Fine root dynamics along an elevational gradient in the southern Appalachian Mountains, USA

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Abstract

Attributes of fine roots (<2.0 mm diameter) were quantified in five southern Appalachian plant communities along an elevational gradient. These attributes include the seasonal dynamics of fine root mass and length, the depth distribution of fine roots, fine root width and, most importantly, the annual appearance and disappearance of fine roots. The principal objectives of this study were two-fold: (1) to compare these attributes of fine roots between plant communities and (2) to compare the results of the two methods used to quantify the attributes: (1) harvesting roots from forest soil with soil cores and (2) photographing roots growing against the windows of minirhizotron boxes. The plant communities that were sampled are characteristic of the region and are designated as follows from lowest elevation (782 m) to highest elevation (1347 m): (1) xeric ridge, (2) cove hardwoods, (3) low elevation mixed oak, (4) high elevation mixed oak, and (5) northern hardwoods. Fine root mass varies seasonally in this temperate region with lowest and highest mass in the spring and autumn, respectively. Fine root mass and fine root mass appearance were lowest in the cove hardwood community and highest in the low elevation mixed oak community. The total length of fine roots was highest in the xeric ridge community and lowest in the low elevation mixed oak community. The high total root length in the xeric ridge community was due to the presence of an exceptionally dense mat of very fine roots found there. The width of these roots was significantly less than that of roots on all other plots. Subsequent regression illustrates two strong patterns in the data. First, fine root mass, fine root mass appearance and leaf production were positively correlated. Second, fine root length and soil moisture were negatively correlated. The accumulation of root mass in these communities was linked to overall site productivity and the development of root length in response to moisture stress. Only the timing of root growth initiation was related to elevation and the associated parameter of soil temperature. The best estimates of fine root appearance and disappearance were generated by harvesting roots rather than photographing them. Some methodological problems with root photography implemented in this study are addressed.
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1. Introduction

Fine roots play an important role in forest ecosystems. While fine roots often constitute as little as 1% of total forest biomass, the annual fine root production may constitute more than 50% of the net primary

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production of forests (Fogel, 1985; Vogt et al., 1996). In these systems growing roots are "turning over" faster than the growing components of shoots, and rates of fine root decomposition are often greater than rates of litter decomposition (McClaugherty et al., 1982). In some systems more nitrogen is returned to the soil via decomposition of fine roots than by decomposition of litterfall (Vogt et al., 1996).

Among different ecosystems and geographic regions, southern Appalachian forests are relatively under-represented in the root literature (Pregitzer et al., 2002). And, although elevation, aspect and topographic differences in forest composition and structure have been extensively described (Day et al., 1988; Whittaker, 1956), there are no corresponding studies of differences in root production and turnover. In this study, we measured fine root mass and dynamics along an elevational temperature/moisture gradient as part of an effort to understand how fine root abundance and activity varied across the southern Appalachian landscape.

Specifically, our objectives were to (a) quantify the seasonal dynamics of fine roots by both harvesting and imaging methods and (b) quantify relationships between these root dynamics and various types of environmental data, including soil temperature and moisture. We hypothesized that fine root biomass and length would be positively correlated with foliar production. Relatively few studies have explicitly examined the relationship between fine root and foliar production or biomass in temperate deciduous forests. Raich and Nadelhoffer (1989) predicted that total allocation to roots should increase with increasing litterfall, but their model does not address standing root mass or length. Hendrick and Pregitzer (1992) summarized data from several studies in which both fine roots and foliar production were measured. The ratio of fine root production to foliar production ranged from 0.26 to 3.10, but there was no clear relationship between absolute amounts of root and foliage production. For example, fine root production in a number of sugar maple forests ranged from about 4000 to 8000 kg ha^{-1} per year, but the ratio of fine root to foliar production was 1.4 times where root production was least, 1.9 where it was greatest, and 3.1 in the middle of the range. In addition, foliage production was 4 times greater than root production at the least productive site. We also hypothesized that fine root

biomass and length would increase with decreasing soil moisture because plants enduring moisture stress will allocate more biomass to roots.

2. Materials and methods

2.1. Site description

The study was conducted at the US Forest Service Coweeta Hydrologic Laboratory, Nantahala National Forest, near Franklin, North Carolina (35°03′N, 83°27′W). Climate, land use and research history are described in Swank and Crossley (1988). Changes in forest processes of production, decomposition, nutrient cycling, plant community structure and plant demography were investigated in five intensive study plots along an elevation temperature gradient commencing in 1991. Plot locations were selected to represent typical plant communities at Coweeta (Knoepp et al., 2000). Plant community types are distributed over the varied topography in relation to elevation and topographic position (Day et al., 1988) where topographic positions are ridge (convex terrain), coves (concave terrain) and slopes (intermediate terrain).

2.2. Study plot descriptions

Site 1: Xeric ridge, aspect 180°, slope 34°, and an elevation of 782 m. Principal canopy species on this south-facing ridge site are *Pinus rigida* and *Quercus coccinea* (nomenclature follows Radford et al. (1968)). *Carya glabra* and *Quercus prinus* also occur. The understory is a thicket of *Kalmia latifolia* shrubs.

Site 2: Cove hardwoods, aspect 340°, slope 21°, and an elevation of 795 m. The principal canopy species in this cool, north-facing community are *Liriodendron tulipifera*, *Acer rubrum*, *Betula lenta* and *C. glabra*.

Site 3: Low elevation mixed oak, aspect 15°, slope 34°, and an elevation of 865 m. This community on plots 3 and 4 is the most common at Coweeta. The canopy is comprised of *Quercus rubra*, *Q. prinus*, *A. rubrum*, and *C. glabra* with an understory of *Rhododendron maximum*, which grows in dense thickets. Because this mixed hardwood community is

ubiquitous in the southern Appalachians across a wide range of elevations, both low (plot 3) and high (plot 4) elevation plots were established.

Site 4: High elevation mixed oak, aspect 75°, slope 33°, and an elevation of 1001 m.

Site 5: Northern hardwoods, aspect 20°, slope 33°, and an elevation of 1347 m. Vegetation is more similar to that of Appalachian forests at higher latitudes than vegetation at other plots at Coweeta. Canopy species include *Q. rubra*, *B. lenta*, *Acer saccharum* and *C. glabra*.

These plots were situated 40 m along the slope and 20 m up slope, fitted with board walks, numerous sampling sub-plots, sampling instruments, meteorological stations, and root observation boxes.

2.3. Estimating root mass dynamics on each plot by harvesting roots

Fine root mass was estimated from soil cores (10 cm diameter × 15 cm length) taken from each of the five study plots on 3 July 1993, 1 August 1993, 5 September 1993, 10 October 1993, 1 November 1993, 8 April 1994, and 16 July 1994. Soil cores were taken at random positions along the perimeter of the 20 × 40 plot and >2 m apart. Samples were sealed in plastic bags and stored in a cold room at 4 °C within 48 h of collection. Roots were separated from soil and plant litter by hand, and washed free of soil with a water spray. Fine roots were separated from thicker roots (>2 mm) and dried at 65 °C to constant weight.

Some soil samples contained mats of roots and litter that were difficult to disentangle. For these, a 10% sub-sample was taken from the root-litter mat and processed as usual. Root dry weight in the total sample was estimated as the dry weight of the sub-sample multiplied by 10.

2.4. Comparing root mass across plots and dates

We tested for differences in root mass across sites and dates using multiple comparisons of means of dry root mass with a Student–Newman–Keuls (SNK) multiple range test on all effect means (SAS Institute Inc., 1989). The SNK test used determines significant differences at $P < 0.05$ in root mass by plot and by sampling date.

If two or more mean values are within this critical range of difference, they are grouped together.

2.5. Estimating root length dynamics on each plot by photographing roots

The length of fine roots on each plot was estimated by analyzing photographs of roots growing against the observation windows on the outsides of minirhizotron boxes. Design details are described in Davis (1997). Briefly, boxes were constructed of opaque polyvinyl chloride (PVC) sheets 0.6 cm thick cemented to a frame of 3 cm × 3 cm PVC pieces. Boxes were 65 cm long, 57 cm wide, 71.5 cm tall at one end and 39.5 cm high at the other end. The viewing window 30 cm long and 15 cm high, was countersunk into the short end wall. Boxes were covered with an overlapping PVC lid containing a gasket to exclude water and small organisms from the interior of the minirhizotron.

Two minirhizotron boxes were installed in the summer of 1992 just outside of the perimeter of each of the five gradient plots in order to minimize disturbances within the plots. No photographs were taken during the first year after installation, to allow the boxes to settle into stable positions and to allow roots to grow against the observation window.

Twelve 17.3 mm × 12.5 mm areas within the observation window were designated for photograph sampling, hereafter referred to as *frames*. We were able to take photographs at magnifications up to 10×. Frames were situated along three horizontal transects of the viewing window. Each of the three transects was located within one of three soil depths: 0–5, 5–10, and 10–15 cm, referred to as *depths* throughout this text. Because roots are present at a higher density near the surface of the soil and at a low density at greater depths, a stratified sampling method was employed. Photographs were taken at the most shallow depth in six regularly spaced frames, at the second depth in four regularly spaced frames and at the third depth in two regularly spaced frames. An 'x' was etched into the glass at the center of each frame to insure that photographs would be taken at exactly the same positions as photographs taken earlier. Photographs were taken on the following four sampling dates: 19 July 1994, 26 August 1994, 1 October 1994 and 25 April 1994.

We used the following categories of root status: (1) new—the root is not seen on images of the same frame

from earlier dates; (2) white—the root is seen on images of the same frame from earlier dates and colored white; (3) brown—the root is seen on images of the same frame from earlier dates and colored brown; (4) missing—the root is not visible in a clear image, i.e. the root has disappeared; (5) unknown—the root is not visible in an unclear image. The status of the root is unknown.

The minirhizotron image analysis program ROOTs was used to calculate the length and diameter of each root when it first appeared, and then to track the fate of individual roots at subsequent sampling dates (Hendrick and Pregitzer, 1996).

A total of 3664 observations of root segments were made from 480 photographs (4 sampling dates × 5 plots × 2 boxes per plot × 12 frames per box). At each date, individual root lengths were summed to obtain per frame values, and are reported as such in the results. Mean values were calculated for each depth using combined plot data at each site. Mean values per site were calculated from all three depths using procedures for calculating means and standard errors for stratified samples (i.e. different numbers of frames per depth) using standard formulas (Freese, 1962).

Next, these values of root length observed against the window of the minirhizotron boxes were converted to root length in a volume of soil assuming a 'depth-of-field' in the photographic images of 2 mm.

Two deviations from the approach described above were necessary in a few instances. First, in some frames at site 1, the entire frame contained only roots, with no soil visible. This was due to a dense fine root mat that is often present in this xeric ecosystem. In these frames, individual roots could not be traced and labeled, and a 1/30th sub-sample was taken by tracing the roots in a smaller frame (2.8 mm × 2.5 mm). A second modification of the procedure was necessary to correct for root observations whose status was recorded as 'unknown'. Some of the images of the frames were unclear and thus some roots were given a status of 'unknown'. Images were unclear for two reasons, either due to condensation of water on the observation window or a few of the photographs were underexposed or out of focus.

Nearly 7% of all root database records were recorded as 'unknown'. Because the analytical procedure of this study involves finding the sum of all roots within a sampling field and then averaging these sums by depth by plot, an uneven distribution of roots with status 'unknown' between depths or between plots will generate bias in the summaries of the data. To correct for this bias, the sum of the length of all roots within a depth was multiplied by 1 plus the ratio of roots of 'unknown' status to roots of 'known' status. The correction was based upon the assumption that the missing values are equal to the mean of all other values observed within that treatment (depth, plot and date combination). Since only 7% of root observations were 'unknown', this correction was very small.

2.6. Estimating root appearance and disappearance by harvesting roots

Changes in fine root mass from sampling date to sampling date were used to estimate rates of fine root mass appearance and disappearance. To estimate root mass appearance for the duration of the study, all occasions of net root mass appearance between sampling dates were summed. Likewise, to estimate root mass disappearance for the duration of the study, all occasions of net root mass disappearance between sampling dates were summed. We refer to this method as 'sums of net changes in fine root mass' throughout the rest of the manuscript.

2.7. Estimating root appearance and disappearance by photographing roots

Estimates of root appearance and disappearance were derived from the repeated measurement of the individual roots in each frame. Positive changes in the length of roots between sampling dates were summed to determine gross root length appearance, and negative changes in the length of roots between sampling dates were summed to determine values of gross root length disappearance. To estimate root length appearance and disappearance for the duration of the study, the values of gross root length appearance and disappearance between sampling dates were independently summed. The values of root length appearance and disappearance were converted to units of mass with the independently derived specific lengths of fine roots from each plot.

The specific length of samples of fine roots from each plot was determined by dividing the dry mass of the samples by their fresh length. Two soil blocks were collected from the upper 15 cm of the soil on each plot

in April and stored at 4 °C until further processing, at which time roots were teased free of the blocks by hand and washed with fine streams of water. Roots and root segments with diameters greater than 2 mm were discarded while fine root branching structures with diameters of 2 mm or less down to their ultra-fine terminal ends were retained for measurement.

The total length of roots in each sample was determined by a gridline intersect method developed by Marsh (1971), which is a refinement of Newman's method of (1966). After the length of the fresh roots was determined, the roots were transferred to paper envelopes and dried to a constant weight.

2.8. Data acquisition and analysis

The four data gathering methods and the data that they generated were: (1) harvesting roots at multiple dates—root mass dynamics, (2) photographing roots at multiple dates—root length dynamics, (3) harvesting roots at one time—specific root length, and (4) data collection by other investigators to plot-scale environmental and soil data.

The root mass dynamics data were used to estimate root mass appearance and disappearance via the 'sums of net changes in root mass' procedure. The root length dynamics data were used to estimate root length appearance and disappearance using the 'sums of gross changes in root length' procedure. These estimates were converted from units of length to units of mass with specific root length data. Next, the estimates of root appearance and disappearance were compared.

3. Results

3.1. Fine root mass dynamics

The seasonal dynamics of fine root mass on all five plots are reported in units of g dry fine root mass/m^2 to
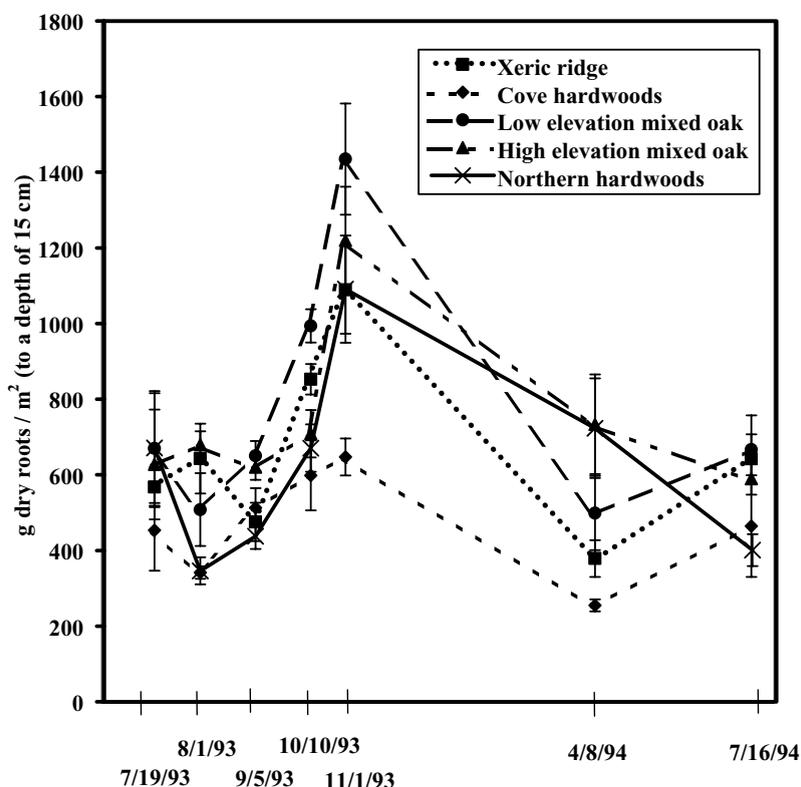

Fig. 1. Seasonal dynamics of fine root mass in five plant communities at the Coweeta Hydrologic Laboratory on seven dates. The error bars represent ±1 S.E.

a depth of 15 cm (Fig. 1). In general, fine root mass fluctuated periodically, with maximum values evident late in the growing season and minimum values prior to the growing season. The mean values of fine root mass were compared across plots and across sampling dates with a two-way analysis of variance. Multiple comparisons of means of dry root mass were conducted using the SNK test for significant differences by plot and by sampling date. Plots 3 and 4 constituted a group with high fine root mass ($P < 0.0001$), plots 1 and 5 constituted a group with lower fine root mass ($P < 0.0001$), and fine root mass on plot 2 was significantly lower ($P < 0.0001$) than all other plots.

Sampling date 10 October 1993 had significantly higher fine root mass, 1 November 1993 was second significantly highest, and all other sampling dates together had low fine root mass. These differences reflected the autumnal increase in root mass seen in Fig. 1.

3.2. Fine root length dynamics

In general, the root length values on plot 1 (xeric ridge) were much greater than the values for the other four plots (Fig. 2). There was little significant difference in fine root length within a plot during the growing season for all five plots. Significant differences between sampling dates for plots 1 and 5 over the winter occurred when a large amount of fine root length disappeared.

3.3. Average root diameter

The diameter of each root was recorded during the analysis of root images and the summary statistics of mean root diameter $\pm$ S.E. were calculated. The most notable attribute of root diameter (Fig. 3) is that roots on plot 1 were smaller (about 0.3 mm) than roots of the other plots (about 0.45–0.6 mm). These data substantiate the visual observation of a root mat of extremely fine roots on plot 1 (xeric ridge).
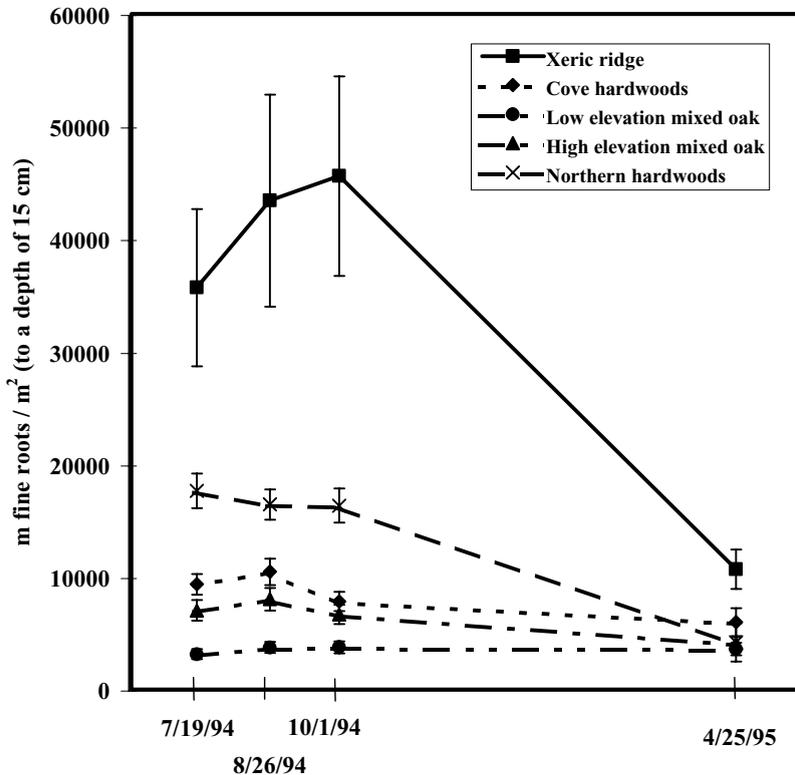

Fig. 2. Mean length density of fine roots in five plant communities at the Coweeta Hydrologic Laboratory at four dates. The error bars represent ± 1 S.E.
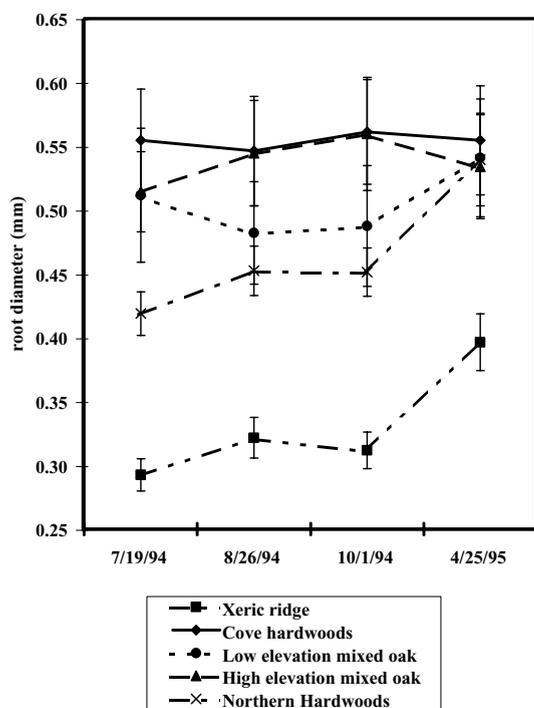
Fig. 3. Average diameter of fine roots on five plant communities at the Coweeta Hydrological Laboratory at four dates. The error bars represent ±1 S.E.

Table 1
Specific root length of fine roots (g dry mass/m fresh length) determined intensively (mass and length data from the same samples) and extensively (mass data from soil cores and root data from minirhizotron boxes)

Plot community	Mean ± S.E.	
	Intensively	Extensively
Xeric ridge	0.041 ± 0.005	0.018 ± 0.010
Cove hardwoods	0.053 ± 0.004	0.050 ± 0.151
Low elevation mixed oak	0.061 ± 0.010	0.213 ± 0.206
High elevation mixed oak	0.040 ± 0.008	0.084 ± 0.095
Northern hardwoods	0.047 ± 0.005	0.023 ± 0.028

3.4. Depth distribution of fine root length

The distribution of fine root length among the three soil depths on all five plots is portrayed in Fig. 4 (on 19 July 1994). On plot 1, xeric ridge, a majority of the root length was concentrated in the upper 5 cm of the soil. In plot 2, cove hardwoods a majority were located in 0–15 cm depth on this mesic plot. Plots 3 and 4, the high and low elevation mixed oak plots, were very similar with respect to the depth distribution of fine root length, with 35–45% in the upper depth, about 35–45% in the middle depth and 10% in the lower depth. The depth distribution of fine root length on plot 5, northern hardwoods, was different than on all other plots: about 25–40% of fine root length was in the upper depth, 30–50% in the middle depth and 20% in the lower depth.

3.5. Specific root length

The specific length of roots (g dry weight/m fresh length) from each plot is reported in Table 1. The first column of data, 'intensive', was obtained by harvest-

ing roots, determining their length with the gridline intersect method, and then determining the dry weight of those same roots. The second column of data, 'extensive', was obtained by combining root mass data determined by harvesting roots in soil cores and root length data determined by photographing roots. Specifically, an estimate of the dry mass of fine roots in a volume of soil that were harvested in July 1994 was divided by an estimate of the fresh length of fine roots present in an equal volume of soil that was photographed 3 days later.

Data from the intensive and extensive methods within plots (Table 1) were within the same order of magnitude. These data were also within 1 S.E. of each other on all five plots. The data from both methods were closest for plot 2, less close for plots 1, 4 and 5, and least close for plot 3.

The application of specific root length values in this study converted root length data to root mass in order to compare between the two. When conducting these conversions, we used only the intensively obtained specific root length data. We desired to make a proper comparison of the two, wherein each data set was obtained and analyzed independently of the other. We used only the root length appearance and disappearance data to convert all root length data sets to units of root mass. The principal benefit of photographing roots as opposed to harvesting roots is realized when estimating root appearance and disappearance over time.

3.6. Fine root appearance and disappearance

Two procedures were used to estimate fine root appearance and disappearance over time: (1) sums of
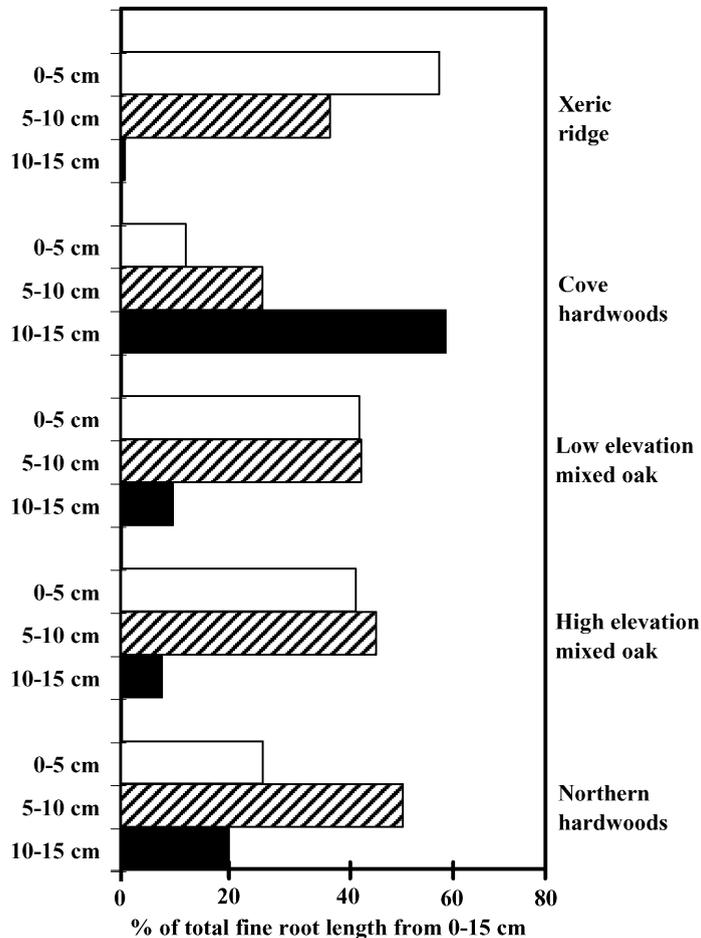
Fig. 4. Depth distribution of fine root length across three soil depths in five plant communities at the Coweeta Hydrologic Laboratory.

net changes in fine root mass and (2) sums of gross changes in fine root length. The results of the second procedure were converted to units of mass with specific root length data. The results of both these procedures are presented in the units of g fine root dry weight/m^2 plot area to a 15 cm depth per 9 months. Only 9 months of root photographs could be analyzed. We used a 9-month period, July–April.

Rates of fine root appearance and disappearance, determined by calculating the sums of net changes in fine root mass, showed the largest amount of root appearance and disappearance in plot 3 while plot 2 had the smallest amounts. The other three plots were not significantly different.

The simultaneous appearance and disappearance of fine root length is portrayed in Fig. 5 as the continuous variable in units of m fine root length/m^2 plot area. The activity of fine roots in plot 3 was less than the activity of roots in the other four plots. Plots 4 and 5 had large disappearances of roots during the winter (interval 3), while plots 1 and 2 had large disappearances earlier in the year (interval 2).

In all cases, estimates from harvesting roots had larger absolute values than corresponding estimates from photographing roots. For plots 1, 2, and 5, the difference between results from the two methods were not greatly different—less than 1 S.E. separated the pairs of two. However, in plots 3 and 4, there were
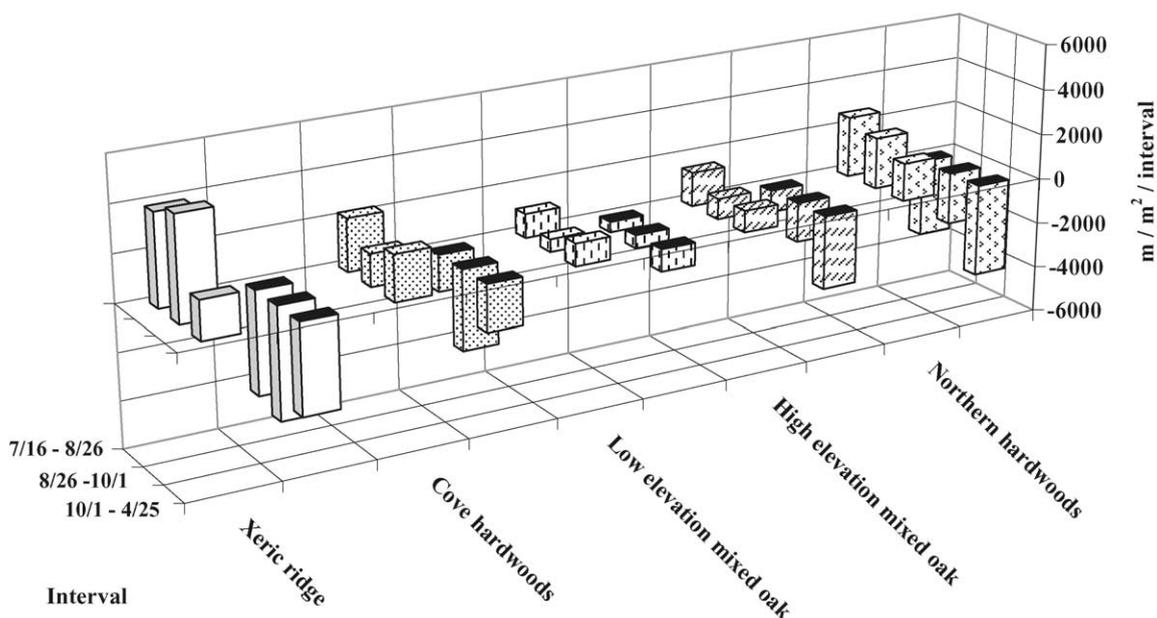
Fig. 5. Simultaneous appearance and disappearance of fine root length in five plant communities at the Coweeta Hydrologic Laboratory. Positive and negative changes in fine root length over each of the three intervals between sampling dates are shown.

larger differences between the results of the two methods. These large differences suggest that at least on the mixed oak plots, there was a methodological problem with one or both of these methods.

3.7. Related plot data comparison

A variety of data on aspects of root growth have been presented. Likewise, a variety of additional data has been collected on the five gradient plots by other researchers. Annual litterfall was highest on the mixed oak plots (3 and 4), followed by plot 1 (xeric ridge). Plots 2 and 5 (cove hardwoods and northern hardwoods), exhibited the lowest litterfall levels. Soil nitrate levels were extremely high on the high elevation plot 5 and much lower on all other plots. Soil ammonium levels were also highest on plot 5, but vary gradually through the other plots in the following order: 2, 3, 4, and 1. A well-defined soil temperature gradient exists and corresponds to the elevational gradient, with temperature decreasing with elevation. A similar trend with respect to soil moisture is not evident. The topographic position of the plot is more predictive of soil moisture than elevation. At the 20 cm depth, plot 2 has the highest soil moisture followed by plot 3, 5, 4 and

finally plot 1. Note that plots 2 and 5 are similar with respect to these parameters as are plots 3 and 4. Plot 1 remains separate.

3.8. Location of archived data

The data from this study can be found online at http://coweeta.ecology.uga.edu/webdocs/1/metatdata_home.html. These results are also reported in greater detail in Davis (1997).

4. Discussion

4.1. Consideration of the hypotheses presented in Section 1

Our specific objectives were to test five hypotheses:

(1) Fine root mass and fine root length will be higher in plots with greater annual leaf production. Only one component of this hypothesis was supported. Plots 3 and 4 exhibited the largest annual leaf production and the largest fine root mass, but the fine root length on these plots was significantly less than the fine root length on all other plots.

(2) Fine root mass and fine root length will be higher on plots with drier soils. Only one component of this hypothesis was supported. Plot 1, the driest site, did have the highest fine root length, but the values of fine root mass and fine root appearance were not significantly different from those of plots 2 and 5, the wettest sites.

(3) Fine root mass data quantified by harvesting will be positively correlated with corresponding fine root lengthy data quantified by photographing roots. First, a regression of fine root mass on each plot determined by photographing roots versus fine root mass on each plot determined by harvesting roots, all from sample collected within a 3-day period in July, gave an R^2 of 0.0023. Second, a regression of root mass appearance determined by photographing roots versus root mass appearance by harvesting provided an R^2 of 0.09. Data had been scaled to same units of length, volume and time. These results are attributed to methodological problems with minirhizotron photography and are considered later.

(4) Root growth will be initiated earlier in the year on the warmer, low elevation plots on this elevational gradient. This hypothesis is supported by data presented in Fig. 1 where net appearance of roots occurred between April and July on plots 1, 2 and 3 (lower elevation), but not on plots 4 and 5 (higher elevation).

(5) Estimates of root appearance and disappearance derived from photographing roots will be larger than estimates of root appearance and disappearance derived from harvesting roots. This hypothesis was not supported. In fact, the estimates derived from harvesting roots were larger than the estimates derived from photographing roots. This result is attributed to methodological problems with minirhizotron photography.

4.2. Plot comparisons

Through the use of ranked comparisons of the plot data the plots can be divided into three groups: plots 3 and 4, plot 1, and plots 2 and 5.

Plots 3 and 4 share many attributes. The plant communities on both plots are classified as mixed oak. Fine root mass and litterfall mass were high on these plots. Across all plots, these variables were positively correlated. This is expected, as forested sites with a large mass of leaves are more able to support the carbohydrate requirements of a large root system.

Plot 1, the xeric ridge, has two very distinctive attributes. The site is extremely xeric and the total length of fine roots on this plot is much greater than on the other plots. Across all plots, root length and soil moisture were strongly negatively correlated. The large total root length on plot 1 was mostly concentrated in the top 5 cm of the soil in an extremely dense, fibrous root mat. The proliferation of this fibrous root mat is most likely due to the xeric conditions on the plot.

Plot 2 (cove hardwoods) and plot 5 (northern hardwoods) constitute the final group. Although the plant communities on these plots differ in species composition, both of these plots are situated on mesic, north-facing terrain. Unlike plots 3 and 4, litterfall and fine root mass were low. Unlike plot 1, soil moisture was high and fine root length low. These observations are related to the strong positive correlations between litterfall and root mass and between soil moisture and root length.

4.3. 'Better' estimates of fine root appearance and disappearance

The estimates of fine root appearance and disappearance are presented here for two purposes: (1) for comparisons of the rates of root appearance and disappearance between plots and (2) for comparisons of the two methods employed to estimates these rates. To generate most accurate estimates of root appearance and disappearance on the plots, the best estimates from either root harvesting or root photography were subjected to additional calculations to scale estimates to the units of g dry roots/m^2 per year. Estimates of fine root appearance and disappearance derived from harvesting roots were expected to be less than corresponding estimates derived from photographing roots. In fact, the opposite was true (see Fig. 6). Since the estimates derived from harvesting roots were greater in all cases, they are presented as 'better' estimates.

Estimates of root appearance and disappearance that were derived from harvesting roots and utilized in comparisons between plots and between methods are presented in Fig. 7. These estimates were
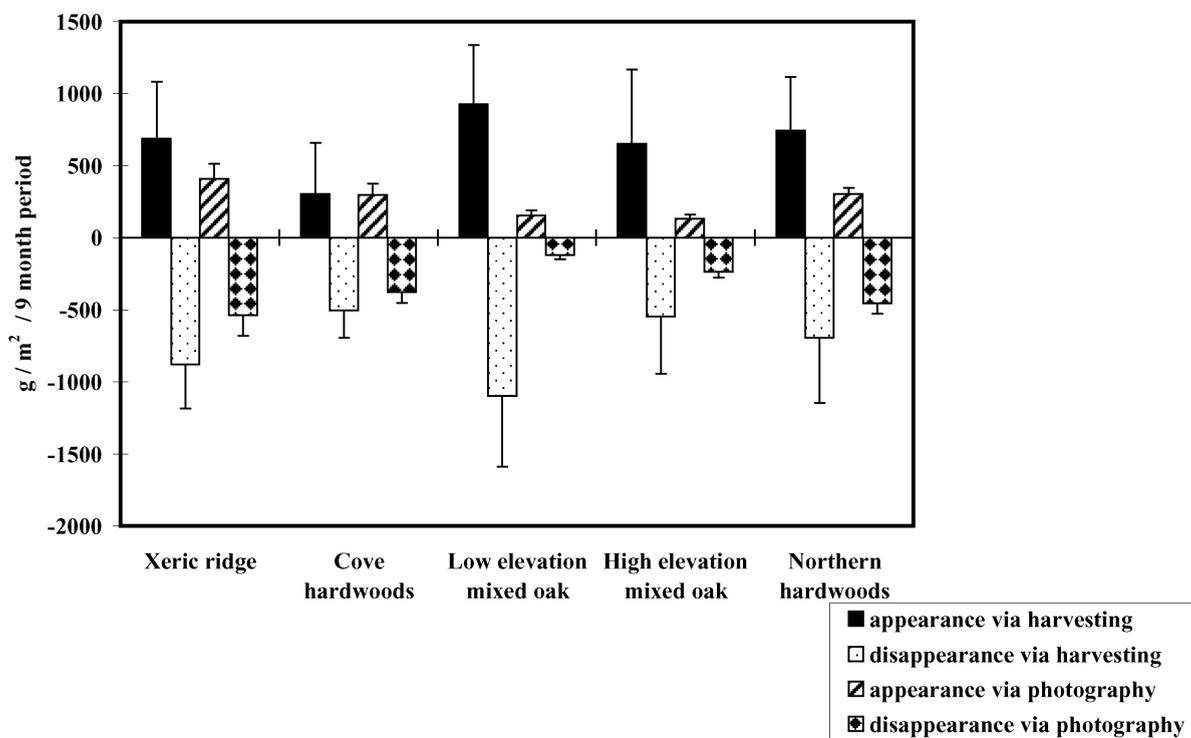
Fig. 6. A comparison of the estimates of fine root appearance and disappearance that are generated by harvesting roots and by photographing roots.

generated by extending the 'sums of net changes in root mass' calculations to include data collected 12 months after the first sampling date. These estimates are likely to be underestimates because net, rather than gross, changes in root mass between sampling periods can be detected by harvesting roots. In addition, these estimates of root appearance and disappearance are also likely to be underestimates for two other reasons: First, roots were harvested only to a depth of 15 cm, because only these soil depths were visible through the window of the minirhizotron box. Undoubtedly fine roots occur below 15 cm. Although deeper roots were not directly measured in this study, their mass can be estimated to a depth of 1m using an equation provided by McGinty (1976). To develop this equation, he harvested roots from a hardwood forest at Coweeta and estimated the percentages of root mass that were present at various soil depths. For example, he estimated that 47% of roots are present from 0 to 10 cm and 95% of all roots are present from 0 to 60 cm. According to his observations, the

mass of fine roots decreases logarithmically with depth and the equation that fits this logarithmic decline is reported as

$$\log 10y = 1.8902 - 0.25x \tag{1}$$

where x is the depth (cm) and y is the percentage of fine root mass present in the 10 cm strata from $x - 10$ to x cm.

However, when a curve is fit to the data reported in the same article (McGinty, 1976), a different equation is obtained. The linear term reported is incorrect by an order of magnitude. The correct equation follows:

$$\log 10y = 1.8902 - 0.025x \tag{2}$$

where x is the depth (cm) and y is the percentage of fine root mass present in the 10 cm strata from $x - 10$ to x cm.

With this equation, the percentage of total fine root mass that is present in the soil depth of 0–15 cm could be estimated. Approximately 60% of the total fine root mass was present in this layer. Therefore, to approach
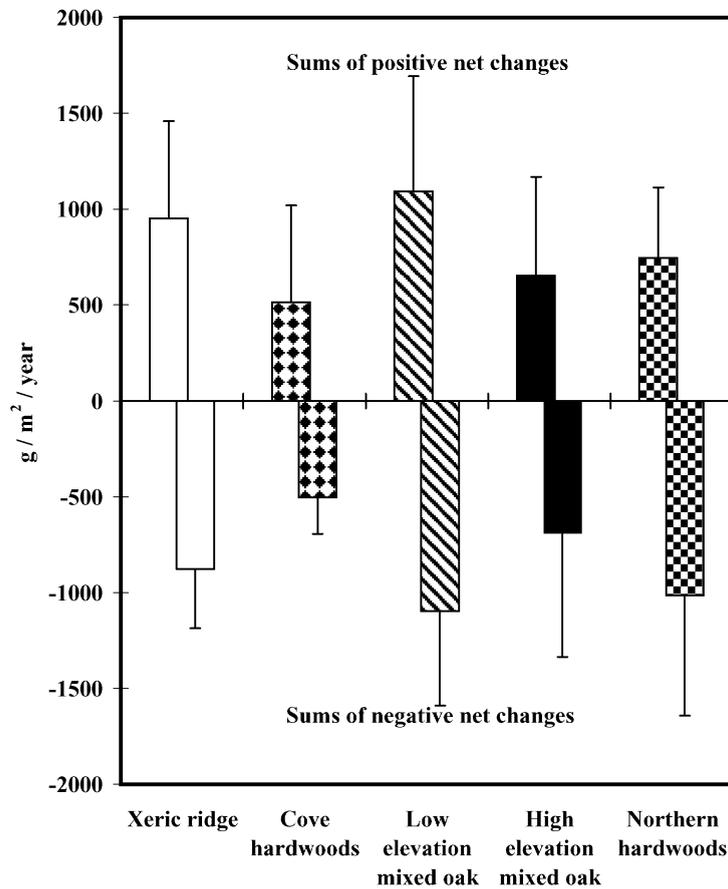
Fig. 7. Appearance and disappearance of fine root mass in five plant communities at the Coweeta Hydrologic Laboratory. The sums of net changes in harvested root mass between sampling dates were totaled over a 12-month period.

more accurate estimates of fine root mass appearance and disappearance, the data should multiplied by 1.67.

Second, it is inevitable that some roots will be fragmented and lost when root samples are sorted from soil in the laboratory. These roots could be recaptured by hydropneumatic elutriation of soil and water fractions derived from the sorting process (Smucker, 1982). Hydropneumatic elutriation was less practical in this study since fine roots were often entangled with decaying litter. As much as 30% of fine roots may be lost to fragmentation during hand sorting (J.P. Davis, unpublished data). Likewise, to approach more accurate estimates of fine root mass appearance and disappearance, the best estimates should be multiplied by 1.30. To correct for both of these factors, the best estimates should be multiplied by 2.17 (Table 2).

Table 2
Appearance and disappearance of fine root mass (g/m^2 per year)[a]

Plot community	Mean ± S.E.	
	Appearance	Disappearance
Xeric ridge	2068 ± 1100	−1906 ± 669
Cove hardwoods	1118 ± 1097	−1094 ± 411
Low elevation mixed oak	2376 ± 1299	−2383 ± 1069
High elevation mixed oak	1416 ± 1121	−1498 ± 1405
Northern hardwoods	1617 ± 802	−2203 ± 1363

[a] Sums of net changes in fine root mass over a 12-month period were calculated from soil cores taken to a depth of 15 cm. By using an equation reported in McGinty (1976), the appearance and disappearance of fine roots were estimated to the soil depth of 60 cm. These data also include corrections for roots lost to fragmentation during collection and processing.

4.4. Other modes of carbon movement below ground

The appearance and disappearance of root mass detected here are only two modes of carbon movement from plants to other soil organisms. Other modes include mycotrophy, root exudation and root respiration. If these processes are quantified for these forests, a more complete picture of carbon cycling in these ecosystems should emerge. It will also be useful in later studies to distinguish the quantity of root mass that disappears by being transferred to the soil via these processes and the quantity of root mass that disappears by being reallocated to shoot systems during the spring. Appearance and disappearance due to reallocation of carbohydrates between shoots and roots before and after winter are likely to be large components of the appearance and disappearance reported here. Much of this pulse could be attributed to the thickening, but not elongation of roots during the process of carbon reallocation from shoots to roots.

4.5. Methodological issues

One of the principal objectives of this study was to compare the results of root harvesting and root photography. As described in Section 1, root harvesting requires less sophisticated equipment and provides good estimates of root mass at one point in time. Most of the published data on root growth in forests is derived from harvesting roots. At this point in time, root photography has not been used as much as root harvesting. However, because root photography is non-destructive, and therefore permits the investigator to detect simultaneous root appearance and disappearance, it is being used with increasing frequency.

In Section 1, we hypothesized that estimates of root mass appearance and disappearance derived from root photography would be greater than estimates derived from root harvesting. They were not (see Fig. 6). We also hypothesized that data derived from harvesting roots would be correlated with the corresponding data derived from photographing roots. They were not. According to these results, the newer and more sophisticated method of root photography, as we have implemented it, cannot supplant the older and simpler method of root harvesting. This is unfortunate because implementing both methods to describe fine root

dynamics may be prohibitively expensive or time consuming.

We suspect that these problematical results can be attributed to methodological problems with root photography as we have used it. We will consider these methodological problems in light of two assumptions in our rhizotron research; (1) the presence of the observation window does not make root systems atypical and (2) the sample size is sufficiently large.

If the first assumption is false, then artificial variation in root length within and among plots may be introduced into the data collected. If the second assumption is false, then the natural variation in root length within plots may not be accurately characterized.

The first problematical result of this study is that estimates of fine root appearance and disappearance derived from photographing roots were in all cases lower than the corresponding estimates derived from harvesting roots (see Fig. 6). One explanation of this result involves the assumption that the depth of field of the photographs is exactly 2 mm. If this assumption is false, the scaling of root length data from window-scale to plot-scale would be inaccurate since this calculation involves the estimated depth of field. If the true depth of field is less than 2 mm, then the final estimates of root appearance and disappearance derived from photographing roots would be greater than we have calculated them.

The error generated by an inaccurate estimate of depth of field would be proportional to the original data and not too difficult to correct. For future studies, it would be useful to attempt to determine the depth of field experimentally. One way to do this would be to photograph roots growing against a rhizotron window and then harvest a rectangular soil block containing these same roots. The length of roots observed in the window could be calculated with the ROOTs program and the length of roots harvested in the soil block could be calculated with the gridline intersect method. The ratio of root length photographed over root length harvested could be multiplied by the thickness of the soil block to determine the depth of field visible in the photograph.

The second problematical result is that estimates of fine root mass determined by the two methods were not correlated. If the first assumption, namely that the presence of the observation window does not make root systems atypical, is false, artificial variation

between root growth near and away from the observation window is introduced. Perhaps the presence of the window may affect the growth patterns of roots growing on different plots differently.

The largest discrepancies between results derived from root harvesting and root photography are plots 3 and 4, the mixed oak plots (Fig. 6). Here, the estimates derived from root harvesting were very high and the estimates derived from root photography very low. The terminal ends of oak roots of this region are typically referred to as 'club-shaped', as they are short and thicker than sections of the root closer to the stem. These club-shaped roots are typically surrounded by an ectomycorrhizal sheath and have an enlarged cortex where hyphae can proliferate between the cortical cells. Ectomycorrhizal hyphae also extend from the fungal sheath out into the surrounding soil.

Should these types of root systems encounter the observation window of a minirhizotron box, these types of roots may not continue to grow. Roots that are not club-shaped, but are thin and fibrous (such as those of plot 1) may continue to grow when encountering a window and look like the 'pot-bound' roots of a plant that has outgrown its small pot. Under these conditions, the presence of the observation window may affect root systems such that horizontal spread of these systems and root density near the window is not representative of these parameters away from the root system.

If the second assumption, namely that the sample size is sufficiently large, is false, the natural variation between root growth near and away from the window is inaccurately characterized. The sample size of two minirhizotrons per plot may not be sufficient to characterize the variability in root growth within a plot. Large differences in root length were observed between the two boxes on many of the plots (Fig. 5). As a percentage of the largest value of average root length per frame across all dates there was an 85% difference on plot 1, a 48% difference on plot 4, a 36% difference on plot 3, a 22% difference on plot 5, and an 11% difference on plot 2. These data suggest that root growth in the plots was spatially heterogeneous. Photographs were taken at only two locations per plot while roots were harvested all around the perimeter of the plots. Thus, if root growth was spatially heterogeneous the results of the two methods may not be correlated.

Comparing interbox differences in root length, the largest differences were observed on the driest sites and the smallest intersite differences were observed on the wettest plots. This suggests that root length is more patchy in space on the drier sites and more uniform in space on the wetter plots.

One strategy to ameliorate these two problems is to use minirhizotron tubes rather than minirhizotron boxes. The effects of the minirhizotron tube on growing conditions and behavior of roots near the tube may be less than the effects of the minirhizotron box. Minirhizotron tubes have a narrower profile to be encountered by growing roots. Since minirhizotron tubes are less expensive per unit than minirhizotron boxes, more tubes could be installed on a site to better characterize the spatial heterogeneity in root length in forest soils. In addition, the use of minirhizotron tubes would also permit studies of roots growing at soil depths much deeper than depth of 0–15 cm investigated in this study. The labor required to install a minirhizotron box at deeper depths is great and the soil disturbance generated by the installation is likewise large.

Minirhizotron boxes do, however, permit the investigator to take highly magnified and highly resolved photographs of fine roots and smaller rhizosphere organisms, such as mycorrhizae and microarthropods. For studies of these organisms, minirhizotron boxes are more appropriate. But for this study, only photographs taken at the lowest magnification were analyzed to assess root growth. The scale of these photos was the same as the scale of typical video images recorded with minirhizotron tubes.

4.6. Intersite comparisons of fine roots

From a literature review of root dynamics from around the world compiled by Vogt et al. (1996), and from more recent papers, data from warm temperate broad leaved forests and from cold temperate broad leaved forests have been selected for comparison with data from Coweeta (Table 3). Data for fine root mass and turnover in the present study were smaller than those of McGinty (1976) but in the same range as values from the other studies (Table 3). Values from the present study do not include corrections for roots deeper than 15 cm or for roots lost to fragmentation during processing. If corrections were

Table 3
Fine root data collected at the Coweeta Hydrolic Laboratory compared with other sites in the eastern deciduous forest

Site	Plant community	Fine root size class	Mass (g/m^2)	Production/Appearence/ Turnover (g/m^{-2} yr.$^{-1}$)	Reference
Coweeta	xeric ridge	<2.0 mm	668	953	Davis, 1997
Coweeta	cove hardwoods	<2.0 mm	468	515	Davis, 1997
Coweeta	low elevation mixed oak	<2.0 mm	793	1095	Davis, 1997
Coweeta	high elevation mixed oak	<2.0 mm	765	652	Davis, 1997
Coweeta	northern hardwoods	<2.0 mm	657	745	Davis, 1997
Coweeta	hardwoods	<2.5 mm	2722	600	McGinty, 1976
Oak Ridge, TN	yellow poplar	<5 mm	680	N/A	DeAngelis et al., 1981
Oak Ridge, TN	oak-hickory	<5 mm	790	N/A	DeAngelis et al., 1981
Bartlett Exp. Station, NH	hardwoods	<3.0 mm	1246	N/A	Safford, 1974
Harvard Forest	hardwoods	<3.0 mm	610	410–1140	McClaugherty et al., 1982
Hubbard Brook	hardwoods	<2.0 mm	471	254	Fahey and Hughes, 1994

made to values from the present study by multiplication by 2.17, the values would be closer to those of McGinty (1976). McGinty's ''fine roots'' were larger than ''fine roots'' in the present study. There is substantial variability between root system attributes between sites, but there are insufficient data to indicate if variability is due to local or regional variability. Cross-site studies of roots involving sampling of numerous sites per region with identical methods would be very useful in understanding variations in root attributes at multiple scales in the deciduous forests of eastern North America.

4.7. Roots, the elevational gradient and environmental heterogeneity

Do differences in elevation along a gradient determine community properties and ecosystem processes at Coweeta? This is one of the principal questions posed at the inception of the Coweeta gradient study (Knoepp et al., 2000). The present study of roots is a small part of the gradient study and the central question is, do differences in elevation along a gradient determine the size and activity of root systems at Coweeta?

The terrain of each of the plots can be described with reference to two abiotic parameters of elevation and topographic position (ridge, slope or cove). Of these two, topography appears to have a greater effect on root system attributes. Plots 1 (ridge topography), 2 (cove topography) and 3 (slope topography) are within 43 m of each other in elevation, but exhibit striking differences with respect to root system attributes. Plots 3 and 4 differ by 136 m in elevation, but root system attributes on these plots are very similar. These two plots are situated on slope topography, and are within the same type of plant community.

The only observation that suggests that elevation has an influence on root system activity is that root appearance is greater than root disappearance in the early spring on the lower three plots only (Fig. 1), most likely due to temperature differences along the gradient.

Since the variations in root system attributes reported here are not closely linked to elevation, the results of this study are best considered in the more general context of studies of ecosystem heterogeneity, rather than studies of ecological gradients.

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References

Davis, J.P., 1997. Fine root dynamics along an elevational gradient in the southern Appalachian Mountains, USA. M.S. Thesis in Botany. University of Georgia, Athens, GA, 83 pp.

Day, F.P., Phillips, D.L., Monk, C.D., 1988. Forest communities and patterns. In: Swank, W.T., Crossley Jr., D.A. (Eds.), Forest Hydrology and Ecology at Coweeta. Springer, New York, pp. 141–149.

DeAngelis, D.L., Gardner, R.H., Shugart, H.H., 1981. Productivity of forest ecosystems studied during the IBP: the woodlands data set. In: Reichle, D.E., (Ed.), Dynamic Properties of Forest Ecosystems. IBP 23. Cambridge University Press, London, UK, pp. 567–672.

Fahey, T.J., Hughes, J.W., 1994. Fine root dynamics in a northern hardwood forest ecosystem, Hubbard Brook Experimental Forest, NH. J. Ecol. 82, 533–548.

Fogel, R., 1985. Roots as primary producers in below-ground ecosystems. In: Fitter, A.H., et al. (Eds.), Ecological Interactions in Soil. Blackwell Scientific Publications, Oxford, UK, pp. 23–36.

Freese, F., 1962. Elementary Forest Sampling. Agriculture Handbook No. 232. US Department of Agriculture, Washington, DC.

Hendrick, R.L., Pregitzer, K.S., 1992. The demography of fine roots in a northern hardwood forest. Ecology 73, 1094.

Hendrick, R.L., Pregitzer, K.S., 1996. Temporal and depth-related patterns of fine root dynamics in northern hardwood forests. J. Ecol. 84, 167–176.

Knoepp, J.D., Crossley Jr., D.A., Coleman, D.C., Clark, J., 2000. Biological indices of soil quality: an ecosystem case study of their use. For. Ecol. Manage. 138, 357–368.

Marsh, B., 1971. Measurement of length of random arrangements of lines. J. Appl. Ecol. 8, 265–267 (short communication).

McClaugherty, C.A., Aber, J.D., Melillo, J.M., 1982. The role of fine roots in the organic matter and nitrogen budgets of two forested ecosystems. Ecology 63, 1481–1490.

McGinty, D.T., 1976. Comparative root and soil dynamics on a white pine watershed and in the hardwood forest in the Coweeta basin. Ph.D. Dissertation. University of Georgia, Athens, GA.

Newman, E.I., 1966. A method of estimating the total length of root in a sample. J. Appl. Ecol. 3, 139–145.

Radford, A.E., Ahles, H.E., Bell, R.B., 1968. Manual of the Vascular Flora of the Carolinas. University of North Carolina Press, Chapel Hill, NC.

Raich, J.W., Nadelhoffer, K.J., 1989. Belowground carbon allocation in forest ecosystems: global trends. Ecology 70, 1346–1354.

Safford, L.O., 1974. Effect of fertilization on biomass and nutrient content of fine roots in a beech-birch-maple stand. Plant and Soil 40, 349–363.

SAS Institute Inc., 1989. SAS/STAT User's Guide, Version 6, 4th ed., vol. 1. SAS Institute Inc., Cary, NC, USA.

Smucker, A.J.M., 1982. Quantitative separation of roots from compacted soil profiles by the hydropneumatic elutriation system. Agron. J. 74, 500–503.

Swank, W.T., Crossley, D.A., Jr., 1988. Introduction and site description. In: Swank, W.T., Crossley, D.A. (Eds.), Forest Hydrology and Ecology at Coweeta. Springer, New York, pp. 3–16.

Vogt, K.A., Vogt, D.J., Palmiotto, P.A., Boon, P., O'Hara, J., Asbjornsen, H., 1996. Review of root dynamics in forest ecosystems grouped by climate. Plant and Soil 187, 159–219.

Whittaker, R.H., 1956. Vegetation of the Great Smoky Mountains. Ecological Monographs 26, 1–80.