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# DETRITAL DYNAMICS IN A MATURE OAK FOREST: HUTCHESON MEMORIAL FOREST, NEW JERSEY[1]

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*Abstract.* The William L. Hutcheson Memorial Forest is a mixed oak stand located on the New Jersey Piedmont, and is believed to have remained uncut and unburned for >250 yr. Abundant canopy gaps and large fallen boles indicate old-age status. Patterns of detritus distribution appear different from younger or disturbed forests. Consequently, we studied organic matter and element content in 12 distinct detritus components, litter deposition, element ratios, element turnover rates, and latitudinal oak forest detritus affinities.

Total detrital organic matter (ash-free) was 27.6 kg/m$^2$, with 86% located in the mineral soil horizons. Of the 3.8 kg/m$^2$ of detritus lying above the mineral soil, 71% was in fallen boles and large branches. Detrital organic matter exceeds aboveground biomass. In the forest floor and associated decaying wood, N was the most abundant element (81 g/m$^2$), followed by Ca (22 g/m$^2$), Mg (11 g/m$^2$), K (10.5 g/m$^2$), and P (4.5 g/m$^2$). The thin humus layer, averaging 0.5 centimetres thick, had a much higher total element content per square metre than other detrital components due to high element concentration values. Concentrations of each element increased as branch diameter decreased, and as leaf, branch, and bole litter decomposed. Organic matter:element ratios exhibited the same trend as carbon:element ratios, a decrease with decreasing branch diameter, increasing forest floor depth, and increasing bole decay.

Average annual litter deposition (ash-free) was 616 g/m$^2$. Nitrogen, P, and K content of litter deposition was higher in summer than in autumn. Leaves returned the majority of each element followed by small branches and fruits.

Forest-floor organic matter and element content increase along a latitudinal gradient of eastern oak forests. Organic matter and element turnover times of southern oak forests, including Hutcheson Forest, are similar, despite differing organic matter and element pools and deposition rates.

One interesting aspect of detritus in an old, undisturbed forest is the pronounced role of detrital wood. Large decaying boles represent 10% of aboveground biomass and 9% of total detritus. These boles are a habitat and energy source for detritivores, influence seedling establishment and soil development, and affect hydrologic and biogeochemical cycles. Because of large carbon:element ratios and slow rates of decomposition, boles lying on the forest floor may exhibit a net accumulation and storage of elements until a critical carbon:element ratio is reached and net mineralization occurs. A time delay thus exists for element release which may provide regular elemental supply through time.

*Key words: biogeochemistry; bole decomposition; decomposition; detrital element content; detrital organic matter; detritus; forest floor; litter; litter deposition; New Jersey; oak forest;* Quercus.

## INTRODUCTION

Old-aged forest ecosystems are uncommon features of the natural landscape. They exist mainly as relics, due to chance, having escaped human influences such as logging, agriculture, or urbanization, and persist in areas with a low frequency of natural catastrophic destruction. Such systems are extremely valuable for considering the development of ecosystems, but our knowledge of their structural dynamics, community energetics, and biogeochemistry is limited. Equating structure and function of intermediate-aged forests to that of old-aged forests is probably invalid.

The William L. Hutcheson Memorial Forest is an example of a stand that has been protected for >250 yr (Buell et al. 1954, Buell 1957). There is no evidence of fire since 1711, and the forest has not been logged. With human influences believed insignificant, all vegetational and concomitant ecosystem changes have been natural.

From an ecosystem perspective, Hutcheson Forest should be approaching zero net ecosystem production (Odum 1969). In theory, biomass accumulation including detritus should be in steady state. Detritus is (in this paper) defined as soil-related particulate organic matter in dead organisms or resulting from their decomposition. Standing dead boles and branches are excluded on an operational basis. The detrital pool is a function of rates of decomposition and deposition (Olson 1963). Decomposition, in turn, is primarily a

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function of time, environment, material, and faunal and microbial activity, whereas litter deposition is related to plant productivity and time of year. Seasonal and annual changes are expected for the mass of detritus because of variations in decomposition and deposition rates.

Lang (1974) described the dynamics of forest floor litter and fermentation layers (*sensu* Lutz and Chandler 1946) in Hutcheson Forest. No significant differences in the mass of these layers were noted for samples taken in late summer (August and September) for 3 consecutive yr. In view of the old, undisturbed status of Hutcheson Memorial Forest, with its numerous canopy gaps and fallen trees, and steady state surficial litter horizons, we decided to investigate further detrital pool size and its turnover dynamics. We assumed that the mass of detritus and the organically bound and exchangeable elements in detritus are in steady state. The objectives of this study were to (1) estimate the amount of fallen boles and branches and compare with other soil and litter detritus components in the forest, (2) estimate the element content of various detritus components, (3) determine element input through litter deposition and calculate turnover time, and (4) evaluate affinities of this forest with oak forests of the eastern United States on the basis of detritus structure and dynamics.

## THE STUDY SITE

Hutcheson Memorial Forest (40°30'N, 74°34'W) is a 26-ha mixed oak woods located near East Millstone on the Piedmont of New Jersey (USA). The stand is surrounded by adjoining fields and was not covered by Wisconsinan glaciation. The forest receives ≈112 centimetres of rainfall which is relatively evenly distributed throughout the year (Biel 1958). Average annual temperature is 11.7°C, and the mean monthly temperature ranges from 0.0°C in January to 24.0°C in July (United States Weather Bureau 1959). The moist, humid environment favors the development of a well-drained, podzolic, brown earth soil formed primarily from underlying Triassic red shale (Ugolini 1964). Many facets of this ecosystem have been studied and reported in >80 publications (Small 1973).

The forest has developed a characteristic structure and physiognomy reflecting its mature vegetational status. At present, Hutcheson Forest is best described as a mosaic of small patches created by tree falls occurring within a larger closed-canopy forest matrix. White oak (*Quercus alba* L.), red oak (*Quercus borealis* Michx.), and black oak (*Quercus velutina* Lam.) dominate the overstory (51% basal area for all individuals ≥10.0 centimetres dbh [diameter at breast height] [Forman and Elfstrom 1975]). The canopy is 30 m in height, and some trees exceed 65 cm in diameter and 300 yr in age. The many gaps in the overstory are due to the natural fall of both living and dead, large, mature trees (Reiners and Reiners 1965). Forest regeneration is through gap-phase reproduction (Watt 1947). Weed species, such as Japanese honeysuckle (*Lonicera japonica* L.), rapidly invade these open areas. Flowering dogwood (*Cornus florida* L.) dominates the understory (84% cover), and maple-leaf viburnum (*Viburnum acerifolium* L.) is the dominant shrub (Monk 1957, 1961). Herbaceous mayapple (*Podophyllum peltatum* L.) forms a continuous cover over much of the area in late spring and early summer.

## METHODS

A representative portion of the upland forest community was chosen for intensive sampling. A 100 × 150-m study area, characteristic of the mature, old-aged forest, was established within grid units 19 to 24 of Hutcheson Forest (see Frei and Fairbrothers 1963, Fig. 2, p. 339 for grid designations). Edge effects from adjacent fields were absent.

### *Estimating detrital mass*

Litter (*L*) and fermentation (*F*) layers of the forest floor were sampled in September 1971, August 1972, and August 1973 with 8 randomly placed 0.5 × 1.0-m quadrats. The combined *L* and *F* layers are analogous to the *O*1 organic horizon. Leaf detritus was collected separately for *L* and *F* layers but branches ≤2.5 cm in diameter and fruit parts were pooled from both layers. Samples were transported to the laboratory in paper bags. Leaf material was dried for 24 h at 105°C but branches and fruit parts were dried for 48 h before weighing.

Field measurements of the thickness of *L* and *F* layers were made in August and November 1972. Twenty randomly located points were sampled with a measuring stick after a side profile of the forest floor was established with a hand trowel.

In September 1974, *L* and *F* layers were brushed aside and a 7.6-cm inner diameter soil core was pushed through the humus (*H*) layer (analogous to the *O*2 organic horizon) into the underlying $A_2$ soil horizon at 50 randomly stratified locations. Each core was carefully placed into a round cardboard container, sealed, and transported intact to the laboratory. Separating the humus layer from the $A_1$ soil horizon was extremely difficult. The humus layer was thin and often contained high amounts of inorganic material. A thin $A_1$ horizon was present with high organic matter content. Consequently, the upper organic portion of the $A_1$ was pooled with the humus, but the lower $A_1$ was pooled with the $A_2$ soil horizon. The resulting humus and $A_2$ samples were measured for thickness, separated, dried for 48 h at 105°C, and weighed. Each *H* and $A_2$ sample was then passed through a 2-mm sieve to remove larger roots and gravel. Roots, gravel, and fine particulate soil (≤2 mm) were reweighed separately. Bulk-density estimates were determined for total core weight. Humus and soil for 5 spatially adjacent samples were pooled for ash determination and chemical analysis.

Twenty-eight 5 × 10-m quadrats were established according to a stratified-random design in September 1974 to sample branches lying on the forest floor. All branches within each quadrat were divided into 2 size classes: those >2.5 cm but ≤5 cm in diameter, and those >5 cm but ≤10 cm. Field wet weight was determined for each size class with a spring balance. Subsamples of each size class from each quadrat were collected and weighed in the laboratory. The small size-class material was oven-dried at 105°C for 5 days, the larger class material for 8 days, and reweighed. These time periods were needed to achieve constant dry weight. A dry-weight correction factor for each quadrat was used to convert field weight for each size class to dry-weight values. In addition, the branch samples used to determine correction factors were also divided into 2 states of decay: slight, and moderate-advanced combination (defined below). Comparisons between the 2 decay states were made to describe changes that occurred during decomposition.

In September 1974 and June 1975, fallen boles and large branches (>10 cm in diameter) on the forest floor were sampled in twenty-four 20 × 20-m quadrats using dimensional analysis techniques (Whittaker and Woodwell 1968). The diameter at each end of each bole and the total length of the bole were measured to the nearest centimetre, and the state of decay recorded. A bole was classified as being in a slight, medium, or advanced state of decay according to the following criteria: slight decay—wood hard and not easily penetrable with a surveyor pin; moderate—spongy wood, easily penetrable to 2.5-cm depth with a metal surveyor pin; and advanced—very soft wood, readily broken into small pieces. The total volume for each bole was determined using the equation for the right frustrum of a cone. "Cookie-shaped" discs were cut from 17 boles representing the 3 decay states. These discs were measured for volume, oven-dried for 10 days, and weighed. Density (weight/volume) for each disc was calculated, and the mean density determined for each decay state. The mean density was used to convert estimated volume to dry weight values.

Standing dead boles and branches were not sampled or included in our detritus estimates.

### *Litter deposition*

Separate estimates of leaf, fruit, and branch (≤2.5 cm in diameter) litter deposition were determined over a 2-yr interval, September 1971 to September 1973. Methods were described previously (Lang 1974).

### *Ash determination and organic-matter weight*

Samples were pooled within the various components of detritus and litter deposition material. The general scheme of pooling samples reduced the logistics of analyses but provided an estimate of component variability. The number of samples analyzed is given in the **Results** section.

Subsamples of all material were ground in a Wiley mill to pass a no. 20 stainless steel mesh; an aliquot of this material was further ground to pass a no. 60 mesh sieve.

Approximately 1 g of no. 20 ground material was placed in crucibles, dried for 12 h at 105°C, weighed to the nearest 0.1 mg, and ashed in a muffle furnace at 550°C for 5 h. The resulting ash was weighed. Bole, branch, and forest floor organic matter weights were determined from loss after combustion (dry weight − ash weight = organic matter). This procedure provided a reasonable estimate for material high in organic matter. Organic matter weight may be overestimated in the humus due to the high percentage of ash. Ignition at 550°C will drive off the $H_2O$ bound in clay minerals; clay is high (30–38%) in Hutcheson Forest soils (Ugolini 1964) but no correction was made for this overestimation.

The amount of organic matter in the mineral soil horizons was derived by (soil volume) × (bulk density) × (% organic matter). The percentage of organic matter and bulk density values for the $A_2$ (10–20 cm), *B*, and *C*-horizons were reported by Ugolini (1964, Tables 14 and 16). We used our core data to establish values for the upper $A_2$ (0–10 cm) horizon. An arbitrary minimum depth was established for each horizon based on Ugolini's (1964) soil profiles. The percentage of organic matter was assumed by Ugolini (1964) to be 2 × the percentage of oxidizable carbon determined through chromic acid digestion.

### *Chemical analyses*

Five millilitres of concentrated $HNO_3$ and 5 ml of distilled $H_2O$ were added to the crucibles to dissolve the ash after combustion. The crucibles were heated in a sand bath until the solution evaporated to 5 ml. The solution was then filtered through Whatman® 541 paper into 100 ml volumetric flasks and brought to volume with distilled $H_2O$. Eight millilitres of 2% $La_2O_3$ in 50% HCl were added to each solution to reduce interference from aluminum and silica in the determination of calcium and magnesium. The Ca, Mg, and potassium concentrations of the solution were determined with an atomic absorption spectrophotometer using standard methods (Perkin–Elmer 1973).

The readily oxidizable carbon content of no. 60 ground material was determined using the Walkley–Black wet digestion method with $K_2Cr_2O_7$ (Jackson 1958). The efficiency of this method may have limitations but the amount of carbon should be roughly proportional to the total amount of carbon present in each component, such that relative differences between samples will be indicative.

Total nitrogen was measured using the micro-Kjeldahl method with the modification for nitrate-nitrogen (Jackson 1958). The no. 60 ground material was used for digestion, and the resulting solutions were ana-

TABLE 1. Soil profile for Hutcheson Forest. Forest floor measurements were made on 17 August 1972. Descriptions of the mineral soil were taken from Ugolini (1964)

| Horizon | Measurements ($n$) | Thickness (cm) |  | Description |
|---|---|---|---|---|
|  |  | Range | $\bar{x}$ |  |
| *L* | 20 | 1–4 | 2.5 | Compressed, forming complete cover over fermentation layer; many small twigs present; leaves of oaks intact and recognizable; dogwood and viburnum leaves not recognized |
| *F* | 20 | 1–2.5 | 1.5 | Dark colored, partially decomposed organic matter; many small twigs and acorns present; very friable |
| *H* | 50 | 0–2 | 0.5 | Material unrecognizable to species; few roots present; high inorganic content; ≈50% frequency of occurrence |
| *A* |  | 18–25 |  | Brown; silt or clay loam; abundant roots; well aggregated |
| *B* |  | 30–35 |  | Reddish yellow; loam or clay loam; hard and compact; unweathered red shale fragments increase with depth |
| *C* |  | 10–20 |  | Red shale; sandy loam or sandy clay; fragments of shale throughout |
| *R* |  |  |  | Red shale bedrock of Brunswick Formation |

lyzed with an ion meter and ammonia probe using standard methods (Orion Research, Inc. 1974).

Phosphorus concentration was determined for no. 60 ground samples using dry-ashing procedures without MgOAc (Jackson 1958). Crucibles, plastic bottles and glassware were washed with 50% $H_2SO_4$ and rinsed 5× with distilled $H_2O$ before use. The phosphorus concentration of the solution was measured by the vanadomolybdophosphoric yellow-color method (Jackson 1958) using a colorimeter.

Because of the high inorganic content of the *F* and *H* forest floor layers and the $A_2$ soil horizon, direct comparisons of organic matter weight are best made on an ash-free basis. Elemental concentrations may be underestimated with high amounts of inorganic content due to the binding of elements by silica during dry-ashing (Reiners and Reiners 1970). No test was made of this underestimation. Gosz et al. (1976) did test for underestimation in the humus and determined that the elemental concentration of the organic material probably was not significantly in error.

### *Statistical analyses*

Significant statistical differences between means were determined by either the Kruskal–Wallis or Wilcoxon 2-sample nonparametric tests as in Sokal and Rohlf (1969).

## RESULTS

### *Detrital mass*

The physical structure of the forest floor *L*, *F*, and *H* layers was described during August, when the depth and mass of the organic layers was near minimum (Table 1). The *L* layer averaged 2.5 cm thick, the *F* layer 1.5 cm, and the *H* layer 0.5 cm. Thus, the combined average depth for the forest floor of this old forest at the end of the summer was 4.5 cm. Many samples contained no humus. Though this study focused primarily on the forest floor, we included an abbreviated version of Ugolini's (1964) data for mineral horizons in Table 1 to provide a complete profile description for later use.

In November, after leaf deposition was completed, the *L* layer ranged in thickness from 3.5 to 8 cm, with a 5 cm average. The leaves were loosely interwoven into a soft mat and were easily recognizable to species. The fermentation layer averaged 3 cm in thickness due to further comminution of old litter; separation of the litter layer from the fermentation layer was more difficult. The thickness of the humus layer was not measured in November. Assuming no detectable change in this thickness of humus from the August value of 0.5 cm, the weighted average of the *L*, *F*, and *H* layers was 8.5 cm, almost a 2-fold increase over the August mean.

The mass of detritus (ash-free weight) during August in Hutcheson Forest was 27,634 g/m² (Table 2). This value represents a weighted average, that is, the sum of the averages for the various detrital components excluding dead roots, and is based on a 60-cm soil profile. Autumn litterfall would increase this value for detritus by ≈500 g/m² (Lang 1974). Of the total 27,634 g/m² of detrital mass, 86% was located in the mineral soil horizons (Table 2) and only 14% above the mineral soil. Of the 3,816 g/m² of organic matter present above the mineral soil, 71% (2,717 g/m²) was in decaying boles, branches, and fruit parts of all sizes. The forest floor comprised only 29% of this aboveground organic matter (1,099 g/m²). This is largely a result of the combination of a very thin humus layer and the

TABLE 2. Detritus in Hutcheson Memorial Forest. Bole, branch, and forest floor weights were determined from loss on ignition and are expressed as ash-free values. Forest floor and fruit parts were measured in August and September when weights were at a minimum. Mineral soil data were derived from Ugolini (1964); see text for discussion. (SE, *n*) = standard error of mean, no. of samples

| Component | Bulk density (g/cm³) | Percent organic matter | Percent ash (SE, *n*) | Organic matter (g/m²) | Percent of grand total |
|---|---|---|---|---|---|
| Boles and branches >10 cm diam[1] | | | 1.71 | 2,131 | 7.7 |
| Branches <10 cm diam | | | | 569 | 2.1 |
| Branches 5–10 cm | | | 2.4 (0.3, 15) | 141 | 0.5 |
| Branches 2.5–5 cm | | | 2.2 (0.2, 16) | 75 | 0.3 |
| Branches ≤2.5 cm | | | 4.9 (0.4, 16) | 353 | 1.3 |
| Fruit parts | | | 4.2 (0.4, 8) | 17 | <0.1 |
| **(Subtotal—boles, branches, fruits)** | | | | (2,717) | (9.8) |
| Forest floor (*L*, *F*, *H*) | | | | 1,099 | 4.0 |
| *L*-layer | | | 9.7 (0.5, 24) | 211 | 0.8 |
| *F*-layer | | | 20.6 (1.1, 24) | 199 | 0.7 |
| *H*-layer (0.5 cm) | 0.71 | | 80.6 (2.3, 10) | 689 | 2.5 |
| (Subtotal—boles, branches, forest floor) | | | | (3,816) | (13.8) |
| Mineral soil | | | | 23,818 | 86.2 |
| *A*-horizon (20 cm) | | | | | |
| $A_2$ (0–10 cm) | 0.92 | 6.62 | 90.9 (0.4, 10) | 6,090 | 22.0 |
| $A_2$ (10–20 cm)[2] | 1.07 | 6.10 | 93.8 | 6,527 | 23.6 |
| *B* (30 cm)[2] | 1.42 | 2.40 | 96.4 | 10,224 | 37.0 |
| *C* (10 cm)[2] | 1.48 | 0.66 | 95.7 | 977 | 3.6 |
| **GRAND TOTAL** | | | | 27,634 | 100.0 |

[1] Weighted average derived from the amount of wood in each decay state (Table 3).
[2] Based on data from Ugolini.

large amount of wood, especially fallen boles, lying on the forest floor. This latter feature reflects the old-age character of the forest. The average number of boles measured in each 20 × 20-m quadrat regardless of size and decay state was 11.3, with a range of 6 to 17. The ranking of components above the mineral soil by detritus weight gives: boles and branches greater than 10 cm >> humus >> branches less than 2.5 cm > *L* layer = *F* layer > branches 5–10 cm > branches 2.5–5.0 cm >> fruits.

Our data for bulk density and percentage organic matter in the upper $A_2$ horizon (Table 2) fit well with Ugolini's (1964) values. As expected, bulk density and the percentage of ash increased with profile depth while the percentage of organic matter decreased.

Sample size varied considerably for the different detrital components. To evaluate sample adequacy for each component, the standard error of the mean was compared to the sample mean using dry-weight data. For the *L*, *F*, and *H* layers and the $A_2$ soil horizon, standard errors were <10% of the mean, suggesting a low variation among replicates. A standard error of 20% of the mean was found using twenty 5 × 10-m quadrats to sample total branch weight for both the 2.5–5 cm and 5–10 cm diameter size classes; with 28 quadrats, which represented 9% of the intensive study area, variation among the quadrats was sufficiently high that the standard error was reduced to only 15% of the mean. A standard error of 15% of the mean was found for the total weight of boles and branches > 10 cm among the twenty-four 20 × 20-m quadrats which comprised 64% of the intensive study area. Analysis of the variation in the data revealed that 10 quadrats would give a standard error of 20% of the mean but at least 20 quadrats were needed to reduce the standard error to 15% of the mean. Considerable variation existed among these large quadrats; if the boles were separated by decay states, the variation would be even greater.

### *Detrital element content*

Element content for boles, branches, and forest floor layers are given in Table 4. The rank of elements by total pool size was carbon >> nitrogen > calcium > magnesium = potasium > phosphorus. This order of abundance also holds for the combined forest floor *L*, *F*, and *H* layers. The ranking of detrital components by total element content excluding carbon was humus >> branches less than 2.5 cm ≥ boles and branches greater than 10 cm > *F* layer = *L* layer > branches 5–10 cm > branches 2.5–5.0 cm = fruits. This general ranking would be similar for N and Ca independently. A comparison of component rank by organic matter weight and element content do not agree for reasons described below.

The distribution of any given element among the

TABLE 3. Abundance and composition of fallen boles and branches >10 cm diameter. Each value is the mean of 5 samples with the standard error of the mean in parentheses.[1] Element percentages are for ash-free organic matter

| Decay state | Wood density (g/cm³) | Organic matter[2] (g/m²) | Percentage composition | | | | | | Percentage composition | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Ash | C | N | P | C:N | C:P | Ca | Mg | K |
| Slight | 0.85 (0.13)a | 699 | 0.9 (0.3)a | 42.4 (1.1)a | 0.29 (0.04)a | 0.008 (0.001)a | 146 | 5,300 | 0.057 (0.023)a | 0.011 (0.002)a | 0.063 (0.018)a |
| Moderate | 0.50 (0.14)ab | 1,126 | 1.6 (0.7)ab | 42.4 (0.8)a | 0.33 (0.06)a | 0.011 (0.003)a | 128 | 3,855 | 0.104 (0.041)ab | 0.013 (0.003)a | 0.083 (0.029)a |
| Advanced | 0.20 (0.07)b | 306 | 2.9 (0.8)b | 41.8 (1.7)a | 0.45 (0.05)a | 0.024 (0.005) | 93 | 1,742 | 0.128 (0.031)b | 0.023 (0.007)a | 0.089 (0.032)a |

[1] Statistically similar means ($p < .05$) using Kruskal–Wallis rank test have same lower-case letters (i.e., a, b).
[2] Volume × wood density × (100 − % Ash/100).

detrital components varied considerably. For example, 71% of the carbon was located in the large boles and branches of all sizes lying on the forest floor. The humus contained 71% of the N, 77% of the P, 91% of the Mg, and 75% of the K, but only 19% of the carbon. Calcium showed no pronounced peak distribution within any component. The humus with 36% of the Ca was relatively high. *L* and *F* layers were more or less equal to each other in elemental amounts and always less than the *H* layer. Large boles usually had the same or greater element content than the other branch components combined except for Ca.

Differences in elemental pool sizes are due to variations in the amount of organic matter (Table 2) and the concentration of an element within the different tissue types (Table 5). For boles and branches, the percent carbon was similar but the percent nitrogen increased with a decrease in branch diameter size; small branches had significantly higher percent nitrogen. Therefore, the C:N ratio was reduced proportionate to the increase in N. The N pool (Table 4) was similar for boles and branches <2.5 cm and ≈20 × that of the 2 other branch components. This similar pool size resulted from a combination of mass and element concentration: for boles, a large mass and low concentration, and for branches, a small mass but high concentration. Phosphorus exhibited a response similar to N with regard to concentration and pool size values for boles and branches. However, the percent phosphorus was 10 to 45 × < the percent nitrogen resulting in a proportionate 10- to 45-fold increase in C:P ratio over that for N.

Calcium and, to a lesser extent, Mg concentration tended to increase with decreasing branch diameter. Potassium concentrations did not differ among the branch size-classes. The high concentration of Ca in the small branches <2.5 cm accounts for the large pool size for these elements (Table 4), especially compared to the boles, because the mass for the small branches is only ⅛ that of the boles (Table 2). However, the small differences in percent magnesium and percent potassium for boles and branches means the change in element pool size for the wood tissue primarily reflects changes in organic matter weight for each component.

Fruit parts had high element concentrations (Table 5), but pool sizes (Table 4) were low due to the small mass (Table 2).

Element pool sizes for *L* and *F* layers for all elements were similar (Table 4). This is apparent because both mass (Table 2) and element concentrations (Table 5) are similar for these components. The element content within the humus is always much greater than that of the *L* and *F* layers. This occurred because both mass and element concentrations (excluding carbon) were greatest in the humus.

Ratios of percent organic matter to percent of an element were calculated (Table 5). Though such ratios

TABLE 4. Element content of detritus in Hutcheson Forest. Values are g/m²

| Component | C | | N | | P | | Ca | | Mg | | K | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Boles and branches >10 cm diam | 904 | | 7.16 | | 0.26 | | 1.97 | | 0.30 | | 1.66 | |
| Branches <10 cm diam | 250 | | 8.54 | | 0.24 | | 5.64 | | 0.24 | | 0.39 | |
| Branches 5–10 cm | | 63 | | 0.45 | | 0.04 | | 0.58 | | 0.04 | | 0.13 |
| Branches 2.5–5 cm | | 33 | | 0.31 | | 0.02 | | 0.40 | | 0.02 | | 0.05 |
| Branches ≤2.5 cm | | 154 | | 7.78 | | 0.18 | | 4.66 | | 0.18 | | 0.21 |
| Fruit parts | 7 | | 0.52 | | 0.02 | | 0.10 | | 0.01 | | 0.05 | |
| **(Subtotal—boles, branches, fruits)** | (1,161) | | (16.22) | | (0.52) | | (7.71) | | (0.55) | | (2.10) | |
| Forest floor (*L*, *F*, *H*) | 473 | | 64.81 | | 3.96 | | 14.32 | | 10.23 | | 8.43 | |
| *L*-layer | | 84 | | 3.63 | | 0.23 | | 3.14 | | 0.19 | | 0.27 |
| *F*-layer | | 75 | | 3.98 | | 0.28 | | 3.26 | | 0.26 | | 0.24 |
| *H*-layer | | 314 | | 57.20 | | 3.45 | | 7.92 | | 9.78 | | 7.92 |
| **TOTAL** | 1,634 | | 81.03 | | 4.48 | | 22.03 | | 10.78 | | 10.53 | |

are usually based on carbon alone, we chose the percentage of organic matter on an ash-free basis (100%–%ash, Table 2) as a potentially more convenient and readily usable measure. Tissues with large carbon: element ratios decay more slowly and have lower rates of mineralization than do tissues with small ratios. Organic matter:element ratios should indicate similar relationships.

For all elements except K, organic matter:element ratios decreased as a function of decreasing wood diameter (Table 5). Because the percentage of organic matter is nearly identical across size classes, this trend is directly related to element concentrations. The sequence from litter to humus also showed a decrease in ratios for reasons similar to those described for branch material. Values for humus potentially re-

TABLE 5. Concentration of elements in detrital components. Data are expressed as the percentage of organic matter (OM) (ash-free weight). *N* = number of determinations; SE = standard error. Values for ratios of % OM:% element are dimensionless

| Component | *N* | Percentage composition | | | | |
|---|---|---|---|---|---|---|
| | | C (SE) | N (SE) | P (SE) | C:N | C:P |
| Boles and branches >10 cm diam¹ | | 42.20 | 0.36 | 0.01 | 117 | 4,220 |
| Branches <10 cm diam | | | | | | |
| Branches 5–10 cm | 6 | 44.96 (0.187) | 0.32 (0.063) | 0.03 (0.002) | 141 | 1,499 |
| Branches 2.5–10 cm | 6 | 44.48 (1.398) | 0.41 (0.049) | 0.03 (0.001) | 108 | 1,483 |
| Branches ≤2.5 cm | 5 | 43.68 (2.408) | 2.26 (0.142) | 0.05 (0.006) | 19 | 874 |
| Fruit parts | 4 | 40.40 (0.456) | 3.04 (0.104) | 0.10 (0.007) | 13 | 404 |
| Forest floor (*L*, *F*, *H*) | | | | | | |
| *L*-layer | 5 | 39.59 (0.648) | 1.72 (0.074) | 0.11 (0.002) | 23 | 360 |
| *F*-layer | 5 | 37.48 (1.642) | 2.00 (0.105) | 0.14 (0.007) | 19 | 268 |
| *H*-layer | 5 | 45.62 (3.846) | 8.30 (0.670) | 0.50 (0.057) | 6 | 91 |

| Component | *N* | Percentage composition | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Ca (SE) | Mg (SE) | K (SE) | OM:N | OM:P | OM:Ca | OM:Mg | OM:K |
| Boles and branches >10 cm diam¹ | | 0.10 | 0.02 | 0.08 | 275 | 9,830 | 1,024 | 6,553 | 1,260 |
| Branches <10 cm diam | | | | | | | | | |
| Branch 5–10 cm | 16 | 0.41 (0.071) | 0.03 (0.023) | 0.09 (0.011) | 305 | 3,253 | 238 | 3,253 | 1,084 |
| Branches 2.5–10 cm | 16 | 0.53 (0.054) | 0.03 (0.031) | 0.06 (0.061) | 239 | 3,260 | 185 | 3,260 | 1,630 |
| Branches ≤2.5 cm | 7 | 1.32 (0.110) | 0.05 (0.003) | 0.06 (0.007) | 43 | 1,902 | 72 | 1,902 | 1,585 |
| Fruit parts | 7 | 0.57 (0.117) | 0.08 (0.012) | 0.31 (0.071) | 32 | 958 | 168 | 1,198 | 309 |
| Forest floor (*L*, *F*, *H*) | | | | | | | | | |
| *L*-layer | 8 | 1.49 (0.096) | 0.09 (0.004) | 0.13 (0.007) | 54 | 821 | 61 | 1,003 | 695 |
| *F*-layer | 8 | 1.64 (0.130) | 0.13 (0.013) | 0.12 (0.014) | 40 | 567 | 48 | 611 | 662 |
| *H*-layer | 10 | 1.15 (0.180) | 1.42 (0.140) | 1.15 (0.110) | 2 | 39 | 17 | 14 | 17 |

[1] Values represent the average bole, derived from the proportional contribution by weight of each decay state in Table 3.

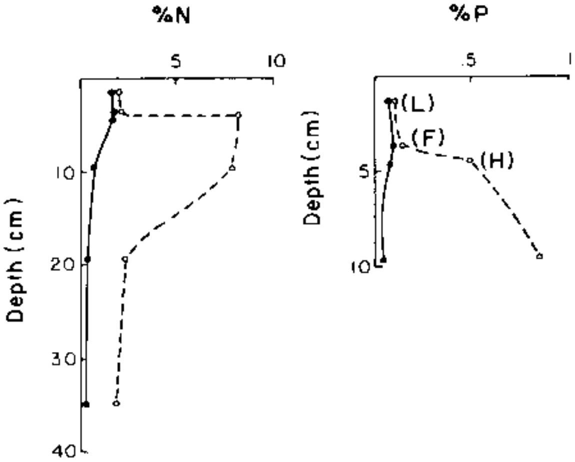

FIG. 1. Change in percentages of nitrogen and phosphorus through the soil profile. Solid lines connect percentages determined on the basis of dry weight of detritus; dashed lines connect percentages determined on the basis of dry weight of detrital organic matter (ash-free). Note the change in scales.

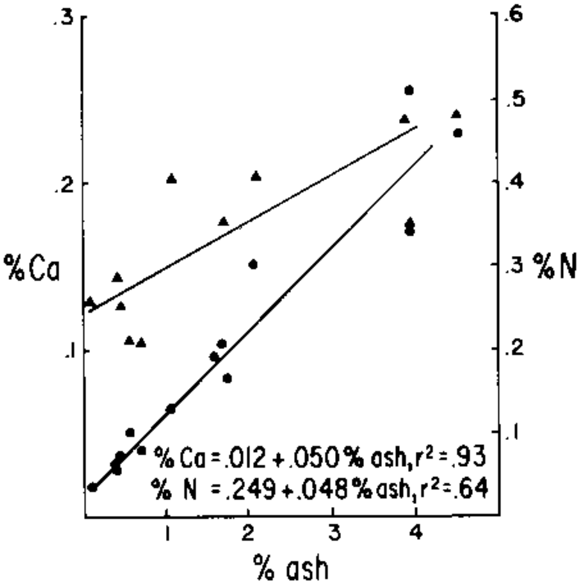

FIG. 2. Relationships of percentages of calcium and nitrogen with percent ash in decaying bole and branches >10 cm diameter. ● represents percent calcium values and ▲ represents percent nitrogen values.

flect the low end of the range for critical ratios where net mineralization occurs. Calcium, Mg, and K have similar ratios in humus because, on an ash-free basis, they have the same concentrations. Phosphorus has the lowest concentration and hence the largest ratio.

Our data for element concentrations have been expressed on an organic matter (ash-free weight) basis. Erroneous comparisons may be made when data are expressed on a dry-weight basis because of variations in ash content from inorganic mineral soil. This is readily apparent in Fig. 1. For the *L* and *F* layers, there was a slight underestimation of element concentration because the amount of mineral soil was low. However, for the humus and underlying mineral horizons, the interpretation changed drastically depending on the manner in which the data were presented. For example, percent nitrogen on a dry-weight basis decreased throughout the profile, but on an ash-free basis increased from the *L* to *F* to *H* layers and then decreased. Carbon and Ca were similar to N but Mg and K behaved more like P.

### *Physical and chemical status of decomposing boles and branches*

For boles and large branches >10 cm in diameter, density decreased along the series of increased decay (Table 3). Concomitantly, percent ash increased with increased decay. Chemical analyses showed no change in percentages of carbon and potassium, an increase in percentages of nitrogen, phosphorus, calcium, and magnesium, and a decrease in the C:N and C:P ratios. Although not calculated, organic matter: element ratios would decrease as decomposition increased. Plotting the element content vs. percent ash showed some interesting trends (Fig. 2). For Ca, a significant correlation was shown ($p = .001$) and 93% of the variation in Ca was explained by regressing on percent ash. Magnesium mimicked Ca quite well ($p = .001$, $r^2 = .82$). No clear relationship existed between K content and percent ash, but, in general, the larger the percent ash, the more K. The absence of a relationship may be partially attributable to the mobility of K and losses through leaching, accumulations from throughfall, and concentration by microflora within the branch. The relationship between percent nitrogen and percent ash (Fig. 2) was also significant ($p = .003$) but only 64% of the variation in the nitrogen content was explainable. Phosphorus mimicked N ($p = .001$, $r^2 = .77$). In general, there appears to be a linear increase in percentage element content as the percent ash increases during branch decomposition.

Ash and element concentrations for boles and branches <10 cm (Table 3) were shown to increase with decomposition. However, standard errors around each mean were large. This is, in part, due to small sample sizes. Also, the variation among boles of a particular decay state can be large and, because decay showed a continuum of change, separation of logs into discrete classes was, at times, difficult. An additional problem with decaying boles was the inherent chemical difference among species. We tried to minimize this problem by doing element analyses only on oak wood, but we could not always be sure a bole or large branch was oak. Differences among the 3 species of oak may contribute to the variation. A clear separation existed between slight and advanced decay states.

Branch material of 2.5- to 5-cm and 5- to 10-cm di-

TABLE 6. Comparison of small branches in different states of decay. Each value is the mean, with the standard error of the mean and the number of samples in parentheses.[1] Branches are 2.5–10 cm in diameter. Moisture content is the percentage of the dry weight that is $H_2O$

| Decay | Moisture content (%) | Ash (%) | N (%) | P (%) | Ca (%) | Mg (%) | K (%) |
|---|---|---|---|---|---|---|---|
| Slight | 62.8 (5.9, 74) | 1.92 (0.215, 16) | 0.27 (0.032, 6) | 0.012 (0.0023, 9)a | 0.37 (0.044, 16)a | 0.039 (0.0033, 16)a | 0.087 (0.010, 16)a |
| Moderate–advanced | 124.3 (11.2, 71) | 2.66 (0.213, 15) | 0.44 (0.052, 6) | 0.018 (0.0058, 6)a | 0.50 (0.059, 16)a | 0.031 (0.0027, 16)a | 0.076 (0.011, 16)a |

[1] Statistically similar means ($p < .05$) using Wilcoxon-rank test have same lower-case letters.

ameter was analyzed for moisture content, ash, and elemental concentration by size-class and decay-state combinations. In all cases, no significant differences existed between the 2 size-classes for a decay state. Therefore, data for 2.5- to 5-cm and 5- to 10-cm branches were pooled according to decay state (Table 6). Slightly decayed branches had significantly less moisture, percent ash, and percent nitrogen than branches in the more advanced state of decay. For the other elements, no significant differences were observed between decay states. These data for smaller branches were consistent with the results for boles and large branches (Table 3).

### *Litter deposition*

Annual and seasonal dynamics for litter deposition for Hutcheson Memorial Forest were described in an earlier paper (Lang 1974). Values reported were on a dry-weight basis. Table 7 has the earlier dry-weight values corrected for percent ash content and also presents element inputs on a yearly basis. Because of the low ash content, there was only a 5% decrease in the earlier dry-weight values. The rank of total element input was N > Ca > K > Mg > P. This rank is similar to that for the forest floor except that K and Mg are reversed. Gosz et al. (1972) report a similar rank of abundance of elements in litter deposition in a northern hardwood forest. Reiners and Reiners (1970) and Cromack and Monk (1975) report the same ranking in oak forests except Ca and N are reversed. The leaf component contributed the largest percentage of each element.

Concentrations of elements in litter deposition are given in Table 9. For all 3 components, the percent carbon was similar, but percentages for other elements varied among the components. These percentages represent weighted values for the year on an ash-free weight basis. Nitrogen and K percentages were highest for fruits, while leaves had the highest percentages of Ca and Mg.

Associated with seasonal changes in litter deposition were changes in element concentrations. For branch and fruit components, there was no significant change ($p < .05$, Wilcoxon $U$-test) in element concentration between summer and autumn (Table 8). For leaves, there was no seasonal change in Ca, Mg, and C ($p < .05$). This was expected, because Ca and Mg are immobile and bound in plant tissue. However, there were significant differences in N, P, K, and ash concentrations (Table 8); in all cases, the percentage was reduced in autumn leaf deposition. These elements are presumably translocated from leaves to branches before leaf fall.

## DISCUSSION

### *Detritus in Hutcheson Forest*

Net aboveground primary production in Hutcheson Forest is estimated at 12 metric tonnes·ha$^{-1}$·yr$^{-1}$ from

TABLE 7. Average annual litter deposition in Hutcheson Forest. Values are $g \cdot m^{-2} \cdot yr^{-1}$. Organic matter is determined from loss on ignition (ash-free weight basis)

| Component | Percent ash (SE, n) | Organic matter | C | N | P | Ca | Mg | K |
|---|---|---|---|---|---|---|---|---|
| Leaf | 6.0 (–, 16)[1] | 440.2 | 174.3 | 5.5 | 0.44 | 5.2 | 0.62 | 1.7 |
| Branches $\leq 2.5$ cm diam | 3.4 (0.10, 20) | 106.9 | 43.5 | 2.4 | 0.05 | 1.1 | 0.05 | 0.1 |
| Flowers and fruits | 3.3 (0.28, 11) | 68.8 | 28.6 | 2.1 | 0.07 | 0.2 | 0.04 | 0.5 |
| **TOTAL** | | 615.9 | 246.4 | 10.0 | 0.56 | 6.5 | 0.71 | 2.3 |

[1] Annual average weighted by seasonal input calculated from Table 8: (6.4 × 1/3) + (5.8 × 2/3).

actual evapotranspiration (Lang 1974). Assuming a 20:1 biomass to production ratio (Whittaker 1975), aboveground biomass for the forest would measure 240 tonnes/ha. Several energetic comparisons can be made. Litter deposition, excluding large boles and branches, represents 2.6% and 51.3% of aboveground biomass and net production, respectively. These values are similar to those reported by Reiners (1972) for a northern pin-oak forest. The remaining 49% of net production is divided disproportionately between herbivore consumption and tree biomass accumulation. If the forest is not harvested, the accumulated biomass is eventually added to detritus, often in a catastrophic event. Because Hutcheson Memorial Forest is old-aged, we assumed the forest floor storage capacity was in steady state. For the *L*, *F*, and *H* layers, this is a reasonable assumption (Lang 1974). However, for the forest floor as a whole, steady state is directly related to the dynamics of bole input. The frequency of bole input and the amount of mass added per unit area may be increasing because of natural forest turnover. Individual tree falls and episodic catastrophes contribute to fluctuations in forest floor storage. A long-term study of bole input is needed to clarify the magnitude of these fluctuations.

Accumulation of detrital mass (Table 2) and elemental pools is related to processes of litter deposition and litter decomposition superimposed over time. The ratio of soil organic matter/aboveground biomass equals 1.15; clearly the detrital pool is a major ecosystem parameter in Hutcheson Forest. Large, decaying boles by themselves represent 9.8% of the aboveground biomass and 8.5% of the detrital pool (Table 2). Litter deposition is a major pathway for elemental recycling, but stemflow and throughfall also contain significant amounts of elemental input (Eaton et al. 1973, Cromack and Monk 1975). No estimates of this input are available, but throughfall inputs can be expected to reduce estimates of overall element turnover times (Gosz et al. 1976).

A decrease in C:element ratios is associated with decomposition. This results in part from the increase in elemental concentration by the action of heterotrophic organisms. Microflora in the forest floor will immobilize elements in inorganic form and incorporate them into protoplasm. Thus, because of biological activities of microorganisms, elements are sequestered and conserved. Once the carbon needed for assimilation by the microflora is limited, elements are no longer readily immobilized and a net release occurs. Thus, in theory, a critical C:element ratio exists, above which there is net element immobilization and below which there is net mineralization. Critical ratios for decomposing leaves and branches are discussed by Gosz et al. (1973).

For the forest floor in Hutcheson Forest, there was an increase in percentages of nitrogen and phosphorus and a decrease in the C:N and the C:P ratios with increased soil depth and increased decomposition (Table 5). The C:N ratio of 6 for humus is at the low end of the general range of 5 to 20 ascribed as the critical ratio for the occurrence of mineralization (Lutz and Chandler 1946, Lyon et al. 1952). These data suggest the net mineralization of nitrogen. Branches $<2.5$ cm, fruits, 1-yr-old litter, and *F*-layer material also fall within this range, but at the high end. The critical C:P ratio for forest soils is debatable. Gosz et al. (1973) report a C:P ratio of 480 for *F*-layer material, but Lunt (1932) gave a ratio of 360 for similar material. One-year-old litter and *F*-layer material in Hutcheson For-

TABLE 8. Seasonal changes in element concentration in leaf litter. Each value is the mean of 4 samples expressed as a percentage of the organic matter (ash-free weight) with standard error of mean (SE)[1]

| | Percentage composition | | | |
|---|---|---|---|---|
| Season (1972) | N (SE) | P (SE) | K (SE) | Ash (SE) |
| Summer (May–Sep) | 2.43 (0.032) | 0.16 (0.009) | 0.75 (0.045) | 6.4 (0.08) |
| Autumn (Sep–Dec) | 1.07 (0.036) | 0.09 (0.002) | 0.33 (0.011) | 5.8 (0.12) |

[1] The means between the 2 seasons for all elements and percent ash are significantly different ($p < .05$) using the Wilcoxon-rank test.

TABLE 9. Concentration of elements in litter deposition. Data are expressed as a percentage of organic matter (ash-free weight). (SE, *n*) is the standard error of the mean, number of samples

| Component | Percentage composition | | | | | |
|---|---|---|---|---|---|---|
| | C (SE, *n*) | N (SE, *n*) | P (SE, *n*) | Ca (SE, *n*) | Mg (SE, *n*) | K (SE, *n*) |
| Leaf | 39.6 (0.47, 8) | 1.25 (–, 8)[1] | 0.10 (–, 8)[1] | 1.18 (0.030, 8) | 0.14 (0.001, 8) | 0.39 (–, 8)[1] |
| Branches ≤2.5 cm diam | 40.7 (0.32, 8) | 2.23 (0.144, 5) | 0.05 (0.002, 4) | 1.01 (0.037, 8) | 0.05 (0.003, 8) | 0.12 (0.012, 8) |
| Flowers and fruits | 41.6 (0.66, 7) | 3.02 (0.104, 4) | 0.10 (0.008, 4) | 0.27 (0.051, 5) | 0.06 (0.004, 5) | 0.75 (0.022, 5) |

[1] Leaf average is proportionally weighted for seasonal concentration and the amount of input.

est have similar ratios, 360 and 268 respectively; the C:P ratio for humus is even smaller, suggesting net phosphorus mineralization.

Gosz et al. (1973) proposed that P may control decomposition because it is present in the least concentration and must recycle rapidly for steady state maintenance (Pomeroy 1970). From the results of Gosz et al. (1973), an average N:P ratio of 16 exists for combined forest floor *L*, *F*, and *H* layers under northern hardwoods. Nitrogen: phosphorus ratios of 15.5 and 11.5 exist for *L*, *F*, and *H* layers in Hutcheson Forest and a northern oak forest (Reiners and Reiners 1970), respectively. It is noteworthy that the N:P ratios for these 3 quite different forests are so similar. This relationship could possibly reflect a more general response as well as a critical ratio for concomitant nitrogen and phosphorus recycling.

The contribution of roots to the turnover of detrital organic matter in the humus pool is problematical. The humus component receives organic carbon inputs from the forest floor *L* and *F* layers, as well as inputs from small roots through exudation of carbon compounds and death of root tissue. These unknown, but potentially significant, inputs may affect humus steady state conditions and estimates of turnover times. We sorted and removed larger roots from humus, but made no attempt to estimate fine roots, some which are alive and others dead. Inclusion of large dead roots would increase the pool size of humus and concomitantly increase turnover time. Removal of small live roots from the humus pool would have the opposite effect. Inputs of carbon from dead roots would also lead to a decrease in turnover time. The net result of these manipulations on our data is unknown, but perhaps significant. Similar considerations are necessary in the mineral soil horizons.

### *Role of bole and branch detritus*

The role of detritus in energy flow and hydrologic and biogeochemical cycles in terrestrial ecosystems has been documented (Odum and de la Cruz 1963, Edwards et al. 1970, Reiners and Reiners 1970, Reiners 1972, Gosz et al. 1976). Decomposing boles and branches lying on the forest floor may play a significant part in the detrital dynamics of forest ecosystems. Their importance, however, has not been fully appreciated because, until recently, little attention has been given to this material. Logistically, this component requires intensive labor to measure. When measured, the amounts of detrital wood have been small compared to the organic matter in the forest floor and consequently dismissed as relatively unimportant. This is partly due to the fact that accumulation is limited in many forests because of past fires or tree harvest. In Hutcheson Forest, the bole and branch detritus accounts for 71% of the organic matter above the mineral soil (Table 2). In this old-age forest with a thin forest floor, the large mass of detrital wood plays an important role in biogeochemical cycling and has several other major functions.

Similar to leaf litter, boles and branches provide a habitat and an energy source for heterotrophic detritivores. Nitrogen-fixing bacteria are 1 example of a particular group of organisms that utilizes decaying wood as both habitat and substrate. With wood having a high C:N ratio, these organisms have a competitive advantage in this niche. Nitrogen fixation in logs has been demonstrated by Cornaby and Waide (1973) and Roskoski (1975). The presence of nitrogen-fixing organisms may regulate the rate of wood decay. In addition, fallen boles in old-age forests may also provide a minor source of nitrogen for the ecosystem. This input is lost with intensive harvesting.

As wood tissue decays, there is an enrichment of soil organic matter. This increase will improve the structure of fine-textured soils, bind course-textured soils into aggregates, improve infiltration and percolation, increase water-holding capacity, and increase cation exchange capacity. In some forests, decaying boles also serve as nurse logs or otherwise affect the establishment of seedlings.

The fall of whole trees onto the forest floor and their subsequent decomposition also has a fundamental role in biogeochemical cycling. Tree harvesting removes elements entirely from the ecosystem. When left to recycle, elemental inputs can be large; small branches contributed 10–20% of total element inputs from litter deposition (Table 7), and this percentage would be higher if estimates for large boles were available. In addition, the element content of detrital wood ranges between 10 and 30% of the total pool (Table 4). These percentages will vary from forest to forest depending on successional status, species composition, and environmental factors.

TABLE 10. Comparison of forest floor organic matter (ash-free weight) and element storage in selected deciduous (primarily oak) forests of eastern United States

| | | | Weight (kg/ha) | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Forest type and age | Location | Components measured | Dry wt | Organic wt | N | P | Ca | K | Reference |
| Northern pin oak with white oak and red maple; ≈50 yr | Cedar Creek, Minnesota (45°N, 275 m elevation) | Forest floor (*L*, *F*, *H*) plus branches | 323,730 | 61,950 | 1,654 | 149 | 454 | . . . | Reiners and Reiners (1970) |
| Northern hardwoods—sugar maple, yellow birch, American beech; ≈60 yr | Hubbard Brook Experimental Forest, New Hampshire (44°N, average 650 m elevation) | Forest floor (*L*, *F*, *H*) | . . . | 46,800 | 1,076 | 68 | 216 | 42 | Gosz et al. (1976) |
| Mixed oak—white, red, black oaks; >250 yr | New Jersey Piedmont (40°30′N, 37 m elevation) | Forest floor (*L*, *F*, *H*)<br>boles, branches, fruits | 40,350<br>28,290 | 10,990<br>27,170 | 648<br>162 | 40<br>5 | 143<br>77 | 84<br>21 | This study |
| Oak forest–red, chestnut, black, and scarlet oaks | Cowetta Hydrologic Laboratory, North Carolina (≈36°N, elevation not given) | Forest floor (*L*, *F*)<br>boles, branches (>2.5 cm diam) | 7,700<br>12,574 | 6,700<br>12,071[4] | 83<br>30 | 10<br>9 | 98<br>19 | 15<br>5 | Yount (1975)<br>Cromack (1973) |
| Black oak; 40 yr | Southeast Missouri (≈37°N, elevation not given) | Forest floor (*L*, *F*, *H*) | . . . | 9,360[2] | . . . | . . . | . . . | . . . | Loomis (1975) |
| Chestnut oak | Walker Branch Watershed, Tennessee (36°N, average 325 m elevation) | Forest floor ($O_1$, $O_2$)<br>boles, branches | 20,000<br>14,500 | 9,465[3]<br>13,920[4] | 232<br>39 | 14<br>2 | 258<br>84 | 21<br>6 | G. S. Henderson (*personal communication*) |
| Oak–hickory—chestnut and white oak–pignut and mockernut hickory | Walker Branch Watershed, Teneeessee (36°N, average 325 m elevation) | Forest floor ($O_1$, $O_2$)<br>boles, branches | 20,900<br>11,600 | 10,175[3]<br>11,136[4] | 267<br>37 | 17<br>2 | 401<br>172 | 21<br>7 | G. S. Henderson, (*personal communciation*) |
| Upland oak—scarlet and black oak; ≈75 yr | Eastern Tennessee (≈36°N, elevation not given) | Forest floor (*L*, *F*, *H*) | 8,400 | 4,200[5] | . . . | . . . | . . . | . . . | Blow (1955) |
| Oak–hickory; 35–92 yr | Ashland Wildlife Area, Missouri (≈39°N, elevation not given) | Forest floor (litter) | 6,070 | 5,160[1] | 137 | 11 | 286 | 12 | Rochow (1975) |
| Pine–oak of southern Appalachians | Appalachian Forest Experiment Station, North Carolina (≈35°N, elevation not given) | Forest floor (*L*, *F*, *H*) | 7,100 | . . . | . . . | . . . | . . . | . . . | Sims (1932) |

TABLE 10. Continued

| Forest type and age | Location | Components measured | Weight (kg/ha) Dry wt | Organic wt | N | P | Ca | K | Reference |
|---|---|---|---|---|---|---|---|---|---|
| Oak–hickory–red and white oak; ≈150 yr | South Carolina Piedmont (≈34°N, elevation not given) | Forest floor (*L*, *F*, *H*) | 13,030 | 8,110 | 134 | . . . | . . . | . . . | Metz (1954) |
| Oak–hickory; ≈150 yr | Georgia Piedmont (≈32°N, elevation not given) | Forest floor (*L*, *F*, *H*) boles, branches | 9,560<br>2,279 | 4,780[5]<br>2,188[4] | . . . | . . . | . . . | . . . | Monk et al. (1970), S. A. Nicholson (*personal communication*) |
| Oak–hickory—live, water, and laurel oak, pignut hickory; >100 yr | Orlando, Florida (28°N, 10 m elevation) | Forest floor (*L*, *F*, *H*) plus boles and branches | . . . | 6,710 | . . . | . . . | . . . | . . . | W. H. Schlesinger (*personal communication*) |

[1] Assumed 15% ash for "litter."
[2] Assumed 10% ash for *L*-layer and 20% for *F*-layer; *H*-layer was corrected.
[3] Assumed 15% ash for $O_1$ and 70% for $O_2$.
[4] Assumed 4% ash.
[5] Assumed a weighted average of 50% ash for profile.

Newly fallen boles and branches have high C:element ratios. As a consequence, these boles show an accumulation of elements through time. Part of this accumulation results from a concentration effect as carbon is disproportionately lost and other elements are immobilized by microbial biomass. In addition, elements may also accumulate from throughfall and winter snowpack as water infiltrates the boles. As mentioned, nitrogen specifically could accumulate through gaseous fixation and thus establish localized areas of more rapid decomposition. Element accumulation continues until a critical C:element ratio is reached, thereafter net mineralization occurs with elemental release from the bole. The presence of nitrogen-fixing bacteria may influence the timing of these events. For the forest ecosystem, decaying boles may accumulate elements and then release them after a time delay. The presence of boles in various states of decay may thus provide a regular yearly supply of elements for recycling. Similar events, but on a smaller and more rapid scale, may occur in small-size branches.

### *Comparisons with selected eastern deciduous forests*

Data for Hutcheson Forest were compared with those for representative oak forests in the eastern United States to look for patterns in forest floor dynamics. A northern hardwoods forest in New Hampshire was also included because forest floor dynamics are thoroughly described (Gosz et al. 1972, 1973, 1976) and because there was only one oak forest located to the north of our study site.

Forest floor (*L*, *F*, *H*) organic matter and element storage were arrayed in Table 10 along a latitudinal gradient. When necessary, we made the conversion to ash-free organic matter from dry-weight values, and estimated latitude to the nearest degree. Although site elevation and aspect, species composition, and stand age varied from forest to forest, there was a progressive increase in organic matter in the forest floor with increasing latitude. Nitrogen and P content in detritus also showed the same trend as organic matter, but data for Ca and K did not correlate as well with latitude. This was not surprising because calcium and potassium contents of an ecosystem can be controlled to a large extent by the nature of the underlying bedrock, rock weathering, and redistribution by plant uptake. Nitrogen and phosphorus contents are primarily under biotic control.

Excluding branches, the total forest floor accumulation in Hutcheson Forest resembled the southern-latitude oak forests more than the 2 northern-latitude stands. This was due in part to the small humus layer in Hutcheson Forest (Tables 1 and 2). Forest floor *L*, *F*, and *H* layers can reach steady state mass accumulation in relatively short periods of time (Covington, fide Gosz et al. 1976, Lang 1973), and thus variations in age and successional status were not critical

TABLE 11. Comparison of annual organic matter (ash-free) and element deposition (in kg/ha) in litter (leaf, branch, fruit) among selected deciduous forests of eastern United States. Turnover times (in years) are calculated as the weight of the forest floor *L*, *F*, and *H*-layers, including small branches (≤2.5 cm) and fruits, divided by annual deposition

| Forest type/location (Reference) | Organic matter | | N | | P | | Ca | | K | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Deposition | Turnover time | Deposition | Turnover time | Deposition | Turnover time | Deposition | Turnover time | Deposition | Turnover time |
| Northern pin oak, Cedar Creek (45°N) (Reiners and Reiners 1970) | 4,394 | 14.1 | 43.8 | 37.8 | 5.4 | 27.6 | 49.6 | 9.2 | . . . | . . . |
| Northern hardwoods, Hubbard Brook (44°N) (Gosz et al. 1974) | 5,702 | 8.2 | 54.2 | 15.3 | 4.0 | 15.4 | 40.7 | 4.8 | 18.3 | 2.0 |
| Mixed oak, New Jersey (40°30′N) (This study) | 6,159 | 2.7 | 100.0 | 7.4 | 5.6 | 7.5 | 65.0 | 3.1 | 23.0 | 5.0 |
| Oak–hickory, Missouri (≈39°N) (Rochow 1975) | 3,316[1] | 1.6 | 31.6 | 4.3 | 3.2 | 3.4 | 70.3 | 4.1 | 6.4 | 1.9 |
| Chestnut oak, Walker Branch (36°N) (Grigal and Grizzard 1975) | 4,294[1,2] | 2.2 | 34.4 | 6.7 | 2.6 | 5.4 | 78.2 | 3.3 | 20.8 | 1.0 |
| Oak–hickory, Walker Branch (36°N) (Grigal and Grizzard 1975) | 4,627[1,2] | 2.2 | 36.0 | 7.4 | 2.7 | 6.3 | 90.1 | 4.5 | 21.9 | 1.0 |
| Mixed oak, Cowetta, North Carolina (≈36°N) (Cromack and Monk 1975) | 3,860[1] | 1.7 | 32.5 | 2.6 | 4.8 | 2.1 | 42.8 | 2.3 | 17.9 | 0.8 |
| Oak–hickory, South Carolina Piedmont (≈34°N) (Metz 1954) | 4,180[1] | 1.9 | 26 | 5.2 | . . . | . . . | 85 | . . . | . . . | . . . |

[1] Assumed 5% ash in dry-weight value.

[2] Assumed elemental concentration in branches and fruits was similar to leaves.

for these comparisons. Successional stage was critical when comparing bole and branch detritus. Hutcheson Forest was initially characterized as an old-age stand. Other stands with detrital branch data were probably not old-age or have been disturbed (i.e., logged) in the recent past. This was apparent in that none of the other stands approach the large amount of wood lying on the forest floor in Hutcheson Forest. Nitrogen, P, and K content in branch detritus was also greater in Hutcheson Forest, but Ca was equal to or less than that in the Tennessee forests.

Although the forest floor organic matter in Hutcheson Forest was similar to that reported by G. S. Henderson (*personal communication*), the amount of stored N and P was appreciably higher than in the Tennessee forests. This was partially explainable by looking at litter deposition data (Table 11). Again the data were arrayed by latitude; variations in both organic matter and element deposition eliminated any general trend with latitude. Hutcheson Forest had the largest input of organic matter, N and P compared to the other forests. These large inputs may help explain the large accumulation in the forest floor when compared to those of Walker Branch and the South Carolina Piedmont.

Forest floor turnover times (forest floor pool size divided by input from litter deposition, Olson 1963) can be calculated from data in Tables 10 and 11. If it is assumed that the forest floor is in steady state, then, over an annual cycle, litter decomposition will equal litter deposition. Turnover times in Table 11 thus represent an estimate of the residence times for organic material or an element in the forest floor. A turnover rate (k) is the reciprocal of turnover time and represents the fractional turnover each year. Turnover rates for N and organic matter as a function of latitude are shown in Fig. 3.

Three major points result from data in Table 11 and Fig. 3. First, turnover times for N and P were longer than for Ca or K in all cases (Table 11). These results are consistent with the original observations of Reiners and Reiners (1970). Potassium is soluble and readily leached from organic matter and therefore recycled faster than structurally bound elements like Ca. Calcium is released at rates similar to those for tissue decomposition. Nitrogen and P are sequestered by microorganisms. The conservative nature of the microbial biomass controls the amount of these elements in the forest floor, and their turnover times are thus markedly longer. For Ca, Mg, and K, confounding effects from differences in geologic parent material are probably present and require finer resolution of the data for evaluation.

Second, forests can be separated into 2 groups,

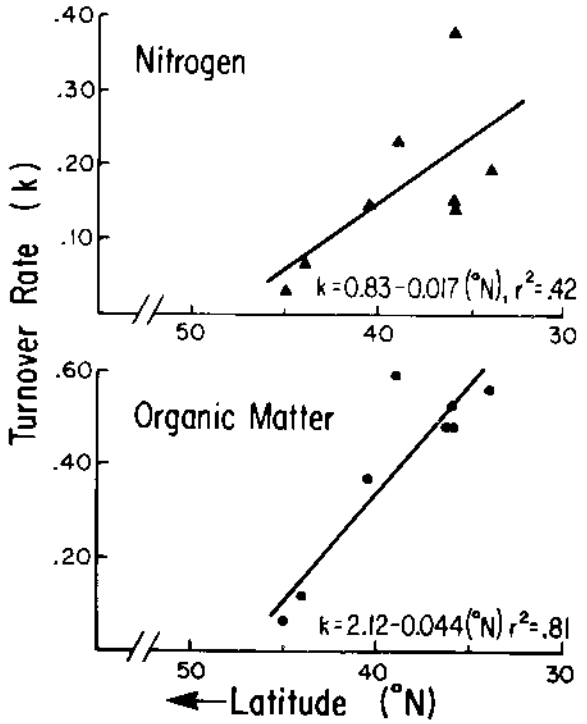

FIG. 3. Relationship of the turnover rate (k) for N and organic matter with latitude. The turnover rate is the reciprocal of the forest floor turnover time given in Table 11.

based on differential conservation of organic matter and elements (Table 11). The northern pin-oak and northern hardwoods forests formed one group characterized by longer turnover times and greater conservation of organic matter, N, and P. The remaining stands formed a second group, in which the turnover times were similar even though litter deposition and forest floor accumulation varied considerably. Turnover times of this second group are much less than that of the first group. The similarity in turnover times suggests that these forests have similar processes or mechanisms functioning in element accumulation and release. This relationship is relative and not absolute. The absolute amount of annual turnover is a function of biological and environmental factors characteristic of each site.

Third, turnover rates for organic matter and N show a nearly linear relationship with decreasing latitude (Fig. 3). The variation is greatest among southern forests, especially for nitrogen. This scatter is possibly due to differences in microbial activity and control of N immobilization and mineralization. Expectations of a better fit for these data may not be warranted. Organic matter turnover rates are highly correlated with latitude. Beech leaves in the northern hardwoods forest at Hubbard Brook have approximately the same substrate quality as oak leaves and similar rates of decomposition. Beech leaves will contribute to a lower turnover rate but leaves from sugar maple and yellow birch will raise k (Gosz et al. 1973, K. Cromack, Jr. *personal communication*). For organic matter turnover, the difference in leaf-type decay characteristics for the forest floor as a whole may not be as significant among the 8 sites as differences in species composition suggests.

The trends for increased accumulation of detrital organic matter, N, and P (Table 11) and their respective decreases in turnover rates (Fig. 3) with increasing latitude, can be related to general climatic changes. Minnesota and New Hampshire forests were located in cold temperate environments where microbial activity is low, decomposition and mineralization are slow, and, as a result, accumulation is large. In the warm, humid climates of the lower latitudes, microbial activity is high, decomposition and element release are fast, and detrital accumulation is small. For the most part, winters in Hutcheson Forest are mild and short compared to New Hampshire, and precipitation is abundant throughout the year. The climate of this New Jersey forest is more analogous to that of Tennessee than New Hampshire.

Because turnover for N and P is slower in colder environments, northern forests are often considered nutrient limited. However, if forest floor detritus is in steady state, with decomposition and mineralization equal to input, the 2 northern forests have as large or larger amounts of net mineralization based on litter input data (Table 11). The slower turnover times may not necessarily indicate nutrient limitation but rather, because of the large pool size, reflect only a greater residence time for an element within the pool. A larger time period is needed to achieve steady state, but once achieved, annual turnover will equal deposition.

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