

Research Article

The High Input of Soil Organic Matter from Dead Tree Fine Roots into the Forest Soil

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The spatial and temporal dynamics of tree fine roots were investigated in six boreal forest types in Eastern Sweden, close to the Swedish Forsmark and Laxemar nuclear power plants. Four dry and two wet forest types were included in the study. The amount of live and dead fine roots in terms of dry weight was estimated in soil cores. The live/dead ratios of fine roots (<1 mm in diameter) decreased with depth; very low ratios were observed in two wet forest sites. The proportions of dead fine roots to the total amounts of fine roots in the mineral soil horizons of those wet sites were 63 and 86%. The corresponding proportions in the mineral soil in dry forest sites were 45 and 45% and 49 and 48% at Forsmark and Laxemar, respectively. Sequential soil core sampling demonstrated a high variation in live and dead amounts of fine roots during the growth period. A high accumulation of carbon from dead tree fine root was found in all six forest types, in particular in the wet forest sites, but also in deeper soil horizons. Consequently, substantial amounts of organic matter from dead fine roots are continuously accumulated in the soil in boreal forests.

1. Introduction

Tree fine roots of forest trees are for their function forced to penetrate dry soil volumes often against mechanical resistance in densely packed soil layers. In spite of those difficulties, tree root systems explore the uppermost parts of the soil profile with a network of growing root tips. For an example, the root system of a 13-year-old Scots pine (*Pinus sylvestris*) reached an area of about 5 m from the tree stem and expanded about 0.4 m yr^{-1} [1, 2]. The high tree density in this forest stand (1095 ha^{-1}) made it clear that the uppermost parts of the soil profile must have been completely interwoven by tree fine roots.

The lateral roots in a nearby 120-year-old Scots pine stand (tree density = 393 ha^{-1}) reached 15–20 m from the tree trunks [3]. The root system of those mature Scots pine trees had expanded about 0.1 m yr^{-1} during the 120-year period leaving an area of about 300 m^{-2} penetrated by tree roots. The wide-spread network of fine roots on the structural roots increases the total surface area and length of the root system [4].

The white coloured area of the root tips behind the region of cell elongation is most active in the uptake processes [5, 6].

This absorption zone is often covered by mycorrhizal fungi or root hairs [7]. The seasonal change in the number of root tips seems to be very well correlated with the changes in the amount and length and surface area of living fine roots [8]. Fine roots are short lived in their effectiveness; death and decay of dead fine roots often take place within a few weeks.

The energy cost of forming and maintaining the fine root system of a single tree is very high [9–13]. The amount of carbon allocated to the root systems is substantial [2, 8, 9, 12, 14–17]. The starch content in living fine roots (<1 mm in diameter) may reach as much as 30% of the dry weight [18]. Live fine root ramifications are constantly replaced and a substantial amount of dead fine-root tissues are formed.

Fine root production and litter formation of fine roots are important components of nutrient and carbon cycles in forest ecosystems [2, 8, 12, 14, 16, 17, 19–25]. Calculating carbon allocation to tree fine roots and turnover time is therefore essential in order to understand the patterns of carbon cycling in forest ecosystems.

The most commonly used methods of estimating fine-root production in forest ecosystems involve the measurements of live and dead amounts of fine roots in terms of dry weight from sequential soil cores. The contribution of

different diameter classes to root biomass and turnover rate may vary [4, 15]. The most substantial turnover rate is to be found in fine roots. Some fine roots are transferred to long-living large-diameter roots [13, 15].

The live/dead ratio of fine roots is a valuable vitality criterion in the soil profile [26]. Persson and Ahlström [27] used the live/dead ratio of fine roots to quantify changes in the “vitality” of fine roots in nitrogen manipulated Norway spruce catchment areas. The fluctuations in the amount of live and dead fine roots during the growth period in these forest areas suggested that climatic alterations were the most important underlying sources of variation. Soil temperature and soil water conditions seem to be the most important factors influencing fine-root growth. The most substantial decomposition takes place in the upper soil layers where high temperature, supplies of air, water, and food allow microorganisms to thrive [28, 29].

The effects of anoxic conditions on the spatial and temporal distribution on the tree fine roots have recently been identified [15, 26, 30]. The live/dead ratio of fine roots may be reduced in water saturated forest soils as a result of oxygen deficiency, a low rate of decomposition, and a substantial accumulation of decomposing organic matter from dead fine roots [31–33].

The boreal forests are in many ways able to keep plant remains from decomposing, thus preventing the release of carbon into the air. Most carbon is accumulated in poorly and very poorly drained soils. A high share of forested wetlands is to be found in the boreal forest region [34–36]. In boreal forests tree fine roots are exposed to large seasonal variations of soil moisture, nutrient availability, and soil temperature [37, 38]. In water-saturated forest stands the accumulation of dead fine roots is expected to be very high.

We hypothesized that soil water saturation plays an important role in regulating the amount of deposited organic matter from dead fine roots. A low live/dead ratio of fine roots is expected in water-saturated forest stands as a result of the high accumulation of dead root tissues. Soil carbon from dead tree roots plays a key role in the global carbon cycle and is an important component in climate models. Humans have, and will likely continue to have, significant impacts on the size of this pool by forest management practices forest such as forest harvesting, clear-cutting, ploughing, and drainage.

2. Material and Methods

Investigations were carried out in six different forest types in areas surrounding two Swedish nuclear power plants at Forsmark and Laxemar [15, 26]. The forest sites at Forsmark were of coniferous *Calluna-Empetrum* type, coniferous fern type, and *Alnus* swamp of herb type [39]. A distinct hummock and hollow microtopography was developed at the *Alnus* forest of swamp herb type at Forsmark.

The sites at Laxemar were of herb rich oak forest type, coniferous *Vaccinium myrtillus* type, and *Alnus* shore forest type. The soil type varied between leptosol/regosols (gleysols at Forsmark and histosols/gleysol at Laxemar (see Table 1). Stone/boulder volumetric content (%) and soil moisture

conditions differed considerably between the different sites [26].

The tree density (the number of trees ha⁻¹) was 1340, 780, and 3340 at the Forsmark and 200, 400, and 1600 at the Laxemar sites, respectively. The mean tree height was 16.3, 19.8, and 18.5 m at the Forsmark sites and 17.1, 21.0, and 11.6 m at the Laxemar sites, respectively. 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 Laxemar sites, respectively (Table 1). The basal area (m²/ha) of the trees was 22.5, 27.0, and 17.9 at the Forsmark sites and 15.0, 15.5, and 17.5 at the Laxemar sites, respectively. The specific basal area was occupied by different tree species.

The *Alnus* swamp forest site at Forsmark consisted besides *Alnus glutinosa* (Table 1; basal area = 7.3 m² ha⁻¹) of *Betula verrucosa*, *Picea abies*, and *Pinus sylvestris* (total basal area = 10.3 m² ha⁻¹). The *Alnus* shore forest at Laxemar consisted of *Alnus glutinosa* (basal area = 17.5 m² ha⁻¹). The coniferous *Calluna-Empetrum* site, the coniferous fern site at Forsmark and the coniferous *Vaccinium* site at Laxemar were dominated by *Picea abies* (basal area = 22.5 and 15.5 m² ha⁻¹) and the herb rich oak forest at Laxemar by *Quercus robur* (basal area = 15.0 m² ha⁻¹). 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.

In total 32 soil cores were taken in each forest site from the four corners of a quadrat covering 200 m², 8 taken randomly in each corner (north, east, south, and west) [15, 26]. Each soil sample was taken as deep as possible, namely, to a depth where stones and larger blocks prevented further penetration by the soil corer.

Soil cores were sampled in the middle of October 2004 for the Forsmark sites and in the end of April 2005 for the Laxemar sites. During the winter months the upper part of the soil profile was deep frozen, and only limited growth of the fine roots could take place. The soil cores were randomly distributed within the hummock and hollow microtopography pattern at the *Alnus* forest of swamp herb type at Forsmark. Half of the soil core samples were taken in the hummocks and the other half in the hollows. In all other forest sites no stratification was applied.

Additional sequential soil core sampling was carried at the coniferous fern forest type at Forsmark on in total 4 sampling occasions [26]. Besides the first sampling in the middle of October in 2004, samplings were carried out in the middle of April, in the beginning of August and in the end of October in 2005 [15]. The depth distribution of fine roots was measured, at intervals of 0–2.5 (H1), 2.5–5 (H2), and 5–10 cm (H3) of the LFH horizon and in 10 cm segments (M1–M3) for the mineral soil profile down to 30 cm.

A cylindrical steel corer, with an inner diameter of 4.5 cm, was used for soil core sampling. In total 32 soil cores were taken, each soil core sample was taken to a depth where stones and larger blocks prevented further penetration by the soil corer. Only few root fragments were found in the deepest soil layer. The uppermost 0–2.5 cm layer consisted of humus in all investigated sites.

The soil samples were transferred into plastic bags and transported to our laboratory and stored in a cold storage

TABLE 1: Site and stand characteristics at Forsmark and Laxemar. *Picea abies* = *P. a.*, *Pinus sylvestris* = *P. s.*, *Betula verrucosa* = *B. v.*, *Alnus glutinosa* = *A. g.*, *Quercus robur* = *Q. r.*

Stand characteristics	Coniferous, <i>Calluna empetrum</i>	Coniferous fern	<i>Alnus</i> swamp herb	Herb rich oak forest	Coniferous <i>Vaccinium</i> <i>myrtillus</i>	<i>Alnus</i> shore forest
Soil moisture class ¹	Fresh	Fresh/moist	Moist	Fresh	Fresh	Moist
Soil type ¹	Leptosol	Regosol/Gleysol	Gleysol	Histosol/Gleysol	Histosol	Histosol
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 (<i>P. a.</i>)	0.31 (<i>P. a.</i>)	0.36	0.32	0.14
Basal area (m ² /ha)	22.5 (<i>P. a.</i>)	20.5 (<i>P. a.</i>) 6.5 (<i>B. v.</i>)	5.3 (<i>B. v.</i>) 7.3 (<i>A. g.</i>) 3.0 (<i>P. a.</i>) 2.3 (<i>P. s.</i>)	15.0 (<i>Q. r.</i>)	15.5 (<i>P. a.</i>)	17.5 (<i>A. g.</i>)

¹[40, 41].

at -4°C ; a temperature that did not damage the live tissue and caused no change in ion concentrations [42]. The roots were sorted out from the soil cores immediately after thawing. In order to distinguish live roots from dead roots distinct morphological characteristics were used [43].

Live fine roots (<1 mm in diameter) 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 [43, 44]. 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 dry weight (at least for 24 hours).

The fine-root production and turnover rates were calculated from significant (Student's *t*-test) increments of live, dead, and live + dead fine roots at the coniferous fern forest at Forsmark. Comprehensive descriptions of calculation methods used are to be found in [8]. By turnover rate, in this context, was meant the annual fluxes in the live, dead, or in the live + dead fine-root compartment. Root turnover rate (yr^{-1}) was calculated from the annual increments in live, dead and, live + dead fine roots divided by the average amounts in those categories during the year of sampling.

From these calculations only minimum estimates of turnover rate can be obtained since the sampling frequency (only four sampling occasions) covered only some of the major fluctuations, but certainly not all increases. The risk for overestimation 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 [8].

3. Results

A substantial variation with depth in the total amount of live and dead tree fine roots was observed at the different forest sites (Figure 1). High amounts of dead fine roots were indicated in the mineral soil horizons. The proportion of dead fine roots varied at all sites and in all horizons from 6 to 88% (Table 2). The highest proportions of dead fine roots were found in the two *Alnus* forest sites at Forsmark and Laxemar, which were both classified as “moist,” with a high topographic wetness index (cf. Table 1). The live/dead ratio of fine roots (<1 mm in diameter) varied in all sites from 14.1 in the uppermost 2.5 cm of the humus layer to 0.2 in the deepest parts of the mineral soil horizon (Table 2). The live/dead ratio is calculated only for soil cores with both live and dead fine roots.

Low amounts of live fine roots were found in the uppermost 2.5 cm of soil of the moist *Alnus* shore forest at Laxemar compared with the same soil segments at other forest sites (Figure 1 and Table 2). The total amounts of fine roots were very low at the latter site and substantial amounts of dead fine roots were found in the total soil profile. At the moist *Alnus* swamp forest at Forsmark, a more substantial proportion of live fine roots were observed in the total soil profile, resulting in a comparatively high live/dead ratio, in particular in the humus layers (Table 2).

The rooting density (g dm^{-3}) was low at all sites in the mineral soil horizons compared with in the humus layers except for in the coniferous fern forest at Forsmark (Figure 1). A low live/dead ratio of fine roots was found in the deepest soil horizons, where the rooting density was very low (Table 2). Extremely low rooting density was observed in the mineral soil horizons at the *Alnus* swamp forest at Forsmark, at the herb rich oak forest at Laxemar and at the *Alnus* shore forest. The soil corer was driven in all sites to depths in the mineral soil horizon (at least 2 dm) where only

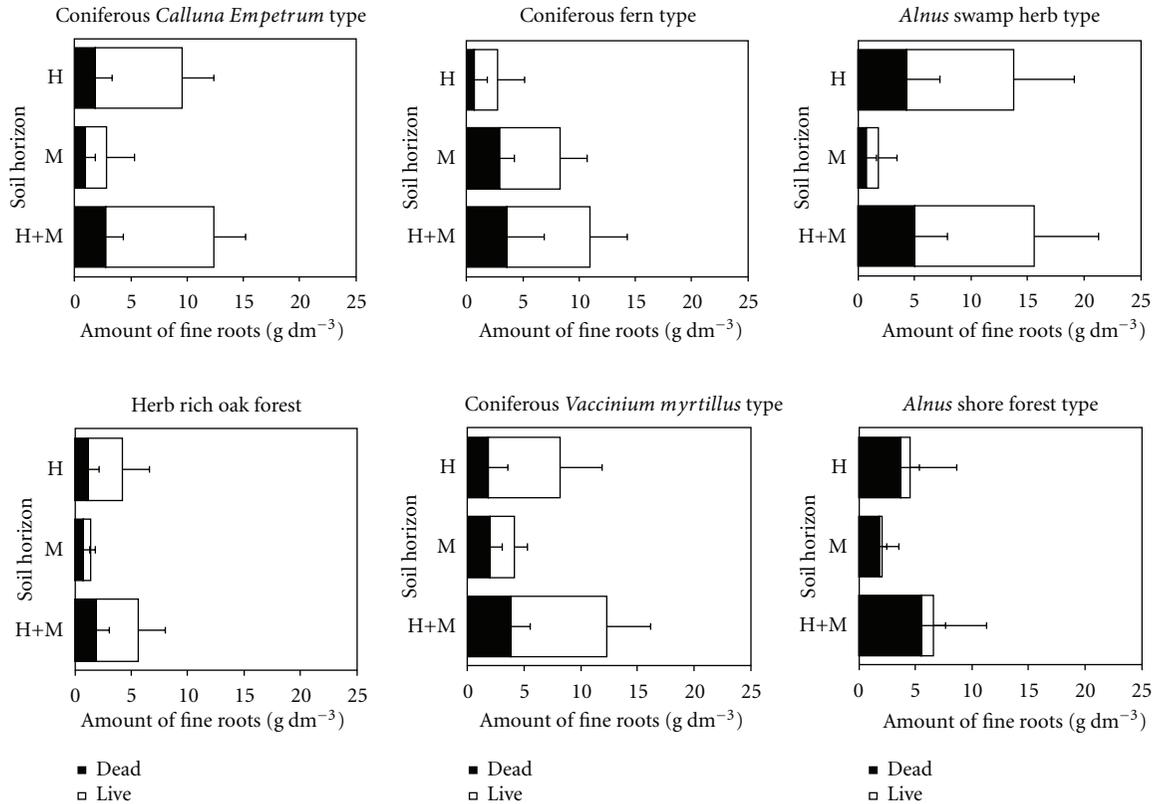


FIGURE 1: The amount of live and dead tree fine roots (g dm^{-3} ; <1 mm in diameter) in the humus layer (H) and in the mineral soil horizon (M) compared with in the total soil profile (H+M) at different Swedish forest sites.

limited amounts of live or dead fine-root fragments were observed (Table 2).

The mean amount of live tree fine roots in the humus layer in relation to the total amount of live + dead fine roots in the soil profile was 48, 7, and 48% for the three Forsmark sites and 35, 25, and 6% for the three Laxemar sites, respectively (Figure 1, Table 2). The related amount of dead fine roots in the humus layer was 13, 2, and 30% for the Forsmark and 13, 2, and 28% for the Laxemar sites, respectively. Proportionally more live than dead fine roots were observed at all sites in the humus compared with in the mineral soil horizon, except for at the *Alnus* shore forest site at Laxemar (Figures 1 and 2). The density estimates (Figure 1; g dm^{-3}) give a more correct picture of the extensive distribution of live fine roots in the humus layer than simply the distribution per unit area in different soil layers (Figure 2 and Table 2; g m^{-2}).

The proportion of dead fine roots (<1 mm in diameter) of the total amount of fine roots in the humus layer (Table 2) was high in both moist *Alnus* forest at Forsmark and Laxemar sites (38 and 82%, resp.). A distinct hummock and hollow microtopography was developed at the *Alnus* forest of swamp herb type at Forsmark and tree fine roots were more frequently found in the uppermost aerated parts of hummocks. The tree layer consisted of a mixture of *Betula verrucosa*, *Picea abies*, and *Pinus sylvestris* (Table 1). At the water-saturated *Alnus glutinosa* shore forest at Laxemar, no

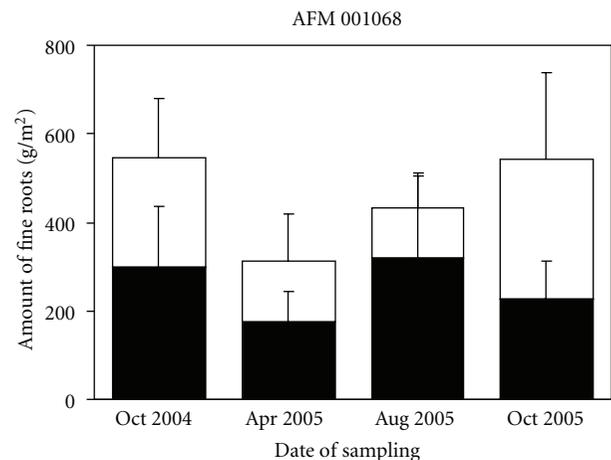


FIGURE 2: The amount of live (unfilled bar) and dead (black bar) fine roots (<1 mm in diameter) on the four sampling occasions in the coniferous fern site at Forsmark during 2004-2005. Mean values \pm SD.

hummocks were found and anaerobic conditions reached even the uppermost parts of the soil horizon.

Substantial variations in live and dead amounts of fine roots and live/dead ratios were observed in the coniferous fern site at Forsmark during the sampling period confirming

TABLE 2: The distribution of live and dead amounts of tree fine roots (<1 mm in diameter), live/dead ratios, and dead (%) at different depths (H = humus; M = mineral soil) at the forest sites: Forsmark-1 (Coniferous, *Calluna Empetrum* type), Forsmark-2 (Coniferous fern type) and Forsmark-3 (*Alnus* swamp herb type) and Laxemar-1 (herb-rich oak forest), Laxemar-2 (Coniferous *Vaccinium myrtillus* type), and Laxemar-3 (*Alnus* shore forest type) forest sites. The live/dead ratio is calculated from the mean amounts of live and dead tree fine roots. Estimates are given as mean values \pm SD ($n = 31-32$).

Site	Horizon	Tree roots (g m^{-2})			
		Live	Dead	Live/dead ratio	Dead (%)
Forsmark-1	H 0–2.5	48 \pm 42	3 \pm 9	13.3	6
	H 2.5–5	64 \pm 29	15 \pm 22	4.2	19
	H 5–10	60 \pm 63	21 \pm 25	2.9	26
	H 10–15	9 \pm 20	9 \pm 21	0.9	50
	H 15–20	2 \pm 9	2 \pm 12	1.0	50
	M 0–10	71 \pm 96	58 \pm 63	1.2	45
	M 10–20	13 \pm 59	10 \pm 21	1.3	43
Forsmark-2	H 0–2.5	30 \pm 35	4 \pm 5	7.5	12
	H 2.5–5	4 \pm 12	4 \pm 11	1.1	50
	H 5–10	2 \pm 6	3 \pm 10	0.6	60
	M 0–10	228 \pm 138	136 \pm 70	1.7	37
	M 10–20	51 \pm 67	73 \pm 60	0.7	59
	M 20–30	2 \pm 8	5 \pm 15	0.4	71
Forsmark-3	H 0–2.5	56 \pm 58	11 \pm 11	5.1	16
	H 2.5–5	46 \pm 36	23 \pm 21	2.0	33
	H 5–10	55 \pm 52	51 \pm 40	1.1	48
	H 10–15	28 \pm 35	25 \pm 33	1.1	47
	H 15–20	13 \pm 30	9 \pm 16	1.5	41
	H 20–25	3 \pm 9	6 \pm 22	0.5	67
	M 0–10	29 \pm 73	45 \pm 55	0.6	61
	M 10–20	6 \pm 11	14 \pm 21	0.4	70
Laxemar-1	H 0–2.5	24 \pm 28	7 \pm 10	3.4	23
	H 2.5–5	34 \pm 37	15 \pm 16	2.3	31
	H 5–10	21 \pm 28	8 \pm 12	2.6	28
	M 0–10	57 \pm 42	48 \pm 34	1.2	46
	M 10–20	3 \pm 7	9 \pm 23	0.3	82
Laxemar-2	H 0–2.5	102 \pm 61	18 \pm 23	5.6	15
	H 2.5–5	48 \pm 52	17 \pm 21	3.0	26
	H 5–10	10 \pm 29	11 \pm 30	0.9	52
	M 0–10	132 \pm 69	71 \pm 48	1.8	35
	M 10–20	51 \pm 49	71 \pm 37	0.7	58
	M 20–30	25 \pm 49	31 \pm 32	0.8	38
	M 30–40	4 \pm 10	26 \pm 34	0.2	87
Laxemar-3	H 0–2.5	14 \pm 17	47 \pm 79	0.3	77
	H 2.5–5	5 \pm 9	38 \pm 57	0.1	88
	H 5–10	1 \pm 4	7 \pm 19	0.1	33
	M 0–10	17 \pm 25	115 \pm 104	0.1	87
	M 10–20	7 \pm 16	35 \pm 40	0.2	85
	M 20–30	3 \pm 8	21 \pm 33	0.1	84
	M 30–40	2 \pm 8	10 \pm 14	0.2	83

TABLE 3: The amount of live, dead, and live + dead fine roots (<1 mm in diameter) and differences on different sampling occasions, annual means, Σ annual increases of fine roots and turnover rate of live, dead, and live + dead fine roots at a fresh/moist coniferous fern forest site at Forsmark.

Sampling number	Live	Dead	Live + dead
(1)	317 \pm 196	226 \pm 88 ^a	543 \pm 205
(2)	113 \pm 79 ^a	321 \pm 184 ^a	434 \pm 212
(3)	150 \pm 112	180 \pm 62 ^b	330 \pm 136 ^a
(4)	248 \pm 134 ^a	299 \pm 136 ^b	546 \pm 212 ^a
Annual means	207	257	463
Σ Annual increases	135	214	216
Turnover rate	0.7	0.8	0.5

Sampling took place on 4 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 \pm SD ($n = 32$). Significant increases are marked by ^a and ^b. Differences are significant at $P = 0.05$ (Student's t -test).

a high turnover rate in live, dead, and live + dead fine roots (Table 3). Low amounts of dead fine roots were found at the remaining sites at Forsmark and Laxemar, in particular in the upper well-oxidized parts of the humus layer. Although, no sequential soil coring was carried out at the two moist *Alnus* forest sites, high turnover rates of live fine roots must explain the high accumulation rate of dead fine roots. Thus, anoxia may play an important role in regulating the rate of organic matter accumulation in forest soils.

4. Discussion

The methods used of estimating fine-root production and mortality should involve the measurements of live and dead dry weight of fine roots from soil cores in undisturbed soil horizons. The often reported discrepancy in the estimates of root litter formation in data from sequential coring may partly be due to imprecise definition of vitality and size classes of the fine roots. In our case distinct morphological characteristics were used in order to separate live and dead fine roots [8, 43]. In roots considered as dead, the stele was brownish and easily broken, and the elasticity was reduced [43]. Dark coloured tissues are frequently found in live fine roots and the colour in itself is not a reliable criterion of vitality. Depending on the pattern of cell death, several root functions can cease even before cell dies [45].

Substantial variations in live and dead fine roots and live/dead ratios usually occur in tree stands confirming our calculations of turnover rates [4, 17, 23, 27, 39, 46–50]. The dead amounts of fine roots normally do not persist for long in well-oxidized conditions, decay or complete disappearance is accomplished in a few days only [8, 49, 51]. Under anoxic conditions there is an accumulation of dead fine roots, since the decomposition will be reduced [33, 52, 53]. Under long-term anoxic conditions, for example, the case, at the *Alnus* swamp forest of herb type at Forsmark and at the *Alnus* shore forest at Laxemar, an accumulation of dead fine roots was observed.

Fine roots respond quickly to environmental changes and are rapidly penetrating favourable the soil horizons.

We know that fine roots are sensitive to drought and that their live/dead ratios are decreasing with less water availability in the soil [54–57]. In water-saturated forest ecosystems the primary production of fine roots may exceed the decomposition of dead roots, also leading to a decreased live/dead ratio [32, 58, 59]. In many cases death takes place as a result of ageing, reduced carbohydrate supply, the influence of different climatic stress factors such temperature changes and frost [49, 60]. Increased fine-root herbivory especially in nutrient-rich patches is furthermore expected to significantly influence the carbon cycling patterns [61].

Although our sampling occasions were few, our data from the coniferous fern site at Forsmark suggest that substantial increases/decreases in live, dead, and live + dead fine roots will take place during the growth period (Table 3). The annual above-ground litter fall (mainly *Picea abies* needles) was 135 g m² compared with the annual below-ground fine-root litter supply of 257 g m² [62] (Table 3). Our study suggests that the annual above-ground tree litter fall from leaves/needles is less important in terms of dry weight than the annual belowground formation of fine-root litter.

Available information in the literature suggests a fine-root production with a seasonal pattern different from needle or leaf production [26, 63, 64]. Fine roots respond quickly to environmental changes and their life span is relatively short. Our investigation confirms that the growth pattern of the fine roots depends on where in the soil profile they are developed and that the live/dead ratio is decreasing with depth (Table 2).

“Vitality” in terms of live/dead ratios of fine roots should be expected to be high in the humus layer, since the extensive mycorrhizal infection in that layer makes the fine roots functional over a prolonged period of time [65–68]. Although no distinct seasonal pattern is reported in the literature a high growth and death rate of fine roots should be expected during the summer months [8, 69]. A high death rate was observed during the winter month and early spring (Table 3). Dead fine roots are decomposed quickly in well-oxidized soil layers ensuring a high live/dead ratio of fine roots.

Detritus from above-ground and below-ground plant tissues constitutes the primary source of carbon for soil organic matter [28]. The presence of soil organic matter improves the nutrient availability and reduces soil strength. Tree fine roots may play a more important role for the formation of soil organic matter than the needles/leaves [8, 22, 26, 70–73]. In strongly seasonal climates, the length of the growing season often increases the lifespan of needles/leaves, but fine roots may stay alive less long.

Sequential coring data at the ecosystem scale suggest an annual production of fine roots, frequently higher than the average amount of live fine-roots [8, 17, 22, 26, 74–78]. Most observations on fine-root turnover are underestimates and the costs and benefits of exudation, root hairs and the mycorrhizal fungi is not yet sufficiently clarified [43]. Techniques for obtaining root data are still in a formative stage. As more research is conducted on root methods, techniques will become more refined and standardized. Obtaining root data is essential for all kind of long-term field experiments, because plant responses may occur in the shifts in carbon allocation between above- and below-ground plant components.

Decomposition of fine roots is determined mainly by the interactions between soil temperature and oxygen accessibility [79]. Other factors regulating the fate of dead fine roots in the soil are the soil pH, the availability of decomposer organisms, and litter quality [22, 80, 81]. Only few studies have considered the interactions between all these factors [32, 33, 35, 52, 53, 71, 79, 82–84]. Estimates of root respiration to the total CO₂ efflux range from 10% to 90%, with considerable methodological uncertainties [35, 84].

The high amount of dead fine roots accumulated in our two anoxic forest sites unveils a high turnover rate of live fine roots. The changes between anoxic and well-oxidized soil conditions in a forest soil may cause death of both fine roots and mycorrhiza [33, 52]. The effects of anoxia on the metabolic cost on the plant root system and the mycorrhizal infection have so far received limited attention [32, 59, 85]. Uncertainties in the belowground carbon balances limit the establishment and improvement of policies regulating the atmospheric CO₂ concentrations.

Trees constitute major reservoirs of carbon in terrestrial ecosystems; large amounts of carbohydrates are annually transported from the shoots to the roots and stored in the root systems [4, 5, 9, 11, 13, 21, 25, 48, 64, 72]. High amounts of live and dead fine roots are found in forest ecosystems [8, 12, 15, 55, 80]. The vitality of the fine roots seem to depend on where in the soil profile they are developed; it is therefore essential, while studying the distribution of fine roots in forest ecosystems, to relate to the natural soil-horizons [15, 46]. The often well-developed organic-rich humus layer in the forest soil most effectively buffers the root system against drought and nutrient deficiencies [15, 69]. Few studies have so far examined patterns in live/dead ratios of fine roots in relation to soil water and mineral nutrient availability during the growth period [15, 24, 74]. Fine roots of trees in many ways are indicators of environmental change, soil nutrient status, and forest health [14, 16, 47].

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