



## Fine-root biomass and production in Scots pine stands

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*Academic dissertation*

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# Original publications

This thesis is based on the following articles, which will be referred to by their Roman numbers.

- I Makkonen, K. & Helmisaari, H-S. 1998. Seasonal and yearly variations of fine-root biomass and necromass in a Scots pine (*Pinus sylvestris* L.) stand. *Forest Ecology and Management* 102:283-290.
- II Makkonen, K. & Helmisaari, H.-S. 1999. Assessing Scots pine fine-root biomass — comparison of soil core and root ingrowth core methods. *Plant and Soil* 210:43-50.
- III Makkonen, K. & Helmisaari, H.-S. 2001. Fine-root biomass and production in Scots pine stands in relation to stand age. *Tree Physiology* 21:193-198.
- IV Helmisaari, H.-S., Makkonen, K., Kellomäki, S., Valtonen, E. and Mälkönen, E. 2001. Below- and above-ground biomass, production and nitrogen use in Scots pine stands in eastern Finland. *Forest Ecology and Management* (in print).

The studies in papers I-III were carried out mainly by Kirsi Makkonen. The research plan and establishment of field studies were done in co-operation with H.-S. Helmisaari as a part of the large research project "Nutrient dynamics and biomass production of Scots pine". Kirsi Makkonen performed experimental work and is responsible for writing and interpretation of the results in papers I-III. In paper IV, Kirsi Makkonen is responsible for writing and interpretation of the results on below-ground biomass and production in Scots pine stands.

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## Corrections to the original papers

In the article I, the data on tree characteristics of the 35-year-old stand in table 2 was changed with an adjacent 35-year-old stand.





# 1. Introduction

## 1.1. Structure and function of roots

Roots are an important functional link between the soil and the above-ground vegetation. Especially fine roots represent a large and dynamic portion of the below-ground biomass and a significant part of primary production in boreal forests (Santantonio et al. 1977, Persson 1978). Living and dead roots provide pathways for the movement of water, nutrients and air in the soil, and their presence modifies the soil to such an extent that they can be considered to have a major influence on soil profile development. Root development is modified and controlled by soil properties, the degree of control depending on the tree species.

The root system of coniferous trees consists of various types of morphologically and functionally different roots. The major part of the root system consists of fine roots (Lyr and Hoffmann 1967). As the various types of roots play different physiological roles, recognition of the different types is a prerequisite for the meaningful description and interpretation of root systems (Sutton 1969).

The three main components of the tree root system are structural roots (coarse roots), fine roots and mycorrhizas. Fine roots consist of "long" roots, which bear lateral "short" roots, and when these roots become infected, they produce mycorrhizas (Bowen 1985). The major mycorrhiza type of Scots pine is ectomycorrhiza and it arises from infection of the short laterals (Harley and Smith 1983). Mycorrhizal associations are essential for conifers, because they enhance nutrient uptake by increasing the surface area of the roots. Mycorrhiza hyphae are widely distributed throughout the uppermost layers of the soil and can penetrate between smaller soil particles than roots (Eissenstat and Van Rees 1994). Mycorrhizas can greatly improve the acquisition of water and nutrients by plant roots (Smith and Read 1997). Mycorrhizas can also change the quality of root exudates; mycorrhizal roots produce exudates that are different from those of non-mycorrhizal roots of the same plant (Leyval and Berthelin 1993). Mycorrhizas can also protect plants against certain pathogens (Schenck 1981).

Roots and root systems have different definitions based on rooting depth, strategy of root growth and root diameter. Roots can be divided, according to rooting depth, into horizontal roots, which grow horizontally from the rootstock and are located in the 0 to 100 cm thick soil layer, and vertical roots, which grow vertically downwards along holes in the soil (Sutton and Tinus 1983). Kalela (1949) found, that in 30–110-year-old Scots pine (*Pinus*

*sylvestris* L.) stands in Finland, 58% of Scots pine horizontal roots were located in the 0–10 cm thick mineral soil layer and that the mean depth of the root system varied between 7.3–9.5 cm depending on stand age. Stone and Kalisz (1991) reported that the maximum rooting depth of different pine species varied from 1 m to as much as 24 m in different forest site types.

The root systems of coniferous trees can be divided, according to the strategy of root growth, into taproot, heartroot and plateroot systems (Sutton 1969, Sutton and Tinus 1983). Scots pine usually has a typical taproot system: 64% of Scots pines, which grow in sand or glacial till soil, have a taproot (Laitakari 1927).

When classified according to diameter, roots can be divided into fine roots and coarse roots (Böhm 1979, Persson 1980b, Sutton and Tinus 1983). Most investigators have defined fine roots as being less than 1 or 2 mm in diameter. Root investigators have also used arbitrary root diameter size classes varying from <1 to <10 mm (Vogt and Persson 1991). In most cases, there is no functional reason for the diameter class chosen. However, for most tree species, subdividing and separating roots into less and more than 1 mm in diameter has a sound morphological basis. Fine roots less than 1 mm in diameter consist of fine ramifications with mycorrhizal root tips, which are morphologically very distinctive from the rest of the root system (Vogt and Persson 1991). The fine-root fraction may account for a high proportion of the total root length. According to Persson (1980b), the <1 mm root fraction constitutes as much as 80% of total root length in Scot pine.

Coarse roots, in this case roots more than 1 mm in diameter, tend to be secondary roots in which the epidermis and cortex have sloughed off and the xylem has become enclosed by a cylinder of phloem with an outside layer of suberized tissue. Tree roots increase in diameter through cambial growth. Organic matter returned to the soil by sloughing of the epidermis and cortex may represent approximately half of the dry matter of young root (Vogt and Persson 1991).

The root systems perform two primary functions: the acquisition of soil-based resources (water and dissolved ions) and anchorage. Other functions, such as storage and synthesis of growth regulators can be considered secondary functions (Fitter 1991). In order to fulfil these functions, roots extend downwards and outwards from the base of the stem, and ramify throughout the accessible regions of the upper layers of the soil in the search for available water and nutrients. Rooting depth is strongly influenced by soil characteristics.

The first root developed by a seedling arises from the root promeristem of

the embryo as the primary or tap root (Esau 1977). Lateral roots originating from the taproot are termed secondary roots, which in turn give rise to tertiary roots. Many of the fine, lateral and tertiary roots die after a short period of activity and are replaced by new roots growing out from the stem or from mother roots. During every growing season old root channels are re-explored by newly formed roots, and previously unexplored volumes of the soil may be penetrated for the first time (Waid 1974). The extension growth and secondary thickening of roots creates and widens channels within the soil, and these channels can persist after the disappearance of the roots. Such channels modify the physical environment of the soil and improve soil aeration, drainage and the waterholding capacity.

One of the important effects of roots in the soil results from the high turnover of fine roots. Fine root mortality transfers significant amounts of organic matter and nutrients into the soil and it is an important part in forest nutrient cycles (Aber et al. 1985). The estimates of fine root turnover rates vary. According to Vogt and Bloomfield (1991), the turnover of fine roots may be only a few weeks in some ecosystems. Lyr and Hoffman (1967) suggested, that fine roots may live for two years, whereas Orlov (1968) observed that fine roots can live for as long as eight years.

The decomposition rates of dead fine roots are frequently considered to be regulated by the interaction between soil organisms, environmental conditions and chemical quality (Fogel and Cromack 1977, Berg and Staaf 1980, Melillo et al. 1982), and in roots particularly the lignin concentration (Berg 1984). Nutrient are released from plant litter either by mechanical leaching or the breakdown of structural organic components by soil organisms. The hemicellulose and cellulose components decompose first, then the lignin. The lignin fraction does not start to degrade until the other components have degraded to a certain extent (Berg and Staaf 1980). The quantity and quality of below-ground litter may vary between different tree species (Finér et al. 1997, Scott 1998) and within individual species (Berg 1984). In Scots pine, root lignin concentrations decreased with increasing diameter from very fine to larger roots (Vogt et al. 1991). According to several studies (Persson 1982, Berg 1984, McClaugherty et al. 1984, Gholz et al. 1986), the fine-root decomposition rates of different pine species varied between 15–30% annual weight loss depending on the method used to determine it.

An extremely wide range of soil organisms are associated with the cycles of root formation, functioning, death and decay. Decomposing root tissues provide energy and nutrients to support the growth of organisms such as earthworms, fungi and bacteria, which, in turn, can improve soil structure or strengthen and thus preserve desirable soil aggregates. Dead roots can act as reservoirs of infection for soil-borne plant pathogens (Waid 1974)

## 1.2. The environment of roots

### Soil properties affect the growth of fine roots

It is well known, that the fine-root growth of forest trees is affected by age and species of tree, carbon allocation and water and nutrient supply, and abiotic factors such as soil temperature, soil density and compaction, aeration and toxicity (Hertz 1935, Lyr and Hoffmann 1967, Persson 1992).

In general, the temperature of the soil is lower than that of the air in the boreal forest, and is less subject to rapid change, particularly at lower depths. Soil temperature affects both directly the cells in the roots and indirectly the physical, chemical and biological properties of the soil (Helmisaari et al. 2000). Soil temperature regulates root growth through nutrient availability, photosynthetic production and carbon allocation. The transport of nutrients in the soil and their release in microbial decomposition are also dependent on temperature. Fine-root growth is greatest in late summer and early autumn probably because of the slow increase in soil temperature throughout the summer. When Scots pine and Norway spruce (*Picea abies* (L.) Karst.) plants were grown in hydroponic culture, the fine roots did not start their growth until the temperature was more than 8 °C (Vapaavuori et al. 1992).

Soil water can directly influence the growth rate and distribution of fine roots. Rooting depth and rooting density may increase in response to a decrease in soil water content (Persson et al. 1995). Changes in soil water potential have a substantial influence on the activity of root systems (McMichael and Quisenberry 1993). The death of fine roots is often caused by extensive drying of the upper soil layers (Deans 1979). When soil dries out rapidly, the turgor pressure of the roots decreases and the roots consequently shrink. A layer of air is left between the roots and soil particles, leading to a reduction in the rate of water transport. A root system that has suffered from drought for a long period, may not be able to utilise an increase in available water until new root tips have been formed (Kramer 1950). Soil drying does not presuppose a period without any precipitation. It is the quantity of precipitation that is the decisive factor. Canopy retention is relatively greater when the amount of precipitation is small than during heavy rainfall. Thus the soil becomes wet only during rain events that last for a sufficient period of time. Elevated temperatures may increase water evaporation from the surface of the soil (Helmisaari et al. 2000).

The forest site and the soil nutrient content also affect fine-root growth. On fertile sites, the trees obtain water and nutrients from a smaller area than those growing on nutrient-poor sites, and the root systems of the individual trees are smaller. In fertile soil, root branching increases and root elongation decreases, while in poor soil root branching is limited, but elongation fast (Laitakari 1927). On fertile site the trees compete especially for light, but on poor site

for water and nutrients. Disturbances such as drought may, however, have a stronger effect on the trees on a fertile site because the surface area of the transpiring canopy is large. High soil fertility increases foliage growth to a relatively greater extent than root growth (Ryan et al. 1996).

The timing of fine-root growth is determined by the physiological state of the trees and soil factors, especially soil temperature (Lyr and Hoffmann 1967). Growth of the above-ground parts of trees in Finland mainly takes place between early May and late July (Helmisaari et al. 2000). During this period the trees use large amounts of photosynthates for the growth of the above-ground parts. When the above-ground growth stops, the trees can then allocate more photosynthates to root growth. According to Lyr and Hoffmann (1967), the growth of Scots pine fine roots is limited during the formation of shoots and needles, but increases immediately after needle elongation.

### **Roots as a part of soil biota**

Roots are an essential part of the soil biota. The other components are soil microbes (bacteria, algae, fungi) and a variety of invertebrate animals (soil fauna). Together they make up the biological community of the soil, and produce intra- and extracellular enzymes that are responsible for much of the biogeochemical cycling in the soil (Killham 1994).

Root systems are almost always associated with an adjacent volume of soil containing a denser distribution of microbes. This zone around the root is called the rhizosphere. The rhizosphere is that portion of the soil in which the abundance and composition of the microbial population is influenced by the presence of roots (Kimmins 1987). The extent of the rhizosphere is generally considered to be a diffuse cylinder of soil that roots exploit and into which they release exudates.

The rhizosphere soil can be distinguished from the bulk soil on the basis of the physical, chemical and biological properties of the soil: the pathway for water, nutrient, microbial and microfaunal movement may be more convoluted in the rhizosphere soil than in the surrounding bulk soil. The organic matter released by the root may accumulate close to the root. The water potential regime of the rhizosphere is lower than that of the bulk soil. This causes a net mass flow of water towards the roots, and can set up a nutrient gradient across the rhizosphere. The chemical nature of the rhizosphere is different from that of the bulk soil as a result of the release of carbon from the roots and the selective uptake of ions from the soil solution (Killham 1994).

Bacteria are known to colonize root surfaces soon after seedlings germinate. The root apices are free of bacteria, but in the zone of root elongation bacteria can be seen as single cells or in clusters on the root surface. As roots age the

bacterial populations on the root surfaces become very large, and extensive colonies can be seen (Waid 1974).

The soil animals (soil fauna) influence the process of decomposition. The direction and degree of this influence is strongly dependent on the type of soil animal, the chemical composition of the litter (especially lignin concentration) and the season of the year (Crossley 1977, Berg et al. 1980).

The mechanisms by which soil animals influence litter decomposition are many: they consume dead organic matter and microorganisms, produce faeces and change the chemical composition. They also change the structure of the litter through fragmentation and mix it into the soil (Crossley 1977).

Soil animals have been classified into five groups according to their feeding habits: saprovores, bacterivores, fungivores, carnivores and herbivores (Wallwork 1958). The soil fauna of coniferous forest has been studied intensively in Finland (e.g. Haimi 1993, Huhta et al. 1986, Setälä 1990). In boreal coniferous forest, the enchytraeid *Cognettia sphagnetorum* (Vedj.) is one of the most important species and forms the major part of the soil fauna biomass (Huhta 2000). Many animals can vary their feeding habits, e.g. *Cognettia sphagnetorum* (Vedj.), is considered to be 50% saprovores, 25% fungivore and 25% bacterivore (Latter and Howson 1978).

Animals undoubtedly play an important role in the final stages of root decay (e.g. Huhta and Setälä 1984, Huhta et al. 1998). Soil animals may occur at a later stage in root decomposition than fungi or bacteria. The dead roots of trees are finally disposed of by saprophagous mites that gnaw away the decaying tissues, which are protected by the outer layers of suberized bark that are more resistant to decay processes. Fine roots are excavated by tiny oribatid larvae and nymphs. As a result of this animal activity, a network of passages remains in the soil replacing the original root system. New roots can grow into this network of passages and presumably benefit from the presence of well-aerated channels enriched in nutrients (Ghilarov 1968, Waid 1974).

Soil organisms decompose the organic substrates and release carbon dioxide, water and mineral nutrients. According to a number of different estimates, the microorganisms release 80–99% and the soil animals 1–20% of the non-root losses of carbon dioxide from various types of soil (Huhta and Koskenniemi 1975, Persson and Lohm 1977, Coulson and Whittaker 1978).

### **1.3. Roots as a carbon sink and source**

In general, fine roots contribute to soil organic matter accumulation because

of their high production and fast turnover leading to high annual litter inputs with fast decay rates (Vogt et al. 1991). The accumulation of forest floor can be as much or more the result of the production and death of fine roots and mycorrhizal fungi as it is of aboveground litterfall (Kimmins 1987).

The living and dead roots contain a store of reduced carbon and nutrients (Waid 1974). Below-ground tissues (i.e. roots) contribute to soil organic pools and accumulation while they are alive, as well as after senescence while they are decomposing. Live roots may contribute carbon to the soil environment in several ways, by root respiration, by exudation of carbon compounds from roots (Smith 1976), by carbon allocation through roots to mycorrhizal hyphae, and through the production of volatile organic compounds (Rovira et al. 1979). These carbon inputs play also an important role in the soil by regulating the decay rate of senesced plant tissues. This is accomplished by sustaining the microbial populations that are involved in litter decay and nutrient mineralization (Vogt et al. 1991). According to a recent Swedish study, root–mycorrhizal respiration estimates in a Scots pine stand were 52–56% of soil overall CO<sub>2</sub> efflux (Högberg et al. 2001).

Estimates of proportion of carbon from root mortality and decay of total carbon annually added to the soil have varied from 25–36% (McClagherty et al. 1984), 54–81% (Gholz et al. 1986) and 78–84% (Fogel and Hunt 1983) according to tree species and forest site types. Vogt et al. (1982) estimated, that although only about 1% of the biomass of Pacific silver fir (*Abies amabilis* Forb.) stands was mycorrhizal fungi, about 15% of the net primary production was allocated into these fungi.

## 1.4. Root research

Root research in forest soils in Finland has earlier concentrated on the morphology and ecology of root systems (Laitakari 1927, 1934, Kalela 1949, Yli-Vakkuri 1953, Heikurainen 1958), with only a few studies carried out on root dynamics (Heikurainen 1955, Kalela 1955). Since then, attention has been paid to the distribution patterns of fine roots.

During the last few decades Finnish root research has focused on the nutrient concentration of roots, fine root production and dynamics, and methods for studying roots both in mineral soils (Helmisaari 1991, Messier and Puttonen 1993, Finér et al. 1999, Makkonen and Helmisaari 1998, 1999, 2001, Helmisaari and Hallbäck 1999) and in peatlands (Paavilainen 1966, Finér 1991, 1992a, 1992b, Finér and Laine 1998, 2000).

In other countries, root research has focused on the dynamics of root biomass

(Santantonio et al. 1977, Vogt et al. 1981, 1983, Aber et al. 1985), and root distribution and production (Fogel 1983, Persson 1978, 1979, 1980a, 1980b, 1983, Heindrick and Pregitzer 1992). Part of the research has concentrated on methodical problems (Böhm 1979, Aber et al. 1985, Fairley and Alexander 1985, Vogt et al. 1986, Kurz and Kimmins 1987, Santantonio and Grace 1987, Persson 1990, Vogt and Persson 1991, Hendrick and Pregitzer 1992, Nadelhoffer and Raich 1992, Majdi and Persson 1993, 1994, 1995).

Even though a number of reports have been published on the stand below-ground biomass during the last two decades, only a few of the studies examine the variation in fine-root biomass with stand age (Persson 1978, 1980a, b, Grier et al. 1981, Vogt et al. 1981, 1983, 1987). Only a few studies report on both the above- and below-ground production of conifers (e.g. Ågren et al. 1980, Grier et al. 1981, Keyes and Grier 1981, Naderhoffer et al. 1985, Gower et al. 1992). Below-ground production data especially, and the factors that control biomass allocation to the roots, remain a large uncertainty in forest biomass production budgets (Vogt et al. 1991, Gower et al. 1994, Bartelink 1998).

## 2. The aim of this thesis

The overall aim of this study was to investigate the seasonal variation in fine-root biomass and production in Scots pine stands of different age using different methods for studying fine roots.

More detailed aims were

- to determine the seasonal variation of fine-root mass and production in a 15-year-old sapling stand (Paper III), in a 35-year-old pole stage stand (Paper I and III), and in a 100-year-old mature stand (Paper III),
- to compare different methods for estimating fine-root production (Paper II), and
- to determine the role of fine roots in the allocation of stand biomass and production (Paper IV).



# 3. Materials and methods

## 3.1. Site description

The study (I–IV) was carried out in three Scots pine (*Pinus sylvestris* L.) stands at Ilomantsi (62° 47' N; 30° 58' E; 144 m a.s.l.) near the Mekrijärvi Research Station of the University of Joensuu.

The experimental stands were a naturally regenerated 15-year-old sapling stand, a 35-year-old pole stage stand and a 100-year-old mature stand (III, Table 2). In each of the stands, one sample plot (area 400 m<sup>2</sup>, 500 m<sup>2</sup> and 875 m<sup>2</sup>, respectively) was established in May 1983. The site type was the *Vaccinium* type according to the classification of Cajander (1949). The field layer in the sapling stand was dominated by heather (*Calluna vulgaris* (L.) Hull.), in the pole stage stand by cowberry (*Vaccinium vitis-idaea* L.) and heather, and in the mature stand by cowberry and blueberry (*Vaccinium myrtillus* L.). The bottom layer was dominated by the red-stemmed feather moss (*Pleurozium schreberi* (Brid.) Mitt.) with some reindeer lichens (*Cladina* sp.) in both the sapling and pole stage stand. In the mature stand the bottom layer was almost completely dominated by the red-stemmed feather moss and *Dicranum* moss (*Dicranum scoparium* Hedw.).

The stands were situated on sites of similar nutrient content and soil type at a distance of less than 500 m from each other. Even though the stands were situated on a similar type of soil, the soil moisture content varied between the stands. The soil in the sapling stand was drier than that in the pole stage or mature stand because of the deeper groundwater level and lower stand density. The groundwater level was about two times deeper in the sapling stand (groundwater level varied between 128–376 cm) than in the mature stand (groundwater level varied between 21–239 cm).

The mean annual temperature was 1.0 °C and the annual precipitation was 699 mm during the study period (1985–1988). The long-term annual averages (1961–1990) were 1.9 °C and 649 mm, respectively (The Finnish Meteorological Institute 1991). Temperature and precipitation data are from the Ilomantsi Station of the Finnish Meteorological Institute (62° 40' N; 30° 57' E; 162 m a.s.l.), located about 12 km from the stands (The Finnish Meteorological Institute 1986, 1987, 1988, 1989). About 40% of the annual precipitation falls as snow, and there is a permanent snow cover from October to May.

The soil type (III, Table 2) is a ferric podzol (FAO–Unesco 1988) and is relatively infertile. The mineral soil down to a depth of 60 cm is sorted

glacio-fluvial sand. The proportions of clay and coarse sand are about 2 and 50%, respectively. Compact till occurs below the sorted layer (Helmisaari and Mälkönen 1989).

### **3.2. Root sampling and analysis**

Soil samples were taken during four growing seasons in 1985–1988 using two methods: the soil core (I–IV) method and the root ingrowth core method (II).

In the soil core method, altogether ten samplings were made in the sapling stand and eleven in the pole stage and mature stands during the growing seasons in the years 1985–1988. Twenty soil cores (volumetric samples, core diameter 36 mm) per sampling and stand were taken for fine-root biomass determinations. The soil cores were divided into three layers by depth: humus, 0–10 cm and 10–30 cm mineral soil layers.

In the root ingrowth core method, a total of 114 ingrowth core samples were collected during the growing seasons 1986–1988. In August 1985, 120 root-free mesh bags ( $\varnothing$  5.7 cm) were inserted into the soil of each stand. The mesh bags were filled with homogeneous, sieved mineral soil and placed in the holes made with a soil corer down to a depth of 30 cm in the mineral soil. A piece of oven-dried humus was placed on top of the mesh bag. The mesh size of the bags was 5.5 mm. The first root ingrowth core samples were removed using a special spade in July 1986 and the last ones in October 1988.

In both techniques, the samples were transported from the field to the laboratory and stored frozen ( $-18\text{ }^{\circ}\text{C}$ ) until analysis.

#### **Laboratory analysis**

In the laboratory, the roots were washed free of soil and classified into trees or understorey vegetation as well as according to diameter and physiological status (living and dead). Living Scots pine roots were distinguished from living understorey roots on the basis of their mycorrhizas, colour and thickness. Dead roots were distinguished from living roots on the basis of their colour and consistency (Vogt and Persson 1991).

In the soil core method the living Scots pine roots were separated into three classes according to diameter:  $<2$  mm, 2–5 mm and 5–10 mm. The living understorey roots and the dead roots (necromass) were separated into diameter classes  $<2$  mm and  $>2$  mm. Roots with a diameter  $<2$  mm were classified as fine roots (Persson 1983, Vogt et al. 1983) and  $>2$  mm as coarse roots. Fine roots are generally defined as non-woody, small diameter roots (Nadelhoffer

and Raich 1992), but there is no established convention defining the diameter range of fine roots (Fogel 1983). The fraction "dead roots" included both Scots pine and understory dead roots.

The frozen root ingrowth core samples were divided in the laboratory into three layers: humus, 0–10 cm mineral soil, and the remaining mineral soil (length measured). As in the soil core method, the roots were separated from the soil by washing, and sorted by hand into living Scots pine roots, living understory roots and dead roots. The sorted roots were then separated into different classes according to diameter: living pine roots were subdivided into <2 mm and 2–5 mm, and both living understory roots and the dead roots (necromass) into <2 mm and >2 mm.

After classification, the roots were dried at 70 °C for 5 days and weighed to determine the oven-dry biomass.

### **3.3. Tree stand measurements and analysis**

The biomass and annual production of stems, needles, cones, stembark, branches (wood and bark) and coarse roots were calculated for the whole stand using biomass measurements made on different components of felled sample trees and on the tree stand (Helmisaari 1992, Helmisaari and Siltala 1989).

The tree stands were measured twice, in May 1983 and 1988. The diameter (1.3 m above ground level) of all the trees on the sample plots was determined, and the height of 50 trees in the sapling stand, 36 trees in the pole stage stand and all the trees in the mature stand was measured. In 1988 also the annual radial growth of the sample trees was determined from core samples taken at a height of 1.3 m.

Twelve trees (four in each stand) were selected for destructive sampling in May, July and September 1985 and February 1986 in order to measure the biomass and nutrient contents of the tree components. The sample trees were subjected to the following basic measurements: stem, height, height of the bottom limit of the living and dead crown, age (on the basis of radial growth), crown, height and diameter of each branch, living and dead branches, and branch age and biomass calculations. The mass of needles, branches, stemwood, stembark, cones and coarse roots of the sample trees were estimated on the basis of the whole tree analysis. These results, together with the basic measurements, were then used to estimate the corresponding quantities for the trees not sampled. A detailed description of the tree sampling is given in article IV.

### 3.4. Data calculation and statistical analysis

The basic data for this study consisted of the fine root biomass and the necromass of Scots pine, dwarf shrub, and grass fine roots in stands of three different stages of development. The Scots pine fine root biomass and the fine root biomass of the understorey vegetation were determined on the basis of the samples, and the fine root necromass of Scots pine was estimated from the total fine root necromass using the ratio between the Scots pine fine root biomass and the total fine root biomass.

The biomass data were analyzed using one- and two-way analysis of variance (BMDP 1990) in order to determine the differences within years, between stands and between years, except for 1986. In 1986, the samples were combined to give a composite sample (one sample per sampling in each stand) and statistical analyses could therefore not be performed.

The total fine root production was calculated by balancing the living and dead fine root biomass compartments according to the decision matrix presented by Santantonio (1980), McClaugherty et al. (1982) and Fairley and Alexander (1985):

		LIVE		
		increase	decrease	
			$\Delta B_{\text{dead}} > \Delta B_{\text{live}}$	$\Delta B_{\text{live}} > \Delta B_{\text{dead}}$
DEAD	increase	$P = \Delta B_{\text{live}} + \Delta B_{\text{dead}}$	$P = \Delta B_{\text{live}} + \Delta B_{\text{dead}}$	$P = 0$
	decrease	$P = \Delta B_{\text{live}}$	$P = 0$	

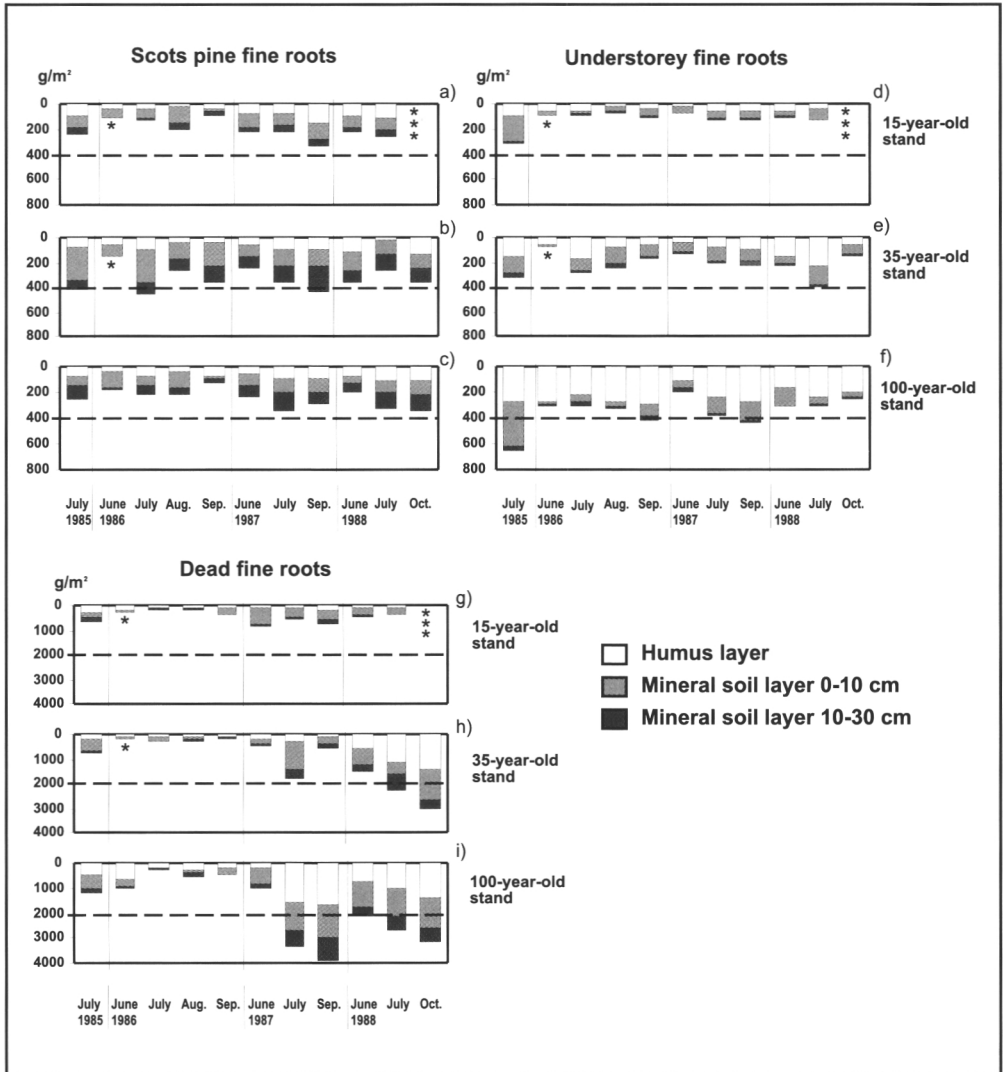
$P$  = fine-root production,  $B$  = mass,  $\Delta = B_i - B_0$ ,  
 live = living fine roots, dead = dead fine roots

The differences in fine root production between the years in the different stands could not be tested because of the lack of replicate stands.

# 4. Results

## 4.1. Seasonal variation of fine-root mass and production in stands of different age

The amount of fine-root biomass and necromass varied during the seasons, between years and between soil layers, but the differences were rarely statistically significant (Figs. 1a-i).



**Figures 1a-i:**

The Scots pine fine-root biomass variation in a 15-year-old sapling, a 35-year-old pole stage and a 100-year-old mature stands (a-c), the fine-root biomass variation of understorey vegetation in a 15-year-old sapling, a 35-year-old pole stage and a 100-year-old mature stands (d-f), and fine-root necromass variation in a 15-year-old sapling, a 35-year-old pole stage and a 100-year-old mature stands (g-i). Asterisks indicate missing values.

### **The variation of Scots pine fine-root biomass**

The fine-root biomass ( $\text{g/m}^2$ ) varied between the stands of different ages (I, II, III, IV). The mean annual biomass of Scots pine fine roots (in the humus layer and the 30 cm mineral soil layer) was  $200 \pm 25 \text{ g/m}^2$  in the 15-year-old sapling stand,  $357 \pm 21 \text{ g/m}^2$  in the 35-year-old pole stage stand and  $259 \pm 26 \text{ g/m}^2$  in the 100-year-old mature stand during three successive growing seasons (1986–1988).

There was no clear seasonal variation of Scots pine fine root biomass in the different stands (Figs. 1a–c). In the sapling and the pole stage stands, the seasonal differences down the whole soil profile (in the humus layer and the mineral soil layers) were not statistically significant during the study period. In the mature stand, the differences were significant ( $p < 0.01$ ) only in 1988: the mass of fine roots was smaller in June than in July or in October.

The seasonal differences of Scots pine fine root biomass in the different soil layers were statistically significant only in the humus layer of the pole stage stand in 1988: the mass of fine roots was greater in June than in July, and smaller in July than in October.

### **The variation of understorey fine-root biomass**

The fraction "the understorey vegetation roots" consisted of all living dwarf shrub and grass fine roots (Figs. 1d–f). The mean fine-root biomass of the understorey vegetation (in the humus layer and 30 cm mineral soil layer) was  $159 \pm 54 \text{ g/m}^2$ ,  $244 \pm 30 \text{ g/m}^2$  and  $408 \pm 81 \text{ g/m}^2$  in the sapling, pole stage and mature stands, respectively.

In the whole soil profile, the seasonal variation of fine-root biomass of the understorey vegetation (dwarf shrub and grass roots) was very small in 1987 and 1988 in the different stands. The differences were significant ( $p < 0.01$ ) only in the pole stage stand in 1988: the mass of fine roots was greater in July than in October.

In the different soil layers, the biomass of dwarf shrub and grass fine roots showed larger seasonal variation than the Scots pine fine-root biomass (I, III). The seasonal differences of understorey fine-root biomass were statistically significant in the pole stage and in mature stands. In the pole stage stand in 1988, in the humus layer the biomass was greater in July than in October, and in the upper mineral soil layer (0–10 cm) the biomass was smaller in June than in July, and greater in July than in October. In the mature stand, the seasonal differences of dwarf shrub and grass fine-root biomass were statistically significant only in the humus layer in 1987: the fine-root biomass was smaller in June than in September.

### **The variation of fine-root necromass**

The necromass fraction "dead roots" consisted of both dead Scots pine and dead dwarf shrub and grass roots (I, III). The mean fine-root necromass (in the humus layer and 30 cm mineral soil layer) was  $500 \pm 112$  g/m<sup>2</sup>,  $1047 \pm 452$  g/m<sup>2</sup> and  $1895 \pm 607$  g/m<sup>2</sup> in the sapling, pole stage and mature stands, respectively.

As was the case for the living biomass, there was no clear seasonal variation of necromass during the study period in the different stands (Figs. 1g–i). The seasonal differences of fine-root necromass down the whole soil profile were significant ( $p < 0.01$ ) in the pole stage and mature stand. In the pole stage stand, the mass of dead fine roots was smaller in June than in July in 1987, and in July than in September in 1988. In the mature stand, the mass of dead fine roots was smaller in June than in July and in July than in September in 1987, and it also was smaller in June than in October in 1988.

The necromass varied seasonally in all three soil layers. In the sapling stand, the differences were statistically significant only in 1987: in the humus layer the mass of dead fine roots was smaller in June and July than in September, in the upper mineral soil layer (0–10 cm) the mass of fine roots was greater in June than in September, and in the lower mineral soil layer (10–30 cm) the mass of dead fine roots was smaller in June than in September. In the pole stage stand, the necromass varied in both the humus layer and the upper mineral soil layer in 1987: the necromass was smaller in June than in July, and greater in July than in September in both layers. In 1988 the seasonal differences were statistically significant only in the humus layer: the necromass was smaller in June than in October. In the mature stand, the necromass varied significantly only in 1987: in the humus layer, the necromass was smaller in June than in July or in September, and in the upper mineral soil layer, the necromass was smaller in June than in September.

### **The annual biomass production of fine roots in Scots pine stands**

The fine-root production of the stands varied according to stand age. The mean annual production of Scots pine fine roots was 165 g/m<sup>2</sup> in the sapling stand, 775 g/m<sup>2</sup> in the pole stage stand and 860 g/m<sup>2</sup> in the mature stand (from the humus layer to the lower mineral soil layer) (III, Table 4, IV, Table 2).

The mean annual total fine root production of Scots pine was 181 g/m<sup>2</sup>, 1039 g/m<sup>2</sup> and 1360 g/m<sup>2</sup> in the sapling, pole stage and mature stands, respectively (III).

The fine-root production obtained by the two methods was different. The annual fine-root production in the pole stage stand varied from approximately 370 g/m<sup>2</sup> to 1630 g/m<sup>2</sup> in the individual soil cores, and between 210–490 g/m<sup>2</sup> in the individual ingrowth cores in the 30 cm thick mineral soil layer (II).

## **4.2. The proportion of fine roots in the tree stand biomass and biomass production**

The portion of fine-root mass and production of tree stand biomass and biomass production varied between different stand age (IV, Table 2). The belowground biomass was 25%, 21% and 13% of the total tree biomass, and the proportion of fine roots 58%, 32% and 14% of all the roots in the sapling, pole stage and mature stands. The mean fine-root biomass was greatest at canopy closure in the pole stage stand, but there was no general trend in fine root biomass between the stands. The relative proportion of fine roots and the ratio of below-ground/above-ground biomass decreased with stand age.

The proportion of the annual fine-root biomass production out of the total belowground production was greater in the sapling and pole stage stands (about 94%) than in the mature stand (88%).

The annual biomass production of fine roots increased with stand age, as well as the relative proportion of fine roots out of stand total production, too (IV, Table 2). Fine-root annual biomass production was 43, 59 and 60% of the total stand biomass production in the sapling, pole stage and mature stands, respectively.

There was no clear relationship between the fine-root biomass and biomass production of fine roots (IV, Table 2). There was an increase in the fine-root production with stand age, and respectively, the ratio of fine-root biomass production/fine-root biomass also increased. Thus, fine-root turnover (annual biomass production per unit of biomass) was fastest in the oldest stand.



# 5. Discussion

## 5.1. The variation of fine-root mass

The Scots pine fine-root biomass was greatest in the pole stage stand that had just reached canopy closure, and lowest in the sapling stand (IV, Table 2). In contrast, the fine-root biomass of the understorey vegetation increased according to stand age. In the pole stage stand, there may be less root competition between trees and thus more space, nutrients and water for root growth. According to Gower et al. (1994), in boreal pine forests the belowground proportion of stand biomass was 27% of the total stand biomass, which is comparable to the 25% in the mature stand of this study.

Several researchers have studied the seasonal variation of fine-root biomass in different stands. Some studies have reported tree stands showing no distinct seasonal pattern (Persson 1978) and some with one (McClaugherty et al. 1982) or two (Grier et al. 1981) statistically significant root biomass peaks. In this study (I, III), there were no distinct seasonal variations in either the fine-root biomass of the Scots pine, dwarf shrub and grass roots or in the fine-root necromass of the different stands.

The spatial variation of fine roots is one reason for the large variation in the mass of organic matter in forest soil. Depending on soil factors, the variation in the fine-root mass is great even within a small area. In this study, the amount of Scots pine fine roots varied in individual samples (in the humus layer and two mineral soil layers) between 1–993 g/m<sup>2</sup> in the sapling stand, between 2–813 g/m<sup>2</sup> in the pole stage stand and between 1–550 g/m<sup>2</sup> in the mature stand. The growth of fine roots depends particularly on soil moisture and temperature (Lyr and Hoffmann 1967). Tryon and Chapin (1983) suggest that every tree species tends to allocate less reserves to root growth during the most active periods of shoot growth, but this seasonal pattern of allocation is strongly modified by the soil conditions.

The fine-root biomass has been reported to vary between different tree species and forest site types. In this study, the fine-root biomass estimates were at the same level (100–735 g/m<sup>2</sup>) to those of reported by McClaugherty et al. (1982) for a 53-year-old Red pine stand, Aber et al. (1985) for a young White pine (*Pinus strobus* L.) stand, Vogt et al. (1987) for a 13–160-year-old Douglas fir stand, Helmisaari and Hallbäcken (1999) for 44–181-year-old Norway spruce stands, and Oleksyn et al. (1999) for a 12-year-old and Vanninen and Mäkelä (1999) for 15–178-year-old Scots pine stands. The amount of fine-root biomass in this study was greater than the value Persson (1980b) reported for 15–20-year-old Scots pine stands and McKay and Malcolm

(1988) for a 15-year-old Sitka spruce (*Picea sitchensis* (Bong.) Carr.) stand. The discrepancy could be due to differences in site quality and tree species, although it may also be associated with differences in root sampling and classification methods.

The root system shows variability between soil layers in both vertical and horizontal direction. Most of the Scots pine fine roots, about 81–85%, are located in the humus layer and in the upper mineral soil horizons (e.g. Messier and Puttonen 1993, Oleksyn et al. 1999). In this study, the major part of the dwarf shrub roots and grass roots — most of which are shallow-rooted (Fitter 1986) — was located in the humus layer and in the immediate underlying mineral soil, while most of the Scots pine roots were in the mineral soil layers. According to Fogel (1983), the distribution of fine roots is dependent on soil aeration and fertility. In boreal forests, the steep temperature decline down the soil profile, the presence of loosely packed soil in the superficial soil horizons, and the dependence on litterfall for nutrients, are factors partially responsible for the concentration of roots in the uppermost soil horizons (Tryon and Chapin 1983).

The seasonal variation of dwarf shrub roots and grass roots was related to their seasonal growth dynamics. In this study, particularly in the pole stage and mature stands, the biomass of dwarf shrub and grass fine roots decreased and the amount of dead roots increased at the end of the growing season in October 1988. Fitter (1986) reported two different active groups of grasses: less productive and shallower-rooted early-active species, and more productive, deeper-rooted and later-active species. In all the grass species studied, the rooting productivity and activity decreased in the upper soil layer (5 cm) and increased in a deeper soil layer (25 cm) towards the end of summer.

In addition to the growth strategy, the weather conditions may also affect the variation of fine-root biomass and necromass. During this study, the weather in 1988 differed clearly from that in the earlier years. Although the variation in precipitation was not abnormal in 1988 (I, Fig.2.), the amount of precipitation was relatively low in July 1988. From the middle of June to the end of July in 1988 it was also unusually warm. This may have resulted in a low soil moisture content due to the rapid evaporation of rainwater before it had percolated into the soil. At the same time, the groundwater level was relatively low especially in the sapling and pole stage stands. For these reasons, the Scots pine fine roots especially may have suffered from drought in the humus layer. In the humus layer of the pole stage stand, the amount of living Scots pine fine roots decreased in July 1988, while the biomass of dwarf shrub roots and grass roots increased. Heindrick and Pregitzer (1993) have reported correspondent effects on roots from drought as in this study.

A similar increase in the amount of dead roots has been reported after a severe winter (Jalkanen et al. 1995, Raitio 2000, Tikkanen and Raitio 1990). In this study, the reason for the large amount of dead fine roots is not likely to have been due to the harsh winter. Even though winter 1987-88 was extremely cold and included many days with the temperature below zero, the snowcover was thick and protected the fine roots from the damaging effect of cold.

## **5.2. The mortality and decomposition of fine roots**

Roots contribute to soil organic pools and accumulation while they are alive, as well as after senescence when they are decomposing. Compared to coarse roots, fine roots contribute more carbon to organic matter accumulation because of their higher annual litter inputs and faster rate of decay. Fine-root mortality will contribute to a more spatially homogeneous distribution of organic matter compared to that from the larger root diameter classes (Vogt et al. 1991).

The mean annual fine-root necromass increased with increasing stand age. In this study, the fine-root necromass of different stands was similar to those reported by McKay and Malcolm (1988) and McClaugherty et al. (1982), but greater than that reported by Persson (1979, 1983).

The necromass proportion of all fine roots increased according to stand age, being 58% in the sapling stand, 68% in the pole stage stand and 75% in the mature stand. At the same time, the proportion of live/dead roots decreased according to stand age. Thus, the older the stand, the smaller the proportion of living fine roots. These results are comparable to the 80% reported by McKay and Malcolm (1988), or the 71% reported by Santantonio and Santantonio (1987), but more than the 45% reported by Persson (1980b).

In this study, the dead fine roots (necromass) included both those roots that have died recently but are still definitely fine roots and those that have already decomposed to varying degrees, but are not yet part of the soil organic matter. The colour and consistency of dead roots differ from those of living roots, but the reliability of classifying roots into living and dead categories and sorting dead roots from the soil organic matter decreases with diminishing diameter. This may have introduced some errors. The necromass values for the bulked samples in 1986 could here have been underestimated because of the difficulties in separating dead fine-root particles less than one mm long from the soil organic matter.

According to Berg (1984), the decomposition rate decreases according to root diameter: larger roots decompose slower. 1–2 mm diameter Scots pine fine

roots lost about 30% of their mass in two years. This is less than the value reported by McEnroe and Helmisaari (2001) for the same pole stage stand as in this study: the 2 mm diameter Scots pine fine roots lost about 51% of their mass during one year. The decomposition rate of fine roots might be even faster than that reported, because the litterbag technique underestimates fine-root decomposition (Vogt et al. 1991), and both Berg (1984) and McEnroe and Helmisaari (2001) used this method.

### **5.3. The fine-root biomass production**

The fine-root production, both Scots pine and total production, increased from the sapling stand to the mature stand. In this study (II, IV), the production was greater than that reported by Persson (1979,1983) for the 15 to 120-year-old Scots pine stands, but comparable to the results of Aber et al. (1985) for young White pine stands.

In the pole stage and the mature stands, fine roots produced more biomass than all of the above-ground tree components combined, 59 and 60% respectively (IV, Fig.1b). According to Ågren et al. (1980), a 14-year-old Scots pine used 57% of its net photosynthetic production for fine root growth, which was slightly more than that in the 15-year-old sapling stand in this study. In a 53-year-old Red pine (*Pinus resinosa* Ait.) plantation, the total annual fine root production was 1090 g/m<sup>2</sup> (McClaugherty et al. 1982), which is comparable with the values for the pole stage and mature stands in this study. In a 40-year-old Douglas fir (*Pseudotsuga menziesii* Mirb.), the total root production (including coarse, small and fine root biomass) was 53%, and the proportion for fine roots was 36% out of total net primary production (Keyes and Grier 1981). This is less than the value obtained for the 35-year-old pole stage stand in this study.

### **5.4. Critical observations on methods for estimating fine-root biomass production**

In this study, I used two different methods to compare the results obtained for the same forest site. According to the results (II), there are some problems and errors associated with the two methods. The root ingrowth core method gives a lower estimation of fine-root production than the soil core method. During the three first years, the density of fine roots grown into the ingrowth cores was still smaller than in the surrounding bulk soil. In the soil core method, the amount of dead fine roots influences the estimate of production: if there is a lot of necromass, as in July 1987 in this study, the fine-root production estimate will be greater.

Because the fine roots were still growing into the ingrowth cores, comparison between these two methods, especially for living fine roots, is difficult. The space available for the growth of living fine roots is different in soil cores than in ingrowth cores. According to some observations, new healthy fine roots of pine trees can grow in the old root channels of the previous pine crop (Nambiar and Sands 1992). The ingrowth cores have no such channels.

In dead roots, the problem is the timing. In the soil core method, all the dead fine roots are included in the sample. In the ingrowth core method, the oldest dead fine roots will be there from the time when the single ingrowth core was inserted into the soil.

Special problems arise when using the root ingrowth core method. The sieved soil will not be replaced to form the same horizons in the ingrowth core; the typical podsol profile will be disturbed. The bulk density of the soil, initially repacked into the mesh bags, will be different from that naturally present on the site. The sieved soil in the ingrowth cores may also be drier or moister than the surrounding soil. During the first years, there is no root competition in the soil of the ingrowth cores, and the roots can grow faster into the ingrowth core than into the surrounding soil — especially because the injured roots around the ingrowth core after installation may favour the growth of adventitious roots.

The soil core method also has its problems. The soil core sample is only a momentary representation of the fine root biomass. The spatial variation of the fine roots may be greater than the temporal variation between sampling.

Both techniques thus have their sources of error. The soil core method can be used for studying the annual and seasonal variation in fine-root biomass. For estimating production, however, sampling should be done at short intervals. The ingrowth core method is more suitable for comparing the potential of annual fine root production between different site types. However, both methods are useful for studies on the dynamics of fine roots.

Another problem is the procedure used for calculating fine-root production. There are no standard methods for determining or calculating production, and researchers have used a number of different methods (Persson 1980, Keyes and Grier 1981, Singh et al. 1984, Vogt et al. 1989). When the total below-ground production is calculated by balancing the living and dead root biomass compartments (e.g. Fairley and Alexander 1985), the cumulative estimates are dependent on the sum of the differences between a series of observations. A considerable error may build up in the calculation process, depending on the precision of the biomass estimates each month. Fairley and Alexander (1985) thus recommend that only significant differences between individual biomass

estimates should be included in the cumulative estimates of production. In this study the biomass and necromass varied greatly during the study period, but the variation was significant only at a few occasions, and the consequent calculation based only on significant variation was not possible. Thus, the fine-root production determined by soil the core method (II, III) might have been overestimated with about 30–35% (Fairley and Alexander 1985, Finér and Laine 1994).

## 6. Conclusions

This study was carried out in three Scots pine stands in eastern Finland during 1985–1988. The stands represented different stages of stand development: a 15-year-old sapling, a 35-year-old pole stage and a 100-year-old mature stands.

One of the aims was to determine the seasonal variation of fine-root mass and production in the different stands. The results from this study show that fine-root biomass, necromass and production varied considerably during the growing season. The variation was especially dependent on soil temperature and moisture.

The results are from Scots pine stands of three different stages growing on *Vaccinium* site type. Even though all the stands were classified as the same forest site type, the variation in soil factors — especially soil moisture and temperature — may have influenced the fine-root biomass variation.

The second aim was to compare two methods for estimating fine-root production: the soil core method and the root ingrowth method. According to the results of this study, the soil core method is rather suitable for studying the annual and seasonal variation in fine-root biomass. For estimating production, sampling by the soil core method should be done at short intervals. The ingrowth core method is more suitable for comparing the potential of annual fine root production between different site types.

Both methods are very time-consuming and laborious. But, as Dr. Wolfgang Böhm wrote in his book (1979), ” *Every method has shortcomings. Although nearly every research worker who has done ecological root studies has altered existing methods or has created better techniques, most of the root-study methods are still tedious and time-consuming. Generally it can be said that the more accurate the method, the more laborious it is.*”

The third aim was to determine the role of fine roots in the distribution of stand biomass and production. In the Scots pine stands the proportion of stemwood (including bark) out of tree stand biomass was about 25–68% while the proportion of fine root was 2–15%, depending on stand age (IV). According to the same study, the proportion of stemwood production was 24%, 21% and 15% out of stand production in the sapling, pole stage and the mature stands, respectively. The proportion of root production was 46, 62 and 68% in the sapling, pole stage and mature stands, respectively. Most of the root production is fine-root production. Thus, the older the tree, the greater is the proportion of production it has to allocate to the below-ground part of the tree instead of the economical important stemwood.

In the carbon cycle, fine roots form an important component. Fine roots contribute to the soil organic pools and accumulation while they are alive, as well as after senescence when they are decomposing. The carbon inputs into the soil in fine-root litter may be several times larger than the inputs from above-ground litter (Hendrick and Pregitzer 1993, Ruess et al. 1996, Scheffer and Aerts 2000). A large proportion of the organic carbon in the mineral soil originates from fine-root litter (Scheffer and Aerts 2000). The amount of carbon in forest ecosystems depends on the stage of stand development. Seedling and young stands bind much more carbon than is released through respiration or decomposition (Karjalainen and Kellomäki 1991).

The vegetation and forest soil may act as sinks or sources of atmospheric carbon dioxide. Most estimates of the global carbon cycle have been calculated on the basis of national forest inventory data from around the world (e.g. Dixon et al. 1994) or by large-scale models using the inventory and research data. At the moment, the carbon budget of forest soil is much more poorly known than the budget of trees. As many other countries, the national carbon budget of Finland is presently mainly based on the trees (Karjalainen and Kellomäki 1991, Karjalainen et al. 1995, Tomppo 2000) and the role of forest soil has not yet been determined.

In this study, one of the main aims was to determine the seasonal variation of living and dead fine root mass and production in Scots pine stands. A recent study by Högberg et al. (2001) indicated, that the seasonal pattern of below-ground carbon allocation may be more important than soil temperature in determining root respiration. The authors concluded, that seasonal variation in carbon allocation fluxes need to be considered if realism is to be achieved in assessing global carbon budgets. The large proportion of below-ground biomass production determined in this study indicate, that below-ground carbon allocation should be taken into account in all carbon budgets. The results of this study agree with the conclusion by Chapin and Ruess (2001), that the current measures of global terrestrial production may be serious underestimates of the true values.



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*Kirsi Mälkönen*

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## **PAPER I**

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## Seasonal and yearly variations of fine-root biomass and necromass in a Scots pine (*Pinus sylvestris* L.) stand

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### Abstract

Seasonal variations of the Scots pine (*Pinus sylvestris* L.), dwarf shrub and grass fine-root biomass and necromass were studied in a pole stage Scots pine stand in eastern Finland during three successive growing seasons. The biomass of Scots pine fine roots varied annually and seasonally in the humus layer between  $19 \pm 5 \text{ g m}^{-2}$  to  $139 \pm 22 \text{ g m}^{-2}$ , in the upper mineral soil layer between  $90 \pm 14 \text{ g m}^{-2}$  to  $279 \pm 0 \text{ g m}^{-2}$ , and in the lower mineral soil layer between  $68 \pm 17 \text{ g m}^{-2}$  to  $217 \pm 73 \text{ g m}^{-2}$ . The seasonal minimum and maximum of understory vegetation fine-root biomass were in the humus layer  $35 \pm 6 \text{ g m}^{-2}$  and  $235 \pm 42 \text{ g m}^{-2}$ , in the upper mineral soil layer  $26 \pm 0 \text{ g m}^{-2}$  and  $165 \pm 0 \text{ g m}^{-2}$ , and in the lower mineral soil layer  $14 \pm 0 \text{ g m}^{-2}$  and  $36 \pm 5 \text{ g m}^{-2}$ . The seasonal fine-root necromass varied in the humus layer from  $2 \pm 0 \text{ g m}^{-2}$  to  $1398 \pm 236 \text{ g m}^{-2}$ , in the upper mineral soil layer from  $86 \pm 0 \text{ g m}^{-2}$  to  $1267 \pm 366 \text{ g m}^{-2}$ , and in the lower mineral soil layer from  $8 \pm 0 \text{ g m}^{-2}$  to  $753 \pm 306 \text{ g m}^{-2}$ . The major part of the living Scots pine fine roots (62%) was in the mineral soil immediately below the humus layer, but almost all dwarf shrub roots and grass roots were in the humus and in the upper mineral soil layers. Most dead fine roots (82%) were in the humus layer and in the uppermost mineral soil layer. The variations of Scots pine fine-root biomass, dwarf shrub and grass fine-root biomass and necromass did not show a distinct and clear pattern within any growing season although there were significant differences between the same month during different growing seasons. Some of the observed variations could be explained by climatic factors related to drought. © 1998 Elsevier Science B.V.

**Keywords:** Biomass; Fine-root; *Pinus*; Scots pine; Seasonal variation

### 1. Introduction

The production, death and decomposition of roots are major processes in the carbon and nutrient dynamics of forest ecosystems. Fine roots are constantly in flux, with death and replacement taking place simultaneously. Even though the proportion of the total tree biomass represented by fine roots and

mycorrhizas is not large, their growth and maintenance use a major part of total net primary production (Fogel, 1983). Despite this, fine roots have seldom been studied in relation to stand biomass and nutrient dynamics, since it is a very laborious task.

Many authors have reported changes in fine-root biomass during the growing season (Heikurainen, 1955; Kalela, 1955; Murach, 1987; Persson, 1978, 1980b; Vogt et al., 1981). The main factors affecting the root growth of forest trees are age and tree

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species, carbon allocation, nutrient and water supply, abiotic factors such as soil temperature, soil strength (density and compaction) and aeration and, finally, toxicity (Persson, 1992). The major part of the root system of understory vegetation and trees is found in the humus layer and in the upper mineral soil (Kalela, 1949). Seasonal variations in the environmental factors in different soil layers affect fine root activity. Drought or shortage of nutrients may disturb fine roots: fine-root damage is often described as a decline in the amount of living fine roots, with a related increase in the amount of dead versus living fine roots (Murach, 1987; Puhe et al., 1986; Persson, 1992).

Soil acidity can also inhibit the growth of fine roots (Matzner et al., 1986; Persson et al., 1995). During acidification, the solubility of metals increases and  $H^+$  ions can displace the metal ions from the surface of soil particles into the soil water. Metals, especially aluminum, can exert toxic effects to plants by reducing root function and inhibiting nutrient uptake (Persson et al., 1995), particularly when  $pH_{\text{water}}$  is below 3.5 (Derome, 1989).

The objective of this study was to determine the seasonal and yearly variations of fine-root biomass and necromass in a Scots pine (*Pinus sylvestris* L.) stand in eastern Finland. The study is a part of a project concentrated on nutrient dynamics and biomass production of Scots pine (Helmisaari, 1995).

## 2. Materials and methods

### 2.1. Experimental stand

The study was carried out in a Scots pine stand in Ilomantsi (62°47'N; 30°58'E; 144 m a.s.l.) near the Mekrijärvi research station of the University of Joensuu.

The experimental stand was a naturally regenerated pole stage stand (Table 1) on a 500 m<sup>2</sup> plot. The site type was *Vaccinium*-type, according to the classification of Cajander (1949). The field layer was dominated by cowberry (*Vaccinium vitis-idaea* L.) and heather (*Calluna vulgaris* (L.) Hull.). The bottom layer was dominated by the moss species red-stemmed feathers (*Pleurozium schreberi* (Brid.) Mitt.) with a few reindeer lichens (*Cladina* sp.).

Table 1

Some characteristics of the experimental tree stand in 1985.

Age (yr)	37
Number of trees ha <sup>-1</sup>	2980
Mean stem diameter (cm)	7.4
Mean height (m)	6.4
Basal area (m <sup>2</sup> ha <sup>-1</sup> )	14
Stem volume (m <sup>3</sup> ha <sup>-1</sup> )	56.6
Volume increment (m <sup>3</sup> ha <sup>-1</sup> yr <sup>-1</sup> )	11.3

Mean annual temperature was 1.0°C and annual rainfall was 699 mm during the study period (1985–1988). The long-term annual averages (1961–1990) were 1.9°C and 649 mm, respectively (The Finnish Meteorological Institute, 1991). About 40% of the annual precipitation consists of snow and the ground is covered by snow from October to May (Helmisaari and Mälikönen, 1989).

Temperature and precipitation data are from the Ilomantsi meteorological station of the Finnish Meteorological Institute (62°40'N; 30°57'E; 162 m a.s.l.), about 12 km from Mekrijärvi research station.

The soil type is a Ferric Podzol according to the FAO classification (FAO–UNESCO, 1988), relatively poor in plant-available nutrients. The thickness of the soil horizons are: humus 2.5 cm, eluvial horizon 5.0 cm, and illuvial horizon 11.0 cm. The surface soil layer is clearly sorted to a depth of 40–60 cm. The proportion of coarse fine sand in this layer is about 50%, while the proportion of clay is only about 2%. Compact till occurs below the sorted layer.

Soil leachate was collected with percolation lysimeters placed beneath the humus layer (Helmisaari and Mälikönen, 1989). pH of the leachate was determined with a Metrohm 605 pH-meter immediately after sampling. Aluminum in soil leachate samples was determined with a flameless atomic absorption spectrophotometer (Perkin-Elmer AS 40).

### 2.2. Root sampling

Eleven samplings were carried out during the growing seasons in the years 1985–1988. Twenty soil cores (volumetric samples, core diameter 36 mm) per sampling were systematically taken for fine-root biomass determinations. The soil cores were divided into three layers by depth: humus, the first

10 cm (denoted 0–10 cm) and next 20 cm (denoted 10–30 cm) of the mineral soil. Samples were transported to the laboratory and stored frozen ( $-18^{\circ}\text{C}$ ) until analysis.

### 2.3. Laboratory analysis

In the laboratory, roots were washed free of soil and separated into Scots pine living roots, understory living roots and dead roots. The Scots pine living roots were separated into three classes by diameter:  $< 2$  mm, 2–5 mm and 5–10 mm, and the understory roots and the dead roots (necromass) into diameter classes  $< 2$  mm and  $> 2$  mm. Scots pine living roots were distinguished from understory living roots by their mycorrhizas, colour and thickness. Pine roots have generally but not always dichotomously branched mycorrhizas. Dead roots were distinguished from living roots by their colour and consistency.

Fine roots are generally defined as nonwoody, small-diameter roots (Nadelhoffer and Raich, 1992), but there is no established convention defining the diameter-size range of fine roots (Fogel, 1983). In this study, roots smaller than 2 mm were regarded as fine roots (Persson, 1983; Vogt et al., 1983) and roots smaller than 10 mm as small roots.

The separated roots were dried at  $70^{\circ}\text{C}$  for 5 days and weighed to determine the oven-dry biomass.

### 2.4. Data processing

The basic data for this study comprised biomass and necromass of Scots pine roots and dwarf shrub roots and grass roots. The data was treated using one- and two-way analyses of variance for examining the variation within seasons and between years, except the year 1986. In 1986, samples were combined to give a composite sample (one sample per sampling), and consequently statistical analyses could not be performed.

Table 2

The mean and standard error of total amount of living and dead roots ( $\text{g m}^{-2}$ ) in different soil layers in 1985–1988

Years	Living Scots pine roots				Living dwarf shrub roots				Dead roots			
	$< 2$ mm		$> 2$ mm		$< 2$ mm		$> 2$ mm		$< 2$ mm		$> 2$ mm	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
<i>Humus layer</i>												
1985	73	19	0	0	157	106	0	0	160	17	78	22
1986	55	13	0	0	91	26	0	0	69	27	46	14
1987	81	11	196	0	68	11	136	31	197	23	118	27
1988	88	13	105	27	147	23	368	269	1026	114	110	20
Mean	74	7	75	47	115	21	126	86	363	222	87	16
<i>Mineral soil layer 0–10 cm</i>												
1985	263	78	0	0	136	19	0	0	474	67	121	28
1986	178	36	0	0	88	22	0	0	118	18	22	9
1987	119	11	197	45	96	11	149	70	510	91	91	21
1988	123	13	333	79	94	11	298	199	799	136	65	15
Mean	170	33	132	81	103	11	111	71	474	139	74	20
<i>Mineral soil layer 10–30 cm</i>												
1985	68	17	0	0	26	5	0	0	72	13	0	0
1986	103	23	0	0	23	5	0	0	24	11	5	0
1987	138	28	125	42	23	4	0	0	208	48	29	0
1988	107	12	79	15	22	3	0	0	488	114	1004	0
Mean	103	14	51	30	23	1	0	0	198	104	259	248
<i>Mean sum for all three soil layers</i>												
	348		258		242		237		1035		422	

### 3. Results

#### 3.1. The variation of Scots pine fine-root biomass

The amount of fine roots varied between layers (Table 2). The major part of both the living Scots pine small roots below 10 mm (62%) and the fine roots less than 2 mm in diameter (46%) was found in the upper mineral soil immediately below the humus layer. Most roots (75%) in the humus layer had a diameter less than 2 mm. Almost all thicker Scots pine roots (diameter greater than 2 mm) were in mineral soil.

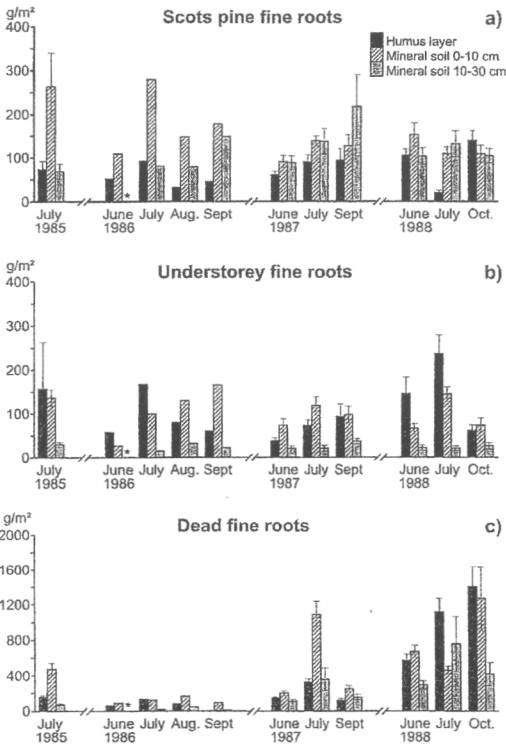


Fig. 1. The seasonal variation of (a) Scots pine fine-root biomass (< 2 mm diameter) and (b) dwarf shrub and grass fine-root biomass (< 2 mm diameter) in different soil layers ( $\text{g m}^{-2}$ ) and (c) dead roots (< 2 mm diameter), including both Scots pine and other fine roots ( $\text{g m}^{-2}$ ). Standard error of the mean is indicated by bars on the columns (not calculated for 1986 data). Stars indicate missing data.

During the study period, the seasonal variation of Scots pine fine-root biomass did not show a clear pattern in the different soil layers (Fig. 1a). The biomass of Scots pine fine roots varied seasonally only in the humus layer. The seasonal variation in the humus layer was significant only in June ( $p < 0.01$ ) and October ( $p < 0.001$ ) than in July (Fig. 1a). In the mineral soil layers, the seasonal and between-year variations were not significant.

There were no statistical differences in fine-root biomass between seasons. However, in July differences in fine-root contents of humus layer samples between different years were significant. There were significant differences in humus layer between 1985 and 1988 ( $p < 0.05$ ), and between 1987 and 1988 ( $p < 0.01$ ).

About 50% of the sampled Scots pine roots had diameters greater than 2 mm. In these thicker roots there were no statistical differences in biomass between layers, seasons or years.

#### 3.1.1. The variation of understorey fine-root biomass

The separated fraction designated "understorey roots" consisted of all living dwarf shrub and grass roots. The amount of fine roots decreased below the humus layer (Table 2). All thicker roots were in the humus layer or in the upper mineral soil layer.

Seasonal variations of dwarf shrub and grass roots did not show a clear pattern (Fig. 1b). The variation in the humus layer was statistically significant only in 1988; the amount of roots was significantly greater ( $p < 0.01$ ) in July than in October. In the upper mineral soil layer, the seasonal variation of living dwarf shrub and grass roots was significant in 1987 and 1988. In 1987, the amount of fine roots was significantly greater ( $p < 0.05$ ) in the middle of the summer than at the beginning of the season. In 1988, the amount of roots differed significantly ( $p < 0.01$ ) between June and July and between July and October.

There were no statistically significant differences in the living dwarf shrub root biomass between years.

#### 3.1.2. The variation of dead roots

The "dead roots" (necromass) portion consisted of both dead Scots pine roots and dead dwarf shrub

and grass roots. The major part of dead roots (82%) was in the humus layer and the upper mineral soil layer (Table 2).

Similar to living biomass, there was no clear seasonal variation of necromass during the study period (Fig. 1c). In the humus layer, the seasonal variation of dead roots was statistically significant in 1988; the root necromass differed significantly between June and October 1988 ( $p < 0.001$ ). In the mineral soil, the seasonal variation was significant only in the upper layer from June to July 1987 ( $p < 0.05$ ).

There were statistical differences in the humus layer between years 1985, 1987 and 1988; differences in July between 1985 and 1988 and in 1987 and 1988 were significant ( $p < 0.001$ ). The amount of dead roots was much greater in 1987 and 1988 than in 1985 or 1986 both in the humus layer and in the mineral soil.

#### 4. Discussion

Despite of their small diameter, the portion of fine roots of the tree biomass can be large. In several studies (Fogel, 1983; Santantonio et al., 1977), the proportion of root biomass varied between 18% and 45% of total tree biomass depending on age and site. According to Helmisaari (1995), in the same stand as investigated in this study, total tree biomass was 5323 g m<sup>-2</sup>, of which 78% was aboveground and 22% belowground biomass. The portion of fine roots in 1985 was 36% of all roots.

The total biomass (Scots pine, dwarf shrub and grass root biomass) varied between 369 g m<sup>-2</sup> and 742 g m<sup>-2</sup> during research years and the necromass 106–3082 g m<sup>-2</sup>. According to Persson (1980b), in a 15 to 20-yr-old Scots pine stand, the fine-root biomass was 139 g m<sup>-2</sup> and the necromass 118 g m<sup>-2</sup>. McKay and Malcolm (1988) reported that the fine-root biomass was 112 g m<sup>-2</sup> and the necromass 457 g m<sup>-2</sup> in a pure 15-yr-old Sitka spruce (*Picea sitchensis* (Bong.) Carr.) stand and 57 g m<sup>-2</sup> and 257 g m<sup>-2</sup>, respectively, in mixed stand of Scots pine. In our stand, the fine-root biomass was greater than those reported by Persson (1980b) and McKay and Malcolm (1988), but the necromass was comparable.

Table 3

The fine-root biomass:necromass ratio during the study periods in 1985–1988.

Time	1985	1986	1987	1988
June	*	1.66	0.81	0.39
July	1.05	2.64	0.33	0.28
August	*	1.72	*	*
September	*	5.82	1.28	*
October	*	*	*	0.17

\* Missing data.

The total fine-root biomass:necromass ratio was the highest in July 1986 and very low in October 1988 (Table 3). The ratio of dead fine roots to living fine-root biomass varied between different years. In the beginning of the study, the amount of living roots was greater and the ratio of fine-root:necromass was over one. In the end of the study the amount of necromass increased. During the research period, dead fine-root mass (diameter less than 2 mm) was 64% of total fine roots (all living and dead roots). This is less than what was reported by McKay and Malcolm (1988) or Santantonio and Santantonio (1987), 80% and 71% respectively, but more than the 45% reported by Persson (1980b).

Dead fine roots include both those roots that have died recently and those that have already decomposed to varying degrees. Dead roots differ from living roots in their colour and consistency, but the reliability of classifying roots into living and dead categories and differing dead roots from the soil organic matter decreases with diminishing diameter and this may have introduced some errors. The necromass values for the two first study years could be underestimated because of the difficulties in separating less than one mm long dead fine-root particles from soil organic matter.

In this study, a major part of dwarf shrub roots and grass roots were in the humus layer and in the mineral soil below it, while most Scots pine roots were in the mineral soil layers. Related results have been reported by Persson (1980a, 1983) and Santantonio and Santantonio (1987). Differences between species groups depend on their strategies of root growth. According to Tryon and Chapin (1983), a sharp temperature decline through the soil profile, loosely packed soil in superficial soil horizons, and

dependence on litterfall for nutrients, are factors partially responsible for the concentration of roots in the uppermost soil horizons of boreal forests.

The biomass of Scots pine fine roots in the humus layer was lowest in August 1986, in June 1987, and in July 1988, and the biomass of dwarf shrub and grass fine roots was lowest in June 1986 and 1987, and in October 1988. Tryon and Chapin (1983) suggested that every tree species tends to allocate less reserves to root growth during the most active periods of shoot growth, but this seasonal pattern of allocation is strongly modified by the soil environment. The growth of fine-roots depends particularly on soil moisture and temperature (Lyr and Hoffmann, 1967).

In the present study, the year 1988 differed from the earlier ones. In the humus layer, the amount of living Scots pine fine roots decreased in July 1988 while the biomass of dwarf shrub roots and grass roots increased. The sudden decrease of living Scots pine fine roots may be related to a change in the environmental factors such as temperature and precipitation.

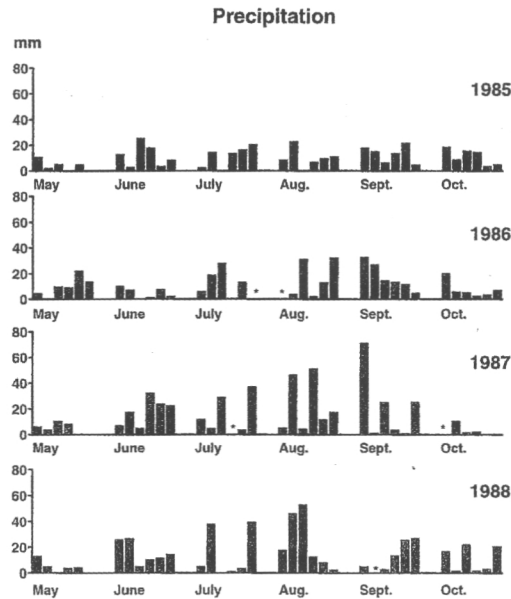


Fig. 2. The variation of precipitation (mm) during growing seasons in 1985–1988. The precipitation is calculated for periods of five days. Stars indicate missing data.

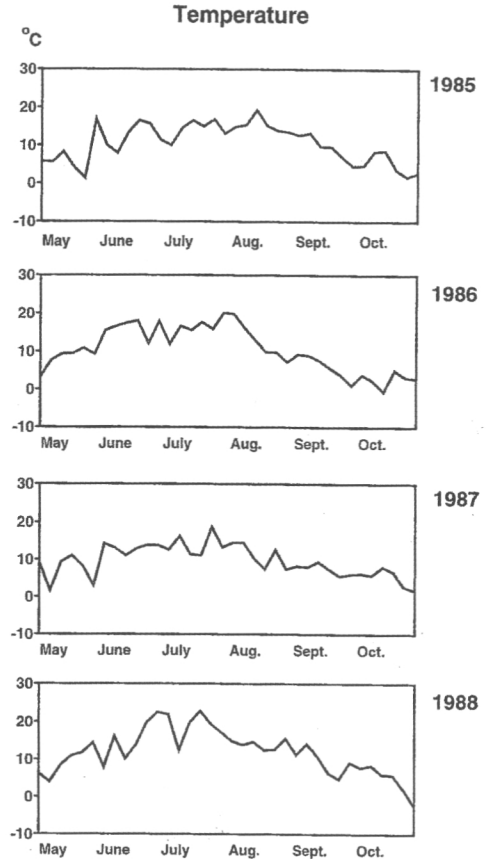


Fig. 3. The variation of daily average temperature (°C) during growing seasons in 1985–1988. The average temperature is calculated for periods of five days.

Although the variation in precipitation was not unusual in 1988 (Fig. 2), the precipitation amount was relatively low in July 1988. The temperature differed in July 1988 from the other years studied (Fig. 3). From the middle of June to the end of July in 1988 it was unusually warm. This may have resulted in low soil moisture due to rapid evaporation of rainwater before it had percolated into the soil. For that reason, the fine roots may have suffered from drought in the humus layer.

The chemical properties of soil also affects the growth of fine-roots. The pH of the soil water in 1988 was lower than at any other time during the



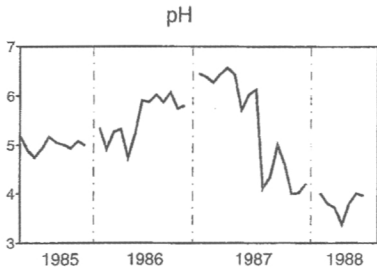


Fig. 4. The variation of pH in soil leachate collected with percolate lysimeters beneath the humus layer during growing seasons in 1985–1988.

study period (Fig. 4), particularly in July 1988 compared with previous years. The concentration of aluminum in the soil leachate was relatively high in July 1988. Aluminum often accumulates in the roots (Goldbold et al., 1988) and leads to root damage and poor root growth. According to Mengel and Kirkby (1979), the solubility of Al increases sharply in acid soils at pH values below 5.5, and can cause toxic effects.

In the humus layer, the major portion of the aluminum is expected to be present as insoluble organic complexes nontoxic for roots (Nilsson and Bergkvist, 1983). In the present study, the content of organic matter in the soil percolate water was not determined, and the aluminum concentration was determined in the soil percolate water leachate samples as total aluminum, which includes both insoluble and soluble aluminum complexes. The total aluminum concentration in soil leachate from 1985 to 1988 is presented in Fig. 5. However, since in laboratory experiments no toxic effects on roots could

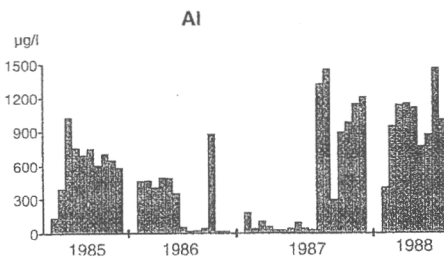


Fig. 5. The total aluminum concentration ( $\mu\text{g l}^{-1}$ ) in soil leachate collected with percolation lysimeters placed beneath the humus layer during growing seasons in 1985–1988.

be observed during periods of even higher aluminum concentrations than in July 1988 (Janhunen et al., 1995), root decline caused by aluminum toxicity seems not likely. The relation to water availability seems to be the most likely cause of the sudden fine-root decline.

Studies of the seasonal variations in living root biomass have reported tree stands showing no distinct seasonal pattern (Persson, 1978) and those with one (McClagherty et al., 1982) or two (Grier et al., 1981) statistically significant root biomass peaks. In this study, there were distinct seasonal variations neither in the fine root mass of the Scots pine nor in the fine root mass of dwarf shrubs and grasses. However, there were statistically significant differences between months in different years.

The seasonal variation of dwarf shrub roots and grass roots was related to their seasonal growth dynamics. Fitter (1986) has found two different active groups of grass; less productive and shallower-rooted early-active species and more productive, deeper-rooted and latter-active species. In all researched grass species the rooting productivity and activity decreased in the upper soil layer (5 cm) and increased in a deeper soil layer (25 cm) to the end of summer (Fitter, 1986). In this research, the biomass of other fine roots decreased and the amount of dead roots increased in October at the end of the growing season. In July 1988, the death of Scots pine fine roots seemed to provide an opportunity for a rapid increase in dwarf shrub roots and grass roots. It seems that dwarf shrubs and grasses can grow their roots deeper faster, thus being not so sensitive to drought as Scots pine.

The results from this study show that fine-root biomass varies considerably but without a distinct and clear pattern during the growing season. However, seasonal variations should be considered when interpreting biomass results from different experiments based on sampling in single occasions.

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## PAPER II

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## Assessing fine-root biomass and production in a Scots pine stand – comparison of soil core and root ingrowth core methods

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### Abstract

Soil core and root ingrowth core methods for assessing fine-root (< 2 mm) biomass and production were compared in a 38-year-old Scots pine (*Pinus sylvestris* L) stand in eastern Finland. 140 soil cores and 114 ingrowth cores were taken from two mineral soil layers (0–10 cm and 10–30 cm) during 1985–1988. Seasonal changes in root biomass (including both Scots pine and understorey roots) and necromass were used for calculating fine-root production. The Scots pine fine-root biomass averaged annually 143 g/m<sup>2</sup> and 217 g/m<sup>2</sup> in the upper mineral soil layer, and 118 g/m<sup>2</sup> and 66 g/m<sup>2</sup> in the lower layer of soil cores and ingrowth cores, respectively. The fine-root necromass averaged annually 601 g/m<sup>2</sup> and 311 g/m<sup>2</sup> in the upper mineral soil layer, and 196 g/m<sup>2</sup> and 159 g/m<sup>2</sup> in the lower layer of soil cores and ingrowth cores, respectively. The annual fine-root production in a Scots pine stand in the 30 cm thick mineral soil layer, varied between 370–1630 g/m<sup>2</sup> in soil cores and between 210 – 490 g/m<sup>2</sup> in ingrowth cores during three years. The annual production calculated for Scots pine fine roots, varied between 330–950 g/m<sup>2</sup> in soil cores and between 110 – 610 g/m<sup>2</sup> in ingrowth cores. The horizontal and vertical variation in fine-root biomass was smaller in soil cores than in ingrowth cores. Roots in soil cores were in the natural dynamic state, while the roots in the ingrowth cores were still expanding both horizontally and vertically. The annual production of fine-root biomass in the Scots pine stand was less in root ingrowth cores than in soil cores. During the third year, the fine-root biomass production of Scots pine, when calculated by the ingrowth core method, was similar to that calculated by the soil core method. Both techniques have sources of error. In this research the sampling interval in the soil core method was 6–8 weeks, and thus root growth and death between sampling dates could not be accurately estimated. In the ingrowth core method, fine roots were still growing into the mesh bags. In Finnish conditions, after more than three growing seasons, roots in the ingrowth cores can be compared with those in the surrounding soil. The soil core method can be used for studying both the annual and seasonal biomass variations. For estimation of production, sampling should be done at short intervals. The ingrowth core method is more suitable for estimating the potential of annual fine-root production between different site types.

### Introduction

In many forest ecosystems on mineral soils, fine-root dynamics, production, death and decomposition of roots appear to play a very important role in carbon and nutrient cycling. Even though the proportion of the total tree biomass represented by fine roots and mycorrhizas is not large, in average 15–25%, their growth and maintenance use a major part, perhaps

as much as 67–70%, of total net primary production (Fogel, 1985).

About 11–57% of the carbon assimilated annually by Scots pine trees is used for the growth of root systems (Persson, 1992). Fine root production may account for 8 to 67% of net primary production (Keyes and Grier, 1981; Grier et al., 1981). The detritus input to the soil from the fine roots may be greater than that from the above-ground compartments (Finer and Laine, 1994). Despite this, there are not many studies in relation to stand biomass and nutrient dynamics.

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Table 1. Some characteristics of the experimental tree stand in 1985

Age, years	37
Number of trees/ha	2660
Mean stem diameter, cm	8.2
Mean height, m	7.5
Basal area, m <sup>2</sup> /ha	15.3
Stem volume, m <sup>3</sup> /ha	70.3
Volume increment, m <sup>3</sup> /ha/year	9

Several methods have been used to estimate fine-root biomass, production and turnover (Santantonio and Grace, 1987; Heindrick and Pregitzer, 1992; Nadelhoffer and Raich, 1992). The sequential soil core method has been widely used (Persson, 1980, 1983; Ahlström et al., 1988; Comeau and Kimmins, 1989; Yin et al., 1989; Kummerow et al., 1990a, 1990b) but is believed to underestimate fine-root production (Kurz and Kimmins, 1987; Hendrick and Pregitzer, 1992). This method is also quite expensive and labour-intensive.

The ingrowth core method has been used alone or in association with the sequential core method to estimate fine-root production (Persson, 1979, 1980; Ahlström et al., 1988; Yin et al., 1989; Messier and Puttonen, 1993). A problem with ingrowth core method is that it greatly modifies the root growth environment. But, on the other hand, it allows the direct calculation of fine-root production and is thus especially suitable for comparison of fine-root production between sites or treatments (Messier and Puttonen, 1993).

Ecophysiological root research has been quite restricted for several reasons: a lack of standardization in methods, and the time and effort needed for root processing. In the future, when more research has been conducted on root methods, techniques will become more refined and standardization will occur among different studies (Vogt and Persson, 1991).

The objective of this study was to assess Scots pine (*Pinus sylvestris* L.) fine-root biomass and production by comparison of soil core and root ingrowth core methods.

## Materials and methods

### Experimental stand

This study was carried out in a Scots pine (*Pinus*

*syilvestris* L.) stand at Ilomantsi (62° 47' N; 30° 58' E; 144 m a.s.l.), near the Mekrijärvi Research Station of the University of Joensuu.

The experimental stand was a naturally regenerated, pole stage stand (Table 1) on a 500 m<sup>2</sup> plot. The site type was *Vaccinium*-type, according to the classification of Cajander (1949). The field layer was dominated by cowberry (*Vaccinium vitis-idaea* L.) and heather (*Calluna vulgaris* (L.) Hull.). The bottom layer was dominated by red-stemmed feathers (*Pleurozium schreberi* (Brid.) Mitt.) with a few reindeer lichens (*Cladonia* sp.).

The mean annual temperature was 1.0°C and the annual rainfall was 699 mm during the study period (1985–1988). The long-term annual averages (1961–1990) were 1.9°C and 649 mm, respectively (The Finnish Meteorological Institute, 1991). About 40% of the annual precipitation consisted of snow and the ground is covered by snow from October until May (Helmisaari and Mälikönen, 1989).

The soil type is a Ferric Podzol according to the FAO classification (FAO-Unesco 1988) and relatively poor in plant-available nutrients. The depths of the soil horizons were: humus layer 2.5 cm, eluvial horizon 5.0 cm, and illuvial horizon 11.0 cm. The surface soil layer is clearly sorted to a depth of 40–60 cm. The proportion of coarse fine sand in this layer is about 50%, while the proportion of clay is only about 2%. Compact till occurs below the sorted layer.

### Root sampling

For comparison of soil core and root ingrowth core methods, samples were taken by two methods during four consecutive growing seasons during the period 1985–1988.

In the soil core method, ten samplings, including a total of 140 soil cores, were systematically taken for fine-root biomass determinations during the period 1986–1988. The soil cores were divided into three layers by depth: humus, 0–10 cm and 10–30 cm of the mineral soil.

In the root ingrowth core method, a total of 114 ingrowth core samples were collected during the growing seasons 1986–1988. In August 1985, 120 root-free mesh bags (Ø 5.7 cm) were systematically placed into the soil of the research stand. Mesh bags were filled with homogenous sieved mineral soil and placed at a depth of 30 cm in the mineral soil. An oven-dried humus clod was placed on top of the mesh bag. The mesh size of the bags was 5.5 mm. The first root ingrowth

core samples were taken, using a special spade, in July 1986 and the last in October 1988.

In both techniques, the samples were transported from the stand to the laboratory and stored frozen ( $-18^{\circ}\text{C}$ ) until analysis.

#### Laboratory analysis

In the laboratory, roots from samples taken by the soil core method were washed free of soil and separated into Scots pine living roots, understorey roots and dead roots. The Scots pine living roots were separated into three classes by diameter:  $< 2$  mm, 2–5 mm and 5–10 mm, and the understorey living roots and the dead roots (necromass) were separated into diameter classes  $< 2$  mm and  $> 2$  mm. The fraction 'dead roots' included both Scots pine and understorey dead roots. The separation of fine roots between the three groups was possible because of differences in root morphology, resilience and colour.

Frozen root ingrowth core samples were divided in the laboratory into three layers: humus, 0–10 cm mineral soil and the rest of the mineral soil. As in the soil core method, roots were separated from soil by washing and sorted by hand into Scots pine living roots, understorey living roots and dead roots.

The sorted roots were then separated into different classes by diameter: living pine roots were subdivided into  $< 2$  mm and 2–5 mm, living understorey roots into  $< 2$  mm and  $> 2$  mm and the dead roots (necromass) into  $< 2$  mm and  $> 2$  mm.

The classified roots were dried at  $70^{\circ}\text{C}$  for 5 days and weighed to determine the oven-dry biomass.

In this study, only fine roots smaller than 2 mm in diameter from the two mineral soil layers (0–10 cm and 10–30 cm) were studied. The soil core data of all three layers (humus layer and the two mineral soil layers) is presented in the article by Makkonen and Helmisaari (1998).

#### Data processing

The Scots pine fine-root biomass was estimated using the collected samples and the fine-root necromass of Scots pine was extrapolated from the total necromass using the ratio of Scots pine fine-root biomass to total fine-root biomass.

The total below-ground production was calculated by balancing the living and dead root biomass compartments according to the decision matrix presented by Fairley and Alexander (1985).

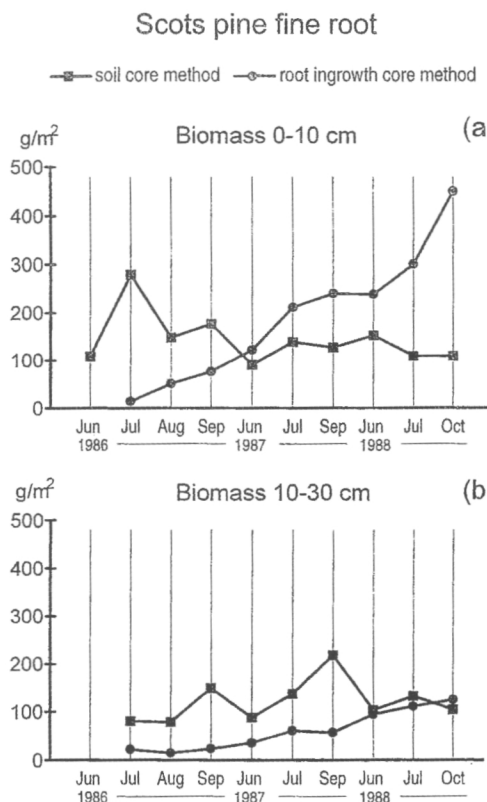


Figure 1. The seasonal variation of Scots pine fine-root biomass ( $\text{g}/\text{m}^2$ ) in (a) the upper (0–10) and (b) the lower (10–30 cm) mineral soil layer comparison of soil core and root ingrowth core methods.

## Results

#### Variations of Scots pine fine-root biomass and necromass

In both of the mineral soil layers, the Scots pine fine-root biomass and necromass varied both vertically and horizontally between the different soil horizons. There was no clear seasonal variation in the Scots pine fine-root mass either in the soil cores or in the ingrowth cores (Figure 1). The greatest proportion of fine roots (live and dead), 67% in the soil cores and 71% in the ingrowth cores, was in the upper mineral soil layer. In the soil cores, 40% of all living fine roots and 67% of all dead fine roots were in the upper mineral soil layer. In the ingrowth cores, the respective values were 77% and 66%.

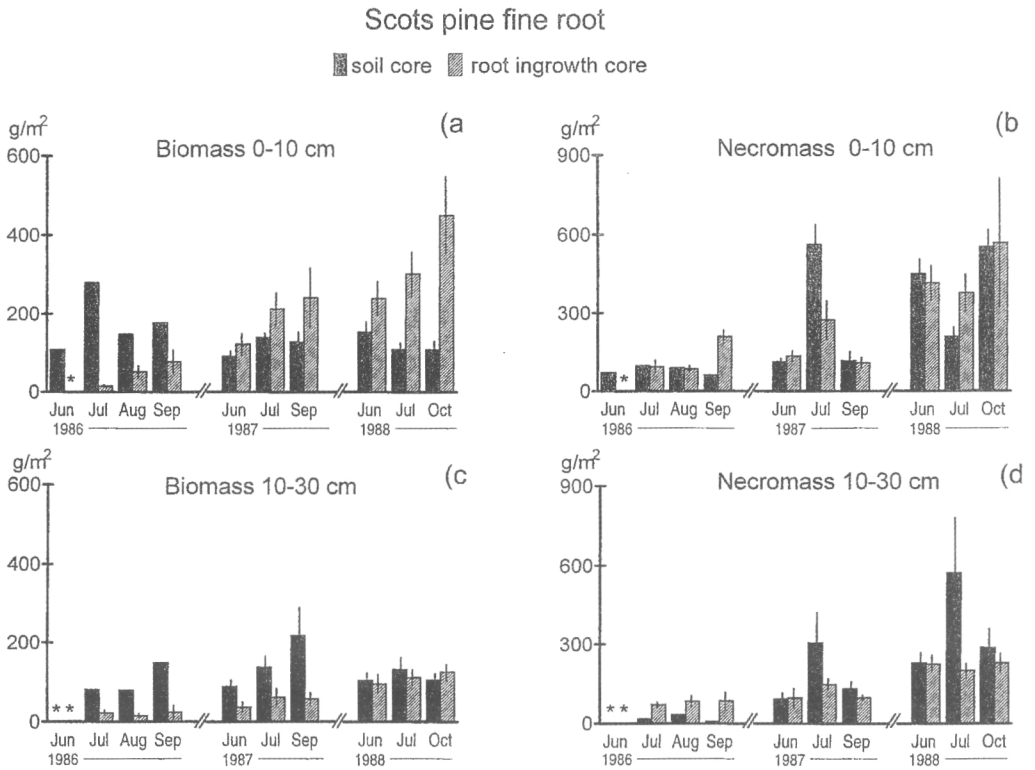


Figure 2. The seasonal variation of Scots pine fine-root (a) biomass (g/m<sup>2</sup>) and (b) necromass (g/m<sup>2</sup>) in the upper mineral soil layer (0–10 cm), and the seasonal variation of Scots pine fine-root (c) biomass (g/m<sup>2</sup>) and (d) necromass (g/m<sup>2</sup>) in the lower mineral soil layer (10–30 cm) comparison of soil core and root ingrowth core methods. Standard error of the mean is indicated by bars on the columns (not calculated for 1986 soil core data). Stars indicate missing data.

Table 2. The annual mean biomass and necromass of Scots pine fine roots (g/m<sup>2</sup>) sampled by two methods

Year	Soil layer	Soil core method				Root ingrowth core method			
		Living	Se	Dead	Se	Living	Se	Dead	Se
1986	0–10 cm	178	37	78	7	38	9	100	15
1987		119	11	278	47	191	31	168	28
1988		123	13	474	40	327	41	450	84
1986	10–30 cm	104	23	19	7	12	3	47	10
1987		148	28	192	43	49	10	107	14
1988		113	12	420	77	108	12	211	19

The biomass and necromass of roots varied spatially even in a small area. In this study the plot size was 500 m<sup>2</sup>, and the biomass of Scots pine fine-roots in different soil core samples varied between 8–813

g/m<sup>2</sup> in the upper mineral soil layer and between 2–649 g/m<sup>2</sup> in the lower one. The total fine-root necromass of Scots pine stand varied between 86–4307 g/m<sup>2</sup> and 9–3071 g/m<sup>2</sup> respectively. In the ingrowth cores, the biomass varied in different samples between 0–1529 g/m<sup>2</sup> in the upper mineral soil layer and between 0–334 g/m<sup>2</sup> in the lower one. The necromass varied between 15–4151 g/m<sup>2</sup> and 5–558 g/m<sup>2</sup> in the upper and lower mineral soil layers, respectively (Table 2).

In the upper mineral soil layer the maxima of Scots pine fine-root biomass estimated using soil cores were in July 1986 (Figure 2a) and in the lower layer in September 1987 (Figure 2c). The fine-root biomass estimated using ingrowth cores continued expanding throughout the duration of the research period, from July 1986 to October 1988, in both layers.



### The total fine root necromass

■ soil core    ▨ root ingrowth core

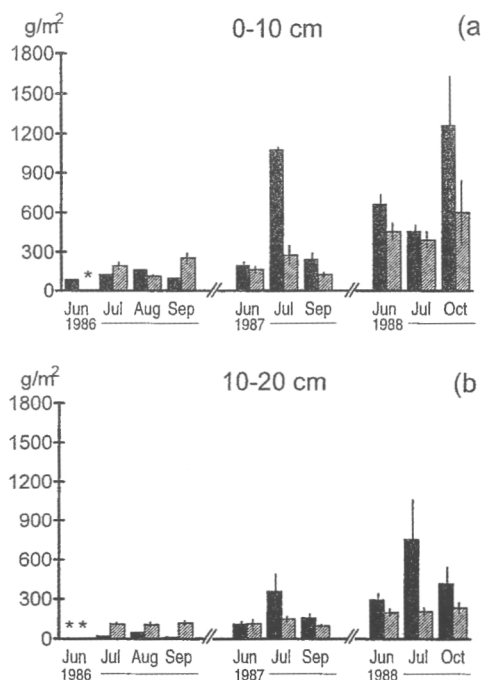


Figure 3. The seasonal variation of total fine-root necromass ( $\text{g/m}^2$ ) (a) in the upper mineral soil layer (0–10 cm) and (b) in the lower mineral soil layer (10–30 cm) comparison of soil core and root ingrowth core methods. Standard error of the mean is indicated by bars on the columns (not calculated for 1986 data). Stars indicate missing data.

There was no clear seasonal variation in the total ne-root necromass (including both Scots pine and understorey necromass) (Figure 3a, b). In July 1987 and October 1988, there were clear maxima in the upper mineral soil layer. In the lower layer, the maximum necromass during the whole research period was in July 1988. In the ingrowth cores, there was no clear seasonal variation in the upper mineral soil layer, but the necromass in both layers increased throughout the research period, from July 1986 to October 1988.

In the soil core samples the maxima of Scots pine necromass were in July 1987, June 1988 and October 1988 in the upper mineral soil layer and in July 1987 and July 1988 in the lower layer and there was no clear seasonal variation (Figure 2b, d). In the ingrowth core samples, the mass of dead roots increased from July

Table 3. Production of fine roots ( $\text{g/m}^2$ ) determined by soil core and root ingrowth core methods according to Fairley and Alexander (1985). Stars indicate missing data. SCR = soil core roots, ICR = ingrowth core roots

Mineral soil layer	Production of total belowground		Production of Scots pine		
	SCR	ICR	SCR	ICR	
0–10 cm	8606/07	281	*	193	*
	8607/08	0	36	0	54
	8608/09	0	164	29	26
	8706/07	973	188	520	302
	8707/09	0	49	0	29
	8806/07	35	59	0	406
8807/10	0	357	559	149	
10–30 cm	8606/07	*	*	*	*
	8607/08	16	0	45	21
	8608/09	69	17	57	10
	8706/07	301	65	276	76
	8707/09	355	0	96	0
	8806/07	416	30	416	16
8807/10	0	42	0	42	

1986 to October 1988, but there was no clear seasonal variation.

#### The annual production of fine-root biomass in a Scots pine stand

The annual fine-root production (seasonal growth and death) in a Scots pine stand (including both Scots pine and understorey fine roots), in the 30-cm-thick mineral soil layer, varied approximately from 350  $\text{g/m}^2$  to 1380  $\text{g/m}^2$  in the soil cores and between 224–490  $\text{g/m}^2$  in the ingrowth cores (Table 3).

The fine-root production calculated by the ingrowth core method was 31% of that in the soil cores. The biomass of ingrowth core roots increased throughout the whole research period and there was no levelling off during the three growing seasons.

The annual production (seasonal growth and death) of Scots pine fine roots in the 30 cm thick mineral soil layer varied approximately from 330  $\text{g/m}^2$  to 950  $\text{g/m}^2$  in the soil cores and between 110–620  $\text{g/m}^2$  in the ingrowth cores.

#### Discussion

In forest ecosystems, the proportion of roots of the tree biomass can be large, varying between 9% and 45%

of the total tree biomass, depending on age and site (Fogel, 1983; Santantonio et al., 1977). According to Helmisaari (1995), in the same stand as in this study, total tree biomass was  $5323 \text{ g/m}^2$ , of which 78% was above-ground and 22% below-ground biomass. The proportion of fine roots in 1985 was 36% of all roots.

In this study, the three-year average of Scots pine fine-root biomass was  $261 \text{ g/m}^2$  in soil cores and  $241 \text{ g/m}^2$  in ingrowth cores. According to Persson (1983), in a 15–20 and a 120-year old Scots pine stand, the Scots pine fine-root biomasses were  $26 \text{ g/m}^2$  and  $123 \text{ g/m}^2$ , respectively. Helmisaari and Hallbäcken (1998) reported that the fine-root biomass varied between  $210$  and  $528 \text{ g/m}^2$  in 48–186 year old Norway spruce (*Picea abies* (L.) Karst.) stands. Aber et al. (1985) reported that the fine-root biomass was  $289 \text{ g/m}^2$  in a White pine (*Pinus strobus* L.) stand. In this study, fine-root biomass values were greater than Persson (1983) reported, but comparable to those reported by Aber et al. (1985) and Helmisaari and Hallbäcken (1998).

The total necromass was  $304 \text{ g/m}^2$  in the soil cores and  $156 \text{ g/m}^2$  in the ingrowth cores. In soil cores, the calculatory part of dead Scots pine fine roots was  $203 \text{ g/m}^2$ . This is significantly more than that reported by Persson (1983):  $68 \text{ g/m}^2$  in a young Scots pine stand and  $64 \text{ g/m}^2$  in the old one. The differences in results between this study and those reported by Persson (1983) may have been caused by differences in research methods: it is very difficult to separate the partly decomposed dead roots from the soil organic matter.

The total annual fine-root production (Scots pine and understorey vegetation) was  $814 \text{ g/m}^2$  as determined by the soil core method and  $335 \text{ g/m}^2$  as determined by the root ingrowth core method. The Scots pine fine-root production was  $721 \text{ g/m}^2$  and  $376 \text{ g/m}^2$  respectively (calculated results). This is greater than Aber et al. (1985) reported:  $162 \text{ g/m}^2$  for fine-root production of White pine, but less than that reported by Grier et al. (1981):  $924 \text{ g/m}^2$  in a 23-year old and  $1279 \text{ g/m}^2$  in a 180-year old Pacific silver fir (*Abies amabilis* Forb.) stand.

The root system shows variability both vertically and horizontally. Most fine roots are in the top 20 cm of the soil, in the humus layer and in the upper mineral soil horizons (Messier and Puttonen, 1993). The distribution is dependent on soil aeration and fertility (Fogel, 1983). In this stand, most Scots pine fine roots were in the upper mineral soil layer. The Scots pine fine-root biomass was about 13% smaller in the lower mineral soil layer than in the upper layer estimated by

the soil core method, and even 53% smaller estimated by the ingrowth core method. These differences are related to the soil structure: in the soil core method the stratification of soil genetic layers still remains – the eluvial horizon is included in the upper layer and the illuvial horizon in the lower layer, while in the ingrowth core method mesh bags are filled by mixed sand. Grier et al. (1981) have reported similar results: 40% of conifer roots were in the upper mineral soil layer (A-horizon) and 11 % in the lower layer (B-horizon).

Almost all dead roots were in the upper mineral soil layer, with only 34% of the total fine-root necromass being in the lower layer. This is comparable with McClaugherty et al. (1982):  $130 \text{ g/m}^2$  in the upper layer (0–15 cm) and  $50 \text{ g/m}^2$  in the lower one (15–30 cm). Also the Scots pine fine-root necromass, as measured by the soil core method, was 23% smaller in the lower layer than in the upper one, and 49% smaller when measured by the ingrowth core method.

In the upper mineral soil layer, the annual mean biomass of Scots pine soil core roots was about 24% less than ingrowth core roots (in a three-year period), but in the lower layer the biomass of ingrowth core roots was 53% greater. In both layers the necromass of soil core roots was greater than that of ingrowth core roots, in the upper layer by 13% and in the lower layer by 42%. The reason might be the lack of root competition in the mesh bags: after a three-year period, there is still free space for roots to expand.

The fine-root biomass and necromass varied spatially in the research plots. In the forest, fine roots seek places where the soil properties are optimal for their growth and development. Trees induce heterogeneity in soil properties. The soil, under the influence of a forest, develops properties that vary spatially with relation to the location of trees. This variation in soil properties is frequently reflected in the distribution of the various species of the understorey. The tree has maximum influence under its crown canopy, and the influence decreases outwards from the tree (Liski, 1995).

Estimates of the fine root biomass and production differed substantially depending on the method of calculation employed. There are some methodological problems which influence the results of both methods, and individual differences in root sorting may affect the results. It is quite difficult to separate the fine roots from the mineral soil, even by washing. Small mineral particles adhere strongly to mycorrhizal hyphae and a part can be left after washing. This may influence

the results. One difficulty often encountered in root sorting is the inability to distinguish dead fine root material from soil organic matter. Freezing damages root tissues, resulting in some loss of structural integrity. It is impractical and almost impossible to sort all of the small dead root fragments. This necessitates restricting sorting to whole fragments over a certain length of recognisable root material (Persson, 1990).

The time interval between root sampling can be too long, and the intervening variation can thus be lost. In this study, the time interval was 6–8 weeks, and therefore root growth and death occurring between sampling dates could not be accurately estimated. Decomposition of fine roots may also have affected the necromass values (of the ingrowth cores). According to Berg (1984), 1–2 mm diameter Scots pine fine-roots lost about 30% of their mass in two years.

There are some errors originating from the different methods used. The root ingrowth core method gives a lower estimation of production than the soil core method. In this study, the biomass in ingrowth cores increases from July 1986 to October 1988. After three years, the root system was still expanding. In the soil core method, the amount of dead roots influences the estimate of production; if there is a lot of necromass – as in July 1987 in this study – the production estimate will be greater.

Because the roots are still expanding into the ingrowth cores, comparison between these two methods, especially for living roots, is difficult. Living roots have different space for their growth in soil cores than in ingrowth cores. According to some observations, new healthy roots of standing trees of pine can grow through old decomposing roots of the previous pine crop, in old root channels (Nambiar and Sands, 1992). In ingrowth cores there are no channels, and thus new roots may not use this easy way to grow.

Instead of living roots, dead roots are ecologically occupying the same space in both methods. The problem is their dying at different times; thus calculation of the necromass according to the biomass does not give accurate results.

Special problems arise when using the root ingrowth core method. The sieved soil cannot be reconstructed into horizons in the ingrowth core; the typical podsol profile will be disturbed. The bulk density of soil, initially repacked into the cylinders, will be different from that naturally present in the soil of the site. The sieved soil in the ingrowth cores may, furthermore, be drier than the surrounding soil. After a short period, there is no root competition in the soil of the

ingrowth cores, so the roots can grow into the ingrowth core faster than into the surrounding soil – particularly because the injured roots around the ingrowth core after their installation may favour the growth of adventitious roots.

The soil core method also has its own problems. The soil core sample is only a momentary representation of fine-root biomass; the growth of fine roots cannot be followed. The spatial variation can be greater than the variation in time.

Both techniques thus have their sources of error. The soil core method is suitable for studying the annual and seasonal fine-root biomass variation. For estimating production, sampling should be done at short intervals. The ingrowth core method is more suitable for comparing the potential of annual fine root production between different site types. However, both methods are useful for studies on the dynamics of Scots pine fine roots.

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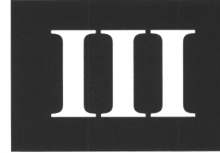
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## **PAPER III**

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## Fine root biomass and production in Scots pine stands in relation to stand age

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**Summary** We determined fine root biomass and production of 15-, 35- and 100-year-old Scots pine (*Pinus sylvestris* L.) stands during three growing seasons. Fine roots were sampled by the soil core method. Mean ( $\pm$  SE) annual fine root biomass of Scots pine in the 15-, 35- and 100-year-old stands was  $220 \pm 25$ ,  $357 \pm 21$  and  $259 \pm 26$  g m<sup>-2</sup>, respectively. Fine root biomass of the understory vegetation was  $159 \pm 54$  g m<sup>-2</sup>,  $244 \pm 30$  and  $408 \pm 81$  g m<sup>-2</sup>, and fine root necromass was  $500 \pm 112$ ,  $1047 \pm 452$  and  $1895 \pm 607$  g m<sup>-2</sup> in the sapling, pole stage and mature stands, respectively. Both understory and Scots pine fine root production increased with stand age. Mean annual Scots pine fine root production was  $165 \pm 131$ ,  $775 \pm 339$  and  $860 \pm 348$  g m<sup>-2</sup> year<sup>-1</sup> in the sapling, pole stage and mature stand, respectively. The respective mean annual production of all fine roots (Scots pine and understory) was  $181 \pm 129$ ,  $1039 \pm 497$  and  $1360 \pm 869$  g m<sup>-2</sup> year<sup>-1</sup>. The Scots pine and understory fine root biomass, necromass and production varied in relation to stand age, although the variation was not statistically significant.

**Keywords:** maturity, necromass, *Pinus sylvestris*.

### Introduction

Fine roots account for most of the surface area and length of coniferous forest root systems, and are therefore important components of forest biomass (Persson 1983). Root biomass (coarse and fine roots) as a proportion of total tree biomass varies between 18 and 45%, depending on the species, age and site (Santantonio et al. 1977, Fogel 1983). More than 50% of annual production is allocated belowground in many forests (Harris et al. 1977, Fogel and Hunt 1979, Grier et al. 1981, Keyes and Grier 1981, Santantonio and Hermann 1985, Vogt et al. 1990, Ruess et al. 1996, Steele et al. 1997).

Fine root growth occurs relatively independently of shoot growth, and the temporal variation in root growth is largely determined by environmental conditions, especially soil temperature, water content, strength (density and compaction) and aeration (Lyr and Hoffmann 1967, Tryon and Chapin 1983, Persson 1992, Steele et al. 1997). Competition among individuals of the same species, as well as among different plant populations, influences the process of root growth (Persson 1983).

Despite the important role of fine roots in stand dynamics,

relatively few studies have been carried out on fine root biomass or production in relation to stand age. Fine root biomass values have been reported for 15- to 178-year-old Scots pine (*Pinus sylvestris* L.) stands (Vanninen and Mäkelä 1999), 15- to 20- and 120-year-old Scots pine stands (Persson 1983, 1984), 11- and 163-year-old Douglas-fir (*Pseudotsuga menziesii* Mirb.) stands (Vogt et al. 1983, 1987), and 23- and 180-year-old Pacific silver fir (*Abies amabilis* (Dougl.) Forbes) stands (Grier et al. 1981).

The aim of this study was to estimate fine root biomass and production in three Scots pine stands (15-year-old sapling stand, 35-year-old pole stage stand and 100-year-old mature stand) in eastern Finland during three successive growing seasons.

### Materials and methods

#### Site description

The study was carried out in Scots pine stands near the Mekrijärvi research station of the University of Joensuu, at Ilomantsi (62°47' N, 30°58' E, 144 m a.s.l.). The stands represented different stages of stand development: sapling, pole stage and mature. One study plot without replicates was established in each stand (Table 1). The stands were situated on sites of similar fertility and soil type within 500 m of each other. The soil type (Table 2) is a ferric podzol (FAO-Unesco 1988) and is relatively infertile. The mineral soil down to a depth of 60 cm is sorted glacio-fluvial sand. The proportions of clay and coarse sand are about 2 and 50%, respectively. Compact till occurs below the sorted layer (Helmisaari and Mälikönen 1989).

The site is a *Vaccinium* forest site type, according to the classification of Cajander (1949). Although the stands were situated on a similar type of soil, soil water content varied among the stands. The soil in the sapling stand was drier than in the pole stage or mature stand because of a deeper groundwater level and lower stand density. The soil in the mature stand had a higher water content than that of the average *Vaccinium* forest site type because of a higher groundwater level.

Mean annual temperature was 1.0 °C and annual precipitation was 699 mm during the study period (1985–1988). The

Table 1. Characteristics of the study stands in 1985.

	Sapling	Pole stage	Mature
Age (years)	17	37	102
Plot area (m <sup>2</sup> )	400	500	875
Number of trees ha <sup>-1</sup>	7425	2660	432
Mean stem diameter (cm)	2.2	8.2	27.4
Mean height (m)	2.5	7.5	20.5
Basal area (m <sup>2</sup> ha <sup>-1</sup> )	3.8	15.3	25.9
Stem volume (m <sup>3</sup> ha <sup>-1</sup> )	11.9	70.3	264.9
Volume increment (m <sup>3</sup> ha <sup>-1</sup> year <sup>-1</sup> )	2.4	9	3.3

long-term annual means (1961–1990) were 1.9 °C and 649 mm, respectively (Finnish Meteorological Institute 1991). Temperature and precipitation data are from the Ilomantsi station of the Finnish Meteorological Institute (62°40' N, 30°57' E, 162 m a.s.l.), located about 12 km from the stands. About 40% of annual precipitation falls as snow, and there is a permanent snow cover from October to May (Helmisaari and Mälikönen 1989).

#### Root sampling

Ten sampling rounds were carried out in the sapling stand, and 11 sampling rounds in the pole stage and mature stands during the growing seasons of 1985–1988. Twenty soil cores (volumetric samples, core diameter 36 mm) per sampling were taken. The soil cores were divided into three layers by depth: the humus layer, and the 0–10 cm and 10–30 cm mineral soil layers. The samples were stored at –18 °C until analyzed.

#### Laboratory analysis

In the laboratory, the roots were washed free of soil and classified into those of trees or understory vegetation, and then further classified according to diameter and physiological status (living and dead). Living Scots pine roots were distinguished from living understory roots on the basis of their mycorrhizae, color and thickness. Dead roots were distinguished from living roots on the basis of their color and consistency (Vogt and Persson 1991). The roots were sorted into two diameter classes: fine (< 2 mm) roots (Persson 1983, Vogt et al. 1983) and coarse (> 2 mm) roots. Fine roots are generally defined as non-woody, small diameter roots (Nadelhoffer and Raich 1992), but there is no established convention defining the diameter range of fine roots (Fogel 1983).

Table 2. The thickness (cm) of the soil horizons in the profiles of the experimental stands.

Horizons	Sapling	Pole stage	Mature
O	2.5	2.5	6.5
E	4	5	8
Bs	10	11	7
BC	12	19	11

The sorted roots were dried at 70 °C for 5 days and weighed. Ash content of the fine roots was determined by combusting the fine root samples for 3 h at 550 °C in a muffle furnace (Halonen et al. 1983). Fine root necromass of Scots pine was estimated from total fine root necromass based on the ratio between Scots pine fine root biomass and total fine root biomass. Total fine root production was calculated by balancing the living and dead fine root mass compartments according to the decision matrix presented by Santantonio (1980), McLaugherty et al. (1982) and Fairley and Alexander (1985).

#### Calculations and statistical analysis

The biomass data were analyzed by one- and two-way analysis of variance (BMDP 7D ver. 1990, SPSS, Inc., Chicago, IL) to determine differences between stands and between years, except for 1986. In 1986, the samples were combined to give a composite sample (one sample per sampling in each stand), so no statistical analyses could be performed.

Differences in fine root production between years in different stands could not be tested because of the lack of replicate stands.

#### Results

Fine root biomass (g m<sup>-2</sup>) varied between stands of different age (Figure 1a–i). Mean annual biomass of Scots pine fine roots varied (in the humus layer and the 30 cm mineral soil layer) between 135 and 259 g m<sup>-2</sup> in the 15-year-old sapling stand, between 311 and 419 g m<sup>-2</sup> in the 35-year-old pole stage stand, and between 184 and 293 g m<sup>-2</sup> in the 100-year-old mature stand during the 3-year measurement period (Figure 1a–c).

The understory vegetation fraction consisted of all living dwarf shrub and grass fine roots. The mean fine root biomass of the understory vegetation varied from 79 to 320 g m<sup>-2</sup>, from 189 to 323 g m<sup>-2</sup>, and from 286 to 646 g m<sup>-2</sup> in the sapling, pole stage and mature stands, respectively (Figure 1d–f).

The dead root (necromass) fraction consisted of dead Scots pine, dwarf shrub and grass fine roots. The mean fine root necromass varied annually from 202 to 721 g m<sup>-2</sup>, 203 to 2325 g m<sup>-2</sup>, and 572 to 2762 g m<sup>-2</sup> in the sapling, pole stage and mature stands, respectively (Figure 1g–i).

The depth distribution of biomass and necromass of fine roots varied with stand age. Most of the Scots pine fine roots were located in the mineral soil in the mature and pole stage stands. In the sapling stand, most fine roots were in the humus layer and upper mineral soil layer. Almost all the fine roots of the understory vegetation in the three stands were located in the humus layer and upper mineral soil layer. Most of the necromass was present in the upper soil layers.

The seasonal variation of Scots pine fine root biomass in the different stands was statistically significant only in the mature stand between June and July, 1988 ( $P < 0.001$ ) and June and October, 1988 ( $P < 0.01$ ). The fine root biomass of the understory vegetation varied seasonally only in the pole stage stand between July and October, 1988 ( $P < 0.001$ ).



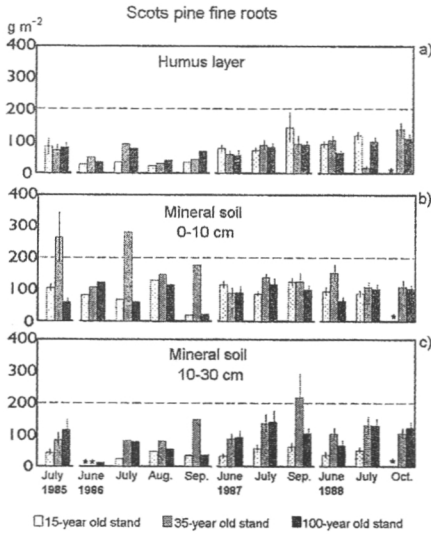


Figure 1a-c. Living Scots pine fine root biomass in three stands in 1985–1988. Asterisks indicate missing values.

Fine root necromass varied seasonally in both the pole stage and the mature stand in 1987: in the pole stage stand between June and July ( $P < 0.001$ ) and July and September ( $P < 0.001$ ), and in the mature stand between June and July ( $P < 0.001$ ) and June and September ( $P < 0.001$ ). In 1988, there was significant variation in fine root necromass between June and October both in the pole stage stand ( $P < 0.01$ ) and in the mature stand ( $P < 0.01$ ).

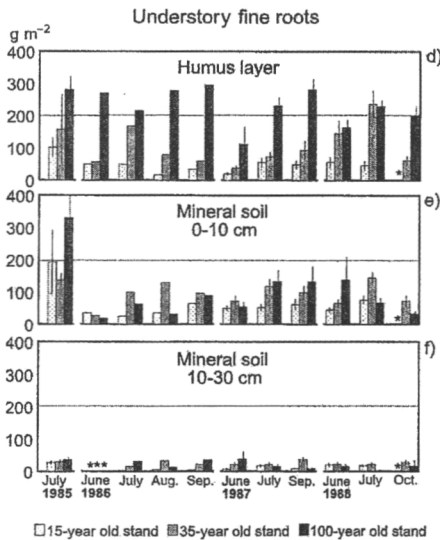


Figure 1d-f. Living fine root biomass of understory vegetation in three stands in 1985–1988. Asterisks indicate missing values.

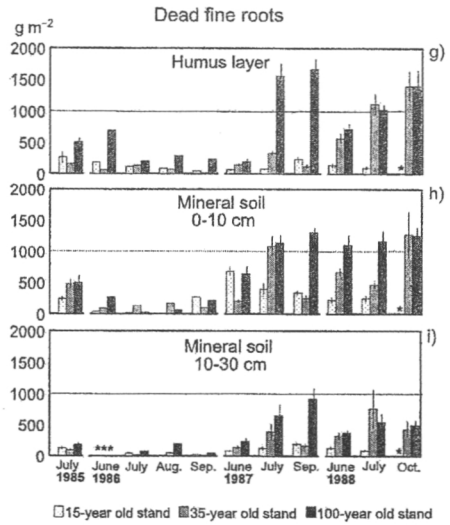


Figure 1g-i. Necromass of Scots pine and understory vegetation in three stands in 1985–1988. Asterisks indicate missing values.

There were several significant differences between the stands in fine root biomass of the understory vegetation and total necromass, but only one instance of a significant difference between stands in Scots pine fine root biomass (Table 3). Most significant differences were found between the sapling and mature stand or between the pole stage and mature stand.

Mean annual production of Scots pine fine roots was  $165 \text{ g m}^{-2} \text{ year}^{-1}$  in the sapling stand,  $775 \text{ g m}^{-2} \text{ year}^{-1}$  in the pole stage stand and  $860 \text{ g m}^{-2} \text{ year}^{-1}$  in the mature stand (Table 4). Mean annual fine root production of the trees, dwarf shrubs and grasses in the Scots pine stands was 181, 1039 and  $1360 \text{ g m}^{-2} \text{ year}^{-1}$  in the sapling, pole stage and mature stands, respectively.

## Discussion

Tree biomass and its distribution between the above- and belowground tree components vary among species and among stands of different age. In boreal pine forests, belowground biomass is 37% of aboveground biomass and 27% of total tree biomass (Gower et al. 1994). According to a study carried out by Helmisaari (1995) on the same stands used in this study, the relative proportions of above- and belowground biomass were 73 and 27%, 78 and 22%, and 87 and 13% in the sapling, pole stage and mature stands, respectively.

Scots pine fine root biomass was greatest in the pole stage stand and lowest in the sapling stand, whereas fine root biomass of the understory vegetation increased with increasing stand age. In the pole stage stand, there may have been less root competition between species and thus more space, nutrients and water available for tree root growth.

Our fine root biomass values were greater than values reported by Persson (1979, 1983) and McKay and Malcolm

Table 3. The statistically significant differences in fine root biomass and necromass between sapling, pole stage and mature stands during 1985–1988.

Date	Comparison	P-Value
<i>Scots pine fine root biomass</i>		
June 1988	Sapling stand versus pole stage stand	< 0.01
<i>Fine root biomass of understory vegetation</i>		
June 1987	Sapling stand versus mature stand	< 0.001
July 1987	Sapling stand versus mature stand	< 0.001
	Pole stage stand versus mature stand	< 0.001
September 1987	Sapling stand versus mature stand	< 0.001
July 1988	Sapling stand versus pole stage stand	< 0.001
	Pole stage stand versus mature stand	< 0.001
<i>Fine root necromass</i>		
July 1985	Sapling stand versus mature stand	< 0.01
June 1986	Sapling stand versus pole stage stand	< 0.01
	Pole stage stand versus mature stand	< 0.001
July 1987	Sapling stand versus pole stage stand	< 0.01
	Sapling stand versus mature stand	< 0.001
	Pole stage stand versus mature stand	< 0.001
September 1987	Sapling stand versus mature stand	< 0.001
	Pole stage stand versus mature stand	< 0.001
June 1988	Sapling stand versus pole stage stand	< 0.001
	Sapling stand versus mature stand	< 0.001
July 1988	Pole stage stand versus mature stand	< 0.001
	Sapling stand versus mature stand	< 0.001

(1988) for Scots pine. However, results comparable with ours have been reported by Aber et al. (1985) for white pine (*Pinus strobus* L.), McClaugherty et al. (1982) for red pine (*Pinus resinosa* Ait.), Oleksyn et al. (1999) for Scots pine, Steele et al. (1997) for jack pine (*Pinus banksiana* Lamb.), Vanninen and Mäkelä (1999) for Scots pine, Vogt et al. (1983, 1987) for Douglas-fir and Helmisaari and Hallbäck (1999) for Norway spruce (*Picea abies* (L.) Karst.).

Mean annual fine root necromass decreased with decreasing stand age. Persson (1979, 1983) reported that the necromass was 125 g m<sup>-2</sup> in a 15- to 20-year-old and 114 g m<sup>-2</sup> in a 120-year-old Scots pine stand, which is less than the necromass obtained in our study. In contrast, the results presented

by McKay and Malcolm (1988) and McClaugherty et al. (1982) are comparable with our results.

The ratio of necromass to total fine root biomass increased with increasing stand age, with values of 58% in the sapling stand, 68% in the pole stage stand and 75% in the mature stand. At the same time, the ratio of live to dead roots decreased with decreasing stand age. Thus, the older the stand, the greater the proportion of dead fine roots. Our results are comparable with the values of 80% reported by McKay and Malcolm (1988), and 71% reported by Santantonio and Santantonio (1987), but more than the value of 45% reported by Persson (1980).

In our study, the dead fine roots included both roots that had

Table 4. Fine root production (g m<sup>-2</sup>) in the Scots pine stands. Asterisks indicate missing values.

Date	Sapling		Pole stage		Mature	
	Total	Scots pine	Total	Scots pine	Total	Scots pine
July 1986	*	*	*	*	68	47
August 1986	*	*	0	0	246	118
September 1986	*	*	48	111	17	0
July 1987	38	0	1524	918	2552	1003
September 1987	272	297	88	74	537	256
July 1988	52	34	844	0	661	822
October 1988	*	*	615	1224	0	334

died recently, and those that had already decomposed to some degree, but could still be identified as roots. Dead roots differ from living roots in their color and consistency, but the reliability of classifying roots as living or dead and distinguishing dead roots from soil organic matter decreases with decreasing root diameter, which may have introduced some errors. Small mineral soil particles may be tightly bound to the mycorrhizae, thus affecting the dry weight values. However, in our study the ash content of the fine roots in the pole stage stand was less than 10%.

The depth distribution of roots in stands of different ages varies. In our study, the majority of dwarf shrub roots and grass roots—most of which are shallow-rooted—were in the humus layer and in the mineral soil lying immediately below it, whereas most of the Scots pine roots were located in the mineral soil layers. Similar results have been reported by Mälkönen (1974), Oleksyn et al. (1999), Persson (1979, 1983) and Santantonio and Santantonio (1987).

Both Scots pine and total fine root production increased in the order: sapling < pole stage < mature stand. Our production values were greater than that reported by Persson (1979, 1983) of 60–200 g m<sup>-2</sup> year<sup>-1</sup> in 15- to 120-year-old Scots pine stands. However, our results are comparable with those of Aber et al. (1985), who reported the annual fine root production of young white pine stands varied between 140 and 162 g m<sup>-2</sup> year<sup>-1</sup> depending on the calculation method.

The great variation in biomass and necromass and the high fine root production in this study might be caused by environmental factors, particularly precipitation, soil water and temperature and their interannual variation. The warm and dry July of 1988 may have resulted in a low soil water content as a result of rapid evaporation of precipitation before it had percolated into the soil (Makkonen and Helmisaari 1998). The Scots pine fine roots, in particular, may have subsequently suffered from drought; Scots pine roots are more sensitive to drought than those of dwarf shrubs and grasses (Heindrick and Pregitzer 1992).

Although all three Scots pine stands were growing on the same *Vaccinium* site type, the existing gradient in soil water may also have contributed to the variation among stands. Water content in the litter and humus layers and fine root distribution are correlated. This relationship could be attributed to high growth rates in the frequently wet soil or high root mortality in the dry parts of the sites, or both (e.g., Comeau and Kimmins 1989, Gower et al. 1992). Variation in soil water content is largely responsible for the spatial heterogeneity of roots (Deans 1979). The main effect of increased soil water content is an increase in the rate of decomposition and mineralization of dead roots, which increases the availability of critical nutrients in the soil. Fine root production may also vary substantially from year to year, and the annual variation may be even greater than the variation among sites (Persson 1984).

Another possible explanation for the high fine root production observed in this study may be associated with calculation procedure. When total belowground production is calculated by balancing the living and dead root biomass compartments,

the cumulative estimates are dependent on the sum of the differences observed between a series of observations. Thus, variation in the precision of the biomass estimates from month to month may have affected the calculated production values. Fairley and Alexander (1985) and Vogt et al. (1986) thus recommend that only significant differences between individual biomass estimates should be included in the cumulative production estimates. The biomass and necromass varied considerably during the study period, but the variation was significant on only a few sampling occasions. Consequently, the calculations could not be based only on significantly different values. Thus, the fine root production in our study may have been overestimated by a maximum of 30–35% (Fairley and Alexander 1985).

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## **PAPER IV**

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## Below- and above-ground biomass, production and nitrogen use in Scots pine stands in eastern Finland

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### Abstract

The below- and above-ground biomass and the annual biomass production of sapling (15-year-old), pole stage (35-year-old) and mature (100-year-old) Scots pine (*Pinus sylvestris* L.) stands were studied in eastern Finland. The fine-root (diameter < 2 mm) biomass (including mycorrhizal root tips), necromass and biomass production were determined for the organic layer and the upper 30 cm mineral soil layer by soil core samplings. The biomass and the annual production of needles, cones, stemwood and stembark, branches (wood and bark), and coarse-roots were calculated for the whole stand using biomass measurements of different components of felled sample trees, and measurements of the tree stand.

Below-ground biomass accounted for 25, 21 and 13% of the stand biomass in the sapling, pole stage and mature stands; 15, 7 and 2% consisting of fine-roots, respectively. The mean fine-root biomass was 220, 357 and 259 g/m<sup>2</sup> in the sapling, pole stage and mature stands. The mean annual fine-root biomass production was 165, 775 and 860 g/m<sup>2</sup>, corresponding to 43, 59 and 60% of the total stand biomass production in the sapling, pole stage and mature stands, respectively. Thus, even though the proportion of fine-roots of the total tree biomass was not large, their growth accounted for a major part of stand biomass production.

Fine-roots annually used 0.9, 4.1 and 4.5 g N/m<sup>2</sup> for biomass production in the sapling, pole stage and mature stands, respectively. This accounted for 45–63% of the nitrogen used annually in total stand biomass production. Needle production accounted for 27–34%, and production of the woody components 9–21% of the nitrogen used annually in biomass production.

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**Keywords:** Dry matter partitioning; Fine-roots; Foliage; Growth; *Pinus sylvestris*

### 1. Introduction

The temporal development of stem volume of pines is well known in managed forests throughout the boreal region. There are also a number of research

reports on the development of stand above-ground biomass, some of them including chronosequence data (e.g. Forrest and Ovington, 1970; Albrektson, 1980; Gower et al., 1994, 1996). A number of reports on stand below-ground biomass have been published during the last two decades, but only a few of them examine variation in fine-root biomass with stand age (Grier et al., 1981; Persson, 1978, 1980; Vogt et al., 1981, 1983; Vanninen et al., 1996). Fine-root biomass

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46 in stands of different age varies also in response to  
47 changes in nutrient availability which makes the  
48 comparisons of age-series more difficult (Keyes and  
49 Grier, 1981; Vogt et al., 1983, 1985).

50 Only a few studies report on both above- and below-  
51 ground production of conifers (e.g. Ågren et al., 1980;  
52 Grier et al., 1981; Keyes and Grier, 1981; Nadelhoffer  
53 et al., 1985; Gower et al., 1992). Especially, below-  
54 ground production data and the factors that control  
55 biomass allocation to roots remain a large uncertainty  
56 in forest biomass production budgets (Gower et al.,  
57 1994; Bartelink, 1998).

58 The availability of mineral nitrogen is normally the  
59 factor restricting tree growth in mineral soils in Fin-  
60 land (Kukkola and Saramäki, 1983). Fine-roots and  
61 their mycorrhizas take up nutrients and also use them  
62 for their own growth and survival. However, from the  
63 boreal region there are not many estimates on how  
64 much nitrogen is used for biomass production of  
65 different tree parts, e.g. fine-roots.

66 The present study is a part of an integrated research  
67 started in 1983 in eastern Finland in three Scots pine  
68 stands representing different stages of stand develop-  
69 ment for determining the nutrient dynamics and bio-  
70 mass production of Scots pine. Previous articles report  
71 on, e.g. nutrient retranslocation (Helmisaari, 1992a,b),  
72 nutrient cycling (Helmisaari, 1995), and fine-root  
73 dynamics (Makkonen and Helmisaari, 2001) in the  
74 same stands. The aim of this study was to present a  
75 synthesis on the distribution of both below- and above-  
76 ground biomass, annual biomass production and nitro-  
77 gen use. Especially, this study aims at determining the  
78 share of fine-roots of total stand biomass, production  
79 and nitrogen use.

## 80 2. Materials and methods

### 81 2.1. Experimental stands

82 The research was carried out in three naturally  
83 regenerated Scots pine stands in the province of north-  
84 ern Carelia, eastern Finland, in the vicinity of Mekri-  
85 järvi Research Station, University of Joensuu  
86 (62°47'N, 30°58'E, 145 m a.s.l.). The stands represent  
87 different stages of development — sapling, pole stage  
88 and mature stages (Table 1). The stands had been  
89 treated as normal managed forests; the oldest stand

Table 1  
Some characteristics of the research stands in 1983

Characteristic	Sapling stand	Pole stage stand	Mature stand
Plot area (m <sup>2</sup> )	400	500	875
Age (years)	15	35	100
Number of trees (per ha)	7425	2660	432
Canopy cover (%)	60	56	63
Mean diameter (cm)	1.6	7.7	27.3
Mean height (m)	2.0	6.8	20.1
Basal area (m <sup>2</sup> /ha)	2.2	13.8	25.7
Stem volume (m <sup>3</sup> /ha)	7.9	57.7	258.1
Volume increment (m <sup>3</sup> /ha per year)	1.8	5.2	3.5

had earlier been treated with thinnings. One experi- 90  
mental plot of 400 m<sup>2</sup> (the youngest stand), or 500 m<sup>2</sup> 91  
(the pole stage stand) or 875 m<sup>2</sup> (the mature stand) was 92  
established in each stand in spring 1983. The plots 93  
could not be replicated, and therefore, statistical ana- 94  
lysis of the data is not justified. The stands were 95  
situated on a similar site and soil type at a distance 96  
of <500 m from each other. 97

The soil type is an iron podzol, relatively poor in 98  
available nutrients (Helmisaari and Mälkönen, 1989). 99  
The surface soil layer is clearly sorted to the depth of 40– 100  
60 cm below the humus layer. The proportion of coarse 101  
fine sand in this layer is about 50%, while the proportion 102  
of clay is only about 2%. Below the sorted layer, there is 103  
tightly compacted till. The site type, according to the 104  
classification of Cajander (1949), is *Vaccinium* type; the 105  
field layer vegetation being dominated by *Vaccinium* 106  
*vitis-idaea* L., *Vaccinium myrtillus* L. and *Calluna* 107  
*vulgaris* (L.) Hull. *Pleurozium schreberi* (Brid.) Mitt. 108  
is dominant in the bottom layer, but *Cladonia* species are 109  
also common, especially in the sapling stand. 110

The study area was located in a boreal climate 111  
region. The long-term (1961–1990) mean annual tem- 112  
perature and precipitation was 1.9°C and 649 mm, 113  
respectively (The Finnish Meteorological Institute, 114  
1991). The mean annual temperature at the site for 115  
the 5-year research period (1983–1987) was 1.4°C and 116  
precipitation 690 mm. 117

### 118 2.2. Tree biomass and biomass production

#### 119 2.2.1. Above-ground

In May 1983 and 1988, the diameter (1.3 m above- 120  
ground level) distribution of all trees of the sample 121



plots was determined. The heights of 50 trees in the sapling stand, 36 trees in the pole stage stand (selected using a sampling method based on the cumulative basal area) and all trees in the mature stand were then measured. In 1988 also the annual radial growth of the sample trees at the height of 1.3 m was determined from core samples. The height and the height of crown bottom was measured for the sample trees, for non-sample trees they were calculated by regression equations on the annual basis for the period 1983–1988. The diameters and heights for the years 1984–1987 were calculated from the measured diameters and heights in 1983 and 1988 and from the diameter and height growth for the years 1983–1987.

Twelve trees (four in each stand) were selected for destructive sampling in spring 1985 for measuring the biomass and nutrient contents of tree components. The samples were taken during different phases of the annual growth cycle; one of the four trees in each stand was felled in May, July and September 1985 and February 1986 (there is a seasonal variation in N concentrations, Helmisaari and Siltala, 1989). Because of the labour in separating tree components, no replicate trees could be sampled at different sampling times.

The sample trees were subjected to the following basic measurements; stem, height, height of the bottom of living and dead crown, age (on the basis of radial growth), crown, height and diameter of each branch, living and dead branches, age of branch. The mass of needles, branches, stemwood, stembark and cones of the sample trees were estimated on the basis of the whole-tree analysis. These results together with the basic measurements, were then used to estimate the same quantities for the trees not sampled. The mass of stemwood, bark and branches in the sample trees were converted to an areal basis by applying regression models.

Sample discs were cut at the heights of 5, 20, 40, 60, 80 and 90% of total tree height for the measurements of wood density and N concentrations. The bark of the discs was removed and divided into living and dead. In addition, the terminal leaders formed during the last 4 years were cut.

For stem analysis, additional sample discs were taken from the heights of 1, 10, 30, 50, 70, and 90% of the total tree height. From all discs, under-bark disc diameters were measured, with the discs

being divided for the latest 5 years (the sapling and pole stage stands), and for the latest 10 years (the mature stand). The over-bark and under-bark volume of stem and volumes of stemwood of different ages were estimated by the integration of taper-curves. Biomass was then calculated from volume using density curves. The measured mass values of living and dead bark were converted into mass per length unit.

The common form of the models for sample trees was  $\ln(D_b(z)) = \ln(a) + bz$ , where  $D_b(z)$  is the bark density at the relative height,  $z$  from the stem butt and  $a$  and  $b$  are parameters. The integration of the equation over the interval (0, 1) multiplied by the height of the tree gave the total mass of the bark,  $S_b$  for the stem, this operation giving the form  $S_b = h(a/b)(e^b - 1)$ .

The stand stemwood biomass each year was estimated using the stemwood biomass per sample tree and the measured tree dimensions of sample trees and all the trees in the stand. The mass of sample tree stembark was converted to an areal basis by applying regression models, the masses being regressed to the dimensions of the stem.

The sample of living branches included every fourth living branch starting from the southernmost branch of the uppermost whorl. From the sample branches, the length and the base diameter of the last four internodes of the first-order lateral, the mass of needles in age classes, the mass of living and dead bark and wood in the above internodes (separately for each and collectively for the rest of the branch), the mass of bark and wood (collectively in second- and higher-order lateral), the mass of dead branches, and the thickness of the last five annual rings at the base of the branch were measured.

The mass of branches in the sample trees was estimated using the sample branch measurements and the measurements of age, diameter, length, and the relative position of all branches. The common form of the models was  $\ln(B_{mc}) = \text{constant} + b \ln(d_b) + c \ln(l_b) + fz_b + gz_b^2$ , where  $B_{mc}$  (g) is the mass of the component,  $d_b$  (cm) the diameter of the branch outside the butt swell,  $l_b$  (cm) the length of the branch and  $z_b$  the relative position of the branch in the living crown, i.e.  $z_b = (h - h_b)/(h - h_c)$ , where  $h$  is the height of the tree,  $h_b$  the height of the branch and  $h_c$  the height of the crown bottom. As in the case of stemwood, the mass of branch components was converted to an areal basis by regression.

218 The needle mass of all the sample trees was esti-  
 219 mated on the basis of the sample branches. The  
 220 parameters of the regression models were estimated  
 221 for the dry mass of the two youngest needle age classes  
 222 of the branch. The dry masses of the older needle age  
 223 classes were calculated in the youngest stand  
 224 from their survival rates determined by counting the  
 225 number of green and brown needles on one shoot on  
 226 12 trees weekly during July and September in 1984  
 227 (Katainen and Valtonen, 1985). The needle biomass of  
 228 individual trees was estimated on the basis of needle  
 229 biomass on sample branches and measurements of  
 230 branch diameter. These models were of the form  
 231  $\ln(B_n) = \text{constant} + b \ln(d_b) + cy_b + fy_b^2$ , where  $B_n$   
 232 is the dry mass (g) of the needle age class of the  
 233 branch,  $d_b$  the diameter (cm) of the branch and  $y_b$  the  
 234 relative value of the sum of square of branch diameter,  
 235 when summing starts from the uppermost living  
 236 branch.

237 The needle biomass for the whole stand was then  
 238 estimated using the needle biomass of sample trees,  
 239 their diameter at breast height and the measured  
 240 diameter at breast height for all trees in the stand.

241 Nitrogen used in annual biomass production was  
 242 calculated as the product of the new biomass produc-  
 243 tion and the biomass weighted nitrogen concentra-  
 244 tions. Sampling for measuring nutrient concentrations  
 245 is described in detail in Helmisaari (1992b). All plant  
 246 and soil samples were dried at 70°C for 48 h, then  
 247 weighed and sieved. Nitrogen was determined using  
 248 the Kjeldahl method.

249 The annual stemwood production in the stand was  
 250 estimated as the difference in the stemwood biomass  
 251 of successive years (1983–1987). The annual produc-  
 252 tion of sample branches was estimated from the  
 253 measurements of the branch diameter growth and  
 254 the biomass of annual shoots. Annual bark production  
 255 was estimated from the stemwood production assum-  
 256 ing that stembark grows in proportion to stem wood  
 257 growth. The youngest age class biomass was consid-  
 258 ered to be the same as the annual needle production.  
 259 Cone production was determined by measuring the  
 260 biomass of recently matured cones. In the 1st year of  
 261 growth, Scots pine cones grow to about 7% of their  
 262 final dry mass (Cousens, 1988). In the following  
 263 growing season cones mature by August–September.  
 264 The measurements of tree dimensions, and the esti-  
 265 mation of biomass production of tree components are

also described in Helmisaari (1992b) and Helmisaari 266  
 and Siltala (1989). 267

### 2.2.2. Below-ground 268

269 The coarse-root samples for biomass and nutrient  
 270 determinations and the fine-root samples for nutrient  
 271 determinations (Helmisaari, 1991) were taken from  
 272 the same trees used for sampling stem and branches.  
 273 The stump was divided into four sectors according to  
 274 exposure, one of which was randomly selected for root  
 275 sampling. The root collar diameters were measured on  
 276 all roots. All lateral roots (depth < 30 cm from soil  
 277 surface) were excavated in one randomly chosen  
 278 sector, beginning at the stump and following the roots  
 279 up to a thickness of 2 mm. The excavated roots were  
 280 divided into the following diameter classes: <2, 2–10,  
 281 10–50 and >50 mm. Roots in the >2 mm diameter  
 282 classes (coarse-roots) were then sectioned into the  
 283 following components, outer bark (dead), inner bark  
 284 (living, phloem and recently produced root wood) and  
 285 woody matter (xylem). For a detailed description of  
 286 this sampling, see Helmisaari (1991, 1992b).

287 The coarse-root biomass in a stand was calculated  
 288 using regression equations developed from the sample  
 289 trees. The root biomass of an individual tree was  
 290 estimated by calculating the biomasses of all roots  
 291 by using regressions between the biomasses of sample  
 292 roots and their root collar diameters. The coarse-root  
 293 biomass in a stand was then calculated by using the  
 294 tree diameters at breast height and the sample tree root  
 295 biomasses. Annual coarse-root production was esti-  
 296 mated using the measured percentage of the inner bark  
 297 (including new recently produced root wood, the latest  
 298 annual ring) of the measured coarse-root biomass  
 299 (Helmisaari, 1992b).

300 The fine-root samples for biomass determinations  
 301 were means of 10 samplings during 1985–1988. From  
 302 each stand, 20 soil cores to the depth of 30 cm mineral  
 303 soil were taken with a cylindrical soil corer (diameter  
 304 36 mm), and samples divided for humus, 0–10 cm  
 305 mineral soil, and 10–30 cm mineral soil (Makkonen  
 306 and Helmisaari, 2001). Roots were separated from soil  
 307 by careful wet sieving and sorted into Scots pine living  
 308 roots, other living roots, and dead roots. Roots were  
 309 divided into the following diameter classes, <2, 2–5,  
 310 5–10 and >10 mm. Roots <2 mm were regarded as  
 311 fine-roots (Persson, 1983; Vogt et al., 1983), and they  
 312 included mycorrhizal short root tips. The biomass

313 production of fine-roots was calculated by balancing  
 314 all living and dead root biomass compartments at  
 315 various samplings (Makkonen and Helmisaari, 1999)  
 316 according to the decision matrix presented by Santan-  
 317 tonio (1980); McClaugherty et al. (1982) and Fairley  
 318 and Alexander (1985). For a detailed description of the  
 319 fine-root sampling, sorting and sources of error, see  
 320 Makkonen and Helmisaari (1998, 1999, 2001).

321 The nitrogen use estimates were based on the  
 322 biomass production and the mean nitrogen concentra-  
 323 tions in the root inner bark (Helmisaari, 1991) in a  
 324 stand weighted with their biomasses.

### 325 3. Results

#### 326 3.1. Biomass

327 The biomass of needles and all woody components,  
 328 including coarse-roots, increased with stand age  
 329 (Table 2). The biomass of coarse-roots increased  
 330 the most after stemwood. The mean fine-root biomass  
 331 was greatest at canopy closure in the pole stage stand,  
 332 but there was no general trend in the fine-root biomass  
 333 between stands on individual samplings (Makkonen  
 334 and Helmisaari, 2001).

335 The relative share of stemwood of the total stand  
 336 biomass increased with stand age, while that of the  
 337 branches and fine-roots decreased (Table 2). Branches  
 338 were the greatest biomass component in the sapling  
 339 stand, but in the pole stage and mature stands the  
 340 biomasses of stem and supporting coarse-roots were  
 341 the greatest. The share of the needle biomass of the  
 342 total stand biomass was at the same level in the two  
 343 youngest stands, and clearly smaller in the oldest stand  
 344 (Fig. 1).

345 The ratio of below-ground/above-ground biomass  
 346 decreased with stand age, and the ratio of fine-root/  
 347 needle biomass decreased, respectively (Table 2). In  
 348 the sapling stand, the fine-root biomass was greater  
 349 than the needle biomass. The ratio of coarse-root  
 350 biomass/above-ground biomass did not have a clear  
 351 trend in relation to stand age.

#### 352 3.2. Biomass production and nitrogen use

353 The annual biomass production of needles, coarse-  
 354 roots and fine-roots increased with stand age, while

355 that of stemwood and bark was greatest in the pole  
 356 stage stand, and branches in the sapling stand  
 357 (Table 2). The relative share of stemwood, stembark  
 358 and branch biomass production of the total stand  
 359 production decreased with stand age while that of  
 360 coarse and fine-roots increased (Fig. 1). Needle pro-  
 361 duction was relatively greatest in the fast growing  
 362 sapling stand.

363 The annual above-ground production accounted for  
 364 31–54% of the total stand biomass production (Table 2,  
 365 Fig. 1). Stemwood accounted for 15–23% of the total  
 366 stand production, needles for 12–15% and coarse-  
 367 roots for 3–8%. The fine-root annual biomass produc-  
 368 tion was between 43 and 60% of the total stand  
 369 biomass production.

370 There was no clear relation between the fine-root  
 371 biomass production and the fine-root biomass  
 372 (Table 2). Because of the increase in the fine-root  
 373 production with stand age, the ratio of fine-root bio-  
 374 mass production/fine-root biomass also increased.  
 375 Thus, fine-root turnover (annual biomass production  
 376 per unit of biomass) was fastest in the two oldest  
 377 stands.

378 Fine-roots and needles alone used 79–91% of all  
 379 nitrogen annually used for biomass production  
 380 (Table 2). Fine-roots annually used 0.9–4.6 g N/m<sup>2</sup>  
 381 for biomass production. This accounted for 45–63%  
 382 of the nitrogen used annually in total stand biomass  
 383 production. Above-ground production (including  
 384 coarse-roots) used 1.0–2.3 g N/m<sup>2</sup>. Growth of the  
 385 current needles accounted for 27–34%, and growth  
 386 of the woody components 9–21% (stemwood 2–3%)  
 387 of the nitrogen used annually in biomass production.

### 4. Discussion 388

#### 4.1. Biomass 389

390 The total biomass of the stands was comparable to  
 391 those in similar conditions (e.g. Mälkönen, 1974;  
 392 Albrektson, 1980). Our fine-root biomass results were  
 393 also in the same range as those reported for Scots pine  
 394 by Vanninen and Mäkelä (1999), for red and white  
 395 pine by Nadelhoffer et al. (1985), and for red pine by  
 396 McClaugherty et al. (1982). In the study by Vanninen  
 397 and Mäkelä (1999), fine-root biomass varied between  
 398 118 and 412 g/m<sup>2</sup> in 23–178 years old Scots pine

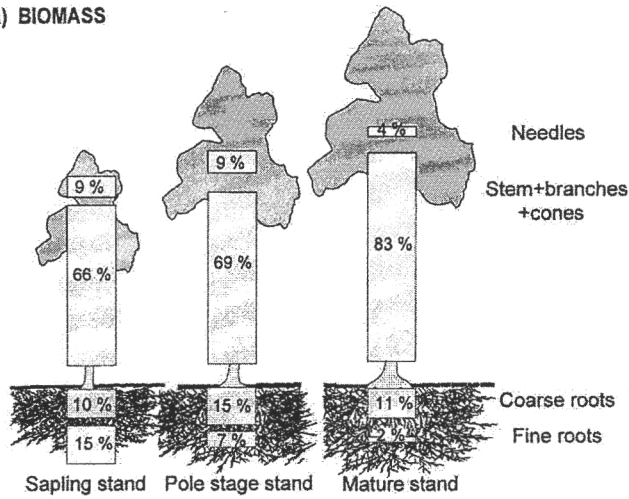
Table 2  
Biomass and biomass production in (a) sapling, (b) pole stage and (c) mature Scot pine stands at Mekrijärvi<sup>a</sup>

Component	Biomass (g/m <sup>2</sup> )	S.D.	Biomass (% of stand total)	Annual biomass production (g/m <sup>2</sup> )	S.D.	Production (% of stand total)	N use for annual biomass production (g/m <sup>2</sup> )	N use (% of stand total)
<b>(a) Sapling stand</b>								
Stemwood	378	129	25.3	89.0	26.9	23.3	0.063	3.3
Living stembark	45	17	3.0	11.5	2.9	3.0	0.054	2.8
Dead stembark	56	9	3.8					
Living branches	427	65	28.6	42.2	7.3	11.0	0.226	11.7
Dead branches	72	18	4.8					
Needles	131	49	8.8	57.9	20.7	15.2	0.647	33.6
Cones	6	5	0.4	5.5	5.0	1.4	0.018	0.9
Above-ground total	1115		74.7	206.1		53.9	1.008	52.3
Coarse-roots	159	65	10.6	11.1	3.9	2.9	0.044	2.3
Fine-roots	220	51	14.7	165.0		43.2	0.875	45.4
Below-ground total	379		25.3	176.1		46.1	0.919	47.7
Stand total	1494		100.0	382.2		100.0	1.927	100.0
<b>(b) Pole stage stand</b>								
Stemwood	2532	434	47.4	271.0	59.7	20.5	0.214	3.2
Living stembark	225	20	4.2	11.9	2.2	0.9	0.059	0.9
Dead stembark	116	10	2.2					
Living branches	744	75	13.9	40.8	22.1	3.1	0.240	3.6
Dead branches	126	26	2.4					
Needles	462	32	8.6	160.0	9.0	12.1	1.776	26.6
Cones	18	17	0.3	18.3	16.5	1.4	0.079	1.2
Above-ground total	4223		79.0	502.0		38.0	2.367	35.5
Coarse-roots	767	90	14.3	45.1	5.1	3.4	0.195	2.9
Fine-roots	357	42	6.7	775.0		58.6	4.108	61.6
Below-ground total	1124		21.0	820.1		62.0	4.303	64.5
Stand total	5347		100.0	1322.1		100.0	6.670	100.0
<b>(c) Mature stand</b>								
Stemwood	9491	347	67.9	216.3	30.7	15.1	0.131	1.8
Living stembark	391	5	2.8	4.0	1.3	0.3	0.014	0.2
Dead stembark	210	2	1.5					
Living branches	1287	15	9.2	<sup>b</sup>			0.000	0.0
Dead branches	122	5	0.9					
Needles	583	8	4.2	192.4	4.4	13.4	2.008	27.9
Cones	41	33	0.3	40.7	33.5	2.8	0.137	1.9
Above-ground total	12125		86.8	453.4		31.6	2.290	31.8
Coarse-roots	1586	16	11.3	120.8	1.2	8.4	0.355	4.9
Fine-roots	259	54	1.9	860.0		60.0	4.558	63.3
Below-ground total	1845		13.2	980.8		68.4	4.913	68.2
Stand total	13970		100.0	1434.2		100.0	7.203	100.0

<sup>a</sup> Dead remaining components (branches and bark) are included in the table.

<sup>b</sup> Net branch production was negative in the mature stand. Above-ground biomass and biomass production are mean values of the years 1983–1987 (Helmisaari, 1992a,b). Fine-root biomass and production are mean values of the years 1985–1988 (Makkonen and Helmisaari, 2001), S.D. is standard deviation of the mean.

a) BIOMASS



b) BIOMASS PRODUCTION

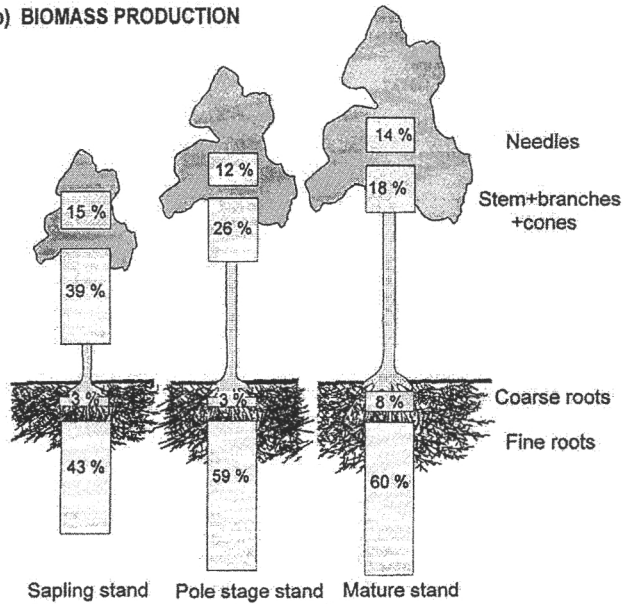


Fig. 1. (a) Biomass and (b) biomass production in three Scots pine stands in eastern Finland. For explanations, see Table 2.

399 stands. Our 15-year-old stand had a fine-root biomass  
 400 of 218 g/m<sup>2</sup>, which is also comparable to the fine-root  
 401 biomass range of 130–330 g/m<sup>2</sup> reported by Oleksyn  
 402 et al. (1999) for 19 studied populations of 12-year-old  
 403 Scots pine trees growing on a provenance experiment.

The distribution of biomass in the 15-year-old Scots pine stand was also comparable to that presented by Oleksyn et al. (1999).

The mean fine-root biomass was highest in the pole stage stand that had just reached canopy closure, but

the differences between stands could not be statistically tested. Also Vogt et al. (1983, 1985) reported that fine-root biomass in Douglas-fir stands peaked at canopy closure. Vanninen and Mäkelä (1999) reported that in Scots pine stands the amount of fine-roots was not correlated with stand age on a poor CT (*Calluna* type) site, whereas on a more fertile MT (*Myrtillus* type) site there was no relationship or the fine-root biomass decreased with stand age.

In our stands, the ratios of below-ground/above-ground biomass and fine-root/needle biomass decreased with stand age. Also Ovington (1957) showed by using chronosequence data from Scots pine plantations that the root/shoot ratio declined from age 7 to 55, at which age the ratio was 0.29, which is comparable to 0.27 at age 35 in our study. Vanninen et al. (1996) reported that the fine-root/needle biomass ratio of individual Scots pine trees increased with tree age, but Vanninen and Mäkelä (1999) also reported that based on stand level data, the same ratio was independent of stand age in Scots pine stands on the poor CT site.

#### 4.2. Biomass production and nitrogen use

Even though the proportion of fine-roots out of the total tree biomass was not large, their growth accounted for a major part of the stand biomass production for the studied Scots pine stands growing on a nutrient-poor VT site. Fine-roots also used most of the nitrogen bound by annual biomass production. In the two oldest stands, fine-roots produced more biomass than all aboveground components.

It has been found in many other studies, too, that trees allocate a great proportion of photosynthate carbon to fine-roots and mycorrhiza as means of obtaining nutrients required for growth (e.g. Vogt et al., 1983). The carbon budget of a 14-year-old Scots pine stand in Sweden showed that about 60% of the total net primary production was invested in the growth and maintenance of the root system (Ågren et al., 1980). Santantonio and Hermann (1985) reported that even 80% of available assimilates may be allocated to fine-roots. McLaugherty et al. (1982) reported that a 53-year-old red pine plantation had fine-root production of 1090 g/m<sup>2</sup>, which is comparable to our estimates from the older stands. In the study by Keyes and Grier (1981) the total root produc-

tion (including coarse-roots) was 53% of total in a 40-year-old Douglas-fir stand, which is close to the 62% in our 35-year-old Scots pine stand. Reviews by Vogt (1991) and Gower et al. (1995) reported that 7–76% of total net primary production by temperate forests is allocated to fine-roots.

Our fine-root production values in the sapling stand were at the same level as reported by Persson (1983) for a 20-year-old Scots pine stand (183 g/m<sup>2</sup> per year). However, our estimates from the pole stage and mature stands were higher than those reported by Persson (1983) for a 120-year-old stand (159 g/m<sup>2</sup> per year).

Fine-root annual biomass production and nitrogen use for biomass production increased with stand age both absolutely and relatively. The fine-root turnover (the annual fine-root biomass production, g/m<sup>2</sup> per year, per mean fine-root biomass, g/m<sup>2</sup>) was fastest in the oldest stands. These results contradict those of Persson (1983), who showed that the ratios of fine-root production to average fine-root standing crop were 2.0 in a 20-year-old *Pinus sylvestris* stand, and 0.7 in a 120-year-old stand.

Fine-root production is difficult to measure, and the production estimates relate to the methods used (Nadelhoffer et al., 1985; Nadelhoffer and Raich, 1992; Neill, 1992; Publicover and Vogt, 1993; Makkonen and Helmisaari, 1999). Most authors agree that the calculations based on soil cores may underestimate production (e.g. Kurz and Kimmins, 1987; Hendrick and Pregitzer, 1992). Because significant differences between individual sampling occasions (Fairley and Alexander, 1985; Vogt et al., 1985) could not be used in our study, the fine-root production could have been overestimated by a maximum of 30–35% (Makkonen and Helmisaari, 2001).

However, also other methods for estimating fine-root production have their sources of error. Therefore, it is advisable to use several different methods for estimating fine-root production. Makkonen and Helmisaari (1999) compared soil cores and in-growth cores in estimating fine-root production in the pole stage stand of this study, and concluded that during the 3rd year after installing the in-growth cores, the fine-root production of Scots pine was similar by using both methods.

Many authors conclude that variation in fine-root growth is largely determined by changes in environ-

503 mental conditions (e.g. soil moisture, temperature and  
504 nutrients) (e.g. Lyr and Hoffman, 1967; Chapin, 1980;  
505 Tryon and Chapin, 1983). Our stands were situated on  
506 similar site and soil types, but soil moisture may have  
507 been higher in the pole stage and mature stands than in  
508 the sapling stand (Makkonen and Helmisaari, 2001).  
509 The humus layer was thicker and the groundwater  
510 layer less deep in the two oldest stands than in the  
511 sapling stand. This may also have affected the fine-  
512 root production values in individual stands.

513 Even if the fine-root biomasses in the sapling and  
514 mature stands were at the same level, fine-root bio-  
515 mass production was much greater in the mature stand.  
516 Even if the data are only from three stands, it appears  
517 that the above-ground production and nitrogen use  
518 were related to the fine-root production. However, no  
519 regressions could be shown because the study was  
520 done in three stands only. In a study by Helmisaari and  
521 Hallbäck (1999), the fine-root growth was posi-  
522 tively correlated with the stem volume growth in  
523 Norway spruce stands on nutrient-poor soils in north-  
524 ern Finland. According to Nadelhoffer and Raich  
525 (1992) in a large data set, there was no overall pattern  
526 between fine-root production and above-ground pro-  
527 duction. However, independent analyses of forest C  
528 and N budgets indicated that below-ground production  
529 increased with above-ground production and sug-  
530 gested that these two components of net primary  
531 production are linked and are limited by the same  
532 factors (Nadelhoffer and Raich, 1992).

533 This study showed that even though the proportions  
534 of fine-roots of the total tree biomass were not large in  
535 Scots pine stands growing on a poor site type, their  
536 growth accounted for a major part of stand biomass  
537 production, especially in the two older stands. Thus,  
538 fine-roots are a strong sink of carbohydrates, and their  
539 death and decomposition transfer large amounts of  
540 carbon into soil. Fine-root growth, death and decom-  
541 position represent major pathways of carbon and  
542 nitrogen in boreal forests, and should be considered  
543 in all stand level studies dealing with carbon and  
544 nutrient dynamics in forest ecosystems.

#### 545 ~~Uncited references~~

546 Marklund (1988), Pregitzer et al. (1990), Ryan et al.  
547 (1996).

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