

Decomposition and nutrient dynamics of hardwood leaf litter in the Fernow Whole-Watershed Acidification Experiment

M.B. Adams^{*}, T.R. Angradi

USDA Forest Service, Timber and Watershed Laboratory, Parsons, WV, USA

Accepted 20 November 1995

Abstract

Two watersheds are part of an on-going long-term artificial acidification experiment: the treatment watershed (WS3) has received $60.5 \text{ kg S ha}^{-1} \text{ year}^{-1}$ and $54 \text{ kg N ha}^{-1} \text{ year}^{-1}$ via aerial applications of ammonium sulfate fertilizer since 1989. After 3 years of treatment, freshly fallen leaves of four hardwood tree species (*Liriodendron tulipifera*, *Prunus serotina*, *Acer saccharum*, and *Betula lenta*) were collected and placed in litter bags, which were placed in stands in the treatment and control watersheds. Decay rates differed for *L. tulipifera*, *Prunus serotina*, and *B. lenta* between the two watersheds, with litter from WS3 decaying more slowly over the 2 year study period than litter from the control watershed. Initial concentrations of N, Ca, and K differed between treatment and control watersheds, but these differences disappeared after 2 years. Nutrient loss rates did not vary with treatment.

Keywords: Organic matter; Nitrogen; Calcium; Nutrient ratio

1. Introduction

Decomposition of annual leaf fall in hardwood forests releases nutrients for cycling within the stand (Johnson, 1995), and provides carbon and nutrients to other organisms in a more available form. Leaf litter can also serve as a temporary sink for nutrients such as N, S and P (Peterson and Rolfe, 1982; Blair, 1988b; White et al., 1988). Because of the important role of litter decomposition in regulating nutrient fluxes, factors influencing litter decomposition have important implications for long-term productivity of forest ecosystems. Forests of the central Appalachian Mountains are in increasing demand for forest products and recreation and as wildlife habitat, all of

which assume continued high forest productivity. In addition, these ecosystems receive some of the highest levels of nitrogen deposition in North America ($20\text{--}25 \text{ kg ha}^{-1} \text{ year}^{-1}$, National Atmospheric Deposition Program, 1992). Most forests have been assumed to be N-limited (Melillo, 1981), recently, however, a concern has arisen about excess nitrogen of atmospheric origin resulting in leaching of base cations (Aber et al., 1989) and soil acidification, with negative implications for long-term forest productivity.

A whole-watershed acidification experiment has been in progress since 1989 on the Fernow Experimental Forest, West Virginia, with the objective of understanding the responses of Appalachian forest ecosystems to increases or accumulations of S and N (Adams et al., 1993; Edwards et al., 1993; Adams et

^{*} Corresponding author.

al., 1995). This experiment provided an opportunity to examine effects of elevated N and S inputs on litter decomposition in forest stands. The objectives of this study were to compare decay rates of litter of different tree species in stands with different treatment histories, and to compare patterns of nutrient loss, focusing on N, P, K, Ca and Mg. We hypothesized that changes in litter nutrient concentrations and/or changes in soil chemistry associated with elevated N and S inputs would result in different rates of decay and nutrient immobilization/mineralization.

2. Methods

2.1. Description of watersheds

Two adjacent watersheds on the Fernow Experimental Forest (FEF) near Parsons, West Virginia, were used for this study. Watershed 3 (WS3) is the treatment watershed, and watershed 7 (WS7) serves as a control. The FEF, located on the unglaciated Allegheny plateau of the Appalachian mountains, is characterized by steep slopes and shallow soils (less than 1 m). Precipitation is distributed evenly between dormant and growing seasons; average precipitation pH is 4.2, but pH values below 4.0 are common in summer (Edwards and Helvey, 1991). The predominant soil type is Calvin channery silt loam (loamy-skeletal, mixed, mesic Typic Dystrochrept) underlain with fractured sandstone and shale of the Hampshire formation (Losche and Beverage, 1967). Stands on both watersheds have similar species composition and originated at the same time (Table 1). Although aspect varies between the two watersheds, average soil temperatures (10 cm depth) do not vary greatly (K.G. Mattson, unpublished data, 1992).

Ammonium sulfate fertilizer was evenly applied to all of WS3 three times per year beginning in 1989. March and November applications consisted of 33.6 kg fertilizer ha⁻¹, which corresponds to 8.1 kg ha⁻¹ and 7.1 kg ha⁻¹ of S and N, respectively. July applications consisted of 100.8 kg fertilizer ha⁻¹, or 24.4 kg ha⁻¹ and 21.2 kg ha⁻¹ S and N, respectively. Thus, the total amount of S and N deposited annually on the treatment watershed was 60.5 kg S

Table 1

Description of stands on two experimental watersheds. Fernow Experimental Forest, Parsons, WV

	Watershed 3	Watershed 7
Age (years)	25	25
Area (ha)	34.3	24.2
Aspect	S	ENE
Minimum elevation (m)	735	725
Maximum elevation (m)	860	855
Average annual precipitation (mm)	1471	1417
Average annual stream flow (mm)	666	882
Average annual litterfall (mt ha ⁻¹)	3.3	3.2
Mean summer soil temp. at -10 cm depth (°C)	17.5	17.8

and 53.8 kg N ha⁻¹, or approximately three times the ambient inputs to the control watershed (WS7).

This study was begun after 3 years of artificial acidification treatment. Freshly fallen leaves of yellow-poplar (*Liriodendron tulipifera* L.), black cherry (*Prunus serotina* L.), red maple (*Acer saccharum* Marsh.) and black birch (*Betula lenta* L.) were collected in the fall of 1992 from both watersheds. These species were selected for study because they are the most common tree species in these stands. The leaves were air-dried and placed into 20 cm × 20 cm fiberglass screen bags (2 mm mesh). Approximately 5 g of leaves were placed in each bag, which was then closed and weighed. Five 2 m × 2 m plots were established on each watershed at five different topographic locations (streamside flat, east-facing ridge top, east-facing mid-slope, west-facing mid-slope, and ridge) and 16 litterbags of each tree species were placed randomly in each plot in November 1992. Bags were placed directly on the mineral soil, and litter was placed on the watershed from which it originated. Four soil samples per plot (0–15 cm depth) were collected at time of bag placement and composited for analyses.

Two bags of each species were collected per plot and returned to the laboratory to calculate handling loss. Litter bags were thereafter collected every 2 months during the first year, and then again at the end of year 2 (November 1994). Samples were oven-dried (70°C, 48 h) and weighed. Loss on ignition (550°C, 4 h) was determined on an approximate 1 g subsample to calculate ash-free dry mass (AFDM). Remaining material was ground and com-

Table 2

Mean initial soil chemical properties (0–15 cm) on two watersheds in the Fernow Experimental Forest. Standard errors are given in parentheses

	Watershed 3	Watershed 7
Total N (%)	0.21 (0.02)	0.23 (0.02)
Organic C (%)	8.60 (0.51)	8.40 (0.85)
pH	4.34 (0.12)	4.52 (0.06)
CEC (meq per 100 g)	6.14 (0.58)	5.16 (0.41)
Ca (mg kg ⁻¹)	84.00 (15.42)	88.00 (14.43)
K (mg kg ⁻¹)	78.40 (3.17)	84.40 (8.68)
Mg (mg kg ⁻¹)	13.66 (1.45)	16.20 (1.45)
P (mg kg ⁻¹)	1.32 (0.24)	1.76 (0.47)

posited for nutrient analysis at the University of Maine Analytical Laboratory. Total Kjeldahl-N was determined by autoanalysis following block digestions with H₂SO₄ and K₂SO₄/CuSO₄. Other elements were determined by plasma emission spectrophotometry following dry ashing and extraction with HCl and HNO₃. Soil pH was determined in water (1:1, w:v) and soil nutrients determined by

NH₄Cl extraction at 1:20 (w:v). Differences were evaluated using analysis of variance.

Litter decay rates were calculated from percent AFDM remaining using a negative exponential model $X/X_0 = e^{-kt}$, where X/X_0 is fraction mass remaining at time t , and k is the annual decay constant (Olson, 1963). Annual constants (k) were calculated for the first year of data, and for both years of data. Analysis of covariance was used to test the interactions of treatment (watersheds) \times time and species \times time. To test watershed differences for each species, one-sided t -tests of the mean difference between watersheds were used.

Nutrient analyses were conducted on samples collected at time 0, and after 2, 4, 6, 12, and 24 months. Because so little material remained after 2 years in the field, samples were composited by species and watershed to provide sufficient material for analyses. Percent nutrient remaining at time t was calculated as the product of percent AFDM remaining and nutrient concentration in the residual material at time t divided by initial nutrient concentration. Paired

Table 3

Decay rates (SE) and r^2 values for leaf litter in the Fernow Experimental Forest during 1 year and for both years 1 and 2 (overall)

Species	Watershed	Year 1 k	Year 1 r^2	Overall k	Overall r^2
Black birch	3	-0.893 (0.140)	0.447	-0.384 (0.093)	0.234
	7	-0.917 (0.123)	0.499	-0.434 (0.066)	0.389
Yellow-poplar	3	-0.890 (0.088)	0.606	-0.482 (0.058)	0.475
	7	-1.141 (0.094)	0.672	-0.834 (0.084)	0.568
Black cherry	3	-1.442 (0.225)	0.451	-0.706 (0.148)	0.290
	7	-1.381 (0.138)	0.613	-1.156 (0.112)	0.611
Red maple	3	-1.268 (0.174)	0.502	-0.430 (0.113)	0.188
	7	-1.425 (0.177)	0.498	-0.667 (0.112)	0.328
Black birch	Pooled ^a	-0.910 (0.093)	0.478	-0.414 (0.055)	0.309
Yellow-poplar	Pooled	-1.014 (0.0665)	0.625	-0.567 (0.050)	0.451
Black cherry	Pooled	-1.413 (0.125)	0.528	-0.918 (0.093)	0.433
Red maple	Pooled	-1.350 (0.123)	0.502	-0.481 (0.077)	0.209

^a Pooled across watersheds.

t-tests were used to test for watershed differences for each sampling date. Nutrient decay rates were calculated as for litter decay rates. Carbon:nutrient ratios (e.g. C:N, C:P) were calculated based on the assumption that C content equalled 50% of AFDM.

3. Results

3.1. Soil chemistry

Soil chemical properties of the two watersheds did not differ significantly at the initiation of this study (Table 2) despite 3 years of elevated inputs of N and S to WS3. Gilliam et al. (1996) also found no differences in total soil N, or C:N after 5 years of treatment in the same experiment. Thus, it is unlikely that soil chemistry explains variability in litter decomposition between the two watersheds.

3.2. Litter decomposition

Decay rates did not vary among topographic positions, so data were pooled by watershed. Litter from the four species decomposed at different rates (Table 3) and the rates of decay of the four species varied over time. In the first year, black cherry litter decomposed most rapidly, followed by red maple and yellow-poplar then black birch. Over the two years, black cherry litter decomposed most rapidly, followed by yellow-poplar, red maple and black birch. AFDM appeared to increase from 400 to 700 days, although these increases were not all statistically significant. We attribute this to increased variability with smaller samples (less sample remaining over time) and possibly to increasing microbial/detritivore biomass in the samples.

Decay rates did not differ significantly between watersheds when all species were included in the

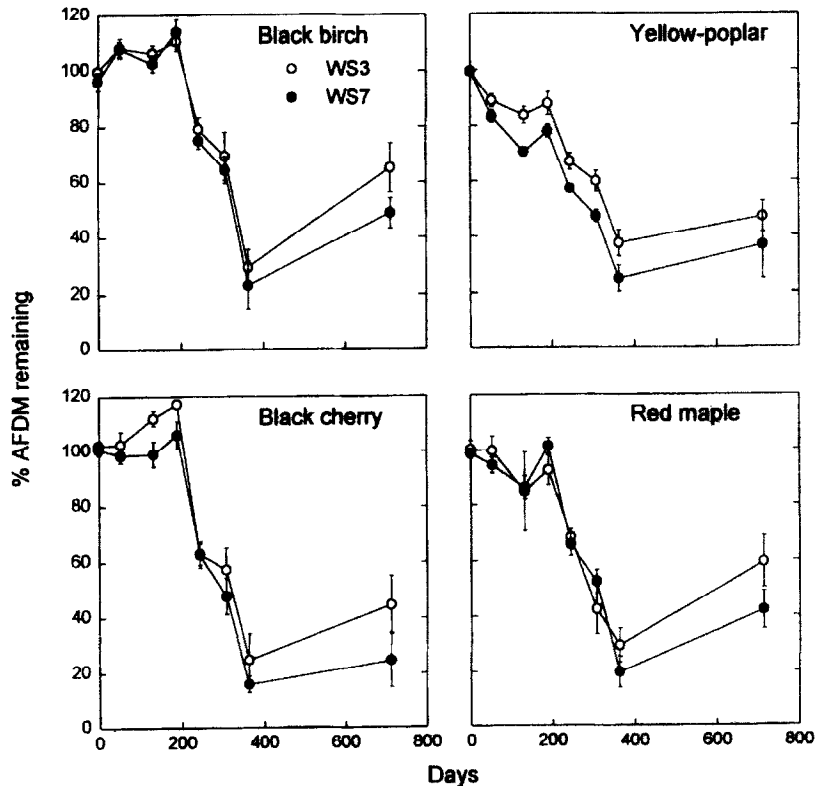


Fig. 1. Percent ash-free dry mass (%AFDM) remaining in leaf litter of four hardwood species as a function of time. Values are means \pm 1 SE.

analysis, but did vary over time. The watershed \times time interaction was statistically significant across species, suggesting that the effect of treatment on mass loss varied over time for at least one of the species. Specifically, watershed differences were statistically significant for yellow-poplar and black cherry ($P < 0.05$) and marginally significant for black birch ($P = 0.063$), and litter from WS3 decayed more slowly over the 2 year study period than litter from WS7 (Fig. 1). K.G. Mattson (unpublished data) reported lower CO_2 evolution from WS3 than from WS7, also suggesting lower decomposition.

3.3. Litter nutrient levels

Initial nutrient concentrations varied among species (Table 4). Yellow-poplar contained the highest concentrations of all nutrients except Mg. Initial N, K, and Ca concentrations differed significantly

Table 4

Mean nutrient concentrations in litter at initiation of study, and after 1 and 2 years in the field. Values are expressed in mg kg^{-1} , except nitrogen (%)

Nutrient	Black birch	Yellow-poplar	Black cherry	Red maple
Nitrogen				
Initial	1.42	1.5	1	0.91
Year 1	2.11	2.49	1.93	1.82
Year 2	1.97	1.93	1.59	1.65
Phosphorus				
Initial	492	915	421	458
Year 1	1034	1207	855	782
Year 2	1068	1080	910	1065
Potassium				
Initial	4515	11018	9498	4358
Year 1	2547	2378	2028	2670
Year 2	2997	3145	2620	2922
Calcium				
Initial	8572	12947	11518	10681
Year 1	6487	8892	10100	8422
Year 2	4407	5165	3715	5245
Magnesium				
Initial	994	1602	2137	802
Year 1	1212	1155	1118	1318
Year 2	878	860	806	884

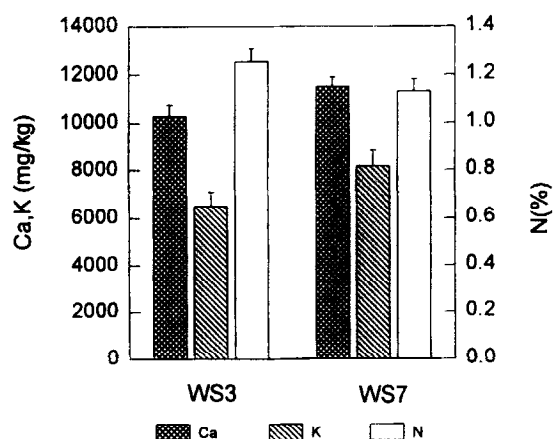


Fig. 2. Initial N (%), Ca and K concentrations (mg kg^{-1}) in freshly-fallen leaf litter from the treated stand (WS3) and control (WS7). Bars represent 1 SE of the mean.

between the two watersheds (Fig. 2). Nitrogen concentrations were higher in the litter from WS3 than WS7; K and Ca values were significantly lower on WS3 than on WS7. After 1 year, these differences were negligible and had disappeared after 2 years. Nutrient decay rates did not vary significantly between the two watersheds.

Litter nutrient concentrations varied between years and among species (Table 4). Nitrogen concentrations increased during the first year of the study, then decreased during the second year. Phosphorus concentrations increased through the course of the study except in yellow-poplar litter. K, Ca and Mg decreased during the first year and then continued to decrease (Ca, Mg) or increased slightly during the second year.

The absolute amount of N in litter increased during the initial 6 months in the field, then decreased to approximately 30–50% of the original amount at the end of the first year (Fig. 3). N then increased or remained constant (yellow-poplar) during the second year. This pattern did not vary significantly between the two watersheds. Phosphorus content increased during the first 6 months for all species except yellow-poplar (Fig. 4), then decreased to the end of the first year, and increased or remained constant (yellow-poplar) through the second year. K was released rapidly, presumably due to its high

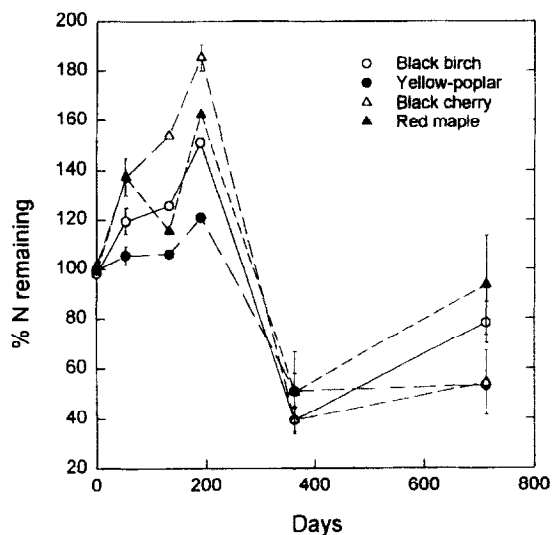


Fig. 3. Percentage of initial N content in leaf litter of four hardwood species as a function of time.

solubility and consequent rapid leaching, with only slight changes after the initial 2 months. Calcium content increased initially in black birch and black cherry, then decreased by the end of the first year so that all species contained nearly the same amount of Ca (approximately 20% of original). There was little change during the second year. Magnesium declined rapidly, although not as quickly as K, then increased slightly (black birch, red maple) or decreased further (yellow-poplar, black cherry).

Carbon:nutrient ratios varied over time (Fig. 5), reflecting initial immobilization and release for N and P, and rapid leaching losses for K and Mg. Two peaks in immobilization/release were apparent for Ca. With the exception of Ca, there was little change in C:nutrient ratios after the first year. Some ratios also varied significantly between the two watersheds (Table 5). C:Ca differed significantly between the watersheds for all species except yellow-poplar, and

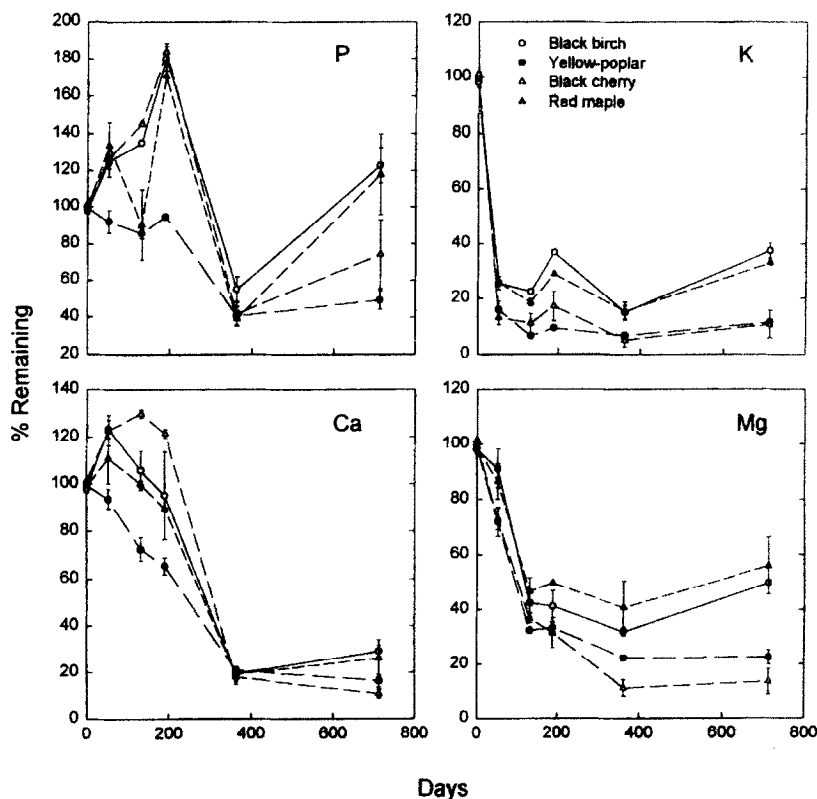


Fig. 4. Percentage of initial P, K, Ca, and Mg content in leaf litter as a function of time.

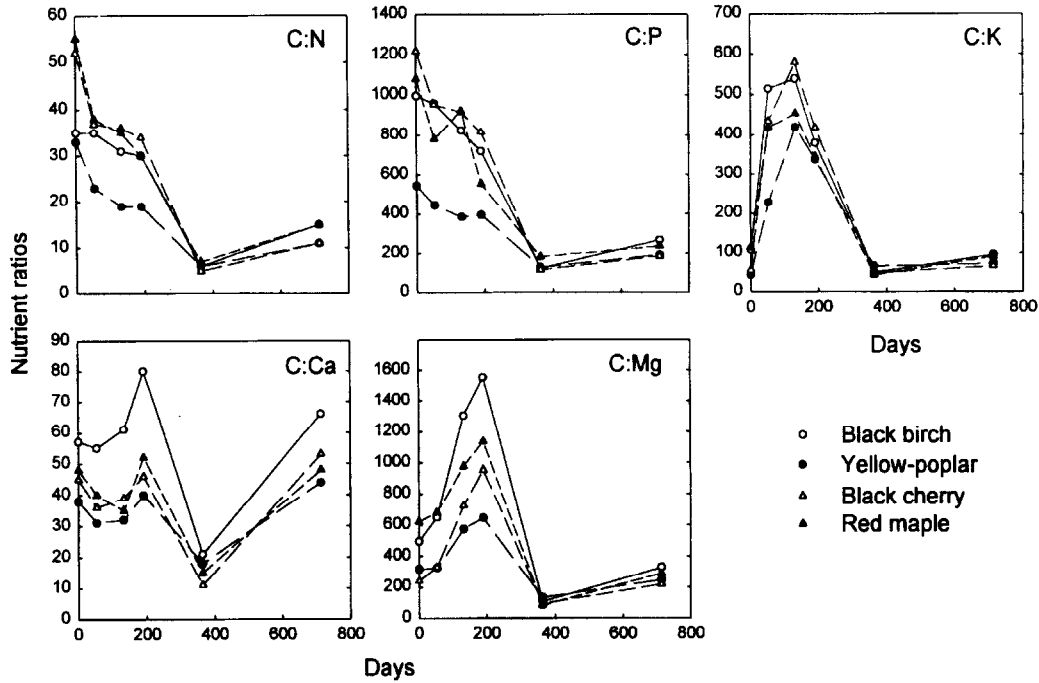


Fig. 5. C:nutrient ratios of leaf litter as a function of time.

C:N varied between the watersheds for yellow-poplar and red maple (Table 5). C:K and C:P ratios for the two watersheds were significantly different for yellow-poplar, while C:K and C:Mg differed for black cherry.

4. Discussion

Only red maple decomposition rates did not differ significantly between the two watersheds. Black birch, yellow-poplar and black cherry decomposed more rapidly on the control watershed (WS7) than on the treated watershed (WS3), suggesting that the treatment may have resulted in slower litter decomposition. Other researchers have reported contradictory results. Fenn (1991) reported that elevated N deposition from air pollution increased site fertility, specifically soil N, in the San Bernardino Mountains, leading to changes in litter quality, and faster decomposition of litter of Jeffrey pine (*Pinus jeffreyi* Grev. and Balf.). Wright and Tietema (1995) reported decreased decomposition of *Calluna vulgaris* litter in

an alpine catchment in Norway as a result of 9 years of N additions, but with no change in foliar N contents. Emmett et al. (1995) found no changes in litter decomposition with only a slight increase in foliar N levels in current-year foliage of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) in Wales following 2.5 years of N additions. Differences in results among these studies possibly reflect whether litter quality was substantially changed as a result of elevated N inputs.

Litter quality has been variously defined and is a function of more than just changes in total N concentration or content of foliage. Lignin (Fogel and Cromack, 1977; Meentemeyer, 1978) and C:N ratios (Taylor et al., 1989) have been used to examine litter quality in more detail. No lignin or other N fractions were measured in this study, therefore we limit the following discussion to nutrient ratios. C:nutrient ratios have been used to predict immobilization or nutrient release (McClagherty et al., 1985; Blair, 1988b). Above a critical C:nutrient ratio, nutrients are immobilized in microbial biomass. When the critical ratio is reached (as C is mineralized) nutrient

Table 5

C:nutrient ratios in litter of four hardwood tree species in the Fernow Experimental Forest, WV. Values are means of five collection dates

	Black birch	Yellow-poplar	Black cherry	Red maple
C:N				
WS3	25	20 *	27	31 *
WS7	25	17	30	29
C:P				
WS3	638	391 *	675	638
WS7	659	307	727	629
C:K				
WS3	290	235 *	295	252
WS7	272	156	241	249
C:Ca				
WS3	64 *	38	48 *	45 *
WS7	50	29	28	34
C:Mg				
WS3	760	387	488 *	649
WS7	718	362	365	626

* Significant effects of WS at $\alpha = 0.05$.

loss is roughly proportional to mass loss. In our study, C:N ratios declined to about 6 by the end of the first year, with a slight increase for all species during the second year (Fig. 5), suggesting a critical ratio between 5 and approximately 25.

Absolute N increased through much of the first year in the field, then decreased by the end of the first year, reflecting initial N immobilization in the litter, then eventual N release. Blair (1988b) reported similar results, except that his initial leaching phase was not observed in this study. Differences between the studies, in timing of litter bag placement (Blair's bags were placed in January, ours were placed in November) and differences in climate (our climate being cooler but drier) may explain this lack of initial leaching. McClaugherty et al. (1985) and Mudrick et al. (1994) also reported nitrogen accumulation during initial stages of decomposition. The increase in N concentration is correlated with C loss, suggesting that the accumulation of N is microbially mediated. Litter appears to act as a short-term reservoir for N, but significant retention does not occur over longer time spans.

Phosphorus and Ca also showed early immobilization, except in yellow-poplar, generally followed by

release after approximately one year. The apparent increase in P in litter of black birch and red maple during the second year suggests a new immobilization or reimmobilization of P, which is reflected in only a slight change in the C:P ratio. Blair (1988b) showed near constant (continuous) immobilization of P in red maple and chestnut oak litter during 2 years of incubation. Other research has suggested critical C:P ratios between 360 and 480 (Gosz et al., 1973). This value obviously varies with species and climate but we hypothesize lower critical C:P ratios for all four species at the FEF. Ca showed two peaks of immobilization followed by release, based on the C:Ca ratios. This probably reflects the loss of structural Ca after approximately 1 year.

Potassium and Mg were lost rapidly from the litter, as has been reported elsewhere (Blair, 1988a). Biological immobilization of Mg has been reported for Scots pine litter in the latter stages of decay or in litter with low initial Mg concentrations (Staaf and Berg, 1982). However, K and Mg release in this study did not appear to depend on biotic activity, but were the result of physical leaching.

In summary, although mass loss of three of the four species studied did differ significantly among the two watersheds, the rates of nutrient loss or immobilization did not vary, and there were few significant differences in nutrient concentrations or amounts between the treated and untreated watershed after 2 years in the field. We conclude that three years of the artificial acidification treatment has only minimally affected the quality of the litter on WS3. Although four species of differing litter quality were selected, the results might be different with species such as oak, which contain higher quantities of lignin and other recalcitrant compounds. Although elevated N and S inputs are of concern for many ecological processes, in the hardwood forest ecosystem we studied, the implications for changes in nutrient cycling due to changes in litter decomposition rate are not great.

References

- Aber, J.D., Nadelhoffer, K.J., Streudler, P. and Melillo, J., 1989. Nitrogen saturation in northern forest ecosystems. *BioScience*, 39: 378–386.

- Adams, M.B., Edwards, P.J., Wood, F. and Kochenderfer, J.N., 1993. Artificial watershed acidification on the Fernow Experimental Forest, USA. *J. Hydrol.*, 150: 505–519.
- Adams, M.B., Kochenderfer, J.N., Angradi, T.R. and Edwards, P.J., 1995. Nutrient budgets of two watersheds on the Fernow Experimental Forest. In: K.W. Gottschalk and S.L. Fosbroke (Editors), Proc. 10th Central Hardwood Forest Conf., 5–8 March 1995, Morgantown, WV. Gen. Tech. Rep. NE-197, USDA Forest Service, Northeastern Forest Experiment Station, pp. 199–130.
- Blair, J.M., 1988a. Nutrient release from decomposing foliar litter of three tree species with special reference to calcium, magnesium and potassium dynamics. *Plant Soil*, 110: 49–55.
- Blair, J.M., 1988b. Nitrogen, sulfur and phosphorus dynamics in decomposing deciduous leaf litter in the southern Appalachians. *Soil Biol. Biochem.*, 20: 693–701.
- Edwards, P.J. and Helvey, J.D., 1991. Long-term ionic increases from a central Appalachian forested watershed. *J. Environ. Qual.*, 20: 250–255.
- Edwards, P.J., Kochenderfer, J.N. and Adams, M.B., 1993. Effects of repeated ammonium sulfate applications on soil leachate chemistry on the Fernow Experimental Forest in West Virginia, USA. In: L. Rasmussen, T. Brydges and P. Mathy (Editors), *Experimental Manipulations of Biota and Biogeochemical Cycling in Ecosystems*, 18–20 May 1992, Copenhagen, Denmark, *Ecosyst. Res. Rep. No. 4*. Commission of the European Communities, Brussels, pp. 122–124.
- Emmett, B.A., Brittain, S.A., Hughes, S. and Kennedy, V., 1995. Nitrogen additions (NaNO_3 and NH_4NO_3) at Aber forest, Wales: II. Response of trees and soil nitrogen transformations. *For. Ecol. Manage.*, 71: 61–73.
- Fenn, M., 1991. Increased site fertility and litter decomposition rate in high-pollution sites in the San Bernardino Mountains. *For. Sci.*, 37: 1163–1181.
- Fogel, R. and Cromack, K., Jr., 1977. Effects of habitat and substrate quality on Douglas fir litter decomposition in western Oregon. *Can. J. Bot.*, 55: 1632–1640.
- Gilliam, F.G., Adams, M.B. and Yurish, B.T., 1996. Ecosystem nutrient responses to chronic nitrogen inputs at Fernow Experimental Forest, West Virginia. *Can. J. For. Res.*, 26: 196–205.
- Gosz, J.R., Likens, G.E. and Bormann, F.H., 1973. Nutrient release from decomposing leaf and branch litter in the Hubbard Brook Forest, New Hampshire. *Ecol. Monogr.*, 43: 173–191.
- Johnson, D.W., 1995. Role of carbon in the cycling of other nutrients in forested ecosystems. In: W.W. McFee and J.M. Kelly (Editors), *Carbon Forms and Functions in Forest Soils*. Soil Science Society of America, Madison, WI, pp. 299–328.
- Losche, C.L. and Beverage, W.W., 1967. Soil survey of Tucker County and part of northern Randolph County, West Virginia. US Soil Conservation Service, Forest Service and W. Va. Agricultural Experiment Station, US Government Printing Office, Washington, DC, 78 pp.
- McClougherty, C.A., Pastor, J., Aber, J.D. and Melillo, J.M., 1985. Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. *Ecology*, 66: 266–275.
- Meentemeyer, V., 1978. Macroclimatic and lignin control of litter decomposition rates. *Ecology*, 59: 465–472.
- Melillo, J.M., 1981. Nitrogen cycling in deciduous forests. In: E.F. Clark and T. Rosswall (Editors), *Terrestrial Nitrogen Cycles*. *Ecol. Bull. NFR*, 33: 427–442.
- Mudrick, D.A., Hoosein, M., Hicks, R.R., Jr. and Townsend, E.C., 1994. Decomposition of leaf litter in an Appalachian forest: effects of leaf species, aspect, slope position and time. *For. Ecol. Manage.*, 68: 231–250.
- National Atmospheric Deposition Program, 1992. NADP/NTN annual data summary: precipitation chemistry in the United States. Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO.
- Olson, J.S., 1963. Energy storage and the balance of producers and decomposers in ecological systems. *Ecology*, 44: 322–331.
- Peterson, D.L. and Rolfe, G.L., 1982. Nutrient dynamics and decomposition of litterfall in floodplain and upland forests of central Illinois. *For. Sci.*, 28: 667–681.
- Staaf, J. and Berg, B., 1982. Accumulation and release of plant nutrients in decomposing Scots pine litter: Long-term decomposition in a Scots pine forest. II. *Can. J. Bot.*, 60: 1561–1568.
- Taylor, B.R., Parkinson, D. and Parsons, W.F.J., 1989. Nitrogen and lignin content as predictors of litter decay rates: a new microcosm test. *Ecology*, 70: 97–104.
- White, D.L., Haines, B.L. and Boring, L.R., 1988. Litter decomposition in southern Appalachian black locust and pine-hardwood stands: litter quality and nitrogen dynamics. *Can. J. For. Res.*, 18: 54–63.
- Wright, R.F. and Tietema, A., 1995. Ecosystem response to 9 years of nitrogen additions at Sogndal, Norway. *For. Ecol. Manage.*, 71: 133–142.