canopy coverages of the individual species, was compared with the structure based on basal areas using the parallel tree measurement data. The mean range of the diameter distribution was examined in the above-mentioned categories. The canopy coverages and species number for peatland forests were also compared with those for mineral soil forests in the 1995 inventory.

2 Material and Methods

2.1 Sampling and Field Work

The study material consists of the measurements and observations made on the permanent sample plots (300 m^2) in the Finnish National Forest Inventory (NFI) in 1995. The inventory was based on clusters of four permanent sample plots arranged in a north-south direction, located systematically 400 m apart (in northern Finland three plots 600 m apart). The distance between the clusters in both the north-south and east-west direction was 16 km, and in northern Finland 24 and 32 km, respectively (Pysyvien koealojen... 1995).

The main groups of forested peatland site types, i.e. spruce mires and pine mires, were included in the data (Table 1). Spruce mires are usually

characterized by *Picea abies* with varying admixtures of *Betula pubescens* and/or other deciduous species. Ombrotrophic and oligotrophic pine mires are generally dominated by *Pinus sylvestris*, whereas on more fertile sites especially *B. pubescens* and/or *P. abies* usually mix with *P. sylvestris* (Eurola et al. 1984, Paavilainen and Päivänen 1995). These main groups applied to both undrained and drained peatlands. Among the drained mires there were sites, which originally have been open mires but after drainage and afforestation are classified either into the pine mires or spruce mires (e.g. Tomppo et al. 2001). The species nomenclature follows Hämet-Ahti et al. (1989).

In the site quality classification used in the Finnish National Forest Inventories, peatland sites are grouped into six classes according to nutrient status (and estimated post-drainage tree stand productivity) (e.g. Paavilainen and Päivänen 1995). This classification is primarily based on the ground vegetation. The site quality (fertility, trophic) classes were I = eutrophic, II = herb-rich (mesotrophic), III = *Vaccinium myrtillus* and tall-sedge (meso-oligotrophic), IV = *Vaccinium vitis-idaea* and small-sedge (oligotrophic), V = cottongrass and dwarf-shrub (poor ombro-oligotrophic bogs), and VI = *Sphagnum fuscum* (ombrotrophic bogs) (Kuusela and Salminen 1969, Huikari 1974, Paavilainen and Päivänen 1995). The spruce mires belong to classes I–IV and the pine mires to classes I–VI.

The post-drainage vegetation succession (drainage) phase was divided into four classes: undrained (Finnish abbreviation lt), recently drained (oj; slight effect on ground vegetation, no or little effect on tree stand), transforming drained (mu; clear effect on ground vegetation and tree stand), and transformed drained (tkg; vegetation resembles corresponding heath forest site type, tree stand forest-like) mires (Sarasto 1961, Pysyvien koealojen... 1995) (Table 1).

The tree stand treatment during the 10-year-period before the 1995 inventory was grouped as follows: 0 = no treatment, 1 = cleanings, commercial thinnings or preparatory cut, 2 = removal of overstorey trees, special cuttings such as cuttings for opening drainage or road construction or cuttings for repairing detected forest damages, 3 = artificial regeneration, natural regeneration (cf.

Table 2. Number of sample plots in the reference mineral soil forests in the 1995 inventory by site quality class. Mature forests include development class 6, i.e. stands ready for regeneration (Pysyvien koealojen … 1995). I = grove (herb-rich forest); II = grove-like, III = fresh, IV = dryish, and V = dry heath.

	Mature forests	All development classes
I	4	32
II	66	338
III	204	815
IV	71	464
V	13	75
Total	358	1725

Tomppo et al. 1997).

In the NFI, mineral soil forests are also classified into six fertility (site type) classes. These classes are comparable with those for peatland sites (e.g. Kuusela and Salminen 1969). The reference material of mineral soil forests on permanent plots in 1995 consisted of site quality classes I–V: I = grove (herb-rich forest), II = grove-like (herb-rich) heath forest, III = fresh (mesic) heath forest, IV = dryish (sub-xeric) heath forest and, V = dry (xeric) heath forest (e.g. Frey 1973). Site quality class VI (barren heath forest) was omitted because it contained only one sample plot. Exposed bedrock, cliff or sandy forestry land (class VII), as well as timber line forests including mountains (VIII), were also excluded (Table 2).

The canopy layers applied were as follows: 1 = overstorey (trees clearly taller, > 2 m, or clearly older, > 40 years, than the dominant trees), 2 = dominant (> 80% of the length of the highest dominant trees – this main storey consists of those trees which are the principal object of silvicultural stand-treatment measures), 3 = intermediate (70–80% of the length of the dominant trees), 4 = suppressed (< 70% of the dominants), and 5 = under-growth layer (trees considerably shorter and generally > 40 years younger than the dominants). Classes 1 and 5 are distinctly different tree cohorts than the 2–4 (Kuusela and Salminen 1969, Reinikainen and Nousiainen 1985, 1995, Pysyvien koealojen...1995, Korpela 2004).

Projection coverages (in %) for the shrub and tree species in the shrub layer (trees 0.5 to 1.5 m

and genuine shrub species, i.e. those species generally not reaching tree height and form, without an upper limit) and for the tree species in five vertical canopy layers were estimated visually on the plots of 300 m^2. This was made with the help of information about the diameter of the single tree canopy. The canopy (crown) diameter was not measured on all trees on the plot, but instead, examples of tree species belonging to different canopy layers were taken for diameter measurements. The estimated locations of the crown margins were marked on the ground, and the diameter was measured with a tape measure. The sum coverages by species were then calculated for the different layers. During the field work, the measurements and estimations of the individual inventory group were compared and calibrated by the other inventory groups.

Trees on the plots with a diameter at breast height ($dbh_{1.3}$) of over 4.5 cm were tallied (Pysyvien koealojen...1995). Their basal areas were calculated. Treewise basal areas were then summed by tree species and canopy layers. Finally, the basal areas were extrapolated to the hectare level according to the size of the plot. The basic size of the sample plot (300 m^2) was applied for trees with a dbh of over 10.5 cm. Sub-sample plot of size of 100 m^2 was applied for trees 4.5 cm < dbh ≤ 10.5 cm. Tree seedlings capable for further development with a diameter < 4.5 cm were also tallied on this sub-sample plot (their basal area was included in the basal area figures). Description of the under-growth layer (5) according to the basal area abundances was complemented by the number of tree seedlings (tree height > 1.5 m and dbh < 4.5 cm) obtained from the so-called small-tree data file (Pysyvien koealojen...1995). This file includes the number and mean height of all seedlings (height > 0.2 m and dbh < 4.5 cm) counted from the above-mentioned sub-sample plot of 100 m^2.

The range of the diameter distribution was calculated as the difference in dbh between the largest and the smallest measured tree on the sample plot (Uuttera et al. 1996, 1997). Tree species or canopy layers were not taken into account in these calculations.

2.2 Statistical Analyses

Pearson correlation coefficients between coverages in different canopy layers, and between the coverages and effective temperature sum (threshold +5°C), were calculated (SPSS 11.0 for Windows) for spruce mires and pine mires. Similarly, the coefficients were calculated for the species number. The temperature sum was calculated for the individual sample plots by the method of Ojansuu and Henttonen (1983). For the spruce mires and pine mires, correlation coefficients were also calculated between the total crown coverage and stand basal area of trees.

The GLM (General Linear Model) multivariate variance procedure (SPSS 11.0 for Windows) was applied to test the variation of the total coverage and species number in different canopy layers between site quality classes (sq) and drainage phases (dp). The multivariate procedure was performed separately for the coverage and species number. The tree stand treatment (trt) during the 10-year-period before the 1995 inventory was used as the third grouping factor. Pairwise interactions, sq×dp, sq×trt, and dp×trt, were examined one by one by adding it to (and removing from) the main effect model to keep the model simple enough for interpretation. The results were calculated separately for spruce mires and pine mires. In the analyses, the regional variation was taken into account by using the effective temperature sum as a covariate. The mean range of the diameter distribution was investigated in a corresponding fashion, but using the univariate procedure.

For the species number in the different canopy layers and in the canopy layers combined, as well as for the total coverage of the shrub layer, repeated and simple contrasts (in the GLM) were used to identify significant differences between individual main type groups (spruce mires, pine mires, mineral soil forests) in corresponding fertility classes. Otherwise the comparisons between peatland and mineral soil forests were performed graphically. For the mean range of the diameter distribution, the contrasts were used to localize differences between individual site quality classes and drainage succession phases.

3 Results

3.1 Abundance in Canopy Layers

3.1.1 Coverage

The correlations between the coverages of different canopy layers were weak, especially on spruce mires. Clearly the highest correlation was between the intermediate and suppressed layer (Table 3).

In general, temperature sum (ts) correlated positively, although not very strongly, with the coverages of the different canopy layers (Table 3). On spruce mires, there was no correlation between ts and total coverage of the shrub layer (Table 3) (there was, however, a slight positive correlation $r = 0.14$, $p = 0.026$ between ts and the coverage of tree shrubs and a slight negative correlation $r = -0.12$, $p = 0.050$ between ts and the coverage of genuine shrubs, cf. Table 4).

Table 3. Pearson correlation coefficients between coverages in different canopy layers and between the coverages and temperature sum (ts) for spruce mires (upper triangle) and pine mires (lower triangle). 1 = overstorey, 2 = dominant, 3 = intermediate, 4 = suppressed, 5 = under-growth, and S = shrub layer. * = $p \leq 0.05$, ** = $p \leq 0.01$, *** = $p \leq 0.001$.

					Spruce mires			
		1	2	3	4	5	S	ts
	1	–	–0.08	–0.01	0.04	–0.08	0.03	0.13*
	2	–0.06	–	0.14*	0.16**	0.09	–0.05	0.23*
	3	0.01	0.25***	–	0.37***	–0.08	–0.13*	–0.04
Pine mires	4	0.00	0.25***	0.38***	–	–0.07	–0.02	0.08
	5	–0.07	0.20***	0.15***	0.08	–	0.01	0.24***
	S	–0.01	0.16***	0.06	0.11**	0.18***	–	–0.00
	ts	–0.13**	0.29***	0.11**	0.11**	0.19***	0.14**	–

Table 4. Significance (F, p) of multivariate analysis of variance for the total coverage in different canopy layers. (cf. Figs 1–4). ts = temperature sum (covariate), sq = site quality class, dp = drainage phase, trt = stand treatment with cuttings. 1–5 = tree layers combined. S = shrub layer, t = trees in the shrub layer, g = genuine shrubs.

	ts		sq		dp		trt	
	F	p	F	p	F	p	F	p
Spruce mires								
1	2.0	0.155	0.0	0.997	1.7	0.171	1.1	0.344
2	7.7	0.006	4.2	0.006	2.4	0.066	5.3	0.001
3	2.9	0.088	2.7	0.046	3.0	0.030	3.7	0.012
4	2.3	0.129	1.6	0.180	0.2	0.893	2.0	0.109
5	28.1	<0.001	2.2	0.089	2.7	0.048	0.5	0.690
1–5	17.7	<0.001	4.5	0.004	2.5	0.058	7.5	<0.001
S	0.0	0.938	1.0	0.415	0.6	0.629	0.4	0.767
t	5.2	0.024	0.5	0.691	0.6	0.603	0.3	0.795
g	4.3	0.039	3.1	0.026	0.6	0.641	0.2	0.878
Pine mires								
1	7.0	0.008	0.8	0.523	0.9	0.458	2.2	0.084
2	31.0	<0.001	10.3	<0.001	21.6	<0.001	4.9	0.002
3	2.8	0.096	2.4	0.036	7.1	<0.001	2.5	0.058
4	3.3	0.071	3.5	0.004	6.6	<0.001	1.6	0.179
5	14.7	<0.001	4.9	<0.001	4.5	0.004	1.1	0.356
1–5	35.1	<0.001	15.7	<0.001	29.4	<0.001	5.8	0.001
S	7.9	0.005	4.8	<0.001	1.6	0.191	6.4	<0.001
t	7.6	0.006	1.3	0.267	1.9	0.125	7.2	<0.001
g	1.2	0.278	7.1	<0.001	0.3	0.842	1.1	0.354

**Spruce mires, 1995**   **Pine mires, 1995**
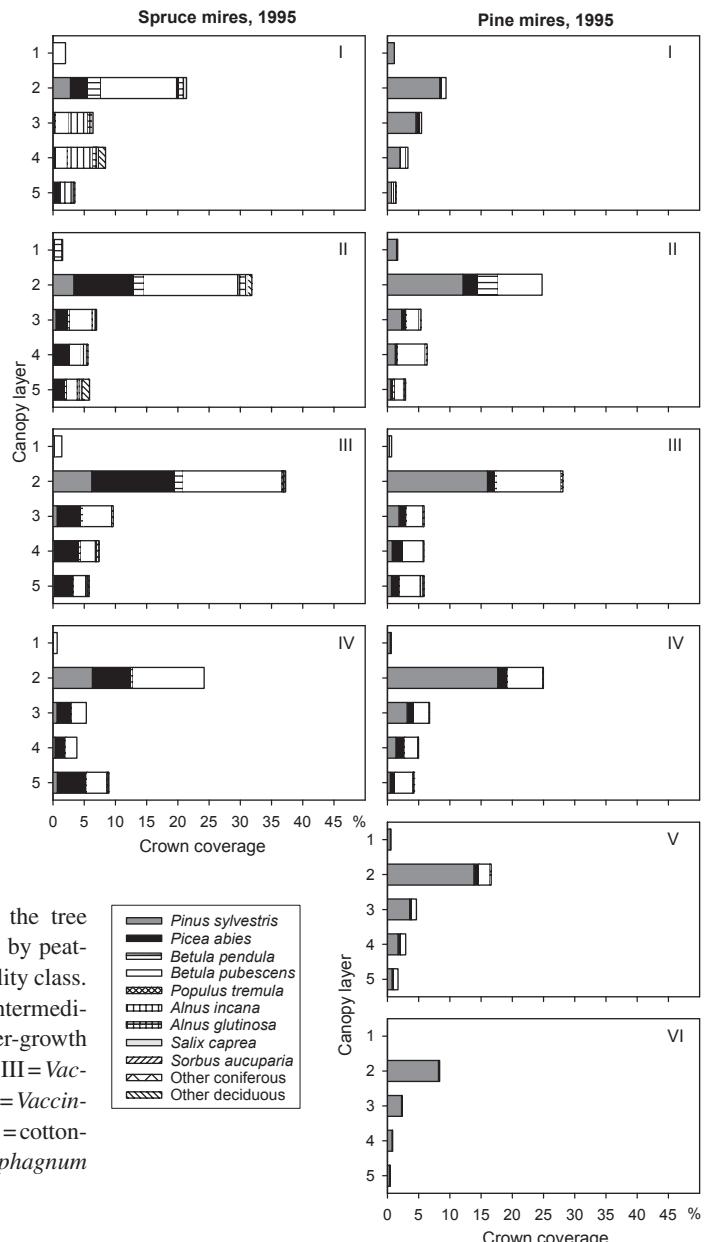
Fig. 1. Average crown coverages of the tree species in different canopy layers by peatland main type group and site quality class. 1 = overstorey, 2 = dominant, 3 = intermediate, 4 = suppressed, and 5 = under-growth layer. I = eutrophic, II = herb-rich, III = *Vaccinium myrtillus* and tall-sedge, IV = *Vaccinium vitis-idaea* and small-sedge, V = cottongrass and dwarf-shrub, and VI = *Sphagnum fuscum* mires.

The site quality class (sq) and drainage succession phase (dp) affected the coverages of the tree layers in both of the main site type groups (Figs 1 and 2, Table 4). The effects were stronger in the pine mire material with respect to most of the canopy layers, especially the dominant tree layer. Temperature sum was a significant covariate for most of the canopy layers (Table 4).

The highest coverage values were found on meso-oligotrophic sites. The abundance relationships of species (in different canopy layers) naturally varied between the site quality classes. On spruce mires, for example, *Alnus incana* was most abundant, whereas *P. abies* was the scantiest in class I. On pine bogs (classes V and VI), the tree storey consisted almost exclusively of *Pinus*
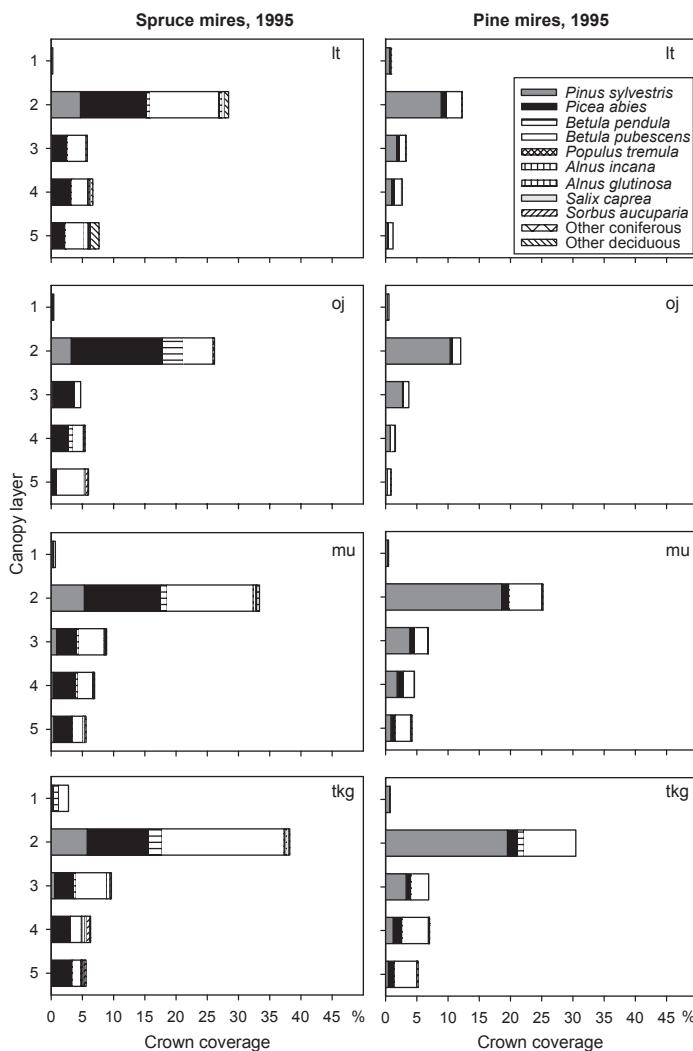
Fig. 2. Average crown coverages of the tree species in different canopy layers by peatland main type group and drainage succession phase. lt=undrained, oj=recently drained, mu=transforming drained, and tkg=transformed drained mires.

sylvestris (Fig. 1).

The coverage of the dominant tree layer increased along with the drainage succession phase – especially on pine mires (Fig. 2, Table 4). On spruce mires this was specifically due to the increase in the abundance of *B. pubescens*, and on pine mires also due to the increase of other species, especially *P. sylvestris*.

On spruce mires, the total coverage of the under-growth layer slightly decreased along with the drainage succession gradient (Fig. 2, cf. also Fig. 9). However, the pattern was relatively complicated as indicated by the interaction term sq×dp (F=2.3, p=0.020): in site quality class

IV the coverage increased after the transforming (mu) phase mainly due to *P. abies* (App. 1). The decrease in the under-growth layer did not concern *P. abies* in any of the site quality classes. In addition to the interaction sq × dp (F=2.1, p=0.009) for the overstorey on pine mires, the above-mentioned was the only significant interaction for different tree layers in both of the main type groups.

Stand treatment with cuttings had a significant effect by reducing the coverage of dominant and intermediate tree layers in both main type groups (cf. Table 4). During the ten-year period before the 1995 inventory, about 19% (n=50) of the
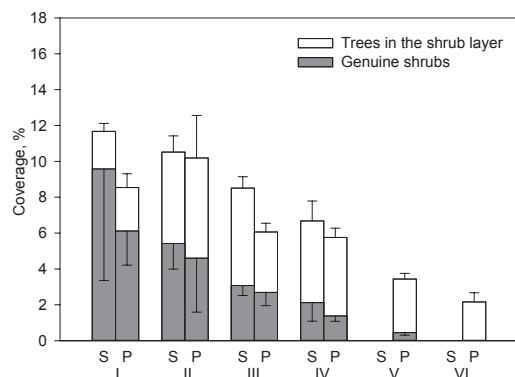
Fig. 3. Coverage of the shrub layer by peatland main type group (S = spruce mires, P = pine mires) and site quality class (mean, standard error of the mean) (cf. Table 5).

Fig. 4. Coverage of the shrub layer by peatland main type group and drainage succession phase (mean, standard error).

spruce mires and 10% (n=60) of the pine mires had been treated to different kinds of cutting.

Site quality class had a significant effect on the total abundance of genuine shrub species: the coverage increased along the fertility gradient from nutrient-poor to richer sites in both main type groups (Table 4, Fig. 3).

The frequencies and average coverages of individual genuine shrub species were, in general, low (Table 5). *Juniperus communis* was, however, abundant on fertile pine mires and *Salix phylicifolia* on spruce mires. No genuine shrub species were found on the poorest pine bogs (VI). *P. abies* and *B. pubescens* were the most abundant species in the shrub layer on spruce mires; *A. incana* was also common in class I and *P. sylvestris* in class IV. On pine mires, in addition to *B. pubescens*, *P. sylvestris* was frequent and relatively abundant, especially on ombro-oligotrophic sites. *P. abies* was also common, except in class VI.

On spruce mires, no significant effects of the dp on the coverage of shrub layer were found (Table 4). On pine mires, the coverage of the shrub layer presumably seemed to increase along with the drainage succession gradient (Fig. 4). However, the effect of dp was not significant (Table 4). Cuttings significantly affected the coverage of the shrub layer. The coverage was higher in treated stands than in the untreated stands, which was caused by the high coverage of the tree species in the shrub layer. However, the pattern was rela-

tively complex, as indicated by the interaction term dp×trt for the shrubs as a whole (F=5.8, p<0.001) and for the trees in the shrub layer (F=2.8, p=0.007). When the treated stands were removed from the analyses, the effect of dp was significant for the total shrub layer (p=0.026) and for the tree shrubs (p=0.032): the coverages increased along with the drainage succession gradient from recently drained mires (oj) onwards.
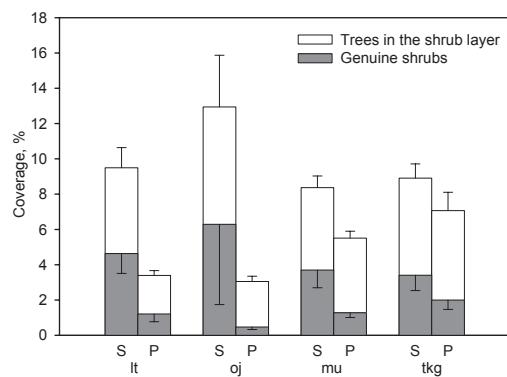
3.1.2 Peatland Forests vs Mineral Soil Forests

The dominant tree layer was, in general, only slightly more pronounced in mineral soil forests than in peatland forests (Figs 1 and 5). The coverage of *B. pubescens* was higher on spruce mires than the sum coverage of *B. pubescens* and *Betula pendula* on mineral soil sites in corresponding site quality classes. This was also the case on pine mires in classes III–V, as well as in class II except for the dominant layer; however, the total coverage of *Betula* in the dominant layer in class II was higher than that in the mineral soil forests. On fertile sites, the proportion of other deciduous tree species in the dominant layer was greater in mineral soil forests than in peatland forests.

In classes I–III, the proportion of *P. abies* in the dominant layer was greater on mineral soil sites than on spruce mires (or on pine mires naturally). In site quality classes IV–V, the forests on

Table 5. Coverages (mean %, all sample plots included) and frequencies (parentheses: % proportion of sample plots on which the species occurred) of the shrub layer species by peatland main type group and site quality class. Coverage<0.05%=+, frequency<0.5%=+.

| | Spruce mires | | | | Pine mires | | | | | |
	I	II	III	IV	I	II	III	IV	V	VI
GENUINE SHRUBS:										
Betula nana x *pubescens*	–	–	+ (1)	–	–	–	–	–	–	–
Frangula alnus	0.1 (10)	0.1 (17)	0.1 (10)	–	+ (11)	0.1 (21)	+ (4)	+ (3)	+ (+)	–
Juniperus communis	0.3 (30)	0.3 (20)	0.6 (24)	0.5 (20)	5.6 (89)	0.7 (53)	0.9 (24)	0.3 (13)	0.1 (3)	–
Ribes alpinum	–	–	–	–	–	–	+ (1)	–	–	–
R. spicatum	–	+ (1)	–	–	–	–	–	–	–	–
Rubus idaeus	0.2 (40)	0.9 (18)	0.2 (11)	+ (4)	–	0.3 (5)	0.5 (7)	+ (1)	–	–
Salix aurita	–	0.3 (14)	1.3 (23)	+ (4)	–	0.5 (11)	0.6 (15)	0.7 (16)	0.2 (4)	–
S. cinerea	–	0.4 (12)	0.1 (9)	0.2 (8)	–	2.1 (5)	0.1 (12)	0.1 (5)	+ (1)	–
S. glauca	0.2 (10)	–	–	–	–	–	–	–	–	–
S. lapponum	0.5 (10)	0.4 (4)	+ (2)	0.6 (8)	0.6 (11)	0.3 (26)	+ (3)	+ (2)	+ (1)	–
S. myrsinifolia	0.1 (20)	+ (1)	+ (5)	–	–	–	0.1 (1)	+ (1)	+ (+)	–
S. myrtilloides	–	+ (1)	+ (1)	–	–	–	+ (4)	+ (1)	–	–
S. phylicifolia	6.7 (40)	3.0 (33)	0.7 (30)	0.8 (28)	–	0.6 (32)	0.3 (20)	0.2 (14)	0.2 (6)	–
S. repens	–	–	+ (1)	–	–	–	–	+ (1)	+ (1)	–
S. rosmarinifolia	–	–	–	–	–	–	–	+ (+)	–	–
Salix spp	1.6 (30)	+ (3)	+ (2)	–	–	–	–	+ (1)	+ (+)	–
S. starkeana	–	–	–	–	–	–	+ (1)	–	–	–
Sambucus racemosa	–	–	–	–	–	–	0.1 (1)	–	–	–
TREES IN THE SHRUB LAYER:										
Alnus glutinosa	–	–	+ (1)	–	0.2 (11)	–	–	+ (+)	–	+ (3)
A. incana	0.8 (50)	0.2 (20)	0.1 (13)	–	0.4 (22)	0.1 (11)	+ (4)	+ (3)	+ (+)	–
Betula pendula	0.1 (10)	0.1 (5)	0.1 (8)	+ (4)	0.3 (11)	1.8 (11)	0.1 (5)	0.1 (5)	+ (6)	+ (5)
B. pubescens	0.2 (40)	1.7 (51)	1.9 (67)	2.5 (80)	0.1 (18)	2.2 (63)	1.4 (55)	2.5 (71)	1.0 (52)	0.2 (27)
Picea abies	0.4 (60)	1.9 (51)	2.4 (80)	1.3 (64)	0.6 (33)	0.6 (47)	0.7 (51)	0.8 (56)	0.5 (36)	0.2 (11)
Pinus sylvestris	–	0.2 (9)	0.1 (18)	0.5 (56)	0.5 (33)	0.7 (47)	0.7 (43)	0.5 (51)	1.4 (75)	1.7 (78)
Populus tremula	–	0.1 (9)	+ (7)	+ (4)	–	+ (16)	+ (5)	+ (2)	+ (1)	+ (3)
Prunus padus	+ (10)	+ (7)	–	–	–	–	–	–	–	–
Salix caprea	0.4 (40)	0.3 (18)	0.5 (20)	0.1 (16)	–	0.1 (11)	0.1 (15)	0.1 (11)	+ (2)	–
S. pentandra	0.1 (10)	0.1 (1)	–	–	0.2 (11)	–	+ (1)	+ (+)	–	–
Sorbus aucuparia	0.1 (30)	0.4 (47)	0.4 (45)	0.2 (24)	–	0.1 (26)	0.2 (26)	0.2 (9)	+ (2)	–

Fig. 5. Average crown coverages of the tree species in different canopy layers in mineral soil forests by site quality class. All = all development classes included, Mature = development class 6 i.e. stands ready for regeneration. I = grove (herb-rich forest); II = grove-like, III = fresh, IV = dryish, and V = dry heath.
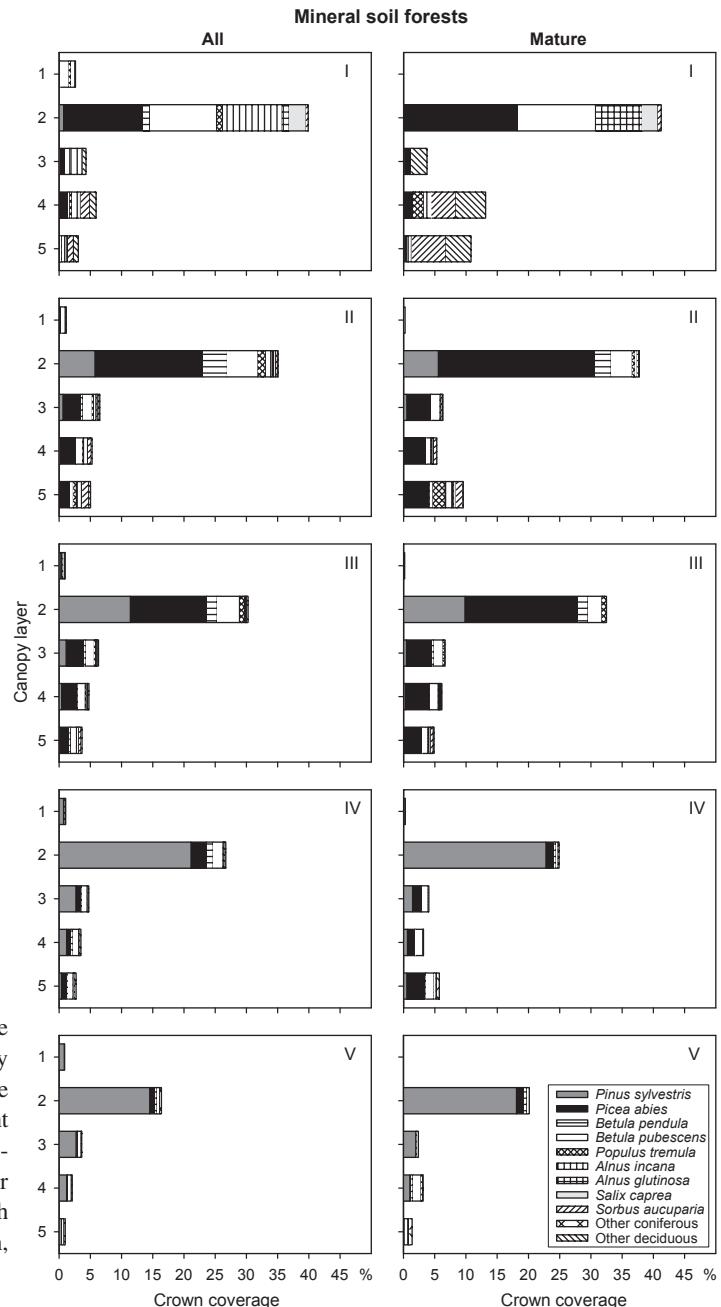
pine mires closely resembled those on mineral soil sites, however, with greater proportion of *B. pubescens*. In mature, fertile mineral soil forests the under-growth layer was more abundant than in peatland forests.

Compared to the mineral soil forests, the shrub layer had a significantly higher coverage on mesotrophic (p=0.027) and meso-oligotrophic (p<0.001) spruce mires (all development classes included) (Figs 3 and 6). The within-class variation was large, in particular on most fertile sites and mesotrophic pine mires (Fig. 3).
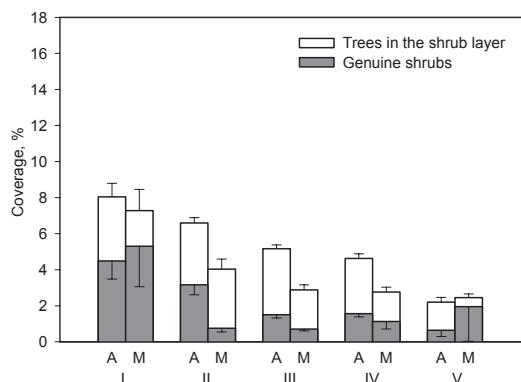
Fig. 6. Coverage of the shrub layer by site quality class in mineral soil forests (mean, standard error). A = all development classes, M = mature forests.

3.1.3 Coverage vs Basal Area

The correlations between the basal area (G) and total crown coverage (C) of trees were $r = 0.45$ ($p < 0.001$) for spruce mires and $r = 0.70$ ($p < 0.001$) for pine mires (cf. Fig. 7).

In the average values based on G, the dominant tree layer was more pronounced compared to the values calculated from C (Figs 2 and 8).

On spruce mires, the proportion of *P. abies* in the dominant layer especially was, in most cases, somewhat greater in the G-based material than in the C material. The generally small proportion of *B. pendula* was even smaller in the G material than in the C material. The proportional total abundance of the under-growth layer based on basal areas was smaller than the abundance based on the coverages. This was due to the minor proportions of *P. abies* and *B. pubescens*. In contrast, the abundance of *P. sylvestris* was more marked in the G figures than in the C figures in the under-growth layer.

On pine mires, the proportions of *P. sylvestris* in the dominant and under-growth layers were emphasized in the G-based values compared to those of the C values (Figs 2 and 8). In contrast, the proportion of G of *B. pubescens* was smaller than that of C, especially in the under-growth layer.

When the G-based estimation for the under-growth layer was complemented by the number of small trees (> 1.5 m) (Fig. 9), the species pool
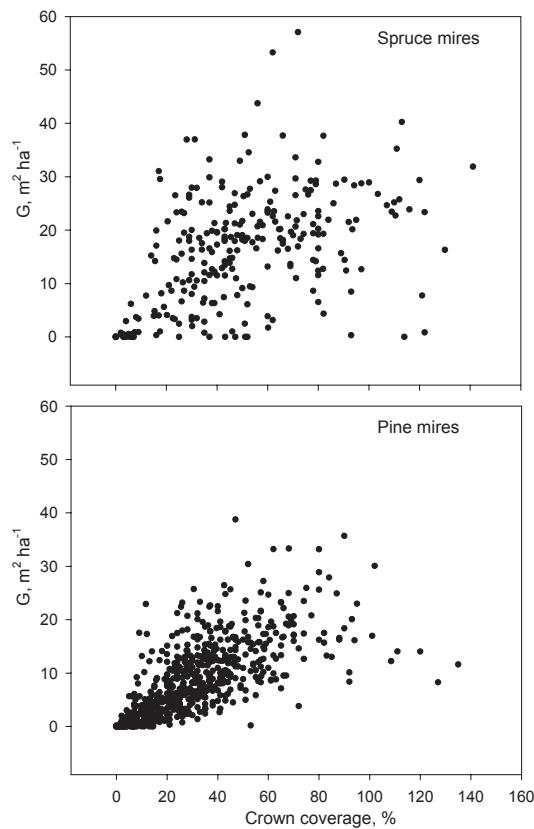
Fig. 7. Scatterplot of canopy coverage (%) against stand basal area (G) of trees by peatland main type group.

and proportional abundances became more similar with those in the C estimation in both main type groups.

3.2 Species Number in Canopy Layers

3.2.1 Peatland Forests

The correlations between the species number of different canopy layers were relatively low but generally positive, in particular on pine mires. As in the case of coverages, clearly the highest correlations were between the intermediate and suppressed layers (Table 6).

In general, temperature sum (ts) correlated positively, although not very strongly, with the species number of the different canopy layers. On spruce
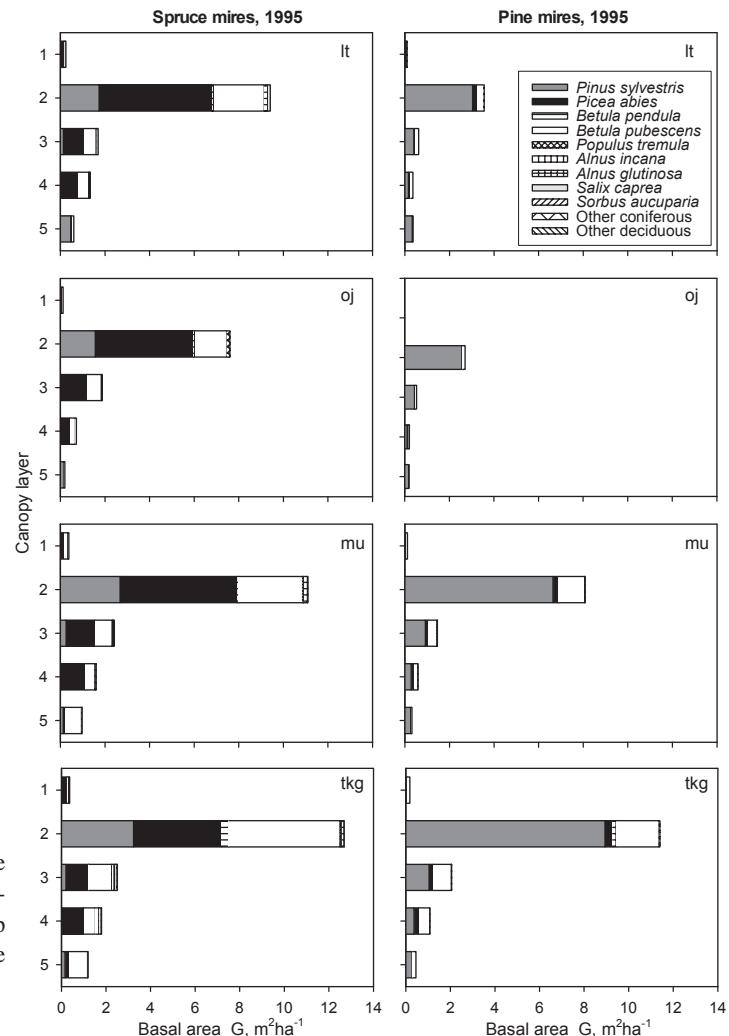
Fig. 8. Average basal area of the tree species in different canopy layers by peatland main type group and drainage succession phase (cf. Fig. 2).
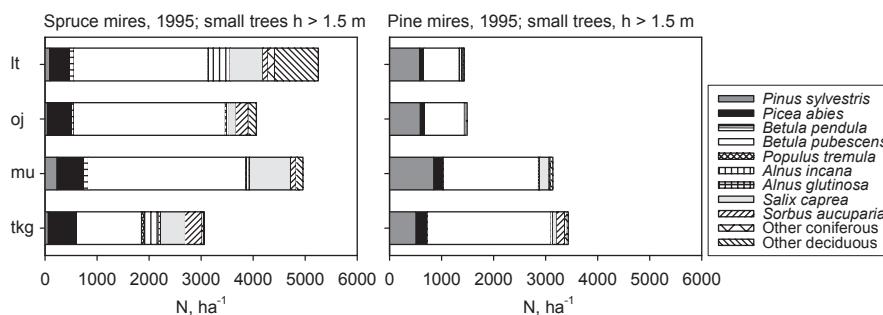
Fig. 9. Average number of tree seedlings (tree height > 1.5 m and diameter at breast height < 4.5 cm) by peatland main type group and drainage succession phase.

Table 6. Pearson correlation coefficients between species number in different canopy layers and between the species number and temperature sum (ts) for spruce mires (upper triangle) and pine mires (lower triangle). For explanations, see Table 3.

		1	2	3	Spruce mires 4	5	S	ts
	1	–	–0.01	–0.03	–0.01	–0.13*	0.25***	0.09
	2	0.07	–	0.12	0.04	0.09	0.14*	0.17**
	3	0.02	0.28***	–	0.42***	0.02	0.05	–0.12
Pine mires	4	0.02	0.22***	0.46***	–	–0.04	0.11	0.08
	5	–0.08*	0.14**	0.09*	0.08*	–	0.22***	0.31***
	S	0.01	0.29***	0.18***	0.23***	0.23***	–	0.29***
	ts	–0.11**	–0.00	0.04	–0.02	0.22***	0.13**	–

**Table 7.** Significance (F, p) of multivariate analysis of variance for the species number per sample plot in different canopy layers (cf. Figs 10–13). 1–5 = tree layers combined. ts = temperature sum (covariate), sq = site quality class, dp = drainage phase, trt = stand treatment with cuttings. S = shrub layer.

	ts F	p	sq F	p	dp F	p	trt F	p
Spruce mires								
1	1.6	0.210	1.0	0.409	0.6	0.637	1.6	0.200
2	7.6	0.006	0.3	0.860	1.1	0.331	7.8	<0.001
3	3.4	0.068	1.4	0.247	1.4	0.240	4.5	0.005
4	0.8	0.377	1.2	0.295	0.7	0.537	1.4	0.251
5	31.7	<0.001	0.5	0.706	1.0	0.390	2.1	0.096
1–5	45.1	<0.001	0.2	0.896	0.3	0.825	8.1	<0.001
S	19.2	<0.001	1.4	0.250	0.3	0.807	1.3	0.263
Pine mires								
1	3.9	0.048	1.7	0.139	2.1	0.095	3.3	0.021
2	0.8	0.369	14.2	<0.001	4.6	0.003	4.5	0.004
3	0.1	0.731	6.0	<0.001	5.5	0.001	3.7	0.012
4	1.6	0.207	6.7	<0.001	10.6	<0.001	2.5	0.055
5	20.7	<0.001	4.5	0.001	11.4	<0.001	0.6	0.593
1–5	4.3	0.039	21.1	<0.001	13.2	<0.001	2.3	0.079
S	9.1	0.003	18.3	<0.001	6.0	<0.001	0.9	0.452

mires, the significant correlations were for the under-growth, shrub and dominant layers; on pine mires, they were for the under-growth and shrub layers (Table 6, cf. Table 7). The correlations between ts and the species number of the tree layers (1–5) combined were r = 0.39 (p < 0.001) for spruce mires and r = 0.12 (p = 0.003) for pine mires.

On spruce mires, neither the site quality class nor drainage succession phase had any significant effect on the species number (Table 7, Figs 10–13). However, there was significant interaction term sq × dp (F = 2.2, p = 0.028) for the dominant layer, which meant that the pattern along with the succession gradient varied between site quality classes: in classes I and II, the species number was the highest in the transformed (tkg) phase, whereas in classes III and IV slightly in the transforming (mu) phase. No other significant interactions were found for spruce mires.

Among the pine mires, mesotrophic sites (Class II) showed generally the highest and *S. fuscum* bogs (VI) the lowest species number in the canopy layers (Fig. 10). This concerned the shrub layer, too (Fig. 12). On spruce mires, the species number in the shrub layer was the highest on eutrophic sites (I) but, due to the large within-class variation in class I, the differences between I and the other
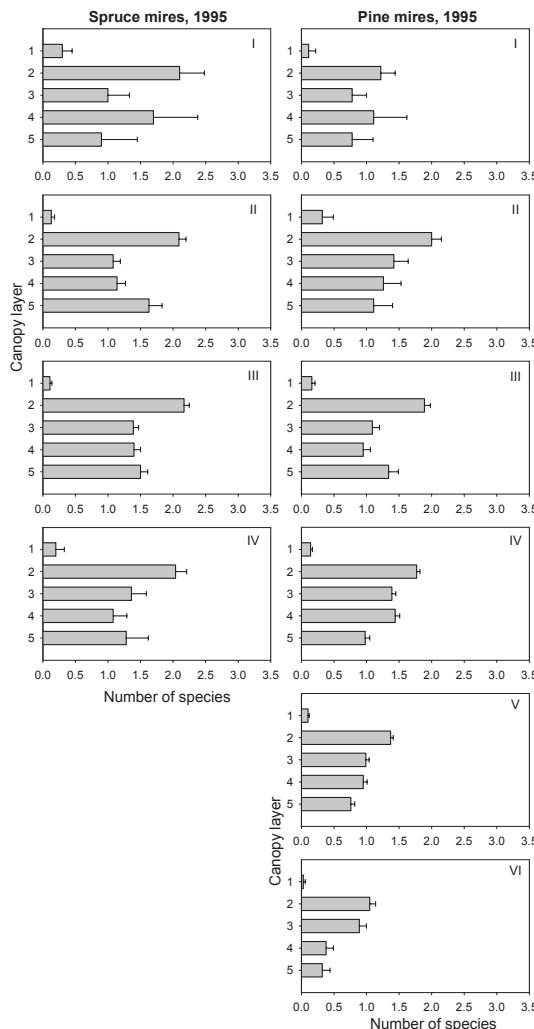
Fig. 10. Species number per sample plot in different canopy layers by peatland main type group and site quality class (mean, standard error).

Fig. 11. Species number per sample plot in different canopy layers by peatland main type group and drainage succession phase (mean, standard error).

classes were not significant.

Excluding the overstorey, the drainage phase significantly affected the species number in all the canopy layers on pine mires (Table 7, Figs 11 and 13). The species number was the highest in the tkg or in the mu phase. The only significant interaction sq dp (F = 1.9, p = 0.027) was for the shrub layer.

Stand treatment with cuttings had a significant effect by reducing the species number, especially in the dominant and intermediate layers (cf. Table 7).
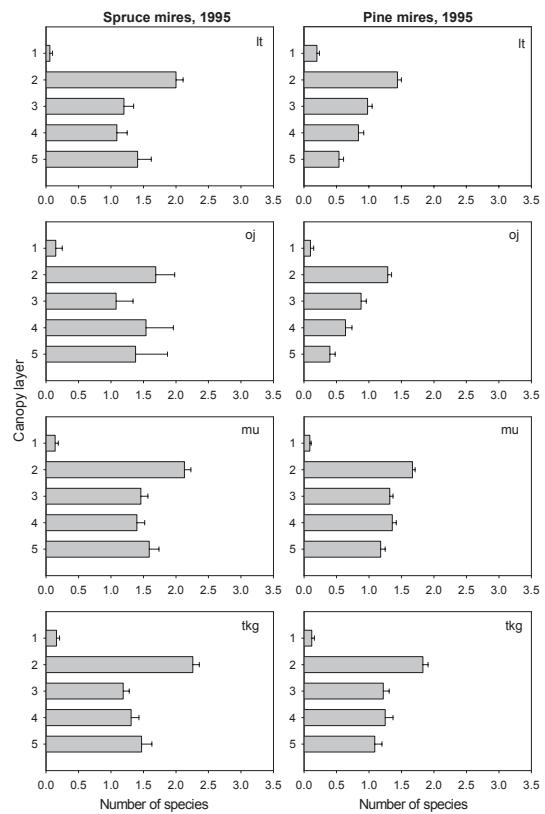
3.2.2 Peatland Forests vs Mineral Soil Forests

Although the average species number seemed, in some cases, to be slightly higher on mineral soil sites (all development classes included) than on spruce mires, no significant differences were found in corresponding site quality classes in any canopy layer between these two site type groups (Figs 10, 12, 14 and 15). There were also no statistical differences in the species number for the combined tree layers (1–5), nor for the combined tree and shrub layers, between these two groups. There were either no significant differences between any of the main type groups in site quality class II, respectively.
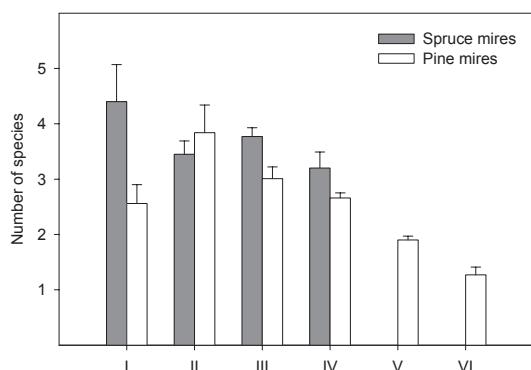
Fig. 12. Species number per sample plot in the shrub layer by peatland main type group and site quality class (mean, standard error).


Fig. 13. Species number per sample plot in the shrub layer by peatland main type group and drainage succession phase (mean, standard error).
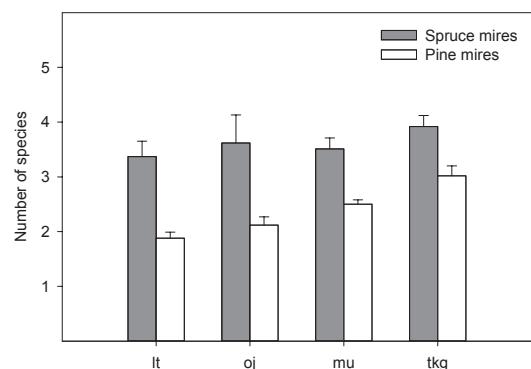
Fig. 14. Species number per sample plot in different canopy layers in all and in mature mineral soil forests by site quality class (mean, standard error).

The detected significant differences were: *in site quality class I*, the species number in the shrub layer (p=0.001 – 0.033) and in the combined tree and shrub layers (p<0.001 – 0.019) were higher on mineral soil sites and spruce mires than on pine mires; the dominant layer (p=0.012) and the combined tree layers (1–5) (p=0.002) were more species rich on mineral soil sites than on pine mires.

In class III, the shrub (p=0.008 – 0.024), suppressed (p=0.009 – 0.023), combined tree (p<0.001 – 0.009) and combined tree and shrub layers (p<0.001 – 0.001) were more species rich on mineral soil sites and spruce mires than on pine mires.

In class IV, the species number in the shrub (p<0.001), under-growth (p=0.002), combined tree (p<0.001) and combined tree and shrub layers (p<0.001) was higher in mineral soil forests than on pine mires but in the intermediate layer slightly lower (p=0.013).

In class V, only the total species number in the combined tree and shrub layers (p=0.001) was higher in mineral soil forests than on pine mires.

Table 8. Significance (F, p) of univariate analysis of variance for the mean range of the diameter distribution (cf. Figs 16–17). ts = temperature sum (covariate), sq = site quality class, dp = drainage phase, trt = stand treatment with cuttings.

| | ts | | sq | | dp | | trt | |
	F	p	F	p	F	p	F	p
Spruce mires	25.4	<0.001	2.0	0.108	1.3	0.265	7.2	<0.001
Pine mires	7.8	0.005	9.4	<0.001	15.4	<0.001	4.9	0.002
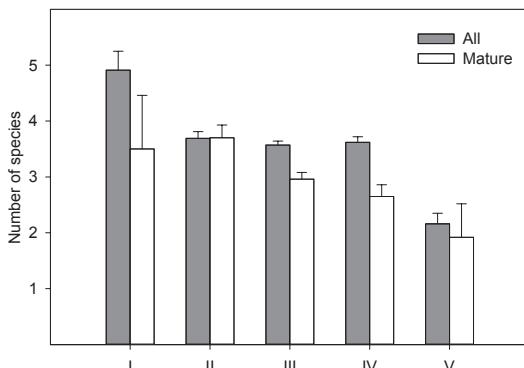
Fig. 15. Species number per sample plot in the shrub layer in all and in mature mineral soil forests by site quality class (mean, standard error).
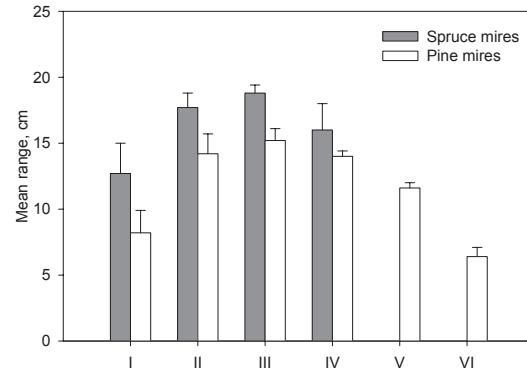

Fig. 16. Mean range of the diameter distribution by peatland main type group and site quality class (mean, standard error).

3.3 Range of Diameter Distribution

Site quality class (sq) and drainage succession phase (dp) had a significant effect on the mean range of the diameter distribution only on pine mires. Temperature sum (ts) as a covariate, and tree stand treatment (trt) by reducing the mean range of the diameter distribution, were significant in both main site types (Table 8). The correlations with ts and mean range of the diameter distribution were r = + 0.28 (p < 0.001) for spruce mires, and r = + 0.16 (p < 0.001) for pine mires. No significant interactions were observed.

The highest values occurred on the meso-oligotrophic sites, whereas the lowest ones were on the poorest and richest sites (Fig. 16). This seemed to be the case also with spruce mires, although there were no statistical differences. On pine mires, the values in site quality classes I and VI were lower (p < 0.001) than the values in the other classes (II–V). With respect to adjacent classes, there was also a significant difference between classes IV and V (p < 0.001).
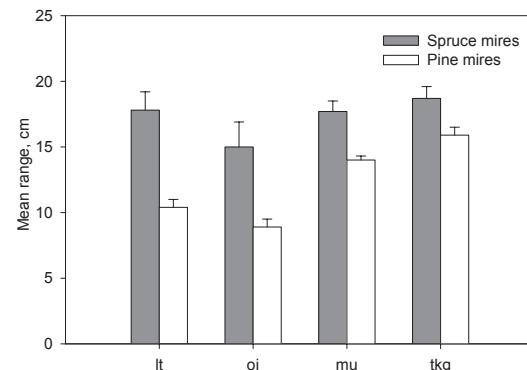
Fig. 17. Mean range of the diameter distribution by peatland main type group and drainage succession phase (mean, standard error).

In both main groups, the range of the diameter distribution received its lowest values (although not significantly different) in the recently drained (oj) mires (Fig. 17). In the pine mire material, the values of the undrained (lt) and oj mires differed significantly from the higher values of the transforming (mu) and transformed drained mires (tkg) (p < 0.001). There were no statistical differences between lt and oj, nor between mu and tkg.

4 Discussion

4.1 Abundance

The correlations between the temperature sum and the coverages of different canopy layers were, almost without exception, positive, although not strong. It is well known that the density, volume and growth of peatland (and mineral soil) forests decrease on moving northwards (e.g. Heikurainen and Seppälä 1973, Gustavsen and Päivänen 1986, Hökkä et al. 2002). However, particularly genuine shrubs, e.g. *Salix* spp. on spruce mires (and *Juniperus* on pine mires), may form dense populations in some places in the north (Eurola et al. 1984, Eurola 1999, Reinikainen 2000a). This could explain the observed slight negative correlation between temperature sum and the coverage of genuine shrub species on spruce mires.

The effects of both site quality class and drainage succession phase were stronger on pine mires than on spruce mires. Compared to spruce mires, the fertility gradient is longer on pine mires containing the whole scale from eutrophy (I) to ombrotrophy (V, VI) (e.g. Eurola et al. 1984). In their natural state, stands on spruce mires are denser and they have a more closed canopy than those on pine mires (e.g. Heikurainen 1971). Thus, there is larger potential free growing space on the pine mires (e.g. Hånell 1984). Composite (combination) types with an open mire influence and wet surfaces unsuitable for tree growth (Eurola et al. 1984) are more common on pine mires than on spruce mires (e.g. Keltikangas et al. 1986). For example, all the pine mires in classes I–III belong, in principle, to the composite types. Composite types do not, especially in their natural state and on young drained areas, have as complete a tree cover as the genuine mire site types. Consequently, the effect of drainage on the tree cover is stronger on pine mires.

The peatland forests with the greatest coverage – especially with respect to the dominant canopy layer – were found on meso-oligotrophic sites (class III). The growing conditions on more fertile sites are generally better, but it is obvious that different kinds of cutting strongly affect the prevailing situation in quickly developing stands on fertile sites, in particular those on spruce mires

(Paavilainen and Päivänen 1995, cf. Hökkä et al. 2002). On pine mires, the total coverages and the coverages of *Betula pubescens* were small in site quality class I due to the fact that the sample plots were concentrated in the classes of undrained and recently drained mires.

Clear changes emerged in the tree species composition and abundances after drainage. Irrespective of the treatments that were most probably directed at *B. pubescens* (Paavilainen and Päivänen 1995), the biotic power of this species in the secondary succession (Hökkä and Laine 1988, Reinikainen 2000a) was well reflected in most of the canopy layers on spruce mires and minerotrophic pine mires. In a selected spruce mire material from the 8th inventory in 1985–86 (Korpela 2002), the clearest change after drainage was the increased coverage of *B. pubescens* in the dominant layer, and mostly also in the intermediate and suppressed layer. It is also clear that extensive past fertilizations, carried out especially in the 1960–1980's (Metsätilastollinen vuosikirja 2002), have hastened the development of drained peatland forests (e.g. Paavilainen and Päivänen 1995).

In the transformed phase on most spruce mires, however, *B. pubescens* seemed to weaken in the under-growth and shrub layers, probably due to competition in low light conditions. On spruce mires, the coverage of the under-growth layer (but not that of *P. abies*) slightly decreased along with the drainage succession gradient, except in the oligotrophic class (IV) where it was higher in the transformed phase than in the transforming phase mainly due to *P. abies* (partly due to *B. pubescens*). Similar results were reported in Korpela's (2002) data – also on oligotrophic sites, due to *B. pubescens*.

On spruce mires, no significant effects of the drainage phase on the coverage of shrub layer were found. There are, however, species, which are affected by the drainage. For example, the occurrence of *Rubus idaeus* was primarily restricted to transformed sites (also Reinikainen 2000b). The abundance of *P. abies* in the shrub layer slightly increased along with the drainage succession gradient in both main type groups (cf. also Lukkala 1946, Saarinen 1989), and *B. pubescens* from the oj phase onwards on pine mires. *P. sylvestris* was the scantiest on transformed sites in both groups.

On spruce mires, drainage especially increased the coverages of the dominant and intermediate trees. On oligotrophic spruce mires, particularly, the increased coverage of *P. sylvestris* was also obvious in the intermediate and dominant layers (also Korpela 2002). The relatively high admixture of *P. sylvestris* in the growing stock on poor spruce mires is a common feature (e.g. Laine and Vasander 1990). On pine mires, when the potential growing space is released after drainage (see Hånell 1984), all the layers except the overstorey became more abundant; thus, there were also generally positive (but relatively weak) correlations between the different canopy layers. Clearly the strongest positive correlations were those between the intermediate and suppressed layers (also for the species number) in both main type groups, which means that if there was one of these layers then there was on many occasions the other layer as well.

Compared to mineral soil forests, in addition to having a higher coverage of *B. pubescens*, the dominant layer was not quite as pronounced in peatland forests. Mineral soil forests have been thinned (from below) at all fertility levels for a longer time than peatland forests, where extensive drainage was mainly performed in the 1960's and 1970's and where the most (especially regeneration) cuttings are primarily directed at fertile sites (cf. Tomppo 2000, Tomppo et al. 2001, Hökkä et al. 2002, Metsätilastollinen vuosikirja 2002). Thus, the dominant layer is generally well developed in mineral soil forests and the coverages decrease relatively evenly from fertile sites to poor sites.

The coverage of the shrub layer in peatland forests, particularly on mesotrophic and meso-oligotrophic spruce mires, was higher than that in mineral soil forests. Compared to a slight decrease of the shrub layer in mineral soil forests since 1950's, most probably due to intensive forestry practices (Reinikainen 2000a), the opposite trend in peatland forests is mainly explained by the above-mentioned power of *B. pubescens* in the drainage succession, as well as by the persistence and regeneration capacity of *P. abies* (and *P. sylvestris* on pine bogs) (Heikurainen 1959, Saarinen 1989, Laiho et al. 1997). However, in mature nutrient-rich mineral soil forests the combined under-growth and shrub layer were more abundant than these layers combined in peatland forests.

The under-growth together with the shrub layer may offer an important potential source for stand regeneration on peatlands (Saarinen 1993, Laiho et al. 1997, Moilanen and Saksa 1998, cf. Sarkkola et al. 2002). Correct determination of the under-growth has proved to be somewhat difficult in practice (e.g. Moilanen and Saksa 1998, cf. Pysyvien koealojen...1995).

4.2 Species Number

On spruce mires, the site quality class and drainage succession phase had no clear effect on the species number. In contrast, the temperature sum (ts) was an important factor; on pine mires ts was significant for the under-growth and shrub layers. This is expected since many tree and shrub species are restricted to southern and central Finland (Hämet-Ahti et al. 1989, Eurola 1999). Site quality class generally affects the species number, especially in the field and bottom layer (e.g. Sarasto 1961, Eurola et al. 1984). However, the number of species does not always decrease in a rectilinear manner on moving from the most fertile to poor sites (Hotanen et al. 1999). In this study, the low number of observations and subsequent large within-site variation on eutrophic spruce mires (class I) have partly contributed to the non-significant differences between site quality classes.

The average species number did not differ significantly between spruce mires and mineral soil forests in corresponding site quality classes. Spruce mire vegetation contains many characteristic features of mesic and herb-rich mineral soil forests due to the supplementary nutrient (mire margin) effect (Eurola et al. 1984, Eurola and Huttunen 1990). Relatively high species richness of the tree and shrub layer in undrained conditions belongs to those characteristics (Eurola et al. 1984). The spruce mire influence, which means that the vegetation receives additional nutrients directly from the underlying mineral soil or through the transport of moving water deeper in the peat, seems to be tolerant against the drainage (Eurola and Huttunen 1990) and can even strenghten against the other ecological influ-

ences (gradients) (Hotanen et al. 1999). Thus, the effects of drainage are not necessarily reflected in the number of species, but instead at the qualitative level, in the relationship between individual species (Reinikainen 2002a).

On pine mires, both the site quality class and drainage succession phase significantly affected the species number – most probably for the same reasons as in the case of the abundances, i.e. the long fertility gradient and potential release of growing space. Mesotrophic pine mires, i.e. site quality class II, showed high species number in both the tree layers and shrub layer. In its natural state, this site type often exhibits a supplementary nutrient effect usually through the influence of surface water (Eurola et al. 1984, Eurola and Huttunen 1990, Reinikainen 2002b). The inflow of surface water has a long-lasting effect in the peat via the transport of mineral material and nutrients (Westman 1981, Eurola and Huttunen 1990). The peat thickness in this type varies, but on the average it is only about one meter (e.g. Laine and Vasander 1990, cf. Reinikainen 2002b). When drained, the growing conditions are therefore generally favourable for a well-developed, variable tree and shrub layer. Eutrophic pine mires include two mire site types, eutrophic pine fen and eutrophic pine fen with *Sphagnum fuscum*, the latter being relatively poor in tree and shrub species (Eurola et al. 1984, 1994).

Drainage results in compaction and, due to increased aeration, an accelerated rate of mineralization of the surface peat (e.g. Lieffers 1988, Minkkinen and Laine 1998, Laiho et al. 1999). After the water-level drawdown, these processes take place at a faster rate on originally wet and fertile sites and in shallow peat layers than on more infertile sites and in thick peat layers (e.g. Minkkinen and Laine 1998). The changes enable spruce mire species and mineral soil species to occupy and grow on pine mires. In addition to the fact that a lot of thin-peated spruce mires have changed into mineral soil forests due to mineralization of the peat after long-lasting drainage, a part of the minerotrophic pine mires have most probably changed into spruce mires during the last five decades (Tomppo 2000, Tomppo et al. 2001, cf. Hökkä et al. 2002).

However, due to their demands favouring mineral soil before thick peat substrate (Hämet-Ahti

et al. 1989), several common deciduous species (e.g. *Alnus incana*, *Betula pendula*, *Populus tremula*, *Sorbus aucuparia*) will most probably remain less abundant on peatland sites. Consequently, the peatland forests especially on pine mires hardly reach (at least for a long period of time) the level of species (alpha) diversity of mineral soil sites on the average.

There were generally significant, but not very strong, positive correlations for the species number between the shrub layer and most tree layers. As a result of occupation of the released growing space, these relationships were more common on pine mires than on spruce mires. The relationships are also assumed to be generally stronger in undrained and untreated stands than in treated stands, where cuttings may decrease some species in certain tree layers, as was the case in the dominant and intermediate layers in this study. It can be concluded from different sources that there is positive correlation at least between the number of tree species and species number in the field and bottom layer, and most probably between the number of tree species and that of shrub species (Ruuhijärvi 1960, Eurola 1962, Eurola et al. 1984, 1994, Laine and Vasander 1990, Korpela 1999).

4.3 Coverage vs Basal Area

There seemed to be close relationships between the average values based on the crown coverages (C) and basal areas (G) of the trees. However, the correlation between the C and G-based values was not very strong, in particular on spruce mires. This is most probably caused by the (relatively linear but) changing relationship between the stem and canopy diameters during tree development from young to mature trees in different conditions (site, stem density) (Ilvessalo 1950, Jakobsons 1970, Muinonen 1995). In addition, this relationship apparently differs from one tree species to another (Ilvessalo 1950, Horn 1971).

The relationship between stand basal area and crown coverage is also affected by the fact that, after canopy closure, the amount (and G) of the tree stock continues to increase. Correspondingly, when this is related to remote sensing the same phenomenon is called the saturation of forest

reflectance (Nilson and Peterson 1994). After canopy closure, the observed spectral values of remote sensing images do not change markedly, although the volume of the tree stock increases (Ardö 1992, Trotter et al. 1997). It is obvious that, on spruce mires, canopy closure is a more common feature than on pine mires where the tree stock is usually sparse.

The inter-observer variation in the coverage estimations presumably weakens the correlations (cf. Tonteri 1990). The between-species differences in the properties of the canopy (foliage/needles: colour, size, pattern, asymmetry) also probably have an additional effect on the visual estimation (cf. Kuusipalo 1985). In a material collected in mature forest stands, Kuusipalo (1985) found that the canopy coverage was more strongly associated with the total basal area than in this study. In addition to using only mature forests, he also standardized the measurements by using a set of hemipherical photographs in the cover assessments. In fact, the oblique projections of stems in hemipherical images are included in canopy coverage values, which naturally strengthens the relationship between basal area and 'canopy' coverage (Kari T. Korhonen, pers. comm.).

The relationship is maybe also weakened by the fact that the basal areas of trees with a diameter at breast height of 4.5 cm < dbh ≤ 10.5 cm were calculated from the sub-sample plot of size of 100 m^2 (although generalized to the hectare level), whereas the crown coverage estimations were performed on the whole plot (300 m^2). In addition, also the basal areas of tree seedlings capable for further development with a diameter < 4.5 cm (dbh$_{1.3}$) were calculated from this sub-sample plot. Instead, the crown coverages of trees of dbh < 4.5 cm were counted (summed) on the whole plot if these trees belonged to any of the tree layers.

The simple measure, the crown coverages in different canopy layers, sometimes criticized (Parker and Brown 2000), produced reasonable and interpretable results in this study. As a field method this kind of structural analysis (for use in extensive inventories and mappings) is maybe easier and quicker than any stand measurement. The assessment procedure can be made more accurate in conditions different to NFI's busy field work.

4.4 Mean Range of Diameters

In both site type groups, the values of the mean range of the diameter distribution were slightly higher than those in comparable site quality classes in central Finland and North Karelia (Uuttera et al. 1996, 1997). On spruce mires, the values were lower than those in corresponding classes in Russian Karelia where the peatlands have not been drained (Uuttera et al. 1997). This is probably due to the fact that the undrained peatlands in Finland also are not necessarily in a natural state (Heikurainen 1971, Uuttera et al. 1997). Part of these peatland forests, especially on fertile sites and with a thin peat layer, may have been treated to selective cuttings at the same time as the surrounding mineral soil forests were managed (Heikurainen 1971, Gustavsen and Päivänen 1986). In this study, during the ten-year period before the 1995 inventory, 1.9% of the undrained spruce mires and 1.1% of the undrained pine mires had been cut (the corresponding values ten years earlier were 4.0% and 2.9%, respectively).

The temporary slight decrease in the mean range of the diameter distribution after drainage may be due to the improvement cuttings and ditch lines made concomitantly with the drainage (Uuttera et al. 1996). In addition, according to the definition of recently drained mires (oj), the growth of the trees has not yet markedly increased (Sarasto 1961). After drainage and possible improvement cutting, the regeneration of new seedlings is, however, rapid from the early transforming (mu) phase onwards, especially on fertile sites (Kaunisto and Päivänen 1985).

Possible explanations for the fact that the mean range of the diameter distribution exceeds (in this study significantly on pine mires) that of the undrained mires at the latest in the transformed phase are: the growth of the existing stock has increased while tree seedlings are still present, or larger trees have higher relative growth rates than suppressed smaller trees, i.e. one-sided (asymmetric) competition (for light) (Cannell and Grace 1993, Schwinning and Weiner 1998). Furthermore, the release growth effect of drainage is different at different distances from the ditch (Seppälä 1972), which causes an increase in the structural diversity of the stand. The phenomenon may also be partly based on the fact that

the undrained peatlands are not necessarily in a natural state.

On spruce mires, the values for undrained and transformed sites were almost equal. The results for central Finland, based on sampling by the relascope method in the 8th inventory, were relatively similar: the values for undrained and transformed spruce mires were close to each other (Uuttera et al. 1996). In the undrained spruce mire forests, the growing conditions are frequently favourable due to the supplementary nutrient effects (Eurola et al. 1984). It is also clear that different kinds of cutting on drained peatlands, which so far have been more common on spruce mires than on pine mires, generally decrease the mean range of the diameter distribution (Uuttera et al. 1997).

The pattern for pine mires along with the drainage succession gradient was almost identical to that reported in the study of Uuttera et al. (1996). In their material, the mean range of the diameter distribution decreased significantly from undrained to recently drained mires, and continued to increase significantly from transforming to transformed sites. In our study, however, the decrease and increase between the above-mentioned phases were not statistically significant.

According to Hökkä and Laine (1988) and Sarkkola et al. (2002, 2003), the size inequality among trees may increase during the first 20–30 years after drainage. The structural inequality may subsequently remain relatively constant or slightly increase, which suggests a simultaneous component of symmetric competition (Weiner 1990, Schwinning and Weiner 1998, Sarkkola et al. 2003). Drained peatland forests maintain their uneven-sized structure for a relatively long period of time. However, later on in the transformed phase, the increasing competition for growing space together with the development of a raw humus layer decreases the receptivity for regeneration (Kaunisto and Päivänen 1985).

Recent results based on repeated measurements in the same (Scots pine) stands show, that after the increase (20–30 years) in structural heterogeneity, the subsequent development towards a more homogeneous stand structure was obvious (Sarkkola et al. 2004, 2005). Thinnings hastened this development (Sarkkola et al. 2005). There are also reports that, over a longer time period, drainage may cause a decline in tree size inequality

due to reduced variability in growth rates among trees (Macdonnald and Yin 1999). Thus, a stand structure variation resembling natural peatland forests is perhaps difficult to maintain (Uuttera et al.1996, Sarkkola et al. 2002).

The sources of tree inequality on peatland sites during the first post-drainage tree generation are the original vertical structure of stands, the mosaic of micro-sites and their receptivity for regeneration. After regeneration the importance of these properties seems to decrease (Saarinen 1997).

Acknowledgements

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Addendix 1. Mean crown coverages of the tree species by peatland main type group, canopy layer (1–5), site quality class (I–VI) and drainage succession phase (lt, oj, mu, tkg) in 1995. Coverage<0.05 %=+. For the species abbreviations, see Fig. 1.

		Psyl	Pabi	Bpen	Bpub	Ptre	Ainc	Aglu	Scap	Sauc	ocon	odec
SPRUCE MIRES												
1 I	lt oj mu tkg	– – –	– – –	– – –	2.3 – 2.2	– – –	– – –	– – –	– – –	– – –	– – –	– – –
1 II	lt oj mu tkg	– – 0.1 0.1	– – 0.2 0.3	– – – 2.4	– – 0.3 0.1	– – – –	– – – –	– – – –	– – – –	– – – –	– – – –	– – – –
1 III	lt oj mu tkg	0.1 – 0.4 0.2	0.1 0.6 + 0.3	– – – –	– – 0.2 2.5	– – – –	– – – –	– – – –	– – – –	– – – –	– – – –	– – – –
1 IV	lt oj mu tkg	– 0.3 0.1 –	– – – –	– – 0.2 –	– – 0.9 0.4	– – – –	– – – –	– – – –	– – – –	– – – –	– – – –	– – – –
2 I	lt oj mu tkg	– – 4.7	4.5 – 2.3	– – 3.5	11.3 25.0 10.4	– – –	– – 0.5	– – 1.3	– – 0.8	– – –	– – –	– – –
2 II	lt oj mu tkg	3.9 – 1.2 4.5	6.9 18.0 11.6 9.2	1.5 – 1.7 1.9	13.5 – 13.1 17.6	– – – +	0.1 – – 0.4	1.5 – 2.2 0.4	1.4 – – 0.2	– – – 0.1	– – – –	1.8 – – 0.2
2 III	lt oj mu tkg	6.3 4.7 6.4 6.3	14.8 14.3 13.7 11.8	0.1 4.8 0.8 2.2	10.6 6.6 14.6 21.0	0.1 0.3 0.2 0.2	0.1 – 0.4 0.1	– – 0.2 –	– – – 0.3	– + + +	– – – –	– – – –
2 IV	lt oj mu tkg	1.8 – 7.8 10.8	4.3 13.0 7.4 2.6	0.8 – 0.3 –	5.0 1.0 9.8 27.0	– – – –	– – – –	– – – –	– – – –	– – – –	– – – –	– – – –
3 I	lt oj mu tkg	– – –	1.3 – –	– – 0.2	3.3 2.0 1.5	– – –	– – 5.0	2.3 – –	– 1.0 –	– – –	– – –	– – –
3 II	lt oj mu tkg	0.2 – 0.4 0.8	1.2 – 2.6 1.9	0.6 – 0.3 0.3	2.4 4.5 1.6 5.2	– – 0.5 –	– – 0.1 0.7	0.2 – + +	0.1 – – 0.3	– – – –	– – – –	– – – –
3 III	lt oj mu tkg	0.2 0.3 1.1 0.4	3.3 4.4 3.4 4.3	0.1 0.1 0.6 0.5	3.2 0.1 4.9 5.3	– – + +	– – + –	– – 0.1 +	– – + +	– – – 0.1	– – – –	– – 0.2 –
3 IV	lt oj mu tkg	0.3 0.3 0.6 1.4	1.2 3.0 3.3 1.0	– – 0.2 –	1.8 1.0 3.2 1.2	– – – –	– – – –	– – – –	– – – –	– – – –	– – – –	– – – –

		Psyl	Pabi	Bpen	Bpub	Ptre	Ainc	Aglu	Scap	Sauc	ocon	odec
4 I	lt	+	0.7	–	4.0	–	–	2.3	0.7	–	–	–
	oj											
	mu	–	–	–	3.0	–	–	–	–	–	–	–
	tkg	–	0.5	–	0.5	0.2	6.7	–	–	0.2	–	1.7
4 II	lt	–	2.3	–	1.2	–	0.4	0.1	0.6	–	–	0.6
	oj	–	4.5	–	1.0	–	–	–	–	–	–	–
	mu	0.1	2.5	–	2.1	–	0.3	+	0.1	–	–	–
	tkg	0.2	2.6	0.2	1.9	–	0.5	–	0.5	0.1	0.1	–
4 III	lt	0.1	4.2	0.2	3.6	–	–	–	+	+	–	0.1
	oj	0.1	3.0	0.9	1.9	0.1	0.1	–	0.1	+	–	–
	mu	0.4	4.4	0.5	2.3	+	+	+	+	0.1	0.1	+
	tkg	0.1	3.5	–	1.8	–	+	0.1	0.2	0.7	–	–
4 IV	lt	0.3	2.3	–	0.5	–	–	–	–	–	–	–
	oj	–	0.5	–	1.0	–	–	–	–	–	–	–
	mu	0.6	1.9	0.2	2.7	–	–	–	–	–	–	–
	tkg	–	0.8	–	1.2	–	–	–	–	+	–	–
5 I	lt	–	1.6	–	0.2	–	6.7	–	–	–	–	–
	oj											
	mu	–	–	–	–	–	–	–	–	–	–	–
	tkg	–	1.5	–	0.2	–	–	–	0.2	0.2	–	0.1
5 II	lt	–	1.6	0.6	2.6	–	0.3	0.1	0.2	0.1	+	3.8
	oj	–	0.5	–	1.3	–	–	–	–	0.5	–	–
	mu	0.1	1.5	0.5	2.5	+	0.1	–	0.1	0.2	–	+
	tkg	0.2	2.2	0.1	0.8	0.2	0.3	0.2	0.4	0.3	+	0.2
5 III	lt	+	1.5	0.1	1.8	0.1	0.5	–	–	0.2	0.3	+
	oj	–	1.2	–	6.1	+	0.1	–	0.2	0.4	0.1	–
	mu	0.5	3.8	0.1	1.6	+	0.1	+	0.3	0.1	+	0.1
	tkg	+	3.2	0.3	1.6	–	0.1	–	+	0.1	+	0.1
5 IV	lt	1.4	6.2	0.3	10.0	0.1	–	0.5	–	0.2	0.1	–
	oj	–	–	–	–	–	–	–	–	–	–	–
	mu	0.8	0.6	0.2	0.9	–	–	–	+	0.1	–	–
	tkg	–	14.4	–	1.6	–	–	–	+	–	–	–

PINE MIRES

		Psyl	Pabi	Bpen	Bpub	Ptre	Ainc	Aglu	Scap	Sauc	ocon	odec
1 I	lt	–	–	–	–	–	–	–	–	–	–	–
	oj	3.3	–	–	–	–	–	–	–	–	–	–
	mu	–	–	–	–	–	–	–	–	–	–	–
	tkg											
1 II	lt	0.1	–	–	–	–	–	–	–	–	–	–
	oj	3.8	0.3	–	0.5	–	–	–	–	–	–	–
	mu	1.8	–	–	–	–	–	–	–	–	–	–
	tkg	1.3	–	–	–	–	–	–	–	–	–	–
1 III	lt	0.3	0.3	–	0.1	–	–	–	–	–	–	–
	oj	–	–	–	7.0	–	–	–	–	–	–	–
	mu	0.5	–	–	0.2	–	–	–	–	–	–	+
	tkg	0.2	–	–	–	–	–	–	–	–	–	–
1 IV	lt	0.6	0.3	+	–	–	–	+	–	–	–	–
	oj	–	–	–	–	–	–	–	–	–	–	–
	mu	0.3	0.1	–	0.1	–	–	–	–	–	–	–
	tkg	0.9	+	–	–	–	–	–	–	–	–	–
1 V	lt	1.0	0.1	–	–	–	–	–	–	–	–	–
	oj	0.1	–	–	–	–	–	–	–	–	–	–
	mu	0.3	–	–	+	–	–	–	–	–	–	–
	tkg	0.5	–	–	0.3	–	–	–	–	–	–	–

			Psyl	Pabi	Bpen	Bpub	Ptre	Ainc	Aglu	Scap	Sauc	ocon	odec
1		lt	0.1	–	–	–	–	–	–	–	–	–	–
		oj	–	–	–	–	–	–	–	–	–	–	–
VI		mu	–	–	–	–	–	–	–	–	–	–	–
		tkg	–	–	–	–	–	–	–	–	–	–	–
2		lt	3.6	–	–	1.0	–	–	–	–	–	–	–
		oj	14.3	–	–	0.3	–	–	–	–	–	–	–
I		mu	9.0	2.0	–	–	–	–	–	–	–	–	–
		tkg											
2		lt	6.3	3.0	–	11.4	–	–	–	–	–	–	–
		oj	10.5	0.3	–	2.1	–	–	–	–	–	–	–
II		mu	23.0	–	–	9.5	–	–	–	–	–	–	–
		tkg	13.0	5.8	15.5	1.8	–	–	–	–	–	–	–
2		lt	10.6	0.7	0.1	5.0	0.1	–	–	–	–	–	–
		oj	–	–	–	–	–	–	–	–	–	–	–
III		mu	16.9	2.1	–	11.4	0.1	–	–	–	–	–	–
		tkg	21.0	0.6	1.1	14.1	0.7	–	–	–	–	–	–
2		lt	13.3	1.1	–	2.4	0.1	–	–	–	+	–	–
		oj	13.1	0.4	–	3.9	–	–	–	–	–	–	–
IV		mu	19.2	1.4	0.4	6.3	–	–	–	–	–	–	0.1
		tkg	19.4	2.2	0.1	7.3	–	–	–	–	+	–	–
2		lt	5.8	1.1	–	1.0	–	–	–	–	–	+	–
		oj	10.6	0.6	–	0.7	–	–	–	–	–	–	–
V		mu	18.3	0.8	0.1	2.1	–	–	+	–	–	0.2	–
		tkg	19.5	0.5	–	5.3	–	–	–	–	–	–	–
2		lt	6.8	–	0.1	–	–	–	–	–	–	–	–
		oj	6.7	–	–	0.3	–	–	–	–	–	–	–
VI		mu	27.5	–	–	–	–	–	–	–	–	–	–
		tkg	18.0	–	–	–	–	–	–	–	–	–	–
3		lt	–	0.5	–	0.5	–	–	–	–	–	–	–
		oj	6.7	–	–	–	–	–	–	–	–	–	–
I		mu	10.5	2.0	–	–	–	–	–	–	–	–	–
		tkg											
3		lt	0.7	0.6	–	3.7	–	0.7	–	–	–	0.1	–
		oj	2.8	–	–	–	–	–	–	–	–	–	–
II		mu	5.5	0.8	–	2.3	–	–	–	–	–	–	–
		tkg	1.3	1.3	1.5	–	–	–	–	–	–	–	–
3		lt	1.5	0.4	–	0.8	–	–	–	–	0.1	–	–
		oj	–	–	–	–	–	–	–	–	–	–	–
III		mu	1.6	1.8	–	4.3	0.1	+	–	0.2	–	–	–
		tkg	2.7	1.0	0.7	1.8	–	–	–	–	–	–	–
3		lt	1.9	1.1	+	1.5	–	–	–	–	–	–	–
		oj	2.2	1.3	–	2.4	–	–	–	–	–	–	–
IV		mu	3.9	1.1	0.2	2.2	+	+	–	–	–	–	0.1
		tkg	2.7	0.8	0.1	3.5	–	–	+	–	–	–	–
3		lt	2.0	0.3	+	0.2	–	–	–	–	–	–	–
		oj	2.9	0.1	–	0.5	–	–	–	–	–	–	–
V		mu	4.2	0.3	+	1.1	–	–	–	–	–	–	–
		tkg	6.9	0.3	–	1.5	–	–	–	–	–	–	–
3		lt	1.7	0.1	–	0.1	–	–	–	–	–	–	–
		oj	2.2	–	–	+	–	–	–	–	–	–	–
VI		mu	7.5	–	–	–	–	–	–	–	–	–	–
		tkg	3.0	–	–	–	–	–	–	–	–	–	–

		Psyl	Pabi	Bpen	Bpub	Ptre	Ainc	Aglu	Scap	Sauc	ocon	odec
	lt	0.5	0.1	–	0.8	–	0.8	–	–	–	–	–
4	oj	2.0	0.3	–	0.3	–	–	–	–	–	–	–
I	mu	5.0	–	–	1.5	–	–	–	–	–	–	–
	tkg											
	lt	0.5	0.3	–	9.2	–	0.6	–	–	0.3	–	–
4	oj	–	–	–	–	–	–	–	–	–	–	–
II	mu	2.5	0.8	–	4.5	–	–	–	–	–	–	–
	tkg	2.5	–	0.8	–	–	–	–	–	–	–	–
	lt	0.4	0.9	–	1.7	–	–	–	–	–	–	–
4	oj	–	–	–	–	–	–	–	–	–	–	–
III	mu	1.4	2.0	+	1.5	–	+	–	–	0.1	–	–
	tkg	0.3	1.9	0.5	7.2	+	+	–	–	–	–	–
	lt	1.2	1.0	–	0.9	+	–	–	+	–	–	–
4	oj	1.4	1.0	–	0.9	–	–	–	0.4	–	–	–
IV	mu	1.5	1.5	0.1	1.9	+	+	–	+	–	–	+
	tkg	1.1	1.6	+	3.9	–	0.1	+	+	+	+	+
	lt	1.2	0.3	–	0.3	–	–	–	–	–	–	–
4	oj	0.5	+	–	0.6	–	–	–	–	–	–	–
V	mu	2.2	0.5	+	1.1	+	–	–	+	–	–	–
	tkg	2.7	0.9	–	0.9	–	–	–	0.2	–	–	–
	lt	0.5	0.1	–	+	–	–	–	–	–	–	–
4	oj	0.7	–	–	0.1	–	–	–	–	–	–	–
VI	mu	4.0	–	–	–	–	–	–	–	–	–	–
	tkg	–	–	–	–	–	–	–	–	–	–	–
	lt	0.3	0.3	–	0.5	–	0.8	–	–	–	–	–
5	oj	0.7	–	–	–	–	–	0.2	–	–	–	–
I	mu	1.5	–	–	–	–	–	–	–	–	–	–
	tkg											
	lt	0.3	0.3	–	1.3	+	–	–	–	0.1	–	–
5	oj	0.5	–	–	1.8	–	–	–	–	–	–	–
II	mu	–	–	–	0.3	–	0.3	–	–	–	–	0.3
	tkg	1.5	1.3	1.3	2.5	–	–	–	–	0.6	0.1	–
	lt	0.2	0.2	+	0.6	–	0.1	–	–	–	–	–
5	oj	–	–	–	–	–	–	–	–	–	–	–
III	mu	0.9	1.7	0.2	3.6	+	0.1	–	0.7	+	–	0.1
	tkg	0.6	1.8	+	5.6	0.1	–	–	+	0.5	–	–
	lt	0.3	0.6	–	1.0	–	–	–	–	+	–	+
5	oj	0.2	–	–	0.6	–	–	–	–	–	–	–
IV	mu	0.6	0.8	0.2	3.6	+	+	–	0.1	+	–	+
	tkg	0.3	0.9	+	3.3	–	+	+	–	+	–	–
	lt	0.3	0.3	–	0.2	–	–	–	–	–	–	–
5	oj	0.6	+	+	0.4	–	–	–	–	–	–	–
V	mu	1.0	0.4	+	0.9	–	+	+	–	+	+	+
	tkg	0.5	+	–	1.3	–	–	–	–	–	–	–
	lt	0.4	–	+	–	–	–	–	–	–	–	–
5	oj	0.1	–	–	–	–	–	–	–	–	–	–
VI	mu	1.5	0.5	–	0.3	–	–	–	–	–	–	–
	tkg	1.0	–	1.0	2.0	–	–	–	–	–	–	–