

## **Nutrient Dynamics**

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# FOLIAR NITROGEN AND PHOSPHOROUS DYNAMICS OF BLACK CHERRY AND RED MAPLE TREES GROWING IN GREAT SMOKY MOUNTAINS NATIONAL PARK

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**Abstract**—The overall goal of this investigation was to determine foliar nutrient dynamics (N and P) of black cherry and red maple trees growing at two locations differing in elevation, ozone, exposure, and other microsite and edaphic attributes within Great Smoky Mountains National Park. At the low elevation site, the two species both exhibited smaller amounts and proportions of leaf P remaining in abscised foliage (i.e., lower magnitude and efficiency) compared with the higher elevation site. Red maple was more efficient than black cherry regarding phosphorous (i.e., maple retains less P in abscised foliage) retranslocation. There are strong indications that translocation of mobile nutrients from senescing foliage is of greater magnitude and efficiency at the higher compared to the lower elevation site. These indications are strongest during the first year of sampling (1994) and are primarily associated with P, although some differences do occur for N as well. The tendency for greater differentiation to occur in terms of P translocation (both magnitude and efficiency) suggests that soil P availability is the primary nutritional distinction between the two elevations. It is likely that this cycling differential exists because the higher elevation soils have lower P availability compared to the lower elevation soils.

## INTRODUCTION

Switzer and Nelson (1972) found that approximately 40 percent and 60 percent of the annual requirements of N and P in loblolly pine (*Pinus taeda* L.) could be accounted for by internal nutrient cycling. Similar results have been reported for other plant species (Chapin and Kedrowski 1983, Killinbeck 1996). However, our understanding of this phenomenon and its subsequent effect on plant growth, nutrient cycling, and adaptation to environmental stresses remains very limited (Killinbeck 1996).

Nutrient resorption is dependent on many factors including site fertility, water, and light (Chapin and Moilanen 1991, Hocking 1982, Killinbeck 1996, Small 1972). In addition, internal nutrient cycling has been shown to be altered by environmental factors such as acid rain (Oren and Schulze 1989) and ozone (Wright and others 1991).

The overall goal of this investigation was to determine foliar nutrient dynamics (N and P) over a 2-year period (1994 through 1995), for black cherry (*Prunus serotina* Ehrh.) and red maple (*Acer rubrum* L.) growing at two locations differing in elevation, ozone exposure, and other microsite and edaphic attributes within Great Smoky Mountains National Park (GRSM).

Specific objectives include an estimation of N and P internal translocation associated with foliage of red maple and black cherry, and a comparison of the magnitude and efficiency of this translocation for both species between two sites that differ in elevation as well as other attributes (soil characteristics, aspect, slope, site history, etc.). The terms “magnitude or quantity” refer to the amount of an element (N or P) undergoing translocation on an individual leaf basis (NT or PT), while “efficiency” is defined relative to the proportion of summer foliar content of N or P that is removed prior to foliage senescence (NTC or PTC).

Findings from this study will provide supplemental data to the Tennessee Valley Authority for parameterization of a physiologically based process model (TREGRO) (Weinstein and Yanai 1994). Results will also give a linkage information gathered on the physiological responses of these selected trees from the two locations in GRSM (Samuelson and Kelly 1997).

## METHODOLOGY

### Location

The study was located at two sites differing in elevation within GRSM. Twin Creeks, a low elevation site [600 meters (m)] is located 2 kilometers (km) from Gatlinburg, TN. Cove Mountain is a high elevation site (1200 m) located approximately 15 km from Gatlinburg. Scaffolding (two towers per site) was constructed at each site to access the upper canopies of mature, dominant black cherry and red maple. Soils were a loamy-skeletal, siliceous, mesic Typic Hapludult at Twin Creeks and a loamy-skeletal, siliceous, mesic Typic Haplumbrept at Cove Mountain (Samuelson and Kelly 1997). For more detailed site descriptions, refer to Samuelson and Kelly (1997).

### Data Collection

Leaves were collected within the crowns of trees in July (live) and November (senesced), 1994 and 1995. Leaves were collected in groups of five (one sample). Sample numbers varied by year, site, and species, depending on tree size and availability of leaf material (table 1). Black cherry samples were collected from two trees at Cove Mountain and three trees at Twin Creeks. Regarding red maple, samples were collected from one and two trees for 1994 and 1995, respectively, at Cove Mountain. At Twin Creeks, samples were collected from two and three trees in 1994 and 1995, respectively.

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Table 1—The amount of P and N (mg per leaf ) remaining in abscised foliage by species and location for 1994 and 1995<sup>a</sup>

Year and species	Location <sup>b</sup>	N <sup>c</sup>	PT	N	NT
1994					
Red maple	TC	7	0.149 a	7	3.702 a
	CM	8	0.462 a	8	2.600 a
Black cherry	TC	12	0.055 a	14	1.866 a
	CM	9	0.310 b	11	2.388 a
Both species	TC	19	0.090 a	21	2.477 a
	CM	17	0.382 b	19	2.478 a
1995					
Red maple	TC	18	0.393 a	18	3.192 a <sup>d</sup>
	CM	11	0.649 b	11	4.221 b
Black cherry	TC	17	0.002 a	17	1.149 a
	CM	2	0.064 a	2	1.066 a
Both species	TC	35	0.203 a	35	2.200 a
	CM	13	0.559 b	13	3.736 b

<sup>a</sup> PT=mg per leaf of phosphorus, NT=mg per leaf of nitrogen; means in rows followed by the same letter are not significantly different ( $p < 0.05$ ) according to t-tests.

<sup>b</sup> TC=Twin Creeks, CM=Cove Mountain.

<sup>c</sup> N=number of samples (5 lvs per sample).

<sup>d</sup> Significant at  $p < 0.10$ .

### Laboratory Analysis

Before determination of N and P, leaves were dried to a constant weight (70 °C), ground to pass a 20-mesh sieve, then analyzed for total N and P. Reference samples were analyzed in duplicate (at least every 20 samples,  $\geq 5$  percent) to determine accuracy and precision.

Total N was determined by thermal conductivity (Sweeney and Rexrod 1987) using a Leco N Determinator (Model FP 228, Leco Corp., St. Joseph, MI) for 1994 samples. A Perkin-Elmer 2400 Series 2 C, H & N analyzer (Perkin-Elmer Corp., Norwalk, CT) was used for 1995 samples. Phosphorus was determined colorimetrically (Milton Roy Co., Rochester, NY, Spectronic 501) on samples dry-ashed at 500 °C for 8 hours and taken up in dilute HCL (Jackson 1958).

The potential for foliage from the two sites to differ in terms of N and P leachability was assessed by placing randomly selected leaves in zippered plastic bags containing 50 ml distilled, deionized H<sub>2</sub>O. Samples were agitated for 1 hour and then the solution was chemically analyzed (ICAP).

### Data Analysis

Statistical analysis consisted of t-tests for comparison of response variables between species and the two sites. Differences with probability levels less than or equal to 5 percent are discussed.

## RESULTS AND DISCUSSION

### Phosphorus

In 1994 at the low elevation site (Twin Creeks), the two species both exhibited smaller amounts and proportions of leaf P being retained in abscised foliage (i.e., lower magnitude and efficiency) compared with the higher elevations (tables 1 and 2). This was also true in 1995 for red maple analyzed individually and when both species were included simultaneously in the statistical analysis. No differences between locations were evident in 1995 for black cherry (tables 1 and 2).

Since red maple is more active in internal translocation of P than black cherry (table 3), it is possible that the 1995 P results for both species combined may be driven by differences in species composition of samples between the two sites. Red maple is indicated in table 3 to be more efficient than black cherry (i.e., maple retains less P in abscised foliage) and composed the majority of the 1995 samples (n) at the high elevation site (Cove Mountain). In 1994, red maple and black cherry sample numbers (n) were very similar at both sites. Consequently, skewed results due to over-representation of red maple are unlikely in that year.

Some caution should be exercised concerning P translocation data for red maple. There were indications that greater tendencies existed for P to leach from the foliage of that species at the high elevation site (data not shown). Consequently, some differences between summer

Table 2—The proportion of P and N (percent) July foliar content remaining in abscised foliage by species and location for 1994 and 1995<sup>a</sup>

Year and species	Location <sup>b</sup>	N <sup>c</sup>	PTC	NTC
1994				
Red maple	TC	7	10.1a	71.2 a
	CM	8	53.6b	57.3 b
Black cherry	TC	12	6.9 a	61.0 a
	CM	9	42.1a	57.4 a
Both species	TC	19	8.1 a	64.4 a
	CM	17	47.5b	57.4 a
1995				
Red maple	TC	18	51.1a	72.9 a
	CM	11	70.6b	72.6 a
Black cherry	TC	17	11.9a	59.2 a
	CM	2	13.7a	56.9 a
Both species	TC	35	32.1a	66.2 a
	CM	13	61.8b	70.2 a

<sup>a</sup> PTC=percent phosphorus remaining, NTC=percent nitrogen remaining; means in rows followed by the same letter are not significantly different ( $p < 0.05$ ) according to t-tests.

<sup>b</sup> TC=Twin Creeks, CM=Cove Mountain.

<sup>c</sup> N=number of samples (5 lvs per sample).

Table 3—Species comparisons within each location<sup>a</sup>

Location <sup>b</sup>	Year	Species	PT	NT	PTC	NTC
TC	1994	Red maple	0.149 a	3.702 a	10.1 a	71.2a
		Black cherry	0.055 a	1.866 b	6.9 a	61.0b
	1995	Red maple	0.393 a	3.192 a	51.1 a	72.9a
		Black cherry	0.002 b	1.149 b	11.9 b	59.2b
CM	1994	Red maple	0.462 a	2.600 a	53.7 a	57.3a
		Black cherry	0.310 a	2.388 a	42.1 a	57.4a
	1995	Red maple	0.649 a	4.221 a	70.6 a	72.6a
		Black cherry	0.064 b	1.066 b	13.7 a	56.9a

<sup>a</sup> PT=mg per leaf of phosphorus, NT=mg per leaf of nitrogen, PTC=percent phosphorus remaining, NTC=percent nitrogen remaining; means in rows followed by the same letter are not significantly different ( $p < 0.05$ ) according to t-tests.

<sup>b</sup> TC=Twin Creeks, CM=Cove Mountain.

verses autumn foliage contents may not be due to internal translocation alone.

Greater efficiency of internal translocation for P at the high elevation site may be reasonable given that extractable soil P is lower there (Samuelson and Kelly 1997). Levels of extractable soil P at the high elevation probably reflect P deficiency for many deciduous tree species while those at the low elevation are marginal to nondeficient. Some contend that efficiency is inversely related to nutrient availability (Killinbeck 1996).

## Nitrogen

There are fewer indications of meaningful differences between sites for N translocation than was the case for P (table 1). The magnitude of N translocation was quite similar for all species when compared between sites in 1994. However, there was an indication that N translocation was more efficient at the low elevation site for red maple in 1994 (table 2). In 1995, greater quantities of N were translocated in red maple and both species combined at the higher elevation, but no differences occurred in efficiency (tables 1 and 2).

Again, comparisons of N translocation between the two species within locations indicated that red maple was more active in translocation than black cherry. This was particularly true at the lower elevation site where both N magnitude and efficiency were highest for maple (table 3).

The 1995 results could be caused by (1) a heavier weighting toward red maple sampling at high elevation (i.e., since red maple at both sites was more efficient than black cherry) or

(2) lower soil N availability at the upper elevation. The latter possibility is conjecture since total soil N and ammonium levels were higher at the upper elevation. However, mineralization rates there may be less rapid than at the lower site due to greater extremes in temperature and, if so, greater efficiency in N translocation could be a credible adaptation.

## CONCLUSIONS

There are strong indications that translocation of mobile nutrients from senescing foliage is of greater magnitude and more efficient at the higher elevation site (Cove Mountain) compared with the lower (Twin Creeks). In comparisons of the two species evaluated, red maple also appears to transfer greater quantities of N and P and to be more efficient in this process. These indications are strongest during the first year of sampling (1994) and are primarily associated with P, although some differences do occur for N as well (tables 1-3). The tendency for greater differentiation to occur in terms of P translocation (both magnitude and efficiency) suggests that P availability is the primary nutritional distinction between the two elevations. While both sites are likely deficient in soil N (although this study was not designed to ascertain the degree to which deficiencies exist), the differential between the two is greatest for P. It is likely that this cycling differential exists because the high elevation is P deficient while the lower is not.

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# FOLIAR AND BELOWGROUND NUTRIENT DYNAMICS IN MIXED HARDWOOD FOREST ECOSYSTEMS

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**Abstract**—Many hardwood forest stands are composed of mixtures of species. The contribution of each species to ecosystem processes, including nutrient cycling, is poorly understood. This research was designed to quantify aboveground and belowground nutrient cycling processes in mixed hardwood forests. Nitrogen and phosphorus retranslocation rates were determined for a variety of species found in these forests. There were significant differences in nutrient retranslocation rates between the species sampled. Leaf litter decomposition followed a linear decay pattern, while decomposition of fine root tissue followed an exponential decay pattern. Patterns of nutrient immobilization and mineralization in fine root tissue differed markedly from those of decaying leaf tissue. These results indicate that the decay patterns of both above- and belowground components should be measured to fully elucidate nutrient cycling processes in forest systems.

## INTRODUCTION

In natural ecosystems, nutrients are often limiting to plant growth with nitrogen (N) and phosphorus (P) commonly the most limiting nutrients. Many studies have examined the patterns of carbon (C), N, and P storage and cycling in forest ecosystems. In second-growth aggrading forest stands, large quantities of nutrients are stored in the woody biomass, but mortality of this component can be low and trees that die exhibit slow decomposition rates of the large woody components. These components can immobilize nutrients for prolonged periods during the decay process and subsequent nutrient mineralization can take many decades (Alban and Pastor 1993). A large proportion of the nutrient transfer processes occur through the production, senescence, death, and subsequent decomposition of annual aboveground litterfall and belowground fine root biomass (Binkley 1986).

Nutrient retranslocation can be an effective mechanism by which both individual members of the forest community and the forest ecosystem as a whole conserve nutrients (Chapin and Kedrowski 1983, Ostman and Weaver 1982). At the individual plant level, plants capable of efficient retranslocation have a significant ecological advantage over individuals that are inefficient at nutrient retranslocation. May and Killingbeck (1992) demonstrated that preventing normal nutrient retranslocation in *Quercus ilicifolia* reduced plant growth by approximately 50 percent and seed production by 90 percent. Differing rates of nutrient retranslocation can also have a direct impact on the chemical characteristics of the leaf-fall that is produced in a forest stand. These differences in foliar chemistry may directly affect nutrient cycling processes in forest stands (Blair 1988, McClaugherty and others 1985). In this way, either positive or negative feedback mechanisms influencing nutrient cycling processes can be established.

The specific objectives of this study were:

- (1) To quantify the patterns of foliar nutrient retranslocation in various species during autumnal leaf senescence.
- (2) To determine the patterns of leaf decomposition of individual species and a cohort of leaf tissue consisting of a mixture of leaf types in proportion to the annual leaf-fall in the stand.
- (3) To determine decomposition dynamics of the indigenous mix of fine root tissues from a mesic forest stand.

## METHODS

### Study Site Description

The site selected for this study is located in Putnam County in west-central Indiana. The soil at this site is a Russell silt-loam (fine-silty, mixed, mesic Typic Hapludalf) which developed from moderately thick loess deposits [70 to 100 centimeters (cm)] overlying glacial till. The vegetation, in decreasing order of total basal area, is dominated by white oak, *Q. alba* (56.7 percent); sugar maple, *Acer saccharum* (12.7 percent); mixed hickories, including *Carya ovalis*, *C. ovata*, and *C. cordiformis* (11.9 percent); northern red oak, *Q. rubra*, (9.6 percent), and black walnut, *Juglans nigra* (3.7 percent) with these species composing 95 percent of the basal area. The site index for oak is approximately 90 feet at a base age of 50 years and approaches the highest productivity levels for upland oak-hickory stands in the Midwest. The soil is characterized by high N availability and moderate to moderately high soil P availability based on comparisons to other oak-hickory dominated forests (Kaczmarek 1995).

### Foliar Nutrient Retranslocation

Nutrient retranslocation rates were determined for eight different species. The species selected—white oak, northern red oak, sugar maple, yellow poplar (*Liriodendron*

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*tulipifera*), shagbark hickory, beech (*Fagus grandifolia*), black walnut, and flowering dogwood (*Cornus florida*) are common associates in many mixed hardwood forests, and the presence of all these species on this single site allows nutrient retranslocation rates to be determined under uniform environmental and edaphic conditions. Six individuals of each species were selected. All trees sampled occupied dominant or codominant canopy positions in the overstory with the exception of sugar maple, beech, and flowering dogwood, which occurred as sapling size individuals in the understory. Leaves from the midcrown position were shot from the overstory trees. Leaves from the understory sugar maple, beech, and dogwood were collected with pruning poles. At the conclusion of the growing season, senescent leaves were collected from the identical trees that were sampled during the summer season. The autumnal sampling consisted entirely of senescent foliage collected as it fell from the tree. Both N and P retranslocation rates were calculated as fall nutrient concentrations divided by midsummer nutrient concentrations.

Analysis of variance was used to determine whether statistically significant differences existed between summer and fall N and P concentrations and nutrient retranslocation efficiencies (percentages). All comparisons were made with the General Linear Model (GLM). If this model revealed significant differences among species, then mean separation tests were performed using Duncan's Multiple Range Test (SAS Institute 1985).

### Leaf Litter and Fine Root Decomposition Dynamics

Litter decomposition dynamics were determined for two types of litter. The first litter type was white oak litter, which represented approximately 55 percent of the total leaf-fall mass. The second type of litter consisted of mixed litter of white oak, sugar maple, and hickory leaf litter in the relative proportion of 55 percent, 30 percent, and 15 percent, respectively. This is the same proportion as that of the total leaf-fall accounted for by these species. Litter bags were constructed from 1.5 millimeter (mm) nylon mesh, measured 20 cm by 20 cm, and contained 4 grams (g) of leaf tissue. Litter decomposition bags were placed in the field in December and natural movement of the litter layer due to wind and snowfall events incorporated these bags into the forest floor by the following spring.

Decomposition rates were determined over a period of 780 days. At sampling intervals of 0, 143, 233, 353, 503, and 780 following placement in the field, four litter bags of white oak litter and mixed species litter were retrieved and oven-dried at a temperature of 65 °C. Total N and P concentrations were determined for samples on each collection date. Initial mass and N and P concentrations were used with the mass remaining and N and P concentrations at each subsequent sampling period to determine patterns of net immobilization and mineralization. Initial N and P contents and the total N and P contents at each of the five sampling times were calculated. Increases in total nutrient content from the initial

time were considered as net immobilization of the nutrient, while decreases in total nutrient content were considered to be net mineralization of the nutrient.

The indigenous fine roots (2 mm or less in diameter) were collected. No effort was made to sort the fine root tissue into various species. Decayed fine roots were discarded. Fine roots were washed under distilled water to remove the adhering silt and clay particles. Root decomposition bags were formed by placing 500 milligrams (mg) of fine root tissue in 0.5 mm nylon mesh bags measuring 8 cm by 8 cm.

The decomposition study was initiated in August 1993 and spanned the period lasting through March 1995. At the beginning of the study, 72 total fine root decomposition bags were placed in the mineral soil at a depth of 10 cm. At each of the sampling times, nine fine root decomposition bags were retrieved. Following installation of the decomposition bags in August 1993, sampling occurred at 30, 90, 210, 270, 330, 390, 450, and 570 days. After the decomposition bags were retrieved from the field, they were rinsed under distilled water on a 0.106 mm sieve to remove any silt and clay particles adhering to the tissue. The root tissue was dried at a temperature of 65 °C for a period of 48 hours. Mass loss was determined as the difference between initial weight and the weight remaining at each given sampling period. Nitrogen and P concentrations were measured and total nutrient contents calculated as described for leaf litter.

## RESULTS AND DISCUSSION

### Summer and Fall Foliar N and P Concentrations

Summer foliar N and P concentrations exhibited wide species differences. Summer foliar N concentrations ranged from 1.83 percent in flowering dogwood to 2.69 percent in black walnut (table 1). The dominant overstory species in this stand—white oak, hickory, sugar maple, and northern red oak—had summer foliage N concentrations that fell within a relatively narrow range (2.0 to 2.2 percent). Nitrogen concentrations of black walnut and yellow-poplar foliage were higher than these of most other species present in the stand. Summer foliar P concentrations did differ significantly by species, but these differences were generally of a smaller magnitude than differences in foliar N concentrations (table 2). Black walnut had the highest foliar P concentrations at 0.21 percent, while flowering dogwood and beech had the lowest summer P concentrations of 0.15 percent. The remaining species had midsummer foliar P concentrations ranging from 0.18 to 0.19 percent.

Nitrogen concentrations in senescent foliage ranged from 0.7 percent in yellow-poplar foliage to 1.2 percent in black walnut foliage (table 1). Nitrogen concentrations in beech and black walnut foliage were significantly higher than N concentrations in most other species. For these two species, high summer foliar N concentrations were also reflected in high N concentrations in the senescent foliage.

Table 1—Mean<sup>a</sup> summer and fall nitrogen concentrations (percentage of dry mass) and nitrogen retranslocation efficiencies of white oak, northern red oak, sugar maple, yellow-poplar, shagbark hickory, beech, black walnut, and flowering dogwood

Species	Summer foliage (N)	Fall foliage (N)	Nitrogen retranslocation
----- Percent -----			
White oak	2.19 cd	0.84 cd	61.7 b
Red oak	2.05 de	0.89 bc	56.4 bc
Sugar maple	1.97 de	0.77 cd	60.7 bc
Poplar	2.48 ab	0.68 d	72.5 a
Hickory	2.09 cd	0.78 cd	62.8 b
Beech	2.31 bc	1.05 ab	54.2 bc
Walnut	2.69 a	1.20 a	55.1 bc
Dogwood	1.83 e	0.87 c	51.6 c

<sup>a</sup> Means in the same column followed by the same letter do not differ significantly from one another at the 5 percent level using Duncan's Multiple Range Test.

Table 2—Mean<sup>a</sup> summer and fall phosphorus concentrations (percentage of dry mass) and phosphorus retranslocation efficiencies of white oak, northern red oak, sugar maple, yellow-poplar, shagbark hickory, beech, black walnut, and flowering dogwood

Species	Summer foliage (N)	Fall foliage (N)	Phosphorus retranslocation
----- Percent -----			
White oak	0.188 ab	0.071 ab	62.0 ab
Red oak	0.180 b	0.089 a	51.2 bc
Sugar maple	0.178 b	0.062 ab	64.1 ab
Poplar	0.180 b	0.047 b	73.9 a
Hickory	0.175 b	0.071 ab	55.7 abc
Beech	0.150 c	0.076 ab	49.3 bc
Walnut	0.208 a	0.089 a	55.9 abc
Dogwood	0.148 c	0.081 a	43.1 c

<sup>a</sup> Means in the same column followed by the same letter do not differ significantly from one another at the 5 percent level using Duncan's Multiple Range Test.

In contrast, yellow-poplar midsummer foliage was characterized by high N concentrations, but by low N concentrations in the senescent foliage. The remaining species had similar N concentrations in senescent foliage with concentrations ranging from 0.77 to 0.89 percent. Phosphorus concentrations in senescent foliage showed an

approximate twofold range of values (table 2). Yellow-poplar had the lowest P concentrations of approximately 0.05 percent, while P concentrations in black walnut and northern red oak were almost twice that level (0.09 percent). Species can be grouped into several categories based on nutrient characteristics in the senescent foliage. Black walnut had high N and P concentrations, white oak and sugar maple had medium N and P concentrations, while yellow-poplar had low N and P concentrations.

### Nitrogen and Phosphorus Retranslocation Efficiencies

Nitrogen retranslocation rates, expressed as the difference in midsummer and fall foliar nutrient concentrations, ranged from 52 percent in flowering dogwood to 73 percent in yellow-poplar (table 1). Yellow-poplar, on the basis of high summer nutrient status and low N concentrations in the fall foliage, had higher N retranslocation rates than any other species sampled. The range of N retranslocation values obtained in this study (52 to 73 percent) are within the range of N retranslocation values commonly reported for deciduous hardwood species. Ostman and Weaver (1982) found that N retranslocation of chestnut oak foliage in southern Illinois ranged from 76 to 80 percent. Boerner (1984), working in mixed oak forests in Ohio, found that N retranslocation was 50 and 48 percent for chestnut oak, and 46 and 31 percent for white oak growing on xeric and mesic sites, respectively. Pregitzer and others (1992) investigated foliar N retranslocation in sugar maple stands throughout Michigan and Minnesota and found that N retranslocation efficiency ranged from 47 to 63 percent.

Chapin and Kedrowski (1983) reported P retranslocation efficiencies that ranged from 11 to 89 percent in various temperate deciduous tree species. Phosphorus retranslocation efficiencies were 51 to 59 percent for chestnut oak stands in southern Illinois (Ostman and Weaver 1982). Boerner (1984) found that P retranslocation efficiencies were 44 and 45 percent for chestnut oak, and 66 and 52 percent for white oak growing on xeric and mesic sites, respectively. Phosphorus retranslocation in sugar maple has been found to exhibit wide variability (38 to 65 percent) across the species range (Pregitzer and others 1993).

The results of the current study support the findings of previous studies which have shown that N and P retranslocation is a significant nutrient conservation mechanism. The current study is unique in that nutrient retranslocation efficiencies were determined for a large number of species within a single uniform environment. Significant differences in nutrient retranslocation between species suggest that these species could respond differently to gradients in soil N and P availability. Once nutrient demands are initially satisfied by the soil supply, efficient nutrient retranslocation may tend to conserve internal nutrient supplies and reduce the quantities of nutrients that must be obtained from the soil to support each new foliage cohort. In this sense, efficient nutrient retranslocation can serve to decouple seasonal fluctuations in plant nutrient demand from seasonal changes in soil

nutrient supply. Differences in nutrient retranslocation rates can also influence characteristics of the leaf-fall at individual sites, thereby affecting nutrient cycling processes.

### Leaf Litter Decomposition Dynamics

Initial leaf litter N concentrations ranged from 0.79 percent for white oak to 1.05 percent for hickory leaf litter (table 3). The initial nutrient concentration of the mixed bag litter was calculated as the weighted mean of white oak, sugar maple, and hickory litter. Mean P concentrations in the individual species leaf litter ranged from 0.057 percent for sugar maple leaves to 0.080 percent for hickory leaves with a weighted mean P concentration of 0.065 percent for the mixed species litter (table 3).

Leaf litter decomposition for both the white oak and mixed species litter followed a linear decay pattern (fig. 1). Mass loss progressed at a relatively constant rate throughout the 780-day period. The similar pattern for white oak and mixed species litter is probably due to the inclusion of a

Table 3—Initial nitrogen and phosphorus concentrations of white oak, sugar maple, hickory, mixed foliage, and fine roots

Tissue type	Nitrogen Concentration	Phosphorus Concentration
	----- Percent -----	
White oak leaves	0.79	0.065
Sugar maple leaves	0.90	0.057
Hickory leaves	1.05	0.080
Weighted mean for mixed foliage	0.86	0.065
Fine roots	1.71	0.133

large percentage of white oak litter in the mixed species bags. Previous studies have demonstrated that *Quercus* species often exhibit slow decomposition rates due to their chemical characteristics. The current study indicates that the inclusion of sugar maple and hickory leaves with white oak leaves does not increase decomposition rates. Any “priming effect” of hickory and sugar maple on white oak decomposition rates is negligible for litter on this site and litter composition. The time required for 50 percent of the leaf litter to decompose is 1.8 years for white oak litter and 1.6 years for mixed litter. The time for 80 percent of the litter to decompose increases to 3 years for white oak and 2.7 years for mixed litter. The rates of litter decomposition measured in this study compare relatively closely to the rates measured in other studies in similar climates with similar litter composition. McClaugherty and others (1985) reported similar rates of mass loss for white oak and sugar maple foliage in southern Wisconsin. Kelly and Beauchamp (1987) observed similar rates of mass loss for mixed oak foliage in Tennessee. Decomposition rates of chestnut oak foliage in North Carolina (Blair 1988) were also comparable. The similar rates of decomposition of oak-dominated foliage across various sites may be related to the similar chemical composition of many types of oak foliage. This suggests that litter chemical characteristics, rather than site environmental conditions, may be the primary control over decomposition. Site characteristics exert an indirect effect on decomposition by determining species composition of the stand and the chemical characteristics of the litter produced on the site (Prescott 1995), but may have a relatively minor direct influence on decomposition rates.

Changes in N and P concentrations show similar trends for both litter types during the decay process (figs. 2 and 3). Nitrogen concentrations show gradual increases from initial levels of approximately 0.8 percent to 1.5 to 2.0 percent after 780 days in the field. Phosphorus concentrations in both litter types also demonstrated increases over the 780-day period from 0.065 percent to approximately 0.15 percent for white oak litter, and 0.19 percent for mixed litter. When changes in litter mass are combined with changes in nutrient concentrations over time, patterns of nutrient immobilization and mineralization become clear. For N, nutrient dynamics may be best described as a three-phase model. Both litter types exhibit net N mineralization over the initial 143-day period (fig. 2). Following this initial net release of N, N is immobilized in both leaf litter types. Sampling at 503 days demonstrated that significant quantities of N were released from the previous sampling interval. While N was released from the peak period of immobilization, both litter types still retained approximately 85 percent of their initial N contents. At this time, both litter types converged to the same point. At the final sampling interval (780 days), both litter types retained 80 percent of their initial N content. This suggests that relatively little N is released for over 2 years following leaf-fall and that freshly fallen leaf tissue serves as a minor source of nutrients. Using an annual leaf production rate of approximately 4,900 kilograms (kg) per hectare (ha) per year (Kaczmarek and others 1995), less than 10 kg per ha of N would be released from a single cohort of leaf litter after

### Leaf Litter Decomposition Rates

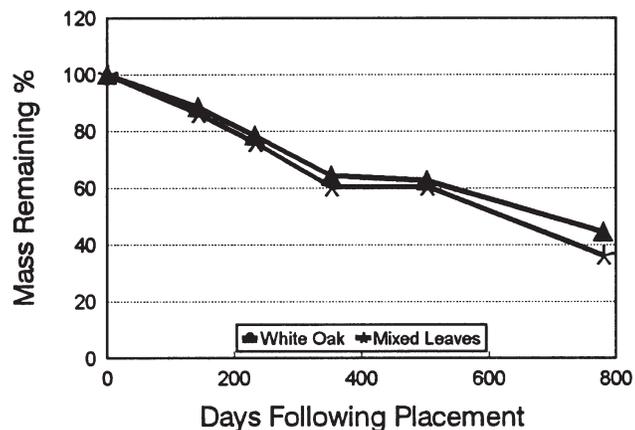


Figure 1—Rates of mass loss for white oak and mixed litter.

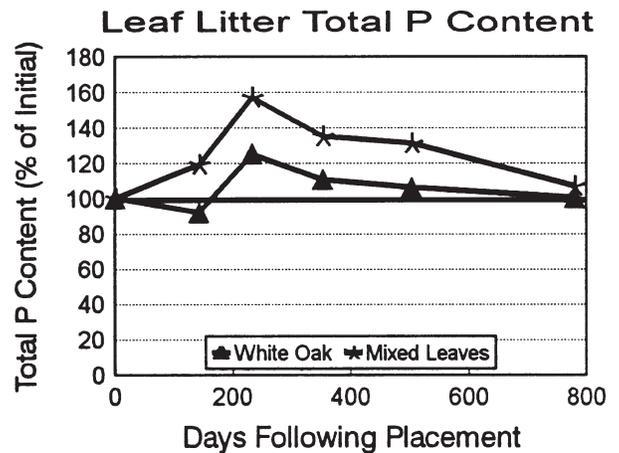
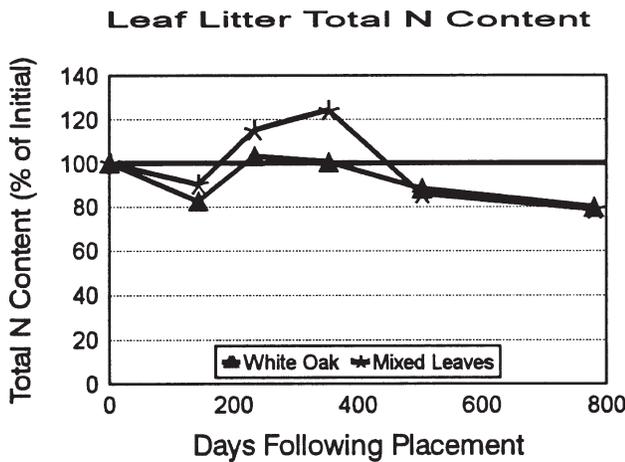
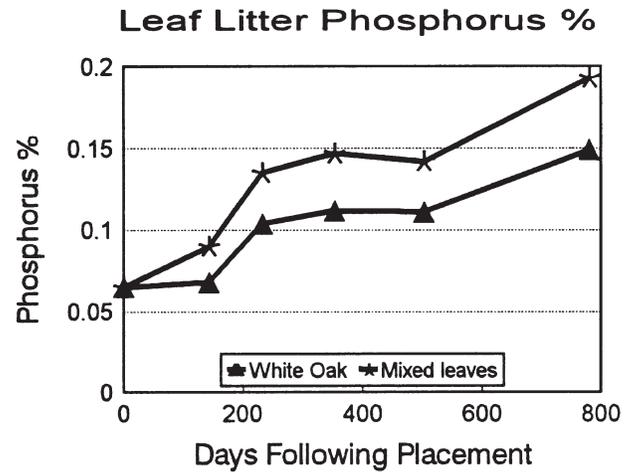
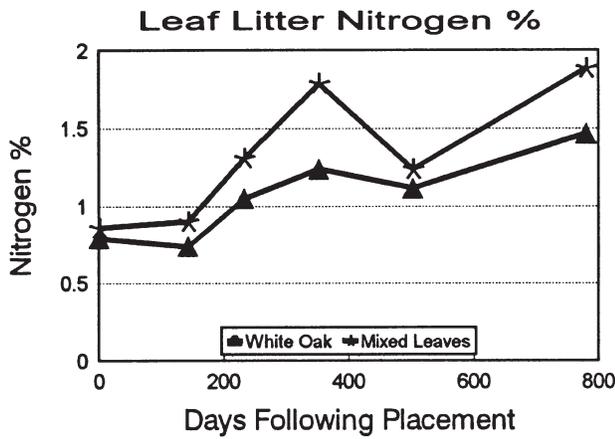


Figure 2—Nitrogen concentrations (top graph) and changes in total N content (bottom graph) for white oak and mixed litter. Points above the 100-percent line indicate net N immobilization while points below the 100-percent line represent net N mineralization.

Figure 3—Phosphorus concentrations (top graph) and changes in total P content (bottom graph) for white oak and mixed litter. Points above the 100-percent line indicate net P immobilization while points below the 100-percent line represent net P mineralization.

approximately 2 years. Longer time periods are clearly necessary for a cohort of leaf tissue to become a large net source of N in this stand.

Patterns of P immobilization and mineralization (fig. 3) for white oak litter show similar trends in the pattern of N mineralization. White oak litter exhibited a three-phase decomposition model with an initial period of P mineralization followed by periods of immobilization and, finally, mineralization. Mixed litter did not show an initial P release phase, but rather exhibited P immobilization followed by mineralization. At the end of the 780-day period, both litter types had released significant quantities of P, which were immobilized during earlier phases of decomposition, but total P contents were approximately equal to total P contents at time 0. By the end of this period, both litter types had converged to similar points which, as for N, demonstrates that initial differences in litter characteristics are most pronounced early in the decomposition process. As decomposition proceeds, initially different litter types appear to be converted into more similar chemical components, and

further decomposition dynamics appear to follow convergent paths.

Similar patterns of N and P immobilization and mineralization have been found in many but not all studies. Blair (1988) and Bockheim and others (1991) observed the general pattern of small initial net mineralization of N followed by varying degrees of N immobilization. The degree of N mineralization appears to be time-dependent. The decay sequence should be carried out for a sufficient time period to observe all phases of the decomposition process. Melillo and others (1989) proposed that a three-phase model incorporating initial periods of net N mineralization followed by immobilization, and finally substantial N mineralization, was a general step in the process of the conversion of organic debris to stable soil organic matter. Patterns of P retention and release have been found to be more variable. Blair (1988) found wide species differences in patterns of P retention and release. Bockheim and others (1991) likewise observed large differences in P dynamics during the decomposition process. Rustad and Cronan (1988), working with species

characterized by high initial P concentrations, found immediate net P mineralization without any P immobilization throughout the decomposition process. Polglase and others (1992) found that high soil P availability led to the production of leaf litter with high inorganic P concentrations. This inorganic P was labile and subject to rapid leaching losses during the early phases of decomposition.

### Fine Root Decomposition Dynamics

Fine roots collected from this stand were characterized by high N concentrations and moderate to moderately high P concentrations based on comparisons of fine root tissue collected from other oak-hickory dominated stands (Kaczmarek 1995). Decomposition rates during the early phase of decomposition of this tissue, based on comparisons to leaf litter discussed previously, were rapid. In contrast to leaf litter decomposition, which followed linear decay dynamics, the native fine root mix followed an exponential decay pattern (fig. 4). Mass loss was rapid and approached 50 percent within 1 year in the field. Based on exponential decay functions, approximately 1.2 years would be required for 50 percent mass loss to take place and 80 percent of the mass would be lost within 2.8 years. The time required to reach 80 percent mass loss for root tissue (2.8 years) compares closely to the time required for the mixed litter to lose 80 percent of its mass (2.7 years). The difference in linear and exponential decay models reveals that there are clear differences in the early stages of decomposition, but also suggest that these different tissues reach convergent points during the latter stages of decomposition.

Changes in N concentrations (fig. 5) in the decaying fine root tissue showed a similar pattern to decaying leaf litter. Following an initial decrease in N concentrations after 30 days in the field, N concentrations rose steadily, reaching 2.2 percent by the end of the study. Phosphorus concentrations were more variable throughout the sampling period; following a sharp decrease after 30 days, they generally followed an increasing trend for the remainder of the study. The patterns of N and P immobilization and mineralization of fine root tissue was distinctly different

### Fine Root Decomposition Rates

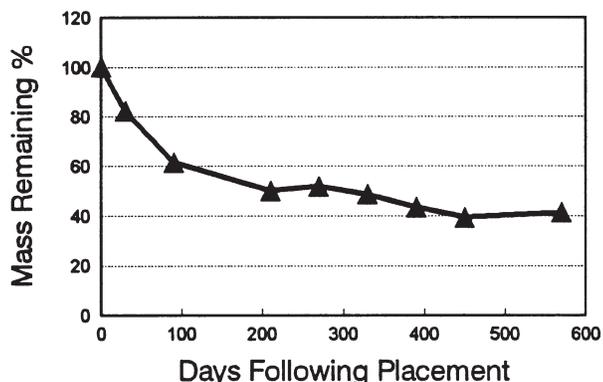


Figure 4—Rates of mass loss for fine root tissue.

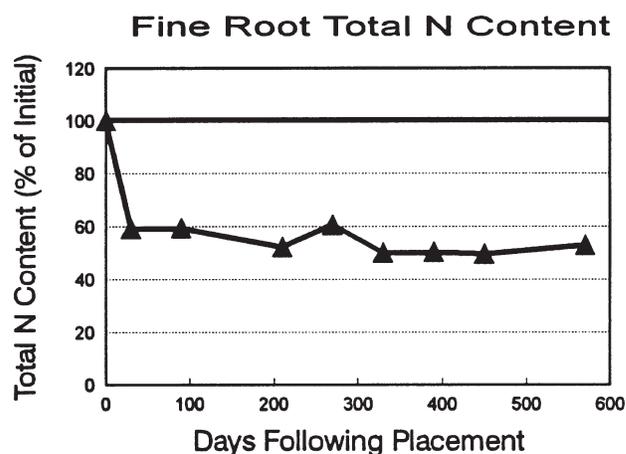
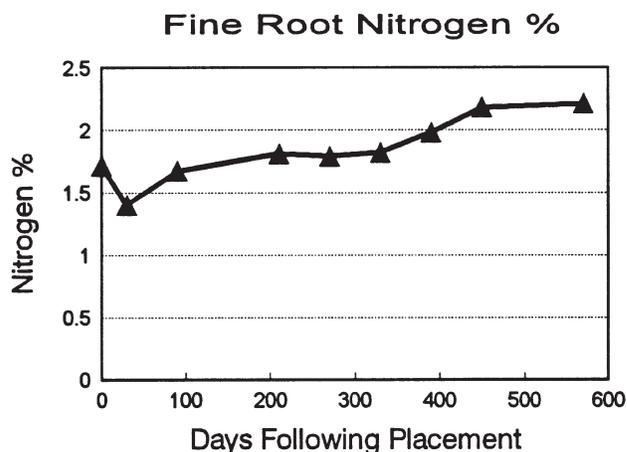


Figure 5—Nitrogen concentrations (top graph) and changes in total N content (bottom graph) for fine root tissue. Points above the 100-percent line indicate net N immobilization while points below the 100-percent line represent net N mineralization.

from the patterns observed for leaf litter. Within 30 days of placement in the field, more than 60 percent of the total N contained in the fine root tissue was released. After this point, little additional N was released. Changes in total P content (fig. 6) exhibited a similar trend with approximately 45 percent of the total P content being released within 30 days in the field. Further releases of P were slow and steady with more than 60 percent of the total P content being released by the end of the study. Combined, these data indicate that belowground nutrient dynamics follow a distinctly different pattern from the patterns observed in decaying leaf tissue. The possible reasons for these differences between nutrient release patterns for fine roots and leaf litter may relate to wide differences in initial N and P concentrations. Both N and P concentrations in fine root tissues were approximately double the concentrations of the leaf litter utilized in the study. High P concentrations in the fine root tissue may have made this nutrient subject to rapid leaching during the early phases of decomposition. The high N concentrations of the fine root tissue may have made C, rather than N, the primary factor controlling decomposition rates.

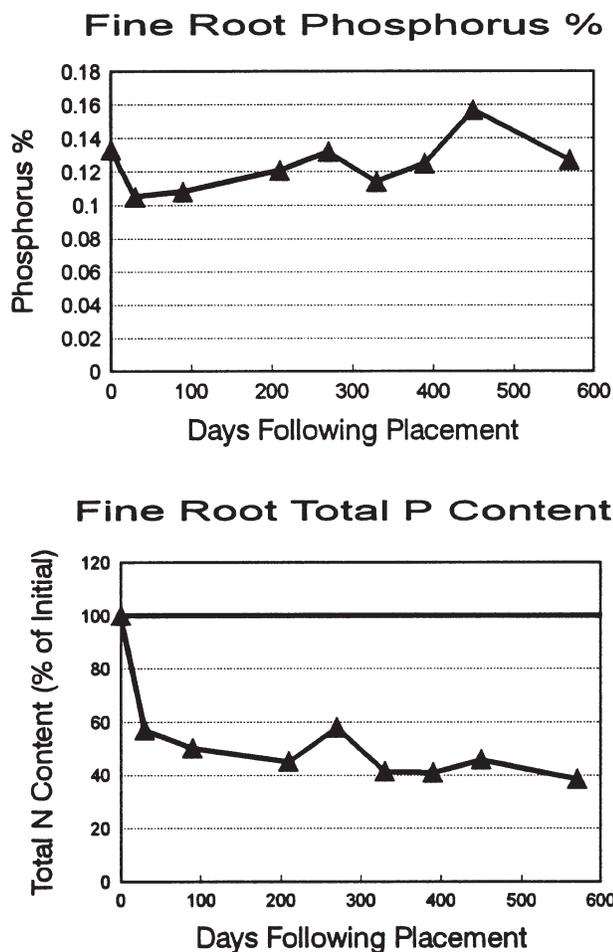


Figure 6—Phosphorus concentrations (top graph) and changes in total P content (bottom graph) for fine root tissue. Points above the 100-percent line indicate net P immobilization while points below the 100-percent line represent net P mineralization.

## CONCLUSIONS

There were significant differences in nutrient retranslocation rates between the species sampled. These differences may, in themselves, have important ecological consequences under nutrient-limited conditions. Differing nutrient retranslocation rates may also influence chemical characteristics of the leaf litter produced on a given site. These differences may then be reflected in differences in decomposition dynamics. This study also clearly indicates that belowground organic matter components must be considered to fully understand nutrient cycling processes. Belowground decomposition dynamics clearly differed from the aboveground measurements in this study. In particular, patterns of nutrient immobilization and mineralization differed significantly between aboveground and belowground tissues.

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

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**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<sup>2</sup> 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<sup>2</sup> per ha. The overstory basal area is dominated by white oak (12 m<sup>2</sup> per ha), with sugar maple (2 m<sup>2</sup> per ha), and hickory [*C. ovata* (Miller) K. Koch and *C. glabra* (Miller) Sweet] (2 m<sup>2</sup> 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<sup>2</sup> 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

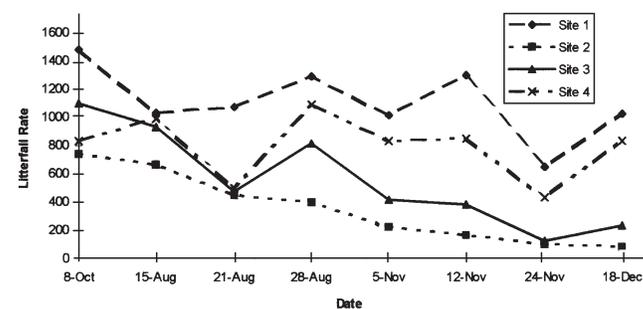


Figure 1—Effect of season upon fine root decomposition (g per m<sup>2</sup>- day) across a 100-year chronosequence of upland hardwood forest stands.

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

Collection date	Total fine root biomass collected			
	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

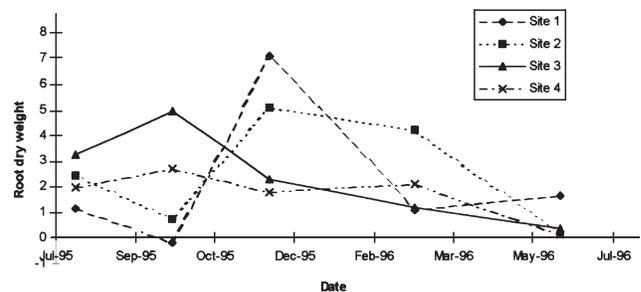


Figure 2—Changes in weekly aboveground autumnal litterfall rates (kg per ha-week) across a 100-year chronosequence of upland hardwood forest stands.

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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