Root turnover and root necromass accumulation of Norway spruce (*Picea abies*) are affected by soil acidity

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Summary   Fine root distribution and turnover were investigated in ca. 40-year-old pure Norway spruce (*Picea abies* Karst.) stands in Germany, growing on four sites that differed in soil acidity (Ebergötzen < Barbis < Fichtelgebirge = Harz). The density of fine root biomass and necromass in different soil horizons differed among the sites. At one of the most acidic sites (Harz), fine root density in the humus layer was more than twice that at the least acidic site (Ebergötzen). At the two most acidic sites, Fichtelgebirge and Harz, the ratio of biomass to necromass was significantly lower than at Ebergötzen and Barbis, particularly in the subsoil layer. In each stand, clear vertical gradients in fine root length density and root tip density were observed. Most of the roots and the root tips were in the humus layer and in the first mineral soil horizon (0–10 cm). There was a significantly different decrease in specific root length (cm g_{DM}^{-1}) and specific root tip density (root tips g_{DM}^{-1}) in the more acidified stands Fichtelgebirge and Harz compared with Ebergötzen and Barbis. Fine root production estimated by ingrowth cores and a net method was approximately twice as high in the more acidic stands Fichtelgebirge and Harz compared with Ebergötzen and Barbis. Rates of living fine root biomass turnover were higher at the Fichtelgebirge and Harz sites than at the Ebergötzen site. Rates of necromass turnover were similar at all sites. The results suggest that the accumulation of necromass was not due to a slower disappearance at the more acid sites, but to earlier root death. Roots contributed 46% to root + needle litter and 32% to root + total aboveground litter at the Harz site in 1997.

Keywords: fine roots, litter fall, root necromass.

Introduction

Fine root turnover has been estimated to account for as much as 33% of global annual net primary production (NPP) (Jackson et al. 1997). In trees, belowground NPP may exceed 50% of total NPP, with fine roots comprising a substantial part of total belowground NPP (Nadelhoffer and Raich 1992). On a global scale root turnover is primarily influenced by temperature (Gill and Jackson 2000), but on a local scale it is related to precipitation and soil factors (Norby and Jackson 2000). Rates of fine root turnover have large consequences for belowground nutrient cycling and C incorporation into soil. In beech forest, nutrient return through fine root turnover provides 20–30% of N inputs (Wu et al. 2001). Vogt et al. (1986) showed that root turnover contributed between 20 and 80% of total forest floor detritus. In many forests throughout much of Scandinavia (Tamm and Hallbäcken 1989), Western and Central Europe (Büttner 1984, Blaser et al. 1999) and areas of the eastern USA (Drohan and Sharp 1997), forest soils have become significantly acidified in recent decades as a result of atmospheric deposition. Soil acidification reduces the base saturation of the cation exchange sites of the mineral soil, leading to a decrease in the storage of base cations such as Mg and Ca and an increase in the availability of potentially toxic ions such as Al (Ulrich 1994). Although it is known that Al affects root growth of small tree seedlings in nutrient solutions (Godbold et al. 1988), there has been contention as to whether Al affects root growth in forest soils. Recently, it has been shown that subsoil acidity affects the distribution of fine roots of Norway spruce (Jentschke et al. 2001), confirming ideas expressed in earlier work (Murach and Matzner 1995). However, differences in rates of fine root turnover have never been investigated in relation to differences in soil acidification, despite the large potential implications for global C sequestration.

Rates of root production and turnover are difficult to measure and estimates are often biased by the methods used (Steele et al. 1997, Rytter 1999, Hertel and Leuschner 2002). In this work, we estimated the rates of fine root turnover in four ca. 40-year-old Norway spruce stands growing on soils that differed in degree of acidification. In one stand, we estimated the importance of fine root turnover to total biomass inputs to the forest floor.

Materials and methods

Study sites

The study was conducted in four ca. 40-year-old pure Norway spruce (*Picea abies* Karst.) stands in Germany, growing on sites that formed a gradient of soil acidity (Ebergötzen < Barbis < Fichtelgebirge = Harz). Three stands, Ebergötzen, Barbis and Lange Bramke, Harz, are in southern Lower Saxony, and the fourth is in northeast Bavaria in the Fichtelgebirge. Diameter at breast height (DBH) and tree height differed among the stands; trees were smallest at the Harz stand and largest at Barbis (Table 1). Mean summer temperature is 14.5 °C at Ebergötzen and Barbis and 9.9 and 11.0 °C at Fichtelgebirge and Harz, respectively. Annual precipitation is higher at Fichtelgebirge and Harz (1100 mm) than at Ebergötzen and Barbis (750 mm). Precipitation is distributed equally between summer and winter in all stands. During the study period, precipitation in all stands was 96 to 124% of the long-term average in 1995, 80 to 84% in 1996 and 89 to 97% in 1997.

The stands differed in the degree of soil acidification (Table 1) and were well drained and the soils showed no signs of waterlogging (Jentschke et al. 2001). The humus layer depth increased from 2 cm at Ebergötzen to 10 cm at the Harz site (Table 1). Soils differed greatly in their chemical properties, especially in their base saturation. Base saturation at 0–10 cm soil depth was 19% at Ebergötzen compared with 5% at Fichtelgebirge and 4% at Harz. At 10–20 cm soil depth the base saturation was 47% at Ebergötzen, 15% at Barbis and only 3 and 6% at Fichtelgebirge and Harz, respectively. Exchangeable Al in the 0–10 cm soil layer was two- to threefold higher at the Fichtelgebirge and Harz sites than at Ebergötzen. The difference was even greater in the 10–20 cm soil layer. At Barbis, the amount of exchangeable Al had an intermediate value in both soil layers. The molar Ca to total Al ratio in the soil solution at 0–10 cm soil depth ranged from high values at Ebergötzen to very low values indicative of Al toxicity (Cronan and Grigal 1995) at Fichtelgebirge and Harz.

Trees had low needle Mg concentrations at Fichtelgebirge and Harz (Ende and Evers 1997). The sites are described in full by Jentschke et al. (2001).

Fine root biomass

Fine root biomass was determined in soil cores. In each stand, six permanent 10-m^2 plots were established. In each plot, two soil cores (4 cm diameter × 40 cm deep) were randomly collected at each sampling and separated into the organic layer and three mineral soil layers from 0–10 cm, 10–20 cm and 20–40 cm depths. Minimal distance between the plots was 30 m, six- to tenfold the distance between trees in all stands. Therefore, each experimental plot was considered an independent replicate within the stand comparison approach. At the Harz stand, a high proportion of coarse fragments in the soil prevented systematic sampling of the 20–40 cm mineral soil layer. At all stands, samples were taken monthly between May and October 1995 and bimonthly between May and October 1996 as well as between April and October 1997. In total, cores were collected on 14 dates. Samples were stored in plastic boxes at 4 °C until processed. Each sample was washed over a 1-mm sieve, and all roots collected. On account of the sparsity of the understory and forest floor vegetation, roots found in the cores were almost all *Picea abies* roots. Occasionally, roots of grasses or blueberry were found in the cores and discarded. Fine roots (< 2 mm diameter) were classified as live or dead based on color, texture and shape (Vogt and Persson 1991) and dried to constant mass at 70 °C.

Root length and number of root tips of the fine roots were determined by analyzing photocopies of the live root segments with Mac/WinRhizo 3.1 (Regent Instruments, Quebec).

Table 1. Stand characteristics and soil properties of the study sites (Fritz 1999).

	Ebergötzen	Barbis	Fichtelgebirge	Harz
Stand characteristics				
Tree age (1996) (years)	35	40	41	45–53
Tree height (m)	21	22	18	15
Stem diameter at breast height (cm)	23	25	22	17
Soil properties				
Humus layer (cm)	2	3	8	10
pH (H$_2$O)				
0–10 cm	4.7	4.2	3.8	3.6
10–20 cm	5.0	4.4	4.0	4.1
Base saturation (%)				
0–10 cm	19	12	5	4
10–20 cm	47	15	3	6
Exchangeable Al (mmol kg^{-1})				
0–10 cm	46	71	101	139
10–20 cm	27	57	112	112
Soil solution (40 cm) (molar Ca:Al)	3.7	2.9	0.3	1.3

Root production

Root production was estimated using ingrowth cores (Vogt and Persson 1991) and a net method. Because root production data from ingrowth cores may be biased by a delay in root regrowth into the cores (Lukac and Godbold 2001), we separated root regeneration after cutting the cores from recolonization of the cores by putting a mechanical barrier in the soil for one year before roots were allowed to recolonize the cores. In May 1996, 30 soil cores (4 cm diameter × 20 cm deep) were cut in each stand. Plastic PVC tubes (5 cm outer diameter × 25 cm length) were placed into the core holes and left in place for one year to allow the root systems to recover from damage inflicted by the soil auger. Tubes were filled with polyurethane foam to protect the surrounding soil from changes in temperature due to the missing soil core. In May 1997, the tubes were carefully removed, and the holes refilled. Root-free native soil was placed by soil layer in 10 of the holes in each stand, and the original litter layer replaced. Soil cores were separated into mineral soil and an organic layer (F and H layers), and sieved through a 4-mm mesh to remove roots. The remaining 20 holes per stand were refilled with quartz sand (0.7–1.2 mm particle size) or fertilized peat (TSK2, Compo, Münster, Germany). We used different substrata in all stands because root production data by the ingrowth technique may be biased by the substrate used to refill the cores (Vogt et al. 1998). Ingrowth cores were collected in October 1997. All ingrowth cores including surrounding soil were collected with an 8-cm diameter corer, and the surrounding soil and roots separated from the cores. Samples were stored in plastic boxes at 4 °C until processed. Cores were washed over a 1.5-mm sieve, and all roots collected. To estimate fine root production, the mass of live and dead roots with a diameter less than 2 mm was determined after drying to constant mass at 70 °C. Because root growth responded to the different substrata similarly in all stands (Jentschke et al. 2001), we used average root ingrowth over all substrata as a measure of relative root production.

In April 1997, 50 nylon meshes (5 cm × 10 cm, 1-mm mesh size) were placed in the uppermost 10 cm of the soil in each stand. To do this, the litter layer was removed, the soil cut to a depth of 10 cm with a bricklayer's trowel and the mesh placed vertically in the slit. The litter layer was then replaced. Unfortunately, wind damaged the Barbis stand in late-summer 1997, leaving only 17 meshes intact. In October 1997, all remaining meshes including the surrounding soil were removed with a spade. Care was taken to keep soil monoliths intact while excavating them. Soil embedded in the meshes was removed with brushes and forceps, and the number of roots crossing the meshes counted. Roots were removed from the meshes and dried to constant mass at 70 °C.

Rates of biomass and necromass turnover were calculated as annual root production divided by maximal standing biomass or necromass (Gill and Jackson 2000).

Aboveground litter collection

At the Harz site at Lange Bramke, total litter fall was collected monthly with 50 × 50 cm plastic-mesh litter collectors suspended 70 cm aboveground in wooden frames. Litter was sorted into needles and woody components and dried at 70 °C.

Statistical analysis

To compare four Norway spruce stands with differing soil acidity, permanent plots were established within each stand, and considered independent replicates. This is a point comparison approach rather than a replicated experiment on the ecosystem scale. To increase homogeneity of variance when necessary, data were log-transformed. A two factor (site by depth) repeated measures (sample date) analysis of variance was carried out. Significance among means was tested by the Tukey-Kramer test.

Results

Fine root density

The density of fine root biomass and necromass in the soil profile differed at the four sites (Figure 1). The density of biomass and necromass in the humus layer increased with increasing soil acidification (Figures 1a and 1b), and at the Harz site was more than double that at the Ebergötzen site. Unlike biomass density, density of necromass was also higher in the 0–10 cm and 10–20 cm mineral soil layers at Fichtelgebirge and Harz than at Ebergötzen. Total biomass (g m^{-2}) was lowest at Ebergötzen, but did not differ among the other sites (Figure 1a). However, we were unable to systematically sample the 20–40 cm soil layer at the Harz site. The available measurements suggest that total biomass was 20 g m^{-2} in this layer (H.-W. Fritz, unpublished data). Total necromass at the Fichtelgebirge and Harz sites was more than twice that at Ebergötzen (Figure 1b). The higher density of necromass was reflected in the ratio of biomass to necromass (Figure 2). At the two most acidic sites, Fichtelgebirge and Harz, the ratio of biomass to necromass was significantly lower than that at Ebergötzen and Barbis, particularly in the subsoil layer.

In each stand, clear vertical gradients in fine root length density and root tip density were observed (Table 2). Most of the roots and the root tips were in the humus layer and in the first mineral soil horizon (0–10 cm). Means for the whole horizon of root length density and root tip density were not significantly different between the stands, even when root length and number of root tips were calculated on an area (m^{-2}) basis (data not shown). This was in contrast to the higher fine root biomass found at the Fichtelgebirge and Harz sites compared with the other sites. In an attempt to relate biomass to root length and root tip density, specific root length (cm g$_{DM}^{-1}$) and specific root tip density (root tips g$_{DM}^{-1}$) were calculated (Table 3). There was a significant decrease in specific root length and specific root tip density in the more acidified stands Fichtelgebirge and Harz compared with Ebergötzen and Barbis, but the values for the Harz were also significantly lower than for the Fichtelgebirge.

Fine root production and turnover

Values of root production determined by ingrowth cores and
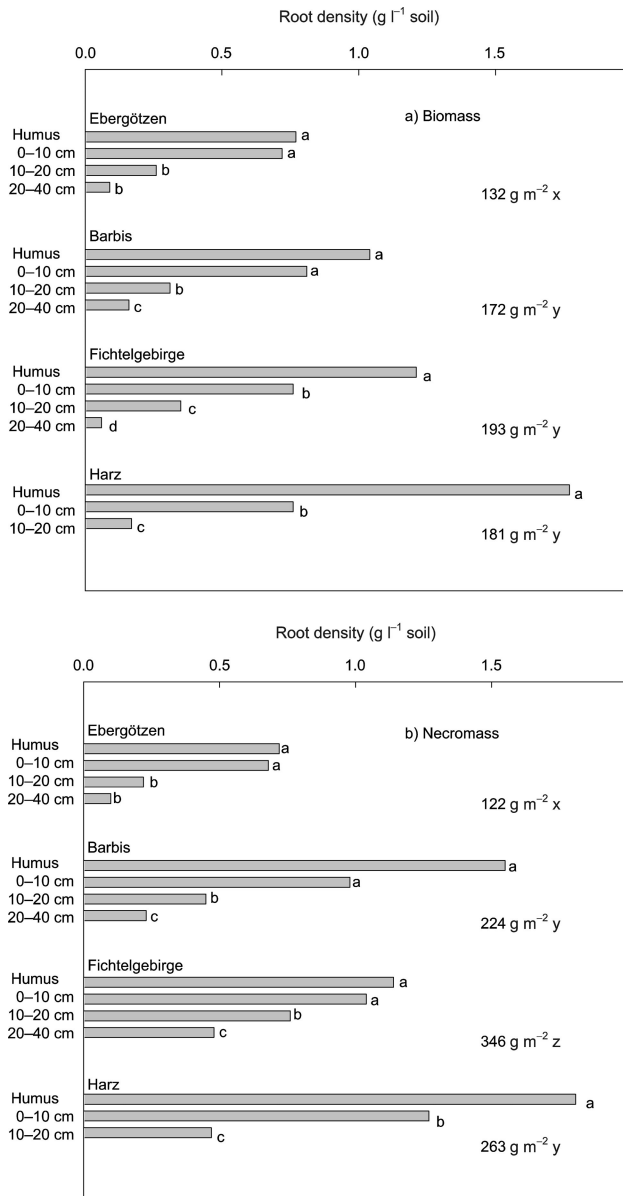
Figure 1. Fine root density in different soil horizons and total fine root mass of the four *Picea abies* stands differing in soil acidity. For the Ebergötzen, Barbis and Fichtelgebirge sites the soil profile was sampled to 40-cm depth, and for the Harz site to 20-cm depth. Values are means of 14 sampling times 1995–1997. Within a site, fine root density values with different letters are significantly different ($P \leq 0.05$). Values for total mass with different letters are significantly different ($P \leq 0.05$).
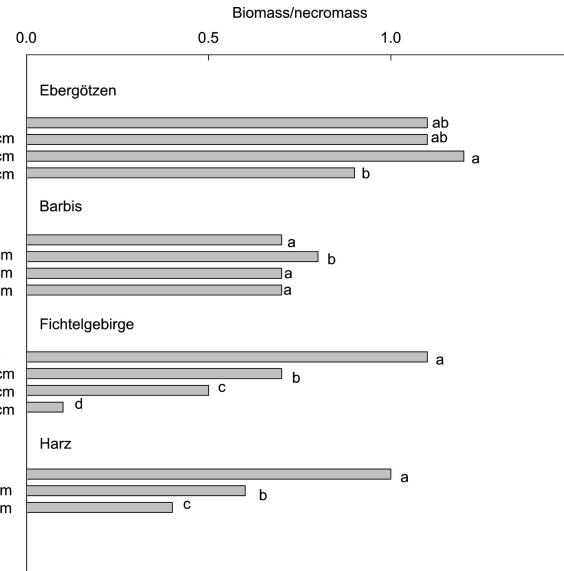

Figure 2. Fine root biomass to necromass ratio in different soil horizons of four *Picea abies* stands differing in soil acidity. Values are means of 14 sampling times 1995–1997. Within a site, bars with different letters are significantly different ($P \leq 0.05$).

ber using nets or from May to October using ingrowth cores. Differences were found between the rates of root turnover based on the two estimates of root production (Table 5). However, rates of biomass turnover were clearly higher at the Fichtelgebirge and Harz sites than at the Ebergötzen site. No clear differences in necromass turnover could be seen between the sites. The ratio of biomass to necromass turnover was higher at the Fichtelgebirge and Harz sites than at the Ebergötzen site. An intermediate value was calculated for the Barbis site.

Aboveground litter fall

At the Harz site, the amount of needle litter fall in 1997 was similar to that in other years, whereas total litter fall was slightly higher (Table 6). Comparing litter fall with the root turnover values obtained by the net method at the Harz site, where the net was in the humus layer only, gives the relative contributions of above- and belowground biomass to the humus layer. Root production was 46% of the root + needle litter or 32% of root + total aboveground litter.

Discussion

The distribution of fine roots in the soil profile differed among the stands; a much shallower rooting pattern was found beneath the stands with more acidified soil. This is consistent with the findings of Jentschke et al. (2001), showing that the effect was due to subsoil acidity, not differences in precipitation, temperature, nitrogen deposition or soil physical properties. In our study, a higher fine root biomass was found for the total soil profile at the more acidic sites.

Estimates of the size of root systems as absorptive organs are biased by the inclusion of a large amount of tissue that is

the net method were similar, even though the methods measured different soil depths. Fine root production was approximately twice as high at Fichtelgebirge and Harz as at Ebergötzen and Barbis (Table 4).

In calculating rates of root turnover, maximal standing biomass or necromass was determined for 0–10 cm or 0–20 cm soil depth to correspond with the depth for net or ingrowth core measurements, respectively. Annual root production was estimated from root production measured from April to Octo-

Table 2. Fine root length and fine root tip density in different soil horizons of four *Picea abies* stands. Values are means of 14 sampling times 1995–1997. Within a site, values for a horizon with different letters are significantly different ($P \leq 0.05$). Mean values for sites are not significantly different ($P \leq 0.05$).

Soil depth	Root length density (cm l^{-1} soil)	Root tip density (tips l^{-1} soil)
Ebergötzen		
Humus (2 cm)	1110 a	3530 a
0–10 cm	950 a	2800 a
10–20 cm	330 b	950 b
20–40 cm	100 b	290 c
Mean	620	1890
Barbis		
Humus (3 cm)	860 a	2590 a
0–10 cm	830 a	2310 a
10–20 cm	320 b	850 b
20–40 cm	150 c	400 c
Mean	540	1540
Fichtelgebirge		
Humus (8 cm)	1480 a	4620 a
0–10 cm	650 b	1930 b
10–20 cm	250 c	760 c
20–40 cm	30 d	90 d
Mean	600	1850
Harz		
Humus (10 cm)	1150 a	3800 a
0–10 cm	500 b	1510 b
10–20 cm	110 c	330 c
Mean	590	1880

Table 3. Specific root length and specific fine root tip density of roots from the whole soil profile (40 cm except Harz, which was 20 cm) at four *Picea abies* stands. Data are means of 14 samples taken in 1995–1997. Within a column, values with different letters are significantly different ($P \leq 0.05$).

Site	Specific root length (cm g_{DM}^{-1})	Specific root tip density (root tips g_{DM}^{-1})
Ebergötzen	1.1 a	3.4 a
Barbis	1.1 a	3.1 a
Fichtelgebirge	0.9 b	2.5 b
Harz	0.6 c	2.0 c

Table 4. Root production determined using nets (0–10 cm soil depth) and ingrowth cores (0–20 cm soil depth) in four *Picea abies* stands in 1997. Within a column, means with different letters are significantly different ($P \leq 0.05$).

Site	Fine root production (kg ha^{-1})	
	Net	Ingrowth cores
Ebergötzen	322 b	501 a
Barbis	762 b	329 ab
Fichtelgebirge	1036 a	1111 c
Harz	1534 a	1705 bc

not involved in absorption of nutrients and water (Pregitzer 2002). In an attempt to overcome this problem we determined root length and number of fine root tips. The distribution of fine root tips was similar to the distribution of fine roots (g_{DM}^{-1}). The highest root length and number of root tips were found in the humus and upper mineral soil layers. In the humus layers, similar values for root tip and root length density were found at each site, as for the whole soil profile. The significant differences in specific length density and specific root tip number between sites suggest that fine roots at Fichtelgebirge and Harz are thicker than at Ebergötzen and Barbis. The in-

creased thickness of fine roots is reflected in the significantly higher fine root biomass density at Harz compared with the other sites.

Rates of fine root turnover were lower at Ebergötzen than at the other sites. The calculated turnover rates are similar to those collated for several temperate conifer ecosystems in a recent review (Gill and Jackson 2000). In sugar maple (*Acer saccharum* Marsh.), fine root life span was shortened, and thus root turnover increased by high temperature and low N availability (Hendrick and Pregitzer 1993), but Burton et al. (2000) subsequently showed that the differences were mostly due to differences in N availability. However, it is difficult to explain the higher turnover rates at the more acidic sites based on temperature and N availability. At the Ebergötzen site, maximum soil temperature in August was slightly higher (18 °C) than at the Fichtelgebirge (14 °C) and Harz (15 °C) sites (Jentschke et

Table 5. Rates of root biomass and necromass turnover, and the ratio of biomass to necromass turnover rate of four *Picea abies* stands in 1997. Rates of turnover were calculated as annual root production divided by maximal standing biomass or necromass.

Site	Turnover (year^{-1})				Biomass:necromass turnover	
	Biomass		Necromass		0–10 cm	0–20 cm
	0–10 cm	0–20 cm	0–10 cm	0–20 cm		
Ebergötzen	0.47	0.47	0.38	0.40	1.24	1.18
Barbis	0.81	0.25	0.58	0.18	1.40	1.41
Fichtelgebirge	1.09	0.78	0.59	0.33	1.85	2.39
Harz	0.84	0.66	0.49	0.38	1.71	1.72

Table 6. Amounts of total and needle litter fall for 1995–1997 of a *Picea abies* stand at the Lange Bramke site in the Harz mountains.

Year	Litter fall (kg ha^{-1})	
	Needle	Total
1995	1810	2580
1996	1220	1770
1997	1830	3420
Mean (1993–2000)	1630	2490

al. 2001). Furthermore, N concentrations in needles were only slightly lower at Ebergötzen than at the other sites (Jentschke et al. 2001). Jentschke et al. (2001) showed that differences in rooting pattern between the sites were due to subsoil acidity and low Ca:Al ratios in the subsoil and fine roots. Even in the upper mineral soil (0–10 cm), the concentration of exchangeable Al was higher at the Fichtelgebirge and Harz sites than at the other sites. Because the concentration of available Al in soil solution is lower in the humus layer than in mineral soil, it is unlikely that Al directly increases the rate of root turnover in the humus layer, but higher soil acidity could be a cause. The pH of the humus layer ranged from 3.7 at Ebergötzen to 2.6 at the Harz site. Perhaps, under adverse soil conditions, the fine roots have to be renewed more often to maintain similar numbers, and hence physiological function. Several other studies have shown a relationship between soil chemical conditions and rates of root turnover (Keyes and Grier 1981, Hayes and Gower 1995). In Norway spruce stands in Sweden, acidification caused by addition of ammonium sulfate resulted in faster rates of root death (Clemensson-Lindell et al. 1995, Majdi et al. 1996).

The calculated rates of necromass turnover were similar for all sites. Berg (1984) found similar rates of decomposition (0.2–0.6 year^{-1}) for fine roots of *Pinus sylvestris* L. in central Sweden. At the Fichtelgebirge and Harz sites, the biomass: necromass ratio was lower than at the Ebergötzen and Barbis sites, particularly in the deeper soil layer. The rates of biomass and necromass turnover are analogous to the rates of root death and disappearance suggested by Mäkelä and Vanninen (2000). Thus, these results imply that the accumulation of necromass is not due to a slower disappearance at the more acid sites, but to a high rate of root death.

A comparison of the contributions of needle and root litter to the humus layer at the Harz site showed that root litter was 46% of the needle fall in 1997. If total litter fall is considered, the contribution of fine roots decreases to 32%. However, the total litter fall in 1997 was 37% higher than the long-term (1993–2000) mean. These values are similar to those found for other coniferous ecosystems (Person 1987, Vogt et al. 1981, 1983, McClaugherty et al. 1982). These results exemplify the importance of root turnover for cycling and sequestration in the forest floor.

Our results suggest that root turnover is affected by soil acidity. Rates of root death seem to be of primary importance in the accumulation of root necromass, and hence C sequestra-tion. In models of global C sequestration in forest soils, single estimates or even default values are often used for root turnover. Our data show that rates of C input can vary greatly among similar forest stands, and that the rates of C input from fine roots may change as soil acidification progresses.

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