Fine Root Productivity and Dynamics on a Forested Floodplain in South Carolina

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ABSTRACT

The highly dynamic, fine root component of forested wetland ecosystems has received inadequate attention in the literature. Characterizing fine root dynamics is a challenging endeavor in any system, but the difficulties are particularly evident in forested floodplains where frequent hydrologic fluctuations directly influence fine root dynamics. Fine root (≤3 mm) biomass, production, and turnover were estimated for three soils exhibiting different drainage patterns within a mixed-oak community on the Coosawhatchie River floodplain, Jasper County, South Carolina. Within a 45-cm-deep vertical profile, 74% of total fine root biomass was restricted to the upper 15 cm of the soil surface. Fine root biomass decreased as the soil became less well drained (e.g., fine root biomass in well-drained soil > intermediately drained soil > poorly drained soil). Fine root productivity was measured for 1 yr using minirhizotrons and in situ screens. Both methods suggested higher fine root production in better drained soils but showed frequent fluctuations in fine root growth and mortality, suggesting the need for frequent sampling at short intervals (e.g., monthly) to accurately assess fine root growth and turnover. Fine root production, estimated with in situ screens, was 1.5, 1.8, and 0.9 Mg ha^{-1} yr^{-1} in the well-drained, intermediately drained, and poorly drained soils, respectively. Results from minirhizotrons indicated that fine roots in well-drained soils grew to greater depths while fine roots in poorly drained soils were restricted to surface soils. Minirhizotrons also revealed that the distribution of fine roots among morphological classes changed between well-drained and poorly drained soils.

PRODUCTIVITY OF FORESTED WETLAND ECOSYSTEMS has been the focus of numerous studies. Most commonly, productivity is estimated using aboveground parameters such as litterfall and stemwood production (Brinson et al., 1980; Conner and Day, 1992; Conner et al., 1993; Conner, 1994; Megonigal et al., 1997). Many investigators have acknowledged, however, that failure to include belowground data will seriously underestimate forest ecosystem productivity (Vogt et al., 1986a; Day and Megonigal, 1993). It has been suggested that fine root production accounts for up to 75% of total net primary production (NPP) in some forests (Nadelhoffer and Raich, 1992). Similar to aboveground foliage, large amounts of fine roots die annually and can contribute a quantity of litter similar in magnitude to foliar litter (McClaugherty et al., 1984). Fine root dynamics, therefore, represent a significant source of energy and nutrient flow through forested systems, particularly for those systems that are subject to periodic disturbances that increase the frequency and extent of fine root turnover.

Forested wetlands are considered among the most dynamic of all forested ecosystems, and vegetation productivity within these systems has been addressed in many studies (Mitsch and Gosselink, 1993; Megonigal et al., 1997; among others). However, only a few investigations have characterized belowground productivity and the processes that contribute to fine root dynamics in forested wetlands (Powell and Day, 1991; Megonigal and Day, 1992; Day and Megonigal, 1993; Jones et al., 1996). Day and Megonigal (1993) suggested that omission of belowground data might cause previously accepted relationships between flooding and vegetation to be less accurate. Results from their study indicated that flooding reduced belowground allocation although aboveground production might remain similar across flooding regimes. Similarly, Brinson (1990) has summarized reports indicating that belowground production may be much more sensitive to changes in soil oxidation–reduction potential than aboveground production. The latter observation agrees with findings from upland systems (Vogt et al., 1993) in relation to the highly responsive nature of fine roots to relatively subtle changes in microenvironment. It is clear that to understand the critical productivity function of forested wetlands, additional data on belowground production and the factors controlling fine root dynamics are needed.

The lack of root data associated with studies of forested ecosystems is often noted (e.g., Vogt et al., 1986b; Megonigal et al., 1997; Lockaby and Walbridge, 1998). The aversion to conducting root studies involves inherent difficulties associated with methodologies for studying root systems. Most methods for estimating standing stocks of root biomass and/or production involve three tasks: excavation, washing, and weighing (Caldwell and Virginia, 1989); the former two are particularly labor-intensive and time-consuming. The common method for estimation of root turnover requires sequential excavation to identify temporal fluctuations in biomass that may be associated with production and mortality (Symbula and Day, 1988; Caldwell and Virginia, 1989). A major challenge to this approach is identifying the appropriate intervals at which to conduct sampling to accurately detect fluctuations in fine root biomass (i.e., production and mortality). Vogt et al. (1986b) and Kurz and Kimmins (1987) stressed that sampling should be conducted at both peak and trough periods of fine root biomass to avoid underestimation of production and mortality. Such timing is not as complicated for systems in which fine root growth and mortality occur predict-

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Abbreviations: ID, intermediately drained (drainage condition); NPP, net primary production; PD, poorly drained (drainage condition); WD, well-drained (drainage condition).

ably. In the upland north–temperate hardwood forest studied by Burke and Raynal (1994), for example, root growth was largely governed by temperature. In southern floodplain forests, however, production and mortality are governed not only by temperature but also by periodic flood events that occur at irregular and unpredictable intervals. This prompts the need for more intensive sampling efforts at more frequent intervals—requiring considerably greater labor expenditure. The development of reliable sampling procedures that are less labor-intensive and time-consuming would be extremely helpful for characterizing belowground dynamics, particularly in southern forested floodplains.

While the processes controlling NPP in forested wetlands are complex, it is generally accepted that hydroperiod is the dominant controlling influence (Mitsch and Gosselink, 1993). There is disagreement, however, as to whether the flood events that are typical of forested wetlands represent a stress or a subsidy to vegetation in these systems (Conner and Day, 1976; Mitsch and Ewel, 1979; Megonigal et al., 1997). For example, Burke et al. (2000b) found continuously flooded stands were more productive than periodically flooded stands. In contrast, Megonigal et al.'s (1997) recent synthesis of studies characterizing productivity of numerous forested wetlands concluded that flooding tended to reduce aboveground NPP. Both suggested, however, that their conclusions considered only aboveground components, and that incorporation of belowground data would greatly improve our understanding of the productivity of entire wetland ecosystems.

It is important to consider not only the immediate effects of flooding on belowground productivity and turnover, but also the indirect effects resulting from many years of flood events, which shape floodplain landscapes and create a myriad of microsites within a single floodplain. It is common for an individual floodplain to exhibit a variety of soil microsites resulting from floodwater encroachment and recession (Jones et al., 1996). The vegetation mosaic created by the pattern of microsites within a single floodplain confounds the characterization of vegetation productivity, both above- and belowground, with each assemblage often exhibiting distinct production and allocation patterns. Often, such microsites differ in terms of soil chemistry, bulk density, and more dramatically, drainage characteristics. These characteristics in turn can play a significant role in fine root growth, production, and turnover.

The objectives of this study were to (i) determine the vertical distribution of roots in three floodplain soils with different morphologies and drainage properties, (ii) estimate and compare production of fine roots within each of these soils, and (iii) examine the feasibility of two recent methods for estimating fine root production and phenology within a floodplain forest. Specifically, we hypothesized that (i) most of the fine root biomass would be in the uppermost soil horizons; (ii) fine root biomass would be lower in soils that were less well drained; (iii) fine roots would have a more shallow distribution in soils that were less well drained; and (iv) net fine root production would be reduced in soils that were less well drained.

METHODS

Study Site

This study was conducted in a bottomland oak community adjacent to the Coosawhatchie River, Jasper County, South Carolina, on land owned by Westvaco Corporation (approximately 31° N, 81° W). Vegetation in the study area ranged from mixed oak at the higher portion of the study site to laurel oak–sweetgum–maple at the lower portion. The mixed oak stand had >30% of the basal area in *Quercus phellos* L., *Q. nigra* L., and *Q. falcata* var. *pagodaefolia* Ell., with some *Pinus taeda* L. in the overstory. The laurel oak–sweetgum–maple stand had >40% of the basal area in *Q. laurifolia* Michx., *Liquidambar styraciflua* L., and *Acer rubrum* L. These stand descriptions were based on a vegetation classification and ordination study and vegetation map by Burke et al. (2000a).

During the 1970s, USDA soil survey staff mapped the study area as a single unit: the Santee Association. A more intensive recent survey using 100 locations systematically located revealed and mapped nine distinct soil series throughout the floodplain (Murray et al., 2000). The site at which our study was located contained three soil series. According to the recent soil survey (Murray et al., 2000), the highest part of the site was classified in the Coosaw series (loamy, siliceous, semiactive, thermic Aquic Arenic Hapludults) with silicious, sandy, and sandy loam surface layers exhibiting well-developed horizons and formed in older terrace sediments. The intermediate elevation at the site was in the Meggett series (fine, mixed, active, thermic Typic Albaqualfs). The lower, more poorly drained part of the site was classified in the Brookman series (fine, mixed, superactive, thermic Umbric Endoaqualfs). These soils have thick, black loamy surface layers and dark gray clayey subsoils.

Preliminary observations of the study site revealed a tendency for floodwaters to remain above the soil surface for different lengths of time among the three soil series. The Coosaw series drained most rapidly followed by the Meggett series and the Brookman series, respectively. As some authors point out, surface flooding and hydroperiod represent only a fraction of actual hydrodynamics in floodplain ecosystems—the majority occurs below the soil surface and thus is not readily observable (Day et al., 1988; Day and Megonigal, 1993; Megonigal et al., 1997). Therefore, it was reasonable to assume that similar differences occurred belowground on this site and that these differences manifested themselves even in the absence of surface flooding. It was hypothesized that these differences were driven by differences in drainage conditions among the three soil series, and that this drainage gradient would be distinct even in the absence of flooding above the soil surface. The primary focus of this study was the difference in belowground production among the three soils resulting from this drainage differential. It should be recognized that the shift in vegetation, driven by the difference in drainage and water tolerance of the species present, as described above would have some effects on belowground processes such as fine root production, distribution, phenology, and nutrient dynamics. We make no attempt in this study to eliminate this source of variability.

Soil Characteristics

Five parallel transects (each 110 m long and 20 m apart) were installed and soil and fine root data were collected along each (Fig. 1). The transects were installed across at least two of the soil series to test fine root response in relation to different soil drainage conditions. Soil temperature was monitored using six portable temperature recorders (Onset Computer Corporation, Pocasset, MA), each of which was placed just

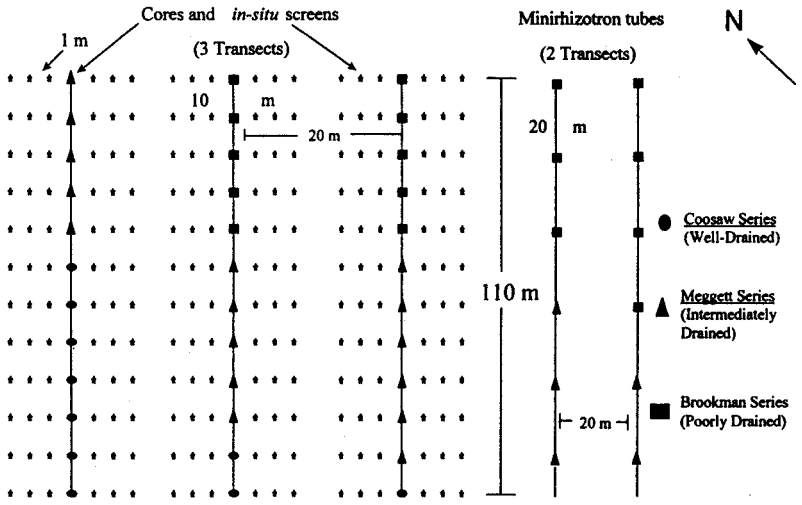

Fig. 1. Transect and sample point layout for soil cores, in situ screens, and minirhizotron tubes in a mixed-oak community on the Coosawhatchie River floodplain, Jasper County, South Carolina.

below the soil surface, at 20-m intervals, along one of the transects. Steel welding rods were installed at the same locations to track monthly patterns of soil oxidation and Fe reduction (Bridgham et al., 1991). To complement welding rod measurements, soil coring was conducted to determine the depth to redoximorphic features (i.e., mottling, gleying). Bulk density measurements were taken in November 1995 using a 5-cm diam. bulk density probe to determine if the Coosaw, Meggett, and Brookman soil series differed in terms of bulk density. Exchangeable soil Ca, Mg, and K were determined on a Perkin-Elmer 373 Atomic Absorption Spectrophotometer (Perkin-Elmer, Norwalk, CT) following a double-acid extraction (Mehlich, 1953), and soil P was determined according to Watanabe and Olsen (1965). Soil pH was determined using a 1:1 soil/water ratio.

Fine Root Distribution

The term *fine roots* is defined here as those roots having a diameter ≤3 mm. Although other studies have defined fine roots as being <2 mm, the 3-mm designation was chosen because a natural division seems to occur at approximately 3 mm since roots larger than this usually have secondary xylem thickening and tend to be perennial (McClaugherty et al., 1982).

Fine root distribution was sampled along three of the transects, each containing 12 sample points, 10 m apart (Fig. 1). At each sampling point, three soil cores from each of three depths (0–15, 15–30, and 30–45 cm) were extracted using a 5-cm diam. bucket auger, for a total of 108 samples in March 1995. Sampling was confined to the top 45 cm of soil, since previous studies in similar systems have indicated that approximately 66% of fine roots may be restricted to that zone (Brown, 1990; Farrish, 1991). Samples were promptly placed in coolers, returned to the lab, and refrigerated at 4°C to maintain live roots until they could be analyzed (within 1 mo). Soil cores were washed and sieved using a hydropneumatic root elutriator (Gillison's Variety Fabrication, Benzonia, MI). Root length was estimated using the line-intercept method (Newman, 1966) as described in Bohm (1979). After fine root length was determined, samples were oven-dried to a constant mass at 70°C, and dry mass was recorded for each depth.

Fine Root Dynamics and Phenology

Two methods were employed to assess fine root phenology and growth—in situ screens and minirhizotrons. While both methods have been used in upland systems (Fahey et al., 1989; Hendrick and Pregitzer, 1992), to our knowledge, their applicability in floodplain systems had not been determined.

In Situ Screens

Melhuish and Lang (1968, 1971) have described a relationship between the number of intersections that growing roots make with a plane of known area and estimated fine root length. In this study, six screens (Phifer fiberglass [Phifer, Tuscaloosa, AL] 18/14 holes in^{-2}, 7.6 × 15.2 cm), 1 m apart, were placed (using a sharpshooter or narrow, elongated spade) in the soil in April 1995 on a line perpendicular to the existing transect at each sampling point (Fig. 1). Screens were oriented randomly with respect to aspect (i.e., N, S, E, or W) to prevent sampling bias in direction of root growth. Screens were inserted at 45° angles in the soil to correct for anisotropic root growth (Brown and Roussopoulos, 1974; Fahey and Hughes, 1994). One screen from each point along each transect was randomly selected for sampling during the first week of May, June, July, August, and November 1995 and April 1996. Screens were removed with a post hole digger and returned to the laboratory under refrigeration to be processed and analyzed as described above for soil core samples. Roots were separated from the screen and soil by hand since mechanical techniques are not appropriate for this task. The following procedure was used to estimate fine root length and biomass production for each screen:

$$I_{cm2} = (I/SA) \quad [1]$$

$$L_{cm3} = 2I_{cm2} \quad [2]$$

$$B = L_{cm3}b \quad [3]$$

$$G = B107\,700 \quad [4]$$

where I_{cm2} = no. of root intersections cm^{-2} screen, I = no. of intersections roots make with each screen, SA = surface area of a screen (cm^{-2}), L_{cm3} = root length cm^{-3} soil, 2 = constant used to express length cm^{-2} of screen on volume basis (cm^{-3}), B = biomass (g) of root cm^{-3} of soil, b = biomass (g) of each cm of root, G = root biomass (g) m^{-2} of soil surface to 10.77-cm depth, 107 700 = expansion factor to achieve total biomass m^{-2}. See below for explanation of 2, B, b, G, and 107 700.

The number of intersections that fine roots made with each screen was counted (I). Based on the area sampled by each screen (SA = 116.13 cm^2), the number of intersections made

with each cm^2 of the screen could be estimated (Eq. [1]). Melhuish and Lang (1968, 1971) demonstrated that random lines intersecting a cube, regardless of volume, would have a mean length of 0.6667 (the units corresponding to the volume of the cube under consideration). Multiplying this constant by the number of intersections that the lines make with one face of the cube (I_{cm2}), multiplying by six to consider all faces of the cube, and dividing by 2 to account for each line intersecting the cube twice yields the equation $L_{cm3} = 2 \times I_{cm2}$ [e.g., $L_{cm3} = (6 \times 0.6667 \times I_{cm2})/2$]. Therefore, Melhuish (1968) and Melhuish and Lang (1968, 1971) suggested that doubling the number of intersections that random lines make with one face of a cube (a plane) will accurately reflect the length of those lines within that cube. Their research using roots of cotton plants suggested that this approach would be useful for determining root length per unit volume of soil by simply examining one face (e.g., a plane or screen) of the cube. However, this approach assumes the following: (i) roots grow in a straight line for an infinitely short distance on either side of the plane; (ii) roots are growing randomly in all angular directions; and (iii) roots grow in all directions and at all places along the plane with equal probability (Melhuish and Lang, 1968).

In their studies, Melhuish (1968) and Melhuish and Lang (1968, 1971) discussed root length. While root length has been an important variable to consider, primarily in agronomic situations, root biomass is a preferred response variable for forested ecosystems since it enables interpretation of nutrient pools. Biomass per unit of volume of soil can be estimated by utilizing a simple length-to-biomass conversion. To accomplish this, a subsample of roots intersecting each screen at every sampling interval was taken. Roots were separated from the screens and length was estimated using the line-intercept method (Newman, 1966). Roots were then oven-dried to a constant mass, and total mass was divided by total length for each sample to yield a constant for biomass per cm of root at each sampling period (b). Using the estimates of root length per unit volume of soil (L_{cm3}) derived from Eq. [2], biomass per unit volume of soil was estimated using Eq. [3]. The expansion factor (107 700) expressed estimates on a square-meter basis (Eq. [4]) (to an approximate depth of 10.7 cm) and was derived using the following: 100 cm × 100 cm × 10.77 cm (vertical depth of screens in soil).

Virtually no dead roots were observed with in situ screen samples. It is likely that dead, and perhaps brittle, fine roots were lost during extraction of the screens. Mortality, therefore, was not directly measured but inferred from significant decreases in fine root biomass across sampling intervals.

Fine root N concentration was determined by thermal combustion using a Perkin-Elmer 2400 CHN-analyzer on subsamples taken from fine roots intersecting screens at each time period. Fine root P concentration was determined colorimetrically using an ammonium vanadate solution (Jackson, 1958) on a HCl extract following dry-ashing at 500°C for 4 h. Fine root N and P contents were determined by multiplying fine root N and P concentration by biomass as estimated with in situ screens for each time period.

Minirhizotrons

The minirhizotron technique was also used to monitor fine root dynamics on the study site. Six clear acetate butyrate tubes (5-cm inside diam., 5.7-cm outside diam., 1.8-m length) were placed 20 m apart on each of the two remaining transects, for a total of 12 tubes (Fig. 1). Tubes were installed during June 1995, when the water table was well below the soil surface. Installation of the tubes when the soil was saturated may have resulted in inadequate seating and stability, thereby adversely influencing root growth estimates. Tubes were inserted at 45° to limit the potential for roots to grow along the soil/tube interface (Bragg et al., 1983). Aboveground portions of the tube were wrapped in duct tape and capped to prevent entry of light and water. Care was taken to anchor tubes to ensure that the fluctuating water table did not push tubes out of the soil. Standard metal conduit (5-cm diam.) was hammered to a depth of ≈1.5 m and anchored to each tube with a clamp and duct tape.

A fiberoptic periscope video camera (Bartz Technology, Santa Barbara, CA) was used to monitor root growth once each month from August 1995 through July 1996. The camera was equipped with a locking shaft to permit consistent, incremental lowering of the camera through tubes to a depth of 30 cm. Each time the camera was lowered, the number of root intersections with a predetermined grid (the left and bottom sides of the monitor, in this case) was counted on the video monitor and recorded for that depth. Roots were identified as live or dead based on their appearance and placed into one of three morphological categories. Roots that appeared brown and exhibited characteristics of secondary xylem thickening were classified as Brown. Roots that were translucent or white and appeared succulent were classified as White. Extremely small-diameter (<0.5 mm) fine roots were classified as Hair-like. All roots classified as Brown or White were larger than 0.5 mm in diam. Fine root length was determined for the field counts using a variation of the line intercept method (Newman, 1966; Bohm, 1979; Buckland et al., 1993). The Bartz camera was also equipped with an ultraviolet (UV) light source that is designed to permit identification of live vs. dead roots in situ. According to Wang et al. (1995), live roots will fluoresce when exposed to UV light. This feature is designed to eliminate subjectivity in distinguishing live vs. dead roots.

In addition to quantifying fine root length in the field using the video monitor, a video recording was made one time each in August and September 1995 and every other month thereafter through July 1996. Recorded video images were then examined in the laboratory to test whether more intensive analyses were feasible. Video images were digitized to computer using the Snappy Video Snapshot (Play Inc., Rancho Cordova, CA), which connects to a parallel port on an IBM-compatible personal computer. The Snappy Video Snapshot provided a low-cost alternative (approximately $100) to expensive, hardware-intensive frame-grabbers. Each time the video camera was lowered, a new depth, or field of view, was recorded on video tape. Each of these images was individually digitized as a frame on which subsequent analyses could be conducted. On each frame, roots were classified as described above for field counts. An image-analysis software package (Optimas 6.0, Optimas, Houston, TX) was used to trace the perimeter of sufficiently large-diameter roots (Brown and White) and estimate their diameter and planar surface area. Although automation is possible with this software, tracing was conducted manually because the heterogeneity of the soil matrix in this system made automation impractical. Due to their small diameter (e.g., <0.5 mm), the perimeter of Hair-Like roots could not be traced; rather a single line was drawn along the length of these structures. Calibrated according to the area being analyzed (13.5 × 18 mm), Optimas returned the surface area of roots classified as either Brown or White and the length of the Hair-Like roots. Roots classified as Brown or White were treated as cylinders and the lengths of these structures were estimated using the diameter and surface area estimates generated by Optimas (length = surface area / $2\pi r$). Tracing was conducted manually because the heterogeneous soil background made automation difficult and subject to error.

Statistical Analyses

Differences in fine root response variables (biomass, length, production) among soil series, depth, and sample date were identified using the Student's *t*-test (PROC TTEST, SAS Institute, 1991). Student's *t*-test was chosen rather than ANOVA because the study design was based on one experimental unit for each soil series. Specifically, Student's *t*-tests were used within each soil series to compare differences in fine root biomass and necromass among depths as well as differences within depths among soil series. Also, production of fine root biomass was estimated using in situ screens and was compared between soil series. Fine root length, as estimated using the minirhizotron method, was compared using Student's *t*-test between soil series within each depth and fine root morphological category. Using the same approach, fine root length among depths and morphological categories were also compared within each soil series. Differences between means were considered statistically significant at $\alpha = 0.10$. The less-conservative 90% level of significance was chosen due to the highly variable nature of fine root data.

RESULTS

Soil Characteristics

Although bulk density and soil temperature data were collected during this study, no differences in these variables were detected among drainage categories. Welding rod measurements taken several times throughout the study indicated that the depth to reduced soil conditions was lower in the Brookman series compared with the Meggett series at every sampling period (Table 1), and these differences were statistically significant in October 1995 and April 1996. Although welding rod data were not available for the Coosaw series, soil coring to determine the depth to mottling or gleying was conducted in May 1997 and confirmed that the depth to Fe reduction was greatest in this series. Each comparison between the Brookman series and the other two series was statistically significant, indicating less well-drained conditions in the Brookman series (Table 1). Results from both the welding rod measurements and the soil-coring efforts confirmed that subsurface hydrology differed among the three soil series and revealed the hypothesized drainage differences, which decreased in the order Coosaw, Meggett, and Brookman. Hereafter, these series will be discussed in terms of their drainage conditions: well-drained (WD), intermediately drained (ID), and poorly drained (PD), respectively. These terms are used as descriptors relative to each other and do not refer to any uniformly defined soil-drainage categories or classifications.

Analysis of mineral elements in the three drainage categories indicated that the concentration of extractable P was greatest in the order: WD > PD > ID. Concentration of extractable K increased as soil drainage decreased such that WD < ID < PD. The patterns of extractable Ca and Mg were identical; concentration increased as successively less well-drained soils were encountered (WD < ID < PD, Table 1).

Table 1. Descriptive characteristics of a well-drained (WD), an intermediately drained (ID), and a poorly drained (PD) soil within a mixed-oak community on the Coosawhatchie River floodplain, Jasper County, South Carolina. Standard errors of the means are in parentheses.

	Depth to reduction† (cm)		
		ID	PD
Date		Meggett Series	Brookman Series
Aug. 1995		64 (9)a‡	48 (5)a
Oct. 1995		19 (7)a	8 (1)b
Nov. 1995		37 (6)a	17 (3)a
Apr. 1996		24 (6)a	8 (1)b
June 1996		55 (9)a	22 (5)a
	Depth to mottling/gleying (cm)		
	WD	ID	PD
Date	Coosaw Series	Meggett Series	Brookman Series
May 1997	56 (7)a	21 (5)a	3 (3)b
	Chemistry (mg kg^{-1})§		
	WD	ID	PD
Parameter	Coosaw Series (0–18 cm)	Meggett Series (0–15 cm)	Brookman Series (0–18 cm)
pH	4.5	4.4	4.7
P¶	30.06	8.18	10.10
K	31.20	58.50	89.70
Mg	19.20	43.20	189.60
Ca	54.00	86.00	960.00

† Measured with steel welding rods.
‡ Means with same lowercase letter in a row are not statistically different ($\alpha = 0.10$).
§ Murray et al. (2000).
¶ This study.

Fine Root Distribution

In March 1995, the majority of fine roots (74%) in this mixed-oak community were located in the upper 15 cm of soil, compared with 17% in the 15- to 30-cm depth and 9% in the 30- to 45-cm depth, respectively (Fig. 2). Fine root biomass tended to decrease with decreasing drainage and depth (Fig. 2). Because the majority of fine roots were located in the upper 15 cm

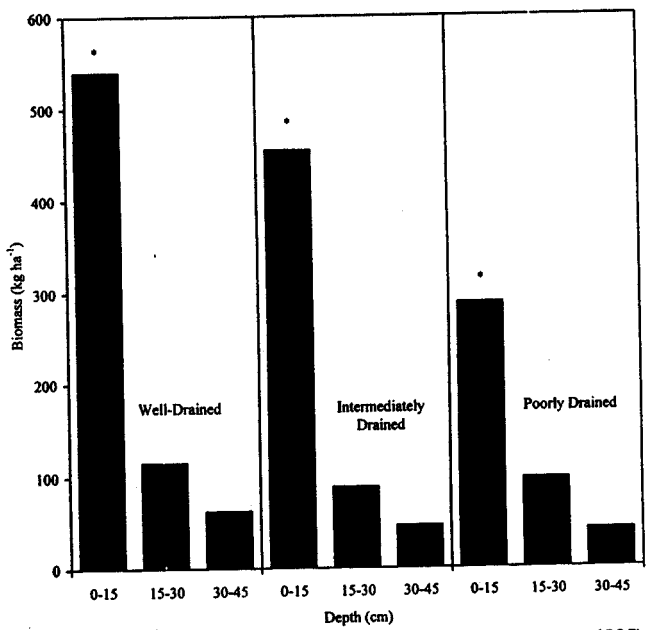

Fig. 2. Depth distribution of fine root biomass (taken in March 1995) in a mixed-oak community within the Coosawhatchie River floodplain, Jasper County, South Carolina. An asterix denotes a significant difference between fine root biomass among depths within each drainage category ($\alpha = 0.10$).

Table 2. Monthly and annual fine root production estimates (kg ha^{-1}) for a well-drained (WD), an intermediately drained (ID), and a poorly drained (PD) soil, to a depth of 11 cm, as measured with in situ screens for a mixed-oak community on the Coosawhatchie River floodplain, Jasper County, South Carolina. Fine root growth was assumed to be zero at the time in situ screens were installed.

	WD	Monthly NPP†	ID	Monthly NPP	PD	Monthly NPP
May 1995	84.10a‡	84.10§**	91.83a	91.83**	115.76b	115.76**
June 1995	941.18ab	857.08**	808.92a	717.09**	937.12b	821.36**
July 1995	604.56a	−336.62	603.99a	−204.93	533.43a	−403.69
Aug. 1995	1202.54a	597.98**	1604.99a	1001.00**	700.11a	166.68
Nov. 1995	1736.24a	533.7	1608.99a	4.00	1510.16a	810.05
Apr. 1996	1624.45b	−111.79	1529.73b	−79.26	793.46a	−716.70
Fine root NPP (yr^{-1})¶		2072.86		1813.92		1913.85
Fine root NPP (yr^{-1})#		1539.16		1809.92		937.12

† NPP represents net primary production.
‡ Lowercase letters compare means between drainage categories for each month.
§ ** indicates statistically significant positive net increases in fine roots over previous month.
¶ Calculation of annual fine root NPP by summing increases in fine roots over the previous month.
# Calculation of annual fine root NPP using only statistically significant increases in fine roots over previous month (Fairley and Alexander, 1985; Kurz and Kimmins, 1987; Publicover and Vogt, 1993).

of soil on the study site, subsequent efforts were directed toward fine roots in these surface soils.

Fine Root Dynamics and Phenology

In Situ Screens

Monthly estimates of fine root growth from in situ screen samples are presented in Table 2. Statistical comparisons of fine root growth since installation of in situ screens indicated few significant differences among the three drainage categories for each month. There was little difference between the WD and ID soils in terms of fine root production, and these differences were never statistically significant (Table 2). However, in April 1996, fine root production was significantly greater in the WD and ID soils compared with production in the PD soil. Only in May 1995 did fine root production in the PD soil exhibit the greatest fine root production among the three drainage categories. In June 1995, fine root production in the PD soil was significantly greater than in the ID soil, but not in the WD soil.

Changes in nutrient content throughout the year are illustrated in Fig. 3 and indicate the pool of each element contained in fine roots at each sampling interval. In terms of N content, the only significant differences among drainage categories were observed between the PD and ID soils. Only in June 1995 did the PD soil exhibit significantly higher fine root N content than the ID soil. The pattern observed was largely driven by the biomass of fine roots because few differences in N concentrations were observed among the drainage categories (data not shown, see Baker, 1998). Exceptions to this occurred in June 1995 when fine root N concentration was significantly greater in the PD soil compared with the WD and ID soils, and in November 1995 when fine root N concentration was significantly greater in the WD soil compared with the PD soil (Baker, 1998). Generally, fine root P content decreased such that WD > ID > PD, except during August 1995 (Fig. 3). Similar to patterns observed for N content, differences in P content among drainage categories were driven largely by the biomass of roots sampled (Baker, 1998). Ratios of N to P suggest subtle differences among the three drainage categories in terms of fine root litter quality but a consistent pattern across all sample dates was maintained such that ratios decreased in the order PD > ID > WD (4.96, 3.54, and 2.60, respectively—data not shown).

Minirhizotrons

Field Counts. Field counts using the minirhizotron revealed a clear periodicity of fine root growth over the 12-mo sampling period (Fig. 4). Results are presented as root length density per unit of minirhizotron tube surface (mm cm^{-2}), similar to that reported by Day et

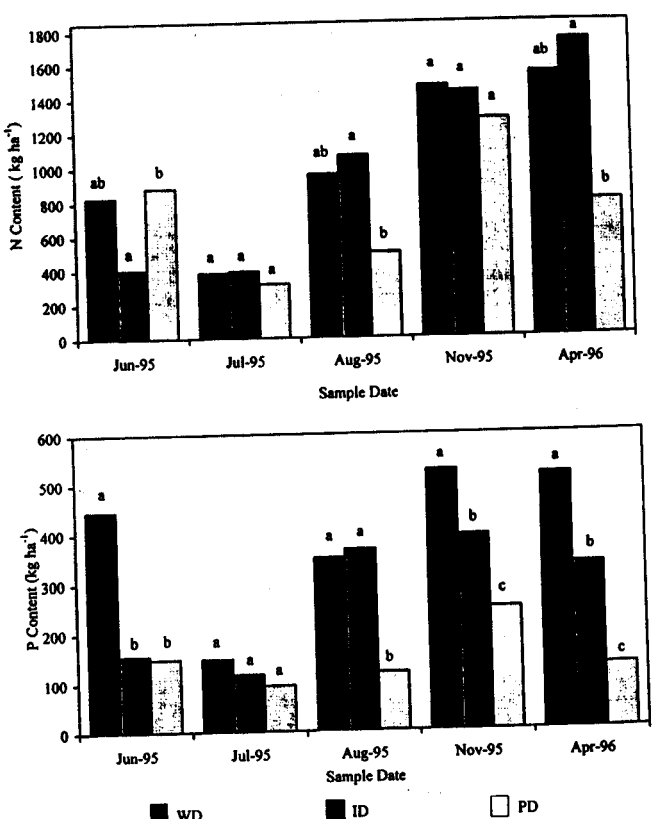

Fig. 3. Fine root N (top panel) and P (bottom panel) contents in surface soil of well-drained (WD), intermediately drained (ID), and poorly drained (PD) soils in a mixed-oak community on the Coosawhatchie River floodplain, Jasper County, South Carolina. Different lowercase letters denote significant differences ($\alpha = 0.10$) among fine root nutrient concentrations within each drainage category for each sample date.

al. (1996). However, our determination of root length differed in that we estimated root lengths based on the number of intersections with a grid on the screen in the field rather than through measurement of digitized images. Fine root length decreased from August 1995 to January 1996 with the exception of one short growth interval from October to November 1995. During the months of January 1996 through April 1996, fine root length fluctuated mildly but exhibited a brief increase from January to February 1996. As indicated on the May 1996 sample date, fine root growth accelerated during April 1996 and continued to increase in length until the final sample period in July 1996. With the exception of August and December 1995, the ID soil contained significantly higher root length density than the PD soil (Fig. 4).

One of the advantages of using the minirhizotron method is the opportunity to examine root growth and morphological changes in situ. Relative changes in the proportion of each morphological category can be monitored over time and with regard to particular environmental variables, which may influence the distribution of roots among morphological classes. For the purpose of illustration, Fig. 5 compares the proportional distribution of fine roots encountered in the three morphological classes between the ID and PD soils. Within both drainage categories, the vast majority of fine root length was in the Hair-Like category. However, a greater proportion of fine roots in the PD soil fell into either the White or Brown classification.

Digitized Images. Similar to results from field counts, root length density across the entire depth sampled (0–30 cm) was statistically higher in the ID soil than in the PD soil for each sample period during which video images were recorded (data not shown). Preliminary analysis, as well as the results from the soil core samples collected in March 1995, suggested that frequency and distribution of fine roots began to decline beyond a certain depth. Therefore, the original 30-cm sampling depth was divided into two separate strata, 0 to 15 cm and 15 to 30 cm, for further analyses. Root length density was greater in the surface horizons than in the lower stratum for each drainage category, and these differences were statistically significant in all months except August 1995, for the PD soil (Table 3). Statistical analysis showed that within the 0- to 15-cm depth, the ID soil contained greater root length density than the PD soil for every sample period and these differences were statistically significant except in May 1996 (Table 3). In the lower depth (15–30 cm), however, the PD soil contained higher root length density in August and September 1995. Apart from these two dates, the ID soil exhibited significantly higher root length density in the other months.

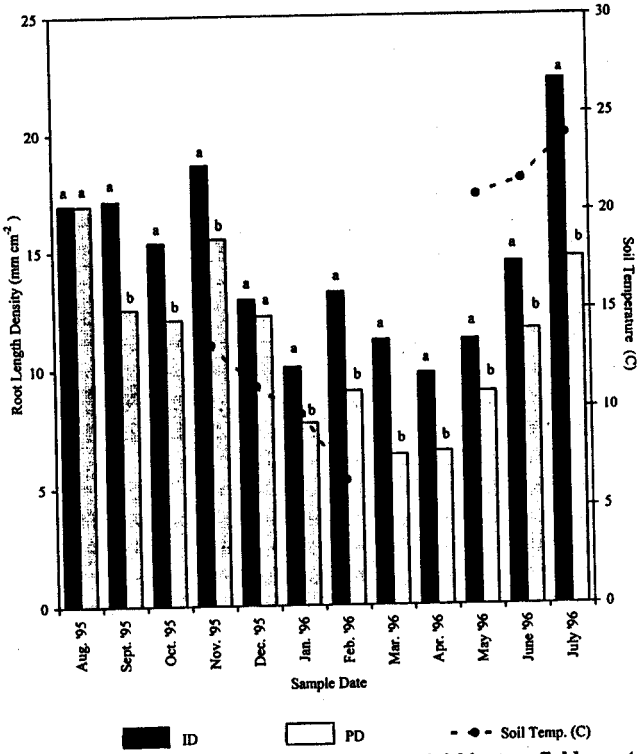

Fig. 4. Fine root length as determined from minirhizotron field counts for intermediately drained (ID) and poorly drained (PD) soils in a mixed-oak community on the Coosawhatchie River floodplain, Jasper County, South Carolina. Sample dates are listed on x-axis and actually measure fine root growth during the previous month. Different lowercase letters denote significant differences ($\alpha = 0.10$) in root length density between drainage categories for each sample date. Soil temperature represents average between the two drainage categories since no significant differences were detected between the two.

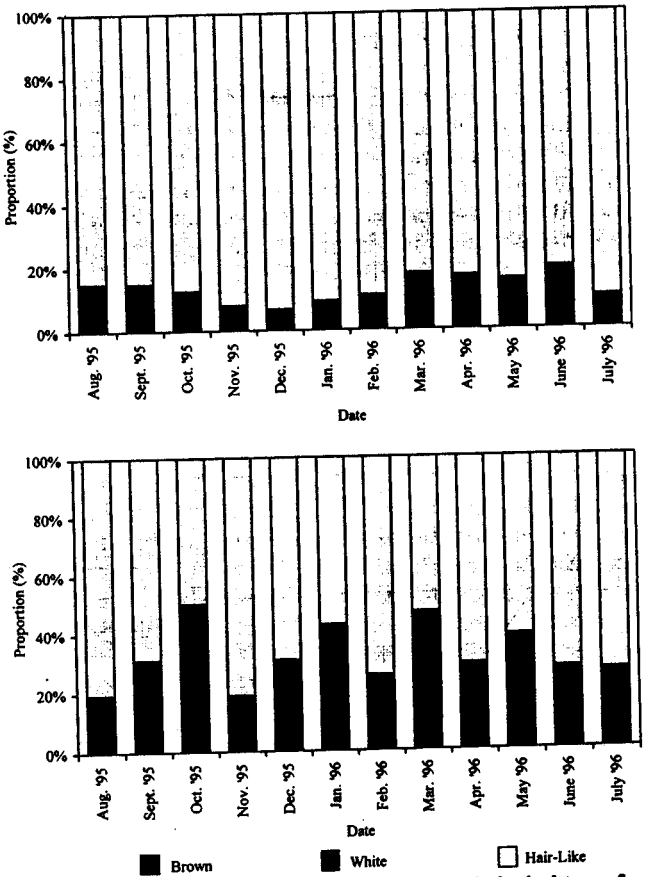

Fig. 5. Proportional distribution of fine root morphological types for intermediately drained (ID, top panel) and poorly drained (PD, bottom panel) soils in a mixed-oak community on the Coosawhatchie River floodplain, Jasper County, South Carolina. Proportions based on root lengths.

Table 3. Statistical comparison of root length density between an intermediately drained (ID) and a poorly drained (PD) soil within two depth strata using digitized images from minirhizotron sampling, Coosawhatchie River floodplain, Jasper County, South Carolina. Standard errors of the means are in parentheses.

	Root length density					
	0–15 cm depth			15–30 cm depth		
Date	ID	PD	$P > F$	ID	PD	$P > F$
	— mm cm^{-2} —			— mm cm^{-2} —		
Aug. 1995	5.63 (0.89)	3.11† (0.37)	0.001	1.76 (0.33)	1.92† (0.36)	0.001
Sept. 1995	4.92 (0.93)	2.37 (0.31)	0.001	1.20 (0.32)	1.35 (0.27)	0.001
Nov. 1995	5.47 (0.96)	3.19 (0.51)	0.001	1.09 (0.26)	0.46 (0.14)	0.030
Jan. 1996	2.81 (0.51)	1.84 (0.29)	0.001	0.73 (0.17)	0.27 (0.10)	0.001
Mar. 1996	4.01 (0.81)	1.83 (0.34)	0.001	0.60 (0.18)	0.17 (0.08)	0.001
May 1996	3.86 (0.76)	2.68 (0.56)	0.125	0.72 (0.21)	0.27 (0.07)	0.095
July 1996	8.33 (1.58)	5.46 (0.94)	0.037	2.35 (0.51)	0.60 (0.13)	0.035

† Indicates the only instance where root length density was not significantly greater in 0 to 15-cm strata.

DISCUSSION

Soil Characteristics

Even though welding rod data were collected only intermittently for the ID and PD soils, and drainage data for the WD soil were based on soil cores, the hypothesized drainage pattern among the three soil series existed and was consistent such that WD > ID > PD, in terms of the depth to Fe reduction on the welding rods. It should be noted that measurements of the depth to Fe reduction on welding rods provide only an approximate estimate of water-table fluctuations between sampling intervals and do not produce estimates as reliable as more intensive, well-monitoring data. Similarly, measurements based on soil morphological characteristics such as depth to mottling and gleying record longer-term hydrologic properties of soils.

All three soils exhibited low pH (Table 1). It is puzzling that soil-P concentration did not follow the gradient in drainage conditions (Table 1). Under successively waterlogged conditions, the concentration of P typically increases as Fe and Al complexes with P are reduced, thereby making the latter more available (Mitsch and Gosselink, 1993). Soil data in this study suggested the opposite trend, however, namely that P decreased as soil drainage decreased (WD > PD > ID, Table 1). It is probable that differences in the origin and genesis of each of the three soils, particularly the WD soil, accounted for the disparity in the observed pattern, but this was not tested.

Fine Root Distribution

In a bottomland hardwood system in Louisiana, Farrish (1991) found that 64% of fine root biomass occurred in the top 20 cm of soil. Although Farrish (1991) sampled fine roots to a much greater depth, results from our study agree that the majority tend to be concentrated in the surface soils. Similarly, Symbula and Day (1988) and Powell and Day (1991) found greater fine root biomass in surface soils than at lower depths in the Great Dismal Swamp. Fine roots are the structures primarily responsible for acquisition of water and nutrients (Marshall and Waring, 1985; Farrish, 1991) and under conditions of comparatively low moisture, plants may allocate more resources to the construction of fine roots (Powell and Day, 1991; Marschner, 1995). The decrease in fine root biomass associated with poorer drainage observed in this study supports the hypothesis that fine root biomass increases along a gradient of decreasing soil moisture. However, it is unclear from our results whether the lower fine root biomass can be attributed to differences in vegetation across drainage categories, reduced growth in response to adequate moisture, hypoxia under poorly drained and thus poorly aerated conditions, or vegetation nutrient status.

Fine Root Dynamics and Phenology

In Situ Screens

Several points need to be made regarding the differences between the work described by Melhuish and Lang (1968, 1971) and its application here. Their earlier study was conducted on roots of cotton grown in a barrel of soil, and made the assumptions discussed above in the Methods section. The present study was conducted in a natural environment and may not adhere as stringently to the assumptions made by Melhuish and Lang (1968, 1971). However, it was assumed for this study that roots grew in all directions as well as in angular directions. To capture growth in all directions, screens were oriented randomly throughout the study site. It was also assumed that roots grew at all places along the screen with equal probability, despite the fact that the majority of growth occurred in a fairly narrow band at the top of the screens. In two subsequent studies, Lang and Melhuish (1970) and Melhuish and Lang (1971) discussed the implications for their technique in populations of roots that exhibit anisotropy and offered an anisotropy parameter to be used in calculating root length under those conditions. Because the degree to which roots were anisotropic could not be determined in the present study, this parameter was not used and our results are qualified by assuming that root growth is not only isotropic, but also fulfills the assumptions set forth in Melhuish and Lang's (1968, 1971) earlier studies.

Although several approaches for calculating production from changes in fine root biomass between sampling intervals have been discussed in the literature, only statistically significant increases in fine root standing stock between sample periods will be discussed in this study (Fairley and Alexander, 1985; Kurz and Kimmins, 1987; Symbula and Day, 1988; Publicover and Vogt, 1993). Several authors have contrasted this approach against simply summing all positive differences. For the purpose of comparison, we present estimates based on all positive increases between sampling intervals (Table 2).

Using only statistically significant increases in fine root biomass between sampling intervals, annual fine root NPP was 1539, 1810, and 937 kg ha^{-1} yr^{-1} to a depth of 10.77 cm for the WD, ID, and PD soils, respectively (Table 2). Inclusion of all increases, not just those that were statistically significant, would have resulted in considerably higher estimates of annual fine root NPP, and may have overestimated actual production. It is difficult to compare fine root production estimates reported in the literature. While most studies use similar diameter class designations, they vary in the use of a wide range of soil depths, time periods, and methods of calculating production. However, estimates from this study are within the ranges reported for other wetland systems. Jones et al. (1996) reported that fine root (≤5 mm) production to a depth of 20 cm ranged between 1030 and 6320 kg ha^{-1} yr^{-1} in a maple–gum community along a low-order blackwater stream in Alabama using the sequential coring technique. Symbulla and Day (1988) reported higher fine root (≤5 mm) production to a depth of 40 cm in a maple–gum community in the Great Dismal Swamp in Virginia; 5970 to 7830 kg ha^{-1} 11 mo^{-1} and 6450 to 8860 kg ha^{-1} 11 mo^{-1} using the implant bag and sequential coring techniques, respectively. Using the sequential coring technique, Powell and Day (1991) compared fine root (≤5 mm) production to a depth of 40 cm between a mixed-hardwood community (3540–9890 kg ha^{-1} yr^{-1}) and a maple–gum community (590–910 kg ha^{-1} yr^{-1}).

Based on estimates derived from in situ screens, fine roots experienced several pulses of growth and mortality throughout the year (Table 2). While it is possible that the decreases in fine root biomass observed in July 1995 and April 1996 could be the result of spatial variability in fine root biomass among sampling points, the fact that fine roots in all three drainage categories experienced mortality during the same months suggests that this was related to other edaphic factors. The decrease in biomass observed for the three drainage categories between June and July 1995 cannot be explained with the information presented here. However, these months are typically dry in this region and precipitation through July 1995 was 17.70 cm below normal, based on historic data collected at the nearest National Oceanic and Atmospheric Administration (NOAA) station in Ridgeland, SC. Drought has been implicated in root mortality by earlier studies (Fogel, 1983). However, it has also been suggested that fine roots would respond to such conditions with increased growth (to a point) rather than the observed mortality (Keyes and Grier, 1981; Marschner, 1995).

In this floodplain community, it is unlikely that drought during the study was severe enough to significantly increase fine root mortality. Also, although contraction of heavy soils during extended dry spells has been shown to discourage fine root elongation (Marschner, 1995), this does not explain the observed mortality since the in situ screens were not installed deep enough to contact soils with appreciable clay content (see soil descriptions in Methods). It has been speculated that plants may respond to dry conditions by shifting root growth to greater depths where water may be more abundant (Owensby et al., 1994). If this is true, the in situ screens may not receive new intersecting roots and may, in fact, lose fine roots as resources are allocated to greater depths. It should be noted that virtually no dead fine roots were observed intersecting in situ screens in this study, perhaps due to loss during extraction or rapid decay. This method did not, therefore, directly estimate fine root mortality—rather it was implied in the reduction of quantities observed between sample periods.

Just as it is likely that fine root mortality during the dormant season accounted for some of the decrease in observed fine root biomass in April 1996, it is also likely that poorly drained conditions led to fine root mortality (Vogt et al., 1993; Marschner, 1995). Welding rod data for April 1996 suggest that the water table was within 8 cm of the soil surface within the PD soil during the preceding months (Table 1). Mortality under poor drainage is also supported by the gradient of fine root biomass estimated with the in situ screens: the WD soil maintained the greatest biomass followed by the ID soil and finally the PD soil (Table 2). By far, the greatest mortality was inferred in the PD soil.

Conversely, it also could be speculated that the relative position of the PD soil among the drainage categories in terms of fine root growth in May and June 1995 may be the result of its closer proximity to moisture during these dry months. Root growth that occurred in the PD soil as a result of plants searching for moisture may have reversed the gradient of fine root growth among the drainage categories from what was observed during wet months. In June 1996, however, the WD soil exhibited the greatest fine root biomass and this phenomenon may be the result of fine root growth exploiting a greater volume of soil for moisture uptake. Fine roots in the ID and PD soils may not have responded similarly because conditions may not have been as droughty in those soils.

These results indicate that fine roots in floodplain forests may experience several pulses of production and mortality annually. This phenomenon suggests that studies of fine root production and mortality must consider more intensive sampling intervals than would be appropriate for other, less dynamic systems. Approaches that measure fine root standing stocks only twice each year may not reveal actual increases and decreases in fine root biomass and may, therefore, seriously underestimate belowground production in floodplain systems (Vogt et al., 1986a; Kurz and Kimmins, 1987). The maximum–minimum method for estimating fine root production and mortality would not be appropriate in the mild climates of the southeastern United States, particularly in floodplain forests where dynamic hydrologic processes contribute substantially to the production and turnover of fine roots.

Although no significant patterns emerged with respect to fine root N contents determined from samples intersecting in situ screens, P content of fine roots appeared to be more sensitive to soil drainage differences. Although P availability generally increases as soils be-

come progressively waterlogged and reduction of Fe and Al phosphates occurs (Mitsch and Gosselink, 1993), fine root P content in these soils do not appear to respond to this predicted P fertility gradient. Results from this study suggested that P cycling through fine root turnover is greatest along the drainage gradient in the order: WD > ID > PD.

Although blackwater rivers are usually associated with low primary productivity, net productivity in this forested floodplain was among the highest reported for floodplain forests in the South (Burke et al., 2000b). This may be due, at least in part, to underlying marl deposited during interglacial periods (Murray et al., 2000) that contribute to the relatively high P and Ca economy on the site. In a community that would normally be considered P-limited, the Coosawhatchie site appears non-deficient in this element. It is not clear what effect, if any, this may have on the patterns of fine root P concentration observed among the three drainage categories under consideration.

Low ratios of N/P in fine roots that intersected in situ screens suggested that this floodplain was not P-limited. Generally N/P ratios >15 suggest that the latter element is limiting and microbial populations that utilize detritus will tend to immobilize P during decomposition (Vogt et al., 1986b). On the nearby blackwater Ogeechee River in Georgia (approximately 100 km west), Lockaby et al. (1996) found that P was immobilized during decomposition of litterfall exhibiting N/P ratios greater than 15. In the present study, N/P ratios of fine roots in all three drainage categories remained well below this threshold value. It is interesting to note, however, that fine root N/P ratios increased as drainage decreased.

Minirhizotrons

Ultraviolet illumination failed to allow us to distinguish between live and dead roots in situ. This problem has been identified in at least one other study (Wang et al., 1995). Despite numerous field trials throughout the course of this investigation, ultraviolet light did not reliably create fluorescence with roots that were known to be alive. Therefore, analyses that relied on ultraviolet determination of live and dead roots were abandoned due to lack of confidence in the procedure. Very few obviously dead roots were observed, and in most cases these were difficult to distinguish from the soil matrix. An excellent review of the minirhizotron method, particularly estimating root mortality, is presented in Hendrick and Pregitzer (1996).

Both the minirhizotron field counts and the digitizing procedures revealed seasonal fluctuations in root length density (Fig. 4). Fine root growth and mortality were temporally similar to the patterns observed for roots sampled with in situ screens (Table 2). Although water contamination and launch failures with temperature recorders precluded temperature estimates for some months, the trend illustrated in Fig. 4 suggests that root elongation covaried with soil temperature.

Although minirhizotrons were installed only on the ID and PD soils, a pattern similar to that observed with in situ screens was evident: the better-drained Meggett series maintained greater root length density than the poorly drained Brookman series. As several authors point out, it is not clear whether plants attempt to acquire resources (i.e., water and nutrients) by exploiting more thoroughly a given volume of soil or by exploring a greater volume of soil (Rogers et al., 1994; Day et al., 1996). This question is difficult to answer with the minirhizotron since only small areas can be sampled. Results in this study suggested that fine roots tend to grow deeper during dry months, which supports the hypothesis that these roots explore a greater volume of soil in search of resources. Comparisons of the ID and PD soils suggested that roots in the ID soil exploited a greater soil volume than roots in the PD soil. It is unclear why the PD soil contained greater root length density of White and Brown roots than the ID soil. It would be expected that plants growing in the PD soil would be less likely to invest in more permanent structures, given the tendency for these soils to become inundated.

Although similar patterns were obtained using both field counts and digitized images for gathering minirhizotron data, actual estimated root length densities differed between the two approaches. Despite good correlation (correlation coefficient, 0.78) between root length densities between field counts and digitized images, estimates from field counts were consistently higher than results from analysis of digitized images. It is inevitable that the soil matrix contains inconsistencies and voids that present challenges to viewing roots at the tube/soil interface. During field sampling, the camera operator has the ability to use the focusing mechanism to improve the field of view. Once digitized, however, video images from minirhizotron samples are two-dimensional and the ability to improve the field of view is lost. This phenomenon may have contributed to the discrepancies between the two approaches and resulted in higher estimates for field counts. Other studies have reported good agreement between root lengths estimated from field counts and digitized images (e.g., $r^2 = 0.74$; Burch, 1995). That study was conducted in an upland system where less organic matter and lighter-colored, more homogenous soil would provide a better background against which roots could be observed during both procedures. This complication may have been exacerbated in this study by a frequently fluctuating water table that often obscured images and may have shifted soil materials around the minirhizotron tubes.

CONCLUSIONS

As we hypothesized, in a 45-cm soil profile within this floodplain oak community, most (74%) of the roots were restricted to the upper 15 cm of the soil. Our results also supported the hypothesis that fine root biomass would be lower in poorly drained soils compared with more well-drained soils. Whereas well-drained soils contained higher fine root biomass in their surface depths compared with poorly drained soils, the poorly drained soils contained a higher proportion of fine root biomass in their surface depths compared with deeper strata.

Fine root production was within the range reported in other bottomland hardwood studies. Although fine root NPP was greater in the well-drained and intermediately drained soils using only statistically significant increases in biomass between sampling intervals, our results did not clearly support the hypothesized decrease in fine root production with decreasing drainage. Although mortality was not estimated directly, relative mortality inferred from in situ screens and minirhizotrons suggested that greater quantities of fine roots turn over annually in well-drained soils, despite the fact that mortality appeared to be proportionally higher, and perhaps more frequent, in poorly drained soils. In this landscape, fine roots in well-drained soils may contribute greater quantities of higher-quality substrate to soil communities than poorly drained soils.

Both the minirhizotron and in situ screen techniques revealed seasonal phenologies in relation to soil temperature and, more significantly, soil drainage class. Both techniques appear to be useful tools for monitoring fine root distribution and production and for estimating mortality in frequently flooded, hydrologically dynamic floodplain ecosystems. Because these methods are less time- and labor-intensive than traditional belowground sampling techniques, they permit the more frequent sampling required in these systems. However, it should be stressed that both techniques sample only small volumes of soil and are subject to the high spatial and temporal variability inherent in fine root measurement. Therefore, increasing the number of samples taken or points measured should be considered during their use. The application of these techniques may be most useful for making comparisons among treatments since there is, as yet, no reliable standard with which to compare actual production and mortality estimates (Hendricks et al., 1993).

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