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Summary

1 Patterns of fine root biomass, morphology, growth and longevity were examined in the northern hardwood zone of Hubbard Brook Experimental Forest to aid understanding of the role of roots in ecosystem function.

2 Fine root biomass in the mature hardwood forest was 471 $g\,m^{-2}$ for < 2 mm roots in June 1987 and was concentrated in the surface soil, with 43% in the forest floor horizons. After clearcutting, fine root biomass accumulated rapidly in the regrowing forest, reaching 71% of that in the mature forest after only four years of recovery.

3 Fine root diameter distributions and specific root length (*SRL*; length/mass) differed among species. *SRL* was higher in the forest floor than mineral soil horizons, and decreased with increasing root diameter.

4 Fine root production in the mature forest, measured with in-growth cores, averaged 254 $g\,m^{-2}$ $year^{-1}$, but this method probably underestimated production. Rapid disappearance of fine roots was observed for roots growing through *in situ* screens, and these ephemeral roots are difficult to quantify.

5 The initiation of fine root growth in the forest floor was coincident with leaf expansion in the forest canopy; root growth in the mineral soil began 1–2 weeks later. Root growth was most rapid in early summer (mid-June to early July), and the lifespan of these early season roots averaged about 8–10 months across three years of study. This estimate of longevity was consistent with that obtained from the ratio of fine root biomass to production, after correcting the production value for the observed root disappearance from *in situ* screens (about 50% of fine roots disappeared from screens within an annual cycle). These longevity estimates also appeared to be consistent with an analysis of the soil C budget based upon soil and fine root respiration and total root allocation. Fine root production was apparently nearly twice as high as leaf production in this ecosystem.

6 These fine root production and turnover estimates are not consistent with results from previous studies of fine root decomposition, and we suggest that fine root decay has been underestimated because existing methods inhibit the saprotrophic activity of rhizosphere organisms.

Keywords: biomass, longevity, respiration, techniques

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Introduction

The fine root systems of plants play crucial roles in the fluxes of energy and matter in the biosphere and carry out the essential functions of soil resource acquisition, but, because of difficulties in measuring their activity *in situ*, our knowledge of the ecology of fine roots is woefully inadequate. A better understanding of the dynamics of fine roots in forest ecosystems awaits additional information on controls of their distribution in soil, growth and physiological activity, morphology and demography, and especially the inter-relationships among these characteristics and their connections with other ecosystem components. The objective of this study was to quantify fine root dynamics in a northern hardwood ecosystem, as part of a continuing effort to characterize the ecology of the intensively-studied Hubbard Brook Experimental Forest in New Hampshire (Likens 1985).

Recent studies have greatly advanced our understanding of fine root dynamics. Both theoretical and empirical investigations have illustrated the strategies

of root growth and root system architecture for optimizing soil resource capture (Caldwell & Richards 1986; Fitter 1991; Grime *et al.* 1991). Furthermore, Eissenstat (1991) has summarized the advantages of and constraints on fine root diameters. Fine root lifespans have been estimated in forest ecosystems using indirect (Nadelhoffer *et al.* 1985; Santantonio & Grace 1987; Schoettle & Fahey 1994) and direct approaches (Hendrick & Pregitzer 1992; 1993), and these estimates generally appear to be consistent with belowground carbon budgets (Nadelhoffer & Raich 1992). In this study we attempted to characterize the growth, longevity, demography, and morphology of fine roots – and to integrate these results with observations of ecosystem dynamics in a northern hardwood forest.

We employed some simple new methods of root study and evaluated the results over several years of study.

Study area

This research was carried out at Hubbard Brook Experimental Forest (HBEF) in north-central New Hampshire (43°56′N, 71°45′W). Likens (1985) provides a detailed summary of the characteristics of this study area. The present study was conducted in the northern hardwood forest zone between 500 and 700 m a.s.l. The forest under study (hereafter 'mature forest') was heavily logged between 1910 and 1919 but has not been disturbed since that time. The overstory was dominated by sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.) and yellow birch (*Betula alleghaniensis* Brit.), with a patchy understory of hobblebush (*Viburnum alnifolia* Marsh.), ferns and other herbaceous plants. Soils are well-drained spodosols (mostly Haplorthods) of sandy loam texture with a 4–6-cm-thick organic layer at the surface.

Most of the research reported here was conducted in the mature forest located between the areas known as watershed 4 and watershed 5 at HBEF. We also report some results from within watershed 5 (hereafter 'W5'), a catchment which was logged in a whole-tree harvest during the dormant season in 1983–84, and from a 0.2 hectare clearcut (hereafter 'small clearcut') located adjacent to the mature forest site at 500 m elevation. The latter was cut during May 1988.

Methods

FINE ROOT BIOMASS

We measured fine root biomass at 30 random locations along a transect from 500 to 600 m a.s.l. in the mature forest in early June and again in mid October 1987. At each location a 4-cm × 4-cm block was removed to the base of the forest floor and the depth of this layer was measured; standard criteria for this study area were employed to distinguish forest floor and mineral soil in the field (Federer 1982). A 1.9-cm-diameter steel corer was used to obtain mineral soil samples to the depth of obstruction (usually boulders) or to 45 cm deep. Samples were returned to the laboratory and stored in a refrigerator for up to four weeks until they were processed. Two samples were destroyed during processing, and the total sample size was 29 for both spring and fall sampling.

In October 1987 we measured fine root biomass for the northern hardwood zone of W5. Sampling was carried out in a randomly-chosen set of seventeen 5-m × 5-m plots from 520–670 m a.s.l. In each plot four random samples were obtained by the same method as described above for the mature forest. The four samples were pooled and thoroughly mixed and a subsample was taken for sorting of roots.

Roots from organic horizon samples were sorted by hand because wet sieving proved ineffective. Average sorting time for the organic horizon samples was about 12 h. A two-stage procedure was used for mineral soil: roots were wet-sieved using a 2-mm-mesh screen, and root fragments were hand-sorted from the material that passed the screen. Two size classes were distinguished in both horizons: < 1 mm and 1–2 mm in diameter. All roots and root fragments were classified as live or dead on the basis of gross morphology and condition. Dead roots were usually brittle and dark in colour or were notable for the ease of separating stele and cortex (Vogt & Persson 1991). Roots were dried to constant mass at 70 °C and weighed to $\pm$ 0.1 mg. Significant differences between dates and soil horizons were detected with the student's t statistic.

FINE ROOT MORPHOLOGY

In mid-summer 1989, fine roots (defined as < 1 mm in diameter) were collected by species for detailed analysis of morphology and diameter distributions. Sugar maple, beech and yellow birch roots were obtained by collecting samples within monospecific groves of each species in the mature forest; we followed lateral roots originating from woody roots of known species., because although it was not easy to distinguish fine roots by species, woody roots of these three species could be distinguished on the basis of bark morphology. Extreme care was taken in this sampling so that 'pure' samples of each species from both organic and mineral soil were obtained. All measurements were made on air-dried roots.

The diameter distribution was measured on a root length basis by dispersing fine roots on a grid and classifying the diameter at intersection with the grid for several thousand roots of each species and soil layer (organic and mineral). Diameter classes (< 0.2, 0.2–0.3, 0.3–0.4, 0.4–0.6 and ≥ 0.6 mm in diameter) were distinguished under a dissecting microscope using black lines of measured thickness as a guide.

Specific root length (length/mass) was calculated for each size class from total length and dry mass of subsamples. In 1987 specific root length was measured in W5 in the same manner except that roots were not separated by species or by diameter class. Unfortunately, no measure of statistical variation was available for all these measurements because samples were pooled.

ROOT PRODUCTION: IN-GROWTH CORES

Fine root production was measured using an in-growth core technique (Steen 1984; Vogt & Persson 1991) in the mature forest, in W5 and in the small clearcut. In mid-July 1988, 50 in-growth cores were established at random locations along a transect from 500–600 m a.s.l. in the mature forest, 80 cores along a parallel transect in W5 and 18 in the small clearcut. Soil cores (5 cm in diameter) were extracted to the depth of obstruction and separated into organic and mineral horizons. Soil was sieved through a 2-mm-mesh screen to remove most roots and stones and then replaced and packed to about the original bulk density, with the organic and mineral horizons retained. Samples from the mature forest were collected from the center of the core with a 1.9 cm diameter steel corer in October 1988 (17 samples), early August (12) and October 1989 (11), and early August 1990 (9), and about 1 week earlier for W5 and the small clearcut. In-growth core samples were returned to the laboratory and either hand sorted (organic horizons) or wet sieved (mineral horizons) to separate live and dead fine roots as described earlier. Root samples were dried to constant mass at 70 °C and weighed to $\pm$ 0.1 mg. Significant differences in total fine root biomass among collection dates were detected by one-way ANOVA with post-hoc analysis of means using Fisher's PLSD.

Root growth was also measured with in-growth cores in W5 during the first 3 years after the whole-tree harvest. In midsummer 1984 soil monoliths approximately 25 cm in diameter were excavated to a depth of about 40 cm using a shovel. Most roots were removed by sieving through a 5-mm-mesh screen, and the mixed organic and mineral soil was replaced in the holes. Forty-eight in-growth cores were established in this way at 6 randomly chosen points within each of 8 intensive study plots (25-m × 25-m; see Hughes & Fahey 1991) in the northern hardwood zone of W5 (520–670 m a.s.l.). Each in-growth plot was divided into four quadrants and root cores were collected with a 1.9-cm-diameter steel corer from one quadrant in each plot in October 1985, May 1986 and October 1986. Few dead roots were observed and no quantitative attempt was made to distinguish live and dead roots. All roots < 1 mm diameter were sorted by hand from each core and dried to constant mass at 70 °C before weighing.

IN SITU ROOT SCREENS

Angle screens

The *in situ* screen method measured the growth of roots through mesh screens inserted in the soil, to estimate the growth in length or biomass of fine roots per unit ground area. Melhuish and Lang (1968) demonstrated a simple relationship between the number of isotropically distributed roots intersecting a square plane of dimension (N), and the probable length of roots (L) per unit soil volume (X^3): $L = 2N$. If root orientation is anisotropic, a correction factor must be based upon the number of intersections with three mutually perpendicular planes (Melhuish & Lang 1971). Placement of screens in this manner would be difficult for perennial vegetation, so we positioned screens at about 45° angles at random orientations to avoid some of the bias associated with anisotropy (Brown & Roussopoulos 1974). The principal problem with this approach is the disturbance to the root system associated with insertion of the screens, as with the in-growth core method. The effect of this disturbance on root growth could not be assessed directly.

Root sampling with *in situ* root screens was carried out in the mature forest, W5 and the small clearcut. Nylon-coated fiberglass screens (5 cm wide; hole size = 2.9 mm^2) were inserted to the depth of obstruction into slits in the soil made with a sharp, straight-edged tool. In early May 1988, 300 screens were randomly positioned in the mature forest between 500 and 600 m a.s.l. Forty screens were selected in a stratified random manner for sampling during the first week of June, July, August and September 1988, early June and August 1989, and early July 1990. Another 120 screens were inserted in this forest in May 1989, and a sub-set was sampled in early July, August, September and October 1989 and early July 1990. All roots growing through the screens were counted by carefully peeling the screens away from the soil. For lower depths (10–30 cm) this required some excavation of soil from one side of the screen. Visual criteria were used to distinguish live from dead roots.

In early May 1988, 400 screens were positioned at random locations between 500 and 600 m a.s.l. in W5. Eighty screens were measured during the last week of May, June, July, August and September 1988. In 1989, 120 screens were inserted in W5 in late May, with 30 screens sampled during the first week of July, August, September and October.

Finally, for the small clearcut 18 screens were positioned along a transect across the small block clearcut in October 1988 and six were sampled in early October 1989 and late June and mid-September 1990. These collections were coordinated with the in-growth core sampling in an effort to calibrate the root screen results against root production estimates by in-growth cores under conditions where the disturbance effect from both methods was minimal (i.e. newly colonizing root systems).

Horizontal screens

One of the crucial problems for understanding the dynamics of fine roots is quantifying their longevity and demographic transitions (Hendrick & Pregitzer 1992; Fahey 1992). In some forests, horizontal *in situ* screens can provide a non-destructive method for assessing the demography and longevity of fine roots growing near the soil surface. In this case, rather than inserting the screens vertically, we positioned screens at the top of the rooting zone in the O_e layer of the forest floor and periodically observed the life history of individual roots that had grown up through the screen into overlying litter. Following some successful trials with this method in 1989, we carried out detailed surveys and experiments in the mature forest in 1990, 1991 and 1992.

In early May of 1990, 1991 and 1992, horizontal *in situ* screens were installed in the mature forest at HBEF. The O_i and upper O_e litter was carefully removed down to the depth where many fine roots were observed, and a 15-cm × 15-cm screen was positioned on top of this layer. The litter layers were then replaced on top of the screen and the corners anchored and marked. In June the position and morphology (length; branching; colour) of roots growing through the screens were recorded. These screens were revisited in August and October or early November and in late spring or early summer the next year, and the fate of each mapped root was recorded. Root observations were made on cool days and roots were misted with distilled water during observation to avoid desiccation injury. Attempts to follow these root cohorts into a second summer were difficult because the development of a dense root mat often made it impossible to identify the mapped roots without damaging them.

In 1990, 1107 roots on 115 screens were mapped in early June. Seventy screens (627 roots) were remeasured in mid-August and mid-October and 43 screens (480 roots) were remeasured in mid-July 1991. On each date the length, number of branches and visual appearance (colour; live/dead; secondary thickening) of each root were recorded.

In 1991, 569 roots were mapped on 43 new screens in late June. To examine the effect of root assessment on mortality, 20 of the 43 screens (266 roots) were chosen randomly to be remeasured only in October while the other 23 (303 roots) were remeasured in both mid-August and October. The 20 screens that were remeasured only in October also were remeasured in May, 1992. Finally, in 1992 a cohort of 300 roots was mapped on 20 new screens in late June and remeasured in mid-August, early November, and in May.

In 1990, an experiment was performed using the horizontal screens to quantify the effects of nutrient availability on root growth and survival. In early June 100 screens were positioned as described above. Twenty five screens were assigned randomly to each of four treatments: continuous fertilization, pulse fertilization, nutrient depletion and control. The continuous fertilizer treatment received a complete fertilizer (including micronutrients) with a total application in $g\,m^{-2}$ of N = 16.7, P = 5.8, K = 25.4, Ca = 31.0, and Mg = 3.7. These doses were achieved via six applications at 2-week intervals from 10 July to 18 September. For each addition the equivalent of 0.6 cm of water was added as a fertilizer carrier. The nutrient pulse treatment received fertilizer only on the first date at the rate of one-sixth of the values above. The nutrient depletion treatment received a sucrose solution on the same schedule as the continuous fertilizer treatment (total dose = 11.25 kg sucrose m^{-2}) as well as 1 kg m^{-2} of sawdust. This treatment was designed to lower the availability of N by immobilizing mineralized N in microbial biomass (Waring & Pitman 1985). Control screens received 0.6 cm of distilled water on the same schedule as the fertilization treatment; there was no water-only control for the nutrient pulse treatment.

In early July, all roots that had grown through each of the 100 screens were counted. During the last week of August, 15 screens in each treatment were remeasured by counting the number of live and dead roots for each screen. These screens also were remeasured in mid-July 1991. The other ten screens in each treatment were remeasured in early November 1990. Also, for an additional six screens, about 10 roots per screen were mapped (as described earlier) in early July and remeasured in late August and in early November. As before, the morphology of each root was recorded on each date. Differences among treatments on each date were analyzed statistically by one-way ANOVA, with *post-hoc* analysis using Fisher's PLSD.

ROOT RESPIRATION

Direct measurements of fine root respiration were made on detached roots from the mature forest using a cuvette system. Samples of the dense fine root mat in the forest floor horizons were removed and quickly washed free of most adhering litter debris in a nearby stream. Time from sample collection until measurement was less than 5 min during which samples were kept moist. Samples consisting of 0.1–0.3 g (dry mass) of fine roots were sealed in a 1.0-L chamber and the production of CO_2 was monitored for about one minute using a Li-Cor LI-6200 CO_2 analysis system, programmed to accommodate increasing CO_2 concentrations associated with respiration. Sequential measurements of the same root samples indicated that respiration rates did not change significantly across about three minutes of sampling, but significant declines occurred after about five minutes, possibly as a result of desiccation. Root respiration measurements were made just after sunrise on 28–29 June and

15–16 August 1990 when air (and chamber) temperature was within 1–2 °C of soil temperature. Sample size was 12 on each date.

Results

FINE ROOT BIOMASS

In early June 1987, live fine root biomass (≤ 1 mm diameter) in the mature forest at HBEF averaged 408 g m^{-2} to a mean sampling depth of 32 cm (Table 1). Of this total, 46% was in forest floor horizons. An additional 63 g m^{-2} of roots 1–2 mm diameter was sorted from the soil in the June sampling.

In mid-October 1987, live fine root biomass and the proportions of fine root biomass in forest floor and mineral soil horizons also were not significantly different from the June values. However, biomass of dead roots was significantly higher in October because of an increase in the mineral soil horizons (183 vs. 107 g m^{-2} for roots < 2 mm; Table 1). Much of the variation among samples of live and total fine root biomass in forest floor horizons could be explained by the thickness of the forest floor horizon ($r^2 = 0.79$ and 0.57, respectively; $P < 0.001$), which ranged from 1.5 to 11.5 cm (mean = 4.5 cm).

In October 1987, live fine root biomass in the 4-year-old forest on W5 was 274 g m^{-2} or about three-quarters that in the adjacent mature forest (Table 1). Based upon measurements of growth into root-free cores, fine root biomass accumulated steadily from year 2 to year 4 of recovery from harvest. Dead fine root biomass was very low in W5, only about 20% of the value in the mature forest.

FINE ROOT MORPHOLOGY

Size-class distributions of air-dried fine roots in the forest floor horizons during midsummer were very similar for yellow birch and beech, with about two-thirds of total root length (≤ 1 mm diameter) in the 0.2–0.3-mm-diameter class (Fig. 1). In contrast, many of the fine roots of sugar maple were slightly smaller than 0.2 mm. Root diameters in mineral soil were larger than in the forest floor with 35–40% of root length in the 0.3–0.4-mm-diameter class across all species (Fig. 1).

The specific root length (length/mass) of fine roots of beech and sugar maple appeared to be higher for forest floor than mineral soil roots in the mature forest whereas the opposite was true for the very fine yellow birch roots (Fig. 2). Specific root length decreased markedly with increasing root diameter class for all species (Fig. 2). Thus, when average specific root length was calculated for all ≤ 1-mm-diameter roots, the values were much lower than for ≤ 0.5-mm roots (26.1 vs. 32.8 m g^{-1}). On W5 in 1987, specific root length was much higher for fine roots from the 5-year-old forest (mostly pin cherry roots; Mou *et al.* 1993) than for the mature forest (43.9 vs 26.1 m/g for < 1 mm roots).

ROOT PRODUCTION: IN-GROWTH CORES

Root growth into root-free cores was measured over a 2-year period from midsummer 1988 through mid-

Table 1 Fine root biomass in (A) a mature northern hardwood forest in 1987, and (B) an adjacent forest recovering after whole-tree harvest performed in fall and winter 1983–84, at Hubbard Brook Experimental Forest, New Hampshire

(a) Mature Forest – 1987		g m^{-2} (standard error; $n = 29$)			
		June		October	
Horizon	Size class (mm)	Live	Dead	Live	Dead
Organic	< 1	187	ND	165	ND
	1–2	16	ND	13	ND
	Total	203 (24)	69 (8)	178 (17)	86 (11)
Mineral	< 1	221	ND	199	ND
	1–2	47	ND	55	ND
	Total	268 (27)	107 (16)	254 (34)	183 (18)
Grand total		471	176	432	269

(b) Regrowing Forest (W5)			g m^{-2} (standard error)	
Sampling date	n	Horizon	Live fine roots (< 1 mm)	Dead
October 1985	48	organic plus mineral	96 (11)	
May 1986	48	organic plus mineral	104 (9)	
October 1986	48	organic plus mineral	200 (15)	
October 1987	17	organic	121 (19)	19
		mineral	142 (24)	32
		Total	274	51

ND = not determined

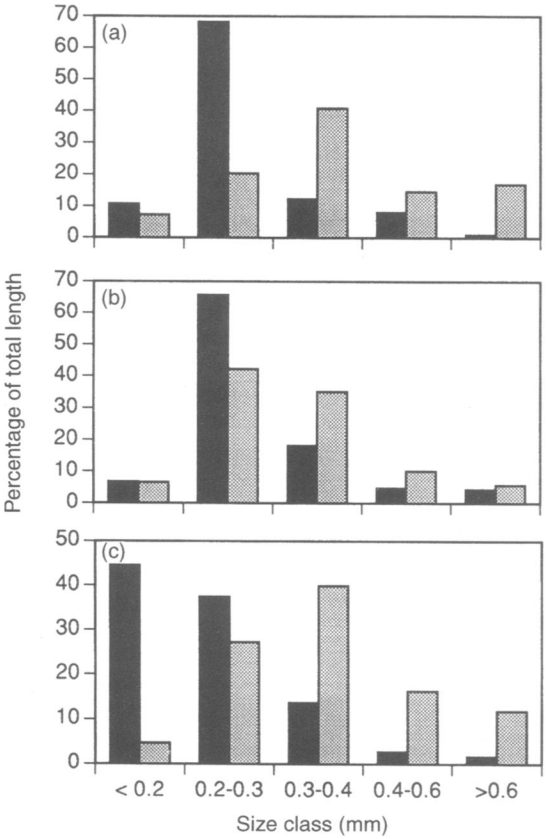

Fig. 1 Diameter distributions of fine roots of (a) beech, (b) yellow birch and (c) sugar maple collected in midsummer from the organic horizons (solid bars) and mineral soil (hatched bars) of a mature northern hardwood forest at Hubbard Brook Experimental Forest, New Hampshire.

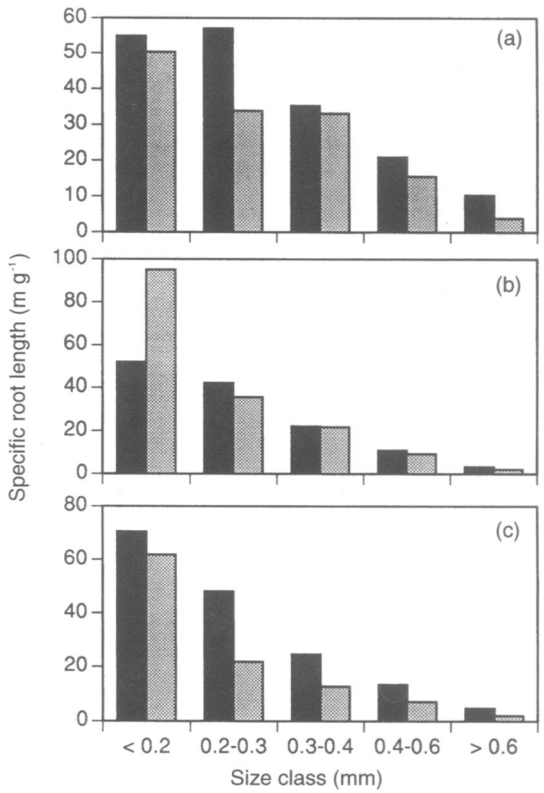

Fig. 2 Specific root length of fine roots of (a) beech, (b) yellow birch and (c) sugar maple across diameter classes. Roots were collected in midsummer from organic (solid bars) and mineral (hatched bars) soil horizons at Hubbard Brook Experimental Forest, New Hampshire.

summer 1990 in the mature forest and W5. In the year to August 1989 total fine root biomass accumulation in the mature forest averaged 241 g m^{-2} with nearly equal amounts in the forest floor and mineral soil (Table 2) compared with 267 g m^{-2} in the year to October 1989. The ratio of dead to live roots in the in-growth cores was higher (0.63) during summer 1989 than during the fine root biomass survey in 1987 (0.50; Table 1). Although we would have expected fine root biomass to continue to accumulate in the cores during 1990 (because biomass values were much lower than for the survey; Table 1), live and dead fine root biomass in the forest floor of the in-growth cores actually decreased significantly during summer 1990. Particularly notable was the highly significant decline in dead fine roots from fall 1989 to midsummer 1990 (Table 2). In contrast, live biomass continued to increase in mineral soil in-growth cores during summer 1990, and the proportion of total fine root biomass in mineral soil increased markedly on the last collection date.

Fine root production was also measured using in-growth cores in W5 during year 2 and 3 after whole-tree harvest (1985, 1986). As expected, the value for live plus dead fine root ($\leq$ 1 mm) accumulation during the second growing season after harvest (96 g m^{-2}; Table 1) was much lower than for the mature forest. At the end of the third growing season live plus dead fine root biomass for in-growth cores on W5 was 200 g m^{-2}, indicating a production of 104 g m^{-2} plus any disappearance and decay of second-year roots. By year 5, annual root production for in-growth cores in the regrowing forest on W5 was not significantly different from the mature forest (Table 3), at g m^{-2}, and 193 g m^{-2} for the years to August and October, respectively. Ratios of dead to live biomass generally were higher for W5 than the mature forest, contrasting with the observations from the root biomass surveys in 1987. A significant decline in dead root biomass was observed in the forest floor between October 1989 and late July 1990, matching the result for the mature forest.

Root in-growth was also measured in the small block clear-cut for the interval from October 1988 (4 months after harvest) through August 1990. During the second growing season after forest harvest, accumulation of live plus dead fine roots averaged 152 g m^{-2}, significantly higher than for W5 at the same stage of regrowth. By late June 1990 this value had increased to 254 g m^{-2}, with roughly equal amounts of live and dead fine roots observed. Unfortunately, disturbance by large mammals interfered with the forest floor layer in-growth cores in late summer 1990.

Table 2 Fine root biomass in in-growth cores in a mature northern hardwoods forest and a regrowing pin cherry-dominated forest (harvested during fall 1983 and winter 1984) at Hubbard Brook Experimental Forest. Cores were initiated in July 1988, and values represent biomass in $g\,m^{-2}$ with standard deviations in parentheses. For total fine root biomass, values with the same letter in each site were not significantly different ($P = 0.05$)

		Organic			Mineral		
Organic	*n*	Live	Dead	Total	Live	Dead	Total
Mature forest							
October 1988	17	45 (34)	T	45[a]	41 (26)	T	41[a]
August 1989	12	74 (75)	44 (11)	118[b]	66 (47)	57 (23)	123[b]
October 1989	11	105 (67)	70 (33)	175[c]	98 (61)	80 (46)	178[bc]
August 1990	9	90 (57)	28 (13)	118[b]	158 (124)	40 (32)	198[c]
Watershed 5							
October 1988	25	69 (40)	T	69[a]	35 (22)	T	35[a]
July 1989	16	71 (35)	65 (18)	136[b]	64 (46)	86 (46)	150[b]
October 1989	19	85 (45)	74 (45)	159[b]	74 (39)	64 (29)	138[b]
July 1990	18	115 (75)	44 (26)	159[b]	89 (69)	87 (85)	176[b]

T = trace amounts

Table 3 Comparison of fine root (< 1 mm diameter) production estimates (all values in $g\,m^{-2}$) based upon in-growth cores in 1988–89 and *in situ* screens for the mature forest and watershed 5 at Hubbard Brook Experimental Forest, New Hampshire. In-growth core values are calcualted from Table 2 for two time intervals. *In situ* screen values are calculated as described in the text from the 1989 data presented in figures 3 and 4

	Mature forest			Watershed 5		
	in-growth cores			in-growth cores		
Horizon	August	October	*in situ* screens	July	October	*in situ* screens
Forest floor	118	130	84	136	90	ND
Mineral soil	123	137	125	150	103	ND
Total	241	267	209	286	193	109

ND = not determined

ROOT GROWTH THROUGH ANGLE *IN SITU* SCREENS

In fall 1987, *in situ* screens were installed in the mature forest, and by early June 1988 (day 160) an average of 12.2 roots (< 1 mm in diameter) was observed for each 5-cm-wide screen (Fig. 3). Significantly more roots had grown in forest floor than mineral horizons. Late spring 1988 was very dry and hot with only 68 mm of rainfall during June, about half the long-term average (Federer *et al.* 1990). Root growth during June 1988 was not very rapid, as the total number of roots per screen increased to 29.1, of which about one-third appeared to be dead. This result was significantly different from a new set of screens measured in the wetter early summer of 1989; about twice as many roots were observed and only about 10% were dead or morbid (Fig. 3). However, most of this difference was made up for by higher midsummer growth rates in 1988 when rainfall was above average. The total number of roots intersecting screens did not change significantly in late summer and fall in either year, but the proportion classified as dead increased, to 57% in 1988 and to 35% in 1989.

Total root length per unit ground area estimated from the *in situ* screens was converted to biomass using the weighted average specific root length value measured for fine roots (≤ 1 mm) from the forest floor and mineral soil (Fig. 2). The resulting fine root biomass estimate for the mature forest was $209\,g\,m^{-2}$ (Table 3) or about half of the live fine root biomass measured with cores in June 1987 and 57% of that in October 1987. This fine root biomass estimate was somewhat lower than the root production estimate based on in-growth cores (241 or $267\,g\,m^{-2}$, depending upon the time interval used).

Root screen measurements were made in W5 during 1988 and 1989 (year 4 and 5 of regrowth) for comparison with the other root measurement methods. Patterns of growth were comparable to those observed in the mature forest, and only a few significant differences were observed between these forests in either year (Fig. 4). Again, higher early summer growth was observed in the wetter 1989 than in 1988, and no increases in the number of root intersections were observed after late summer. Estimated fine root production for the screens was much lower

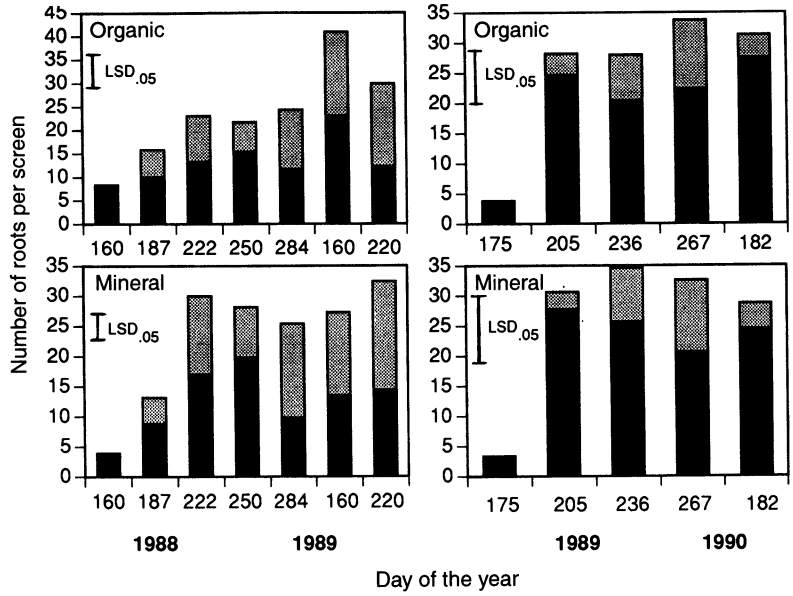

Fig. 3 Root growth through 5-cm-wide *in situ* screens in the organic (top) and mineral (bottom) horizons of a northern hardwood forest at Hubbard Brook Experimental Forest, New Hampshire. Solid bars indicate live roots and hatched bars dead roots, and the error bars indicate the least significant difference ($P = 0.05$).

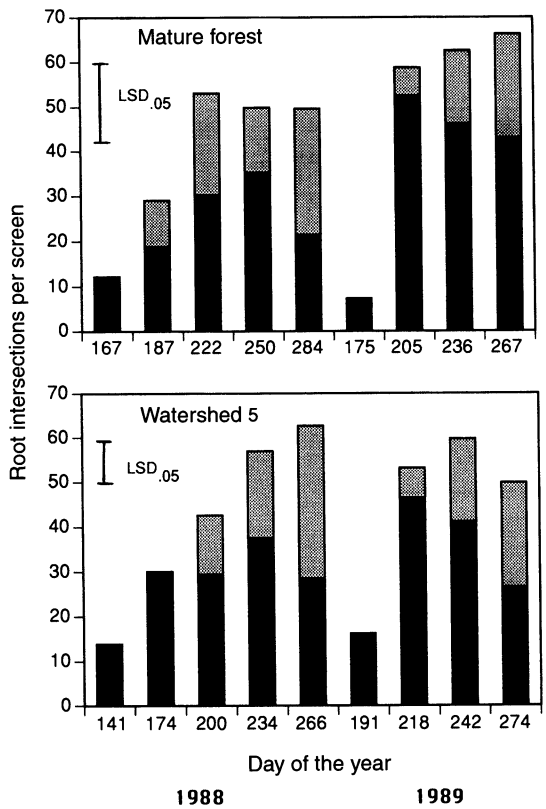

Fig. 4 Root growth through 5-cm wide in situ screens in the mature northern hardwood forest and an adjacent regrowing clearcut site at Hubbard Brook Experimental Forest, New Hampshire. Solid bars indicate live roots and hatched bars dead roots, and the error bars indicate the least significant difference ($P = 0.05$).

for W5 than the mature forest (Table 3) because specific root length was much higher for the pin cherry-dominated W5 than for the mature forest, as noted earlier. This result contrasted with measurement of fine root production using in-growth cores.

Finally, we compared the *in situ* screen method with the in-growth core method on the small clearcut from fall 1988 through late summer 1990. Values of live plus dead biomass calculated for *in situ* screens were about 50% and 70% of those for in-growth cores for the forest floor and mineral soil horizons, respectively.

ROOT GROWTH THROUGH HORIZONTAL SCREENS

We followed cohorts of forest floor roots that grew through horizontal screens in late spring of three different years (1990–1992). By mid-August, about 70% of these roots were still alive in each year (Table 4). Surprisingly, of the dead roots about two-thirds had disappeared completely from the screens, suggesting either rapid decay or consumption by herbivores. By mid-autumn, additional fine root mortality was observed, with 50% survivorship in 1990, 62% in 1991 and 56% in 1992. Although not significant, the difference among years was accounted for by higher disappearance in 1990 and 1992 as the percent dead (but still visible) was quite similar in 1990 and 1991, and much lower in 1992.

Repeated observation of 'dead' roots allowed us partially to verify the accuracy of our visual criteria of vitality. In 1990, only three out of 98 roots that were classified as dead in August were growing again by October, whereas in 1991 no 'dead' roots showed growth or recovery. Thus, our visual criteria appeared to be adequate for assessing root mortality. We had no way of evaluating whether any dead roots were

Table 4 Percentages of near-surface roots, initiated in early June of 1990, 1991 or 1992 in a northern hardwood forest, that were still alive, dead or disappeared in subsequent remeasurements. Values in parentheses are standard errors and sample sizes (*n*) represent number of locations (screens) sampled for each date and year

	1990	1991	1992
# roots mapped	1107	569	300
August			
n	68	23	19
%Live	71 (3.2)	69 (5.9)	75 (4.6)
% Dead	6 (1.7)	14 (4.4)	6 (3.4)
% Gone	23 (3.2)	17 (4.8)	18 (3.3)
October			
n	67	43	19
% Live	50 (3.1)	62 (4.4)	56 (5.1)
% Dead	16 (2.3)	14 (2.4)	6 (1.9)
% Gone	34 (3.1)	24 (4.0)	38 (4.7)
Late spring/Early summer			
n	43	31	20
% Live	28 (2.9)	36 (5.2)	45 (3.1)
% Dead	24 (3.1)	15 (3.0)	12 (2.4)
% Gone	48 (3.6)	49 (5.3)	43 (3.0)

classified as live. Observations in the late spring and early summer of the subsequent year indicated that only 28–45% of the fine roots lived longer than a year. It is notable that the lowest value coincided with measurements made about a month later (in 1991) than for the higher values (in 1992 and 1993); perhaps mortality is relatively high early in the second season for overwintering fine roots.

The effect of root measurement on subsequent mortality was examined in 1991. Somewhat lower average mortality was observed in October for screens that were being remeasured for the first time than for a group that had been remeasured previously, in August (Table 5); however, statistical comparisons indicated that the differences were not significant. Moreover, the mean percentage survival in mid-August (first remeasurement of the screens that were remeasured twice) was about the same as that in October for the first remeasurement. Thus, these two sets of screens do not appear to have been equivalent as this result would suggest that little mortality had occurred during late summer and early fall, which seems unlikely in light of the previous observations. In fact, there was a highly significant tendency ($P < 0.001$; based on chi-square analysis) for root mortality to occur contagiously; that is, many screens had very low and many screens very high mortality, relative to the mean (also note the relatively high standard errors in Table 4). Additional study of the effects of remeasurement on root growth and survival in horizontal screens is needed.

Table 5 The effect of repeated observation on root survival and disappearance for a cohort of near-surface roots mapped in early June 1991 in a northern hardwood forest in New Hampshire. Values in parentheses are standard errors

	Once	Twice
N (screens)	20	23
n (roots)	266	303
August		
% dead	–	14.2 (4.5)
% gone	–	17.3 (4.5)
October		
% dead	9.9 (3.5)	18.5 (4.4)
% gone	21.5 (4.6)	25.9 (5.0)

Patterns of root growth and branching were quite consistent for the three years of study (Table 6). Of the roots that survived from June to August, additional extension growth was observed for a range of 23 to 39% across the three years. The average increases in root length ranged from 1.3 to 1.7 cm among years, with a strongly skewed distribution as most of the growing roots increased by 1 cm or less while a small proportion showed much higher length growth (up to 8 cm). From August to October only about 12% of the surviving roots increased in length. From June to August, 26– 34% of the surviving roots showed additional branching with an average of about four new branches per root (Table 6). In contrast to length growth, which declined considerably in late summer and fall, continued branching was observed during the second interval in each year. Finally, by October the percentage of the original root cohort that showed obvious secondary thickening was 2.7% in 1990, 2.5% in 1991 and 2.3% in 1992.

RESPONSES TO ALTERATION OF NUTRIENT AVAILABILITY

As expected, fertilization resulted in significant increases in root growth in the forest floor. The treatment receiving biweekly (hereafter; 'continuous') fertilization had about six times as many new roots in August as the control, and the single-pulse fertilization treatment had about three times as many (Table 7). In this experiment 'new' roots refers to the

Table 6 Percentage of near-surface roots, initiated in early June in 1990, 1991, and 1992 in a northern hardwood forest, that exhibited subsequent growth and branching during two intervals. Values are expressed as a percentage of those roots surviving through the time interval

		root %		root mean growth	branches/
Interval	*n*	grew	branched	(cm)	root
June-Aug					
1990	446	33	26	1.5	4.3
1991	416	39	34	1.7	4.1
1992	151	23	28	1.3	3.8
Aug-Oct					
1990	303	12.2	22	1.7	5.1
1991	369	11.6	25	1.6	5.5
1992	48	10.4	17	1.0	2.6

Table 7 Root growth through horizontal *in situ* screens in the O_e horizon of a northern hardwood forest: responses to alteration of nutrient availability. Values represent number of new roots growing through 15-cm × 15-cm screens. In columns values with different letters are significantly different ($P = 0.05$)

		August 1990		November 1990		July 1991	
August 1990	*N*	New*	Dead	New†	Dead	New‡	Dead
Control	49	22a	9a	33a	16a	28a	2a
Fertilizer-continuous	20	128c	34c	164c	32b	30a	30b
Fertilizer-pulse	27	64b	11a	105bc	24ab	ND	ND
Depletion	21	17a	22b	50ab	41b	187b	30b

*New = Live + dead in August minus total in June.
†New = Live + dead in November minus total in June.
‡New = Live + dead in July, 1991 minus Live + dead in August, 1990.
ND = not determined.

difference in number of live roots per screen in early July (beginning of treatments) and late August. The average number of new roots in the nutrient depletion treatment was lower than the controls, but the difference was not significant. However, the total number of dead roots was significantly higher in the depletion treatment, and for 50% of the screens an absolute decline in the total number of roots (live plus dead) occurred between June and August. The total number of dead roots was highest for the continuous fertilization treatment, but the percentage dead was lowest for this treatment.

The last treatments were applied on 21 September 1990, and by early November the number of additional new roots (i.e. difference from late-August values) was similar in the continuous fertilizer, pulse fertilizer and depletion treatment, all of which were significantly higher than the control. In July 1991, screens in the continuous fertilizer, depletion and control groups were reassessed. Surprisingly, root growth for the depletion screens was about six times higher than the fertilizer and control (Table 7).

About 50 roots on six screens in each treatment were mapped prior to initiation of the treatments, and these roots were re-assessed in August and November. There was a trend towards higher percent survival of the roots in the continuous fertilizer treatment (40% by early November) compared with the other treatments (25 to 30%), but this difference was not statistically significant.

FINE ROOT AND SOIL RESPIRATION

Despite higher soil temperatures in mid-August than late June (14° vs. 12 °C at 5 cm and 12° vs 10 °C at 20 cm), average respiration rates of fine roots from the O_e horizon were significantly higher in June (8.0 nmol cg^{-1} DM s^{-1}) than August (5.2). The high values in June may be associated in part with the rapid root growth at that time (van der Werf *et al.* 1988). Assuming that these respiration rates are maintained throughout the day and that these values are representative of the entire root system, then fine root respiration would be about 3.9 g CO_2-C m^{-2} day^{-1} in mid June and about 2.5 g CO_2–C m^{-2} day^{-1} in August. By comparison, soil respiration rate in the study site was measured at 4.5 g CO_2-C m^{-2} day^{-1} in midsummer (Goreau 1981; Yavitt & Fahey, unpublished).

Discussion

FINE ROOT MORPHOLOGY

In theory, soil resources should be acquired most efficiently by minimizing root diameter and maximizing specific root length (*SRL*; Fahey 1992; Yanai *et al.* 1994). Eissenstat (1992) noted that roots of high *SRL* and low diameter may be capable of rapid proliferation in resource-rich environments. The fine roots of the northern hardwoods, particularly those in the forest floor, supported this assertion; diameter distributions were smaller and *SRL* values larger in the resource-rich forest floor than in the resource-poor mineral soil (Fig. 2), and these values were more extreme than most observations for trees. Differences in soil temperature between forest floor and mineral soil also could influence *SRL* (Cooper 1973). In general, the diameters of fine roots in the northern hardwood forest at HBEF were similar to herbaceous legumes and desert shrubs, larger than most grasses and smaller than coniferous and broadleaf evergreen trees (Eissenstat 1992). Some bias may be inherent in these comparisons because some root shrinkage occurs upon drying and not all studies have specified moisture conditions of measured roots.

Diameter distributions and *SRL* differed among the dominant species (Figs 1 and 2). The mean diameter of sugar maple roots was similar to the values reported for red maple (*Acer rubrum* L.) in Massachusetts (Lyford & Wilson 1964). These values are lower than those measured by minirhizotron for a sugar maple forest in Michigan (Hendrick & Pregitzer 1992). This discrepancy is probably explained by shrinkage resulting from air drying in our study. Hendrick & Pregitzer (1992) observed that root diameters

increased with soil depth, which is consistent with our results.

Diameter distributions and *SRL* of fine roots may be constrained by a variety of other trade-offs in form and function. For example, root longevity can have important effects on the efficiency of roots in soil resource acquisition (Yanai *et al.* 1994), and root longevity may be positively correlated with diameter (Fernandez & Caldwell 1975; Kummerow *et al.* 1978). Wilson and Horsley (1970) demonstrated that relatively large diameter, 'long roots' of red maple lived much longer than smaller diameter roots, so that the need to explore the soil for resources with patchy distributions influences the average root diameter and *SRL*. Mycorrhizal infection also is influenced by root diameter: both the smallest roots (Pope *et al.* 1983; Graham & Syvertsen 1985), and the larger primary roots (Hooker *et al.* 1992) are rarely infected. Finally, larger roots may be capable of withstanding greater soil impedance before buckling (Whitely *et al.* 1982), possibly explaining the generally larger diameters and lower *SRL* values for roots in mineral soil than forest floor (Fig. 1 and 2).

FINE ROOT BIOMASS

Hendrick & Pregitzer (1994) recently summarized observations of fine root biomass for mature temperate deciduous forests, and our values fell in the middle of the range. In the spodosols that are characteristic of most northern hardwood forests fine roots are concentrated in the forest floor horizons. Within-site and between-site variation in fine root biomass in these organic horizons may be largely explained by the horizon thickness; for example, Simmons (1993) measured much higher fine root biomass (390 $g\,m^{-2}$) in the thicker forest floor (10.0 cm) of a mature northern hardwood forest in the Adirondack Mountains of New York than for our site.

After clearcutting, fine root biomass accumulated rapidly in the pin cherry-dominated forest. Our coring data indicated that fine root biomass was 25, 52 and 71% of that in the mature forest after 2, 3 and 4 years of forest regrowth, respectively. The rate of recovery of fine root biomass was similar to that for foliage biomass, as analogous values for foliage were 36, 45 and 61% for years 2, 3 and 4 of regrowth for the same study site (Mou *et al.* 1993). These values suggest that the ratio of fine root to foliar biomass increased during the period of canopy closure after an early minimum (in years 1 and 2). This pattern probably resulted from initially high soil resource availability favouring aboveground carbon allocation to utilize the light resource, followed by rapidly declining soil resource availability and greater belowground carbon allocation. Similar changes in the proportions of fine root and foliage biomass were observed in shrub-dominated vegetation on clearcut conifer forest sites in British Columbia, but the rate of change was slower (Messier & Kimmins 1991).

The rate of recovery of fine root biomass in the Hubbard Brook forest was slower than that in a cut-over tropical rainforest at LaSelva, Costa Rica where 92% of the mature forest value was observed one year after cutting (Raich 1980). Six years after clearcutting a *Quercus*-dominated ecosystem in Wisconsin, Yin *et al.* (1989) observed that fine root biomass of the fern and shrub dominated vegetation was 50% higher than the adjacent forest. They suggested that some of the measured roots may have been part of the residual root system of the forest as abundant sprouting from stumps was observed. Although some stump and root sprouting occurred on our study site, most of the fine root biomass was associated with colonizing trees and shrubs (Mou *et al.* 1993). Zeimer (1981) measured fine root biomass of shrub-dominated vegetation on a 12-year-old clearcut site in northwestern California at 82% of that in the adjacent mature forest. In sum, the rate of recovery of fine root biomass following large-scale forest disturbance probably follows complex patterns that depend upon a variety of vegetation, soil and climatic features, and additional systematic study will be necessary to develop a general understanding of this phenomenon.

FINE ROOT PRODUCTION AND TOTAL ROOT ALLOCATION

Our in-growth core estimate of fine root production (dry weight basis: 254 $g\,m^{-2}\,year^{-1}$) is within the range obtained by a variety of methods for temperate deciduous forests (85–990 $g\,m^{-2}\,year^{-1}$; Nadelhoffer & Raich 1992; Hendrick & Pregitzer 1994). However, the in-growth core technique suffers from some potential problems (Vogt & Persson 1991) including the effect of cutting roots during core establishment, soil disruption within the core and root disappearance during the incubation interval. A correction for the last effect was possible using our observations of root disappearance for the horizontal *in situ* screens. Assuming that 50% of the roots growing into in-growth cores disappeared during the annual sampling interval (Table 4), then the in-growth core estimates of production should be doubled, yielding annual fine root growth of 508 $g\,m^{-2}$. Any major differences in root disappearance between forest floor and mineral soil would affect these estimates. Using the same assumption for the 5-year-old forest on W5 yields a root production estimate of 480 $g\,m^{-2}$; however, no confirming data were available for root disappearance in that stand.

Hendrick & Pregitzer (1994) estimated fine root production and mortality in two sugar maple forests in Michigan using a combination of mini-rhizotrons and root coring. They observed 40% mortality of fine roots during the interval from June to September, comparable to our estimate. However, fine root pro-

duction was much higher in the Michigan forest (730–800 g m^{-2} $year^{-1}$), as were fine root and leaf biomass. The causes of higher fine root and foliage production in the Michigan stands than for sugar maple stands in Wisconsin (Aber *et al.* 1985) and northern hardwoods in New Hampshire deserves further study.

Fine root production during the fifth year of recovery following whole-tree harvest was not significantly different from the mature forest, based upon ingrowth cores (Table 3). Similarly, foliage production at this site in the fifth year (268 g m^{-2} $year^{-1}$; Mou *et al.* 1993) was not significantly different from the mature forest (260 g m^{-2} $year^{-1}$; Fahey, unpublished data), illustrating the rapid recovery of ecosystem function in the northern hardwood forest (Marks & Bormann 1972).

Our measurements of fine root dynamics can be checked for consistency with other C flux estimates for the Hubbard Brook forest. If soil C pools are not changing from year to year, then inputs from root mortality (which would equal fine root production) and litterfall should equal outputs from total soil respiration plus small amounts of organic C leaching. Carbon concentration in fine roots at Hubbard Brook averaged 48% dry mass (Fahey *et al.* 1988), and fine root production in the mature forest based upon ingrowth cores averaged 244 g C m^2 year. Litterfall in the study site averaged 261 g C m^{-2} $year^{-1}$ and did not change significantly between 1968–69 and 1987–88 (Gosz *et al.* 1972; Hughes & Fahey 1994). Soil respiration has been measured at about 600 g C m^{-2} $year^{-1}$ (Yavitt & Fahey, unpublished). Because forest floor C pools appear to be in steady state for this forest (Siccama; unpublished data), these results suggest a large, additional soil C input, presumably from root exudation and rhizodeposition.

These values can be further cross-checked using our root respiration measurements and literature values for total root allocation (Raich & Nadelhoffer 1989). A simple extrapolation through the year of our root respiration measurements, based on the Q_{10} value suggested by Ryan (1991), would place fine root respiration at about 400 g C m^{-2} $year^{-1}$. Raich and Nadelhoffer (1989) estimated C allocation to roots based upon the correlation between soil respiration and aboveground litterfall for 30 forest ecosystems worldwide. Assuming that belowground C allocation is equal to the difference between soil respiration and litterfall, they developed a regression equation to predict total root allocation (*TRA*) of C from litterfall ($TRA = 130 + 1.92 \times$ litterfall mass; units are g m^{-2} $year^{-1}$). Application of this equation yields a *TRA* value of 631 g C m^{-2} $year^{-1}$ for the mature forest at Hubbard Brook. The difference between *TRA* and fine root production (631–244 = 387 g C m^{-2} $year^{-1}$) should equal root respiration plus exudation.

These values are not consistent when compared with the previous estimates of the soil C budget and root respiration; for example, the *TRA* calculation would suggest little C flux via exudation/rhizodeposition. Perhaps the most likely causes of these discrepancies are (1) overestimation of fine root respiration because extrapolations were based on measurements only of forest floor roots; (2) error in the regression equation for *TRA* (for example; this ignores C allocation to mycorrhizal fungi and assumes steady-state soil organic matter); (3) error in the estimate of total soil respiration; and (4) error in the ingrowth core estimate of fine root production.

A comparable exercise in soil C budgeting was presented recently (Bowden *et al.* 1993) for a mixed hardwood forest in central Massachusetts. Soil C fluxes in that forest were lower than at Hubbard Brook (litterfall = 138 g C m^{-2} $year^{-1}$; soil respiration = 371; root mortality = 110; root respiration = 123). As a percentage of total soil respiration, C flux via root mortality appeared to be higher at Hubbard Brook (40%) than in Massachusetts (30%). These differences in soil C fluxes probably result from contrasting forest composition, soils and land-use histories, as well as possible measurement errors.

FINE ROOT PHENOLOGY, LONGEVITY AND DEMOGRAPHY

Our observations of root growth through *in situ* screens indicated that root production was most rapid in early summer but continued at a reduced rate through late summer in the northern hardwood forest (Fig. 3), consistent with previous observations (McClaugherty *et al.* 1982; Nadelhoffer *et al.* 1985; Hendrick & Pregitzer 1992). Near-surface roots in the O_e horizon rapidly elongated into overlying leaf litter between mid-May and early June if the soil layer was moist at that time (as in 1990 and 1991). Thus, initiation of root growth in the upper forest floor seems to coincide with completion of leaf expansion in the forest canopy which normally occurs during the last two weeks of May at HBEF (C. A. Federer; personal communication). In contrast, Morrow (1950) observed that the most rapid growth of sugar maple roots in surface mineral soil occurred in March and April, prior to leaf out, on mull soils in central New York. During a very dry late spring in 1992, little root elongation occurred at HBEF until 6 cm of rainfall re-wetted the O_e horizon in mid-June. Simmons (1993) observed a highly significant shift in live fine root biomass from the O_e to the O_a horizon during an unusually dry summer in a mature northern hardwood forest at Woods Lake, New York. Thus, it appears that the timing and distribution of root growth in forest floor horizons in this northern hardwood ecosystem depends upon both seasonal factors (probably soil temperature) and resource availability. Because a high proportion of fine root biomass is located in the forest floor, the forest C budget could be profoundly influenced by drought via effects on root mortality or growth patterns.

The drought effects and our experimental manipulations of soil resource availability (Table 7) demonstrated that fine roots are capable of responding to environmental fluctuations. However, despite natural environmental variation across three years of study, the demography of the near-surface roots was remarkably constant. For example, among the roots born in late spring and surviving into the summer, in each year about one-third exhibited additional growth by mid-August, and about 12% showed continuing growth into early autumn (Table 6). Similarly, average length of elongation and frequency and degree of branching were very consistent between years. Observations of this sort are not available for other forests, and additional observations are needed to verify the generality of this pattern.

We also observed that 2.3–2.7% of the near-surface roots exhibited secondary thickening, and continued observation of several of these indicated that most would become part of the perennial woody root system of the trees. Fahey *et al.* (1988) found that 13.3% of the root biomass in the organic horizons of this forest consisted of small woody roots (1–5 mm in diameter), and the concentration of these roots was much higher in the forest floor than mineral soil. The probability that a fine root develops into a woody root seems to be related to the amount of soil resources it transports. For example, Simmons (1993) introduced two fine roots through holes into forest floor microcosms in a northern hardwood forest, and these roots quickly proliferated within the microcosms: one to two years later, nearly all of the root axes growing through the holes had developed into woody roots.

Measurements of survivorship in these cohorts of fine roots provided a partial picture of root longevity patterns in the forest floor of the northern hardwood forest at Hubbard Brook. The median longevity of roots equals the time to 50% survivorship, and our observations (Table 4) would indicate a median longevity of about six months. Observations of a set of 353 roots in a maple-beech forest in south-central New York gave similar results, with 59% of the root cohort still alive after 5 months (Fahey; unpublished data). If root longevity is normally distributed the mean and median values would be equal, but rhizotron observations for northern hardwood fine roots in Michigan suggest that the distribution of longevity may be skewed (Hendrick & Pregitzer 1993).

Our observations were restricted to the late-spring flush of fine roots in the forest floor. This cohort of roots is probably the most important because it is the largest (Figs 3 and 4) and the most active in nutrient uptake (Yanai 1992); however, the demography of roots born at other times and depths may be somewhat different. For example, Hendrick & Pregitzer (1993) suggested that roots born in spring in northern hardwood forests live longer than the average for all fine roots. Also, there is limited evidence that roots in deeper soil horizons live longer than surface roots (Persson 1983; Gholz *et al.* 1986; Schoettle & Fahey 1994).

Fine root longevity also could be estimated from the ratio of average biomass to production. Based upon the production estimate from the in-growth cores (corrected for root disappearance) for the mature forest (508 g m^{-2}), this approach would yield a longevity estimate of 0.77 years, which appears somewhat longer than observations for the horizontal *in situ* screens. It should be noted that the root screen observations measure longevity on a root length basis whereas the biomass/production ratio is calculated on a root mass basis. If root longevity varies markedly among size classes, these approaches could yield quite different longevity estimates. For example, if finer roots have shorter lifespans, then because they contribute proportionately more to total root length than to root mass, a length-based estimate of longevity should be shorter than a mass-based value; this matches our observations. Our current estimate of root longevity is comparable to other estimates for northern hardwood forests (Hendrick & Pregitzer 1992; 1993).

Perhaps the most striking result from these studies was the evidence of rapid disappearance of fine roots. First, live plus dead root biomass measured for ingrowth cores in the organic horizons of the mature forest declined significantly between October 1989 and August 1990, with most of this 30% decline in the dead root category (Table 2). Thus, rapid decay must have occurred during winter and early summer. This result is consistent with the high live-to-dead ratios observed during summer in this study (2.7:1; Table 1), but not with very low decay rates observed in root decomposition studies at HBEF (Fahey *et al.* 1988) and other northeastern forests (McClaugherty *et al.* 1982).

Secondly, direct evidence of rapid fine root disappearance was obtained with the horizontal *in situ* screens in the forest floor (Table 4). In all three study years a large fraction of the roots mapped in early June disappeared during the summer, suggesting either consumption by herbivores or rapid decomposition. In several cases, nearly all the mapped roots on a particular screen or section of a screen disappeared, contributing to high spatial variation in root survival. In most of these cases, a proliferation of gray fungal hyphae was observed at the location where roots disappeared, and rapid decay of roots by fungi is postulated. Although larvae and adults of arthropods were occasionally observed in the vicinity of screens, previous energetic calculations have suggested that soil arthropods are unlikely to consume significant amounts of fine root biomass, except perhaps during irruptive outbreaks (Ausmus *et al.* 1977).

Thirdly, evidence of rapid root disappearance in mineral soil horizons also was seen. Although declines in total and dead root biomass for mineral soil ingrowth cores were less pronounced than for organic

horizons (Table 2), a significant decline in the number of dead roots intersecting the angle *in situ* screens in mineral soil was observed in summer 1988 in the mature forest (Fig. 3). Moreover, total root intersections declined abruptly in early autumn 1989 in the 5-year-old forest on W5 (Fig. 4).

Hendrick & Pregitzer (1992) also observed rapid disappearance of fine roots in mineral soil of a northern hardwood forest in Michigan using mini-rhizotrons.

These results call into question the methods used to measure fine root decomposition in eastern deciduous forests. Fahey (1992) commented previously on the difficulty of reconciling the low decay rates observed by McClaugherty *et al.* (1982) and Fahey *et al.* (1988) with the apparent lack of accumulation of large quantities of dead root tissue in these forests. Three possible explanations were advanced: (1) underestimation of fine root decay, (2) underestimation of fine root longevity and (3) significant, chronic fine root herbivory. The present studies would seem to support the first explanation. As discussed above fine root longevity appears to average somewhat less than 1 year. No evidence was obtained for a soil arthropod irruption, which probably would be required to explain the observed consumption of up to one-third of fine root production. Moreover, Hendrick & Pregitzer (1992) reported no evidence of faecal material that should be associated with invertebrate consumption of roots.

Why have studies of fine root decomposition failed to demonstrate rapid decay? One possible explanation is that contact between roots and soil is important to the decay organisms; however, Fahey *et al.* (1988) observed relatively slow decay even when roots were in direct contact with soil either tethered on strings or incubated in bags containing soil. Moreover, nitrogen immobilization in very fine roots incubated with humus inside mesh bags was very different from that observed for roots decaying *in situ* following forest harvest (Fahey & Arthur 1994). A probable explanation is that procedures of removing roots from the complex mycorrhizosphere environment fundamentally altered the normal decay process, which may be carried out by rhizosphere organisms or perhaps by mycorrhizal fungi.

FINE ROOT RESPONSE TO ALTERED NUTRIENT AVAILABILITY

The nutrient availability treatments were designed to simulate microsite variations, rather than large-scale fertilization or nutrient depletion. Thus, the 6-fold increase in root growth observed on the fertilized plots represents the short-term response of roots to enriched microsites under unrestricted carbon supply for root growth, and this result agrees with other studies of microscale variation in root growth (St. John *et al.* 1983; Crick & Grime 1987; Jackson & Caldwell 1989). Although the response of root turnover or longevity to microsite enrichment has not been measured, it has been argued that fine root longevity should increase under very high nutrient conditions because depletion zones might not develop around absorbing roots (Schoettle & Fahey 1994; Yanai *et al.* 1994). Our results supported this argument, as the proportion of dead roots was significantly lower in the fertilized microsites (16.3%) than the controls (32.6%), and fine root survivorship in the continuously fertilized treatment (40% survival over 12 months) tended to be higher (though not significantly) than the control and single-pulse fertilized treatments (25–30%). These results match very closely those for a mixed deciduous forest in Michigan (Pregitzer *et al.* 1993). Conversely, the nutrient depletion treatment resulted in a significant decline in the live-to-dead ratio as well as a slight but non-significant decline in survivorship. The only significant root growth response to the nutrient depletion treatment was observed in the early summer of the next growing season when these screens exhibited root growth comparable to that observed the previous year in the continuous fertilization treatment (Table 7). Perhaps nutrients that had been immobilized by microbes during treatments in the previous growing season were re-mineralized as microbes died and root growth was greatly stimulated.

ROOT SCREEN METHODOLOGY

The *in situ* screen methods provide an inexpensive alternative to coring and mini-rhizotron techniques. In forests with surface organic horizons, the horizontal screens allow observation of the demography of cohorts of fine roots with minimal disruption of the soil environment.

The angle root screen method offers advantages over coring techniques because roots do not need to be sorted from soil, but the value of this method for quantifying root production and biomass is unproven. In the low bulk density soils at Hubbard Brook, root measurement in the upper 15 cm was not a problem. Our estimate of root production using these *in situ* screens was 209 $g\,m^{-2}$ $year^{-1}$, which was about 82% of that from in-growth cores. This value also should be adjusted for root disappearance. Both techniques suffer from potential problems associated with severing of fine roots during installation. The in-growth core technique might stimulate root growth if disruption of soil structure increases nutrient availability; this would not be true for the *in situ* screens, and might help to explain their lower root production values. However, anisotrophy in root orientation might explain the fact that live fine root biomass from root cores (growing season average = 386 $g\,m^{-2}$) exceeded the value calculated from the observed peak in root screen intersections after 2–3 years in the ground (270 $g\,m^{-2}$). Thus, using the correction factor of Melhuish & Lang (1971) with the *in situ* screen

technique appears to result in systematic underestimation of fine root biomass and production by about 20–30% compared with coring and in-growth core techniques. Whether a systematic correction for this apparent bias can be obtained must await further research.

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