A Decrease in Oak Litter Mass Changes Nutrient Dynamics in the Litter Layer of a Central Hardwood Forest

Kathryn B. Piatek, Prinith Munasinghe, William T. Peterjohn, Mary Beth Adams, and Jonathan R. Cumming

ABSTRACT

The abundance of oak is declining in the central hardwood forest, resulting in structural and functional changes in the litter layer. We hypothesized that a decline in oak litter mass associated with a lower oak component will result in an increase in nutrient cycling rates in the litter layer. To test this hypothesis, we compared mass loss and C, N, P, and Ca dynamics in pure oak litter and in litter made of 48% oak plus 52% five other deciduous species in a central hardwood forest in West Virginia. In 12 months of litter decomposition, pure oak litter decomposed more slowly, retained more C and N, immobilized more and subsequently did not release P, and released less Ca than litter consisting of 48% oak plus five other species. Annual stand-level nutrient fluxes in pure oak and in 48% oak plus five other species litter were correspondingly +4.1 and −4.4 kg ha^{-1} N, +0.22 and −0.17 kg ha^{-1} P, and −9.3 and −16.7 kg ha^{-1} Ca. These results indicate that a decline in oak will cause more rapid nutrient cycling in the litter layer of affected central hardwood stands.

Keywords: central hardwoods, litter, oak decline, nutrient cycling

The central hardwood forest spans the area approximately from Massachusetts and Wisconsin to Alabama and from Missouri to West Virginia (Hicks 1998, Fralish 2003, Kromroy et al. 2008). The most prominent characteristic of the central hardwood forest is the dominance of oaks, with 18 species of oak distinguishing the core central hardwoods from zones of transition into other forest types (Fralish 2003). The average oak component within the oak-hickory type reaches 93% in Iowa and Missouri, and it declines to <10% in other hardwood types (Kromroy et al. 2008). Historical records of species abundance indicate that oaks became dominant in the eastern United States forests after the last glacial maximum (Watts 1979, Davis 1981). The long history of oak domination was facilitated primarily by widespread and frequent fires (Abrams 1992, Abrams et al. 1997, Nowacki and Abrams 2008).

In more recent history, oak abundance has been decreasing in various parts of the range, a pattern that is attributed mainly to fire suppression (Dwyer et al. 2007, Luppold and Alderman 2007, Kromroy et al. 2008, Nowacki and Abrams 2008). Regeneration failures of oak are widespread (Cho and Boerner 1991, Smith 1992). At the Fernow Experimental Forest in West Virginia, the importance values for red oak in the understory declined between 1958 and 1997 from 4.3 to 0 in stands that were commercially clearcut and from 2.3 to 0 in uncut stands (Schuler and Gillespie 2000). In addition to the elimination of fire, outbreaks of the gypsy moth (*Lymantria dyspar*), deer browsing, and oak mortality due to the oak-decline syndrome (Manion 1991, Jones et al. 1993, Liebhold et al. 1995, Dwyer et al. 2007) suggest that oak dominance will continue to decline. A long-term change in species composition from fire-dependent oak, pine, and chestnut to fire-sensitive, mostly shade-tolerant maples, cherry, beech, and hemlock is already evident in the central hardwood forest (Nowacki and Abrams 2008).

A major decline of dominant species may acutely and chronically affect forest ecosystem structure and function, including the fluxes of nutrients (Ellison et al. 2005). Some of the first effects include a decrease in the relative mass of that species in the litter layer and concomitant changes in overall litter chemistry and its functional characteristics. Oak has among the highest lignin contents of the different species litters in the hardwood forests, resulting in a slow rate of decomposition and nutrient release from oak litter (Cromack and Monk 1975, Hobbie et al. 2006). A decline in oak abundance and the corresponding decrease in the relative mass of oak litter may result in a significant increase in the rate of nutrient cycling in the forest floors of the central hardwood forest.

Foliar litter plays a significant role in nutrient cycling processes because it temporarily ties up nutrients via microbial immobilization during decomposition, and subsequently releases nutrients via mineralization. Nitrogen (N), for example, is almost ubiquitously immobilized in foliar litter, reflecting a limitation both to litter decomposition and forest growth (Vitousek and Howarth 1991).

Manuscript received July 27, 2009, accepted February 19, 2010.

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This article uses metric units; the applicable conversion factors are: millimeter (mm): 1 mm = 0.039 in.; centimeters (cm): 1 cm = 0.39 in.; meters (m): 1 m = 3.3 ft; hectares (ha): 1 ha = 2.47 ac; kilograms (kg): 1 kg = 2.2 lb; gram (g): 1 g = 0.035 oz.

Phosphorus (P) is also commonly immobilized (Osono and Takeda 2004), whereas calcium (Ca) tends to be immobilized briefly or not at all (Adams and Angradi 1996, Piatek and Allen 2001). The magnitude and duration of each of these processes have significant consequences for site productivity.

Faster nutrient turnover in the litter layer may enhance forest productivity. However, faster nutrient cycling in addition to atmospheric N deposition may increase the risk of nitrate exports to surface water. Inputs of atmospheric N in some hardwood forests in the northeastern United States have exceeded the biological demand for N, resulting in nitrate and Ca exports (Peterjohn et al. 1996, Aber et al. 1998, Adams et al. 2006). Forests dominated by sugar maple are particularly prone to nitrate leaching, whereas forests dominated by oak retain N (Christenson et al. 2009). Therefore, a greater understanding of the consequences of a decline in the relative oak abundance for nutrient cycling processes in the litter layer will be important for the management of site productivity and water quality.

Nutrient dynamics in decomposing foliar litter is conveniently studied in litter bags. The litter bag technique is a versatile tool that allows ecologists to follow a known amount and composition of litter through changes as litter decomposes. Litter bag contents can be manipulated to reflect litter compositions that allow testing of specific hypotheses. Typically, different litters are applied on the same site to alleviate the confounding effects of different soil types. The premise of such manipulations is that the manipulated litter functions within the forest floor of the study site as it would within its own type of forest floor. The validity of that assumption is supported in the literature (Prescott 1995, Piatek and Allen 2001). By applying stand-level, species-specific litterfall mass, stand-level nutrient pools and fluxes can be calculated.

The litter bag technique has been used in many studies aimed at elucidating differences in decomposition of mixed versus single-species litters (Gartner and Cardon 2004, Hobbie et al. 2006, and many others). We know from these studies that litters of closely related species decompose faster when placed together in a mixture than when decomposing alone (Chapman and Koch 2007). Furthermore, as litter decomposition progresses, nutrient contents of species that decompose together in mixtures become increasingly similar to each other despite potentially substantial differences in initial litter chemistry (Piatek and Allen 2001, Osono and Takeda 2004).

In an earlier study, we determined that oak litter decomposing *within* a mix of other hardwood species decreases potential total litter N, P, and Ca mineralization (Piatek et al. 2009). However, the implications of a change in the mass of oak litter on litter nutrient fluxes have not been considered. We conducted this study to determine the potential implications of a decrease in oak litter mass in the central hardwood forests on nutrient immobilization and release patterns from the litter layer. We hypothesized that a decline in oak litter will result in an increase in the rates of litter nutrient cycling. To test this hypothesis, we conducted a litter bag study in a central hardwood forest in West Virginia with two litter types: 100% oak and a litter mix made of 48% oak plus 52% five other species common to West Virginia (from here on called the ambient mix). Pure oak litter was prepared by selecting only oak collected at the site, whereas ambient litter reflected the natural litter mix at the site. We chose these divergent litters because we wanted to approximate the oak proportions found across the range of the hardwood forest (Kromroy et al. 2008). Less than 48% oak in the mix may have not resulted in measurable differences in nutrient dynamics, whereas no oak at all was thought to be unlikely in the central hardwoods because of how they are defined (Fralish 2003, Kromroy et al. 2008) and the substantial efforts associated with stimulating oak regeneration (Smith et al. 1992, Brose et al. 2008). A pure-oak litter and a half-oak mix satisfied our requirements of being representative of possible stand conditions, ensuring measurable differences, and allowing us to consider potential implications of a change in oak mass for nutrient cycling.

Materials and Methods

Study Site

We conducted our study in the Long-Term Soil Productivity Plots at the Fernow Experimental Forest in Tucker County, West Virginia (latitude 39°04′N, longitude 79°41′W). Mean annual precipitation at the site is 1,422 mm (56 in.; Gilliam et al. 1996). Soils are generally thin (<1 m depth), acidic, sandy-loams of the Inceptisol order (Gilliam et al. 1994). The Long-Term Soil Productivity Study was established in 1996 following a whole-tree harvest. Several treatments were imposed in a randomized complete block design to study the effects of simulated acidic deposition, and details of that study design are provided in Adams et al. (2004). Briefly, four adjacent blocks were established along a slope gradient at elevation of 798–847 m. All plots (treated and not treated) are 0.2 ha, with a buffer strip treated in the same manner. Today, this is a naturally regenerated young hardwood stand. For the purpose of the study reported here, we used the one unamended control plot in each block (total of four plots).

Litter Bag Preparation

We collected foliar litter from the top of the forest floor from one unamended plot per block in early December 2005. Late collection ensured that most of the oak litter fell to the ground. We separated leaves by species into an oak group, consisting of northern red oak (*Quercus rubra*) plus a minor white and chestnut oak (*Quercus alba*) presence, and maple (*Acer rubrum* and *Acer saccharum*), yellow-poplar (*Liriodendron tulipifera*), magnolia (*Magnolia acuminata* and *Magnolia fraserii*), sweet birch (*Betula lenta*), and cherry (*Prunus serotina* and *P. pennsylvanica*). We then combined all collected litter within species, thoroughly mixed it within species, and air-dried it for 10 days. We determined the weight proportions of species to be 48% oak, 19% yellow-poplar, 14% maple, 12% magnolia, 4% cherry, and 3% sweet birch. Using these proportions, we made our ambient litter mix. Also from these collections, oak litter alone comprised our pure oak litter type.

Litter collected in early December is most likely free of easily leachable nutrient components that may make up a small proportion of total litter nutrients. Thus, our initial nutrient contents and subsequent changes may be underestimated by the amount that had leached before collection; however, assuming that litter falls over a period of time, some litter of each species likely remained longer on the ground than other litter of the same species, and nutrient dynamics during subsequent decomposition will reflect an average of the litter conditions.

Approximately 10 g (total air-dried weight) of either oak or ambient litter was placed in nylon litter bags, with a 2-mm mesh size and dimensions of 22 × 25 cm. Eight litter bags of each litter type were made for each of the four planned collection times. Additionally, three litter subsamples of each species (18 samples total) were

Table 1. Initial C, N, P, Ca, and lignin concentrations and selected ratios for oak and ambient litter (48% oak, 19% yellow poplar, 14% maple, 12% magnolia, 4% cherry, and 3% birch).

	C	N	P	Ca	Lignin	C:N	C:P	N:P	Lignin:N	Lignin:P
	. . . .(%)		(mg/kg)	. . . . .(%)						
Oak	49.7	0.9	481	1.2	28.6	55	1,033	19	32	595
Ambient litter	48.4	1.1	526	1.37	24.5	47	940	21	24	475

oven-dried at 65°C for 48 hours to determine their oven-dry weights. The difference between oven-dry and air-dry weights of these subsamples was used to calculate oven-dry weights of initially air-dried samples in litter bags. Later, these three subsamples of each of the species were used to determine initial litter nutrient concentrations (analytical replicates only).

Litter Bag Placement and Collections

Litter bags were placed in a random fashion directly on the mineral soil in each of the blocks after snow had melted in March 2006. Earlier placement was not possible for logistical reasons. The process of decomposition is primarily a function of initial litter chemistry. Therefore, it was assumed to proceed at similar magnitudes whether litter bags are set out in March, as in this study, or directly after litterfall. This assumption is supported by evidence from a study in a neighboring watershed in which N immobilization peaked at 6 months of decomposition (Adams and Angradi 1996), just as in our study.

We collected two bags per block (8 total) of each litter type 3, 6, 7, and 12 months later. The 7-month collection was made to detect the switch from net immobilization to net mineralization.

Mass Loss Measurements and Nutrient Analysis

After collection, litter bags were immediately transported to the laboratory, where they were cleaned of debris. Litter was taken out of the mesh bags, oven-dried for 48 hours at 65°C, and weighed to the nearest hundredth gram. Mass loss over time was calculated as oven-dry mass of litter at time t over initial mass, in percent. The rate of decomposition in each litter type was calculated as the decay rate constant k using the exponential decay model (Olson 1963):

$$-k = (\ln X/X_0)/t,$$

where k is the linear decay rate constant per year, X is the sample mass at time t, X_0 is the initial sample mass, X/X_0 is the mass fraction remaining at time t, and $t = 1$ year.

Oven-dried litter was ground on a Wiley mill (60 mesh). The mill was vacuum-cleaned between samples. Ground litter was redried, and 0.3–0.5 g was analyzed for total C and N on a Carlo Erba 1500 NCS elemental analyzer with a Micro Dumas combustion procedure. For P and Ca, 0.2 g of ground litter was digested in 5 ml of concentrated nitric acid and 30% hydrogen peroxide at 125°C on a digestion block until colorless (5–7 hours). The volume of digest was diluted with deionized water and filtered with 0.45-μm nylon filter papers. Total P was measured on a VIS spectrophotometer (Shimadzu UV 160U, Japan). Total Ca was measured on a Varian Spectra 220 atomic absorption spectrophotometer at 225 nm in nitrous oxide/acetylene gas. Nutrient contents in each litter type were calculated as litter mass times the concentration at time t. The percentage of initial contents remaining at collection time t was calculated as nutrient contents at time t over initial nutrient contents; initial litter nutrient contents were equal to 100%.

Lignin Analysis

Subsamples of ground initial litters were analyzed for lignin concentration by Dairy One Forage Laboratory (Ithaca, NY). Subsamples were digested for 75 minutes in an ANKOM A200 Digestion Unit. Residues were further digested in 72% weight/weight sulfuric acid for 3 hours at ambient temperature (Dairy One 2007).

Calculations of Litter Nutrient Pools and Fluxes

Nutrient pools were calculated as products of litter mass per hectare and initial nutrient concentrations multiplied by percentage of initial contents remaining at the time of collection. Litter mass per hectare was obtained by collecting litter fall between August and December in three litter traps per plot, oven-drying at 65°C, and weighing the total contents. Mass used in calculating stand-level pools in pure oak litter was set equal to that of the collected ambient litter.

Three types of fluxes were estimated. First, peak N and P pools were subtracted from initial pools to estimate the amounts of N and P immobilized into microbial biomass (an increase in N or P). For C and Ca, which mineralized (decreased) over time, the midperiod pools were subtracted from initial pools to calculate the 6-month mineralization rate. Second, 12-month pools were subtracted from peak or midperiod pools to estimate the 6- to 12-month mineralization rate. Finally, end-of-period pools were subtracted from initial pools to determine net annual fluxes in the litter layer.

Statistical Analysis

Analysis of variance was used to test for the main effects of block (blocks 1–4) and litter type (oak versus ambient) with no interaction effects (insufficient degrees of freedom) on mass loss; decay rate constant; and C, N, P, and Ca contents using SAS statistical software (SAS Institute 1985). The analysis was performed separately for each collection time because the effect of collection time is large, and nutrient dynamics at each collection time are independent of each other.

Results

Characteristics of Initial Litters

The initial concentrations of C, N, P, Ca, and lignin and the C:N, C:P, lignin:N, and lignin:P ratios in oak and in ambient litter mix are shown in Table 1. Statistical analysis could not be performed because of the lack of plot-level replication of initial samples (only analytical replicates were obtained).

Litter Decomposition Rates

Changes in mass and decay rate constant k indicated that mass loss in oak litter was significantly slower than in ambient litter mix (Table 2). After 12 months, oak litter lost 47% of its original mass, whereas the ambient mix lost 63%. Carbon closely followed the mass-loss pattern; differences between litter types in C dynamics

Table 2. Changes in mass (percentage remaining) and decay rate constant (k, year^{-1}) (±SD) after 3, 6, 7, and 12 months of decomposition in oak and in ambient litter mix, with corresponding P values for the null hypothesis of no difference between oak and ambient litter.

	Mass				k			
	3 months	6 months	7 months	12 months	3 months	6 months	7 months	12 months
Oak	96.3 (1.1)	83.3 (0.7)	77.4 (1.4)	53.3 (1.6)	0.15 (0.04)	0.37 (0.02)	0.44 (0.03)	0.63 (0.03)
Ambient	90.7 (2.6)	69.8 (4.7)	59.2 (1.5)	37.2 (1.4)	0.39 (0.11)	0.72 (0.13)	0.89 (0.04)	0.99 (0.04)
P value	0.0147	0.0111	0.0004	0.0003	0.0162	0.0137	0.0005	0.0003

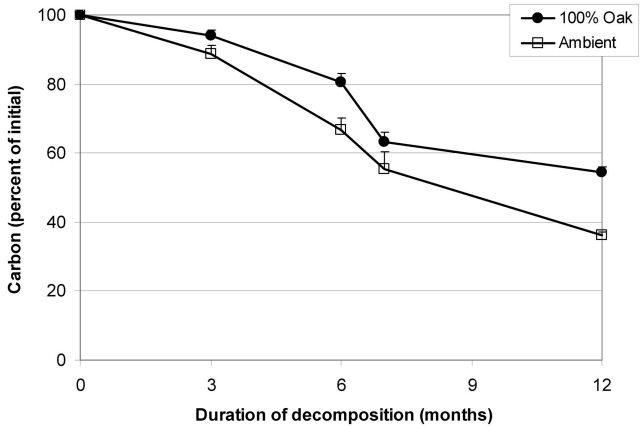

Figure 1. Carbon dynamics in decomposing oak and in ambient litter. Standard deviations (+1 SD) are shown as rising bars. Significant differences are indicated in Table 3. 0 indicates October.

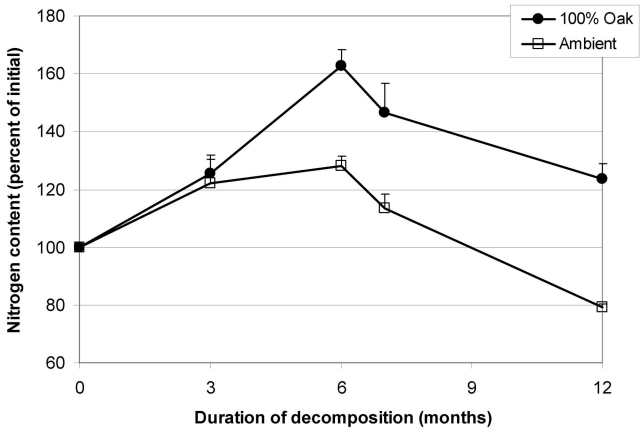

Figure 2. N dynamics in decomposing oak and in ambient litter. Standard deviations (+1 SD) are shown as rising bars. Significant differences are indicated in Table 3. 0 indicates October.

Table 3. Significant P values for the litter type effects (100% oak versus ambient mix) on C, N, P, and Ca content (mass × concentration) at each collection time. Block effects were not significant. Interaction of block × litter type was not tested because of insufficient degrees of freedom. Empty cells indicate $P > 0.05$.

	3 months	6 months	7 months	12 months
C		0.008		<0.0001
N		0.004	0.019	0.0003
P			0.024	0.0003
Ca	0.004	0.009	0.001	0.0001

were significant for each period (Figure 1). Block effects were not significant.

N Retention versus Release

Differences between litter types in N dynamics became significant in the sixth month of decomposition. Oak litter at that time immobilized 35% more N than ambient litter, resulting in a difference in net immobilization of 4.9 kg ha^{-1} more N in oak than in ambient litter (Table 3, Figure 2). After 1 year of decomposition, oak litter still contained 4.1 kg ha^{-1} more N than it started with, whereas ambient litter had released 4.4 kg ha^{-1} N (Table 4).

P Retention versus Release

At peak P immobilization, ambient litter mix immobilized more P, and its rate of immobilization was faster than that of oak litter (Figure 3). However, these differences were not statistically significant in the third and sixth months of decomposition (Table 3). In the seventh month of decomposition, these trends reversed, and net immobilization of P in oak litter became significantly higher than in ambient litter (Figure 3). After 1 year, oak litter still contained 0.22 kg P ha^{-1} more than it did initially (continued net immobilization), whereas the ambient mix had released 0.17 kg P ha^{-1} (net release; Table 4). Litter differences in P in month 12 of decomposition were also significant.

Calcium Release

Both litter types mineralized Ca from the beginning of the decomposition experiment. Ca release from oak was significantly slower than the release from ambient litter at all collection times. After 12 months, a total of 9.3 kg Ca ha^{-1} was released from oak, and 16.7 kg Ca ha^{-1} was released from ambient litter (Figure 4, Table 4).

Discussion

Effects of Initial Litter Chemistry

Oak litters exhibit among the lowest decay rates among hardwood species; contain lower initial N, P, and Ca levels in fresh litters; and immobilize more nutrients longer (Table 5). Even decomposing within a mix of other species litters, which are known to be easily decomposable, oak decomposition lags behind that of the other litters (Piatek et al. 2009). The overall lower decomposability of oak litter has been attributed to higher lignin content and higher lignin-to-nutrient ratios (Aber and Melillo 1982, Osono and Takeda 2004, Hobbie et al. 2006, Moore et al. 2006). These characteristics of oak litters were also reflected in this study. Initial stand-level nutrient pools in oak litter contained more C and less N, P, and Ca on a per-hectare basis than ambient litter, and this was due to the differences in initial nutrient concentrations between the study litters. Oak-only litter also lost mass and C more slowly (Table 2,

Table 4. Pool sizes and fluxes (+ or −) of nutrients in oak and in ambient litter, in kg ha^{-1}.

Element	Litter type	Initial pool (0)	Peak pool	Flux 1 (peak-0)	End pool[a]	Flux 2 (end-peak)	Total flux (end-0)
C	Oak	958.2	771.4	−186.8	522.2	−249.1	−436.0
C	Ambient	933.2	622.4	−310.7	338.7	−283.7	−594.5
N	Oak	17.4	28.2	+10.9	21.4	−6.8	+4.1
N	Ambient	21.2	27.2	+6.0	16.8	−10.0	−4.4
P	Oak	0.93	1.3	+0.37	1.15	−0.15	+0.22
P	Ambient	1.01	1.63	+0.61	0.84	−0.78	−0.17
Ca	Oak	23.1	16.9	−6.2	13.8	−3.1	−9.3
Ca	Ambient	26.4	14.3	−12.2	9.7	−4.6	−16.7

[a] End is 12 months after litter decomposition started.
Litter mass used (1928.0 kg ha^{-1}) is for ambient litter mix in our study stand (10-year-old hardwood); oak litter pools and fluxes are calculated based on the same weight as for ambient litter. Pools are product of litter mass and initial nutrient concentration from Table 1 and percent contents at corresponding times (see Figures). Fluxes are differences between pools.

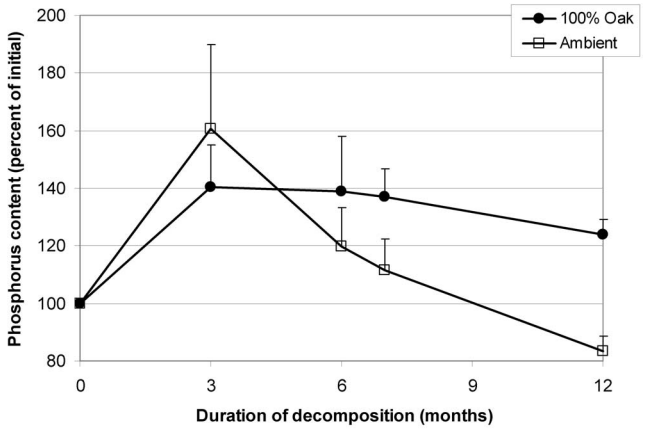

Figure 3. P dynamics in decomposing oak and in ambient litter. Standard deviations (+1 SD) are shown as rising bars. Significant differences are indicated in Table 3. 0 indicates October.

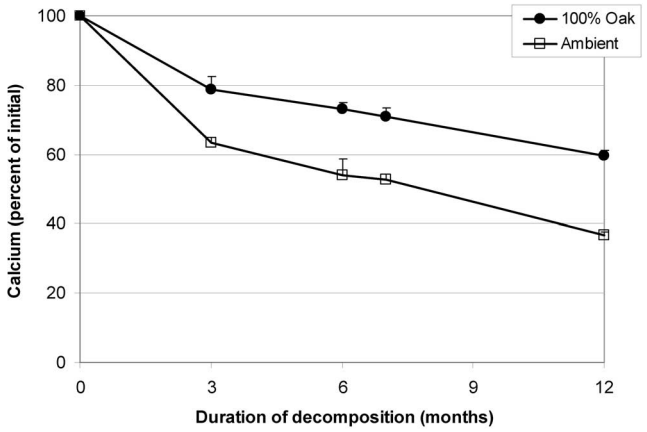

Figure 4. Ca dynamics in decomposing oak and in ambient litter. Standard deviations (+1 SD) are shown as rising bars. Significant differences are indicated in Table 3. 0 indicates October.

Figure 1) and had significantly higher N immobilization, significantly longer P immobilization, and significantly less Ca mineralization than ambient litter (Tables 3 and 4), with significant implications for stand-level nutrient dynamics.

Stand-Level N and P Retention in Litter

There are several implications of the higher N and P immobilization in oak than in ambient litter (Table 3). First, the microbe-mediated process of N immobilization in foliar litter results in a temporal N retention on site. The central hardwood forest is affected by some of the highest rates of atmospheric N deposition in the United States, (Adams et al. 2000), which can result in nitrate leaching to surface waters, posing a threat to aquatic ecosystems (Gilliam et al. 1996, Peterjohn et al. 1996). Therefore, an increased capacity for N retention in oak litter over ambient litter is beneficial in these forests. Stands in which the litter layer is composed of half oak and half other central hardwood species appears less efficient at N retention via litter immobilization than stands with a nearly pure oak component in the litter. On the basis of the results of this study, a difference in peak litter immobilization in these two litter types of 4.9 kg N ha^{-1} means that approximately 45% *more* atmospheric N can be potentially retained in near-pure oak stands in the first 6 months of litter decomposition than in stands with our ambient species mix (based on the area's average atmospheric inputs of 11 kg N ha^{-1} per year; Adams et al. 2000).

Second, the central hardwood forest may become P-limited as a result of long-term N additions with atmospheric deposition (Gress et al. 2007). Enzymatic evidence suggests that as forests become increasingly more N-rich under chronic atmospheric N deposition, P becomes more limiting to forest growth (Gress et al. 2007). Near-pure oak litter may contribute to P limitation, as microbes using the 100% oak litter sequestered but did not mineralize much P during decomposition (Table 3). On the other hand, it is unlikely that P immobilized by microbes during the first few months of litter decomposition would have been taken up by trees instead. Namely, when litter falls and decomposition begins in October, nutrient uptake by trees shuts down in our region, and it remains shut down for up to 6 months. Therefore, the differences between litter types in P fluxes are probably less important for tree growth during the immobilization phase than at other times of the year. In addition, P immobilization may be a mechanism of P storage, not unlike the retention of N. Phosphorus storage in litter via immobilization and subsequent P release at a time when plant uptake starts later in spring would support tree nutrition; however, oak litter released P more slowly than ambient litter, with likely lower benefit to productivity than the faster P release from ambient litter.

Stand-Level Implications of N, P, Ca, and C Release from Litter

Faster rates of mineralization between peak immobilization and the 12-month decomposition period released more N from ambient litter than from oak litter (flux 2, Table 3). At our site, this period falls between approximately April and October of the year after the litterfall; therefore, litter-released N may be taken up by trees. September, however, marks the end of the growing season, suggesting

Table 5. Cross-study comparison of litter decay rates and biomass and litter nutrient contents after 1 year of decomposition of hardwood tree species.

Species	Decay rate constant (year $^{-1}$)	Biomass	N	P	Ca	Study location
			(%)			
N. red oak[a]	0.13					Poland
European red oak[a]	0.36					Poland
Beech[b]	0.08	92	152			Hubbard Brook Exp. For., NH
Sugar maple[b]	0.25	78	155			Hubbard Brook Exp. For., NH
Paper birch[b]	0.34	73	131			Hubbard Brook Exp. For., NH
Pin cherry[b]	0.35	71	155			Hubbard Brook Exp. For., NH
Red maple[b]	0.42	66	145			Hubbard Brook Exp. For., NH
Chestnut oak[c]	0.33	73	92	80	75	Otto, NC
Oak[d]	0.63	53	122	125	60	Fernow Exp. For., WV
Ambient mix[e]	0.99	37	80	83	38	Fernow Exp. For., WV
Black birch[f]	0.92	22	41	55	20	Fernow Exp. For., WV
Black cherry[f]	1.38	18	41	40	20	Fernow Exp. For., WV
Red maple[f]	1.43	20	50	39	20	Fernow Exp. For., WV
Yellow poplar[f]	1.14	23	50	40	20	Fernow Exp. For., WV

[a] Reich et al. 2005.
[b] Melillo et al. 1982.
[c] Blair 1988.
[d] Over 90% northern red oak; this study.
[e] Ambient mix is made of 48% oak, 19% yellow poplar, 14% maple, 12% magnolia, 4% cherry, and 3% birch; this study.
[f] Adams and Angradi 1996.
Blank cells indicate that data were not available. Exp. For., Experimental Forest.

rapidly decreasing tree nutrient uptake. With net mineralization starting in ambient litter at about month 9 of decomposition, or September (Figure 2), litter-mineralized N may have a greater chance of being leached than being taken up by vegetation, possibly contributing to N exports from forests. The slower mineralization rates in pure oak resulted in a continued net retention of N at the end of the 12 months of decomposition (Table 3, Figure 2). Thus, N retention in annual pure-oak litterfall would last until and beyond the following October/November, when a new litter layer forms and the immobilization cycle we described begins again. In effect, pure oak litters can be considered efficient at N retention.

Ambient litter contributed more P to the system than oak litter; the slow P release from oak resulted in a continued P storage in litter until the next litter fall and P-immobilization cycle (past 12 months of decomposition). Analogous to N, net P mineralization from ambient liter at month 9 again suggests a misalignment with plant P demand (Table 3, Figure 3). Unlike N, however, which can be converted to nitrate and subsequently leached, P is not a mobile element in soils, and it remains in the system for possible uptake into microbial biomass decomposing the newly deposited litter.

Ca is important for site productivity in the central hardwood forest. Periodic removals of Ca-rich woody biomass in combination with leaching resulting from acidic atmospheric deposition may deplete Ca in soils (Adams et al. 2000, 2006). Calcium release from decomposing litter may serve as an important Ca source for forest trees. However, the benefit of that release during the first 6 months of litter decomposition is in question, as plant nutrient uptake stops in winter. Slower Ca release from pure oak litter than from ambient litter allows for longer Ca storage in litter and a greater synchrony of litter Ca release and plant uptake.

Management Implications

The magnitudes of annual nutrient fluxes in litter relative to potential stand nutrient use are relatively small, although they will grow larger as this stand matures. Still, they are important in both young and old stands for at least three reasons: (1) annual N immobilization into decomposing litter can account for almost all of the incoming atmospheric N inputs, suggesting that N immobilization in litter may retain or help retain N on site and potentially prevent nitrate leaching to surface waters; (2) P limitation to forest growth in stands affected by N inputs may be exacerbated because P is released from foliar litter during dormant rather than the growing season; and (3) Ca release from litter may be one of the most important sources of Ca to trees, and more than half of it occurs in the dormant season when tree uptake is shutdown, whereas losses to streams may continue as precipitation moves leachable soil elements through the profile. Our results show that pure oak litter is much more efficient at each of these processes than litter containing only half the oak mass. This supports our hypothesis that a lower oak litter mass accelerates nutrient cycling rates. These results further suggest that the current reduction of oak regeneration at the Fernow and other locations in the central hardwood forest will accelerate future rates of nutrient cycling, possibly increasing N loss from forests and nitrate inputs to surface waters. Also, because oak releases C at slower rates than does ambient litter, a lower oak component will decrease short-term C storage capacity in the litter layer of our forests.

Application of These Findings to Other Forest Types

The litter-nutrient dynamics we described were for pure oak litter and a litter mix made of 48% oak plus 52% other hardwood species. The choice of litter was aimed at simulating stand conditions with high and medium oak components. Oak litter in this study was composed primarily of northern red oak, although minor quantities of white and chestnut oaks were also present. Few hardwood forests are composed of 100% oak, although some oak-hickory forests closely approach that (Kromroy et al. 2008). Our mixed litter represented stand conditions at the site and, in addition to oak, was composed of red and sugar maple, black and pin cherry, Frasier and cucumber magnolia, yellow-poplar, and sweet birch, making up 52% of the litter mass found. Because of their low lignin content, these species produce litter that decomposes relatively easily and releases nutrients relatively fast. Nutrient dynamics are affected not only by the relative mass of oak in the litter (and, within that, possibly by the relative amounts of red to white oak) but also by the

particular mix of the other species and their functional characteristics, which affect decomposition (Hooper and Vitousek 1998). For example, a change from 100% oak in litter to 50%–50% oak–beech or oak–hickory is unlikely to result in substantially increased cycling rates, as both beech and hickory also have high lignin contents in litter. Increased nutrient cycling rates will be possible only with an increase in the content of easily decomposable litter relative to recalcitrant litter.

Forest stands at our study site are young, and they exhibit a mostly closed canopy. Large changes in nutrient concentrations due to tree age are not expected. Older hardwood stands, however, produce greater litter masses, on average 4,000 kg ha^{-1} on an annual basis, as observed in a neighboring watershed at the Fernow (Adams 2008). Therefore, pools and fluxes of C, N, P, and Ca will be at least twice as great as for our study litters (Table 3), as pools are a product of litter mass and element concentration and in older stands will be driven by the greater litter mass. This means that N retention capacity is likely to increase further in pure oak litters and decrease in ambient litters, with corresponding implications for nitrate leaching to surface waters. P limitation in oak and P mineralization in ambient litter will also increase, although the increase in mineralization will occur at the time of the year when it is unlikely to be assimilated by trees; Ca release will increase correspondingly.

Conclusions

On the basis of these results, we conclude that a substantial decrease in the relative proportion of oak in the hardwood forest ecosystem will precipitate changes in nutrient dynamics in the litter layer, with faster decomposition and therefore shorter C storage, further loss of N retention capacity, and increased P limitation to decomposition but greater levels of Ca release. Furthermore, these effects will exacerbate symptoms of N saturation in forests already affected by acidic atmospheric deposition; such as increased nitrate and Ca leaching, and potential P limitation to tree growth.

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