Technical Report

TR-07-11

Growth dynamics of fine roots in a coniferous fern forest site close to Forsmark in the central part of Sweden

Hans Persson, Ingela Stadenberg
SLU, Department of Ecology and Environmental Research

December 2007

Svensk Kärnbränslehantering AB
Swedish Nuclear Fuel
and Waste Management Co
Box 250, SE-101 24 Stockholm
Tel +46 8 459 84 00

Growth dynamics of fine roots in a coniferous fern forest site close to Forsmark in the central part of Sweden

Hans Persson, Ingela Stadenberg
SLU, Department of Ecology and Environmental Research

December 2007

Keywords: Field layer, Fine roots, Fine-root growth, Live/dead ratio, Root distribution, Sequential core method, Soil horizons.

Summary

The seasonal growth dynamics of live and dead roots for trees and the field layer species (g m^{-2}, varying diameter fractions) and live/dead ratios were analysed at a fresh/moist coniferous fern forest site close to the nuclear power plant at Forsmark in the central eastern parts of Sweden. The changes in depth distribution of fine roots were observed at depth intervals of the top humus horizon down to 40 cm in the mineral soil profile.

The bulk of living fine roots of trees (< 1 mm in diameter) were found in the mineral soil horizon the total profile down to 40 cm of the mineral soil, where 89, 82, 83 and 89% of the total amount in the whole profile were found. The upper 2.5 cm part of the humus layer contained 83, 81, 100 and 100% of all roots of the humus layer on the four different sampling occasions. High amounts of living fine roots were found in the upper 10 cm of the mineral soil horizon *viz.* 84, 76, 91 and 69% of the total mineral soil layer. Consequently, both the top soil horizons of the humus and the mineral soil layers were heavily penetrated by living fine roots.

The highest proportion of living fine roots was found in the top 2.5 cm of the humus layer. Accordingly, the live/dead ratio of fine roots (< 1 mm in diameter) decreased from the top of the humus layer to the lower part of mineral soil horizon from 8.0–0.3, 0.8–0.2, 4.4–0.4 and 3.3–0.7 (g g^{-1}) for the four sampling occasions, respectively. We concluded that the decrease in the live/dead ratio was related to decreased vitality with depth of the fine roots in the soil profile. The highest live/dead ratio was found in the upper 2.5 cm of the humus layer for both the tree and field-layer species. This distribution pattern was most evident for tree fine roots < 1 mm in diameter.

The mean fine-root biomass (live tissue < 1 mm in diameter) of tree species for the total profile varied on the four sampling occasions between 317, 113, 139 and 248 g m^{-2}. The related fine-root necromass (dead tissue) varied between 226, 321, 176 and 299 g m^{-2}. The total quantity of fine roots (live + dead) amounted to 543, 434, 314 och 546 g m^{-2}. Considerable quantities of fine roots (< 1 mm in diameter) were attributed to field-layer species (about 18% of the total biomass during the whole period of investigation). The turnover rate (the rate of construction of new roots) for tree fine roots < 1 mm in diameter amounted to at least the size of the average fine-root biomass.

Our methods of estimating fine-root production and mortality, involved periodic measurements of live and dead dry weight of the fine roots from sequential core samples of the forest soil. The collected data give a proper and instant measure of the spatial and temporal distribution of fine roots in the undisturbed soil-profile. Data from other fine-root investigations suggest turnover rates in agreement with our present findings. Differences between root growth and turnover should be expected between trees of different age, tree species and different forest sites, but also between different years. Substantial variations in fine-root biomass, necromass and live/dead ratios are found in different forest sites.

Correct methods for estimating the amount of live and dead fine-roots in the soil at regular time intervals are essential for any calculation of fine-root turnover. Definition of root vitality differs in literature, making it difficult to compare results from different root investigators. Our investigation clarifies the importance of using distinct morphological criteria when sorting fine roots into live and dead tissues. Our data suggest that the often-reported discrepancy in the data of fine roots in literature most frequently is due to lack of precision in the detection the vitality of the excavated root-fragments. The live/death ratio of the fine roots in this context is reflecting the vitality of the fine roots, both temporarily and spatially in the soil profile. The live/dead ratio seems to be a most powerful vitality criterion of the fine roots.

Sammanfattning

Tillväxtdynamiken hos levande och döda finrötter (g m^{-2}; torrvikt 65° C; vid skilda diameterfraktioner), kvoten levande/döda finrötter (g g^{-1}) studerades vid fyra skilda provtagningar under en tillväxtperiod för träd och fältskiktsarter i ett barrskogsbestånd av ormbunkstyp nära Forsmark. Finrötternas fördelning på djupet bestämdes i segment från det övre humusskiktet till 40 cm ned i mineraljorden.

Den största andelen levande finrötter (< 1 mm i diameter) av träd återfanns i mineraljordskiktet, dvs 89, 82, 83 och 89 % vid provtagningarna. Det övre 2.5 cm av humusskiktet innehöll 83, 81, 100 och 100 % av den levande mängden finrötter i humusskiktet vid de fyra provtagningarna. En stor andel levande finrötter återfanns även i det övre 10 cm mineraljordsskiktet – 84, 76, 91 och 69 % av den totala mängden i detta skikt. Humus och mineraljordskikt är således i sina övre skikt är väl genomvävda av levande finrötter.

Kvoten levande/döda finrötter (< 1 mm i diameter) minskade från det övre 2.5 cm humusskiktet till det lägsta mineraljordsskiktet med 8.0–0.3, 0.8–0.2, 4.4–0.4 och 3.3–0.7 (g g^{-1}) vid dessa fyra provtagningstillfällen. En stor andel av de levande finrötterna i det övre 2.5 cm humusskiktet bestod förutom trädrötter av rötter från fältskiktsarter. Vi tolkade nedgången i levande/döda kvoten hos finrötter med djupet i markprofilen som en indikation på en avtagande vitalitet.

Trädens levande mängd finrötter (biomassa, < 1 mm i diameter) i hela markprofilen uppgick till 317, 113, 139 och 248 g m^{-2} för de fyra provtagningar. Den motsvarande vikten vid provtagningarna för döda finrötter (nekromassa) var 226, 321, 176 och 299 g m^{-2}. Totalt uppgick mängden levande + döda finrötter vid provtagningarna till 543, 434, 314 och 546 g m^{-2}. En stor mängd finrötter kunde härledas till fältskiktsarterna i hela markprofilen (ca 18 % under undersökningsperioden).

Våra undersökningar omfattade mätningar av mängden levande och döda finrötter i markproppar under en hel tillväxtperiod. Våra resultat ger en direkt av provtagningsmetodiken opåverkad bild av den rumsliga och tidsmässiga fördelningen av finrötterna i marken. Den levande/död kvoten definierar därför vitaliteten hos finrötterna, både rumsligt och tidsmässigt. De processer som inverkar på levande/död kvoten hos finrötterna är tillväxt, avdöende och nedbrytning.

Våra undersökningar understryker betydelsen av att använda väldefinierade morfologiska kriterier vid sortering och kvantifiering av finrotmängder. Kraftiga differenser i finrotbiomassa, nekromassa och levande/dödkvot uppträder mellan skilda skogsbestånd beroende på beståndsbeskaffenhet. Omsättningen av finrötter hos träd (< 1 mm i diameter) beräknades till minst storleken av finrotbiomassan. Resultat från andra undersökningar med avseende på mängd, omsättning och fördelning i marken av finrötter anger även omsättning i denna storleksordning.

Skillnader mellan rottillväxt och omsättning kan förväntas mellan träd av olika ålder, trädart, beståndstäthet men också mellan skilda år. Stora skillnader finns mellan olika trädbestånd beträffande variationer i mängd finrotbiomassa, nekromassa och levande/död kvot.

Bra metoder för att bestämma mängden levande och döda finrötter i markprofilen vid upprepade tillfällen under tillväxtperioden är väsentliga före att beräkna omsättningen av finrötter. Osäkerheten i beträffande biomassafördelning ovan och under mark i många skogsekosystemstudier har varit stor på grund av brister vid bestämning av vitaliteten hos de sorterade rotfragmenten. Vid rotundersökningar inkluderas ofta i rotbiomassan en okänd andel döda rotfragment (nekromassa). Levande/död kvoten tycks vara ett kraftfullt vitalitetskriterium för finrötter, som ger information om var i markprofilen rötterna växer samt när under tillväxtperioden.

Contents

1	**Introduction**	7
2	**Material and methods**	9
3	**Results**	13
4	**Discussion**	23
5	**References**	29

1 Introduction

A forest tree consists basically of an aboveground assimilating part, which captures energy and carbon, and a belowground part that captures water and mineral nutrients. Trees have usually evolved in mixed ecosystems, in which survival in a competitive and varying environment is essential and not necessary high productivity. Roots comprise a substantial and varying proportion of the total dry weight in forest ecosystems /Persson 2002/. Generally, tree roots account for 15–30% of the total tree biomass.

Data for structural coniferous and deciduous root systems under different environmental conditions show a remarkable consistent relationship between root system dry weight of structural roots and diameter at breast height /Santantonio et al. 1977/. The amount of energy partitioned to the roots depends on the relative demands of the roots and the aboveground parts. Many woody roots remain alive as long as the trees stay alive; in temperate regions up to > 100 years. Tree fine roots form an integrated spatially and temporarily variable network in the forest soil, decreasing in density from the soil surface downwards /Jackson et al. 1996/.

To function efficiently, root systems must be extensive and active enough to meet the need of aboveground plant parts of water and mineral nutrients. Fine roots are opportunistic and exploitive in their growth habits, adapting rapidly to climatic variation and to changes in mineral nutrient and water supply. Therefore a substantial variation in fine-root biomass (live), necromass (dead) and the live/dead ratios normally should be expected during the growth period /Persson 1980, 1983/. Production of new roots represents a great carbon expenditure of in the plant system and appears to be a significant phenomenon in a variety of ecosystems. The high turnover of fine roots is usually explained as an “adaptive strategy” /Persson 2000/.

Increasing fine-root biomass and decreasing live/dead ratios with age is to a great extent overshadowed by site factors favouring growth such as increased water and mineral nutrient availability. A reverse relationship is often observed between the amount of fine roots and nutrient availability /Persson 2000/. Fine-root characteristics such as the amount of fine roots in terms of dry weight in different soil horizons, rooting density and the live/dead ratios seem to be depending on a variety of abiotic and biotic factors specific for different forest stands /Persson 2000/.

The highest live/dead ratio is usually detected in the uppermost humus layer /cf. Persson et al. 1995, Persson and Ahlström 2002, Puhe et al. 1986/. There is a substantial flow of root litter to the forest soil from dead fine roots during the growth period. Root litter is normally decomposed quite fast. The rate of decomposition is influenced by soil temperature and soil water conditions /Santantonio and Hermann 1985/.

Tree roots can be separated by size into different categories: coarse supportive roots with low turnover rates, small diameter roots with low turnover rates that act as conduits for water and mineral nutrients and very fine /mycorrhizal roots; < 1 mm in diameter), with high degree of soil penetration and high turnover rates /Vogt and Persson 1991/. Tree roots perform many significant functions. High fluctuation rates in fine-root biomass and necromass are found in a great variety of European forest ecosystems /cf. e.g. Persson 1978, Helmisaari and Helmisaari 1992, Helmisaari and Hallbäcken 1999, Bakker et al. 2000, Persson and Ahlström 2002, Helmisaari et al. 2002, Stober et al. 2000, Helmisaari et al. 2007/.

On a global scale, a substantial fraction of the atmosphere CO_2 originates from dead decomposing root tissues /Norby and Jackson 2000/. At the ecosystem level, the input of root litter is an important contributor to the ecosystem processes (e.g. nutrient cycling). Together with litter from aboveground parts of the tree, the decaying root material forms the bases for the complex biological cycles in the soil that includes bacteria, fungi and soil animals.

The distribution of fine roots in various soil horizons, are essential for mineral nutrient uptake, biomass production and plant health /Marschner 2002/. Since the most efficient fine roots are superficially distributed, they are easily influenced by different kinds of environmental stress, e.g. frost and drought /Raitio 1990/. Research into root senescence is complicated by the fact that cessation of root penetration is not synonymous with root death. Substantial changes in the amount of fine roots, occurring at intervals during the period of study, suggest that climatic alterations may be one underlying source of variation /Persson and Ahlström 2002/.

Root damage may be visualised by a decreased live/dead ratio of the fine roots /Persson and Ahlström 2002/. Few studies have so far examined patterns in live/dead ratios of fine roots in relation to soil water and mineral nutrient availability /cf. Persson 2000, 2002, Santantonio and Hermann 1985/. With regards to the sustainability of the forest ecosystems, decreased levels of cations and increased levels of nitrogen have increased the risk of damage symptoms /Daldoum and Ranger 1994, Persson et al. 1995/.

The aims of our project which was carried out in a fresh/moist coniferous fern forest site forest types at Forsmark on the four sampling occasions were to:

– to describe the changes during the growth period in the amount of live and dead fine-roots (biomass and necromass) of tree species and field-layer species in different diameter fractions.

- To evaluate the seasonal variation of the depth distributions of fine roots.
- To estimate the turnover rate.
- To evaluate of live/dead ratios as a vitality criterion of fine roots.
- To compare the obtained results with results from other studies in similar environments.

Roots are separated into tree species (mainly *Picea abies* and *Betula verrucosa*), dwarf shrubs and the field layer. The turnover is intended to be described in terms of living (biomass) and living + dead (necromass) dry weight within the soil profile.

The investigation is part of the activities performed within the site investigations at Forsmark and this report is the second report describing roots at the site. The earlier report /Persson and Stadenberg 2007/ described root biomass at six localities in Forsmark and Laxemar investigation areas. The locality investigated in this report was also a part of the earlier study.

2 Material and methods

The field studies were carried out within a forest site close to the village of Forsmark in the central eastern parts of Sweden and about 10 km from the Forsmark nuclear power plant. The site was of a coniferous fern type /Nordiska Ministerrådet 1978/ and the soil type was a Regisol/ Gleysol (Table 2-2). The average thickness of the humus layer was 5.2 cm. The soil pH (H_2O) was varying between 6.7–7.9, the raw-humus layer was fairly extensively developed /Lundin et al. 2004, 2005/. The mean tree height was 19.8 m and the tree density (number of trees/ha) was 780 (Table 2-2). See Tables 2-1 and 2-2 for detail information of the site and the map in Figure 2-1 for the location of the site.

The sequential core method /Vogt and Persson 1991/ was used to describe root distribution with depth/LFH-horizon and the mineral soil as deep as possible) of both living (biomass) and dead (necromass) fine roots in terms of dry weight. The depth distribution of tree species and dwarf shrubs were described, using the depth intervals 0–2.5, 2.5–5, 5–10 cm of the top LFH horizon and in 10 cm segments for the mineral soil profile down to 40 cm.

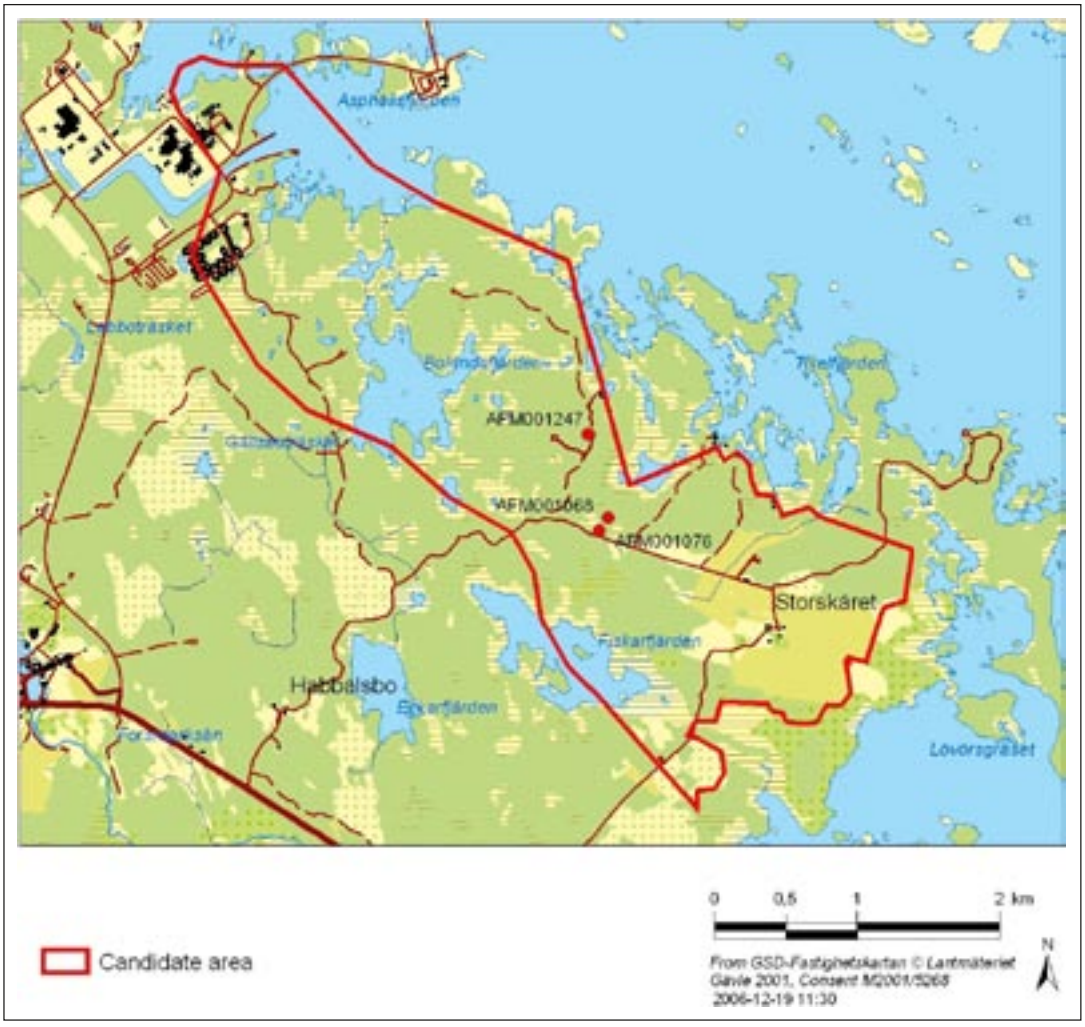

Figure 2-1. *Map of the Forsmark region with the investigated sites indicated. The investigated site is marked by FM001068. The other sites marked on the map (AFM001247 and AFM001076), besides the present one, were used for a comparison between the root distribution at Forsmark and three sites at Laxemar /cf. Persson and Stadenberg 2007/.*

Table 2-1. A general site characteristic of the investigated forest stand at Forsmark /Johansson and Öhman 2008/.

Characteristics	
Latitude, longitude	E 60° 22’ N, 18° 11’ W
Mean annual temp. 2004–2006	+6,9°C
Min–max daily temp	–14 – +25°C
Mean precipitation (mm)	537
Vegetation period	May–September
Vegetation period (No of days > 5°C)	210

Table 2-2. Site characteristics of the investigated forest stand (FG1, AFM001068) at Forsmark.

Variables	
Soil moisture class (Ståndortskart.)	Fresh/moist
Soil pH (H_2O) H 0–30	6.7
Soil pH (H_2O) M 0–10	7.2
Soil pH (H_2O) M 10–20	7.4
Soil pH (H_2O) M 55–65	7.9
Lundin’s id.	FG1
Soil type	Regosol/Gleysol
Stone/boulder, volumetric content in M 0–30 (%)	43
Topographic wetness index (TWI)	9.3
Number of trees /ha	780
Basal area (m^2/ha)	20.5 (*Picea abies*) 6.5 (*Betula verrucosa*)
Tree age	80–88
Tree height (m)	19.8
Dominant height at 100 years /Hägglund 1973/	G 20
Diameter at breast height (dbh in cm)	0.26
Above field-layer biomass (g m^{-2})	24
Veg. types /Nordiska Ministerrådet 1978/	Coniferous fern-type
Field-layer species	*Maianthemum bifolium, Anemone nemorosa, Hepatica nobilis, Listera ovata, Rubus saxatilis*
Ground-layer species	*Hylocomium splendes, Ptilium crista-castrensis*

The soil sampling was carried out during 2004 in the mid of October and during 2005 in the mid of April, in the beginning of August and in the end of October. A steel corer, with an inner diameter of 4.5 cm, was used for the soil sampling. In total 32 soil cores were taken from the four corners of a quadrate covering 200 m^2, 8 in each corner (north, east, south and west). Each soil sample was taken as deep as possible, *viz.* to a depth where stones and larger blocks prevented further penetration by the soil corer. Sampling was avoided at a distance of less than 0.5 m from the holes from the earlier soil cores.

The specific spot, within which the soil corer was taken, was chosen with the help of a sharp iron stick driven down into the soil profile. The aim of this procedure was to make sure that at least 10 cm of the soil profile was included in the soil samples from the mineral soil.

While sampling in a stony soil an increased concentration of roots along the surface area of the stones should be expected. These roots are extremely difficult to include by the soil corer in the soil samples. On the other hand, the method of deliberately sampling spots where at least 10 cm of the mineral soil is included and then extrapolated to a square metre suggest that the estimate of fine-root dry weight to some extent will be overestimated in the mineral soil. How this would affect the distribution pattern of roots in the soil areas between the stones is not known. Therefore any correction of the distribution pattern of the fine roots for the total soil profile was not carried out.

The soil corer was driven into the mineral soil as deep as possible, at those depths only limited live root fragments were sampled (with a low live/dead ratio). Thus, the live (biomass) and dead (necromass) fine roots were not underestimated in the deeper horizons, since only small root fragments were found in those horizons**.**

The thickness of humus horizon was measured in each soil core. The uppermost 0–2.5 cm layer consisted of humus in all sites. The thickness of humus layer was rather variable within the 6 different sites. The soil samples were transferred into plastic bags and transported as soon as possible to our laboratory and stored in a cold-storage at –4°C (a temperature that did not damage the live tissue and caused no change in ion concentrations; /cf. Clemensson-Lindell and Persson 1992/ until the final sorting took place.

The roots were sorted out from the soil cores immediately after thawing. To distinguish biomass (live roots) from necromass (dead roots) the fine roots were separated into live and dead categories based on morphological characteristics /Vogt and Persson 1991/. Separation was carried out for both tree roots and roots of other vascular species (dwarf shrubs, herbs and grasses).

It is essential to use distinct morphological criteria while sorting the root fragments into live and dead fine roots. Live fine roots were defined as roots that were white or to a varying degree brownish/suberized and often well branched, with the main part of the root tips light and turgid or changed to mycorrhizal ramifications /Agerer 1987–2002/.

In cases when there was a difficulty to judge if a root fragment was live or dead, it was cut lengthwise with a sharp dissection knife and the judgement was based on the colour between cortex and periderm. The stele of live roots was white to slightly brown and elastic. In roots considered as dead, the stele was brownish and easily broken, and the elasticity was reduced. Dead fragmented root fragments with a length < 1 cm were regarded as soil organic matter. The dry weight was estimated for all root fractions after drying in an oven at 65°C to constant weight (at least 24 hours).

Roots were classified into the following root diameter fractions: < 1, 1–2, 2–3, 3–4, 4–5 and 5–10 mm and separated into tree and field-layer species. The diameter measurements were carried out in the mid of each fragment using a pair of vernier callipers. For most forest trees, roots < 1 mm in diameter consist of ramifications with mycorrhizal root tips, morphologically very distinctive from the rest of the root system. In the past, researchers have arbitrarily chosen root diameter size classes to describe what have been called fine roots varying from < 1 to 10 mm /Vogt and Persson 1991/.

The remaining soil from the soil cores (the rhizosphere and bulk soil) was stored in a cold-storage at –4°C until the chemical analyses were carried out. The rhizosphere soil was distinguished from the root fragments by shaking the root fragments with their attached soil gently in a glass jar. The rhizosphere soil was defined as the few millimetres of soil surrounding the plant roots and influenced by their activity /cf. Gobran et al. 2001/. Chemical data for the rhizosphere and bulk soil for some other SKB sites are reported in /Hannu and Karlsson 2006, Hannu et al. 2007/.

The fine-root production and turnover rates were calculated from significant increments/decrements (t-test) of live and dead fine roots and live + dead fine roots (Table 3-9). Comprehensive descriptions of our calculation methods used are to be found in /Persson 1978, 1980/. Turnover rate, in this context, means the annual rate of replacement of a certain fine-root category. By definition it is at that rate that special root cathegory is replaced during a year.

Only data from our sequential coring program of fine roots were used for our calculations. These calculations give minimum estimates since the sampling frequency (on 4 sampling occasions) covered only some of the major fluctuations, but certainly not all increases or decreases that actually occurred. On the other hand, the risk for overestimation (e.g. the difference between the sum of the observed increments and the corrected sum of these increments, due to the random variations in the means) is low with a low number of sampling occasions /Persson 1978, 1980/.

Fine-root growth studied by other techniques, such as the use of root windows etc, are strongly affected in their growth pattern, by the environmental conditions in the soil volume close to the transparent windows /Stober et al. 2000/. The minirhizotrons furthermore influence the vitality and life span of fine roots /Witington et al. 1996/. It is obvious that these data do not represent the growth conditions in a natural forest stand.

3 Results

Living tree-fine roots were concentrated to the uppermost part of both the humus and mineral soil layers respectively. The proportion of live tree fine roots was high especially in the top 2.5 cm of the humus layer and in the top 10 cm of the mineral soil (Tables 3-1, 3-2, 3-3). The density of fine roots (expressed as g l^{-1}) emphasizes the quantitative importance of those two top soil horizons (Table 3-4).

This distribution pattern is evident especially for the fine roots < 1 mm in diameter, but also common for other diameter fractions (< 2 mm, < 10 mm in diameter). In most soil layers, except for the deepest ones, the tree fine-root biomass was > the tree fine-root necromass (Table 3-8). With increasing depth, less living tree roots were found. The live/dead ratio was at the same time > 1.

A substantial seasonal variation in the amount of live and dead tree fine roots (< 1 or < 2 mm in diameter) were observed in different soil horizons (Tables 3-1; 3-2; Figure 3-1). The mean fine-root biomass (< 1 mm in diameter) of tree species for the total profile varied on the four sampling occasions between 317, 113, 139 and 248 g m^{-2} (Table 3-5). The related fine-root necromass (dead tissue) varied between 226, 321, 176 and 299 g m^{-2}. The total quantity of fine roots (live + dead) amounted to 543, 434, 314 och 546 g m^{-2} for the four sampling occasions.

The tree fine-root biomass was simultaneously changed into fine-root necromass and finally the fine root necromass into soil organic matter. Reverse fluctuations were to some extent found during the period of investigations between fine-root biomass and necromass (< 1 mm, < 2 mm and < 10 mm in diameter) on different sampling occasions (Table 3-5, 3-6 and 3-7). A high fine-root biomass figure was often followed on the next sampling occasion by a high necromass figure. This was also reflected in the live/dead ratio for different diameter fractions (Table 3-8).

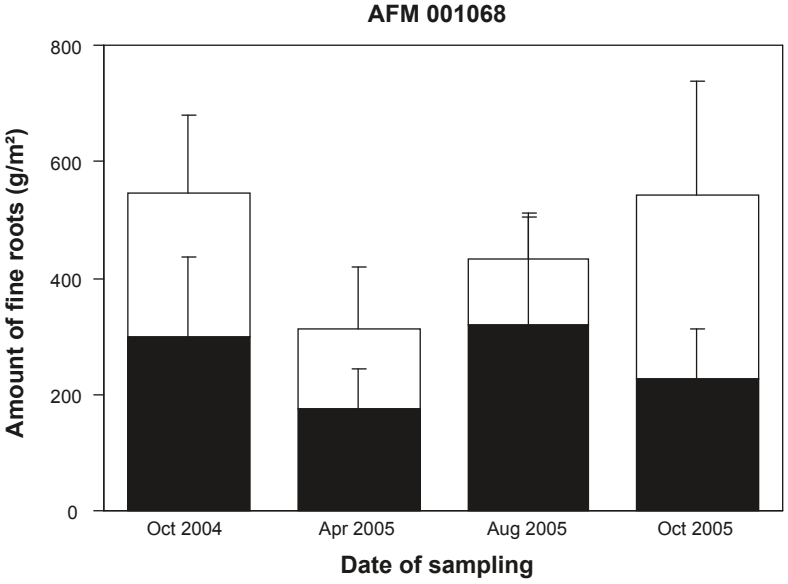

Figure 3-1. *The amount of live (unfilled bar) and dead (black bar) fine roots (< 1 mm in diameter) on the four sampling occasions. Mean values ± SD.*

The dry weight of fine roots decreased considerably with depth (Table 3-5, 3-6 and 3-7). Root sampling took place to a depth where only few roots occurred and only small dead root fragments were observed. Therefore we may conclude that most fine roots were sampled and that only insignificant amounts were left behind. Most roots of the field-layer species were concentrated to the humus layer (Table 3-5, 3-6 and 3-7). Most of both fine and coarse roots of the trees were concentrated to the top 10 cm of the mineral soil.

The mean dry weight of the fine-root biomass of the field-layer species on all those sampling occasions were 115, 99, 78 and 85 g m^{-2} (Table 3-5). The related fine-root necromass were 41, 52, 24 and 37 g m^{-2}. Proportionally less fine-root necromass was observed for the field-layer species than for the trees. The total quantity of fine roots (live + dead) of field layer species amounted to 155, 152, 102 and 123 g m^{-2}. These figures of the fine roots of the field layer amounted, on an average, to 29% of the dry weight figures of tree fine roots.

Tree roots are generally distributed deeper than roots from the field-layer species. Therefore, they are to a limited degree influenced by competition from the roots of the field-layer species. The field-layer vegetation was extensively developed in this fairly open forest site (the above ground dry weight of the field layer at time of peak biomass was 24 g m^{-2}).The roots from the field-layer species in the present site coincide with a comparatively low number of trees in the forest stand (780 trees/ha).

The average change in tree fine-root dry weight for the total soil profile, during the period of investigation, for all sampling occasions, were in the same average level for the fine-root biomass and necromass (Tables 3-8, 3-9). The live/dead ratio for the total soil profile was then close to 1. However, as a result of the heavy fluctuations high amounts of the tree-fine root biomass were dying off during the season and simultaneously changed into fine-root necromass. The fluctuations did not occur concurrently in the humus and mineral soil horizons.

A most substantial increase in fine-root biomass of 146 g m^{-2} (production) took place during the growth period in the humus + mineral soil horizons (Table 3-9). An even higher increase in biomass + necromass was observed at the humus + mineral soil g horizons of 296 g m^{-2} (production) at the same time. In both cases a conservative estimate of the annual fine-root production was calculated since changes occurring between the different sampling occasions can not be included in the calculated figures.

The accumulation in necromass (senescence) was higher than in biomass (359 versus 146 g m^{-2}). In a healthy forest ecosystem it is reasonable to assume that the production of fine roots should at least exceed the senescence of fine roots or be in the same order assuming a steady state. Our results indicate that, at the ecosystem level, inputs of dead roots to the forest soil are an important contribution to nutrient cycling and decomposition.

Table 3-1. The distribution of fine roots (< 1 mm in diameter) at different depths (H=humus; M=mineral soil) during a growth period at the fresh/moist coniferous fern forest site (AFM001068) at Forsmark. Estimates are given as mean values ± SD (n=32). Sampling took place on four sampling occasions: October 20th, 2004 (S-1), April 18th, 2005 (2), August 2nd , 2005 (S-3) and October 28th, 2005 (S-4).

Site	Horizon	Tree roots (g m^{-2})			Roots of field-layer species (g m^{-2})		
		Live	Dead	Total	Live	Dead	Total
S-1 20/10							
2004	H 0–2.5	30±35	4±5	34±38	15±23	1±2	16±23
	H 2.5–5	4±12	4±11	8±22	1±6	8±22	8±28
	H 5–10	2±6	3±10	5±16	4±21	0	4±21
	M 0–10	228±138	136±70	364±165	74±55	36±122	109±129
	M 10–20	51±67	73±60	124±82	14±15	3±6	17±18
	M 20–30	2±8	5±15	7±16	1±4	0	1±4
	M 30–40	0	0	0	0	0	0
S-2 18/4	H 0–2.5	17±28	23±25	40±43	18±21	3±4	21±22
2005	H 2.5–5	4±14	4±12	8±23	4±11	1±2	4±13
	H 5–10	0	0	0	0	0	0
	M 0–10	69±62	195±141	256±160	69±90	42±70	110±118
	M 10–20	19±24	83±55	103±69	9±10	6±9	15±13
	M 20–30	4±8	15±25	19±27	1±2	1±2	1±3
	M 30–40	0	0	0	0	0	0
S-3 2/8	H 0–2.5	24±24	6±7	30±29	8±14	2±4	11±14
2005	H 2.5–5	0	0	0	0	0	0
	H 5–10	0	0	0	0	0	0
	M 0–10	104±89	111±50	215±107	60±39	19±19	79±47
	M 10–20	22±34	62±40	84±54	12±15	3±7	15±19
	M 20–30	0	2±6	2±6	0	0	0
	M 30–40	0	0	0	0	0	0
S-4 28/10	H 0–2.5	27±30	8±11	35±36	9±11	2±4	10±12
2005	H 2.5–5	1±3	0	1±3	1±3	0	1±5
	H 5–10	0	0	0	0	0	0
	M 0–10	152±100	188±103	340±166	66±53	30±32	96±77
	M 10–20	69±54	101±50	169±80	10±10	5±11	15±15
	M 20–30	0	2±8	2±8	0	0	0
	M 30–40	0	0	0	0	0	0

Table 3-2. The distribution of fine roots (< 2 mm in diameter) at different depths (H=humus; M=mineral soil) at the fresh/moist coniferous fern forest site (AFM001068) at Forsmark. Estimates are given as mean values ± SD (n=32). Sampling took place on four sampling occasions: October 20th, 2004 (S-1), April 18th, 2005 (2), August 2nd , 2005 (S-3) and October 28th, 2005 (S-4).

Site	Horizon	Tree roots (g m^2)			Roots of field-layer species (g m^2)		
		Live	Dead	Total	Live	Dead	Total
S-1	H 0–2.5	36±41	5±10	42±45	17±25	2±7	19±28
	H 2.5–5	6±18	7±19	13±34	9±26	1±6	10±31
	H 5–10	5±20	3±11	8±30	2±25	0	5±25
	M 0–10	281±149	160±78	441±179	84±60	36±122	120±130
	M 10–20	79±84	110±78	189±95	15±17	3±6	18±20
	M 20–30	3±11	8±21	10±25	1±4	0	1±4
	M 30–40	0	0	0	0	0	0
S-2	H 0–2.5	22±33	25±27	47±47	30±35	4±6	34±36
	H 2.5–5	6±25	6±19	11±38	4±15	2±6	6±21
	H 5–10	0	0	0	0	0	0
	M 0–10	126±101	247±149	373±173	91±95	48±73	136±125
	M 10–20	61±66	119±72	180±111	11±12	10±19	21±23
	M 20–30	10±19	27±49	37±58	1±6	1±2	2±6.4
	M 30–40	0	0	0	0	0	0
S-3	H 0–2.5	24±24	7±10	31±31	10±15	2±4	13±16
	H 2.5–5	0	0	0	0	0	0
	H 5–10	0	0	0	0	0	0
	M 0–10	151±121	160±75	311±139	69±45	23±23	92±58
	M 10–20	48±55	114±68	162±89	12±15	4±8	16±20
	M 20–30	1±3	2±6	2±8	0	0	0
	M 30–40	0	0	0	0	0	0
S-4	H 0–2.5	30±34	11±17	42±45	11±14	2±4	13±15
	H 2.5–5	1±3	0	1±3	1±5	1±1	2±7
	H 5–10	0	0	0	0	0	0
	M 0–10	216±137	241±121	456±191	86±58	35±37	121±92
	M 10–20	111±83	136±64	247±107	11±12	6±13	17±20
	M 20–30	0	2±8	2±8	0	0	0
	M 30–40	0	0	0	0	0	0

Table 3-3. The distribution of roots (g m^{-2}, < 10 mm in diameter) at different depths (H=humus; M=mineral soil) at the fresh/moist coniferous fern forest site (AFM001068) at Forsmark. Sampling took place on four sampling occasions: October 20th, 2004 (S-1), April 18th, 2005 (2), August 2nd , 2005 (S-3) and October 28th, 2005 (S-4). Estimates are given as mean values ± SD. (n=32).

Sampling	Horizon	Tree roots (g m^{-2})			Roots of field-layer species (g m^{-2})		
		Live	Dead	Total	Live	Dead	Total
S-1	H 0–2.5	41±54	6±11	47±59	35±74	2±7	36±74
	H 2.5–5	22±79	7±19	28±95	34±133	1±6	35±139
	H 5–10	8±36	4±13	12±48	8±43	0	8±43
	M 0–10	549±342	222±126	772±373	103±88	36±122	139±140
	M 10–20	262±448	232±307	494±544	15±17	3±6	18±20
	M 20–30	6±24	10±29	16±39	1±4	0	1±4
	M 30–40	0	0	0	0	0	0
S-2	H 0–2.5	24±38	30±36	54±63	32±36	4±6	36±37
	H 2.5–5	6±26	6±19	11±37	4±15	2±6	6±21
	H 5–10	0	0	0	0	0	0
	M 0–10	355±422	315±236	670±469	116±104	48±73	165±135
	M 10–20	284±473	224±181	508±476	11±12	10±11	21±23
	M 20–30	26±67	61±153	87±174	2±9	1±2	3±9
	M 30–40	0	0	0	0	0	0
S-3	H 0–2.5	49±106	10±23	59±107	11±20	4±10	15±28
	H 2.5–5	0	0	0	0	0	0
	H 5–10	0	0	0	0	0	0
	M 0–10	247±248	227±144	474±276	93±67	31±44	123±87
	M 10–20	160±259	253±376	414±469	12±15	4±8	16±20
	M 20–30	1±3	2±6	2±8	0	0	0
	M 30–40	0	0	0	0	0	0
S-4	H 0–2.5	39±56	14±20	53±64	20±27	2±4	21±29
	H 2.5–5	1±3	0	1±3	1±5	0	1±7
	H 5–10	0	0	0	0	0	0
	M 0–10	608±500	414±308	1021±578	127±169	35±36	162±187
	M 10–20	383±489	333±395	716±592	11±12	6±13	17±20
	M 20–30	3±17	2±8	5±25	0	0	0
	M 30–40	0	0	0	0	0	0

Table 3-4. The amount of fine roots (< 1 mm in diameter) per soil volume (g l^{-1}) at different depths (H=humus; M=mineral soil) at the fresh/moist coniferous fern forest site (AFM001068) at Forsmark. Sampling took place on four sampling occasions: October 20th, 2004 (S-1), April 18th, 2005 (2), August 2nd , 2005 (S-3) and October 28th, 2005 (S-4). Estimates are given as mean values ± SD (n=32).

Site	Horizon	Tree roots (g l^{-1})			Roots of field-layer species (g l^{-1})		
		Live	Dead	Total	Live	Dead	Total
S-1	H 0–2.5	1.4±1.5	0.3±0.6	1.7±1.9	0.6±0.9	0.03±0.08	0.6±0.9
	H 2.5–5	0.4±0.9	0.2±0.5	0.6±1.4	0.3±1.0	0.06±0.25	0.4±1.2
	H 5–7.5	0.3±0.8	0.2±0.5	0.4±1.3	0.04±2.11	0	0.04±2.11
	M 0–10	3.6±1.6	1.8±1.3	5.3±2.7	0.7±0.5	0.4±1.2	1.1±1.3
	M 10–20	1.7±1.2	1.1±0.7	2.7±1.6	0.2±0.2	0.04±0.10	0.2±0.3
	M 20–30	0.2±0.4	0.1±0.3	0.3±0.7	0.01±0.04	0	0.01±0.04
	M 30–40	0	0	0	0	0	0
S-2	H 0–2.5	0.7±1.1	0.9±1.0	1.6±1.7	0.7±0.8	0.1±0.2	0.9±0.9
	H 2.5–5	0.2±0.7	0.2±0.5	0.3±1.0	0.2±0.5	0.03±0.1	0.2±0.6
	H 5–7.5	0	0	0	0	0	0
	M 0–10	0.7±0.6	2.0±1.4	2.6±1.6	0.7±0.9	0.4±0.7	1.1±1.2
	M 10–20	0.2±0.2	0.9±0.6	1.2±0.7	0.1±0.1	0.07±0.11	0.2±0.2
	M 20–30	0.04±0.10	0.18±0.28	0.22±0.30	0	0	0
	M 30–40	0	0	0	0	0	0
S-3	H 0–2.5	1.0±1.0	0.3±0.3	1.3±1.2	0.4±0.6	0.08±0.15	0.4±0.6
	H 2.5–5	0	0	0	0	0	0
	H 5–7.5	0	0	0	0	0	0
	M 0–10	1.0±0.9	1.1±0.5	2.2±1.1	0.6±0.4	0.2±0.2	0.8±0.5
	M 10–20	0.3±0.4	0.8±0.5	1.1±0.7	0.2±0.2	0.05±0.12	0.2±0.3
	M 20–30	0	0	0	0	0	0
	M 30–40	0	0	0	0	0	0
S-4	H 0–2.5	1.1±1.2	0.4±0.5	1.4±1.5	0.37±0.43	0.06±0.18	0.4±0.5
	H 2.5–5	0.06±0.33	0	0.6±0.33	0.05±0.31	0.04±0.21	0.09±0.51
	H 5–7.5	0	0	0	0	0	0
	M 0–10	1.5±1.0	1.9±1.0	3.4±1.7	0.7±0.5	0.3±0.3	1.0±0.8
	M 10–20	0.9±0.8	1.3±0.7	2.3±1.1	0.2±0.2	0.1±0.1	0.2±0.2
	M 20–30	0	0	0	0	0	0
	M 30–40	0	0	0	0	0	0

Table 3-5. The amount of live and dead fine roots (< 1 mm in diameter) in different soil layers (H=humus; M=mineral soil) at the fresh/moist coniferous fern forest site (AFM001068) at Forsmark. Sampling took place on four sampling occasions: October 20th, 2004 (S-1), April 18th, 2005 (2), August 2nd , 2005 (S-3), and October 28th, 2005 (S-4). Estimates are given as mean values ± SD (n=32).

Sampling	Horizon	Tree roots (g m^{-2})			Roots of field-layer species (g m^{-2})		
		Live	Dead	Total	Live	Dead	Total
S-1	H	35±44	11±23	46±61	27±49	2±6	29±54
	M	272±190	208±91	480±213	88±58	39±122	126±130
	H+M	317±196	226±88	543±205	115±87	41±122	155±145
S-2	H	21±33	27±27	47±51	22±26	4±4	25±28
	M	91±73	294±183	386±206	78±90	49±74	126±123
	H+M	113±79	321±184	434±212	99±93	52±74	152±131
S-3	H	24±24	6±7	30±29	8±14	2±4	11±14
	M	127±104	169±62	284±130	69±49	22±21	91±61
	H+M	150±112	176±70	330±136	78±56	24±21	102±67
S-4	H	27±31	8±11	35±36	9±12	2±5	11±14
	M	220±123	291±133	511±200	76±60	35±40	111±88
	H+M	248±134	299±136	546±212	85±65	37±41	123±92

Table 3-6. The amount of live and dead fine roots (< 2 mm in diameter) in different soil layers (H=humus; M=mineral soil) at the fresh/moist coniferous fern forest site (AFM001068) at Forsmark. Sampling took place on four sampling occasions: October 20th, 2004 (S-1), April 18th, 2005 (2), August 2nd , 2005 (S-3) and October 28th, 2005 (S-4). Estimates are given as mean values ± SD (n=32).

Sampling/ root fraction	Horizons	Tree roots (g m^{-2})			Roots of field-layer species (g m^{-2})		
		Live	Dead	Total	Live	Dead	Total
S-1	H	47±62	16±33	63±89	31±53	3±9	34±59
	M	363±201	278±98	641±206	101±64	39±122	140±130
	H+M	410±207	294±107	704±211	132±97	42±122	174±149
S-2	H	28±43	31±32	59±60	34±40	5±10	40±46
	M	197±151	393±183	590±246	103±95	58±78	161±137
	H+M	224±162	424±184	649±251	137±100	64±78	200±150
S-3	H	24±24	7±10	31±32	10±15	2±4	13±16
	M	200±153	276±95	475±157	81±53	26±27	107±70
	H+M	224±162	282±98	506±170	91±61	29±26	120±77
S-4	H	31±35	11±17	42±46	12±17	2±5	14±19
	M	327±172	378±167	704±235	97±73	41±44	138±102
	H+M	358±176	389±174	747±248	109±79	43±44	152±106

Table 3-7. The amount of live and dead tree roots (< 10 mm in diameter) in different soil layers (H=humus; M=mineral soil and H+M) at the fresh/moist coniferous fern forest site (AFM001068) at Forsmark. Sampling took place on four sampling occasions: October 20th, 2004 (S-1), April 18th, 2005 (2), August 2nd , 2005 (S-3) and October 28th, 2005 (S-4). Estimates are given as mean values ± SD (n=32).

Sampling/ root fraction	Horizons	Tree roots (g m^{-2})			Roots of field-layer species (g m^{-2})		
		Live	Dead	Total	Live	Dead	Total
S-1							
	H	73±141	16±35	88±172	77±208	3±9	80±214
	M	349±437	230±248	579±545	11±20	3±5	14±23
	H+M	890±581	480±309	1370±675	195±230	42±122	237±245
S-2	H	30±47	35±39	65±73	36±41	5±10	42±47
	M	665±588	600±335	1265±600	129±104	59±78	188±145
	H+M	695±587	635±339	1330±601	165±102	65±78	229±153
S-3	H	49±105	19±23	59±107	11±20	4±10	15±28
	M	408±406	482±396	890±545	105±71	34±50	139±96
	H+M	457±400	493±395	949±544	116±79	38±51	154±105
S-4	H	39±56	14±20	54±64	21±28	2±5	23±31
	M	993±740	749±516	1742±785	138±176	41±44	179±195
	H+M	1032±743	763±523	1795±795	158±184	43±44	202±203

Table 3-8. The live/dead ratio of fine roots at various root diameters (< 1, < 2, < 5 and < 10 mm in diameter) at different depths (H=humus; M=mineral soil) at the fresh/moist coniferous fern forest site (AFM001068) at Forsmark. Sampling took place on four sampling occasions: October 20th, 2004 (S-1), April 18th, 2005 (2), August 2nd , 2005 (S-3) and October 28th, 2005 (S-4). Estimates are given as mean values ± SD (n=32).

Sampling	Horizon	Tree roots (g g^{-1})				Roots of field-layer species (g g^{-1})			
		< 1	< 2	< 5	< 10	< 1	< 2	< 5	< 10
S-1	H 0–2.5	8.04	6.69	8.05	6.83	23.88	9.95	19.00	19.75
	H 2.5–5	1.01	0.95	1.64	3.19	5.73	6.79	25.50	25.48
	H 5–10	0.64	1.41	2.24	2.24	–	–	–	–
	M 0–10	1.67	1.75	2.12	2.47	2.07	4.67	2.84	4.67
	M 10–20	0.70	0.72	0.96	1.13	4.58	4.67	4.67	4.67
	M 20–30	0.34	0.37	0.62	0.62	31.18	34.30	34.30	34.30
	H	3.38	3.05	3.87	4.29	14.59	10.15	24.42	24.84
	M	1.31	1.31	1.57	1.76	2.28	2.57	3.01	3.01
	H+M	1.41	1.40	1.67	1.85	2.82	3.13	4.56	4.59
S-2	H 0–2.5	0.76	0.86	0.74	0.81	6.00	7.56	8.08	8.08
	H 2.5–5	0.99	1.07	1.07	1.07	5.79	2.93	2.93	2.93
	H 5–10	–	–	–	–	–	–	–	–
	M 0–10	0.35	0.51	0.70	1.13	1.62	1.90	2.40	2.40
	M 10–20	0.23	0.51	0.68	1.27	1.52	1.06	1.03	1.03
	M 20–30	0.23	0.37	0.86	0.43	0.82	2.65	3.64	3.64
	H	0.79	0.90	0.79	0.85	5.96	6.28	6.65	6.65
	M	0.31	0.50	0.70	1.11	1.60	1.76	2.17	2.17
	H+M	0.35	0.53	0.71	1.09	1.91	2.15	2.55	2.55
S-3	H 0–2.5	4.30	3.48	3.48	4.68	4.11	4.52	2.92	2.92
	H 2.5–5	–	–	–	–	–	–	–	–
	H 5–10	–	–	–		–	–		
	M 0–10	0.93	0.94	0.97	1.09	3.19	3.04	3.02	3.02
	M 10–20	0.36	0.42	0.76	0.63	3.51	3.23	3.23	3.23
	M 20–30	0	0.34	0.34	0.34	0	0	0	0
	H	4.30	3.48	3.48	4.68	4.11	4.52	2.92	2.92
	M	0.72	0.73	0.89	0.85	3.23	3.07	3.04	3.04
	H+M	0.83	0.79	0.94	0.93	3.31	3.18	3.03	3.03
S-4	H 0–2.5	3.25	2.70	2.72	2.72	5.44	6.83	12.28	12.28
	H 2.5–5	0	–	–	0	1.47	2.60	2.60	2.59
	H 5–10	–	–	–	–	–	–	–	–
	M 0–10	0.81	0.90	1.01	1.47	2.22	2.45	3.25	3.61
	M 10–20	0.68	0.81	0.91	1.15	1.80	1.79	1.79	1.79
	M 20–30	0	0	1.76	1.76	0	0	0	0
	H	3.32	2.75	2.77	2.77	4.68	6.04	10.48	10.48
	M	0.76	0.86	0.98	1.33	2.16	2.35	3.03	3.34
	H+M	0.83	0.92	1.02	1.35	2.29	2.52	3.37	3.67

Table 3-9. The amount of live and dead fine roots (< 1 mm in diameter) and differences between different sampling occasions in different soil layers (H=humus; M=mineral soil) at the fresh/moist coniferous fern forest site (AFM001068) at Forsmark. Significant differences are given without parenthesis. Increases are indicated by +, decreases –. Sampling took place on four sampling occasions: October 20th, 2004 (S-1), April 18th, 2005 (2), August 2nd, 2005 (S-3) and October 28th, 2005 (S-4). Estimates are given as mean values ± SD (n=32). ns=not significant.

Sampling	Horizons	Tree roots (g m^{-2})					
		Live	Difference	Dead	Difference	Total	Difference
S-1	H	35±44		11±22		46±61	
			–15		+16		(–1)
S-2	H	21±33		27±27		47±51	
			(+3)		–21		–16
S-3	H	24±24		6±7		30±29	
			(+3)		(+2)		(+5)
S-4	H	27±31		8±11		35±36	
Σ increases			15		16		ns
Σ decreases			ns		21		16
Average		27±11		13±8		40±16	
S-1	M	272±190		208±91		480±213	
			–181		+86		–94
S-2	M	91±73		294±183		386±206	
			+36		–124		–102
S-3	M	127±104		169±62		284±131	
			+93		+122		+227
S-4	M	220±123		291±133		511±200	
Σ increases			181		208		227
Σ decreases			129		86		196
Average		178±35		241±44		415±67	
S-1	H+M	317±196		226±88		543±205	
			–204		+95		–109
S-2	H+M	113±79		321±184		434±212	
			+37		–141		–220
S-3	H+M	150±112		180±62		330±136	
			+109		+123		+296
S-4	H+M	248±134		299±136		546±212	
Σ increases			146		359		296
Σ decreases			204		141		329
Average		207±48		257±45		463±69	

4 Discussion

The long-lived woody framework of structural roots support a mass of short-lived nonwoody fine roots associated with mycorrhizal fungi. It is not advisable, due to the high variability of the fine roots, to estimate the fine-root biomass as a proportion of total root biomass or to use other structural parts of the tree for such estimations /Vogt and Persson 1991/. The total carbon investment in those finer ramifications is generally higher than in the structural roots /Persson 2002/. Fine-root biomass and necromass, in stands of different age, varies in response to water and nutrient availability, which make a comparison between age-series of forest trees difficult (Table 4-1).

Quantification of fine roots in forest ecosystem studies is necessary due to their important role as carbon sinks and sources input of soil organic matter. Growth dynamic of fine roots varies considerably between different forest ecosystems, tree species, latitudes and climatic conditions (Table 4-1). Therefore, attempts to correlate fine-root development in forest trees with environmental factors have so far often yielded in inconclusive results /Persson 1996, Santantonio and Hermann 1985/.

The amount of fine-root biomass and necromass at the study area (Table 4-1) were within the range of data from other investigations, taking into consideration the high seasonal variability of the fine roots /cf. Persson 2000/. Tree fine roots grow most vigorously in those soil layers since organic nitrogen compounds are present in large quantities. The presence of soil organic matter generally improves the nutrient availability and reduces soil strength. There is always much higher root and mycorrhizal proliferation in the uppermost part of the soil horizon than in deeper soil horizons, since the surface soil is rich in organic matter and nutrients /Persson 1980/.

Fine-root characteristics such as the amount of live and dead fine roots and the live/dead ratio seem to depend on a variety of abiotic and biotic factors specific for certain forest stand /Persson 1996/. Our data clarify that it is necessary to sort the fine roots in both live and dead categories, to get a general picture of the spatial and temporal distribution of fine roots (Figure 3-1). It is necessary to relate to the natural soil-horizons since the distribution pattern of the fine roots seems to depend to a great extent on where in the soil profile they were excavated.

The live/dead ratios in our case (between 0.2–1.4 for tree species < 1 mm in the total soil profile) did not differ very much from available data in literature (Table 4-1). Live/dead ratios in literature varied between 0.2–5.3 g/g for coniferous forest and between 0.2–3.0 g/g and for deciduous forest (Table 4-1). The highest live/dead ratio is always to be found in the humus layer.

The fine roots in the uppermost horizons (< 1 mm in diameter) are to a great extent infected by mycorrhizal fungi. The number of mycorrhizal root tips per unit root length are consequently more frequently found in the humus layer /Person 1978/. Mycorrhizal root tips are morphologically very different from non-infected root tips. In terms of numbers they constituted the main part of the total number of living tree fine-root tips. Data verifying a high live/dead ratio in the top of the soil profile decreasing with depth are found in the quoted literature (Table 4-1).

Fine-root “vitality” in terms of live/dead ratios of the fine roots should be expected to be high in the humus layers, since the extensive mycorrhizal infection in that layer makes the fine roots functional over a prolonged period of time /Persson and Ahlström 1999/.

The degree of root penetration in the different soil horizons, as revealed from the live/dead ratio, is regarded as a vitality criteria of the forest stand /Persson 1996/. The efficiency of root penetration depends on soil conditions as well as the degree of suberization and frequency of mycorrhizal infection. Under unfavourable conditions (drought, frost and insufficient carbohydrate supply) fine roots may die back to a great extent, but they are rapidly formed again once environmental conditions become more favourable. Tree fine roots exposed to a relatively low nutrient availability are highly dependent on the mycorrhizae for their function in nutrient uptake /cf. e.g. Marschner 2002/.

Table 4-1. Amount of live (biomass), dead (necromass) fine roots (DW g m^2) and live/dead ratios (g g^1) in some natural forest ecosystems. Np = not published.

Forest type/Species	Stand age	Diameter (mm)	Biomass (g m^{-2})	Necromass (g m^{-2})	Live/dead ratio (g/g)	References
Fagus sylvatica	90	< 1	118	193	0.6	/van Praag et al. 1988/
–	122	< 1	94	75	1.2	/Stober et al. 2000/
–	122	< 1	43	139	0.3	–
–	122	< 1	120	111	1.1	–
–	122	< 1	79	74	1.1	–
–	123	< 1	77	151	0.5	–
–	140	< 1	474	861	5.5	/Sandhade–Hofmann and Zech 1992/
–	140	< 1	407	828	4.9	–
Quercus petraea	15	< 2	536	335	1.6	/Bakker 1998/
–	24	< 2	277	721	3.8	–
–	25	< 2	359	277	2.4	–
–	42	< 2	654	328	2.0	–
–	44	< 2	362	196	1.9	–
–	48	< 2	330	118	2.8	–
–	49	< 2	285	131	2.2	–
–	50	< 2	695	290	2.4	–
–	51	< 2	325	131	2.5	–
–	55	< 2	346	153	2.3	–
–	76	< 2	436	264	1.7	–
Quercus robur	112	< 1	137	87	1.6	/Persson and Stadenberg 2007/
–	112	< 2	179	123	1.5	–
Alnus glutinosa	85–95	< 1	235	184	1.3	–
–	85–95	< 2	332	285	1.2	–
–	34	< 1	50	271	0.2	–
–	34	< 2	82	381	0.2	–
Coniferous – *Calluna*	59–60	< 1	267	119	2.2	–
–	59–60	< 2	365	167	2.2	–
Coniferous –*V. myrt.*	55	< 1	371	245	1.5	–
–	55	< 2	499	344	1.5	–
Coniferous fern	80–88	< 1	317	226	1.4	This study
–	–	< 1	113	321	0.4	–
–	–	< 1	139	176	0.8	–
–	–	< 1	248	299	0.8	–
–	80–88	< 2	410	294	1.4	–
–	–	< 2	224	424	0.5	–
–	–	< 2	224	282	0.8	–
–	–	< 2	358	389	0.9	–
Nortern hardwood	80	< 0.5	132	117	1.1	/Burke and Raynal 1994/
–	4	< 1	274	54	5.1	/Fahey et al. 1994/
Oak-hornbeam forest	78	< 2	1259	236	5.3	/Simonovic 1978/
Picea abies	10	< 2	108	65	1.7	/Puhe 1993/
–	18	< 2	197	105	1.9	–
–	28	< 2	238	168	1.4	–
–	13	< 2	154	4875	0.3	–

Forest type/Species	Stand age	Diameter (mm)	Biomass (g m^{-2})	Necromass (g m^{-2})	Live/dead ratio (g/g)	References
–	22	< 2	227	238	1.0	–
–	23	< 2	181	394	0.5	–
–	26	< 2	492	174	2.8	/Majdi and Persson 1993/
–	28	< 1	273	728	0.4	/Persson et al. 1995/
–	31	< 1	131	253	0.5	/Püttsepp et al. 2006/
–	35	< 1	134	391	0.3	/van Praag et al. 1988/
–	40	< 2	276	381	0.7	/Hansen and Thomsen 1991/
–	44	< 2	Np	Np	0.9	/Helmisaari and Hallbäcken 1999/
–	58	< 2	Np	Np	2.3	–
–	88	< 2	Np	Np	1.5	–
–	181	< 2	Np	Np	1.4	–
–	45	< 2	301	363	0.8	–
–	66	< 2	725	1719	0.4	–
–	47	< 1	70	45	1.6	/Stober et al. 2000/
–	47	< 1	63	64	1.0	–
–	47	< 1	56	38	1.5	–
–	47	< 1	40	37	1.1	–
–	48	< 1	57	97	0.6	–
–	60	< 1	94	137	0.7	/Ostonen et al. 2005/
–	53	< 2	273	297	0.9	/Murach and Schünemann 1985/
–	62	< 2	440	150	2.9	/Murach et al. 1993/
	62	< 2	345	130	2.7	–
–	80	< 2	360	330	1.1	/Puhe et al. 1986/
–	106	< 2	350	170	2.1	–
–	115	< 2	510	260	2.0	–
–	85	< 2	220	74	3.0	/Ulrich et al. 1984/
–	80–100	< 1	173	234	0.7	/Persson and Ahlström 2002/
–	–	< 1	119	250	0.5	–
–	–	< 1	167	135	1.2	–
–	–	< 1	194	184	1.0	–
–	–	< 1	220	106	2.2	–
Pinus sylvestris	20	< 2	26	68	0.4	/Persson 1979/
–	37	< 2	404	706	0.6	/Makkonen and Helmisaari 1998/
–	38	< 2	336	280	1.2	–
–	39	< 2	338	1195	0.3	–
–	40	< 2	351	2313	0.2	–
–	40	< 2	107	34	3.1	/Vanguelova et al. 2005/
–	41	< 2	74	59	1.3	–
–	41	< 2	147	50	3.0	–
–	41	< 2	138	94	1.5	–
–	120	< 2	123	64	1.9	/Persson 1979/
–	120	< 2	236	145	1.6	/Persson 1982/
–	120	< 2	256	123	2.1	–

Forest type/Species	Stand age	Diameter (mm)	Biomass (g m^{-2})	Necromass (g m^{-2})	Live/dead ratio (g/g)	References
Pinus radioata	12	< 1	437	1494	0.3	/Santantonio and Santantonio 1987/
Pseudotsuga menziesii						/Santantonio and Hermann 1985/
– dry	70	< 1	253	1067	0.2	
– moderate	170	< 1	350	816	0.4	–
– wet	120	< 1	315	406	0.8	–
– low productivity	11	< 2	13	6	2.3	/Vogt et al. 1983/
–	12	< 2	14	44	0.3	–
–	33	< 2	360	126	2.8	–
–	49	< 2	171	69	2.5	–
–	67	< 2	157	89	1.8	–
–	69	< 2	316	200	1.6	–
–	150	< 2	60	67	0.9	–
–	163	< 2	146	68	2.3	–
– high productivity	13	< 2	21	10	2.2	–
–	14	< 2	11	5	2.3	–
–	45	< 2	116	97	1.2	–
–	46	< 2	134	100	1.3	–
–	65	< 2	15	20	0.8	–
–	75	< 2	15	19	0.8	–
–	150	< 2	21	3	6.6	–
–	160	< 2	13	15	0.9	–
Larix leptolepis	40	< 2	72	23	3.1	/Son and Hong Hwang 2003/
Mixed hardwood	78	< 2	794	164	4.8	/Powel and Day 1991/
Maple-gum	52	< 2	243	100	2.4	–
Cedar	57	< 2	500	165	3.0	–
Cypress	86	< 2	230	80	2.9	–

The root function is extremely costly and is enhanced by a high carbohydrate supply /Ågren et al. 1980, Marshall and Waring 1985/. Available information in literature suggests substantial fine root production with a seasonal pattern different from needle or leaf production /Persson 1983/. Data from various forest stands, obtained by sequential coring, suggest annual turnover rates of 0.6–2.4 times the average fine-root biomass (Table 4-2). All those turnover rates are conservative since turnover occurring between the sampling occasions remained undetermined. In our case the turnover rate was obtained from four sampling occasions during a period of one year (Figure 3-1). Only significant alterations were included in our calculations.

If the sampling had been carried out at more frequent intervals, it should have been necessary to excavate an even larger number of soil core samples on each sampling occasion in order to detect significant changes. The cost of excavating our soil core samples then should have increased drastically. Problems with determining an adequate sampling frequency suggest that most estimates of turnover rates, using the sequential coring method, are rather conservative (Table 4-2). Since only significant changes were used in those calculations, the limited sampling frequency, but also the limited the number of samples on each sampling occasion, are affecting the calculated figures. Turnover rates higher than those given in Table 4-2 are therefore likely to be expected.

Table 4-2. Fine-root production, average biomass and turnover rates (minimum estimates) at different forest sites obtained by the sequential coring method. The turnover rate is calculated for the figures of production and the average amount of fine roots. Calculations were made for * live fine roots; ** live + dead fine roots.

Forest ecosystem	Diameter (mm)	Stand age	Production (g m^{-2} yr^{-1})	Average amount of fine roots (g m^{-2})	Turnover rate (yr^{-1})	Reference
Picea abies	< 1	92	78	57	1.4	/Stober et al. 2000/*
Picea abies	< 1	120	131.4	133.5	1.0	/van Praag et al. 1988/*
Pinus sylvestris	< 2	15–20	61	26,1	2.4	/Persson 1979/*
Pinus sylvestris	< 2	15–20	183	93.7	2.0	/Persson 1979/**
Pinus sylvestris	< 2	120	139	122.5	1.1	/Persson 1979/*
Pinus sylvestris	< 2	120	192	186.8	1.0	/Persson 1979/**
Fagus sylvatica	< 1	161	137	83	1.7	/Stober et al. 2000/*
Fagus sylvatica	< 1	35	11.8	117.8	0.1	/van Praag et al. 1988/*
Northern hardwood	< 0.5	80	230	132	1.7	/Burke and Raynal 1994/*
Pseudotsuga menziesi – high productivity	< 2	40	41	27	1.5	/Keyes and Grier 1981/*
– low productivity	< 2	40	81	83	1.0	/Keyes and Grier 1981/*
Coniferous fern forest site	< 1	80–88	146	207	0.7	This study*
Coniferous fern forest site	< 1	80–88	296	463	0.6	This study**

Other destructive methods of estimating fine-root turnover, such the ingrowth core or the rhizotron/minirhizotron method, are highly affecting the fine-root growth and spatial distribution of the fine roots. Fine roots, produced close to observation windows, rhizotron tubes, or in ingrowth cores, generally behave differently with regards to the live/dead ratios, longevity and spatial distribution /Stober et al. 2000/. These fine roots may stay alive for a longer period and differ considerably with regards to their spatial and temporal growth patterns /Persson and Ahlström 1994/. Therefore, we have deliberately chosen not to compare with such data. Only data from sequential coring of fine roots in natural conditions have been used for our calculations of rates of fine-root production (Table 3-9).

Most studies on fine roots in forest ecosystems have been concentrated on tree fine roots, while roots of the field-layer species although often most important in terms of dry weight have been neglected /cf. Palviainen et al. 2005, Persson 1978/. Our investigation confirms the quantitative importance of the fine roots of field-layer species in open forest ecosystems (Table 3-8). Forest-trees are usually evolved in mixed ecosystems, in which survival in a competitive environment, not necessarily high production, is important.

Subsequent changes in the live/dead ratios of fine-roots are frequently connected with soil water availability. Fine roots are sensitive to drought and their live/dead ratios are decreasing with less water availability in the soil /cf. Olsthorn 1991, Persson et al. 1995, Santantonio et al. 1977, Santantonio and Hermann 1985/. Temporary rain showers affect mainly the upper humus layers during the summer months. Fine roots respond quickly to environmental changes and are rapidly penetrating those wet horizons.

A high death rate in the finest < 1 mm diameter root fraction should be expected during summer drought. In boreal forest ecosystems, the well-developed organic-rich podzol profiles, most effectively buffer the soil system against drought and nutrient deficiencies. Most dead fine roots (necromass) are then found in the mineral soil. The high necromass concentration in this soil horizon is probably due to harsher environmental conditions, a high penetration and death rate, counterbalanced by invasion of new fine roots from the upper organic soil horizon.

Substantial variations in fine-root biomass, necromass and live/dead ratios usually occur in tree stands depending on site quality /Clemensson-Lindell and Persson 1995, Ostonen et al. 1999, Persson 2002, Persson and Ahlström 2002, Raich and Nadelhoffer 1989/. The contribution of different species and diameter classes to growth pattern in the soil profile may vary considerable, but few investigators seem to be aware of this problem.

It was impossible, in our case to calculate significant turnover rates of large-diameter roots (2–10 mm in diameter) due to their higher variability. The amount fine-root biomass of the field layer species (Table 3-5) were significantly decreasing during the period of study, suggesting that only few new roots were formed. The high variability of the field-layer fine roots makes it impossible to calculate their turnover rates.

Concluding remarks

The often-reported discrepancy in the data on turnover rates of fine roots may partly be due to imprecise definition of size classes (diameter), vitality of the root fragments (biomass and necromas) or species (tree or field-layer species).

Turnover rates of tree fine-roots in forest ecosystems are high and the annual production of fine roots may amount to the average fine-root biomass during the growth period.

The methods of estimating fine-root production, mortality and turnover should involve the periodic measurements of live and dead dry weights of fine roots in soil cores in the undisturbed soil horizons in the field.

It is essential to use data obtained by the sequential soil coring technique. Other destructive techniques such as observation windows, the use of minirhizotrons or ingrowth cores etc, are not applicable to the growth conditions in undisturbed forest stand.

The sampling frequency applied should cover the main fluctuations during the growth period. It is necessary to excavate a sufficient number of soil cores on each sampling occasion in order to detect significant changes.

The live/dead ratio is a powerful vitality criterion of fine roots, revealing when new roots are formed.

5 References

Agerer R, ed, 1987–2002. Colour atlas of ectomycorrhizae. Einhorn-Verlag, Eduard Dietenberger Gmbh, Germany.

Bakker M, 1998. Effet des amendements calciques sur les racines fines de chênes (Quercus petrea et robur): conséquences des changements dans la rhizosphère. Doctoral thesis, INRA, Champenoux.

Bakker M R, Garbaye J, Nys C, 2000. Effect of liming on the ectomycorrhizal status of oak. Forest Ecology and Management 126: 121–131.

Burke M K, Raynal D J, 1994. Fine root growth phenology, production, and turnover in a northern hardwood forest ecosystem. Plant Soil 162: 135–146.

Clemensson-Lindell A, Persson H, 1992. Effects of freezing on rhizosphere and root nutrient content using two soil sampling methods. Plant and Soil 139:39–45.

Clemensson-Lindell A, Persson H, 1995. Fine-root vitality in 30-year-old Norway spruce stand subjected to varying nutrient supplies. Plant and Soil 168–169: 167–171.

Cramér P, Stendahl S, Erhag T, 2007. Nationellt ansvar för använt kärnbränsle i en utvidgad europeisk union? SKB R-07-01, Svensk Kärnbränslehantering AB.

Daldoum M A, Ranger J, 1994. The biochemical cycle in a healthy and highly productive Norway spruce (*Picea abies*) ecosystem in the Vosges, France. Can. J. For. Res. 24: 839–849.

Fahey T J, Hughes J W, 1994. Fine root dynamics in a northern hardwood forest ecosystem, Hubbard Brook Experimental Forest, NH. J. Ecology: 533–548.

Gobran G R, Fenn L B, Persson H, Al-Windi I, 1991. Beneficial use of soluble calcium for stimulating plant growth: Forest species. In: Persson, H (ed). Above and below ground interactions in forest trees in acidified soils. Air Pollution Research Report 32: 162–174.

Hannu S, Karlsson S, 2006. Forsmark site investigation. Chemical characterisation of deposits and biota. Forsmark site investigation, SKB TR-06-220, Svensk Kärnbränslehantering AB.

Hannu S, Ternsell A, Engdahl A, 2007. Oskarshamn site investigation. Chemical characterisation of deposits and biota. Oskarshamn site investigation, SKB TR-07-XXX, Svensk Kärnbränslehantering AB.

Hansen H B R, Thomsen L, 1991. Rodundersoegelser og biomassemålinger på tre danske roedgranlokaler. Rapport Laboratoriet Oekologi og Miljoelaere, Danmarks Tekniske Höjskole, Lyngby, Denmark, 112 pp.

Helmisaari H, Helmisaari H-S, 1992. Long-term forest fertilization experiments in Finland and Sweden. Swed. Environm. Prot. Adency, Pep. 4099, 123 pp.

Helmisaari H-S, Hallbäcken L, 1999. Fine-root biomass and necromass in limed and fertilized Norway spruce (*Picea abies* (L.) Karst.) stands. Forest Ecology and Management 119:99–110.

Helmisaari H-S K, Makkonen S, Kellomäki E, Valtonen E, Mälkönen E, 2002. Below- and above-ground biomass, production and nitrogen use in Scots pine stands in eastern Finland. Forest Ecology and Management 165: 317–326.

Helmisaari H-S, Derome J, Nöjd P, Kukkola M, 2007. Fine root biomass in relation to site and stand characteristics in Norway spruce and Scots pine stands. Tree Physiology 27: 1493–1504.

Hägglund B, 1973. Om övre höjdens utveckling för gran i södra Sverige: Royal College of Forestry, Department of Forest Yield Research, Research Notes 24, 49 p.

Jackson R B, Canadell J, Ehleringer J R, Mooney H A, Sala O E, Schulze E D, 1996. A global analysis of root distribution for terrestrial biomes. Oecologia 108: 389–411.

Janssens I A, Sampson D A, Curiel-Yuste J, Carrara A, Ceulemans R, 2002. The carbon cost of fine root turnover in a Scots pine forest. Forest Ecology and Management 168: 231–240.

Johansson P-O, Öhman J, 2008. Presentation of meteorological, hydrological and hydro-geological monitoring data from Forsmark. Site descriptive modelling. SDM-Site Forsmark. SKB R-08-10, Svensk Kärnbränslehantering AB.

Keyes M, Grier C, 1981. Above- and below-ground net production in 40-year-old Douglas-fir stands on low and high productivity sites. Can. J. For. Res. 11: 599–605.

Lundin L, Lode E, Stendahl J, Melkerud P-A, Björkvall L, Thorstensson A, 2004. Soil and site types in the Forsmark area. SKB R-04-08, Svensk Kärnbränslehantering AB.

Lundin L, Lode E, Stendahl J, Björkvall L, Hansson J, 2005. Soil and site types in the Oskarshamn area. SKB R-05-15, Svensk Kärnbränslehantering AB.

Löfgren A, 2005. Estimation of biomass and net primary production in field and ground layer, and biomass in litter layer in different vegetation types in Forsmark and Oskarshamn. Oskarshamn/Forsmark site investigation, SKB TR-05-80, Svensk Kärnbränslehantering AB.

Majdi H, Persson H, 1993. Spatial distribution of fine roots, rhizosphere and bulk-soil chemistry in an acidified *Picea abies* stand. Scand. J. Forest Res. 8: 147–155.

Makkonen K, Helimisaari H-S, 1998. Seasonal variation of fine-root biomass in a Scots pine (*Pinus sylvestris* L.) stand. Forest Ecology and Management 102:283–290.

Marschner H, 2002. Mineral nutrition of higher plants. Second edition. Academic Press, 889 pp.

Marshall J D, Waring R H, 1985. Predicting fine root production and turnover by monitoring root starch and soil temperature. Canadian Journal of Forest Research 15: 791–800.

Murach D, 1983. Die Reaktion von Fichtenfeinwurzeln aufzunehmende Bondenversauerung. AFZ 38: 683–686.

Murach D, 1984. Die Reaktion der Feinwurzeln von Fichten (Picea abies (L) Karst) auf zunehmende Bodenversäurung. Göttinger Bodenkd. Ber. 77: 1–126.

Murach D, Shünemann E, 1985. Reaktion der Feinwurzeln von Fichten auf Kalkungsmassnahmen. AFZ: 1151–1154.

Norby R J, Jackson R B, 2000. Root dynamics and global change: seeking an ecosystem perspective. New Phytol. 147: 3–12.

Nordiska Ministerrådet, 1978. Vegetationstyper. Representativa naturtyper och hotade biotoper i Norden. Remissupplaga November 1978.

Olsthoorn A F M, 1991. Fine root density and root biomass of two Douglas-fir stands on sandy soils in the Netherlands. 1. Root biomass in early summer. Netherlands Journal of Agricultural Science 39: 49–60.

Ostonen I, Lõhmus K, Lasn R, 1999. The role of soil conditions in fine root ecomorphology in Norway spruce (Picea abies (L.) Karst.). Plant and Soil 2008: 283–292.

Ostonen I, Lõhmus K, Pajuste K, 2005. Fine root biomass, production and its proportion of NPP in a fertle middle-aged Norway spruce forest: Comparision of soil core and ingrowth core methods. Forest Ecology and Management 212: 264–277.

Palviaiainen M, Finer L, Mannerkoski H, Piirainen S, Starr M, 2005. Changes in the above- and below-ground biomass and nutrient pools of ground vegetation after clear-cutting of a mixed boreal forest. Plant and Soil 275: 157–167.

Persson H, 1975. Deciduous woodland at Andersby, eastern Sweden: field-layer and below-ground production. Acta phytogeogr, suec. 62: 1–71.

Persson H, 1978. Root dynamics in a young Scots pine stand in Central Sweden. Oikos 30: 508–519.

Persson H, 1979. Fine-root production, mortality and decomposition in forest ecosystems. Vegetatio, 41, 101–109.

Persson T, 1979. Structure and Function of Northern Coniferous Forests. Ecol. Bull. (Stockholm) 32: 1–609.

Persson H, 1980. Spatial distribution of fine root growth, mortality and decomposition in a young Scots pine stand in Central Sweden. Oikos 34: 77–87.

Persson H, 1980. Structural properties of the field and bottom layers at Ivantjärnsheden. Ecol. Bull. (Stockholm) 32: 153–163.

Persson H, 1983. The distribution and productivity of fine roots in boreal forests. Plant and Soil 71: 87–101.

Persson H, Ahlström K, 1994. The effects of alkalizing componds on fine-root growth in a Norway spruce stand in Southwest Sweden. J. Environ. Sci. Health A 29(4): 803–820.

Persson H, Majdi H, Clemensson-Lindell A, 1995. Effect of acid deposition on tree roots. Ecol. Bull. 44: 158–167.

Persson H, Von Fircks Y, Majdi H, Nilsson L O, 1995. Root distribution in a Norway spruce (Picea abies (L.) Karst.) stand subjected to drought and ammonium-sulphate application. Plant and Soil 168–169: 161–165.

Persson H, 1996. Fine-root dynamics in forest trees. Acta Phytogeogr. Suec. 81: 17–23.

Persson H, Ahlström K, 1999. Effect of nitrogen deposition on tree roots in boreal forests. In: Going underground – Ecological studies in forest soils. Commission of the European Communities. Ed. H. Persson. Air Pollution Report 32: 221–238.

Persson H, 2000. Adaptive tactics and characteristics of tree fine roots. Dev. Plant Soil Sci.33: 337–346.

Persson H, 2002. Root system in arboreal plants. In Waisel, Y, Eshel, A. and Kafksfi, U. (eds.) Plant roots – the Hidden Half. 3rd ed., pp. 187–204.

Persson H, Ahlström K, 2002. Fine-root response to nitrogen in nitrogen manipulated Norway spruce catchment areas. Forest Ecology and Management 168: 29–41.

Persson H, 2007. Reliable data on fine-root turnover from sequential soil coring in an old carbon (C) budget for a 14-year old Scots pine from the late 1970's. Scandinavian Journal of Forest Research xx: xxx–xxx.

Persson H, Stadenberg I, 2007. Distribution of fine roots in forest areas close to the Swedish Forsmark and Oskarshamn nuclear power plants. SKB TR-07-01,
Svensk Kärnbränslehantering AB.

Powel S W, Day F P, 1991. Root production in four communities in the great dismal swamp. American Journal of Botany 78:288–297.

Puhe J, Persson H, Börjesson I, 1986. Wurzelwachtum und Wurzelshäden in Skandinavischen Nadelwäldern. AFZ 20: 488–492.

Puhe J, 1993. Die Wurzelentwicklung der Fichte (*Picea abies* [L.] Karst.) bei unterschiedlichen chemischen Bodenbedingungen. Ber. Forschungszentrum Waldökosysteme (Göttingen), 108 pp.

Püttsepp Ü, Lõhmus K, Persson H Å, Ahlström K, 2006. Fine-root distribution and morphology in an acidic Norway spruce (Picea abies (L.) Karst.) stand in SW Sweden in relation to granulated wood ash application. Forest Ecology and Management 221: 291–298.

Raich J W, Nadelhoffer K J, 1989. Belowground carbon allocation in forest ecosystems: global trends. Ecology 70: 1346–1354.

Raitio H, 1990. Decline of young Scots pines in a dry heath forest. Acta Univ. Ouluensis, Ser. A, Sientiae Rerum Naturalium 216, Acad. Diss., Oulu.

Sandhage-Hoffmann A, Zech W, 1993. Dynamik und Elemwentgehalte von Fichtenfeinwurzeln in Kalksteinsböden am Wank (Bayerische Kalkalpen). Z. Pflanzenernähr. Bodenk. 156: 181–190.

Santantonio D, Hermann R K, Overton W S, 1977. Root biomass studies in forest ecosystems. Pedobiologia 17: 1–31.

Santantonio D, Hermann R K, 1985. Standing crop, production, and turnover of fine roots on dry, moderate, and wet sites of mature Douglas-fir in western Oregon. Ann Sci. For. 42: 113–142.

Santantino D, Santantino E, 1987. Effect of thinning on production and mortality of fine roots in a *Pinus radiata* plantation on a fertile site in New Zealand. Can. J. For. Res. 17: 919–928.

Simonovic V, 1978. A quantitative study of roots in the forest ecosystem. Biologia (Bratislava) 33: 543–550.

SMHI, 2004. Väder och vatten, No13, SMHI, Norrköping.

Son Y, Hong Hwang J, 2003. Fine root biomass, production and turnover in a fertilized *Larix Leptolepis* plantation in central Korea. Ecological Research 18:339–346.

Stober C, Eckart G A, Persson H, 2000. Root growth and response to nitrogen. In: Carbon and nitrogen cycling in European forest Ecosystems. Schulze, E.-D. (Ed.). Ecological studies 142: 99–121.

Ulrich B, Pirouzpanah D, Murach D, 1984. Bezeihungen zwischen Bodenversauerung ind Wurzelentwicklung von Fichten mit unterschiedlich starken Schadsymtomen. Forstarcviv 55127-134.

Vanguelova E I, Nortcliff S, Moffat A J, Kennedy F, 2005. Morphology, biomass and nutrient status of fine roots of Scots pine (Pinus sylvestris) as influenced by seasonal fluctuations in soil moisture and soil solution chemistry. Plant and Soil 270: 233–247.

Van Praag H J, Sougnez-Remy S, Weissen F, Carlett F G, 1988. Root turnover in a beech and a spruce stand at the Belgian Ardennes. Plant and Soil 105: 87–103.

Vogt K A, More E E, Vogt D J, Redlin M J, Edmonds R L, 1983. Conifer fine root and mycorrhizal root biomass within the forest floors of Douglas-fir stands of different ages and site productivities. Ca. J. For. Res. 13: 429–436.

Vogt K A, Persson H, 1991. Measuring growth and development of roots. – In: Techniques and Approaches in Forest Tree Ecophysiology. Eds. Lassoie JP, Hinckley TM, CRS, Press, pp. 477–501.

Withington J M, Elkin A D, Bulaj B, Olesinski J J N, Bouma T J, 2003. The impact of material used for minirhizotron tubes for root research. New Phytologist 160: 533–544.

Ågren G, Axelsson B, Flower-Ellis J G K, Linder S, Persson H, Staaf H, Troeng E, 1980. Annual carbon budget for a young Scots pine. Ecol. Bull. 32: 307–313.