

Nutrient release from decomposing foliar litter of three tree species with special reference to calcium, magnesium and potassium dynamics

JOHN M. BLAIR

Department of Entomology and Institute of Ecology, University of Georgia, Athens, GA 30602, USA.
Present address: Department of Entomology, The Ohio State University, Columbus, OH 43210, USA

Received 18 November 1987. Revised March 1988

Key words: *Acer rubrum*, calcium, cations, *Cornus florida*, decomposition, litter, magnesium, nitrogen, nutrient release, phosphorous, potassium, *Quercus prinus*, sulfur

Abstract

Calcium, magnesium and potassium dynamics in decomposing litter of three tree species were measured over a two-year period. The species studied were flowering dogwood (*Cornus florida*), red maple (*Acer rubrum*) and chestnut oak (*Quercus prinus*). The order of decomposition was: *C. florida* > *A. rubrum* > *Q. prinus*.

Calcium concentrations increased following any initial leaching losses. However, there were net releases of Ca from all three litter types since mass loss exceeded the increases in concentration. Net release of Ca by the end of two years from all three species combined was 42% of initial inputs in litterfall. Magnesium concentrations increased in the second year, following decreases due to leaching during the first year in *C. florida* and *A. rubrum* litter. Net release of Mg by the end of two years was 58% of initial inputs. Potassium concentrations decreased rapidly and continued to decline throughout the study. Net release of K by the end of two years was 91% of initial inputs.

These data on cation dynamics, and similar data on N, S and P dynamics from a previous study, were combined with annual litterfall data to estimate the release of selected nutrients from foliar litter of these tree species at the end of one and two years of decomposition. The relative mobility of all six elements examined in relation to mass loss after two years was; K > Mg > mass > Ca > S > P > N.

Introduction

Release of nutrients from decomposing litter is an important internal pathway of nutrient flux in forested ecosystems. The release of nutrients from decomposing litter controls their subsequent availability for plant uptake, or loss from the ecosystem, and affects ecosystem primary productivity. Nutrients may be released from litter by leaching or by mineralization (Swift *et al.*, 1979). The rate at which nutrients are released depends on several factors including the composition of the litter (including the initial concentration of the nutrient in the litter), the structural nature of the nutrient in the litter matrix, microbial demand for the nutrient, and the availability of exogenous sources of the nutrient (Seastedt, 1984). The release

of elements that are not limiting to microbial decomposers and are not structurally bound in the litter may exceed mass loss. However, elements which are in short supply relative to microbial demand may be released at a rate slower than mass loss or may even accumulate in the litter during early phases of decomposition (*i.e.*, Berg and Staaf, 1981).

In a recent two-year study of litter decomposition at the Coweeta Hydrologic Laboratory, North Carolina, USA, litter quality was found to affect both rates of mass loss and fluxes of N, P and S during decomposition (Blair, *in press*). Concentrations of N, P and S increased during decomposition, following any initial leaching losses, and there was a net immobilization of these elements in some of the litter types examined. This paper

presents data from the same study regarding the dynamics of three plant macronutrient cations (Ca, Mg and K) during two years of decomposition. Previous decomposition studies have often been one year or less in duration, although longer studies are often necessary to characterize adequately patterns of nutrient flux. The objectives of this study were 1) to quantify changes in the concentrations and absolute amounts of Ca, Mg and K in litter of three hardwood tree species during two years of decomposition and 2) to combine this data with N, S and P flux data from a previous study to estimate total nutrient release from these litter types over a two-year period.

Methods

Site description

This study was conducted at the USFS Coweeta Hydrologic Laboratory from January 1985–January 1987. The Coweeta Laboratory, located in the southern Appalachian Mountains of southwestern North Carolina, USA, (35°00'N latitude, 83°30'W longitude), is a 2185 ha forested basin consisting of numerous smaller watersheds (catchments) that serve as experimental units. The watershed utilized in this study, WS 2, is a 12.3 ha catchment located in the northeastern portion of the Coweeta basin. Elevations on WS 2 range from 709 to 1004 m and the average slope is 60% (Swank and Crossley, 1986). The vegetation is an uneven-aged mixed hardwood association dominated by *Quercus*, *Carya* and *Acer* spp. (Berish and Ragsdale, 1985). Mean annual rainfall on WS 2 is 1770 mm yr⁻¹ and is evenly distributed throughout the year. Mean annual temperature is 13°C.

Decomposition rates and nutrient dynamics

Litter decomposition rates and nutrient dynamics in decomposing litter were quantified using litterbags with an inside area of 10 × 10 cm constructed of fiberglass window screen material (1.6 × 1.8 mm mesh). Senescing leaves of flowering dogwood (*Cornus florida* L.), red maple (*Acer rubrum* L.) and chestnut oak (*Quercus prinus* L.) were collected in October 1984 and air-dried at

22°C. These three species were chosen to represent a range of resource qualities and decomposition rates and because of their abundance on WS 2. Approximately 2.5 g of air-dried leaves were placed in pre-weighed bags. Five bags of each species were oven-dried at 50°C to develop equations relating air-dry to oven-dry mass. On 4 January 1985, 52 litterbags of each species were placed in each of three plots arranged in a transect on a mid-elevational area of WS 2. Plots were spaced approximately 100 to 150 m apart. Litterbags used in the present study were collected randomly from each of the plots at approximately bimonthly intervals throughout 1985 (n = 6 bags/species/date) and 1986 (n = 3 bags/species/date) for a total of 12 collection dates over a two-year period. The last collection date was 6 January 1987 (732 days in the field).

Intact litterbags were oven-dried at 50°C, the litter was reweighed, ground and subsamples were ashed at 500°C for 4 h to determine % AFDM. Litter masses and nutrient concentrations were corrected for any soil contamination (see Blair, in press). Decomposition rates were calculated from percent mass remaining data using a single negative exponential decay model $X/X_0 = e^{-kt}$, where X/X_0 = fraction mass remaining at time t , t = time elapsed in years, and k = the annual decay constant (Olson, 1963). The single negative exponential model was fit to the data by least squares regression of the natural logarithm of mean percent mass remaining over time.

Calcium, Mg and K concentrations in the residual litter were determined by atomic absorption spectrophotometry (Perkin-Elmer 5000) following perchloric-nitric acid digestion (Blanchard *et al.*, 1965). Calcium and Mg concentrations were determined in an air-N₂O flame and K was determined in an air-acetylene flame using acid standards. Details on determination of N, S and P in the samples are given in Blair (in press). Net nutrient fluxes were derived from nutrient concentration and mass loss data. Percent nutrient remaining at time t was calculated as the product of percent mass remaining and nutrient concentration in the residual material at time t divided by the initial nutrient concentration of that litter type. Release rates of cations were estimated in a manner analogous to decay rates using percent nutrient remaining data.

Table 1. Mass loss and nutrient release rates derived from a single negative exponential model (Olson, 1963). Rate constants (k) are based on two years of data

	<i>C. florida</i>	<i>A. rubrum</i>	<i>Q. prinus</i>
Mass			
k (year ⁻¹)	-0.562	-0.393	-0.330
r^2	0.899	0.869	0.962
Calcium			
k	-0.373	-0.227	-0.128
r^2	0.851	0.534	0.600
Magnesium			
k	-0.529	-0.366	-0.223
r^2	0.613	0.359	0.689
Potassium			
k	-1.25	-0.567	-0.747
r^2	0.660	0.434	0.597

Results

Litter of the three species examined decayed in the following order (fastest to slowest): *C. florida* > *A. rubrum* > *Q. prinus*. First year annual decay rates were -0.850, -0.638 and -0.274, respectively. Annual decay rates based on two years of decomposition data were -0.562, -0.393 and -0.330, respectively (Table 1). Patterns of mass loss are presented in Fig. 1. Percent mass remaining at the end of two years for *C. florida*, *A. rubrum* and *Q. prinus* litter was 37, 42 and 54%, respectively.

Changes in the relative concentrations of Ca, Mg and K in litter of each species over a two-year period are presented in Fig. 2. Litter of *C. florida*, which had the highest initial Ca concentration (2.58%), exhibited an initial decrease in Ca concentration, presumably due to leaching, followed by a gradual increase to a maximum of 3.13%. Litter of both *A. rubrum* and *Q. prinus* displayed smaller initial decreases in Ca concentration followed by slower increases to a maximum of 1.37% in *A. rubrum* litter and 1.50% in *Q. prinus* litter. Changes in Mg concentrations were more variable. In both *C. florida* and *A. rubrum* litter there was an initial rapid decrease in Mg concentrations followed by a gradual continued decline for the remainder of the first year. Magnesium concentrations during the second year were more variable, but generally tended to increase as decomposition proceeded. Litter of *Q. prinus* had a lower initial Mg concentration and did not exhibit any

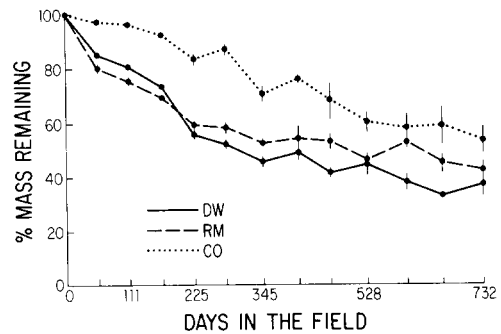


Fig. 1. Changes in mean percent of initial mass remaining in litter of *C. florida* (DW), *A. rubrum* (RM) and *Q. prinus* (CO) over a two-year period. Bars represent one SE.

initial leaching losses. Changes in K concentration were similar in litter of all three species. There were rapid initial decreases in K concentration due to leaching followed by very little change later in de-

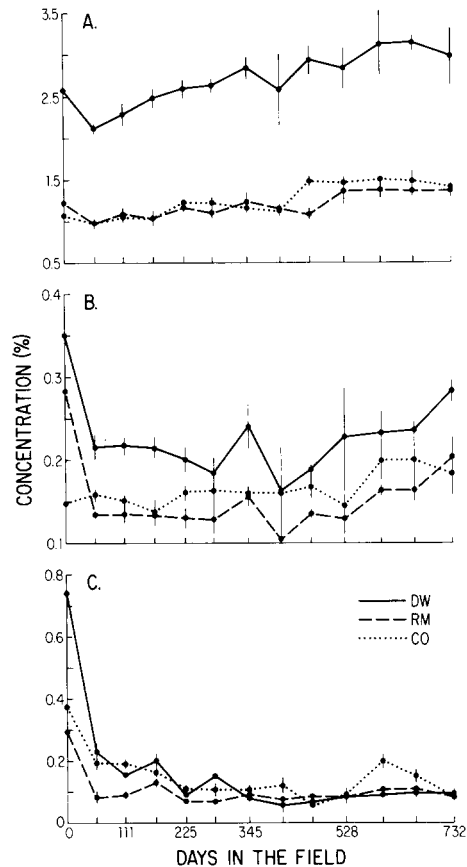


Fig. 2. Changes in mean concentrations of (A) calcium, (B) magnesium and (C) potassium in litter of *C. florida* (DW), *A. rubrum* (RM) and *Q. prinus* (CO) over a two-year period. Bars represent one SE.

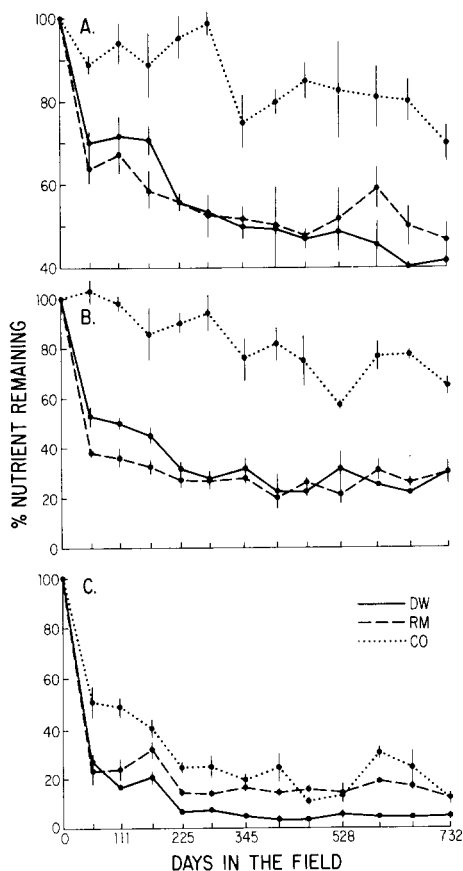


Fig. 3. Changes in absolute amounts of (A) calcium, (B) magnesium and (C) potassium in litter of *C. florida* (DW), *A. rubrum* (RM) and *Q. prinus* (CO) over a two-year period. Bars represent one SE.

composition. Although initial K concentrations ranged from 0.29 to 0.74% the final concentration of K in all three species after two years was between 0.08 and 0.09%.

Change in the absolute amount of a nutrient during decomposition is a function of both mass loss and change in the relative concentration of the nutrient in the remaining litter. Changes in the absolute amounts of Ca, Mg and K in litter of each species, expressed as percent of the initial amount remaining, are presented in Fig. 3. Percent nutrient remaining data for Ca, Mg and K were fit to a negative exponential model to estimate nutrient release rates (Table 1).

In litter of all three species there was a net release of Ca over the two-year study period (Fig. 3A). In the case of *C. florida* and *A. rubrum* there was a

rapid initial loss by day 59 followed by more gradual release for the remainder of the study. *Quercus prinus*, the slowest decomposing species, also released Ca at the slowest rate. By the end of the two-year study period net releases of Ca from litter of *C. florida*, *A. rubrum* and *Q. prinus* were 59, 54 and 30%, respectively, of initial amounts. There was a strong positive correlation ($r^2 = 0.978$) between Ca release rates and decomposition rates of the three litter types.

Magnesium release from all three litter types was somewhat more rapid than Ca release (Fig. 3B) and this is reflected in the higher release rates (Table 1). Litter of *C. florida* and *A. rubrum* exhibited a rapid initial loss of Mg in the first 59 days followed by more gradual release for the remainder of the first year. This was followed by very little change in absolute amounts of Mg during the second year of decomposition. Litter of *Q. prinus* exhibited a small increase in absolute amount (net immobilization) of Mg at day 59 followed by gradual net release for the remainder of the study. By the end of two years net releases of Mg from *C. florida*, *A. rubrum* and *Q. prinus* litter were 67, 77 and 43%, respectively, of initial amounts. Release rates of Mg were also positively correlated with decay rates ($r^2 = 0.952$).

Potassium was released much more rapidly than either Ca or Mg. Changes in absolute amounts of K were similar in litter of all three species (Fig. 3C). There were rapid initial losses of K in the first 59 days followed by continued net release for the remainder of the study. By the end of two years net releases of K from *C. florida*, *A. rubrum* and *Q. prinus* litter were 92, 89 and 89%, respectively, of initial amounts. Estimated K release rates (Table 1) were less strongly correlated to decay rates ($r^2 = 0.749$) than were Ca and Mg release rates. However, K release rates were highly positively correlated with initial K concentrations in the three litter types ($r^2 = 0.993$).

Discussion

Results of this study indicate a relatively rapid release of Ca, Mg and K from *C. florida*, *A. rubrum* and *Q. prinus* litter during the first two years of decomposition, although the relative release rates varied among cations and litter species. This is in contrast to patterns of N, P and S flux in the same

Table 2. Estimated annual inputs of mass and selected nutrients in foliar litter of three species on WS2 and subsequent net changes in the standing stock of each of these components at the end of the first and second years of decomposition. All values are expressed as kg ha⁻¹

Initial input	<i>C. florida</i>	<i>A. rubrum</i>	<i>Q. prinus</i>	Total
Litter mass ^a	170	320	970	1460
Year 1	-92 (54%)	-151 (47%)	-261 (27%)	-504 (35%)
Year 2	-15 (9%)	-35 (11%)	-190 (19%)	-239 (16%)
Net change	-107 (63%)	-185 (58%)	-451 (46%)	-743 (51%)
Calcium	4.4	3.9	10.4	18.7
Year 1	-2.2 (50%)	-1.9 (49%)	-2.6 (25%)	-6.7 (36%)
Year 2	-0.4 (9%)	-0.2 (5%)	-0.5 (5%)	-1.1 (6%)
Net change	-2.6 (59%)	-2.1 (54%)	-3.1 (30%)	-7.8 (42%)
Magnesium	0.6	0.9	1.4	2.9
Year 1	-0.4 (67%)	-0.7 (77%)	-0.4 (29%)	-1.5 (51%)
Year 2	0.0 (0%)	0.0 (0%)	-0.2 (14%)	-0.2 (7%)
Net change	-0.4 (67%)	-0.7 (77%)	-0.6 (43%)	-1.6 (58%)
Potassium	1.3	0.9	3.6	5.8
Year 1	-1.2 (92%)	-0.8 (89%)	-2.9 (81%)	-4.9 (85%)
Year 2	0.0 (0%)	0.0 (0%)	-0.3 (8%)	-0.3 (6%)
Net change	-1.2 (92%)	-0.8 (89%)	-3.2 (89%)	-5.2 (91%)
Nitrogen	1.3	1.8	8.4	11.4
Year 1	0.0 (0%)	+0.1 (+6%)	-0.7 (8%)	-0.6 (5%)
Year 2	-0.1 (8%)	0.0 (0%)	-0.3 (4%)	-0.4 (4%)
Net change	-0.1 (8%)	+0.1 (+6%)	-1.0 (12%)	-1.0 (9%)
Sulfur	0.3	0.2	0.6	1.1
Year 1	-0.2 (67%)	0.0 (0%)	0.0 (0%)	-0.2 (18%)
Year 2	0.0 (0%)	0.0 (0%)	0.0 (0%)	0.0 (0%)
Net change	-0.2 (67%)	0.0 (0%)	0.0 (0%)	-0.2 (18%)
Phosphorus	0.2	0.1	0.5	0.8
Year 1	-0.1 (50%)	0.0 (0%)	-0.1 (20%)	-0.1 (25%)
Year 2	0.0 (0%)	0.0 (0%)	0.0 (0%)	0.0 (0%)
Net change	-0.1 (50%)	0.0 (0%)	-0.1 (20%)	-0.1 (25%)

^a Litterfall data from Risley (1987).

litter substrates. Nitrogen and P were immobilized during the early stages of decomposition in all three litter substrates, as was S in the litter of *A. rubrum* and *Q. prinus* (Blair, in press). The overall relative mobility for the three cations examined was: K > Mg > Ca. These results are similar to those reported for litter of three hardwood species in a northeastern hardwood forest (Gosz *et al.*, 1973), *Pinus ponderosa* litter (Klemmedson *et al.*, 1985) and *Pinus resinosa* litter (Bockheim and Leide 1986). Overall relative mobility of all six elements examined in relation to mass loss was: K > Mg > mass > Ca > S > P > N.

The rapid release of K early in decomposition is a commonly observed phenomenon. Between 50 and 77% of initial litter K was released in the first 59 days. Potassium is not a structural component

of plant litter and is subject to removal by physical leaching. Therefore, K release is not strongly dependent on biotic activity (Alexander, 1977). This may explain why K release rates were more highly correlated with initial K concentrations than with decay rates. Additionally, K inputs to the forest floor via canopy leaching are considerable and often exceed inputs in litterfall (Swank, 1986).

Leaching also appears to play an important role in the early release of Mg from litter of *C. florida* and *A. rubrum*, which had much higher initial Mg concentrations than *Q. prinus* litter. However, following these initial losses Mg concentrations were variable but tended to increase, as they did throughout the decomposition of *Q. prinus* litter. This suggests that microbial immobilization of Mg may be important in the latter stages of decom-

position or in litter types with low initial Mg concentrations. Biological immobilization of Mg was also suggested as a mechanism of Mg retention in the latter stages of Scots pine litter decomposition (Staaf and Berg, 1982).

Initial leaching losses of Ca were much less than for either K or Mg. This is due to the nature of Ca as a structural component of plant litter. Therefore, the release of Ca is more dependent on biotic activity than on leaching. Net fluxes of Ca have been reported to track patterns of mass loss (Gosz, 1973; Staaf and Berg, 1982; Thomas, 1969). However, other studies have reported increased Ca concentrations during decomposition which result in greater retention, or even accumulation, of Ca during early phases of decomposition (Bockheim and Leide, 1986; Klemmedson *et al.*, 1985; Vogt *et al.*, 1983; Yavitt and Fahey, 1986). Some of the retention or accumulation of Ca in litter has been attributed to the formation of calcium oxalate by certain fungi (Cromack *et al.*, 1975). The increased Ca concentrations observed in this study resulted in slightly slower release rates of Ca, relative to mass loss, in the three species examined.

Watershed-level estimates of the net release of selected nutrients (Ca, Mg, K, N, S and P) from foliar litter of these three species may be obtained by combining data on nutrient dynamics, from this study and Blair (in press), with annual litterfall data for WS2 (Risley, 1987). These estimates should be interpreted with caution, however. First, they are based on foliar litter inputs of these three species only. Litter inputs of wood and dead roots in forests can be substantial and will affect estimates of nutrient release from total litter inputs (*i.e.*, Vogt *et al.*, 1983). Secondly, decomposition rates and nutrient fluxes of confined litter may differ from those of unconfined litter on the forest floor (St. John, 1980; Weider and Lang, 1982). However, these estimates do allow the comparison of the relative release rates of selected nutrients from foliar litter of three species that comprise over 46% of total foliar litter inputs on WS2 and represent a range of initial resource qualities.

Annual inputs of mass, Ca, Mg, K, N, S and P in foliar litter of *C. florida*, *A. rubrum* and *Q. prinus* on WS2 are presented in Table 2. Also presented are the net changes in each of these components at the end of the first and second years of decomposition. Annual foliar litter inputs by these three

species (1985–86) totaled 1460 kg ha⁻¹ (Risley, 1987). Net loss of mass from all three species was 743 kg ha⁻¹, or 51% of the initial litter input, by the end of two years. Annual inputs of Ca in litter of these species totaled 18.7 kg Ca ha⁻¹. By the end of year 2 there was a net release of 7.8 kg Ca ha⁻¹, an amount equivalent to 42% of the initial input. Thirty-six percent of initial Ca inputs were released in year 1. Only an additional 6% of initial inputs were released in year 2. Inputs of Mg by these species totaled 2.9 kg Mg ha⁻¹. Net release by the end year 2 was 1.7 kg Mg ha⁻¹, an amount equivalent to 58% of initial inputs. Fifty-one percent of initial Mg inputs were released in year 1 and only an additional 7% was released in year 2. Potassium inputs in litter of these three species totaled 5.8 kg K ha⁻¹. Net release by the end year 2 was 5.2 kg K ha⁻¹, an amount equivalent to 91% of initial inputs. Eighty-five percent of the initial K input was released in year 1 and only an additional 6% was released in year 2.

Net releases of N, S and P in the first two years of decomposition were much less than cation releases (Table 2). Annual inputs of N in litter of these species totaled 11.4 kg N ha⁻¹. By the end of year 2 there was a net loss of 1.0 kg N ha⁻¹, an amount equivalent to 9% of the initial input. Sulfur inputs in these three species totaled 1.1 kg S ha⁻¹. Net loss by the end of year 2 was 0.2 kg S ha⁻¹, an amount equivalent to 18% of initial inputs. The only species to release sulfur in the first year was *C. florida*, which had three times the initial S concentration of *A. rubrum* or *Q. prinus* (Blair, in press). Releases of S in year 2 were negligible. Inputs of P in these species totaled 0.8 kg P ha⁻¹. Net loss at the end of year 1 was 0.2 kg P ha⁻¹, an amount equivalent to 25% of initial inputs. Net release of P in year 2 was also negligible.

These results indicate that the majority of cation release occurs in the first year of decomposition. Release of the remaining cations continues during the second year but at a much slower rate, implying a rapid recycling of cation nutrients from plant litter to the soil where they may subsequently become available for plant uptake. This is in contrast to N, S and P which tend to be retained in the litter (Blair, in press; Staaf and Berg, 1982). Although over 50% of litter mass was lost in the first two years, net losses of N, S and P were relatively small. Thus, foliar litter of these species may

act as a nutrient reservoir or sink during the first two years of decomposition for nutrients limiting to the decomposer community such as N, S and P.

Acknowledgements

I thank B L Haines and D O Wilson for providing technical advice on nutrient analyses and M E Sumner for the use of his atomic absorption spectrophotometer. Thanks to D A Crossley, Jr, R W Parmelee and an anonymous reviewer for helpful comments on earlier drafts of this manuscript. Thanks are due the US Forest Service for their cooperation in the use of the Coweeta Facilities. This research was supported by NSF grant BSR-8012093 to the University of Georgia Research Foundation.

References

- Alexander M 1977 Introduction to Soil Microbiology. John Wiley and Sons, New York, 467 p.
- Berg B and Staaf H 1981 Leaching, accumulation, and release of nitrogen in decomposing forest litter. *In* Terrestrial Nitrogen Cycles: Processes, Ecosystem Strategies, and Management Impacts. Ed. T. Perrson. 33, pp 163–178 Ecol. Bull. (Stockholm).
- Berish C W and Ragsdale H L 1985 Chronological sequence of element concentrations in wood of *Carya* spp. in the southern Appalachian Mountains. *Can. J. For. Res.* 15, 477–483.
- Blair J M Nitrogen, sulfur and phosphorus dynamics in decomposing deciduous leaf litter in the southern Appalachians. *Soil Biol. Biochem.* (*In press*).
- Bockheim J G and Leide J E 1986 Litter and forest-floor dynamics in a *Pinus resinosa* plantation in Wisconsin. *Plant and Soil* 96, 493–406.
- Cromack K Jr, Todd R L and Monk C D 1975 Patterns of basidiomycete nutrient accumulation in conifer and deciduous forest litter. *Soil Biol. Biochem.* 7, 265–268.
- 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.
- Klemmedson J O, Meier C E and Campbell R E 1985 Needle decomposition and nutrient release in Ponderosa pine ecosystems. *For. Sci.* 31, 647–660.
- Olson J S 1963 Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* 44, 322–331.
- Risley L S 1987 Acceleration of Seasonal Leaf Fall by Herbivores in the Southern Appalachians. Ph. D. Dissertation, University of Georgia, Athens, Georgia.
- Seastedt T R 1984 The role of microarthropods in decomposition and mineralization processes. *Annu. Rev. Entomol.* 29, 25–46.
- St. John T V 1980 Influences of litterbags on growth of fungal vegetative structures. *Oecologia* 46, 130–132.
- Staaf H 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.
- Swank W T 1986 Biological control of solute losses from forest ecosystems. *In* Solute Processes. Ed. S T Trudgill. pp 85–139. John Wiley and Sons, Ltd.
- Swank W T and Crossley D A Jr 1986 Coweeta Hydrologic Laboratory background and synthesis. *In* Coupling of Ecological Studies with Remote Sensing. Eds. M I Dyer and D A Crossley, Jr. pp 23–32. U.S. Department of State Publication No. 9504.
- Swift M J, Heal O W and Anderson J M 1979 Decomposition in Terrestrial Ecosystems. University of California Press, Berkeley, 372 p.
- Thomas W A 1969 Accumulation and cycling of calcium by dogwood trees. *Ecol. Monogr.* 39, 101–120.
- Vogt K K, Grier C C, Meier C E and Keyes M R 1983 Organic matter and nutrient dynamics in forest floors of young and mature *Abies amabilis* stands in western Washington, as affected by fine-root inputs. *Ecol. Monogr.* 53, 139–157.
- Weider R K and Lang G E 1982 A critique of the analytical methods used in examining decomposition data obtained from litter bags. *Ecology* 63, 1636–1642.
- Yavitt J B and Fahey T J 1986 Litter decay and leaching from the forest floor in *Pinus contorta* (lodgepole pine) ecosystems. *J. Ecol.* 74, 525–545.