United States
Department of
Agriculture

Forest Service

Southern Research
Station

General Technical
Report SRS-20

Proceedings of the Ninth Biennial Southern Silvicultural Research Conference

Clemson, South Carolina
February 25-27, 1997

Idol, Travis, W.; Pope, Phillip E.; Tucker, Jennifer; Ponder, Felix, Jr. 1998. The role of fine root dynamics in the N and P cycles of regenerating upland oak-hickory forests. In: Waldrop, Thomas A., ed. Proceedings, 9th Biennial southern silvicultural research conference; 1997 February 25-27; Clemson, SC. Gen. Tech. Rep. SRS-20. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station: 136-140.

sil·vics \'sil-viks\ n pl but sing in constr [NL silva] : the study of the life history, characteristics, and ecology of forest trees esp. in stands
sil·vi·cul·tur·al \,sil-və-'kəlch-(ə-)rəl\ adj : of or relating to silviculture — sil·vi·cul·tur·al·ly \-ē\ adv
sil·vi·cul·ture \'sil-və-,kəl-chər\ n [F, fr. L silva, sylva forest + cultura culture] : a phase of forestry dealing with the development and care of forests — sil·vi·cul·tur·ist \,sil-və-'kəlch-(ə-)rəst\ n

Proceedings of the Ninth Biennial Southern Silvicultural Research Conference

Edited by
Thomas A. Waldrop

Clemson, South Carolina
February 25-27, 1997

Hosted by
Clemson University
USDA Forest Service, Southern Research Station

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Southern Industrial Forest Research Council
USDA Forest Service, Southern Research Station
University of Arkansas, Monticello

Published by
USDA Forest Service
Southern Research Station
Asheville, North Carolina
June 1998

CONTENTS

Page

MEASUREMENT AND RESEARCH METHODS

THE ROLE OF FINE ROOT DYNAMICS IN THE N AND P CYCLES OF REGENERATING UPLAND OAK-HICKORY FORESTS

Travis W. Idol, Phillip E. Pope, Jennifer Tucker, and Felix Ponder, Jr.[1]

Abstract—In naturally regenerating hardwood forest stands, inputs of organic matter and nutrients from fine root turnover and decomposition are significant but not well-quantified. Four forest stands in southern Indiana—aged 6, 12, 31, and approximately 100 years since clearcutting at the time of the study—were chosen to represent the different developmental stages of upland temperate hardwood forest stands. Changes in live and dead fine root biomass and fine root growth were monitored to calculate total fine root decomposition. Autumnal aboveground litterfall was collected to compare above- and belowground litter nutrient inputs. Results indicate that, on an annual basis, N and P inputs to the soil from fine root decomposition are greater than or equal to, the total amount of N and P held in the aboveground litterfall for all but the youngest stand. The ratio of aboveground fine root N and P inputs decreases with stand age beginning about 10 years after harvest. This indicates that fine root turnover and decomposition in these upland oak-hickory forests is the major pathway for biological cycling of nutrients from stand ages 10 to 80 years.

INTRODUCTION

Management of many forests in the central hardwood forest region consists of infrequent clearcuts or selective harvests done on the scale of only a few hectares. This is especially true in Indiana since much of the landscape is dissected into private and public lands. Natural regeneration is usually relied upon to reforest harvested sites; often, site preparation and postharvest monitoring of stand regeneration is neglected.

Past research on temperate deciduous stands has revealed that the direction and magnitude of stand development are strongly influenced by the nature of the regenerating vegetation and the nutrient dynamics of the site (Hughes and Fahey 1994, Mattson and Swank 1989, Mroz and others 1985, Palik and Pregitzer 1991, Polglase and Attiwill 1992, Weigel 1996). A few studies have focused on fine root dynamics of regenerating or disturbed stands in tropical ecosystems (Berish and Ewel 1987, Raich 1980, Silver and Vogt 1993), and only one investigated these dynamics in temperate hardwood forests of the United States (Yin and others 1989).

Fine roots, like leaves, tend to be relatively short-lived, both physically (Hendrick and Pregitzer 1993, Joslin and Henderson 1987) and functionally (Kuhns and others 1985), ranging from a few weeks to 1 or 2 years. Therefore, the rapid turnover and eventual decomposition of fine roots and leaves are important carbon and nutrient inputs to the soil (Joslin and Henderson 1987, McClaugherty and others 1982, Ruess and others 1996). Changes in species composition and growth rates in developing forest stands alter the nutrient demands over time. Since leaf area and fine root biomass also change with the age of the stand (Yin and others 1989), the relative importance of the turnover and decomposition of these tissues in supplying N and P to the soil will vary. Quantifying these changes is important in understanding the nutrient cycles of upland temperate hardwood forests.

This study was developed with these factors in mind. Specifically, we wanted to investigate the influence of stand development on the rates of fine root decomposition, the amount of autumnal aboveground litterfall, the N and P contributions of fine root decomposition to the soil, and the total N and P held in the autumnal litterfall.

SITE DESCRIPTIONS

Our study is being implemented at the Southern Indiana Purdue Agricultural Center, located in Dubois County, IN. The area is in the Crawford Upland Section of the Shawnee Hills Natural Region (Homoya and others 1985). The ecological landtype phase most common in these stands is classified as *Quercus alba-Acer saccharum/Parthenocissus* dry-mesic ridges (USDA 1995). The soils are of different series within the family of fine-silty, mixed, mesic Ultic Hapludalfs (USDA 1996). The area is characterized by rolling hills, and all plots in this study are located on 10 to 30 percent slopes with southern and western aspects. All four stands have historically been dominated by oak (*Quercus*) and hickory (*Carya*) species at maturity. Site index for white oak is approximately 20 to 21 meters at 50 years (Kaczmarek 1995). The three regenerating stands were clearcut in 1991, 1985, and 1969, respectively (Sites 1, 2, and 3). The fourth is a mature oak-hickory stand, 80 to 100 years old (Site 4).

Species Composition

The vegetation of the 6-year-old stand (Site 1) is composed of many small tulip poplar (*Liriodendron tulipifera* L.) [28,500 stems per hectare (ha)], white oak (*Q. alba* L.) (19,000 stems per ha), and sugar maple (*Acer saccharum* Marshall) (11,400 stems per ha), saplings with greenbriar (*Smilax* spp.) (11,000 stems per ha), blackberry (*Rubus* spp.) (10,200 stems per ha), and Virginia creeper [*Parthenocissus quinquefolia* (L) Planchon] (10,200 stems per ha) in the understory. In the 12-year-old stand (Site 2), the overstory vegetation is a mixture of black cherry (*Prunus serotina* Ehrhart) (210 stems per ha), red oak (*Q.*

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rubra L.) (200 stems per ha), eastern redbud (*Cercis canadensis* L.) (170 stems per ha), dwarf sumac (*Rhus copallina* L.) (160 stems per ha), and sugar maple (160 stems per ha). The basal area of the 31-year-old stand (Site 3) in 1990 was 14 m^2 per ha. The overstory in this stand is a mixture of sugar maple (700 stems per ha), black cherry (410 stems per ha), and sassafras (200 stems per ha) (Yu, in press). The basal area of the mature stand (Site 4) in 1987 was 16 m^2 per ha. The overstory basal area is dominated by white oak (12 m^2 per ha), with sugar maple (2 m^2 per ha), and hickory [*C. ovata* (Miller) K. Koch and *C. glabra* (Miller) Sweet] (2 m^2 per ha) present in smaller amounts (Kaczmarek 1995). The sapling layer is dominated by sugar maple (740 out of a total of 770 stems per ha) with several American beech (*Fagus grandifolia* Ehrhart) and white ash scattered throughout (Yu, in press).

METHODS

Fine root biomass was sampled over a 30 centimeter (cm) depth, according to the coring method of Joslin and Henderson (1987). Fine root growth was estimated with the ingrowth technique, using soil collected from the site in which the ingrowth cores were placed (Conlin and Lieffers 1993, Joslin and Henderson 1987). Ten to 15 core samples per site were collected approximately every 60 days from July 1995 until December 1995, and then again in 1996 from April to June. Fine roots were separated from the soil in a hydro-pneumatic elutriation machine (Smucker and others 1982). Fine roots were separated into live and dead categories according to tissue integrity, color, and sheath covering (Clemsson-Lindell 1994). All samples were dried in an oven at 65 °C to a constant weight for at least 48 hours before being weighed.

If changes in live and dead fine root biomass and the fine root growth rate over a specific time period are known, then the total fine root decomposition during that time period can be calculated. Because the change in live fine root biomass during any time period is a function of fine root growth (an addition of live fine root mass) and fine root death, or mortality (a subtraction from the live fine root mass), fine root mortality can be calculated by subtracting the change in live fine root mass from the fine root growth rate.

Symbolically, where GROWTH = fine root growth, LFR_1 = live fine root mass at time 1, LFR_2 = live fine root mass at time 2, and MORT = fine root mortality: $LFR_2 - LFR_1$ = GROWTH - MORT. By rearranging the terms of the expression: MORT = GROWTH - ($LFR_2 - LFR_1$).

Similarly, the change in dead fine root mass during any time period is a function of additions to the dead fine root pool due to fine root mortality and subtractions from the dead fine root pool due to fine root decomposition. By knowing the fine root mortality rate, the fine root growth rate, and the change in dead fine root mass during a specific time period, fine root decomposition can be calculated.

Symbolically, where DECOMP = fine root decomposition, DFR_1 = dead fine root mass at time 1, and DFR_2 = dead fine root mass at time 2: $DFR_2 - DFR_1$ = MORT - DECOMP. By rearrangement of the terms of the expression: DECOMP = MORT - ($DFR_2 - DFR_1$) or DECOMP = GROW - ($LFR_2 - LFR_1$) - ($DFR_2 - DFR_1$) .

Ten to 15 littertraps, 0.71 by 0.71 meters on a side or approximately 0.5 m^2 in area and 10 cm deep, were placed within each site. Autumnal litterfall was collected weekly from October 8 to December 18, 1995. Samples were separated according to species and air dried in a greenhouse before being weighed.

Nutrient analyses were performed on representative subsamples of live fine roots and aboveground litterfall. Total N was determined according to the micro-Kjeldahl method (Keeney and Nelson 1982). Total P was determined by digesting approximately 0.1 gram of the ground plant tissue in a mixture of perchloric acid and peroxide at a temperature of approximately 220 C. After the digestion was complete, the samples were diluted with double- distilled water, and the P content of the resulting solution was determined according to the phosphomolybdate blue colorimetric procedure (Olsen and Sommers 1982). The average N and P concentrations from all fine root or litterfall samples within a site were used to calculate N and P inputs or contents of the litter sources.

RESULTS AND DISCUSSION

Patterns of Fine Root Decomposition

Figure 1 illustrates the seasonal patterns of fine root decomposition from July 1995 to July 1996 for all four sites. The peak time for fine root decomposition occurred during the fall and winter of the year, from October 1995 to March 1996. For the four stands in this study, annual rates of fine root decomposition peaked at 10 years of age, and decreased thereafter (table 1).

Patterns of fine root decomposition across stands of varying age are not well understood. The pattern of increasing then decreasing fine root decomposition with stand age (table 1) suggests that the biomass and longevity of fine roots in younger stands are lower than in older stands. As the stand

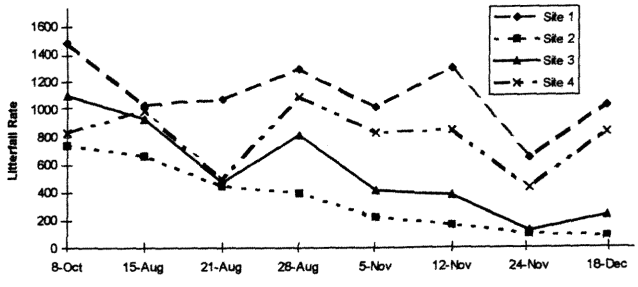

Figure 1—Effect of season upon fine root decomposition (g per m^2- day) across a 100-year chronosequence of upland hardwood forest stands.

Table 1—Annual rates of fine root decomposition, aboveground litterfall, and the N and P contents of litter sources across a 100-year chronosequence of upland hardwood forest stands

Stand age (1995)	Site	Fine root decomp.	Aboveground litterfall	Fine root N return	Fine root P return	Litterfall N content	Litterfall P content
- Years -	No.	*- - - - - - - - - - - - - - - - Kilograms per hectare per year - - - - - - - - - - - - - - - - -*					
4	1	7,150	8,970	57.8	6.51	82.3	7.98
10	2	10,110	2,820	70.5	7.28	27.3	2.71
29	3	7,720	4,480	64.9	4.94	36.7	2.96
80–100	4	6,460	6,360	50.5	3.94	52.2	4.13

ages, there is more fine root mass which can potentially turn over, but less of a percentage of this standing biomass actually turns over during any given time interval. Consequently, total fine root decomposition in younger stands increases over time as long as increases in total fine root biomass are greater than increases in fine root longevity. This presumably is the case in Sites 1 and 2, the 6- and 12-year-old stands. As the dominant canopy trees establish themselves and canopy tree dieback decreases, fine root biomass will reach a maximum level, but fine root longevity will continue to increase. This would mean that total fine root decomposition would decrease over time. This presumably is the case for Sites 3 and 4, the 31- and 80- to 100-year-old stands.

Fine Root Biomass

Table 2 lists the seasonal and annual levels of fine root biomass in the chronosequence of stands investigated. The assumption of increasing fine root biomass with stand age is justified in this case. Total fine root biomass increases from the 6- to the 12-year-old stand, decreases from the 12- to the 31-year-old stand, but then increases again from the 31- to the 80 to 100-year-old stand. The levels of fine root biomass in the 12- and 80 to 100-year-old stands are similar, suggesting that reestablishment of belowground fine root biomass occurs within 10 years after a harvest in these upland hardwood forests.

The decrease in fine root biomass in the 31-year-old stand is perhaps due to a change in canopy species composition. The canopy of this stand is dominated by pioneering species like sassafras and black cherry, whereas the canopy of the 80 to 100-year-old stand is dominated by white oak. Reduced vigor and tree damage or death due to windstorms has been observed in this stand. It is possible that these pioneering species will lose their canopy dominance over the next few decades, being replaced by oak, hickory, and maple species.

Litterfall

Figure 2 illustrates the rates of aboveground litterfall during the autumn of 1995. For the 12- and 31-year-old stands (Sites 2 and 3), litterfall rates generally decreased during the collection period. However, for the 6- and 80 to 100-year old stands (Sites 1 and 4), litterfall rates remained high though the last collection date. Overall, litterfall was highest in the youngest stand, lowest in the 12-year-old stand, and then increased with stand age thereafter (table 1).

The high rate of litterfall in the youngest stand (Site 1) is contrary to what was expected (table 1). With a much lower leaf area than stands with closed canopies, litterfall in very young stands is expected to be low (Gholz and others

Table 2—Seasonal patterns of total fine root biomass (kg per hectare on a dry weight basis) across a 100-year chronosequence of upland hardwood forest stands

	Total fine root biomass collected			
Collection date	Site 1 6 yrs old	Site 2 12 yrs old	Site 3 31 yrs old	Site 4 80-100 yrs old
	- - - - - - - - - Kilograms per hectare - - - - - - - - -			
6/29/95	178	320	265	301
8/27/95	194	275	208	277
10/21/95	388	392	224	290
12/18/95	176	322	200	277
4/13/96	196	190	174	213
6/15/96	203	311	233	270
Average	222	302	217	271

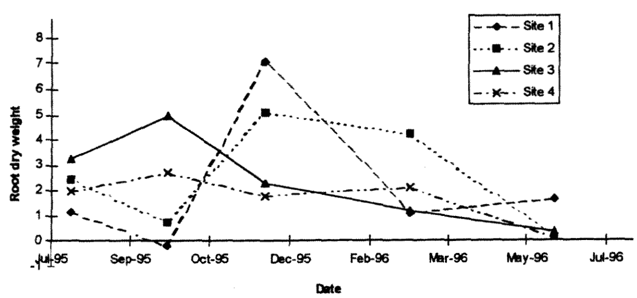

Figure 2—Changes in weekly aboveground autumnal litterfall rates (kg per ha-week) across a 100-year chronosequence of upland hardwood forest stands.

1985, Hughes and Fahey 1994, Polglase and Attiwill 1992). There are two possible explanations for why this is not the case in this study. First, much of the vegetation in Site 1 is herbaceous annuals and short-lived perennial vines and shrubs. Turnover of this material could be high enough to lead to the higher-than-expected values. Adding to this high indigenous litterfall rate is the influx of litter material from surrounding mature stands. From personal observations, it seems that a significant component of the litterfall in Site 1 came from mature trees in stands surrounding the plots in the harvested stand. Together, this seems to yield the higher-than-expected litterfall rates in Site 1. Because the total leaf area of oak and hickory stems within Site 1 is not known, this off-site litter could not be separated from the total litterfall collections.

N and P Inputs

Potential N and P inputs from fine roots in the 12- and 31-year-old stands (Sites 2 and 3) exceeded the total nutrient content present in the litterfall. Since fine root biomass reached preharvest levels more quickly than leaf area, contributions of N and P from fine root decomposition may exceed inputs from aboveground litterfall until maximum leaf area is reached in the stand. If forest floor decomposition is assumed to be approximately equal litterfall in the 80 to 100-year-old stand, then N and P contributions from fine roots are approximately equal to contributions from aboveground litterfall in this stand. In the 6-year-old stand (Site 1), the combination of less fine root biomass, rapid turnover of aboveground biomass, and the influx of litter from outside the stand means that fine root contributions to N and P inputs are less important than inputs from aboveground litterfall. In the 12- and 31-year-old stands (Sites 2 and 3), high fine root biomass and decomposition yield N and P inputs in excess of the amounts of N and P held in annual litterfall.

CONCLUSIONS

Polglase and Attiwill (1992) express the commonly held opinion that nutrient returns to the soil from plant litter are derived mainly from leaf fall and stem death from stand self-thinning. They surmise from their measurements of aboveground productivity and litterfall return that in young mountain ash (*Eucalyptus regnans*) stands, soil nutrient reserves supply the majority of N taken up by the vegetation. Joslin and Henderson (1987) recognized the importance of fine root turnover to the inputs of organic matter and nutrients in mature hardwood forests. Our study suggests that, for upland oak-hickory forests, fine root decomposition is the major pathway for N and P return to the soil from about age 10 years until maturity, at age 80 to 100 years. Mineralization of these organic forms of N probably accounts for the majority of the N taken up by the regenerating vegetation in these stands.

Soil nutrient availability is an important part of understanding soil quality and forest productivity. To adequately quantify the biological sources of plant-available soil N and P, measuring aboveground litterfall returns is not sufficient. Inputs of N and P from fine root decomposition can exceed litterfall inputs from 10 years until 70 or 80 years of age. Fine roots also supply organic N and P compounds to the soil throughout the year, not just during the fall and winter. Because of the high activity of rhizosphere microorganisms, mineralization of the N and P in decomposing fine roots may be more rapid than from forest floor litter. Thus, a complete understanding of nutrient cycling, nutrient availability, and soil quality in upland hardwood forest stands must consider the belowground turnover of plant tissues as well as the aboveground turnover of leaves, branches, and stems.

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