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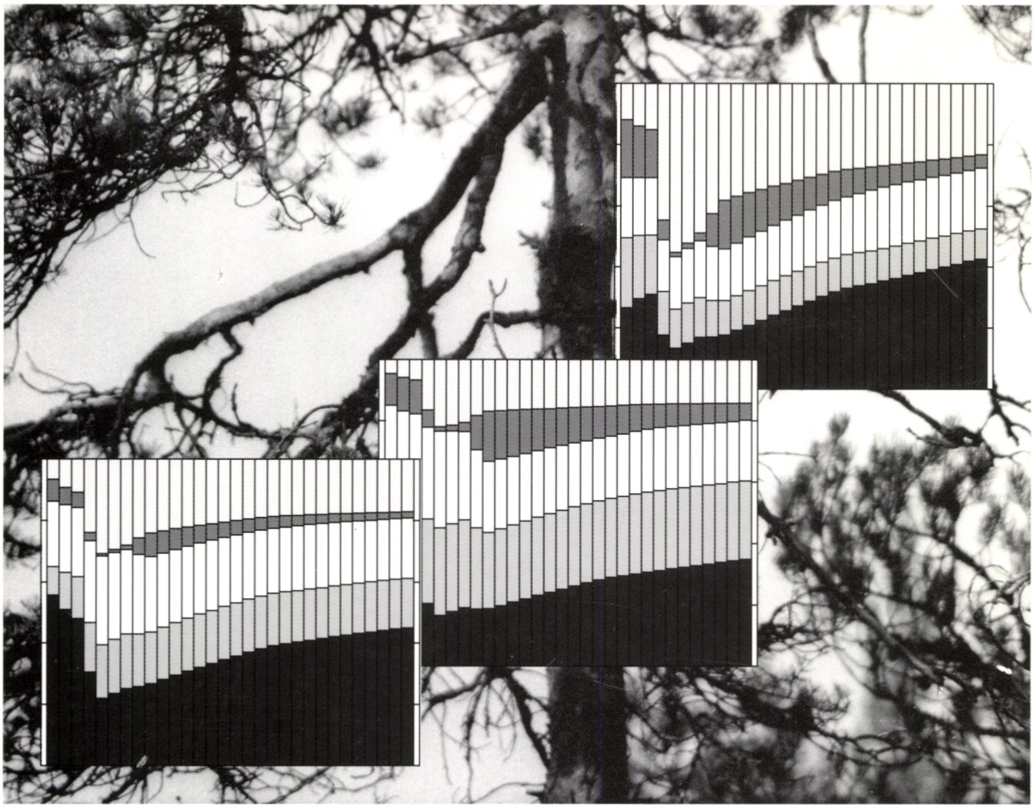

Plant biomass dynamics in drained pine mires in southern Finland

Implications for carbon and nutrient balance

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Academic dissertation

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The main objectives of this study were to follow the changes in total plant biomass, its distribution and nutrient content along the secondary succession caused by forest drainage, and to evaluate the implications of these changes in relation to carbon storage and soil nutrient regimes. The study was limited to a set of pine mire site types commonly drained for forestry. Sites having varying drainage ages (0-55 a) were used to depict the drainage succession.

Soil nutrients and tree stand volumes were measured for both undrained and drained mire sites (n=80) in southern Finland (ca. 61°35' - 61°52'N, 24°05' - 24°25'E). Plant biomass and nutrient contents were measured on a smaller set of intensive study sites (n=6). Equations relating the amount of biomass and nutrient contents to both tree and tree stand dimensions were generated for generalizing the results.

Approximately 50 years after drainage the above-ground tree stand C content on meso-oligotrophic sites had increased, on average, to tenfold that of undrained sites, and on oligo-ombrotrophic sites to sevenfold. The variation was high, however; on meso-oligotrophic sites the range was 2-6 kg C m^{-2} and on oligo-obrotrophic sites 2-4.5 kg C m^{-2}. The estimated maximum C contents in untreated stands ranged from 7 to 10.5 kg C m^{-2} in above-ground biomass and from 10 to 15.5 kg C m^{-2} in total tree stand biomass (excluding fine roots) depending on site type.

On the oldest drained sites studied, the tree stands contained on average 20-30 g m^{-2} N, 1.5-2 gm^{-2} P, 6-7 gm^{-2} K, 10-15 gm^{-2} Ca and 2-3 gm^{-2} Mg, the higher values being for meso-oligotrophic and lower values for oligo-ombrotrophic sites. Developing to the estimated maximum, the tree stands would accumulate a further 50 to 100% of these amounts.

Despite the increasing accumulation of nutrients in the tree stands, the stores of most nutrients remained relatively unchanged in a 0-50 cm surface peat layer during the studied post-drainage period. This may be caused by post-drainage subsidence of the mire surface, due to which the 0-50 cm layer on drained sites does not correspond to the original 0-50 cm layer in the undrained condition, but relates to a thicker layer. The actual losses of base cations from the soil due to uptake and leaching was obvious as decreased gravimetric concentrations.

On the oldest drained sites, the stores of N and P in surface peat were on average 20-30 times higher than the amounts accumulated in the tree stands, and those of Ca and Mg almost 10 times higher. The stores of K in the surface peat were only slightly higher than the amounts in the tree stands. It was concluded that cuttings may cause such K losses that the development of the second-rotation tree stand may be impaired.

Keywords: boreal zone, forest drainage, peatlands, *Pinus sylvestris* L., Scots pine.

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CONTENTS

List of original papers

This thesis is based on the following original papers, referred to according to their Roman numerals:

I Laiho, R. & Laine, J. 1994. Nitrogen and phosphorus stores in peatlands drained for forestry in Finland. Scandinavian Journal of Forest Research 9: 251-260

II Laiho, R. & Laine, J. 1995. Changes in mineral element concentrations in peat soils drained for forestry in Finland. Scandinavian Journal of Forest Research 10: 218-224

III Laiho, R. 1996. Changes in understorey biomass and species composition after water level drawdown on pine mires in southern Finland. Suo 47: 59-69

IV Laiho, R. & Finér, L. 1996. Changes in root biomass after water-level drawdown on pine mires in southern Finland. Scandinavian Journal of Forest Research 11: 251-260

V Laiho, R. & Laine, J. 199x. Tree stand biomass and carbon content in an age sequence of drained pine mires in southern Finland. Forest Ecology and Management (Accepted)

Some as yet unpublished results from further analyses of the materials used in papers I-V are presented in the summary.

List of symbols

d_i	tree stem diameter at height h_i, cm
dm_i	biomass of component i, g
h	tree height, m
h_c	crown limit, m
h_{dom}	tree stand dominant height, m
h_{rel}	relative height of a tree (h/h_{dom})
l_c	tree crown length, m ($h-h_c$)
pi	model parameters
t	time since drainage, a
V	tree stand stem volume with bark, m^3 ha^{-1}

Definitions

Biomass, as used in this study, is more or less synonymous with phytomass; i.e. including not only live (plant) organs but also dead plant tissues still fixed to living individuals (bark, heartwood, dead branches). The amount of biomass is indicated as dry mass, dried in 60°C (fine roots) or 105°C (other components).

Birch means pubescent birch, *Betula pubescens* Ehrh.

Drainage age of a drained peatland site means the time (years) elapsed since the drainage (ditching) of the site.

Fine roots mean all roots with a diameter ≤ 1cm (i.e. fine and small roots as defined by Sutton & Tinus 1983).

Mire means an ecosystem supporting a mire plant community (e.g. Eurola et al. 1984) and characterized by accumulation of organic matter as peat.

Peatland means any site, undrained or drained, with peat soil (at least 75% of dry mass organic matter deriving mainly from plants).

Pine means Scots pine, *Pinus sylvestris* L.

Spruce means Norway spruce, *Picea abies* (L.) Karst.

1. INTRODUCTION

Peatlands are formed and develop when conditions of excessive moisture cause part of the organic matter produced to be deposited as peat. In undrained boreal peatlands, most of the organic matter deposited derives from ground vegetation. The relationship between annual deposition and net primary production in undrained peatlands varies between 3 - 16% (Reader & Stewart 1972, Tolonen 1977, Kozlovskaja et al. 1978, Elina et al. 1984, Tolonen et al. 1988, Francez & Vasander 1995), the mean long-term rate of carbon (C) accumulation in Finnish conditions being ca. 26 g m^{-2} a^{-1} (Tolonen & Turunen 1996, Tolonen et al. 1996). Boreal and subarctic peatlands have been estimated to contain a total of 455 Pg of deposited C (Gorham 1991), which comprises ca. 30% of the estimated global soil C pool.

In Finland, half or more of the mire area, ca. 10 mill. ha before the large-scale drainage started (Paavilainen & Tiihonen 1988), has been drained for forestry (Paavilainen & Tiihonen 1988, Aarne 1993). About 25% of the country's forestry land area consists of peatlands; in some areas this figure is as high as 40% (Mattila & Penttilä 1987, Paavilainen & Tiihonen 1988). The growth of peatland forests may be even more than 25% of the total growth of all Finnish forests (Paavilainen & Tiihonen 1988, Penttilä & Salminen 1991). According to a review by Paavilainen & Päivänen (1995), a total of about 15 million ha of peatlands and wetlands have been drained for forestry in boreal and temperate zones.

After drainage for forestry and the consequent water level drawdown, the aerated surface peat layer increases in thickness. The wetter the site was originally, the more significant is the change in growth conditions caused by drainage. Mire plants adapted to wet conditions decline rapidly, and a secondary vegetation succession towards more forest-like communities begins (e.g. Cajander 1913, Multamäki 1923, Sarasto 1957). The rapidity and extent of the secondary succession depend on the nutrient status and original wetness of the site as well as on the extent of the change in water level (Laine & Vanha-Majamaa 1992, Laine et al. 1995). Biomass production, most of which took place in field and ground layers before drainage is now largely directed to the tree stand (Reinikainen et al. 1984, Sakovets & Germanova 1992), if the site is not too poor in nutrients to sustain forest growth (Vasander 1982). The effects of drainage on stemwood production (e.g. Seppälä 1969, Heikurainen & Seppälä 1973, Hånell 1984, Keltikangas et al. 1986) as well as vegetation composition (e.g. Sarasto 1957, Elina & Kuznecov 1977, Aapala & Kokko 1988, Laine et al. 1995) have been studied rather extensively. Research on the total vegetation biomass on both undrained and drained peatlands has been carried out by e.g. Holmen (1964), Kosonen (1976), Medvedeva et al. (1977), Ouni (1977), Paavilainen (1980), Vasander (1982), Reinikainen et al. (1984 and the references therein), Finér (1989a, 1991), but without focusing on long-term successional dynamics at the stand-level. Only Brække (1986) has related tree biomass dynamics on a drained and afforested mire to the more easily measurable stand stem volume development.

Along with increased aeration of the surface peat, the microbial activity increases after drainage. Thus the oxidation of soil organic matter becomes more effective (e.g. Karsisto 1979, Lieffers 1988, Bridgham et al. 1991) and the flux of C from the soil to the atmosphere rises above pre-drainage level (Silvola 1986, Martikainen et al. 1995, Silvola et al. 1996a, Nykänen et al. 1997), also partly due to an increase in root respiration (Silvola et al. 1996b). Drainage for agriculture or peat harvesting has been found to change a mire from a sink to a source of C for the atmosphere (e.g. Armentano &

Menges 1986, Ahlholm & Silvola 1990, Nykänen et al. 1995). The consequences of forest drainage are not as obvious (e.g. Vompersky et al. 1992, Martikainen et al. 1995). In some cases, accumulation of C in the soil may continue after drainage (Vompersky & Smagina 1984, Minkkinen & Laine 1996, Minkkinen et al. 1996), and the increasing accumulation in tree stands may compensate for the increased flux from the soil for some time (e.g. Sakovets & Germanova 1992, Laine & Minkkinen 1996). It can be concluded from e.g. Vompersky & Smagina (1984), Cannell et al. (1993), Martikainen et al. (1995) and Minkkinen & Laine (1996), that the change in the C balance of both the soil and the whole ecosystem largely depends on the relation between the rates of decomposition and C input via the tree stand, which in turn are mainly regulated by the geohydrological regime of the site as well as the climate. C accumulation in standing stock biomass is cyclical in character. Tree litter shed both above and, especially, below ground may be even more important for the C balance of the site than the accumulation in biomass (cf. Ågren et al. 1980, Fogel & Hunt 1983, Finér et al. 1992). The amount of litterfall naturally varies with the stage of tree stand development.

Carbon cycling is inseparably connected to nutrient cycling. On undrained mires, wetness (aerobicity/unaerobicity) may affect the rates of production (Reinikainen et al. 1984) and decomposition (Bridgham et al. 1991, Szumigalski & Bayley 1996), and, in particular, biomass accumulation in tree stands (Heikurainen 1971, Jeglum 1974, Gustavsen & Päivänen 1986) more than the nutrient regime of the site. On drained mires, however, soil nutrient regime is an important regulating factor (e.g. Tuorila 1933, Vahtera 1955, Kaunisto 1982, Westman 1987, Kaunisto & Paavilainen 1988). Drainage itself also affects the amount of nutrients available for plants in several ways. Increased aerobicity enhances nutrient mineralization in soil (Silvola 1988, Freeman et al. 1993). Leaching of many elements increases at least temporarily with the increased runoff after drainage (Malcolm & Cuttle 1983, Ahtiainen 1988, Lundin 1988). Sallantaus (1992a, 1995) found drainage to cause net leaching of base cations, especially calcium and magnesium. On the other hand, subsidence of mire surface and compaction of peat due to drying may again bring nutrient reserves in the deeper peat layers to within reach of plant roots (cf. Laiho & Laine 1992). Further, increasing foliage biomass may capture nutrients from both dry and wet deposition more than the concentrations in free rainfall would indicate (e.g. Ivens et al. 1990).

The growing tree stand itself is a considerable nutrient sink (e.g. Holmen 1964, Paavilainen 1980, Finér 1989a), accumulating nutrients in standing stock biomass for a relatively long time. This is a great change in the nutrient cycle of most mires (cf. Eurola & Huttunen 1990), where annual cycling of biomass and nutrients through moss and field layer vegetation plays an important role (e.g. Bernard & Hankinson 1979). In peat soils, potassium (K) and/or phosphorus (P) are usually the nutrients limiting tree stand growth (e.g. Paarlahti et al. 1971). K is taken up in considerable amounts compared with the total stores in soil (e.g. Holmen 1964, Paavilainen 1980, Finér 1989a). In tree harvesting, nutrients are removed from the site, and it has been estimated that the amount of K in peat is too small for long-term timber production without repeated fertilization even on many extensively drained mire site types (Kaunisto & Paavilainen 1988).

The dynamics of plant, especially tree, biomass and its accumulation of C and nutrients play an important role in the post-drainage secondary successional changes in the respective cycles on peatland sites. Knowing these dynamics is essential in predicting the long-term consequences of drainage, e.g. those for C balance and sufficiency of nutrients for timber production. Recently, studies on the impact of drainage for forestry has also gained new significance, as it has been suggested that this drainage effect could be used to simulate the effects of predicted climate changes (Martikainen et al. 1993, Laine et al. 1996). Though systematic drainage for forestry has been practiced for ca. 90 years (Paavilainen & Päivänen 1995), little systematic knowledge of the total plant biomass dynamics and the effects on C and nutrient balance on drained peatland sites has been accumulated. This is understandable bearing in mind the time span and variety of mire site types to be dealt with, and the laboriousness of such studies. The aim of this study was to investigate the issue using a set of common pine mire site types in southern Finland. The overall aim was divided into the following more specific objectives:

1) to study the post-drainage changes in the amount and distribution of plant biomass;

2) to provide tools for taking into account the whole plant biomass C pool in C balance calculations by relating it to tree stand stem volume;

3) to study the post-drainage changes in the amount and distribution of nutrients bound in the plant biomass;

4) to study the post-drainage changes in the nutrient stores of surface peat.

2. MATERIALS AND METHODS

21. Approach

No true time series were available for studying actual changes taking place after drainage at certain sites. Therefore, the study was based on comparing sites belonging to the same original site types at various stages of the post-drainage secondary succession; i.e. the sites having varying drainage ages depict the drainage succession. Thus, there was an underlying assumption that the sites belonging to the same original site type were similar before drainage and have developed similarly after drainage. It has been shown, however, that there may be considerable variation between sites belonging to the same site type in e.g. the chemical properties of peat (Westman 1981) as well as the volume of the pre-drainage tree stand (Heikurainen 1971). Consequently, the sites were selected carefully in order to ensure as good a comparability as possible (I).

Because of the approach, it was considered that the material should be as extensive as possible within the site types under investigation and collected from a macroclimatically homogenous area so that natural variation in the studied characteristics would not mask the changes caused by drainage. Thus a limited number of common pine mire site types were chosen as the subjects of the study, namely 1) herb-rich sedge birch-pine fen (RhSR), 2) tall-sedge pine fen (VSR), 3) cottongrass-sedge pine fen (TSR), 4) low-sedge *Sphagnum papillosum* pine fen (LkR) and 5) cottongrass pine bog (TR) (for the Finnish classification system see Cajander 1913, and e.g. Laine & Vasander 1996 for current terminology; short site type descriptions are given in paper I). About 35% of the peatland area drained for forestry in Finland consists of these mire site types (Keltikangas et al. 1986). Typical of all these site types is a mosaic-like pattern of treed hummocks and treeless lawn hollows. They cover a wide geohydrological continuum from meso-eutrophy (RhSR) to oligotrophy and ultimately ombrotrophy (TR).

22. Basic material

The framework for sampling was the mire sites belonging to the site types mentioned above and located in the former Pirkka-Häme Forestry Board District, in the municipalities of Juupajoki, Kuorevesi, Orivesi, Ruovesi and Tampere. The area is part of the southern boreal coniferous forest zone (Ahti et al. 1968) and the eccentric raised bog region (Ruuhijärvi 1982).

To locate the drained sites, the drainage plan documents filed by the Board were checked for sites classified as the chosen site types, and the sites were further checked before sampling. The sites finally chosen for sampling had to meet the following conditions: 1) a proper site type in a more or less homogenous area of at least 0.5 ha, 2) no signs of drainage of unknown age before the year given in the drainage plan documents, 3) thickness of peat layer at least 1 m, 4) a distance of at least 40 m to the mire margin, 5) a satisfactorily effective drainage on the drained sites, 6) no peculiarities in the peat, like thick layers of charcoal or water-borne mineral grains, 7) at least ten trees on the plot (sized 10x30 m) with breast height diameter of at least 5 cm, 8) the site not treated with cuttings (with the exception of possible improvement cutting along with ditching).

The basic material (I, II) consists of 80 peatland sites, 11 undrained and 69 drained at different times (Table 1). The oldest drainage areas sampled had been drained 55 years earlier.

The sample plots were placed along contour ditches with the longer side of the plot parallel to the ditch to standardize hydrological conditions. The tree stand was measured for stem volume estimation and peat samples were taken for nutrient analyses (I, II).

The material was grouped into two site type groups. The "meso-oligotrophic" site type group consisted of RhSR and VSR site types, which are closely related to each other in terms of vegetation (cf. e.g. Hotanen & Vasander 1992) and peat composition (sedge peat). The "oligo-ombrotrophic" site type group consisted of more nutrient-poor site types, TSR, LkR and TR, which have *Sphagnum*-dominated peat.

23. Intensive study sites

231. Selection

Out of the basic material, six sites of the tall-sedge pine fen (VSR) type were selected for more intensive studies (III-V). Tall-sedge pine fen was chosen as the main subject of the study, because it is the site type most commonly drained for forestry in Finland (Keltikangas et al. 1986), and it has been suggested to represent the 'nutrient-level median' of the drained peatlands (Laine & Minkkinen 1996). The sites were selected to represent as wide a drainage age variation as possible within the chosen site type, so that on the drained sites, the tree stand volume would be close to the average for the drainage

Table 1. Site type and drainage age distribution in the basic material. For site type descriptions, see Chapter 21.

Site type	Drainage age class				
	undrained	1-20	21-40	41-55	*all*
RhSR	2	3	6	3	*14*
VSR	3	10	6	11	*30*
TSR	3	4	3	7	*17*
LkR	2	6	4	2	*14*
TR	1	1	1	2	*5*
all	*11*	*24*	*20*	*25*	*80*

age. Two of the sites were undrained while the rest had been drained 8, 22, 30 and 55 years earlier. The general features of these sites are described in Table 1 of papers III-V, and the ground vegetation composition in paper III.

232. Field measurements and sampling

Sampling was done in mid June 1991 on sites 2 and 5, and at the end of June 1992 on the other sites. Understorey species composition was analyzed (III), and all vegetation components were sampled for biomass and nutrient content determinations (III-V).

All trees on the sample plots (henceforward called tally trees) were measured for $d_{1.3}$ (0.5 cm precision) and d_6 (1 cm precision; for trees higher than 7 m), bark thickness (1 mm precision), total height, and height to the base of the live crown (both 0.1 m precision). Eight pine biomass sample trees per plot (only six on plot 1; henceforward called sample trees; Table 2) were chosen with stratified random sampling to cover the whole range of diameters. Depending on the tree species composition of the sites, varying numbers of birch and spruce sample trees, as well as dead trees, were also chosen. The sampling procedure is described in detail in paper V.

Ground vegetation, litter layer and peat for fine root biomass determination were sampled at 16-20 systematically chosen locations. Tree seedlings ($d_{1.3} < 1.5$ cm) were measured and sampled on five circular subplots with a radius of 2 m, laid systematically on the diagonals of the sample plots.

Volumetric peat samples (490 or 640 cm^3) were taken from depths of: 0-10, 10-20, 25-35, and 50-60 cm, at the same locations as the ground vegetation and fine root samples were taken (III, IV). The samples were dried in 105°C to constant mass and ground to pass through a 2 mm sieve.

233. Estimation of tree stand volume and plant biomass

The total stem volume (with bark) at each site was calculated using KPL software (Heinonen 1994). Tree-level stem volumes were calculated as

$$V=f(\text{tree species}, d_{1.3}, h) \qquad (1)$$

using volume functions by Laasasenaho (1982), and summed up to obtain stand-level stemwood volumes.

Above-ground tree stand biomass was estimated by the regression method (e.g. Satoo & Madgwick 1982) as described in paper V. The estimation method for the biomass of stumps and coarse roots, not sampled for this study, is described in paper IV. Understorey and fine root biomasses were estimated per unit area as described in papers III and IV.

Table 2. Some sample tree characteristics for the intensive study sites.

	Pine undrained		Pine drained		Birch		Spruce	
n	14		33		17		8	
$d_{1.3}$, cm	9.9	± 4.2	14.8	± 6.2	6.7	± 3.3	6.2	± 2.7
height, m	6.0	± 2.0	10.9	± 4.5	8.2	± 2.9	5.4	± 2.4
crown limit, m	2.9	± 0.8	5.1	± 2.8	2.8	± 1.6		
stemwood, kg	12.5	± 9.9	47.7^{b}	± 46.7	9.3	± 9.2	5.1	± 5.4
stembark, kg	2.3	± 1.9	5.5^{b}	± 4.6	1.6	± 1.6	1.1	± 1.0
branches, kg	2.9	± 3.1	11.1	± 9.6	2.1	± 2.1	3.8^{d}	± 3.4
dead branches, kg	1.6	± 1.1	4.4	± 5.1	0.3^{c}	± 0.3	0.4	± 0.4
foliage, kg	1.1^{a}	± 1.3	5.3	± 3.5	0.6	± 0.6		

[a] n=12, [b] n=32, [c] n=16

[d] including foliage

234. Carbon and nutrient analyses

For nutrient analyses, the biomass samples were combined either *per* sample tree or *per* sample plot. The following sample discs of stemwood and bark were combined *per* sample tree: 0-10%, 20-50% and 60-90% relative height. Live branches and needles were combined *per* sample tree. Dead branches had already been combined *per* sample tree for biomass determination. All biomass samples of some of the largest sample trees were analyzed for nutrient concentrations to check the reliability of the combined sample results. Understorey and litter samples were combined *per* component and sample plot. Peat samples were combined *per* layer and sample plot.

Concentrations of P, K, calcium (Ca) and magnesium (Mg) were measured on an ICP analyzer (ARL 3580) after nitric acid-perchloric acid digestion. Nitrogen (N) and C concentrations of a subset of samples were measured on a Leco CHN 600 analyzer. The analyses were checked for a subset of samples by parallel measurements.

The element contents of the various biomass components *per* sample plot were calculated by multiplying the biomass values by the mean concentrations given in Table 2 in paper V (carbon) and Appendices 1-3 (other elements). The element contents of stumps and coarse roots were estimated using the concentrations presented by Finér (1989a) for pine growing on a VSR site and birch on a RhSR site. The values were corrected with the ratio of Finér's stemwood concentrations to those measured in this study. Spruce was left out of this estimation because its stump and coarse root biomass was small on the sites of this study. Standing dead trees were also excluded because there is no information on the changes in their element concentrations after death.

235. Analysis of the stand-level past growth

The past annual stem diameters without bark at the 11 heights where stem analysis discs had been taken (V) were reconstructed for each sample tree back to five years before drainage using tree ring data measured from the stem analysis discs. Past annual height estimation was based on the number of annual rings. It was assumed that each disc had been situated in the middle of an annual shoot. For instance, if there were two annual rings in the uppermost disc, it was assumed that there had been one and a half shoots between the uppermost disc and the tree top. If the distance between discs in the tree was 20 cm, the two previous past growths would have been 20/1.5 = 13.3 cm a^{-1}. The height growth between the lower discs was obtained by dividing the distance between discs by the difference in the number of annual rings in the discs. The corresponding annual stem volumes for each sample tree were then obtained by fitting and integrating a taper curve, smoothed by a spline function, to each year's diameter data set using KPL software (Heinonen 1994).

The previous year's diameter increment at breast height, as well as the height increment of the sample trees were then regressed against the current $d_{1.3}$ by KPL. Applying the regressions to the recorded diameters at breast height resulted in the $d_{1.3}$ and height of each tree a year earlier. This procedure was repeated until the fifth pre-drainage year, or until the tree's $d_{1.3}$ became zero. Bark thickness was then added to the diameters using the bark equations of KPL, as it was found that the bark estimates thus obtained did not differ from the estimates calculated using the bark thickness values measured from the sample trees. Thus, estimates of the annual $d_{1.3}$ and height distributions of the tree stands were obtained for as far back as the fifth pre-drainage year.

On site 5 there was a rather abundant number of standing dead trees due to Scleroderris canker (*Ascocalyx abietina* Lagerb.) epidemics in the mid 1980s (V). On the basis of a tree ring analysis of the dead sample trees, the average year when their radial growth had ended was found. This was chosen as the year when all the dead trees were removed from the analysis of the living tree stand. Their previous growth was estimated as described above using the values of living sample trees, because there were no evident differences in the growth of dead and living sample trees until the growth of the former suddenly ended. On other sites, the mortality was assumed to have been of no significance due to the small size and number of dead trees.

236. Reconstructing the past tree stand biomass dynamics

For estimating the past tree component and total biomasses, a new set of regression equations was made from the combined sample tree data (Tables 3 and 4). The plotwise equations used in paper V were not considered generally applicable because biomass allocation ratios change along with tree stand development (e.g. Ruark et al. 1987).

Only two birch sample trees had been felled on the undrained sites. On *a posteriori* basis, birch biomass on the undrained sites was estimated using equations derived from the birch data of the drained sites; leaf biomass values, however, were corrected as shown in Table 3. The number of spruce sample trees was so small that equations were made only for estimating total and stem (wood + bark) biomasses, and crown (branches

Table 3. Equations for estimating total and component tree-level biomasses (g). A lacking parameter value indicates that the independent variable in question was not included in the corresponding equation. Parameter standard errors are given in brackets.

	p1	p2	p3	p4	p5
Pine: undrained sites		$dm_i = p1 \cdot d_{1.3}^{p2} \cdot h^{p3}$			
Stemwood	68.408 (15.347)	2.052 (0.104)	0.183 (0.090)		
Stembark	10.452 (4.267)	1.411 (0.169)	1.117 (0.196)		
Live branches	3.324 (1.174)	2.857 (0.131)			
Dead branches	57.981 (48.587)	1.443 (0.325)			
Foliage	0.451 (0.200)	1.987 (0.140)	1.592 (0.233)		
Total above ground	66.758 (15.988)	1.883 (0.102)	0.658 (0.142)		
Pine: drained sites		$dm_i = p1 \cdot d_{1.3}^{p2} \cdot h^{p3} \cdot h_c^{p4} \cdot h_{rel}^{p5}$			
Stemwood	14.422 (3.206)	1.840 (0.095)	1.185 (0.073)		
Stembark	5.658 (2.543)	2.251 (0.203)	0.249 (0.133)		
Live branches	3.992 (3.326)	3.285 (0.311)		-0.804 (0.102)	
Dead branches	3101.458(5047.502)	0.307 (0.554)			5.275 (1.639)
Foliage	33.203 (15.816)	2.132 (0.182)		-0.502 (0.078)	
Total above ground	53.677 (17.734)	2.143 (0.149)	0.510 (0.102)		
Birch:		$dm_i = p1 \cdot d_{1.3}^{p2} \cdot h^{p3} \cdot h_{rel}^{p4} - d_{1.3}^{p5}$			
Stemwood	6.329 (1.316)	1.820 (0.065)	1.580 (0.115)		
Stembark	5.156 (4.129)	1.197 (0.236)	1.456 (0.448)		
Live branches	3.775 (4.290)	2.966 (0.459)		-0.745 (0.355)	
Dead branches	1130.121(1294.469)	1.693 (0.339)	-2.146 (0.457)		
Foliage	13.180 (4.550)	1.978 (0.149)			2.987[a](0.040)
Total above ground	37.437 (10.789)	2.031 (0.106)	0.799 (0.107)		
Spruce:		$dm_i = p1 \cdot d_{1.3}^{p2} \cdot h^{p3}$			
Stem (wood + bark)	38.711 (4.802)	1.789 (0.066)	0.901 (0.039)		
Total above ground	92.558 (55.238)	1.652 (0.319)	0.855 (0.196)		

[a] for undrained

Table 4. Some statistics for the biomass equations presented in Table 3; r.s.d. = residual standard deviation of the model, kg, (* = standard error of estimate from the observation / estimate -regression, see text), coefficient = observation / estimate -ratio (its standard error in brackets).

	R^2	r.s.d.	n	coefficient		R^2	r.s.d.	n	coefficient
Pine: undrained sites									
Stemwood	0.996	1.05	14	1.001 (0.016)	Dead branches	0.915	0.62	14	1.000 (0.084)
Stembark	0.989	0.35	14	1.000 (0.030)	Foliage	0.996	0.12	12	1.001 (0.020)
Live branches	0.993	0.40	13	1.000 (0.025)	Total above ground	0.997	1.51	12	1.001 (0.016)
Pine: drained sites									
Stemwood	0.996	4.26	32	0.999 (0.011)	Dead branches	0.823	2.85*	33	0.999 (0.082)
Stembark	0.983	0.96	32	0.997 (0.019)	Foliage	0.971	1.13	33	1.001 (0.031)
Live branches	0.960	3.06	33	0.999 (0.036)	Total above ground	0.991	9.78	32	0.998 (0.017)
Birch									
Stemwood	0.999	0.47	15	1.001 (0.009)	Dead branches	0.900	0.16	13	1.001 (0.097)
Stembark	0.981	0.29	15	0.999 (0.037)	Foliage	0.983	0.12	17	0.999 (0.032)
Live branches	0.960	0.67	15	1.001 (0.054)	Total above ground	0.995	1.44	17	1.002 (0.017)
Spruce									
Stem	0.999	0.25	8	1.001 (0.009)					
Crown	0.920	1.60*	8	0.998 (0.111)	Total above ground	0.987	1.97	8	1.000 (0.043)

+ foliage) biomass was calculated as the difference between total and stem biomass values.

Estimates of the crown limit for pines, i.e. height to the base of the live crown, were made by fitting the following empirical equation to the combined pine tally tree data for the drained intensive study sites:

$$h_c = p0 + h^{p2} \bullet h_{dom}^{p3} \qquad (2)$$

obtaining parameter values (± asymptotic standard errors) $p0 = -94.452 \pm 10.452$, $p2 = 0.742 \pm 0.022$ and $p3 = 0.520 \pm 0.057$. The degree of determination was 0.972 and the residual standard deviation 0.95 m. The unit of tree-level variables h_c and h was cm and that of stand-level variable h_{dom} m. The relation of the tallied $h_c(1)$ to a more accurately measured $h_c(2)$ was checked in the sample tree data, being

$$h_c(2) = 0{,}949 \bullet h_c(1) \qquad (3)$$

with a standard error of estimate of 0.76 m and a degree of determination of 0.984. The crown limit estimates obtained with Equation 2 were corrected accordingly for this slight systematic overestimation. For trees growing on the undrained sites, the crown limit related poorly to any other measured dimensions, so an estimation of the past crown limit was limited to the post-drainage period.

The reconstructed annual tree data were divided by tree species into 1 cm diameter classes. The mean $d_{1.3}$ and height value of each diameter class (or $d_{1.3}$ and crown limit/crown length obtained fitting the mean height into Equation 2) were fitted into the biomass equations. The biomasses obtained were multiplied by the number of trees in each diameter class and summed up over each diameter class.

For pine, the 'undrained' vs. 'drained' equations were applied in the following way:

Dead branches:
$t \leq 2$: $dm_i = dm_i0$
$2 < t < 5$: $dm_i = avg(dm_i0, dm_i3)$
$5 \leq t < 10$: $dm_i = dm_i3$
$10 \leq t < 12$: $dm_i = avg(dm_i3, dm_i1)$
$t \geq 12$: $dm_i = dm_i1$

Other components and total biomass:
$t \leq 2$: $dm_i = dm_i0$
$2 < t < 5$: $dm_i = avg(dm_i0, dm_i1)$
$t \geq 5$: $dm_i = dm_i1$

where dm_i0 = value obtained with the undrained sites' equation (Table 3); dm_i1 = value obtained with the drained sites' equation (Table 3), dm_i3 = value obtained with the equation specific for site 3 (paper V, not shown) and avg = average. The grounds for this smoothing were derived from *a posteriori* examination of the plotwise biomass values (V) and from the observations of e.g. Lukkala (1929) concerning the timing of the effect of drainage in the size and amount of needles and the diameter and height growth of trees. The amount of dead branches on the recently drained sites could not be corrected with a dummy variable because the equation thus constructed produced negative values for trees with small $d_{1.3}$'s.

As simple statistical biomass component models never completely sum up to equal the total estimate (e.g. Cunia & Briggs 1984), the component estimates were used only in describing the dynamics of the component proportions in time.

237. Reconstructing the past tree stand nutrient dynamics

To estimate the nutrient content of individual trees, regression equations were derived from the sample tree data (Table 5, Figs 1-3, App. 4-7). The equations were applied similarly to the biomass equations described above.

On the recently drained site 3 the pine foliage K contents in relation to $d_{1.3}$ were significantly higher than on the other sites. Thus a correction factor ($d_{1.3}^{p6}$) was added to the drained sites' equation, which was applied for 12 years after drainage in a manner similar to that for the dead branch biomass shown above, with the exception that smoothing was started in the year of ditching. In the foliage P equation a similar correction factor reduced the residual standard deviation and was included.

The nutrient content of dead branches could be estimated with equations only in the undrained site pine data. For pines on drained sites, the corresponding values were calculated by multiplying the biomass estimates by concentrations related to $d_{1.3}$ (App. 8). Dry mass weighted mean concentrations were used for birches. It was not possible to make a total N equation for birch because the number of observations was too small. Instead, biomass estimates and the average N concentration in total biomass (4.069 mg g^{-1}) were used.

Table 5. Equations for estimating total tree-level nutrient contents (g); r.s.d. = residual standard deviation (g), coefficient = observation / estimate -ratio. Standard errors are given in brackets.

	p1		p2		R^2	r.s.d.	n	coefficient	
Pine: undrained sites			$c_i = p1 \cdot d_{1.3}^{p2}$						
N	0.0793	(0.055)	2.714	(0.253)	0.996	8.438	5	1.000	(0.033)
P	0.0171	(0.009)	2.237	(0.198)	0.987	0.608	9	1.003	(0.041)
K	0.158	(0.095)	2.033	(0.224)	0.980	3.967	9	0.999	(0.050)
Ca	0.0896	(0.045)	2.603	(0.186)	0.991	7.046	9	1.000	(0.034)
Mg	0.0567	(0.033)	2.008	(0.217)	0.982	1.272	9	0.999	(0.048)
Pine: drained sites			$c_i = p1 \cdot d_{1.3}^{p2}$						
N	1.360	(1.704)	1.862	(0.412)	0.953	78.876	12	1.001	(0.070)
P	0.0410	(0.027)	2.125	(0.213)	0.963	3.879	27	1.001	(0.038)
K	0.310	(0.172)	1.906	(0.184)	0.970	13.625	27	1.000	(0.035)
Ca	0.658	(0.435)	1.858	(0.219)	0.948	33.206	27	1.001	(0.046)
Mg	0.0249	(0.012)	2.438	(0.156)	0.984	3.989	27	0.995	(0.025)
Birch			$c_i = p1 \cdot d_{1.3}^{p2}$						
P	0.0174	(0.030)	2.636	(0.726)	0.920	2.100	10	0.998	(0.098)
K	0.184	(0.097)	2.074	(0.225)	0.983	2.613	10	1.002	(0.043)
Ca	0.415	(0.212)	2.025	(0.218)	0.984	5.207	10	0.999	(0.043)
Mg	0.0598	(0.047)	2.188	(0.335)	0.969	1.536	10	0.997	(0.060)

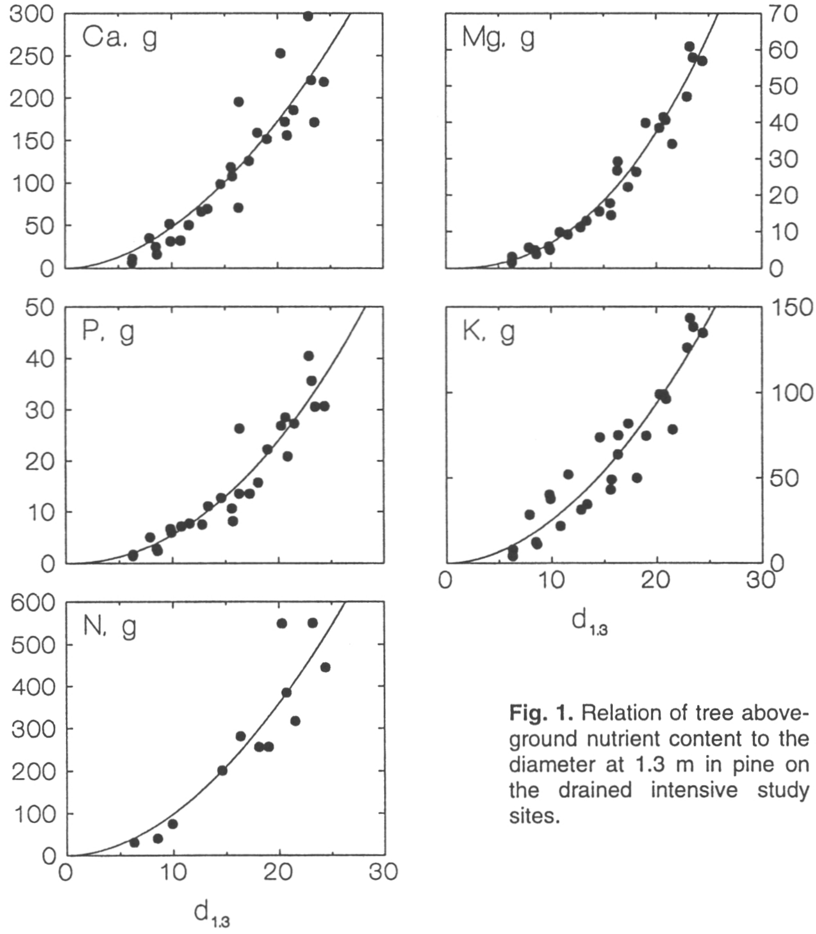

Fig. 1. Relation of tree above-ground nutrient content to the diameter at 1.3 m in pine on the drained intensive study sites.

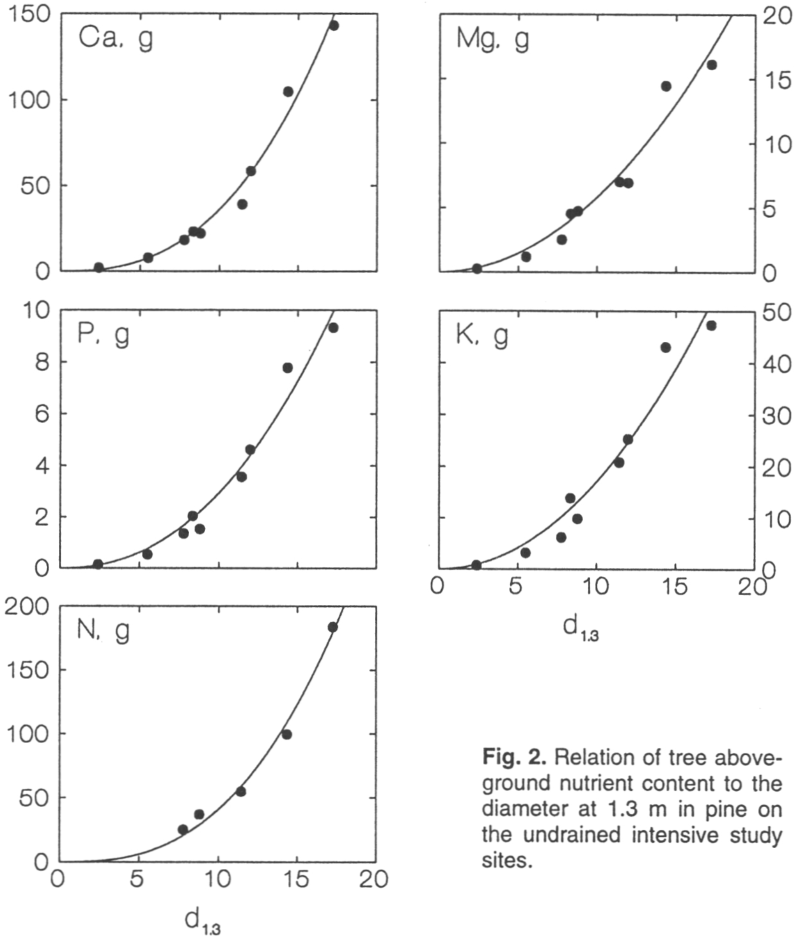

Fig. 2. Relation of tree above-ground nutrient content to the diameter at 1.3 m in pine on the undrained intensive study sites.

24. Estimating tree stand carbon and nutrient content in the basic material

Tree stand C and nutrient contents were estimated for the basic material sites using the results from the intensive study sites. The stand level equation relating the C content to tree stand stem volume presented in paper V was used for C. The tree level equations presented in Chapter 237 were used for nutrients. This was done because the proportion of birch varied considerably in the basic material, which was presumed to affect the tree stand nutrient content more than C content (cf. e.g. Perry et al. 1987). With the tree level equations this variation could be accounted for better than with the stand level equations to be presented for pine-dominated stands in Chapter 321.

The new nutrient content estimates were used to replace the ones calculated earlier for papers I and II, using the constant nutrient concentration values per m^3 stemwood from Paavilainen (1980) and Finér (1989a) (I).

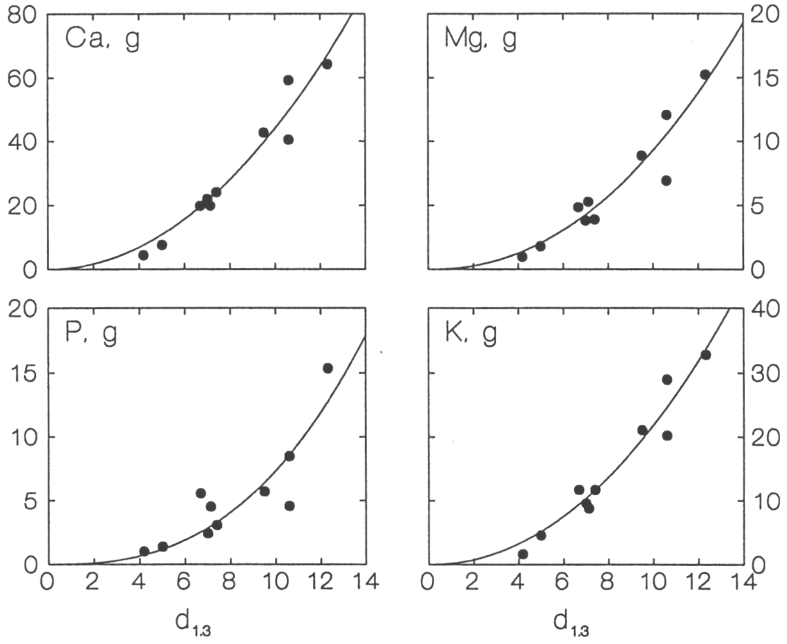

Fig. 3. Relation of tree above-ground nutrient content to the diameter at 1.3 m in birch on the intensive study sites.

3. RESULTS

31. Biomass and carbon

311. Distribution and dynamics along the drainage succession on the intensive study sites

The total above-ground plant biomass varied from 1040 g m^{-2} on an undrained site to 8310 g m^{-2} on the site drained 55 years earlier (Table 6). The proportion of tree stand was smallest on undrained site 1 and on site 3, drained eight years earlier, being 38 and 43% respectively. On sites 4-6, drained 22-55 years earlier, it was 92-96% of the total above-ground plant biomass. The total understorey biomass (including tree seedlings) was almost 600 g m^{-2} on average on the undrained sites, and increased up to almost 1000 g m^{-2} soon after drainage. Later on in the drainage succession, the understorey biomass first decreased to minimum values on the sites drained 22-30 years earlier, but had again risen on the oldest drained site to reach a level similar to that on the undrained sites. Within-site variation in the understorey biomass was much higher on the drained than on the undrained sites.

The total amount of fine roots somewhat increased along with the increasing drainage age; site 5 was exceptional in this respect. Fine roots of Cyperaceous field layer were reduced to a minimum of 11 g m^{-2} on the oldest drained site while those of trees and

Table 6. The amount of plant biomass and above-ground detritus (g m^{-2}) on the intensive study sites. Standard deviations are given in brackets. Sites 1-2 undrained, drainage age of site 3: 8 years, site 4: 22 years, site 5: 30 years and site 6: 55 years.

	Site					
	1	2	3	4	5	6
Above-ground						
Tree stand (V) [a]	380	1930	720	4444	5810	7647
Tree seedlings (III)	21 (31)	26 (26)	19 (23)	112 (77)	18 (22)	21 (12)
Ground vegetation (III)	634 (108)	497 (61)	992 (175)	263 (213)	262 (117)	643 (293)
Vegetation total	**1035**	**2453**	**1731**	**4819**	**6090**	**8311**
Standing dead trees (V)	229	31	50	71	358	37
Litter layer	199 (166)	147 (38)	268 (164)	769 (294)	581 (426)	683 (434)
Detritus total	**428**	**178**	**318**	**840**	**939**	**720**
Below-ground						
Coarse roots (IV)	175	916	291	1387	2109	2932
Fine roots (IV)	456 (236)	597 (191)	481 (177)	840 (316)	437 (305)	886 (345)
Live roots total	**631**	**1513**	**772**	**2227**	**2546**	**3818**

[a] dbh ≥ 1.5 cm

shrubs more than tripled during the drainage succession (IV). The estimated living tree stump and coarse root biomass had a positive linear correlation to the tree stand stem volume, increasing clearly during the drainage succession (IV).

The amount of above-ground detritus was lowest on undrained site 2 and highest on the site drained 30 years earlier (Table 6). It clearly increased after drainage, being almost threefold on the oldest drained sites in comparison to the undrained sites and the youngest drained site.

The amount of C contained in plant biomass was closely related to the tree stand stem volume (Fig. 4 and Table 7). Within the drainage succession studied (0-55 years since drainage), this C pool had increased by ca. 5000 g m^{-2}.

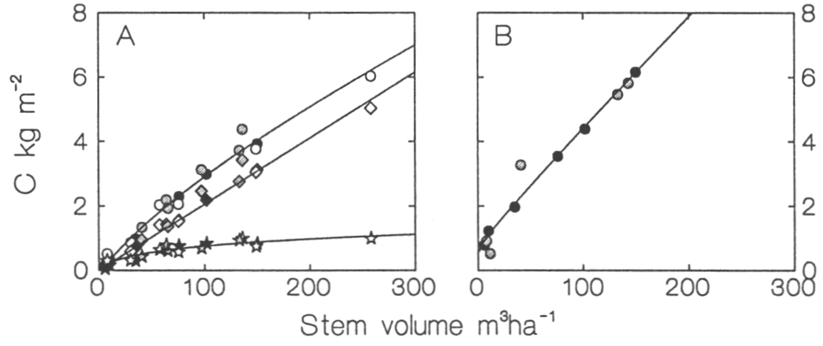

Fig. 4. Relations between A: tree stand stem volume and the C content in total above-ground tree stand biomass (uppermost line, circles), stem component biomass (wood + bark, middle line, diamonds) and crown component biomass (needles + all branches, lowermost line, stars), and B: tree stand stem volume and the C content in total plant biomass (above- and below-ground, all vegetation layers). Black symbols depict the intensive study sites of this study, grey symbols peatland sites with natural pine-dominated stands but with varying nutrient regime studied by Holmen (1964), Medvedeva et al. (1977), Paavilainen (1980), Finér (1989a, 1991), Håland (1994) and open symbols upland sites of Mälkönen (1974) and H.-S. Helmisaari & K. Makkonen (unpublished) with a nutrient regime approximately corresponding to the sites of this study. The cited material has been converted to C estimates by multiplying the reported biomass values by 0.50. Lines were drawn using the equations shown in Table 7.

Table 7. Regression equations for the relation of above-ground tree stand and total plant biomass carbon contents (y, kg C m^{-2}) to tree stand stem volume (x, m^3 ha^{-1}); s.e. = parameter standard error, SEE = standard error of estimate. 'Tree stand' equation from V.

Component	p1	s.e.	p2	s.e.	p3	s.e.	SEE	R^2	n
Tree stand:									
$y = p1 \cdot x + p2 \cdot (\ln x)^{p3}$	0.012	0.012	0.012	0.008	3.241	0.745	0.090	0.999	6
Total vegetation:									
$y = 0.5 + p1 \cdot x + p2 \cdot \ln x$	0.034	0.001	0.108	0.029			0.10	0.998	6

312. Reconstructed tree stand biomass dynamics on the drained intensive study sites

Above-ground tree stand biomass has increased almost linearly in relation to the drainage age of the sites, and the rate of accumulation has not yet decreased even on the oldest drained site (Fig. 5). On site 4 the recent annual above-ground biomass accumulation has been ca. 250 g m^2 a^{-1}. The development on site 5 has been similar to that on site 4 except for the disturbance caused by Scleroderris canker. On the oldest drained site, 6, the recent biomass accumulation has been somewhat slower, ca. 200 g m^2 a^{-1}. The average annual biomass accumulation during the whole post-drainage period has been less than 50 g m^{-2} a^{-1} on site 3, almost 200 g m^{-2} a^{-1} on sites 4-5, and 150 g m^{-2} a^{-1} on site 6. During the five-year period before drainage it was 5-10 g m^{-2} a^{-1} for the current tree stands.

Recent annual stump and coarse root biomass accumulation has been 50-90 g m^{-2} a^{-1}, and average annual accumulation less than 20 g m^{-2} a^{-1} on site 3 and 40-60 g m^{-2} a^{-1} on the older drained sites (Fig. 5). Before drainage the annual accumulation was 2-6 g m^{-2} a^{-1}.

The current above-ground biomass estimates obtained with the general equations are slightly higher than the ones obtained with the site-specific equations (V), especially for site 6.

Drainage sharply increased the proportions of foliage and branches but later on the proportion of stemwood increased steadily (Fig. 6).

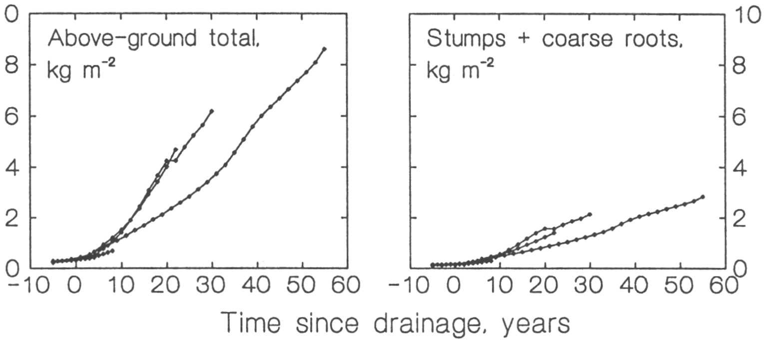

Fig. 5. Reconstructed biomass accumulation in the tree stands on the drained intensive study sites. Note the difference in scales.

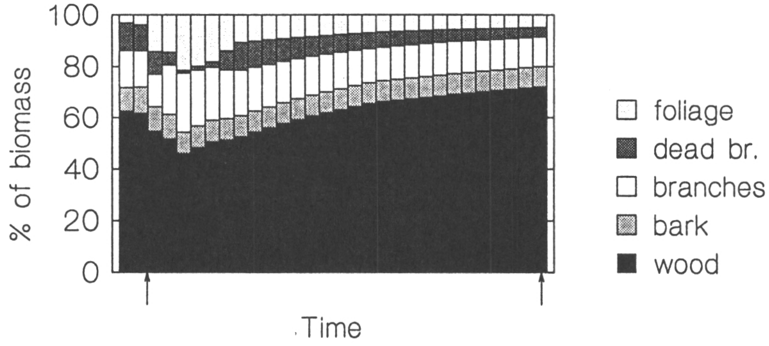

Fig. 6. Reconstructed dynamics of the biomass proportions of above-ground tree components on intensive study site 6 (drained 55 years earlier). The arrows point at the year of drainage (left) and the year 55 after drainage (right).

313. General situation in the basic material

The above-ground tree stand C store has clearly increased after drainage. On sites drained ca. 50 years earlier, it was on average over tenfold that on undrained sites in the meso-oligotrophic group (RhSR and VSR) and ca. sevenfold in the oligo-ombrotrophic group (TSR, LkR and TR) (Fig. 7). The variation was high, the maximum being ca. 6 kg C m^{-2} and minimum ca. 2 kg C m^{-2} on the meso-oligotrophic sites; on the oligo-ombrotrophic sites the corresponding figures were 4.5 and 2 kg C m^{-2}, respectively.

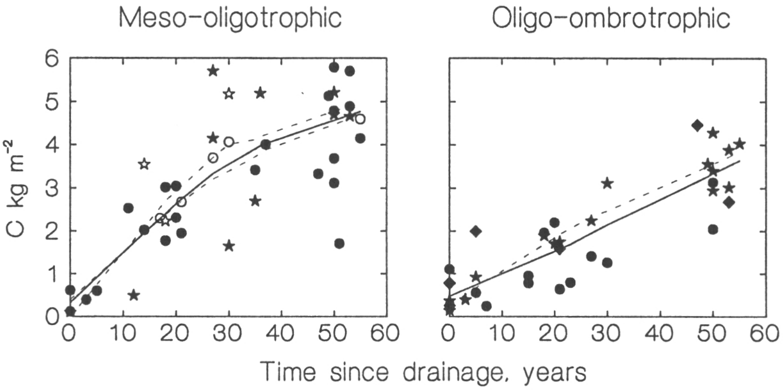

Fig. 7. Estimated total above-ground C contents in the tree stands of the basic material. Stars = RhSR (left) and TSR (right), dots = VSR and LkR, diamonds = TR. Open symbols depict sites where the proportion of birch out of the total stand stem volume was ≥ 50 %, and where the estimates are thus less reliable (see text). Solid lines are for the site type groups and dotted lines for individual site types.

32. Nutrients

321. Distribution and dynamics along the drainage succession on the intensive study sites

The nutrient concentrations in various tree components varied between sites (App. 1-3), so the total amounts of some nutrients in tree stand biomass did not follow as clear a pattern in relation to tree stand stocking as biomass itself (Fig. 8, Table 8). The tree stand on site 5 contained relatively little N and much P. The larger the tree stand, the higher amount of N, K, Ca and Mg in the stemwood component. The nutrient amounts accumulated in the tree stands may be represented rather well by equations relating them to stem volume (Fig. 9, Table 9).

The relative proportions of the major nutrients in the tree stand differed from those in the peat soil (0-50 cm layer) (Fig. 10), the most striking differences being the overwhelming proportion of N and small proportion of K in the soil, as compared with those in the tree stand. The relative proportions of N and P in the tree stand were slightly higher on the drained than on the undrained sites, whereas the opposite was found for

Table 8. Nutrient contents, g m^{-2}, in vegetation and litter layer on the intensive study sites.

Site and component		N	P	K	Ca	Mg
1	Tree stand, above-ground	0.94	0.04	0.27	0.66	0.12
	Ground vegetation, -"-	5.89	0.25	2.33	1.90	0.67
	Stumps + coarse roots [a]	0.75	0.02	0.26	0.33	0.07
	Litter layer	1.61	0.07	0.39	0.43	0.08
	0-50 cm surface peat [b]	474.50	13.29	5.75	63.60	16.24
2	Tree stand, above-ground	5.14	0.32	1.72	4.35	0.58
	Ground vegetation, -"-	4.55	0.31	2.66	1.63	5.26
	Stumps + coarse roots [a]	3.41	0.13	1.19	1.39	0.24
	Litter layer	1.07	0.05	0.31	0.45	0.07
	0-50 cm surface peat [b]	1105.00	27.02	13.33	155.88	26.92
3	Tree stand, above-ground	3.37	0.22	1.31	1.64	0.26
	Ground vegetation, -"-	10.87	0.62	2.85	2.77	0.85
	Stumps + coarse roots [a]	1.05	0.04	0.37	0.45	0.07
	Litter layer	2.78	0.13	0.50	0.83	0.17
	0-50 cm surface peat [b]	836.20	27.25	9.56	70.48	20.18
4	Tree stand, above-ground	16.67	0.96	3.76	8.35	1.46
	Ground vegetation, -"-	3.81	0.18	0.43	0.81	0.19
	Stumps + coarse roots [a]	4.87	0.30	1.32	1.91	0.35
	Litter layer	11.26	0.46	0.61	3.35	0.46
	0-50 cm surface peat [b]	1035.5	34.22	7.87	190.69	14.72
5	Tree stand, above-ground	17.07	1.46	4.13	9.39	1.79
	Ground vegetation, -"-	3.71	0.29	1.33	0.76	0.30
	Stumps + coarse roots [a]	8.46	0.30	1.32	1.91	0.35
	Litter layer	6.98	0.38	0.61	2.91	0.42
	0-50 cm surface peat [b]	1714.30	36.48	8.09	216.74	18.45
6	Tree stand, above-ground	22.44	1.40	5.69	9.70	2.35
	Ground vegetation, -"-	8.69	0.58	2.25	2.43	0.69
	Stumps + coarse roots [a]	13.37	0.47	2.54	3.36	0.81
	Litter layer	7.44	0.35	0.61	2.40	0.32
	0-50 cm surface peat [b]	1355.80	50.91	12.19	84.14	12.56

[a] estimated using concentrations given by Finér (1989), as described in Chapter 234.

[b] including fine roots

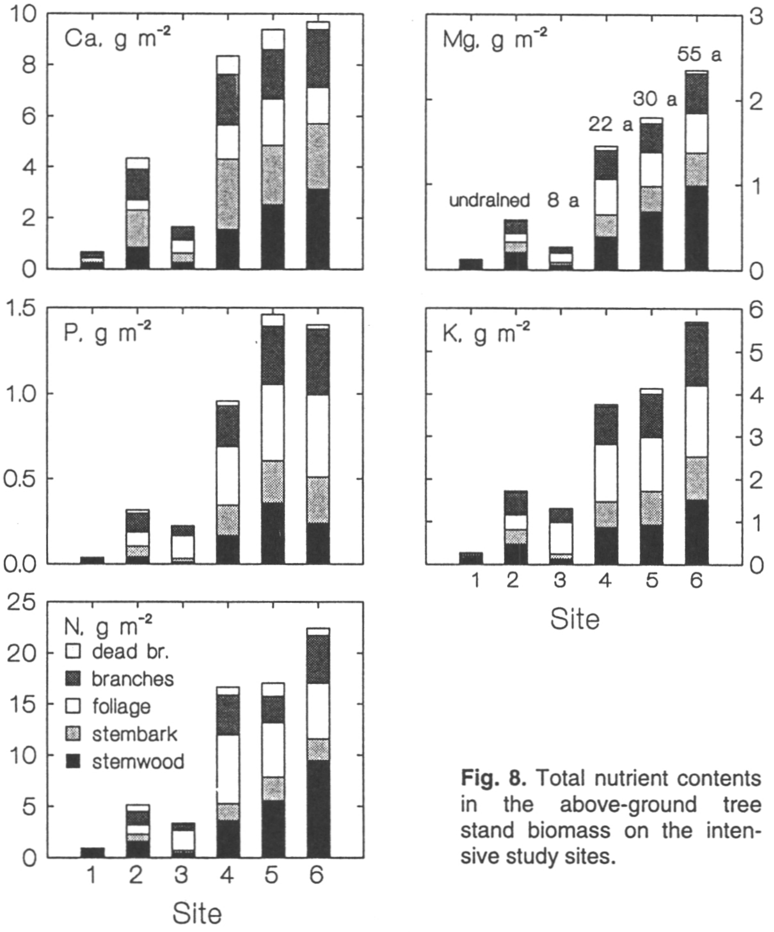

Fig. 8. Total nutrient contents in the above-ground tree stand biomass on the intensive study sites.

Ca. The relative proportion of K in the tree stand was highest on the youngest drained site, 3. In the surface peat the relative proportions of K and Mg were slightly higher on the undrained than on the drained sites; otherwise no patterns were found except that the proportions of N and P on the oldest drained site, 6, were higher than on the other sites.

The proportion of ground vegetation of the total nutrients in above-ground plant biomass decreased due to drainage, but not as much as the respective biomass proportion; on the oldest drained site the proportion was still 20-30% for all major nutrients (Table 8).

In 0-50 cm surface peat the proportion of N, P and Ca actually in fine roots was in general 1% or less, that of Mg 1-4% and K up to 8% (Table 8).

In general, more than 90% of the total nutrient amounts in the system studied (0-50 cm peat layer, litter layer and vegetation including roots) were found in peat (Table 8). Exceptional in this respect were Ca and Mg on site 6 (ca. 85 and 75% in peat, respectively) and K, of which ca. 70% was found in peat on sites 1-3 and only ca. 50% on sites 4-6.

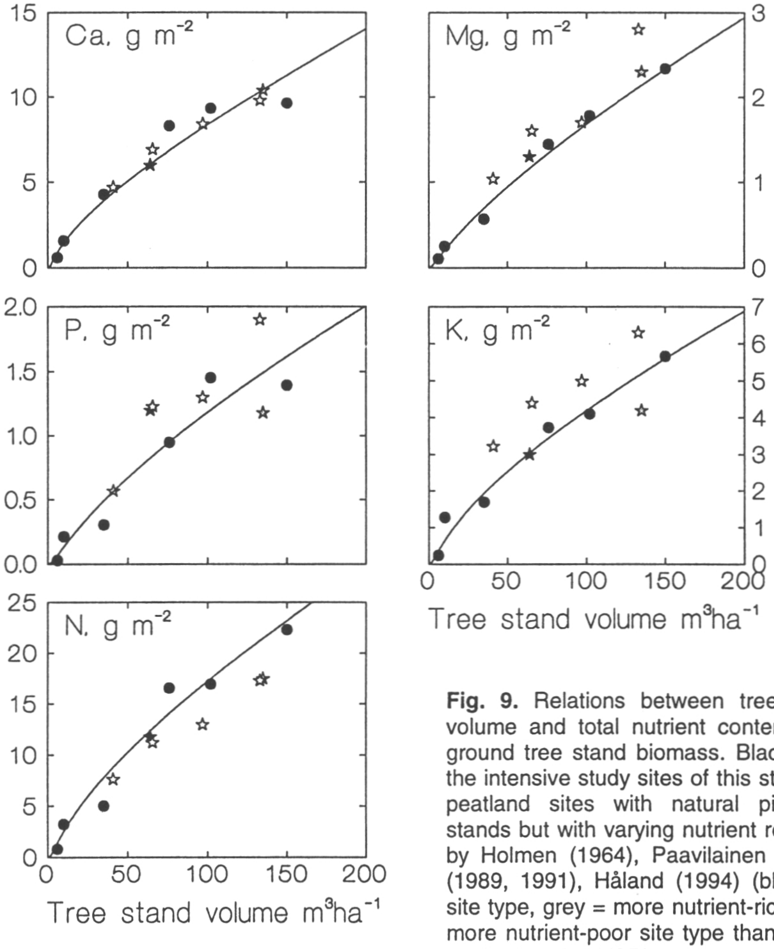

Fig. 9. Relations between tree stand stem volume and total nutrient contents in above-ground tree stand biomass. Black dots depict the intensive study sites of this study and stars peatland sites with natural pine-dominated stands but with varying nutrient regime studied by Holmen (1964), Paavilainen (1980), Finér (1989, 1991), Håland (1994) (black = similar site type, grey = more nutrient-rich and open = more nutrient-poor site type than the intensive study sites, i.e. VSR).

Table 9. Regression equations for the relation of above-ground stand-level nutrient contents (y, g m^{-2}) to tree stand stem volume (x, m^3 ha^{-1}); s.e. = parameter standard error, SEE = standard error of estimate. The linear part p1 • x represents the stem (wood + bark) component (n = 6) and p2 • (lnx) ^{p3} the crown component (n = 6), which were estimated separately.

$y = p1 \cdot x + p2 \cdot (\ln x)^{p3}$	p1	s.e.	p2	s.e.	p3	s.e.	SEE	R^2
N	0.076	0.001	0.235	0.307	2.430	0.856	1.756	0.986
P	0.0039	0.0004	0.0069	0.007	3.087	0.736	0.174	0.971
K	0.017	0.001	0.063	0.068	2.406	0.702	0.347	0.991
Ca	0.044	0.004	0.187	0.129	1.996	0.454	1.086	0.978
Mg	0.009	0.0002	0.011	0.010	2.785	0.585	0.078	0.997

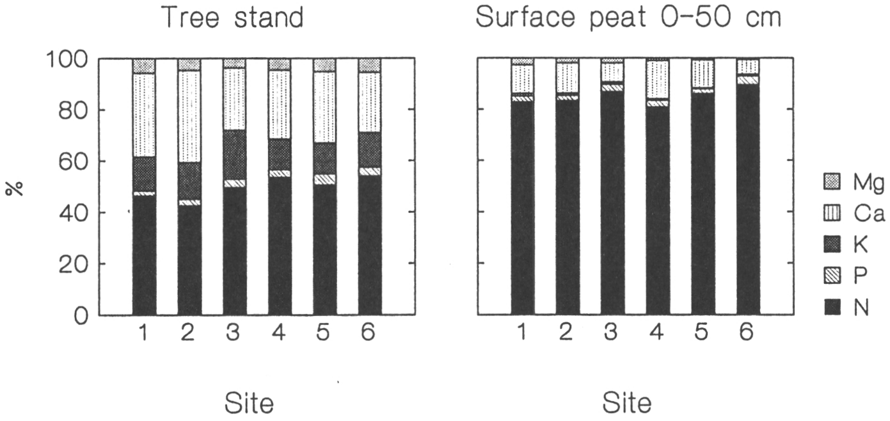

Fig. 10. Relative proportions of major nutrients in the tree stand and 0-50 cm peat layer on the intensive study sites.

322. Reconstructed tree stand nutrient dynamics on the drained intensive study sites

The estimated post-drainage accumulation of nutrients in the tree stands has been almost linear and has not yet slowed down even on the oldest drained site (Fig. 11). The average annual post-drainage accumulation of N on sites 5 and 6 has been 0.6 and 0.4 g m^{-2} a^{-1} respectively, that of P 0.04 and 0.03 g m^{-2} a^{-1}, K 0.2 and 0.1 g m^{-2} a^{-1}, Ca 0.3 and 0.2 g m^{-2} a^{-1}, and Mg 0.06 and 0.04 g m^{-2} a^{-1}.

The current values obtained using the equations (Fig. 11) are in many cases somewhat higher than those obtained using biomass estimates and mean nutrient concentrations (Fig. 8). This is especially true for site 4. Thus the accumulation values for site 4 would also be overestimates.

Drainage immediately increased the proportion of nutrients found in foliage, which also remained at a relatively high level afterwards (Fig. 12). After a temporary drop, the proportions of N, Ca and Mg in stemwood increased steadily after drainage, but those of K and P only slightly.

323. General situation in the basic material

The gravimetric concentrations of most major nutrients in the surface peat were lower on the oldest drained sites than on the undrained sites, with the exception of N and P on the oligo-ombrotrophic sites (I, II). The volumetric nutrient stores in a 0-50 cm peat layer, however, remained rather constant after drainage. On the meso-oligotrophic sites, there were no statistically significant differences between the drainage age classes. On the oligo-ombrotrophic sites, stores of N and P in the oldest drainage age class were higher than those in the other age classes (I, II).

On the drained meso-oligotrophic sites, the average relative proportion of N out of the major nutrients in peat slightly increased along with drainage age, while that of Ca slightly decreased (Fig. 13). In the oligo-ombrotrophic group no patterns could be found, though the proportion of N was highest and Ca lowest in the oldest drainage age group.

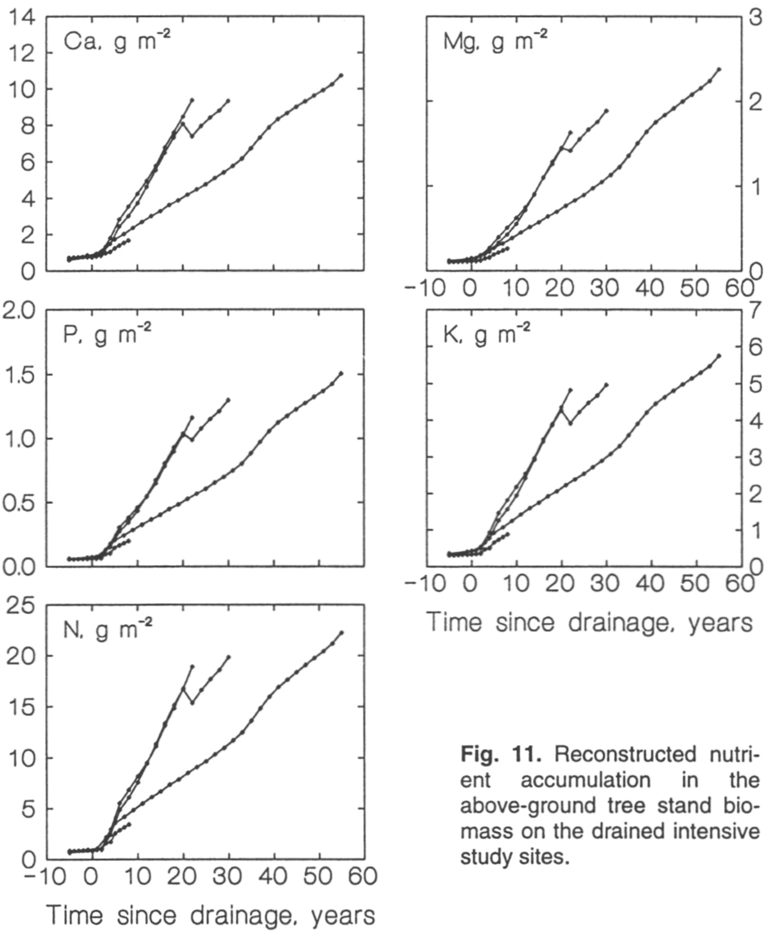

Fig. 11. Reconstructed nutrient accumulation in the above-ground tree stand biomass on the drained intensive study sites.

On the oldest drained sites, the stores of N and P in surface peat were on average 20-30 times higher than the amounts accumulated in the tree stands, and those of Ca and Mg almost 10 times higher (Figs 14-18). The stores of K in the surface peat were only slightly higher than the amounts in the tree stands. The tree stand nutrient amounts estimated here were clearly smaller than the preliminary estimates presented in papers I and II, which were based on constant conversion factors.

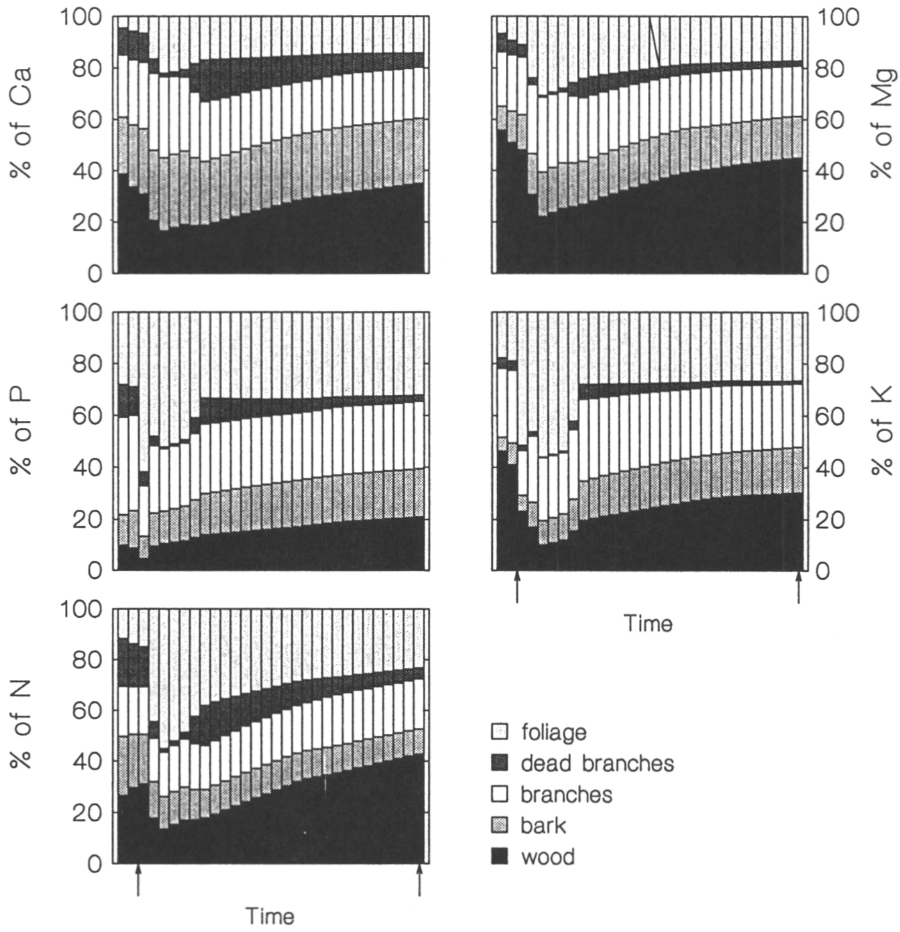

Fig. 12. Reconstructed dynamics of the proportions of major nutrients in the above-ground tree stand biomass components on intensive study site 6 (drained 55 years earlier). The arrows point at the year of drainage (left) and the year 55 after drainage (right).

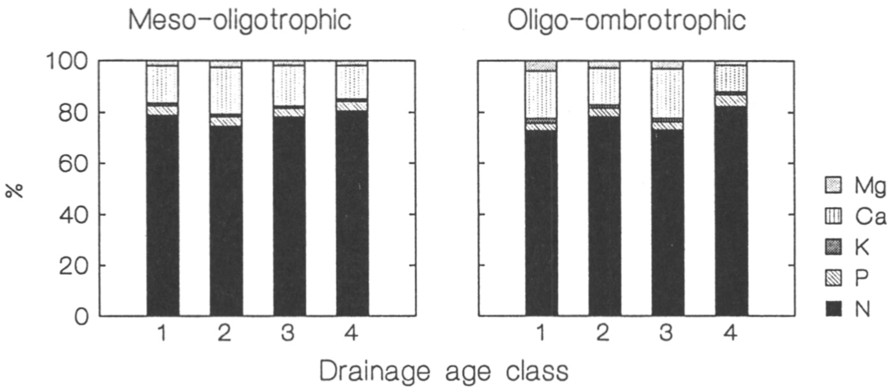

Fig. 13. Relative proportions of major nutrients in the 0-50 cm peat layer on the sites of the basic material. Drainage age classes: 1 = undrained, 2 = drained 1-20 years earlier, 3 = drained 21-40 years earlier, 4 = drained 41-55 years earlier.

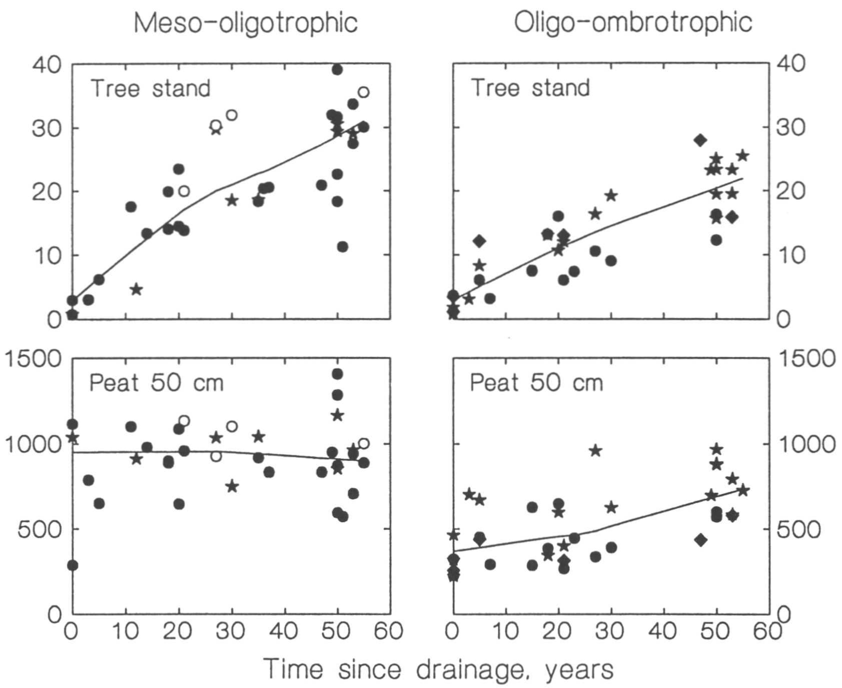

Fig. 14. Total N, g m^{-2}, in the tree stand and 0-50 cm peat layer on the sites of the basic material. Tree stand values were estimated using the tree-level equations presented in chapter 237. Stars = RhSR (left) and TSR (right), dots = VSR and LkR, diamonds = TR. Open symbols depict sites where the proportion of birch out of the total stand stem volume was ≥ 50 %.

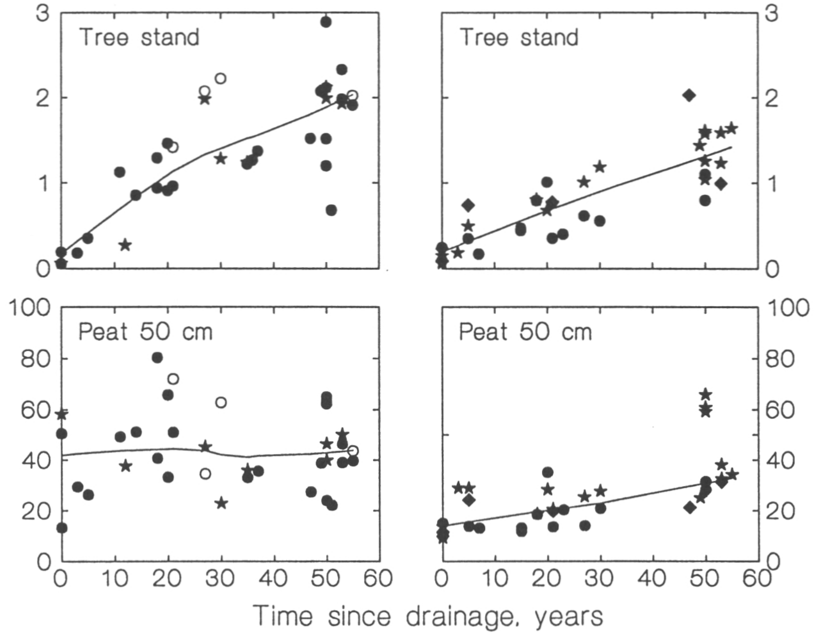

Fig. 15. Total P, g m^{-2}, in the tree stand and 0-50 cm peat layer on the sites of the basic material. See Fig. 14 for explanations.

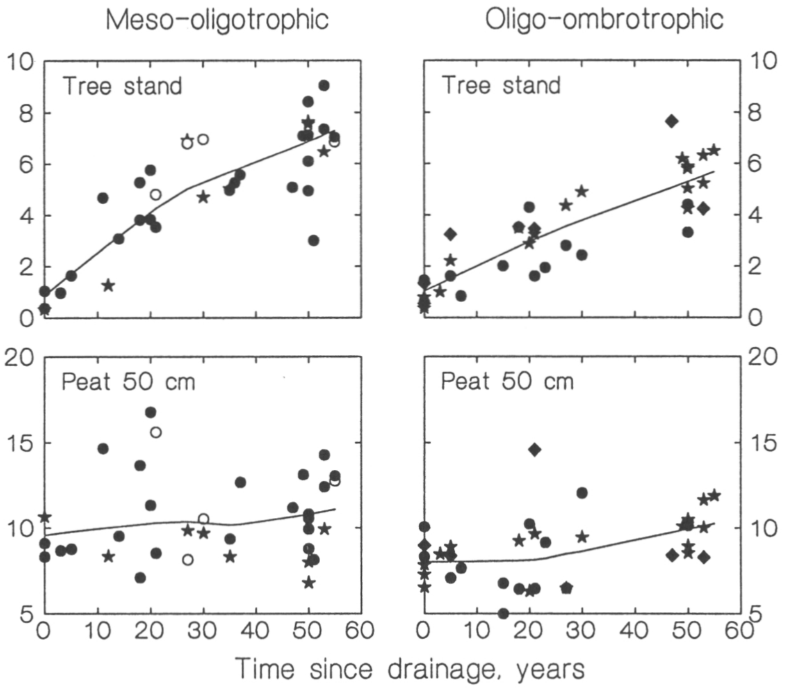

Fig. 16. Total K, g m^{-2}, in the tree stand and 0-50 cm peat layer on the sites of the basic material. Tree stand values were estimated using the tree-level equations presented in chapter 237. Stars = RhSR (left) and TSR (right), dots = VSR and LkR, diamonds = TR. Open symbols depict sites where the proportion of birch out of the total stand stem volume was ≥ 50 %.

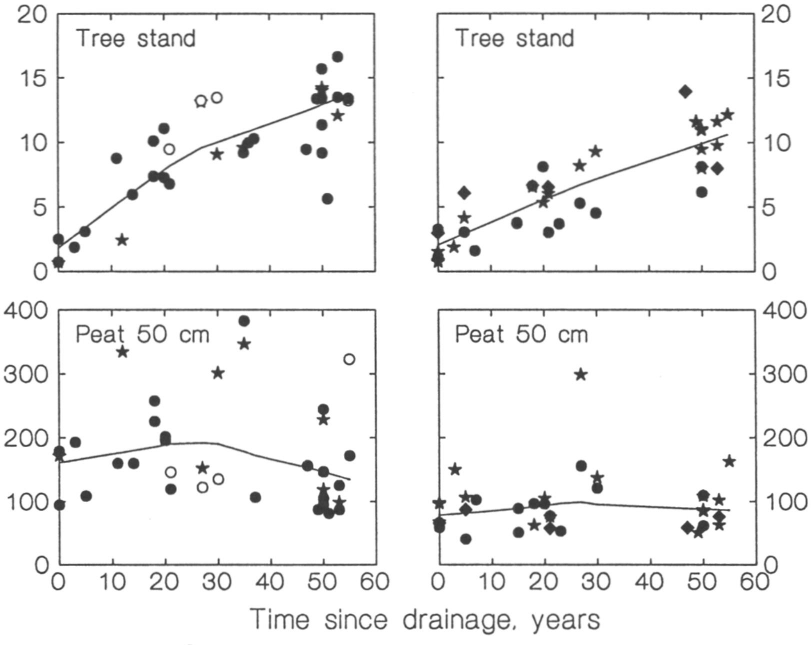

Fig. 17. Total Ca, g m^{-2}, in the tree stand and 0-50 cm peat layer on the sites of the basic material. See Fig. 16 for explanations.

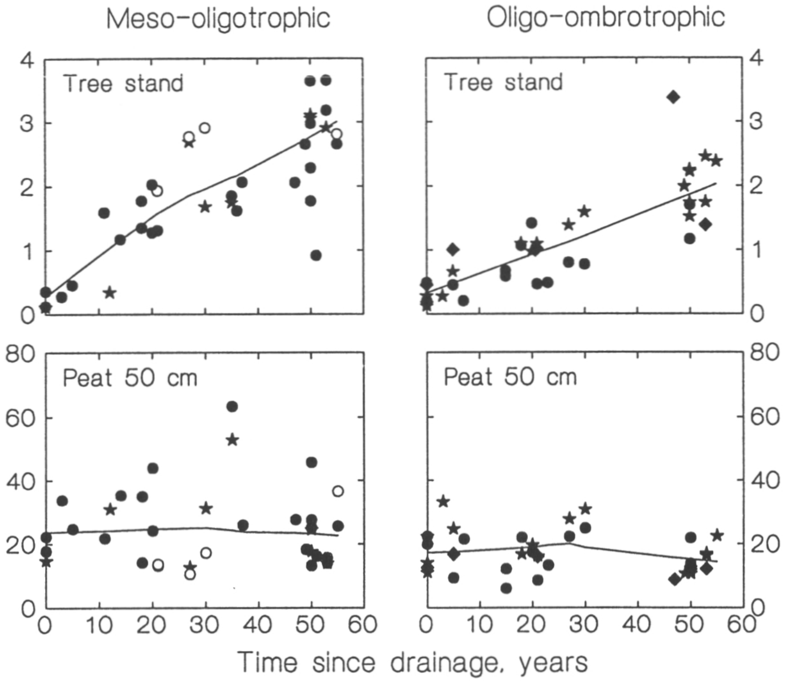

Fig. 18. Total Mg, g m^{-2}, in the tree stand and 0-50 cm peat layer on the sites of the basic material. Tree stand values were estimated using the tree-level equations presented in chapter 237. Stars = RhSR (left) and TSR (right), dots = VSR and LkR, diamonds = TR. Open symbols depict sites where the proportion of birch out of the total stand stem volume was ≥ 50 %.

4. DISCUSSION

41. Validity of biomass estimates

411. Tree stand, above-ground

Choosing sample plot size and the number of trees for destructive harvesting is a trade-off between increased accuracy and reliability of estimates and increased effort and cost. E.g. Woods et al. (1991) have shown that improvement of regression models has only a secondary effect on the total estimation error. The sample plot size on the intensive study sites of this study corresponded to the recommendations for inventory studies (e.g. Satoo & Madgwick 1982). The number of sample trees was in line with common practise, and the sampling intensity within sample trees was efficient (Satoo & Madgwick 1982 and the references therein, Finér 1989a, 1991).

Two sets of biomass equations were applied to the tree stands on the drained intensive study sites: site-specific in paper I to obtain as accurate estimates as possible for the time of sampling (e.g. Crow & Schlaegel 1988, Woods et al. 1991) and the more general equations, presented in this summary paper, for estimating the biomass at different stages of drainage succession. The total biomass estimates, obtained with the general equations computed from the combined sample tree data, deviated ± 5% from the estimates obtained with the site-specific equations, except for site 6 where the difference was 10%. It cannot be said which estimates would actually be more correct, because no information was available on the within-site variations in biomass for any range of $d_{1.3}$, and thus the representativeness of the sample trees for each site. According to their $d_{1.3}$/height-curves the sample trees were good representatives of the site-level tree populations.

When computing the more general equations, a mixed model technique, applied successfully by e.g. Lappi (1986) and Penner et al. (1995) for estimating the variance components of hierarchically nested stand-level and tree-level characteristics, was tested in an attempt to account for a possible site effect (i.e. 'stage of tree stand development' effect). However, none of the random parameters tried proved significant, either because there were no significant differences in biomass ratios between sites or because the number of sites was too small for the technique. A variable allometric ratio, suggested by Ruark et al. (1987), was also tested but it did not prove significant.

Nonlinear fitting of tree-level equations was used instead of applying logarithmic transformation and a correction factor, a commonly used procedure which may result in slightly biased estimates (e.g. Madgwick 1983, Sprugel 1983). However, the bias deriving from nonlinear fitting has not been tested. A prerequisite for the method is homoscedasticity of variance along the range of the independent variable (e.g. Ratkowsky 1990), which is not the case in any biomass data. So a correct procedure would be to use weighted least squares regression instead of simple least squares (e.g. West 1980). This was not done, however, because as Ratkowsky (1990) points out, the solutions differ only when heteroscedasticity is very strong. Moreover, the equations seemed to produce unbiased estimates for the material used here, and they were not designed for more general use.

The tree-level equations were forced through origin, which is theoretically incorrect because none of the characteristic values would be exactly zero when $d_{1.3}$ is zero. Adding a constant term, however, would not have improved the estimates. The value of the constant term would usually have been negative. In addition, it always would have had a very large standard error and caused an increase in the residual standard deviation of the equation. In general, in published equations with a form similar to that applied in this study, the constant term has also been omitted (e.g. Satoo & Madgwick 1982, Crow & Schlaegel 1988).

The tree-level biomass equations were tested in an independent data set provided by Finér (1989a). Depending on the biomass component, 95-100% of the variation in the data could be accounted for. On sites where the stem volume of the stand was within the range of the intensive study sites (Fig. 19; 4 kg C m^{-2} equals to the stand on intensive study site 6), the tree-level equations produced estimates which, when summed up and converted to C, were well comparable with estimates obtained with the stand-level equations compiled in paper V. For stands with higher stem volumes the tree-level equations produced systematic overestimates.

The stand-level total C equation was tested using data from several studies dealing with pine-dominated stands on southern boreal zone (cf. Fig. 4). Ninety-nine percent of the variation could be accounted for, the standard error of estimate being 0.3 kg C m^{-2}. Thus the equation seems generally applicable, for stands on upland sites as well. Although on tree level, stand density and nutrient availability cause variation in the biomass proportions (e.g. Valinger 1993, Mäkelä & Vanninen unpublished), on stand level, total biomass and stem volume seem to be rather firmly correlated.

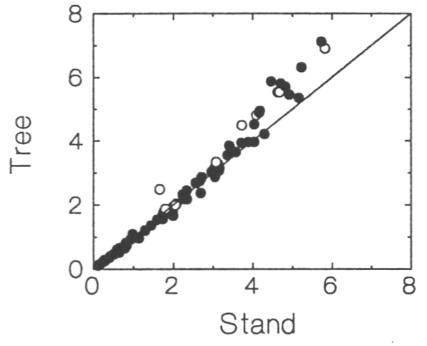

Fig. 19. Tree stand above-ground C content estimates, kg m^{-2}, obtained by summing up tree-level biomass estimates (converted to C with the average C ratio 0.52) *vs.* stand-level equations, for the basic material. Open symbols depict sites where the proportion of birch out of the total stand stem volume was ≥ 50 %.

Tree stand measurements of the basic material were made on rather narrow strips along drainage ditches excluding the ditch area, so actual drained area biomasses would be somewhat smaller. Including the ditch area would have reduced the values by ca. 3-4%, and extending the measurements further from the ditch maybe by 2-3% on average (Seppälä 1972, Heikurainen 1980, Lukin 1988).

412. Other components

The ground vegetation and fine root biomasses varied considerably within most sites (III, IV). With the sampling intensity used, the maximum error of the sample mean of the total ground vegetation biomass was less than 10% for sites 1-3, but more than 20% for the older drained sites ($p = 0.05$). For the various components the maximum error was generally higher, e.g. for shrub biomass on sites 4 and 5 it was as high as 70%. The maximum error in the total fine root biomass estimates was 15-18% for all sites except 1 and 5, where it was 24 and 33% respectively.

The accuracy of the estimates could have been increased by increasing the number of samples (III, Fig. 3), or possibly by using geostatistical methods taking into account the spatial autocorrelation (Robertson 1987). Unfortunately, no information was available on the variation in the respective biomasses between sites in the same stage of the secondary succession, so it cannot be estimated how 'typical' the intensive study sites were in this respect.

Estimation of coarse root and stump biomass was based solely on data presented in earlier studies (cf. IV). There seemed to be a strong correlation between this biomass and tree diameter, but the data set available was still rather small.

42. Validity of nutrient estimates

The nutrient concentrations in most tree components vary within and between years (e.g. Tamm 1955, 1968, Helmisaari & Siltala 1989, Helmisaari 1990), but the between-year variation in the total content is smaller (Helmisaari 1990). In the sampling of the intensive study sites of this study, the aim was to capture within-year maximum plant biomass, and thus probably also maximum total nutrient content. In reality, the trees may not quite have completed their growth by the time of sampling (e.g. Huikari & Paarlahti 1967), which may have resulted in slightly underestimated values. In contrast to nutrient content, the maximum nutrient concentrations in e.g. needles can be found during the dormancy period (e.g. Helmisaari 1990).

According to Comerford & Leaf's (1982a, b) evaluation of techniques for sampling tree nutrient content, the tree-level stem component estimates for the intensive study sites of this study should have less than 5% maximum error ($p = 0.05$), as five sampling heights would be enough to approximately reach that accuracy level for the nutrients studied here. For foliage with the sampling intensity used (ca. 20% systematic sample on tree level), the error should be within 5% for N, P and Mg, and within 10% for K and Ca. For branchwood, the error should be within 10% for all other nutrients except K. On site-level estimates, these errors combine with the biomass estimate errors.

For ground vegetation and fine roots on the intensive study sites, the nutrient analyses were made of site-level composite samples. Thus, the nutrient content estimates cannot be more accurate than the respective biomass estimates.

The nutrient estimates for stumps and coarse roots are highly speculative, as they were based on an assumption of constant concentration ratios between this component and stemwood. There is not much evidence of such constant ratios, however, even though those used here were rather close the ones found in the Håland (1994) material. In any case, these ratios may vary, at least between different site types (cf. e.g. Finér 1989a).

The total above-ground tree stand nutrient content on the intensive study sites corresponded well to values obtained in other studies of pine-dominated stands (Fig. 9). The tree N concentrations measured here, and thus also N contents, were systematically slightly higher than those presented by e.g. Paavilainen (1980) and Finér (1989a), which may be due to the different analysis method. More N is extracted by the LECO-analyzer used in this study than by the Kjeldahl-method frequently used in earlier studies (Griepink & Maier 1989).

The tree-level and stand-level equations produced rather similar total nutrient content estimates for the sites of the basic material (Fig. 20). In the K content estimates there was a systematic difference. For stands where the proportion of birch was more than 30% of the total tree stand stem volume (i.e. beyond the range within the intensive study sites) the estimates obtained with the stand-level equations were smaller, especially for N and P. The P and Mg content relative to tree size was higher in birch than in pine. The difference for N may depend on the estimation method used for birch (see Chapter 24), which was not very accurate.

For the basic material, tree nutrient data from one site type only (VSR) was used to estimate the tree stand nutrient content for all site types. Thus the values should be considered indicative only, as it has been shown that stand age, site quality and growth rate affect tree nutrient concentrations (Mälkönen 1974, Miller et al. 1980, Finér 1989a). However, the differences in the total nutrient contents among pine-dominated tree stands on varying peatland sites do not seem large (Fig. 9), though there seems to be relatively more K in stands on poorer site types.

43. Comparability of the sites

The peat nutrient regime varied both in the basic material and among the intensive study sites. The basic material was so extensive that the trends found were assumed to be reliable. It should be borne in mind, however, that these data do not describe actual changes

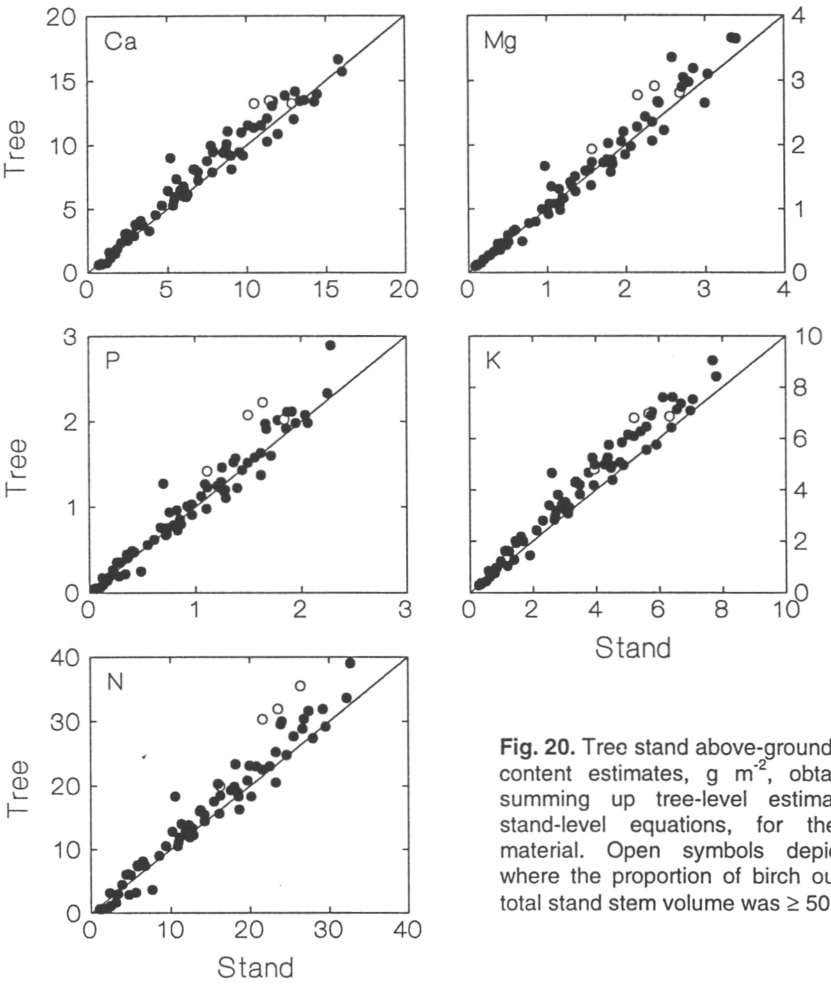

Fig. 20. Tree stand above-ground nutrient content estimates, g m^{-2}, obtained by summing up tree-level estimates *vs.* stand-level equations, for the basic material. Open symbols depict sites where the proportion of birch out of the total stand stem volume was ≥ 50 %.

taking place following drainage on individual sites; they only show an average trend on sites with varying drainage age.

The post-drainage tree stand development has been faster on intensive study sites 4 and 5 than on site 6. There are no obvious reasons for this in the peat nutrient content of the sites. In addition, the tree stand stocking at the time of drainage as well as the later dominant height development, based on the standing stock at the time of sampling, seem to have been rather similar on all drained sites (Fig. 21). An explanation might be that timber would have been selectively harvested on site 6 some time after drainage, although this was not noticed when the site was selected. Thus, first stronger competition and, after the cutting, decreased stand density would have caused the observed lower net accumulation of tree biomass.

Based on reconstruction from the standing stocks at the time of sampling, the tree stand stocking on the drained intensive study sites at the time of drainage resembled that on undrained site 1 rather than site 2. This, however, may be due to possible improve-

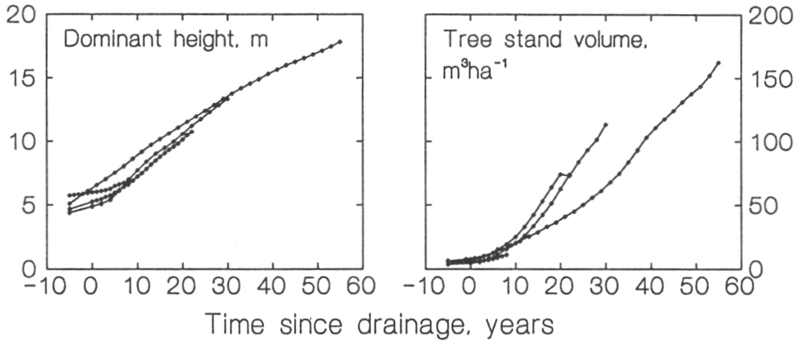

Fig. 21. Reconstructed development of tree stand dominant height and stem volume on the drained intensive study sites.

ment cuttings done at the time of drainage as the tree stand volume on site 1 was clearly below the average of this site type in southern Finland (Heikurainen 1971).

Finding 'truly' comparable stands is difficult and can finally be verified only after stem analysis. This does not greatly impair making conclusions about the biomass or C dynamics, because these characteristics can be related to tree stand size, e.g. stemvolume (V), but one must be more careful when estimating the changes in e.g. soil nutrient characteristics. For instance, making comparisons within various small subsets from the basic material could evidently lead to very different conclusions about the post-drainage development of soil nutrient stores (I, II).

The proportion of birch in the stand volume varied both on the meso-oligotrophic sites of the basic material and on the intensive study sites. The variation on the intensive study sites corresponded well with the average variation in relation to drainage age in the basic material. Occurrence of some birch is typical for both undrained and drained RhSR and VSR sites (e.g. Keltikangas et al. 1986, Laine & Vasander 1990).

The peat nutrient contents were rather similar within the meso-oligotrophic (RhSR, VSR) and oligo-ombrotrophic (TSR, LkR, TR) site type groups. However, on RhSR sites there was on average more Ca in the surface peat than on VSR sites (cf. also Vahtera 1955), and on TSR sites more N and P than on LkR and TR sites. The differences between site types, especially between RhSR and VSR, were smaller than those found by Westman (1981) for undrained sites. The contents of all studied nutrients differed significantly between the site type groups. The differences in tree stand stocking in relation to drainage age were also very small within the site type groups (e.g. Fig. 7). Generally speaking, the most nutrient-rich old RhSR drainage areas with high tree stand volumes may have already been cut, and thus automatically excluded from the material.

44. The role of plant biomass in the carbon balance in drained pine mires

During the 55-year post-drainage time span studied, the tree stands have not by any means reached their maximum, expressed as either biomass or stem volume. If the future tree stand development is estimated by drawing parallels to upland sites in the way suggested by Laine (1989), the increase in total stem volume in untreated RhSR stands would level out at a value of more than 500 m^3 ha^{-1} in ca. 120 years. After this the increase would still continue, but slowly (Ilvessalo & Ilvessalo 1975). The respective values for VSR-TSR sites would be ca. 400 m^3 ha^{-1} in 140 years, and for LkR-TR sites almost 300 m^3 ha^{-1} in 160 years (Ilvessalo & Ilvessalo 1975). The average tree stand volume development in the basic material relates rather well to the development on the parallel upland site types, except that the tree stand volumes in the oldest RhSR drainage areas did not differ from those on VSR sites, which may be an artefact as discussed above. When the above-mentioned values are used as conservative estimates of the average maximum tree stand volumes for untreated stands, the respective maximum above-ground tree stand C content, estimated using the equation presented in Table 7, would be ca. 10.5 kg C m^{-2} for RhSR, 9 kg C m^{-2} for VSR-TSR, and 7 kg C m^{-2} for LkR-TR sites.

The corresponding maximum stump and coarse root C content, estimated using the biomass equation presented in IV and a C ratio of 0.52, would be 5 kg C m^{-2} for RhSR, 4 kg C m^{-2} for VSR-TSR and 3 kg C m^{-2} LkR-TR sites. These may be overestimates if the increase in stump and coarse root biomass in relation to stem volume levels out at bigger stem volumes, as discussed in paper V. Recently, however, Vanninen et al. (1996) found the relation of coarse root biomass to above-ground biomass on tree-level to be linear for a wide range of pine sizes in upland stands in southern Finland; this indicates that the relation to stem volume might remain linear, in stand-level as well, since stem volume and stem biomass have a linear relationship.

The amount of tree fine roots could not be related to tree stand volume in this study, perhaps at least partly due to the variation caused by two different sampling years (IV). It has been suggested that fine root biomass reaches a rather constant level after canopy closure (Kalela 1949, 1955, Albrektson 1980, Vogt et al. 1983, 1987). This supports the idea of the so-called functional balance (e.g. Brouwer 1962) which would determine the ratio between fine roots and foliage to be constant by site quality. In the material of Vanninen et al. (1996), however, the fine root biomass increased with the stand basal area. On the intensive study sites of this study, the fine root biomass on the site drained 22 years earlier (76 m^3 ha^{-1}) was nearly as high as on the site drained 55 years earlier (150 m^3 ha^{-1}). If it remained on the same level later on, it would mean nearly 0.5 kg C m^{-2}, which would generally be counted into the soil C store.

Totals of 15.5, 13 and 10 kg C m^{-2} in tree biomass (excluding fine roots) on RhSR, VSR-TSR and LkR-TR sites respectively, would be equal to the amount of C in peat layers of ca. 36, 44 and 37 cm on undrained sites of the corresponding site types, according to average peat bulk densities in this region (I, Minkkinen unpublished; cf. Minkkinen & Laine 1996). The above-ground tree stand biomasses would correspond to peat layers of 28, 35 and 28 cm in terms of C content.

The ground vegetation C store showed no permanent change after drainage on the intensive study sites. In general, the ground vegetation biomass has been found to vary in relation to the tree stand size; the larger the stand, the less ground vegetation (e.g. Long & Turner 1975, Reinikainen et al. 1984, Brække 1988).

The increase in the oxidation rate of ‘old’ (pre-drainage) peat caused by drainage for forestry has not yet been unambiguously quantified. Silvola et al. (1996a) found that drainage increased the C flux from soil as CO_2 by ca. 70 g C m^{-2} a^{-1} on VSR and ca. 50 g C m^{-2} a^{-1} on TR sites. The amount of root biomass and thus probably also root litter increases after drainage (biomass estimates in IV, turnover estimates in Finér & Laine 1996, Saarinen 1996), and about 40% of the increase in C efflux may be attributed to increased root and root-associated respiration and decomposition (Glenn et al. 1993, Silvola et al. 1996b). The above-ground litterfall also increases after drainage (Laiho &

Laine 1996) and its decomposition probably accounts for a part of the remaining increase in the C efflux. Sallantaus (1992b) found that drainage increased the leaching rate of C very little, 1 g m^{-2} a^{-1}. Laine & Minkkinen (1996) estimated an average annual net loss of 14 g C m^{-2} a^{-1} after drainage for a VSR site drained 30 years earlier. On the other hand, the long term changes in peat C store estimated for the site types studied here by Minkkinen & Laine (1996) were, in southern Finland, negative only for RhSR; for VSR-LkR the net change varied between + 5-20 kg C m^{-2} during 60 years (i.e. ca. 80-330 g C m^{-2} a^{-1}). Thus, it seems that on all site types studied, with the exception of RhSR, tree litter production - and on LkR-TR sites also probably *Sphagnum* litter (cf. *Sphagnum* coverages in Laine et al. 1995) - is enough to keep the C balance of the soil positive (Karsisto et al. 1996 have shown that the decomposition potential of fresh plant litter is not necessarily higher on drained than undrained sites). This means that the accumulation of C in the tree stand would represent a net increase of C in the C balance of the whole ecosystem. On RhSR sites, if the annual net loss of C from soil was as high as 100 g m^{-2} a^{-1} (cf. Minkkinen & Laine 1996), its accumulation in an untreated tree stand would compensate for the loss for about 150 years (about 100 years if only above-ground parts are considered).

In production forests where regular cuttings are applied, the time-averaged so-called equilibrium C storage in a tree stand is, depending on the length of rotation, about half or less of the maximum storage (Harmon et al. 1990, Dewar & Cannell 1992, Cannell et al. 1993, Laine & Minkkinen 1996). In managed forests, the maximum storage of C would probably be somewhat smaller than in untreated stands. On the other hand, so far there is little information about total yields of managed stands on drained peatland sites, and there is some evidence that on the site types studied here the maximum yields might actually be close to the yield estimates for untreated stands presented earlier (Hökkä & Penttilä unpublished). Anyway, biomass accumulation in the tree stand would keep the C balance of managed RhSR sites positive during the first tree stand rotation at the most.

After harvesting, C efflux from soil has been found to increase (e.g. Trettin et al. 1995 and the references therein). On mineral soil sites, it has been observed that forest floor organic matter declines following cutting, requiring 30-80 years to recover to the precut level (Aber et al. 1978, Covington 1981, Nakane & Lee 1995). Olsson et al. (1996) found a 0-7% decrease in soil C pool 15 years after harvesting of upland pine sites in Sweden. The changes induced in drained peatland sites have not been quantified.

On average there is more tree stand biomass and thus also more C in relation to stem volume in peatland stands than in upland stands, when southern boreal Scots pine - dominated stands are examined (V). The difference is mainly due to the bigger amount of below-ground biomass on peatland sites. In peatland pine stands, if the stem component alone (wood + bark) is taken into account in the C store estimations, one third or more of the actual C store is ignored, most of this in the stump - coarse root system.

45. The role of plant biomass in the nutrient balance in drained pine mires

Miller (1995) in his review has stated that nutrient accumulation into a developing tree stand is very rapid at first, but once the canopy is closed, up to two thirds of the nutrients required for growth can be obtained by retranslocation from older or dying tissues. The net demand from soil is further reduced by the cycle through the litter layer. Consequently, nutritional problems would be most likely to arise in the early years while the green crown is being constructed.

On the intensive study sites of this work, the estimated nutrient accumulation was still unreduced even on the oldest drained site studied. When comparing the uptake values presented by Finér (1989a) and accounting for retranslocation and litterfall, the reconstructed nutrient accumulation trends seem credible. In pine stands studied by Helmisaari (1992) there were no differences in the importance of retranslocation of N, P, K and Mg between pine stands of 50 and 250 m^3 ha^{-1}. Thus it seems that the net accumulation of nutrients in the tree stand will still continue on the sites studied. In this respect, it is essential that the accumulation in stemwood has apparently not declined (cf. also e.g. Mälkönen 1974, Turner 1981).

The share of ground vegetation in the nutrients bound in above-ground plant biomass was much higher than their biomass proportion, as has also been found by e.g. Paavilainen (1980) and Finér (1989a). On the oldest drained intensive study site, 20-30% of the plant biomass nutrients were still found in ground vegetation. If the ground vegetation biomass decreases later on when the tree stand increases, at least a part of its nutrient reserve will be available for the trees.

Although the nutrient amounts accumulated in the tree stand increased almost linearly with time after drainage in the basic material, on average the volumetric contents in soil (0-50 cm) were rather similar on sites drained at different times. This surprising feature was probably caused mainly by subsidence of mire surface (e.g. Lukkala 1949) and compaction of the peat soil after drainage, shown as higher bulk densities (I), due to which the 0-50 cm layer on drained sites included peat, and nutrients, from depths that were below the 50 cm layer before drainage. Another factor that may have significance especially for K stores is the ability of trees to trap dry deposition (Miller et al. 1979, Lim & Cousens 1986, Laiho & Laine 1992).

Using the soil data, it is very difficult to estimate the actual net loss of base cations from soil, shown as the decrease in their gravimetric concentrations (II), since the 0-50 cm layer on drained sites does not correspond to a 0-50 cm layer in undrained conditions. The average net subsidence of mire surface in the study area has been 23 cm in 60 years for RhSR-VSR and 14 cm for TSR-LkR (Minkkinen & Laine 1996), but we do not know exactly in which layers the subsidence actually takes place. If all the compaction took place in the 0-50 cm layer, the subsidence value could simply be subtracted from 50 cm on an old drainage area to get the layer corresponding to 50 cm on an undrained site, but Minkkinen & Laine (1996) have found some evidence that compaction may take place even deeper than 80 cm. Moreover, so-called raw humus may accumulate on top of the pre-drainage mire surface after drainage (e.g. Kaunisto & Paavilainen 1988) which further hampers the comparability of layers.

There is a 30-50% difference in the gravimetric concentrations of K, Ca and Mg between undrained sites and the drained sites belonging to the oldest age group (II). This cannot be said to represent the net loss, because changes in the organic matrix also have taken place. If 30% of the corresponding average nutrient amounts in a 50 cm thick peat layer on the undrained sites was estimated as the loss, it would be ca. 3 g m^{-2} K, 45 g m^{-2} Ca and 6 g m^{-2} Mg in 51 years (average age of the oldest drainage age group) in the meso-oligotrophic group (excluding one very high Ca value). The amount of K accumulated in the tree stand (above-ground) after drainage would be double the respective loss, whereas for Mg the loss would be double the amount in the tree stand, and fourfold for Ca. These net losses of Ca and Mg from the studied system would match well with the base cation leaching values presented by Sallantaus (1995) for drained VSR. Thus, it seems that vegetation conserves K in the system very efficiently (cf. also e.g. Stone & Kszystyniak 1977, Miller et al. 1979), but net leaching of Ca and Mg takes place from peat soil after drainage. This has also been shown in the leaching studies of Sallantaus (1992a, 1995). In the basic material it may already be seen as the decreased relative proportion of Ca on the oldest drained sites (Fig. 13).

According to estimates using the equations in Table 9, the developing tree stands (basic material) would still accumulate from 50% (oligo-ombrotrophic sites) to 100% (meso-oligotrophic sites) of the amounts of nutrients now found in them. On the oldest drained sites studied, the amounts of all other nutrients but K in surface peat were still manyfold compared to those accumulated in the tree stands.

In clear cutting (only stems harvested), 50 - 60% of tree stand K, the sufficiency of which seems to be the primary potential problem, would be removed from the site (e.g. Fig. 12, cf. also Kaunisto 1996). In addition, K could be lost through leaching, as large quantities of it would be released from logging residuals, especially from needles, and simultaneously the binding potential of plant biomass would be reduced. Potassium is quickly released from needle litter (Laskowski et al. 1996), most of the loss taking place during the first year (Paavilainen 1980, Berg et al. 1987). During the first two years after clear-cutting, Ahtiainen (1988) found a fivefold increase in the leaching of K from a peatland-dominated catchment. Thus, this study gives some support to the hypothesis of Kaunisto & Paavilainen (1988) that harvesting is a great risk for the K status of the site, and long-term timber production might not be possible on the site types studied without repeated K fertilization. On mire sites treeless before drainage the peat K reserves may already become insufficient during the first post-drainage tree stand rotation (e.g. Kaunisto & Tukeva 1984, Kaunisto 1992). On the other hand, the present study indicates that the peat K content may remain on average rather stable throughout the whole first tree stand rotation on these originally forested site types (cf. also Moilanen et al. 1996). The variation was very high, however, especially in the meso-oligotrophic group. It would be essential to study the leaching of K in different cutting regimes with the nutrient balance of the site as the point of view to quantify the risks. Recovering ground vegetation (e.g. Hannerz & Hånell 1993, Penttilä & Laiho unpublished), as well as the remaining trees after thinnings (e.g. Mugasha et al. 1991, Hökkä et al. 1996) may capture a part of the released nutrients.

The sufficiency of Ca and Mg may also become a problem later on if continuous net leaching of these cations takes place. The current stores in the 50 cm peat layer on the oldest drained sites of the basic material only corresponded to the estimated maximum needs of ca. five tree stands.

It is very difficult to make exact nutrient sufficiency calculations. Most tree fine roots can be found in the 30 cm surface peat layer (e.g. Paavilainen 1966, Finér 1989b) but the dynamics of this ‘layer’ in organic soil depends on the decomposition and compaction of the ‘old’ soil as well as new litter material and is still insufficiently known. Trapping of dry deposition by trees, though known as a process, is difficult to quantify (Lovett & Lindberg 1984, Lindberg & Lovett 1985, Lim & Cousens 1986, Ahmad-Shah & Rieley 1989). Furthermore, although surface flow is cut off by ditches, it is still possible that water movements may transport nutrients to the rooting zone from deeper layers (Mannerkoski 1980, cf. also Hill & Siegel 1991). However, the significance of this process is not known. The changes in the leaching rates after cuttings on organic soil are still insufficiently known as well.

5. CONCLUSIONS AND PROSPECTS FOR FURTHER RESEARCH

On the oldest drained sites studied (50-55 years), the above-ground tree biomass in the untreated tree stands contained on average ca. 4.5 kg C m^{-2} on RhSR-VSR sites and 3.5 kg C m^{-2} on TSR-TR sites. The estimated maximum above-ground C content was ca. 10.5 kg C m^{-2} for RhSR, 9 kg C m^{-2} for VSR-TSR, and 7 kg C m^{-2} for LkR-TR sites. The values including stumps and coarse roots were 15.5, 13 and 10 kg C m^{-2} respectively. In regularly managed production forests, the equilibrium stores would be about half of the above-mentioned values. According to the preliminary results by Minkkinen & Laine (1996), the peat soil C balance would generally be positive on drained VSR-TR sites. Thus these tree stands would represent an additional C storage in the ecosystem. On RhSR sites the tree stand would compensate for C losses from soil for more than one hundred years if untreated, or ca. one tree stand rotation in production forests, after which the C balance of the site would become negative. However, more information is still needed on the changes taking place in peat soil after drainage.

The nutrient regime seemed to remain stable during the post-drainage period studied, when the stores of most nutrients remained relatively unchanged in a 0-50 cm surface peat layer. As the nutrient contents in the tree stands increased after drainage in some cases, the total nutrient contents in the studied system also increased. The actual losses of nutrients from the soil could be observed as decreasing gravimetric nutrient concentrations. The total stores of K were rather limited compared to the tree stand needs.

The direct effect of cuttings on the C and nutrient balance could be studied by simulating the changes in tree stand volume and applying equations for estimating the respective C and nutrient contents. This study material covered only a relatively short time span, so, to avoid extrapolation, it should be expanded to older drainage areas with larger tree stands. The loss of nutrients from the sites through leaching after harvesting should be studied with the site nutrient regime in mind.

The dynamics of tree litterfall and its role in the post-drainage C balance will be investigated later when more data has been obtained on the relation of litterfall to stand biomass, and decomposition dynamics on the sites studied (Finér & Laine 1994, Laiho & Laine 1994, Domisch et al. 1996).

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Appendices

App. 1. The average nutrient concentrations (mg g^{-1}) weighted with respective sample tree component biomasses, for pine on the intensive study sites. The figures in brackets show the number of sample trees analysed, for all other nutrients/N.

Site	N	P	K	Ca	Mg	N	P	K	Ca	Mg
Pine	Stemwood					Stembark				
1 (6/3)	1.651	0.025	0.458	1.006	0.255	3.977	0.168	0.908	4.301	0.405
2 (8/4)	1.420	0.031	0.387	0.685	0.158	2.772	0.266	1.429	5.924	0.504
3 (8/3)	1.386	0.033	0.388	0.764	0.159	4.131	0.341	1.781	5.540	0.557
4 (8/5)	1.239	0.049	0.293	0.624	0.155	4.351	0.422	1.538	5.812	0.721
5 (8/4)	1.520	0.077	0.263	0.703	0.187	4.014	0.516	1.745	5.020	0.676
6 (6/6)	1.693	0.035	0.272	0.555	0.187	2.711	0.440	1.773	3.433	0.678
	Foliage					Live branches				
1 (5/4)	10.737	0.962	4.155	3.660	1.156	3.012	0.226	1.341	2.714	0.420
2 (8/4)	7.857	0.747	3.058	3.715	0.882	4.136	0.343	1.689	3.884	0.454
3 (8/4)	12.118	0.832	4.650	3.098	0.656	4.123	0.365	2.074	3.300	0.455
4 (9/7)	15.904	0.959	3.410	2.830	0.905	4.621	0.295	1.087	2.389	0.425
5 (8/4)	13.273	1.156	3.135	5.098	0.879	3.203	0.367	1.175	2.181	0.405
6 (8/4)	9.744	1.087	3.831	2.743	0.904	5.229	0.434	1.710	1.965	0.559
	Dead branches									
1 (6/4)	2.754	0.092	0.248	1.626	0.187					
2 (8/4)	4.270	0.123	0.239	2.903	0.130					
3 (8/4)	4.164	0.066	0.198	1.304	0.072					
4 (8/5)	2.225	0.085	0.156	2.031	0.140					
5 (8/4)	2.883	0.142	0.274	1.727	0.144					
6 (7/4)	2.132	0.077	0.169	0.884	0.118					

App. 2. The average nutrient concentrations (mg g^{-1}) weighted with respective sample tree component biomasses, for birch on the intensive study sites. The figures in brackets show the number of sample trees analysed, for all other nutrients/N. A concentration value in brackets is a mean of the other sites, calculated for trees with $d_{1.3} < 10$ cm.

Site	N	P	K	Ca	Mg	N	P	K	Ca	Mg
Birch	Stemwood					Stembark				
2 (2/0)	(1.464)	0.116	1.045	1.873	0.540	(4.861)	0.326	1.732	7.713	0.721
4 (3/2)	1.695	0.090	0.421	0.559	0.143	2.319	0.302	0.896	5.559	0.330
5 (5/1)	1.345	0.172	0.184	0.527	0.161	7.197	0.519	1.286	3.783	0.457
6 (4/4)	2.286	0.090	0.345	0.603	0.164	5.579	0.423	1.270	4.547	0.414
	Foliage					Live branches				
2 (2/1)	20.400	2.009	10.788	5.780	2.767	6.284	0.442	2.041	4.154	0.574
4 (5/2)	29.927	1.123	5.383	6.988	2.099	5.776	0.333	1.124	3.027	0.450
5 (4/4)	30.019	2.373	7.335	7.138	2.902	2.530	0.604	1.261	2.742	0.510
6 (6/3)	31.279	1.508	5.724	6.435	2.399	3.031	0.391	1.266	2.987	0.445
	Dead branches									
2 (1/0)	(4.357)	0.242	0.535	4.070	0.387					
4 (5/2)	3.744	0.099	0.240	3.174	0.269					
5 (4/1)	4.331	0.259	0.504	2.346	0.354					
6 (4/1)	4.416	0.107	0.217	1.875	0.147					

App. 3. The average nutrient concentrations (mg g^{-1}) weighted with respective sample tree component biomasses, for spruce and standing dead trees on the intensive study sites. Material from all sites was combined.

	N	P	K	Ca	Mg	N	P	K	Ca	Mg
Spruce	Stemwood (7/2)					Stembark (4/1)				
	0.890	0.129	0.257	1.082	0.128	5.080	0.488	1.426	11.154	0.715
	Branches [a] (7/1)									
	8.970	0.626	2.193	4.601	0.602					
Dead	Stemwood (7/5)					Stembark (4/2)				
	0.916	0.015	0.106	0.716	0.142	4.526	0.344	0.537	4.858	0.372
	Branches (9/4)									
	3.489	0.214	0.284	1.233	0.082					

[a] including needles

App. 4. Equations for estimating tree-level component nutrient contents (g) for pine on undrained sites. Parameter standard errors are given in brackets.

	p1		p2		p3	
Pine: undrained sites			$c_i = p1 \cdot d_{1.3}^{\,p2} \cdot h^{\,p3}$			
Stemwood						
N	0.0123	(0.020)	1.895	(0.802)	1.406	(0.582)
P	$0.621 \cdot 10^{-6}$	(0.142 10^{-5})	5.234	(0.819)		
K	0.0820	(0.025)	1.766	(0.118)		
Ca	0.0664	(0.038)	2.119	(0.215)		
Mg	0.0304	(0.024)	1.864	(0.297)		
Stembark						
N	0.125	(0.171)	1.753	(0.508)		
P	$0.344 \cdot 10^{-3}$	(0.246 10^{-3})	0.580	(0.211)	3.116	(0.419)
K	$0.411 \cdot 10^{-3}$	(0.591 10^{-3})	0.262	(0.396)	4.213	(0.855)
Ca	0.00147	(0.001)	2.512	(0.273)	1.506	(0.345)
Mg	$0.617 \cdot 10^{-3}$	(0.617 10^{-3})	1.007	(0.336)	2.628	(0.655)
Live branches						
N	$0.590 \cdot 10^{-3}$	(0.813 10^{-3})	3.999	(0.495)		
P	0.00112	(0.638 $10^{-3)}$	1.808	(0.219)	1.303	(0.283)
K	0.00540	(0.004)	1.945	(0.271)	1.160	(0.357)
Ca	0.00273	(0.002)	2.494	(0.251)	1.198	(0.330)
Mg	0.00170	(0.751 10^{-3})	2.171	(0.180)	0.806	(0.201)
Dead branches						
N	0.211	(0.140)	1.418	(0.251)		
P	0.0108	(0.009)	0.778	(0.415)	0.573	(0.486)
K	0.0183	(0.018)	1.336	(0.387)		
Ca	0.0273	(0.032)	0.889	(0.457)	1.534	(0.683)
Mg	0.00362	(0.007)	2.645	(0.986)	-1.132	(0.666)
Foliage						
N	0.00298	(0.002)	1.908	(0.253)	1.769	(0.310)
P	$0.719 \cdot 10^{-3}$	(0.302 10^{-3})	1.587	(0.135)	1.726	(0.238)
K	0.00290	(0.002)	1.969	(0.202)	1.267	(0.334)
Ca	$0.583 \cdot 10^{-4}$	(0.100 10^{-3})	2.409	(0.332)	2.655	(0.758)
Mg	$0.180 \cdot 10^{-3}$	(0.245 10^{-3})	1.057	(0.335)	3.113	(0.762)

App. 5. Equations for estimating tree-level component nutrient contents (g) for pine on drained sites. Parameter standard errors are given in brackets.

	p1	p2	p3	p4	p5	p6
Pine: drained sites		$c_i = p1 \cdot d_{1.3}^{p2} \cdot h^{p3} \cdot h_c^{p4} \cdot l_c^{p5} + d_{1.3}^{p6}$				
Stemwood						
N	0.114 (0.026)	1.733 (0.924)	1.554 (0.740)			
P	0.00118(0.002)	2.717 (0.444)				
K	0.00928(0.004)	1.718 (0.187)	1.007 (0.144)			
Ca	0.0215 (0.011)	1.919 (0.224)	0.763 (0.158)			
Mg	0.00342(0.002)	1.538 (0.219)	1.420 (0.178)			
Stembark						
N	0.315 (0.316)	1.545 (0.336)				
P	0.00833(0.004)	1.517 (0.255)	0.623 (0.195)			
K	0.0232 (0.011)	1.621 (0.208)	0.627 (0.158)			
Ca	0.137 (0.118)	2.488 (0.441)	-0.673 (0.289)			
Mg	0.0115 (0.005)	1.649 (0.224)	0.505 (0.172)			
Live branches						
N	0.00186(0.004)	4.065 (0.788)		-0.864 (0.168)		
P	0.00402(0.003)	2.688 (0.279)		-0.359 (0.100)		
K	0.0650 (0.038)	2.172 (0.219)		-0.306 (0.092)		
Ca	0.0281 (0.022)	3.024 (0.292)		-1.015 (0.115)		
Mg	0.00486(0.003)	2.781 (0.261)		-0.489 (0.095)		
Foliage						
N	0.419 (0.355)	2.361 (0.315)		-0.917 (0.127)		
P	0.0267 (0.018)	1.485 (0.271)			0.629 (0.291)	0.141[a] (0.192)
K	0.124 (0.080)	1.166 (0.252)			0.924 (0.288)	1.068[a] (0.054)
Ca	0.199 (0.145)	1.826 (0.283)		-0.350 (0.129)		
Mg	0.0178 (0.009)	2.247 (0.200)		-0.427 (0.082)		

[a] for early drained situation, see text.

App. 6. Equations for estimating tree-level component nutrient contents (g) for birch. Parameter standard errors are given in brackets.

	p1	p2	p3	p4
Birch		$c_i = p1 \cdot d_{1.3}^{p2} \cdot h^{p3} - d_{1.3}^{p4}$		
Stemwood				
N	$0.552\ 10^{-3}$ (0.001)	2.125 (0.486)	2.631 (1.034)	
P	$0.874\ 10^{-4}$ ($0.216\ 10^{-3}$)	4.164 (1.013)		
K	0.128 (0.092)	1.608 (0.312)		
Ca	0.0130 (0.008)	1.376 (0.193)	1.452 (0.358)	
Mg	0.00171 (0.001)	1.381 (0.183)	1.765 (0.347)	
Stembark				
N	0.0521 (0.234)	2.446 (1.871)		
P	$0.968\ 10^{-5}$ ($0.138\ 10^{-4}$)	1.269 (0.317)	3.648 (0.749)	
K	$0.202\ 10^{-3}$ ($0.330\ 10^{-3}$)	1.141 (0.369)	2.933 (0.853)	
Ca	0.166 (0.103)	1.856 (0.267)		
Mg	$0.338\ 10^{-3}$ ($0.490\ 10^{-3}$)	1.019 (0.327)	2.382 (0.752)	
Live branches				
N	0.241 (0.100)	1.861 (0.189)		
P	$0.941\ 10^{-5}$ ($0.103\ 10^{-4}$)	2.188 (0.354)	2.994 (0.571)	
K	0.00467 (0.004)	1.773 (0.274)	1.223 (0.332)	
Ca	0.102 (0.068)	2.077 (0.286)		
Mg	0.00227 (0.003)	1.802 (0.354)	1.090 (0.627)	
Foliage				
N	0.366 (0.280)	2.016 (0.325)		1.561[a] (0.069)
P	$0.166\ 10^{-4}$ ($0.165\ 10^{-4}$)	1.583 (0.261)	3.372 (0.501)	
K	0.00225 (0.002)	1.522 (0.228)	1.929 (0.332)	
Ca	0.00252 (0.003)	1.439 (0.365)	1.997 (0.537)	
Mg	$0.417\ 10^{-3}$ ($0.456\ 10^{-3}$)	1.491 (0.312)	2.277 (0.490)	

[a] used for undrained situation, $d_{1.3} > 2$cm

App. 7. Some statistics for the component nutrient equations presented in App. 4-6; r.s.d. = residual standard deviation of the model, kg, (* = standard error of estimate from the observation / estimate -regression), coefficient = observation / estimate -ratio (its standard error in brackets).

	R^2	r.s.d.	n	coefficient		R^2	r.s.d.	n	coefficient
Pine: undrained sites									
Stemwood					Dead branches				
N	0.863	12.27	7	1.000 (0.163)	N	0.981	1.20	7	0.999 (0.057)
P	0.929	0.17	14	0.999 (0.077)	P	0.902	0.07	14	1.002 (0.091)
K	0.991	0.65	14	0.999 (0.027)	K	0.877	0.18	14	0.998 (0.104)
Ca	0.975	2.20	14	1.001 (0.045)	Ca	0.919	1.55	14	0.999 (0.082)
Mg	0.945	0.77	14	1.000 (0.067)	Mg	0.815	0.17	14	1.001 (0.132)
Stembark					Foliage				
N	0.958	3.07	5	1.001 (0.104)	N	0.996	1.55	7	0.998 (0.027)
P	0.991	0.09	10	0.999 (0.031)	P	0.996	0.09	11	1.000 (0.014)
K	0.976	0.88	10	1.001 (0.052)	K	0.992	0.56	11	1.000 (0.028)
Ca	0.990	2.49	10	1.002 (0.033)	Ca	0.983	1.07	11	1.000 (0.042)
Mg	0.978	0.30	10	1.000 (0.050)	Mg	0.979	0.25	11	1.000 (0.046)
Live branches									
N	0.981	3.44	8	0.999 (0.053)					
P	0.986	0.18	13	1.004 (0.039)					
K	0.978	1.16	13	1.000 (0.043)					
Ca	0.985	2.31	13	1.000 (0.033)					
Mg	0.991	0.21	13	1.001 (0.024)					
Pine: drained sites									
Stemwood					Dead branches				
N	0.855	57.01	18	1.008 (0.101)	N	0.951	4.29*	17	0.898 (0.051)
P	0.882	1.21	30	1.000 (0.068)	P	0.932	0.20*	31	1.177 (0.058)
K	0.986	2.34	30	1.000 (0.022)	K	0.831	0.62*	31	1.133 (0.093)
Ca	0.980	6.12	30	1.009 (0.026)	Ca	0.946	2.53*	31	1.115 (0.048)
Mg	0.980	1.85	30	1.002 (0.026)	Mg	0.957	0.19*	31	1.192 (0.046)
Stembark					Foliage				
N	0.931	7.74	16	1.001 (0.071)	N	0.962	18.86	19	1.001 (0.047)
P	0.965	0.64	30	1.000 (0.036)	P	0.956	1.46	33	0.990 (0.038)
K	0.977	1.96	30	1.000 (0.028)	K	0.965	4.62	33	1.006 (0.034)
Ca	0.918	9.98	30	1.001 (0.056)	Ca	0.916	6.04	32	0.998 (0.054)
Mg	0.972	0.84	30	1.001 (0.031)	Mg	0.970	0.98	33	0.998 (0.031)
Live branches									
N	0.952	17.65	17	1.000 (0.056)					
P	0.963	1.05	33	1.000 (0.035)					
K	0.964	3.88	33	0.999 (0.034)					
Ca	0.946	8.18	33	1.003 (0.042)					
Mg	0.966	1.28	33	1.000 (0.032)					
Birch									
Stemwood					Dead branches				
N	0.979	5.54	7	0.999 (0.033)	N	0.997	0.07*	4	0.955 (0.029)
P	0.934	0.51	11	1.000 (0.084)	P	0.842	0.04*	13	1.077 (0.135)
K	0.948	1.08	11	1.001 (0.074)	K	0.871	0.07*	13	1.124 (0.125)
Ca	0.992	0.86	11	1.002 (0.028)	Ca	0.948	0.38*	13	1.133 (0.076)
Mg	0.993	0.22	11	1.002 (0.022)	Mg	0.949	0.03*	13	1.103 (0.074)

App. 7. Continued.

	R^2	r.s.d.	n	coefficient			R^2	r.s.d.	n	coefficient	
Birch											
Stembark						Foliage					
N	0.814	8.51	6	1.001	(0.214)	N	0.956	6.37	10	1.047	(0.079)
P	0.986	0.15	10	0.999	(0.039)	P	0.981	0.23	17	0.999	(0.035)
K	0.976	0.53	10	1.001	(0.052)	K	0.976	0.89	17	1.000	(0.044)
Ca	0.976	1.81	10	0.993	(0.052)	Ca	0.933	1.65	17	0.998	(0.056)
Mg	0.979	0.16	10	1.001	(0.049)	Mg	0.956	0.49	17	1.003	(0.054)
Live branches											
N	0.989	1.22	7	1.000	(0.044)						
P	0.975	0.25	17	1.000	(0.040)						
K	0.964	0.83	17	1.000	(0.048)						
Ca	0.948	2.09	17	1.001	(0.061)						
Mg	0.962	0.32	16	0.999	(0.051)						

App. 8. Regression equations for the relation of nutrient concentrations in dead branches to tree $d_{1.3}$ for pines on drained intensive study sites; SEE = standard error of estimate. All parameters were statistically significant ($p< 0.01$).

	p1		p2		R^2	SEE	n
	$\text{Concentration} = p1 + p2 \bullet d_{1.3}$						
N, mg g^{-1}	6.481	(0.654)	-0.195	(0.039)	0.601	1.087	17
P, mg g^{-1}	0.269	(0.034)	-0.00905	(0.00212)	0.365	0.073	31
K, mg g^{-1}	0.670	(0.138)	-0.0252	(0.0086)	0.202	0.297	31
Ca, mg g^{-1}	3.347	(0.306)	-0.0989	(0.0191)	0.463	0.658	31
Mg, mg g^{-1}	0.234	(0.035)	-0.00617	(0.00217)	0.191	0.075	31

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Nitrogen and Phosphorus Stores in Peatlands Drained for Forestry in Finland

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Nitrogen and phosphorus concentrations were determined for surface peat samples for 78 sites on both undrained and drained pine mires. The oldest areas had been drained 55 years earlier. Generally, the N and P stores in a 0–50 cm peat layer increased with increasing drainage age in oligo-ombrotrophic sites, and remained unchanged in meso-oligotrophic sites, even if large quantities were bound up in the increasing tree stand biomasses. This was mainly caused by post-drainage subsidence of the mire surface and the consequent compaction, which increased the peat bulk densities and brought new stores from deeper peat layers into the layer under observation. Measured stand volumes and published values for N and P concentrations of tree stand compartments were used to estimate the amounts of N and P bound up in the tree stands. The estimates of N and P in the tree stands of the oldest drainage areas were considerable (ca. 400 kg N and 40 kg P ha^{-1} in the meso-oligotrophic and ca. 300 kg N and 30 kg P ha^{-1} in the oligo-ombrotrophic sites), but were small when compared to the stores in the peat (ca. 10 000 kg N and 400 kg P ha^{-1} in the meso-oligotrophic and ca. 7000 kg N and 300 kg P ha^{-1} in the oligo-ombrotrophic sites in the 0–50 cm layer). *Key words: Nitrogen, phosphorus, drainage, pine mires.*

INTRODUCTION

Nitrogen in peat comes from three main sources: microbial N fixation, atmospheric deposition, and ground water input. The most important source of N in peat is—or has been—the microbial fixation of atmospheric N. The highest reported fixation rates have been found in minerotrophic mires, which are characterised by high nutrient levels, high pH, and high water table level (e.g. Waughman & Bellamy 1980, Chapman & Hemond 1982). The higher fixation rates are accordingly reflected in the higher contents of N in minerotrophic peats with higher mineral nutrient levels (Westman 1981, Starr & Laine 1988, Laine & Vanha-Majamaa 1992). During the last few decades, atmospheric deposition may have exceeded microbial fixation as a source of N, especially for ombrotrophic bogs (Urban & Eisenreich 1988). Nitrogen concentrations in inflowing ground water are low in Finland, but the interception of N from water by plants integrated over the growing season may be of importance. A major part of the N input is immobilised in the peat (e.g. Urban & Eisenreich 1988).

As long as the peat layer is shallow, plants are able to take up P released by weathering directly from the mineral soil below. A part of this primary P cycles between the vegetation and the aerobic surface peat, and is gradually moved upwards by vegetation as the peat layer grows thicker. Another important P source for minerotrophic mires is the input from inflowing ground water. In southern Finland, P input through atmospheric deposition appears to exceed the leaching losses from undrained mires (Sallantaus 1992).

Drainage of a mire is followed by a lowering of the water table level. Consequently, the thickness of the aerated surface peat layer increases and the organic matter is increasingly exposed to efficient aerobic microbial activity. Thus, the loss of carbon and release of nutrient ions from the organic matrix are raised above pre-drainage levels (e.g. Lieffers 1988, Silvola 1988).

Tree stand biomasses increase after drainage. The increase is greatest in nutrient-rich mires having favourable macroclimate conditions (e.g. Keltikangas et al. 1986). Along with an increase in the total biomass, drainage causes a shift in the relative proportions of the biomass components in the mire ecosystem. The proportion of tree stands increases and correspondingly the proportions of field and, especially of ground layers, decrease (Reinikainen 1981). The developing tree stands accumulate large quantities of nutrients, N being quantitatively the most important. On drained meso-oligotrophic sites in Finland, the annual uptake of N was about tenfold that of P (N 26–42 and P 2.5–3.4 kg ha^{-1}; Finér 1989).

Along with increased annual runoff (e.g. Seuna 1988), drainage usually increases the leaching of N and P from mires (e.g. Ahtiainen 1988). However, there is some evidence that the annual runoff approaches, and possibly goes below the pre-drainage level as the transpiration and interception of the tree stands increase (Seuna 1981).

Drainage initiates subsidence of the mire surface. At first, the removal of water causes a physical collapse and compression in peat, and later, decomposition of the organic matrix further contributes to the subsidence (Laine & Laiho 1992). Subsidence brings a part of the nutrient stores immobilised in the deeper layers during peat accumulation back to nutrient cycling in the drained peatland forest ecosystem.

Thus, the net change in the nutrient stores of surface peat after drainage is determined by the balance between input processes (deposition, addition from deeper peat layers through subsidence), and output processes (leaching, immobilisation in the biomass).

The aims of the present study are (i) to determine how the stores of N and P in the surface peat are affected by drainage, and (ii) to estimate the amounts of N and P bound up to tree stands in order to analyse the effect of uptake on the peat nutrient stores. The results are based on the assumption that drained sites belonging to the same original site type were similar before drainage. This study is a part of a project dealing with the nutrient status of peatlands drained for forestry.

MATERIAL AND METHODS

Research area and sample plots

The studied mires are located in central Finland in a region between 61°35′–62°05′ N and 23°50′–24°55′ E. The elevation of the sites varies between 105 and 170 m a.s.l. The mean annual temperature of the region is 3 °C and that of July 16 °C. The mean annual temperature sum (accumulated mean daily temperatures $\geqslant 5$ °C) varies between 1150 and 1250 d.d. The annual precipitation is about 650 mm, of which nearly 240 mm is snowfall.

As all the sample plots representing a certain site type were to be comparable, they were carefully selected from a larger material prechosen from the drainage archives of the local District Forestry Board. The selected sites had to have a peat layer thicker than 1 m and the stands should not have undergone cuttings.

Altogether, measurements were made at 78 sample plots on sites, both undrained and drained, which belong to following mire site types in the Finnish classification system (Cajander 1913, see Laine et al. 1986 for current terminology): 1) herb-rich sedge birch-pine fen (RhSR), 2) tall-sedge pine fen (VSR), 3) cottongrass-sedge pine fen (TSR), 4) low-sedge *Sphagnum papillosum* pine fen (LkR) and 5) cottongrass pine bog (TR). The oldest drainage areas sampled had been drained 55 years earlier. Of the nearly 5.3 million ha of peatland drained for forestry in Finland, about 35% consists of these mire site types (Keltikangas et al. 1986). They form a succession continuum from meso-eutrophy (RhSR) to oligotrophy and ultimately ombrotrophy (TR). Typical of these site types is a mosaic-like pattern of treed hummocks and treeless lawn hollows.

In virgin state the tree stands are sparse and dominated by Scots pine (*Pinus sylvestris* L.). Birch (*Betula pubescens* Ehrh.) is abundant in RhSR sites but diminishes gradually and does not occur in TR sites. Mire dwarf shrubs (e.g. *Betula nana* L., *Ledum palustre* L., *Vaccinium uliginosum* L.) occur on hummocks in all sites types. Occurrence of mesotrophic herb species (e.g. *Potentilla palustris* (L.) Scop.) is restricted to RhSR sites. Minerotrophic tall sedge species (*Carex lasiocarpa* Ehrh., *Carex rostrata* Stokes) are abundant in RhSR and VSR sites, and are still found sporadically in LkR sites. Oligo-ombrotrophic *Sphagna* (e.g. *Sphagnum fallax* (Klinggr.) Klinggr., *Sphagnum angustifolium* (Russ.) C. Jens.) are predominant in all sites types, whereas mesotrophic species (e.g. *Sphagnum subsecundum* Nees., *Sphagnum riparium* Ångstr.) are found only in RhSR sites. The surface peat is *Carex* dominated in RhSR and VSR sites, but the proportion of *Sphagnum* residues increases along the gradient towards ombrotrophy.

Special attention was paid to the determination of the original site type on the drained sites. Post-drainage vegetation changes are rapid and drastic, especially on the more nutrient-rich sites. Sedges and mire herbs disappear, and dwarf shrubs gain dominance in the field layer. On the more nutrient-rich sites, mire dwarf shrubs give way to *Vaccinium myrtillus* L. and *Vaccinium vitis-idaea* L. as the shading from the tree stand canopy increases (Laine & Vanha-Majamaa 1992). The determination of the original site type on drained sites was based on the following features: (i) microtopography, (ii) floristic composition of the surface peat, (iii) indicator species of the original site types on younger drained sites, and (iv) indicator species of the drained peatland forest types on older sites. A parallel between drained peatland forest types and the original, natural mire site types can be drawn since the post-drainage vegetation succession of each natural site type is sufficiently known (Laine 1989).

The tree stands on drained sites had developed from sparse pre-drainage stands and gradually become fully stocked through natural regeneration. The stands thus typically have a very uneven-aged structure.

To standardise hydrological conditions, the sample plots (10 × 30 m) were placed along contour ditches with the longer side of the plot being parallel to the ditch. Three sampling points were chosen, as equally spaced as possible, about 5 m from the ditch at lawn-level to avoid possible variation caused by microtopography. Undisturbed samples (746 cm^3) were taken from four depths: 0–10, 10–20, 25–35, and 50–60 cm. These sampling depths were chosen for the determination of vertical distributions of various peat characteristics which are not dealt with in the present paper. Zero-level was taken as the upper level of the rooting zone, which often corresponds to the lower level of the living moss layer. The samples were stored in a freezer until further treatment.

The diameter at 1.3 m height was measured (± 1 cm) of all trees having a diameter $\geqslant 5$ cm. Ten sample trees per sample plot were chosen using systematic random sampling, and measured for bark thickness, diameter at 6 m, and height.

Analyses

The peat samples were dried at 105 °C, weighed for bulk density calculations, and ground to pass through a 2 mm sieve. Roots with diameter $\geqslant 1$ cm, if present, were removed before grinding. For each sample plot, the samples from all three sample points representing the same depths were combined and mixed thoroughly before chemical analyses.

Phosphorus concentrations were measured on an ICP-analyser after $HNO_3-H_2SO_4-HClO_4$ digestion. Nitrogen contents were measured on a Leco CHN 600 analyser.

Because the number of plots representing some original site types was too small, the plots were grouped into two site type groups. The "meso-oligotrophic" site type group consists of RhSR and VSR site types, which are closely related to each other in terms of vegetation and peat composition (sedge peat). The "oligo-ombrotrophic" site type group consists of more nutrient-poor site types: TSR, LkR and TR (*Sphagnum*-peat).

Because of the clustered distribution in relation to drainage age, we divided the material for statistical analyses into four "drainage age" classes according to time passed since drainage: undrained plots, plots drained 1–20 years, 21–40 years, and 41–55 years before sampling. To test the effect of drainage age on the nutrient stores in peat we used ANOVA.

Nutrient stores were calculated for the 0–50 cm surface peat layer which was considered to be the layer for nutrient uptake during the first tree stand rotation, taking into account the depth distribution of fine roots (Holmen 1964, Håland & Brække 1989, Finér 1991) and the subsidence of the mire surface (Laine & Laiho 1992). These stores were calculated as weighted means of the sampled layers. The depth of the peat layer represented by each peat sample was used as the weight (sampling did not cover the whole 0–50 cm layer).

To estimate the nutrient amounts bound into the tree stands, we used nutrient concentrations given by Finér (1989) and Paavilainen (1980) for site types comparable with those in our study. Calculations were made separately for pine and birch, and for four stand compartments: stemwood, crown, stumps plus coarse roots, and fine roots. Nutrient concentrations for each compartment, calculated per m^3 of stemwood, were multiplied with stemwood $m^3\ ha^{-1}$ values from our plots.

To illustrate the trends in the measured parameters after drainage, we used a robust locally weighted regression for smoothing scatter plots (Cleveland 1979, Wilkinson 1989).

RESULTS

The amounts of N and P in the surface peat (0–50 cm layer) were unaltered by drainage in the meso-oligotrophic group but increased in the oligo-ombrotrophic group with the increasing drainage age (Figs. 1, 2). The increase was statistically significant (Table 1); peat of the oldest age class had higher amounts of N and P than the younger age classes (probabilities for contrasts: $p < 0.05$ for N and $p < 0.01$ for P).

In the meso-oligotrophic sites, the volumetric N concentrations in the two uppermost layers (0–10 and 10–20 cm) showed a trend to increase slightly up

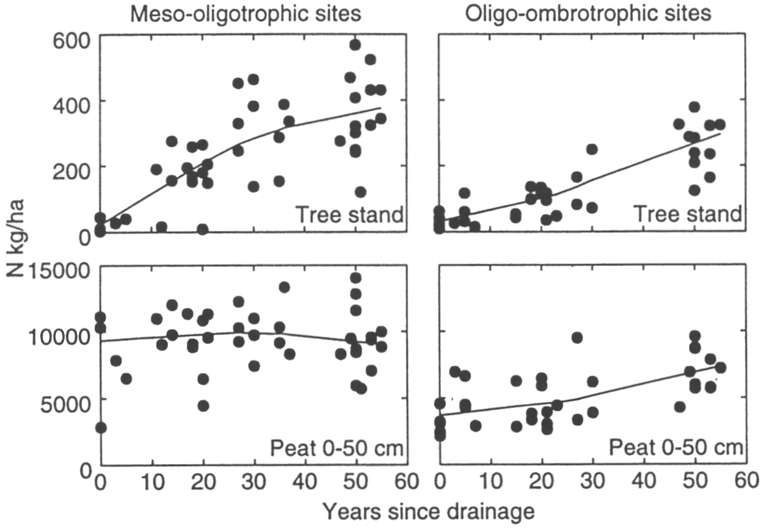

Fig. 1 The nitrogen stores in tree stands and in the 0–50 cm peat layer as a function of drainage age for each site type group.

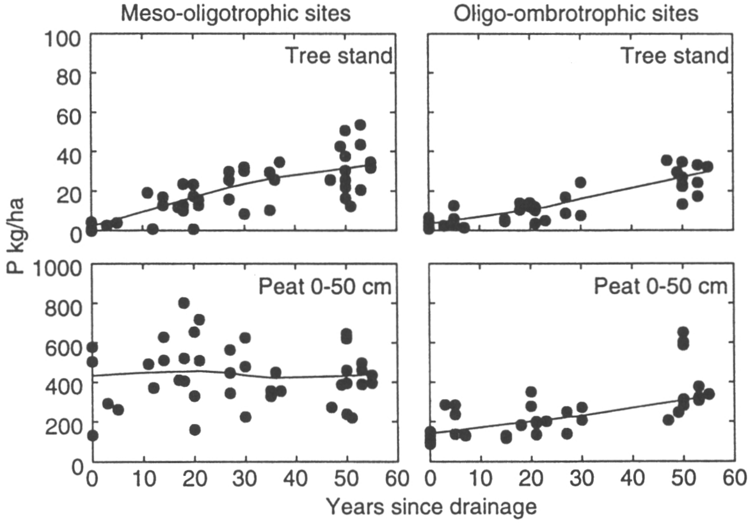

Fig. 2. The phosphorus stores in tree stands and in the 0–50 cm peat layer as a function of drainage age for each site type group.

Table 1. *Results of one-way ANOVA for N and P stores (kg ha^{-1}) in the 0–50 cm peat layer with drainage age class (years since drainage) as a grouping factor*

	Meso-oligotrophic sites		Oligo-ombrotrophic sites	
	F	p	F	p
Nitrogen	0.94	0.433	7.88	0.000
Phosphorus	0.09	0.963	11.60	0.00
degrees of freedom	3, 38		3, 32	

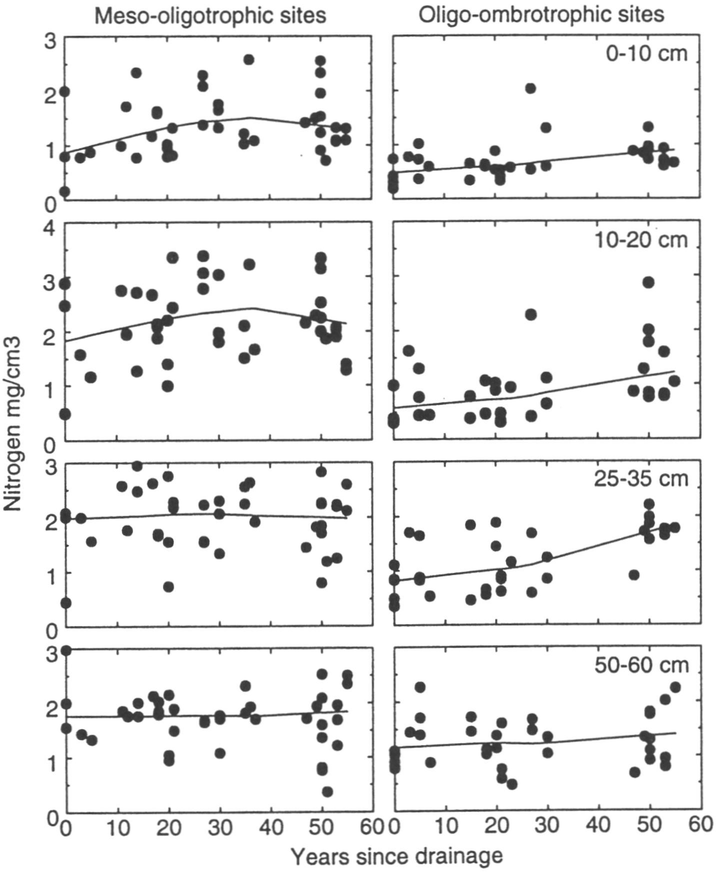

Fig. 3 Total nitrogen concentrations in different peat layers as a function of drainage age for each site type group.

to 20–30 years after drainage (Fig. 3, Table 2). For P concentrations, a similar trend was seen in the 0–10 cm layer only (Fig. 4, Table 2). In the oligo-ombrotrophic sites N and P concentrations increased with increasing drainage age, even in the 25–35 cm layer (Figs. 3, 4).

After drainage, increasing amounts of N and P were bound up in the developing tree stands (Figs. 1, 2, Table 3). However, these quantities were small compared to the stores of these nutrients in the peat (0–50 cm layer). The amounts of N and P in the studied ecosystems (peat plus stand) appear to have increased with increasing time since drainage (Figs. 1, 2). Most of the N and P in the tree stands was found in the crowns but the amounts bound in the stems relatively increased the most as the stands matured (Table 4).

DISCUSSION

The underlying assumption in this study is that sites belonging to same site types were originally similar and that their post-drainage development has proceeded similarly. The same approach has been used by Starr (1982). However, the variation in nutrient contents of the surface peat layer of undrained sites belonging to the same site types has been shown to be considerable (Westman 1981). Thus, the assumption in our approach may be questioned. Nonetheless, in view of the extent of our material, we consider the post-drainage changes in N and P stores we have outlined to be reliable.

As the sample plots were located close to the ditches, the water table levels were deeper than average in the sites. Consequently, the effects of drainage, including those on nutrient uptake and leaching, may

Table 2. *Mean values ± standard deviations of peat volumetric (v, mg cm^{-3}) and gravimetric (g, mg g^{-1}) N and P concentrations*

The values are given separately for site type groups, drainage age classes (years since drainage), and peat layers

Years since drainage		Layer, cm 0–10	10–20	25–35	50–60	n
		Meso-oligotrophic sites				
Undrained	Nv	1.009 ± 0.935	1.974 ± 1.276	1.534 ± 0.925	2.202 ± 0.729	3
	Ng	12.8 ± 7.3	19.6 ± 8.4	18.1 ± 7.4	20.8 ± 4.1	
	Pv	0.059 ± 0.045	0.102 ± 0.064	0.071 ± 0.044	0.108 ± 0.059	
	Pg	0.773 ± 0.366	1.024 ± 0.413	0.839 ± 0.364	0.993 ± 0.352	
1–20	Nv	1.271 ± 0.484	1.930 ± 0.596	2.025 ± 0.628	1.722 ± 0.392	13
	Ng	13.8 ± 3.5	17.6 ± 3.2	17.9 ± 3.1	16.0 ± 3.1	
	Pv	0.077 ± 0.032	0.107 ± 0.052	0.095 ± 0.037	0.073 ± 0.034	
	Pg	0.860 ± 0.193	0.896 ± 0.257	0.754 ± 0.198	0.649 ± 0.275	
21–40	Nv	1.565 ± 0.540	2.551 ± 0.694	2.093 ± 0.404	1.748 ± 0.286	12
	Ng	16.0 ± 2.6	20.3 ± 3.2	19.0 ± 2.5	18.7 ± 2.9	
	Pv	0.091 ± 0.030	0.113 ± 0.041	0.085 ± 0.030	0.070 ± 0.027	
	Pg	0.933 ± 0.186	0.895 ± 0.236	0.772 ± 0.258	0.756 ± 0.306	
31–55	Nv	1.450 ± 0.523	2.276 ± 0.639	1.914 ± 0.571	1.654 ± 0.664	14
	Ng	14.3 ± 2.5	16.5 ± 3.3	15.7 ± 3.6	15.2 ± 3.7	
	Pv	0.085 ± 0.037	0.116 ± 0.040	0.080 ± 0.030	0.064 ± 0.028	
	Pg	0.827 ± 0.207	0.834 ± 0.199	0.653 ± 0.184	0.595 ± 0.203	
		Oligo-ombrotrophic sites				
Undrained	Nv	0.396 ± 0.183	0.464 ± 0.244	0.675 ± 0.292	0.970 ± 0.151	6
	Ng	6.7 ± 0.8	7.7 ± 1.5	10.2 ± 2.8	12.7 ± 2.8	
	Pv	0.021 ± 0.007	0.022 ± 0.005	0.025 ± 0.009	0.027 ± 0.008	
	Pg	0.419 ± 0.086	0.421 ± 0.082	0.414 ± 0.100	0.386 ± 0.043	
1–20	Nv	0.653 ± 0.187	0.837 ± 0.375	1.121 ± 0.550	1.407 ± 0.375	11
	Ng	8.5 ± 1.7	10.4 ± 3.6	12.6 ± 4.3	14.1 ± 2.0	
	Pv	0.040 ± 0.012	0.039 ± 0.017	0.045 ± 0.027	0.049 ± 0.019	
	Pg	0.606 ± 0.139	0.537 ± 0.179	0.493 ± 0.178	0.481 ± 0.090	
21–40	Nv	0.810 ± 0.579	0.836 ± 0.657	1.003 ± 0.365	1.141 ± 0.472	8
	Ng	10.2 ± 3.6	9.9 ± 4.8	11.5 ± 3.1	11.9 ± 3.5	
	Pv	0.055 ± 0.020	0.037 ± 0.016	0.039 ± 0.009	0.036 ± 0.015	
	Pg	0.758 ± 0.218	0.466 ± 0.113	0.451 ± 0.089	0.373 ± 0.102	
41–55	Nv	0.880 ± 0.191	1.351 ± 0.669	1.720 ± 0.324	1.377 ± 0.526	11
	Ng	10.8 ± 1.3	12.3 ± 2.4	13.9 ± 1.3	12.7 ± 2.6	
	Pv	0.062 ± 0.024	0.090 ± 0.056	0.086 ± 0.034	0.058 ± 0.030	
	Pg	0.741 ± 0.167	0.798 ± 0.238	0.685 ± 0.178	0.532 ± 0.186	

have been more pronounced. Still the N and P concentrations (both gravimetric and volumetric) for our sites are in general agreement with those reported by Westman (1981) for undrained sites, and those of Kaunisto & Paavilainen (1988) and Laine & Vanha-Majamaa (1992) for drained sites belonging to the same original site types.

The amounts of N and P bound in the tree stands have been calculated assuming that the ratios of crown and root biomasses to stem volume remain constant as the stem volumes increase. However, these ratios have been found to change in relation to increasing stand age and stem volume (e.g. Albrektson 1980). Nutrient concentrations for tree stands

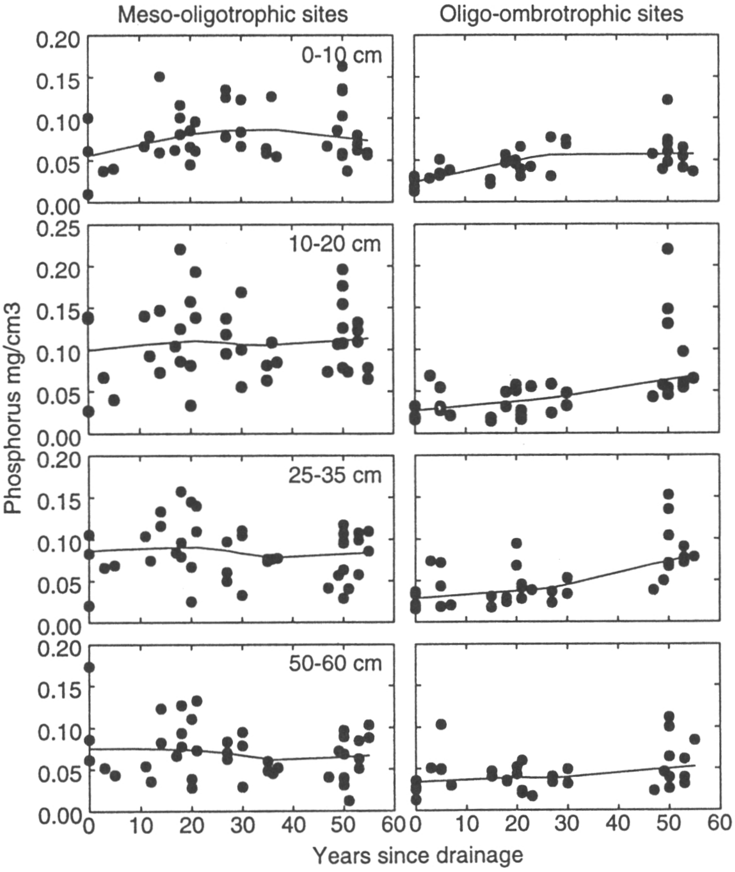

Fig. 4. Total phosphorus concentrations in different peat layers as a function of drainage age for each site type group.

Table 3. *Tree stand stemwood volumes (m^3 ha^{-1}) in different drainage age classes for each site type group. Values are means ± standard deviations*

	Years since drainage Undrained	1–20	21–40	41–55
Meso-oligotrophic sites	11 ± 9	68 ± 42	149 ± 58	178 ± 55
Oligo-ombrotrophic sites	16 ± 12	40 ± 23	54 ± 29	127 ± 33

growing on the same site types as in our study were available only for a few stands in a certain stage of development (Paavilainen 1980, Finér 1989). It is also well documented that nutrient concentrations of tree stand biomasses per unit volume of stemwood may vary. For example, nutrient concentrations are higher in older (and larger biomass) Scots pine stands than in younger (and smaller biomass) stands (e.g. Mälkönen 1974). Site quality and the growth rate of tree stands have also been shown to affect biomass nutrient concentrations (Miller et al. 1980, Finér 1989). Thus, the calculated nutrient stores in tree stand biomasses should be considered as indicative only. In particular, the nutrient stores of crown and fine root compartments in stands with high stem volumes are probably overestimates.

The nutrient stores of fine roots are the most uncertain. These nutrients are included in the peat

Table 4. *Estimated N and P stores (kg ha^{-1}) in the tree stands*

Calculated using nutrient concentration data given by Finér (1989) and Paavilainen (1980), and stemwood m^3 ha^{-1} values measured from the studied sample plots

Years since drainage		Stems	Crowns	Stumps + coarse roots	Fine roots
	Meso-oligotrophic sites				
Undrained	N	4	15	4	4
	P	<1	2	<1	<1
1–20	N	32	92	27	22
	P	3	8	2	2
21–40	N	68	175	55	42
	P	5	14	4	3
41–55	N	73	226	61	60
	P	6	21	6	5
	Oligo-ombrotrophic sites				
Undrained	N	5	21	6	7
	P	<1	2	<1	<1
1–20	N	13	52	14	17
	P	2	5	2	2
21–40	N	19	73	19	22
	P	2	7	2	2
41–55	N	46	174	45	52
	P	5	17	5	5

nutrient store in our study. In the 0–10 cm layer, where most of the roots are found (e.g. Håland & Brække 1989, Finér 1991), fine root nutrient stores consisted of less than 5% of the N and about 5% of the P stores in the oldest drainage age class when estimated according to the data of Finér (1989) and Paavilainen (1980). Fine roots also increase the bulk density of the surface peat (Mannerkoski 1982), which affects the volumetric nutrient store calculations.

We have not presented N and P balances for individual or average stands because components such as deposition inputs and leaching losses were not determined for our sample sites. The preliminary balance calculations showed that the use of regional deposition and leaching values led to arbitrary relationships between the various components of the balances, indicating that regional values should not be used when computing nutrient balances for individual ecosystems. Deposition and leaching of nutrients have often been assumed to be balanced (e.g. Kaunisto & Paavilainen 1988), and they have been omitted from nutrient sufficiency calculations. Recent results have shown, however, that the deposition of N may be much larger than leaching losses from drained peatlands, and there may be a net output of P (Sallantaus 1992).

The amounts of N and P in the surface peat (0–50 cm) did not decrease, even if considerable amounts were bound up in the developing tree stands after drainage. These losses have been largely compensated for by the subsidence of the mire surface and the compaction of peat after drainage (see bulk densities in Table 5). The 50 cm thick surface layer on drained sites included peat layers from depths that were below the 50 cm layer before drainage. How much, depended on the amount of subsidence; if all the subsidence took place in the original 50 cm layer, the added thickness of peat would equal the amount of subsidence.

Since subsidence is greatest nearest a ditch (Lukkala 1949), the sampling procedure used at our sites means that the mire surfaces have subsided more than average. Annual average subsidences in the region (over a 50 year period) have been estimated to be 0.6 cm for site types corresponding to our meso-oligotrophic group, and 0.4 cm for site types corresponding to the oligo-ombrotrophic group (Laine & Laiho 1992). It is not possible to calculate the amounts of nutrients that subsidence has brought into the 0–50 cm layer as we do not know how deep the subsidence proceeds. However, even very conservative estimates give values that would fully compensate for the amounts bound up in the tree stand biomass.

Most of the above-ground N and P in the tree stands was bound in the crowns (Table 4, see also Finér 1989). The amounts removed by traditional stemwood harvesting would thus be less than half of the above-ground stores (10–20 kg ha^{-1} P and 100–150 kg ha^{-1} N at the most) at the end of the first rotation on these site types (Kaunisto & Paavilainen 1988). Whole tree harvesting, however, might have serious implications for the P conditions of the surface peat (Holmen 1964, Finér 1989).

In conclusion, the N and P stores in the surface peat have either remained unaltered or slightly increased during the first tree stand rotation after drainage, and are relatively large compared to stores in the biomasses, even in the oldest studied drainage areas.

Table 5. *Mean values ± standard deviations of peat bulk density (g cm^{-3})*

The values are given separately for site type groups, drainage age classes (years since drainage), and peat layers

Years since drainage	Layer, cm 0–10	10–20	25–35	50–60	n
	Meso-oligotrophic sites				
Undrained	0.066 ± 0.034	0.091 ± 0.034	0.078 ± 0.025	0.105 ± 0.022	3
1–20	0.087 ± 0.019	0.114 ± 0.034	0.124 ± 0.034	0.113 ± 0.031	13
21–40	0.096 ± 0.018	0.124 ± 0.018	0.111 ± 0.020	0.096 ± 0.023	12
41–55	0.099 ± 0.021	0.137 ± 0.028	0.122 ± 0.026	0.106 ± 0.035	14
	Oligo-ombrotrophic sites				
Undrained	0.050 ± 0.009	0.053 ± 0.006	0.059 ± 0.012	0.070 ± 0.013	6
1–20	0.067 ± 0.009	0.072 ± 0.012	0.088 ± 0.027	0.102 ± 0.024	11
21–40	0.073 ± 0.022	0.077 ± 0.019	0.086 ± 0.011	0.094 ± 0.026	8
41–55	0.082 ± 0.013	0.105 ± 0.032	0.123 ± 0.021	0.106 ± 0.024	11

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Changes in Mineral Element Concentrations in Peat Soils Drained for Forestry in Finland

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The concentrations of Ca, Mg, K, Fe, Mn, Al, Cu, Zn, Mo, Pb, Cr and Cd were determined for surface peat samples for 80 sites on both undrained and drained pine mires in Finland. The oldest areas had been drained 55 years earlier. Although the gravimetric concentrations of many elements tend to decrease with increasing drainage age, the stores in the 0–50 cm peat layer do not change much along the drainage age gradient. This is possible because compaction of peat takes place after drainage, and, consequently, the 0–50 cm layer in the drained plots includes peat that was below the 50 cm limit before the sites were drained. The fact that elements are removed from soil by uptake by tree stands and by leaching is thus indicated by the decreasing, or unchanging, gravimetric concentrations only. *Key words: drainage, heavy metals, nutrients, pine mires.*

INTRODUCTION

In the early phases of mire formation, plants have several sources of nutrients: the mineral soil below, ground-water flowing from the surrounding upland areas, the decomposing organic remains forming the still thin peat layer, and atmospheric deposition. As the peat layer grows thicker, the root contacts with the mineral soil and ground-water become weaker, and the vegetation becomes ever more dependent on the two last-mentioned sources. Some of the nutrients in dead decomposing plant material are cycled between the living vegetation and the aerated surface peat, but more and more are buried out of reach in the increasing bulk of peat. Various aspects of the biogeochemistry of undrained mires have been studied by e.g. Mattson & Koutler-Andersson (1954), Malmer (1962), Damman (1978, 1986), Hemond (1980), Damman et al. (1992), Verry & Urban (1992).

Drainage for forestry and the consequent water level drawdown causes many changes in the site properties from the plants' point of view, as outlined by, e.g., Laiho & Laine (1994). The oxidation/reduction conditions change (Lähde 1969), and the increased aeration of the surface peat allows for an accelerated rate of nutrient mineralization (e.g. Lieffers 1988, Freeman et al. 1993). The subsidence of the mire surface brings new nutrient reserves from deeper peat layers back to where they can be reached by plant roots (Laiho & Laine 1994). On the other hand, leaching of many elements increases, at least temporarily, with the increased runoff after drainage (Ahtiainen 1988, Lundin 1988, Sallantaus 1992), and in deep peat, all ground-water contact is usually cut off by the ditches.

Tree-stand growth increases after drainage, because of an increased oxygen supply for roots in the aerated surface peat (Boggie 1977). The increasing tree biomass accumulates nutrients taken up from the soil. Calculations based on static physical post-drainage rooting zone volume have produced results that indicate that nutrient, especially K, stores will be depleted in many site types as early as at the end of the first or during the second tree-stand rotation (Kaunisto & Paavilainen 1988, Finér 1989). Long-term studies on the actual changes in post-drainage nutrient stores have, however, not been done.

The aim of the present study is to examine how drainage for forestry affects the stores of mineral elements in surface peat of a selection of mire site types most commonly drained in Finland. Phosphorus has already been dealt with in an earlier paper (Laiho & Laine 1994) together with N.

MATERIAL AND METHODS

The selection of the material and the sampling procedure are described in detail in Laiho & Laine (1994), and are thus summarized only briefly here.

The mires studied are located in central Finland in a region between 61°35′–62°05′ N and 23°50′–24°55′

E. The elevation of the sites varies between 105 and 170 m a.s.l. The mean annual temperature of the region is 3°C and that of July 16°C. The mean annual temperature sum (accumulated mean daily temperatures ⩾5°C) varies between 1150 and 1250 d.d. The annual precipitation is about 650 mm, of which nearly 240 mm is snowfall.

Altogether, measurements were made at 80 sample plots on sites, both undrained and drained, which belong to the following mire site types in the Finnish classification system (Cajander 1913, see Laine et al. 1986 for current terminology): (1) herb-rich sedge–birch–pine fen (RhSR), (2) tall-sedge–pine fen (VSR), (3) cottongrass–sedge–pine fen (TSR), (4) low-sedge–*Sphagnum papillosum*–pine fen (LkR) and (5) cottongrass–pine bog (TR). Short site type descriptions are also given in Laiho & Laine (1994). In addition to the material in Laiho & Laine (1994), two new sample plots were measured, one on an undrained herb-rich sedge–birch–pine fen and one on an undrained tall-sedge–pine fen.

When selecting the sites, special attention was paid to their comparability, especially in the case of drained sites, where the vegetation differs significantly from that of the same site types in their natural condition (Laine 1989, Laine et al. 1995).

To standardise hydrological conditions, the sample plots (10 × 30 m) were placed along contour ditches with the longer side of the plot being parallel to the ditch. Three series of undisturbed peat samples were taken from four depths: 0–10, 10–20, 25–35 and 50–60 cm. Zero-level was taken as the upper level of the rooting zone, which often corresponds to the lower level of the living moss layer.

The peat samples were dried at 105°C, weighed for bulk density calculations, and ground to pass through a 2 mm sieve. Roots with diameter ⩾1 cm, if present, were removed before grinding. For each sample plot, the samples from all three sample points representing the same depths were combined and mixed thoroughly. Element concentrations were measured on an ICP analyser (ARL 358) after HNO_3–H_2SO_4–$HClO_4$ digestion at 200°C (see Allen 1974).

The Pb concentrations obtained for some samples were disregarded because a very high Pb concentration was inexplicably found in the blank sample used to control that particular sample set.

Nutrient stores for the 0–50 cm surface peat layer were calculated as weighted means of the sampled layers. The depth of the peat layer represented by each peat sample was used as the weight (sampling did not cover the whole 0–50 cm layer).

Because the number of plots representing some original site types was too small, the plots were grouped into two site type groups. The "meso-oligotrophic" site type group consists of RhSR and VSR site types, which are closely related to each other in terms of vegetation and peat composition (sedge peat). The "oligo-ombrotrophic" site type group consists of more nutrient-poor site types: TSR, LkR and TR (*Sphagnum* peat). According to the amount of time passed since drainage, the material was divided into four "drainage age" classes: undrained plots, plots drained 1–20 yrs, 21–40 yrs, and 41–55 years before sampling.

To illustrate the trends in the measured parameters after drainage, we used a robust locally weighted regression for smoothing scatter plots (Cleveland 1979, Wilkinson 1989).

RESULTS

Almost all of the mineral elements studied were found in larger quantities in the surface peat on the meso-oligotrophic, clearly minerotrophic, sites (Figs. 1–4). Only K and Pb occur in similar amounts on both site type groups, and there was more Zn on oligo-ombrotrophic than on meso-oligotrophic sites.

The variation in the stores of the studied elements in peat was large (Table 1, Figs. 1–4). In general, the stores did not change much along the drainage age gradient. Only the amounts of Ca and Fe seemed to have decreased on meso-oligotrophic sites with increasing drainage age. On oligo-ombrotrophic sites, the amount of Mg decreased and that of Al increased, especially in the layer below 20 cm. Also the amount of K seemed to slightly increase on oligo-ombrotrophic sites with increasing drainage age.

The amounts of heavy metals in peat (Figs. 3, 4) were too small to allow any conclusions concerning their relationship to the drainage age.

The average gravimetric concentrations of K, Ca, Mg and Mn tended to decrease towards the oldest drainage age class, especially on the meso-oligotrophic sites (Table 1). Concentrations of Al and heavy metals did not show a clear trend along the drainage age gradient.

DISCUSSION

The study was based on an assumption that drained sites belonging to the same original site type were similar before drainage and have developed in a similar manner after drainage. The validity of the

Table 1. *Mean values (±SD) of the gravimetric concentrations of some mineral elements in peat (0–50 cm layer)*
The values are given separately for site type groups and drainage age classes (years since drainage). The values in brackets show the number of sites for which Pb concentrations could be given

		Years since drainage			
	Mineral	0	1–20	21–40	41–55
Meso-oligotrophic sites	K (mg g^{-1})	0.295 ± 0.087	0.202 ± 0.050	0.199 ± 0.038	0.193 ± 0.041
	Ca (mg g^{-1})	5.652 ± 4.994	3.936 ± 1.108	3.869 ± 1.924	2.579 ± 1.127
	Mg (mg g^{-1})	0.531 ± 0.270	0.603 ± 0.282	0.487 ± 0.331	0.413 ± 0.145
	Mn (mg g^{-1})	0.114 ± 0.140	0.061 ± 0.078	0.073 ± 0.054	0.037 ± 0.024
	Fe (mg g^{-1})	8.569 ± 6.517	3.118 ± 2.002	6.362 ± 2.644	2.845 ± 1.920
	Al (mg g^{-1})	1.982 ± 1.239	2.225 ± 0.680	1.665 ± 0.758	1.998 ± 0.857
	Zn (mg g^{-1})	0.015 ± 0.008	0.012 ± 0.006	0.014 ± 0.011	0.015 ± 0.006
	Cu (μg g^{-1})	7.330 ± 7.103	7.555 ± 2.379	3.973 ± 2.319	5.949 ± 2.282
	Mo (μg g^{-1})	1.619 ± 1.004	0.997 ± 0.476	1.391 ± 0.503	0.896 ± 0.454
	Cd (μg g^{-1})	0.643 ± 0.478	0.290 ± 0.170	0.365 ± 0.107	0.339 ± 0.104
	Cr (μg g^{-1})	4.850 ± 3.189	3.718 ± 1.204	4.093 ± 1.965	3.296 ± 1.380
	Pb (μg g^{-1})	6.260 ± 2.701	3.640 ± 1.611	3.986 ± 1.592	4.757 ± 1.773
n		5	13 (9)	12	14
Oligo-ombrotrophic sites	K (mg g^{-1})	0.308 ± 0.036	0.215 ± 0.032	0.253 ± 0.100	0.211 ± 0.040
	Ca (mg g^{-1})	2.737 ± 0.715	2.308 ± 0.658	2.943 ± 1.450	1.705 ± 0.597
	Mg (mg g^{-1})	0.620 ± 0.166	0.478 ± 0.164	0.506 ± 0.161	0.293 ± 0.101
	Mn (mg g^{-1})	0.030 ± 0.015	0.022 ± 0.014	0.018 ± 0.012	0.023 ± 0.030
	Fe (mg g^{-1})	1.213 ± 0.433	1.268 ± 0.597	1.113 ± 0.509	1.259 ± 1.063
	Al (mg g^{-1})	0.673 ± 0.315	1.171 ± 0.585	0.633 ± 0.196	1.466 ± 0.446
	Zn (mg g^{-1})	0.038 ± 0.010	0.022 ± 0.010	0.025 ± 0.014	0.022 ± 0.025
	Cu (μg g^{-1})	3.070 ± 0.829	3.610 ± 1.106	2.692 ± 0.672	4.639 ± 1.555
	Mo (μg g^{-1})	0.754 ± 0.292	0.608 ± 0.306	0.665 ± 0.346	0.655 ± 0.197
	Cd (μg g^{-1})	0.438 ± 0.186	0.293 ± 0.182	0.397 ± 0.080	0.301 ± 0.082
	Cr (μg g^{-1})	3.140 ± 0.783	2.713 ± 1.233	1.993 ± 0.793	2.327 ± 0.935
	Pb (μg g^{-1})	9.559 ± 3.327	7.195 ± 2.106	7.771 ± 3.513	5.553 ± 2.706
n		6 (5)	11 (7)	8	11

approach has been discussed by Laiho & Laine (1994). It should be borne in mind that our data cannot be used to make any conclusions about actual changes taking place on individual sites, they show an average trend only within a relatively large amount of material.

The stores of the elements studied in a 50 cm surface peat layer seem to remain rather constant after drainage. This observation may seem rather surprising at first, because we know that after drainage of forested peatlands an increasing amount of mineral elements is bound by the tree stands, and that the leaching of most elements increases at least in the beginning of the drainage succession.

The studied elements taken up most readily by trees are Ca, K and Mg. We estimated the amounts of these elements bound by the tree stands on our sample plots, using concentration values found by Paavilainen (1980) for ombrotrophic sites and those found by Finér (1989) for meso-oligotrophic site types (see Laiho & Laine 1994). According to our estimates, the tree stands on the oldest drained meso-oligotrophic sites had bound, on average, approximately 200 kg ha^{-1} Ca, 90 kg ha^{-1} K and 40 kg ha^{-1} Mg in their above-ground biomass after drainage. The corresponding figures for oligo-ombrotrophic sites were 120, 70 and 30 kg ha^{-1}, respectively. The amount of K in the oldest tree stands was approximately the same as the amount in the surface peat, whereas the amounts of Ca and Mg found in the tree stands were ca. 20% of the remaining stores in the surface peat.

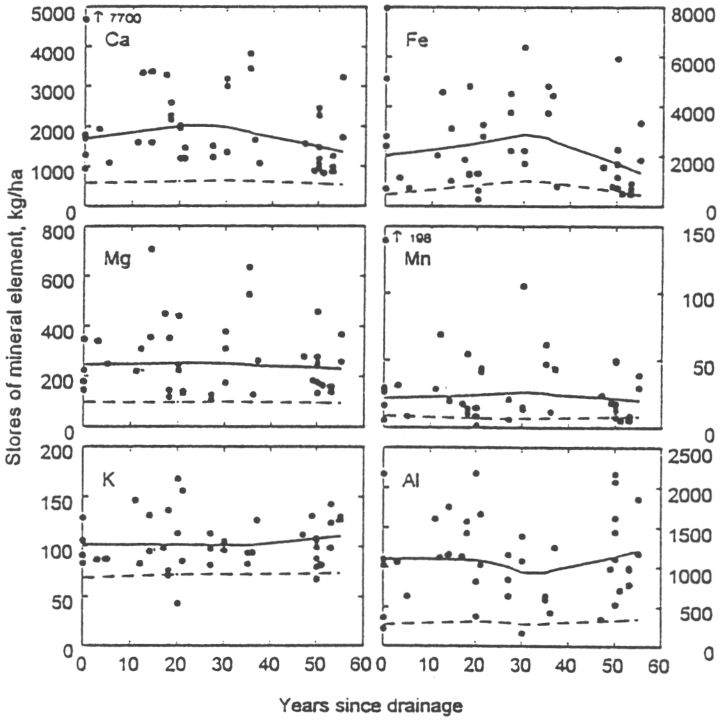

Fig. 1. The stores of Ca, Mg, K, Fe, Mn and Al in the 0–50 cm peat layer of the meso-oligotrophic sites, as a function of drainage age. The lower dashed lines show the stores in the 0 –20 cm peat layer.

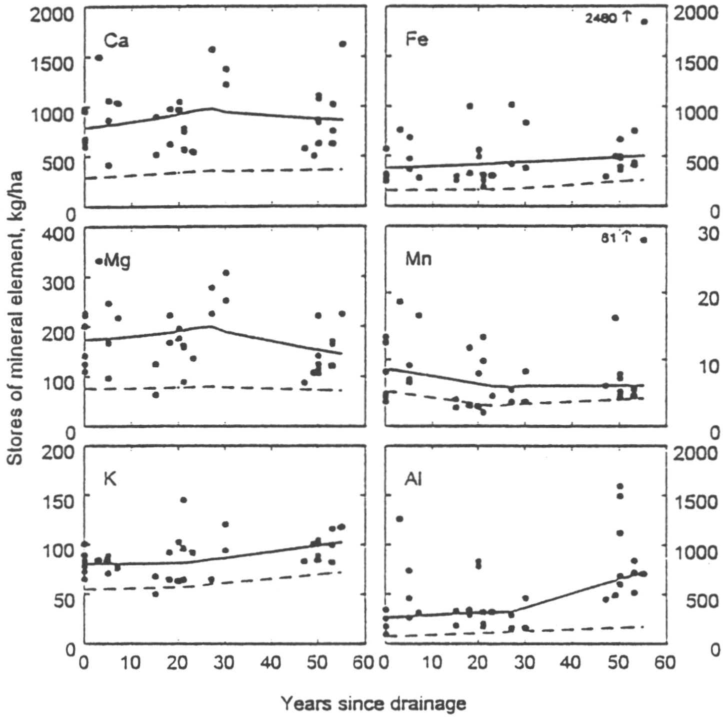

Fig. 2. The stores of Ca, Mg, K, Fe, Mn and Al in the 0–50 cm peat layer of the oligo-ombrotrophic sites, as a function of drainage age. The lower dashed lines show the stores in the 0–20 cm peat layer.

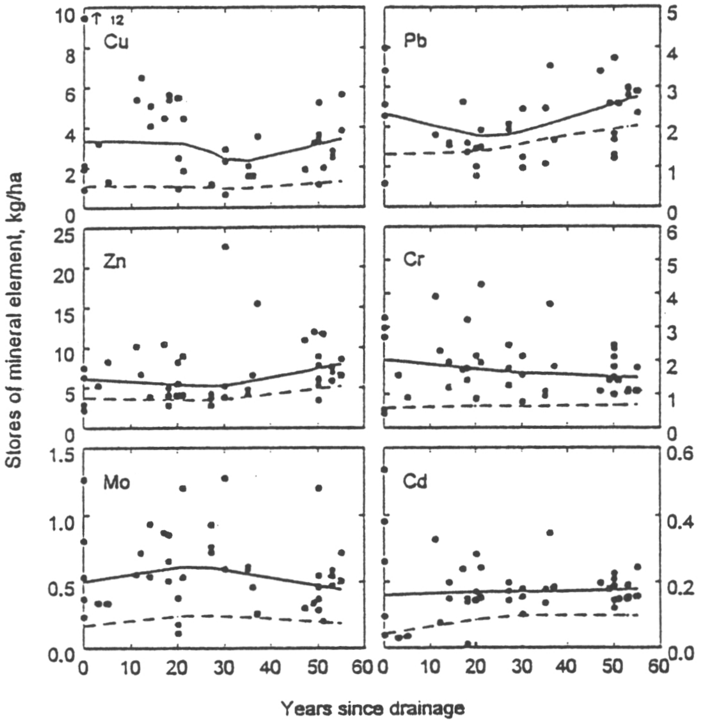

Fig. 3. The stores of Cu, Zn, Mo, Pb, Cr and Cd in the 0–50 cm peat layer of the meso-oligotrophic sites, as a function of drainage age. The lower dashed lines show the stores in the 0–20 cm peat layer.

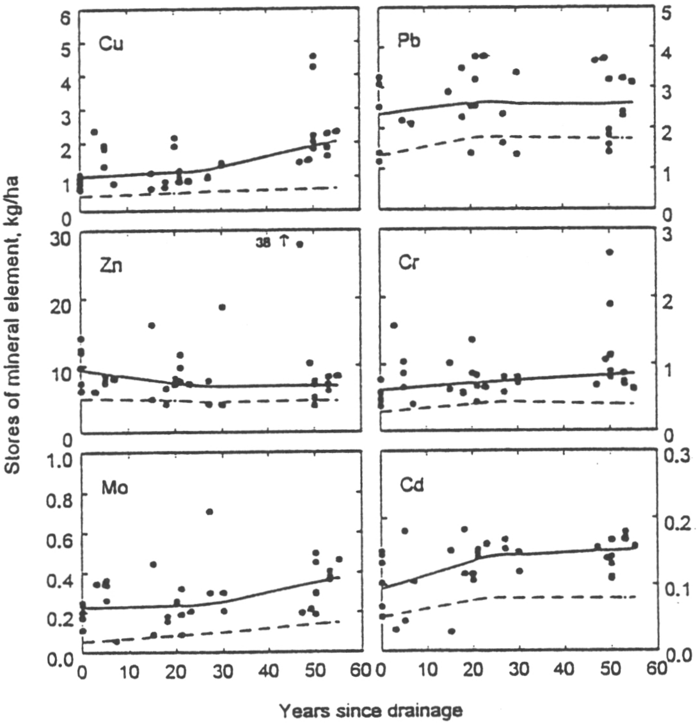

Fig. 4. The stores of Cu, Zn, Mo, Pb, Cr and Cd in the 0–50 cm peat layer of the oligo-ombrotrophic sites, as a function of drainage age. The lower dashed lines show the stores in the 0–20 cm peat layer.

Sallantaus (1992) found a net loss of Ca, Mg and K with runoff water from drained mire catchments, whereas on the undrained parts of the same catchments, the inputs and outputs of these elements were more or less balanced. Magnesium and Ca were leached relatively more easily than K, which is retained effectively by the vegetation, as concluded by e.g. Laiho & Laine (1992). In our drained material, the ratio of K to Ca and Mg in peat was highest in the oldest drainage age class.

The removal of elements from peat can be seen as a decrease in the gravimetric concentrations of most elements after drainage (Table 1). If the gravimetric concentrations decrease but the volumetric ones remain the same, it means that compaction of peat must take place simultaneously. The bulk density values of peat, presented in an earlier paper (Laiho & Laine 1994), indeed increase after drainage. Thus the compaction of peat, which brings "new" peat material from below to the layer studied (always 50 cm), compensates for the losses of elements when a certain peat volume is observed. The amount of some elements may even increase, depending on the relationship between the rates of peat compaction and element removal. The fact that elements are actually removed from peat is thus shown as decreasing gravimetric concentrations only. The mechanism of peat compaction is discussed in more detail by Laiho & Laine (1994).

In addition to peat compaction, another factor compensating for the removal of elements from the surface peat, may be the ability of increased tree-stand canopy biomass to capture dry deposition, which, as a process, is generally acknowledged but difficult to quantify (e.g. White & Turner 1970, Lindberg & Lovett 1985, Hicks et al. 1987).

The gravimetric concentrations of Al and some heavy metals remained, on average, approximately the same after drainage. The same holds for Fe on oligo-ombrotrophic sites; on meso-oligotrophic sites the very large variation in the Fe concentration made it difficult to draw any firm conclusions. This is explained partially by the fact that these elements are not actively taken up by the plants, as most of them are toxic. Information concerning their leaching rates from peatlands, and the effect of drainage, is scanty and partly contradictory (e.g. Ahtiainen 1990, Bergquist et al. 1984). As the concentrations of Al and Fe in our material do not increase even if the surface peat is compacted, it may be concluded that these elements are leached to some extent from the surface peat assuming that no significant amounts are bound into the tree stand biomass.

Our values for heavy metals, especially Cd, Cr, Mo and Pb, may be considered as being indicative only, showing the magnitude of their presence in peat. Their concentrations were close to the detection limits of the assay method used, and the quantitative effect of possible contamination of samples during sampling and further treatment could not be estimated.

Harvesting may considerably affect the nutrient capital of these ecosystems. Relatively large quantities of some cations, e.g. K, are removed in harvested stemwood (Kaunisto & Paavilainen 1988, Finér 1989), and whole-tree harvesting would further increase element losses. The leaching losses of most elements have been found to increase after harvesting as well (e.g. Ahtiainen 1988).

Earlier studies concerning nutrient stores on drained peatlands have been based on rather small data sets. The very large variation included in our material shows that making comparisons within various small subsets could lead to very different conclusions about the post-drainage changes. On an average, however, it seems that the first post-drainage tree generation does not essentially deplete the nutrient supplies of surface peat in the site types studied.

ACKNOWLEDGMENTS

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III

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 references 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 *Vuosia ojituksesta*	–	–	8	22	30	55
Living tree stand volume, m^{3}ha^{-1} *Elävän puuston tilavuus, m^{3}ha^{-1}*	6	35	10	76	102	150
Proportion pine/birch/spruce [a] *Puulajisuhteet mänty/koivu/kuusi* [a]	100/–/–	95/5/0	100/-/0	69/31/0	83/15/2	88/9/3
Number of living stems, ha^{-1} *Runkoluku, kpl ha^{-1}*	444	1567	554	4750	1782	2786
Ditch spacing, m *Sarkaleveys*	–	–	30	37	37	32
Sample plot size, m^2 *Koealan koko, m^2*	900	600	1263	1158	1190	1328

[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°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 m^2 per location, other components on an area of 0.19 m^2. 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 oxycoccos*), 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 ± their asymptotic standard errors for the regression equation $dm_s = p1\ h^{p2}$ for estimating tree seedling biomass, where dm_s = total dry mass of the seedling (g), h = seedling height (m), p1, p2 = parameters, r.s.d. = residual standard deviation.

Taulukko 2. Puuntaimien biomassan estimointiin käytetyn regressioyhtälön $dm_s = p1\ h^{p2}$ *parametrien arvot ja niiden asymptoottiset keskivirheet;* dm_s = *taimen kokonaiskuivamassa (g),* p1, p2 = *parametrit,* r.s.d. = *jäännösvaihtelu.*

Species	p1	p2	r^2	r.s.d.	n
Pine – *mänty*	136.4 ± 20.56	2.715 ± 0.355	0.948	54.9	16
Birch – *koivu*	40.1 ± 29.18	1.338 ± 0.820	0.749	70.2	8
Spruce – *kuusi*	207.8 ± 36.15	1.248 ± 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 peittävyydet tutkimuskohteilla.

	Site – *Kohde*					
	1	2	3	4	5	6
Salix aurita	–	+	–	+	–	–
Andromeda polifolia	1	1	3	3	+	+
Betula nana	1	10	20	20	1	+
Calluna vulgaris	–	–	–	+	–	–
Empetrum nigrum	1	1	10	5	20	–
Ledum palustre	–	–	–	5	+	2
V. microcarpum	+	+	+	–	–	–
V. myrtillus	–	–	–	1	+	40
V. oxycoccos	1	3	2	10	+	+
V. uliginosum	+	+	1	20	2	1
V. vitis-idaea	–	–	–	20	1	40
Carex chordorrhiza	–	+	–	–	+	–
C. dioica	–	+	–	–	–	–
C. echinata	–	+	–	–	+	–
C. lasiocarpa	10	20	1	–	–	–
C. magellanica	+	+	+	+	+	–
C. nigra	–	–	–	–	+	–
C. pauciflora	+	1	+	–	+	–
C. rostrata	–	2	–	–	–	–
Eriophorum angustifolium	–	+	–	–	+	–
E. vaginatum	5	10	10	20	30	1
Agrostis canina	–	–	–	–	+	–
Calamagrostis arundinacea	–	–	–	–	+	–
C. purpuraea	–	–	–	–	+	–
Deschampsia cespitosa	–	–	–	–	+	–
Dactylorhiza maculata	–	+	+	–	–	–
Drosera rotundifolia	+	+	–	–	–	–
Dryopteris carthusiana	–	–	–	–	+	–
Epilobium angustifolium	–	–	–	–	+	–
Equisetum fluviatile	–	+	–	–	–	–
Melampyrum pratense	–	+	–	+	+	+
Menyanthes trifoliata	–	5	–	–	–	–
Potentilla palustris	–	+	–	–	+	–
Pyrola media	–	–	–	–	+	–
Rubus chamaemorus	2	–	1	1	+	5
Trientalis europaea	–	–	–	+	+	+
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 peittävyydet tutkimuskohteilla.

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

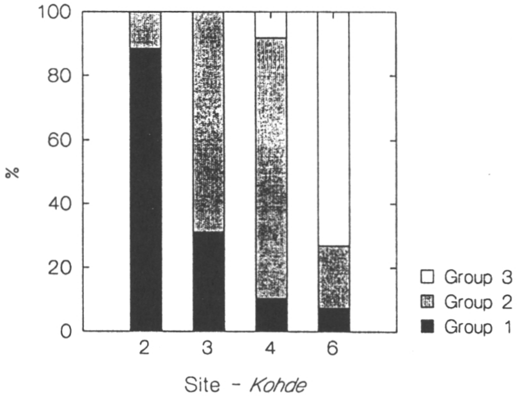

Fig. 1. Distribution of dwarf shrub biomass between species groups at different stages of the drainage succession: Group 1 = shrubs typical of treeless mires (*Andromeda polifolia* and *Vaccinium oxycoccos*), Group 2 = shrubs typical of pine mires (*Betula nana, Empetrum nigrum, Ledum palustre, Vaccinium 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 kuivumissukkession eri vaiheissa. Group 1 = nevavarvut, Group 2 = rämevarvut, Group 3 = metsävarvut; lajit kuten yllä (esim. Eurola ym. 1984). Kohteiden ojitusiät Taulukossa 1.

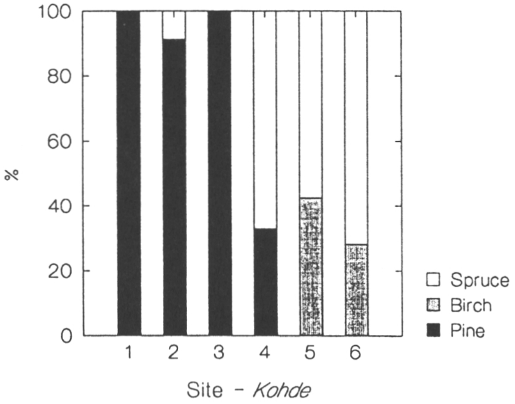

Fig. 2. The biomass proportions of Scots pine, pubescent birch and Norway spruce seedlings at different stages of the drainage succession. Drainage ages of the sites in Table 1.

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

DISCUSSION

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

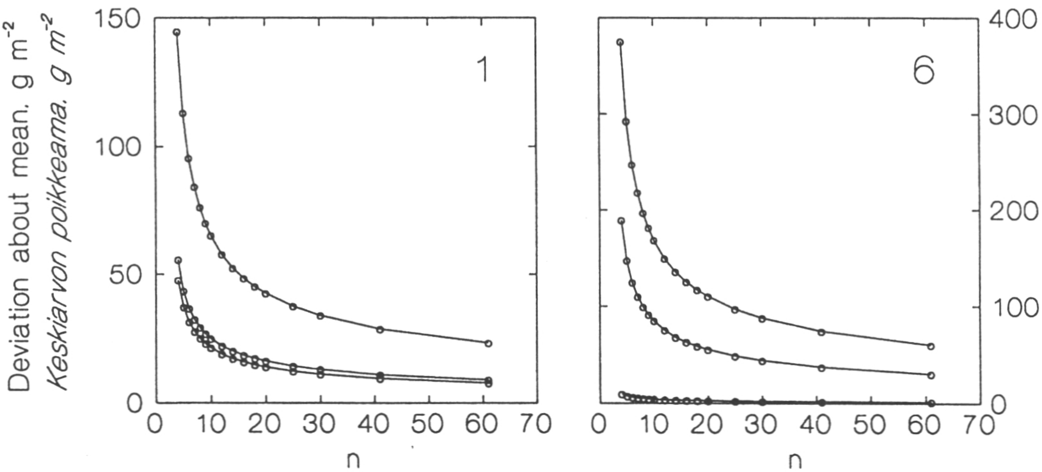

Fig. 3. Maximum deviation of the estimated mean biomass (Table 5) with a 95 % confidence level as a function of the number of samples for sites 1 and 6. The uppermost lines represent moss biomass, the middle lines shrub biomass and the lowermost lines other field layer biomass.

Kuva 3. Otoskeskiarvon (Taulukko 5) suurin poikkeama populaation keskiarvosta todennäköisyydellä 95 % näytemäärän funktiona kohteille 1 ja 6. Ylimmät käyrät ovat sammalbiomassalle, keskimmäiset 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 suluissa 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)

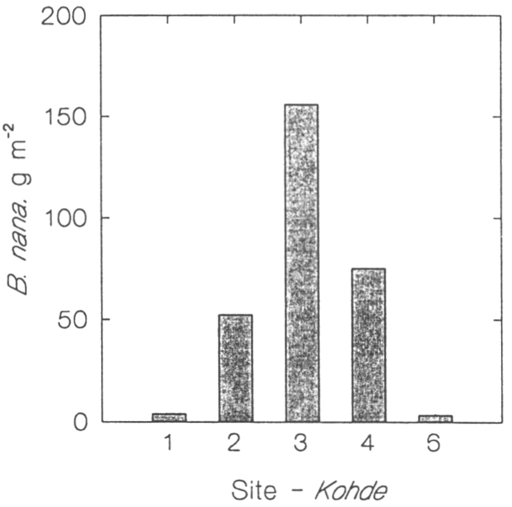

Fig. 4. The biomass of *Betula nana* at different stages of the drainage succession. Drainage ages of the sites in Table 1.

Kuva 4. Vaivaiskoivun (B. nana) *biomassa kuivumissukkession eri vaiheissa. Kohteiden ojitusiät 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. Eurola 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 sekundäärisukkession myötä tapahtuvia muutoksia varsinaisen sararämeen (VSR, esim. Laine & Vasander 1990), Suomen yleisimmin ojitetun suotyypin, pintakasvillisuudessa, erityisesti sen biomassassa. Mittauksia tehtiin kuudella kohteella, joista kaksi oli ojittamattomia ja neljä eri-ikäisiä ojitusalueita (Taulukko 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 kuivumissukkession eri vaiheita ja olivat keskenään mahdollisimman vertailukelpoisia.

Ojittamattomilla kohteilla koealat sijoitettiin kasvillisuudeltaan mahdollisimman homogeeniseen ja tyypillisesti VSR:ttä 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 peittävyydet 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 m^2 alalta ja muu kenttäkerros sekä pohjakerros 0,19 m^2 alalta kultakin näytteenottokohdalta. Jako maanalaiseen ja maanpäälliseen osaan tehtiin sen perusteella, missä juuristokerros alkoi. Ositteet kuivattiin näytteenottokohdittain vakiomassaisiksi 105°C:ssa ja punnittiin. Puuntaimista mitattiin pituus viideltä koealan lävistäjille sijoitetulta ympyräkoealalta, 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 biomassa pienenee selvästi ojituksen jälkeen. Varpu- ja sammalbiomassa kasvaa aluksi ojituksen jälkeen ja pienenee sitten väliaikaisesti suurimman lajistomuutoksen tapahtuma-aikana. Vanhimmalla tutkitulla ojitusalalla varpubiomassaa oli enemmän ja sammalbiomassaa noin yhtä paljon kuin ojittamattomilla kohteilla. Lajisto oli tällöin kuitenkin muuttunut tyypillisten metsälajien vallitsemaksi; poikkeuksen muodosti varvikkorahkasammal *Sphagnum russowii* pohjakerroksessa.

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

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Changes in Root Biomass after Water-level Drawdown on Pine Mires in Southern Finland

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Changes in living and dead root biomass were monitored in the succession created by drainage for forestry on six sites from undrained to 55-yr-old drained tall-sedge pine mires in southern Finland. This was done to evaluate the role of root biomass in carbon cycling in drained peatland ecosystems. The total living Scots pine (*Pinus sylvestris* L.) root and stump biomass varied from 190 g m^2 on an undrained site to 3060 g m^2 on the oldest drained site. The pine fine root biomass reached the maximum level within 22 yrs of drainage with a pine stand volume of 81 m^3 ha^{-1}. The pine coarse root and stump biomass increased with the age of the stand, comprising 90% of the total living root biomass on the 55-yr-old drained site. The drainage also increased the root biomass of field layer species; however, the roots of sedges were replaced by those of shrubs and trees. The dead fine root biomass was smallest on the two oldest drained sites, which could have resulted from a higher decomposition rate after improved aeration in the surface peat. *Key words: drainage, ground vegetation, peatlands, Pinus sylvestris, roots.*

INTRODUCTION

Mire ecosystems are characterized by a high water table level, which reduces the growth substrate gas volume and oxygen content unfavourably low for many vascular plants, e.g. conifers. Mire plants adapted to wet conditions have specific cell tissues for transporting oxygen to roots, and their roots may reach very deep into anaerobic peat (Metsävainio 1931, Saarinen et al. 1994). On treeless, wet mires most of the vascular plant biomass is below ground (e.g. Sjörs 1991, Wallén 1992, Saarinen et al. 1994), whereas on forested mires, relatively more biomass accumulates above ground (e.g. Reader & Stewart 1972).

After drainage for forestry, mire plants are replaced gradually by forest species (e.g. Laine et al. 1995) and tree stand becomes the main carbon binding body of the peatland ecosystem (Reinikainen et al. 1984), provided that lack of nutrients does not essentially restrain growth (Vasander 1982). The total biomass accumulation of vascular plants also shifts from below-ground to above-ground (Vasander 1982). Results from mineral soil sites suggest, however, that fine roots may account for a major part of biomass production also in forested peatland ecosystems (e.g. Ågren et al. 1980, Keyes & Grier 1981, Persson 1983, Santantonio & Santantonio 1987).

The root systems of Scots pine (*Pinus sylvestris* L.) growing on peatland sites have been found to differ from those on mineral soil sites; peatland pines usually lack the main tap root, and the root system is more superficial (e.g. Kokkonen 1923, Laitakari 1927). After drainage and the consequent water-level drawdown, tree roots can grow deeper. However, in most cases it has been found that the average depth of fine roots increases only very little (Heikurainen 1955a, Paavilainen 1966). On very nutrient-rich drained sites, tree roots have been found to reach as deep as 75 cm (Holmen 1964).

When assessing the effect of water-level drawdown on the carbon balance of peatlands, the significance of estimating the root production has become evident. The increase in the C accumulation in the tree stand biomass will have a positive effect on the total C balance of the ecosystem at the beginning (50–200 yrs; Cannell et al. 1993), but in the long run it will be critical whether the litter production of the tree stand compensates for the decay of the peat organic matter. The amount and decomposition rate of subsurface litter is very important in this respect (Finér & Laine 1994).

The aim of this study was to examine the changes in root biomass of pine mires after water-level drawdown by comparing sites at different stages of succes-

Table 1. *General features of the sites*

	Site					
	1	2	3	4	5	6
Years since drainage	–	–	8	22	30	55
Tree stand volume (m^3 ha^{-1})	6	35	10	76	102	150
Proportion pine/birch/spruce	100/–/–	95/5/0	100/–/0	69/31/0	83/15/2	88/9/3
Number of stems (ha^{-1})	878	1700	594	5320	2328	2982
Ditch spacing (m)	–	–	30	37	37	32
Sample plot size (m^2)	900	600	1263	1158	1190	1328

sion caused by forest drainage. This is a part of a study investigating the role of biomass in carbon cycling in peatland ecosystems (Laiho & Laine 1994*b*) as part of the project "Carbon balance of peatlands and climate change" within the Finnish Research Programme on Climate Change.

MATERIAL AND METHODS

Study sites

For the study, six sample plots were established on pine mire sites in southern Finland (61°35′–61°52′ N, 24°05′–24°25′ E) (Table 1). Two of the sites (1, 2) were undrained whereas the rest (3–6) had been drained 8, 22, 30 and 55 yrs earlier. 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, with one ditch counted in the area. Site 2 is slightly affected by a ditch ca. 40 m away from the sample plot. The undrained sites are very wet, with the water-table level at or close to the mire surface. On the drained sites, the water table has fluctuated between the following approximate limits during the time from early spring until late autumn: 10–25 cm (site 3), 35–50 cm (site 4), 35–60 cm (site 5) and 50–75 cm (site 6) below the mire surface. These values are from the middle of the strip between ditches.

The sites were selected from an earlier study dealing with the effect of drainage on peat properties and vegetation (Laiho & Laine 1994*a*, Laine et al. 1995). The original sites were selected very carefully to allow comparison between different stages of the post-drainage succession (see Laiho & Laine 1994*a* for details). The sites of the present study were chosen to obtain as wide a drainage age variation as possible within one site type. Tall-sedge pine fen (VSR, according to the Finnish site type classification system, e.g. Ruuhijärvi (1983) and Eurola et al. (1984); see Laine & Vasander (1990) for the current terminology) was chosen because it is the mire site type most frequently drained for forestry in Finland (Keltikangas et al. 1986).

A mosaic-like pattern of low treed hummocks and treeless lawns (intermediate level between dry hummock and wet hollow level) is typical of this site type in its natural (undrained) state. The tree stand is sparse and dominated by Scots pine (*Pinus sylvestris* L.), usually with some white birch (*Betula pubescens* Ehrh.). Mire dwarf shrubs (e.g. *Betula nana* L., *Ledum palustre* L., *Vaccinium uliginosum* L.) occur on hummocks. Minerotrophic tall sedge species (*Carex lasiocarpa* Ehrh., *Carex rostrata* Stokes) dominate the field layer of lawns. In the moss layer, oligo-ombrotrophic *Sphagna* (e.g. *Sphagnum fallax* (Klinggr.) Klinggr., *Sphagnum angustifolium* (Russ.) C. Jens.) are predominant. The peat is *Carex* dominated. After drainage, sedges disappear fairly soon. Mire dwarf shrubs usually increase at first, and then decrease gradually with increasing tree stand growth, giving way to forest species such as *Vaccinium vitis-idaea* L. Vegetation changes after drainage are described in more detail by Laine et al. (1995).

Sampling and analyses

Living and dead fine and small root (∅ ⩽ 10 mm) biomasses were determined by the core method (e.g. Böhm 1979). Sixteen to twenty peat cores were taken systematically on each plot from the 0–30 cm peat layer. This limit was chosen because most of the fine roots are to be found in the 0–30 cm layer on both undrained and drained mires (e.g. Paavilainen 1966, Håland & Brække 1989, Sjörs 1991, Saarinen et al. 1994). Zero-level was taken as the upper level of the rooting zone, which corresponded approximately to

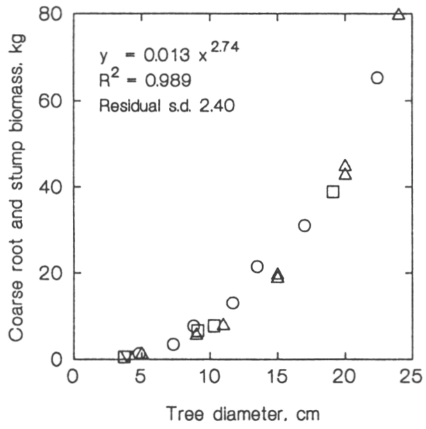

Fig. 1. Relationship between Scots pine stem diameter at 1.3 m and biomass of stump and coarse roots on peatland sites, according to data from Vasander (1982; triangle (downward)), Håland & Brække (1989; squares) and Finér (1989*a*; triangles (upward), 1991; circles).

the lower level of the living moss layer. The area of the core was 49 or 64 cm^2 on the undrained sites and 24 cm^2 on the drained ones. The cores were divided into three subsamples 10 cm long, starting from the surface down. Sampling was done in mid June 1991 on sites 2 and 5 and at the end of June 1992 on the other sites. The samples were frozen for storage until treatment.

Roots were extracted by hand from the cores. The root fraction included both the morphological roots and the rhizomes. Living roots were separated into three species groups: Scots pine, other tree species and shrubs, and Cyperaceae (*Carex* L. spp. sedges and cottongrass, *Eriophorum vaginatum* L.). Dead roots were separated into two groups: Scots pine, and all others combined. Roots were further divided into four diameter classes as follows: <1 mm, 1–2 mm, 2–5 mm, and 5–10 mm, except for Cyperaceae roots, almost all of which had a diameter smaller than 1 mm. Roots of all these size classes will henceforth be called fine roots. They were dried at 60°C to constant mass and weighed with 0.001 g precision. Distinguishing living roots from dead was based on the colour, resilience and ease of breaking. Some checking was done by staining with fluorescein diacetate (e.g. Widholm 1972). Only the thickest dead roots and rhizomes of sedges could be counted, because the peat originated mainly from the remnants of sedge roots. Both living and dead roots extracted will be referred to as biomass (Sutton & Tinus 1983).

For this study, the stumps and coarse roots could not be excavated for the biomass measurements. Therefore, existing data for peatlands, with the same diameter limit for fine and coarse roots as in this study (10 mm), were used. For Scots pine, the data of Vasander (1982), Håland & Brække (1989) and Finér (1989*a*, 1991) were combined, and an equation relating the biomass of stumps and coarse roots to tree stem diameter at 1.3 m ($d_{1.3}$) was calculated (Fig. 1). Only the unfertilized part of the material was used. For white birch and Norway spruce (*Picea abies* (L.) Karsten), the equations presented by Finér (1989*a*, appendix 19; $+a_2 d$ should be $+a_2 \ln d$) were used. On the sample plots, $d_{1.3}$ of all living and standing dead trees with $d_{1.3} \geq 1.5$ cm was measured so that the equations could be applied.

RESULTS

The living Scots pine fine root (∅ ⩽ 10 mm) biomass is small on the undrained sites (Table 2). It increases

Table 2. *Mean fine root (∅ ⩽ 10 mm) biomass, g m^{-2}, in the 0–30 cm surface peat layer on the sites studied*
Standard deviation in parentheses

Site	n	Pine	Trees and shrubs[a]	Cyperaceae	Living total	Dead pine	Dead other	Dead total
1	20	15 (27)	215 (151)	226 (150)	456 (236)	23 (37)	343 (137)	366 (136)
2	16	47 (64)	276 (146)	275 (93)	597 (191)	37 (53)	406 (209)	443 (232)
3	20	64 (50)	235 (189)	182 (133)	481 (177)	31 (49)	249 (95)	280 (94)
4	20	342 (249)	486 (323)	12 (17)	840 (316)	89 (56)	309 (174)	398 (206)
5	18	275 (284)	147 (190)	15 (23)	437 (305)	44 (37)	173 (91)	218 (106)
6	20	363 (275)	513 (285)	11 (7)	886 (345)	94 (46)	180 (96)	274 (107)

[a] Excluding pine.

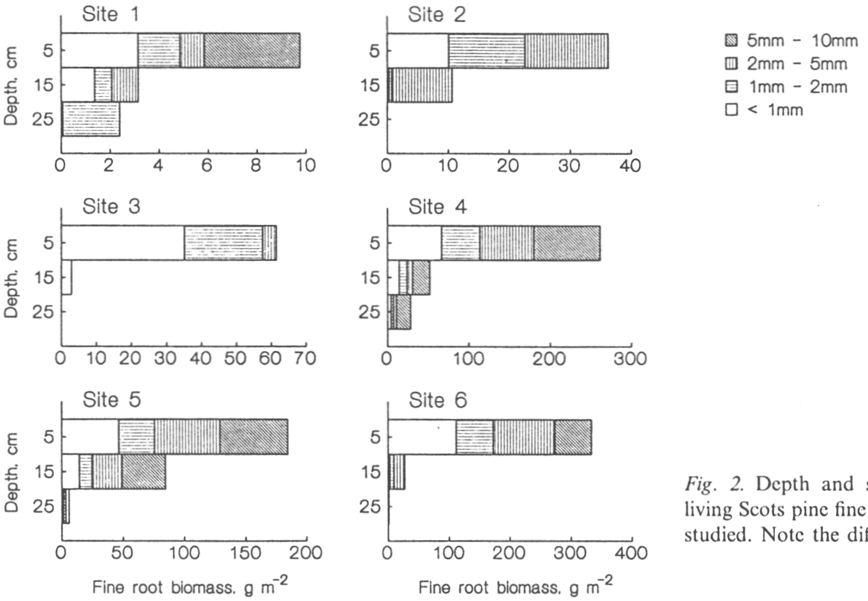

Fig. 2. Depth and size class distribution of living Scots pine fine root biomass on the sites studied. Note the difference in scales.

soon after drainage and reaches a maximum level on the site drained 22 yrs ago. The living root biomass of the other tree species and shrubs also increases after drainage, although the change is smaller than for pine roots. The change in the fine root biomass of Cyperaceae is the opposite to that of pine. Living roots of Cyperaceae are suppressed within 22 yrs of water-level drawdown. The total living fine root biomass has increased by more than 50% on the 22- and 55-yr-old drained sites compared with the undrained ones.

The dead pine fine root biomass changes parallel that of the living biomass, although the increase is much smaller (Table 2). The other dead root biomass

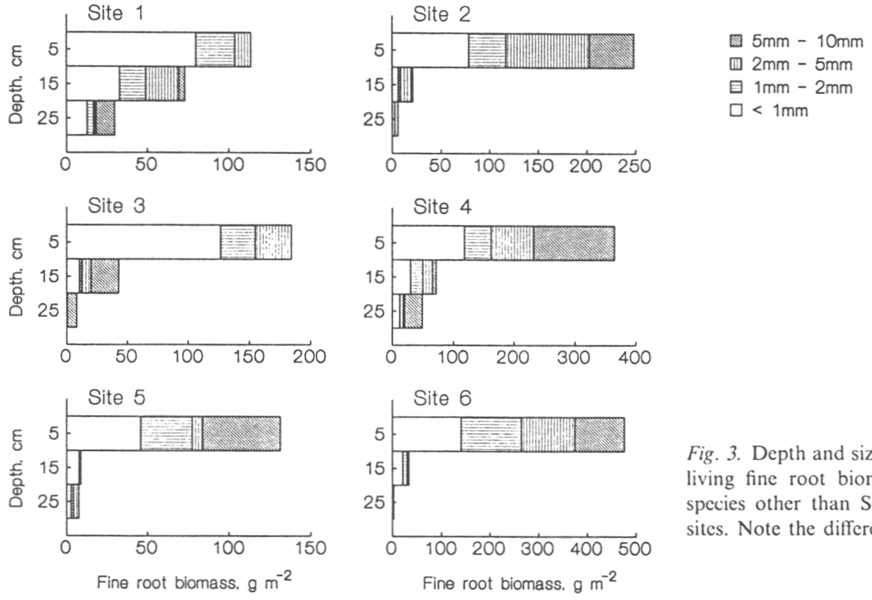

Fig. 3. Depth and size class distribution of the living fine root biomass of shrubs and tree species other than Scots pine on the studied sites. Note the difference in scales.

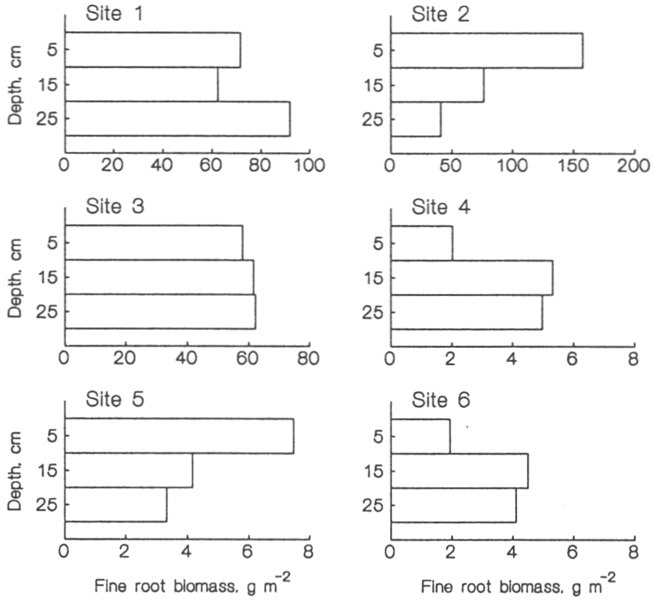

Fig. 4. Depth distribution of Cyperaceae fine root biomass on the sites studied. Note the difference in scales.

fraction is somewhat smaller in the two oldest sites compared with the other sites. The total dead root biomass is smallest on the two oldest drained sites.

Most living tree and shrub fine roots are found in the topmost 10-cm peat layer (Figs. 2, 3), both on undrained and drained sites. The depth distribution of sedge roots shows no consistent pattern (Fig. 4). The dead pine roots are distributed more superficially on the three oldest drained sites than on the other sites, thus resembling more the depth distribution of the living pine roots (Fig. 5). The depth distribution of the dead root biomass of the other species has not

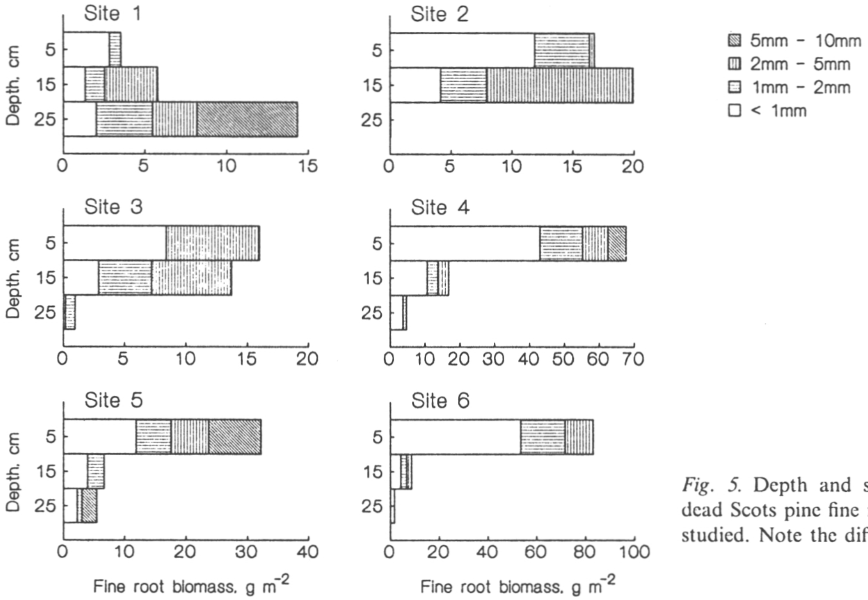

Fig. 5. Depth and size class distribution of dead Scots pine fine root biomass on the sites studied. Note the difference in scales.

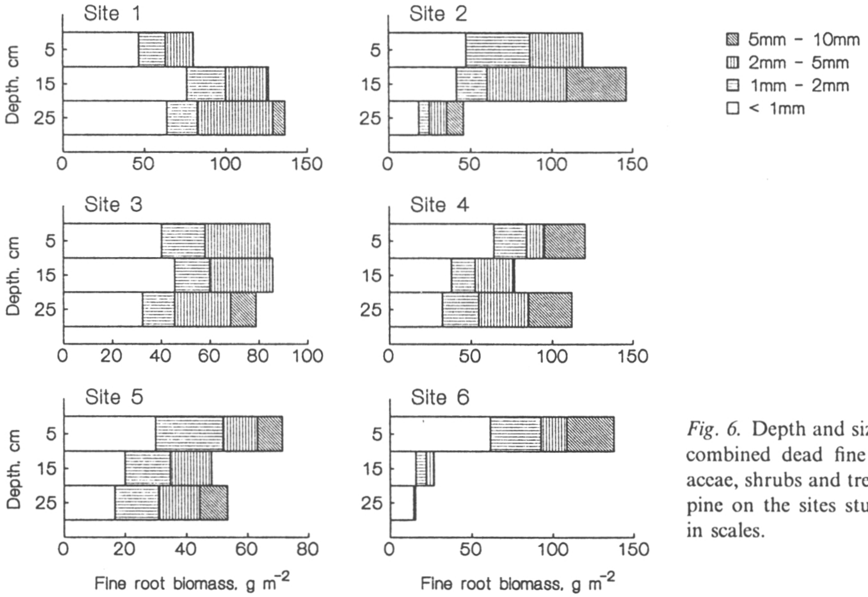

Fig. 6. Depth and size class distribution of the combined dead fine root biomass of Cyperaceae, shrubs and tree species other than Scots pine on the sites studied. Note the difference in scales.

been affected by drainage, except on the oldest drained site, where it has become more superficial (Fig. 6).

The living coarse root and stump biomass increases after drainage (Table 3), with a linear relationship to the stem volume (total biomass kg $m^{-2} = 0.02 \times$ total stem volume m^3 ha^{-1}, SEE = 0.130; stem volumes in Table 1).

Total living pine root and stump biomass varies from 190 g m^{-2} on one undrained site to 3060 g m^{-2} on the oldest drained site. The proportion of fine roots out of the total pine root biomass is less than 10% on the undrained sites, increasing to ca. 20% on the 8- and 22-yr-old drained sites, and decreasing again to around 10% on the oldest drained sites.

DISCUSSION

The amount of living fine roots varies both between and within years (e.g. Heikurainen 1955*b*), so one sampling gives no absolute information on the amount of fine roots on the sites studied. The spatial variation in the fine root biomass within a site is also very high, as has already been shown in previous studies (Håland & Brække 1989, Finér 1991). The relevance of this study is more in comparing the situation on sites at different stages of post-drainage succession. Because the amount of Scots pine fine roots has been found to reach its maximum at the end of June (Heikurainen 1955*b*, Finér et al. 1992), our values are probably near the annual maximum.

Table 3. *Estimated stump and coarse root (∅ > 10 mm) biomass, g* m^{-2}*, on the sites studied*

Site	Pine	Birch	Spruce	Living total	Dead pine	Dead other[a]	Dead total
1	175	0	0	175	124	0	124
2	884	28	4	916	12	2	14
3	291	0	<1	291	30	0	30
4	1122	260	6	1387	25	<1	25
5	1879	208	22	2109	183	0	183
6	2693	155	84	2932	7	4	10

[a] Birch and spruce.

Field layer vegetation roots and dead roots have not shown any seasonal pattern (Finér et al. 1992). The dynamics of fine root production on peatland sites is still rather poorly known, but ongoing work by Finér & Laine (1994) will shed more light on this. Our fine root biomass values are in agreement with those reported for drained tall-sedge pine mires in Finland (Finér 1989*b*, Finér et al. 1992, Finér & Laine 1994). As extracting fine roots from peat soil is difficult and laborious, our values may still be underestimated, especially those of Cyperaceae on the undrained sites (cf. Sjörs 1991).

Our results confirm the observation that the amount of pine fine roots on peatland sites reaches its maximum fairly soon after drainage with a small tree standing stock (Heikurainen 1955*a*). On mineral soil sites, the fine root biomass of tree stands has been found to reach its maximum at canopy closure (Kalela 1949, 1955, Albrektson 1980, Vogt et al. 1983, 1987). The seemingly smaller amount of pine fine roots (both living and dead) on the site drained 30 years ago, as compared with those drained 22 and 55 yrs ago, may still be within natural variation or is due to the different sampling year. Early summer 1991 was colder than 1992 (5°C threshold temperature sum June 15th: 128 d.d. in 1991, 354 d.d. in 1992), and the tree stands were not quite at the same phase of the annual growth cycle (e.g. Andersen et al. 1986). Thus the amount of pine fine roots on undrained site 2, also sampled in 1991, may also be relatively too small. On the other hand, soil frost may melt earlier on undrained sites than on drained sites (Eurola 1975), and the soil temperature conditions between years are more even on wet undrained sites because of the flowing water, so the values from site 2 are probably more comparable with the others than those of site 5. The difference between undrained sites 1 and 2 is due mostly to hydrological differences, site 1 being very wet with slowly-moving water deficient in oxygen, whereas site 2 is slightly affected by a drainage system further away on the mire, due to which the surface water, though still at a high level, moves faster towards the ditch. This difference is clearly reflected in tree stand volumes (Table 1).

Although Scots pine accounts for by far the biggest proportion of above-ground biomass on the sites studied (Laiho & Laine 1994*b*), the fine root biomass of other tree species and shrubs exceeds that of pines. White birch has been found to have more fine roots than Scots pine (Heikurainen 1958, Finér 1989*b*), and the shrub layer alone may have as much fine roots as the tree layer, although its above-ground biomass is relatively small (e.g. Paavilainen 1980, Finér & Laine 1994).

The ratio between dead and living fine root biomass decreases from 43–45% on the undrained sites to 23% on the oldest drained site. The ratio is lower on the oldest drained site than it has been on mineral soil sites (e.g. Persson 1980), although comparable to that measured on other drained sites (Finér 1991, Finér et al. 1992). The higher decomposition rate or lower turnover rate or both may explain these differences. Dead roots are abundant also in deeper peat layers. This is especially obvious on undrained sites, and may result from a low rate of decomposition in anaerobic conditions (Brække & Finér 1990). The proportion of the finest root fraction ($\varnothing <$ 1 mm) is larger in dead than living roots, probably reflecting the high turnover rate also observed in other studies (e.g. Persson 1983, Finér et al. 1992).

The amount of carbon fixed in fine root standing stock is fairly small. The significance of fine roots is more in their role as a continuous source of litter below ground. The below-ground litter input has been found to be larger than that above ground in forested ecosystems (Vogt et al. 1986). Some of the carbon accumulation into peat, which has occurred on drained peatlands (Laine et al. 1994) can thus probably be explained by the fine root litter input.

Coarse roots and stumps accumulate carbon for a longer period of time than fine roots. Thus their proportion of the total living root biomass increases as the tree stand grows (e.g. Mälkönen 1974). The relationship between stump and coarse root biomass and tree diameter of peatland pines seems to be very strong and solid because the data from different sites were so similar in that respect. The total number of observations was still rather low, however. On the whole, pine stands on peatland sites seem to allocate relatively more dry matter to coarse roots and stumps than stands with a similar stem volume on mineral soil sites (e.g. Mälkönen 1974, Paavilainen 1980, Finér 1989*a*, 1991, Håland & Brække 1989, Helmisaari 1995). The coarse root biomass of dead, still standing trees was estimated here with the same equations as that of living trees; because the wood density of 5-cm stemwood discs from the stump upwards did not differ between dead and living sample trees, this was considered to be adequate. The dead trees on undrained site 1 are mostly rather old, whereas on site 5 most of them have died from the Scleroderris canker (*Ascocalyx abietina* Lagerb.) epidemics in the 1980s.

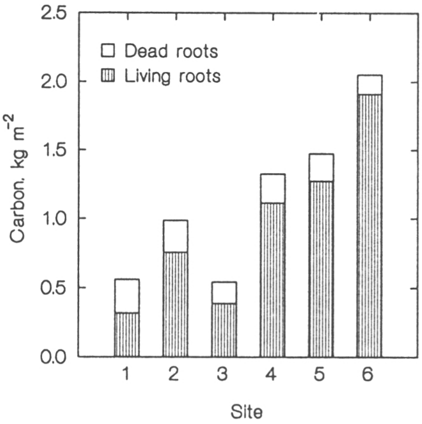

Fig. 7. The total carbon content of living and dead roots on the studied sites. Carbon content estimated to be 50% of root dry mass.

If all living and dead roots are totalled and estimated to have a carbon content of 50% of dry mass (e.g. Matthews et al. 1991, Karjalainen & Kellomäki 1993), a little more than 2 kg m^{-2} of C is fixed in roots on the oldest (55 yrs) drained site (Fig. 7). The tree stand volume on this site is slightly larger than the average for this site type with the same drainage age in southern Finland (Keltikangas et al. 1986).

If the average tree stand development on this site type is assumed to be similar to that on natural *Vaccinium vitis-idaea* type mineral soil sites, as has been done elsewhere (e.g. Laine 1989), the tree stands could reach a maximum standing stock volume of about 400 m^3 ha^{-1} about 150 yrs after drainage (Ilvessalo & Ilvessalo 1975). Assuming a similar allometric relationship between $d_{1.3}$ and stump and coarse root biomass as in Fig. 1, and a similar linear relationship between tree stand volume and total stump and coarse root biomass as within the sites of this study, a 400 m^3 ha^{-1} tree stand would have about 8 kg m^{-2} biomass (4 kg m^{-2} C) in stumps and coarse roots. Assuming that the biomass of fine roots would be similar to that in site 6, about 4.5 kg m^{-2} of C as a whole could be fixed in living roots.

In conclusion, following water-level drawdown caused by drainage for forestry, the living root biomass increases considerably on tall-sedge pine fens. In the beginning of the post-drainage succession, the increase is due mainly to the increase in tree and possibly shrub fine roots, which replace the roots of mire species such as *Carex* spp. sedges. This increased fine root production may partly compensate for the cessation of carbon sequestration in peat by sedge roots, and the accelerated decay of peat organic matter after drainage. Later on, the increase in root biomass is due to the long-term carbon accumulation in coarse roots and stumps. Root production is a considerable carbon sink, and its role in the carbon balance of peatlands should be given special attention.

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Tree stand biomass and carbon content in an age sequence of drained pine mires in southern Finland

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Abstract

Biomass and carbon accumulation into tree stand and distribution between tree stand components was studied in two undrained and four drained Scots pine (*Pinus sylvestris* L.) dominated peatland stands in southern Finland. On the drained sites, the amount and distribution of biomass above-ground was rather similar to pine-dominated stands on upland sites when drainage age of the site was thought to represent the stand age. The proportion of estimated below-ground biomass of the total pine biomass was ca. 30 % on all sites studied which is more than on upland sites with supposedly similar growth potential. Due to the bigger amount of below-ground biomass, there is on average more biomass and thus also carbon in relation to stem volume in peatland stands than upland stands, when southern boreal Scots pine stands are examined. Equations for estimating the amount of carbon accumulating in the tree stand along with increasing stem volume are presented.

Keywords: carbon balance; drainage; peatland; Scots pine

1. Introduction

In Finland, ca. 25 % of the forestry land area consists of peatlands, in parts of northern Finland as much as 40 %. The growth of peatland forests may be about one third of the total growth of all Finnish forests (Paavilainen & Tiihonen 1988, Penttilä & Salminen 1991). About half of the mire area (originally ca. 10 mill. ha) has been drained for forestry.

In undrained boreal mires, most of the organic matter deposited as peat derives from ground vegetation. Following drainage for forestry, peat-forming *Carex* and *Sphagnum* species rapidly decline (Laine et al., 1995), and tree stand becomes the main carbon binding body of the ecosystem. The post-drainage carbon balance, or net ecosystem production (NEP), is thus largely dependent on the relation between carbon loss from the soil due to enhanced oxidation, and the carbon input via the tree stand, both as an increase in the standing stock, and the input to the soil as above-ground and root litter (e.g. Vompersky and Smaginā, 1984; Sakovets and Germanova, 1992; Vompersky et al., 1992; Cannell et al., 1993; Laine and Minkkinen, 1996).

When the effect of drainage of mires on the carbon efflux to the atmosphere became a matter of concern on a larger scale, it was first hypothesised that drainage would categorically change mires from a sink to a source of carbon into the atmosphere (e.g. Armentano and Menges, 1986; Silvola, 1986). Later on, e.g. Laine and Minkkinen (1996) have shown that the situation is more complicated. Increasing carbon accumulation into the tree stand may keep the NEP positive for some 300 years after drainage and in some cases there may even also be net carbon accumulation into the peat soil after drainage (Laine and Minkkinen, 1996).

When assessing the drainage effect on the carbon store and balance of the peatland forests of Finland (or any area), reliable estimates of plant biomass in various stages of the drainage succession are of prime importance. The dynamics of the various biomass components in drained boreal peatland forests are still poorly known (cf. Brække, 1986). The structure of these forests differs from that of forests on upland sites at least during the whole first tree stand rotation, due to site properties and the initial uneven-aged and -sized structure of peatland forests before drainage (e.g. Gustavsen and Päivänen, 1986; Hökkä and Laine, 1988). For that reason, data from upland sites may not be directly applied before it is shown that there are no significant differences in carbon binding and allocation between stands on upland and peatland sites. This should also be taken into account when modelling the carbon balance of the forest sector in general. Recently, e.g. Karjalainen (1996a, 1996b) has modelled the carbon sequestration potential of boreal forest stands, but so far, no special attention has been paid to the carbon sequestration dynamics of drained peatland forests.

The aim of this study was to examine the effect of water level drawdown caused by forest drainage on (1) the total biomass and carbon content of tree stands on pine mires and (2) the relations between various biomass components. This is part of a study dealing with the role of plant biomass in carbon cycling in mire ecosystems within the Finnish Research Programme on Climate Change (Laiho and Laine, 1994b). Below-ground biomass has been dealt with in an earlier paper (Laiho and Finér, 1996).

2. Material and methods

2.1. Study sites

Tall-sedge pine fen was chosen as the object of the study because it is the site type most commonly drained for forestry in Finland (Keltikangas et al., 1986) and also represents the "nutrient-level median" of the forest drainage areas. This site type is always forested (a stunted, slow-growing Scots pine stand) in natural, undrained, condition, and after drainage, the existing tree stand usually forms the basis of the production forestry stand and no afforestation measures are needed.

The sites of the study (Table 1) are situated in southern Finland (61°35' - 61°52'N, 24°05' - 24°25'E), and are described in more detail by Laiho and Finér (1996).

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 and Laine, 1994a, Laine et al., 1995). The sites of the present study were chosen to obtain as wide a drainage age variation as possible within the chosen site type to cover the whole transition period from a mire ecosystem to a forest-like ecosystem. The underlying assumption in this study is that sites belonging to the same site type were originally similar and that their post-drainage development has proceeded similarly.

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 has 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.

Table 1. General features of the sites.

	Site					
	1	2	3	4	5	6
Years since drainage	-	-	8	22	30	55
Live tree stand volume, m^3ha^{-1}	6	35	10	76	102	150
Proportion pine/birch/spruce[a]	100/-/-	95/4/1	100/-/0	69/31/1	84/15/1	87/9/3
Number of stems, ha^{-1}	444	1567	554	4750	1782	2786
Ditch spacing, m	-	-	30	37	37	32
Sample plot size, m^2	900	600	1263	1158	1190	1328

[a] of volume; Scots pine (*Pinus sylvestris* L.), pubescent birch (*Betula pubescens* Ehrh.), Norway spruce (*Picea abies* (L.) Karst.)

2.2. Tree stand measurements and sampling

All trees with a dbh (diameter at 1.3 m) ≥1.5 cm were measured for dbh and d_6 (diameter at 6 m), bark thickness, total height, and height to the base of the live crown. Stem volumes and stem numbers per hectare (Table 1) were computed separately for Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* (L.) Karst.) and pubescent birch (*Betula pubescens* Ehrh.) on each sample plot.

Eight pine biomass sample trees per plot (only six on plot 1) were chosen with stratified random sampling so that they represented the whole diameter range, with slightly more weight on larger trees. Depending on the tree species composition of the stands, varying number of birch and spruce sample trees, as well as dead trees, were also chosen.

The crown was divided into ten equally long components. All live branches were cut along the stem, their length and diameter at 1 cm from the base were measured, and their position (crown component) was recorded. From each crown component, one branch was randomly chosen as a sample branch. Sample branches were separated into foliage and branchwood (including bark). They were dried at 105°C to constant mass, and data was recorded by branch.

The dry mass of dead branches was obtained by multiplying their total fresh mass with the dry mass percentage of a subsample.

Each stem was divided into 11 sections by removing a 5 cm disc from the base of the stem and from relative heights of 5 % and each full 10 %. The diameter and volume of each disc was measured both with and without bark. The volume was obtained making use of Archimedes' principle, i.e. the net mass of the disc immersed in water was measured. Bark and wood samples were dried at 105°C to constant mass, and data recorded by disc.

Dead sample trees were separated into branches, bark (if remaining), and wood. These components were handled like dead branches of the live sample trees. Some of the largest stems were divided into sections like those of the live sample trees.

2.3. Biomass calculations

The over-bark and under-bark volumes of the sample trees were calculated by integrating the taper curves smoothed by a cubic spline function. The volume of bark was obtained as the difference between these volumes. The dry mass of stemwood and bark was calculated for each stem section, by multiplying their volume with respective density values (averages of the discs from lower and upper ends of the sections), and summed up.

The total dry masses of live branches and foliage per sample tree were estimated using equations derived from the sample branch data, relating the dry mass to measured branch characteristics. Various biomass variables determined for the sample trees were regressed against diameter, height and crown characteristics, and the equations then used to estimate corresponding values for the whole tree stands of the sample plots.

Equation parameters were computed using nonlinear estimation with a least squares loss function (SYSTAT, 1992). The equations finally used were chosen so that the smallest standard error of estimate, and a coefficient of the linear regression between measured and estimated values closest to 1.000 were achieved in addition to a high degree of determination. The best fits were obtained with allometric functions with a general form $y = p_1 x_1^{p2} x_2^{p3}$, commonly used in biomass studies (e.g. Satoo and Madgwick, 1982 and references therein).

In many cases, two intercorrelated independent variables were used to increase the fit. This was accepted here because the equations were meant only for estimation of the biomass of the sites studied, and the data sets of which the equations were derived covered the whole variation range of the tree stands where the equations were applied. So the equations were applied like interpolation polynomials, and the fit of estimates within data was good. The degree of determination was generally above 0,95. Using nonlinear fitting we avoided logarithmic transformation and use of correction factor, a commonly used procedure which is not without problems (e.g. Madgwick, 1983; Sprugel, 1983).

Estimated stump and coarse root biomasses for all tree species as well as fine root biomass values for pine on the sites studied were obtained from Laiho and Finér (1996).

2.4. Carbon analyses

The carbon contents of a subset of samples were measured on a Leco CHN 600 analyser. The C concentrations of various biomass components per tree species given in Table 2 were calculated as weighted means with the dry mass proportion represented by individual samples as the weight (several samples per each tree were analysed).

Table 2. The mean dry mass weighted carbon concentrations (% of dry mass) in different tree biomass components in the material studied. The values in brackets show the number of trees analysed/the total number of samples analysed/s.d. of all samples analysed *per* component.

Species	Stemwood	Bark	Foliage	Live branches	Dead branches
pine	51.8 (17/59/0.9)	53.2 (8/20/1.7)	53.8 (23/76/0.7)	53.1 (18/44/0.4)	52.7 (19/19/0.7)
birch	49.7 (3/9/0.2)	55.7 (3/9/1.3)	52.1 (8/25/0.9)	52.3 (5/5/0.3)	52.5 (4/4/0.4)
spruce	50.9 (2/6/0.2)	51.8 (1/1)	[54.0] (1/10/0.3)	52.6[a] (2/4/0.6)	51.8 (2/2/0.1)
dead pine	51.8 (6/32/1.2)	54.0 (2/4/0.9)			52.8 (4/4/1.2)

[a] including needles

3. Results

The total above-ground biomass of the tree stand increases after drainage at the whole age range of the drained sites (Table 3, Fig. 1). The increase in the stemwood biomass continues during the whole post-drainage time period under observation, but the increase in the amount of branches and foliage appears to have levelled out already at the 22-year-old site.

The development of the carbon store closely follows that of the biomass (Fig. 2). More than 70 % of the total tree stand carbon store of ca. 40 tonnes per hectare of the oldest drained site is found in the stemwood component (with bark). Using a conversion factor of 0.50, frequently applied in biomass carbon estimations, would have lead to on average 5.6 % smaller C store values than those obtained with using the measured C concentrations.

In pine, the amount and proportion of foliage are the first to increase after drainage (Figs 1 and 3). The proportion of foliage is clearly highest at the younger drained sites (3 and 4), and diminishes towards the older sites (Fig. 3). The development of live branch biomass is rather similar. The proportion of stemwood increases steadily after drainage. The proportion of above-ground biomass is approximately 70 % at all sites.

The total pine biomass calculated *per* m^3 of stemwood (with bark) gradually decreases after an initial post-drainage increase (Table 4). This is caused by the similar trend in the crown biomass - stemwood volume -ratio because the corresponding ratio for stem biomass is rather stable.

Table 3. Total above-ground tree stand component dry masses (g m^{-2}) at the sites studied.

Species component	Site 1	2	3	4	5	6
Pine						
stemwood	239	1070	326	1537	3026	4632
stembark	43	213	67	263	368	453
branches	49	288	151	580	635	622
foliage	11	101	156	252	283	338
dead branches	38	145	18	246	437	293
total	380	1817	718	2878	4749	6338
Birch						
stemwood	0	53	0	991	678	613
stembark	0	22	0	216	111	124
branches	0	8	0	189	142	123
foliage	0	3	0	89	49	52
dead branches	0	6	0	43	18	24
total	0	92	0	1528	998	936
Spruce						
stem[a]	0	12	1	19	37	210
crown[b]	0	9	1	19	26	163
total	0	21	2	38	63	373
Live total	380	1930	720	4444	5810	7647
Standing dead						
stemwood	220	26	46	57	317	33
stembark	0	3	1	9	11	1
dead branches	9	2	3	5	30	3
total	229	31	50	71	358	37

[a] including wood and bark

[b] including all branches and foliage

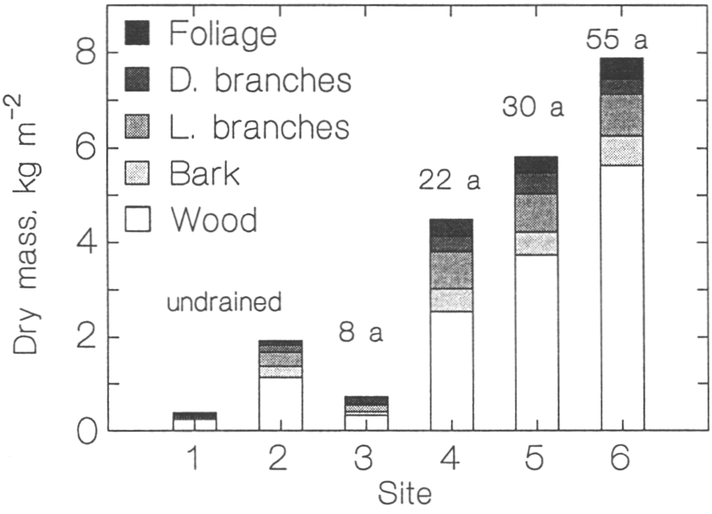

Fig. 1. Total biomass of the above-ground components of the tree stands (dead trees excluded) on the sites studied (D. = dead, L. = living). Drainage age of the sites is shown above the bars.

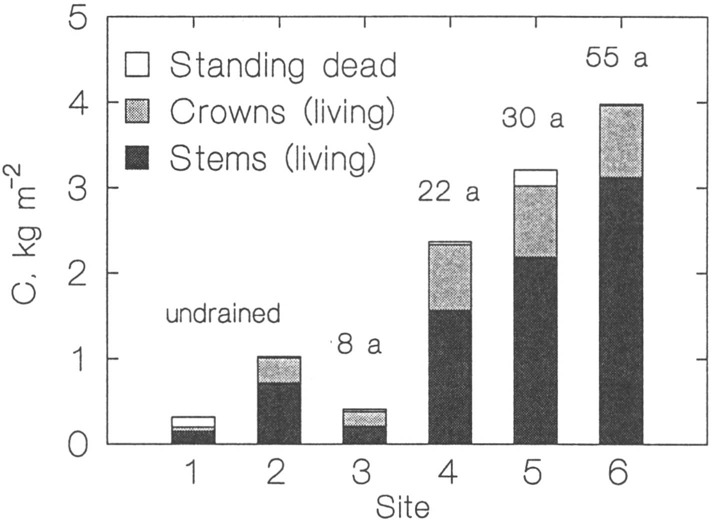

Fig. 2. Carbon fixed in the above-ground parts of the tree stands on the sites studied.

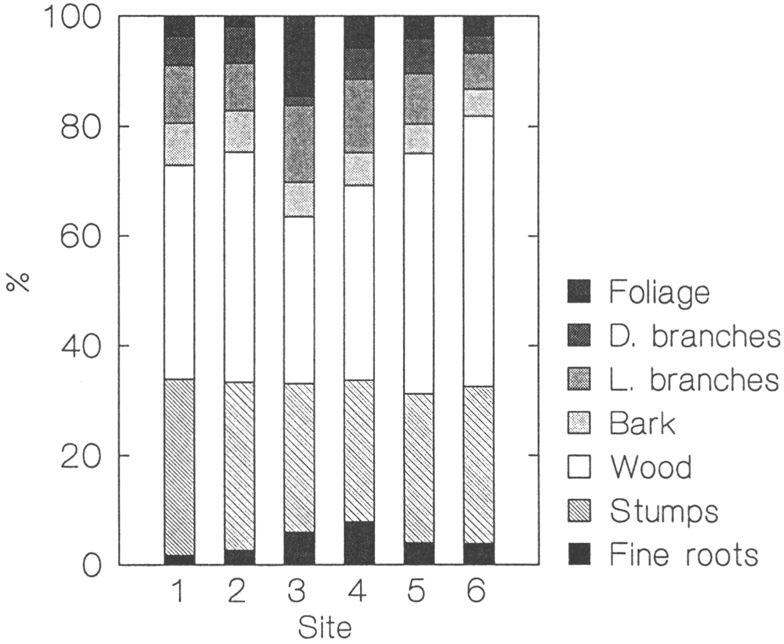

Fig. 3. Percental distribution of biomass between tree components in pine (*Pinus sylvestris* L.) on the sites studied. 'Stumps' include coarse roots. Root data from Laiho and Finér (1996).

Table 4. Total above-ground pine biomass *per* pine stem volume (with bark), kg m^{-3}.

	Site					
Component	1	2	3	4	5	6
Stemwood + bark	470	389	393	346	395	388
Branches + foliage	163	162	325	207	158	96
Total	633	551	718	553	552	484

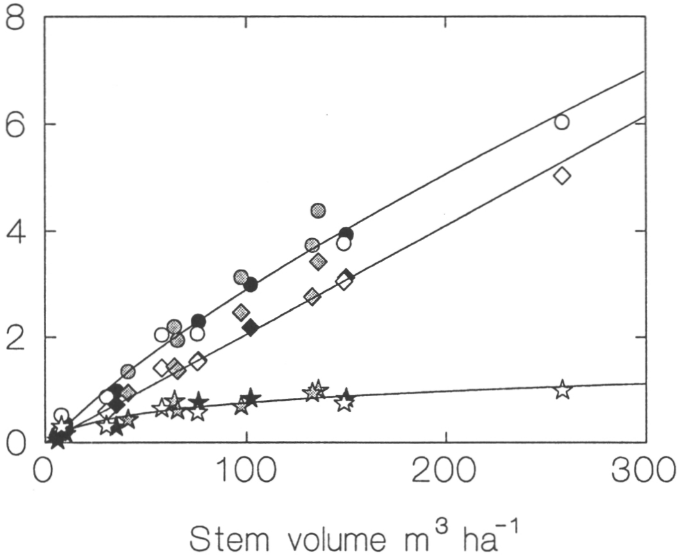

Fig. 4. Relations between stand stem volume and total above-ground tree stand biomass (uppermost line, circles), stem component biomass (wood + bark, middle line, diamonds) and crown component biomass (needles + all branches, lowermost line, stars). Black symbols depict the sites of this study, grey symbols peatland sites with natural pine-dominated stands but with varying nutrient regime studied by Holmen (1964), Paavilainen (1980), Finér (1989, 1991), Håland (1994) and open symbols upland sites of Mälkönen (1974) and Helmisaari and Makkonen (unpublished) with a nutrient regime approximately corresponding to the sites of this study. The cited material has been converted to C estimates by multiplying the reported biomass values with 0.50. Lines drawn using the equations shown in Table 8.

Table 5. Regression equations for the relation of above-ground biomass carbon contents (y, kg m^{-2} C) and tree stand stem volume (x, m^3 ha^{-1}). s.e. = parameter standard error, SEE = standard error of estimate.

Component	p1	s.e.	p2	s.e.	p3	s.e.	SEE	r^2	n
Total:									
$y = p1x + p2\ln x^{p3}$	0.012	0.012	0.012	0.008	3.241	0.745	0.090	0.999	6
Stemwood + bark:									
$y = p1x$	0.021	<0.001					0.029	1.000	6
Branches + foliage:									
$y = p1\ln x^{p2}$	0.020	0.016	2.380	0.514			0.090	0.981	6

4. Discussion

Pine stands on undrained mires clearly carry less needles and live branches and more dead branches than stands with a similar amount of stem mass on upland sites (cf. e.g. Albrektson, 1980). This is due to the unfavourable growth conditions, mainly a lack of oxygen for roots, which is also reflected in the small amount of pine fine roots (Laiho and Finér, 1996).

The drainage effect is first seen in the amount, and thus also proportion of needles that increase rapidly, a phenomenon that has been noted in all studies on the effect of drainage on tree growth (e.g. Lukkala, 1929). Only when a larger amount of photosynthesising needle mass can be maintained, may growth in general increase. The proportion of dead branches rapidly decreases during tree growth revival after drainage until canopy closure when it temporarily increases again. The large amount of dead branches on site 5 is a consequence of Scleroderris canker (*Ascocalyx abietina* Lagerb.) epidemics in mid 1980's.

On drained peatland sites, the proportions of pine needles and living branches and their amount in relation to stem volume are rather similar to those of pine stands on upland sites whereas the proportion of dead branches is slightly bigger on peatland sites (e.g. Mälkönen, 1974; Albrektson, 1980; Helmisaari, H.-S. and Makkonen, K., unpublished data).

The differences between sites in the relation of stem (wood + bark) dry mass to stem volume mainly reflect variation in wood density (generally highest on undrained sites due to slow growth, here especially high on site 1) and the proportion of bark which is bigger in smaller trees. There seems to be no difference between stands on drained peatlands and upland sites with supposedly similar growth potential (Mälkönen, 1974; Helmisaari and Makkonen, unpublished). In general, wood density varies with climatic conditions and site nutrient regime (e.g. Hakkila, 1979).

The proportion of below-ground parts in peatland pine stands is bigger than that of pine stands with similar stem volumes on upland sites (Hakkila, 1972; Mälkönen, 1974; Paavilainen, 1980; Finér, 1989, 1991; Håland and Brække, 1989; Helmisaari, 1995). Thus the root system biomass also increases more rapidly in relation to tree stand stem volume than on upland sites. On the sites studied the estimated stump and coarse root biomass (kg ha^{-1}) relation to stem volume (m^3 ha^{-1}) was linear with a coefficient of 0.02 (Laiho and Finér, 1996) whereas in the combined material of Mälkönen (1974) and Helmisaari and Makkonen (unpublished) the coefficient for the linear part of the relationship is 0.01 and the increase in the stump and coarse root biomass seems to level off at about a stem volume of 150 m^3 ha^{-1}. An explanation for the higher below-ground biomass proportion might be that when growing in peat soils that have much smaller bulk density than mineral soils, trees need a larger coarse root system for support.

On average there is more tree stand biomass and thus also carbon in relation to stem volume in peatland stands than upland stands, when southern boreal Scots pine -dominated stands are examined. The difference is mainly due to the bigger amount of below-ground biomass on peatland sites. If all available material is combined, the difference is also statistically significant with a 5 % risk level, but within sites of supposedly similar growth potential (e.g. Laine, 1989), the amount of material is too small for analysis.

If the stands on our drained sites are compared with stands on natural *Vaccinium vitis-idaea* type upland sites, the total stand stem volumes in relation to drainage age of the site are comparable to the average volume in relation to tree stand age given by Ilvessalo and Ilvessalo (1975). If the stand development later followed a pattern similar to upland sites (cf. Seppälä, 1969), the volume increment would culminate at the age of ca. 90 years after drainage, and the stands would reach a maximum volume of ca. 400 m^3 ha^{-1} at the age of ca. 150 years (cf. Ilvessalo and Ilvessalo, 1975). If the relation of the stand carbon content to stem volume remained similar to the one shown in Fig. 4 and Table 5, the above-ground parts of the stand would finally store a maximum of ca. 9 kg m^{-2} of C.

The development of the below-ground parts is more difficult to predict because there are less direct measurements to rely on. Laiho and Finér (1996) presented an estimate of a maximum of 4 kg m^{-2} C in stumps and coarse roots, but that may be an overestimate, for the increase in stump and coarse root biomass in relation to stem volume may level off at bigger stem volumes also on peatland sites.

A total of 13 kg m^{-2} C (130 tonnes per hectare) would be equal to the amount of C in a peat layer of ca. 35 cm on undrained sites of this site type on average in this region (Laiho and Laine, 1994a). This amount of carbon sequestration in the tree stand would compensate for the peat carbon oxidation loss given by Laine and Minkkinen (1996) for more than 300 years.

In many forest sector carbon balance calculations so far, tree stand components other than stemwood have been excluded (e.g. Karjalainen et al., 1995). The equation relating the total above-ground tree stand biomass C store to the stem volume of the stand (Table 5) provides a simple tool for estimating the C content of Scots pine -dominated southern boreal peatland stands when e.g. assessing the effect of forest drainage on the carbon balance of mire ecosystems. For the below-ground parts the study by Laiho and Finér (1996) may be referred to. To produce models for making more refined estimates, variation caused by geographical location and site nutrient regime should be accounted for (cf. e.g. Hakkila, 1979), and measurements should be extended to stands with larger stem volumes.

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