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REGULAR ARTICLE

Fine root dynamics in a Norway spruce forest (*Picea abies* (L.) Karst) in eastern Sweden

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Abstract The annual dynamics of live and dead fine roots for trees and the field layer species and live/dead ratios were investigated at a coniferous fern forest (*Picea abies* L. Karts) in Sweden. Our methods of estimating the average amount of fine roots involved the periodic sampling of fine roots in sequential cores on four sampling occasions. The highest live/dead ratio was found in the upper part of the humus layer for both tree and field-layer species and decreased with depth. Most tree fine roots on the four sampling occasions were found in the mineral soil horizon, where 86, 81, 85 and 89% of <1 mm and 89, 88, 89 and 92% of <2 mm diameter of the total amounts of live fine roots in the soil profile were found. The mean amounts of live fine roots of tree species for the total soil profile on the four sampling occasions was 317, 150, 139 and 248 g m^{-2} for <1 mm and 410, 225, 224 and 351 g m^{-2} for <2 mm diameter fine roots. The related amount of dead fine roots was 226, 321, 176 and 299 g m^{-2} and 294, 424, 282 and 381 g m^{-2}, respectively. Average amounts of live and dead fine-roots and live/dead ratios from other *Picea abies* forest ecosystems were within the range of our estimates. The production of fine roots, <1 and <2 mm in diameter, estimated from the annual increments in live fine roots, was 207 and 303 g m^{-2}. The related accumulation of dead fine roots was 257 and 345 g m^{-2}, The turnover rate of tree fine roots <1 mm in diameter in the total soil profile amounted to 0.7 yr^{-1} for live and 0.8 yr^{-1} for dead fine roots. The related turnover rates for tree fine roots <2 mm were 0.4 yr^{-1} and 0.7 yr^{-1}. Our data, although based on minimum estimates of the annual fluxes of live and dead fine roots, suggests a carbon flow to the forest soil from dead fine-roots even more substantial than from the needle litter fall. Fine-root data from several *Picea abies* forest ecosystems, suggest high turnover rates of both live and dead tree fine-roots.

Keywords Fine roots · Fine-root growth · Fine-root production · Live/dead ratio · Root distribution · Root turnover · Sequential core method

Introduction

Roots comprise a substantial fraction of the total plant dry weight in forest ecosystems (Persson 2002). Tree roots can be separated by size and function into three different categories:

- coarse supportive roots with low turnover rates;
- small diameter roots with low turnover rates acting as conduits of water and mineral nutrients;

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- fine roots (mycorrhizal roots; <1 mm or <2 in diameter), with a high degree of soil penetration and a high turnover rate (cf. Vogt and Persson 1991).

Fine roots are most frequently defined as <1 or <2 mm in diameter in literature. In order to be able to compare with results from other investigations both diameter fractions were included in our calculations.

Fine roots are exploitive and adapt rapidly to changes in mineral nutrient and water supply. Linné (1772) stated with regards to the function of fine roots: “The roots, their mouths are thin threadlike straws, by the help of which they suck up a watery tincture from the soil, as most exquisite from the top-soil”. The fine roots form an active and spatially variable threadlike network in the soil with a high density in the top soil, decreasing in density downwards in the soil profile (cf. Bakker 1999; Bakker et al. 2006; Borken et al. 2007; Konôpka et al. 2005; López et al. 2001; Makkonen and Helmisaari 1999; Persson 1979; Stober et al. 2000).

A substantial variation in live and dead fine-roots and in the live/dead ratios should be expected during the growth period related to the high root penetration of the soil horizons (cf. John et al. 2001; Makkonen and Helmisaari 1999; Persson 1980a; Persson 1983; Stober et al. 2000). The production of new fine roots is usually substantial during the growth period in forest ecosystems (cf. Persson 1978; Persson 2000; Persson and Ahlström 2002; Helmisaari et al. 2002; Santantonio et al. 1977; Santantonio and Hermann 1985; Stober et al. 2000; Helmisaari et al. 2007). At the same time, a substantial inflow of dead fine-root litter into the soil takes place.

The rate of decomposition of different kind of plant litter is affected by soil temperature and soil moisture conditions (Bowen 1991; Marshall and Waring 1985; Persson 1996; Prescott et al. 2004; Santantonio and Hermann 1985). The decomposition of fine roots, which takes place most extensively in the upper soil layers, is strongly dependent on most specialised microorganisms in the rhizosphere and the fresh carbon supply from dead fine roots (cf. Cheng et al. 2003; Fontaine et al. 2003; Fontaine et al. 2004). Traditional estimation of litter mass loss, through the use of mesh litter bags, which includes some experimental sources of errors, was avoided in our study (cf. Prescott et al. 2004). Fine-root characteristics such as the amount of live and dead roots in terms of dry weight (g m^{-2}) in different soil horizons, the rooting density in terms of dry weight per soil volume (g dm^{-3}) and the live/dead ratio, depend on a variety of abiotic and biotic factors specific for different forest stands (Persson 2000).

A reverse relationship is frequently found between the amount of fine roots and nutrient availability (Clemensson-Lindell and Persson 1995; Persson 1996; Persson and Ahlström 1999). With regards to the sustainability of the forest ecosystems, decreased levels of cations and increased levels of nitrogen have increased the risk of root damage symptoms (Daldoum and Ranger 1994; Persson et al. 1995a; Persson et al. 1995b; Puhe 1993; Ulrich et al. 1984; Vanguelova et al. 2005). Root proliferation around pockets of fertilizers is commonly observed in forestry practice (Bowen 1984). In forest stands there appear to be limited relationships between the total amounts of tree fine roots extracted from soil cores and the distance to the nearest tree (Kalisz et al. 1987; Moir and Bachelard 1969; Persson 1980a; Safford and Bell 1972).

On a global scale, a substantial fraction of the atmosphere CO_2 is originating from dead and decomposing root tissues (Norby and Jackson 2000). The input of root litter is an important contributor to the ecosystem processes with regards to carbon and nutrient cycling. High fluctuations in live and dead fine roots are found in many forest ecosystems (cf. e.g. Bakker 1998; Bakker et al. 2000; Finér et al. 2007; Persson 1978; Persson 1979; Persson and Ahlström 2002; Helmisaari and Helmisaari 1992; Helmisaari and Hallbäcken 1999; Helmisaari et al. 2002; Helmisaari et al. 2007; Stober et al. 2000). Characterizing turnover times of fine roots and carbon allocation in trees is essential in order to understand the patterns of carbon cycling in forest ecosystems.

Fine roots exert a great influence on their environment by accumulating organic matter and redistributing mineral nutrients in the soil profile (Persson 2000). 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 annual patterns in live/dead ratios of fine roots in relation to soil water and mineral nutrient availability (cf. Persson 2000; Persson 2002; Persson et al. 1995a; Santantonio 1980; Santantonio and Hermann 1985). Together with litter from aboveground tree parts, the decaying root material forms the bases for the complex biological cycles in the soil that includes bacteria, fungi and soil animals (cf. Cheng et al. 2003; Fontaine et al. 2003).

The aims of our project, which was carried out in a fresh/moist coniferous fern forest site, on the four sampling occasions, at Forsmark in the central eastern part of Sweden, were:

- to describe the changes during the growth period in the amount of live and dead fine-roots and rhizomes of tree species and field-layer species in different diameter fractions.
- to describe the seasonal variation in depth distribution of fine roots.
- to evaluate the live/dead ratio as a vitality criterion of fine roots.
- to estimate the production and turnover rate.
- to compare our results with data from other studies in Norway spruce stands.

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 (Persson and Stadenberg 2007, 2008, 2009). The mean tree height was 19.8 m and the tree density was 780 number of trees/ha (Table 1). The site was of a coniferous fern type (Nordiska Ministerrådet 1978) and the soil type was a Regisol/Gleysol. The tree layer consisted mainly of *Picea abies* and some suppressed *Betula verrucosa* tree with a basal area of 20.5 m^2/ha and 6.5 m^2/ha, respectively. The above-ground tree litter fall was relatively low and consisted mainly of *Picea abies* needles (135 g m^2; Mjöfors et al. 2007). Dominant species in the field-layer were *Maianthemum bifolium*, *Anemone nemorosa*, *Hepatica nobilis*, *Listera ovata* and *Rubus saxatilis* and dominant ground-layer species were *Hylocomium splendens and Ptilium crista-castrensis*. The average thickness of the humus layer was 5.2 cm. The soil pH (H_2O) was between 6.7 and 7.9. The raw-humus layer was extensively developed (Lundin et al. 2004).

The sequential core method (Vogt and Persson 1991) was used to describe root distribution with depth (in the LFH-horizon and mineral soil layer as deeply as possible) of both live and dead fine roots in

Table 1 Site characteristics of the fresh/moist coniferous fern forest site at Forsmark (cf. Persson and Stadenberg 2007, 2008)

Latitude, longitude	E 60° 22′ N, 18° 11′ W
Mean annual temperature	5.5°
Mean precipitation (mm)	758
Vegetation period (No of days >5°C)	199
Soil pH (H_2O) in the humus layer 0–30 cm	6.7
Soil pH (H_2O) in the mineral soil 0–10 cm	7.2
Soil pH (H_2O) in the mineral soil 10–20 cm	7.4
Soil pH (H_2O) in the mineral soil 55–65 cm	7.9
Soil type (Lundin et al. 2004)	Regosol/Gleysol
Vegetation type (Nord. Ministerråd 1978)	Coniferous fern type
Number of trees (ha^{-1})	780
Basal area (m^2 ha^{-1})	20.5 (*Picea abies*), 6.5 (*Betula verrucosa*)
Aboveground forest tree litterfall (gm^{-2} yr^{-1}; Mjöfors et al. 2007)	135
Tree age (years)	80–88
Tree height (m)	19.8
Dominant height at 100 years (Hägglund 1973)	G 20
Diameter at breast height (dbh in cm)	26
Above-ground field-layer biomass (g m^{-2} ; Löfgren 2005)	24
Dominant field-layer species	*Maianthemum bifolium, Anemone nemorosa, Hepatica nobilis, Listera ovata, Rubus saxatilis*
Dominant ground-layer species	*Hylocomium splendens, Ptilum crista-castrensis*

terms of dry weight. The depth distribution of roots of tree and field-layer species was measured, at depth intervals of 0–2.5 (H1), 2.5–5 (H2), 5–10 cm (H3) of the LFH horizon and in 10 cm segments (M1–M3) for the mineral soil profile down to 30 cm.

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. The sampling interval between the 2nd and 3rd sampling was more than 3 month, why fluxes in live and dead fine roots and turnover are underestimated during that period. A cylindrical 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 area, within which the soil corer was taken, was chosen with the help of a sharp iron stick driven down into the soil profile. An increased concentration of roots along the surface area of the stones should be expected in the forest soil. These roots were not completely included in the soil samples by the soil corer. On the other hand, the method of deliberately choosing the sampling area by the help of the iron stick to some extent causes an overestimation of the fine roots in the deeper parts of mineral soil. The soil corer was driven to a depth where only few root fragments were sampled in the deepest soil layer (cf. Persson and Stadenberg 2009).

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 soil samples were transferred into plastic bags and transported 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).

The roots were sorted out from the soil cores immediately after thawing. In order to distinguish live roots from dead roots morphological characteristics were used (Vogt and Persson 1991). Separation into live and dead categories was carried out for both tree roots and roots and rhizomes of other vascular species (dwarf shrubs, herbs and grasses). It is essential to use distinct criteria while sorting the root fragments. Live fine roots were defined as roots with a varying degree of brownish/suberized tissues, often well branched, with the main part of the root tips light and turgid or changed into mycorrhizal root tips (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 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 h).

Roots were classified into the following root diameter fractions: <1, 1–2, 2–3, 3–4, and 4–5 and 5–10 mm and separated into tree and field-layer species. The following diameter fractions are only reported here: <1 and <2 mm. Additional data for larger diameter fractions are available in Persson and Stadenberg 2007, 2008, 2009. The diameter separation was carried out for both tree roots and roots and rhizomes of other vascular species (dwarf shrubs, herbs and graminaceous 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).

Mycorrhizal root tips and long root tips in our study were included within the <1 or <2 mm diameter range. The selection of fine roots and rhizomes were unbiased; all fragments were sampled without specification to special roots, species or branching orders etc. (cf. Persson 1979; Pregitzer et al. 2002; Xiangrong et al. 2007).

The fine-root production and turnover rates were calculated from significant (Student's t-test) increments of live and dead fine roots. The t-statistic assumes that the individual data values are normally distributed. Since the distribution pattern of fine roots in the different soil cores was symmetric, the large number of samples (n=32) were expected to result in means which are normally distributed. Comprehensive descriptions of calculation methods used are to be found in (Persson 1978; Persson 1980a). By turnover, in this context, was meant the annual fluxes in the live or dead fine-root compartment. Root turnover rate (yr^{-1}) was calculated as annual increments in live and dead fine roots divided by the mean of each of these compartments during the year. We used mean live and mean dead instead of minimum or maximum estimates of these categories during the period of investigation to calculate turnover rates (cf. Eissenstat and Yanai 2002).

Data from our sequential coring program of fine roots were used for our calculations of turnover rates. These calculations give minimum estimates since the sampling frequency (on four sampling occasions) covered only some of the major fluctuations, but not all increases. On the other hand, the risk for overestimation (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 and a high number of samples on each sampling occasion (Persson 1978; Persson 1980a).

Results

The growth-pattern of the fine roots seemed to depend on where in the soil they were developed. Live tree-fine roots (<1 mm in diameter) were concentrated to the uppermost part of both the humus and mineral soil layers respectively (Tables 2; Fig. 1). In most soil layers, except for in the deepest ones, the live amount of tree fine roots was extensively developed compared with dead fine roots. 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. The high density of fine roots (g dm^{-3}) emphasized the importance of those soil horizons for fine-root development (Fig.1). Relatively more roots and rhizomes of field-layer species were concentrated to the humus layer than tree roots (Table 2). Most tree roots were found in the top 10 cm of the mineral soil. Consequently the tree roots were only to a limited extent influenced by the competition from field-layer species.

A substantial seasonal variation in the amount of live and dead tree fine roots was observed in all soil horizons (Table 2). The live/dead ratio decreased in the mineral soil substantially with depth (Table 3). Most fine roots (both live and dead) were found in the mineral soil. The highest live/dead ratio of tree fine roots <1 mm in diameter (0.8–8.0) was found in the uppermost 2.5 cm humus layer, the lowest ratio (0–0.3) in the deepest part of the mineral soil horizon. This distribution pattern was found for both fine roots <1 mm and <2 mm in diameter (Table 3).

A higher live/dead ratio was found in the humus layer than in the mineral soil for both tree roots and roots and rhizomes of field-layer species for all root fractions (Table 3). In the forest soil, the live tree fine-roots are subsequently changed into dead fine-roots and the dead fine roots into soil organic matter. The live/dead ratio of the fine roots gives an indication of the rate of growth and death in different soil horizons and may be used as a vitality criterion.

A substantial seasonal variation during the year in the amount of dead and dead tree fine roots was observed in all soil horizons (Table 2). The mean amounts of live fine roots of tree species for the total soil profile on the four sampling occasions were 317, 113, 150 and 248 g m^{-2} for <1 mm and 410, 225, 224 and 358 g m^{-2} for <2 mm fine roots. The related mean amounts of dead fine roots for <1 and <2 mm diameter fine roots were 226, 321, 176 and 299 g m^{-2} and 294, 424, 282 and 389 g m^{-2}, respectively. A higher live/dead ratio was found in the humus layer than in the mineral soil for both tree roots and roots and rhizomes of field-layer species for all root fractions (Table 3).

The live/dead ratio of the fine roots gives an indication of the rate of growth and decomposition in different soil horizons and may be used as a vitality criterion. The live/dead ratio was increasing with a larger diameter both for the fine roots of tree and for field-layer species (Table 3). The fluctuations in the live/dead ratio were reflected in the amounts of live and dead fine roots during the period of investigation (Table 2). High amounts of live fine roots were then followed, on the next sampling occasion, by high amounts of dead fine roots.

The field-layer vegetation was extensively developed in this fairly open forest site (780 trees/ha); the above ground dry weight of the field layer was 24 g m^{-2} at the time of peak development (Löfgren 2005; Table 1). The amount of live fine roots of the field layer species was significantly decreasing during

Table 2 The dry weight distribution (g m^{-2}) of fine roots (<1 mm in diameter) at different depths and in different soil layers (H=humus; M=mineral soil) during a year at the fresh/moist coniferous fern forest site at Forsmark. The average thickness of the humus layer was 5.2 cm. The corer was driven as deeply as possible into the deepest mineral soil layer

Sampling	Horizon	Tree species	Dead	Field-layer species	
	Depth (cm)	Live		Live	Dead
(1)	H 0–2.5	30±35	4±5	15±23	1±2
	H 2.5–5	4±12	4±11	1±6	8±22
	H 5–10	2±6	3±10	4±21	–
	M 0–10	228±138	136±70	74±55	36±122
	M 10–20	51±67	73±60	14±15	3±6
	M 20–30	2±8	5±15	1±4	–
	H	35±44	11±23	27±49	2±6
	M	272±190	208±91	88±58	39±122
	H+M	317±196	226±88	115±87	41±122
(2)	H 0–2.5	17±28	23±25	18±21	3±4
	H 2.5–5	4±14	4±12	4±11	1±2
	H 5–10	–	–	–	–
	M 0–10	69±62	195±141	69±90	42±70
	M 10–20	19±24	83±55	9±10	6±9
	M 20–30	4±8	15±25	1±2	1±2
	H	21±33	27±27	22±26	4±4
	M	91±73	294±183	78±90	49±74
	H+M	113±79	321±184	99±93	52±74
(3)	H 0–2.5	24±24	6±7	8±14	2±4
	H 2.5–5	–	–	–	–
	H 5–10	–	–	–	–
	M 0–10	104±89	111±50	60±39	19±19
	M 10–20	22±34	62±40	12±15	3±7
	M 20–30	–	2±6	0	0
	H	24±24	6±7	8±14	2±4
	M	127±104	169±62	69±49	22±21
	H+M	150±112	176±70	78±56	24±21
(4)	H 0–2.5	27±30	8±11	9±11	2±4
	H 2.5–5	1±3	–	1±3	–
	H 5–10	–	–	–	–
	M 0–10	152±100	188±103	66±53	30±32
	M 10–20	69±54	101±50	10±10	5±11
	M 20–30	–	2±8	–	–
	H	27±31	8±11	9±12	2±5
	M	220±123	291±133	76±60	35±40
	H+M	248±134	299±136	85±65	37±41

Estimates are given as mean values ± SD (n=32). Sampling took place on four sampling occasions: October 20th, 2004 (1), April 18th, 2005 (2), August 2nd, 2005 (3) and October 28th, 2005 (4)

the period of study, suggesting that only few new roots and rhizomes were formed (Table 2). The mean dry weight of live fine roots (<1 mm in diameter) of the field-layer species was 115, 99, 78 and 85 g m^{-2} on the different sampling occasions (Table 2). The related amount of dead fine roots was 41, 52, 24 and 37 g m^{-2}. Proportionally less dead fine-roots was observed for field-layer species than for trees.

As a result of the heavy seasonal fluctuations of the tree fine roots, high amounts of live fine roots were continuously transferred into dead fine roots. These fluctuations did not occur concurrently in the humus

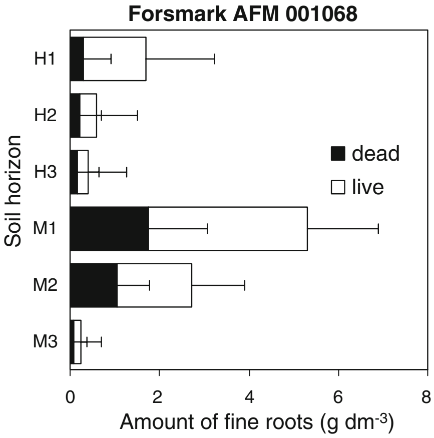

Fig. 1 The amount of live and dead fine roots (g/dm^{-3}) in different soil horizons on the first sampling occasion in October 20th, 2004. The depth intervals in the humus layer are of H1= 0–2.5 cm, H2=2.5–5 cm, H3=5–10 cm (the average depth was 5.2 cm). The mineral soil was separated into 10 cm segments (M1, M2 and M3)

and mineral soil horizons. A most substantial production in live fine-roots (<1 mm and <2 mm in diameter) of 135 g m^{-2} and 134 g m^{-2} was calculated during the year of investigation (Table 2 and 4). The related accumulation of dead fine-roots was furthermore substantial, *viz.* 214 g m^{-2} and 237 g m^{-2}. In all cases conservative estimates of the annual fine-root production and accumulation in dead fine roots were calculated since changes in the amount of fine roots occurring between the different sampling occasions were not included in these figures. The accumulation of dead fine roots exceeded the annual litterfall from needles and other above-ground components returned to the forest floor, which amounted to 135 g m^{2} (Mjöfors et al. 2007).

In forest ecosystems, at a steady state, it is reasonable to assume that the annual accumulation of fine roots should be in the same order in terms of dry weight for the live and dead. In our investigation, this was more or less the case. The turnover rates of tree fine-roots <1 mm in diameter for the total soil profile were 0.7 yr^{-1} for live and 0.8 yr^{-1} for dead fine roots, respectively. The related figures for fine roots <2 mm in diameter were 0.4 yr^{-1} and 0.7 yr^{-1}. The turnover rate of <1 mm fine roots seems to be faster than of <2 mm fine roots.

The most substantial turnover of tree fine roots took place in the mineral soil, where 86, 81, 85 and 89% of live fine roots <1 mm were distributed. The related figures for fine roots <2 mm in diameter were 89, 88, 89 and 92%, respectively. It was impossible, in our case to calculate significant turnover rates of large diameter roots (2–10 mm in diameter) due to their high variability.

Discussion

Fine-root characteristics such as the amount of live and dead fine roots (g m^{-2}), rooting density (g dm^{-3}) and the live/dead ratio depend on a variety of abiotic and biotic factors specific for different forest stands. The amounts of live and dead tree fine roots at our site (113–317 g m^{-2} for live and 176–321 g m^{-2} for dead fine roots <1 mm in diameter and 224–410 g m^{-2} for live and 282–424 g m^{-2} for dead fine roots <2 mm in diameter) did not differ from other European *Picea abies* stands, taking into consideration the high seasonal variability of the fine roots. The amount of live fine roots at our site is slightly over the range of 184–370 g m^{-2} for live fine roots (<2 mm in diameter) in 8 *Picea abies* stands throughout Finland (Helmisaari et al. 2007). Low amounts of fine roots were obtained in a 60 year old fertile *Picea abies* stand in Estonia of 94 and 137 g m^{-2} live fine roots and 142 and 154 g m^{-2} for dead fine roots, <1 and <2 mm in diameter, respectively (Ostonen et al. 2005). Low mean amounts of fine roots of live and dead fine roots were obtained on five sampling occasions in a 93 year old *Picea abies* stand in France at the northeastern side of the Vosges Mountains (67 and 56 g m^{-2} for live and dead fine roots <1 mm in diameter; Stober et al. 2000).

The mean amounts of live fine roots (<1 mm in diameter) in *Picea abies* chronosequence in southeast Norway 10, 30, 60 and 120 years of age, were 22, 217, 107 and 75 g m^{-2}, respectively (Børja et al. 2008). The mean amounts of live fine roots (<2 mm in diameter) from two sampling occasions, in spring and autumn, in four German *Picea abies* stands, 5, 24, 42 and 97 years of age, were 119, 497, 399 and 346 g m^{-2} (Claus and George 2005). There was a clear effect of stand age on fine-root biomass in the latter study, confirmed also by two more forest chronosequences of similar age dominated by *Fagus sylvatica* and *Quercus robur*, suggesting that the highest amounts of live fine root are in the adult but not mature stands.

The live/dead ratio in the total soil profile for tree fine roots <1 mm in diameter from our site (range

Table 3 The live/dead ratio of fine roots <1 and <2 mm in diameter at different depths (H=humus; M=mineral soil) at the fresh/moist coniferous fern forest site at Forsmark

Sampling	Horizon	Tree roots	<2	Roots and rhizomes of field-layer species	
	Depth (cm)	<1		<1	<2
(1)	H 0–2.5	8.04	6.69	23.88	9.95
	H 2.5–5	1.01	0.95	5.73	6.79
	H 5–10	0.64	1.41	–	–
	M 0–10	1.67	1.75	2.07	4.67
	M 10–20	0.70	0.72	4.58	4.67
	M 20–30	0.34	0.37	31.18	34.30
	H	3.18	2.94	13.50	10.33
	M	1.31	1.31	2.26	2.59
	H+M	1.40	1.29	2.80	3.14
(2)	H 0–2.5	0.76	0.86	6.00	7.56
	H 2.5–5	0.99	1.07	5.79	2.93
	H 5–10	–	–	–	–
	M 0–10	0.35	0.51	1.62	1.90
	M 10–20	0.23	0.51	1.52	1.06
	M 20–30	0.23	0.37	0.82	2.65
	H	0.78	0.90	5.50	6.80
	M	0.31	0.50	1.59	1.78
	H+M	0.35	0.53	1.90	2.14
(3)	H 0–2.5	4.30	3.48	4.11	4.52
	H 2.5–5	–	–	–	–
	H 5–10	–	–	–	–
	M 0–10	0.93	0.94	3.19	3.04
	M 10–20	0.36	0.42	3.51	3.23
	M 20–30	0	0.34	0	0
	H	4.00	3.43	4.00	5.00
	M	0.75	0.73	3.14	3.12
	H+M	0.85	0.79	3.25	3.14
(4)	H 0–2.5	3.25	2.70	5.44	6.83
	H 2.5–5	–	–	1.47	2.60
	H 5–10	–	–	–	–
	M 0–10	0.81	0.90	2.22	2.45
	M 10–20	0.68	0.81	1.80	1.79
	M 20–30	–	–	–	–
	H	3.38	2.81	4.50	6.00
	M	0.76	0.86	2.17	2.37
	H+M	0.83	0.92	2.43	2.53

Sampling took place on four sampling occasions: October 20th, 2004 (1), April 18th, 2005 (2), August 2nd, 2005 (3) and October 28th, 2005 (4). Soil core samples with only very small amounts of either live or dead fine-root fragments are indicated by "–"

0.4–1.4) for all four sampling occasions was within the range of equivalent data (<1 mm in diameter) for other *Picea abies* forest stands (Table 5). Nor did the live/dead ratio calculated for tree fine roots <2 mm in diameter (range 0.5–1.4) differ very much. Nevertheless, the contribution of different diameter classes and species to the general growth pattern of roots in the soil may vary considerable.

Our investigation confirms the quantitative importance of the fine roots of field-layer species in an open forest site (Table 2). In the boreal forest ecosystems trees are frequently sparsely distributed and a sub-

Table 4 The amount of live and dead fine roots (<1 mm and <2 mm in diameter) on different sampling occasions, annual means, production of live and accumulation of dead fine roots (Σ increases) and the turnover rate in the total soil profile at the fresh/moist coniferous fern forest site at Forsmark

Diameter/Sampling	Live	Dead
<1 mm		
(1)	317±196	226±88^a
(2)	113±79^a	321±184^a
(3)	150±112	180±62^b
(4)	248±134^a	299±136^b
Annual means	207	257
Σ Increases	135	214
Turnover rate	0.7	0.8
<2 mm		
(1)	410±207	294±107^a
(2)	225±162	424±184^a
(3)	224±162^a	282±98^b
(4)	358±176^a	389±174^b
Annual means	303	345
Σ Increases	134	237
Turnover rate	0.4	0.7

Sampling took place on four sampling occasions: October 20th, 2004 (1), April 18th, 2005 (2), August 2nd, 2005 (3) and October 28th, 2005 (4). Estimates are given as mean values ± SD (n=32). Significant increases are marked by ^{a} and ^{b}, respectively. Differences are significant at p=0.005 (Student's t-test)

stantial field layer is developed (cf. Persson 1978; Palviainen et al. 2005; Helmisaari et al. 2007; Persson and Stadenberg 2009). The low tree density, at our site, favoured the development of a luxurious field layer. Investigations carried out in *Calluna* heathland stands suggested a high root turnover rate as a key factor in C, N, and P cycling (cf. Aerts et al. 1992). In oligotrophic mire sites in the Southern Taiga roots of herbs and shrubs show a high contribution (48–55%) to the total carbon storages (cf. Golovatskaya and Dyukarev 2009). The high live/dead ratio of the fine roots and rhizomes of the field layer species in our investigation (Table 5) suggests that they stayed alive longer than tree fine roots, with a lower turnover rate.

Substantial variations in live and dead fine roots and live/dead ratios usually occur in tree stands depending on site quality (Helmisaari et al. 2007; Ostonen et al. 1999; Persson 2002; Persson and Ahlström 2002; Persson and Stadenberg 2009; Raich and Nadelhoffer 1989; Stober et al. 2000; Vogt et al. 1983). Varying climatic and environmental factors influence the rate of changes from one sampling occasion to another and between years. Available information in literature on the live/dead ratios of fine roots of *Picea abies* from measurements in the field is substantial (Table 5).

Fine-root "vitality" in terms of live/dead ratios of the fine roots should be expected to be high especially in the humus layer (cf. Brundrett 2002; Durall et al. 1994; Hooker et al. 1995). The presence of soil organic matter improves the nutrient availability and reduces soil strength. Tree fine roots are highly dependent on the mycorrhizae for their nutrient uptake (cf. Brundrett 2002; Marschner 2002). Roots can be damaged by herbivores, pathogens, but also by drought, water saturation, frost and wind movements (Bloomfield et al. 1996; Hendricks et al. 2000; Pregitzer et al. 2000).

High concentrations of dead fine roots in the mineral soil may be a result of a high death rate and a slow rate of decomposition (Table 3). Low amounts of dead fine roots are most frequently found in the humus layer in most forest sites (cf. e.g. Helmisaari et al. 2007; Makkonen and Helmisaari 1999; Persson 1983; Persson and Stadenberg 2009). Although the amounts of dead fine roots may be low, a high turnover rate of fine roots should be expected in humus layer. Thus, Persson and Stadenberg (2009) investigating six different Swedish forest stands, including our present stand, observed a high accumulation of dead fine roots in the humus layer of two of the water saturated forest stands. In the latter two wet forest stands, a high death rate and a low decomposition rate of fine roots due to oxygen deficiency caused an accumulation of dead roots in the humus layer and in the whole soil profile, not to be found to such an extent in the other forest stands.

Fine roots are intensively penetrating wet and nutrient rich horizons. Subsequent changes in the live/dead ratios of fine-roots are frequently connected with soil water availability. Plant root systems can rapidly change their spatial pattern of water uptake in response to increased water availability (Čermák et al. 1993; Nadezhdina et al. 2006). But fine roots are sensitive to drought and their live/dead ratios are decreasing with less water availability (cf. Olsthoorn 1991; Persson et al. 1995b; Puhe et al. 1986; Santantonio et al. 1977; Santantonio and Hermann 1985). Under summer

Table 5 The amount of live and dead fine roots (DW g m^2) and live/dead ratios in some natural *Picea abies* forest stands of fine roots <1 mm and <2 mm in diameter

Diameter (mm)	Stand age	Live	Dead	Live/dead ratio	References
<1	28	273	728	0.4	Persson et al. (1995a)
<1	31	131	253	0.5	Püttsepp et al. (2006)
<1	35	134	391	0.3	van Praag et al. (1988)
<1	55	371	245	1.5	Persson and Stadenberg (2009)
<1	59–60	267	119	2.2	–
<1	60	94	137	0.7	Ostonen et al. (2005)
<1	80–100	173	234	0.7	Persson and Ahlström (2002)
<1	80–100	119	250	0.5	–
<1	80–100	167	135	1.2	–
<1	80–100	194	184	1.0	–
<1	80–100	220	106	2.2	–
<1	80–88	317	226	1.4	This study
<1	80–88	113	321	0.4	–
<1	80–88	150	180	0.8	–
<1	80–88	248	299	0.8	–
<1	93	70	45	1.6	Stober et al. (2000)
<1	93	63	64	1.0	–
<1	93	56	38	1.5	–
<1	93	40	37	1.1	–
<1	93	57	97	0.6	–
<2	10	108	65	1.7	Puhe (1993)
<2	18	197	105	1.9	–
<2	28	238	168	1.4	–
<2	13	154	4875	0.3	–
<2	22	227	238	1.0	–
<2	23	181	394	0.5	–[1]
<2	26	492	174	2.8	Majdi and Persson (1993)
<2	40	276	381	0.7	Roehrig Hansen and Thomsen (1991)
<2	45	301	363	0.8	–
<2	53	273	297	0.9	Murach and Schünemann (1985)
<2	55	499	344	1.5	–
<2	60	142	154	0.9	Ostonen et al. (2005)
<2	62	440	150	2.9	Murach et al. (1993)
<2	62	345	130	2.7	–
<2	59–60	365	167	2.2	Persson and Stadenberg (2009)
<2	66	725	1719	0.4	Roehrig Hansen and Thomsen (1991)
<2	85	220	74	3.0	Ulrich et al. (1984)
<2	80	360	330	1.1	Puhe et al. (1986)
<2	80–88	410	294	1.4	This study
<2	80–88	225	424	0.5	–
<2	80–88	224	282	0.8	–
<2	80–88	358	389	0.9	–
<2	106	350	170	2.1	Puhe et al. (1986)
<2	115	510	260	2.0	–

drought they die back to a great extent, but they are rapidly recovered if environmental conditions become more favourable (Puhe et al. 1986; Santantonio and Hermann 1985; Persson 1978). Sporadically occurring rain showers affect the upper soil layers during the summer months and a high rate of death and decomposition of fine roots should be expected temporarily (cf. Bowen 1991; Gaul et al. 2008).

Root production of fine roots, live/dead ratios and mineral nutrient concentrations are strongly influenced by nitrogen availability in the soil, which also affects the rate of decomposition of root litter (King et al. 2002; Persson 1980a; Persson 1980b; Pregitzer et al. 2000; Pregitzer et al. 2002; Puhe 2003; Vanguelova et al. 2005). Root proliferation in nutrient-rich patches is an important mechanism increasing nutrient capture by plants (Bowen 1984, Gross et al. 1993; Moar and Wilson 2006; Pregitzer et al. 1993). Nitrogen tends to limit plant growth on young soils in young postglacial soils in Western Europe and North America, while phosphorous becomes more limiting in other ancient soil types exposed to long-range weathering and erosion (Lambers et al. 2008).

Tree fine roots are concentrated with regards to dry weight and length in diameters <1 mm (Ford and Deans 1977; Persson 1978; Roberts 1976; Vogt and Persson 1991). Available information in literature suggests a high fine root production with a seasonal pattern different from needle or leaf production (cf. e.g. Bakker et al. 2000; Finér et al. 2007; Helmisaari et al. 2007; Janssen et al. 2002; Makkonen and Helmisaari 1999; Persson 1983; Tateno et al. 2004).

Fine-root data from several *Picea abies* forest stands, suggest high turnover rates of live and dead fine roots. Thus, van Praag et al. (1988) reported substantial turnover rates in a 80–88 year old stand in Belgium of 1.0 yr^{-1} for live fine roots and 1.0 yr^{-1} and dead fine roots (<2 mm in diameter). Stober et al. (2000) calculated turnover rates of 0.3 yr^{-1} for live and 0.5 yr^{-1} for dead fine roots (<1 mm in diameter) in a 120 year old stand in the northern parts of France. Ostonen et al. (2005) obtained a high turnover rate of 1.8 yr^{-1} for live fine roots (<2 mm in diameter) in a fertile 60-year old stand in Estonia. The latter authors furthermore, reported a turnover rate of 1.4 yr^{-1} of fine roots in ingrowth cores installed in the same stand. From these data we may conclude that in *Picea abies* forest stands, the turnover in the amounts of live or dead fine-roots may exceed their annual means.

Tree fine roots enrich the soil with organic matter and nutrients and they may quantitatively play a more important role than the needles/leaves (Helmisaari et al. 2007; Persson 1978; Ruess et al. 1996; Ruess et al. 2003; Scheffer and Aerts 2000; Scarascia-Mugnozza et al. 2000; Vanninen and Mäkelä 1999). Trees maintain a large and more resistant fine-root system at poor forest sites at the expensive of above-ground growth (Ares and Peinemann 1992; Bloomfield et al. 1996; Persson 2002; Helmisaari et al. 2002).

The root function is costly and is enhanced by a high carbohydrate supply (Ågren et al. 1980; Ericsson and Persson 1980; Hallgren et al. 1991; Johansson 1993; Kobe 1997; Langley et al. 2002; Lippu 1998; Marshall and Waring 1985; Oren et al. 1988). High starch reserves are accumulated in tree roots, supporting a high turnover rate (Ericsson and Persson 1980). The below-ground starch reserves are mobilized at the time of root growth and shoot elongation (cf. Ericsson and Persson 1980; Marshall and Waring 1985). Confounding effects of the starch storage in the entire tree root systems, limited knowledge of translocation and transport of carbohydrate between different root tissues, make it difficult to conclude anything about the actual carbon residence times in different root tissues (cf. Matamala et al. 2003; Strand et al. 2008; Trumbore and Gaudinski 2003).

Concluding remarks

Amounts of fine roots and fine-root production in forest ecosystem vary with tree species, tree density and soil fertility. The long-lived woody framework of structural roots of forest trees support a mass of short-lived nonwoody fine roots associated with mycorrhizal fungi. Fine-root growth is the result of metabolic processes and therefore regulated by soil temperature and soil water conditions. Our understanding of the turnover rates of fine roots under field conditions in forest ecosystems is still incomplete, as well as the mechanisms of root litter formation (cf. Gill and Jackson 2000; Helmisaari et al. 2002; Meier and Leuschner 2008; Persson 1978; Richter et al. 2007; Vogt et al. 1983). Research into root senescence is complicated by the fact that cessation of root penetration is not synonymous with root death (Durall et al. 1994; Enstone et al. 2001; Leshem 1965; Taylor and Peterson 2000; Wilcox 1954).

There is always a vital root and mycorrhizal proliferation in the upper parts of the soil profile. Mycorrhizal root tips are morphologically very different from non-infected root tips and they constitute a high proportion of the total number of root tips. A large part of the fungal mycelium is outside the root; the longevity of these hyphae was shown by different investigators to be very short. Much more work is still needed to quantify the role of mycorrhizas in the carbon budgets of forests.

Correct methods for estimating the amount of live and dead fine-roots in the forest soil are essential for any calculation of average amounts of fine roots (mycorrhizal and non-mycorrhizal) and turnover rates. Results from our investigations clarify the importance of using distinct morphological criteria when sorting fine roots into live and dead tissues. Our investigation revealed that amounts of live and dead fine roots vary greatly with respect to season, distribution in the soil profile and vegetation components. The live/death ratio of the fine roots in this context reflected the vitality of the fine roots, both temporarily and spatially in the soil profile.

The highest live/dead ratio in our study was found in the top of the humus layer for both the tree and field-layer species, and the lowest in the deepest part of the mineral soil. On the other hand, a substantial amount of the root dry weight was concentrated to the mineral soil horizon. Average live/dead ratios from different *Picea abies* forest ecosystems confirm that live/dead ratios in our investigation were within the range of available data in literature. The live/dead ratio was proved to be a powerful vitality criterion of fine roots, revealing when new roots are formed.

Our methods of estimating fine-root production and the average amount of fine roots, involved periodic measurements of live and dead dry weight of the fine roots from sequential core samples of the forest soil. These data give instant measure of the spatial and temporal distribution of fine roots in the undisturbed soil-profile. The methods of estimating fine-root production, mortality and turnover in the field should involve the periodic measurements of both live and dead dry weights of fine roots in undisturbed soil horizons.

Fine-root data (<1 mm or <2 mm in diameter) from *Picea abies* forest ecosystems suggest substantial production and turnover rates of live and dead fine roots in relation to the average values of those categories. All calculated turnover rates are conservative since growth occurring between sampling occasions are not be included. Our turnover rates (0.7 and 0.8 of fine roots <1 mm and 0.6 and 0.7 of fine roots <2 mm in diameter respectively) were obtained from four sampling occasions during a period of one year. The contribution of different diameter classes and species to the general growth pattern of roots in the soil may vary considerable.

The annual production of fine roots in *Picea abies* forest stands may amount to or exceed the average amount of live fine roots during the same year.

Quantification of the amounts of fine roots is highly desirable due to their important role as carbon sinks and sources of input of soil organic matter to the soil. It is essential to obtain data from sequential coring, if an instant measure of the spatial and temporal distribution of roots in the undisturbed soil profile is a primary goal. The sampling frequency should preferable cover the main fluctuations during the growth period. A sufficient number of sequential soil cores must be excavated on each sampling occasion in order to detect significant changes.

The root function is extremely costly and is enhanced by a high carbohydrate supply. Besides the forest trees, the field-layer species in forest stands are heavy contributors of soil organic matter. High annual fluctuations in fine-root growth and turnover rates are to be found in forest stands of different age, tree density and vegetation type.

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References

Aerts R, Bakker C, de Caluwe H (1992) Root turnover as determinant of the cycling of C, N and P in a dry heathland ecosystem. Biogeochemistry 15:175–190

Agerer R (ed) (1987–2002) Colour Atlas of Ectomycorrhizae. Einhorn-Verlag, Eduard Dietenberger Gmbh, Germany

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

Ares A, Peinemann N (1992) Fine-root distribution of coniferous plantations in relation to site in southern Buenos Aires, Argentina. Can J For Res 22:1575–1582

Bakker M (1998) Effet des amendements calciques sur les racines fines de chêne (*Quercus petrea* et *robur*): conséquences des changements dans la rhizosphère. Doctoral thesis I'Université Henri Poincaré, Nancy

Bakker MR (1999) The effect of lime and gypsum application on a sessile oak (*Quercus petrea* (M.) Liebl.) stand at La Croix-Scaille (French Ardennes) II. Fine root dynamics. Plant Soil 2006:109–121

Bakker MR, Garbaye J, Nys C (2000) Effect of liming on the ectomycorrhizal status of oak. For Ecol Manage 126:121–131

Bakker MR, Augustin L, Achat DL (2006) Fine root distribution of trees and understory in mature stands of maritime pine (*Pinus pinaster*) on dry and humid sites. Plant Soil 286:37–51

Bloomfield J, Vogt K, Wargo PM (1996) Tree root turnover and senescence. In: Waisel Y, Eshel A, Kafkafi U (eds) Plant Roots – the Hidden Half, 2nd edn. pp 363–384

Børja I, De Wit HA, Steffenrem A, Majdi H (2008) Stand age and fine root biomass, distribution and morphology in a Norway spruce chronosequence in Southeast Norway. Tree Physiol 28:773–784

Borken W, Kossmann G, Matzner E (2007) Biomass, morphology and nutrient contents of fine roots in four Norway spruce stands. Plant Soil 292:79–92

Bowen GD (1984) Tree roots and the use of nutrients. In: Bowen, GD, Nambiar, EKS (eds) Nutrition of plantation forests, pp 147–179

Bowen GD (1991) Soil temperature, root growth, and plant function. In: Waisel Y, Eshel A, Kafkafi U (eds) Plant Roots – the Hidden Half, 1st edn. pp 309–330

Brundrett MC (2002) Coevolution of roots and mycorrhizas of land plants. New Phytol 154:275–304

Čermák J, Matyseek R, Kucera J (1993) Rapid response of large, drought stressed beech trees to irrigation. Tree Physiol 12:281–290

Cheng W, Johnson DW, Fu S (2003) Rhizosphere effects on decomposition: controls of plant species, phenology and fertilization. Soil Sci Soc Am J 67:1418–1427

Claus A, George E (2005) Effect of stand on fine-root biomass and biomass distribution in three European forest chronosequences. Can J For Res 35:1617–1625

Clemensson-Lindell A, Persson H (1992) Effects of freezing on rhizosphere and root nutrient content using two soil sampling methods. Plant 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 Soil 168–169:167–171

Daldoum MA, 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

Durall DM, Marshall JD, Jones MD, Crawford R, Trappe JM (1994) Morphological changes and photosynthate allocation in ageing *Hebeloma crustuliniforme* (Bull.) Quel. and *Laccaria bicolor* (Maire) Orton mycorrhizas of *Pinus ponderosa* Dougl. ex. Laws. New Phytol 127:719–724

Eissenstat DM, Yanai RD (2002) Root life span, efficiency, and turnover. In: Waisel Y, Eshel A, Kafkafi U (eds) Plant Roots – the Hidden Half, 3rd edn. pp 221–238

Enstone DE, Peterson CA, Hallgren SW (2001) Anatomy of seedling tap roots of loblolly pine (*Pinus taeda* L.). Trees 15:98–111

Ericsson A, Persson H (1980) Seasonal changes in starch reserves and growth of fine roots of 20-year old Scots pines. Ecol Bull Stockh 32:239–250

Finér L, Helmisaari HS, Lohmus K, Madji H, Brunner I, Borja I, Eldhuset T, Godbold D, Grebenc T, Konopka B, Kraigher H, Mottonen MR, Ohashi M, Oleksyn J, Ostonen I, Uri V, Vanguelova E (2007) Variation in fine root biomass of three European tree species: beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* L. Karst.) and Scots pine (*Pinus sylvestris* L.). Plant Biosystems 141:394–405

Fontaine S, Mariotti A, Abbacies L (2003) The priming effect of organic matter: a question of microbial competition? Soil Biology & Biochemistry 35:837–843

Fontaine S, Bardoux G, Abbadie L, Mariotti A (2004) Carbon inputs to soil may decrease soil carbon content. Ecol Lett 7:314–320

Ford ED, Deans JD (1977) Growth of a Sitka Spruce Plantation: spatial distribution and seasonal fluctuations of lengths, weights and carbohydrate concentrations of fine roots. Plant Soil 47:463–485

Gaul D, Hertel D, Borken W, Matzner E, Leuschner C (2008) Effects of experimental drought on the fine root system of mature Norway spruce. For Ecol Manage 256:1151–1159

Gill R, Jackson RB (2000) Global patterns of root turnover for terrestrial ecosystems. New Phytol 147:13–31

Golovatskaya EA, Dyukarev EA (2009) Carbon budget of oligotrophic mire sites in the Southern Taiga of Western Sibiria. Plant Soil 315:19–34

Gross KI, Peters A, Pregitzer KS (1993) Fine root growth and demographic responses to nutrient patches in four old-field plant species. Oecologia 95:61–64

Hägglund B (1973) Om övre höjdens utveckling för gran i södra Sverige. Royal Coll For, Dept For Yield Res, Res Notes 24, 49 pp

Hallgren SW, Taver CG, Lock JE (1991) Fine root carbohydrate dynamics of loblolly pine seedlings grown under contrasting levels of soil moisture. For Sci 37:766–780

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

Helmisaari H, Helmisaari H-S (1992) Long-term forest fertilization experiments in Finland and Sweden. Swed Environ Prot Agency Rep 4099, 123 pp

Helmisaari H-S, Makkonen K, Kellomäki S, Valtonen E, Mälkönen E (2002) Below- and above-ground biomass, production and nitrogen use in Scots pine stands in eastern Finland. For Ecol Manage 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 Physiol 27:1493–1504

Hendricks JJ, Aber JD, Nadelhoffer KJ, Hallett RD (2000) Nitrogen controls on fine root substrate quality in temperate forest ecosystems. Ecosystems 3:57–69

Hooker JE, Blank KE, Perry RL, Atkinson D (1995) Arbuscular mycorrhizal fungi induced alteration to root longevity of poplar. Plant Soil 172:327–329

Janssen IA, Sampson DA, Curiel-Yuste J, Carrara A, Ceulemans R (2002) The carbon cost of fine root turnover in a Scots pine forest. For Ecol Manage 168:231–240

Johansson T (1993) Seasonal changes in contents of root starch and soluble carbohydrates in 4–5-year old Betula pubescens and Populus tremula. Scand J For Res 8:94–106

John B, Pandey HN, Tripathi RS (2001) Vertical distribution and seasonal changes of fine and coarse root mass in *Pinus kesiya* Royle Ex. Gordon forest of three different ages. Acta Oecol 22:293–300

Kalisz PJ, Zimmermaan RW, Müller RN (1987) Root density, abundance and distribution in the mixed mesophytic forest of eastern Kentucky. Soil Sci Soc Am J 51:220–225

King JS, Albaugh TJ, Allen M, Buford H, Strain BR, Dougherty PM (2002) Below-ground carbon input to soil is controlled by nutrient availability and fine root dynamics in loblolly pine. New Phytol 154:389–398

Kobe RK (1997) Carbohydrate allocation to storage as basis of interspecific variation in sapling survivorship and growth. Oikos 80:236–233

Konôpka B, Yuste JC, Janssens IA, Ceulemans R (2005) Comparison of fine root dynamics in Scots pine and pedunculate oak in sandy soil. Plant Soil 276:33–45

Lambers H, Raven JA, Shaver GR, Smith SE (2008) Plant nutrient-acquisition strategies change with soil age. Trends Ecol Evol 23:95–103

Langley JA, Drake BG, Hungate BA (2002) Extensive belowground carbon storage supports roots and mycorrhizae in regenerating scrub oaks. Oecologia 131:542–548

Leshem B (1965) The annual activity of intermediary roots of the Aleppo pine. For Sci 11:291–298

Linné C von (1772) Deliciae Naturæ. Facsimile copy published in 1954 by Almqvist & Wiksell, Uppsala

Lippu J (1998) Redistribution of ^{14}C-labelled reserve carbon in *Pinus sylvestris* seedlings during shoot elongation. Silva Fennica 32:3–10

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

López B, Sabate S, Gracia CA (2001) Annual and seasonal changes in fine root biomass of a *Quercus ilex* L. forest. Plant Soil 230:125–134

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

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

Makkonen K, Helmisaari H-S (1999) Assessing fine-root biomass and production in a Scots pine stand – comparison of soil core and ingrowth core methods. Plant Soil 210:43–50

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

Marshall JD, Waring RH (1985) Predicting fine root production and turnover by monitoring root starch and soil temperature. Can J For Res 15:791–800

Matamala R, Conzales-Meler MA, Jastrow JD, Norby RJ, Schlesinger WH (2003) Impacts of fine root turnover on forest NPP and soil C sequestration potential. Science 302:1385–1387

Meier IC, Leuschner C (2008) Genotypic variation and phenotypic plasticity in the drought response of fine roots of European beech. Tree Physiol 28:297–309

Mjöfors K, Johansson M-B, Nilsson Å, Hyvönen R (2007) Input and turnover of forest tree litter in the Forsmark and Oskarshamn areas. SKB R-07-23, Svensk Kärnbränslehantering AB

Moar SEL, Wilson SD (2006) Root responses to nutrient patches in grassland and forest. Plant Ecol 184:157–162

Moir WH, Bachelard EP (1969) Distribution of fine roots in three *Pinus radiata* plantations near Canberra, Australia. Ecology 50:658–662

Murach D, Schünemann E (1985) Reaktion der Feinwurzeln von Fichten auf Kalkungsmassnahmen. AFZ 45:1151–1154

Murach D, Klaproth F, Wiedemann H (1993) Feinwurzeluntersuchungen auf den Versuchsflächen des Dach-Expieriments im Solling. Forstarchiv 64:188–191

Nadezhdina N, Cermák J, Gašpárek J, Nadezdin V, Prax A (2006) Vertical and horizontal water redistribution in Norway spruce (*Picea abies*) roots in the Moravian Upland. Tree Physiol 26:1277–1288

Norby RJ, Jackson RB (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 AFM (1991) Fine root density and root biomass of two Douglas-fir stands on sandy soils in the Netherlands. 1. Root biomass in early summer. Netherl J Agric Sci 39:49–60

Oren R, Schulze E-D, Werk KS, Meyer J, Schneider BU, Heilmeier H (1988) Performance of two *Picea abies* (L.) Karst. Stands at different stages of decline. I. Carbon relations and stand growth. Oecologia (Berlin) 75:25–37

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

Ostonen I, Lõhmus K, Pajuste K (2005) Fine root biomass, production and its proportion of NPP in a fertile middle-aged Norway spruce forest: Comparison of soil core and ingrowth core methods. For Ecol Manage 212:264–277

Palviainen M, Finér 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 Soil 275:157–167

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

Persson H (1980b) Fine-root dynamics in a Scots pine stand with and without near-optimum nutrient and water regimes. Acta Phytogeogr Suec 68:101–110

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

Persson H (1996) Fine-root dynamics in forest trees. In: Persson H, Baitulin I (eds) Plant root systems and natural vegetation, pp 17–23

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, Kafkafi U (eds) Plant Roots – the Hidden Half, 3rd edn. pp 187–204

Persson H, Ahlström K (1999) Effect of nitrogen deposition on tree roots in boreal forests. In: Persson H (ed), Going Underground – Ecological Studies in Forest Soils. Commission of the European Communities. Air Poll Rep 32:221–238

Persson H, Ahlström K (2002) Fine-root response to nitrogen in nitrogen manipulated Norway spruce catchment areas. For Ecol Manage 168:29–41

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

Persson, H, Stadenberg I (2008) Growth dynamics of fine roots in a coniferous fern forest site close to Forsmark in the central part of Sweden. SKB TR-07-11, Svensk Kärnbränslehantering AB

Persson H, Stadenberg I (2009) Spatial distribution of fine roots in boreal forest in eastern Sweden. Plant Soil 318:1–14

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

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

Pregitzer KS, Hendrick RL, Fogel R (1993) The demography of fine roots in response to patches of water and nitrogen. New Phytol 125:575–580

Pregitzer KS, King JS, Burton AJ, Brown SE (2000) Responses of tree fine roots to temperature. New Phytol 147:105–115

Pregitzer KS, DeForest JL, Burton AJ, Allen MF, Ruess RW, Hendrick RL (2002) Fine root architecture of nine North American trees. Ecol Monogr 72:293–309

Prescott CE, Blevins LL, Staley C (2004) Litter decomposition in B.C. forests: controlling factors and influences of forestry activities. BC J Ecosyst Managem 5:30–43

Puhe J (1993) Die Wurzelentwicklung der Fichte (*Picea abies* [L.] Karst.) bei unterschiedlichen chemishen Bodenbedingumgen. Diss. Forstwissenschaftlichen Fachbereichs der Georg-August-Universität Göttingen, 131 pp

Puhe J (2003) Growth and development of the root system of Norway spruce (*Picea abies*) in forest stands—a review. For Ecol Manage 175:253–273

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

Püttsepp Ü, Lõhmus K, Persson HÅ, 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. For Ecol Manage 221:291–298

Raich JW, Nadelhoffer KJ (1989) Belowground carbon allocation in forest ecosystems: global trends. Ecology 70:1346–1354

Richter AK, Walthert L, Frossard E, Brunner I (2007) Does low soil base saturation affect fine root properties of European beech (*Fagus sylvatica* L.)? Plant Soil 293:69–79

Roberts J (1976) A study of root distribution and growth in a *Pinus sylvestris* L. (Scots pine) plantation in Thetford Chase, East Anglia. Plant Soil 44:607–621

Roehrig Hansen HB, Thomsen L (1991) Rodundersøgelser og biomassemålinger på tre danske rødgranlokaler. Rapport Laboratoriet Økologi og Miljølaere, Danmarks Tekniske Højskole, Lyngby, Denmark, 112 pp

Ruess RW, van Cleve K, Yarie J, Viereck LA (1996) Contributions of fine root production and turnover to the carbon and nitrogen cycling in taiga forests on the Alaskan interior. Can J For Res 26:1326–1336

Ruess RW, Burton AJ, Pregitzer KS, Sveinbjornsson B, Allen MF, Maurer E (2003) Coupling fine root dynamics with ecosystem carbon cycling in black spruce forests of interior Alaska. Ecolol Monogr 73:643–662

Safford LO, Bell S (1972) Biomass of fine roots in a white spruce plantation. Can J For Res 2:169–172

Santantonio D (1980) Seasonal dynamics of fine roots in mature stands of Douglas-fir on different water regimes – a preliminary report. In: Riedacker A, Gagnaire-Michard J (eds) Symposium root physiology and symbiosis, Nancy, France. Centre Nationale de Recherches Forestière, Seichamp

Santantonio D, Hermann RK (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

Santantonio D, Hermann RK, Overton WS (1977) Root biomass studies in forest ecosystems. Pedobiologia 17:1–31

Scarascia-Mugnozza G, Bauer GA, Persson H, Matteucci G, Masci A (2000) Tree biomass, growth and nutrient pools. In: Schulze ED (ed) Carbon and Nitrogen Cycling in European Forest Ecosystems. Ecol Stud 142:49-62

Scheffer RA, Aerts R (2000) Root decomposition and soil nutrient and carbon cycling in two temperate fen ecosystems. Oikos 91:541–549

Stober C, Eckart GA, Persson H (2000) Root growth and response to nitrogen. In: Carbon and nitrogen cycling in European forest Ecosystems. Schulze E-D (ed). Ecol Stud 142:99–121

Strand AE, Pritchard SG, McCormack ML, Davis MA, Oren R (2008) Irreconcilable differences: fine root life spans and soil carbon persistence. Science 319:456–458

Tateno R, Hishi T, Takeda H (2004) Above- and belowground biomass and net primary production in a cool-temperate deciduous forest in relation to topographical changes in soil nitrogen. For Ecol Manage 193:297–306

Taylor JH, Peterson CA (2000) Morphometric analysis of *Pinus banksiana* Lamb. Root anatomy during a 3-month field study. Trees 14:239–247

Trumbore SE, Gaudinski JB (2003) Atmospheric science: the secret lives of roots. Science 302:1344–1345

Ulrich B, Pirouzpanah D, Murach D (1984) Bezeihungen zwischen Bodenversauerung und Wurzelentwicklung von Fichten mit unterschiedlich starken Schadsymptomen. Forestarchiv 55:127–134 van Praag HJ, Sougnez-Remy S, Weissen F, Carlett FG (1988) Root turnover in a beech and a spruce stand at the Belgian Ardennes. Plant Soil 105:87–103

Vanguelova EI, Nortcliff S, Moffat AJ, 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 Soil 270:233–247

Vanninen P, Mäkelä A (1999) Fine root biomass of Scots pine stand differing in age and soil fertility in southern Finland. Tree Physiol 19:823–830

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

Vogt KA, Moore EE, Vogt DJ, Redlin MR, Edmonds RL (1983) Conifer fine roots and mycorrhizal root biomass within the forest floors of Douglas-fir stands of different ages and site productivities. Can J For Res 13:429–437

Wilcox H (1954) Primary organization of active and dormant roots of noble fir, *Abies procera*. Am J Bot 41:812–821

Xiangroung W, Zhengquan W, Yourzhi H, Jiancun G, Dali G, Li M (2007) Variations of fine root diameter with root order in Manchurian ash and Dahurian larch plantations. Front Forest China 2:34–39