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**BIOMASS AND NUTRIENT DYNAMICS OF SCOTS PINE ON
A DRAINED OMBROTROPHIC BOG**

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**BIOMASS AND NUTRIENT DYNAMICS OF SCOTS PINE ON
A DRAINED OMBROTROPHIC BOG**

LEENA FINÉR

ACADEMIC DISSERTATION

To be presented, with the permission of the Faculty of Agriculture and Forestry of the University of Helsinki, for public criticism in Auditorium II of Metsätalo, Unioninkatu 40 B, Helsinki, on September 11th, 1992, at 12 o'clock noon.

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The present article is a summary of four publications in a series of articles concerning biomass and nutrient cycling on a drained ombrotrophic pine bog in eastern Finland. The distribution of biomass and nutrients between different tree compartments and between the vegetation and surface peat are presented. Tree biomass production and nutrient uptake from the peat are estimated. The role of atmospheric deposition and the effects of harvesting on the nutrient status of the site are discussed. The initial effects of fertilization on tree biomass and nutrient dynamics are studied. The fate of fertilizer nutrients in the ecosystem are traced.

Key words: accumulation, drainage, dry mass, fertilization, peatland, *Pinus sylvestris*, production, uptake

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LIST OF ORIGINAL PAPERS

The thesis is based on the following papers referred to in the text by Roman numerals:

- I Finér, L. 1991. Effect of fertilization on the growth and structure of a Scots pine stand growing on an ombrotrophic bog. Tiivistelmä: Lannoituksen vaikutus rämemännikön kasvuun ja rakenteeseen. Suo 42(5): 87-99.

- II Finér, L. 1991. Effect of fertilization on dry mass accumulation and nutrient cycling in Scots pine on an ombrotrophic bog. Seloste: Lannoituksen vaikutus männyn kuivamassan kertymään ja ravinteiden kiertoon ombrotrofisella rämeellä. Acta Forestalia Fennica 223. 42 p.

- III Finér, L. 1991. Root biomass on an ombrotrophic pine bog and the effects of PK and NPK fertilization. Tiivistelmä: Ohutjuurten biomassa lannoitetulla ja lannoittamattomalla ombrotrofisella rämeellä. Silva Fennica 25(1): 1-12.

- IV Finér, L. 1992. Nutrient concentrations in *Pinus sylvestris* L. growing on an ombrotrophic pine bog, and the effects of PK and NPK fertilization. Scandinavian Journal of Forest Research 7: 205-218.

1 INTRODUCTION

1.1 Biomass and nutrient dynamics on virgin ombrotrophic bogs

Peat accumulates on waterlogged sites where net primary production is higher than decomposition. In favourable conditions the peat layer may become so thick that the nutrient input from the underlying and surrounding mineral soil is stopped; this is the starting point for the formation of ombrotrophic peat. On ombrotrophic bogs the sources of nutrients for the vegetation are the nutrient stores in the surface peat and the input from atmospheric deposition (Fig. 1).

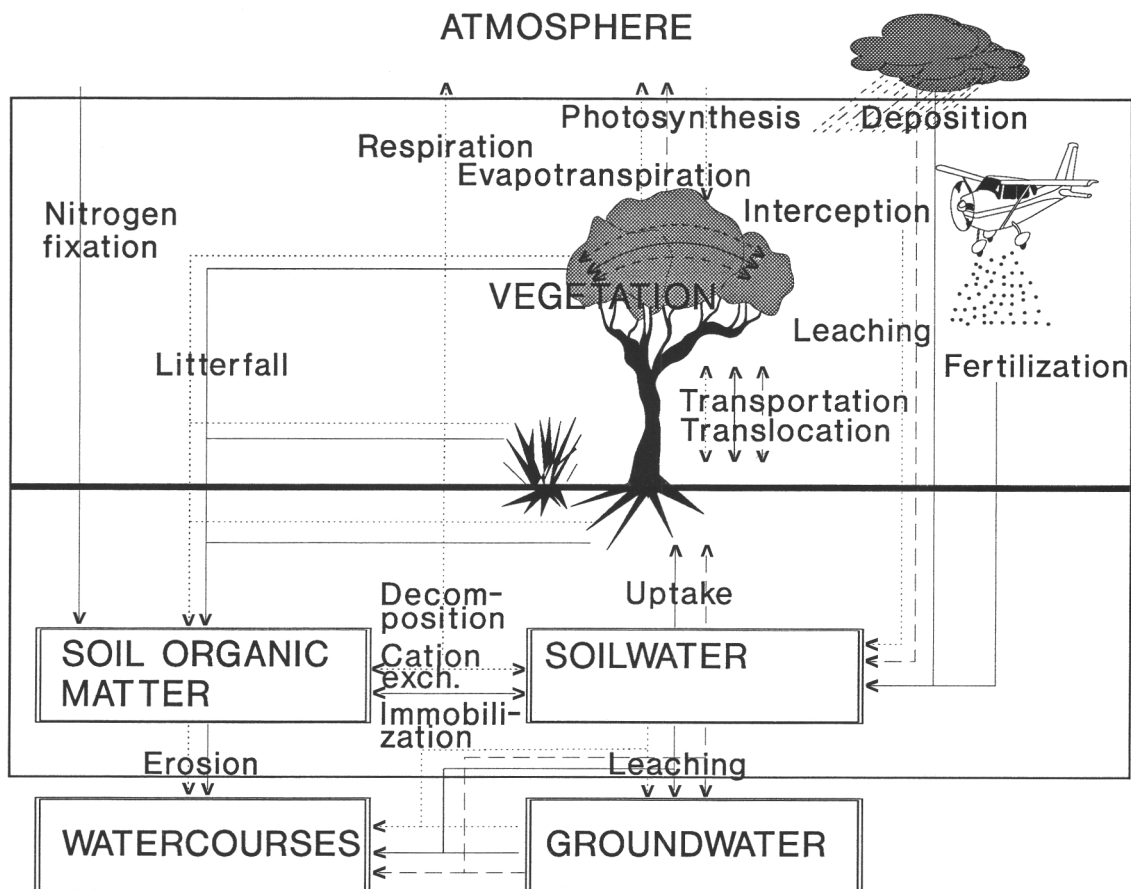


Fig. 1. Schematic presentation of the cycling of carbon (....), water (----) and nutrients (—) on ombrotrophic bogs.

The nutrient input from atmospheric deposition varies geographically (e.g. Overrein et al. 1980, Järvinen 1986, Kulmala et al. 1990). Marine aerosols, soil particles and air pollutants are the main sources of nutrients in deposition. Atmospheric nitrogen is also fixed in the peat (Chapman & Hemond 1982, Dickinson 1983). The nutrient stores in ombrotrophic bogs are small, because the nutrient input from atmospheric deposition is low and the accumulation of peat results in a part of the nutrients being trapped in the lower peat layers. Nutrients are also lost from bogs through leaching. Ombrotrophic surface peat and the ground vegetation have a net input of N and S and a net output of K, Ca and Mg (Brække 1981).

Only few plant species survive on ombrotrophic bogs. *Sphagnum* species cover most of the bottom layer, although some lichens and forest mosses grow on hummocks. In Fennoscandia, dwarf shrubs (e.g. *Andromeda polifolia*, *Betula nana*, *Calluna vulgaris*, *Empetrum nigrum*, *Ledum palustre*, *Vaccinium oxycoccus*, *Vaccinium uliginosum*), and *Eriophorum vaginatum* and *Rubus chamaemorus* dominate in the field layer, and Scots pine (*Pinus sylvestris*) is the only tree species that can form the tree layer. These species mainly take up nutrients from the surface peat layer (see Metsävainio 1931, Heikurainen 1955, Paavilainen 1966, Wallen 1986, Håland & Brække 1989).

The total above-ground biomass of ombrotrophic bogs increases with an increase in the tree biomass, and the relative distribution of the biomass simultaneously shifts from the field and bottom layers to the tree layer (Reinikainen et al. 1984, Vasander 1990). Biomass production is not very closely connected to that of the tree layer, but is positively correlated with the vitality of the bottom and field layers (Reinikainen et al. 1984, Vasander 1990).

1.2 Changes caused by drainage

Approximately half a million hectares of ombrotrophic bogs have been drained for forestry in Finland (Keltikangas et al. 1986). Drainage has an effect on the nutrient stores and fluxes on these bogs (see Fig. 1). The aerobic peat zone becomes thicker, thus increasing microbial activity and the mineralization of nutrients (Silvola et al. 1985, Silvola 1986, 1988). The surface peat subsides as a result of physical compaction and the loss of dry matter caused by increased microbial activity. Physical compaction is highest a few years after drainage (Lukkala 1949, Päivänen 1982, Kurimo & Hovi 1984). Subsidence increases the amounts of nutrients in the root zone. The amounts of organically bound nutrients, especially N, P and S, may increase as a result of compaction (see Huttunen & Karhu 1981, Westman 1981, Kaunisto & Paavilainen 1988, Laiho 1991).

The outflow of water and nutrients increases for a number of years after drainage (e.g. Heikurainen et al. 1978, Kenttämies & Laine 1984, Ahtiainen 1990). Increased leaching of N, P, K, Ca, Mg and S have been reported in watercourses soon after the digging of ditches (Ahtiainen 1988, 1990). Leaching losses from old drainage areas are connected to the development of the vegetation (see Ahtiainen 1988, 1990). Potassium, Ca and Mg are more susceptible to leaching than N and P, which are primarily organically bound in peat (e.g. Kaunisto & Paavilainen 1988).

Drainage changes the composition of the vegetation. *Sphagnum* species of the bottom layer are replaced by mosses and lichens spreading from the hummocks (e.g. Sarasto 1957, 1961). In the field layer dwarf shrubs, and to some extent *Eriophorum vaginatum* and *Rubus chamaemorus*, also grow on drained sites. The growth of Scots pine is improved and its roots penetrate to a greater depth in the peat (Heikurainen 1955, Paavilainen 1966). However, nutrient uptake mainly occurs in the uppermost 20 cm-peat layer on drained bogs, too. The total biomass and biomass production of the vegetation increase, and there is a shift

from the bottom and field layers to the tree layer, and from the above-ground compartments to the roots (Reinikainen et al. 1984, Vasander 1990). However, the nutrient status of the peat may be so poor that the increase in the field and tree layer biomasses cannot compensate for the decrease in the ground layer biomass, and the total biomass therefore decreases (Vasander 1982).

Tree stands on virgin ombrotrophic bogs are usually small, sparse and of an uneven size distribution (Gustavsen & Päivänen 1986). Because the oldest and tallest trees do not improve their growth after drainage (Heikurainen & Kuusela 1962) they are usually harvested. After drainage the stem number increases (Hökkä & Laine 1988), and stand development most probably follows that of young evenaged stands. The total tree biomass and biomass production increase for many years after drainage unless the development is interrupted by thinning, damage or nutrient deficiencies.

In the early stages of stand development the biomass mainly accumulates in the foliage, branches (Albrektson 1980, Brække 1986) and fine roots (Heikurainen 1955). Later on accumulation shifts to the stems, stumps and coarse roots. The biomass of the foliage, branches and fine roots reaches a maximum soon after canopy closure, somewhat earlier than the maximum rate of total biomass accumulation (Albrektson 1980, Miller 1986). The production of tree biomass culminates at the same time as maximum foliage biomass is reached (see e. g. Albrektson 1980). A large proportion of the production is subsequently lost as litterfall instead of accumulating in the tree biomass.

It is still unclear whether the rate of biomass production is greater than the rate of decomposition on ombrotrophic bogs after drainage. Some preliminary results indicate that this would be the case (Laine & Vasander 1991, Laine et al. 1991, 1992), although net losses of organic matter may also occur (Brække 1987, Silvola 1988, Laine et al. 1992).

The nutrient dynamics in tree stands differ from those of the biomass (e. g. Switzer & Nelson 1972, Miller 1984, 1986). Nutrient concentrations in the foliage, inner bark and fine roots are higher than those in the outer bark and stemwood (e.g. Holmen 1964, Mälkönen 1974, Paavilainen 1980, Finér 1989, Helmisaari & Siltala 1989, Helmisaari 1990a, 1991). The nutrient accumulation rate is rapid before canopy closure, but declines later on because nutrients are accumulated primarily in the woody compartments of trees (e. g. Switzer & Nelson 1972, Cole & Rapp 1981, Miller 1984, 1986). As the development of the tree stand progresses, more and more nutrients are accumulated in the long-living compartments of trees. On drained ombrotrophic pine bogs the main stores of K, Mn, Zn and B may shift from the peat to the trees (Holmen 1964, Paavilainen 1980, Kaunisto & Paavilainen 1988).

Before canopy closure the annual nutrient requirements of trees are primarily satisfied by uptake from the soil, and most of the nutrients are accumulated in the tree stand (e. g. Cole & Rapp 1981, Miller 1981, 1984, 1986, Gosz 1984). After canopy closure, retranslocation of nutrients from the senescing foliage, branches and roots accounts for a considerable proportion of the N, P, K and Mg requirements (e. g. Viro 1955, Mälkönen 1974, Lim & Cousens 1986, Helmisaari 1990b, 1992). At canopy closure, significant amounts of nutrients are also released back into the soil in the litterfall, and Ca, K and Mg are partly even leached from the canopy to the soil (e. g. Päivänen 1974, Helmisaari & Mälkönen 1989, Hyvärinen 1990, Ragsdale et al. 1992). The maximum demand for soil nutrients occurs at or slightly before the time of canopy closure (Miller 1986).

Sooner or later the trees are harvested from drainage areas. This removes nutrients from peatlands, and may be detrimental for the K, Mn, Zn and B stores of ombrotrophic bog ecosystems (Holmen 1964, Kaunisto & Paavilainen 1988). Whole-tree harvesting removes more nutrients than stem harvesting (see e. g. Mälkönen 1976, Kaunisto & Paavilainen 1988, Finér 1989). Harvesting

operations also increase nutrient losses through leaching and erosion (Ahtiainen 1988, 1990).

1.3 Effects of fertilization

Small stores of K, Mn, Zn and B, low mineralization rates of N and P, and a low net input of nutrients create a poor nutrient regime for plant growth on ombrotrophic bogs (see e. g. Kaunisto & Paavilainen 1988). After drainage, nutrition is further impaired by the increased accumulation of nutrients in the long-living compartments of trees and nutrient losses through leaching and harvesting. The nutrients most limiting for tree growth on ombrotrophic bogs are N, P and K (e. g. Meshechok 1967, Brække 1977a, 1979, Paavilainen 1979a, 1979b, 1984, Kaunisto 1982, 1987). On inland sites a low supply of B has also restricted the balanced development of trees (e. g. Huikari 1977, Brække 1979, 1983, Veijalainen 1983, Veijalainen et al. 1984, Kaunisto 1987). The poor nutrient status of ombrotrophic bogs can, however, be improved by fertilization.

Only a few studies have been carried out on the effects of fertilization on tree biomass and biomass production on peatlands (see Brække 1977b, 1986, Paavilainen 1980, Vasander 1982, Finér 1989). According to these studies and those made in mineral soil stands, the improved nutrition brought about by fertilization increases biomass production and alters its relative allocation within the trees (Miller & Miller 1976, Satoo & Madgwick 1982, Linder & Rook 1984, Mead et al. 1984, Axelsson 1986, Axelsson & Axelsson 1986). The relative distribution of biomass production shifts from the roots to the shoots (Vasander 1982, Axelsson 1986), from the stems to the crowns (Vasander 1982, Axelsson 1986) and, within the crowns, from the foliage to the branches (Madgwick 1975, Mead et al. 1984). However, the changes in biomass production and allocation between different tree compartments are closely connected to the time elapsed since fertilization and the amounts of nutrients applied (see e. g. Miller & Miller 1976, Mead et al. 1984). The foliage biomass responds first, followed by that of

the branches and stem (e. g. Miller & Miller 1976). Maximum foliage biomass occurs in pine stands in the third to fourth year after a single N fertilization, simultaneously with the maximum of stemwood production (see Fagerström & Lohm 1977). Stem growth is usually increased for 10-15 years after NPK fertilization on drained ombrotrophic bogs (e. g. Paavilainen 1977, Heikurainen & Laine 1985).

The developmental stage of a tree stand affects the trees' ability to utilize fertilizer nutrients (Miller 1981, 1986). Before canopy closure, when the nutrient requirements of trees are mainly satisfied by uptake from the soil, a strong fertilizer response is expected. After full development of the crown the total nutrient requirements are largely satisfied by retranslocation, and net uptake from the soil declines. Nutrient application at this stage is less significant, and the growth responses may be small. However, reducing the foliage biomass before fertilization, e. g. by thinning, may increase the response (see Brix & Ebell 1969, Jonsson & Möller 1977, Haapanen et al. 1979, Saramäki & Silander 1982).

Large doses of fertilizer nutrients are usually applied (see e. g. Huikari 1961, Paavilainen 1979a, Moilanen & Penttilä 1988), which do not correspond to the annual uptake of nutrients by trees. It is thus probable that only a minor portion of the fertilizer nutrients are in fact taken up by the trees (see Paavilainen 1973, Melin et al. 1983, Ballard 1984, Melin & Nömmik 1988, Nömmik & Larsson 1989). The excess is fixed by the ground vegetation and soil (e. g. Paavilainen 1973, Melin & et al. 1983, Melin & Nömmik 1988, Nömmik & Larsson 1989), or even leached into the watercourses (see Harriman 1978, Malcolm & Cuttle 1983, Lundin & Bergquist 1985).

1.4 The aim of the study

More information is needed about the biomass and nutrient dynamics of ombrotrophic pine bog ecosystems in the context of a changing nutrient status, e. g. due to drainage, harvesting, fertilization and increased atmospheric inputs. The aim of the present study was to investigate the following factors in a Scots pine stand growing on a drained ombrotrophic bog:

- 1) biomass and nutrient distribution between different tree compartments and the effects of fertilization (II,III,IV),
- 2) biomass and nutrient accumulation and release in tree stands and the effects of fertilization (II,III,IV),
- 3) the commonly used stem and stem growth parameters (I); this information is required when attempting to link these parameters to the biomass and nutrient dynamics (II,III).

2 MATERIAL AND METHODS

2.1 Background

This study is a part of a Nordic project, the main objectives of which were to study the distribution and cycling of nutrients on drained ombrotrophic pine bogs in different climatic conditions, and the changes caused by fertilization (see Paavilainen 1990). The experiments were set up in Norway, Sweden and Finland. The field work was started in Norway and Finland in 1984 and one year later in Sweden. The final measurements were carried out in 1987 and 1988. In addition to the tree stand, the studies were also directed at the biomass and nutrient dynamics in the peat (Brække & Finér 1990, 1991) and ground vegetation (Finér & Brække 1991a, 1991b). The quality of precipitation and water percolating down through the surface peat to the ground water was monitored (Finér & Brække 1991c). The material of this study was collected from the Finnish experimental field of the project.

2.2 Study site

The Finnish experimental field is located in eastern Finland (64 km SE of Joensuu 62° 14' N; 29° 50' E, 81 m a. s. l.). The climatic data are presented in publications II and III. According to the classification of Heikurainen and Pakarinen (1982), the site was a low-shrub pine bog. A detailed description of the vegetation is presented by Finér & Brække (1991a). The site was drained in 1967 with a 50 m ditch spacing. The fluctuations in the groundwater table were monitored during 1984-1987 (II, III).

The peat layer is over one-metre thick and consists of slightly decomposed ombrotrophic *Sphagnum* peat on the surface. Below a depth of 20 cm there are some remnants of *Carex* species. Detailed descriptions of the peat properties are

presented by Brække & Finér (1991). The Scots pine (*Pinus sylvestris* L.) stand growing on the site is unevenaged, the average age being 85 years (I).

The field experiment was established in 1984 and fertilized in spring 1985. A 3 * 3 Latin-square design with a 1500 m² plot size was used. The plots extended from the middle of a ditch to the middle of the next ditch. The treatments were as follows: 1) control, 2) PK(MgB), 3) NPK(MgB). The amounts of different elements (kg ha⁻¹) applied were: N 150, P 53, K 100, Ca 135, Mg 25, S 28, Cl 95 and B 2.4. The fertilizers were given as ammonium nitrate, raw phosphate, potassium chloride, magnesium sulphate and sodium borate.

2.3 Collection of the material

The material for tree stand biomass and nutrient determinations was collected by the harvesting method (see e. g. Satoo & Madgwick 1982). Determination of the biomass in the above-ground tree compartments and stumps and coarse roots was done by the regression method, and that of fine roots and litterfall by the unit area method (see e. g. Hakkila 1989). In this study the term biomass has the same meaning as dry mass.

The breast height diameter, total height and length of the living crown of each tree were measured on the sample plots in 1984, 1987 and 1991 (see I). The sampling for biomass and nutrient determinations was carried out twice, in 1984 and 1987. On both occasions 27 sample trees were chosen. The stump and coarse roots of every fourth sample tree were excavated in 1984. In 1987 only one sample tree per plot was sampled for stump and coarse root nutrient analyses. The small and fine roots were sampled using the core method (III). Litterfall was collected with littertraps on each plot from 1984 to 1987.

All samples were dried at 60 °C to a constant weight. A subsample was dried at 105 °C for dry mass determination. Nitrogen was analyzed by the Kjeldahl

method. The concentrations of K, Ca, Mg, P, S, B, Fe, Mn, Zn and Cu were determined by inductively coupled plasma emission spectrophotometry (ARL 3580) after nitric acid-perchloric acid digestion. The sampling for the biomass and nutrient determinations is described in full in publications II, III and IV.

2.4 Calculations and definitions

The stem volume of the tree stand was calculated in 1984, 1987 and 1991 (I). The growth was determined as the difference between the volumes in 1991, 1987 and 1984. The sample tree data were used for deriving regression functions for the different biomass compartments of the trees (II). These functions were used to calculate the biomass of the tree stands in 1984 and 1987. The difference between the biomasses in 1987 and 1984 was regarded as *biomass accumulation*. The above-ground *biomass production* was determined by adding the litterfall to the accumulation of biomass between 1984 and 1987. The change in dry mass according to needle age was taken into account in the foliage production estimate (II, Appendices 4, 10, see also Mälkönen 1974, Satoo & Madgwick 1982). Nutrient amounts in the different tree compartments were calculated by multiplying the dry masses (II,III) with the corresponding nutrient concentrations (IV). The nutrient content of litterfall was calculated by multiplying the nutrient concentrations of the litter at each sampling with the corresponding amount of litter (II).

The difference between the nutrient amounts in the trees in 1987 and 1984 was called *nutrient accumulation*. The above-ground *nutrient uptake* from the soil was calculated as the sum of the nutrient accumulation in the above-ground compartments and the nutrient content of the above-ground litterfall during the same period.

The differences in the estimated variables between years 1984 and 1987 were tested with the paired t-test. The differences between the effects of different treatments were tested using F tests after analysis of variance.

3 RESULTS AND DISCUSSION

3.1 Stand structure and biomass dynamics

The stem volume of the Scots pine stand was $81 \text{ m}^3 \text{ ha}^{-1}$ in 1984 and the volume growth $6 \text{ m}^3 \text{ ha}^{-1} \text{ a}^{-1}$ (I). These figures are greater than the average values for low-shrub pine bogs twenty years after drainage in South Finland (see Keltikangas et al. 1986). The stem number was high, $2300 \text{ trees ha}^{-1}$, and the canopy was closed. The vigorous development of the tree stand may have been partly due to the nutrient input from the *Carex-Sphagnum*-peat layers lying below the shallow ombrotrophic *Sphagnum*-peat layer (see Brække & Finér 1991).

The total biomass of the tree stand was 78 t ha^{-1} , of which the stem with bark accounted for 52 %, branches 11 %, foliage 5 % and the below-ground compartments 31 % (II, III). The accumulation of biomass mainly occurred in the stems, dead branches and stump and coarse roots (II, Table 5). The living fine root biomass did not change, and that of the living branches increased only slightly during the study period. The foliage biomass decreased, most probably due to the increased mortality of the oldest needles caused by the exceptionally cool and rainy weather in 1987 (see Tikkanen & Raitio 1990). The stand had probably reached its maximum living fine root biomass (see Heikurainen 1955), but not passed the stage where the foliage and branch mass culminates (see Albrektson 1980, Brække 1986, Miller 1986).

The annual above-ground biomass production of the stand was 6.3 t ha^{-1} (II, Table 7). The production of stemwood with bark was lower than that of foliage and branches combined. This is characteristic of Scots pine stands after crown closure, before the culmination of biomass production (see Albrektson 1980). A high proportion (49 %, 3.1 t ha^{-1}) of the production was lost through litterfall. However, the amount of litter collected was only $1.7 \text{ t ha}^{-1} \text{ a}^{-1}$. The difference,

1.4 t ha⁻¹ a⁻¹, could be explained by the leaching of organic matter from the tree crowns, decomposition of the litter before reaching the soil (see Bray & Gorham 1964, Tukey 1970, Rosén & Lundmark-Thelin 1985, Alenäs & Skärby 1988) and retranslocation of carbohydrates during the senescence of foliage and branches (e. g. Smith et al. 1981).

The total tree biomass and biomass production in the pine stand was higher than those of all vegetation layers combined on virgin ombrotrophic bogs (see Vasander 1982, Reinikainen et al. 1984). The amount of tree biomass was within the same range, and the production higher, than those presented for Scots pine stands growing on drained peat and mineral soil sites in Fennoscandia (II, Fig. 5 and Table 13). The greater production obtained for this site could result from site and stand factors, and also the different methods used for branch and foliage production estimation.

3.2 Distribution and cycling of nutrients

The studied nutrients accounted for 0.49 % (392 kg ha⁻¹) of the dry mass of the trees (II, Table 8). The proportions of the main nutrients, N, Ca and K, out of the total amount of nutrients were 44 %, 23 % and 15 %, respectively. The remainder (18 %) was distributed fairly evenly between P, Mg, S and micronutrients combined. The total nutrient concentration of the tree biomass (% d. w.) was lower than that in the ground vegetation (Finér & Brække 1991b).

Nutrient concentrations varied between the different tree compartments (IV, Figs. 1 and 2). The stemwood had the lowest concentrations of most nutrients. The highest concentrations were found in the foliage, living branches, stembark and fine roots. The distribution of nutrients within the trees differed from that of the biomass (II, Fig. 4). The importance of foliage and branches as nutrient stores was greater, and that of stemwood smaller than would be expected on the basis of their proportions of the biomass.

The amounts of nutrients in the biomass of the trees were within the range reported for the other Scots pine stands in Fennoscandia (II, Figs. 6 and 7). The Mn, Zn and Cu stores in the surface peat were greater, and those of the other nutrients equal to those of old drained ombrotrophic bogs in Finland (see Paavilainen 1980, Kaunisto & Paavilainen 1988, Laiho 1991). The trees had almost the same amounts of K and Mn, and even more B in their biomass than in the surface peat (Fig. 2, see also Holmen 1964, Paavilainen 1980, Kaunisto & Paavilainen 1988, Finér 1989, Laiho 1991). The other nutrients were mainly stored in the peat. Manganese stores were also high in the ground vegetation. It could be assumed that, without any nutrient inputs, accumulation in the trees would exhaust the K, Mn and B stores in the root zone before the end of the first rotation even.

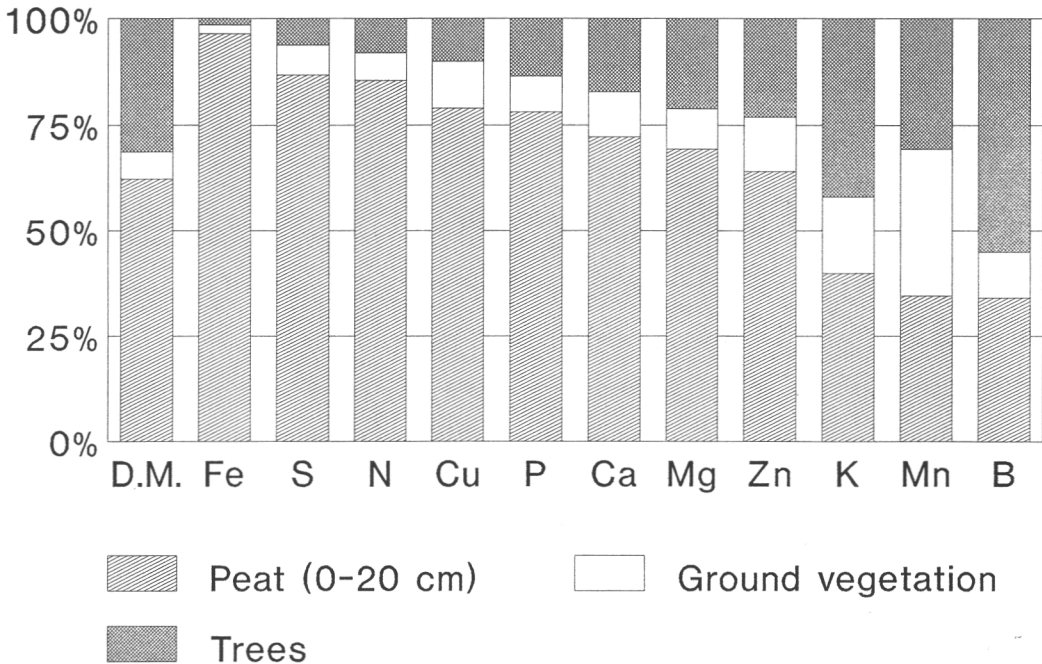


Fig. 2. Average percentual distribution of dry mass (D.M.) and nutrients between the surface peat (Brække & Finér 1991), ground vegetation (Finér & Brække 1991b) and trees on the study site.

Nutrients will be removed from the bog in connection with harvesting. A change in harvesting practices from traditional harvesting of merchantable stem to whole-tree harvesting will considerably increase the nutrient losses (see also Mälkönen 1976, Kaunisto & Paavilainen 1988, Finér 1989). Nutrient removal will more than double in the first stand thinning if whole-tree harvesting is used instead of stem harvesting (II, Table 8).

In mature stands the annual nutrient requirements of trees are satisfied from two sources: retranslocation from the storage organs of trees, and uptake from the soil (e. g. Miller 1984, 1986). In this study the measurements were not designed for determining retranslocation. The estimated annual uptake of nutrients from the peat was as follows: N 15.6, Ca 12.8, K 4.1, P 1.3, Mg 1.7 and S and Mg 1.5 kg ha⁻¹ (II, Table 10). The uptake of Fe and Zn was 510 and 130 g ha⁻¹, respectively, and that of B and Cu less than 100 g ha⁻¹. Except for K and Fe, less than half of the annual uptake accumulated in the trees. Nutrients mainly accumulated in the stems and dead branches, as was the case for biomass (see also Miller 1984).

Annual nutrient uptake and accumulation are known to be closely connected to biomass production and accumulation (e. g. Cole & Rapp 1981, Miller 1984, Brække 1990). There was considerable variation in nutrient uptake and accumulation between this and the other Scots pine stands studied in Fennoscandia (see Holmen 1964, Mälkönen 1974, Paavilainen 1980, Finér 1989, Brække 1990).

The nutrients leached from the tree crowns and litter were not included in the nutrient uptake estimate. Consequently the results were underestimates, especially for the Ca, Mg, K and Mn uptake (see Päivänen 1974, Helmisaari & Mälkönen 1989, Hyvärinen 1990, Ragsdale et al. 1992). The leaching of N, P and S is less significant (Helmisaari & Mälkönen 1989, Hyvärinen 1990, Lovett 1992, Lindberg 1992). The inclusion of the portion of nutrient uptake consumed

by the root systems would have given considerably higher nutrient uptake estimates (see Meier et al. 1985, Vogt et al. 1986).

Atmospheric deposition ($\text{kg ha}^{-1} \text{ a}^{-1}$) of 8.4 N, 7.2 S, 3.1 Ca, 1.7 K and 0.7 Mg was measured on an open field outside the study site (Finér & Brække 1991c). The deposition of N was somewhat greater, and those of the other nutrients close to the average values for eastern Finland (see Järvinen 1986). Atmospheric deposition of these nutrients seems to have been higher than the amounts that had accumulated in the trees during the about 85-year lifetime of the tree stand. The annual deposition of N, S and Mg was greater and that of Ca and K lower than the current annual accumulation. In eastern Finland the deposition level of $140 \text{ g ha}^{-1} \text{ a}^{-1}$ for P (Järvinen 1986) and of less than $10 \text{ g ha}^{-1} \text{ a}^{-1}$ for B (Wikner 1983) have less significance. The net input of nutrients into the bog could not be evaluated because dry deposition and the leaching of nutrients were not known. The annual leaching losses of K from drained forested ombrotrophic bogs have been $0.05\text{-}1.5 \text{ kg ha}^{-1}$ and for P below 0.04 kg ha^{-1} (Ahti 1983). These figures indicate a net input of K and P.

Atmospheric deposition could account for all of the annual uptake of S, and a considerable proportions of the uptake of N, K, Ca and Mg. However, the annual nutrient uptake was largely satisfied by the release of nutrients from the surface peat. This was especially the case because nutrient uptake to the tree roots was not taken into account, and the ground vegetation and micro-organisms compete with the trees for nutrients.

3.3 Effects of fertilization

3.3.1 Volume growth and biomass accumulation

Fertilization had no effect on the total biomass or biomass production of the tree stand within the three-year study period (II). However, it did change biomass allocation in the crowns of the trees. The needle biomass increased and that of dead branches decreased, resulting in a higher biomass of living branches on the NPK fertilized plots (see also Miller & Miller 1976, Mead et al. 1984). The stem biomass or volume was not affected by fertilization (I,II).

The volume growth, however, increased significantly during the second, three-year period after fertilization (I). This suggests that there was also an increase in stem biomass. The increase in volume growth given by NPK and PK fertilization within six years, $6.3 \text{ m}^3 \text{ ha}^{-1}$ and $4.3 \text{ m}^3 \text{ ha}^{-1}$ respectively, was similar to that obtained in previous studies (see Hämäläinen & Laakkonen 1983, Almqvist & Carlsson 1988). The fertilization response most probably followed a pattern in which the biomass increase in the tree crowns preceded that in the stems (see Miller & Miller 1976). The high density of the stand may have somewhat diminished the fertilization effect (see Brix & Ebell 1969, Jonsson & Möller 1977, Haapanen et al. 1979, Saramäki & Silander 1982, Mead et al. 1984).

3.3.2 Nutrient dynamics

The foliar concentrations indicated a low supply of N, P, K and B on the study site (IV). Fertilization almost doubled the annual uptake of these nutrients (II, Table 10), and the annual accumulation was as much as three to four times greater than before fertilization (II, Table 9). These extra nutrients mainly accumulated in the crowns of the trees, where the biomass and nutrient

concentrations also increased the most (II, IV). One third of the increased uptake of B had already returned to the soil in litterfall.

The increased accumulation in the trees accounted for only 20 - 25 % of the applied N and K, and about 10 % of the P and B (Table 1). These proportions cannot be regarded as low, since the amounts applied were many times greater than the annual uptake by the unfertilized trees and, except for N, also higher than the total amounts in the trees before fertilization. The ground vegetation and peat had probably accumulated a part of the fertilizer nutrients (Table 1). However, considerable amounts of fertilizer nutrients seemed to have been lost through leaching; this phenomenon was also supported by the increased nutrient concentrations in the groundwater (see Finér & Brække 1991c).

Table 1. The increased accumulation of fertilizer nutrients in the trees, ground vegetation and peat (kg ha^{-1}) and as a proportion (%) of the amount of nutrients applied.

		Trees		Ground vegetation ¹⁾		Peat ²⁾ (0-50 cm)		Total	
		PK	NPK	PK	NPK	PK	NPK	PK	NPK
N*	kg ha^{-1}		29	-	-	-	-		29
	%		20	-	-	-	-		20
P	kg ha^{-1}	6.0	5.4	10.0	6.0	-	-	16.0	11.4
	%	11	10	19	11	-	-	30	22
K	kg ha^{-1}	27	25	-	-	27	40	54	65
	%	27	25	-	-	27	40	54	65
B	kg ha^{-1}	0.22	0.23	0.06	0.07	0.90	0.90	1.20	1.20
	%	9	10	3	3	38	38	49	49
Ca	kg ha^{-1}	-	-	25	13	-	-	25	13
	%	-	-	18	9	-	-	18	9
Mg	kg ha^{-1}	-	-	-	-	-	-	-	-
	%	-	-	-	-	-	-	-	-
S	kg ha^{-1}	2.3	3.6	-	-	-	-	2.3	3.6
	%	8	13	-	-	-	-	8	13

* the change on the PK fertilized plots taken into account

1) Finér & Brække 1991b

2) calculated from Brække & Finér 1991

3.4 Reliability of the results

The harvesting method used in this study is almost exclusively used for determining biomass and nutrient amounts in peatland ecosystems. However, the method is associated with possible errors resulting from sampling and measurements.

The number of sample trees was small. However, the homogeneity of the tree stands on the sample plots before fertilization probably reduced some of the errors associated with the small sample size. The samples for determining biomass and nutrient concentrations were taken more intensively from the upper than the lower parts of the crowns. This could introduce a varying amount of bias in the different biomass and nutrient parameters.

Although the instruments were carefully handled, regularly serviced and calibrated, the possibility of systematic errors could not be totally excluded. In the laboratory the quality of the chemical analyses was followed by analyzing every fifth sample twice, by performing the analyses by two different methods, except N, and by taking part in interlaboratory calibrations (see Finér & Brække 1990).

The allometric functions used for predicting the biomass in different tree compartments are commonly applied in biomass studies (e. g. Satoo & Madgwick 1982). The derived tree and branch biomass functions explained, except for cones, over 80 % of the biomass variation (II, Appendices 7, 8 and 9). The relative standard errors for the different crown compartments were higher than those for the stemwood, stem bark and stump and coarse roots (see also Mälkönen 1974, Paavilainen 1980, Finér 1989).

Some of the problems in the determination of biomass and nutrient stores and dynamics are connected to the date of sampling and the time interval chosen. The processes involved may have both seasonal and between-year variation.

Biomass growth and retranslocation of nutrients have a physiologically controlled seasonal rhythm. Climatic factors and damage cause between-year variation. In this study the sampling for biomass and nutrient stores was done at the same time during the growing season on both occasions, and was close to the annual maximum in biomass and nutrient concentrations (see Helmisaari 1990a).

The estimation of biomass production and nutrient uptake was associated with some problems derived from the short study period and biomass losses due to mortality. The dead needles and branches which were not attached to the trees at the end of the study period were collected in littertraps. The number of littertraps was low and probably gave an underestimate of the amount of bark and branch litter (see Bray & Gorham 1964, Mälkönen 1974, Satoo & Madgwick 1982). The needle litterfall in pine stands is known to vary considerably between years, and a 3 to 4 year collection period is regarded as a minimum (Bray & Gorham 1964, Flower-Ellis 1985).

The needle dry mass decreased considerably at the senescence (II, Appendix 4), which could be due to decomposition, leaching and the retranslocation of organic compounds. The production was probably somewhat overestimated, because the role of retranslocation was not studied.

The tracing of fertilizer nutrients was somewhat inaccurate with the methods used, because the natural variation obscured nutrient doses that were small compared to the stores in the ecosystem. Isotope techniques would have given more accurate estimates of the fate of some fertilizer elements, although these methods also have some methodological and technical problems (see e. g. Böhm 1979, Head 1980, Andreux et al. 1990, Nömmik 1990).

4 CONCLUSIONS AND PROSPECTS

The studied Scots pine stand growing on the ombrotrophic bog had developed more rapidly after drainage than the average for this type of site. This could indicate a nutrient input from the layers lying below the ombrotrophic, 20 cm-thick, surface peat layer.

Macronutrient stores in the surface peat were low, as is usually the case on ombrotrophic bogs. The amounts of K and Mn in the tree stand were equal to, and that of B higher than those in the surface peat. Harvesting will have a great impact on the K, Mn and B stores of the bog, especially. Compensating nutrient inputs from atmospheric deposition and from the deeper peat layers are significant and require further study.

Tree growth was limited by a low supply of N, P, K and B. Atmospheric deposition had an effect on the annual supply of S, N, K, Ca and Mg especially. However, the nutrient uptake of the vegetation seemed to mainly depend on the nutrient supply from peat.

Fertilization affected the biomass of the foliage and branches within the three-year study period. The period was probably too short for detecting any stem growth response. The high density of the stand may have diminished the fertilization effects.

Only relatively small amounts of the applied nutrients seemed to have become fixed in the ecosystem. The losses would probably have been smaller if the amounts of nutrients applied had better corresponded to the demand of the trees and the fixing capacity of the peat (see e. g. Ingestad 1982, 1987, 1988). However, these factors are not easily determined and satisfied in practice (see Axelsson 1986, Chapin et al. 1986).

This study supports and supplements the results of the other studies on the tree biomass and nutrient dynamics of drained ombrotrophic pine bogs in Fennoscandia (see Holmen 1964, Paavilainen 1980, Vasander 1981, 1982, Brække 1977b, 1986, 1987, 1990). Further generalizations require studies on other sites with different tree stands and more detailed investigations on the individual processes involved. In the near future the results from the other sites of the Nordic project will become available (see already Håland & Brække 1989, Brække & Finér 1990, 1991, Brække & Håland 1990, Finér & Brække 1991a, 1991b, 1991c).

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LEENA FINÉR

EFFECT OF FERTILIZATION ON THE GROWTH AND STRUCTURE OF A SCOTS PINE STAND GROWING ON AN OMBROTROPHIC BOG

Lannoituksen vaikutus rämemännikön kasvuun ja rakenteeseen

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NPK fertilization increased volume growth by 6.3 m³ ha⁻¹ and PK fertilization by 4.3 m³ ha⁻¹ within six years after nutrient application. The results indicate that dominant and co-dominant trees respond to fertilization better than suppressed ones, and that the trees close to the ditches benefit almost as much from fertilization as those in the middle of the strip. NPK fertilization also increased the mortality of the intermediate trees.

Keywords: bog, drainage, increment, *Pinus sylvestris*, tree class

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INTRODUCTION

The effect of fertilization on the tree stand depends on factors such as the age and density of the stand, and on the fertility and water regime of the site. Many fertilization experiments have been carried out in pine stands on peat soils. Phosphorus and potassium are the growth limiting nutrients on most drained peatlands (e. g. Paavilainen 1979a). On ombrotrophic sites nitrogen is also essential to obtain a growth increase (e. g. Meshechok 1968, Brække 1977, 1983, Paavilainen 1977, 1979a). The effect of nitrogen fertilization lasts for nearly ten years, and that of PK fertilization up to 15 years (e.g. Paavilainen 1972, 1977, 1979b, Paavilainen and Simpanen 1975, Heikurainen and Laine 1985). The growth response is at its greatest after 3 to 5 years of treatment (Paa-

vilainen 1972, Paavilainen and Simpanen 1975, Karsisto 1976).

Vigorous stem growth presupposes that the crowns of the trees have good light conditions. Different tree classes are affected by fertilization in different ways (Tamm 1966, Viro 1967, Fahlroth 1969, Gustavssen 1976, Kukkola 1978). Suppressed trees are not able to compete for nutrients and light with the trees in dominant tree classes. In dense stands, a shortage of light limits the growth of most trees. Thinning before fertilization thus guarantees the best results (Brix and Ebell 1969, Jonsson and Möller 1977, Haapanen et al. 1979, Saramäki and Silander 1982). On peat soils, effective drainage also improves the response to fertilization (Hui-kari and Paarlahti 1967, Heikurainen and

Veijola 1971, Heikurainen and Laine 1976).

The aim of this report is to describe the short-term growth responses after PK and NPK fertilization of Scots pines in different tree classes and at different distances from the ditches on a drained ombrotrophic pine bog. This study is part of a Nordic project the main objectives of which are to evaluate the amount, distribution and circulation of mineral nutrients after the drainage and fertilization of ombrotrophic pine bogs in different climatic conditions.

MATERIAL AND METHODS

Study site

The material was collected from an experimental field in northern Karelia (65 km SE of Joensuu 62°14' N; 29°50' E, 81 m

a. s. l.). The site was drained in 1967 with a 50 m ditch spacing. Climatic data are given by Finér and Brække (1991). The depth of the groundwater table was monitored during 1984–1987 (Table 1). The site has a 1–3 metre-thick, nutrient-poor peat layer (see Brække and Finér 1991). The naturally regenerated Scots pine (*Pinus sylvestris* L.) stand growing on the experimental field is about 85 years old. The site is a low-shrub pine bog according to the classification of Heikurainen and Parkarinen (1982, see also Finér and Brække 1991).

The field experiment was started in June 1984, and fertilization carried out at the beginning of June, 1985. A 3 x 3 Latin square design was used with a plot size of 1 500 m². The buffer zone between the plots on the strips was ten meters. The treatments were as follows: 1) unfertilized (0), 2) PK(MgB), 3) NPK(MgB). The

Table 1. Groundwater level (cm) during June–September, 1984–1987. The values are average distances to the water table measured from the soil surface.

Taulukko 1. Pohjaveden pinnan taso (cm) kesä–syyskuussa vuosina 1984–1987. Arvot ovat etäisyyksiä mitattuna maanpinnasta pohjavesipintaan.

Year Vuosi	Treatment Käsittely	Distance from ditch Etäisyys ojasta					
		\bar{x}	12.5 m max	min	\bar{x}	25m max	min
1984	0	47	68	20	49	69	19
	PK	49	72	20	45	67	19
	NPK	51	73	21	44	64	19
1985	0	33	48	23	33	50	21
	PK	31	47	20	30	47	22
	NPK	32	49	22	30	45	20
1986	0	38	58	18	39	59	16
	PK	41	63	19	39	59	18
	NPK	41	62	18	37	56	15
1987	0	26	40	18	25	40	17
	PK	26	41	18	26	39	18
	NPK	27	43	18	24	37	16

amounts of elements (kg ha^{-1}) applied were: N 150, P 53, K 100, Ca 135, Mg 25, S 28, Cl 95, B 2.4. The fertilizers were given as ammonium nitrate, raw phosphate, potassium chloride, magnesium sulphate and sodium borate.

Field measurements

All the trees on the sample plots were numbered, mapped and a cross painted at breast height in late June 1984. The breast height diameter from two opposite directions (mm), height (dm) and crown length (dm) were measured. The trees were classified into different tree classes as follows: 1) dominant, 2) co-dominant, 3)

intermediate, 4) suppressed 5) emergent 6) undergrowth. The breast-height diameters and height were remeasured in August 1987 and in early spring, 1991. The breast height diameters were measured at exactly the same points on all occasions. Dead and badly damaged trees were harvested during the course of the experiment.

Calculations

The over-bark stem volume of the trees was calculated by means of volume equations based on breast height diameter and height (Laasasenaho 1982). The increment in diameter, height, and stem volume with bark were determined as the difference

Table 2. Tree stand characteristics of all the trees before fertilization (1984) and dead or badly damaged trees during the experimental period and the F-values of treatments, (standard deviation and significance of F-value in parentheses), (d = arithmetic mean diameter (over bark), h = arithmetic mean height, g = over bark basal area, v = over bark stem volume, n = number of trees).

Taulukko 2. Puustotunnukset ennen lannoitusta (1984) koaloilla laskettuna erikseen kaikille ja tutkimusjaksolla kuolleille ja pahoin vioittuneille puille sekä käsittelyn F-arvot, (keskihajonta ja F-arvon merkitsevyys suluissa), (d = aritmeettinen kuorellinen keskiläpimitta, h = aritmeettinen keskipituus, g = kuorellinen pohjapinta-ala, v = kuorellinen runkokuu tilavuus, n = puiden lukumäärä).

Treatment Käsittely	d cm	h m	g m^2ha^{-1}	v m^3ha^{-1}	n Stems ha^{-1} Runkoa ha^{-1}
All trees in 1984 — Kaikki puut 1984					
0	8.7 (0.16)	8.9 (0.12)	15.4 (0.52)	80.9 (4.5)	2364 (103)
PK	8.7 (0.44)	8.8 (0.56)	15.3 (0.68)	80.3 (7.4)	2310 (230)
NPK	8.8 (0.22)	8.9 (0.40)	15.6 (1.18)	82.4 (9.9)	2335 (91)
F-value F-arvo	0.06 (0.95)	0.26 (0.79)	1.05 (0.49)	0.32 (0.76)	0.14 (0.88)
1984–1991 dead and badly damaged trees 1984–1991 kuolleet ja pahoin vioittuneet puut					
0	6.1 (0.20)	6.8 (0.32)	0.8 (0.22)	3.9 (0.8)	302 (166)
PK	6.2 (0.21)	6.9 (0.22)	1.0 (0.43)	4.8 (2.2)	317 (123)
NPK	6.1 (0.20)	7.1 (0.32)	1.8 (0.44)	8.1 (2.5)	563 (112)
F-value F-arvo	0.12 (0.89)	0.59 (0.63)	27.75 (0.04)	13.58 (0.07)	60.12 (0.02)

between the values measured in 1991, 1987 and 1984.

The differences between treatments were tested with the F-test after analysis of variance. The tests were done using the MANOVA procedure of the SPSS-X statistical package (SPSS-X...1983).

RESULTS AND DISCUSSION

Tree stand growth

The volume of the tree stand (Table 2) was almost the same ($93 \text{ m}^3 \text{ ha}^{-1}$), while the increment (Table 3) was 2–3 $\text{m}^3 \text{ ha}^{-1}$

year⁻¹ and number of stems per hectare 400–800 higher than those usually recorded on drained pine bogs of the same site type and development class in South Finland (see Keltikangas et al. 1986, Hökkä and Laine 1988). The stem size frequency distribution was typical of drained low-shrub pine bogs and did not differ very much from that on mineral sites of similar fertility (Fig. 1, see Ilvessalo 1920, Hökkä and Laine 1988).

Fertilization increased the diameter and volume increment of the tree stand during the study period. The effect of NPK fertilization on the diameter growth was sig-

Table 3. Tree stand growth (excluding badly damaged and dead trees) during 1984–1987, 1988–1990 and 1984–1990 on the control, PK and NPK fertilized plots and the F-values of treatments, (standard deviation and significance of F-values in parentheses), (i_d = arithmetic mean diameter increment, i_h = arithmetic mean height increment, i_v = over-bark stemwood volume increment).

Taulukko 3. Puuston kasvu (ilman pahoin vioittuneita ja kuolleita puita) vuosina 1984–1987, 1988–1990 ja 1984–1990 lannoittamattomilla, PK- ja NPK-lannoitetuilla koelohjoilla sekä käsitellyn F-arvot, (keskihajonta ja F-arvon merkitsevyys suluisissa), (i_d = aritmeettisen keskiläpimitan kasvu, i_h = aritmeettisen keskipituuden kasvu, i_v = kuorellinen runkopuun tilavuuskasvu).

Treatment Käsittely	i_d cm		i_h m		i_v $\text{m}^3 \text{ ha}^{-1}$	
1984–1987						
0	0.66	(0.08)	0.88	(0.02)	18.2	(1.2)
PK	0.69	(0.10)	0.93	(0.05)	18.7	(0.5)
NPK	0.83	(0.11)	0.96	(0.11)	20.2	(1.6)
F-value	55.50	(0.02)	0.49	(0.67)	1.82	(0.35)
<i>F-arvo</i>						
1988–1990						
0	0.65	(0.06)	0.76	(0.15)	21.2	(2.5)
PK	0.79	(0.07)	0.86	(0.11)	24.9	(1.9)
NPK	0.85	(0.06)	0.94	(0.03)	25.4	(0.2)
F-value	320.17	(0.00)	4.15	(0.19)	27.85	(0.04)
<i>F-arvo</i>						
1984–1990						
0	1.31	(0.14)	1.64	(0.17)	39.3	(3.7)
PK	1.48	(0.17)	1.79	(0.08)	43.6	(2.3)
NPK	1.68	(0.17)	1.90	(0.11)	45.6	(1.6)
F-value	151.23	(0.01)	2.25	(0.31)	8.76	(0.10)
<i>F-arvo</i>						

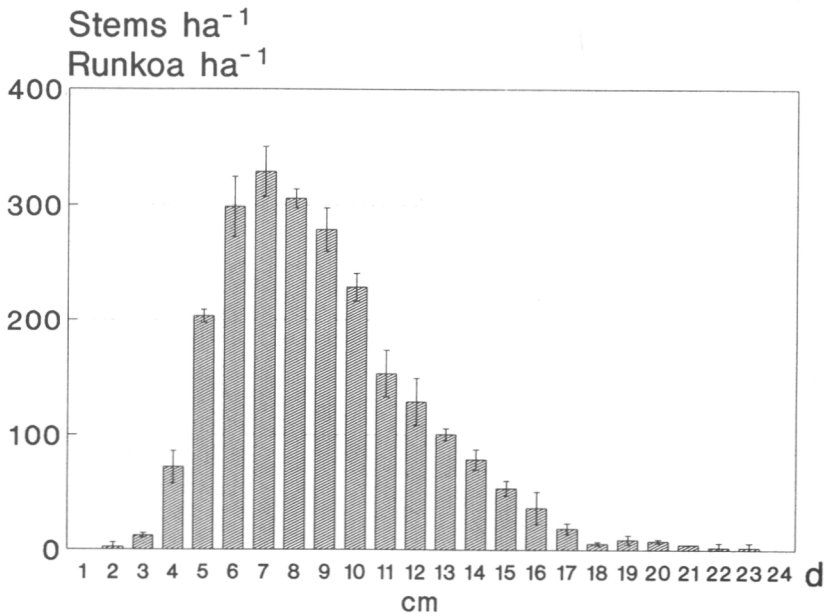


Fig. 1. The mean diameter distribution of all the trees in 1984.

Kuva 1. Keskimääräinen kaikkien puiden runkolukusarja käsittelyillä ($n=3$) vuonna 1984.

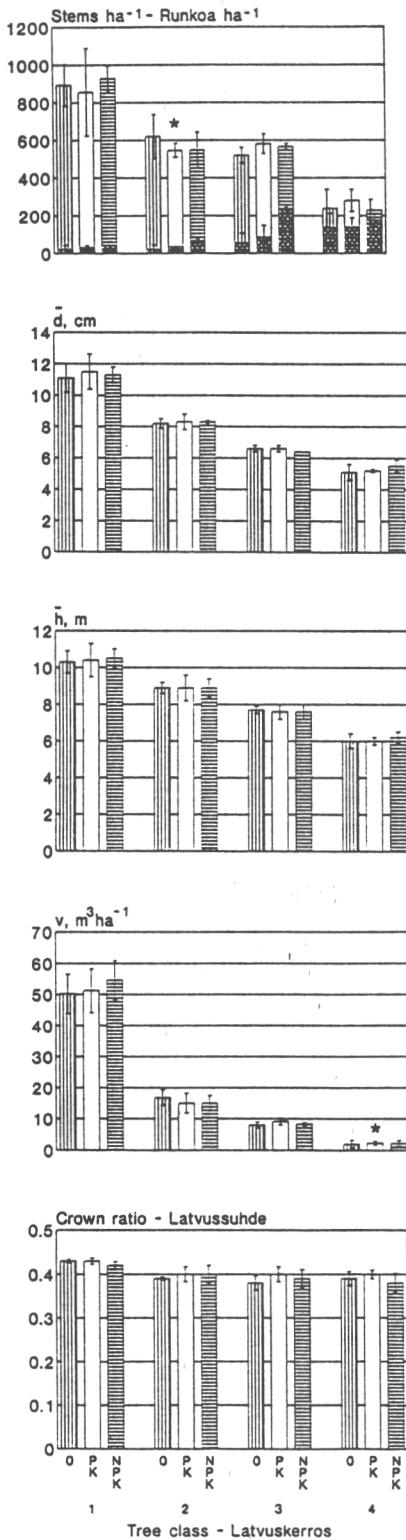
nificantly greater than that of PK fertilization ($p \leq 0.05$). The volume growth increased $6.3 \text{ m}^3 \text{ ha}^{-1}$ (16%) on the NPK and $4.3 \text{ m}^3 \text{ ha}^{-1}$ (11%) on the PK fertilized plots during the six-year study period. The better response to NPK fertilization was consistent with earlier studies in which nitrogen together with phosphorus and potassium, has been found to limit growth on low-shrub pine bogs (Paavilainen 1977, 1979a, 1984). The diameter growth increment in pine stands on peatlands is usually highest during the third and fourth year after fertilization, and that of height growth a few years later (Paavilainen 1972, Paavilainen and Simpanen 1975, Karsisto 1976).

During the study period more trees suffered from damage on the NPK plots than on those with the other treatments (Table 2). In most cases the damaged trees were the smallest ones, irrespective of the treatment, and suffered mainly from snow breakage. Fertilization is known to in-

crease the needle biomass (e. g. Miller and Miller 1976), and the crowns cannot carry the increasing mass of snow during winter. An increase in competition for light as a result of greater needle biomass could also increase self-thinning mortality on the fertilized plots. A minor Scleroderris canker (*Gremmeniella abietina* (Lagerb.) Morelet) epidemic damaged the trees, but the effect of fertilization on the frequency of canker damage was not studied. NPK fertilization with and without micronutrients has been found to increase Scleroderris canker damage on ombrotrophic pine bogs (Mannerkoski and Miyazawa 1983, Vasander and Lindholm 1985, Pätilä and Uotila 1990, see also Kaunisto 1989).

Growth in different tree classes

The very few emergent and undergrowth trees were excluded from the study. The dominant trees were approximately 4 m



higher and 6 cm thicker, and had almost the same crown ratio (height of crown/height of whole tree) as the suppressed trees (Fig. 2). Although only 40% of the trees were dominant, their share of the total volume of the stand was 70%. Less than 10% of the dominant and co-dominant trees died or were badly damaged on the unfertilized plots during the study period. The corresponding percentage for the intermediate and suppressed trees was higher, 44 and 73 respectively.

The diameter growth of the dominant trees increased by 15–21% and that of the co-dominant trees by 17–22% after fertilization (Fig. 3, Table 4). There were no significant differences between the fertilizer treatments ($p > 0.05$). The diameter growth of the other tree classes was not

Fig. 2. Stem number, mean diameter (d), mean height (h), volume (v) and mean crown ratio of all trees in different classes before fertilization, 1 — dominant, 2 — co-dominant, 3 — intermediate, 4 — suppressed. The lower part of the column in the uppermost subfigure indicates the number of trees that died or became badly damaged during the study period. The treatments are presented in all subfigures in the same way as in the lowermost subfigure. SD is indicated on the columns by lines. Values marked with * differ significantly according to variance analysis, $p < 0.05$.

Kuva 2. Kaikkien puiden runkoluku, keskiläpimitä (d), keskipituus (h), tilavuus (v) ja keskimääräinen latvussuhde eri latvuskerroksissa ennen käsittelyä, 1 — päävaltapuu, 2 — lisävaltapuu, 3 — välipuu, 4 — aluspuu. Ylimmän osakuvan pylväiden alaosassa on esitetty tutkimusjaksolla kuolleiden tai pahoin vahingoittuneiden puiden runkoluku. Eri käsittelyt on esitetty alimman osakuvan tavoin kaikissa osakuvissa. Keskihajonta esitetty janoin. Tähdillä merkityt eroavat merkitsevästi toisistaan varianssianalyysin perusteella, $p < 0.05$.

affected. The height growth of the suppressed trees on the fertilized plot was higher than on the controls during 1988–1990. The significant volume growth increase of the suppressed trees after PK fertilization was probably artificial as the volume was significantly higher on the PK fertilized plots already before nutrient application. The mortality of the intermediate trees increased significantly after NPK fertilization.

In Norway spruce (Gustavssen 1976, Kukkola 1978) and Scots pine (Tamm 1966) stands on mineral soil sites, trees in all classes have increased their growth within 5–11 years after N and NPK fertilization; small trees relatively more than larger trees, and larger trees in absolute terms more than smaller trees. Large spruces and pines have responded more rapidly to nitrogen addition than smaller ones (Shimansky and Pobedov 1976,

Kukkola 1978, see also Viro 1967). The high density of the studied plots probably resulted in severe competition for light, and the intermediate and suppressed trees were less able to benefit from the improved nutritional status.

Fig. 3. The increment in mean diameter (i_d), mean height (i_h) and stand volume (i_v) in different classes during the experimental period (excluding dead and badly damaged trees). For numbers see fig. 2. The lower part of the column indicates the period 1984–1987 and the upper part the period 1988–1990. SD for the whole six-year period is indicated on the columns by lines. The treatments are presented in all subfigures in the same way as in the lowermost subfigure.

Kuva 3. Puiden keskiläpimitan (i_d), keskipituuden (i_h) ja kokonaistilavuuden (i_v) kasvu eri latvuserroksissa tutkimusjakson aikana (ilman kuolleita ja pahoin vioittuneita puita). Numerot ks. kuva 2. Pylväiden alaosassa esitetään jaksot 1984–1987 ja yläosassa jaksot 1988–1990 kasvut. Keskihajonta koko kuuden vuoden tutkimusjaksolle esitetty janoain. Eri käsitellyt on esitetty kaikissa osakuvissa alimman osakuvan tavoin.

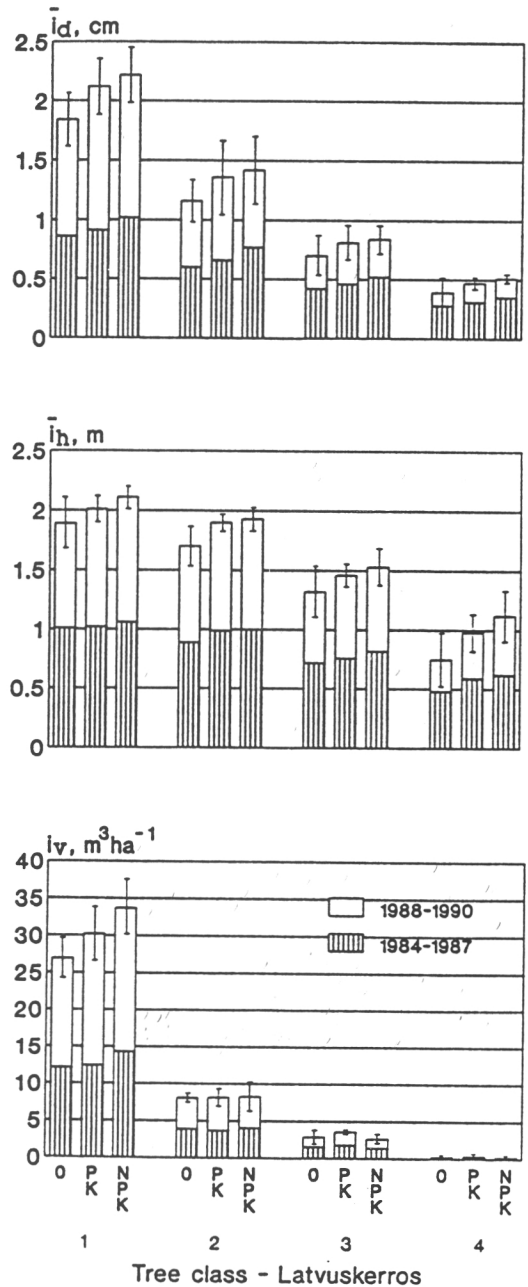


Table 4. The F-values (F) of the variance analyses and their significance (p) for variables i_d , i_h , i_v (see Table 3) in different tree classes and distances from the ditches in 1984–1987, 1988–1990 and 1984–1990.

Taulukko 4. Varianssianalyysien F-arvot (F) ja niiden merkitsevyys (p). Selittävinä muuttujina i_d , i_h ja i_v (ks. taulukko 3) eri latvuserroksissa ja etäisyyksillä ojasta vuosina 1984–1987, 1988–1990 ja 1984–1990.

Dependent variable <i>Selitettävä muuttuja</i>		Treatment — <i>Käsittely</i>					
		1984-1987		1988-1990		1984-1990	
Tree class		F	p	F	p	F	p
<i>Latvuserros</i>							
Dominant	i_d	8.81	0.10	17.96	0.05	13.36	0.06
<i>Päävaltapuu</i>	i_h	0.10	0.91	1.87	0.35	0.87	0.53
	i_v	3.40	0.23	5.02	0.17	4.95	0.17
Co-dominant	i_d	91.08	0.01	20.28	0.05	34.37	0.03
<i>Lisävaltapuu</i>	i_h	1.74	0.37	5.30	0.16	3.94	0.20
	i_v	0.37	0.73	0.22	0.82	0.04	0.96
Intermediate	i_d	4.28	0.19	0.63	0.61	1.84	0.35
<i>Välipuu</i>	i_h	3.44	0.23	1.21	0.45	1.97	0.34
	i_v	1.19	0.46	4.05	0.20	2.32	0.30
Suppressed	i_d	3.00	0.25	0.21	0.83	1.40	0.42
<i>Aluspuu</i>	i_h	0.96	0.57	21.67	0.04	3.84	0.21
	i_v	15.05	0.06	10.20	0.09	16.87	0.06
Distance from ditch		F	p	F	p	F	p
<i>Etäisyys ojasta</i>							
0-5 m	i_d	10.49	0.09	7.72	0.12	16.98	0.06
	i_h	1.30	0.44	15.01	0.06	2.31	0.30
	i_v	0.82	0.55	3.72	0.21	1.80	0.36
5-10 m	i_d	31.48	0.03	9.88	0.09	14.50	0.06
	i_h	0.18	0.85	2.31	0.30	1.19	0.46
	i_v	1.71	0.37	1.55	0.39	1.49	0.40
10-15 m	i_d	30.78	0.03	103.30	0.01	60.46	0.02
	i_h	0.55	0.65	6.60	0.13	2.05	0.33
	i_v	0.55	0.65	6.42	0.14	2.46	0.29
15-20 m	i_d	7.54	0.12	15.00	0.06	10.48	0.09
	i_h	1.51	0.40	1.30	0.44	2.56	0.28
	i_v	1.57	0.39	5.67	0.15	2.82	0.26
20-25 m	i_d	132.60	0.01	33.48	0.03	51.16	0.02
	i_h	0.76	0.57	18.63	0.05	3.14	0.24
	i_v	2.27	0.31	2.32	0.30	0.40	0.72

Growth at different distances from the ditches

The distance between each tree and the middle of the ditch was measured, the open ditch area being included in the 0–5 m zone. Thus the number of trees in the middle of the strips was greater than that near the ditches (Fig. 4). Probably as a result of the better light regime and more aerobic conditions in the root zone, the trees near the ditches had grown 1.5–2 cm thicker and 0.8–0.9 m taller, and had a larger crown ratio than those in the middle of the strips. They were also less vulnerable to damage since the mortality increased on the unfertilized plots from 13% to 30% according to increasing distance from the ditch.

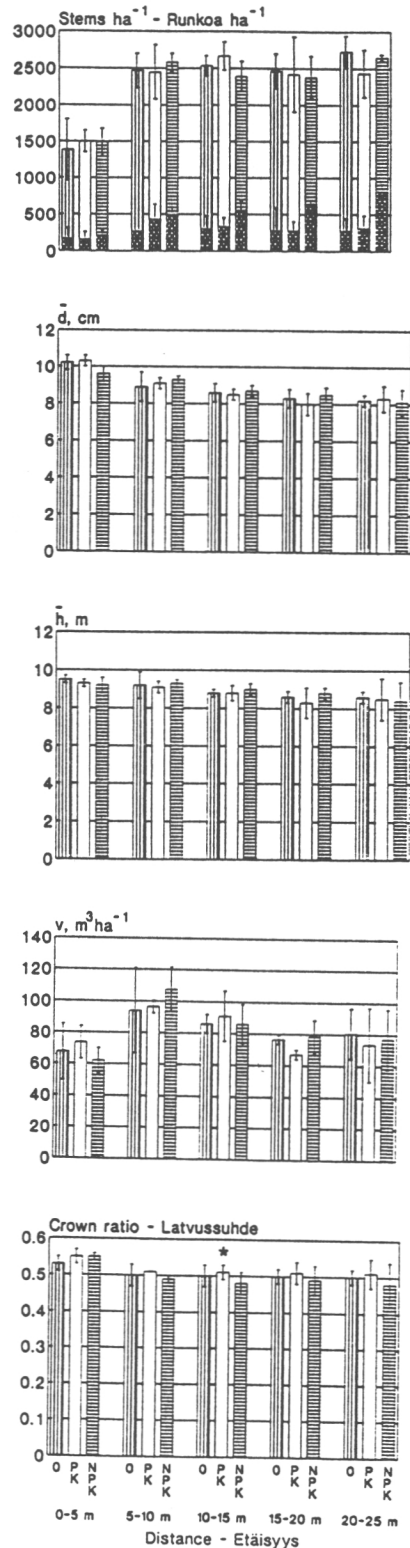


Fig 4. Stem number, mean diameter (d), mean height (h), volume (v) and mean crown ratio of all trees at different distances from the ditches before fertilization. The lower part of the column in the uppermost subfigure indicates the number of trees that died or became badly damaged during the study period. The treatments are presented in all subfigures in the same way as in the lowermost subfigure. SD is indicated on the columns by lines. Values marked with * differ significantly according to variance analysis, $p < 0.05$.

Kuva 4. Kaikkien puiden lukumäärä, keskiläpimitta (d), keskipituus (h), tilavuus (v) ja keskimääräinen latvussuhde eri etäisyyksillä ojasta ennen käsittelyä. Ylimmän osakuivan pylväiden alaosa on esitetty tutkimusjaksolla kuolleiden tai pahoin vahingoittuneiden puiden runkoluku. Eri käsittelyt on esitetty alimman osakuivan tavoin kaikissa osakuivissa. Keskihajonta esitetty janoin. Tähdillä merkityt eroavat merkitsevästi toisistaan varianssianalyysin perusteella, $p < 0.05$.

The diameter growth of the trees increased after fertilization irrespective of the distance from the ditch (Fig. 5, Table 4). The effect of NPK fertilization was significantly greater in the middle of the strip than that of PK fertilization ($p \leq 0.05$).

The growth increase after PK fertilization was relatively smaller, whereas that of NPK fertilization was slightly greater in the middle of the strips than closer to the ditches. This could result from the faster rate of nitrogen mineralization near the ditches, promoted by the deeper penetration of thermal radiation and the deeper aerobic zone in the soil. Some earlier studies have shown that efficient drainage improves the effect of fertilization (Heikurainen and Veijola 1971, Heikurainen and Laine 1976, see also Huikari and Paarlahti 1967).

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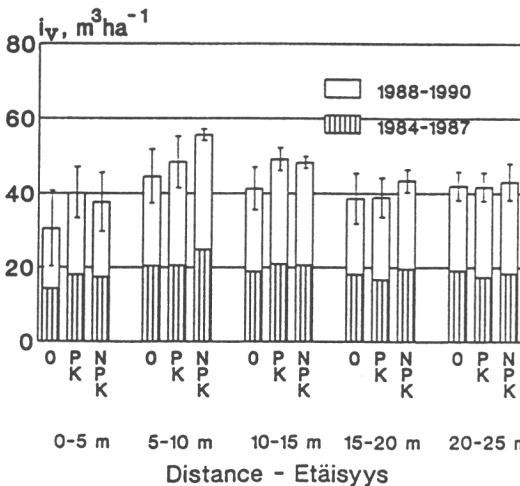
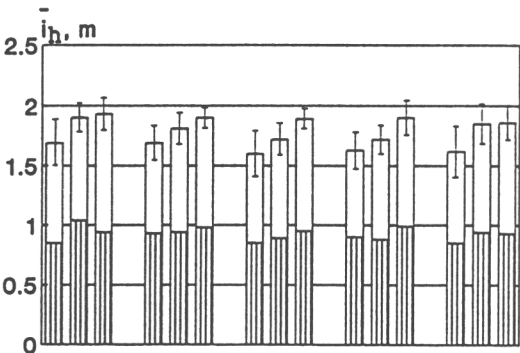
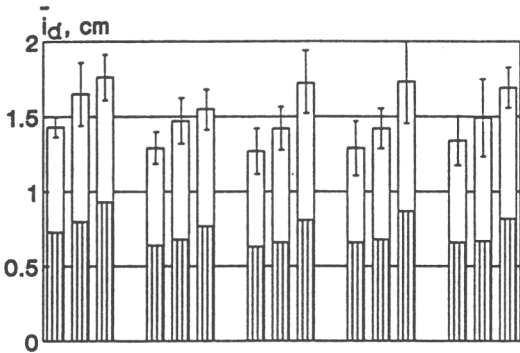


Fig. 5. Increment in mean diameter (i_d), mean height (i_h) and stand volume (i_v) at different distances from the ditches during the experimentation period (excluding dead or badly damaged trees). The lower part of the column represents the period 1984–1987 and the upper part the period 1988–1990. SD for the whole six-year period is indicated on the columns by lines. The treatments are presented in all subfigures in the same way as in the lowermost subfigure.

Kuva 5. Puiden keskiläpimitan (i_d), keskipituuden (i_h) ja kokonaistilavuuden (i_v) kasvu eri etäisyyksillä ojasta tutkimusjaksolla (ilman kuolleita tai pahoin voittuneita puita). Pylväiden alaosassa esitetään jaksos 1984–1987 ja yläosassa jaksos 1988–1990 kasvut. Keskiahajonta koko tutkimusjaksolle esitetty janoin. Eri käsittelyt on esitetty kaikissa osakuivissa alimman osakuivan tavoin.

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TIIVISTELMÄ:

LANNOITUKSEN VAIKUTUS RÄMEMÄNNIKÖN KASVUUN JA RAKENTEESEEN

Tutkimuksessa tarkastellaan lannoituksen vaikutusta puuston pituus-, läpimitanja tilavuuskasvuun kuutena lannoituksen jälkeisenä vuotena eri latvuskerroksissa ja eri etäisyyksillä ojista. Tutkimuksen aineisto kerättiin kokeelta, joka oli perustettu Pohjois-Karjalaan isovarpuiselle räme muuttumalle yhteispohjoismaisen "Ravinteiden kierto ja jakaantuminen suoekosys-

teemissä eri ilmasto-olosuhteissa"-projektin yhteydessä. Puusto mitattiin lannoitusta edeltävänä vuotena ja kolme sekä kuusi vuotta lannoituksen jälkeen. Kokeessa oli kolme käsittelyä ja kolme toistoa. Käsittelyt olivat: lannoittamaton (0), PK(MgB), NPK(MgB) ja käytetyt lannoitemäärät (kg ha⁻¹): N 150, P 53, K 100, Mg 25, B 2,4.

Lannoitus lisäsi läpimitan ja tilavuuden kasvua (taulukko 2). NPK-lannoituksella saatiin kuudessa vuodessa kasvunlisäystä $6,3 \text{ m}^3 \text{ ha}^{-1}$ ja PK lannoituksella vastaavasti $4,3 \text{ m}^3 \text{ ha}^{-1}$. Lannoitus lisäsi selvemmin valtapuiden ja lisävaltapuiden kuin alem-

pien lasvuserrosten puiden läpimitankasvua (kuva 3, taulukko 4). NPK-lannoitus lisäsi välipuiden kuolleisuutta. Puun etäisyys ojasta ei vaikuttanut merkittävästi eri tunnuksin mitattuihin lannoitusreaktioihin (kuva 5).

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II



ACTA FORESTALIA FENNICA 223

EFFECT OF FERTILIZATION ON DRY MASS
ACCUMULATION AND NUTRIENT CYCLING IN
SCOTS PINE ON AN OMBROTROPHIC BOG

Lannoituksen vaikutus männyn kuivamassan kertymään ja ravinteiden
kiertoon ombrotrofisella rämeellä

Leena Finér

Approved on 29.11.1991

Finér, L. 1991. Effect of fertilization on dry mass accumulation and nutrient cycling in Scots pine on an ombrotrophic bog. *Seloste: Lannoituksen vaikutus männyn kuivamassan kertymään ja ravinteiden kiertoon ombrotrofisella rämeellä*. Acta Forestalia Fennica 223. 42 p.

The first three-year effects of PK(MgB) and NPK(MgB) fertilization on the dry mass accumulation and nutrient cycling were studied in a Scots pine (*Pinus sylvestris* L.) stand growing on a drained low-shrub pine bog in eastern Finland. The total dry mass of the tree stand before fertilization was 78 t/ha, of which the above-ground compartments accounted for 69 %. The annual above-ground dry mass production was 6.3 t/ha, 51 % (3.2 t/ha) of it accumulating in the tree stand.

The study period was too short for detecting any fertilization response in the stems. The total dry mass accumulation was not affected, because the increase in foliar and cone dry masses after both fertilization treatments, and that of the living branches after NPK fertilization, were compensated by the decrease in the dry mass of dead branches.

The nutrients studied accounted for 392 kg/ha (0.49 %) of the total dry mass of the tree stand before fertilization. The amounts were as follows: N 173 kg/ha (44 %), Ca 90 kg/ha (23 %), K 58 kg/ha (15 %). The rest (18 %) consisted of P, Mg, S and micronutrients combined, each 13–22 kg/ha.

The unfertilized trees took up the following amounts of nutrients from the soil: N 15.6, Ca 12.8, K 4.1, P 1.3, Mg 1.7 and S and Mn 1.5 kg/ha/a. The uptake of Fe and Zn was 510 and 130 g/ha and that of B and Cu less than 100 g/ha. More than 50 % of the nutrient uptake, except for that of K and Fe, was released in litterfall. The results indicated very efficient cycling of K, Mn and B between the soil and trees.

The fertilized stands accumulated more N, P, K and B than the unfertilized ones during the three-year study period. The increased accumulation corresponded to 35 % (52 kg/ha) of the N applied on the NPK fertilized plots, 10 % (6 kg/ha) of the P, 25 % (25 kg/ha) of the K and 10 % (0.2 kg/ha) of the B on the PK and NPK fertilized plots. The increased amount of B released in litterfall after fertilization was equivalent to 4 % of the applied B. Fertilization inhibited the uptake of Mn and Ca.

Keywords: accumulation, biomass, litterfall, nutrient, peatland, *Pinus sylvestris*, production, uptake.
FDC 237 + 114.4 + 174.7 *Pinus sylvestris*

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PK(MgB) ja NPK(MgB) -lannoituksen vaikutusta männyn kuivamassan kertymään ja ravinteiden kiertoon tutkittiin kolmen lannoituksen jälkeisen vuoden ajan ojitetulla isovarpuisella rämeellä Pohjois-Karjalassa.

Ennen lannoitusta puuston kuivamassa oli 78 t/ha, josta maanpäällisten osien osuus oli 69 %. Puuston vuotuinen kuivamassan tuotos oli 6,3 t/ha, ja siitä 51 % kerääntyi puustoon.

Lannoitusvaikutus ei näkynyt rungon kuivamassan lisäyksenä tutkimusjaksolla. Lannoitus ei myöskään vaikuttanut kuivamassan kokonaiskertymään. Tosin neulasten ja käpyjen massa lisääntyi sekä PK- että NPK-lannoitetuilla koaloilla ja elävien oksien massa myös NPK-lannoitetuilla koaloilla, mutta samanaikaisesti kuolleiden oksien massa pieneni molempien lannoituskäsitteilyjen vaikutuksesta.

Tutkittujen ravinteiden osuus puuston kuivamassasta oli 0,49 % (392 kg/ha) ennen lannoitusta. Tästä tyyppiä oli 173 kg/ha (44 %), kalsiumia 90 kg/ha (23 %), kaliumia 58 kg/ha (15 %) ja loppu (18 %) jakaantui melko tasaisesti fosforin, magnesiumin, rikin ja hivenravinteiden kesken.

Lannoittamaton puusto otti maasta vuositain tyyppiä 15,6, kalsiumia 12,8, kaliumia 4,1, fosforia 1,3, magnesiumia 1,7 sekä rikkiä ja mangaania 1,5 kg/ha. Rautaa ja sinkkiä puusto otti vastaavasti 510 ja 130 g/ha sekä kuparia ja booria alle 100 g/ha. Yli puolet näistä ravinemääristä, rautaa ja kaliumia lukuunottamatta palasi karikkeiden mukana takaisin maahan. Tulokset antoivat viitteitä kaliumin, mangaanin ja boorin tehokkaasta kierrosta puuston ja maan välillä.

Lannoitetussa puuston kuivamassassa oli enemmän tyyppiä, fosforia, kaliumia ja booria kuin lannoittamattomassa kolmen vuoden kuluttua lannoituksesta. Lisääntynyt ravinteiden kertymä vastasi 10 % (6 kg/ha) käytetystä lannoitefosforista, 25 % (25 kg/ha) lannoitekaliumista ja 10 % (0.2 kg/ha) lannoiteboorista. Vastava osuus typen kohdalla oli 35 % (52 kg/ha) NPK-lannoitetuilla koaloilla. Lannoitus vähensi kalsiumin ja mangaanin ottoa.

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Symbols – Merkinät

Tree – *Puu*

- d over-bark, breast-height diameter – *kuorellinen rinnankorkeusläpimitta*, cm
h height – *pituus*, dm
cl crown limit – *latvusraja*, dm
cr crown ratio – *latvussuhde*, $\frac{h - cl}{h}$
v over-bark volume – *kuorellinen tilavuus*, l

Branch – *Oksa*

- d_b diameter of branch at 3 cm distance from the stem – *oksan läpimitta 3 cm etäisyydellä rungosta*, mm
 h_b length – *pituus*, cm
pos relative branch position in the living crown measured from the base of the living crown – *oksan suhteellinen sijainti elävässä latvuksessa, määritettynä elävän latvuksen alarajalta*, %

Equations – *Yhtälöt*

- R^2 coefficient of determination – *selitysaste*
 S_e residual standard deviation – *jäännöshajonta*
 $S_e\%$ relative standard error – *suhteellinen keskivirhe*, $100 * \sqrt{e^{s_e^2} - 1}$

Other – *Muut*

- n number of observations – *havaintojen lukumäärä*
a year – *vuosi*
C current year needles – *uusin neulaskerta*
C + 1 one-year-old needles – *vuoden vanha neulaskerta*
C ≥ 2 two-year-old and older needles – *kaksi vuotta vanha ja vanhempi neulaskerta*

Preface

The present study was financed by the Nordic Forest Research Cooperation Committee, The Finnish Forest Research Institute and the Academy of Finland. Ms. Anki Geddala, Ms. Seija Taskinen, Mr. Markku Tiainen and Mr. Pekka Järviluoto have helped in the collection of material. Ms. Leena Karvinen has given technical help. Professors Finn H. Brække, Seppo Kaunisto, Eero Paavilainen, and Juhani Päivänen and Jussi Saramäki, Lic. For. and Mr. Jaakko Hei-

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Joensuu, November 1991

Leena Finér

1. Introduction

Drained peatland ecosystems in Fennoscandia usually have more organic matter and macronutrients in the root zone than in the vegetation (see e.g. Holmen 1964, Paavilainen 1980, Brække 1988, Kaunisto & Paavilainen 1988, Finér 1989). Potassium is often an exception, because it occurs in almost equal amounts in the vegetation and in the surface peat. Harvesting removes nutrients from the ecosystem, exhausting potassium stores sooner than those of the other nutrients (Kaunisto & Paavilainen 1988, Finér 1989).

Tree growth on ombrotrophic peatlands in Finland is dependent on the pool of available nutrients in the root zone, because nutrient input from the atmosphere is low (see e.g. Järvinen 1986). A shortage of phosphorus, potassium and nitrogen usually limits tree growth on bogs (e.g. Meshechok 1967, Brække 1977a, 1979, Paavilainen 1979). On inland sites, additional boron is also often necessary for balanced growth (Brække 1977a, 1979, 1983, Huikari 1977).

Fertilization has been a common practice in peatland forestry in Finland. The stem height, diameter and volume growth responses of Scots pine to fertilization have been documented in

many studies on peat soils. Changes in nutrient concentrations, mostly in the foliage, are also frequently observed. Conclusions about the effect of fertilization on the dry mass and nutrient status in the other tree compartments, however, have to be drawn primarily from the results of only a few studies (see Paavilainen 1967, 1968, 1969, 1980, Vasander 1982, Brække 1986, Finér 1989).

The nutrient doses used in single fertilization treatments are large and not always balanced with the annual uptake of trees. Only relatively small amounts of the fertilizer nutrients usually accumulate in the trees (see e.g. Paavilainen 1973, Ballard 1984, Melin & Nömmik 1988). Most of the added nutrients are fixed in the understorey vegetation and soil or leached out.

The aim of the present study is to determine the effects of fertilization on the dry mass accumulation and nutrient cycling of Scots pine (*Pinus sylvestris* L.) growing on an ombrotrophic pine bog. This study is a part of a Nordic project, the main objectives of which are to study the distribution and cycling of nutrients on drained ombrotrophic pine bogs in different climatic conditions.

2. Material and methods

21. Study site

The experimental field is located in North Karelia (64 km SE of Joensuu 62°14' N; 29°50' E, 81 m a.s.l.). The climatic data are presented in Table 1. The year 1987 was cooler with more precipitation than the others, and the surface peat did not thaw until two weeks after the beginning of the growing season. According to the classification of Heikurainen and Pakarinen (1982), the site type has originally been a low-shrub pine bog. A detailed description of the vegetation is presented by Finér and Brække (1991a). The site was drained in 1967 with a 50 m ditch spacing, and fluctuations in the groundwater table were monitored during 1984-1987 (Table 2).

The peat layer is over one-meter thick and consists of slightly decomposed (vonPost, H3-H5) *Sphagnum* peat with wood in all layers and some *Carex* remnants below a depth of 20 cm (see Brække & Finér 1991). A naturally regenerated 85-year-old Scots pine (*Pinus sylvestris* L.) stand is growing on the site (Table 3) (see also Finér 1991a).

The field experiment was established in 1984 and fertilized in spring 1985. A 3 * 3 Latin-square design with 1500 m² plot size was used. The treatments were as follows: 1) unfertilized (0), 2) PK(MgB), and 3) NPK(MgB). The amounts of different elements (kg/ha) applied were: N 150, P 53, K 100, Ca 135, Mg 25, S 28, Cl 95, B 2.4. The fertilizers were given as ammonium nitrate, raw phosphate, potassium chloride, magnesium sulphate and sodium borate.

22. Collection of the material

General

The breast height diameter (mm), height (dm) and length of the living crown (dm) of each tree were measured on the sample plots in 1984 and 1987 (Finér 1991a). The trees were classified into different classes in 1984 as follows: 1) dominant 2) co-dominant, 3) intermediate, 4) suppressed trees. The sampling for dry mass and nutrient determinations was carried out twice, in September-October 1984 and 1987. On both occasions 27 sample trees were chosen, three per sample plot using stratified random sampling based on breast-height diameter. In 1984 the trees were chosen from outside the plots, and in 1987 from inside the plots. The sample tree characteristics are presented in Appendix 1.

Stem measurements

The sample trees were cut as close to the ground as possible and discs were sawn from different relative heights (0, 10, 20, 30, 40, 50, 60, 70, 80, 90 %) and breast height. The over-bark and under-bark diameters (0.01 mm) were measured from the discs in two oppos-

ing directions, and the number of annual rings was counted. For the density measurements the fresh volume of the stemwood and stembark was determined by immersing the discs in water.

Branch measurements

The locations of the living branches were defined to 0-30, 30-50, 50-60, 60-70, 70-80, 80-90, 90-100 % of the living crown starting from the lower limit of the living crown. The branch length (cm) and the base diameter (mm) from two opposite directions at a distance of three centimeters from the stem were measured. All dead branches and also all the cones in 1987 were detached and their fresh mass (g) weighed. The branch characteristics are presented in Appendix 2.

Seven living branches were chosen from each sample tree at relative heights of 15, 40, 55, 65, 75, 85, 95 % from the lower limit of the living crown. The branches were divided in the laboratory into cones, current needles (C), one-year-old needles (C + 1), older needles (C ≥ 2) and branchwood with bark. The age of the branches was also determined (Appendix 3). In 1987 the 1000-needle mass was determined in different age classes on one sample tree on every sample plot (Appendix 4). All cones (1987) and ten dead branches were also randomly chosen from each sample tree for dry mass determinations.

Below-ground compartments

Stump and coarse roots ($\varnothing > 10$ mm) of every fourth sample tree were excavated in 1984. In 1987 the stump and coarse roots of one sample tree per plot were sampled for nutrient analyses. The small and fine roots ($\varnothing \leq 10$ mm) were sampled using the core method (see Finér 1991b).

Litterfall

Litterfall was collected on each sample plot with five systematically placed collectors (25 × 25 cm) from September 1984 to September 1987. The collectors were emptied and the nutrient content determined six times per year. The amount of litterfall is presented in Appendix 5. In 1987 the dry mass of 1000 litter needles was determined at each sampling (Appendix 4).

Dry mass and nutrient determinations

All samples were dried at 60 °C to constant weight and weighed. A subsample was dried at 105 °C for dry mass determination.

Nitrogen was analyzed by the Kjeldahl method and K,

Table 1. Length of the growing season, temperature sum (threshold 5 °C) and accumulated precipitation during 1984–1987. The values measured at the synoptic climatic station Tohmajärvi are given in parentheses.

Taulukko 1. Kasvukauden pituus, lämpösomma (kynnysarvo 5°C) ja sademäärä vuosina 1984–1987. Ilmatieteen laitoksen Tohmajärven asemalla mitatut arvot on esitetty suluissa.

Year <i>Vuosi</i>	Length of growing season, days <i>Kasvukauden pituus, vrk</i>	Temperature sum <i>Lämpösomma</i>	Precipitation, mm	
			1.6.–30.9	1.1.–31.12
1984	165 (168)	1107 (1243)	238 (249)	– (618)
1985	141 (169)	1097 (1129)	282 (350)	582 (755)
1986	128 (151)	1026 (1135)	240 (302)	573 (650)
1987	173 (173)	939 (967)	478 (474)	698 (749)

Table 2. Groundwater level during June–September in 1984–1987. The values are average distances to the water table measured from the soil surface, in wells spaced across the plots at right angles to the ditch direction (n = 12).

Taulukko 2. Pohjavesipinnan etäisyys maanpinnasta kesä-syyskuussa vuosina 1984–1987 mitattuna tasaisin välein poikkisaran sijoitetuista kaivoista (n = 12).

Year <i>Vuosi</i>	Treatment <i>Käsittely</i>	Mean <i>Keskiarvo</i>	Max cm	Min
1984	0	48	69	20
	PK	48	70	20
	NPK	48	70	20
1985	0	36	49	27
	PK	33	47	25
	NPK	34	47	27
1986	0	42	58	21
	PK	44	62	23
	NPK	44	60	23
1987	0	25	41	18
	PK	25	40	18
	NPK	25	41	18

Table 3. Tree stand characteristics for trees living in 1987.

Taulukko 3. Puustotunnukset jakson lopussa eläville puille.

Treatment <i>Käsittely</i>	Stem volume o.b. <i>Rungon kuorellinen tilavuus</i> m ³ /ha		Volume growth o.b. <i>Rungon kuorellinen tilavuuskasvu</i> m ³ /ha/a	Stems/ha <i>Runkotuuku, kpl/ha</i>
	1984	1987		
0	79.7	97.3	5.9	2219
PK	78.8	97.4	6.2	2178
NPK	79.4	99.1	6.6	2072

Ca, Mg, P, S, B, Fe, Mn, Zn and Cu by inductively coupled plasma emission spectrophotometer (ARL 3580) after nitric-perchloric acid digestion (see also Finér 1992).

23. Calculations

231. Equations

Stem, stump and coarse root dry mass

The over-bark and under-bark volumes of the sample trees were calculated by integrating the taper curve smoothed by a cubic spline-function. The volume of bark was obtained as the difference between these volumes. The dry mass of stemwood and stembark (Appendix 6) was calculated by multiplying the volume with the corresponding density obtained as the dry mass-weighted mean of the wood and bark densities of the discs (Appendix 1).

Regression equations based on breast height diameter and tree height were made for stemwood and stembark (Appendix 7). The breast height diameter was used to predict the stump and coarse root dry mass combined (Appendix 7).

Crown dry mass

Formulation of the crown dry mass equations was started from the branch dry mass equations. The dry mass of the foliage was accordingly predicted by branch diameter, length and position in the crown and the dry mass of the branchwood with branch diameter and length only (Appendix 8). The foliar and branchwood dry masses of each sample tree were calculated using these equations (see Appendix 6). The stem diameter at breast height and crown ratio were used to predict the tree foliar and branchwood dry masses, and the breast height diameter only for prediction of the dry mass of dead branches and cones (Appendix 9).

232. Dry mass and dry mass production

The above-ground, stump and coarse root dry masses of the tree stand on each plot in 1984 and 1987 were obtained by summing up the calculated dry masses of each tree (living in 1987) using the equations (see Ap-

pendices 7 and 9). The small and fine-root dry mass ($\varnothing \leq 10$ mm) (Finér 1991b) and the litterfall had been measured at the stand level.

The difference between the tree stand dry mass in 1987 and 1984 was regarded as *dry mass accumulation*. The mean above-ground *dry mass production* in the stand during 1984–1987 was estimated by summing up the production in the different tree compartments. The stem, stump and coarse root production was assumed to equal the accumulation. The needle, branch and cone production was calculated from the tree stand dry masses in 1984 and 1987 and litterfall (see Appendix 10). The change in the dry mass by needle age was regarded in the foliage production estimate by assuming no fertilization effect.

233. Nutrient accumulation

The nutrient contents in different tree compartments in the stand before (1984) and three years (1987) after the fertilization treatments were calculated by multiplying the dry masses of the different compartments with the corresponding nutrient concentrations (Finér 1992). The nutrient contents of the litterfall were calculated by multiplying the concentration at each sampling with the corresponding amount of litter. The dry-weight weighted, mean nutrient concentrations are presented in Appendix 11.

The difference between the nutrient contents of the tree stand in 1987 and 1984 was regarded as *nutrient accumulation*. The *nutrient uptake* from the soil to the above-ground compartments was calculated as the sum of the nutrient accumulation in the above-ground compartments and the nutrient content of the above-ground litterfall.

234. Statistical tests

The differences between the results for 1984 and for 1987 were tested with paired t-tests, and the effect of fertilization with analysis of variance and covariance. The differences between the effects of different treatments were tested with the F test after analysis of variance. The tests were done using the T-TEST PAIRS and MANOVA procedures of the SPSS-X statistical package (SPSS-X... 1983).

3. Results

31. Dry mass and its accumulation

Before fertilization in 1984 the average total dry mass of the trees on the sample plots was 77.7 t/ha, of which the above-ground compartments accounted for 69 % (Table 4). The proportion of stemwood was 47 %, and that of the stump and coarse roots 23 %. The dry mass of the living branches and fine roots was almost the same, 8 %, and that of the stembark and foliage, each 5 %. The dead branches accounted for about 3 % of the total dry mass.

64 % of the total above-ground stand dry mass was in the dominant tree class (Fig. 1). The above-ground dry mass was not distributed in the different tree compartments in the same way in all tree classes. The dry mass of stemwood and living branches was proportionally greater in the upper tree classes, and that of stembark, foliage and dead branches in the lower tree classes.

The mean annual dry mass accumulation during 1984–1987 was 3.7 t/ha (4.7 %) on the unfertilized plots (Table 5). Approximately 58

% of this was located in the stemwood, 6 % in the living branches, 12.5 % in the dead branches and 27 % in the stump and coarse roots. The needle dry mass of the oldest age class decreased during the observation period (Tables 5 and 6).

There were statistically significant differences in the stand stembark and foliar dry masses between the treatments before fertilization (Table 6). However, their use as a covariate did not increase the coefficient of determination when the effect of fertilization was tested, and the covariate was omitted from the tests.

Fertilization had no significant effect on the total stand dry mass or dry mass accumulation (Tables 5 and 6). The distribution of dry mass, however, changed in the crowns of the trees. In 1987 the total needle dry mass was 10 % higher on the PK and 7 % higher on the NPK fertilized plots than on the unfertilized ones. In 1984 the corresponding percentages were 2 % and –2 %. The dry mass of the youngest needles increased only on the PK plots due to fertilization (Tables 4, 5 and 6, Fig. 2). The dry mass of needles

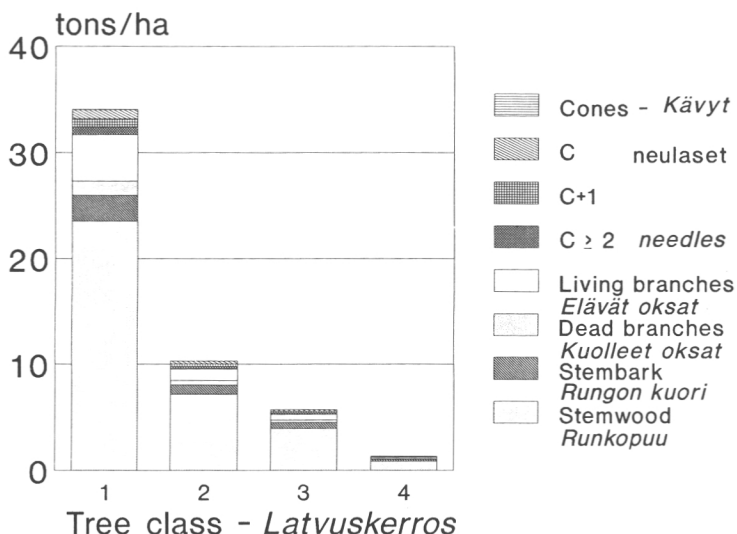


Fig. 1. Distribution of the above-ground dry mass in different tree compartments in different tree classes on the sample plots in 1984, (1 = dominant, 2 = co-dominant, 3 = intermediate, 4 = suppressed).

Kuva 1. Maanpäällisen kuivamassan jakaantuminen puuston eri osiin eri latvuskerroksissa vuonna 1984, (1 = valta puut, 2 = lisävalta puut, 3 = välipuut, 4 = aluspuut).

Table 4. Distribution of dry mass in different tree compartments in 1984 (n = 9) and 1987 (n = 3) on the unfertilized, PK and NPK fertilized plots, (standard deviation in parentheses).
 Taulukko 4. Kuivamassan jakaantuminen puuston eri osiin vuonna 1984 (n = 9) ja vuonna 1987 (n = 3) lannoittamattomilla (0), PK- ja NPK-lannoitetuilla koelaitilla (keskihajonta suluisissa).

	1984		1987					
			0	PK	NPK			
	kg/ha							
Cones – Kävyt	38	(1)	49	(7)	77	(7)	229	(28)
Needles – Neulaset								
C	1387	(29)	1461	(38)	1550	(40)	1380	(58)
C + 1	1218	(25)	1164	(27)	1610	(66)	1532	(48)
C ≥ 2	1216	(21)	747	(29)	551	(22)	689	(40)
Living branches – Elävät oksat	6408	(146)	7001	(328)	7424	(103)	7607	(378)
Dead branches – Kuolleet oksat	2122	(10)	3512	(128)	3011	(92)	2984	(234)
Stembark – Rungon kuori	4232	(48)	5723	(142)	5664	(295)	5646	(319)
Stemwood – Runkopuu	36737	(290)	43471	(1840)	42493	(4760)	42294	(4362)
Above-ground – Maanpääll.	53356	(233)	63128	(2840)	62380	(5124)	62361	(5399)
Stump and coarse roots Kanto ja paksujuuret	17994	(39)	21001	(784)	21099	(534)	21438	(1518)
Small and fine roots – Ohutjuuret	6365	(458)	4423	(1027)	5997	(55)	6510	(2399)
Below-ground – Maanal.	24359	(419)	25424	(1700)	27096	(575)	27948	(3872)
Total dry mass Kokonaiskuivamassa	77716	(186)	88552	(4179)	89476	(5657)	90309	(9163)

which had been formed in the second year (C + 1) after fertilization was greater in all tree classes as a result of both fertilization treatments. The dry mass of the oldest needles (C ≥ 2) on the dominant trees decreased most clearly after PK fertilization. These needles had mostly been formed in the year of fertilization. The cone dry mass increased in all tree classes, and more after NPK than after PK fertilization.

NPK fertilization increased the living branch dry mass (Tables 5 and 6); in 1987 it was 9 % higher on the NPK plots than on the unfertilized ones (Table 4). The response was measured only in the dominant trees (Fig. 3). The dry mass of dead branches decreased. In 1987 it was 14–15 % smaller on the fertilized plots than on the unfertilized plots. The decrease was relatively smaller in the dominant than in the other tree classes.

Fertilization had no effect on the stemwood or stembark in any of the tree classes. The stump and coarse root dry mass and the small and fine-root dry masses were not affected by fertilization (see also Finér 1991b).

32. Dry mass production

The annual above-ground dry mass production was 6.3 t/ha on the unfertilized plots (Table 7). About 40 % of the above-ground production occurred in the stems, almost the same proportion in the foliage and the remaining 20 % in the branches and cones. 51 % of the above-ground production accumulated in the standing crop, the rest was lost as litter.

Fertilization had no effect on the total above-ground production. However, the branch and cone production increased by 23 % after NPK fertilization.

33. Nutrient content

The studied nutrients accounted for 0.49 % (392 kg/ha) of the dry mass of the trees on the sample plots in 1984 (Table 8). The proportions were N 44 %, Ca 23 % and K 15 %, and the remainder (18 %) was fairly evenly distributed between P, Mg, S and micronutrients combined. Manganese was the dominant micronutrient, followed by Fe, Zn, B and Cu.

Table 5. Mean annual dry mass accumulation during 1984–1987 in different tree compartments on the unfertilized (0), PK and NPK fertilized plots and the F values of the analyses of variance (standard deviation in parentheses).
 Taulukko 5. Kuivamassan kertymä vuosina 1984–1987 puuston eri osissa lannoittamattomilla (0), PK- ja NPK-lannoitetuilla koealoilla sekä varianssianalyysien F-arvot (keskihajonta suluisissa).

	0	PK	NPK	F value – F-arvo
	kg/ha/a			
Cones – Kävyt	5 (1)	13 (2)	63 (5)	1421 ***
Needles – Neulaset				
C	25 (21)	45 (10)	7 (18)	43.6 *
C + 1	-18 (16)	122 (3)	113 (11)	178 **
C ≥ 2	-157 (13)	-228 (11)	-168 (17)	143 **
Living branches – Elävät oksat	225 (114)	282 (29)	429 (82)	9.0
Dead branches – Kuolleet oksat	460 (21)	297 (22)	290 (17)	284 ***
Stembark – Rungon kuori	487 (29)	469 (91)	490 (30)	0.2
Stemwood – Runkopuu	2149 (127)	2017 (569)	1849 (209)	0.6
Above-ground – Maanpääll.	3176 (256)	3017 (693)	3073 (71)	0.1
Stump and coarse roots	989 (92)	1037 (99)	1160 (101)	20.1
Kanto- ja paksujuuret				
Small and fine roots – Ohutjuuret	-487 (402)	-139 (240)	-96 (914)	0.6
Below-ground – Maanal.	502 (328)	898 (212)	1064 (814)	1.2
Total dry mass – Kokonaiskuivamassa	3678 (419)	3915 (811)	4137 (824)	1.9

* p < 0.05, ** p < 0.01, *** p < 0.001

Table 6. The results of the paired t-tests and the analyses of variance. Different dry mass compartments in 1984 and 1987 as dependent variables in the t-tests, and different dry mass compartments in different treatments in 1984 and 1987 as dependent variables in the variance analyses.

Taulukko 6. Parittaiten t-testien ja varianssianalyysien tulokset. T-testien selitettävänä muuttujina kuivamassat puuston eri osissa vuosina 1984 ja 1987 ja varianssianalyysissä kuivamassat puuston eri osissa eri käsittelyillä vuosina 1984 ja 1987.

	0	PK	NPK	1984	1987
	t-value – t-arvo			F value – F-arvo	
Cones – Kävyt	-11.2**	-14.3**	23.7***	0.1	140.4**
Needles – Neulaset					
C	-2.0	-7.6*	-0.7	82.9**	196.3**
C + 1	1.9	-61.0***	-17.2***	45.4*	287.3***
C ≥ 2	20.3***	35.0***	17.0***	35.5*	272.5***
Living branches – Elävät oksat	-3.4	-17.1***	-9.1**	1.3	125.1**
Dead branches – Kuolleet oksat	-37.4***	-23.5***	-29.3***	0.1	43.1*
Stembark – Rungon kuori	-29.2***	-8.9**	-28.4***	65.2*	0.4
Stemwood – Runkopuu	-29.4***	-6.1*	-15.3***	0.2	0.2
Above-ground – Maanpääll.	-40.7***	-13.8**	15.3***	0.1	0.1
Stump and coarse roots	-18.6***	-18.2***	-19.9***	0.0	0.6
Kanto- ja paksujuuret					
Small and fine roots – Ohutjuuret	2.1	1.0	0.2	1.0	2.6
Below-ground – Maanal.	2.7	7.3*	2.3	6.5	2.7
Total dry mass – Kokonaiskuivamassa	-15.2***	-8.4**	-8.7***	0.1	0.3

* p < 0.05, ** p < 0.01, *** p < 0.001

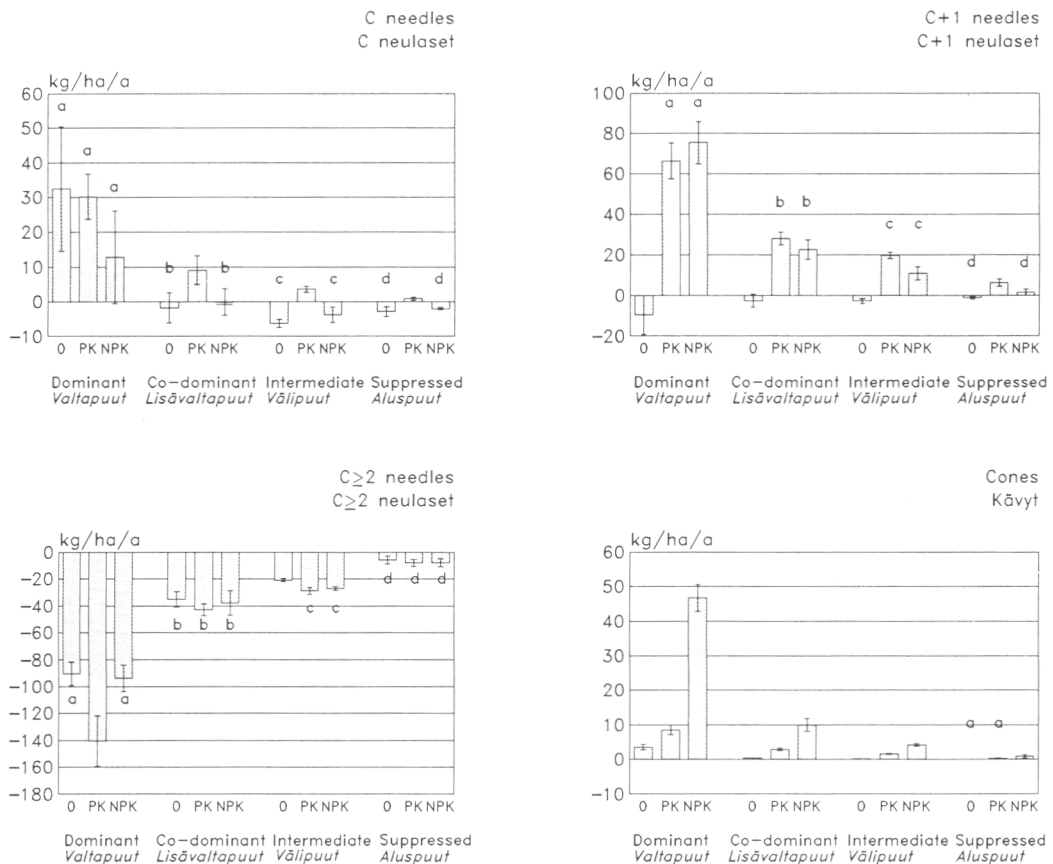


Fig. 2. Annual foliar and cone dry mass accumulation in different tree classes on the control, PK and NPK fertilized plots during 1984–1987. Mean values with the same letter do not differ significantly from each other according to the F test ($p > 0.05$).

Kuva 2. Keskimääräinen vuotuinen neulasten ja käpyjen kuivamassan kertymä eri latvuskerroksissa lannoittamattomilla, PK- ja NPK-lannoitetuilla koealoilla vuosina 1984–1987. Samalla kirjaimella merkityt keskiarvot eivät poikkea merkitsevästi toisistaan F-testin perusteella ($p > 0.05$).

Table 7. Mean annual above-ground dry mass production after fertilization and the F values of variance analyses (standard deviation in parentheses).

Taulukko 7. Keskimääräinen vuotuinen kuivamassan tuotos lannoituksen jälkeen ja varianssianalyysien F-arvot (keskihajonta suluisissa).

Compartment – Osite	0	PK	NPK	F value F-arvo
		kg/ha/a		
Needles – Neulaset	2445 (215)	2303 (351)	2423 (293)	0.35
Branches & Cones – Oksat & kävyt	1178 (150)	1022 (155)	1445 (309)	26.0*
Stem with bark – Runko kuorineen	2636 (107)	2486 (660)	2339 (210)	0.2
Total – Koko	6259 (448)	5810 (980)	6208 (628)	0.27

* $p < 0.05$

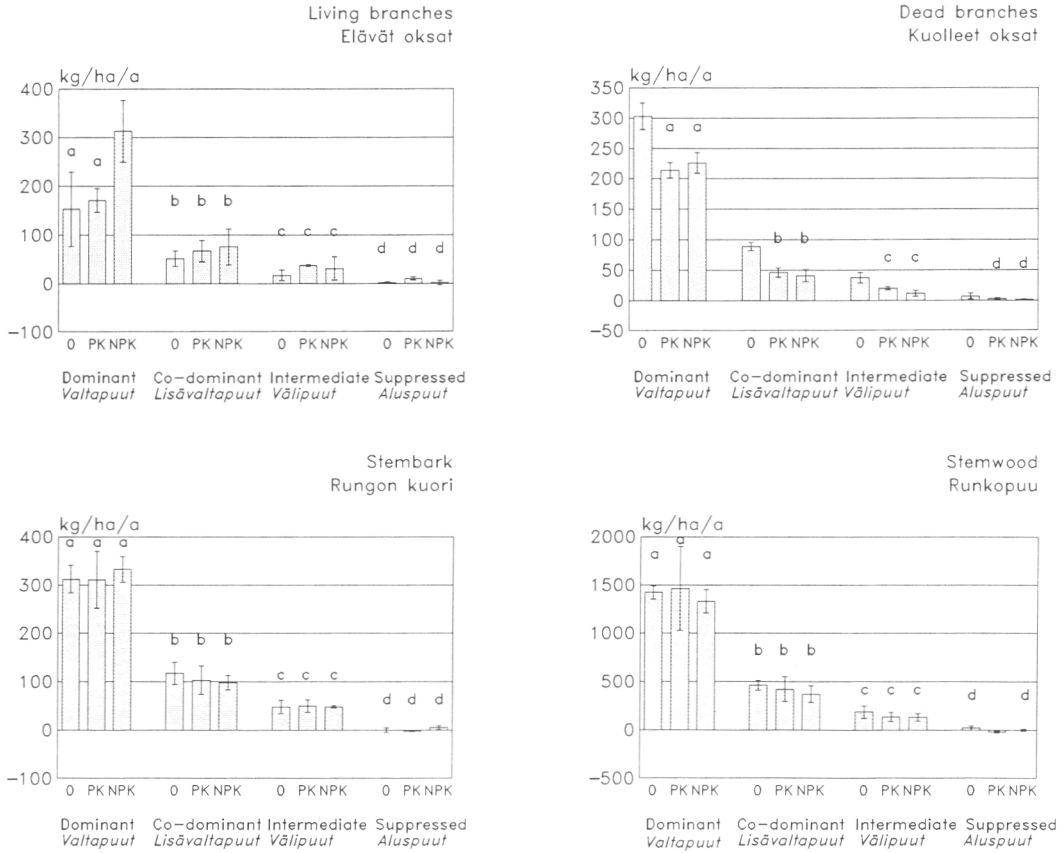


Fig. 3. Annual branch and stem dry mass accumulation in different tree classes on the control, PK and NPK fertilized plots during 1984–1987. Mean values with the same letter do not differ significantly from each other according to the F test ($p > 0.05$).

Kuva 3. Keskimääräinen vuotuinen oksien ja rungon kuivamassan kertymä eri latvuseroksissa lannoittamattomilla, PK- ja NPK-lannoitetuilla koealoilla vuosina 1984–1987. Samalla kirjaimella merkityt keskiarvot eivät poikkea merkittävästi toisistaan F-testin perusteella ($p > 0.05$).

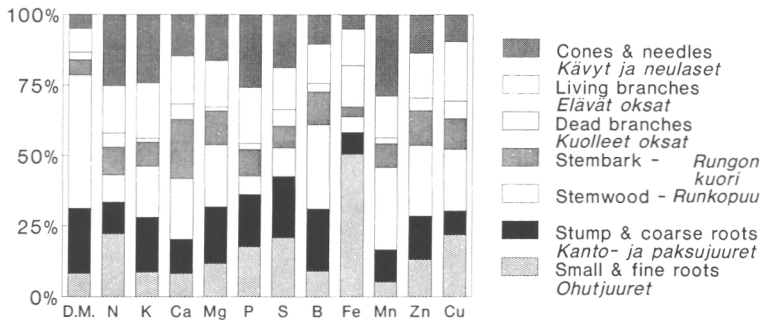


Fig. 4. Average percentual distribution of dry mass and nutrients in the different tree compartments on the sample plots in 1984.

Kuva 4. Kuivamassan ja ravinteiden keskimääräinen prosentuaalinen jakaantuminen puuston eri osiin koealoilla vuonna 1984.

Table 8. Average amounts of nutrients in different tree compartments in 1984 on the sample plots (n = 9), (standard deviation in parentheses).

Taulukko 8. Eri puuston osien keskimääräiset ravinnemäärät koaloilla (n = 9) vuonna 1984, (keskihajonta suluisissa).

	N	K	Ca kg/ha	Mg	P
Cones – Kävyt	0.12 (0.03)	0.06 (0.01)	0.01 (0.00)	0.02 (0.00)	0.01 (0.00)
Needles – Neulaset					
C	15.53 (0.62)	5.48 (0.22)	3.13 (0.12)	1.48 (0.06)	1.75 (0.07)
C + 1	14.13 (0.54)	4.40 (0.17)	4.42 (0.17)	1.15 (0.04)	1.38 (0.05)
C ≥ 2	13.86 (0.52)	4.10 (0.15)	5.53 (0.21)	0.96 (0.04)	1.32 (0.05)
Living branches – Elävät oksat	28.90 (0.99)	11.34 (0.39)	15.32 (0.52)	3.66 (0.12)	3.44 (0.12)
Dead branches – Kuolleet oksat	8.74 (0.47)	0.84 (0.04)	4.88 (0.26)	0.32 (0.02)	0.39 (0.02)
Stembark – Rungon kuori	17.10 (0.63)	4.95 (0.18)	19.00 (0.70)	2.68 (0.10)	1.64 (0.06)
Stemwood – Runkopuu	16.75 (1.33)	10.51 (0.83)	19.36 (1.53)	4.89 (0.39)	1.12 (0.09)
Above-ground – Maanpääll.	115.13 (4.05)	41.68 (1.57)	71.65 (2.90)	15.15 (0.62)	11.05 (0.37)
Stump and coarse roots					
Kanto- ja paksujuuret	19.61 (1.17)	11.34 (0.67)	10.98 (0.65)	4.50 (0.77)	3.24 (0.19)
Small and fine roots	38.51 (4.45)	5.03 (0.58)	7.32 (0.85)	2.61 (0.30)	3.05 (0.35)
Ohutjuuret					
Below-ground – Maanal.	58.12 (4.17)	16.37 (0.71)	18.30 (0.86)	7.11 (0.32)	6.29 (0.33)
Total – Koko	173.25 (4.98)	58.05 (1.97)	89.95 (3.22)	22.26 (0.78)	17.34 (0.48)

The nutrient stores in the foliage and branches were greater and that in the stem smaller than their proportion of the dry mass (Fig. 4). The stump and all roots combined accounted for a smaller proportion of the Ca and Mn and a higher proportion of the P, S and Fe stores than their proportion of the dry mass.

The foliage contained almost the same amounts of N, K, Mg, P and S as the living and dead branches combined. Manganese was the only element that was more abundant in the foliage than in the branches. Except for Fe, the living branches had larger nutrient stores than the dead ones. The dry mass of the stembark was small compared to that of the stemwood. However, it contained more P and almost equal amounts of N and Ca as the stemwood. The small and fine roots ($\varnothing \leq 10$ mm) had fixed, except for Fe, also more N and Cu than the stumps and coarse roots.

34. Nutrient accumulation

Annually 5.3 kg/ha of N, 3.7 kg/ha of K, 4.3 kg/ha of Ca and 0.9 kg/ha of P were accumulated in the trees on the unfertilized plots (Table 9). The annual accumulation of Mn, Fe, Mg and S was

317, 244, 213 and 70 g/ha, and that of Zn, B and Cu only 28, 24 and 5 g/ha, respectively. The major part of the nutrients was distributed in the above-ground compartments, especially in the stemwood, stembark and dead branches. The dry mass of the oldest needles was smaller in 1987 than in 1984; this also had an effect on the foliar nutrient stores. However, the foliar P, K and B contents did not decrease. The small and fine root nutrient stores decreased during 1984–1987.

Fertilization had an effect on the total accumulation of all nutrients except Mg, Fe, and Zn (Tables 9 and 10). The fertilized stands accumulated more N, K, P, S, Cu and B and less Ca and Mn. The effect of NPK fertilization was greater on the N, S and Mn contents and smaller on the Ca and Cu contents than that of PK fertilization ($p \leq 0.05$). The nutrient contents of the stump and coarse roots, foliage and living branches were, in relative terms, the most strongly affected by fertilization.

The increased nutrient accumulation corresponded to about 35 % of the N applied on the NPK fertilized plots, and 25 % of the K, 10 % of the P, S and B on the NPK and PK plots within the three-year period. When the increase in N accumulation on the PK fertilized plots was

Table 8 continued.
Taulukko 8 jatkuu.

S		B		Fe		Mn		Zn		Cu	
kg/ha											
0.01	(0.00)	0.000	(0.000)	0.000	(0.000)	0.001	(0.000)	0.001	(0.000)	0.000	(0.000)
1.18	(0.05)	0.019	(0.001)	0.041	(0.002)	0.587	(0.023)	0.059	(0.002)	0.004	(0.000)
1.10	(0.04)	0.016	(0.001)	0.057	(0.002)	0.808	(0.031)	0.061	(0.002)	0.004	(0.000)
1.10	(0.04)	0.013	(0.001)	0.068	(0.003)	0.906	(0.036)	0.064	(0.002)	0.004	(0.000)
2.67	(0.09)	0.065	(0.002)	0.417	(0.014)	1.192	(0.041)	0.219	(0.007)	0.027	(0.001)
1.07	(0.06)	0.014	(0.001)	0.477	(0.026)	0.171	(0.009)	0.062	(0.003)	0.008	(0.000)
1.40	(0.05)	0.054	(0.002)	0.116	(0.004)	0.677	(0.025)	0.170	(0.006)	0.014	(0.001)
1.84	(0.14)	0.140	(0.011)	0.178	(0.014)	2.340	(0.185)	0.344	(0.027)	0.028	(0.002)
10.37	(0.38)	0.321	(0.015)	1.354	(0.056)	6.682	(0.280)	0.980	(0.043)	0.089	(0.004)
3.96	(0.24)	0.103	(0.006)	0.257	(0.015)	0.927	(0.055)	0.214	(0.013)	0.011	(0.001)
3.75	(0.43)	0.042	(0.005)	1.649	(0.190)	0.414	(0.048)	0.180	(0.021)	0.028	(0.003)
7.71	(0.41)	0.145	(0.006)	1.906	(0.185)	1.341	(0.058)	0.394	(0.020)	0.039	(0.003)
18.08	(0.56)	0.466	(0.020)	3.260	(0.172)	8.023	(0.310)	1.374	(0.049)	0.128	(0.004)

taken into account, a maximum of 20 % of the N fertilizer accumulated in the trees on the NPK fertilized plots from 1984 to 1987.

Although fertilization had an effect on the accumulation of most nutrients, it did not have any significant effect on the dry mass accumulation (chapter 31.). Consequently the trees on the fertilized plots used the N, K, P, S, B and Cu less effectively, and the Ca and Mn more effectively than those on the unfertilized plots (see Table 11).

35. Above-ground nutrient uptake and turnover

The annual nutrient uptake of the trees on the unfertilized plots was as follows: N 15.6, Ca

12.8, K 4.1, P 1.3, Mg 1.7 and S and Mn 1.5 kg/ha (Table 10). The annual uptake of Fe and Zn was 510 and 130 g/ha and that of Cu and B less than 100 g/ha. Only part of the uptake accumulated in the standing crop. About 30 % of the K, 40 % of the Fe, 50 % of the P, 60 % of the B, 70 % of the N, Ca, Mg, S, Zn and over 80 % of the amount of Mn and Cu uptake were released to the soil in litterfall (Table 10). The needle litter accounted for 40 % of the Cu, 55 % of the Fe and over 70 % of the release of the other nutrients (Table 12).

Fertilization increased only the B content in the litterfall ($p = 0.07$) (Tables 10 and 12). The increase was equivalent to 4 % of the applied B.

Table 9. Annual nutrient accumulation during 1984–1987 in the different tree compartments on the unfertilized (0), PK and NPK fertilized plots and the results of the analyses of variance. Those with NS do not differ significantly from each other, $p > 0.05$ (standard deviation in parentheses).

Taulukko 9. Ravinteiden vuotuinen sitoutuminen puuston eri osiin vuosina 1984–1987 lannoittamattomilla (0), PK- ja NPK-lannoitetuilla koealoilla ja varianssianalyysien tulokset. Ne jotka eivät eroa toisistaan merkitsevästi ($p > 0.05$) on merkitty NS:llä (keskihajonta suluisa).

	0	PK	NPK	0	PK	NPK	0	PK	NPK
				kg/ha/a					
	N			K			Ca		
Cones	0.015	0.040	0.255	0.016	0.045	0.175	0.000	0.001	0.008
<i>Kävyt</i>	(0.002)	(0.005)	(0.021)	(0.002)	(0.002)	(0.017)	(0.000)	(0.000)	(0.000)
Needles	-1.793	-0.624	1.098	0.168	2.092	1.982	-0.804	-1.347	-1.031
<i>Neulas</i>	(0.574)	(0.195)	(0.518)	(0.205)	(0.020)	(0.192)	(0.165)	(0.090)	(0.157)
Living branches	0.873	1.224	4.038	0.561	1.341	2.508	0.654	-0.859	0.213
<i>Elävät oksat</i>	(0.507)	(0.128)	(0.423)	(0.209)	(0.062)	(0.197)	(0.278)	(0.048)	(0.183)
Dead branches	2.106	1.555	1.563	0.275	0.217	0.182	1.631	0.412	0.687
<i>Kuolleet oksat</i>	(0.094)	(0.095)	(0.096)	(0.011)	(0.010)	(0.011)	(0.068)	(0.047)	(0.041)
Stembark	1.586	3.027	3.259	1.218	2.210	1.872	1.195	-1.652	-0.303
<i>Rungon kuori</i>	(0.108)	(0.417)	(0.193)	(0.049)	(0.184)	(0.108)	(0.107)	(0.279)	(0.020)
Stemwood	2.226	3.498	3.113NS	0.455	1.866	1.629	1.495	0.567	1.059NS
<i>Runkopuu</i>	(0.065)	(0.547)	(0.240)	(0.039)	(0.307)	(0.121)	(0.064)	(0.245)	(0.109)
Above-ground	5.013	8.720	13.326	2.693	7.771	8.348	4.171	-2.878	0.633
<i>Maanpäälliset</i>	(1.278)	(1.188)	(1.112)	(0.459)	(0.545)	(0.494)	(0.582)	(0.629)	(0.277)
Stump and coarse roots	3.388	5.209	6.838	1.673	4.943	3.661	0.673	0.843	0.565
<i>Kanto- ja paksujuuret</i>	(0.142)	(0.055)	(0.286)	(0.075)	(0.063)	(0.144)	(0.057)	(0.056)	(0.072)
Small and fine roots	-3.081	-1.059	2.457NS	-0.665	0.090	0.054NS	-0.590	0.000	-0.176NS
<i>Ohutjuuret</i>	(2.406)	(1.448)	(6.600)	(0.261)	(0.191)	(0.768)	(0.457)	(0.277)	(1.028)
Below-ground	0.307	4.150	9.295NS	1.008	5.033	3.715	0.083	0.844	0.389NS
<i>Maanalaiset</i>	(2.358)	(1.486)	(6.884)	(0.229)	(0.254)	(0.912)	(0.411)	(0.258)	(0.957)
Total	5.320	12.870	22.621	3.701	12.804	12.063	4.254	-2.034	1.022
<i>Koko</i>	(3.066)	(2.565)	(7.767)	(0.598)	(0.704)	(1.374)	(0.834)	(0.862)	(0.982)
	Mg			P			S		
Cones	0.002	0.004	0.023	0.004	0.009	0.035	0.002	0.004	0.023
<i>Kävyt</i>	(0.000)	(0.001)	(0.002)	(0.001)	(0.000)	(0.003)	(0.000)	(0.000)	(0.002)
Needles	-0.169	-0.230	-0.178NS	-0.003	0.341	0.372	-0.200	-0.169	-0.047
<i>Neulas</i>	(0.047)	(0.023)	(0.042)	(0.064)	(0.010)	(0.056)	(0.043)	(0.019)	(0.039)
Living branches	0.075	0.010	0.278	0.090	0.231	0.552	0.012	0.053	0.290
<i>Elävät oksat</i>	(0.063)	(0.014)	(0.047)	(0.060)	(0.016)	(0.053)	(0.044)	(0.011)	(0.037)
Dead branches	0.093	0.059	0.041	0.125	0.083	0.062	0.307	0.188	0.172
<i>Kuolleet oksat</i>	(0.004)	(0.003)	(0.002)	(0.005)	(0.004)	(0.004)	(0.013)	(0.012)	(0.010)
Stembark	0.274	0.234	0.135	0.323	0.497	0.414	0.179	0.265	0.270
<i>Rungon kuori</i>	(0.018)	(0.055)	(0.009)	(0.014)	(0.050)	(0.024)	(0.010)	(0.035)	(0.016)
Stemwood	0.300	0.297	0.373NS	0.069	0.195	0.138	0.068	0.122	0.146NS
<i>Runkopuu</i>	(0.017)	(0.079)	(0.029)	(0.004)	(0.032)	(0.010)	(0.007)	(0.031)	(0.011)
Above-ground	0.575	0.374	0.672NS	0.608	1.356	1.573	0.368	0.463	0.854
<i>Maanpäälliset</i>	(0.127)	(0.159)	(0.068)	(0.138)	(0.101)	(0.120)	(0.104)	(0.088)	(0.079)
Stump and coarse roots	-0.103	0.189	-0.067	0.528	1.382	0.781	0.078	0.439	0.398
<i>Kanto- ja paksujuuret</i>	(0.025)	(0.026)	(0.050)	(0.023)	(0.017)	(0.023)	(0.020)	(0.017)	(0.012)
Small and fine roots	-0.259	-0.077	-0.104NS	-0.263	0.133	0.323NS	-0.376	-0.082	0.030NS
<i>Ohutjuuret</i>	(0.153)	(0.098)	(0.352)	(0.187)	(0.177)	(0.569)	(0.219)	(0.141)	(0.570)
Below-ground	-0.362	0.112	-0.171NS	0.265	1.515	1.104NS	-0.298	0.357	0.428NS
<i>Maanalaiset</i>	(0.128)	(0.088)	(0.302)	(0.179)	(0.134)	(0.591)	(0.200)	(0.137)	(0.558)
Total	0.213	0.486	0.500NS	0.873	2.871	2.677	0.070	0.820	1.282
<i>Koko</i>	(0.200)	(0.228)	(0.334)	(0.269)	(0.221)	(0.686)	(0.247)	(0.217)	(0.608)

Table 9 continued.
Taulukko 9 jatkuu.

	0	PK	NPK	0	PK g/ha/a	NPK	0	PK	NPK
	B			Fe			Mn		
Cones	0.09	0.27	1.00	0.07	0.11	0.62	0.06	0.31	1.26
<i>Kävyt</i>	(0.01)	(0.01)	(0.10)	(0.01)	(0.02)	(0.05)	(0.01)	(0.06)	(0.05)
Needles	1.92	35.93	36.57	-6.99	-17.69	-12.38	-160.23	-257.21	-297.84
<i>Neulasat</i>	(0.74)	(1.09)	(1.72)	(2.17)	(1.21)	(1.95)	(29.26)	(16.86)	(28.68)
Living branches	-0.30	6.57	11.68	0.16	-9.08	25.11	4.46	-43.97	-24.84NS
<i>Elävät oksat</i>	(1.03)	(0.34)	(1.03)	(6.74)	(1.49)	(5.27)	(19.45)	(4.01)	(13.93)
Dead branches	1.69	1.61	2.79	145.62	80.86	81.19	59.64	35.94	15.59
<i>Kuolleet oksat</i>	(0.10)	(0.14)	(0.17)	(6.16)	(5.13)	(4.92)	(2.46)	(1.96)	(0.92)
Stembark	2.04	6.19	3.07	14.82	7.51	7.36	64.57	27.82	-26.99
<i>Rungon kuori</i>	(0.27)	(1.18)	(0.21)	(0.83)	(2.28)	(0.48)	(4.32)	(12.72)	(1.38)
Stemwood	13.57	13.37	13.97NS	138.66	7.52	105.96	286.17	127.05	-11.89
<i>Runkopuu</i>	(0.47)	(2.80)	(0.99)	(5.28)	(2.51)	(9.91)	(8.62)	(36.07)	(20.14)
Above-ground	19.01	63.94	69.08	292.34	69.23	207.86	254.67	-110.06	-344.71
<i>Maanpäälliset</i>	(2.29)	(4.12)	(3.05)	(19.91)	(9.98)	(16.37)	(60.50)	(61.91)	(40.95)
Stump and coarse roots	7.04	25.60	13.04	56.14	21.86	70.90	118.82	20.33	-33.86
<i>Kanto- ja paksujuuret</i>	(0.54)	(0.29)	(0.14)	(2.20)	(5.13)	(2.42)	(5.72)	(5.83)	(11.81)
Small and fine roots	-2.48	7.68	17.59NS	-104.11	32.04	-63.95NS	-56.74	-43.00	-58.32NS
<i>Ohutjuuret</i>	(2.81)	(1.66)	(12.58)	(108.38)	(62.69)	(223.09)	(21.10)	(15.27)	(41.66)
Below-ground	4.56	33.28	30.63NS	-47.96	53.90	6.95NS	62.08	-22.67	-92.18
<i>Maanalaiset</i>	(2.42)	(1.84)	(12.46)	(108.38)	(62.17)	(225.51)	(18.03)	(13.10)	(30.23)
Total	23.57	97.22	99.71	244.38	123.13	214.81NS	316.75	-132.73	-436.89
<i>Koko</i>	(3.92)	(5.21)	(15.51)	(117.52)	(72.15)	(240.02)	(69.52)	(71.71)	(26.39)
	Zn			Cu					
Cones	0.13	0.26	1.38	0.01	0.03	0.02			
<i>Kävyt</i>	(0.02)	(0.02)	(0.12)	(0.00)	(0.01)	(0.00)			
Needles	-11.06	-11.05	-7.87NS	-0.35	-0.27	-0.73			
<i>Neulasat</i>	(2.30)	(1.10)	(2.12)	(0.16)	(0.06)	(0.14)			
Living branches	-2.84	0.48	18.67	0.62	-0.36	1.08			
<i>Elävät oksat</i>	(3.40)	(0.85)	(2.88)	(0.47)	(0.10)	(0.33)			
Dead branches	13.46	13.03	10.40	1.90	1.15	1.31			
<i>Kuolleet oksat</i>	(0.62)	(0.71)	(0.63)	(0.09)	(0.09)	(0.08)			
Stembark	7.51	8.98	7.98NS	1.17	1.25	0.87NS			
<i>Rungon kuori</i>	(0.88)	(3.26)	(0.55)	(0.09)	(0.29)	(0.06)			
Stemwood	29.27	5.72	31.85	2.48	7.29	5.73			
<i>Runkopuu</i>	(1.13)	(3.87)	(2.29)	(0.09)	(1.08)	(0.45)			
Above-ground	36.47	17.42	62.41	5.83	9.09	8.28NS			
<i>Maanpäälliset</i>	(7.26)	(8.74)	(4.28)	(0.80)	(1.48)	(0.60)			
Stump and coarse roots	11.07	11.63	0.23	2.83	10.47	2.13			
<i>Kanto- ja paksujuuret</i>	(1.09)	(1.19)	(2.16)	(0.11)	(0.20)	(0.04)			
Small and fine roots	-19.84	-14.32	-16.61NS	-3.32	-2.21	-3.24NS			
<i>Ohutjuuret</i>	(10.15)	(6.69)	(21.07)	(1.53)	(1.04)	(3.05)			
Below-ground	-8.77	-2.69	-16.38NS	-0.49	8.26	-1.11			
<i>Maanalaiset</i>	(9.19)	(6.20)	(18.95)	(1.51)	(1.23)	(3.10)			
Total	27.70	14.73	46.03NS	5.34	17.35	7.17			
<i>Koko</i>	(12.94)	(14.20)	(21.75)	(1.87)	(2.58)	(3.60)			

Table 10. Amounts of nutrients in the dry mass in 1984 and 1987, nutrient accumulation and uptake between 1984–1987 on the unfertilized (0), PK and NPK fertilized plots and the results of the analyses of variance. Those with NS do not differ significantly from each other, ($p > 0.05$), (standard deviation in parentheses).

Taulukko 10. Puuston ravinnemäärä vuosina 1984 ja 1987, ravinteiden sitoutuminen ja maastaotto vuosina 1984–1987 lannoittamattomilla (0), PK- ja NPK-lannoitetuilla koealoilla sekä varianssianalyysien tulokset. Ne jotka eivät eroa merkitsevästi toisistaan ($p > 0.05$) on merkitty NS:llä (keskihajonta suluisissa).

	0	N PK	NPK	0	K PK	NPK	0	Ca PK	NPK
Above-ground – <i>Maan päällä</i> , kg/ha									
In tree stand 1984	115.1	116.7	113.6 NS	41.7	42.2	41.2 NS	71.8	72.3	70.9 NS
<i>Puustossa 1984</i>	(1.23)	(3.0)	(7.0)	(0.6)	(1.1)	(2.7)	(1.4)	(2.1)	(5.1)
In tree stand 1987	130.1	142.8	153.6	49.7	65.5	66.2	84.3	63.6	72.8
<i>Puustossa 1987</i>	(4.5)	(4.9)	(8.9)	(1.7)	(2.5)	(3.9)	(1.6)	(3.2)	(4.9)
Accumulated 1984–1987	15.04	26.16	39.98	8.08	23.31	25.04	12.51	-8.63	1.90
<i>Sitoutunut puustoon 1984–1987</i>	(3.83)	(3.57)	(3.34)	(1.38)	(1.63)	(1.48)	(1.75)	(1.89)	(0.83)
Litterfall 1984–1987	31.81	29.30	38.25NS	4.10	4.89	5.71NS	25.94	24.21	29.11NS
<i>Karikesato 1984–1987</i>	(2.67)	(5.15)	(8.39)	(0.37)	(1.09)	(1.35)	(1.92)	(2.73)	(2.92)
Uptake 1984–1987	46.86	55.45	78.23	12.17	28.21	30.75	38.45	15.58	31.01
<i>Maasta otettu 1984–1987</i>	(5.50)	(6.95)	(10.12)	(1.70)	(2.49)	(2.23)	(2.10)	(2.54)	(3.67)
Below-ground – <i>Maan alla</i> , kg/ha									
In tree stand 1984	55.3	55.4	60.7 NS	16.1	16.4	16.7 NS	17.7	18.3	18.8 NS
<i>Puustossa 1984</i>	(3.6)	(3.4)	(4.8)	(0.7)	(0.4)	(1.0)	(0.9)	(0.5)	(1.1)
In tree stand 1987	56.2	70.9	88.6 NS	19.0	31.5	27.8	18.0	20.9	19.9 NS
<i>Puustossa 1987</i>	(7.0)	(1.1)	(20.6)	(1.2)	(0.7)	(3.6)	(1.6)	(0.4)	(3.6)
Accumulated 1984–1987	0.92	12.45	27.9 NS	3.02	15.10	11.15	0.25	2.53	1.17NS
<i>Sitoutunut puustoon 1984–1987</i>	(7.07)	(4.46)	(20.7)	(0.69)	(0.76)	(2.74)	(1.23)	(0.78)	(2.87)
Total – <i>Koko</i> , kg/ha									
In tree stand 1984	170.3	175.1	174.3 NS	57.7	58.6	57.9 NS	89.5	90.6	89.7 NS
<i>Puustossa 1984</i>	(3.5)	(5.7)	(6.0)	(1.0)	(1.5)	(3.4)	(2.0)	(2.5)	(5.5)
In tree stand 1987	186.3	213.7	242.2	68.8	97.0	94.0	102.3	84.5	92.8
<i>Puustossa 1987</i>	(11.2)	(5.7)	(29.1)	(2.9)	(3.1)	(7.5)	(4.5)	(3.5)	(8.4)
Accumulated 1984–1987	15.96	38.61	67.90	11.10	38.41	36.19	12.76	-6.10	3.07
<i>Sitoutunut puustoon 1984–1987</i>	(9.20)	(7.70)	(23.30)	(1.79)	(2.22)	(4.12)	(2.50)	(2.59)	(2.95)

Table 10 continued.
Taulukko 10 jatkuu.

	0	Mg PK	NPK	0	P PK	NPK	0	S PK	NPK
Above-ground – <i>Maan päällä</i> , kg/ha									
In tree stand 1984	15.2	15.3	15.0 NS	11.0	11.2	10.9 NS	10.4	10.5	10.2 NS
<i>Puustossa 1984</i>	(0.3)	(0.5)	(1.1)	(0.9)	(0.3)	(0.6)	(0.1)	(0.3)	(0.7)
In tree stand 1987	16.9	16.4	17.0 NS	12.9	15.3	15.6	11.5	11.9	12.8
<i>Puustossa 1987</i>	(0.6)	(0.8)	(1.1)	(0.4)	(0.4)	(0.8)	(0.4)	(0.4)	(0.8)
Accumulated 1984–1987	1.73	1.13	2.02NS	1.82	4.07	4.72	1.10	1.39	2.56
<i>Sitoutunut puustoon 1984–1987</i>	(0.38)	(0.48)	(0.20)	(0.41)	(0.30)	(0.36)	(0.31)	(0.27)	(0.24)
Litterfall 1984–1987	3.37	3.50	3.84NS	2.12	2.14	2.64NS	3.31	3.10	3.76NS
<i>Karikesato 1984–1987</i>	(0.31)	(0.67)	(0.29)	(0.18)	(0.37)	(0.52)	(0.23)	(0.60)	(0.85)
Uptake 1984–1987	5.08	4.63	5.86NS	3.94	6.20	7.36	4.42	4.49	6.33
<i>Maasta otettu 1984–1987</i>	(0.59)	(1.03)	(0.22)	(0.48)	(0.59)	(0.73)	(0.46)	(0.68)	(0.95)
Below-ground – <i>Maan alla</i> , kg/ha									
In tree stand 1984	6.9	7.1	7.3 NS	6.1	6.3	6.5 NS	7.4	7.7	8.0 NS
<i>Puustossa 1984</i>	(0.3)	(0.2)	(0.4)	(0.3)	(0.2)	(0.4)	(0.4)	(0.3)	(0.5)
In tree stand 1987	5.8	7.5	6.8 NS	6.9	10.9	9.8	6.5	8.8	9.2 NS
<i>Puustossa 1987</i>	(0.5)	(0.1)	(1.2)	(0.6)	(0.2)	(1.9)	(0.7)	(0.2)	(1.9)
Accumulated 1984–1987	-1.09	0.34	-0.52NS	0.79	4.55	3.31NS	-0.90	1.07	1.29NS
<i>Sitoutunut puustoon 1984–1987</i>	(0.38)	(0.26)	(0.91)	(0.54)	(0.40)	(1.77)	(0.60)	(0.41)	(1.67)
Total – <i>Koko</i> , kg/ha									
In tree stand 1984	22.1	22.4	22.3 NS	17.1	17.5	17.4 NS	17.8	18.2	18.2 NS
<i>Puustossa 1984</i>	(0.5)	(0.4)	(1.3)	(0.3)	(0.5)	(0.7)	(0.4)	(0.5)	(0.8)
In tree stand 1987	22.7	23.9	23.8 NS	19.7	26.2	25.4	18.0	20.7	22.0
<i>Puustossa 1987</i>	(1.1)	(1.0)	(2.3)	(1.0)	(0.6)	(2.7)	(1.1)	(0.5)	(2.6)
Accumulated 1984–1987	0.64	1.46	1.50NS	2.62	8.61	8.03	0.21	2.46	3.85
<i>Sitoutunut puustoon 1984–1987</i>	(0.60)	(0.68)	(1.00)	(0.81)	(0.66)	(2.06)	(0.74)	(0.65)	(1.82)

Table 10 continued.
Taulukko 10 jatkuu.

	0	B PK	NPK	0	Fe PK	NPK	0	Mn PK	NPK
Above-ground – <i>Maan päällä</i> , kg/ha									
In tree stand 1984 <i>Puustossa 1984</i>	0.322 (0.009)	0.324 (0.012)	0.319NS (0.026)	1.35 (0.03)	1.37 (0.04)	1.34NS (0.10)	6.75 (0.13)	6.80 (0.23)	6.67NS (0.48)
In tree stand 1987 <i>Puustossa 1987</i>	0.380 (0.014)	0.515 (0.024)	0.526 (0.035)	2.23 (0.08)	1.58 (0.05)	1.97 (0.14)	7.51 (0.27)	6.47 (0.35)	5.63 (0.39)
Accumulated 1984–1987 <i>Sitoutunut puustoon 1984–1987</i>	0.057 (0.007)	0.192 (0.012)	0.207 (0.009)	0.88 (0.06)	0.21 (0.03)	0.62 (0.05)	0.76 (0.18)	-0.33 (0.19)	-1.04 (0.12)
Litterfall 1984–1987 <i>Karikesato 1984–1987</i>	0.091 (0.330)	0.179 (0.510)	0.192NS (0.350)	0.64 (0.09)	0.58 (0.14)	0.67NS (0.18)	3.68 (0.26)	3.55 (0.54)	3.95NS (0.37)
Uptake 1984–1987 <i>Maasta otettu 1984–1987</i>	0.148 (0.037)	0.371 (0.058)	0.400 (0.044)	1.52 (0.14)	0.79 (0.12)	1.30 (0.23)	4.44 (0.12)	3.22 (0.54)	2.91 (0.43)
Below-ground – <i>Maan alla</i> , kg/ha									
In tree stand 1984 <i>Puustossa 1984</i>	0.142 (0.006)	0.145 (0.003)	0.147NS (0.009)	1.78 (0.14)	1.92 (0.16)	2.02NS (0.22)	1.31 (0.06)	1.34 (0.03)	1.37NS (0.08)
In tree stand 1987 <i>Puustossa 1987</i>	0.155 (0.011)	0.245 (0.005)	0.239 (0.046)	1.64 (0.29)	2.08 (0.02)	2.04NS (0.61)	1.50 (0.09)	1.28 (0.03)	1.09 (0.16)
Accumulated 1984–1987 <i>Sitoutunut puustoon 1984–1987</i>	0.014 (0.007)	0.100 (0.006)	0.092NS (0.037)	-0.14 (0.33)	0.16 (0.19)	0.02NS (0.68)	0.19 (0.05)	-0.07 (0.04)	-0.28 (0.09)
Total – <i>Koko</i> , kg/ha									
In tree stand 1984 <i>Puustossa 1984</i>	0.464 (0.013)	0.468 (0.015)	0.466NS (0.033)	3.14 (0.15)	3.29 (0.16)	3.36NS (0.18)	8.06 (0.16)	8.14 (0.25)	8.03NS (0.53)
In tree stand 1987 <i>Puustossa 1987</i>	0.535 (0.025)	0.760 (0.029)	0.766 (0.080)	3.87 (0.37)	3.66 (0.07)	4.00NS (0.75)	9.01 (0.36)	7.74 (0.37)	6.72 (0.54)
Accumulated 1984–1987 <i>Sitoutunut puustoon 1984–1987</i>	0.071 (0.012)	0.292 (0.016)	0.299 (0.047)	0.73 (0.35)	0.37 (0.22)	0.64NS (0.72)	0.95 (0.21)	-0.40 (0.22)	-1.31 (0.08)

Table 10 continued.
Taulukko 10 jatkuu.

	0	Zn PK	NPK	0	Cu PK	NPK
Above-ground – <i>Maan päällä</i> , kg/ha						
In tree stand 1984	0.98	0.99	0.97NS	0.090	0.090	0.089NS
<i>Puustossa 1984</i>	(0.02)	(0.03)	(0.07)	(0.002)	(0.000)	(0.007)
In tree stand 1987	1.09	1.04	1.16	0.107	0.118	0.114NS
<i>Puustossa 1987</i>	(0.04)	(0.05)	(0.08)	(0.004)	(0.007)	(0.018)
Accumulated 1984–1987	0.11	0.05	0.19	0.018	0.027	0.025NS
<i>Sitoutunut puustoon 1984–1987</i>	(0.02)	(0.03)	(0.01)	(0.002)	(0.004)	(0.002)
Litterfall 1984–1987	0.29	0.30	0.33NS	0.204	0.201	0.225NS
<i>Karikesato 1984–1987</i>	(0.01)	(0.04)	(0.02)	(0.005)	(0.050)	(0.050)
Uptake 1984–1987	0.40	0.35	0.52	0.222	0.228	0.250NS
<i>Maasta otettu 1984–1987</i>	(0.04)	(0.05)	(0.03)	(0.013)	(0.048)	(0.051)
Below-ground – <i>Maan alla</i> , kg/ha						
In tree stand 1984	0.38	0.40	0.41NS	0.037	0.041	0.039NS
<i>Puustossa 1984</i>	(0.02)	(0.01)	(0.02)	(0.003)	(0.004)	(0.003)
In tree stand 1987	0.36	0.39	0.36NS	0.035	0.064	0.037NS
<i>Puustossa 1987</i>	(0.03)	(0.01)	(0.07)	(0.004)	(0.001)	(0.009)
Accumulated 1984–1987	-0.03	-0.01	-0.05NS	-0.001	0.025	-0.003
<i>Sitoutunut puustoon 1984–1987</i>	(0.03)	(0.02)	(0.06)	(0.005)	(0.004)	(0.009)
Total – <i>Koko</i> , kg/ha						
In tree stand 1984	1.36	1.38	1.38NS	0.126	0.130	0.129NS
<i>Puustossa 1984</i>	(0.03)	(0.04)	(0.02)	(0.003)	(0.006)	(0.003)
In tree stand 1987	1.44	1.43	1.51NS	0.142	0.182	0.151NS
<i>Puustossa 1987</i>	(0.07)	(0.06)	(0.15)	(0.008)	(0.008)	(0.017)
Accumulated 1984–1987	0.08	0.04	0.14NS	0.016	0.052	0.022
<i>Sitoutunut puustoon 1984–1987</i>	(0.04)	(0.04)	(0.07)	(0.006)	(0.008)	(0.011)

Table 11. The total amount of nutrients in the dry mass in 1984 and 1987 per dry mass unit and the amount of nutrients accumulated in the dry mass from 1984 to 1987 per unit of dry mass accumulated during the same period on the unfertilized (0), PK and NPK fertilized plots and the results of the analyses of variance. Those denoted NS do not differ significantly from each other, ($p > 0.05$), (standard deviation in parentheses).

Taulukko 11. Puuston koko kuivamassaan 1984 ja 1987 ja kuivamassan kertymään vuosina 1984–1987 sitoutuneiden ravinteiden määrät puuston kuivamassa- ja kuivamassan kertymäyksikköä kohti lannoittamattomilla (0), PK- ja NPK-lannoitetuilla koelajoilla sekä varianssianalyysojen tulokset. Ne jotka eivät eroa merkitsevästi toisistaan ($p > 0.05$) on merkitty NS:llä (keskihajonta suluissa).

		N	K	Ca g/kg	Mg	P	S
1	0	2.20 (0.06)	0.74 (0.01)	1.16 (0.02)	0.28 (0.00)	0.22 (0.01)	0.23 (0.00)
	PK	2.26 (0.11)	0.75 (0.02)	1.17 (0.03)	0.29 (0.01)	0.23 (0.01)	0.23 (0.01)
	NPK	2.24 (0.12)	0.74 (0.02)	1.15 (0.03)	0.29 (0.01)	0.22 (0.01)	0.23 (0.01)
	NS	NS	NS	NS	NS	NS	NS
2	0	2.10 (0.03)	0.78 (0.01)	1.16 (0.00)	0.26 (0.00)	0.22 (0.00)	0.20 (0.00)
	PK	2.39 (0.09)	1.09 (0.03)	0.95 (0.02)	0.27 (0.01)	0.29 (0.01)	0.23 (0.01)
	NPK	2.68 (0.07)	1.04 (0.02)	1.03 (0.01)	0.26 (0.00)	0.28 (0.00)	0.24 (0.01)
	NS				NS		
3	0	1.40 (0.66)	1.00 (0.05)	1.15 (0.10)	0.06 (0.05)	0.23 (0.05)	0.01 (0.06)
	PK	3.29 (0.15)	3.34 (0.49)	-0.56 (0.33)	0.12 (0.04)	0.75 (0.09)	0.21 (0.02)
	NPK	5.38 (0.79)	2.95 (0.29)	0.23 (0.18)	0.11 (0.05)	0.64 (0.05)	0.30 (0.08)
	NS						
		B	Fe	Mn mg/kg	Zn	Cu	
1	0	6.0 (0.1)	40.5 (1.8)	104.0 (1.9)	17.6 (0.3)	1.6 (0.0)	
	PK	6.0 (0.1)	42.3 (3.0)	104.8 (2.4)	17.8 (0.5)	1.7 (0.1)	
	NPK	6.0 (0.1)	43.3 (4.2)	103.2 (2.5)	17.7 (0.5)	1.7 (0.1)	
	NS	NS	NS		NS	NS	
2	0	6.0 (0.0)	43.6 (2.1)	101.8 (0.8)	16.3 (0.0)	1.6 (0.0)	
	PK	8.5 (0.2)	40.9 (1.8)	86.6 (1.5)	15.9 (0.3)	2.0 (0.0)	
	NPK	8.5 (0.1)	44.1 (3.9)	74.5 (1.5)	16.8 (0.1)	1.7 (0.0)	
	NS		NS		NS		
3	0	6.4 (0.3)	65.1 (24.6)	85.5 (10.4)	7.3 (2.6)	1.4 (0.3)	
	PK	25.4 (3.9)	30.0 (14.6)	-37.4 (25.6)	3.4 (3.0)	4.5 (0.3)	
	NPK	24.3 (1.7)	46.0 (45.0)	-108.4 (20.8)	10.8 (2.9)	1.7 (0.5)	
	NS						

1) Fixed in tree stand dry mass in 1984/Dry mass of tree stand in 1984 – Sitoutunut puuston kuivamassaan 1984/Puuston kuivamassa 1984.

2) Fixed in tree stand dry mass in 1987/Dry mass of tree stand in 1987 – Sitoutunut puuston kuivamassaan 1987/Puuston kuivamassa 1987.

3) Fixed in dry mass accumulation 1984–1987/Dry mass accumulation 1984–1987 – Sitoutui kuivamassan kertymään 1984–1987/
Kuivamassan kertymä 1984–1987.

Table 12. The amount of nutrients in the annual litterfall on the unfertilized (0), PK and NPK fertilized plots in 3.9.1984–1.9.1987 (standard deviation in parentheses).

Taulukko 12. Vuotuisen karikesadon sisältämät ravinnemäärät lannoittamattomilla (0), PK- ja NPK-lannoitetuilla koealoilla 3.9.1984–1.9.1987 (keskihajonta suluisissa).

		N		K		Ca kg/ha/a		Mg		P		S	
Needle <i>Neulas</i>	0	7.99	(0.82)	1.04	(0.09)	7.49	(0.60)	0.94	(0.09)	0.51	(0.06)	0.83	(0.06)
	PK	7.37	(1.06)	1.24	(0.22)	7.11	(0.77)	0.98	(0.16)	0.51	(0.08)	0.79	(0.13)
	NPK	8.99	(1.42)	1.35	(0.31)	8.32	(0.90)	1.01	(0.06)	0.61	(0.08)	0.89	(0.11)
Other <i>Muu</i>	0	2.62	(0.14)	0.33	(0.03)	1.15	(0.23)	0.18	(0.01)	0.19	(0.01)	0.27	(0.01)
	PK	2.40	(0.67)	0.39	(0.15)	0.96	(0.23)	0.18	(0.07)	0.20	(0.04)	0.24	(0.08)
	NPK	3.76	(1.61)	0.56	(0.18)	1.38	(0.73)	0.27	(0.10)	0.27	(0.10)	0.36	(0.18)

		B		Fe		Mn kg/ha/a		Zn		Cu	
Needle <i>Neulas</i>	0	0.025	(0.011)	0.118	(0.005)	1.184	(0.085)	0.078	(0.003)	0.027	(0.000)
	PK	0.054	(0.015)	0.110	(0.018)	1.143	(0.168)	0.083	(0.009)	0.025	(0.005)
	NPK	0.055	(0.007)	0.122	(0.005)	1.256	(0.108)	0.089	(0.005)	0.028	(0.002)
Other <i>Muu</i>	0	0.006	(0.000)	0.097	(0.029)	0.041	(0.003)	0.017	(0.002)	0.041	(0.004)
	PK	0.006	(0.002)	0.084	(0.028)	0.041	(0.014)	0.016	(0.005)	0.042	(0.011)
	NPK	0.009	(0.005)	0.102	(0.057)	0.060	(0.031)	0.022	(0.009)	0.047	(0.015)

4. Discussion

4.1. Dry mass and dry mass production

The dry mass and its distribution between the different tree compartments was within the ranges reported for Scots pine stands growing on drained peatlands (Holmen 1964, Brække 1977b, 1986, Paavilainen 1980, Finér 1989) and mineral soil sites (Mälkönen 1974, Albrektson 1980) in Fennoscandia (Fig. 5, Table 13). The development of the stand was delayed by the poor aeration in the soil before drainage. An equal dry mass is reached at a much younger age on well drained sites. The density and age of the tree stand, as well as the fertility of the site, affect the dry mass distribution. In general, the dry mass of branches, foliage and roots decrease in relation to that of the stem along with an increase in stand age (see e.g. Albrektson 1980, Brække 1986). With increasing site fertility the branch dry mass increases in relation to that of the stem, and an increase in stand density has an opposite effect (Kellomäki and Väisänen 1986).

Stem and branch dry masses have increased and that of needles increased only slightly or

remained almost constant in Scots pine stands with the same stem volume as the one studied here (see Brække 1986). However, the foliar dry mass decreased during the observation period on all plots and the decrease was concentrated in the oldest needle class. This can be explained by climatic factors, stand structure and/or diseases. The weather in summer 1987 differed from that during 1984–1986 (see chapter 21.). Summer 1987 was wet and the groundwater table was close to the root zone. Moreover, the frozen soil did not melt until two weeks after the beginning of the growing season. These phenomena may have affected water and nutrient uptake and lead to increased shedding of the oldest needles in 1987. On the other hand, the stand was relatively dense and the poor light conditions in the crown layer may also have increased the mortality of the old needles. However, this is not a probable explanation since Brække (1986) has shown that denser, vigorously growing Scots pine stands have a greater foliage dry mass on ombrotrophic bogs. A light outbreak of *Gremmeniella abietina* (Lagerb.) Morelet, observed

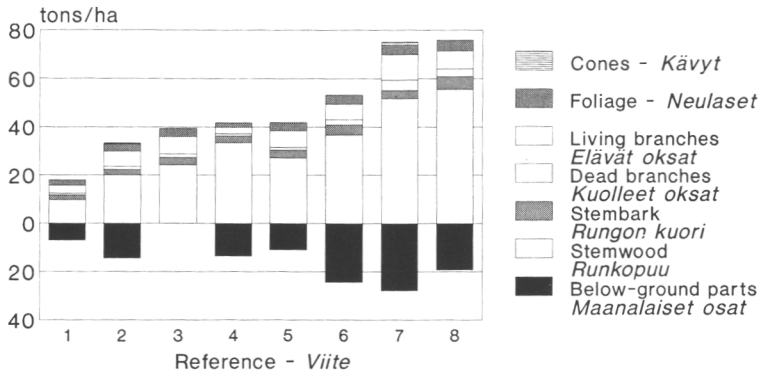


Fig. 5. Distribution of dry mass between the different tree compartments in unfertilized Scots pine stands according to 1) Mälkönen (1974), sample plot no. 1, 2) Finér (1989), VNRmu, 3) Holmen (1964), 4) Finér (1989), RhNRmu, 5) Mälkönen (1974), sample plot no. 2, 6) The present study, 7) Paavilainen (1980), sample plot no. 1, 8) Mälkönen (1974), sample plot no. 3.

Kuva 5. Kuivamassan jakaantuminen puuston eri osiin lannoittamattomissa männyköissä eri tutkimusten mukaan, 1) Mälkönen (1974), koeala no. 1, 2) Finér (1989), VNRmu, 3) Holmen (1964), 4) Finér (1989), RhNRmu, 5) Mälkönen (1974), koeala no. 2, 6) Tämä tutkimus 7) Paavilainen (1980), koeala no. 1, 8) Mälkönen (1974), koeala no. 3.

Table 13. Tree stand characteristics of the unfertilized reference stands (see Figs. 5–7).
Taulukko 13. Lannoittamattomien viitemetsiköiden puustotunnukset (ks. kuvat 5–7).

Site type	Volume	Volume growth	Age	Above-ground dry mass production	Reference
<i>Kasvupaikkatyyppi</i>	<i>Tilavuus</i>	<i>Tilavuuskasvu</i>	<i>Ikä</i>	<i>Maanpäällinen kuivamassan tuotos</i>	<i>Viite</i>
	m ³ /ha	m ³ /ha/a	a	kg/ha/a	
Ledum-pine bog-IR	66	3.6	44	3000	Holmen 1964
Vaccinium-type-VT (mineral soil)	30	2.3	28	2445	Mälkönen 1974 "Sample plot no. 1" "Koeala no. 1"
Vaccinium-type-VT (mineral soil)	75	5.0	47	4055	Mälkönen 1974 "Sample plot no. 2" "Koeala no. 2"
Myrtillus-type-MT (mineral soil)	149	5.9	45	5095	Mälkönen 1974 "Sample plot no. 3" "Koeala no. 3"
Dwarf-shrub pine bog-IR	116	4.5		4690	Paavilainen 1980 "Sample plot no. 1" "Koeala no. 1"
Ordinary sedge pine mire-VNR	48	2.7	40–50	3275	Finér 1989
Herbrich sedge pine mire-RhNR	72	2.0	40–60	2320	Finér 1989
Low shrub pine bog-IR	80	5.9	85	6259	The present study Tämä tutkimus

on the site in 1987, probably had no effect on the oldest needle class.

The above-ground dry mass production was higher than that reported for other Scots pine stands in Fennoscandia (Table 13). In addition to site and stand factors, this could be explained by methodological differences. In young stands more of the dry mass production takes place in the foliage and branches than in the stem (e.g. Albrektson 1980). In old stands the relationship is the reverse. In the studied stand the production of stemwood was equal to that of foliage. Almost one half of the annual dry mass production was lost as litter. This proportion was greater than in stands on mineral soil studied by Mälkönen (1974), and almost the same as those for peatland stands reported by Paavilainen (1980). One half of the produced needle dry mass senesced before the end of the three-year period (see Appendix 10).

The below-ground production was not measured in this study. In previous studies the production of fine roots has accounted for 5–85 % of the total tree stand production (Harris et al. 1977, Grier et al. 1981, Keyes & Grier 1981, Fogel 1985, Joslin & Henderson 1987, Santantonio & Santantonio 1987).

42. Effect of fertilization on dry mass

In previous studies the needle dry mass has increased already during the first growing season after fertilization (Miller & Miller 1976, Brix 1981). This is mainly caused by the increased size and longevity of the needles (Miller & Miller 1976, Turner 1977). This was probably also true in this study, since litterfall decreased during the year of fertilization (Finér, unpublished data). However, no positive fertilization effect was detected in the dry mass of the oldest needles, which had mostly been formed during the fertilization year. The dry mass of the oldest needles was even lowest on the PK fertilized plots in 1987. This is difficult to explain, but the consequences of the weather in 1987, which probably explained the overall decrease in the dry mass of this needle class, could also have had a negative interaction with PK fertilization, e.g. by inducing N deficiency in poor mineralization conditions. Both fertilization treatments increased the dry mass of the needles that developed in the second year after fertilization due to the increased needle weight (see Appendix 4). Some earlier studies have shown

that the needle mass can also increase as a result of the greater number of needles after fertilization (see Brix & Ebell 1969, Miller & Miller 1976, Turner 1977, Brix 1981, Madgwick & Tamm 1987).

NPK fertilization increased the living branch dry mass, most probably due to the decreased mortality of the branches. The branchwood growth and the number of shoots may also have increased (see Brix & Ebell 1969, Saramäki & Silander 1982, Madgwick & Tamm 1987, Nambiar & Fife 1987). PK fertilization did not have any effect on the living branch dry mass, even though the dead branch dry mass decreased. Greater branch litterfall on the PK fertilized plots than on the other plots could be one explanation. It seems also possible that PK fertilization had a negative effect on the branch growth.

Neither the stem dry mass nor the volume increased until the second three-year period after fertilization (Finér 1991a). Stems respond later to fertilization than foliage, often not before the second year (Miller & Miller 1976, Saramäki & Silander 1982). Maximum stem growth usually occurs in the 3rd–4th year after N or NPK fertilization in Scots pine stands (e.g. Viro 1965, Paavilainen 1972, Paavilainen & Simpanen 1975, Saramäki & Silander 1982). The stem dry mass response is relatively smaller than that of the volume, since fertilization decreases the specific gravity of the stemwood (Brix & Ebell 1969, Saikku 1975ab). The total dry mass of the stand was not affected by fertilization. The study period was thus too short for detecting a growth response in the stem, and increases in the foliar and branch dry masses were compensated by the decrease in dead branch dry mass.

43. Nutrient stores

The total above-ground nutrient stores and their distribution between the different tree compartments was inside the ranges reported for the other unfertilized stands studied in Fennoscandia (Figs. 6 and 7). The exceptions were Fe, Cu and B, the reference material for which was rather small.

The total nutrient concentration in the trees was low compared to plant material in general (see e.g. Epstein 1972, Larcher 1980). The composition was also different, the proportions of P and K were low and that of Ca high (see Epstein 1972). However, the concentrations did not

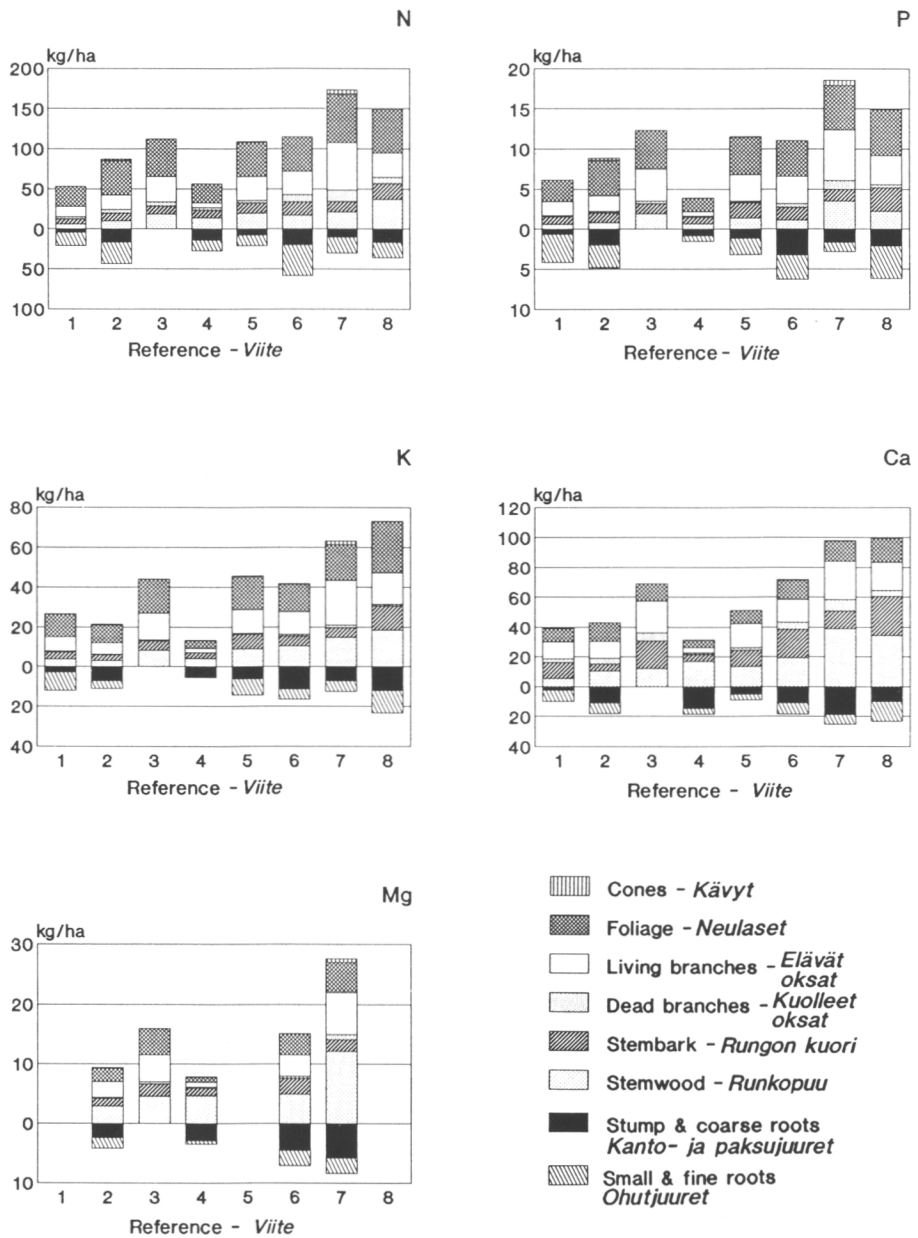


Fig. 6. Distribution of N, K, Ca, Mg and P between the different tree compartments in unfertilized Scots pine stands according to 1) Mälkönen (1974), sample plot no. 1, 2) Finér (1989), VNRmu, 3) Holmen (1964), 4) Finér (1989), RhNRmu, 5) Mälkönen (1974), sample plot no. 2, 6) The present study, 7) Paavilainen (1980), sample plot no. 1, 8) Mälkönen (1974), sample plot no. 3.

Kuva 6. Typen, kaliumin, kalsiumin, magnesiumin ja fosforin jakaantuminen puuston eri osiin lannoittamattomissa männiköissä eri tutkimusten mukaan, 1) Mälkönen (1974), koeala no. 1, 2) Finér (1989), VNRmu, 3) Holmen (1964), 4) Finér (1989), RhNRmu, 5) Mälkönen (1974), koeala no. 2, 6) Tämä tutkimus 7) Paavilainen (1980), koeala no. 1, 8) Mälkönen (1974), koeala no. 3.

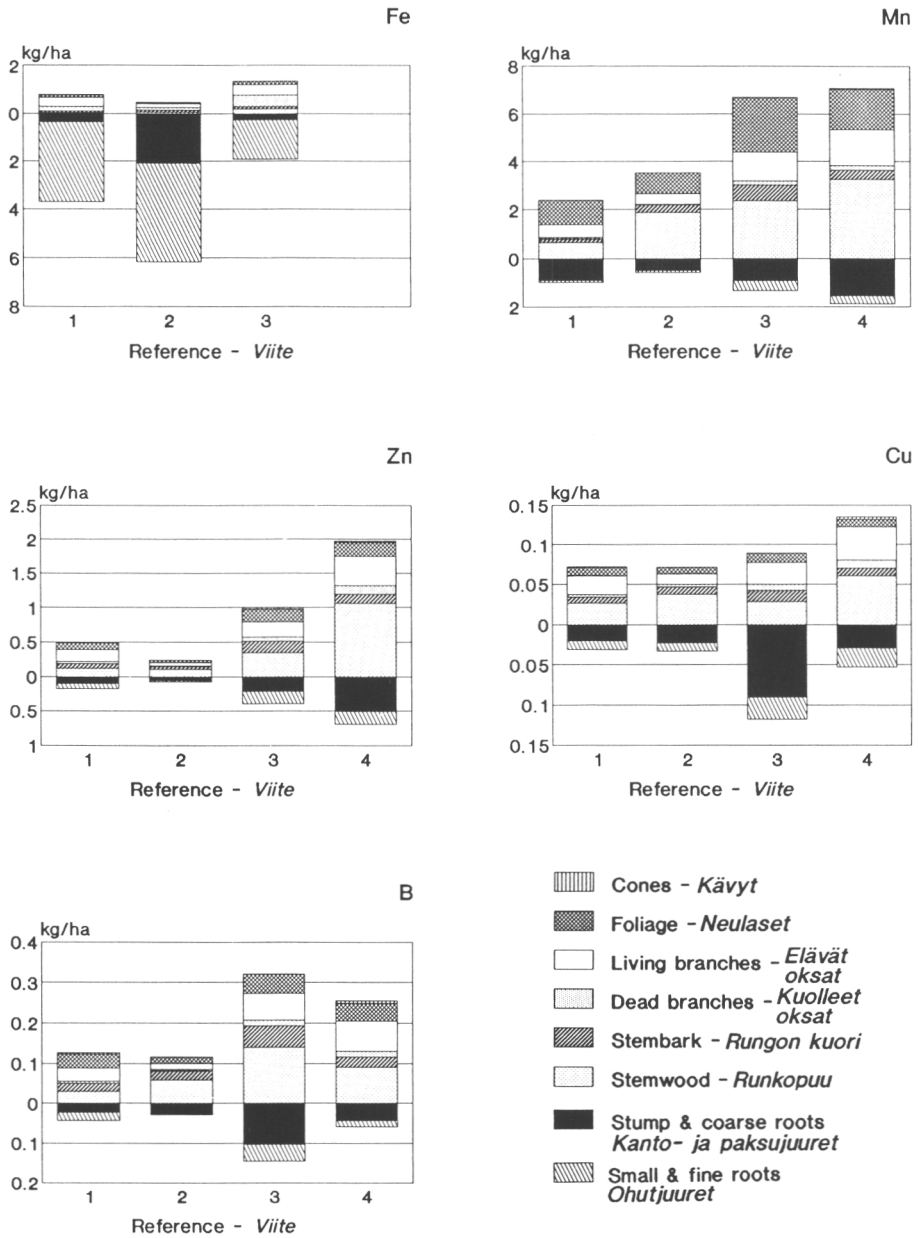


Fig. 7. Distribution of B, Fe, Mn, Zn and Cu between the different tree compartments in unfertilized Scots pine stands according to 1) Finér (1989), VNRmu, 2) Finér (1989), RhNRmu, 3) The present study, 4) Paavilainen (1980), sample plot no. 1.

Kuva 7. Boorin, raudan, mangaanin, sinkin ja kuparin jakaantuminen puuston eri osiin eri tutkimusten mukaan, 1) Finér (1989), VNRmu, 2) Finér (1989), RhNRmu, 3) Tämä tutkimus 4) Paavilainen (1980), koela no. 1.

Table 14. Nutrient stores in the 0–20 cm peat layer in 1984 (Brække & Finér 1991).
Taulukko 14. Ravinnevarat 0–20 cm turvekerroksessa vuonna 1984 (Brække & Finér 1991).

Nutrient Ravinne	kg/ha
N	1912
K	64
Ca	392
Mg	69
P	105
S	258
B	0.36
Fe	213
Mn	10.9
Zn	4.2
Cu	1.1

markedly differ from those observed in other unfertilized Scots pine stands (see Mälkönen 1974, Paavilainen 1980, Finér 1989).

The K, Mn and B pools in the tree stand were close to those in the root zone (Table 14). The other nutrients were more abundant in the surface peat than in the tree stand. The stand was dense and the next silvicultural operation to be carried out on the site would be thinning. It will have a greater effect on the K, Mn and B stores of the site than on the other nutrients (see Kaunisto & Paavilainen 1988, Finér 1989). Stem harvesting, which is the predominant method in Finnish forestry, would remove about one half less of the Ca, Mg, Mn, Zn, B and Cu, one third less of the N, S and K, one fourth less of the P and one fifth less of the Fe from the studied site than whole-tree harvesting. The effect of harvesting methods on the nutritional status of peat soils has been previously emphasized by Kaunisto and Paavilainen (1988) and Finér (1989).

44. Nutrient accumulation and uptake

The relationship between nutrient accumulation and uptake is dependent on the developmental stage of the tree stand (see Miller 1981, 1984). Most of the nutrients taken up from the soil before canopy closure are fixed, but after this stage the proportion of accumulation decreases and a greater part of the nutrients are returned to the soil in litterfall. After crown closure the recycling of nutrients accounts for a large proportion of the annual N, P, K and Mg requirement

of the trees (e.g. Lim & Cousens 1986, Helmissaari 1990). Apart from K and Fe, the release of nutrients through litterfall was great compared to the above-ground nutrient uptake on the studied site. Nutrient accumulation mainly took place in the stems, stumps and coarse roots.

The annual nutrient accumulation and uptake from the soil seems to be largely dependent on the dry mass production of the tree stand and its distribution between the different tree compartments (see e.g. Cole & Rapp 1981, Miller 1984, Brække 1990). Marked differences in nutrient accumulation and uptake are observed between tree stands (see Holmen 1964, Mälkönen 1974, Paavilainen 1980, Finér 1989, Brække 1990).

The figures in Table 10 are underestimates for the above-ground K, Ca, Mg and Mn uptake and release, since these nutrients are leached from the pine canopy by precipitation (see Helmissaari & Mälkönen 1989, Hyvärinen 1990). The total nutrient uptake from the soil also includes the below-ground compartments. Annual nutrient uptake by the fine roots may account for an even larger proportion than that of the above-ground compartments, even though the release by fine root turnover probably compensates for the uptake from the soil (see Meier et al. 1985, Vogt et al. 1986).

The annual atmospheric wet deposition of N, Mg and S was 8.4, 0.69 and 7.2 kg/ha on the site during 1984–1987 (Finér & Brække 1991b). The annual accumulation of these nutrients on the unfertilized plots was lower than the deposition. The annual deposition of 1.7 kg of K and 3.1 kg of Ca per ha was smaller than the accumulation in the trees.

Atmospheric wet deposition could satisfy all of the annual uptake of S, and 54 % of N on the unfertilized plots. The proportion for K and Mg was 40 %, and 23 % for Ca. The deposition of P and micronutrients was not measured on the site, but it was most probably of less significance. Phosphorus deposition in eastern Finland has been 0.14 kg/ha/a (Järvinen 1986).

Except for S, the supply of other nutrients was thus largely dependent on mineralization from the peat on the unfertilized plots. The total pools of N and P were large in the peat compared to uptake by the trees, but the slow rate of mineralization limits their availability (see e.g. Kaunisto & Paavilainen 1988, Brække & Finér 1991). Although a large proportion of the total Ca, Mg, K, Mn and Zn in the surface peat was rather easily extractable (Brække & Finér 1991), the total amounts of Mn and K in the root zone on

the unfertilized plots corresponded to only 7 and 16 years' uptake respectively. The B content in the upper 20 cm peat layer was also only seven times larger than the annual uptake, but most of the B was tightly bound to the peat matrix (see Brække & Finér 1991). It would appear that the B, Mn and K supply is closely dependent on efficient cycling between the soil and the trees if fertilizers are not applied. This also means that the system is easily disturbed. Boron deficiency is probably one of the main reasons for nutritional growth disturbances on peatlands in Finland (Veijalainen et al. 1984), and K deficiency has even caused the death of trees on some sites exceptionally poor in K (Kaunisto & Tuveva 1984).

45. Effect of fertilization on nutrient contents

The foliar nutrient concentrations indicated a restricted supply of N, P, K and B before fertilization (see Finér 1992), and the uptake of these nutrients was promoted by fertilization. One third of the increased B uptake was already released in the litterfall at the end of the three-year study period. The extra elements accumulated primarily in the canopy, where the dry mass and nutrient concentrations (see Finér 1992) also increased the most (see also Melin & al. 1983, Melin & Nömmik 1988, Nömmik & Larsson 1989).

Compared to the annual above-ground uptake on unfertilized plots, the amount of B applied was about 50, P 40 and that of N, Ca, Mg, S and K, 10 to 25 times greater. Fertilization approxi-

mately doubled the annual uptake of N, P, K and B, while the total accumulation of these nutrients was three to four times greater after fertilization. However, the uptake of Mg was not affected and that of Ca and Mn was inhibited. Fertilization has also been observed to decrease Mn uptake in previous studies (Finér 1989). The lower uptake of Mn and also Ca could be explained by the inhibitory effect of the other fertilizer cations or chemical reactions in the peat.

The amount of applied N was lower and that of P, K, Ca, Mg, S and especially B higher than the stores in the tree layer before fertilization. The increased nutrient accumulation was low compared to the applied amounts of fertilizers. However, these observations are in accordance with earlier ones in which the increased accumulation in the tree stand has been less than one half of the applied N, P, K within 0.5–15 years after fertilization (see e.g. Paavilainen 1973, Ballard 1984, Melin & Nömmik 1988, Finér 1989, Nömmik & Larsson 1989). The proportions have also decreased along with increasing fertilizer doses (Miller et al. 1976). The ability of the studied stand to exploit the applied fertilizers was largely dependent on the capacity of the canopy to enlarge its dry mass after fertilization.

The greater amounts of K and B in the surface peat of the fertilized plots could indicate that some of the fertilizers were still left in the peat (Brække & Finér 1991). The remainder was probably taken up by the understorey vegetation (e.g. Päivänen 1970, Paavilainen 1980) or leached out (e.g. Ahti 1983).

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Seloste

Lannoituksen vaikutus männyn kuivamassan kertymään ja ravinteiden kiertoon ombrotrofisella rämeellä

Johdanto

Ojitettujen soiden ravinnevarat ovat sitoutuneet elävään ja kuolleeseen orgaaniseen aineeseen, kasvillisuuteen ja turpeeseen. Kaliumia ja joitakin hivenravinteita lukuunottamatta ravinteita on enemmän juuristokerroksessa kuin kasvillisuudessa (esim. Holmen 1964, Paavilainen 1980, Brække 1988, Kaunisto ja Paavilainen 1988, Finér 1989). Orgaanista ainetta ja ravinteita poistuu soilta huuhtoutumalla ja puunkorjuussa.

Ombrotrofisten soiden puusto kasvaa turpeesta mineralisotuvien ravinteiden varassa, sillä laskeuman mukana tuleva käyttökelpoinen ravinnelisa on pieni. Useimmilla turvemaidella fosforin, kaliumin ja boorin niukkuus rajoittaa puuston kasvua, ja karuimmilla turvemaidella on puutetta myös typestä (esim. Meshechok 1967, Brække 1977a, 1979, 1983, Paavilainen 1979).

Lannoitus on ollut yleistä ojitetuilla soilla maassamme. Lannoituksen vaikutuksia selvittävät tutkimukset ovat kuitenkin keskittyneet suurimmalta osin vain rungon kasvussa ja neulasten ravinnepitoisuuksissa tapahtuvien muutosten tarkasteluun. Puuston muut osat ovat jääneet vähälle huomiolle.

Puuston kuivamassan tuotosta ja ravinteiden kiertoa koskevat tutkimustulokset ovat tarpeen mm. selvittäessä soiden merkitystä orgaanisen aineen ja ravinteiden varastoina, tutkittaessa mahdollisuuksia jatkuvaan kestävään puuntuotantoon turvemaidella sekä tarkasteltaessa lannoiteravinteiden kulkeutumista suoekosysteemissä. Tämän tutkimuksen tarkoituksena on selvittää lannoituksen vaikutusta puuston kuivamassan kertymään ja ravinteiden kiertoon ombrotrofisella rämeellä kasvavassa männikössä.

Aineisto ja menetelmät

Tutkimuksen aineisto kerättiin Pohjois-Karjalasta isovarpuiselta rämeeltä, joka oli ojitettu 20 vuotta ennen kokeen perustamista. Tutkimusalueella kasvoi noin 85-vuotias männikkö (taulukko 3). Mittaukset aloitettiin vuonna 1984 ja koe lannoitettiin keväällä 1985. Koe toteutettiin latinalaisen nelion periaatteen mukaan (3 * 3). Lannoituskäsittelyt olivat 1) lannoittamaton (0), 2) PK (MgB) ja 3) NPK (MgB) ja käytetyt lannoitemäärät (kg/ha): N 150, P 53, K 100, Ca 135, Mg 25, S 28, Cl 95 ja B 2,4.

Tutkimuksessa kerättiin vuosina 1984 ja 1987 aineisto, jonka perusteella laadittiin puukohtaiset rungon, latvuksen ja kanto- ja paksujuurten kuivamassayhtälöt (liitteet 7, 9). Yhtälöillä laskettiin metsikkötason kuivamassa vastaaville ositteille. Ohutjuurten ja karikesadon kuivamassa mitattiin metsikkötasolla. Tämän lisäksi analysoitiin eri ositteiden ravinnepitoisuudet (Finér 1992, liite 11) ravinne-määrien laskemista varten.

Tulokset ja tarkastelu

Kuivamassa ja kuivamassan tuotos

Puuston kuivamassa oli ennen lannoitusta 77,7 t/ha (taulukko 4, kuvat 1 ja 4), josta maanalaisten osien osuus oli 69 %. Runkopuun osuus metsikön kuivamassasta oli 47 % ja elävien sekä kuolleiden oksien yhteensä 11 %. Rungon kuoren ja neulasten osuus kuivamassasta oli 5 %. Kolmen vuoden tarkastelujaksolla puuston vuotuinen kuivamassan kertymä oli 3,7 t/ha (taulukko 5), josta suurin osa kohdistui runkoon. Puuston maanpäällisten osien vuotuinen kokonaistuotos oli 6,3 t/ha, ja siitä 51 % kerääntyi puuston (taulukko 7, liite 10).

Lannoitus ei vaikuttanut kuivamassan kokonaiskertymään, mutta muutti sen jakaantumista latvuksessa (taulukot 4 ja 5). Lannoitus lisäsi neulasmassaa 7–10 % (taulukko 4). Neulasmassa oli kuitenkin kaikilla koealoilla pienempi tarkastelujakson lopussa kuin alussa, minkä tulkittiin johtuneen pääasiassa kylmän kevään 1987 ja koko kesän 1987 korkealla olleen pohjavesipinnan (taulukko 2) vaikutuksesta puiden veden ja ravinteiden ottoon. NPK lannoitus lisäsi myös elävien oksien kuivamassaa n. 9 %:lla (taulukko 4). Molemmat lannoituskäsittelyt vähensivät kuolleiden oksien kuivamassaa 14–15 % ja lisäsivät käpyjen massaa. Runkoon ja maanalaisiin osiin lannoitus ei vaikuttanut. Myöskään rungon tilavuuskasvu ei lisääntynyt ennen toista kolmi-vuotisjaksoa lannoituksen jälkeen (Finér 1991a). Lannoitusvaikutusta koskevat tulokset olivat sopusoinnussa aikaisempien tutkimustulosten kanssa, joiden mukaan männynllä lannoitusvaikutus ilmenee ensimmäisenä latvuksessa ja vasta myöhemmin rungossa (ks. Miller & Miller 1976, Saramäki & Silander 1982).

Ravinteiden kierto

Tutkittujen ravinteiden osuus lannoittamattomien puiden kuivamassasta oli 392 kg/ha (0,49 %) (taulukko 8). Tästä tyypeä oli keskimäärin 173 kg/ha (44 %), kalsiumia 90 kg/ha (23 %), kaliumia 58 kg/ha (15 %) ja loppu (18 %) jakaantui melko tasaisesti fosforin, magnesiumin, rikin ja hivenravinteiden kesken. Puiden kokonaisravinnepitoisuus (% k.a.) oli pieni ja fosforin sekä kaliumin osuus alempi ja kalsiumin korkeampi kuin kasveissa keskimäärin (Epstein 1972, Larcher 1980). Puiden kokonaisravinnepitoisuus oli kuitenkin lähes saman suuruinen kuin aikaisemminkin tutkituissa männiköissä (ks. Mälkönen 1974, Paavilainen 1980, Finér 1989).

Puustossa oli kaliumia, mangaania ja booria lähes yhtä paljon kuin juuristokerroksessa (taulukot 8 ja 14). Muiden ravinteiden varastot olivat suuremmat ylimmässä 20 cm turvekerroksessa kuin puustossa. Juuriston osuus puuston kuivamassasta oli n. 30 % samoin kuin sen osuus puuston sitomasta typen, kaliumin, magnesiumin, fosforin, kuparin, sinkin ja boorin määrästä (kuva 4). Vastaavasti kalsiumia ja mangaania juuristossa oli vähemmän ja rikkiä ja erityisesti rautaa enemmän. Latvuksen kuivamassa oli selvästi pienempi kuin rungon, mutta ravinnevarastona se oli merkityksellisempi. Edellisen perusteella oli pääteltävissä, että puunkorjuulla on vaikutusta erityisesti tutkitun suon kaliumin, mangaanin ja boorin varastoihin, ja kokopuukorjuun vaikutus on voimakkaampi kuin runkopuukorjuun.

Puusto otti maasta vuosittain keskimäärin tyypeä 15,6, kalsiumia 12,8, kaliumia 4,1, fosforia 1,3, magnesiumia 1,7 sekä rikkiä ja mangaania 1,5 kg/ha maanpäällisiin osiinsa (taulukko 10). Rautaa ja sinkkiä puusto otti vastaavasti 510 ja 130 g/ha sekä kuparia ja booria alle 100 g/ha. Karikkeiden mukana palasi maahan ravinteita, rautaa ja kaliumia lukuunottamatta määrä, joka oli yli puolet puuston maasta ottamasta ravinnemäärästä. Rikkiä lukuunottamatta kasvien ravinteiden saanti riippui lannoit-

tamattomilla koealoilla suuresti ravinteiden mineralisaatiosta maassa, sillä laskeuman mukana tuleva ravinnelisiä oli vähäinen (Finér & Brække 1991b). Tulokset antoivat viitteitä kaliumin, mangaanin ja boorin tehokkaasta kierrosta puuston ja maan välillä, ja samalla näiden ravinteiden kierron herkästä järkkymisestä.

Neulasanalyyysien mukaan kasvupaikalla oli ennen lannoitusta tarjolla niukasti tyypeä, fosforia, kaliumia ja booria (Finér 1992). Lannoitus vaikutti magnesiumia, rautaa ja sinkkiä lukuunottamatta kaikkien muiden ravinteiden kertymään (taulukot 9, 10). Lannoitetun puusto kuivamassassa oli enemmän tyypeä, fosforia, kaliumia, rikkiä, kuparia ja booria kuin lannoittamattomassa puustossa kolmen vuoden kuluttua lannoituksesta. Lisääntynyt ravinteiden kertymä vastasi 25 % (25 kg/ha) käytetystä lannoitekaliumista, 10 % (6 kg/ha) lannoitefosforista ja 10 % (0.2 kg/ha) lannoiteboorista. Vastaava osuus typen kohdalla oli 35 % (52 kg/ha) NPK-lannoituksen jälkeen, mutta mikäli myös PK lannoituksesta johtuva typen lisääntynyt kertymä otettiin huomioon, osuus oli vain n. 20 % (30 kg/ha). Noin kolmasosa puuston ottamasta lisäboorista oli jo palannut karikkeiden mukana takaisin maahan.

Lannoitettu puusto otti maasta vähemmän kalsiumia ja mangaania kuin lannoittamaton. Lannoituksen on aikaisemminkin todettu pienentäneen puiden Mn ottoa (Finér 1989), ja sen samoin kuin Ca otton pienemiseen vaikuttivat todennäköisesti toiset lannoitekationit tai maassa tapahtuneet kemialliset reaktiot.

Puuston kertynyt lisäravinnemäärä (N, P, K) on myös muissa tutkimuksissa ollut yleensä alle puolet lannoite-ravinnemäärästä (Paavilainen 1973, Ballard 1984, Melin & Nömmik 1988, Finér 1989, Nömmik & Larsson 1989). Osa lannoiteravinteista on todennäköisesti sitoutunut pintakasvillisuuteen (esim. Päivänen 1970, Paavilainen 1980), osa turpeeseen (ks. Brække & Finér 1991) ja osa on kulkeutunut pois kasvupaikalta (esim. Ahti 1983).

Appendix 1. Sample tree characteristics in 1984 and 1987 on the unfertilized (0), PK and NPK fertilized plots.

Liite 1. Koeputunnuksia vuonna 1984 ja 1987 lannoittamattomilla (0) sekä PK- ja NPK- lannoitetuilla koealoilla.

Characteristic <i>Tunnus</i>		1984		1987	
		all- <i>kaikki</i>	0	PK	NPK
d, cm	\bar{x}	11.5	12.6	12.5	12.9
	min	4.9	6.0	7.0	6.4
	max	22.0	19.1	18.9	23.6
h, dm	\bar{x}	104	116	115	115
	min	64	84	89	84
	max	133	134	147	145
cl, dm	\bar{x}	47	63	57	62
	min	26	52	42	42
	max	64	70	69	78
cr	\bar{x}	0.54	0.45	0.51	0.46
	min	0.40	0.36	0.42	0.37
	max	0.69	0.54	0.60	0.52
v, l	\bar{x}	75	91	88	104
	min	8	13	22	16
	max	269	181	211	281
Age - <i>ikä</i> , a	\bar{x}	85	89	87	91
	min	63	74	75	71
	max	114	98	96	110
Stemwood density <i>Runkopuun tiheys</i> , kg/l	\bar{x}	0.44	0.42	0.41	0.42
	min	0.38	0.38	0.39	0.38
	max	0.52	0.48	0.45	0.47
Stembark density <i>Rungon kuoren tiheys</i> , kg/l	\bar{x}	0.33	0.29	0.28	0.29
	min	0.29	0.28	0.25	0.27
	max	0.39	0.32	0.31	0.33
n		27	9	9	9

Appendix 2. Branch characteristics of sample trees in 1984 and 1987 on the unfertilized (0), PK and NPK fertilized plots.

Liite 2. Lukuoksatunnuksia vuonna 1984 ja 1987 lannoittamattomilla (0) sekä PK- ja NPK- lannoitetuilla koelohilla.

Characteristic Tunnus	1984		0		1987 PK		NPK			
	all	/tree	all	/tree	all	/tree	all	/tree		
	kaikki	/puu	kaikki	/puu	kaikki	/puu	kaikki	/puu		
			Living branches - <i>Elävät oksat</i>							
d _{br} , mm	\bar{x}	13	11	13	12	14	13	14	12	
	min	2	6	2	7	2	9	2	7	
	max	47	19	37	17	41	18	54	19	
h _{br} , cm	\bar{x}	89	77	98	87	98	89	93	83	
	min	4	40	4	63	3	66	2	56	
	max	341	127	288	112	310	128	322	133	
n	\bar{x}	2120	151	673	75	691	77	707	79	
	min		102		44		53		49	
	max		226		94		117		112	
			Dead branches - <i>Kuolleet oksat</i>							
Fresh mass <i>Tuoremassa, g</i>	\bar{x}	49	51	60	63	56	55	64	65	
	min	1	6	1	11	1	14	1	5	
	max	2176	241	1361	250	1177	149	2810	199	
n	\bar{x}	1909	72	873	97	765	85	780	87	
	min		44		76		55		48	
	max		104		122		104		136	

Appendix 3. Characteristics of sample branches in 1984 and 1987 on the unfertilized (0), PK and NPK fertilized plots

Liite 3. Koeoksatunnuksia vuonna 1984 ja 1987 lannoittamattomilla (0) sekä PK- ja NPK- lannoiteilla koealoilla.

Characteristic		1984		1987	
Tunnus		all-kaikki	0	PK	NPK
d _b , mm	\bar{x}	13	13	14	14
	min	3	3	6	4
	max	47	32	34	49
h _b , cm	\bar{x}	89	90	93	90
	min	13	9	19	16
	max	341	226	243	320
Needle dry mass					
Neulaskuivamassa, g					
C	\bar{x}	17.1	19.8	22.0	25.7
	min	0.5	0.8	3.6	0.9
	max	165.6	150.9	99.8	254.1
C+1	\bar{x}	14.4	17.6	22.9	28.0
	min	0.0	0.0	0.0	0.0
	max	139.7	160.5	124.9	306.0
C≥2	\bar{x}	12.2	12.0	9.6	15.0
	min	0.0	0.0	0.0	0.0
	max	121.5	90.2	42.6	248.4
Branch dry mass					
Oksakuivamassa, g					
Age - Ikä, a	\bar{x}	85.4	75.1	85.1	105.6
	min	0.4	0.2	1.8	0.7
	max	2212.5	596.5	693.9	2005.0
Age - Ikä, a	\bar{x}	8	7	7	8
	min	1	1	1	1
	max	38	24	28	38
n		186	63	63	63

Appendix 4. 1000-needle dry mass in different age-classes and litter in 1987 on the unfertilized (0), PK and NPK fertilized plots, (standard deviation in parentheses).

Liite 4. Tuhannen eri-ikäisen elävän ja karikeneulasen painotettu kuivamassa vuonna 1987 lannoittamattomilla (0) sekä PK- ja NPK- lannoitetuilla koealoilla, (keskihajonta suluisissa).

	0	PK	NPK
		g	
Living needles - <i>Elävät neulaset</i>			
C	11 (3.9)	13 (0.5)	11 (0.3)
C+1	16 (5.9)	22 (4.3)	24 (6.2)
C≥2	13 (3.7)	15 (1.6)	13 (1.8)
Needle litter	7.1 (0.9)	7.7 (1.3)	9.0 (1.8)
<i>Neulaskarike</i>			

Appendix 5. Litterfall in 3.9.1984-1.9.1987 on the unfertilized (0), PK and NPK fertilized plots, (standard deviation in parentheses).

Liite 5. Karikesato 3.9.1984-1.9.1987 lannoittamattomilla (0) sekä PK- ja NPK- lannoitetuilla koealoilla, (keskihajonta suluisissa).

	0	PK	NPK
		kg/ha	
Needles - <i>Neulaset</i>	3752 (247)	3450 (494)	3582 (423)
Other - <i>Muu</i>	1465 (96)	1289 (508)	1989 (884)

Appendix 6. Dry mass characteristics of the sample trees in 1984 and 1987 on the unfertilized (0), PK and NPK fertilized plots.

Liite 6. Koeuiden kuivamassatunnuksia vuonna 1984 ja 1987 lannoittamattomilla (0) sekä PK- ja NPK-lannoitetuilla koealoilla.

Characteristic		1984	1987		
Tunnus		all-kaikki	0	PK	NPK
Cone dry mass	\bar{x}		165	120	308
Käpykuivamassa, g	min		0	8	0
	max		928	383	1034
Needle dry mass					
Neulaskuivamassa, g					
C	\bar{x}	1198	1279	1338	1284
	min	134	158	331	203
	max	3613	2620	3565	3915
C+1	\bar{x}	1065	950	1335	1332
	min	113	155	373	253
	max	3220	1803	3309	4057
C≥2	\bar{x}	1005	628	420	740
	min	136	88	125	72
	max	2876	1216	954	2167
Live branch dry mass	\bar{x}	7106	6937	7633	8262
Elävien oksien kuivamassa, g	min	357	628	1100	694
	max	29215	16360	21739	29389
Dead branch dry mass	\bar{x}	1835	3330	2712	3191
Kuolleiden oksien kuivamassa, g	min	216	652	486	276
	max	5838	10910	6953	9848
Stembark dry mass	\bar{x}	3.2	4.4	4.3	4.9
Rungon kuoren kuivamassa, g	min	0.6	1.2	1.4	1.2
	max	11.2	8.4	7.8	12.3
Stemwood dry mass	\bar{x}	32	37	37	42
Runkopuun kuivamassa, kg	min	4	7	9	7
	max	112	77	86	110
Stump and coarse root dry mass					
Kannon ja paksujuurten kuivamassa, kg					
	\bar{x}	20			
	min	1.6			
	max	63			

Appendix 7. Stem, stump and coarse root dry mass equations in 1984 and 1987 on the unfertilized (0), PK and NPK fertilized plots.

Liite 7. Runko- sekä kanto- ja paksujuurikuivamassayhtälöt vuonna 1984 ja 1987 lannoittamattomilla (0), sekä PK- ja NPK- lannoitetuilla koealoilla.

Independent variable Selittävä muuttuja	1984		1987	
	all-kaikki	0	PK	NPK
	Coefficients-Kertoimet			
	ln (Stembark) - ln (Rungon kuori), kg			
Constant-Vakio	-0.7220	-5.7367	-5.3095	-3.4382
ln (d)	2.1274	1.4480	1.5413	1.7949
ln (h)	-0.7392	0.7304	0.5915	0.0582
n	27	9	9	9
R ²	0.97	0.98	0.98	0.99
S _e	0.1328	0.1000	0.0963	0.1144
S _e %	13.3	10.0	9.6	11.4
	ln (Stemwood) - ln (Runkopuu), kg			
Constant-Vakio	-5.7103	-5.9689	-8.1559	-6.6539
ln (d)	1.7256	1.7123	1.4666	1.6551
ln (h)	1.0241	1.0778	1.6665	1.2442
n	27	9	9	9
R ²	0.99	0.99	0.99	0.99
S _e	0.0643	0.0228	0.0622	0.0813
S _e %	6.4	2.3	6.2	8.1
	ln (Stump and coarse roots)- ln (Kanto- ja paksujuuret), g			
Constant-Vakio	-3.3420			
ln (d)	2.4142			
n	7			
R ²	0.99			
S _e	0.1176			
S _e %	11.8			

Appendix 8. Branch dry mass equations in 1984 and 1987 on the unfertilized (0), PK and NPK fertilized plots.

Liite 8. Oksien kuivamassayhtälöt vuonna 1984 ja 1987 lannoittamattomilla (0) sekä PK- ja NPK- lannoitetuilla koealoilla.

Independent variable Selittävä muuttuja	1984		1987	
	all- <i>kaikki</i>	0	PK	NPK
Coefficients - <i>Kertoimet</i>				
$\ln (C- \text{ needles}) - \ln (C- \text{ neulaset}), g$				
Constant - <i>Vakio</i>	-5.2650	-5.0515	-4.2297	-4.2770
$\ln (d_b)$	1.3751	1.9573	1.9317	2.4161
$\ln (h_b)$	0.6310	0.3657	0.1700	-0.1950
pos	0.0426	0.0302	0.0400	0.0524
$\text{pos}^2 \cdot 10^{-4}$	-2.112	-1.453	-2.591	-3.298
n	186	63	63	63
R^2	0.81	0.95	0.91	0.89
S_e	0.4640	0.2469	0.2628	0.3970
$S_e \%$	49.0	25.1	26.7	41.3
$\ln \{ (C+1- \text{ needles})+1 \} - \ln \{ (C+1- \text{ neulaset})+1 \}, g$				
Constant - <i>Vakio</i>	-4.8294	-3.8305	-6.8975	-5.4542
$\ln (d_b)$	1.1403	1.2915	0.2036	1.1634
$\ln (h_b)$	0.7132	0.4893	1.7692	0.8987
pos	0.0506	0.0523	0.0519	0.0633
$\text{pos}^2 \cdot 10^{-4}$	-4.247	-5.018	-4.246	-5.817
n	186	63	63	63
R^2	0.90	0.90	0.94	0.93
S_e	0.3598	0.4013	0.3189	0.3700
$S_e \%$	37.6	42.3	33.1	38.8
$\ln \{ (C \geq 2- \text{ needles})+1 \} - \ln \{ (C \geq 2- \text{ neulaset})+1 \}, g$				
Constant - <i>Vakio</i>	-1.7197	-1.0720	-0.5395	-1.7860
$\ln (d_b)$	1.7754	1.9294	1.8829	2.8341
$\ln (h_b)$	-0.2267	-0.4460	-0.6405	-0.8600
pos	0.0520	0.0538	0.0607	0.0419
$\text{pos}^2 \cdot 10^{-4}$	-6.544	-6.797	-8.5688	-5.524
n	186	63	63	63
R^2	0.86	0.88	0.87	0.81
S_e	0.4991	0.4354	0.4432	0.3040
$S_e \%$	53.6	46.2	47.1	71.2
$\ln (\text{Living branches}) - \ln (\text{Elävät oksat}), g$				
Constant - <i>Vakio</i>	-5.8400	-6.4365	-6.6572	-6.1496
$\ln (d_b)$	1.8800	1.5882	1.7390	1.9250
$\ln (h_b)$	1.0716	1.3576	1.3057	1.092
n	186	63	63	63
R^2	0.97	0.99	0.99	0.99
S_e	0.2628	0.1794	0.1601	0.1932
$S_e \%$	26.7	18.1	16.1	19.5

Appendix 9. Dry mass equations of different crown compartments in 1984 and 1987 on the unfertilized (0), PK and NPK fertilized plots.

Liite 9. Latvuksen eri osien kuivamassayhtälöt vuonna 1984 ja 1987 lannoittamattomilla (0) sekä PK- ja NPK-lannoitetuilla koealoilla.

Independent variable Selittävä muuttuja	1984		1987	
	all-kaikki	0	PK	NPK
Coefficients - Kertoimet				
$\ln (\text{Cones}+1)^* - \ln (\text{Kävyt}+1)^*, \text{ g}$				
Constant - Vakio		9.7570	-4.1570	-3.3124
$\ln(d)$		5.2788	3.2730	3.3491
n				
R^2		0.74	0.65	0.54
S_e		1.3140	0.9240	1.5430
$S_e\%$		215.0	116.1	313.3
$\ln (C- \text{ needles}) - \ln (C- \text{ neulaset}), \text{ g}$				
Constant - Vakio	2.8966	1.8004	2.5858	2.4000
$\ln(d)$	1.9320	2.2770	1.9820	2.1108
$\ln(\text{cr})$	1.1458	0.7551	0.7917	1.1190
n	27	9	9	9
R^2	0.98	0.99	0.96	0.98
S_e	0.1322	0.1011	0.1777	0.1640
$S_e\%$	13.3	10.1	17.9	16.5
$\ln (C+1- \text{ needles}) - \ln (C+1- \text{ neulaset}), \text{ g}$				
Constant - Vakio	2.6514	1.7072	3.2199	3.1822
$\ln(d)$	1.9828	2.0529	1.7782	1.9598
$\ln(\text{cr})$	1.1520	0.2108	0.9352	1.5340
n	27	9	9	9
R^2	0.98	0.99	0.95	0.98
S_e	0.1430	0.1111	0.1991	0.1607
$S_e\%$	14.4	11.1	20.1	16.2
$\ln (C\geq 2- \text{ needles}) - \ln (C\geq 2- \text{ neulaset}), \text{ g}$				
Constant - Vakio	2.6905	0.1588	1.8429	0.8310
$\ln(d)$	1.8779	2.2563	1.7245	2.5454
$\ln(\text{cr})$	0.8357	-0.5938	0.3424	1.3964
n	27	9	9	9
R^2	0.98	0.97	0.94	0.99
S_e	0.1350	0.1631	0.1892	0.1332
$S_e\%$	13.6	16.4	19.1	13.4
$\ln (\text{Living branches}) - \ln (\text{Elävät oksat}), \text{ g}$				
Constant - Vakio	2.7932	1.8239	2.9424	3.7943
$\ln(d)$	2.6708	2.7347	2.5359	2.6129
$\ln(\text{cr})$	1.3568	0.1899	0.9977	2.4262
n				
R^2	0.97	0.99	0.94	0.99
S_e	0.2239	0.1518	0.2866	0.1469
$S_e\%$	22.7	15.3	29.2	14.8
$\ln (\text{Dead branches}) - \ln (\text{Kuolleet oksat}), \text{ g}$				
Constant - Vakio	1.8943	1.8330	1.3496	1.1418
$\ln(d)$	2.2181	2.3913	2.5237	2.5966
n	27	9	9	9
R^2	0.87	0.88	0.93	0.89
S_e	0.3649	0.3732	0.2712	0.4584
$S_e\%$	37.7	38.6	27.6	48.3

* Values below 0=0 - arvot alle 0=0.

Appendix 10. Calculation of the needle dry mass production in 1985-1987. Adjusted for the dry weight changes on the unfertilized plots, (standard deviation in parentheses).

Liite 10. Neulaskuivamassan tuotoksen (kg/ha) laskenta vuosille 1985-1987. Kuivamassan muutokset huomioitu lannoittamattoman aineiston mukaisesti, (keskihajonta suluisissa).

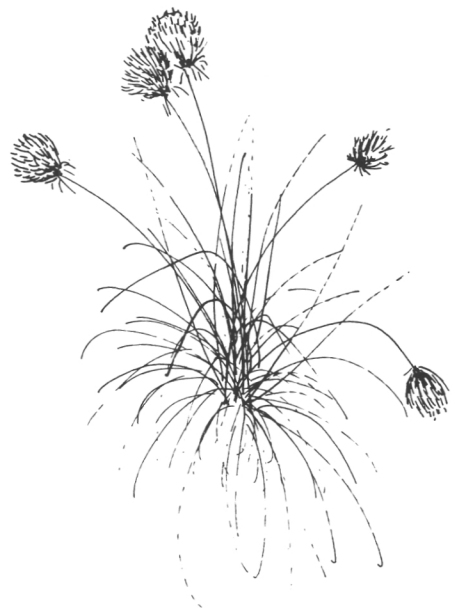
	0	PK kg/ha	NPK
Needle dry mass 1984 - <i>Neulaskuivamassa 1984</i>	4481 (68)	4565 (205)	4392 (214)
Litterfall 1984-1987 - <i>Karikesato 1984-1987</i>	8444 (557)	7763 (1113)	8060 (954)
1985-1987 formed needles in litterfall	3963 (602)	3197 (945)	3668 (748)
<i>1985-1987 syntyneitä neulasia karikesadossa</i>			
Needle dry mass 1987 - <i>Neulaskuivamassa 1987</i>	3372 (93)	3711 (128)	3601 (142)
Needle dry mass production 1985-1987	7335 (645)	6908 (1053)	7269 (878)
<i>Neulaskuivamassan tuotos 1985-1987</i>			

Appendix 11. The mean nutrient concentrations of the litterfall on the unfertilized (0), PK and NPK fertilized plots during 3.9.1984 - 1.9.1987, (standard deviation in parentheses).

Liite 11. Neulas- ja muun karikkeen keskimääräiset ravinnepitoisuudet lannoittamattomilla (0) sekä PK- ja NPK-lannoitetuilla koelaitilla ajalla 3.9.1984-1.9.1987, (keskihajonta suluisissa).

	Needles - <i>Neulas</i>			Other - <i>Muu</i>		
	0	PK	NPK	0	PK	NPK
N %	0.598 (0.023)	0.601 (0.009)	0.703 (0.034)	0.503 (0.032)	0.546 (0.090)	0.540 (0.057)
K %	0.078 (0.004)	0.101 (0.005)	0.105 (0.014)	0.063 (0.004)	0.087 (0.010)	0.082 (0.010)
Ca %	0.561 (0.019)	0.583 (0.044)	0.665 (0.154)	0.223 (0.050)	0.222 (0.051)	0.193 (0.027)
Mg %	0.070 (0.002)	0.080 (0.007)	0.080 (0.012)	0.035 (0.001)	0.040 (0.004)	0.039 (0.005)
P %	0.038 (0.002)	0.042 (0.002)	0.048 (0.001)	0.037 (0.002)	0.047 (0.013)	0.039 (0.004)
S %	0.062 (0.001)	0.064 (0.001)	0.070 (0.001)	0.052 (0.001)	0.054 (0.006)	0.051 (0.005)
B ppm	20 (7)	46 (7)	46 (3)	11 (1)	13 (1)	14 (1)
Fe ppm	88.4 (2.3)	89.3 (3.9)	96.9 (13.3)	187 (63)	189 (22)	145 (29)
Mn ppm	892 (113)	932 (15)	998 (179)	80 (9)	92 (10)	84 (11)
Zn ppm	59 (4)	68 (4)	71 (13)	33 (4)	35 (4)	32 (2)
Cu ppm	20 (1)	20 (1)	22 (3)	79 (11)	98 (20)	71 (23)

III



Root biomass on an ombrotrophic pine bog and the effects of PK and NPK fertilization

Leena Finér

TIIVISTELMÄ: OHUTJUURTEN BIOMASSA LANNOITETULLA JA LANNOITTAMATTOMALLA OMBROTROFISELLÄ RÄMEELLÄ

Finér, L. 1991. Root biomass on an ombrotrophic pine bog and the effects of PK and NPK fertilization. Tiivistelmä: Ohutjuurten biomassa lannoitetulla ja lannoittamattomalla ombrotrofisella rämeellä. *Silva Fennica* 25(1): 1–12.

Scots pine living root biomass ($\varnothing \leq 10$ mm) was 640 g/m^2 on the studied low-shrub pine bog before fertilization, and that of the ground vegetation almost the same. The total root necromass was 23 % of the living root biomass. The length of pine roots was 2440 m/m^2 . The living root biomass and root necromass were superficial. The $\varnothing < 1$ mm pine root fraction accounted for almost 90 % of the pine root length; in contrast, over 50 % of the biomass was in the 1–10 mm thick roots. The NPK(MgB) and PK(MgB) fertilizations did not affect total living root biomass, pine root length, nor the root necromass during the three-year observation period.

Ohutjuurten ($\varnothing \leq 10$ mm) biomassaa tutkittiin Pohjois-Karjalassa sijaitsevalla iso-varpuisella rämeellä. Ennen lannoitusta männyn ja pintakasvillisuuden elävien ohutjuurten biomassa oli lähes yhtä suuri (640 g/m^2) ylimmässä 40 cm turvekerroksessa. Kuolleiden juurten massa oli 23 % elävien juurten massasta. Männyn ohutjuurten pituus oli 2440 m/m^2 . Sekä elävien että kuolleiden juurten massa oli suurimmalta osin ylimmässä 20 cm turvekerroksessa. Alle 1 mm paksuisten juurten pituus oli lähes 90 % männyn ohutjuurten pituudesta, mutta niiden osuus biomassasta oli alle 50 %. NPK(MgB) ja PK(MgB) lannoitukset eivät vaikuttaneet merkittävästi elävien männyn juurten kokonaisbiomassaan, pituuteen, pintakasvillisuuden juurten biomassaan ja kuolleiden juurten massa kolmen vuoden tutkimusjaksolla.

Keywords: *Pinus sylvestris*, ground vegetation, root biomass, peatlands, fertilization. FDC 114.4+237

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1 Introduction

On drained, ombrotrophic pine bogs the root system of Scots pine is superficial even after improved aeration (Heikurainen 1955ab, Paavilainen 1966). Although the length of pine fine ($\varnothing < 1\text{ mm}$) and small ($\varnothing 1\text{--}10\text{ mm}$) roots is considerable – as much as thousands of kilometers per hectare (e.g. Heikurainen 1955ab, Paavilainen 1966, 1967a, Finér 1989, Håland and Brække 1989), their living biomass is equivalent to only a few per cent of the total biomass of the tree stand (Paavilainen 1980, Håland and Brække 1989, Finér 1989). On the other hand, a considerable proportion of the biomass of the ground vegetation is in the root system (Paavilainen 1980, Håland and Brække 1989).

Fine and small roots are short-lived and their production and mortality occur simultaneously during the growing season (e.g. Persson 1979, 1980a, Keyes and Grier 1981, Joslin and Henderson 1987, Santantonio and Santantonio 1987). Root length reaches its maximum on peat soils already in young stands (Heikurainen 1955b). The fluctuations in root biomass during the growing season are caused by e.g. the growth of above-ground compartments, soil temperature (Lyr and Hoffman 1967, Kramer & Kozłowski 1979) and the depth of the groundwater table (Heikurainen 1955b). On drained, ombrotrophic pine bogs tree

growth is limited by a shortage of phosphorus, potassium, nitrogen and boron (see e.g. Meshechok 1968, Brække 1977, 1983, Paavilainen 1979). Roots also respond to fertilization on mineral (Zöttl 1964, Persson 1980b) and peat soils (Paavilainen 1967b, 1968, 1980). The relationships between root development and different ecological factors are, however, not yet fully understood.

The aim of this report is to describe the living root biomass ($\varnothing \leq 10\text{ mm}$) and necromass distribution of Scots pine (*Pinus sylvestris*) and ground vegetation, and the effects of PK and NPK fertilization on a low-shrub pine bog. This study is a part of a Nordic project, the main objectives of which are to evaluate the amount, distribution and circulation of mineral nutrients after drainage and fertilization of ombrotrophic pine bogs in different climatic conditions.

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2 Material and methods

2.1 Study area

The material was collected from an experimental field in northern Karelia, (64 km SE of Joensuu 62° 14'; 29° 50' E, 81 m a.s.l.). The climatic data during 1984–1987 are presented in Table 1. The year 1987 was colder and more rainy than the other years, and the surface peat did not thaw until two weeks after the beginning of the growing

season. According to Heikurainen and Pakarinen (1982), the site is a low-shrub pine bog. A detailed description of the vegetation has been presented by Finér and Brække (1991). The site was drained in 1967 with a 50 m ditch spacing, and the fluctuations in groundwater table were monitored during 1984–1987 (Table 2).

The peat layer is over one meter thick and consists of slightly decomposed (von Post,

Table 1. Length of the growing season, temperature sum and accumulated precipitation during 1984–1987. The values measured at the synoptic climatic station are given in parenthesis.

Taulukko 1. Kasvukauden pituus, lämpösumma ja sademäärä vuosina 1984–1987. Ilmatieteen laitoksen Tohmajärven säähavaintoasemalla mitatut arvot suluissa.

Year	Length of growing season	Temperature sum	Precipitation	
<i>Vuosi</i>	<i>Kasvukauden pituus</i> days – vrk	<i>Lämpösumma</i> dd°	<i>Sademäärä</i> mm	
			1.6.–30.9.	1.1.–31.12.
1984	165 (168)	1107 (1243)	238 (249)	(618)
1985	141 (169)	1097 (1129)	282 (350)	582 (755)
1986	128 (151)	1026 (1135)	240 (302)	573 (650)
1987	173 (173)	939 (967)	478 (474)	698 (749)

H3-H5) ombrotrophic *Sphagnum* peat with some *Carex* below 20 cm depth and remnants of wood in all layers (see Brække and Finér 1991). The Scots pine stand growing on the site is about 85 years old and naturally regenerated (Table 3).

The field experiment was established in June 1984 and fertilized during the first days of June, 1985. A 3 x 3 Latin-square design with a 1500 m² plot size was used. The treatments were as follows: 1) control, 2) PK(MgB), 3) NPK(MgB). The amounts of different elements applied are given in Table 4. The fertilizers were given as ammonium nitrate, raw phosphate, potassium chloride, magnesium sulphate and sodium borate.

2.2 Sampling and calculations

Root sampling was carried out twice: 12.–27.9.1984 and 18.8.–3.9.1987. Twenty square peat cores (24.7 cm²) were systematically taken from each plot. The living moss layer was removed and the cores were divided into subsamples, starting from the surface down, as follows: 0–10, 10–20, 20–40 cm. Only every fifth subsample was taken from the deepest peat layer. The roots ($\emptyset \leq 10$ mm) were extracted by hand from each subsample and separated into three classes: living roots of Scots pine, living roots of ground vegetation, and all dead roots. Pine roots were further divided into $\emptyset < 1$ mm and $\emptyset = 1–10$ mm fractions. The length of pine roots was measured (cm)

Table 2. Depth of the groundwater table (cm) in June–September in 1984–1987. Values are the average distance to the water table from the ground surface at three points across the plots perpendicular to the ditch direction (n=12).

Taulukko 2. Pohjaveden pinnan syvyys (cm) kesä-syyskuussa vuosina 1984–1987. Arvot ovat keskisyvyysmittattuna maanpinnasta pohjavesipintaan kolmesta kaivosta, jotka oli sijoitettu tasavälein saralle kohtisuoraan ojja vastaan.

Year	Treatment	mean	max	min
<i>Vuosi</i>	<i>Käsittely</i>	<i>keskiarvo</i>		
1984	0	48	69	20
	PK	48	70	20
	NPK	48	70	20
1985	0	36	49	27
	PK	33	47	25
	NPK	34	47	27
1986	0	42	58	21
	PK	44	62	23
	NPK	44	60	23
1987	0	25	41	18
	PK	25	40	18
	NPK	25	41	18

before the roots were dried (105 °C) and weighed (0.001 g).

Differences in root biomass, necromass and length between years were tested with the paired t-test. The effect of fertilization was tested with variance analysis.

Table 3. Tree stand characteristics in 1984 and 1987.
Taulukko 3. Puustotunnukset vuosina 1984 ja 1987

Treatment Käsittely	Stem volume o. b. Rungon kuorellinen tilavuus (m ³ /ha)		Trees – 1984	Puuta/ha 1987	Volume growth o. b. Rungon kuorellinen tilavuuskasvu (m ³ /ha/yr – m ³ /ha/vuosi)
	1984	1987			
0	79.7	97.3	2333	2219	5.9
PK	78.8	97.4	2299	2178	6.2
NPK	79.4	99.1	2311	2072	6.6

Table 4. Nutrient elements applied in the different treatments, kg/ha.

Taulukko 4. Lannoituksessa käytetyt ravinnemäärät, kg/ha.

Element Ravinne	PK	NPK
N	–	150
P	53	53
K	100	100
Ca	135	135
Mg	25	25
S	28	28
Cl	95	95
B	2.4	2.4

3 Results

The average amount of Scots pine living root biomass was 637 g/m² on the plots before fertilization (Table 5), and that of the ground vegetation almost the same (Table 6). Root necromass was 23 % of the living root biomass. The variation coefficient of the living pine and ground vegetation root biomass estimate was 11 %, and that of the dead roots 32 %. There were no significant differences in root biomass between the treatments before (1984) and after (1987) fertilization. The total biomass of the ground vegetation roots on the control and PK fertilized plots decreased, and the necromass on the PK fertilized plots increased between 1984–1987 (Table 6).

The mean depth of the living root biomass was 9 cm and that of the pine root length 8 cm in 1984 (Table 7). Fertilization had no effect

on the depth of pine roots. However, the average depth of the ground vegetation roots was greater on the fertilized than on the control plots. More than 60 % of the ground vegetation and over 50 % of the pine root biomass occurred in the 0–10 cm peat layer (see Fig. 1). Only 5 % of the pine and slightly more of the ground vegetation roots were growing in the deepest peat layer, 20–40 cm. The greatest amount of dead roots was separated from the surface layer. Their distribution was more even than that of the living roots. Variance analyses by peat layers did not indicate any significant fertilization response.

The fine roots ($\varnothing < 1$ mm) accounted for 45 % of the total pine root biomass in the 0–10 cm peat layer before fertilization. In the 10–20 cm peat layer the small roots ($\varnothing = 1$ –

Table 5. Living fine and small root biomass (g/m^2) and root length (m/m^2) of Scots pine in 1984 and 1987. F and t-values and their significance, (standard deviation in parentheses).

Taulukko 5. Männyn elävien ohutjuurten biomassa (g/m^2) ja pituus (m/m^2) vuonna 1984 sekä t- ja F-arvot ja niiden merkitsevyys, (keskihajonta suluisissa).

Treatment Käsittely	Size Koko	Biomass – Biomassa				t-value t-arvo	Length – Pituus				t-value t-arvo
		1984		1987			1984		1987		
0	$\text{Ø} < 1 \text{ mm}$	263	(54)	167	(47)	-1.90	2075	(687)	1155	(193)	- 1.85
PK	–”–	276	(45)	208	(26)	-2.18	2050	(214)	1405	(129)	- 2.29
NPK	–”–	308	(21)	249	(99)	-1.01	2428	(302)	1598	(219)	-13.4***
All – Kaikki		282	(42)	208	(67)		2184	(457)	1386	(250)	
F-value		0.52		1.31			0.54		1.77		
<i>F-arvo</i>											
0	$\text{Ø} 1-10 \text{ mm}$	325	(19)	276	(78)	-0.90	237	(56)	161	(38)	- 4.55*
PK	–”–	366	(68)	392	(22)	0.95	257	(57)	201	(34)	- 1.45
NPK	–”–	372	(69)	402	(141)	0.30	277	(12)	186	(50)	- 2.55
All – Kaikki		354	(54)	356	(101)		257	(44)	183	(40)	
F-value		0.49		4.29			0.29		1.10		
<i>F-arvo</i>											
0	$\text{Ø} \leq 10 \text{ mm}$	588	(54)	442	(103)	-2.10	2311	(738)	1316	(191)	- 1.94
PK	–”–	641	(66)	600	(5)	-1.00	2307	(420)	1605	(160)	- 2.19
NPK	–”–	680	(89)	651	(240)	-0.18	2705	(304)	1785	(251)	-11.51***
All – Kaikki		637	(74)	564	(161)		2440	(493)	1569	(270)	
F-value		0.73		1.41			0.04		0.11		
<i>F-arvo</i>											

*** $p < 0.01$, * $p < 0.10$

Table 6. Living biomass of ground vegetation roots and the necromass of all roots in 1984 and 1987 (g/m^2). F and t-values and their significance, (standard deviation in parentheses).

Taulukko 6. Pintakasvillisuuden elävien ja kaikkien kuolleiden juurten biomassa vuosina 1984 ja 1987 (g/m^2), sekä t- ja F-arvot ja niiden merkitsevyys, (keskihajonta suluisissa).

Treatment Käsittely	Ground vegetation Pintakasvillisuus				t-value t-arvo	Dead Kuolleet				t-value t-arvo	
	1984		1987			1984		1987			
0	653	(48)	465	(81)	-4.44**	317	(135)	342	(71)	0.50	
PK	556	(47)	418	(81)	-6.86**	239	(46)	373	(13)	4.19**	
NPK	689	(43)	629	(337)	-0.34	305	(89)	524	(292)	1.05	
All	633	(72)	504	(202)		287	(91)	413	(172)		
<i>Kaikki</i>											
F-value	16.24*		2.50			0.32		1.36			
<i>F-arvo</i>											

** $p < 0.05$, * $p < 0.10$

Table 7. Mean penetration (cm) of living root biomass, necromass and length in 1984 and 1987. F-values and their significance, (standard deviation in parentheses).

Taulukko 7. Keskimääräinen juuriston elävän ja kuolleen biomassan ja pituuden syvyysjakaantuminen (cm) vuosina 1984 ja 1987 sekä F-arvot ja niiden merkitsevyys, (keskihajonta suluisissa).

Treatment <i>Käsittely</i>	Pine <i>Mänty</i>	Biomass – Biomassa		Dead <i>Kuolleet</i>	Pine root length <i>Männyn juurten pituus</i>
		Ground vegetation <i>Pintakasvillisuus</i>			
1984	0	9.3 (0.6)	7.8 (1.2)	13.8 (3.0)	8.1 (0.8)
	PK	9.5 (1.9)	10.9 (2.6)	14.2 (2.0)	8.7 (1.3)
	NPK	9.1 (1.2)	8.1 (0.8)	13.6 (3.5)	8.0 (0.5)
	All – <i>Kaikki</i>	9.3 (1.1)	8.9 (2.1)	13.8 (2.5)	8.2 (0.9)
F-value	0.4	4.4	0.0	1.0	
<i>F-arvo</i>					
1987	0	9.2 (0.9)	6.7 (0.8)	10.1 (0.2)	7.7 (0.2)
	PK	10.7 (0.8)	8.0 (1.7)	12.6 (2.5)	9.7 (1.1)
	NPK	9.8 (0.8)	9.1 (1.7)	12.7 (1.0)	8.8 (0.9)
	All – <i>Kaikki</i>	9.9 (1.0)	8.0 (1.6)	11.8 (1.8)	8.7 (0.9)
F-value	2.4	35.5**	1.6	2.3	
<i>F-arvo</i>					

** p < 0.05

10 mm) dominated, and in the deepest layer the fine roots ($\emptyset < 1$ mm).

The length of pine roots was 2440 m/m² in 1984 (Table 5), with no significant differences between the fertilization treatments. The pine root length decreased, especially on the NPK plots, between the surveys. The root length was more superficial than the biomass (see Table 7, Fig. 2). The fine root fraction ($\emptyset < 1$ mm) accounted for 90 % of the total root length in the 0–10 cm peat layer; in the deeper layers its proportion was smaller.

The biomass/length ratio was not affected by fertilization (Table 8), although according to the t-test the ratio of the 1–10 mm thick pine roots increased on the NPK plots. Scots pine root biomass and length per stem number and stem volume were also calculated (Table 9). They were not affected by the fertilizer treatments.

Table 8. Scots pine living root biomass in g per root length (m) of the two root size classes. F and t-values and their significance.

Taulukko 8. Männyn elävien ohutjuurten biomassa (g) pituusyksikköä (m) kohti eri kokoluokissa sekä t- ja F-arvot ja niiden merkitsevyys.

Treatment <i>Käsittely</i>	Size <i>Koko</i>	1984	1987	t-value <i>t-arvo</i>
0	$\emptyset < 1$ mm	0.13	0.14	0.56
PK	--	0.13	0.14	1.70
NPK	--	0.12	0.15	0.85
F-value		0.39	0.47	
<i>F-arvo</i>				
0	1–10 mm	1.37	1.70	0.76
PK	--	1.44	1.98	1.68
NPK	--	1.34	2.13	6.64**
F-value		0.07	7.14	
<i>F-arvo</i>				

** p < 0.05

Table 9. Scots pine living root biomass and length per stem and stem volume (m^3 o.b.) in different root size classes in 1984 and 1987. F and t-values and their significance.

Taulukko 9. Mäännyn elävien ohutjuurien biomassa ja pituus puuta ja puuston tilavuusyksikköä kohti eri kokoluokissa 1984 ja 1987 sekä t- ja F-arvot ja niiden merkitsevyys.

Treatment Käsittely	Size class Koko	kg/tree - puu		kg/m ³		t-value		km/tree - puu		t-value		km/m ³		t-value	
		1984	1987	1984	1987	1984	1987	1984	1987	1984	1987	1984	1987	1984	1987
0	Ø < 1 mm	1.1	0.8	1.64	17	2.63	9.0	5.2	1.70	260	119	2.32			
PK	"	1.2	1.0	1.72	21	3.51*	8.9	6.5	1.96	260	144	3.31*			
NPK	"	1.3	1.2	0.51	25	2.06	10.5	7.8	15.50***	306	161	8.47**			
F-value - F-arvo		1.14	1.79		1.55		1.21	2.87		0.33	1.86				
0	1-10 mm	1.4	1.2	0.58	28	1.98	1.0	0.73	3.85*	30	17	5.73*			
PK	"	1.6	1.8	-1.61	40	1.60	1.0	0.93	1.04	33	21	2.48			
NPK	"	1.6	2.0	-0.72	41	0.67	1.2	0.90	1.92	35	19	3.34*			
F-value - F-arvo		1.37	5.60		4.40		0.79	1.36		0.21	1.59				
0	Ø ≤ 10 mm	2.5	2.0	1.60	45	3.37*	10	5.9	1.80	290	135	-2.44			
PK	"	2.8	2.8	0.03	61	3.39*	10	7.5	1.84	293	165	3.21*			
NPK	"	2.9	3.1	-0.27	66	1.79	12	8.7	-13.82**	341	180	7.57**			
F-value - F-arvo		3.41	3.32		3.05		1.16	2.61		0.30	1.73				

*** p < 0.05, * p < 0.10

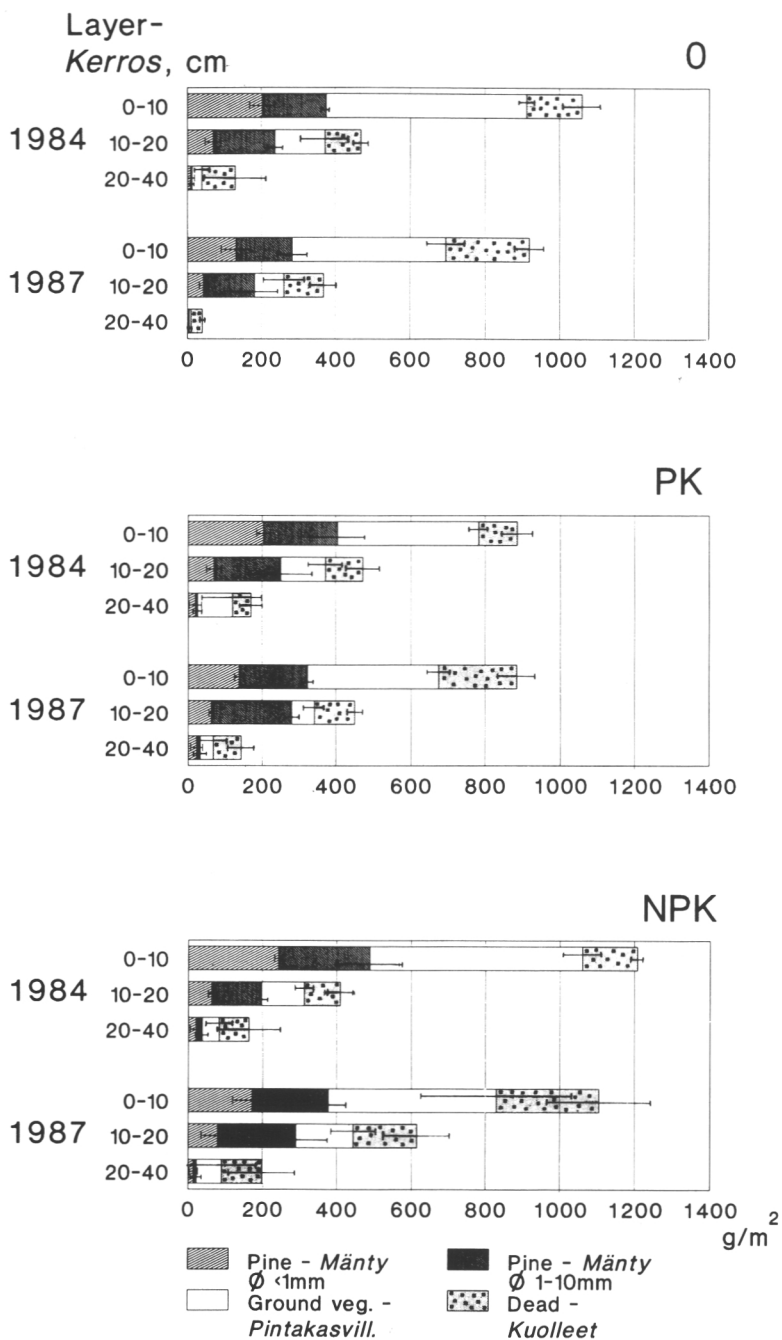


Figure 1. Living root ($\varnothing \leq 10$ mm) biomass and root necromass in different peat layers in 1984 and 1987 on the control, PK and NPK fertilized plots. Standard deviation indicated by lines in the columns.

Kuva 1. Elävien ja kulleiden juurten ($\varnothing \leq 10$ mm) biomassa eri turvekerroksissa vuosina 1984 ja 1987 lannoittamattomilla, PK- ja NPK-lannoitetuilla koealoilla. Keskihajonta esitetty janoin.

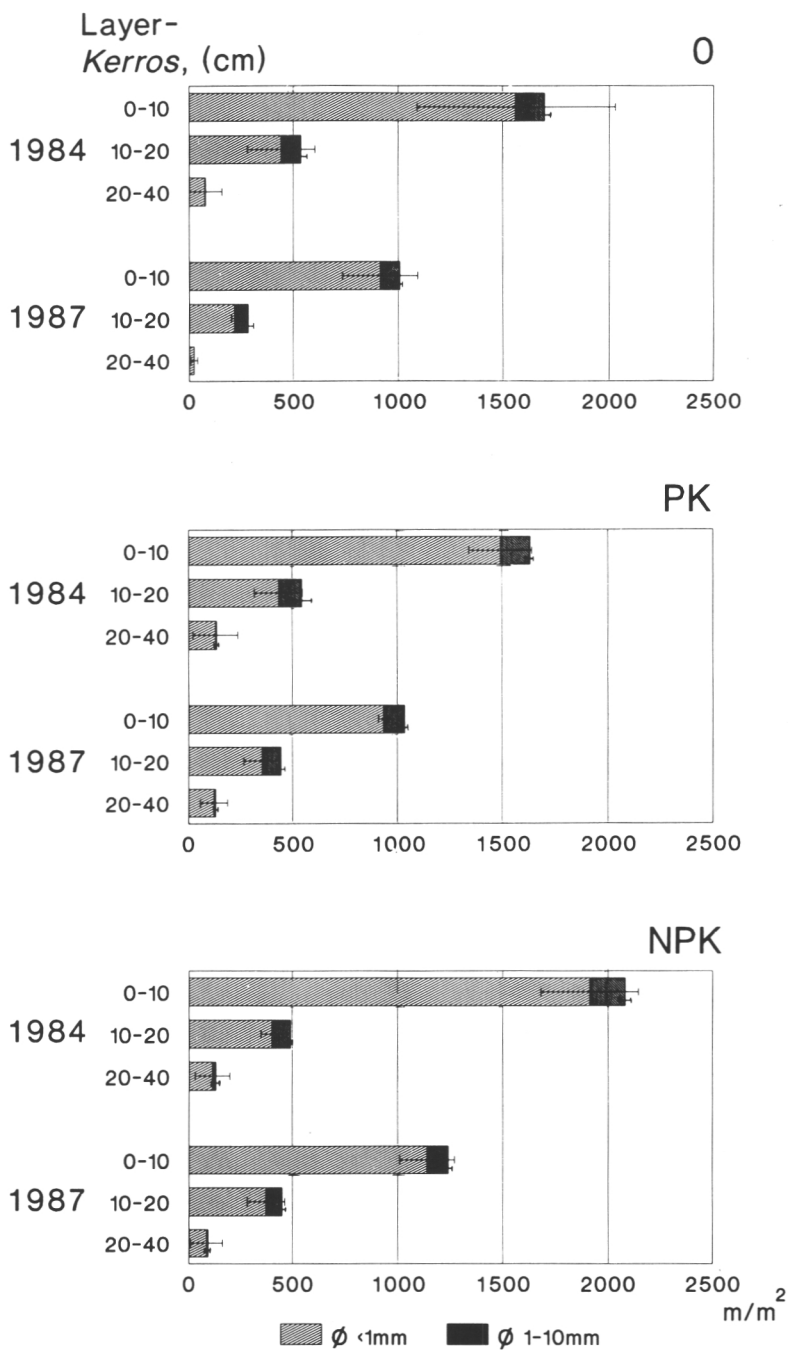


Figure 2. Scots pine root length ($\varnothing \leq 10$ mm) in different peat layers in 1984 and 1987 on the control, PK and NPK fertilized plots. Standard deviation indicated by lines in the columns.

Kuva 2. Männyn juurten ($\varnothing \leq 10$ mm) pituus eri turvekerroksissa vuosina 1984 ja 1987 lannoittamattomilla, PK- ja NPK-lannoitetuilla koealoilla. Keskihajonta esitetty janoin.

4 Discussion

Root length has been studied in Finland (Heikurainen 1955ab, Paavilainen 1966, Finér 1989) and in Norway (Håland and Brække 1989) on pine bogs with almost the same site type and tree stand characteristics as in this study. The root length in proportion to stem volume and tree number was lower on virgin sites studied by Heikurainen (1955b) and Håland and Brække (1989), and almost equal to those reported by Heikurainen (1955b), Paavilainen (1966) and Finér (1989) from drained sites. The pine root biomass was larger than that on the Norwegian site (Håland and Brække 1989), and almost the same as on the Finnish pine bog studied by Finér (1989). These observations are in accordance with results showing that root amount increases after improved drainage (Heikurainen 1955b, Paavilainen 1966).

The root biomass of the ground vegetation was almost equal to those reported by Paavilainen (1980) from a drained low-shrub pine bog in Finland, and Håland and Brække (1989) from a virgin bog in Norway. The proportion of ground vegetation roots compared to pine roots was clearly smaller than on the Norwegian site. After drainage the above-ground biomass of pine increases, whereas the ground vegetation, which is dominated by dwarf shrubs may gradually decrease (Brække 1988). This is probably also true for root biomass.

In general, pine produces a superficial root system on pine bogs (e.g. Heikurainen 1955ab, Paavilainen 1966, 1967, Finér 1989, Håland and Brække 1989). Although the roots penetrate to deeper peat layers after drainage, the change in the depth distribution is not great (Heikurainen 1955b, Paavilainen 1966). The root system on the Norwegian site (Håland and Brække 1989) had a similar distribution pattern to that on the studied site. The nutrient conditions were probably more favourable for the roots near the surface, where the decomposition activity was the highest (see Brække and Finér 1990). The higher temperatures and better aeration in the surface also promote the formation of a superficial root system. The pine roots were thicker in the 10–20 cm peat layer than in the

surface layer. This has also been observed on some other sites (Heikurainen 1955b, Håland and Brække 1989), but not on all (Finér 1989).

The ground vegetation root system was more superficial on the studied site than on the pine bog studied by Håland and Brække (1989). The species composition may explain this phenomenon (see Finér and Brække 1991). The roots of *Eriophorum vaginatum*, which was more dominant on the Norwegian site, penetrate to deeper peat layers than those of bog dwarf shrubs. Scots pine and the ground vegetation had equally deep root systems (compare Paavilainen 1968, Håland and Brække 1989).

No reports on the root necromass of pine bogs were found in the literature. Separating dead roots from peat is a more subjective procedure than that for living roots, and their mass is underestimated by this method. The annual fine root turnover has been estimated to be almost equal to the average, living, fine root biomass in cold temperate and boreal coniferous forests (Vogt et al. 1986). If the same relationship also prevailed on the study site, the root necromass was very low compared to the living root biomass. This may be an indication of a high rate of decomposition of the root litter. The root necromass was more evenly distributed in the different peat layers than the living biomass. This is probably explained by the differences in the decomposition between the peat layers (see Brække and Finér 1990) or a higher mortality rate close to the water table.

The results did not show that fertilization would have had any significant effect on the total root biomass or length (cf. Paavilainen 1980). According to Zöttl (1964, ref. Lyr and Hoffman 1967), the increased increment of stemwood given by fertilization in vigorously growing stands is associated with unstimulated or only slightly increased root systems. On the other hand, in stands with a poor nutrient status, additional growth of the above-ground compartments requires an enlargement of the root systems. Although the studied site was an oligotrophic low-shrub pine bog, the trees were growing

vigourously (Table 3). On oligotrophic pine bogs PK and NPK fertilizations have increased the root biomass and root length of pine seedlings and ground vegetation (Paavilainen 1967b, 1968). The site in this study was at the developmental stage where the amount of roots has already reached its maximum (Heikurainen 1955b). The root zone may have been fully occupied, with little room for root enlargement. In previous studies an increase in fine root biomass has also been observed later, 5–8 years after fertilization (see Paavilainen 1967b, 1968).

Axelsson and Axelsson (1986) found that the ratio of roots to total biomass fell during the 12-year period following fertilization of a Scots pine stand. In this study the amount of fine and small roots per stem volume did not change within the three-year study period. The depth of the ground vegetation root system was greater on the fertilized than on the unfertilized plots in 1987. This may be due to improved nutrition in the deeper layers, or to changes in the species composition after fertilization (see Finér and

Brække 1991).

The variation coefficients obtained for the total biomass estimate of the site can be regarded as small for material of this type (Brække and Håland 1990). However, the small effects of fertilization may have been obscured by the variation between the treatments. Possible responses in root dynamics were not revealed by the method used (see Persson 1980b).

The results indicate that the pine root length and ground vegetation root biomass decreased and the necromass increased between the surveys on both the control and fertilized plots. The root system probably suffered from poor aeration in 1987, when the groundwater table remained for most of the time in the studied peat layer (Table 2). The surface peat did not thaw until two weeks after the beginning of the growing season in 1987. Low temperatures may have prevented elongation and increased the mortality of roots (Kramer and Kozłowski 1979, Andersen et al. 1986).

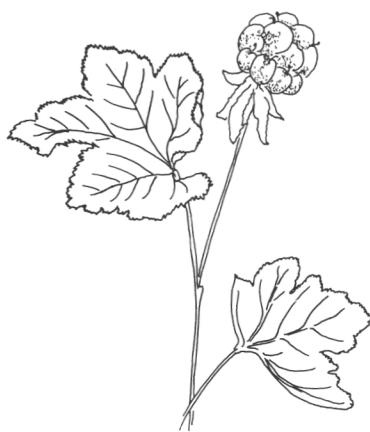
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IV



Nutrient Concentrations in *Pinus sylvestris* Growing on an Ombrotrophic Pine Bog, and the Effects of PK and NPK Fertilization

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Nutrient concentrations in different tree compartments and the effects of PK(MgB) and NPK(MgB) fertilization were studied in a Scots pine (*Pinus sylvestris* L.) stand growing on a low-shrub pine bog in eastern Finland.

The nutrient concentrations in all tree compartments were lower than those for plant material in general, although they did not differ very much from the values obtained from Scots pine in previous studies. The nutrient composition of the current needles were closest to those considered optimum for the development of higher plants. The highest macronutrient concentrations were found in the foliage. Zinc, Cu and B concentrations were also high in the living branches, stembark and small and fine roots. Iron concentrations were highest in the small and fine roots and dead branches. Stemwood had the lowest nutrient concentrations.

The rapidly soluble ammonium nitrate and potassium chloride fertilizers increased the foliar and stemwood N and K concentrations within the three year study period. Nitrogen concentrations also increased in the small and fine roots, and those of K in the living branches. The fertilization effect was greater in the young needles than in the old ones, indicating a delay in nutrient uptake, or retranslocation from the old needles to the youngest ones. Slowly soluble raw phosphate fertilizer clearly increased the small and fine root phosphorous concentrations only. The effect of sodium borate was rapid in the above-ground compartments, where the B concentrations increased in the foliage and living branches. The B concentrations increased more in the older than in the younger needles, which was explained by poor translocation of the fertilizer B in the foliage.

Magnesium sulphate fertilization did not change the Mg concentration in any of the studied tree compartments. The decrease in foliar Fe and Mn concentrations after fertilization could be due to the "dilution effect" of the main nutrient fertilization, inhibited uptake by other fertilizer cations or soil reactions. The foliar N, P, K and B concentrations and N/K and N/P ratios were below the optimum values before fertilization. The foliar N and P concentrations and N/P and N/K ratios remained below the optimum values despite the changes caused by fertilization. The K and B concentrations reached optimum values in the current needles. *Key words: Scots pine, tree compartment, element content, peatland, nutrient application.*

INTRODUCTION

Different tree compartments have separate functions, and their processes and nutrient concentrations therefore differ. Nutrient concentrations are controlled by the consumption of different tissues, the transport of elements between tree compartments, as well as by element uptake and availability in the soil. The storage and growing organs, i.e. needles, inner bark, buds, flowers, cones and fine roots, have the highest concentrations, and the stemwood and outer bark that consist mostly of dead cells have the lowest (e.g. Holmen, 1964; Mälkönen, 1974; Paavilainen, 1980; Lim & Cousens, 1986 a; Finér, 1989; Helmisaari & Siltala, 1989; Helmisaari, 1990 a, b).

At the beginning of the growing season nutrients are transported to the growing tissues from the soil and from storage sites in the tree. At senescence, part of the nutrients are transferred to the storage sites ready for future use by the growing organs (see e.g. Viro, 1955; Mälkönen, 1974; Helmisaari & Siltala, 1989; Helmisaari, 1990 *a*). Although nutrients are stored in the branches, trunks and roots of Scots pine, the needles are the most important storage sites (e.g. Lim & Cousens, 1989 *b*; Helmisaari & Siltala, 1989). The variation in climatic conditions cause between year fluctuations in the nutrient concentrations (e.g. Helmisaari, 1990 *a, b*; Helmisaari & Siltala, 1989). The changes in nutrient concentrations are also connected to the age of the stand (e.g. Mälkönen, 1974; Miller et al., 1981; Helmisaari, 1990 *a, b*; Helmisaari & Siltala, 1989).

On bogs the growth of trees is limited by a shortage of phosphorus and potassium (e.g. Meshechok, 1968; Brække, 1977, 1979; Paavilainen, 1979). On infertile sites nitrogen, and on inland sites boron, are also needed to achieve a growth increase (e.g. Meshechok, 1968; Brække, 1977, 1983; Paavilainen, 1979). The poor nutrient supply is reflected in the needle nutrient concentrations (e.g. Paarlahti et al., 1971), which increase after measures designed to improve the nutritional status of trees (e.g. Brække, 1977, 1979, 1983; Mannerkoski & Miyazawa, 1983; Paavilainen & Pietiläinen, 1983; Kaunisto, 1982, 1987; Paavilainen, 1984). The concentrations in the other tree compartments are also affected (Paavilainen, 1968, 1969, 1980). The changes in nutrient concentrations after fertilization indicate the nutrient status of the trees and the mobility of the fertilizer nutrients in the trees and soil. Determination of nutrient concentrations in different tree compartments is essential not only when studying the nutritional physiology of trees, but also when nutrient budgets are calculated for forested ecosystems.

The aim of this study was to determine the nutrient concentrations in tree compartments of Scots pine (*Pinus sylvestris* L.) growing on a nutrient poor low-shrub pine bog, and to

Table 1. *Tree stand characteristics*

Treatment	Stem volume (overbark) (m ³ ha ⁻¹)		Volume growth (overbark) during 1984–1987 (m ³ ha ⁻¹ a ⁻¹)	Stem number Trees ha ⁻¹
	1984	1987		
0	79.7	97.3	5.9	2219
PK	78.8	97.4	6.2	2178
NPK	79.4	99.1	6.6	2072

Table 2. *Amounts of nutrients applied in the different treatments, kg ha⁻¹*

Element	PK	NPK
N	–	150
P	53	53
K	100	100
Ca	135	135
Mg	25	25
S	28	28
Cl	95	95
B	2.4	2.4

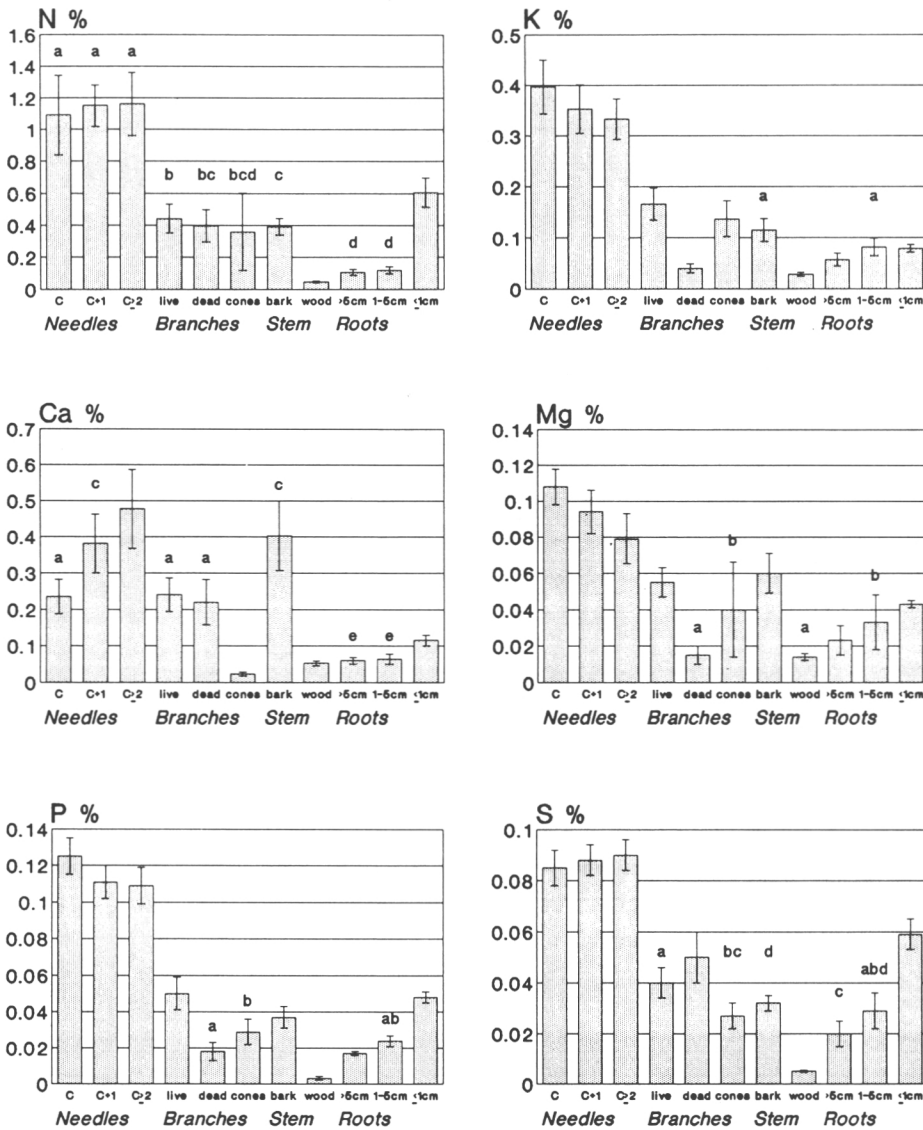


Fig. 1. The concentrations of macronutrients in different tree compartments in 1984. The compartments with the same letter do not differ significantly from each other ($p > 0.05$). Standard deviation is indicated by lines in the columns ($n = 27$). (C = current needles, C + 1 = one-year-old needles, C \geq 2 = two-year and older needles.)

estimate the effects of PK and NPK fertilizations on these concentrations. This study is part of a Nordic project, the main objectives of which are to study the distribution and cycling of nutrients on drained low-shrub pine bogs in different climatic conditions.

MATERIAL AND METHODS

Study site

The material was collected from the Finnish experimental forest (64 km SE of Joensuu, 62°14' N; 20°50' E, 81 m a.s.l.) of the Nordic project. The climatic data have been reported

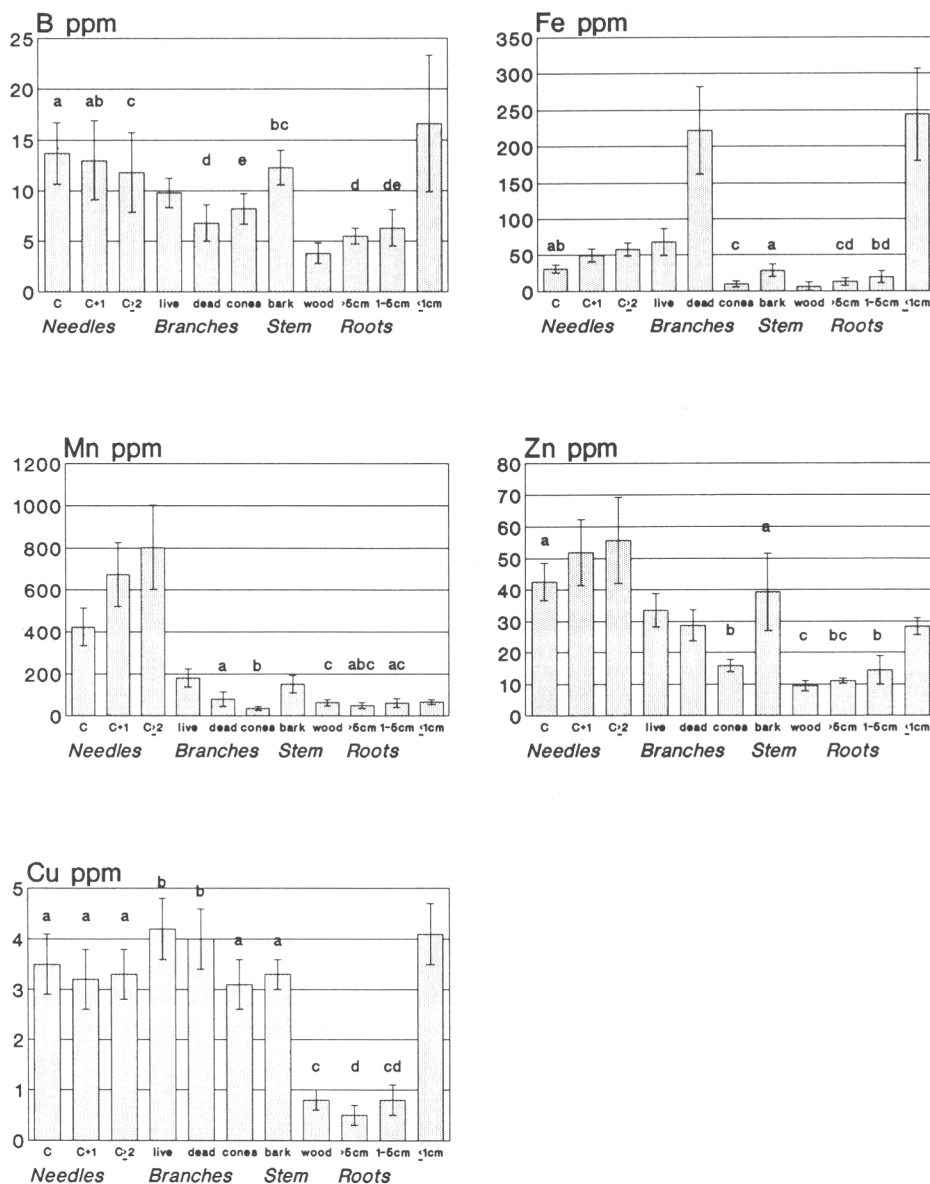


Fig. 2. The concentrations of micronutrients in different tree compartments in 1984. The compartments with the same letter do not differ significantly from each other ($p > 0.05$). Standard deviation is indicated by lines in the columns ($n = 27$). (C = current needles, C + 1 = one-year-old needles, C \geq 2 = two-year and older needles.)

by Brække and Finér (1990). According to the classification of Heikurainen & Pakarinen (1982), the site is a low-shrub pine bog. A detailed description of the vegetation has been presented by Finér & Brække (1991). The site was drained in 1967 with a 50 m ditch spacing, and fluctuations in the groundwater table were monitored during the period 1984–87 (see Finér & Brække, 1991).

The peat layer is over one-meter thick and consists of slightly decomposed (von Post, H3–H5) ombrotrophic *Sphagnum* peat with remnants of wood in the surface layer. The

nutrient contents of the peat have been presented by Brække & Finér (1991). The Scots pine stand growing on the site is 85 years old and was naturally regenerated (Table 1).

The field experiments were established in June 1984 and fertilized at the beginning of June 1985. A 3 × 3 Latin-square design with plots of 1500 m² was used. The treatments were as follows: 1) control, 2) PK(MgB), 3) NPK(MgB). The amounts of different elements applied are given in Table 2. The fertilizers were given as ammonium nitrate, raw phosphate, potassium chloride, magnesium sulphate, and sodium borate.

Sampling

The sampling for the nutrient determinations was carried out in September–October 1984 and again in 1987. On both occasions 27 sample trees were chosen, three per plot, using stratified random sampling based on breast height diameter. The bark and wood of the stem sample discs from relative heights of 0, 10, 20, 30, 40, 50, 60, 70, 80 and 90% were combined. The cones, branchwood with bark and needles of different age classes from seven branches (at 15, 40, 55, 65, 75, 85 and 95% relative heights) in the living crown were pooled. Ten randomly chosen dead branches per sample tree were pooled to give one sample. In 1984 the stumps, coarse ($\emptyset > 5$ cm) and large roots ($\emptyset 1-5$ cm) from every fourth and in 1987 from one sample tree on each plot were sampled for chemical analyses. The small and fine roots ($\emptyset \leq 1$ cm) were sampled on all plots using the core method. The same sample tree and fine root material was used for the dry mass determinations.

Nutrient analyses and calculations

Nitrogen was analyzed by the Kjeldahl method. The concentrations of K, Ca, Mg, P, S, B, Fe, Mn, Zn and Cu were determined by inductively coupled plasma emission spectrophotometry (ARL 3580) after nitric acid-perchloric acid digestion.

Differences in nutrient concentrations between tree compartments were tested by the paired *t*-test in 1984. The fine roots were not included in the tests because they were collected at the stand level. The differences between the treatments were tested by the *F*-test after analysis of variance.

RESULTS AND DISCUSSION

Variation between compartments

The nutrient concentrations in the different tree compartments (Figs. 1 and 2, Tables 3–6) were inside the ranges reported by Holmen (1964), Paavilainen (1968, 1980), and Finér (1989) for Scots pine growing on unfertilized peat soils, and by Wright & Will (1958) and Mälkönen (1974) for mineral soils.

The concentrations of the macronutrients, Mn and Zn were highest in the foliage (Figs. 1 and 2), which has also been observed in previous studies (see Holmen, 1964; Paavilainen, 1980; Reinikainen & Silfverberg, 1983; Finér, 1989). However, the concentrations of Ca and Zn were almost similar in the stembark. Apart from the foliage the B, Zn and Cu concentrations were also high in the other active organs, stembark, living branches (see also Reinikainen & Silfverberg, 1983) and small and fine roots. The Fe concentration was highest in the small and fine roots (see also Helmissaari, 1990 *b*) and dead branches (see also Finér, 1989). The concentrations of all nutrients were lowest in the structural organs, especially the stemwood (see Holmen, 1964; Paavilainen, 1980; Reinikainen & Silfverberg, 1983; Finér, 1989).

The total nutrient content accounted for 2.1–2.3% of the dry weight of the foliage, whilst in the living branches, stembark and small and fine roots the total content was only half of

Table 3. Mean nutrient concentrations (% d.m.) in the different needle age classes in 1987 on the control, PK and NPK fertilized plots and the F-values of variance analyses.

Standard deviation and the significance of F-value in parentheses, $n = 3$ (C = current needles, C + 1 = one-year-old needles, C ≥ 2 = two-year or older needles)

	C				C + 1			
	0	PK	NPK	F-value	0	PK	NPK	F-value
N(%)	1.10 (0.32)	1.11 (0.45)	1.21 (0.44)	75 (0.01)	1.16 (0.05)	1.19 (0.03)	1.31 (0.07)	4.9 (0.17)
K(%)	0.478 (0.023)	0.621 (0.040)	0.600 (0.005)	21 (0.05)	0.400 (0.020)	0.517 (0.016)	0.526 (0.030)	20 (0.05)
Ca(%)	0.193 (0.012)	0.174 (0.031)	0.170 (0.011)	3.1 (0.24)	0.356 (0.019)	0.311 (0.044)	0.310 (0.026)	5.7 (0.15)
Mg(%)	0.092 (0.005)	0.087 (0.006)	0.084 (0.005)	4.0 (0.20)	0.090 (0.006)	0.080 (0.012)	0.079 (0.015)	0.7 (0.59)
P(%)	0.144 (0.006)	0.171 (0.004)	0.171 (0.016)	4.7 (0.17)	0.118 (0.031)	0.132 (0.006)	0.140 (0.013)	14 (0.07)
S(%)	0.079 (0.005)	0.076 (0.002)	0.082 (0.0004)	1.7 (0.37)	0.083 (0.001)	0.082 (0.005)	0.090 (0.002)	5.3 (0.16)
B (ppm)	16.1 (1.4)	33.7 (2.2)	31.1 (3.0)	266 (0.00)	14.0 (2.9)	45.8 (3.9)	41.8 (9.2)	87 (0.01)
Fe (ppm)	33.7 (5.8)	24.8 (0.02)	26.9 (4.4)	3.7 (0.21)	44.8 (4.2)	33.9 (0.4)	36.9 (3.3)	73 (0.01)
Mn (ppm)	352 (12)	290 (36)	261 (59)	13 (0.07)	639 (29)	510 (66)	460 (117)	68 (0.02)
Zn (ppm)	41.3 (2.6)	40.2 (0.2)	42.6 (1.7)	0.70 (0.59)	51.2 (2.6)	43.4 (3.2)	45.2 (5.3)	9.2 (0.10)
Cu (ppm)	3.3 (0.3)	3.5 (0.7)	2.6 (0.2)	7.9 (0.11)	3.2 (1.2)	2.7 (0.3)	2.4 (0.2)	1.4 (0.41)

this figure, and less than 1/10 of it in the stemwood. The total nutrient content even in the needles was lower than that in plant material in general (Epstein, 1972; Larcher, 1980). The current needle nutrient composition was closest to that required for optimum development of higher plants. The needle K, B and Fe concentrations were low, and those of Mn and Zn high in relation to the N content.

The P concentration decreased by 13%, K by 16% and Mg by 28% as the needles aged from current ones to those more than two years old in 1984 (see also Viro, 1955; Paavilainen, 1980; Reinikainen & Silfverberg, 1983; Helmisaari, 1990 *a, b, c*). This would suggest that P is mobile in the foliage. Some K and Mg may also have been leached by precipitation from the old needles (see e.g. Päivänen, 1974; Helmisaari, 1990 *c*; Helmisaari & Mälkönen, 1989), which leads to overestimation of the mobility of these elements.

The high P, K, and Mg concentrations in the living branches and stumps and coarse roots compared to the dead branches and large roots, could also indicate the mobility of these elements in the tree. This conclusion is based on the assumption that the function of stumps and coarse roots does not differ very much from that of large roots.

The N concentration did not change with needle age (Fig. 1). This supports the observations for pine on peat soils (see Paavilainen, 1980; Reinikainen & Silfverberg, 1983; Finér 1989). However, on mineral soils foliar nitrogen concentrations have been found to decrease

C \geq 2

0	PK	NPK	F-value
1.15	1.14	1.24	2.4
(0.05)	(0.02)	(0.06)	(0.30)
0.379	0.451	0.458	6.8
(0.026)	(0.006)	(0.039)	(0.13)
0.469	0.458	0.466	1.7
(0.045)	(0.039)	(0.019)	(0.37)
0.076	0.079	0.070	0.17
(0.010)	(0.014)	(0.015)	(0.85)
0.114	0.120	0.124	1.7
(0.005)	(0.003)	(0.009)	(0.38)
0.086	0.085	0.080	5.2
(0.002)	(0.005)	(0.001)	(0.16)
12.8	59.5	60.4	105
(2.9)	(4.6)	(14.7)	(0.01)
56.0	45.6	50.5	0.84
(11.9)	(4.1)	(5.8)	(0.54)
799	713	652	27.3
(68)	(126)	(187)	(0.04)
51.0	58.0	47.1	0.22
(7.4)	(5.0)	(6.7)	(0.82)
2.5	2.5	2.7	0.29
(0.4)	(0.2)	(0.5)	(0.77)

along with increasing needle age (see Viro, 1955; Malkönen, 1974; Aronsson & Elowson, 1980; Helmisaari, 1990 *a, c*). The Ca concentration increased by 87% and sulphur by 7% as the needles aged from current ones to those more than two years old (see also Viro, 1955; Paavilainen, 1980; Reinikainen & Silfverberg, 1983; Helmisaari, 1990 *a, c*). The needle dry weight increases simultaneously (see e.g. Viro, 1955; Mälkönen, 1974; Helmiassari, 1990 *a, c*), and on the studied site the dry weight of the current needles was 18% lower than that of the oldest ones in 1987 (Finér, 1991). Because the increase in dry weight was clearly lower than the increase in the Ca concentration, this element can be considered to be poorly mobile (see Helmisaari, 1990 *a, c*). The mobility of N and S was probably intermediate. The high N, Ca and S concentrations in the stumps and coarse roots, and also that of S in the dead branches compared to the large roots and the living branches, supported the hypothesis of low mobility of these elements.

Boron was the only micronutrient whose concentration decreased with needle age. This could indicate mobility of B in the foliage (see Helmisaari, 1990 *a, c, d*). The Mn and Fe concentrations were almost 90% higher and Zn 20% higher in the oldest needle age-class than in the current one. The Cu concentrations did not differ between age-classes. Mn and Fe were probably concentrated in the old needles (see Helmisaari, 1990 *a, c, d*). The high Fe concentrations of small and fine roots probably indicated poor mobility of Fe from fine roots

Table 4. Mean nutrient concentrations (% d.m.) in the living and dead branches and cones in 1987 on the control, PK and NPK fertilized plots and the F-values of variance analyses

Standard deviation and the significance of F-value in parentheses, $n = 3$

	Living branches				Dead branches			
	0	PK	NPK	F-value	0	PK	NPK	F-value
N(%)	0.433 (0.014)	0.437 (0.024)	0.503 (0.039)	8.1 (0.11)	0.396 (0.060)	0.424 (0.063)	0.420 (0.074)	0.61 (0.62)
K(%)	0.178 (0.013)	0.206 (0.011)	0.232 (0.017)	20.8 (0.05)	0.043 (0.010)	0.049 (0.009)	0.046 (0.007)	110 (0.01)
Ca(%)	0.231 (0.022)	0.195 (0.015)	0.206 (0.012)	1.8 (0.18)	0.243 (0.028)	0.202 (0.028)	0.217 (0.034)	1.3 (0.44)
Mg(%)	0.052 (0.001)	0.051 (0.001)	0.053 (0.006)	0.22 (0.81)	0.015 (0.007)	0.015 (0.002)	0.014 (0.004)	1.12 (0.89)
P(%)	0.050 (0.003)	0.054 (0.006)	0.062 (0.002)	14.8 (0.06)	0.020 (0.005)	0.020 (0.003)	0.019 (0.001)	0.72 (0.58)
S(%)	0.037 (0.001)	0.039 (0.002)	0.044 (0.003)	26 (0.04)	0.053 (0.005)	0.053 (0.004)	0.053 (0.004)	0.01 (0.99)
B (ppm)	9.0 (0.5)	11.6 (0.5)	12.1 (1.0)	40.8 (0.02)	5.2 (0.6)	5.9 (0.2)	6.6 (0.3)	5.8 (0.15)
Fe (ppm)	61.4 (1.8)	57.2 (9.3)	65.2 (13.8)	5.9 (0.14)	238 (24)	224 (11)	240 (24)	0.50 (0.67)
Mn (ppm)	171 (3)	149 (26)	141 (35)	13 (0.07)	91 (41)	79 (5)	67 (7)	1.0 (0.50)
Zn (ppm)	30.9 (1.9)	31.1 (1.9)	34.2 (0.8)	44 (0.02)	28.9 (4.9)	31.1 (3.0)	29.2 (3.3)	0.35 (0.74)
Cu (ppm)	3.9 (0.6)	3.6 (0.3)	3.9 (0.4)	0.40 (0.71)	3.8 (0.5)	3.7 (0.1)	4.0 (0.3)	0.77 (0.57)

to the other tree compartments (see also Finér, 1989; Helmisaari, 1990 *b*). Zinc and Cu can be regarded as being intermediately mobile in the foliage (see Helmisaari, 1990 *a, c, d*). According to Loneragan et al. (1976), Zn and Cu are transported from senescing needles to new ones only if their concentrations in the plant are high.

Effect of fertilization

There were no significant differences in nutrient concentrations between the plots before fertilization. Nitrogen fertilization increased the nutrient concentrations of the youngest needle age class, stemwood, and small and fine roots (Tables 3–6). The K concentrations in the two youngest needle age classes living branches and stemwood were higher in the fertilized than in the control trees. Although the oldest needle age class on the trees had developed during the fertilization year, the increase in N and K concentrations was highest in the youngest needle-age classes. This could be explained by a delay in nutrient uptake, or more probably by retranslocation from the old needles to the youngest ones. Ammonium nitrate and potassium chloride are readily soluble in the soil solution and the effect of these fertilizers in the foliage of Scots pine has been observed to continue up to the third year after treatment (Paavilainen & Pietiläinen, 1983; Paavilainen, 1984; Kaunisto, 1987). Ammonium nitrate no longer has any effect after five to eight years on peat soils (Kaunisto, 1982, 1987), while that of potassium chloride continues (Kaunisto, 1982, 1987; Paavilainen, 1984).

Cones			
0	PK	NPK	F-value
0.362	0.360	0.402	1.9
(0.046)	(0.051)	(0.117)	(0.34)
0.206	0.272	0.271	3.0
(0.025)	(0.052)	(0.083)	(0.25)
0.014	0.015	0.015	2.8
(0.002)	(0.003)	(0.001)	(0.26)
0.037	0.036	0.036	0.09
(0.004)	(0.001)	(0.001)	(0.92)
0.044	0.052	0.054	0.47
(0.011)	(0.007)	(0.015)	(0.68)
0.031	0.030	0.035	0.66
(0.005)	(0.001)	(0.006)	(0.60)
11.3	13.4	13.1	0.29
(3.2)	(1.0)	(3.4)	(0.77)
12.4	10.7	9.0	1.1
(1.6)	(3.5)	(1.3)	(0.48)
26	26	24	0.37
(3)	(5)	(3)	(0.73)
18.5	17.9	21.2	1.5
(1.7)	(0.9)	(2.2)	(0.41)
3.3	2.7	2.1	12.4
(0.4)	(0.1)	(0.3)	(0.08)

Raw phosphate increased the phosphorus concentrations significantly ($p < 0.05$) only in the small and fine roots. There was no clear phosphorus fertilization effect in the foliage after three years in this study (compare Kaunisto, 1987). Raw phosphate is slowly soluble and does not increase the needle P concentrations as quickly as water-soluble superphosphate (Karsisto, 1976). However, the effect is usually long-lasting, for at least 5–6 years (Kaunisto, 1982, 1987; Paavilainen, 1984).

In 1987 the N/P ratio of current needles was 6.5 on the NPK and 7.1 on the PK fertilized plots, and that of N/K 1.8 and 2.0 respectively. These ratios were below those regarded optimum (see Puustjärvi, 1962 *a, b*; Paavilainen, 1979), and even slightly lower than before fertilization. However, the K concentrations in the current needles rose to the optimum level, and those of N and P remained below.

Sodium borate increased the B concentrations in all needle age classes and living branches. A rapid increase in foliar B concentrations after borate fertilization has been observed in previous studies (see Brække, 1977, 1979; Veijalainen, 1977, 1980; Paavilainen & Pietiläinen, 1983; Paavilainen, 1984; Kaunisto, 1987). In this study the B concentrations in the oldest needle classes even rose above the toxicity level (53 ppm) proposed by Brække (1983). In Brække's (1983) studies the toxicity symptoms occurred at higher boron doses than those used in this study. The change in B concentration was greatest in the oldest needles, which may indicate that most of the fertilizer had been taken up during the first year, and that the

Table 5. Mean nutrient concentration (% d.m.) in the stembark and stemwood in 1987 on the control, PK and NPK fertilized plots and the F-values of variance analyses

Standard deviation and the significance of F-value in parentheses, $n = 3$

	Stembark				Stemwood			
	0	PK	NPK	F-value	0	PK	NPK	F-value
N(%)	0.381 (0.018)	0.436 (0.017)	0.446 (0.026)	3.9 (0.20)	0.056 (0.005)	0.063 (0.008)	0.060 (0.005)	45 (0.02)
K(%)	0.144 (0.012)	0.211 (0.018)	0.180 (0.020)	7.0 (0.13)	0.028 (0.003)	0.037 (0.002)	0.035 (0.001)	41 (0.02)
Ca(%)	0.346 (0.046)	0.266 (0.028)	0.301 (0.042)	2.5 (0.28)	0.054 (0.003)	0.053 (0.004)	0.054 (0.001)	0.11 (0.90)
Mg(%)	0.054 (0.007)	0.059 (0.006)	0.049 (0.009)	1.2 (0.46)	0.013 (0.001)	0.014 (0.0001)	0.014 (0.001)	0.36 (0.74)
P(%)	0.043 (0.003)	0.053 (0.003)	0.048 (0.007)	3.1 (0.25)	0.003 (0.0003)	0.004 (0.001)	0.004 (0.0002)	3.8 (0.21)
S(%)	0.033 (0.001)	0.038 (0.002)	0.038 (0.003)	7.9 (0.11)	0.005 (0.0002)	0.005 (0.0003)	0.005 (0.0001)	19 (0.05)
B (ppm)	10.5 (0.5)	13.1 (1.6)	10.6 (0.4)	4.7 (0.18)	4.0 (0.6)	4.1 (0.9)	4.4 (0.8)	0.13 (0.89)
Fe (ppm)	28.5 (4.2)	24.6 (2.6)	24.9 (2.6)	0.68 (0.60)	11.4 (6.2)	5.5 (2.6)	9.3 (4.1)	2.1 (0.32)
Mn (ppm)	143 (20)	139 (23)	104 (16)	13 (0.07)	74 (6)	65 (13)	56 (13)	7.4 (0.12)
Zn (ppm)	33.0 (3.6)	35.1 (1.1)	33.1 (3.6)	9.5 (0.10)	10.3 (1.6)	8.7 (0.7)	10.3 (1.5)	2.1 (0.32)
Cu (ppm)	3.2 (0.1)	3.5 (0.7)	3.0 (0.2)	0.55 (0.64)	0.9 (0.4)	1.1 (0.3)	1.0 (0.4)	4.9 (0.17)

translocation of the fertilizer in the foliage was not very efficient. The mobility of B may be connected to the B status of the tree; in the control material the foliar B concentration decreased with needle age. Brække (1983) has shown that low Mg levels in the foliage are connected with B deficiency on inland sites, and that the application of B at optimum doses has often also increased Mg concentrations in the needles. Although the needle analyses indicated a low supply of B, the Mg application in water-soluble form did not increase the Mg concentration in any of the tree compartments. Magnesium sulphate fertilization increased the S concentrations in the living branches, stemwood and small and fine roots only.

After fertilization the Fe concentrations decreased in one needle age class, and the Mn concentrations in the two oldest needle classes. The decrease in Fe and Mn concentrations may be due to the "dilution effect" of the main nutrient fertilization (see e.g. Paarlahti et al., 1971; Veijalainen, 1977). Manganese contents have been found to decrease even after Mn fertilization (Finér, 1989), which also indicates that Mn uptake is inhibited by other fertilizer cations or chemical reactions in the soil.

Nitrogen fertilization probably affected the uptake of other nutrients. Thus the K concentrations in the living branches and S concentrations in the fine roots also increased more after NPK than after PK fertilization ($p < 0.05$). The Mn concentrations decreased

more after NPK than after PK fertilization in the foliage and stem bark. PK fertilization also had an effect on N uptake, since the concentrations increased in the stemwood. This could be connected to the overall increased uptake of nutrients or to improved mineralization of N after PK fertilization.

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Table 6. Mean nutrient concentration (% d.m.) in the stump to $\emptyset > 5$ cm, large ($\emptyset 1 - 5$ cm) and small and fine roots ($\emptyset \leq 1$ cm) in 1987 on the control, PK and NPK fertilized plots and the F-values of variance analyses

Standard deviation and the significance of F-value in parentheses

	Stump and coarse roots ($\emptyset > 5$ cm)				Large roots ($\emptyset 1 - 5$ cm)			
	0	PK	NPK	F-value	0	PK	NPK	F-value
N(%)	0.128 (0.014)	0.153 (0.024)	0.153 (0.027)	2.7 (0.27)	0.186 (0.029)	0.211 (0.054)	0.299 (0.059)	6.4 (0.13)
K(%)	0.069 (0.002)	0.110 (0.023)	0.082 (0.033)	1.6 (0.38)	0.104 (0.010)	0.166 (0.067)	0.171 (0.047)	1.2 (0.45)
Ca(%)	0.059 (0.004)	0.062 (0.005)	0.055 (0.008)	59 (0.02)	0.077 (0.024)	0.069 (0.016)	0.070 (0.010)	0.37 (0.73)
Mg(%)	0.018 (0.002)	0.022 (0.003)	0.018 (0.008)	0.75 (0.57)	0.027 (0.006)	0.030 (0.008)	0.028 (0.009)	0.36 (0.74)
P(%)	0.021 (0.002)	0.030 (0.008)	0.021 (0.008)	2.3 (0.30)	0.030 (0.001)	0.048 (0.020)	0.041 (0.008)	1.2 (0.45)
S(%)	0.016 (0.002)	0.021 (0.002)	0.020 (0.004)	1.4 (0.42)	0.035 (0.014)	0.038 (0.013)	0.039 (0.005)	0.72 (0.58)
B (ppm)	5.6 (0.5)	7.1 (1.4)	6.3 (0.5)	3.4 (0.23)	6.7 (0.3)	13.3 (11.9)	7.5 (1.8)	0.94 (0.52)
Fe (ppm)	21.4 (19.8)	14.2 (4.8)	21.7 (18.7)	0.14 (0.88)	16.6 (2.2)	18.6 (7.6)	22.5 (2.2)	2.0 (0.33)
Mn (ppm)	55.3 (1.1)	46.7 (1.3)	38.5 (10.4)	6.2 (0.14)	73.5 (20.2)	47.2 (6.5)	38.0 (12.9)	5.6 (0.15)
Zn (ppm)	10.4 (1.4)	11.5 (2.6)	8.8 (1.0)	1.8 (0.35)	16.2 (6.4)	12.9 (3.2)	13.6 (1.7)	1.4 (0.41)
Cu (ppm)	0.8 (0.4)	1.9 (1.3)	0.7 (0.5)	1.9 (0.34)	1.2 (0.3)	2.3 (2.1)	1.2 (0.3)	0.56 (0.64)

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Small and fine roots ($\emptyset \leq 1$ cm)

0	PK	NPK	F-value
0.596	0.594	0.745	32
(0.043)	(0.025)	(0.002)	(0.03)
0.062	0.089	0.085	13.7
(0.005)	(0.006)	(0.014)	(0.07)
0.112	0.123	0.112	0.88
(0.009)	(0.004)	(0.012)	(0.53)
0.036	0.040	0.038	5.3
(0.003)	(0.0005)	(0.004)	(0.16)
0.043	0.058	0.061	38.8
(0.003)	(0.002)	(0.005)	(0.03)
0.055	0.059	0.063	55.5
(0.004)	(0.002)	(0.005)	(0.02)
7.2	10.9	15.0	7.5
(3.1)	(3.9)	(3.4)	(0.12)
254	293	241	44.4
(72)	(54)	(72)	(0.02)
48	48	41	1.3
(12)	(13)	(1)	(0.53)
25.8	23.1	21.9	2.3
(3.6)	(1.2)	(2.2)	(0.30)
3.4	3.6	3.1	0.81
(1.0)	(0.6)	(0.9)	(0.55)

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