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REGULAR ARTICLE

Spatial distribution of fine-roots in boreal forests in eastern Sweden

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Abstract Investigations were carried out in six forest types in areas surrounding two Swedish nuclear power plants (Forsmark and Laxemar). The aim of the investigation was to determine the spatial distribution of fine-root biomass (live), necromass (dead) and standing crop (live + dead) and to test the use of the live/dead ratio as a vitality criterion. Soil cores were taken to depths with insignificant amounts of roots. The total amount of fine-root biomass (<1 mm in diameter) of tree species in the soil profile was 267, 317 and 235 g m^{-2} for the Forsmark and 137, 371 and 50 g m^{-2} for the Laxemar sites. The related necromass was 119, 226 and 184 g m^{-2} and 87, 245 and 271 g m^{-2}. The biomass in the humus layer was 47, 7 and 48% for the Forsmark and 34, 26 and 7% for the Laxemar sites, as a percentage of the total live + dead fine roots in the soil profile. The related necromass in the humus layer was 13, 2 and 30% for the Forsmark and 13, 2 and 28% for the Laxemar sites. The live/dead ratio decreased with depth for both tree— and field-layer species and seems to be a most powerful vitality criterion of fine roots.

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Introduction

Roots comprise a heavy and varying fraction of the total dry weight of the vegetation in forest ecosystems. Generally, tree roots account for 15–30% of the total tree biomass (Persson 2002). In addition, the roots of field-layer species (dwarf shrubs, herbaceous and graminaceous plant species) account for a substantial fraction.

The excavated root fragments can be separated by size into different categories: fine roots (<1 mm in diameter) with a high degree of soil penetration and a high turnover rate, small diameter roots with a low turnover rate, acting as conduits for water and mineral nutrients and finally coarse supportive roots with low turnover rate (Vogt and Persson 1991). On the framework of the conductive and supporting root system, fine roots are of great importance for the efficiency of water and mineral nutrient uptake. The fine roots must be extensive and active enough to meet the need of the aboveground plant parts.

Tree fine roots play an important role in carbon and nutrient cycling in boreal forest ecosystems, due to the high proportion of carbohydrates allocated belowground and due to the rapid decomposition of the fine-roots relative to above-ground tissues. Fine roots form an integrated spatially and temporarily variable network in the forest soil. They are opportunistic and exploitive in their growth habits and adapt rapidly to climatic variation and to changes in soil solution chemistry or water supply (Bakker et al. 2006; Persson 2000; Richter et al. 2007; Santantonio and Hermann 1985; Vanguelova et al. 2005).

Increased fine-root biomass and increased live/dead ratios in the forest soil are to a great extent caused by site factors favouring growth such as high soil temperature and rich availability water and mineral nutrient (Persson 1980a, 2000). Since most fine roots are superficially distributed, they are affected negatively by different kinds of environmental stress, e.g. drought, frost and wind movements (Persson 2002; Raitio 1990). Increased levels of nitrogen and decreased levels of cations raise the risk of damage symptoms in the tree root systems (Daldoum and Ranger 1994; Roehrig Hansen and Thomsen 1991; Persson et al. 1995; Richter et al. 2007; Vanuguelova et al. 2005).

The network of fine roots is decreasing in density from the soil surface downwards (Bakker et al. 2006; Borken et al. 2007; Konôpka et al. 2006; Makkonen and Helmisaari 1999; Persson 1978; Persson 2000). Coarse roots, which are to a less extent involved in nutrient absorption, are to a greater extent concentrated to the sub-soil horizons (Persson 2002). Root damage may be visualised by a decreased live/dead ratio of the fine roots (Persson and Ahlström 2002). Dead root ramifications are continuously replaced by new root tips quickly exploiting the upper soil horizons. Research into root senescence is complicated by the fact that cessation of root penetration is not synonymous with root death. Roots, which are not developed under the restrictions imposed by the soil or by the aqueous environment, may be functional for a prolonged time (cf. Waisel 2002).

Important fine-root characteristics are the amount of fine roots, in terms of dry weight, in different soil horizons (g m^{-2}), rooting density (g l^{-1}) and the live/dead ratio (g g^{-1}). A substantial variation in fine-root biomass (live), necromass (dead) and the live/dead ratios occurs during the growth period (Persson 1980a, 1983). A high live/dead ratio in the soil profile most frequently occurs in the uppermost part of the humus layer (cf. Puhe et al. 1986; Persson et al. 1995; Persson and Ahlström 2002). We hypothesised that the live/dead ratio is reflecting the rate of production and death of roots with depth in the soil profile.

High rates of fine-root fluctuation are found in many European forest ecosystems (cf. e.g. Persson 1978; Helmisaari and Helmisaari 1992; Helmisaari and Hallbäcken 1999; Bakker et al. 2000; Persson and Ahlström 2002; Roehrig Hansen and Thomsen 1991; Helmisaari et al. 2002; Stober et al. 2000; Helmisaari et al. 2007; Persson and Stadenberg 2008). A substantial flow of carbon and nutrients from root litter into the forest soil at the same time occurs during the growth period. Root litter is decomposed quickly; the rate of decomposition depends on soil temperature and soil water availability (Santantonio and Hermann 1985). The input of root litter to the forest soil is an important contributor to the ecosystem processes, e.g. to nutrient cycling and forest growth.

On a global scale, a substantial fraction of the atmosphere CO_2, is originating from dead and decomposed root tissues (Norby and Jackson 2000). Together with litter from the 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. Few studies have so far examined the spatial distribution pattern of the live/dead ratios of fine roots in the forest soil profile (cf. Persson 2000; Persson 2002).

The main aim of our present project was to describe the spatial distribution of live and dead roots and live/dead ratios in some common forest ecosystems close to two main nuclear power plants in Sweden. The investigated areas were chosen at a distance of about 10 km from the two nuclear power plants. Basic data sets and a more comprehensive description on those forest sites are to be found in Persson and Stadenberg (2007, 2008), Löfgren (2005) and in Löfgren et al. (2006).

Material and methods

The field studies were carried out within three sites close to the Forsmark and three sites close to the Laxemar nuclear power plants in the central eastern and south eastern parts of Sweden (See Tables 1 and 2 for detail information of the sites). The sites at Forsmark were of coniferous *Calluna-Empetrum* type, coniferous fern type and *Alnus* swamp herb-type (Nordiska Ministerrådet 1978). The related forest sites at Laxemar were of herb rich oak forest type, coniferous *Vaccinium myrtillus* type and *Alnus* shore

Table 1 Climate characteristics for Forsmark and Laxemar

Area	Forsmark	Laxemar
Latitude, longitude	E 60° 22′ N, 18° 11′ W	57° 25′ N, 16° 33′ E
Mean annual temp. 2004[1]	+6°C	+7°C
Mean annual temp.	5.5[2]	6.4[3]
Min — max annual temp.	3.4–7.4[2]	4.8–8.4[3]
Mean precipitation (mm)	758[4]	633[3]
Min — max precipitation (mm) 1961–1990	411–1252[4]	403–997[3]
Vegetation period (No of days >5°C)	180[5]	199[6]

1) (SMHI 2004).

2) (From Örskär 1961–2000) (Larsson-Mcann et al. 2002).

3) (From Laxemar 1961–1990) (Larsson-Mcann et al. 2002).

4) From (From Lövsta) (Larsson-Mcann et al. 2002).

5) Data for 1988 from the island of Örskär.

6) Data for 1981 from northern peak of the island of Öland.

forest type. A maritime climate is prevailing in both the Forsmark and Laxemar regions (SMHI 2004). The soil type varied between leptosol/regosols) gleysols at Forsmark and histosols/gleysol at Laxemar (Table 2).

The average thickness of the humus layer was 15.3, 5.2 and 15.3 cm at the Forsmark sites and 11.5, 5.5 and 5.3 cm at the Laxemar sites. The soil pH (H_2O) was about 6.7 for the humus layer (0–30 cm) at

Table 2 Site and stand characteristics at Forsmark (AFM) and Laxemar (ASM). Picea abies = P. a., Pinus sylvestris = P. s., Betula verrucosa = B. v., Alnus glutinosa = A. g., Quercus robur = Q. r. TW1 =

SKB code	AFM001247	AFM001068	AFM001076	ASM001426	ASM001440	ASM001434
Soil moisture class[1]	Fresh	Fresh/moist	Moist	Fresh	Fresh	Moist
Soil type[1]	Leptosol	Regosol/ Gleysol	Gleysol	Histosol/ Gleysol	Histosol	Histosol
Stone/boulder volumetric content in M 0–30 (%)[1]	62	50	66	57	0	0
Tree age	59–60	80–88	85–95	112	55	34
Number of trees /ha	1340	780	3340	200	400	1600
Tree height (m)	16.3	19.8	18.5	17.1	21.0	11.6
Diameter at breast height (dbh in m)	0.21	0.26 (*P. a.*)	0.31 (*P. a*)	0.36	0.32	0.14
Basal area (m^2/ha)	22.5 (*P. a.*)	20.5 (*P. a.*) 6.5 (*B. v.*)	5.3 (*B. v.*) 7.3 (*A. g.*) 3.0 (*P. a.*) 2.3 (*P. s.*)	15.0 (*Q. r.*)	15.5 (*P. a.*)	17.5 (*A. g.*)
Above ground field-layer biomass ($g\ m^{-2}$)[3]	–	24	5	89	27	9
Vegetation types[4]	Coniferous, *Calluna-Empetrum*-type	Coniferous fern type	*Alnus* swamp herb-type	Herb rich oak forest	Coniferous *Vaccinium myrtillus* type	*Alnus* shore forest type

[1] (Lundin et al. 2004) and (Lundin et al. 2005)

[2] (Hägglund 1973)

[3] (Löfgren 2005)

[4] (Nord. Ministerråd. 1978)

the Forsmark sites and about 4.6 (0–30 cm) for the Laxemar sites (Persson and Stadenberg 2007). The related soil pH (H_2O) was, in the top 0–10 cm of the mineral soil, about 7.1 at the Forsmark and 5.3 for the sites at Laxemar. The raw-humus layer at the Forsmark sites was generally deeper than at Laxemar (cf. Lundin et al. 2004, 2005). The calcareous moraine sediments in the Forsmark region caused a high soil pH and a flora extremely rich in plant species (Jerling and Isaeus 2001).

The mean tree height of the trees was 16.3, 19.8 and 18.5 m at the Forsmark and 17.1, 21.0 and 11.6 m at the Laxmar sites, respectively (Table 2). The tree density (number of trees ha^{-1}) was 1340, 780 and 3340 at the Forsmark and 200, 400 and 1600 at the Laxemar sites respectively. The field-layer vegetation was extensively developed at sites with a more sparsely developed tree layers (Löfgren 2005).

The sequential core method (cf. Vogt and Persson 1991) was used to obtain data on the root distribution with depth, in the LFH-horizon and in the mineral-soil horizon as deeply as possible, of living (biomass) and dead (necromass) fine roots in terms of dry weight. The depth distribution of roots of tree and field-layer species was recorded, at depth intervals of 0–2.5 (H1), 2.5–5 (H2), 5–10 (H3), 10–15 (H4), 15–20 (H5), 20–25 (H6) cm of the LFH horizon and in 10 cm segments (M1–M4) for the mineral soil profile down to 40 cm.

The soil sampling was carried out in the mid of October 2004 for the Forsmark sites and in the end of April 2005 for the Laxemar sites. A steel corer, with an inner diameter of 4.5 cm, was used for the soil sampling. In total 32 soil cores were taken randomly in each site from the four corners of a quadrate covering 200 m^2, eight in each corner (north, east, south and west).

Each soil-core sample was taken as deeply as possible, *viz*. to a depth where stones and larger blocks prevented further penetration by the soil corer. The spot where the soil core was taken was chosen with the help of a sharp iron stick driven down into the soil. 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.

The three Forsmark stands and the herb rich oak forest site at Laxemar were stony in the mineral soil horizons resulting in an increased concentration of roots close to the surface area of the stones (cf. Table 2). Therefore, fine roots from these stands were not included completely by the soil corer in the soil samples. On the other hand, the method of deliberately choosing sampling spots with at least 10 cm of the mineral soil included may cause an overestimation of the dry weight of the fine-roots in the mineral soil. The thickness of humus horizon was measured in each soil core. The uppermost 2.5 cm layer consisted of humus in all sites. The soil samples were transferred into plastic bags and transported directly to our laboratory and stored in a cold-storage room at —4°C, until the sorting took place (cf. Clemensson-Lindell and Persson 1992).

The roots were sorted out from the soil cores immediately after thawing. In order to distinguish biomass (live roots) from necromass (dead roots) the fine roots were separated into live and dead categories based on distinct morphological characteristics (Vogt and Persson 1991). It is essential to use well defined morphological criteria while sorting the root fragments into species and live and dead root categories. Root fragments of the different species categories were distinguished from morphological characteristics.

Live fine roots were defined as roots with white or to a varying degree brownish/suberized root tips, often well branched. The main part of their root tips were light and turgid or changed to mycorrhizal ramifications (cf. Vogt and Persson 1991; 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 pieces with a length <1 cm were regarded as soil organic matter. Similar criteria were applied for both tree and field layer species.

The 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 following diameter fractions are reported here: <1, 1–2, 2–5 and 5–10 mm. Data sets for the original diameter fractions are available in Persson and Stadenberg (2007). The diameter separation was carried out for both tree roots and roots 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. The dry weight was estimated for all root fractions after drying in an oven at 65°C to constant weight (at least for 24 h).

Results

The depth of the humus layer and the soil profile differed considerable between the investigated sites. The soil corer was driven into the mineral soil to depths where only limited live root fragments were found (cf. Figs. 1 and 2). A low live/dead ratio was found at those depths and the rooting density (g l^{-1}) was also very low (Fig. 1). Thus, the amounts of live (biomass) and dead (necromass) fine roots were almost completely included in our core samples (Tables 3, 4 and 5).

There was a substantial variation in the amount of live and dead tree fine roots between different soil horizons (Figs 1, 2 and 3). Proportionally, more live tree fine roots were found in the uppermost 2.5 cm segment of the humus layer in all sites (Fig. 1). Tree roots in the latter horizon consisted of heavily branched mycorrhizal ramifications, morphologically different from the rest of the root system. The dry weight and rooting density of tree fine roots decreased with depth (Figs. 1 and 2). Most large diameter tree roots were located in the mineral soil horizon (Tables 3 and 4).

The mean fine-root biomass (<1 mm in diameter) of tree species in the humus layer in relation to the total amount of live + dead fine roots in the soil profile was 47, 7 and 48% for the Forsmark and 34, 26 and 7% for the Laxemar sites, respectively (Table 3). The related necromass in the humus layer was 13, 2 and 30% for the Forsmark and 13, 2 and 28% for the Laxemar sites, respectively. The live/dead ratio decreased with depth for both tree- and field-layer species (Figs. 1, 2 and Table 5).

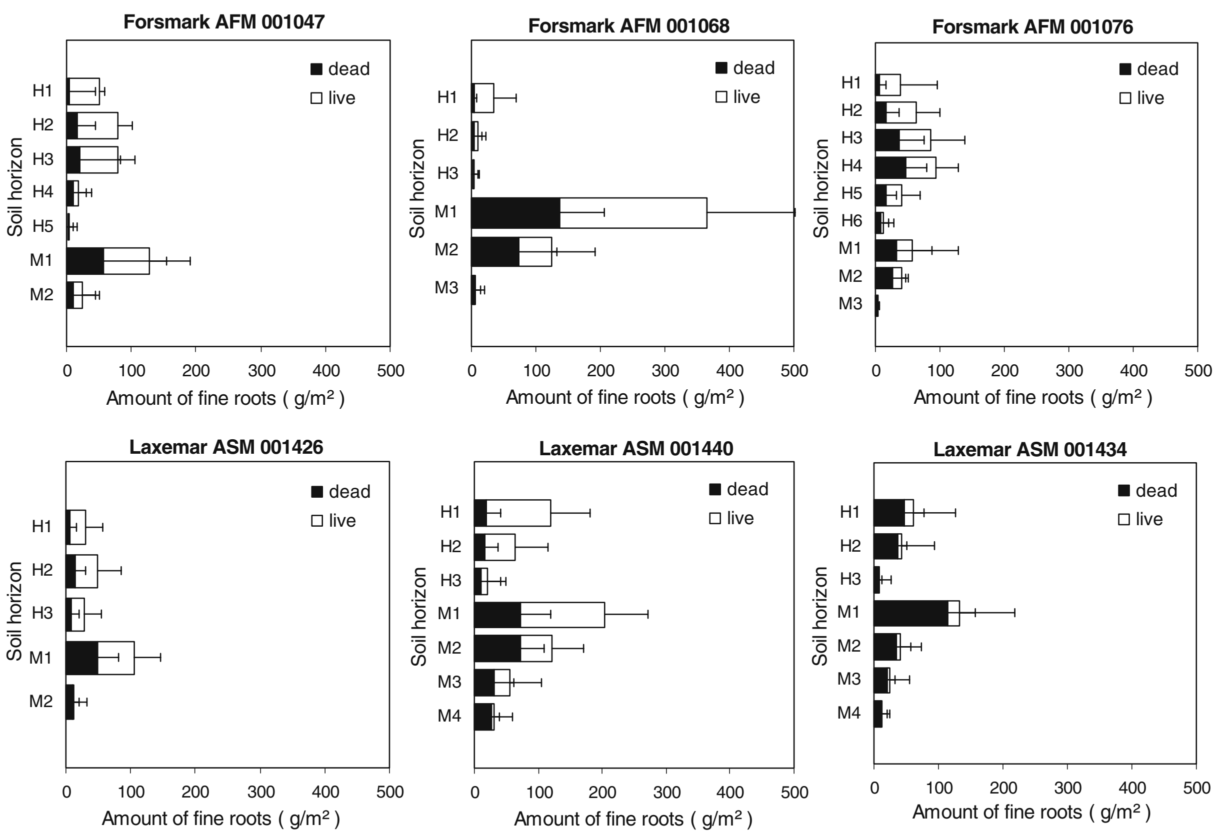

Fig. 1 The depth distribution (g m^{-2}) of tree fine roots (<1 mm in diameter) at the different sites at Forsmark and Laxemar

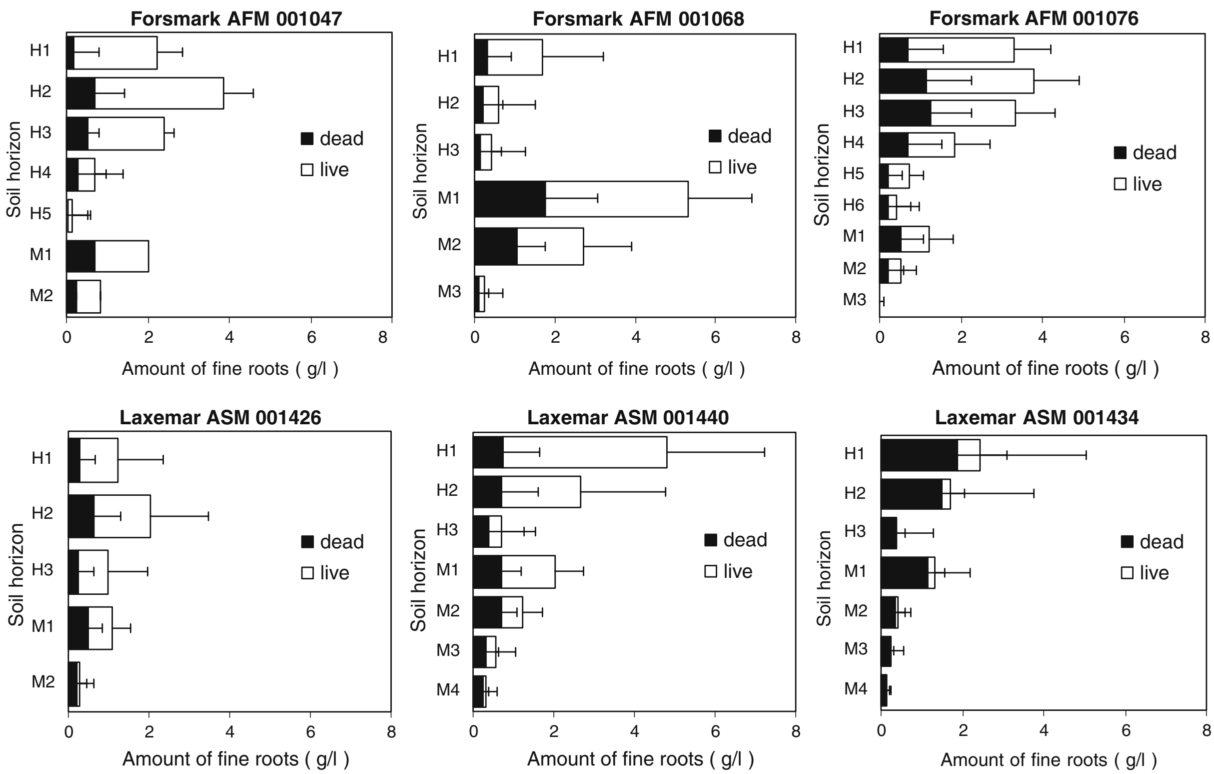

Fig. 2 The rooting density (g l^{-1}) of tree fine roots (<1 mm in diameter) at the different sites at Forsmark and Laxemar

The distribution of roots was rather superficial in the coniferous *Calluna-Empetrum* type forest site (mainly tree roots) at Forsmark and at the herb rich oak forest (roots of both trees and field layer species) at Laxemar (Table 4). The high stone/boulder volumetric content in the soil prevented a deeper penetration of the root systems at those sites (Table 2). High amounts of fine roots of both trees and field layer species were found in the thick humus layer at the *Alnus* swamp forest at Forsmark.

Substantial amounts of fine roots of the field-layer species were found at all sites except for at the *Picea abies-Vaccinium myrtillus* forest at Laxemar, where the field layer was extremely scarcely developed (Table 3). Fine roots of field-layer species (<1 mm in diameter) constituted in the investigated sites as much as 1–58% of the total belowground standing crop (biomass + necromass) of the field layer species. Both coarse and fine-root fractions of the field-layer species were concentrated to the humus layer (Table 4). The amount of live field-layer fine roots was high at the open herb rich oak forest at Laxemar (the number of trees/ha was only 200).

More live than dead tree fine roots were observed in all sites in the humus compared with the mineral soil horizon (Table 3), except for at the *Alnus* swamp of herb-type at Forsmark and the *Alnus* shore forest site at Laxemar. Both those sites were classified as "moist", with a high topographic wetness index (cf. Table 2). The percentage proportion of dead fine roots (<1 mm in diameter) was high in those sites; 44 and 84%, respectively of the total amount of live + dead fine roots. In all other sites and horizons the fine-root biomass was more substantial than the fine-root necromass.

The distribution pattern of the tree roots was to a minor extent influenced by the competition from the root systems of the field layer species. The tree roots were distributed more deeply than roots of field-layer species (Tables 3 and 4). The highest amount of roots from the field-layer species was found in the sites with a low number of trees/ha; *viz*. in the coniferous

Table 3 The amount of live and dead fine roots (<1 mm in diameter) in different soil layers (H = humus; M = mineral soil) at different forest sites at Forsmark (AFM) and at Laxemar (ASM). Estimates are given as mean values ± SD (*n*=32)

Site/root fraction	Horizons	Tree roots (g m^{-2})			Roots of field-layer species (g m^{-2})		
		Live	Dead	Total	Live	Dead	Total
Forsmark							
AFM001247	H	182±91	51±47	233±120	32±46	1±3	33±46
	M	84±116	68±71	152±170	11±20	3±5	15±23
	H + M	267±118	119±74	385±148	43±53	5±6	48±53
AFM001068	H	36±44	11±23	48±62	27±49	2±6	29±54
	M	281±187	215±84	495±198	88±58	39±122	126±130
	H + M	317±196	226±88	543±205	115±87	41±122	155±145
AFM001076	H	201±136	125±97	325±197	16±21	7±10	24±28
	M	35±80	59±72	84±144	3±7	4±11	7±13
	H + M	235±162	184±95	419±229	20±26	11±15	30±33
Laxemar							
ASM 001426	H	77±61	29±25	106±72	163±153	55±58	218±194
	M	60±42	58±45	118±65	62±47	26±72	88±100
	H + M	137±72	87±50	224±80	224±168	82±91	306±220
ASM001440	H	159±97	45±49	205±133	2±9	0	2±9
	M	211±116	199±103	411±172	3±9	0	4±9
	H + M	371±151	245±103	616±211	5±17	0	6±17
ASM001434	H	21±20	90±123	110±134	29±34	12±18	40±47
	M	29±39	181±174	210±200	21±69	24±34	45±88
	H + M	50±52	271±245	321±278	50±84	35±41	85±107

fern type forest at Forsmark (780 trees/ha) and at the herb rich oak forest at Laxemar (200 trees/ha). The age of the forest trees at those sites were 80 and 112 years, respectively.

The Laxemar *Alnus* shore forest site, differed from all other sites since the amount of fine roots was very low and distributed very deeply in the whole soil profile. A substantial amount of dead fine roots of trees and field-layer species were found in the uppermost 0–10 cm part of the mineral soil. The tree density of this fairly young site (34 years) was 1600 trees/ha (Table 2).

The below-ground proportion of the plant tissue from the field-layer species was low in sites with a low tree stem density such as the *Picea abies* site of *Vaccinium myrtillus* type and the herb rich oak forest at Laxemar (Tables 2 and 4). The above-ground field-layer plant parts consisted in those sites mainly of ericaceous dwarf shrubs. In the Forsmark area, the coniferous fern forest with a low stem density showed a high above-ground field-layer biomass (Tables 2 and 4).

The live/dead ratio in all sites was generally high in the upper 2.5 cm of the humus layer for both tree and field-layer species. A high live/dead ratio was most frequently found in the upper part of the mineral soil horizon (Figs 1, 2 and detail data in Persson and Stadenberg 2007). In most soil layers, except for in the deepest ones, the tree fine-root biomass was larger than the related necromass. A high live/dead ratio was found in the humus layer as a whole (Table 5).The live/dead ratio decreased substantially with depth in the mineral soil (Figs. 1 and 2).

The live/dead ratios for the field-layer species in all diameter fractions were higher than for tree roots (Table 5). Extremely high live/dead ratios were found in the field layers of the two coniferous forests of *Calluna-Empetrum* and fern type at Forsmark and at the coniferous forest of *Vaccinium* type at Laxemar. These sites were characterized mainly by coniferous trees in the tree layer and ericaceous shrubs in the field layer. The live/dead ratios for the field layer species were high for fine roots <1 mm in diameter, but extremely high for diameter fractions >2 mm in diameter at the coniferous forest of *Vaccinium myrtillus* type at Laxemar (Table 5). Included in the excavated root fragments in the latter sites were rhizomes and stem parts from above-ground of

Table 4 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 different forest sites at Forsmark (AFM) and at Laxemar (ASM). Estimates are given as mean values ± SD (n=32)

Site and horizons	Tree roots (g m^{-2})			Roots of field-layer species (g m^{-2})		
	Live	Dead	Total	Live	Dead	Total
Forsmark						
AFM001247						
H	425±390	113±136	538±421	46±61	1±3	48±61
M	349±437	230±248	579±545	11±20	3±5	14±23
H + M	774±545	343±271	1117±664	57±69	5±6	62±70
AFM001068						
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
AFM001076						
H	509±409	338±210	847±559	32±61	11±21	43±66
M	178±242	194±192	371±360	11±39	4±11	14±40
H + M	687±444	532±244	1218±594	43±94	14±24	58±99
Laxemar						
ASM001426						
H	147±141	58±69	206±176	209±227	58±61	267±266
M	347±396	252±340	599±496	65±50	32±81	98±108
H + M	494±441	310±355	805±579	274±242	90±100	364±291
ASM001440						
H	307±216	99±147	406±267	12±41	0	13±41
M	674±436	594±354	1268±678	4±13	0	5±13
H + M	981±387	693±404	1674±652	17±51	0	17±51
ASM001434						
H	113±178	184±223	297±357	52±60	14±23	67±73
M	267±499	497±462	764±871	22±69	99±188	121±200
H + M	380±594	681±565	1062±1051	75±105	113±190	188±213

ericaceous dwarf shrub embedded in the moist humus layer. The lowest live/dead ratios in all sites were obtained for herbaceous and graminaceous plants and the highest values for dwarf shrubs.

Discussion

The long-lived woody framework of structural tree roots supports a mass of short-lived nonwoody fine roots associated with mycorrhizal fungi (cf. e.g. Marschner 2002). Tree fine roots are most frequently concentrated in diameters <1 mm (Ford and Deans 1977; Persson 1978; Persson 2002; Roberts 1976; Vogt and Persson 1991). Since most absorption takes place immediately behind the apex of the root tips, the absorption is to a great extent dependent on the growing root tips and a continuous replacement of the area behind the apex of the root tips (Persson 1978). Most tree root tips are short-root endings (mycorrhizas). The seasonal changes in the number of root tips are well correlated with the changes in the amount of fine roots and with the live/dead ratios (cf. Persson 1978; Marshall and Waring 1985; Stober et al. 2000).

Tree fine roots enrich the soil with nutrients and organic matter and may sometimes play a quantitatively more important role than the leaf (needle) litter (cf. Persson 1978). Fine-root death and renewal in trees is a natural process and bears to some extent a resemblance of leaf shedding in evergreen plants. 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; Lippu 1998). High starch reserves (up to 30% of the dry weight) are accumulated in tree roots (Ericsson and Persson 1980). Only a limited share of the reserve carbon is redistributed to the above ground shoots, suggesting that the bulk of the carbon reserves in the

Table 5 The live/dead ratio of fine roots at various root diameters (<1, <2, <5 and <10 mm in diameter) in different soil horizons (H = humus, M = mineral soil and H + M) at different forest sites at Forsmark (AFM) and at Laxemar (ASM). Estimates are given as mean values (n=32)

Site and horizons	Tree roots (g g^{-1})				Roots of field-layer species (g g^{-1})			
	<1	<2	<5	<10	<1	<2	<5	<10
Forsmark								
AFM001247								
H	3.59	3.30	2.96	3.75	25.20	28.40	31.35	36.62
M	1.24	1.36	1.31	1.52	3.32	3.32	3.32	3.32
H + M	2.24	2.19	1.94	2.25	9.39	10.28	11.10	12.57
AFM001068								
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
AFM001076								
H	1.81	1.45	1.33	1.51	2.30	2.98	3.07	2.96
M	0.58	0.64	0.83	0.93	0.92	1.66	3.09	3.08
H + M	1.28	1.17	1.18	1.30	1.84	2.57	3.07	2.99
Laxemar								
ASM001426								
H	2.68	2.51	2.27	2.54	2.95	3.29	3.61	3.63
M	1.04	1.02	1.22	1.37	2.33	1.10	2.02	2.01
H + M	1.59	1.45	1.53	1.59	2.75	2.87	3.04	3.05
fsASM001440								
H	3.51	3.54	3.97	3.10	23.04	41.00	126.70	126.70
M	1.06	1.05	1.04	1.13	8.92	12.09	12.98	12.09
H + M	1.51	1.45	1.43	1.41	11.99	18.38	39.23	37.01
ASM001434								
H	0.22	0.28	0.41	0.61	2.78	3.16	3.65	3.65
M	0.16	0.19	0.37	0.54	0.89	0.58	0.41	0.23
H + M	0.18	0.22	0.38	0.56	1.46	1.22	1.09	0.66

roots is spend on root growth (Lippu 1998; Wargo 1979).

The roots contain considerable amounts of starch during the late autumn and winter. Starch content is to a varying degree found in all diameter fractions of the tree roots and in the tree stump (Ericsson and Persson 1980). Root sampling in our study took place late in autumn and early in spring, when the starch concentrations in the roots were high and the mobilization of carbohydrates for above- and below-ground growth was low (cf. Ericsson and Persson 1980). During that period the climatic conditions in the soil are rather uniform. The soil is frozen in the upper soil layers during the winter months and root growth is restrained and even stopped (cf. Raitio 1990).

It is not advisable, due to the high variability in the amount of tree fine roots, to estimate the fine-root biomass as a proportion of total root biomass or to use above-ground structural parts of the tree for such estimations (Vogt and Persson 1991). The sequential coring method, in this context offers a reliable technique, for direct investigations of the fine-root distribution (Vogt and Persson 1991). Quantification of fine-root distribution of the tree and field layer species is highly required in forest ecosystems, due to the important role of the root systems as carbon sinks and sources of input of soil organic matter (Persson 1979; Jackson et al. 1996).

The spatial distribution of the fine roots is determined to a great extent by the age and composition of the forest stand, by environmental and climatic factors (Persson 2000). The high spatial variability in fine-root biomass and necromass during the growth period makes a comparison of spatial distribution of fine roots between forest-stands difficult (Persson 2000; Persson and Ahlström 1999). Nevertheless, the data of

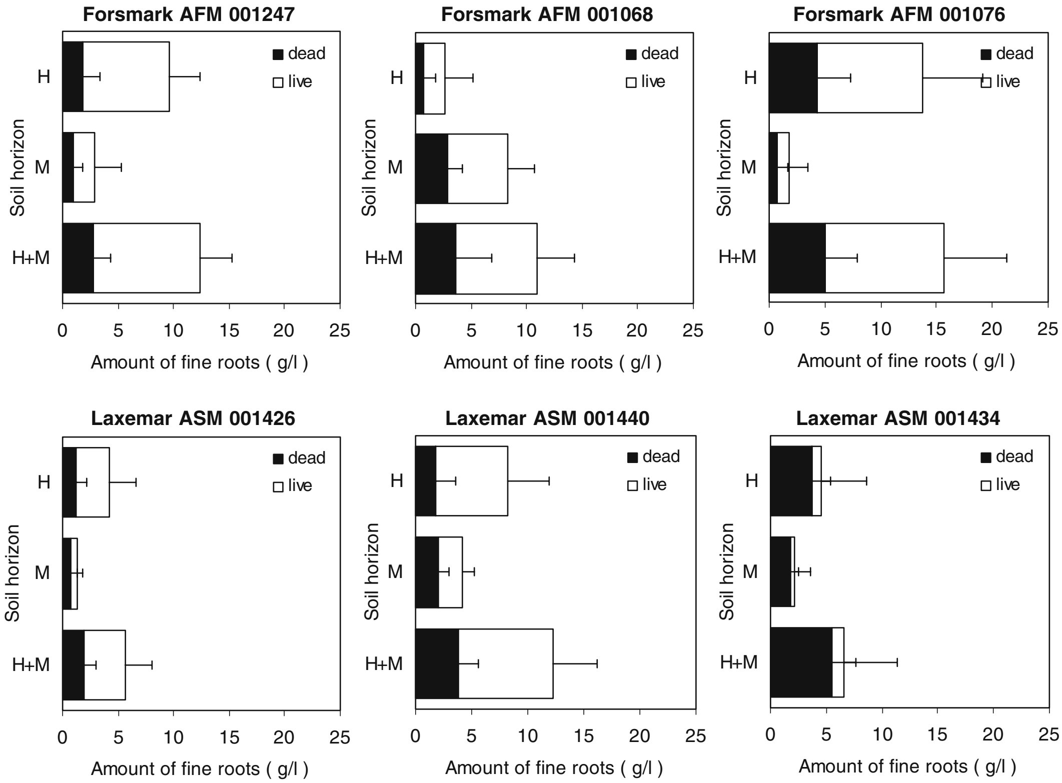

Fig. 3 The amount of live (biomass) and dead (necromass) tree fine roots (g l^{-1}; <1 mm in diameter) in the humus layer, the mineral soil horizon and the total soil profile at different sites at Forsmark and Laxemar

the amount of fine-root biomass and necromass at the Forsmark and Laxemar sites (Table 3 and 4) were within the range of the data from other investigations, using the same technique, taking into consideration the high seasonal variability of the amount of fine roots (cf. Borken et al. 2007; López et al. 2001; Makkonen and Helmisaari 1999; Persson 2000; Persson and Stadenberg 2007; Persson and Stadenberg 2008; Stober et al. 2000; Vanguelova et al. 2005).

All investigated coniferous forest sites, two at Forsmark (coniferous *Calluna-Empetrum* type and coniferous fern type) and one at Laxemar (coniferous *Vaccinium myrtillus* type), indicated high live/dead ratios for both tree and field-layer fine roots (Table 4). The highest live/dead ratio was found in the humus layer. The live/dead ratios in tree fine roots in the total soil profile for the two coniferous sites at Forsmark were 2.2 and 1.4 respectively. The related live/dead ratio for the coniferous site at Laxemar site was 1.5. The live/dead ratio of four *Picea abies* stands (84–99 years in age) in Germany (Borken et al. 2007) were within the range obtained for our coniferous forest sites. The live/dead ratios in 10 different European coniferous forest sites (*Picea abies*) were ranging between 0.4–2.8 (Persson 2000).

The dry weight of fine roots (<1 mm in diameter) at the *Alnus* sites at Forsmark and Laxemar consisted to a great extent of necromass (Table 4). The live/dead ratio in the total soil profile was 1.3 and 0.2 at those sites, respectively. The older more densely developed *Alnus* swamp forest at Forsmark differed considerable from the *Alnus* shore forest at Laxemar with regards to tree density (3340 versus 1600 trees/ha). The basal area of the forest trees was almost the same, 19.9 g m^{-2} at the Forsmark and 19.5 g m^{-2} at Laxemar site (Table 2). At the Forsmark site 59% of the basal area consisted of forest trees other than *Alnus glutinosa* (*Betula verrucosa* 30%, *Picea abies* 17 and *Pinus sylvestris* 13). The high live/dead ratio at Forsmark may be explained by site factors such as a mixed tree stand with a luxuriously developed field layer, a thick humus layer and a soil substrate rich in lime.

The amount of tree fine roots in the herb rich and open oak-forest site at Laxemar was low (200 trees/

ha) and the fine roots of the field layer species occupied more substantially the humus layer. The total amount of fine roots (live + dead) of field layer species (<1 mm in diameter) amounted to 306 g m^{-2}, compared with 224 g m^{-2} for fine roots. The live/dead ratio of the fine roots (<1 mm in diameter) for field layer species was 2.7 for the total soil profile. The related live/dead ratio for tree fine roots was only 1.6. The high live/dead ratio of the fine roots of the field layer species suggests that they stay alive longer than tree fine roots.

Root data on deciduous tree sites comparable to the oak-forest site at Laxemar are few in literature. The live/dead ratio of fine roots (<1 mm in diameter) in a 161 year old European beech (*Fagus sylvatica*) stand in the northern part of France varied between 0.6–2.1 during the season (cf. Stober et al. 2000). The live/dead ratio of fine roots <1 mm in diameter in a 120 year old European beech forest (*F. sylvatica*) in the Belgian Ardennes was 0.6 (cf. Van Praag et al. 1988).

Most studies on fine roots in forest ecosystems have been concentrated on tree fine roots, while roots of the field-layer species, although 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 (Table 3). About 8–27% of the fine root biomass (<1 mm in diameter), in the total soil profile, at the Forsmark and 1–62% at the Laxemar sites consisted of fine roots of field layer species (Tables 3, 4 and 5).

The field layer species were more substantially developed in open forests stands, with a low stem density (Table 3). Roots of tree and field-layer species were generally occupying different soil horizons and therefore to a limited extent competing with each other for water and nutrients. The superficial distribution pattern of the fine roots of field-layer species was confirmed with data from other investigations (Persson 1975, 1978, 1983).

In both moist sites (the *Alnus* swamp at Forsmark and the *Alnus* shore forest at Laxemar) high proportions of dead fine roots (necromass) was found in the total soil profile. In both areas the field-layer species were more substantially developed below-ground than above-ground (Table 3 and 4), in terms of dry weight. The above-ground biomass (living tissue) was only 9 and 11% of the total (above + belowground) field-layer biomass (Tables 2 and 4). Low above to below-ground biomass of the field-layer species (11%) was furthermore found in the coniferous fern type forest (soil moisture class: fresh/moist) at Forsmark. This was in agreement with data from an aspen (*Populus tremula*) site (fresh/moist) in deciduous woodland in the province of Uppland (Persson 1975), where the above-ground field-layer occupied about 16% of the total above and belowground biomass.

High above-ground to below-ground field-layer biomass was recorded at Laxemar in the herb rich oak forest and in the coniferous *Vaccinium myrtillus* forest (Tables 2 and 4). The above-ground biomass was 25% of the total above + belowground biomass (<10 mm in diameter) in the herb rich oak forest and 61% in the coniferous *Vaccinium myrtillus* forest. In all other sites, considerable lower above/belowground ratios were estimated. Both those areas were fairly dry (soil moisture class: fresh) and open (400 and 200 stems/ha, respectively) compared with the other sites. The field layer was dominated by ericaceous dwarf shrubs; *Vaccinium vitis-idaea* at the herb-rich oak forest and *Vaccinium myrtillus* at the other two site.

Two Scots pine (*Pinus sylvestris*) sites, one young and one mature site, in the Jädraås area in Central Sweden are comparable to those open Laxemar sites (Persson 1979, 1980b, 1983). The above-ground field layer occupied 62% of the total field layer in a young stand and 38% in a mature Scots pine stand. Both stands were fairly open (453 and 393 stems/ha, respectively) and dry. The field layer consisted mainly of ericaceous dwarf shrubs (*Calluna vulgaris*).

Fine roots are sensitive to drought and their live/dead ratios are decreasing with decreased water availability in the soil (cf. Olsthoorn 1991; Persson et al. 1995; Santantonio et al. 1977; Santantonio and Hermann 1985). Dry soil conditions have been demonstrated to decrease the live/dead ratio (Santantonio and Hermann 1985). It is reasonable to expect a high death rate in fine roots during summer drought. In boreal forest ecosystems, rain showers affect mainly the upper parts of the humus layer, during the summer months. Fine roots respond quickly to the increased water availability and are rapidly penetrating wet horizons. The concentration of fine roots in the humus layer seems to be dependent on soil water availability. The often well-developed organic-rich podzol profiles with a thick humus layer most effectively buffer the soil system against drought and nutrient deficiencies.

Substantial variations in fine-root biomass, necromass and live/dead ratios furthermore occur in tree stands depending on site quality (Raich and Nadelhoffer 1989; Clemensson-Lindell and Persson 1995; Steele et al. 1997; Ostonen et al. 1999; Persson 2002; Persson and Ahlström 2002; Godbold et al. 2003; Borken et al. 2007). Subsequent changes in the live/dead ratios of fine-roots are connected with their ageing (cf. Persson 2000). The low live/dead ratio at the *Alnus* swamp at Forsmark and the *Alnus* shore forest at Laxemar, in the soil profile, however, must be explained by a decreased rate of decomposition in the water saturated soil environment.

Most dead fine roots (necromass) were found in the mineral soil (Table 5). The concentration of necromass in this soil horizon was probably high due to harsher environmental conditions and a high death rate of new root ramifications penetrating from the humus layer. Low live/dead ratios may indicate stress conditions such as nutrient imbalances, soil acidification, water saturation or drought (Puhe et al. 1986; Godbold et al. 2003; Santantonio and Hermann 1985).

As a result of better moisture and nutrient conditions, there was a much greater proliferation of mycorrhizal fine roots of trees (<1 mm in diameter) in the humus layer (cf. Persson 1978; Persson 2000; Marschner 2002). The importance of the humus horizon for the development of tree fine-root biomass was evident in all investigated vegetation types (Tables 3 and 4). Coarse tree roots were distributed more deeply in the soil profile. The field layer species were most substantially developed in open forests stands, with a low stem density of the trees.

Concluding remarks

Forest-trees are developed in a mixed and competitive environment, in which a long-term strategy for their root function is essential. Fine roots in forest ecosystems are exposed to low nutrient availability and are highly dependent on the mycorrhizae for their survival. High fine-root “vitality” in terms of high live/dead ratios of the fine roots should be expected in the humus layers, since the extensive mycorrhizal infection in that layer increases the uptake area and improve the function of fine roots over a prolonged period of time.

The most common method of estimating the production, mortality and survival of fine roots involve periodic measurements of live (biomass) and dead (necromass) dry weights of fine roots from soil cores. The often-reported discrepancy in the data on root litter formation may partly be due to imprecise definition of size classes (diameter), vitality of the root fragments (live or dead) and species (tree or field-layer species) of the fine roots. Distinguishing live and dead fine roots is a fundamental but difficult part of root investigations.

Methods of studying fine roots, which do not account for live and dead categories, are of limited value for a credible description of the spatial distribution of the fine roots in the soil profile. For most forest tree species, subdividing and separating roots into <1 mm in diameter has a sound morphological basis. Most of the total length and surface area of the tree roots is to be found in the latter diameter fraction. The vitality and distribution patterns of the fine roots seem to depend on where in the soil profile they are developed. Our investigations stress the importance, while studying the distribution of fine-roots in forest ecosystems, to relate to the natural soil-horizons.

Our data clarify the importance of sorting fine roots in both a live and a dead category, in order to get a general picture of the spatial distribution of the fine roots. Our data of the amount of biomass (live), necromass (dead) and standing crop (biomass + necromass) of fine-root at the Forsmark and Laxemar sites were within the range of the data from other investigations taking into consideration the high seasonal variability of the fine roots (see literature above). The live/dead ratio was proved to be a most powerful vitality criterion of fine roots.

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