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Fine root dynamics across a chronosequence of upland temperate deciduous forests

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Abstract

Following a major disturbance event in forests that removes most of the standing vegetation, patterns of fine root growth, mortality, and decomposition may be altered from the pre-disturbance conditions. The objective of this study was to describe the changes in the seasonal and spatial dynamics of fine root growth, mortality, and decomposition that occur following removal of standing forest vegetation. Four upland temperate deciduous forest stands in southern Indiana, USA were chosen for this study. The ages of the stands, as represented as the number of growing seasons since forest overstory removal, were 4, 10, and 29 years at the beginning of the study in 1995. A mature stand, ≈ 80 –100 years since last harvest, was chosen to represent the pre-harvest conditions. A combination of soil cores and ingrowth cores were used to assess stand-level rates of fine root growth, mortality, and decomposition. Results show that fine root growth increases significantly after harvesting, but declines as the stand matures. In all stands, fine root mortality and decomposition are nearly equal to or greater than fine root growth. Fine root growth in the A horizon (0–8 cm) is significantly greater than in the B horizon (8–30 cm) in the 4, 29, and 80–100-year-old stands. In the 4- and 10-year-old stands fine root growth in the A horizon peaks earlier in the year than in the B horizon. Fine root biomass recovers rapidly in these upland hardwood stands following forest removal due to high rates of fine root growth; however, the distribution of fine root growth between the A and B soil horizons differs from pre-harvest conditions during the first 10–30 years. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Fine roots; Chronosequence; Forest regeneration; Soil horizons

1. Introduction

Disturbances that remove the forest overstory, such as clear-cut harvesting, can greatly alter fine root dynamics. Rapid recovery of fine root biomass to

pre-disturbance levels has been found in some studies (Raich, 1980; Yin et al., 1989) while other studies have shown a gradual increase in fine root growth and biomass up to at least 20 years following forest removal (Berish, 1982; Arunachalam et al., 1996). In addition, the seasonal activity and spatial distribution of fine roots are variable in most forest ecosystems (Kuhns et al., 1985; Joslin and Henderson, 1987; Hendrick and Pregitzer, 1993; Burke and Raynal,

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1994; Büttner and Leuschner, 1994). Production and maintenance of fine root systems can utilize a significant portion of the carbon fixed by plants and the nutrients taken up by the fine roots (McClaugherty et al., 1982; Joslin and Henderson, 1987). Understanding the changes in fine root dynamics after harvesting and during stand regeneration is important to make assessments of forest and soil productivity.

To estimate changes in fine root dynamics at various stages of forest development, some studies have employed a chronosequential approach to investigate similar forest stands of different age at the same time. This approach allows for a direct comparison of different-aged stands during the same time period, but effects due to stand age may be confounded with spatial differences in stand locations. Within a physiographic region and forest type, ecological classification schemes have shown that site productivity and species composition of mature forests are related mainly to aspect, slope, and soil properties (Spies and Barnes, 1985; U.S. Department of Agriculture, 1995). Site disturbance and management history can also play an important role (Van Lear and Jones, 1987). If care is taken to minimize differences in these characteristics among stands, the chronosequence approach can yield specific inferences about the biology and ecology of developing forests.

The objective of this study was to investigate the influences of stand age, soil depth, and time of year upon fine root growth, mortality, and decomposition across a chronosequence of upland oak-hickory forests in the Central Hardwood Region of the United States. Specific hypotheses included: (1) rates of fine root growth, mortality, and decomposition will increase following forest removal but decline as the stand reaches maturity; (2) fine root growth will be greater than mortality following forest removal; and (3) fine root growth, mortality, and decomposition will be concentrated in the A horizon following forest removal but become more uniformly distributed as stand age increases. Rapid recovery of fine root biomass to pre-disturbance levels following harvesting requires high rates of fine root growth. The abundance of herbaceous and annual plants that typically dominate temperate forest ecosystems during the first years after harvest tend to exhibit high rates of fine root turnover, as well. Overall increases in fine root biomass, however, would require that fine root growth

exceed fine root mortality in the long-term. Fine roots of tree seedlings and herbaceous vegetation may be concentrated in the upper soil horizons soon after a harvest until sufficient time elapses to allow for penetration and establishment of fine root biomass deeper in the soil profile. Thus, changes in fine root dynamics may occur on both annual and spatial scales in developing forest stands.

2. Materials and methods

2.1. Site descriptions

These studies were installed at the Southern Indiana Purdue Agricultural Center, located in Dubois County, Indiana, USA. The study area is located in the Crawford Upland Section of the Shawnee Hills Natural Region (Homoya et al., 1985). The average annual precipitation is 1170 mm, and the mean annual air temperature is 12.0°C, which ranges from a low of -2.3°C in January to a high of 24°C in July. The soil parent materials are loess deposits over paleosols derived from weathered sandstone and siltstone. Most of the soil types are different series within the family of fine-silty, mixed, mesic Ultic Hapludalfs (Soil Survey Staff, 1996). This area is characterized by rolling hills, and the study areas are located on 10–20% slopes with southern and western facing aspects. The soils within the study area were mapped, described, and classified based on physical characteristics of 1 m deep soil cores taken on a 10 × 10 m² grid. The thickness of the A horizon and the depth to and thickness of the underlying B horizon were measured at each sampling location.

Stand age, identified in the chronosequence, was marked from the date of complete overstory tree removal. Following removal of commercially desirable timber, all remaining overstory trees (>4 cm diameter at breast height) were either herbicide-killed or mechanically removed. The stands were 4, 10, and 29 years old at the beginning of the study (1995). A fourth stand, aged 80–100 years, was chosen to represent the pre-harvest conditions of the sites. Oak (*Quercus*) and hickory (*Carya*) species historically have dominated all stands at maturity. White oak (*Q. alba* L.) is the dominant tree species in the 80–100-year-old stand. The site quality of this stand as

Table 1
Effect of stand age upon the number and species composition of plants within the seedling, sapling, and overstory layers along a 100-year chronosequence of upland hardwood forest stands

Stand age (years)	Seedlings			Saplings			Overstory		
	No./ha	Major species	Percent stems	No./ha	Major species	Percent stems	No./ha	Major species	Percent stems
4	79 000	<i>Smilax</i> spp.	14	95 000	<i>Liriodendron tulipifera</i>	30	—		
		<i>Rubus</i> spp.	13						
		<i>Parthenocissus quinquefolia</i>	13		<i>Quercus alba</i>	20			
					<i>Acer saccharum</i>	12			
10	107 000	<i>Parthenocissus quinquefolia</i>	22	16 000	<i>Asimina triloba</i>	23	1340	<i>Prunus serotina</i>	16
					<i>Sassafras albidum</i>	19		<i>Quercus rubra</i>	15
		<i>Rubus</i> spp.	16		<i>Cercis canadensis</i>	12		<i>Cercis canadensis</i>	13
		<i>Smilax</i> spp.	14					<i>Rhus copallina</i>	12
		<i>Rhus radicans</i>	12					<i>Acer saccharum</i>	12
29	146 000	<i>Rhus radicans</i>	40	1950	<i>Acer saccharum</i>	38	1950	<i>Acer saccharum</i>	36
		<i>Prunus serotina</i>	25		<i>Asimina triloba</i>	28		<i>Prunus serotina</i>	21
								<i>Sassafras albidum</i>	10
80–100	18 300	<i>Parthenocissus quinquefolia</i>	26	770	<i>Acer saccharum</i>	96	710	<i>Acer saccharum</i>	75
		<i>Acer rubrum</i>	24					<i>Quercus alba</i>	13
		<i>Rhus radicans</i>	10						
		<i>Prunus serotina</i>	10						

estimated by site index is 20 m at 50 years for white oak (Kaczmarek, 1995). The ecological land-type phase is classified as a *Quercus alba-Acer saccharum/Parthenocissus* dry mesic ridge (U.S. Department of Agriculture, 1995). Vegetation characteristics for all the stands are given in Table 1.

2.2. Fine root measurements

Three plots, each measuring approximately one-half hectare in size, were selected within the 4, 10, and 80–100-year-old stands. In order to maintain similar physiographic characteristics and a similar disturbance history within the different stands, only two plots were selected within the 29-year-old stand. Fine root growth, turnover, and decomposition were measured using the coring techniques of Persson (1979) as described by Joslin and Henderson (1987). This

method utilizes sequential soil cores and field-incubated ingrowth cores to estimate rates of fine root production, turnover, and decomposition. Sequential soil cores were taken to a depth of 30 cm with a cylindrical coring device in order to measure standing live and dead fine root mass. A mesh bag with holes ≈ 8 mm in diameter was placed inside the soil cavity produced by the corer. Root-free A and B horizon soil taken from the site was packed into each bag to a depth corresponding to the depth of the horizons on the site. Five samples of soil cores and five ingrowth cores were collected within each plot approximately every 60 days from late June 1995 through mid-December 1995. During the mid-December 1995 collection, ingrowth cores were placed in the ground and left until mid-April 1996, ≈ 120 days. A final collection of soil cores and ingrowth cores was made in mid-June 1996, for a total of six collections and five time periods of study.

Samples were processed in a hydro-pneumatic elutriation device (Smucker et al., 1982) in order to extract the fine roots, according to the methods of Kaczmarek (1995). This device uses jets of air and a column of water to disrupt the soil matrix and break apart soil aggregates. Fine roots (less than or equal to 2 mm in diameter) were then washed and collected on a 0.5 mm mesh screen, separated from rocks and other organic matter by hand, and were classified as either live or dead based upon the texture, coloring, and sheath integrity of the roots (Kaczmarek, 1995). For soil and ingrowth cores collected from mid-October 1995 and later, A and B soil horizon samples were processed separately. Fine root samples were dried at 65°C for at least 48 h before being weighed.

Changes in live and dead fine root mass were determined from the changes in standing fine root mass measured from soil cores taken at the beginning and end of a time interval. Fine root growth was estimated from the total amount of fine roots measured in the ingrowth cores after the 60-day incubation period in the field. Fine root mortality and decomposition were calculated according to the method of Joslin and Henderson (1987). Mortality was calculated by subtracting the change in live fine root mass from fine root growth. Decomposition was calculated by subtracting the change in dead fine root mass from fine root mortality.

There are problems with the ingrowth core method as used by Persson (1979), Joslin and Henderson (1987), and others (Yin et al., 1989; Kaczmarek, 1995). In these studies, numerous ingrowth cores were placed in the field at the beginning of the study, and a subset of these cores was extracted at each subsequent time interval. Thus, some ingrowth cores were extracted after 30–60 days, and some remained in the field for up to two years before extraction. Fine root growth was measured as the mass of fine roots extracted from the ingrowth core. Fine roots may respond to being cut by branching and proliferating over a short time period. This would lead to a possible overestimation of fine root growth rates in the short-term. However, ingrowth cores that remain in the soil for more than several months are also problematic. Simultaneous fine root growth and mortality in ingrowth cores will lead to an underestimation of fine root growth rates. Therefore, the longer ingrowth cores remain in the field, the greater the chance that

some of the fine roots that grow into the cores will die and decompose and the greater the underestimation of fine root growth rates.

We decided to modify the ingrowth core method as used in these studies. Instead of installing all of the ingrowth cores at the beginning of the study period and then extracting a subset at sequential time periods, we installed ingrowth cores at the beginning of each time period and extracted them at the end of the same time period. We chose a time period of ≈ 60 days in order to reduce the possible overestimation of short-term fine root growth rates and to minimize the likelihood of death and decomposition of any fine roots that grew into the ingrowth cores.

2.3. Statistics

The design of this experiment was a randomized complete block design. Because the time periods varied with respect to the number of days during which fine root dynamics were assessed, total fine root growth, mortality, and decomposition during a time period were reported as a daily rate. Because of the unique nature of the chronosequence, there is no true replication of stand age. Plots were used as pseudo-replications in all data analyses. This approach may lead to biased error estimates when comparing stand ages, but without true replication of stand age, the degree of bias cannot be estimated. All data were checked for Normality using the Box-Cox procedure (Box et al., 1978). The results suggested that no transformation of the data was necessary to approximate a Normal distribution.

Seasonal differences in fine root growth, mortality, and decomposition across the 30-cm sampling depth were investigated using the ANOVA procedure in SAS (SAS Institute, 1989). Each site was investigated separately. Where a significant difference by time period was indicated, Duncan's multiple range test ($\alpha = 0.05$) was used to identify which time periods were significantly different (SAS Institute, 1989).

A separate ANOVA was used to compare fine root growth, mortality, and decomposition among the different stand ages. Site (stand age) and month (time period) were the treatment variables, plot was the block variable, and fine root growth, mortality, and decomposition ($\text{g/m}^3 \text{ day}^{-1}$) were the dependent variables. The different error terms (block*site, block*

month, and experimental error) were found to be insignificant at $p = 0.25$; therefore, they were combined to create a pooled error term in order to increase the degrees of freedom for the F -test. The pooled error term was used to calculate the error mean square and F -tests in the analysis. Where a significant difference occurred, Duncan's multiple range test ($\alpha = 0.05$) was used to identify which stand ages and time periods were significantly different (SAS Institute, 1989).

Fine root growth, mortality, and decomposition for the A and B horizons within each stand were also compared using the ANOVA procedure in SAS. The rates of fine root growth, mortality, and decomposition ($\text{g/m}^3 \text{ day}^{-1}$) in the A and B horizons were calculated based on the average horizon thicknesses, 8 and 22 cm for the A and B horizons, respectively. Each site was analyzed separately. Horizon (A or B) and month (time period) were the treatment variables, plot was the block variable, and fine root growth, mortality, and decomposition were the dependent variables. The different error terms (block*depth, block*month, and the SAS error) were found to be insignificant at $p = 0.25$; therefore, they were combined into a single pooled error term for calculation of the error mean square and F -tests in the analysis. Duncan's multiple

range test ($\alpha = 0.05$) was used to separate horizon by month interaction means.

3. Results

3.1. Single-depth analysis

Average annual fine root growth is highest for the 10-year-old stand ($8.00 \text{ g/m}^3 \text{ day}^{-1}$), followed by the 4-year-old stand ($7.28 \text{ g/m}^3 \text{ day}^{-1}$), the 29-year-old stand ($6.11 \text{ g/m}^3 \text{ day}^{-1}$), and 80–100-year-old stand ($4.89 \text{ g/m}^3 \text{ day}^{-1}$). Fine root growth in the oldest stand was significantly lower than in the other stands (Table 2). The seasonal growth pattern of fine roots is similar among the four ages of the chronosequence (Fig. 1). All have a single annual period of maximum fine root growth followed by a significant decline and near steady growth. However, there is a difference in the timing of maximum fine root growth by stand age. For the stands aged 4 and 10 years after forest removal, fine root growth was highest from mid-October to mid-December 1995, averaging 11.56 and $12.89 \text{ g/m}^3 \text{ day}^{-1}$, respectively and was significantly greater than fine root growth in the 29 and 80–100-year-old stands

Table 2
Influence of time of year and stand age upon fine root dynamics over a 30 cm depth across a chronosequence of upland hardwood forest stands

Stand age (years)	Fine root parameter	1995			1996		Annual average
		6/29–8/26 ($\text{g/m}^3 \text{ day}^{-1}$)	8/26–10/21	10/21–12/18	12/18–4/14	4/14–6/18	
4	growth	4.73b	10.33a	11.56a	6.00b	5.44b	7.28
	mortality	5.33c	10.00b	14.44a	6.22c	4.22c	7.65
	decomposition	3.77b	–0.56b	23.57a	3.70b	5.44b	18.93
10	growth	4.78c	10.44b	12.89a	7.22c	6.44c	8.00
	mortality	9.44ab	9.89ab	14.67a	8.44bc	2.56c	8.78
	decomposition	8.11bc	2.44bc	18.11a	14.00ab	0.44c	9.22
29	growth	6.11ab	16.11a	6.22b	2.67b	4.00b	6.11
	mortality	13.67ab	19.44a	6.56b	1.67b	3.33b	7.56
	decomposition	10.78ab	16.44a	7.67ab	4.00b	1.22b	7.22
80–100	growth	5.11b	10.00a	5.11b	3.11c	3.22c	4.89 ^a
	mortality	9.11b	16.00a	5.44bc	2.11cd	0.56d	5.67
	decomposition	6.67a	9.00a	6.00a	7.00ab	0.44b	5.89

Note: For a specific stand age, values followed by the same letter within a row do not differ significantly using Duncan's multiple range test with $\alpha = 0.05$.

^a Indicates that Site 4 fine root growth is significantly lower than fine root growth in the other sites using Duncan's multiple range test with $\alpha = 0.05$.

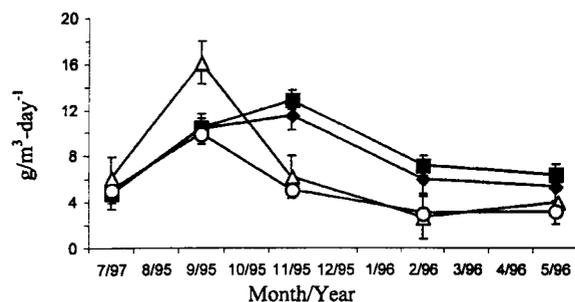


Fig. 1. Effect of season upon fine root ingrowth ($\text{g/m}^3 \text{ day}^{-1}$) in the upper 30 cm of soil along a 100-year chronosequence of upland hardwood forest stands. ■, 4-year-old stand; ◆, 10-year-old stand; △, 29-year-old stand; ○, 80–100-year-old stand.

during this time period. Fine root growth in the 29-year-old and 80–100-year-old stands was greatest from late August to mid-October 1995 (16.11

$\text{g/m}^3 \text{ day}^{-1}$ and $10.00 \text{ g/m}^3 \text{ day}^{-1}$, respectively). Fine root growth in the 29-year-old stand during this time period was significantly greater than fine root growth in any other stand of the chronosequence.

Average annual fine root mortality is highest in the 10-year-old stand ($8.78 \text{ g/m}^3 \text{ day}^{-1}$), followed by the 4-year-old ($7.65 \text{ g/m}^3 \text{ day}^{-1}$), the 29-year-old ($7.56 \text{ g/m}^3 \text{ day}^{-1}$), and the 80–100-year-old stand ($5.67 \text{ g/m}^3 \text{ day}^{-1}$). The seasonal variations in fine root mortality masked any differences by site, but there were time periods during which fine root mortality was significantly different by site (Table 3). Fig. 2 illustrates the seasonal patterns of fine root mortality in these stands. Fine root mortality rates were greatest in the 29 and 80–100-year-old stands (19.44 and $16.00 \text{ g/m}^3 \text{ day}^{-1}$, respectively) during late August to mid-October 1995 and were significantly greater

Table 3
ANOVA for fine root dynamics by site and time period (month) across a 100-year chronosequence of upland oak-hickory forests

Source	DF	ANOVA SS	Mean square	F value	Pr > F
Dependent variable: fine root growth					
Site	3	5.8457	1.9486	12.82	**
Error (a)					
Error (a')	(7)	(0.9291)	(0.1327)		
Month	4	36.4709	9.1177	60.00	**
Site*month	12	16.3681	1.3640	8.98	**
Error (b)					
Error (b')	(28)	(4.3897)	(0.1568)		
Pooled error (a' + b')	35	5.3188	0.1520		
Dependent variable: fine root mortality					
Site	3	3.8477	1.2826	1.97	
Error (a)					
Error (a')	(7)	(2.2111)	(0.3159)		
Month	4	76.0439	19.0110	29.26	**
Site*month	12	43.5943	3.6328	5.59	**
Error (b)					
Error (b')	(28)	(20.5270)	(0.7331)		
Pooled error (a' + b')	35	22.7381	0.6497		
Dependent variable: fine root decomposition					
Site	3	4.7351	1.5784	1.08	
Error (a)					
Error (a')	(7)	(1.4365)	(0.2052)		
Month	4	77.4730	19.3682	13.20	**
Site*month	12	100.629	8.3858	5.71	**
Error (b)					
Error (b')	(28)	(49.9242)	(1.7830)		
Pooled error (a' + b')	35	51.3607	1.4674		

Note: Error (a) and Error (b) are the true error for site and for the site by month interaction, respectively. Because there is no true replication of stand ages, Error (a') and Error (b'), potentially biased error terms that represent block (site) and the block (site) by month interaction, were used in the analysis.

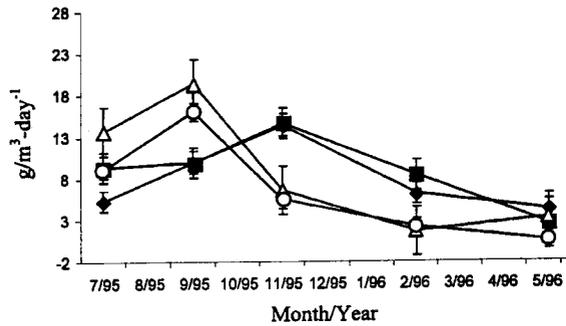


Fig. 2. Effect of season upon fine root mortality ($\text{g/m}^3 \text{day}^{-1}$) in the upper 30 cm of soil along a 100-year chronosequence of upland hardwood forest stands. \blacksquare -, 4-year-old stand; \blacklozenge -, 10-year-old stand; \triangle -, 29-year-old stand; \circ -, 80–100-year-old stand.

than fine root mortality rates in the 4- and 10-year-old stands (10.00 and $9.89 \text{ g/m}^3 \text{day}^{-1}$). During mid-October to mid-December 1995, fine root mortality rates were greatest for the 4- and 10-year-old stands (14.44 and $14.67 \text{ g/m}^3 \text{day}^{-1}$) and were significantly greater than fine root mortality rates in the 29 and 80–100-year-old stands (6.56 and $5.44 \text{ g/m}^3 \text{day}^{-1}$).

On an annual basis, fine root decomposition rates decreased with increasing stand age (Table 2). The seasonal variations in fine root decomposition masked any differences by site, but there were time periods during which fine root decomposition was significantly different by site (Table 3). Fig. 3 illustrates the seasonal patterns of fine root decomposition in these stands. Fine root decomposition rates in the 29 and 80–100-year-old stands were highest during late

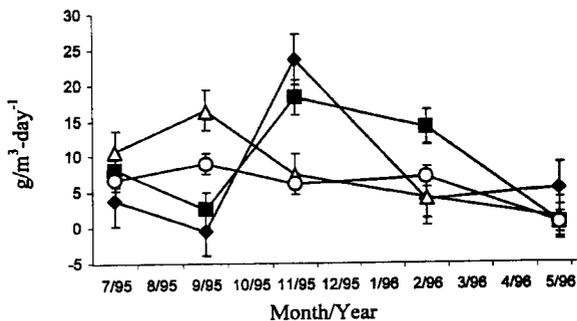


Fig. 3. Effect of season on fine root decomposition ($\text{g/m}^3 \text{day}^{-1}$) in the upper 30 cm of soil along a 100-year chronosequence of upland hardwood forest stands. \blacksquare -, 4-year-old stand; \blacklozenge -, 10-year-old stand; \triangle -, 29-year-old stand; \circ -, 80–100-year-old stand. Error bars represent the least significant difference using Duncan's multiple range test ($\alpha = 0.05$).

August to mid-October 1995 (16.44 and $9.00 \text{ g/m}^3 \text{day}^{-1}$, respectively) and were significantly greater than fine root decomposition rates in the 4- and 10-year-old stands (-0.56 and $2.44 \text{ g/m}^3 \text{day}^{-1}$, respectively). Fine root decomposition rates in the 4- and 10-year-old stands were highest during the following time period, from mid-October to mid-December 1995 (23.57 and $18.11 \text{ g/m}^3 \text{day}^{-1}$) and were significantly greater than fine root decomposition rates in the 29 and 80–100-year-old stands (7.67 and $6.00 \text{ g/m}^3 \text{day}^{-1}$).

3.2. Fine roots: analysis by soil horizon

Fine root growth in the A and B soil horizons was significantly different for the time periods investigated in this study. In all, but the 10-year-old stand, fine root growth in the A horizon was significantly greater than in the B horizon (Table 4). The seasonal patterns of fine root growth in the A and B horizons differ by stand age, as well. For all, but the four-year-old stand, fine root growth in the A horizon peaks during the same time period as fine root growth in the B horizon (Table 5). In the four-year-old stand, fine root growth in the A horizon was at a maximum from late August to mid-October 1995, but fine root growth in the B horizon was greatest from mid-October to mid-December 1995 (Table 4). For the 29 and 80–100-year-old stands, fine root growth in both horizons was greatest from late August to mid-October 1995. For the 10-year-old stand, fine root growth in both horizons was greatest from mid-October to mid-December 1995.

Fine root mortality rates in the A horizon were significantly greater than in the B horizon only in the 29-year-old stand (Table 4). In all age stands fine root mortality was highest in both horizons from mid-October to mid-December 1995. Fine root decomposition rates followed the same pattern as fine root mortality rates in the 4-, 10-, and 29-year-old stands, but there were significant differences by horizon in the 80–100-year-old stand (Table 4). For all but the oldest stand, fine root decomposition was highest in both horizons from mid-October to mid-December 1995. Fine root decomposition in the A horizon of the 80–100-year-old stand was highest from mid-December 1995 to mid-April 1996 and was significantly greater than fine root decomposition in the B horizon. Fine

Table 4
Fine root dynamics for the A and B soil horizons across a 100-year chronosequence of upland oak-hickory forests

Stand age (years)	Soil horizon	Fine root parameter	1995				1996	Average
			6/29–8/26	8/26–10/21 (g/m ³ day ⁻¹)	10/21–12/18	12/18–4/13	4/13–6/15	
4	A	ingrowth		19.08a	10.20bc	3.18d	8.09c	8.65 ^a
	B			7.10c	12.09b	2.06d	4.55d	5.55
	A	mortality			14.95	5.51	3.13	7.21
	B				14.23	2.03	4.09	5.58
	A	decomposition			40.84	5.07	4.78	13.82
	B				17.30	0.58	5.20	5.68
10	A	ingrowth		10.87	11.93	5.25	9.14	8.48
	B			10.88	13.28	2.00	5.58	6.71
	A	mortality			19.72	6.63	0.00	8.11
	B				12.83	3.09	3.66	5.64
	A	decomposition			28.26a	10.52bc	0.00c	12.13
	B				12.84b	5.30bc	5.20bc	7.13
29	A	ingrowth		24.37	7.97	4.07	7.09	9.35 ^a
	B			13.08	5.61	1.82	3.00	4.97
	A	mortality			8.66	4.57	4.04	5.44 ^a
	B				5.73	1.14	2.70	2.68
	A	decomposition			14.99	7.00	1.67	7.57
	B				5.04	1.77	0.73	2.30
80–100	A	ingrowth		13.19	7.30	4.53	6.22	7.09 ^a
	B			8.90	4.42	2.61	2.15	4.07
	A	mortality			7.38	4.00	0.42	3.89
	B				4.74	2.10	0.30	2.28
	A	decomposition			5.92bc	10.54a	0.20d	6.67 ^a
	B				6.06b	2.94cd	0.17d	2.98

Note: For a specific stand age and fine root parameter, row values comparing horizons A and B followed by the same letter do not differ significantly using Duncan's multiple range test at $\alpha = 0.05$.

^a Indicates a significant difference by horizon when averaged over the entire study period.

root decomposition in the B horizon of this stand was highest from mid-October to mid-December 1995.

4. Discussion

4.1. Fine root growth

The results from our study generally support the findings of other studies with respect to fine root growth rates in mature oak-hickory forests (Kaczmarek, 1995) and in regenerating forests following harvesting (Raich, 1980; Berish and Ewel, 1988; Yin et al., 1989). The annual rate of fine root growth in the 80–100-year-old stand in our study (4.89 g/m³ day⁻¹ from June 1995 to June 1996) compares favorably

with the results of Kaczmarek (1995) for a study conducted in the same 80–100-year-old stand (3.8 g/m³ day⁻¹ from March 1993 to March 1994). Fine root growth in a six-year-old clear-cut stand in Wisconsin was 2.28 g/m³ day⁻¹ (Yin et al., 1989), lower than the fine root growth rates in either the 4 or 10-year-old stands in our study (7.28 and 8.00 g/m³ day⁻¹, respectively).

The differences in the annual fine root growth rates between our study and those of Yin et al. (1989) may be due to differences in annual climatic conditions or stand productivity. Our study site in southern Indiana has greater annual precipitation (1170 ml) and mean annual temperature (12°C) than the Wisconsin site of Yin et al. (1989), which receives 792 ml of mean

Table 5
ANOVA for fine root dynamics by horizon across a 100-year chronosequence of upland oak-hickory forests

Source	DF	Anova SS	Mean square	F value	Pr > F
Dependent variable: fine root growth					
Stand age = 4					
Block	2	1.7078	0.8539	0.19	
Month	3	403.5211	134.5070	29.41	**
Error (a)	(6)	(4.8790)	(0.8132)		
Depth	1	81.5963	81.5963	17.85	**
Error (b)	(2)	(31.8892)	(15.9446)		
Month*depth	3	159.8249	53.2750	11.65	**
Error (c)	(6)	(27.2429)	(4.5405)		
Pooled error (a + b + c)	14	64.0111	4.5722		
Stand age = 10					
Block	2	7.3825	3.6912	1.25	
Month	3	285.1646	95.0549	32.13	**
Error (a)	(6)	(23.5762)	(3.9294)		
Depth	1	11.1736	11.1736	3.77	
Error (b)	(2)	(0.0616)	(0.0308)		
Month*depth	3	26.3837	8.7946	2.97	
Error (c)	(6)	(17.7753)	(2.9625)		
Pooled error (a + b + c)	14	41.4131	2.9581		
Stand age = 29					
Block	1	5.8077	5.8077	1.05	
Month	3	600.6710	200.2237	36.23	**
Error (a)	(3)	(37.8462)	(12.6154)		
Depth	1	99.8515	99.8515	18.07	**
Error (b)	(1)	(0.1179)	(0.1179)		
Month*depth	3	55.0351	18.3450	3.32	
Error (c)	(3)	(0.7201)	(0.2400)		
Pooled error (a + b + c)	7	38.6842	5.5264		
Stand age = 80–100					
Block	2	2.7628	1.3814	0.70	
Month	3	207.3719	69.1240	35.14	**
Error (a)	(6)	(13.1535)	(2.1922)		
Depth	1	65.0118	65.0118	33.05	**
Error (b)	(2)	(0.4359)	(0.2180)		
Month*depth	3	5.4455	1.8152	0.92	
Error (c)	(6)	(13.9500)	(2.3250)		
Pooled error (a + b + c)	14	27.5394	1.9671		
Dependent variable: fine root mortality					
Stand age = 4					
Block	2	33.5976	16.7988	0.77	
Month	2	475.3637	237.6818	10.90	**
Error (a)	(4)	(22.3735)	(5.5934)		
Depth	1	5.2509	5.2509	0.24	
Error (b)	(2)	(73.3696)	(36.6848)		
Month*depth	2	15.0583	7.5291	0.34	
Error (c)	(4)	(122.1562)	(30.5391)		
Pooled error (a + b + c)	10	217.8993	21.7899		

Table 5 (Continued)

Source	DF	Anova SS	Mean square	F value	Pr > F
Stand age = 10					
Block	2	36.2969	18.1484	0.98	
Month	2	771.0993	385.5496	20.85	**
Error (a)	(4)	(68.1084)	(17.0271)		
Depth	1	11.2251	11.2251	0.61	
Error (b)	(2)	(34.0169)	(17.0084)		
Month*depth	2	127.3306	63.6653	3.44	
Error (c)	4	(82.7893)	(20.6973)		
Pooled error (a + b + c)	10	184.9146	18.4915		
Stand age = 29					
Block	1	0.8356	0.8356	0.26	
Month	2	45.0151	22.5076	6.91	*
Error (a)	(2)	(3.7893)	(1.8946)		
Depth	1	19.7478	19.7478	6.06	*
Error (b)	(1)	(10.5317)	(0.5317)		
Month*depth	2	2.3981	1.1990	0.37	
Error (c)	(2)	(18.2586)	(9.1293)		
Pooled error (a + b + c)	10	32.5797	3.2580		
Stand age = 80–100					
Block	2	1.3160	0.6580	0.18	
Month	2	97.6066	48.8033	13.49	**
Error (a)	(4)	(20.2072)	(5.0518)		
Depth	1	10.8471	10.8471	3.00	
Error (b)	(2)	(0.2591)	(0.1296)		
Month*depth	2	4.9898	2.4949	0.69	
Error (c)	(4)	(15.7032)	(3.9258)		
Pooled error (a + b + c)	10	36.1695	3.6170		
Dependent Variable: fine root decomposition					
Stand age = 4					
Block	2	209.6066	104.8033	0.91	
Month	2	2546.8755	1273.4377	11.04	**
Error (a)	(4)	(683.7007)	(170.9252)		
Depth	1	381.0902	381.0902	0.33	
Error (b)	(2)	(419.4758)	(209.7379)		
Month*depth	2	480.3532	240.1766	2.08	
Error (c)	(4)	(905.0463)	(226.2616)		
Pooled error (a + b + c)	10	1153.0373	115.3037		
Stand age = 10					
Block	2	58.8950	29.4475	0.88	
Month	2	1470.5012	735.2506	22.05	**
Error (a)	(4)	(207.9083)	(51.9771)		
Depth	1	97.5751	97.5751	2.93	
Error (b)	2	(50.3728)	(25.1864)		
Month*depth	(2)	366.5542	183.2771	5.50	*
Error (c)	(4)	(75.1905)	(18.7976)		
Pooled error (a + b + c)	10	333.4716	33.3472		
Stand age = 29					
Block	1	43.8686	43.8686	1.60	
Month	2	159.2113	79.6057	2.91	

Table 5 (Continued)

Source	DF	Anova SS	Mean square	F value	Pr > F
Error (a)	2	(47.7784)	(23.8892)		
Depth	1	86.6636	86.6636	3.17	
Error (b)	1	(93.0031)	(93.0031)		
Month*depth	2	40.5942	20.2971	0.74	
Error (c)	2	(132.7864)	(66.3932)		
Pooled error (a + b + c)	10	273.5679	27.3568		
Stand age = 80–100					
Block	2	2.2607	1.1303	0.36	
Month	2	154.5077	77.2538	24.72	**
Error (a)	(4)	(10.9239)	(2.7310)		
Depth	1	27.9949	27.9949	8.96	*
Error (b)	(2)	(9.5396)	(4.7698)		
Month*depth	2	58.6826	29.3413	9.39	*
Error (c)	(4)	(10.6616)	(2.6654)		
Pooled error (a + b + c)	10	31.1251	3.1251		

Note: Error (a) represents the block*month interaction. Error (b) represents the block*depth interaction. Error (c) represents the block*month*depth interaction.

annual precipitation and has a mean annual temperature of 7°C. These climatic differences affect the growing season length and number of days during which conditions for fine root growth are favorable. We expect our estimates of fine root growth to be somewhat greater because we modified the ingrowth core method. As described above, we installed and collected ingrowth cores every 60 days, instead of installing all the ingrowth cores at the beginning of the study and collecting a subset every 60 days. Because the results from our study and those from Kaczmarek (1995) compare favorably, the modification in this study of the traditional ingrowth core technique has not seriously compromised estimates of fine root growth.

Fine root growth during the winter (mid-December 1995 to mid-April 1996) and spring (mid-April to mid-June 1996) periods were approximately the same. Fine roots can remain active during the winter as long as soil temperatures remain above freezing; however, higher soil temperatures and a more active above-ground biomass in the spring period suggest greater fine root growth during the spring than during the winter in these temperate hardwood forests. We did not detect a flush of fine root growth during the spring sampling interval (mid-April to mid-June 1996). If an early season fine root growth flush occurred before this time period, we would have included it with the winter

sampling interval. In the Kaczmarek (1995) study of the 80–100-year-old stand, fine root growth rates during the spring (from late March to late May) were also similar to the preceding winter period (from late November to late March). Thus, if an early spring flush of fine root growth does occur in the 80–100-year-old stand, the activity must begin before mid to late March.

The difference in the timing of peak fine root growth rates between the younger (aged 4 and 10 years) and older (aged 30 and 80–100 years) stands may be due to differences in species composition and developmental stages of the forest vegetation. In the 4- and 10-year-old stands, geophytic and other plants with underground storage organs, such as *Rubus* spp. (Jensen et al., 1995) and *Smilax* (Dahlgren et al., 1985), make up the majority of the aboveground and presumably the belowground vegetative biomass (Table 1). Retranslocation of carbohydrates to these storage organs may stimulate a flush of fine root growth, especially with favorable soil temperatures (Fig. 4) and soil moisture potentials (Fig. 5). Larger and more mature trees, such as those in the 29 and 80–100-year-old stands, distribute retranslocated photosynthates among the bole and coarse roots (Larcher, 1995); thus, there is less potential for fine root growth in the older stands, despite favorable soil conditions.

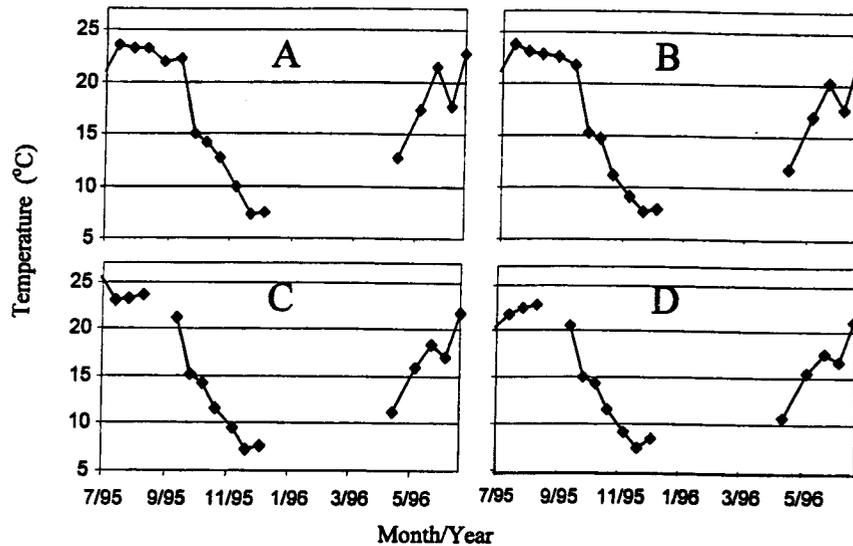


Fig. 4. Effect of season on soil temperature in the upper 30 cm of soil along a 100-year chronosequence of upland hardwood forest stands. (A) 4-year-old stand; (B) 10-year-old stand; (C) 29-year-old stand; (D) 80–100-year-old stand. Error bars represent the least significant difference using Duncan's multiple range test ($\alpha = 0.05$).

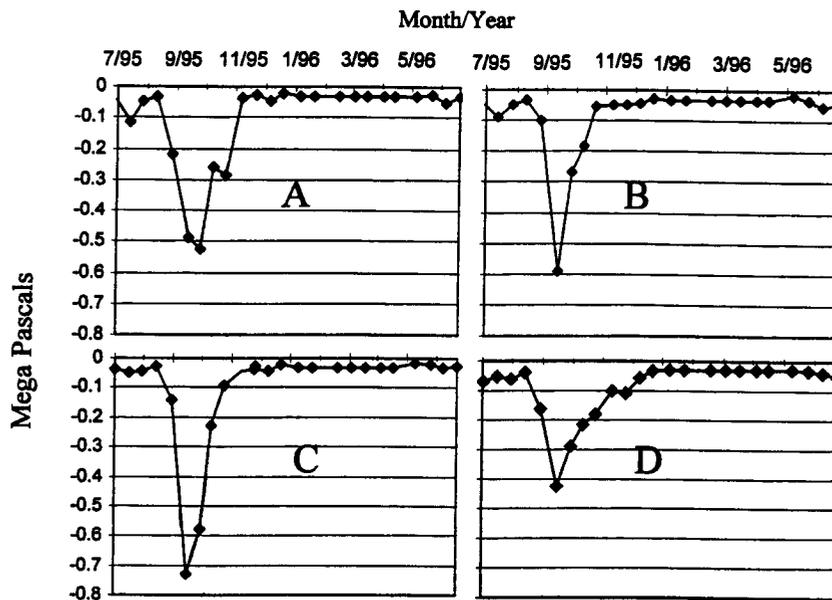


Fig. 5. Effect of season on soil moisture potential in the upper 30 cm of soil along a 100-year chronosequence of upland hardwood forest stands. (A) 4-year-old stand; (B) 10-year-old stand; (C) 29-year-old stand; (D) 80–100-year-old stand. Error bars represent the least significant difference using Duncan's multiple range test ($\alpha = 0.05$).

4.2. Fine root mortality and decomposition

The seasonal patterns of fine root mortality among the stands follow the pattern of fine root growth rates (Fig. 1 and Fig. 2). Although the simultaneous occurrence of increased fine root growth and mortality may seem counter-intuitive, this phenomenon has been singled out as a principal reason why maximum–minimum measurements of fine root production and turnover usually underestimate the true rate of fine root activity (Kurz and Kimmins, 1987; Nadelhoffer and Raich, 1992).

The seasonal patterns of fine root decomposition (Fig. 3) differed from the seasonal patterns of fine root growth (Fig. 1) and mortality (Fig. 2). From July to October 1995, fine root growth and mortality increased significantly in all stand ages except the 29-year-old stand; however, fine root decomposition was not affected in any of the stands (Table 2). Afterwards, fine root mortality and decomposition followed fairly similar patterns in all of the stands of the chronosequence. Since the fine root decomposition rate is calculated based upon the fine root growth rate, there is some influence of fine root growth upon the measurements of fine root decomposition. However, if the patterns of fine root decomposition measured in this study accurately reflect the patterns of fine root decomposition in these stands, then there seems to be a late season period of rapid fine root growth, mortality, and decomposition in all the stands of the chronosequence.

4.3. Fine root dynamics by soil horizon

A decrease in fine root mass and fine root growth with depth is fairly common in many forest ecosystems (Berish, 1982; Joslin and Henderson, 1987; Kelly and Joslin, 1989; Yin et al., 1989; Büttner and Leuschner, 1994; Kätterer et al., 1995; Arunachalam et al., 1996). Yin et al. (1989) found that in red oak (*Quercus rubra* L.) stands, fine root growth was more concentrated in the A horizon in a clear-cut stand than in a mature stand. They suggested that the roots of young trees had not penetrated as deeply in the soil as roots of older trees; thus, fine root growth and biomass were concentrated in the A horizon. The distribution of fine root growth in the 4- and 10-year-old stands of our study does follow the pattern suggested by Yin et al.

(1989) (Table 4). However, this trend reverses itself from the 10 to the 29 and 80–100-year-old stands, as fine root growth is once again significantly greater in the A than in the B soil horizon. After canopy closure and the onset of the stem exclusion stage in forests, increasing competition for limiting soil resources may lead to an increasing concentration of fine root growth in the A horizon.

Seasonal patterns of fine root growth in the two soil horizons were similar for all except the four-year-old stand. The difference in fine root growth patterns by horizon during the fall of the year in the four-year-old stand may be due mainly to the abundance of geophytic plant species (Table 1). Trees and annual plants have their fine roots concentrated in the A horizon, and fine root growth rates declined significantly in this horizon from October to December as soil temperatures declined. Geophytic plant species have underground storage organs located deeper in the soil profile to protect them from freezing (Larcher, 1995). Increased carbohydrate allocation to the underground storage organ during the fall (Larcher, 1995) may lead to increased fine root growth rates in the B horizon from October to December as long as soil temperatures remain favorable (Table 4). Observations of new fine roots originating from these underground storage organs were made not only in the ingrowth and soil core collections of this study but also from individual plant excavations made during October and November of 1998.

Fine root mortality and decomposition by horizon were only measured over three time periods, or approximately eight months (Table 4), so inferences from these results are tentative at best. During this period, both mortality and decomposition showed more complicated patterns of distribution between the A and B horizons than fine root growth. The seasonal patterns of fine root mortality and decomposition by horizon did differ with stand age (Table 4), but no clear patterns emerged that seem to be related to stand age alone.

5. Conclusions

High fine root growth rates following harvesting found in this study support the results of previous studies (Raich, 1980; Berish and Ewel, 1988; Yin et al.,

1989). High fine root mortality and decomposition in the regenerating stands, however, suggest there is little net accumulation of fine root biomass from 4 to 30 years following forest removal. The distribution of fine root growth among the A and B soil horizons differs from the pattern suggested by Yin et al. (1989), who argued that fine root growth is concentrated in the A horizon after forest removal and becomes more uniformly distributed with increasing stand age. We found an increasing concentration of fine root growth in the A horizon from the stands aged 10 to 80–100 years.

Further work is needed to relate these changes in fine root dynamics to other forest processes, such as nutrient cycling, soil microbial activity, and overall forest productivity. It is not known whether significant fine root growth during the winter translates into significant nutrient uptake. The changes with stand age in the contribution of fine root litter to soil organic matter and nutrient pools are largely unknown in most forest ecosystems. This study provides a baseline of information on fine root dynamics that can be used to answer important questions of ecosystem processes and overall forest productivity.

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