Oak contribution to litter nutrient dynamics in an Appalachian forest receiving elevated nitrogen and dolomite

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Abstract: Ecosystem nitrogen (N), phosphorus (P), and calcium (Ca) fluxes are affected by inputs of atmospheric N. Oak litter may additionally affect these fluxes because of its high-lignin content. We analyzed nutrient dynamics in ambient mixed-species litter in an aggrading hardwood stand at the Fernow Experimental Forest in West Virginia. We separated oak from the mix for analysis (oak) and compared it with total litter (all species) to understand how oak affects nutrient fluxes in the litter layer. The study was conducted under ambient atmospheric deposition, under elevated atmospheric deposition, and under elevated deposition plus mitigation with dolomite. N flux between litterfall and 12 months later indicated a net loss in all-species litter of up to 7.3 kg N·ha^{-1} and a retention of up to 0.6 kg N·ha^{-1} in oak. P flux included losses in all species in ambient and in dolomite treatments of up to 0.19 kg P·ha^{-1} and gains of up to 0.12 kg P·ha^{-1} in oak in all treatments. Oak mineralized Ca at an average across treatments of 4.6 kg Ca·ha^{-1} compared with 16 kg Ca·ha^{-1} in all species, with half of that when trees were dormant. Percent immobilization and release over initial litter were greater in oak than in all species, but nutrient fluxes were lower in oak than in all species because of low oak litter mass. Elevated deposition lowered N and increased P immobilization. Dolomite appeared to affect early N dynamics only. With an increase in litterfall mass when forests mature, these effects are also likely to increase.

Résumé : Les apports d'azote atmosphérique influencent les flux d'azote, de phosphore et de calcium dans les écosystèmes. La litière de chêne peut elle aussi influencer ces flux à cause de son taux élevé de lignine. Nous avons analysé la dynamique des nutriments dans la litière ambiante d'espèces mélangées dans un jeune peuplement feuillu à la forêt expérimentale de Fernow, en Virginie-Occidentale. Nous avons extrait le chêne du mélange pour l'analyser séparément et nous l'avons comparé à la litière complète, c'est-à-dire contenant toutes les espèces, pour comprendre comment cette espèce influence le flux des nutriments dans la couche de litière. L'étude a été réalisée dans des conditions de dépôts atmosphériques ambiants et élevés ainsi que dans des conditions de dépôts atmosphériques élevés atténués avec de la dolomite. D'après le flux d'azote pendant la période de 12 mois qui a suivi la chute de litière, il y a eu une perte nette allant jusqu'à 7,3 kg N·ha^{-1} en tenant compte de toutes les espèces et une rétention pouvant atteindre 0,6 kg N·ha^{-1} dans le cas du chêne. En tenant compte de toutes les espèces, le flux de phosphore incluait des pertes qui ont pu atteindre 0,19 kg P·ha^{-1} dans les conditions de dépôts ambiants et élevés avec de la dolomite mais il y eu des gains pouvant atteindre 0,12 kg P·ha^{-1} dans le cas du chêne, peu importe les conditions de dépôt. Le chêne minéralisait 4,6 kg Ca·ha^{-1} comparativement à 16 kg Ca·ha^{-1} pour la litière complète, et la moitié de la minéralisation survenait pendant que les arbres étaient dormants. Les pourcentages d'immobilisation et de libération dans la litière initiale étaient plus élevés dans le cas du chêne comparativement à la litière complète mais les flux de nutriments étaient plus faibles dans le cas du chêne à cause de la faible masse de litière de cette espèce. Des dépôts élevés ont diminué l'immobilisation de l'azote et augmenté celle du phosphore. La dolomite a semblé avoir un effet seulement sur la dynamique initiale de l'azote. Ces effets ont aussi des chances de s'accentuer avec l'augmentation de la masse de litière lorsque les forêts deviendront matures.

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Introduction

Oaks dominate the central hardwood forest, which extends from Massachusetts to Missouri and characterizes the Appalachian Mountains of the eastern US (Hicks 1998). Oaks are among the most important economic commodities in the region, and they provide an essential source of mast for wildlife. Oaks may also play a significant role in nutrient cycling in these forests. Oak litter is highly lignified (Sinsabaugh et al. 2002). High-lignin litters decompose most slowly, possibly resulting in a slower nutrient release (Hobbie et al. 2006). For example, nitrogen (N) retention in red oak litter is greater than in that of sugar maple (Templer et al. 2005), and oaks are known to have lower rates of nitrification than other species (Lovett et al. 2004). Therefore, a high oak component in forests may affect (*i*) carbon storage in the forest floors through lower rates of litter decomposition and (*ii*) potential nutrient availability through a delayed mineralization from litter.

A delayed mineralization from litter may be beneficial in the case of N in the central hardwood forest. Parts of this ecosystem in the Appalachian Mountains receive some of the highest rates of atmospheric N deposition in the US (Adams et al. 2000). Long-term atmospheric N inputs have been strongly linked to N loss as nitrate in surface water (Pregitzer et al. 2004; Stoddard 1994) and appear to be shifting ecosystem nutrient imbalance from N to phosphorus (P) limitation (Gress et al. 2007). Nitrate exports from forests tend to be highly correlated with calcium (Ca) exports, and Ca exports, combined with extraction of Ca in wood, may affect sustainable forest production (Adams et al. 2000). These potential far-reaching effects cause considerable interest in the mechanisms of N retention in forests influenced by atmospheric N deposition.

The Fernow Experimental Forest (Fernow) in West Virginia, located in the north-central Appalachian Mountains, receives about 10–12 kg $N \cdot ha^{-1} \cdot year^{-1}$ and about 17 kg $S \cdot ha^{-1} \cdot year^{-1}$ through atmospheric deposition (Adams et al. 1997). Experimental additions of N and sulfur (S) have resulted in a long-term increase in NO_3-N in stream water (Gilliam et al. 1996; Peterjohn et al. 1996) and in changes in foliar nutrients and stem growth (May et al. 2005). Such changes are consistent with N saturation — a condition in which forests cannot utilize all available N (Aber et al. 1998). Further, enzymatic evidence of P limitation has also been detected in this forest (Gress et al. 2007).

We conducted this study to increase our understanding of (*i*) the importance of oak to ecosystem N retention, P limitation, and Ca cycling, and (*ii*) the potential changes under elevated atmospheric deposition and mitigation with dolomite. We focused on microbial immobilization in fresh foliar litter as one of the N-retention mechanisms with possible consequences for P and Ca nutrition. As immobilization typically switches to mineralization within the first year of litter decomposition, we focused on the first-year nutrient dynamics in litter.

Materials and methods

Study site

We conducted this work at the Long Term Soil Productivity Study at the Fernow Experimental Forest in Tucker County, West Virginia (latitude 39°04′N, longitude 79°41′W). The Long Term Soil Productivity Study was established in 1996 to test the effects of (*i*) simulated acid deposition at three times the ambient rate to accelerate cation leaching from the soil and (*ii*) potential amelioration with dolomite (Adams et al. 1997, 2004). The area was whole-tree harvested, and four blocks were established along a slope at elevation 798–847 m.

We used three treatments: (1) ambient deposition (ambient); (2) annual additions of 36 kg $N \cdot ha^{-1}$ and 40 kg $S \cdot ha^{-1}$ as ammonium sulfate, or 3× ambient N and S deposition rates (elevated); and (3) treatment 2 plus dolomitic lime at 22.5 kg $Ca \cdot ha^{-1} \cdot year^{-1}$ and 11.6 kg $Mg \cdot ha^{-1} \cdot year^{-1}$ (dolomite). A total of 12 experimental plots (four replicates per treatment) were used. Plots are 0.2 ha and include a buffer strip (Adams et al. 2004). Trees originated from natural regeneration, and the canopy was closed at the time of this study, 11 years after harvest.

Foliar litter collection and litter bag preparation

We collected foliar litter directly from the top of the litter layer randomly across the entire area in each treatment plot in early December 2005. We chose this late collection to include all of the oak litter that falls last in the season. We separated leaves by species into northern red oak (*Quercus rubra*), 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 *Prunus pennsylvanica*). Then, keeping species separate, we combined litter by treatment. After thorough mixing, litter was air-dried for 10 days.

We determined the mass proportion of each species in each treatment in our collections and averaged them across treatments; the resulting average of 48% oak, 19% poplar, 14% maple, 12% magnolia, 4% cherry, and 3% sweet birch was used to make our litter bags. We used nylon litter bags, with a 2 mm mesh size and dimensions of 22 cm × 25 cm, and placed approximately 10 g of total mass of air-dried litter in each bag. Before taking bags to the field, we pulled three subsamples of each species litter and oven-dried them at 65 °C for 48 h to determine their oven-dry masses. The difference between oven-dry and air-dry masses of these subsamples was used to back-calculate oven-dry masses of initially air-dried samples in litter bags.

Litter bag placement and collections

We placed eight litter bags randomly in each of the 12 experimental plots after snow melted in March 2006. We placed the litter bags on the mineral soil and secured them with landscape pins. Then we retrieved two replicate bags from each plot and treatment (ambient, elevated, and dolomite) 3, 6, 7, and 12 months later. We made the 7 month collection to better detect the switch from net immobilization to net mineralization, which according to a study by Adams and Angradi (1996) in a neighboring watershed, could be expected around month 6 of decomposition.

Oak vs. all-species litters

After collection, litter bags were immediately transported to the laboratory and manually cleaned off outer debris. Leaves were taken out of the mesh bags within 1 week of

Table 1. Annual litterfall dry masses, initial nutrient concentrations, nutrient ratios, lignin concentration (per dry mass), and ratios of lignin to select nutrients for oak and all-species litters in three treatments.

Treatment	Litter type	Dry mass ($kg \cdot ha^{-1}$)	N (%)	P ($mg \cdot kg^{-1}$)	Ca (%)	N:P	Lignin (%)	Lignin:N	Lignin:P
Ambient	Oak	637.3	0.90	481	1.20	19	28.6	32	595
	All species	1928.2	1.34	526	1.25	21	24.3	18	462
Elevated	Oak	1240.8	1.00	431	1.01	23	31.5	32	731
	All species	1928.2	1.47	525	1.06	23	24.4	17	464
Dolomite	Oak	909.5	0.92	480	1.14	19	28.4	31	592
	All species	1928.2	1.51	511	1.27	22	25.5	17	499
p value			<0.000	0.001	<0.000	0.005	0.007	0.011	0.005

Note: *p* values are for litter type effects (treatment not significant). N, nitrogen; P, phosphorus; Ca, calcium.

collection. Oak was separated from the litter mix for all subsequent drying, weighing, and nutrient analysis, and the results are reported for litter type "oak". Analysis results for the rest of the litter mix together with the results for oak are reported for litter type "all species".

Mass loss measurements and nutrient analysis

Samples were oven-dried for 48 h at 65 °C and weighed to the nearest hundredth gram. The mass loss over time was calculated as the percentage of the initial oven-dry mass of litter. Oven-dried oak and other litters were 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 weighed into tin capsules (0.009 m × 0.005 m), pelleted, and analyzed for total carbon and N on a Carlo Erba 1500 CNS elemental analyzer with a Micro Dumas combustion procedure. For P and Ca analysis, 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 h). Aliquots from the filtrate were analyzed for total Ca on a Varian Spectra 220 atomic absorption spectrophotometer at 225 nm wavelength using nitrous oxide – acetylene gas. Total P was measured on a VIS spectrophotometer (Shimadzu UV 160U, Japan). Analytical precision was maintained by including blanks, analytical standards, and duplicate samples. Nutrient contents at each collection time were calculated from concentration and mass; the remaining contents were calculated as percentages of the initial contents.

Pool sizes and flux calculations

Total annual litterfall mass was obtained by collecting litter in plastic litter traps (2 per plot) in each treatment. Litterfall was separated by species and oven-dried to determine mass. Oven-dry mass was multiplied by the initial litter nutrient concentrations to calculate initial nutrient pools. Peak and final (end) pool sizes were calculated by multiplying the percentage of initial contents at peak and end times by the initial pool sizes. Fluxes were obtained by subtracting peak or end pool sizes from the initial pool sizes. Positive flux values reflect net increases, while negative values reflect net decreases.

Lignin analysis

Initial samples of each species by treatment were analyzed for lignin concentration by Dairy One Forage Laboratory (Ithaca, New York). Aliquots of ground litters were individually weighed into filter bags and digested for 75 min in an ANKOM A200 Digestion Unit. Residues were further digested in 72% (*m*/*m*) sulfuric acid for 3 h at ambient temperature (Dairy One Forage Lab Analytical Procedures, February 2007, www.dairyone.com/Forage/Procedures/default.htm).

Statistical analysis

We used analysis of variance with SAS statistical software (SAS Institute Inc., Cary, North Carolina) to test for the main effects of block (1–4), treatment (ambient, elevated, dolomite), litter type (oak vs. all species), and interaction of treatment and litter type on mass loss and on N, P, and Ca contents at each collection time. We used a significance level of $\alpha \leq 0.05$.

Results

Initial litter characteristics

Initial levels of N, P, Ca, nutrient ratios, or lignin concentration and lignin to nutrient ratios in litter were not statistically significantly different among treatments, but they were different among litter types. Oak litter exhibited lower initial N, P, and Ca, and higher lignin, lignin to N, and lignin to *p* values than all species together (Table 1).

Mass loss in oak litter versus all species together

For the first 6 months, oak litter decomposed consistently slower than litter of all species together. Later, all-species litter in the dolomite treatment decomposed as slowly as the oak litter (Fig. 1). After 12 months of decomposition, oak lost 52% of mass (an average across treatments), while all species together lost 60%.

N, P, and Ca dynamics

N immobilized into oak litter for the entire 12 months regardless of treatment. By contrast, all species together started to mineralize N after 7 months of decomposition (Fig. 2). Peak immobilization occurred at 6 months for most litters. Oak in ambient deposition treatment exhibited a delayed peak at 7 months. The highest N immobilization occurred in oak in both the ambient and dolomite treatments at an average of 152% of initial N. Conversely, lowest N immobilization had an average of 122% of initial N in all species and in oak in the elevated treatment. At 12 months, litter type was highly significant (Table 2), with oak still containing an average of 107% of initial N, while all species together contained an average of only 77% of initial N, a 30% difference.

P dynamics was dominated by microbial immobilization

Fig. 1. Mass loss as a percentage of initial mass in oak litter and all-species litter in three treatments in an aggrading Appalachian hardwood forest. Ambient, ambient deposition levels; elevated, annual triple atmospheric nitrogen + sulphur addition; dolomite, elevated + dolomitic lime addition. Note: oak litter was separated for analysis after decomposing in the all-species litter.

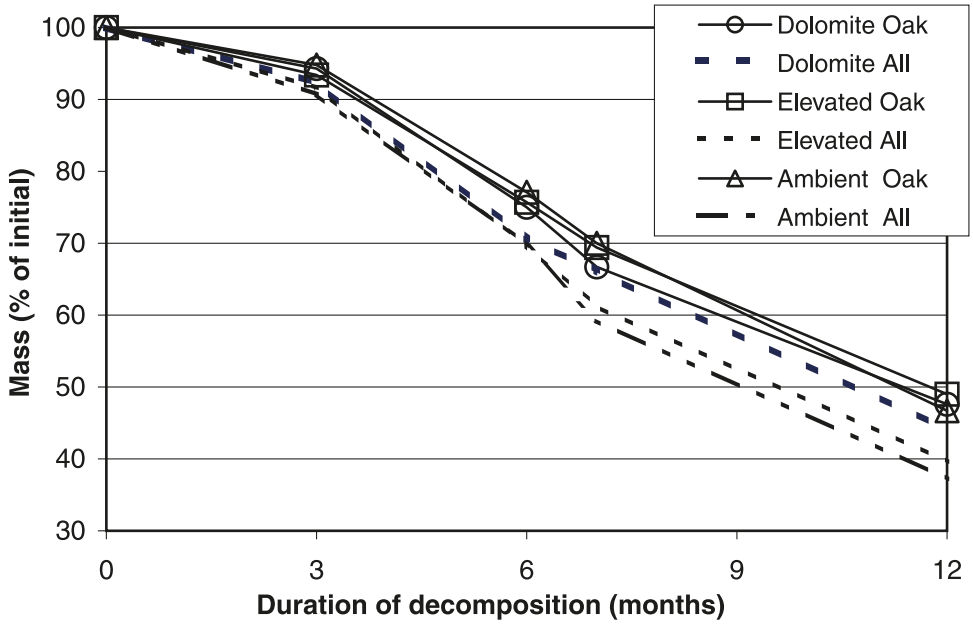
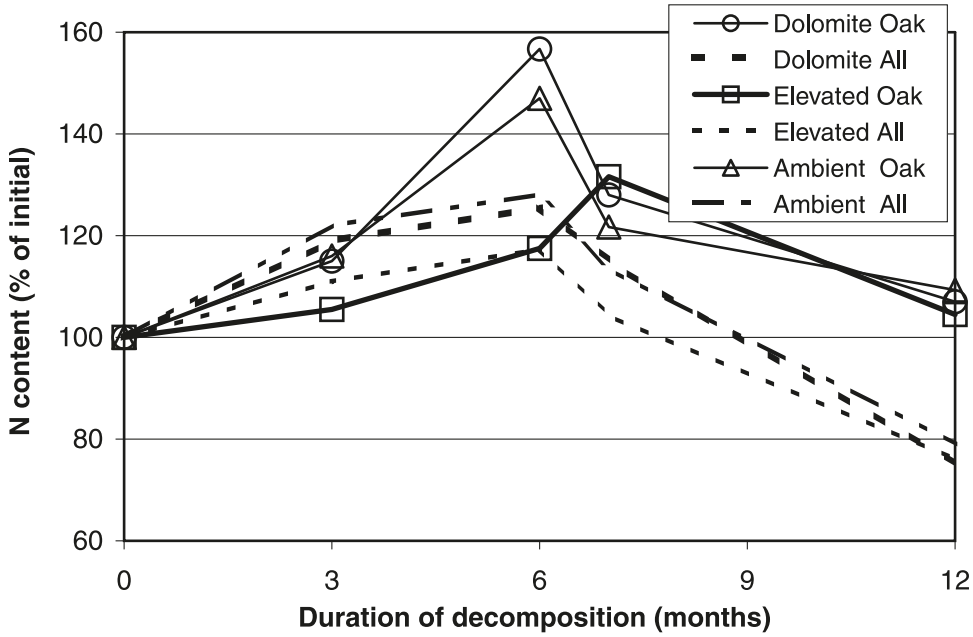


Fig. 2. Nitrogen (N) dynamics as a percentage of initial N mass oak and all-species litters in three treatments in an aggrading Appalachian hardwood forest.



(Fig. 3), peaking at 3 months at 168% of the initial P content in all species together in the ambient and dolomite treatments. Oak in the elevated treatment exhibited a peak later, at 6 months at 165% of initial P. All other litter × treatment combinations lacked a well-defined peak and immobilized much less P overall (Fig. 3). At the end of the 12 months of decomposition, the average P content was 117% of the initial P content in oak in all treatments compared with 94% in all species together in all treatments. This 23% difference was significant (Table 2).

Ca was released from oak litter from the beginning of decomposition. By month 6, an average of 40% of Ca was released. Ca release slowed considerably in the next 6 months in oak and appeared to exhibit some immobilization in the ambient and in the dolomite treatments (Fig. 4). At 12 months, 46% of Ca in oak and 60% in all species was mineralized, with significant differences among litter types (Table 2).

Litterfall nutrient pools and fluxes

Increases in litter pool sizes of N at peak immobilization

Table 2. *p* values for the effects of block, treatment (ambient, elevated, dolomite), litter type (oak, all species), and treatment × litter type interaction on percentage of remaining nitrogen (N), phosphorus (P), and calcium (Ca) at 3, 6, 7, and 12 months of decomposition in an aggrading hardwood forest at the Fernow Experimental Forest, West Virginia.

	Mass				N				P				Ca			
	3	6	7	12	3	6	7	12	3	6	7	12	3	6	7	12
Block	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.0465
Treatment	ns	ns	ns	0.001	0.014	<0.000	ns	ns	ns	ns	0.001	0.002	0.021	0.033	ns	0.010
Litter type	0.001	0.001	<0.000	<0.000	ns	<0.000	<0.000	<0.000	0.003	0.012	ns	<0.000	<0.000	0.002	<0.000	<0.000
Treatment × litter type	ns	ns	0.000	0.002	ns	0.000	0.033	ns	0.006	0.009	ns	ns	<0.000	ns	ns	ns

Note: ns indicates lack of significance ($p \geq 0.05$).

ranged from 2.7 kg·ha^{-1} in oak in the ambient treatment to 7.4 kg·ha^{-1} in all species together in the dolomite treatment (Table 3). N flux between the end and beginning of decomposition indicated a substantial net loss of litter N from all species together (5.4–7.3 kg·ha^{-1}), and continued retention in oak of an average of 0.5 kg N·ha^{-1} (Table 3).

P pools at peak immobilization increased by 0.08 kg P·ha^{-1} in oak in the ambient treatment to 0.89 kg P·ha^{-1} in all species together in the dolomite treatment (Table 4). P flux between the beginning and end of decomposition included losses of up to 0.19 kg P·ha^{-1} in all species together in ambient and in dolomite treatments to gains of up to 0.12 kg P·ha^{-1} in oak in all treatments and in all species together in the elevated treatment (Table 4).

The difference in Ca pools between the beginning and end of decomposition showed mineralization ranging from a low of 3.4 kg Ca·ha^{-1} in oak to a high of 18.3 kg Ca·ha^{-1} in all species together, both in the ambient treatment. On average across treatments, oak released 4.6 kg Ca·ha^{-1}, while all species together released 16 kg Ca·ha^{-1} (Table 5).

Discussion

Mass loss in oak versus all-species litters

Slower decomposition in oak than in all species together appeared to be the function of litter chemistry, not treatment. This effect is most likely related to the lignin to N ratio rather than lignin alone, as oak had a significantly higher lignin to N ratio than other species (Hobbie et al. 2006). Therefore, oak may contribute to somewhat longer carbon storage in the litter layer regardless of deposition rates or Ca amendments. In a neighboring watershed at Fernow, experimental N additions decreased decomposition rates of several other species (no oak) (Adams and Angradi 1996). Hutchinson et al. (1998) also found that the rate of maple litter decomposition decreased after N and S additions. This indicates that in contrast to other species, oak decomposition does not respond to N additions, at least during the first year. Our findings for oak confirm earlier results, where an increase in N availability did not increase leaf decomposition rates (Prescott 1995).

Can oak litter contribute to N retention?

Clearly, oak in these forests can contribute to N retention via N immobilization in leaf litter. While all species together mineralized one-fifth to one-third of the amount of N that is available from ambient and experimentally increased rain, oak litter continued to retain a small portion of the immobilized N at the end of the 12 month decomposition period (Table 3). At that time, a developing new litter layer will start the process of immobilization anew, in effect increasing the overall potential for N retention in litter.

It can be concluded that without oak, more N would be mineralized from the litter of the other species, increasing the N available in the system. These results agree with earlier findings in which N retention in forest floors made of red oak was 13% greater than in that made of sugar maple (Templer et al. 2005).

In terms of the potential ability to retain atmospheric N inputs, peak immobilization into oak in the ambient treatment in our study accounted for 18% of atmospheric N (15 kg·ha^{-1}), with other species accounting for another 30%.

Fig. 3. Phosphorus dynamics as a percentage of initial P in oak and all-species litters in three treatments in an aggrading Appalachian hardwood forest.

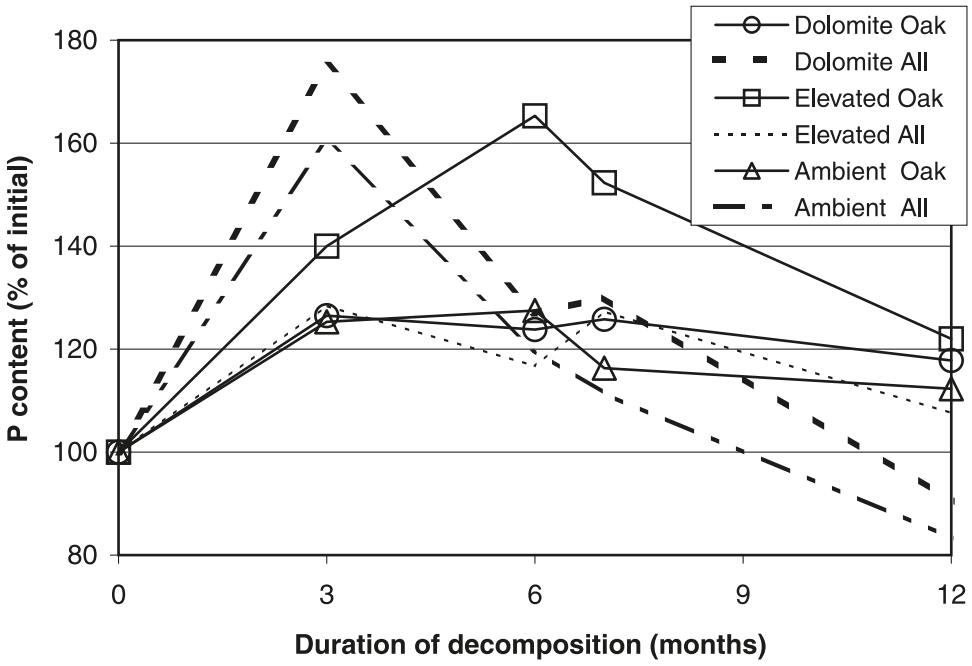
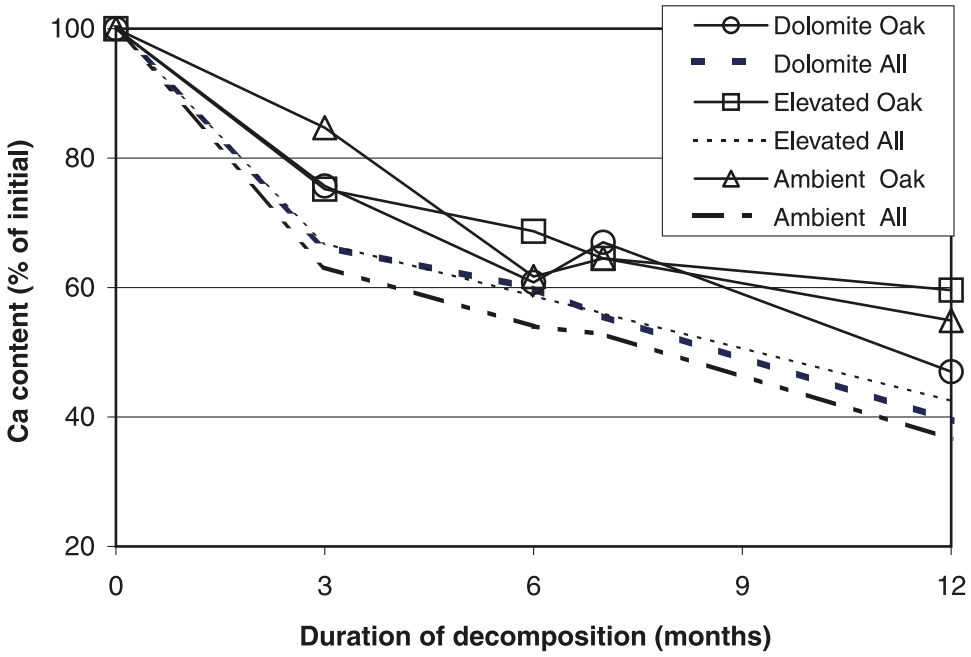


Fig. 4. Calcium (Ca) dynamics as a percentage of initial Ca in oak and all-species litters in three treatments in an aggrading Appalachian hardwood forest.



This relatively low percentage of possible atmospheric N retention despite high immobilization rates is due to the low mass of oak litter in the ambient treatment (Table 1); with more oak litter, more of the atmospheric N could be immobilized. For example, in the increased N and S deposition treatment (i.e., elevated), oak accounted for similar percentages of atmospheric N inputs as other species because more oak litter was present than in the ambient treatment. Litter mass will continue to increase as this aggrading, 11-year-old forest matures; therefore, the importance of immobilization as a potential N retention mechanism will continue to expand.

The amount of initial lignin in litter and, in particular, the lignin:N ratio are two of the indicators of litter N dynamics (Aber and Melillo 1982; Osono and Takeda 2004). That ratio in our oak litter was >31, much higher than the next highest of 20 for tulip poplar (Table 6). Thus, the relatively long residence time of N in oak litter and short residence time in other species seems to reflect the species differences in lignin:N ratio.

Table 3. Litterfall pool sizes and fluxes for nitrogen (N) in oak and in all species together.

Treatment	Litter type	Initial N pool ($kg \cdot ha^{-1}$)	Peak N pool ($kg \cdot ha^{-1}$)	N flux (peak – 0)* ($kg \cdot ha^{-1}$)	End N pool ($kg \cdot ha^{-1}$)	N flux (12 months – 0)† ($kg \cdot ha^{-1}$)
Ambient	Oak	5.7	8.4	+2.7	6.3	+0.6
	All species	25.8	33.1	+7.3	20.4	–5.4
Elevated	Oak	12.4	16.3	+3.9	13.0	+0.6
	All species	28.3	33.3	+5.0	21.5	–6.8
Dolomite	Oak	8.4	13.1	+4.7	8.9	+0.5
	All species	29.1	36.5	+7.4	21.8	–7.3

*Change in N pool from beginning of decomposition (0) to peak immobilization.
†Change in N pool from beginning of decomposition (0) to end of decomposition (12 months).

Table 4. Litterfall pool sizes and fluxes for phosphorus (P) in oak and in all species together.

Treatment	Litter type	Initial P pool ($kg \cdot ha^{-1}$)	Peak P pool ($kg \cdot ha^{-1}$)	P flux (peak – 0)* ($kg \cdot ha^{-1}$)	End P pool ($kg \cdot ha^{-1}$)	P flux (12 months – 0)† ($kg \cdot ha^{-1}$)
Ambient	Oak	0.31	0.39	+0.08	0.34	+0.03
	All species	1.16	1.86	+0.70	0.97	–0.19
Elevated	Oak	0.53	0.88	+0.35	0.65	+0.12
	All species	1.28	1.64	+0.36	1.37	+0.09
Dolomite	Oak	0.44	0.55	+0.11	0.51	+0.07
	All species	1.18	2.07	+0.89	1.07	–0.11

*Change in P pool from beginning of decomposition (0) to peak immobilization.
†Change in P pool from beginning of decomposition (0) to end of decomposition (12 months).

Table 5. Litterfall pool sizes and fluxes for calcium (Ca) in oak and in all species together.

Treatment	Litter type	Initial Ca pool ($kg \cdot ha^{-1}$)	End Ca pool ($kg \cdot ha^{-1}$)	Ca flux (12 months – 0)* ($kg \cdot ha^{-1}$)
Ambient	Oak	7.6	4.2	–3.4
	All species	28.9	10.6	–18.3
Elevated	Oak	12.5	7.5	–5.0
	All species	23.1	9.8	–13.3
Dolomite	Oak	10.4	4.9	–5.5
	All species	27.0	10.6	–16.4

*Change in Ca pool from beginning of decomposition (0) to end of decomposition (12 months).

Table 6. Initial lignin levels (per dry mass), lignin to nutrient ratios, and *p* values for different species.

	Lignin	Lignin:N	Lignin:P
Birch	32.6a	18a	429a
Cherry	31.7ab	15a	375a
Oak	29.5abc	31b	639b
Tulip poplar	22.2cd	20a	365a
Magnolia	17.9d	12a	380a
Maple	15.5d	15a	277a
p value	<0.000	0.000	0.003

Note: Same letters within a column indicate no significant difference (Tukey's studentized range test, $\alpha = 0.05$).

Is P limiting to litter decomposition?

High levels of P immobilization may be indicative of P limitation to decomposition of litter in these forests regardless of treatment or litter type. Clearly, oak litter can contribute to potential P limitation, especially with extended residence time of P in litter. Similar to N, P flux into oak litter in the ambient treatment was limited by the amount of oak litter mass. As these forests mature and leaf biomass increases, potential P limitation to litter decomposition is likely to increase as well. Higher peak immobilization levels for P than for N in all species together in the ambient and dolomite treatments may indicate that P may be more limiting than N to decomposition in these treatments.

Based on an extensive study of litter decomposition across a variety of sites in Canada, Moore et al. (2006) proposed that initial N:P ratios of >16 indicate P immobilization and ratios <16 indicate P mineralization. Initial N:P characteristics of litters in our study and P dynamics during litter decay support the observations of Moore et al. (2006) for litter N:P ratios >16 (Table 1). Moore et al. (2006) also proposed that decomposing litter N:P ratios converge to an average of 16. We did not observe such convergence. Rather, our range of N:P diverged from the initial 19–23 to a final 15–26. P limitation to decomposition in our ecosystem most likely contributes to the observed N:P by probable

disproportionate increases in P relative to N, especially early in decomposition. Other differences in the two studies may include litter chemistry and climate. In Moore et al. (2006), all species except jack pine had lower initial N, and all except beech and birch had substantially lower initial N:P ratios than our oak litter. All of litters in Moore et al. (2006) decomposed above 45°N, while our litter decomposed at 39°N, where optimal temperatures for decomposition last longer. The location differences are reflected in decomposition rates; our litter needed 1 year to lose about 50% of mass, while Moore et al.'s litter needed 6 years to do the same. Therefore, it appears that the changes in litter N:P during decomposition may be dependent on the nature of limitation and on the effects of initial litter chemistry and climate on the rate of decomposition. These effects need to be further examined.

Ca dynamics in oak litter and in all species together

While Ca mineralization occurred in both litter types, oak mineralized much less Ca compared with all species together (Table 5). High rates of mineralization may be desirable in these systems, where substantial amounts of Ca are removed in the harvesting of wood that may be >80 years old (Adams et al. 2000). However, Ca mineralized in the first 6 months after leaf drop may be lost to leaching with nitrate during high discharge events because of a lack of uptake during colder times of the year, November–April.

Effects of elevated N inputs on early litter processes

Since the study inception in 1996, a total of 360 kg N·ha^{-1} was added to elevated and dolomite treatments, and 110 kg Ca·ha^{-1} to dolomite treatments, along with S and Mg. In oak litter, these additions were reflected in the trend of initial N concentrations increasing from ambient to elevated treatments and of Ca concentrations increasing from elevated to ambient and to dolomite treatments (Table 1). Similar results were found in a 25-year-old mixed hardwood watershed at Fernow, which had received a total of 162 kg N·ha^{-1}; in that study, N concentrations were higher in the litter of the species considered (black birch, black cherry, red maple, and yellow poplar; no oak), and Ca concentrations were lower in the treated than in the control watersheds (Adams and Angradi 1996). Some elemental leaching may have affected initial concentrations in our study before we collected litter in the beginning of December; however, it appears that any such effect was proportional across treatments, and treatment differences reflected those in Adams and Angradi (1996).

Elevated N appeared to have lowered the N- and P-immobilization capacity of all species together but increased P immobilization in oak. Less N immobilization under elevated N translates to a lower ability to retain N, with potential consequences for nitrate loss from the system. This effect of elevated N has been described before in forest floors in N-fertilized plots that had a 22% lower ability to retain N than nonfertilized plots (Templer et al. 2005). Lower P immobilization into litter may help alleviate potential P limitation in N-saturated forests; P limitation under elevated N conditions had been described at neighboring watersheds at Fernow based on greater root in-growth into microsites fertilized with P than with N or Ca and on increased soil phosphomonoesterase activity (Gress et al. 2007). Our results indicate that this limitation may also exist for litter decomposition. Elevated N also appeared to shift N- and P-immobilization peaks to 1 month later but only in oak; however, this result must be interpreted with caution because of the relatively low sample size in any 1 month.

Did liming ameliorate deposition effects?

In both oak and all-species litters, dolomitic lime seemed to reverse the conditions in the elevated treatment to those in ambient treatment only for peak N immobilization; the dolomite and ambient treatments were similar.

The ambient and elevated treatments differ in the amount of N and S inputs. The ambient and the dolomite treatments differ in both the amount of N and S and basic cation inputs. The elevated and dolomite treatments differ only by the amount of Ca and Mg added. This suggests that it is the addition of basic cations in the elevated treatment that allows the ameliorating effect, and that an elevated N and S effect is exerted through acidification of the environment and not through elemental addition of N or S. An alternative explanation could involve Ca and Mg limitation to decomposition, but that was clearly not the case for Ca, and we assume the same for Mg.

In general, liming did not exert a strong effect on the litter processes in our study. Of all amendments presently used in forests, liming can potentially change the soil environment the most because it increases soil pH and helps mobilize many macro- and micro-elements; therefore it is surprising that our liming treatment did not result in a strong effect. However, lime applications may exert much less impact in fertile soils than in less fertile ones (Simmons et al. 1996). The Fernow Forest is relatively productive and has areas with a site index of 24 m (80 feet) for red oak, base age 50. The "fertility factor" may extend to the Ca dynamics in the litter layer, although the exact mechanisms are unknown. Also, a lack of influence of the environment — in our case, increased Ca in the dolomite treatment — on litter decomposition and nutrient dynamics appears common and has been observed elsewhere (Prescott 1995; Piatek and Allen 2001). The effects of the environment, including high levels of Ca, may become apparent over time, but a longer-term study would be needed to observe that (Prescott et al. 2004; Chapman and Koch 2007).

Conclusions

1. Oak litter can contribute to atmospheric N retention via N immobilization. N immobilization in oak lasted 12 months, while mineralization in all species together started around month 7 of decomposition. Elevated atmospheric N lowered rates of N immobilization in litters.

2. P was immobilized, possibly indicating P limitation to decomposition; oak litter and all species in elevated treatment immobilized P longer than other litters, while all species in the ambient treatment started mineralizing at month 9. Greater immobilization of P than N suggested that P may be more limiting than N to decomposition in this system.

3. Ca mineralization from litter may not contribute to tree nutrition as much as the magnitude of release would indicate, especially for all species together. This is due to the lack of tree uptake in the first 6 months of Ca mineralization.

4. Dolomitic lime appears to alleviate the effects of N deposition on early N dynamics in litter probably by neutral-

izing acidification. However, further effects of lime may become apparent over time.

5. Litterfall mass will increase as this aggrading forest matures. Assuming no changes in the proportion of litter mass by species, the importance of immobilization to site N retention, especially in oak litter, will continue to increase. At the same time, P limitation may become more acute.

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