

Changes in understorey biomass and species composition after water level drawdown on pine mires in southern Finland

Vedenpinnan alenemisen vaikutus sararämeen pintakasvillisuuden biomassaan ja lajistoon

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Understorey biomass and species composition were analyzed on six sites representing tall-sedge pine fen at different stages of secondary succession caused by drainage for forestry. Two of the sites were undrained controls and the other sites had been drained 8–55 years earlier. Cyperaceous and herbaceous field layer was found to diminish permanently after drainage, whereas shrub and moss layers survived in the drainage succession in terms of biomass allocation although the species composition changed almost completely. On the oldest drained site the ground vegetation was dominated by typical upland forest species with the exception of *Sphagnum russowii*. Total understorey biomass varied from 260 g m⁻² on sites drained 22–30 years earlier to 990 g m⁻² on a site drained 8 years earlier.

Key words: drainage, field layer, ground vegetation, moss layer, peatland, succession

INTRODUCTION

The above-ground plant biomass on undrained mire sites in Finland has been found to vary between 200 g m⁻² in a very wet treeless mesotrophic fen to 15 300 g m⁻² in a *Vaccinium myrtillus* type spruce swamp where most of the biomass is in the tree layer (Reinikainen et al. 1984, see e.g. Eurola et al. 1984 for the site types). In general, there is a significant correlation between the tree stand volume and the total above-ground biomass, and the ground vegetation biomass is in inverse proportion to the tree stand

biomass (Reinikainen et al. 1984, Brække 1988). Nevertheless, on most mire site types found in Finland, most of the organic matter deposited as peat derives from ground vegetation (e.g. Lappalainen & Hänninen 1993). Only on the most nutrient-rich forested mire sites can the proportion of tree litter of the carbon sequestered in the soil be said to be considerable.

Most of the organic matter deposited as peat derives from plant material produced below the mire surface — *Carex* roots and the lower parts of *Sphagnum* mosses — whereas a large part of the carbon

and nutrient pool of the above-ground field and moss layer vegetation is in an annual cycle. When the peat layer grows in thickness, the habitat conditions may gradually change as e.g. a part of the nutrients cycling in the ecosystem are immobilized in the peat, and minerogenic ground water richer in nutrients than rain water is left too deep for the roots to reach. Thus, in natural conditions, mire vegetation is usually under a slow succession towards communities adapted to more nutrient-poor and drier conditions until the mire reaches a steady state determined by climatic conditions and the topography of the site (cf. Clymo 1984, Damman 1996).

If the water table of a mire is permanently lowered, e.g. by drainage for forestry, a secondary vegetation succession towards more forest-like communities is started (e.g. Cajander 1913, Multamäki 1923, Sarasto 1957), the rapidity of which depends on the nutrient status and original wetness of the site and the extent of the change in the water level (Laine & Vanha-Majamaa 1992, Laine et al. 1995). At the same time, the element cycling of the ecosystem changes when the tree stand becomes the main carbon and nutrient binding body of the system, accumulating them for a relatively long period of time.

The changes in vegetation composition of pine mires after water level drawdown were recently outlined by Laine et al. (1995). Ground vegetation biomasses have been reported for several mire site types both in undrained and drained condition (Reinikainen et al. 1984, Vasander 1990 and the ref-

erences therein), but there is no information about the long-term changes along the post-drainage secondary succession. The aim of this study was to examine the changes in the understorey biomass in relation to the changes in species composition after water level drawdown caused by forest drainage. This is a part of a study dealing with the role of biomass in carbon cycling in peatland ecosystems (Laiho & Laine 1994a) within the Finnish Research Programme on Climate Change. The below-ground biomass has been dealt with in an earlier paper (Laiho & Finér 1996).

MATERIAL AND METHODS

Tall-sedge pine fen (VSR or VNR in the Finnish classification system; e.g. Eurola et al. 1984, Laine & Vasander 1990) was chosen as the object of this study because it is the site type most commonly drained for forestry in Finland (Keltikangas et al. 1986) and represents the "nutrient-level median" of the forest drainage areas. This site type is always forested, but it characteristically has large lawns (intermediate level between dry hummock and wet hollow level) dominated by vegetation typical of treeless mires.

The sites of the study (Table 1) are situated in southern Finland (61°35'–61°52'N, 24°05'–24°25'E). The area is part of the southern boreal coniferous forest zone (Ahti et al. 1968) and the eccentric raised bog

Table 1. General features of the sites studied.

Taulukko 1. Tutkimuskohteiden yleistunnuksia.

	Site – Kohde					
	1	2	3	4	5	6
Years since drainage	–	–	8	22	30	55
<i>Vuosia ojituksesta</i>						
Living tree stand volume, m ³ ha ⁻¹	6	35	10	76	102	150
<i>Elävän puuston tilavuus, m³ha⁻¹</i>						
Proportion pine/birch/spruce ^a	100/–/–	95/5/0	100/–/0	69/31/0	83/15/2	88/9/3
<i>Puulajisuhteet mänty/koivu/kuusi ^a</i>						
Number of living stems, ha ⁻¹	444	1567	554	4750	1782	2786
<i>Runkoluku, kpl ha⁻¹</i>						
Ditch spacing, m	–	–	30	37	37	32
<i>Sarkaleveys</i>						
Sample plot size, m ²	900	600	1263	1158	1190	1328
<i>Koalan koko, m²</i>						

^a of volume; Scots pine (*Pinus sylvestris*), pubescent birch (*Betula pubescens*), Norway spruce (*Picea abies*)

^a tilavuudesta

region in central Finland (Ruuhijärvi 1982, Ruuhijärvi 1983). The mean annual temperature in the region is +3°C and that of July is +16°C. The mean annual temperature sum (accumulated mean daily temperatures $\geq +5^\circ\text{C}$) varies between 1150 and 1250 d.d. The annual precipitation is c. 650 mm, of which c. 240 mm is snowfall.

Two of the sites were undrained while the rest had been drained 8, 22, 30 and 55 years earlier. The sites were selected from the material of an earlier study dealing with the effect of drainage on peat properties and vegetation (Laiho & Laine 1994b, Laine et al. 1995). The original material was very carefully selected to allow comparison between various sites at different stages of the post-drainage succession. For details of the selection, see Laiho & Laine (1994b). The sites of the present study were chosen to obtain as wide a drainage age variation as possible within the chosen site type, and so that on the drained sites the tree stand volume would be close to the average of the drainage age.

On undrained sites the sample plots were laid out in the middle of an area where vegetation uniformly represented the chosen site type. On drained sites the sample plots covered a whole strip between ditches. Undrained site 2 was slightly affected by a ditch ca. 40 m away from the sample plot, which was clearly reflected in its tree stand volume. However, both of the undrained sites were very wet with the water table level at or close to the mire surface. On the drained sites, the water table fluctuated between the following approximate limits during the time from early spring till late autumn: site 3: 10–25 cm, site 4: 35–50 cm, site 5: 35–60 cm and site 6: 50–75 cm below the mire surface.

The coverage of each plant species present was determined on the area of the whole plot. This was

done with 1% coverage classes until 10%, after that with 10% coverage classes. The nomenclature follows Moore (1982) for vascular plants and Koponen et al. (1977) for bryophytes. *Sphagnum angustifolium* and *S. fallax* were determined as *S. recurvum* complex (e.g. Flatberg 1992).

Sampling was done in mid June 1991 on sites 2 and 5 and at the end of June 1992 on the other sites. Plant biomass was sampled on 16–20 systematically chosen locations. Shrubs were harvested on an area of 0.5 m² per location, other components on an area of 0.19 m². Zero-level for sampling of both field and moss layers was taken as the upper level of the rooting zone, i.e. the layer where the topmost fine roots could be found. This corresponded approximately to the lower level of the living moss layer. Litter and dead stems of the field layer species were excluded from the material, whereas possible dead branches in shrubs were included. On sites 1, 3, 4 and 6, shrubs were separated by species. On site 2, *Betula nana* was separated. The material was dried at 105°C to constant mass. The shrubs were combined into three species groups: shrubs typical of treeless mires (*Andromeda polifolia* and *Vaccinium oxycoccus*), shrubs typical of pine mires (*Betula nana*, *Ledum palustre*, *Vaccinium uliginosum*, here *Empetrum nigrum* was also counted into this group) and shrubs typical of upland forests (*Vaccinium myrtillus* and *V. vitis-idaea*) (e.g. Eurola et al. 1984). The dry matter of all material harvested will henceforth be referred to as biomass.

Tree seedlings ($d_{1,3} < 1.5$ cm) were measured on five circular subplots with a radius of 2 m laid systematically on the diagonals of the sample plots. Unstable seedlings 1–2 years old, if present, were excluded. The height and species of the seedlings were recorded, and a total of five sample seedlings

Table 2. The parameters \pm their asymptotic standard errors for the regression equation $dm_s = p_1 h^{p_2}$ for estimating tree seedling biomass, where dm_s = total dry mass of the seedling (g), h = seedling height (m), p_1 , p_2 = parameters, r.s.d. = residual standard deviation.

Taulukko 2. Puuntaimien biomassan estimointiin käytetyn regressioyhtälön $dm_s = p_1 h^{p_2}$ parametrien arvot ja niiden asymptoottiset keskivirheet; dm_s = taimen kokonaiskuivamassa (g), p_1 , p_2 = parametrarit, r.s.d. = jännösvaihtelu.

Species	p_1	p_2	r^2	r.s.d.	n
Pine – mänty	136.4 \pm 20.56	2.715 \pm 0.355	0.948	54.9	16
Birch – koivu	40.1 \pm 29.18	1.338 \pm 0.820	0.749	70.2	8
Spruce – kuusi	207.8 \pm 36.15	1.248 \pm 0.320	0.944	71.8	6

per plot were harvested. The seedlings were separated into foliage and woody parts and dried at 105°C to constant mass. Equations relating the total biomass of the sample seedlings to their length (Table 2) were computed for all tree species separately using material from all plots combined. Equation parameters were computed using nonlinear estimation with a least squares loss function (SYSTAT 1992).

The relation between the number of samples and the accuracy of the sample mean was estimated using the central limit theorem (e.g. Ranta et al. 1989,

p. 97) and the sample standard deviation as an estimate of the population s.d. Thus Student's t-distribution fractiles were used.

RESULTS

Species composition

On the undrained sites the field layer was dominated by *Carex lasiocarpa* (Table 3). *Eriophorum*

Table 3. Field layer plant species and their coverage on the sites studied.

Taulukko 3. Kenttäkerroksen kasvilajit ja niiden peittävyudet tutkimuskohteilla.

	Site – Kohde					
	1	2	3	4	5	6
<i>Salix aurita</i>	–	+	–	+	–	–
<i>Andromeda polifolia</i>	1	1	3	3	+	+
<i>Betula nana</i>	1	10	20	20	1	+
<i>Calluna vulgaris</i>	–	–	–	+	–	–
<i>Empetrum nigrum</i>	1	1	10	5	20	–
<i>Ledum palustre</i>	–	–	–	5	+	2
<i>V. microcarpum</i>	+	+	+	–	–	–
<i>V. myrtilus</i>	–	–	–	1	+	40
<i>V. oxycoccus</i>	1	3	2	10	+	+
<i>V. uliginosum</i>	+	+	1	20	2	1
<i>V. vitis-idaea</i>	–	–	–	20	1	40
<i>Carex chordorrhiza</i>	–	+	–	–	+	–
<i>C. dioica</i>	–	+	–	–	–	–
<i>C. echinata</i>	–	+	–	–	+	–
<i>C. lasiocarpa</i>	10	20	1	–	–	–
<i>C. magellanica</i>	+	+	+	+	+	–
<i>C. nigra</i>	–	–	–	–	+	–
<i>C. pauciflora</i>	+	1	+	–	+	–
<i>C. rostrata</i>	–	2	–	–	–	–
<i>Eriophorum angustifolium</i>	–	+	–	–	+	–
<i>E. vaginatum</i>	5	10	10	20	30	1
<i>Agrostis canina</i>	–	–	–	–	+	–
<i>Calamagrostis arundinacea</i>	–	–	–	–	+	–
<i>C. purpurea</i>	–	–	–	–	+	–
<i>Deschampsia cespitosa</i>	–	–	–	–	+	–
<i>Dactylorhiza maculata</i>	–	+	+	–	–	–
<i>Drosera rotundifolia</i>	+	+	–	–	–	–
<i>Dryopteris carthusiana</i>	–	–	–	–	+	–
<i>Epilobium angustifolium</i>	–	–	–	–	+	–
<i>Equisetum fluviatile</i>	–	+	–	–	–	–
<i>Melampyrum pratense</i>	–	+	–	+	+	+
<i>Menyanthes trifoliata</i>	–	5	–	–	–	–
<i>Potentilla palustris</i>	–	+	–	–	+	–
<i>Pyrola media</i>	–	–	–	–	+	–
<i>Rubus chamaemorus</i>	2	–	1	1	+	5
<i>Trientalis europaea</i>	–	–	–	+	+	+
Number of species	12	22	12	15	26	11

vaginatum was the second most common species with a coverage half that of *C. lasiocarpa*. The coverage of shrubs was small except for *Betula nana* on site 2. Some herbs grew on site 2, *Menyanthes trifoliata* being the most abundant.

After drainage *C. lasiocarpa* disappeared completely; it still grew sporadically on the youngest drained site 3 (8 years since drainage), but on other drained sites it could not be found. The coverage of *E. vaginatum* increased at first after drainage, having its maximum on the 30-year-old drained site 5; however on the oldest drained site the coverage had dropped drastically. The coverages of mire dwarf shrubs also increased at first, but on the oldest drained site they had been replaced by upland forest dwarf shrub species (*Vaccinium myrtillus* and *V. vitis-idaea*). *Rubus chamaemorus*, *Melampyrum pratense* and *Trientalis europaea* were the most common herb species on drained sites. On site 5, other herb species as well as several grasses were found sporadically.

On the undrained sites the moss layer was dominated by *Sphagnum recurvum* complex, of other species only *S. magellanicum* was rather abundant (Table 4). Drainage did not have a rapid effect on *S. recurvum* complex, but on the 22-year-old drained site 4 its coverage had already clearly decreased. On the oldest drained sites *S. russowii* had become the dominant moss species, but *Pleurozium schreberi* had also clearly gained coverage after drainage.

Biomass

The biomass of Cyperaceous and herbaceous field layer decreased steadily along with increasing drainage age (Table 5). Shrub biomass had a maximum value on the youngest drained site 3 (8 years), and after a temporary decrease it had the second highest value on the oldest drained site. The moss biomass likewise had its maximum on the youngest drained site and had increased again on the oldest drained site. However this increase was only to a value similar to that on the undrained site, and the variation was high.

When the shrub biomass was divided into the three species groups (Fig. 1), open mire species dominated on the undrained site, pine mire species gained dominance after drainage but lost it to the upland forest species as the drainage age increased.

The number and biomass of tree seedlings were clearly highest on the 22-year-old drained site (Table 6). Scots pine (*Pinus sylvestris*) seedlings were abundant on the undrained sites and the youngest drained site, but on older drained sites they had been replaced by Norway spruce (*Picea abies*) and pubescent birch (*Betula pubescens*) seedlings (Fig. 2).

Total understorey biomass varied from 260 g m⁻² on sites drained 22–30 years earlier to 990 g m⁻² on the site drained 8 years earlier.

Table 4. Moss layer plant species and their coverage on the sites studied.

Taulukko 4. Pohjakerroksen kasvilajit ja niiden peittävytydet tutkimuskohteilla.

	Site – Kohde					
	1	2	3	4	5	6
<i>Sphagnum fuscum</i>	5	+	4	1	+	–
<i>S. magellanicum</i>	30	10	2	10	2	1
<i>S. recurvum</i> complex	60	90	90	5	20	3
<i>S. russowii</i>	–	+	–	5	30	60
<i>Aulacomnium palustre</i>	+	+	–	3	+	+
<i>Dicranum polysetum</i>	–	–	–	3	+	1
<i>D. scoparium</i>	–	–	–	–	–	+
<i>Pleurozium schreberi</i>	+	+	–	+	30	30
<i>Polytrichum commune</i>	–	–	–	–	5	–
<i>P. strictum</i>	1	+	4	20	+	+
<i>Ptilidium pulcherrimum</i>	–	–	–	+	–	–
<i>Cladina</i> spp.	–	–	–	1	–	+
<i>Cladonia</i> spp.	–	–	–	+	–	+
Number of species	6	7	4	11	9	10

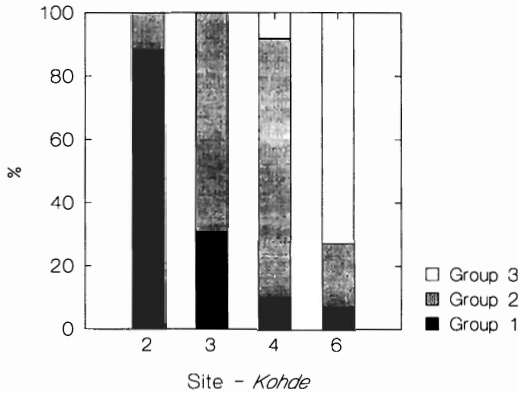


Fig. 1. Distribution of dwarf shrub biomass between species groups at different stages of the drainage succession: Group 1 = shrubs typical of treeless mires (*Andromeda polifolia* and *Vaccinium oxycoccos*), Group 2 = shrubs typical of pine mires (*Betula nana*, *Empetrum nigrum*, *Ledum palustre*, *Vaccinium uliginosum*), Group 3 = upland forest shrubs (*Vaccinium myrtillus* and *V. vitis-idaea*) (e.g. Eurola et al. 1984). Drainage ages of the sites in Table 1.

Kuva 1. Varpubiomassan jakautuminen kolmen lajiryhmän kesken kuivumissukcession eri vaiheissa. Group 1 = ne-
vavarvut, Group 2 = rämevarvut, Group 3 = metsävarvut;
lajit kuten yllä (esim. Eurola ym. 1984). Kohteiden ojitusiät
Taulukossa 1.

DISCUSSION

The vegetation composition on the undrained sites was typical of this site type (Ruuhijärvi 1960, Eurola

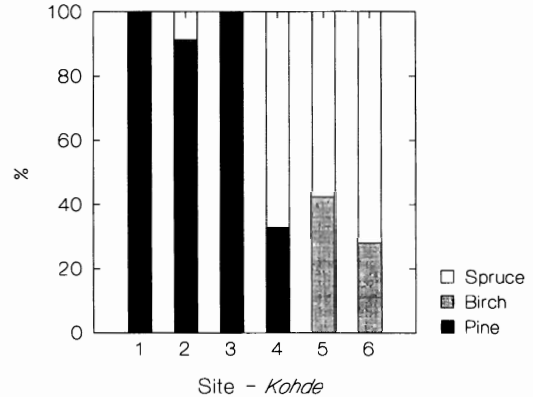


Fig. 2. The biomass proportions of Scots pine, pubescent birch and Norway spruce seedlings at different stages of the drainage succession. Drainage ages of the sites in Table 1.

Kuva 2. Männyn (pine), hieskoivun (birch) ja kuusen (spruce) taimien suhteelliset biomassaosuudet kuivumissukcession eri vaiheissa. Kohteiden ojitusiät Taulukossa 1.

1962). Site 2 was more nutrient-rich than site 1 (unpublished data), which was also reflected in the plant species composition and in the larger number of species. The changes in species composition after drainage follow the general trends outlined by Laine et al. (1995). The coverage values cannot be considered absolute as they were estimated for fairly large areas (Table 1); however, they are very comparable with each other.

Table 5. Ground vegetation biomass (g m^{-2}) on the sites studied. Standard deviations are given in brackets below the mean values.

Taulukko 3. Pintakasvillisuuden biomassa (g m^{-2}) tutkimuskohteilla. Keskihajonnat suluisia keskiarvojen alapuolella.

	Site - Kohde					
	1	2	3	4	5	6
Shrubs	41	76	288	103	54	186
Varvut	(35)	(43)	(133)	(143)	(83)	(119)
Other field layer species	58	72	60	22	15	5
Muu kenttäkerros	(30)	(23)	(42)	(24)	(14)	(6)
Mosses	534	349	644	137	193	452
Sammalet	(91)	(59)	(90)	(172)	(117)	(236)
Total	634	497	992	263	262	643
Yhteensä	(108)	(61)	(175)	(213)	(117)	(293)
n	20 ^a	16	20	20	18	20

^a for field layer excluding shrubs, only 15 (5 samples were damaged before measurements)

^a muulle kenttäkerrokselle kuin varvuille 15 (5 näytettä vaurioitui ennen määrittystä)

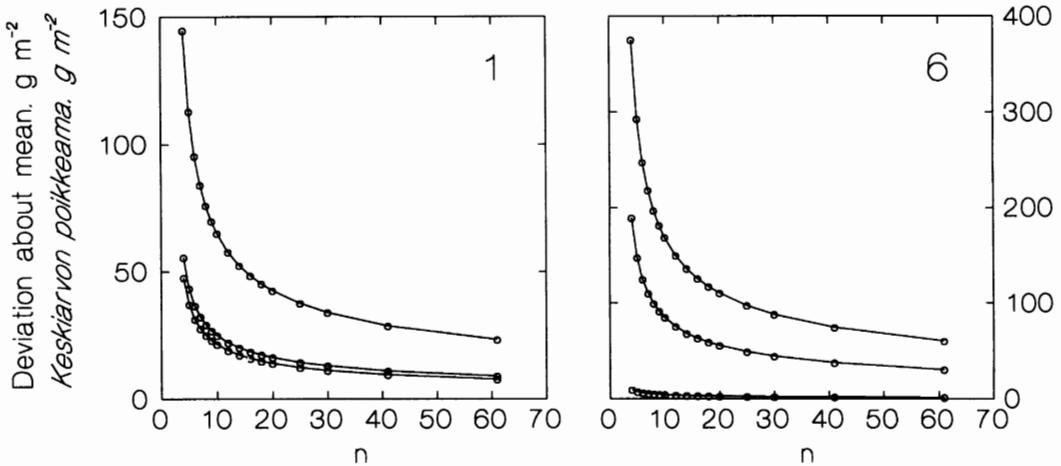


Fig. 3. Maximum deviation of the estimated mean biomass (Table 5) with a 95 % confidence level as a function of the number of samples for sites 1 and 6. The uppermost lines represent moss biomass, the middle lines shrub biomass and the lowermost lines other field layer biomass.

Kuva 3. Otokeskiarvon (Taulukko 5) suurin poikkeama populaation keskiarvosta todennäköisyydellä 95 % näytämäärän funktiona kohteille 1 ja 6. Ylimmät käyrät ovat sammalbiomassalle, keskimäiset varpubiomassalle ja alimmat muulle kenttäkerrokselle.

The biomass values were in accordance with those given by Elina & Kuznecov (1977), Reinikainen et al. (1984) and Vasander et al. (1993) for corresponding site type. For comparing accurately the moss biomass values of different studies, it would be essential to know how the lower limit of harvesting has been chosen. There is no obvious objective zero-level for sampling.

The standard deviations of the biomass values were rather high. On undrained sites this was probably mainly due to the fact that the vegetation consisted of two different community types, hummocks and lawns (cf. e.g. Moore 1989). This still holds true on the recently drained site 3. On the older drained sites shading by trees may be the main factor causing variation in the ground vegetation. On the

undrained sites sampling by communities might have led to more accurate results, but probably not on the drained sites. Increasing the number of samples would have increased the accuracy of the biomass estimates very little in relation to the increased effort (Fig. 3).

Field layer vegetation biomass has been shown to peak in late July–early August (e.g. Vasander 1990). The sampling for this study was done a little earlier and may have led to values smaller than maximum. However, when sampling was repeated for checking for site 2 in August, the biomass values obtained were similar to those of the first sampling except for shrubs for which a smaller biomass value was obtained in the later sampling. The development of the moss layer depends largely on the

Table 6. Tree seedling biomass (g m^{-2}) and number (ha^{-1}) on the sites studied. Standard deviations are given in brackets below the mean values.

Taulukko 4. Puuntaimien biomassa (g m^{-2}) ja lukumäärä (kpl ha^{-1}) tutkimuskohteilla. Keskihajonnat suluiissa keskiarvojen alapuolella.

	Site – Kohde					
	1	2	3	4	5	6
g m^{-2}	21 (31)	26 (26)	19 (23)	112 (77)	18 (22)	21 (12)
n ha^{-1}	2850 (3090)	950 (490)	1940 (2530)	12020 (5880)	5050 (5890)	1120 (430)

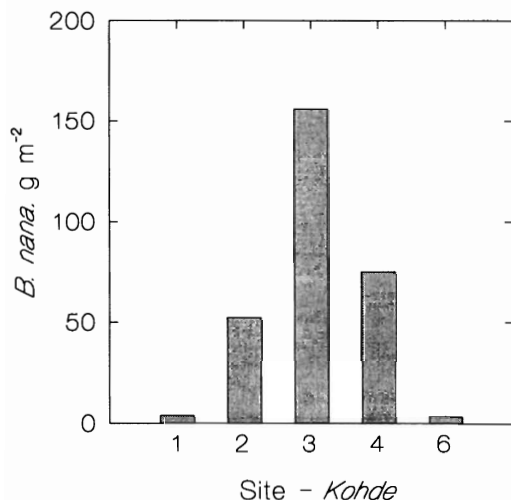


Fig. 4. The biomass of *Betula nana* at different stages of the drainage succession. Drainage ages of the sites in Table 1.

Kuva 4. Vaivaiskoivun (*B. nana*) biomassa kuivumisukcession eri vaiheissa. Kohteiden ojitusikä Taulukossa 1.

weather, especially on moisture conditions (e.g. Lindholm 1990).

The different sampling year may have affected the comparability of the results from sites 2 and 5 to others, as early summer 1991 was clearly colder and wetter than 1992. There is little information on the annual variation in ground vegetation coverages and biomass. Hultgren (1988) found the seasonal maximum biomass of sedges to vary only slightly between years on a mire site with a small water level amplitude. According to Botch (1996), increased precipitation and lower temperature decreased the coverage of ground vegetation on fen sites. The values from site 2 are probably more comparable with the others, as the soil temperature conditions between years are more constant on this wet undrained site, but the values from site 5 may be underestimated compared with the others (cf. Laiho & Finér 1996). This does not affect the conclusions, however.

Coverage and biomass values may give quite a different view on the abundance of some species. For example, the coverage of *Betula nana* was estimated to be 20% on sites 3 and 4, yet the biomass of *B. nana* on site 3 was twice the biomass on site 4 (Fig. 4). After drainage the coverage of *B. nana* usually increases (Laine et al. 1995), and due to the simultaneous considerable increase in the height growth the increase in the biomass may be much larger than that of the coverage. *B. nana* is relatively

sensitive to shading by tree stand and begins to decline when the tree canopy closure increases (Laine et al. 1995). At least at the outset, this change also was relatively more pronounced in biomass than in coverage (Fig. 4, Table 3). Furthermore, the total coverage of Cyperaceous species on the 30-year-old drained site 5 was still as large as on the undrained sites, although the biomass had dropped drastically (Tables 3 and 5). The dominant species was now *Eriophorum vaginatum* instead of *Carex* species, but this probably cannot be the only explanation, for there were clear morphological differences between *E. vaginatum* on undrained and drained sites (e.g. shorter stems on drained sites). In general, the biomass proportion of Cyperaceous and herbaceous field layer is much smaller than the respective coverage (Reinikainen et al. 1984, Vasander 1990).

When examining the drainage succession according to the theory developed by Al-Mufti et al. (1977) and Grime (1979), site 3 was clearly stressed, as it had the smallest number of species and the largest total ground vegetation biomass. Only the most tolerant mire species remained on the site, and the colonization of upland forest species had not yet started. After this 'shock phase' the number of species increased and the total biomass decreased until they reached approximately the same level as on the undrained sites. According to Vasander (1990), after forest amelioration on mires, species richness usually decreased in the field layer and increased in the ground layer, whereas with biomass, the trends were the opposite. These trends were not unambiguous on the site type studied here.

The drainage age variation of 55 years in the material covered approximately the period of rapid change from a functioning mire ecosystem towards an upland-forest-like ecosystem on this site type. The changes in the relative abundance of the three shrub groups depict nicely the progress of the secondary succession. On the oldest drained site the ground vegetation was dominated by typical upland forest species with the exception of *Sphagnum russowii*. On undrained mires this moss species is abundant only in relatively dry site types (e.g. Euroola et al. 1984), but its increase after drainage is typical for this and related site types (Laine et al. 1995). The abundance of *S. russowii* obviously does not indicate inefficient drainage but reflects instead the differences in the growth conditions between upland sites and drained peatland sites.

The gradual disappearance of Scots pine seedlings after drainage was at least initially most probably due to increased shading mainly induced by shrubs (e.g. Fig. 4). Previous studies have suggested that changes in the moss species composition and formation of a so-called raw humus layer may also lead to impaired regeneration in the future (Sarasto & Seppälä 1964, Kaunisto & Päivänen 1985). The tree stands even on the oldest drained sites were probably not dense enough to completely prevent pine seedling development. Pubescent birch also requires much light, but it seems to regenerate more easily than pine on the drained sites studied. On the older drained sites shade-tolerant Norway spruce seedlings have become abundant. Similar changes have been reported by e.g. Mannerkoski (1976). This means that natural regeneration for pine may not be easy on these sites at the end of the first tree stand rotation. For spruce, however, the nutrient regime of sites of this type is in general not sufficient in the long run.

Whereas Cyperaceous and herbaceous field layer permanently diminished after drainage, both moss and shrub biomasses increased again following the decline 20–30 years after drainage. On the oldest drained site, the moss biomass remained at the same level as on the undrained sites, whereas shrub biomass on the oldest drained site was comparatively larger. This shows that on this site type the shrub and moss layers may survive in the drainage succession in terms of biomass allocation, but the species composition changes almost totally due to the changes in growth conditions. With regard to mosses these results vary somewhat from those obtained by Vasander (1990) on a considerably nutrient-poorer site type. This may be due to the rather short time elapsed from drainage in his study (13 years) and the much slower rate of the secondary succession on that site type. For instance, an invasion of new moss species had not yet occurred on the site.

The changes described above might in principle result from long-term water-level drawdown caused by factors other than forest drainage as well. For example, Martikainen et al. (1993) and Laine et al. (1996) have used the forest drainage effect to estimate the consequences of climatic warming. Drier, warmer summer conditions might initiate a similar secondary succession that would, however, probably be considerably slower.

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TIIVISTELMÄ

Vedenpinnan alenemisen vaikutus sararämeiden pintakasvillisuuden biomassaan ja lajistoon

Työssä selvitettiin metsäojituksen aiheuttaman sekundäärisuoksektion myötä tapahtuvia muutoksia varsinaisen sararämeen (VSR, esim. Laine & Vasander 1990), Suomen yleisimmin ojitettun suotyypin, pintakasvillisuudessa, erityisesti sen biomassassa. Mittauksia tehtiin kuudella kohteella, joista kaksi oli ojitettamattomia ja neljä eri-ikäisiä ojitusalueita (Tau-

lukko 1). Kohteet sijaitsivat Pirkka-Hämeessä. Ne valittiin aiemman metsäojituksen vaikutuksia ns. nevarämesarjan soilla selvittäneen tutkimushankkeen aineistosta (esim. Laiho & Laine 1994, Laine ym. 1995) siten, että ne edustivat mahdollisimman pitkän ojituksenjälkeisen kuivumissuoksektion eri vaiheita ja olivat keskenään mahdollisimman vertailukelpoisia.

Ojittamattomilla kohteilla koealat sijoitettiin kasvillisuudeltaan mahdollisimman homogeeniseen ja tyypillisesti VSR:tä edustavaan kohtaan. Ojitusalueilla koealat peittivät koko saran (toinen rajoittavista sarkaojista on mukana pinta-alassa). Ojittamaton kohde 2 sijaitsi suolla, joka oli osittain ojitettu, ja noin 40 m päässä koealasta ollut lähin oja vaikutti lievästi sen hydrologiaan. Molemmat ojittamattomat kohteet olivat kuitenkin hyvin märkiä ja vedenpinta oli koko sulan kauden aikana hyvin lähellä suon pintaa. Ojitetuilla kohteilla vedenpinta vaihteli suunnilleen seuraavilla väleillä: koeala 3: 10–25 cm, koeala 4: 35–50 cm, koeala 5: 35–60 cm ja koeala 6: 50–75 cm suon pinnan alapuolella.

Näytteenotto tapahtui kesäkuun lopulla, kohteilla 2 ja 5 vuonna 1991 ja muilla 1992. Kaikkien koealoilta tavattujen kasvilajien peittävydet arvioitiin koko koealan alalta. Tämä tehtiin yhden prosentin luokissa 10%:iin asti, minkä jälkeen käytettiin 10% luokkia. *Sphagnum angustifolium* ja *S. fallax* määritettiin yhteisellä nimellä *S. recurvum*. Pintakasvillisuudesta otettiin näytteitä 16–20 systemaattisesti valitusta kohdasta. Varvut korjattiin 0,5 m² alalta ja muu kenttäkerros sekä pohjakerros 0,19 m² alalta kultakin näytteenottokohdalta. Jako maanalaiseen ja maanpäälliseen osaan tehtiin sen perusteella, missä juuristokerros alkoi. Ositteet kuivattiin näytteenot-

tokohdittain vakiomassaisiksi 105°C:ssa ja punnittiin. Puuntaimista mitattiin pituus viideltä koealan lävistäjille sijoitetulta ympyräkoevalta, joiden säde oli 2 m, ja kultakin kohteelta otettiin viisi koetainta, joiden kuivamassa määritettiin ja joiden perusteella laadittiin regressioyhtälö taimien biomassan arviointiin (Taulukko 2).

Pintakasvillisuuden lajisto on esitetty Taulukoissa 3 ja 4 ja biomassatunnuksia Taulukoissa 5 ja 6 sekä Kuvissa 1, 2 ja 4. Muun kenttäkerroksen kuin varpujen biomassassa pienenee selvästi ojituksen jälkeen. Varpu- ja sammalbiomassa kasvaa aluksi ojituksen jälkeen ja pienenee sitten väliaikaisesti suurimman lajistomuutoksen tapahtumai-
aikana. Vanhimmalla tutkitulla ojitusalueella varpu-
biomassaa oli enemmän ja sammalbiomassaa
noin yhtä paljon kuin ojittamattomilla kohteilla.
Lajisto oli tällöin kuitenkin muuttunut tyypillisten
metsälajien vallitsemaksi; poikkeuksen muodosti
varvikkorahkasammal *Sphagnum russowii* pohja-
kerroksessa.

Peittävyys- ja biomassatunnusten avulla voi saada melko erilaisen käsityksen joistakin tapahtuvista muutoksista. Esimerkiksi vaivaiskoivun (*Betula nana*) biomassaa ensin kasvaa ja sitten vähenee jyrkemmin kuin peittävyys (Kuva 4, Taulukko 3), mikä johtuu ensin ojituksen ja myöhemmin lisääntyvän varjostuksen vaikutuksista varvun morfologiaan.

Received 1.4.1996, accepted 12.6.1996
(Editor for this article: Harri Vasander)