LITTER DYNAMICS OF A BOTTOMLAND HARDWOOD FOREST IN SOUTHERN ILLINOIS

David L. Peterson and Gary L. Rolfe.[1/]

Abstract.--Patterns of litterfall and subsequent decomposition and nutrient turnover were studied in a bottomland hardwood forest in southern Illinois. Mean litterfall dry weight was 6500 kg ha^{-1} yr^{-1}, and nutrient inputs were in the order Ca > N >> K >> Mg > P > Na. A large proportion of litterfall (16% dry weight) was comprised of reproductive material, primarily sweetgum fruits. Rates of nutrient exchange were determined on the basis of a decomposition experiment and analysis of forest floor litter. Relative to dry weight loss in decomposing leaves, N was strongly accumulated, P was moderately accumulated, Ca was moderately leached, and Mg and K were highly leached. Analysis of forest floor litter indicated that Na may have a slow turnover rate due to uptake by fungi and root exudation. The immobilization of N was perhaps the most significant feature of decomposition in the forest and indicates the strong demand for this element by heterotrophic decomposer organisms. This net assimilation of N represented a gain of 19.3 kg ha^{-1} yr^{-1} beyond that contained in litterfall. Forest floor leaf litter may act as a sink in which N is retained despite long periods of inundation by floodwater.

Additional keywords: Bottomland forest, decomposition, forest floor, litterfall, nutrient cycling, turnover rate.

During the past twenty years, there has been considerable interest in various aspects of nutrient cycling in forest communities (e.g., Duvigneaud and Denaeyer - de Smet 1973; Likens, *et al*. 1977; Rolfe, *et al*. 1978), although few studies have been done on bottomland hardwood forests. Since wetland forests are currently being more extensively utilized commercially and are subject to loss by agricultural and developmental interests (Horwitz 1978), it is surprising that there has not been more work done on bottomland communities. Studies by Brinson (1977) and Brinson, *et al*. (1980) on decomposition and litterfall in a *Nyssa aquatica* L. swamp forest and by Conner and Day (1976) on productivity in an *Acer rubrum* L. - *N. aquatica* forest are among the few to examine aspects of nutrient cycling in bottomland hardwood communities.

Litterfall is an important internal cycling mechanism in forest communities. Subsequent breakdown of organic materials on the forest floor and eventual mineralization provide a major pathway for the return of nutrients to the

[1/] Research Assistant and Professor, Department of Forestry, University of Illinois, Urbana, IL. The authors thank George Weaver and Phil Robertson for permission to use their vegetation data, and the Illinois Department of Conservation for their cooperation in allowing the use of the study site. Tim White collected most of the samples for the study, and Dan Rice and Kate Wroblewski assisted with nutrient analysis. This study was supported by McIntire-Stennis Research Project No. 55-309, under the auspices of the Illinois Agricultural Experiment Station.

soil for potential uptake by plants. In our study of a bottomland hardwood forest we have characterized the litter dynamics of the site by determining: 1) the phenology of and nutrient inputs from litterfall, 2) the quantity and turnover rates of nutrients in forest floor litter, and 3) the rate of leaf dry weight loss and patterns of element exchange in decomposing leaves.

STUDY SITE

The study was conducted on Horseshoe Lake Island in Alexander County, Illinois. The study site supports an undisturbed, old-growth bottomland forest and is representative of the original floodplain forest in the area. *Liquidambar styraciflua* L. is the dominant species, comprising nearly 58% of the basal area in the plots selected for study. The major subdominant species are *Ulmus americana* L., *Acer rubrum*, and *Fraxinus pennsylvanica* Marsh. Understory and herbaceous vegetation is sparse. The vegetation of the Horseshoe Lake bottomland forest has been described in detail by Robertson, *et al.* (1978).

Flooding on the study site is extensive, and is influenced by the hydrology of the lake. The lake area was once part of the Mississippi River and was formed when the stream abandoned the Horseshoe Lake channels (Fisk 1944). A fixed spillway currently maintains a permanent pool in these channels, resulting in an elevated water table and prolonged periods of flooding on the island. During the course of this study, the bottomland forest had standing water at depths of up to 1.4 m from early November, 1977 to early June, 1978 and from late December, 1978 to early August, 1979. Although a small stream connects the forest with the lake when flood levels are greater than about 80 cm, floodwater is generally stagnant.

The soil of the study site is an Okaw silt loam, a Typic Albaqualf (Parks and Fehrenbacher 1968). The A horizon is a thin (0-7 cm) silt loam layer, and the B horizon is a thick (7-100 cm) layer of silty clay.

METHODS

Six .04 ha plots were selected on the basis of uniformity with respect to vegetation compostition and structural characteristics; these plots were representative of the Horseshoe Lake Island bottomland forest community described by Robertson, *et al* (1978). Sixteen 1 x 1 m baskets with wooden sides and aluminum screen bottoms were situated within each plot for litter collection. The baskets were elevated 1.5 m above the soil on fence posts to prevent inundation of litter by floodwater. Litter was normally collected monthly, but was collected weekly during peak litterfall in October and November. Litter for January, February, and March was composited since the presence of snow prevented collection during this period. Litter samples were separated into leaves, wood and bark, and reproductive parts. Collections were conducted for 2 years, beginning on 1 October 1977.

Forest floor litter was collected on 30 September 1977 and 30 September 1978, prior to the onset of substantial autumn litterfall. Ten samples were collected per plot with a 0.06 m^2 quadrat, and only recognizable leaf litter (01 horizon) was collected.

The decomposition rate of leaf litter was determined by measuring weight loss and nutrient variation of a known quantity of leaves. Samples of 72 g (oven dry weight) of fresh leaf litter were placed in closed hardware cloth containers (7 mm mesh) with a bottom surface area of 1650 cm^2, and eight containers were placed in each plot on the old forest floor litter. Containers were placed in the field on 1 December 1977, and samples were collected periodically for 2 years.

Plant tissue samples were oven-dried at 80°C for 48 hr., weighed, and ground to pass a 20-mesh screen prior to nutrient analysis. Decomposing leaves were gently rinsed with deionized water to remove sediment prior to drying. Total nitrogen was determined using an aluminum block digestion method (Gallaher, et al 1976) and semimicro-kjeldahl technique (Bremner 1965.) Samples were ashed and dissolved in 1N HNO_3 prior to other analyses. Phosphorus was determined colorimetrically with a single solution procedure (Murphy and Riley 1962), and Ca, Mg, K, and Na were measured with atomic absorption spectrophotometry (Ediger 1973).

RESULTS

Annual litterfall inputs were very similar for both years of the study, 6448 kg ha^{-1} and 6551 kg ha^{-1}, although the proportions of specific litter components varied considerably. During the first year (1 Oct. 1977-30 Sept. 1978), leaves, wood, and reproductive material comprised 58%, 22%, and 20% of the litter, respectively, while during the second year (1 Oct. 1978-30 Sept. 1979), these components were 74%, 13%, and 13%, respectively. Over 80% of leaf fall occurred during October and November (Fig. 1), and there were large inputs of reproductive litter, primarily sweetgum fruits, during winter and early spring. Woody litter was distributed evenly throughout the year, with the exception of autumn, 1977.

Nutrient inputs via litterfall were in the order: Ca > N >> K >> Mg > P > N (Table 1).

Table 1.--Mean litterfall rates (kg ha^{-1} yr^{-1}) for dry weight and nutrients, based on a two-year study period.

Component	Dry Weight	N	P	K	Ca	Mg	Na
Leaves	4298	39.8	4.6	20.0	54.4	9.0	3.8
Wood	1144	9.5	0.84	2.8	15.0	1.4	0.53
Reproductive	1058	10.7	0.96	2.6	4.8	0.99	0.32
Total	6500	60.0	6.4	25.4	74.2	11.4	4.6

Reproductive litter contributed ≥ 15% of the N and P input, but ≤ 10% of all other elements. The concentration of elements varied for all components during the year, with only leaf litter displaying clear annual patterns (Fig. 2)

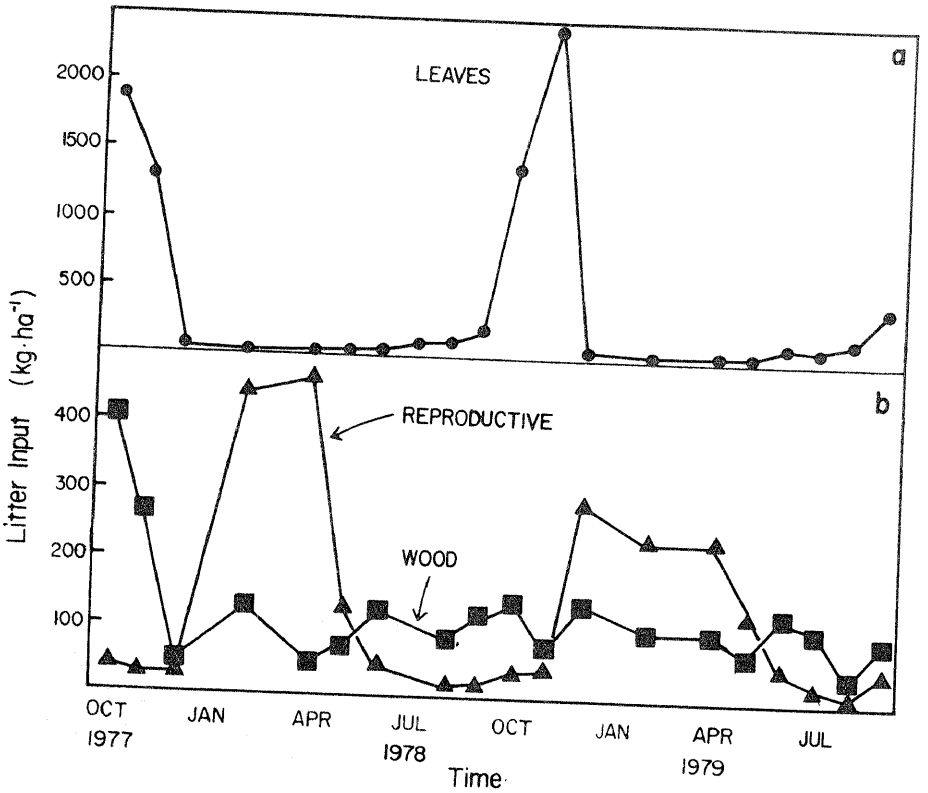

Figure 1.--Patterns of litterfall over a two-year period for (a) leaves and (b) wood and reproductive material. Note change of scale on vertical axis.

Both N and P concentrations in leaf litter rose sharply in the spring, then declined steadily during the growing season. Potassium and Mg also increased during the spring and decreased during the peak litterfall period in autumn. Calcium increased during the growing season, and Na increased slightly before declining in autumn.

The forest floor contained a minimum litter layer (prior to autumn leaf fall) of 12,557 kg ha^{-1}, with nutrient pools in the order: N > Ca >> Na > Mg > P > K (Table 2). The activities of nutrient inputs and standing states (forest floor litter) were compared by calculating the turnover time (Reiners and Reiners 1970) for each element. Turnover time is defined as the mean standing state of an element divided by the annual input, where mean standing state is calculated for forest floor pools by averaging minimum pool size (in September) with maximum pool size (minimum pool size + annual litterfall). Turnover time for leaf litter biomass was 3.4 yr., with element turnover in the order: Na > N > Ca > P > Mg > K, from longest to shortest time. Table 2

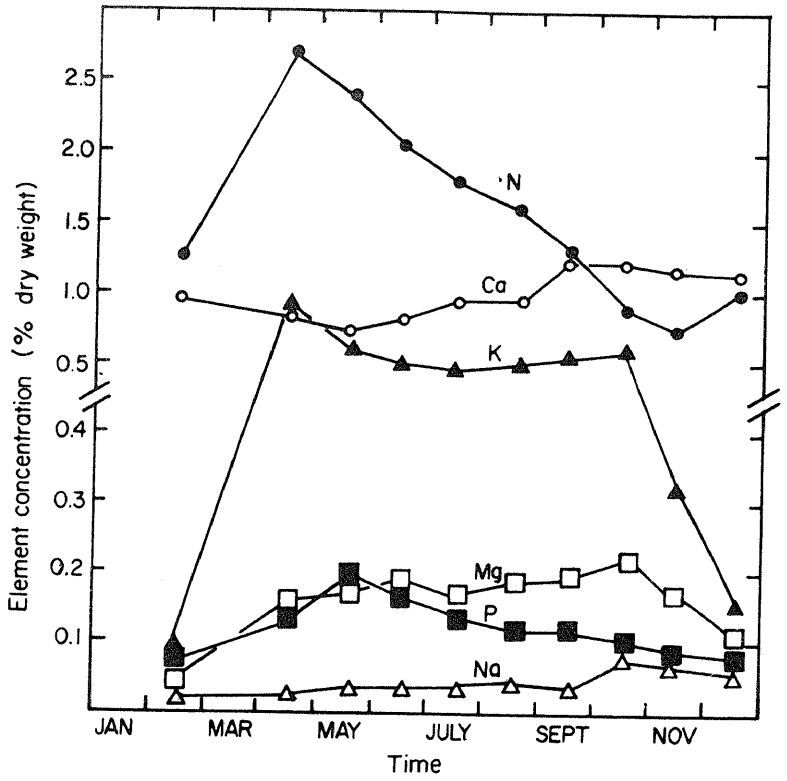

Figure 2.--Annual patterns of variation in the concentration of elements in leaf litter. Each data point represents the mean of two years of collections.

Table 2.--Summary of leaf litter dynamics, based on means for two years of data. Pool size refers to forest floor biomasses.

Component	Annual Litter Input (kg ha^{-1})	Minimum Pool Size (kg ha^{-1})	Mean Pool Size (kg ha^{-1})	Turnover Time (yr)	Fractional Annual Turnover (%)
Dry weight	4298	12,557	13,206	3.4	29.2
N	39.8	176.7	196.6	4.9	20.2
P	4.6	11.4	13.7	3.0	33.6
K	20.0	10.1	20.1	1.0	99.5
Ca	54.4	140.6	167.8	3.1	32.4
Mg	9.0	12.6	17.1	1.9	52.6
Na	3.8	19.0	20.9	5.5	18.2

also indicates fractional annual turnover, which is the reciprocal of turnover time expressed as a percentage.

The decomposition study indicated that although 29% of leaf dry weight was lost during the first year only 32% was lost after 2 years (Fig. 3b). Weight loss as a function of time can be expressed as a power curve. There were two basic patterns of nutrient flux for the six elements analyzed (Fig. 3a): 2 elements were accumulated or retained at their original quantity and 4 elements were subject to various degrees of loss. Nitrogen increased approximately 50% over the 2-year period, and increased 110% in concentration, while P remained at near the original quantity after an initial decrease. Leaf tissue content of K and Mg decreased sharply during the first year of the experiment, while Ca gradually declined and stabilized at about 50% of its original level. Sodium showed an erratic pattern of decrease.

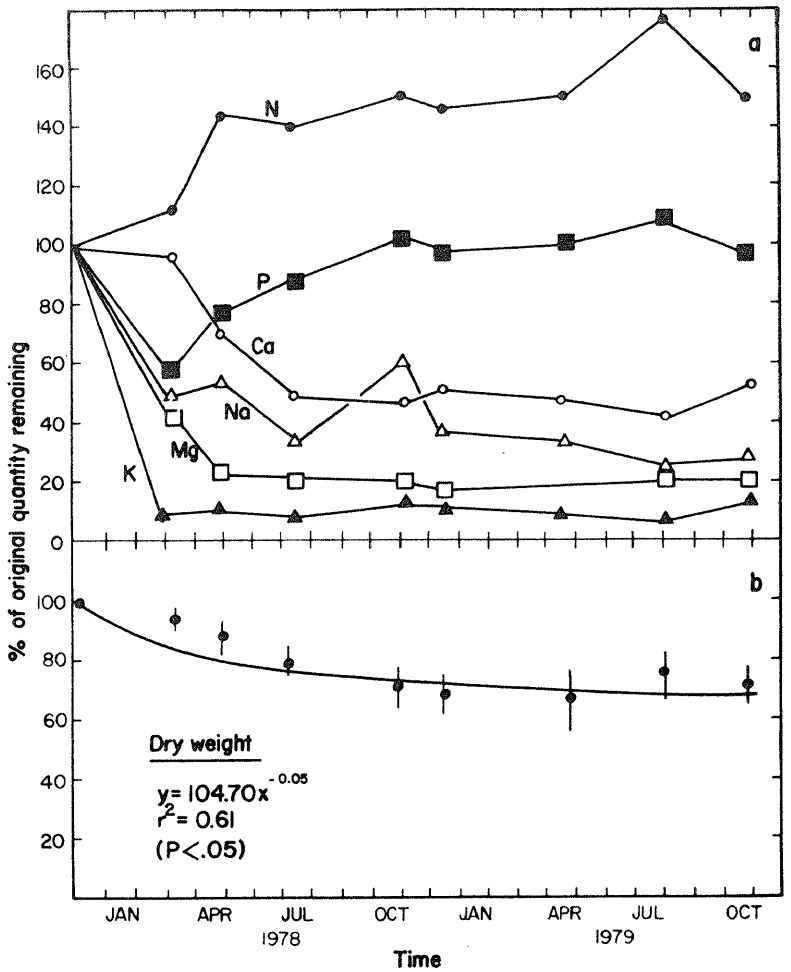

Figure 3.--Change in (a) nutrient concentration and (b) dry weight of decomposing leaves, expressed as percent of the quantity present at the start of the study. Bars represent 1 standard error of the mean. In the regression equation, x = number of days and y = % of original dry weight.

DISCUSSION

Litterfall Patterns

Annual litterfall for the Horseshoe Lake bottomland forest was relatively high compared to other studies of bottomland hardwood forests (Table 3) and was much greater than mean values compiled by Bray and Gorham (1964) for warm and cool temperate forests. Reproductive litter was high compared to values reported in most litterfall studies and represented a major portion of productivity in the forest. Reproductive litter accounted for a large pulse of nutrients, especially N and P, in the winter and early spring. The fact that the proportions of the various litter components varied while the total was nearly equal for the two years of the study suggests a trade-off in resource allocation among these components. A longer term study, including an exam-

Table 3.--Summary of litterfall rates for bottomland hardwood forests and temperate forests.

Community Type	Location	Litterfall Components ($kg\ ha^{-1}\ yr^{-1}$)				Source
		Leaves	Wood	Reproductive	Total	
Bottomland hdwd. (sweetgum)	So. Illinois	4298	1144	1058	6500	This Study
Bottomland hdwd. (red maple-water tupelo)	Louisiana	----	----	----	5740	Conner and Day (1976)
Floodplain (silver maple)	C. Illinois	4226	690	267	5183	Bell, *et al*. (1978)
Alluvial swamp (water tupelo)	No. Carolina	4222	907	1000	6129	Brinson, *et al*. (1980)
Floodplain (silver maple)	C. Illinois	3846	3061	1063	7970	Peterson (unpublished)
Warm temperate forest	Several	3600	1900 (non-leaf litter)		5500	Bray and Gorham (1964)
Cool temperate forest	Several	2500	900 (non-leaf litter)		3500	Bray and Gorham (1964)

ination of the mast fruiting of sweetgum (Schopmeyer 1974), is currently being conducted to observe variation in litterfall patterns.

Seasonal variation in the concentration of elements in leaf litter (Fig. 2) was similar to that observed by Grizzard, et al. (1977). Concentrations of N, P, and K increased significantly in the spring and declined during the rest of the growing season. This decrease has been attributed to leaf expansion and translocation of nutrients to perennial tissue prior to leaf abscission (e.g., Woodwell 1974). In addition, foliar leaching by precipitation is greatest in senescent leaves (Day and Monk 1977), as is suggested by high concentrations of K and Mg in throughfall at the Horseshoe Lake site in October and November (Peterson, unpublished data). Calcium concentration increased during the summer and is associated with incorporation in the cell walls of leaf tissue (Bidwell, 1974). As a structural component, Ca was less subject to leaching and increased relative to other more leachable elements.

Decomposition and Nutrient Turnover

Dry weight loss from decomposing leaves was low compared to a similar study done by Brinson (1977) in a North Carolina swamp forest. Following a decrease of 29% during the first year of the study, weight loss was negligible during the second year. The decomposition constant k can be calculated with the equation

$$X/X_o = e^{-kt}$$

where X = dry weight at time t, X_o = original dry weight, e is the base of natural logarithms, and t is time in years (Olson 1963). The values for decomposing leaves are $k = 0.342$ for 1 year and $k = 0.193$ for 2 years based on the decomposition study.

The rate of nutrient exchange for different elements determines how rapidly elements from decomposing leaves are incorporated into the mineral soil. This exchange process can be characterized through both decomposition studies and an analysis of the content of the forest floor litter. Although there was some disparity in the results obtained with these two methods, several patterns of nutrient exchange were determined.

Nitrogen and Phosphorus.--Heterophic decomposer organisms in leaf litter generally have a strong demand for N and P in addition to a source of carbohydrates (Gosz, et al. 1973). Our decomposition study showed that N and P were the most strongly retained elements in known amounts of leaf litter (Fig. 3a). Analysis of forest floor litter also showed that N had a long turnover time (Table 2), although P appeared subject to losses greater than those suggested by the decomposition experiment.

An increase in N concentration in decomposing leaves was accompanied by an accumulation of N beyond the amount originally present. This striking increase indicates that N was assimilated by decomposer organisms from sources such as floodwater and throughfall, and perhaps by N-fixation. This immobilization of N was an actual gain for the forest community. Calculated on the basis of the decomposition study, this gain was 19.3 kg ha^{-1}, a 32% gain

beyond the absolute quantity of N received by the forest floor via litterfall. In a study of decomposition in a swamp forest, Brinson (1977) observed a substantial but brief period of N immobilization. Our results more closely parallel patterns found by Lousier and Parkinson (1978) for decomposing *Populus tremuloides* Michx. and *P. balsamifera* L. leaves.

The amount of P remaining in decomposing leaves at the end of a 2-year period was similar to the original quantity (Fig 3a). The substantial decline in P indicates that P may have been initially more subject to leaching than N. However, a subsequent increase in P suggests that there is also some assimilation of this element in decomposing leaf litter.

Potassium, Magnesium, and Calcium.--Both K and Mg were rapidly lost from decomposing leaf litter and had fast turnover rates compared to leaf dry weight. These elements have been shown to be readily leached from leaves (Gosz, *et al*. 1975), a process which is greatly enhanced by the presence of floodwater during much of the year. Consequently, the physical process of leaching was the most important factor in the removal of K and Mg from leaves.

Although Ca loss from leaves and turnover rate were slightly faster than for dry weight, Ca content of leaves stabilized at higher levels than K and Mg. Since Ca is an important structural component of the middle lamella in cell walls (Bidwell 1974), it may have been more protected from leaching than other cations. The low initial rate of Ca loss (Fig. 3a) may reflect this lower susceptibility to leaching prior to substantial physical breakdown of leaf tissue.

Sodium.--Although Na was lost from decomposing leaves at a rate intermediate to Ca and Mg, it appeared to have the longest residence time of all elements studied in forest floor litter biomass. These confounding results may be the result of the failure of the decomposition study with mesh containers to accurately simulate the forest floor dynamics of Na.

A slow turnover rate of Na in leaf litter could be attributed to at least three different factors. First, it has been shown that Na is not readily leached from the leaves of several deciduous tree species (Gosz, *et al*. 1975). Second, Stark (1972) and Cromack, *et al*. (1975) have shown that basidiomycetes in forest floor litter can accumulate large concentrations of Na. Finally, Smith (1976) demonstrated that tree root exudates contain large amounts of Na; the forest floor litter at the Horseshoe Lake site contains many fine tree roots, and exudates could be a significant source of Na.

Since decomposer fungi and tree roots may have been slower to occupy the leaves enclosed in the containers, we conclude that the slow turnover of Na as determined in the analysis of forest floor litter is a more realistic interpretation.

CONCLUSIONS

Patterns of litterfall and decomposition should be considered as an important internal cycling mechanism of forest communities. We have examined these patterns in one of the few reported studies on the litter dynamics of a bottomland hardwood forest.

Litterfall rates for the Horseshoe Lake forest were relatively high and may be an indication of the high productivity of this site. In addition, annual variations in the composition of litterfall suggest that there may be some trade-offs in the allocation of resources among components.

Studies of decomposition and nutrient exchange in the forest floor litter showed that N and P were retained, K, Ca, and Mg were leached to various degrees, and Na had a slow turnover time due to certain biotic factors. The assimilation of N in decomposing leaf litter indicates that there is a strong demand for this element by decomposer organisms. The accumulation of N is an important gain for the forest and suggests that decomposing leaf litter may act as a sink for N in a community in which flooding, and therefore leaching, is a common occurrence.

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