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A comparison of four different fine root production estimates with ecosystem carbon balance data in a *Fagus–Quercus* mixed forest

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Abstract

The controversy on how to measure fine root production of forests (*P*) most accurately continues. We applied four different approaches to determine annual rates of *P* in an old-growth temperate *Fagus sylvatica–Quercus petraea* stand: sequential soil coring with minimum–maximum calculation, sequential coring with compartmental flow calculation, the ingrowth core method, and a recently developed root chamber method for measuring the growth of individual fine roots *in situ*. The results of the four destructive approaches differed by an order of magnitude and, thus, are likely to introduce large errors in estimating *P*. The highest annual rates of *P* were obtained from the sequential coring approach with compartmental flow calculation, intermediate rates by sequential coring with minimum–maximum calculation, and low ones by both the root growth chamber and ingrowth core approaches. A carbon budget for the stand was set up based on a model of annual net carbon gain by the canopy and measurements on carbon sink strength (annual leaf, branch and stem growth). The budget implied that a maximum of 27% of the net carbon gain was available for allocation to fine root growth. When compared to the carbon budget data, the sequential coring/compartmental flow approach overestimated annual fine root production substantially; whereas the ingrowth core and root growth chamber approaches grossly underestimated *P* rates. With an overestimation of about 25% the sequential coring/minimum–maximum approach demonstrated the best agreement with the carbon budget data. It is concluded that the most reliable estimate of P in this temperate forest will be obtained by applying the sequential coring/minimum–maximum approach, conducted with a large number of replicate samples taken on a few dates per season, in conjunction with direct root growth observation by minirhizotrons.

Introduction

Fine roots (roots thinner than 2 mm) represent a small, but functionally important, fraction of tree biomass (DeAngelis et al. 1981). Fine root production probably constitutes about 30–50% of the carbon being cycled annually through forest ecosystems (Grier et al. 1981; Vogt et al. 1996). Jackson et al. (1997) estimated that roots consume about 30% of the global annual net primary production. Thus, accurate data on below-ground biomass and root turnover of forests are important for comparing soil carbon storage and fluxes, and to balance the global carbon cycle (Gill and Jackson 2000). Moreover, fine root production and turnover may be a sensitive indicator of changing soil environments. Thus, monitoring the amount and timing of fine root production should reflect tree and ecosystem health (Bloomfield et al. 1996).

Together with root exudation, fine root production is probably the least known process of the carbon cycle of forests. Root production data are much more scarce than root biomass data, and most existing information originates from managed monospecific forest stands of temperate North America and Europe (Fogel 1985; Nadelhoffer and Raich 1992). According to these data, annual fine root production differs by a factor of approximately 10 among various temperate forest stands. However, this high variability in

below-ground productivity of forests may be misleading since productivity measurements were based on different methods that give contrasting results (Singh et al. 1984). Thus, variation in root productivity data among different stands could either reflect real differences in productivity or methodological differences. Moreover, no consensus yet exists on how to best measure fine root production in forests (Majdi 1996, Vogt et al. 1998). Since most techniques are labour-intensive, a recommended method must be sufficiently accurate and feasible. There is an urgent need to test and compare the available methods for estimating root productivity.

The best approach for assessing the reliability of existing methods would be to apply them in parallel at the same place and time, and to compare the results to an independent, non-destructive method. The Ecosystem Carbon Balance Approach (ECBA; Vogt et al. 1996) could serve as a crude independent estimate of below-ground productivity. It aims at a quantification of the total amount of carbon fixed by the trees and might indicate an upper limit for carbon allocation to fine root production. McClaugherty et al. (1982), Aber et al. (1985), Powell and Day (1991), Publicover and Vogt (1993), and Majdi (1996) each compared two or more different production estimates, but they made no attempts to compare measured root production with carbon budget data of the whole stand.

The objectives of our study were: (1) to compare three independent techniques (and four calculation procedures) of measuring fine root production; (2) to relate root production to carbon gain of the stand, as determined by gas exchange measurements in the canopy; and (3) to identify the strengths and weaknesses of the four methods.

Materials and methods

Study site

The investigations were carried out from 1995 to 1997 in a mixed old-growth *Fagus sylvatica* L. /*Quercus petraea* (Matt.) Liebl. forest close to Unterlüss (52°45' N, 10°30' E) in the Lüneburger Heide area (Northwest Germany, state of Lower Saxony; elevation: 115 m a.s.l.). The stand grows on highly acidic and nutrient-poor sandy soils (Spodo-dystric Cambisols; pH(KCl) of the topsoil: 2.6–2.8) derived from fluvioglacial sands of the penultimate ice age. The profile is covered by periglacial drift sand (Leuschner et al. 1993). The stand has a closed canopy and reaches a maximum height of 31 m with *Fagus* trees being 90–110 years old, *Quercus* trees 180–200 years of age. *Fagus* canopies cover 62% of the stand area; those of *Quercus* 38%. A herbaceous layer is absent. A 9–11-cm-thick organic profile (Hemimor to Hemihumimor with Ol, Of and Oh horizons) atop the mineral soil contains a large proportion of tree fine root biomass revealing the very shallow rooting patterns of this community (Büttner and Leuschner 1994; Leuschner et al. 2001). Fine root density (root dry mass per soil volume) decreases exponentially with soil depth resulting in very low values (< 100 g m^{-3}) at horizons below 60 cm. Details on fine and coarse root distribution are given in Hertel (1999) and Leuschner et al. (2001). The ground water table is far below the rooting depth. The climate is cool-temperate and humid suboceanic (mean annual rainfall: 800 mm, air temperature: 8° C). During summer, rainless periods of 20–30 days may occur resulting in water contents < 3 vol.% in the sandy soil profile (Leuschner 1993; Backes and Leuschner 2000).

Four 3 $\times$ 4-m plots were established at random locations in the stand. Earlier investigation had shown that tree fine root biomass is distributed uniformly in this stand, i.e., stem-centred patterns do not exist (Leuschner et al. 2001). The fine root systems of *Fagus* and *Quercus* trees have very large horizontal extensions (diameters > 7 m) with the consequence that fine root endings of both species intermingle thoroughly in the organic layer (Büttner and Leuschner 1994; Hertel 1999). For obtaining average fine root production values of the mixed stand, each study plot was placed in the middle of a *Fagus*/*Quercus* tree pair with an inter-stem distance of 5–7 m. All productivity data were calculated separately for the two species (*Fagus* and *Quercus*), total production being the sum of the two species. Since about 50% of total fine root biomass is located in the organic horizons (Of and Oh) and the mineral topsoil (Ah: 0–5 cm; Leuschner 2001), root production measurements were conducted in these horizons only. Canopy carbon gain, stem growth and litter fall were measured at a distance of 5–10 m from the root study plots (see below). For destructive sampling of above-ground biomass fractions, trees at a distance of approximately 50 m from the study plots were selected.

Fine root growth and production estimates

Three different parameters were used to assess fine root growth: (i) the absolute rate of fine root production (P, i.e. net production of root biomass per horizon and ground area, expressed as g d.m. m^{-2} yr^{-1}), (ii) the mass-related fine root growth rate (MGR, i.e. root increment relative to initial fine root biomass, expressed as g d.m. g^{-1} yr^{-1}), and (iii) the fine root recovery rate after removal of all roots from the soil (R, i.e. regrowth of fine root biomass in the soil cores during a given period in percent of initial fine root mass).

We estimated *P* and MGR with four different approaches: (a) sequential soil coring in combination with a minimum-maximum calculation (SC-MM), (b) sequential coring in combination with a compartmental flow calculation (SC-CF), (c) the ingrowth core method (IC), and (d) an in situ root growth chamber technique (RGC; Hertel 1999; Leuschner et al. 2001). The fine root recovery rate (*R*) was calculated only with the ingrowth core method. The quotient of annual fine root production and annual mean fine root biomass was used to estimate fine root turnover rates (in g g^{-1} $year^{-1}$).

We were not able to conduct all of the labour-intensive experiments synchronously within 1 year, but spread the field measurements over a period of 29 months (April 1995 to August 1997).

Sequential soil coring

Fine root sampling with the sequential coring method (Persson 1978; Vogt and Persson 1991) was conducted with sharp root corers (diameter 33 mm, length 150 mm) that were manually driven 15 cm deep into the topsoil. Twenty samples each were collected at intervals of about 4 weeks from April 1995 to March 1996 (10 sampling occasions). Coring locations were positioned by random coordinates in the four plots (five samples each per plot and sampling date). Duckboards were used to avoid trampling on the plots. For each root sample the thickness of the organic profile was determined by carefully measuring the depth of the Of, Oh and Ah layers prior to sampling. When calculating root densities the sampled humus volume was corrected for the volume lost due to compression. The soil cores were sliced into the organic Of and Oh, and the mineral soil Ah horizons (0–5 cm), transferred to plastic bags, sealed, and transported to the laboratory where processing of stored samples (4° C) took place within 25 days.

In the laboratory, the samples were soaked in demineralized water and soil residues were removed using a 0.25-mm mesh. Large root fractions (> 10 mm length) were extracted by hand. Only fine roots (i.e., roots < 2 mm in diameter) were considered in the analysis. Live (biomass) and dead rootlets (necromass) were distinguished under the dissecting microscope using the degree of cohesion of stele and periderm, root elasticity, and colour. A dark periderm and stele, or a white, but non-turgid, stele and periderm, or the complete loss of the stele were used as indicators of root death. These criteria had been established in 20 root samples that were stained with triphenyltetrazolium chloride (TTC) according to the procedure described by Knievel (1973) and sorted into live and dead according to the presence of the red stain (reduced TTC; Joslin and Henderson 1987). To distinguish the two species, differences in colour (*Fagus*: dark reddish brown; *Quercus*: light yellow), periderm surface structure (*Fagus*: rough with furrows; *Quercus*: smooth) and ramification (*Fagus*: second order rootlets more evenly distributed; *Quercus*: local concentration of rootlets and root tips) were used (Hertel 1999). The mass of small dead rootlets (< 10 mm length) was quantified by removing the larger roots from the sieve manually (van Praag et al. 1988); the residue of a sample was evenly spread on a piece of filter paper (730 cm^2) with 36 squares marked on it. Six of the squares were randomly selected and analysed under the microscope for even smallest dead fine root fragments. These decaying root particles represent the main necromass fraction in organic soil horizons (van Praag et al. 1988; Bauhus and Bartsch 1996). The mass of small dead rootlets was extrapolated to the entire sample by means of the ratio small dead rootlets/large dead roots (> 10 mm length) that was established in the six squares. Root biomass and necromass were dried at 70° C (24 h), and the data expressed as root abundance (g d.m. m^{-2} and $horizon^{-1}$) or root density (g d.m. m^{-3}).

The production of *Fagus* and *Quercus* fine roots was calculated from the sequential coring data by two independent methods:

(i) The 'minimum–maximum method' (SC-MM; Edwards and Harris 1977; McClaugherty et al. 1982) calculates the difference between minimum and maximum of fine root bio- and necromass in the measuring period and equates it with production. In this study, the measuring period lasted from April 1995 until March 1996 (12 months).

Only significant differences between minimum and maximum were considered.

(ii) By quantifying the changes in live and dead root mass in consecutive intervals, and by subtracting the losses of necromass due to decomposition, a mass balance approach allows fine root production to be calculated even for periods of non-synchronous root growth and mortality — the 'compartmental flow method' or 'decision matrix method' (SC-CF; McClaugherty et al. 1982; Santantonio and Grace 1987). We used the decision matrix of Fairley and Alexander (1985), and considered all biomass and necromass differences between two sampling dates whether they were significant or not.

Fine root decomposition rates were determined experimentally by the litter bag method (Fahey et al. 1988). In March 1995, fine roots of the two species were extracted from the organic layers, soil residues removed, and samples of 2 g fresh weight inserted into litter bags (nylon, 10 × 10 mm, mesh size 1.2 mm). Subsamples of the root material were dried (70°C, 48 h) to obtain the water content of the fresh roots. Ten bags each were laid out in the organic Of layer near to the soil coring plots on March 27, June 22, August 7, and October 2, 1995, and covered with 2 cm of fresh litter. The bags were collected after 86 days (March 27–June 22), 46 days (June 22–August 7), 54 days (August 7–October 2) or 58 days (October 2–November 29), and transported to the laboratory where soil residues and fungal hyphae were carefully removed from the root material by rinsing. The loss of root dry mass due to decomposition was calculated from the difference between initial and remaining root mass. It was related to the fine root necromass pool in the soil to obtain seasonal decomposition rates per horizon and sampling interval. To estimate fine root production by the SC-CF approach for any interval between two subsequent sampling occasions 1 and 2, a mass balance approach (Fairley and Alexander 1985) was applied with

$$P_{2-1} = (B_2 + N_2) - (B_1 + N_1) + D_{2-1} \qquad (1)$$

where P is fine root production, B_2, B_1, N_2 and N_2 are fine root biomass and fine root necromass on time 2 and 1, respectively, and D_{2-1} is fine root decomposition rate in the interval 1-2. Fine root production was then calculated from the decision matrix of Fairley and Alexander (1985). We calculated P separately for the three soil horizons to account for different phenologies of the fine roots in these layers (Hertel 1999).

Ingrowth cores

Ingrowth core experiments with local soil material were carried out in the Of, Oh and Ah layers according to the methodology described by Persson (1980), Powell and Day (1991), and Majdi (1996). In close vicinity to the sequential coring plots, 20 cores (diameter 55 mm, depth 15 cm) were cut from the topsoil with a sharp corer in August 1995 (each 10 cores at 0.5 m distance to a *Fagus* or a *Quercus* tree, respectively). The cores were sliced into the three soil horizons, and all macroscopically visible live and dead root material was extracted by hand. Smaller dead rootlets were assumed to dissapear by decomposition during the experiment. The remaining soil material was replaced into the hole and its edges marked at the soil surface. Care was taken that the structure and density of the soil samples was conserved as much as possible. No mesh bags were used in order to minimise disturbance effects. The samples were re-collected with a soil corer in June 1997 after a 645-day long exposure period since no recolonisation and root growth was observed during the experiment's first 12 months. Following Vogt et al. (1998) we then calculated fine root production in the cores as the increase in root biomass from the start of root recolonisation until harvest (period September 1996–June 1997: 280 days). To express root mass in the ingrowth cores as root density, the depth of the three soil horizons was measured in undisturbed profiles near the sample. In the laboratory, root biomass in the cores was measured as described above. Fine root increment in the cores was calculated as g d.w. m^{-2} yr^{-1}. We also calculated the fine root recovery rate (R; in percent of initial root density) in the ingrowth cores. To do so, we related the fine root density in the cores at harvest to the root density in the surrounding, unmanipulated soil, and expressed recovery in percent.

In situ root growth chambers

We constructed plastic chambers that allowed monitoring of the increment and vitality of isolated, but intact, fine root endings in minimally disturbed soil over periods of several months. Each chamber was of 189 cm^3 volume (length, width and height: 90 × 70 × 30 mm), had perforated side walls (1 mm) and were sealed with 1.5-mm mesh at the bottom and top to allow for sufficient gas diffusion and water percolation, but to prevent ingrowth of external roots. This technique, which is described in detail in Hertel (1999) and Leuschner et al. (2001), was successfully introduced

to study root growth of adult trees in the field under near-natural or artificial soil conditions. In this study, the chambers were filled with organic Of/Oh material from which macroscopically visible root material had been removed. Two 5–8-cm long *Fagus* and *Quercus* fine root endings were carefully isolated from the adjacent organic soil material and inserted through small holes (6.5 mm) in the opposite walls of a chamber. By placing one *Fagus* and one *Quercus* root together in the chamber, we attempted to simulate the growth conditions in the soil of this mixed stand. After their installation, the chambers were covered with Ol material and remained for 180 or 438 days in the forest floor. The initial dry mass of the inserted root endings was estimated from measurements of root length inside the chambers and length/mass relationships of the roots. The latter were established at roots sampled in the soil outside the chambers. A rapid recolonisation by mycorrhizal hyphae and root infection indicated that root growth in the chambers may have proceeded under near-natural conditions. Root growth rates were calculated from the difference of initial mass and mass at harvest. Forty chambers were installed near the four sequential coring plots in June 1996, and harvested in December 1996 or August 1997. Chambers with root increments < 5 g m^{-2} yr^{-1} were excluded from the analysis to avoid the possibility that roots had been damaged during installation.

Measurement of canopy carbon gain and ecosystem carbon balance

The 'Ecosystem Carbon Balance Approach' (ECBA; Vogt et al. 1996) was used as an independent reference method. We used leaf gas exchange measurements conducted by Terborg (1998), and data on vertical leaf distribution and canopy light (PAR) distribution in this stand to model the net carbon assimilation (i.e., net assimilation less nocturnal leaf respiration) of the canopy on a daily and annual basis. This allowed us to quantify the annual net carbon gain of the *Fagus–Quercus* canopy based on seasonal courses of PAR, air temperature and vapour pressure deficit measured at three canopy levels. Key functions of the carbon model were (i) the light dependence of photosynthesis, (ii) the temperature and humidity dependence of assimilation, and (iii) the temperature dependence of leaf dark respiration as a function of season.

Maximum steady-state net photosynthesis rates at light saturation (A_{max}, measured at ambient [CO_2]), and corresponding light response curves were determined at intervals of 3–4 weeks in the summers of 1992 and 1993 for sun and shade leaves of *Fagus* and *Quercus* using an open gas exchange measuring system based on a BINOS 3 differential IR gas analyser (Leybold-Heraeus, Hanau, Germany). Several sun-lit branches of two *Fagus* and two *Quercus* trees were assessed from a scaffolding tower at 22–25 m (sun canopy) or 18–22 m height (shade canopy). Earlier measurements made on seven trees from a mobile elevator platform had shown that the trees adjacent to the tower had typical photosynthetic rates. Four *Fagus* leaves of a leaf cluster (or single *Quercus* leaves) were placed horizontally in a fully climatised plexiglass chamber (5000 cm^3, Walz, Effeltrich, Germany) illuminated by a mercury lamp (HQI-400W/D, OSRAM) at saturating photon flux densities (PAR) of 800–900 μmol m^{-2} s^{-1}. Air temperature and air-to-leaf water vapour pressure difference (ALVPD) were kept constant during the experiments (18–20° C, 800 to 1000 mPa Pa^{-1}). At six to 10 occasions during a season, the dependence of A_{max} on air temperature (T_a, 5–30° C) and ALVPD (500–3000 mPa Pa^{-1}) was additionally investigated. All measurements were made between 08:00 to 17:00 local time, and recorded gas exchange rates after attainment of approximate equilibrium values, generally within 20–40 min. Photosynthetically active radiation, air temperature and air humidity were recorded continuously in the canopy with quantum sensors, and air-shielded, ventilated dry and wet bulb thermistors at heights of 19, 24 and 32 m on the tower in the centre of the stand. Further measurement and modelling details are given in Terborg (1998).

The leaf area index and annual leaf and fruit mass production of the stand were determined by positioning 32 litter buckets with a surface area of 0.25 m^2 in a rectangular grid at a height of 1 m near the four root study plots. The area of leaves in fresh litter was measured with a LI-3000 (LiCor, Lincoln, NE, USA) leaf area meter, and weighed to obtain annual leaf and fruit mass production. Larger litter fractions were collected in four nets of 20 m^2 that were laid out on the forest floor. Each six adult *Fagus* and *Quercus* trees of representative diameters were harvested during summer and analysed for their vertical leaf area distribution in height classes comprising 4 m each. Mobile quantum sensors (LI-190 SB, Li-Cor, Lincoln, NE, USA) positioned by rope climbing were used to characterise the light regime inside *Fagus* and *Quercus* canopies. Six classes of relative PAR transmissivity (0.05–0.10, 0.10–0.20, 0.20–0.30 ... 0.80–1.00) were defined in

Fagus and *Quercus* canopies and assigned to the leaf area in the respective canopy sections.

Stem growth as another major carbon sink was measured every other week in terms of cross-sectional area increment at breast height (1.3 m) using 20 dendrometer bands per tree species. The selected trees were representative in their diameters for the five major diameter classes in the stand. The annual increment was calculated as the difference between spring minimum and winter maximum in cross-sectional area. Relationships between dbh and stem, branch (> 7 mm) and twig mass (< 7 mm) were established at the 12 harvested trees.

A crude estimate of the amount of carbon available for fine root growth was obtained by solving the carbon budget equation for P. Carbon invested in branch growth, and leaf and fruit production (litter fall data), or stem growth (dendrometer data) was subtracted from the calculated annual net carbon gain of the canopy. Stem, branch and root respiration were estimated from literature data of temperate forests. The resulting value may indicate the upper limit of carbon consumption by fine root growth in this stand.

Statistical analysis

A non-parametric Mann–Whitney (Wilcoxon) two-sample test with a 5% rejection level was used to test for significant differences between (i) fine root biomass or necromass at two sampling dates of the sequential coring experiment, or (ii) fine root mass at the beginning and end of the litter-bag and root-growth-chamber experiments. Although the number of investigated replicate samples was substantial in the four approaches (20), each a single mean production estimate was obtained only by the two sequential coring approaches which made it impossible to test for significant differences among the four methods.

Results

Sequential coring approaches

The fine root mass of *Fagus* and *Quercus* in two organic (Of and Oh) and one mineral topsoil horizon (Ah) was dominated by dead rootlets and partly decayed root fragments (necromass). Only 20–30% of total fine root mass consisted of live fine roots (biomass). Although root biomass showed only minor fluctuations during the 12-months study period (April 1995–March 1996), necromass varied considerably

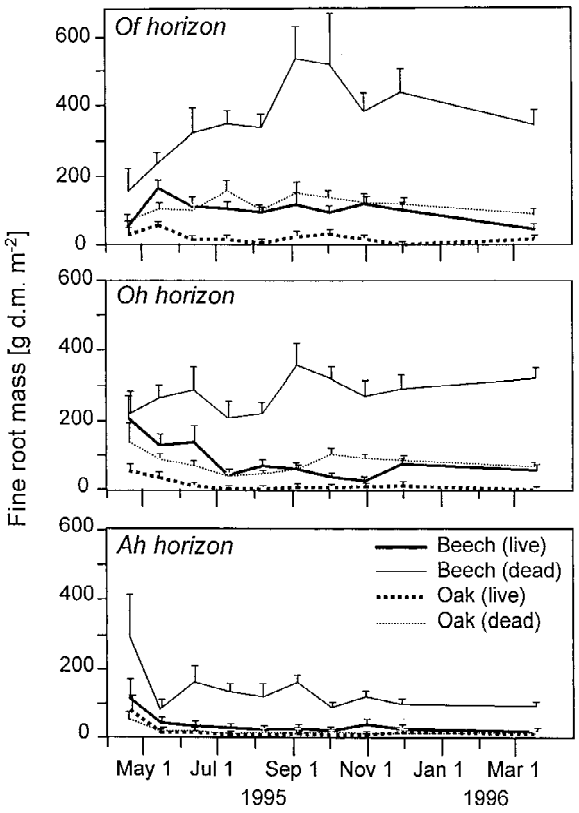

Figure 1. Fluctuation of fine root biomass (live) and necromass (dead) of *Fagus* and *Quercus* trees in the organic Of and Oh layers and the mineral soil Ah horizon of the *Fagus–Quercus* forest during April 1995–March 1996. Given are mean ± 1 SE of 20 soil cores each taken at random coordinates in the study plots.

with particularly large fluctuations in late summer (August/September, Fig. 1). After a period of large soil water deficits in July and August, *Fagus* fine root necromass nearly doubled in the Of and Oh horizons. In contrast, necromass of *Quercus* (and biomass of *Quercus* and *Fagus*) in the three topsoil horizons remained rather stable during this period.

Seasonal maximum and minimum of total fine root mass (bio- and necromass) per unit area differed by factors of 2–6 over the 12-months period. The minimum–maximum differences were significant at $p < 0.05$ in all horizons except for *Quercus* roots in the Ah horizon (Table 1). In contrast, differences in root mass between two subsequent sampling dates (4-week intervals) were significant in a minority of cases only. For example, significant increases existed for *Fagus* necromass in the August–September interval (Of and Oh horizons), and for *Fagus* biomass in the April–May interval (Of horizons, Fig. 1). Most other seasonal

root mass fluctuations in the study period, in particular those of *Quercus* biomass and necromass, were only small and differences not significant at $p < 0.05$ although the number of replicate samples was high ($n = 20$).

Decomposition rates of root necromass were estimated by multiplying the mass loss rates of litter bag material with the total root necromass of the Of, Oh and Ah horizons as determined by soil coring. Rates fluctuated between 0 and 6.4 g m^{-2} 28 $days^{-1}$ for *Fagus* fine roots, and between 1.5 and 12.8 g m^{-2} 28 $days^{-1}$ for *Quercus* fine roots in the study period (March–November 1995, Tab. 2). Apparently, *Fagus* roots decompose more slowly than *Quercus* roots since mass losses of *Fagus* were very small (and not significant at $p < 0.05$) in three of four exposure periods. In comparison to fine root production rates, root decomposition rates as estimated using litter bags were very small in both tree species.

The calculation of fine root production based on the sequential coring data gave highly different results depending on the calculation method used. The 'minimum–maximum method' (SC-MM), which only considers significant differences between seasonal root mass extremes, provided an annual fine root production of 689 g d.m. m^{-2} yr^{-1} for *Fagus*, and of 226 g m^{-2} yr^{-1} for *Quercus* (stand total: 915) in the Of, Oh and Ah horizons (Table 1). Root decomposition is neglected in this approach. In the Ah horizon, zero production was found for *Quercus* roots with this calculation method because maximum and minimum were not significantly different. Fine root turnover rates were estimated from the quotient of annual production and annual mean fine root biomass (P/B). According to the SC-MM approach, the fine root biomass was turned over 2.3–3.8 times per year in the three horizons (Table 1). A much higher, and perhaps unrealistic, turnover rate was calculated for *Quercus* roots in the Oh horizon (12.6 g g^{-1} yr^{-1}).

The 'compartmental flow method' (SC-CF) considers all biomass and necromass differences between two sampling dates whether they are significant or not, and also includes mass losses with root decomposition. With an annual fine root production of 1360 g d.m. m^{-2} yr^{-1} (*Fagus*; 1012, *Quercus*; 348) this method gave by 49% higher values than the minimum-maximum method. According to this approach, peaks of fine root production occurred in April and August, 1995, for *Fagus* (Of and Oh horizons), and in May, July and August for *Quercus* (Fig. 2). In both tree species, production rates decreased from the uppermost

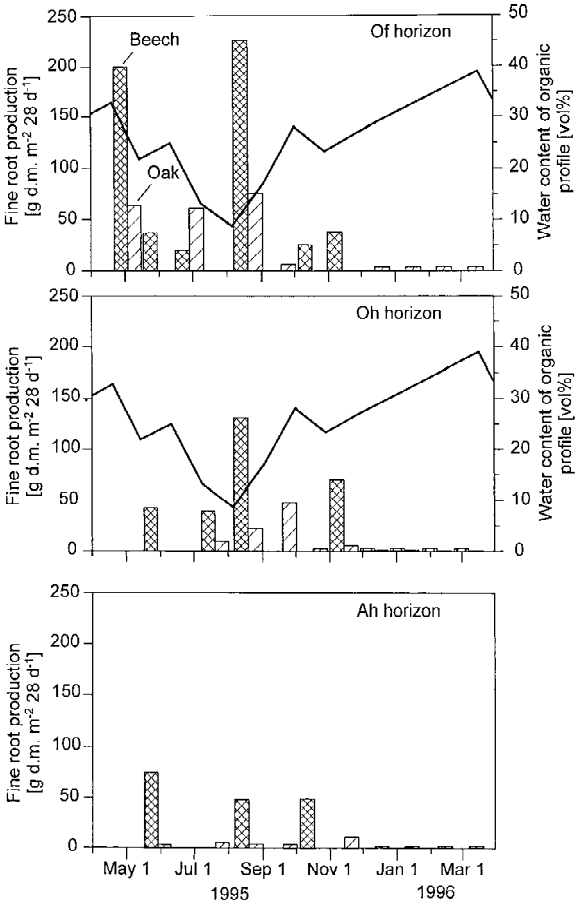

Figure 2. Fine root production of *Fagus* and *Quercus* trees in three topsoil horizons of the *Fagus–Quercus* forest during 28-day-intervals in 1995/1996 as estimated by a sequential coring approach with compartmental flow calculation. The solid line indicates the volumetric water content of the two organic horizons (no measurements in the Ah horizon). Fine root decomposition as determined with root litter bags was added to the production values (see text).

organic Of horizon to the mineral topsoil (Ah horizon). In contrast to the minimum–maximum method, positive production values were calculated with this method for *Quercus* in the Ah horizon (compare Table 1). According to the calculations with the SC-CF approach, fine root biomass was turned over 3.7–7.3 times per year.

Ingrowth core approach

Fagus and *Quercus* fine roots, that recolonised the root-free soil of the ingrowth cores, showed production rates in the topsoil (Of, Oh, Ah horizons) of 110 and 36 g m^{-2} yr^{-1}, respectively (Fig. 3). Similar to the two sequential coring approaches, the ingrowth

Table 1. Seasonal maximum and minimum of fine root mass (biomass and necromass), annual fine root production and fine root turnover rate (production/mean biomass) for *Fagus* and *Quercus* roots in the Of, Oh and Ah horizons of the studied *Fagus–Quercus* forest according to the sequential coring/minimum–maximum approach (period April 1995–March 1996). Profile means are weighted means

Horizon	Fine root biomass and necromass ($g\ m^{-2}$)		Significance of min–max difference[1]	Production ($g\ m^{-2}\ year^{-1}$)	Fine root biomass[2] ($g\ m^{-2}$)	Fine root turnover rate ($g\ g^{-1}\ yr^{-1}$)
	Seasonal maximum	Seasonal minimum				
Fagus						
Of	652	209	*	443	118	3.8
Oh	419	252	*	167	72	2.3
Ah	194	115	*	79	21	3.8
Profile total				689	211	
Profile mean						3.2
Quercus						
Of	170	95	*	75	28	2.7
Oh	194	43	*	151	12	12.6
Ah	–[3]	–[3]	n.s.	0	4	–[3]
Profile total				226	44	
Profile mean						5.6

[1] * marks significant maximum – minimum differences ($p < 0.05$) for a given horizon; [2] Mean of study period; [3] No data are given because none of the seasonal differences were significant.

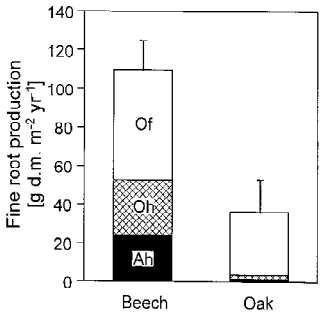

Figure 3. Production of *Fagus* or *Quercus* fine roots in ingrowth cores (55 cm in diameter, 15 cm long, filled with site-specific Of, Oh and Ah material) that were exposed for 645 days (August 1995–June 1997) in the topsoil of the *Fagus–Quercus* forest (mean ± 1 SE of 20 cores).

core method (IC) indicated highest production rates in the uppermost Of horizon and smaller values in the Oh and Ah horizons. However, this method supplied extremely low values for *Quercus* in the Oh and Ah horizons (< 2.5 g m^{-2} yr^{-1}) that contrast with the results of the sequential coring study.

In situ–root growth chamber approach

With the growth chamber (RGC) approach we monitored growth rates of individual *Fagus* and *Quercus* fine root endings in the field under conditions of minimal disturbance. When expressed on a ground area basis, fine root productivities of 40 g m^{-2} (180-day experiment), and 120 g m^{-2} (438-day experiment) were obtained for *Fagus* (Fig. 4). The productivity of *Quercus* roots was much smaller in both experiments (10 and 15 g m^{-2} in the 180- and 438-day intervals, respectively).

Comparison of fine root production rates

Fine root production estimated with the compartmental flow, the minimum–maximum, the ingrowth core, and the root growth chamber method differed by a factor of 12 or more among the four approaches. By far the highest annual production rates were obtained by the SC-CF method (1360 g m^{-2} yr^{-1}) which contrasts sharply with the RGC method (108 g m^{-2} yr^{-1}) (Fig. 5). Very small production values were also found with the ingrowth core method (147 g m^{-2} yr^{-1}). The SC-MM method, which uses a similar data basis as the

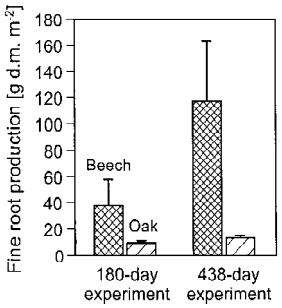

Figure 4. Growth of *Fagus* or *Quercus* fine roots in *in situ* root growth chambers (189 cm^3 volume) that were exposed for 180 days (left) or 438 days (right) in the organic topsoil of the *Fagus–Quercus* forest (1996–1997). The chambers were filled with site-specific Of/Oh humus material. Stated are means (± 1 SE) of 20 chambers each with fine root growth rate expressed per square meter soil surface. Each chamber contained one *Fagus* and one *Quercus* root ending. Roots with an increment > 5 g m^{-2} were included in the analysis only.

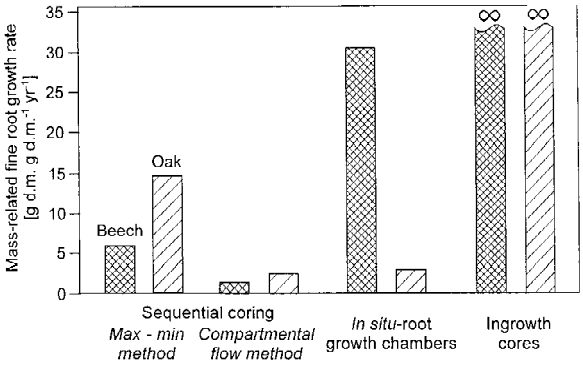

Figure 5. Annual fine root production of *Fagus* and *Quercus* in three topsoil horizons as estimated with four different approaches in the *Fagus–Quercus* forest in 1995–1997.

SC-CF approach, calculated annual growth rates 50% smaller than the SC-CF method. Nevertheless, its values were 8-fold larger than those of the experimental RGC and IC approaches.

Mass-related growth rates of fine roots and root recolonisation rates in root-free soil

By relating the annual root increment to the average root standing crop, we calculated mass-related growth rates (MGR) of *Fagus* and *Quercus* fine roots. MGR values express increases in root mass relative to the existing root biomass and, thus, reflect the 'expansivity' of a root system in a given experiment. Ingrowth cores contain no root biomass at the experiment's beginning and, thus, have infinite MGR values (Fig. 6). Large values (> 30 g g^{-1} yr^{-1}) were also found for *Fagus* roots (but not for *Quercus* roots) in the root chamber experiments. The sequential coring approaches showed the lowest mass-related growth rates of all four methods (2–15 g g^{-1} yr^{-1}).

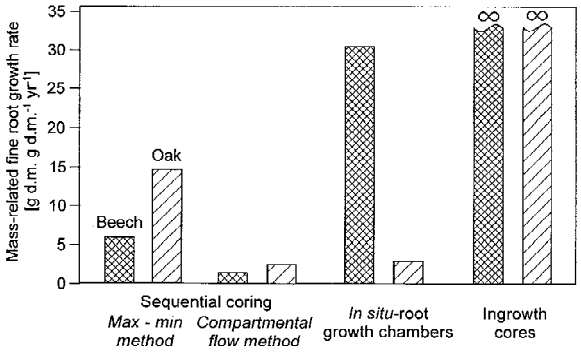

Figure 6. Increment of *Fagus* and *Quercus* fine roots per year as related to the standing crop of fine root biomass at the experiment's beginning, expressed as g d.m. g^{-1} yr^{-1}, mass-related fine root growth rate, MGR) according to four different approaches to estimate fine root production in the *Fagus–Quercus* forest. MGR values are infinite for the ingrowth core technique since the cores were cleaned of roots at the experiment's beginning. MGR values were calculated to express the 'expansivity' of the fine root systems in different experimental settings.

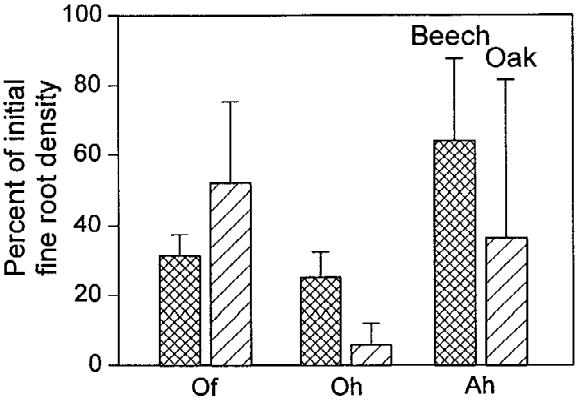

Figure 7. Recovery rates of *Fagus* or *Quercus* fine roots in ingrowth cores following complete extraction of roots in the substrate (i.e.% of initial fine root mass or density that is regrown after a given recovery period). Given are average rates (± 1 SE) for 20 ingrowth cores that were exposed for 645 days in the three horizons of the topsoil in the *Fagus–Quercus* forest.

The ingrowth core experiment, which started with an initially root-free soil, allowed the calculation of a fine root recovery rate (*R*) in the cores. Organic Of material exposed in the cores for 645 days had regained 32% (*Fagus*) and 53% (*Quercus*) of its initial fine root mass per soil volume (Fig. 7). Recovery rates were smaller in the Oh horizon (25 and 8%), but higher in the mineral Ah horizon (67 and 38%).

Table 2. Mass loss due to decomposition rates of dead *Fagus* or *Quercus* fine root mass in the Of, Oh and Ah horizons of the *Fagus–Quercus* forest during four periods in 1995 (expressed as g mass loss m^{-2} 28 $days^{-1}$). Values are means ± 1 SE of 10 replicates each. The specific decomposition rates were derived from root litter bag experiments; the values were then extrapolated to total topsoil root necromass to obtain loss rates on a ground area basis

Species	Period of exposure			
	Mar 27 – Jun 22	Jun 22 – Aug 7	Aug 7 – Oct 2	Oct 2 – Nov 29
Fagus	4.8±3.7*	0	6.4±22.2	0
Quercus	1.5±2.9	6.4±8.2*	8.1±3.7*	12.8±7.7*

*Difference in litter bag mass during the studied interval significant at $p < 0.05$.

Ecosystem carbon balance approach

Based on data of leaf gas exchange, canopy architecture and stand microclimate, the canopy carbon assimilation model of Terborg (1998) allows calculation of an average net carbon gain of 129.9 mol m^{-2} for the seasons 1992 and 1993 in the studied *Fagus-Quercus* stand (Table 3). Since leaf nocturnal respiration losses are included, this number characterizes the carbon source strength of the tree canopy. Litter trapping and dendrometric stem growth measurements indicated that about 37% of this amount (48.7 mol C m^{-2} yr^{-1}) were invested annually into growth of stems, branches, twigs and coarse roots (> 2 mm), and into the production of leaves, fruits and bud scales. The remaining 81.2 mol C m^{-2} yr^{-1} must have been allocated to three major carbon sinks, (1) fine root production, (2) root exudation and C transfer to mycorrhizal fungi, and (3) construction and maintenance respiration of stems, branches and roots. Our fine root production data indicate that 4.6 to 58.4 mol C m^{-2} yr^{-1} (depending on the method used) were consumed by fine root growth and turnover in the three topsoil horizons (Table 3). The smallest value (RGC approach: 4.6 mol C m^{-2} yr^{-1}) equals 3.5% of the annual net carbon gain, the largest value (58.4 mol m^{-2} $year^{-1}$, SC-CF approach) amounts to 45.0% of the carbon input.

Table 3. Annual carbon balance of the *Fagus–Quercus* mixed stand in the Lüneburger Heide (fluxes in mol C m^{-2} yr^{-1}; all data refer to *Fagus* and *Quercus*; mean of the years 1992 and 1993). The four fine root production estimates are for the three topsoil horizons only (extrapolation for a 160-cm deep profile in brackets)

Carbon gain	
Net uptake of leaves[1]	129.9
Carbon allocation into structure	
Stem wood increment[2]	21.9
Twig growth (d < 7 mm)[3]	2.4
Branch growth (d > 7 mm)[3]	2.0
Coarse root increment[4]	2.2
Leaf production[5]	13.0
Production of flowers, buds etc.[5]	2.6
Production of fruits[5]	4.6
Total	*48.7*
Fine root production: SC-MM approach	39.3 *(46.2)*
Fine root production: SC-CF approach	58.4 *(49.6)*
Fine root production: IC approach	5.4 *(6.4)*
Fine root production: RGC approach	4.6 *(5.4)*

[1]Obtained from a canopy carbon model of this stand that uses leaf gas exchange data of the two species, continuous PAR, temperature and air humidity records, and leaf distribution data in the canopy (Terborg 1998); the number refers to daytime net carbon assimilation less the nocturnal respiration loss of the canopy leaf mass. [2]Calculated from band dendrometer readings at each 20 *Fagus* and *Quercus* trees and dbh/stem biomass relationships established at each six *Fagus* and *Quercus* trees (Schmitt, unpubl. results). [3]Estimated from litter fall data measured in 32 litter buckets (fine litter) and four nets of 20 m^2 (coarse litter), [4]Taken as 10% of stem wood increment according to *Fagus* data from the Solling experimental plots (Ellenberg et al. 1986; these data were also used to estimate *Quercus* coarse root growth), [5]Collected in 32 litter buckets. Fine root production was investigated in the years 1995–1997.

Discussion

In comparison to the average fine root production estimates given by Fogel (1985) and Nadelhoffer and Raich (1992) for temperate hardwoods (about 300 g m^{-2} yr^{-1}), the results of the two sequential coring approaches of this study (SC-MM; 915; SC-CF; 1360) were high; whereas the results of the ingrowth

core and growth chamber techniques were considerably lower (147 and 108 g m^{-2} yr^{-1}). As long as a standard procedure has not been established, it may be questionable, however, to average fine root production data from different studies because a broad variety of methods have been used by the authors included in the cited reviews.

Sequential soil coring and the subsequent quantification of live and dead fine root mass probably is the most widespread approach that has been used in forests. Errors in the separation of live and dead root mass, and in the quantitative extraction of fine root necromass in samples that originate in organic soil horizons represent a basic problem of this method. Furthermore, the technique is very labour-intensive and may suffer from a high sample variation in the estimation of root mass, thus introducing substantial errors when calculating production from seasonal mass differences (Lauenroth et al. 1986; Sala et al. 1988). We attempted to reduce sample variation by analysing a comparably large set of replicates (20 cores per date and horizon) but still found typical coefficients of variation of 30–150% for fine root biomass or necromass in the organic horizon samples. Consequently, root mass differences between two subsequent sampling dates were not significant in the majority of intervals in our study since fine root mass fluctuations were only moderate over the year (Hertel 1999).

In principal, there are at least two factors that can result in an underestimation of production by a sequential coring approach as conducted in our study: (1) We may have missed seasonal minima and maxima of root mass with our 4-week sampling scheme (Kurz and Kimmins 1987; Singh et al. 1984). (2) Root necromass decomposition rates (a parameter included in the SC-CF approach), as measured with the litter bag technique, may have been underestimated substantially in our study since fresh fine root biomass with a presumed low decay rate was filled into the bags (Majdi 1996). This error can also be inferred from the fact that our estimates of annual fine root production rates exceeded the measured decomposition rates by a factor of 8 or more. This implies an unrealistic long-term increase of root mass in this stand. This problem awaits a solution since we are aware of no method to measure fine root decomposition accurately in situ.

On the other hand, by including not only significant, but also non-significant, root mass differences in the calculations, the SC-CF approach is particularly sensitive to errors that are likely to result in overestimates of production (Sala et al. 1988). Both the SC-CF and the SC-MM approaches are additionally biased by sampling schemes that measure root standing crop synchronously in more than one soil horizon. This practice can lead to erroneous root biomass and necromass values by incorrectly separating adjacent soil horizons in the cores. To avoid this type of error in the sequential coring approaches, several authors have recommended applying a simple sampling design (one horizon and a limited number of sampling dates only), and relying on significant differences between seasonal root mass maxima and minima only (Neill 1992; Vogt et al. 1986). The majority of studies in forests indeed favoured the minimum–maximum calculation method over the more complex compartmental flow calculation despite the neglect of root decomposition.

In many studies of forest ecosystems, ingrowth cores have been utilized as an alternative to sequential coring. Indeed, the technique is simple and allows a sufficient number of replicates to be investigated (Majdi 1996). However, ingrowth core data suffer from the following shortcomings: (1) the core installation typically represents a heavy disturbance of the rhizosphere with root injury and possible enhancement of mineralisation, (ii) root growth starts only after a period of delay (typically several months after the experiment's onset, Vogt et al. 1998), (iii) fine root growth proceeds at artificially low root densities in the cores during most of the experiment (which may be influential for root growth in nutrient-poor soils), (iv) root disappearance due to decomposition during the experiment is not considered in the data, and (v) the majority of studies used soil substrates other than the local soil as a growth medium. Thus, a number of artefacts are to be expected when using this method (Neill 1992). In acid forest soil, Bauhus and Bartsch (1996) found that fine root mass in the ingrowth cores had regained the density value that existed prior to core installation only after 16 months. Kalhoff and Bornkamm (1992) found only 45–60% of the initial root biomass density in the cores 12 months after their installation. More importantly, these authors detected no fine root necromass in the cores; this indicates a greatly reduced root mortality during the core experiments. In our study, 8–67% (depending on horizon) of the initial root biomass had reestablished itself in the cores after 21 months of exposure, indicating again a greatly reduced fine root density during this experiment. Similar results were obtained by Makkonen and Helmisaari (1999). Indeed, ideal ingrowth cores should have a very small size in order to minimize delays in the recolonization of invading roots.

The in situ root growth chamber technique was developed in our group in order to analyse competition effects between two isolated tree fine root endings experimentally in the field (Leuschner et al. 2001). When the method is applied to estimate fine root growth, it is burdened with shortcomings similar to those of the ingrowth core method (disturbance effect, lowered root densities, no root decay during sample intervals considered). Moreover, growth estimates refer to measurements with one or two root endings per chamber only. Thus, if root production is to be expressed on a ground area basis, an experimental design with a large number of replicates and additional data on fine root densities in the soil are required. In contrast to the situation in the ingrowth cores, however, damage to roots inside the chamber can normally be excluded in this method. This prevents a long delay in root growth and often leads to a rapid reinfection of the enclosed roots by mycorrhizal fungi (Hertel 1999).

Controversy over the most reliable method for quantifying fine root production in forests will continue as long as the results of the various techniques are not checked against an independent nondestructive method. A possible reference is the ecosystem carbon balance approach (ECBA). In the studied *Fagus–Quercus* forest, we compared the results on carbon consumption by fine root growth as estimated by the sequential coring, ingrowth core and root growth chamber methods with the estimated carbon input through assimilation (about 130 mol C m^{-2} yr^{-1} according to data from a canopy carbon gain model). This budget also contains data on carbon consumption by leaf, branch and stem growth. We extrapolated our fine root production data to the entire soil profile since the experimental data (Table 3) refer to the three topsoil horizons only which contained 50% of the total fine root biomass in this forest (profile depth: 160 cm depth, Leuschner 2001). Our root data show a vertical decrease of the root production/root biomass (P/B) ratio in the profile which is in accordance with results obtained by Hendrick and Pregitzer (1996) in a northern hardwood forest. We then estimated root production for the lower profile down to a depth of 160 cm by multiplying extrapolated P/B ratios with fine root biomass data of this profile. With this calculation we estimated fine root production of the lower profile at 15% of the profile total, and obtained fine root production rates of 68.6 mol C m^{-2} yr^{-1} (SC-CF), 46.1 mol C m^{-2} yr^{-1} (SC-MM), 6.4 mol C m^{-2} yr^{-1} (IC) or 5.4 mol C m^{-2} yr^{-1} (RGC) for a 160-cm-deep profile by the four approaches.

To complete the ecosystem carbon balance we estimated the carbon used by maintenance and growth respiration of stems, branches and roots from literature data. Our calculation bases on a quotient of annual fine root respiration loss/fine root biomass (R/B) of 1.32 yr^{-1}obtained by fine root gas exchange measurements in an old-growth *F. sylvatica* forest in the Solling highlands (Central Germany, Gries unpubl. data). This quotient was applied to the fine root standing crop of the *Fagus/Quercus* stand (447 g fine root dry mass m^{-2}, i.e. 18.6 mol C m^{-2}, Hertel 1999). Furthermore, it is assumed that branch, stem and coarse root respiration consume about 15% of annual assimilation in a temperate forest (Ryan et al. 1996). In this manner, we obtained a total annual respiration by heterotrophic plant compartments of about 44.0 mol C m^{-2} yr^{-1} (i.e. 24.5 mol C m^{-2} yr^{-1} fine root respiration, and 19.5 mol C m^{-2} yr^{-1} branch, stem and coarse root respiration). These respiration data are supported by results of Granier et al. (2000) in a 30-year-old *F. sylvatica* stand in France where 33.3 mol C m^{-2} yr^{-1} of root respiration and 16.8 mol C m^{-2} yr^{-1} of branch and stem respiration were estimated.

The carbon cost to plants maintaining ectomycorrhizal associations is estimated to range from 15 to 28% of net carbon fixation (Finlay and Söderström 1992; Fogel and Hunt 1983), but the proportion of carbon that is allocated to extra-radical mycorrhizal mycelium in natural soils remains uncertain (Leake et al. 2001). Those parts of the mycelium that are directly attached to the roots or are a component of the Hartig net are likely to be included in the fine root biomass data. Carbon fluxes to extra-radical hyphae and C losses via root exudation must be neglected in this calculation.

Assuming that the above-mentioned assumptions are valid, we concluded that not more than 37.2 mol C m^{-2} yr^{-1} (or about 890 g dry matter m^{-2} yr^{-1}) could have been allocated to fine root growth in the *Fagus-Quercus* forest. This value as obtained from the ECBA approach is 6–7 times higher than the adjusted fine root production rates obtained with the ingrowth core and root growth chamber methods (6.4 and 5.4 mol C m^{-2} yr^{-1}, respectively). In contrast, the two sequential coring approaches overestimate annual fine root production either slightly (SC-MM approach: 46.1 mol C m^{-2} yr^{-1}, i.e. 25% overestimation) or substantially (SC-CF approach: 68.6 mol C m^{-2} yr^{-1}, i.e. 85% overestimation) when the ECBA approach is used as a reference. Thus, comparison with the ECBA data provided evidence that root production es-

timates based on manipulative experiments (IC and RGC approaches) led to highly misleading results in this temperate forest on nutrient-poor soil.

We speculate that the ingrowth core and growth chamber approaches are more erroneous in nutrient-poor forest soils with a high topsoil fine root density than in fertile soils where root competition is presumed to be less intense (Coomes and Grubb 2000). Ingrowth cores principally measure the regeneration potential of injured roots that invade unexplored soil volume. If root growth is expressed as mass-related growth rate (MGR, growth per standing crop), indeed large differences between the sequential coring approaches (low MGR) and the two manipulative approaches (high MGR) became apparent. We conclude that ingrowth cores may be useful devices to compare fine root growth potentials among different seasons, sites, or tree species under conditions of artificially low root competition. Similarly, the in situ root growth chamber technique proved to be less suitable for ground-area based estimates of root production. This method has been used successfully in experimental studies on root interactions and root growth in altered environments (Leuschner et al. 2001).

We conclude that the appropriate method for estimating fine root production may vary with the study objectives. If ground-area-related data of production are sought, sequential coring with a minimum–maximum calculation approach yields the most reliable estimates in this temperate hardwood forest on poor soil. Satisfactory results were obtained by this approach despite neglecting important processes in the carbon balance of roots such as root decomposition. We speculate that the reliability of the SC-MM approach benefits from the fact that (1) the rhizosphere is disturbed only minimally, (2) measurements are conducted at natural fine root densities, and (3) the number of measured parameters which may introduce errors is kept rather small (seasonal root mass extremes only, no decomposition rates). It should be added that the soil coring technique produces a number of other useful data on structure and dynamics of fine root systems, including root biomass totals, the biomass/necromass ratio, and information on root mass seasonality, that may serve as indicators of soil fertility or stress intensity in the rhizosphere. These data are not provided by other techniques.

However, the potential for errors in the SC-MM approach remains high. In theory, this technique should only work if no roots die between measurements. It also should fail in systems with less seasonality in fine root biomass. Despite a good agreement with the ECBA data in this study, there remains the possibility of simple coincidence or at least some combination of offsetting errors that might occur with any of the tested root production methods. In any case, the reliability of the SC-MM approach has to be evaluated by further comparison with independent methods under a broader range of climates, and forest and soil types. Therefore, the results of this study should not be transferred to forest communities with significantly different structure, seasonality or climate.

Finally, the ECBA approach as used in this study may have introduced certain errors itself (e.g., questionable respiration data, unknown root exudation) that impair the reliability of this reference method. Thus, at the current stage of methods development, we suggest combining two approaches in order to attain a maximum reliability of annual fine root production estimates in forests; (1) sequential coring with minimum–maximum calculation that bases on a reduced number of sampling dates (e.g., four per year) but a large number of replicate samples taken (> 20), and (2) a direct observation technique to monitor root longevity and decomposition in the undisturbed rhizosphere independently. One of the methods that allows direct root observation is the minirhizotron technique (Majdi 1996).

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