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AUTUMN LEAF FALL AND NUTRIENT RETURN IN AN OLD-GROWTH AND A SECOND-GROWTH FOREST IN EASTERN KENTUCKY[1]

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Autumn leaf fall was sampled in two watersheds, one containing an old-growth stand and the other a 35-yr-old second-growth stand of mixed mesophytic forest in eastern Kentucky. Total leaf fall and its composition did not differ between the two watersheds and averaged 291 g/m^2. Weighted average nutrient concentrations exhibited spatial variation, which paralleled a previously established soil fertility gradient. Total nutrient return by autumn leaf fall was greatest on mid-slope sites of both watersheds, where soil pH and nutrient availability are greatest. The combination of bulk nutrient return by leaf fall and of recognized variation in leaf decay rates suggests that the soil fertility gradient within each stand may be tied to internal nutrient cycling characteristics of the vegetation.

Introduction

Litter fall has been recognized as an important process in the nutrient dynamics of forested ecosystems. It is a significant pathway in the internal cycle of mineral elements within an ecosystem (Gosz, Likens, and Bormann 1972; Cromack and Monk 1975), and its dynamics may have been an important determinant in the evolution of temperate zone evergreen forests (Monk 1966). Also, the forest floor to which litter fall contributes is believed to serve as a regulator of ecosystem function (Bormann and Likens 1979). Most studies of litter fall have focused on the dynamics of input of litter to the forest floor on an annual basis and the rates of decomposition once that litter reaches the forest floor (Day 1974; Lang 1974; Rochow 1974). Few studies have assessed the variability in litter fall over important compositional gradients of vegetation or amounts of nutrient return over those gradients (Gosz et al. 1972; Grigal and Grizzard 1975; Bell, Johnson, and Gilmore 1978).

In temperate deciduous forests the two major components of litter fall are woody litter, which accounts for 35%–45% of the total input, and leaf fall (45%–50% of the total input; Rodin and Bazilevich 1967). Additional components, which are of variable and usually marginal magnitude, are bud scales, flowers, fruits, and frass. Woody litter fall is temporally sporadic, being strongly influenced by storms, and spatially very heterogeneous. Leaf fall, on the other hand, is highly pulsed in a temporally regular pattern and is spatially homogeneous. The greater concentrations of major nutrients in leaf litter over woody litter magnify its importance as a major pathway in the dynamics of nutrient cycling and conservation in forested ecosystems. Leaf fall accounts for 55%–90% of total nutrient transfer by litter fall in temperate deciduous forests (Rodin and Bazilevich 1967). The temporally regular occurrence of leaf fall and its spatial homogeneity further contribute to its importance in ecosystem processes.

Foliar nutrient content may vary considerably depending on species, age of the organism, time of season, and nutrient availability in the local substrate (Gosz et al. 1972; van den Driessche 1974; Day and Monk 1977). The influence of nutrient availability on foliar contents is most evident when widely differing substrates are contrasted. In a study of tree foliage from sites of varying limestone content, Bard (1945) found increased P and K content in samples from the more acid sites where exchangeable amounts of these elements were greater. Similarly, Reich and Hinckley (1980) found an important correlation between foliar contents of Ca and Mg and exchangeable levels of these elements in the soil over a significant pH and fertility gradient in a pygmy oak forest in Missouri. However, these same relationships are not always evident over more subtle gradients of nutrient availability and may be expected to be even less clear in fallen leaves that have been subjected to nutrient resorption and leaching during senesence.

As part of a study of the vegetation in the Mixed Mesophytic Forest Region and the structural and compositional recovery of that vegetation following disturbance, autumn leaf fall was sampled in an

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old-growth forest containing beech and beech–hemlock stands, sugar maple–basswood stands, and chestnut oak–red maple stands, and in a 35-yr-old second-growth forest that had developed after clear-cutting and was of similar composition. Objectives of the study were (1) to compare rates of leaf fall and nutrient return by leaf fall within two forests of differing age and structural attributes, and (2) to compare rates of leaf fall and nutrient return by leaf fall along important environmental gradients in the Mixed Mesophytic Forest Region.

Methods

Lilley Cornett Woods is a 148-ha preserve located in the center of the Mixed Mesophytic Forest Region in Letcher County of southeastern Kentucky (83°0′W,37°5′N). Two watersheds were chosen for detailed studies of forest structure and processes. Big Everidge Hollow (52 ha) is located in the southwestern corner of Lilley Cornett Woods and is covered entirely by old-growth forest. Immediately adjacent to it and outside of the Lilley Cornett Woods boundary lies Pollbranch Hollow (89 ha), which was clear-cut in 1945 and allowed to regenerate naturally. The two watersheds are similar in shape, elevational range (335–600 m), aspect (east facing), and geologic substrate. They differ most significantly in forest history. Detailed discussions of the geology and soils of the area are available in PUFFETT (1965), BYRNE et al. (1970), and MARTIN (1975). In spite of the cutting history of Pollbranch, overall composition and structure of the two watersheds are similar. Basal area does not differ significantly between the two stands and averages 29 m^2/ha (MULLER 1982).

Phytosociological analyses of the old-growth forest indicated that strong vegetational gradients exist which are related to distinct topographic and edaphic parameters (MARTIN 1975) and more directly to soil moisture and soil fertility (MULLER 1982). On the basis of these analyses, three communities may be distinguished. Beech and beech–hemlock-dominated stands exist on lower slopes where soil moisture is high and extractable nutrients in the upper 20 cm of soil are intermediate. Sugar maple–basswood-dominated stands occur on mid-slope positions (particularly on north-facing aspects) where soil moisture and extractable nutrients are high. Finally, chestnut oak–red maple-dominated stands occur on upper slope and ridgetop sites where soil moisture and extractable nutrients are low. The second-growth forest exhibits similar composition and species distributions, with an increase in species such as *Liriodendron tulipifera* and *Cercis canadensis,* which occur early in succession. The fertility patterns in the surface soil do not appear to be related to the underlying substrate, which is composed of interbedded layers of sandstone, siltstone, shale, and coal. This is particularly so for nitrogen, which is, in general, an insignificant component of the lithosphere (FORTESCUE 1980).

Forty leaf fall traps were located in each watershed, using plots that had been established in a stratified random manner for analysis of the vegetation (MULLER 1982). Leaf fall traps consisted of a metal hoop (0.22 m^2) held ca. 1 m above the ground by three wooden stakes. Plastic bags, into which small holes were cut for drainage of water, were fixed to the hoop. The traps were set out on September 15, 1979, and collected on November 15, 1979.

This sampling scheme was designed primarily for direct comparison of the two watersheds. Significant, although small, amounts of leaf fall may occur both prior to and following the main body of leaf fall during the autumn. However, visual observation at the beginning and end of the collection period indicated that the main body of leaf fall was collected, and detailed analyses of the temporal pattern of leaf fall in deciduous forests suggest that no more than 10% of the actual total leaf fall may have been missed (ROCHOW 1974; GRIGAL and GRIZZARD 1975).

The collected samples were separated into eight species groups: *Acer rubrum, A. saccharum, Fagus grandifolia, Liriodendron tulipifera, Quercus alba, Q. prinus,* red oaks (which include *Q. coccinea, Q. rubra,* and *Q. velutina*), and all other species. Each subsample was dried to a constant weight at 80 C and weighed to the nearest 0.1 g. The samples were ground for nutrient analysis and analyzed for total N by the Kjeldahl procedure, modified to include nitrate (BREMNER 1965) and wet ashed for analysis of P, K, Ca, and Mg. Ashing consisted of digesting 0.5 g of the sample in 10 ml of nitric-perchloric acid for at least 12 h, drying the sample, and taking up the inorganic components in 1 N HCl. Phosphorus was determined in appropriate dilutions of the ashed sample colorimetrically with a Technicon Auto Analyzer, using a modification of the method of FISKE and SUBBAROW (1925); the cations were determined by atomic absorption spectroscopy.

Comparisons between watersheds were conducted by *t*-test and between phytosociological groups of plots (MULLER 1982) by analysis of variance, using Duncan's multiple range test. Sample sizes for these groups were 14 for lower slope (beech) plots, 11 for mid-slope (sugar maple–basswood) plots, and 15 for upper slope (chestnut oak–red maple) plots in Big Everidge; and 12, 12, and 16, respectively, for the same groups in Pollbranch.

Results and discussion

There were few strong differences in leaf fall biomass or nutrient concentrations between watersheds. The average leaf fall over both watersheds (291 g/m^2; table 1) is at the lower end of

the range of values presented by BRAY and GORHAM (1964) for warm temperate forests and at the upper end of the range for cool temperate forests. The latitudinal location of the study site places it at the boundary of both regions. Among the categories of individual species, *Fagus grandifolia* accounted for the greatest proportion of average leaf fall (19.6%), followed by *Quercus prinus* (15.3%), *Acer saccharum* (9.3%), *A. rubrum* (8.8%), *Liriodendron tulipifera* (4.8%), and *Q. alba* (4.5%). The combined categories of red oaks and others accounted for 37.7% of the average total leaf fall. The only significant difference in leaf fall between watersheds by species group was for the category of "others," which showed 33% greater leaf fall in Pollbranch (91 g/m^2) than in Big Everidge (68 g/m^2). This reflects the significantly greater basal area of species such as *Cercis canadensis, Cornus florida, Robinia pseudoacacia,* and *Sassafras albidum* in the second-growth watershed (MULLER 1982).

The similarity of leaf fall from *L. tulipifera* in the two watersheds may also be related to basal area. Although density of *L. tulipifera* was strongly influenced by the history of the two stands and was much greater in the second-growth stand, its total basal area was not different (MULLER 1982). In spite of its intolerance to heavy shading, *L. tulipifera* is able to maintain itself in old-growth forest by colonizing small gaps and growing to full stature prior to complete canopy closure (BUCKNER and McCRACKEN 1978; SKEEN, CARTER, and RAGSDALE 1980). This is clearly evident in Big Everidge, where it exists as large-statured individuals, average dbh = 35.9 cm, whereas in Pollbranch its average dbh is 16.4 cm.

Nutrient content of leaf fall varied considerably among species, with highest concentrations of N, P, Ca, and Mg in *L. tulipifera* and lowest levels of those elements in the oaks (table 2). Within species, concentrations followed the order of Ca > N > K > Mg > P. PETERSON, ROLFE, and BAZZAZ (1979) found a similar concentration sequence in leaf litter of a bottomland hardwood forest in southern Illinois. Nutrient concentrations showed few strong trends between watersheds. In general, later successional species, such as *A. saccharum, F. grandifolia,* and *Q. prinus,* showed higher elemental concentrations in leaf fall from Big Everidge than in Pollbranch. However, *L. tulipifera* exhibited higher concentrations of K and Ca in Pollbranch than in Big Everidge.

Surface soil (0–20 cm) analyses from the sample locations showed a strong gradient of decreasing fertility from sugar maple–basswood-dominated plots to beech-dominated plots to chestnut oak–red maple-dominated plots (MULLER 1982). CHANDLER (1941) found significant differences in nutrient content of bulk litter collected from sites of varying acidity in New York and attributed these differences to compositional variation of the leaf fall itself. Species growing on more acid sites contained lower concentrations of macronutrients than those on less acid sites. Weighted average nutrient concentrations for the bulk litter on Big Everidge showed similar trends, especially for N, P, and Ca, with highest concentrations in samples from the mid-slope, where *A. saccharum* and *T. heterophylla* were dominant (table 3). Of the leaf fall on those plots, 71% was accounted for by *A. saccharum, F. grandifolia, L. tulipifera,* and "others," all of which contained higher nutrient concentrations than the oaks that are dominant on the upper slope and ridgetop plots. Clearly, species composition is important in the higher concentrations observed in mid-slope samples.

No significant differences were observed in average bulk nutrient return by leaf fall between watersheds, either for total nutrient return or for any of the eight species categories (table 2). Among individual species, the greatest proportion of total

TABLE 1

AUTUMN LEAF FALL (g/m^2) IN AN OLD-GROWTH (BIG EVERIDGE) AND SECOND-GROWTH (POLLBRANCH) FOREST AT LILLEY CORNETT WOODS

Species	Big Everidge	Pollbranch
Acer rubrum	23.1 ± 4.8	28.0 ± 5.1
A. saccharum	26.4 ± 7.7	27.5 ± 7.1
Fagus grandifolia	58.1 ± 11.8	55.8 ± 13.0
Liriodendron tulipifera	12.8 ± 2.7	15.3 ± 3.2
Quercus alba	17.3 ± 5.9	8.8 ± 5.4
Q. prinus	55.8 ± 12.9	33.2 ± 8.1
Red oaks	28.2 ± 4.2	32.3 ± 6.5
Others	68.2 ± 7.9	91.0 ± 8.7
Total	290.5 ± 11.2	291.8 ± 11.3

NOTE.—Values are the average of 40 samples and are given with 1 SE.

TABLE 2

AVERAGE NUTRIENT CONCENTRATION (% of dry weight) AND NUTRIENT RETURN IN AUTUMN LEAF FALL AT LILLEY CORNETT WOODS

	N		P		K		Ca		Mg	
	%	kg/ha	%	kg/ha	%	kg/ha	%	kg/ha	%	kg/ha
Acer rubrum	.75 (.03)	1.9 (.2)	.04 (.005)	.1 (.02)	.50 (.02)	1.3 (.2)	1.19 (.04)	2.9 (.4)	.26 (.01)	.6 (.09)
A. saccharum	1.01 (.03)	2.9 (.5)	.07 (.01)	.3 (.1)	.54 (.02)	1.4 (.3)	1.52 (.05)	4.2 (.8)	.28 (.02)	.7 (.1)
Fagus grandifolia	1.01 (.02)	8.3 (2.8)	.05 (.004)	.3 (.05)	.50 (.02)	2.8 (.4)	1.30 (.07)	6.6 (.9)	.20 (.006)	1.1 (.2)
Liriodendron tulipifera	1.15 (.04)	1.7 (.3)	.09 (.01)	.1 (.02)	.49 (.03)	.7 (.1)	2.08 (.09)	2.8 (.4)	.47 (.02)	.6 (.1)
Quercus alba	.87 (.04)	1.2 (.4)	.04 (.005)	.1 (.02)	.46 (.02)	.6 (.2)	1.15 (.08)	1.5 (.4)	.20 (.01)	.3 (.07)
Q. prinus	.84 (.02)	3.6 (.6)	.03 (.004)	.1 (.03)	.51 (.02)	2.5 (.5)	1.14 (.03)	5.3 (1.0)	.19 (.006)	.8 (.1)
Red oaks	.90 (.02)	2.7 (.3)	.03 (.003)	.1 (.01)	.48 (.02)	1.5 (.2)	1.05 (.05)	3.1 (.4)	.23 (.01)	.7 (.1)
Others	1.27 (.03)	10.0 (.8)	.07 (.005)	.6 (.06)	.63 (.03)	5.2 (.5)	1.76 (.06)	14.4 (1.3)	.36 (.01)	2.9 (.2)
Total		32.2 (2.7)		1.7 (.1)		16.0 (.6)		40.8 (1.5)		7.8 (.2)

NOTE.—Nutrient concentration values are the averages of variable numbers of samples depending on the number of actual collections of a species made. Nutrient return values are the average of 80 samples distributed evenly between the Big Everidge and Pollbranch watersheds. Values in parentheses are SEs of the means.

nutrient return was accounted for by *F. grandifolia* (17.3%), followed by *Q. prinus* (13.3%), *A. saccharum* (9.8%), *A. rubrum* (7.1%), *L. tulipifera* (6.1%), and *Q. alba* (3.9%). The categories of red oaks and "others" accounted for 8.2% and 33.6%, respectively, of total nutrient return by leaf fall. The increased importance of *L. tulipifera* and "others" in litter fall nutrient return over leaf weight alone is the result of higher concentrations of macroelements. The low elemental concentrations in the oaks resulted in proportionally lower bulk nutrient return by those species.

Bulk nutrient return exhibited strong gradients in Big Everidge, which were confirmed, in part, by the data of Pollbranch. For N, P, K, Ca, and Mg in Big Everidge, bulk return in mid-slope plots was significantly greater than in lower slope and/or upper slope plots (table 4). Because of variation among species in elemental composition, these differences are greatly accentuated over those of dry weight alone. For instance, bulk return of N in lower slope and upper slope samples was 71.4% and 66.0%, respectively, of the return observed in mid-slope samples, while dry weight of leaf fall in lower slope and upper slope plots averaged 80.9% and 92.6%, respectively, of that in mid-slope plots. Although not as strong, similar trends appeared in Pollbranch. Bulk return of N, P, K, Ca, and Mg in mid-slope plots was either equal to or greater than return in the other two groups (table 4), even though leaf fall by dry weight was least in mid-slope plots in that watershed. Nutrients returned in leaf fall may be redistributed downslope before mineralization occurs (ORNDORFF and LANG 1981;

TABLE 3

WEIGHTED AVERAGE NUTRIENT CONCENTRATIONS (% of dry weight) IN THE THREE REGIONS OF THE BIG EVERIDGE WATERSHED DISTINGUISHED BY SPECIES COMPOSITION

	N	P	K	Ca	Mg
Lower slope	1.02[ab]	.06[b]	.504	1.258[b]	.261
Mid-slope	1.16[ac]	.09[ac]	.539	1.647[ac]	.265
Upper slope	.83[bc]	.05[b]	.582	1.259[b]	.255

NOTE.—Lower slope plots are dominated by *Fagus grandifolia*, mid-slope plots by *Acer saccharum* and *Tilia heterophylla*, and upper slope plots by *Quercus prinus* and *A. rubrum*.

[a] Values significantly different from upper slope values at .05 level.

[b] Values significantly different from mid-slope values at .05 level.

[c] Values significantly different from lower slope values at .05 level.

TABLE 4

AUTUMN LEAF FALL (g/m^2) AND NUTRIENT RETURN IN LEAF FALL (kg/ha) IN THREE REGIONS OF BIG EVERIDGE AND POLLBRANCH WATERSHEDS

	Leaf fall	N	P	K	Ca	Mg
Big Everidge:						
Lower slope (14)	259.6[b]	26.5[b]	1.4[b]	13.2[ab]	32.6[b]	6.8[b]
Mid-slope (11)	320.9[c]	37.1[ac]	3.1[ac]	17.5[c]	52.7[ac]	8.4[c]
Upper slope (15)	297.1	24.5[b]	1.5[b]	17.5[c]	36.7[b]	7.4
Pollbranch:						
Lower slope (12)	298.9	33.9	1.6	14.4	37.5[b]	6.7[a]
Mid-slope (12)	255.0[a]	29.3	2.2[a]	15.1	48.5[c]	8.0
Upper slope (16)	314.0[b]	29.3	0.9[b]	17.8	40.1	9.0[c]

NOTE.—In both watersheds, lower slope plots are dominated by *Fagus grandifolia*, mid-slope plots by *Acer saccharum* and *Tilia heterophylla*, and upper slope plots by *Quercus prinus* and *A. rubrum*. Sample size of each region given in parentheses.

[a] Values significantly different from upper slope values at .5 level.

[b] Values significantly different from mid-slope values at .05 level.

[c] Values significantly different from lower slope values at .5 level.

WELBOURN, STONE, and LASSOIE 1981; LANG and ORNDORFF 1982), but the extent of such redistribution may vary significantly with local conditions of topography, vegetation, and microstructure of the forest floor. The field sites of this study encompass average slopes of 55% with lengths of 900 m. Clearly, some downslope movement of litter must occur; however, microsite diversity such as windfall pits, logs, rocks, and understory vegetation can serve as effective traps to retain litter in the general vicinity of deposition (LANG and ORNDORFF 1982). Such processes were observed extensively within the study areas; most likely, downslope movement of litter is not great.

The uniformity of leaf fall and nutrient return values in both watersheds is supported by strongly similar structural and compositional characteristics of the two stands (MULLER 1982). The equivalent total leaf fall values for Big Everidge and Pollbranch imply similar leaf area index values and, hence, similar production potential. This suggests that, despite the difference in age, patterns of production and resource utilization may be similar. COVINGTON and ABER (1980) found generally constant leaf fall values in mixed-species stands of northern hardwoods at ages greater than 30 yr following cutting, and MARKS (1974) found a very rapid recovery of leaf area index and production in early successional forests of the northern hardwood region.

MARKS (1974) suggested that, in cutover forests of the northeast, the determinant factors of forest growth, regardless of successional stage or species composition, are the levels of available resources. Early successional forests develop rapidly until complete utilization of resources is achieved. The similar leaf fall and nutrient return of Big Everidge and Pollbranch, along with the similar compositional and structural characteristics of the two watersheds, indicate that the potential exists in southern Appalachian forests for rapid recovery following disturbance. BORING, MONK, and SWANK (1981) found that successional species establishing on a site during the first year following disturbance contributed greatly to the rapid recovery of nutrient cycling processes. The results of our study suggest that components of the mature forest are also capable of rapid establishment and stabilization of the site. Although continued development may be expected in terms of total biomass accumulation and magnitude of nutrient pools, the first 30 yr of succession are clearly important in determining the dynamics of the recovery process.

Vegetation analysis has indicated an important relationship between species distribution and overall soil fertility (MULLER 1982). Surface soils from the mid-slope samples were characterized by higher cation exchange capacity, percentage of base saturation, extractable bases (K, Ca, and Mg), N, and P than soils of either lower or upper slope samples. Site differences in bulk nutrient return of autumn leaf fall support the hypothesis of an important fertility gradient in the distribution of forest vegetation in the southern Appalachians. *Fagus grandifolia* and the species of *Quercus* are characterized by slower rates of decomposition and, hence, nutrient turnover than *A. saccharum* and several of the other dominants in mid-slope plots (MELIN 1930; KUCERA 1959; GOSZ, LIKENS, and BORMANN 1973; BELL et al. 1978). These slower turnover rates, combined with lower nutrient concentrations of leaf litter and lower bulk nutrient return, suggest that along with the gradient of soil fertility occurs a gradient of nutrient cycling dynamics. On mid-slope plots dominated by *A. saccharum* and *T. heterophylla,* fast internal cycling of elements involving relatively large nutrient pools occurs, while slower internal cycling of small nutrient pools occurs on lower slope plots dominated by *F. grandifolia* and on upper slope and ridgetop plots dominated by *Q. prinus* and *A. rubrum.* Such processes, in addition to other factors such as nutrient resorption (RYAN and BORMANN 1982), would contribute to the overall nutrient cycling characteristics of a site and may be important in determining some aspects of landscape diversity.

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