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Seasonal Nutrient Dynamics of Foliage and Litterfall on Walker Branch Watershed, a Deciduous Forest Ecosystem

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SEASONAL NUTRIENT DYNAMICS OF FOLIAGE AND LITTERFALL ON WALKER BRANCH WATERSHED, A DECIDUOUS FOREST ECOSYSTEM

T. Grizzard, G. S. Henderson, E. E. C. Clebsch, and D. E. Reichle

Submitted by Tom Grizzard as a dissertation to the
Graduate School of the University of Tennessee
in partial fulfillment of the requirement
for the degree of Master of Science

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ABSTRACT

A detailed twelve-month study of litterfall, live foliage biomass, and seasonal nutrient (nitrogen, phosphorus, potassium, calcium, sodium, and magnesium) dynamics in tree components was performed for forest types on Walker Branch Watershed, Oak Ridge, Tennessee. Biomass and nutrient content of foliage, reproductive parts and branches were examined for ten dominant trees in order to assess the relative importance of litterfall in returning nutrients to the forest floor in four different forest types. Litterfall, measured in pine, pine-oak-hickory, oak-hickory, and mesophytic hardwood forests, was separated into three components (leaves, reproductive parts, and branches). Seasonal comparisons of those forest types were made for biomass and nutrient inputs for each component and for total litterfall. Each forest type was characterized by total annual input to the forest floor of biomass and individual nutrients for each component as well as total litterfall. Canonical analysis was performed on the yearly totals to test for significant differences among the forest types.

Live foliage from the ten predominant species of trees on the watershed, determined by order of total basal area, was analyzed for biomass, nutrient concentration, and changes in nutrient content through the growing season. Seasonal trends for these variables, including the ranking of nutrient concentrations for spring versus fall, were discussed in relation to differential growth, translocation, and leaching factors. Most of the litterfall in all forest types (77-85%) was in leaves with fall maximum. Reproductive parts (8-14% with spring and fall maxima) and branches (8-11% with no seasonal trend) contributed the remainder.

The ranking of nutrient content in litterfall was similar in spring and fall, except for the replacement of nitrogen by calcium in autumn as the predominant nutrient (followed by K > Mg > P > Na).

Comparisons were made between weight and nutrient content for living leaves and leaf litter input in litterfall. The ranking of total nutrient content per leaf in spring foliage was N > K > Ca > Mg > P > Na. The autumn foliage ranking was the same as that for autumn leaf litterfall (Ca > N > K > Mg > P > Na), the change being due to differing behavior of the particular nutrients (translocation, biomass dilution and removal by leaching).

In the four forest types analyzed, significant differences occurred in the biomass and individual nutrients recycled to the forest floor. The greatest litterfall and amounts of nitrogen input occurred in the pine forest type. Oak-hickory forests had the greatest litter inputs of magnesium and potassium. Calcium return was greatest in the mesophytic hardwood forest. No marked differences in the amounts of sodium and phosphorus return in the forest floor occurred among mesophytic hardwoods and oak-hickory forest types, which were consistently higher than pine and pine-oak-hickory forest values.

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INTRODUCTION

Development of the Problem

Litterfall is one of the most important processes in forest ecosystems, because it is a major pathway for both nutrient and energy recycling to the forest floor (Bray and Gorham 1964). Litter is the substrate upon which nutrient mineralization in the upper soil horizons is based (Carlisle, Brown and White 1966); biological return of elements is particularly important to the nutrition of woodlands on soils of low nutrient status where tree growth depends to a great extent upon the short-term or annual recycling of nutrients. Tree growth can be decreased by removing litter from beneath forests growing on poor soils (e.g., Van Goor and Tiemens 1963). Fallen leaves and other litter components are important sources of nutrients and organic material in forest soils for forest nutrition and continued productivity.

Many chemical elements are contained in woodland plants and have well-defined biogeochemical cycles. Some elements, such as carbon, circulate in large quantities; others, for example, nickel and cobalt, are present only in trace amounts (Warren and Delavault 1954, 1957). Several elements, including calcium, magnesium, potassium, nitrogen, and phosphorus, are essential to plant nutrition. Others such as sodium, are not required in plant biochemistry, but are physiologically essential to other forest organisms in higher trophic levels.

Objective

The objective of this study was to quantify the seasonal dynamics of biomass and nutrients in litterfall components for four forest types on Walker Branch Watershed, ERDA Reservation, Oak Ridge, Tennessee. Leaf weights and nutrient contents of the ten dominant trees in those forest types were analyzed in order to relate changing nutrient values in foliage during the growing season to observed values in litter input to the forest floor. Data were collected on the growth rate of leaves of deciduous and coniferous trees, and the seasonal variation in elemental concentrations and total amount for nitrogen, phosphorus, calcium, sodium, potassium and magnesium. Concomitant measurements were made of total litter inputs to the forest floor for the four forest types which characterize the watershed. Seasonal biomass and nutrient contents of litterfall and its components of leaves, reproductive parts and branches, were determined on a unit area basis. Summaries of the total biomass and element return to the forest floor were developed for the entire watershed, based upon the contribution of area of each forest type to the total watershed. The relative importance of nutrient return in litterfall in each forest type was addressed, as was the importance of biological inputs of elements through litterfall in the recycling of elements from vegetation to soil in forest ecosystems

CHAPTER II

MATERIALS AND METHODS

Site Description and Location

The study was conducted on the 97.53 hectare (ha) Walker Branch Watershed on the ERDA Reservation in Oak Ridge, Tennessee (Figure 1). The watershed is underlain by Knox dolomite, and soils formed over this substrate are well drained and have a high infiltration capacity. Mean annual precipitation is 135 cm/yr, and temperature averages 13.3°C (Curlin and Nelson 1968).

Detailed characterization of the composition and structure of forest types on Walker Branch Watershed has been reported by Curlin and Nelson (1968) and Grigal and Goldstein (1971). The following is a brief summary to clarify the general characteristics of each forest type. The pine forest consists of relatively pure pine stands of planted loblolly (*Pinus taeda*) and natural stands of shortleaf pine (*Pinus echinata*) with few other arboreal species. The understory is poorly developed, and honeysuckle (*Lonicera japonica*) is the predominant ground cover. The pine-oak-hickory forest has codominants of *Pinus echinata*, *Carya* sp. (mainly *Carya tomentosa*) and *Quercus* sp. Other canopy species include black gum (*Nyssa sylvatica*) and sourwood (*Oxydendron arboreum*). The pine-oak-hickory forest has a developed understory of dogwood (*Cornus florida*), red bud (*Cercis canadensis*), and sassafras (*Sassafras albidum*). The oak-hickory forest has the same composition of tree species as the pine-oak-hickory forest type except that pines are absent. The mesophytic hardwood type is characterized by tulip poplar (*Liriodendron tulipifera*) and red maple (*Acer rubrum*)

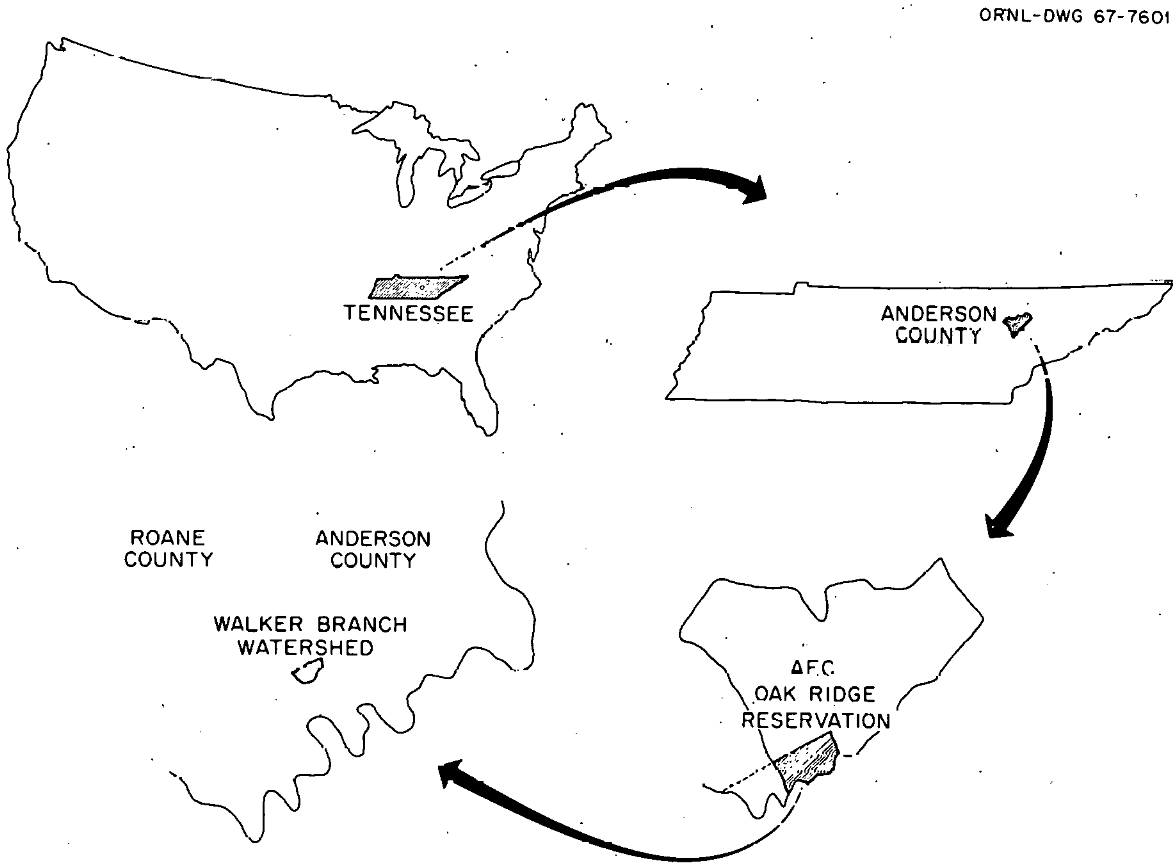

Figure 1. Geographical location of Walker Branch Watershed Project.

with a well-developed canopy of deciduous hardwood characteristic of the deciduous hardwood forest (Braun 1964). Other infrequently occurring tree species that are indigenous to streams and valleys are classified in the mesophytic hardwood forest, e.g., sycamore (*Platinus occidentalis*) and beech (*Fagus grandifolia*). The ground vegetation stratum is well developed with perennial, herbaceous vegetation (Taylor 1974).

Sample Plot Location

On the basis of variance estimates calculated from forest management data collected on the Oak Ridge Reservation, preliminary analyses (Curlin and Nelson 1968) determined that 300 .081-ha plots distributed among the four forest types were needed for dimension analyses to estimate stand composition and productivity within ≃ 15% accuracy on the watershed. Within the core study plots 80 litter traps were allocated according to the range of size classes, age and height categories for each forest cover type (Table 1).

Because pine forest types exhibited greatest consistency among plots for the above characteristics, fewest litter traps were allocated to that category. Mesophytic hardwood and oak-hickory forest types, with greatest range in composition and structure, received the largest allocation of litter traps. The criterion for the number of traps allocated to a single forest type was that of maintaining a coefficient of variation (C.V.) for litter biomass estimation $\leq$ 25%. Actual variation (expressed as C.V.) associated with estimates of annual litter input for each forest type using this experimental design (Table 1) was: 28% for pine, 20% for pine-oak-hickory, 24% for oak-hickory, and 26% for mesophytic hardwoods.

Table 1. Allocation of litter traps based on percentage cover of the four forest types on Walker Branch Watershed

Forest Type	Distribution of Forest Types		Litter Trap Allocation
	Acres	% Area	
1 Pine	17	7	6
2 Pine-Oak-Hickory	35	14	14
3 Oak-Hickory	143	60	35
4 Mesophytic Hardwood	46	19	25

Litterfall Collection and Chemical Analyses

Litterfall collections began on July 1, 1969 and continued for one year. Collections were made monthly during the summer, biweekly during the autumn, and once during the winter. Nine collections were made during the year (Table 2). Litter traps (Figure 2) were one meter square with 25 cm high redwood sides and bottoms of bronze wire mesh (6 mesh per cm). The litter traps were leveled at approximately 60 cm above the ground to prevent input of resuspended windblown materials. Prior examination indicated that all material caught in the traps came directly from aboveground vegetation and was not blown in from the forest floor.

The litter collected from the traps was separated into three components: (1) leaves and needles, (2) branches and bark, and (3) reproductive parts. The material was separated into each component at the trap site, brought into the laboratory, dried for 24 hours at 76°C, weighed, and milled to pass a number 40 screen. Samples weighing approximately one gram were then ashed for 8 hrs at 525°C, dissolved in 2.5 ml of 2 N HCl, filtered through Whatman No. 42 filter paper, and brought to volume with 100 ml distilled water. Calcium, potassium, magnesium, and sodium determinations were made by the Analytical Chemistry Section of the Oak Ridge National Laboratory using a Perkin-Elmer Model 403 Atomic Absorption Spectrophotometer. Strontium was used to reduce anion interference. The procedures used to determine each element are described in Kahn (1971). Phosphorus determinations were made by the sulfuro-molybdate method on a Technicon Auto Analyzer. The details of the method used for the phosphorus determinations are

Table 2. Dates and intervals of litter trap collections on Walker Branch Watershed

Collection Number	Date	Days between Collections
1	July 31, 1969	31
2	September 2, 1969	33
3	October 15, 1969	43
4	October 30, 1969	15
5	November 12, 1969	13
6	December 2, 1969	20
7	March 5, 1970	93
8	June 1, 1970	88
9	July 1, 1970	30

Figure 2. A one meter square litter trap on a study plot used to collect litterfall components.

available in Lundgren (1960). Total nitrogen was determined by the semi-micro Kjeldahl procedure described by Black (1965).

All calculations of chemical contents of sample materials were based upon the mean of replicate analyses of two homogeneous subsamples of $\sim$ 1 g each taken from the dried and homogenated litter component. Precision of chemical determinations (maximum percentage deviation from the mean) based upon National Bureau of Standards orchard leaf standards for the respective analytical procedures was: calcium, 2%; nitrogen, 2%; sodium, 4%; phosphorus, 4%; magnesium 2%; and potassium, 2%. These percentages are the maximum range of individual measurements from mean values and incorporate errors associated with both analytical procedures and variances between subsamples.

Leaf Sampling

The objectives of separate analyses of leaf material were: (1) to determine growth rates of leaves of major species from bud break until abscission and (2) to quantify the seasonal change in concentration of major nutrients in living leaves. Ten tree species, which contributed 88% of the basal area (Table 3) of the watershed, were sampled beginning May 2, 1969 and continuing through May 4, 1970 (phenologically from cessation to cessation of dogwood flowering) on a maximum of 17 different sampling dates (Table 4). Forty trees were sampled across the ten species studied; the same trees were sampled at each collection date. Table 3 summarizes the number of trees, age, and range of diameter at breast height (DBH) of each species.

Canopy foliage was sampled by shooting leaves (25 leaves were sampled) off the trees with a shotgun. On each sampling date 25 conifer

Table 3. Major tree species studied on Walker Branch Watershed with DBH range, age, number of trees sampled and basal area of each

Species[b]	DBH (cm)	Age (years)	Number of Trees Sampled	Basal Area[a] (m^2/ha)
Pinus taeda L. (Loblolly Pine)	21.1-29.0	20-21	3	0.52
Pinus echinata Mill. (Shortleaf Pine)	30.7-38.1	89-121	3	2.48
Quercus rubra L. (Red Oak)	23.9-41.4	28-68	4	1.12
Quercus alba L. (White Oak)	29.2-36.7	41-64	4	2.21
Quercus prinus L. (Chestnut Oak)	26.4-46.0	36-83	6	3.39
Liriodendron tulipifera L. (Yellow Poplar)	22.4-37.9	30-52	5	2.14
Acer rubrum L. (Red Maple)	16.0-26.7	20-32	4	1.44
Nyssa sylvatica Marsh. (Black Gum)	17.0-33.5	27-53	3	0.95
Oxydendrum arboreum (L.) DC. (Sourwood)	7.6-11.7	12-21	3	1.09
Carya tomentosa Nutt. (Mockernut Hickory)	27.9-38.6	38-88	5	2.31

[a]Total basal area of all overstory vegetation on Walker Branch Watershed averages 20.8 m^2/ha with a total of 53 tree species represented (Grigal and Goldstein 1971).

[b]E. L. Little, Jr. 1953. Check List of Native and Naturalized Trees of the United States. Agricultural Handbook No. 41. U. S. Government Printing Office, Washington, 1953. 472 p.

Table 4. Frequency of foliage collections from ten major tree species on Walker Branch Watershed

Collection Number	Date
1	May 2, 1969
2	May 16, 1969
3	June 4, 1969
4	July 2, 1969
5	July 29, 1969
6	August 26, 1969
7	September 13, 1969
8	September 30, 1969
9	October 15, 1969
10	October 29, 1969
11	November 11, 1969
12	November 26, 1969
13	December 30, 1969
14	February 7, 1970
15	March 31, 1970
16	April 15, 1970
17	May 4, 1970

leaves, with each fascicle counting as a single leaf, were collected in the same manner as deciduous leaves. Conifer leaves were also collected during the winter months. Leaf collections were brought to the laboratory, and the same procedures and techniques were used for drying and chemical determinations as for litter trap samples.

Sampling Considerations

Certain sources of error must be acknowledged in sampling vegetation for determination of seasonal nutrient dynamics. One type involves genetically-based physiological variations within a species-population, including differences due to life-history phenomena (Manshard 1933). For conifers, which carry their needles for two of three years, the situation is further compounded (Hoyle 1965). These factors interact with environmental heterogeneity and the two sources of error are often difficult to distinguish. Trees of different ages may have experienced different environmental extremes during their ontogenies, and may occupy divergent soil and atmospheric strata. Both age and environmental conditions were variables involved in the results of foliage data of Murneck and Logan (1932), McClung and Lott (1956), Askew et al. (1959), and Koo and Sites (1956). The situation is further complicated because growing leaves utilize nutrients stored in the perennial tissue in previous years. For these reasons it is risky to transpose results from one year to the next. In the present study no attempt was made to account for genetic variability, and sampling was not biased for age or physical condition, although extreme conditions were avoided. For conifers the newly initiated foliage was not sampled. The soils on the watershed are quite similar (Peters et al. 1970), with the main difference involving topographic position and consequent soil moisture conditions. In regard to soils and extreme moisture conditions (for example solid rock outcroppings and swampy areas) trees occupying highly atypical situations were not considered.

Concerning time of sampling, many investigators (Frank and Otto 1891, Miller 1926, Chibnall 1929, Mitchell 1936, Biddulph 1941, and Phillis and Mason 1942) found significant diurnal changes in foliar concentrations for at least some of the nutrients studied. Mitchell (1936) and Denny (1933) advocated sampling at the same time of the day during each collection. Similar precautions were taken in this study, with all samples being collected within the same 3-4 hour period on each date.

Much work, a great deal of it conflicting in results, has been done concerning the effect of position of leaves on the trees on their nutrient concentrations. These include vertical position (Seiden 1926, Wallihan 1944, White 1954, and Guha and Mitchell 1966), cardinal position (Seiden 1926, Wallihan 1944, Tamm 1951, and White 1954) and position on a twig or branch (Wallihan 1944, and Guha and Mitchell 1965). In the present study those possible effects are integrated into the sampling technique. The leaves from whole twigs or small branches, taken from three cardinal positions at random heights in the canopy, were removed and composited for each sample.

Expression of Data

The literature reveals a general lack of conformity in expressing data on foliar nutrient dynamics. Olsen (1948) and Hoyle (1965) draw attention to the drawbacks in the use of concentration values alone, including reduction of measurement sensitivity, obscuring seasonal gains and losses of nutrients and inability to detect differences in total foliage nutrient levels. While certain phenomena, such as determination of relative changes among different nutrients at a given time for a given species, can be gleaned from concentration data alone, interspecific comparisons and seasonal differences in foliage nutrient levels, even within the same species, are masked due to changes in the dry weight of the leaf material. As such, false impressions regarding translocation to and from the leaves and leaching effects are possible when using just this one measure. Since total content (weight of nutrient per gram dry weight) of a nutrient can be derived quite readily from concentration and dry weight data, and since the inclusion of all three parameters requires no additional field work and no significant amount of additional analytic endeavor, all three measures should generally be reported.

Statistical Analysis

Analysis of variance techniques were used to compare the concentrations of each nutrient considering forest types and litter components as fixed factors in a factorial arrangement of treatments. Nutrient concentrations were based on totals from those traps collecting more than 3 grams (dry weight) of a particular litter component. The $P \leq 0.05$ level of significance was used in the analysis of variance while Duncan's Multiple Range test, also at the $P \leq 0.05$ level, was used to compare means of those factors with significant F ratios.

The total amount of litter collected in a particular trap was quite variable within a forest type and extremely variable when either branches or reproductive parts were compared. This variability in the total nutrient content between litter traps precluded rigourous statistical analysis of either branches or reproductive parts. Variability for total nutrients (sum of leaves, branches and reproductive parts) and nutrients in the leaf component were less variable but differed between the forest types. This was especially true for Ca, Mg and K. Because of these unequal variances, 95% Confidence Intervals were constructed about each mean with non-overlapping intervals used to indicate significant differences at the $P \leq 0.05$ level.

The Multivariate Technique, Canonical Analysis, was performed to test for differences that may exist between the four forest types annually. The total dry weight and the total content of the six nutrients in each component of litterfall and in total litterfall were values used in this evaluation.

CHAPTER III

RESULTS

Seasonal Foliage Weight and Nutrient Dynamics

Weight changes. Loblolly and shortleaf pine leaf weights remained relatively constant throughout the year (Figure 3). The uniform weight is due to the fact that newly initiated leaves were not sampled at any of the collection dates. All deciduous species showed sharp increases in dry weight during May when foliar development was most prominent. Some species, notably red oak and tulip poplar, showed gradual increases in leaf weight after the first of June whereas leaf weight of other species did not change. The oaks and tulip poplar produced the heaviest leaves and values are consistent with those of Bray and Gorham (1964). Mitchell (1936) reported maximum dry weights of 15.4, 13.4 and 5.6 g/25 leaves for red oak, white oak, and red maple leaves, respectively. Corresponding weights in this study were 17.5, 9.4 and 6.3 g/25 leaves.

The deciduous species lost an average of 28% of their maximum weight from two to six weeks prior to abscission. Sampson and Samisch (1935) attributed the 14% weight loss they observed for *Quercus gambelli* prior to abscission to leaching and to translocation of nutrients and other materials from leaves to branches. Viro (1955) reported leaf weights prior to abscission in four deciduous species to average 21% less than weights of leaves during the summer when their weights were greatest.

Timing of leaf abscission. Tulip poplar, black gum, and sourwood leaves fell earliest (late October), followed by red maple, hickory, chestnut oak, and red oak leaves (late October-early November). White oak leaves fell last (mid-November).

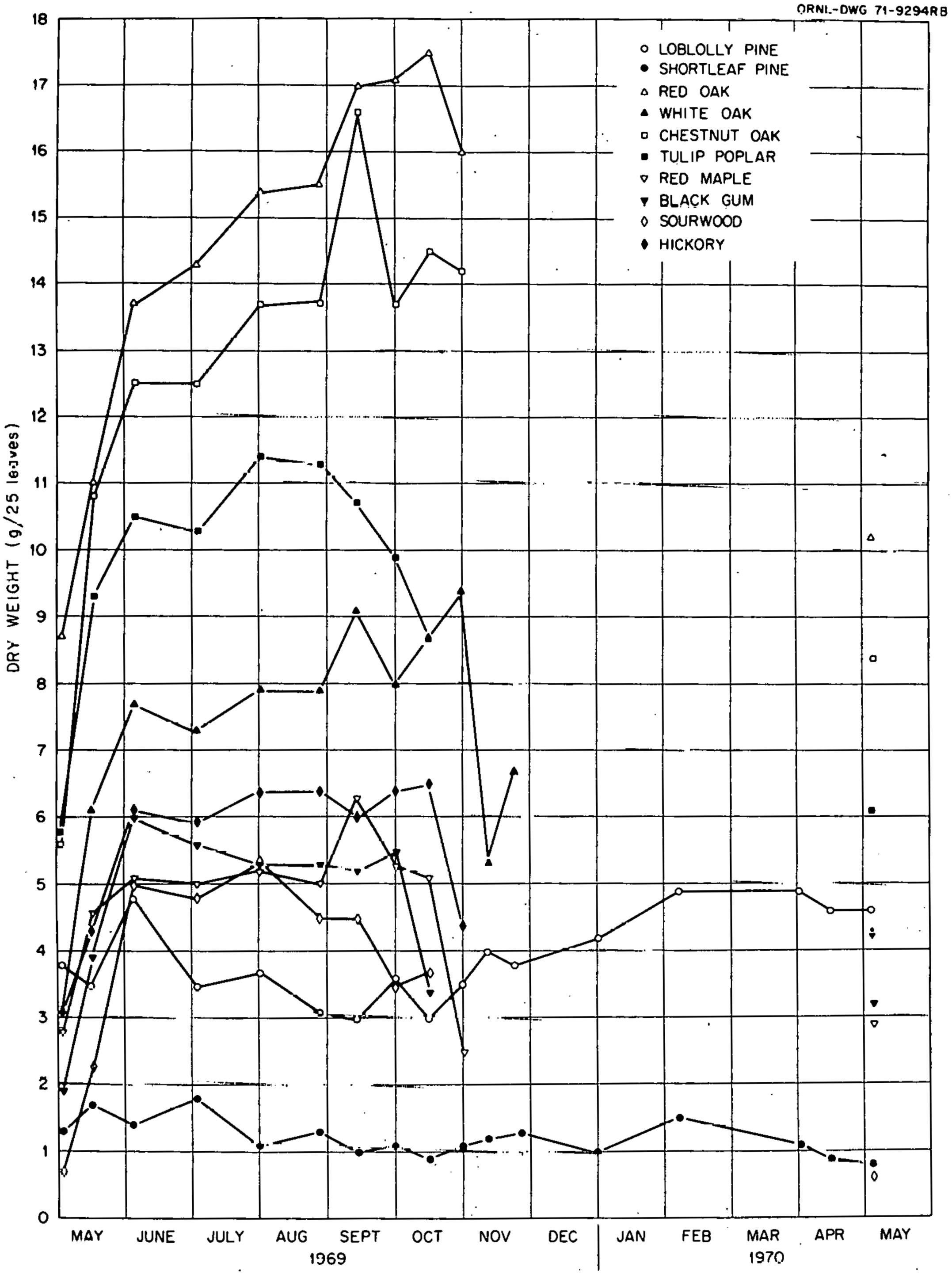

Figure 3. Seasonal patterns of the oven dry weights of leaves of major tree species on Walker Branch Watershed.

Seasonal Foliage Nutrient Changes

Nitrogen. Although leaves of some deciduous species had higher nitrogen concentration than did others at a given time, all exhibited a decrease in nitrogen concentration as leaf development progressed (Figure 4). The decrease in concentration was the result of increases in leaf weight (dilution) as the season progressed. The highest observed concentration on a dry wt basis was 3.6% nitrogen (sourwood) on the early spring collection (May 2). The average nitrogen concentration in the early spring collection (May 2) was 2.9% while the average of the autumn collection (October 29) was 0.5%. Alway, Maki, and Methley (1934) also found the average nitrogen concentration of nine deciduous tree species on five sampling dates (June 1, July 1, August 1, September 1, October 11-16) in Minnesota to range from the high in June of 3.0% to a low in October of 0.8%.

Leaves of the two coniferous species contained generally lower nitrogen concentrations than did deciduous species, and those concentrations remained relatively constant through the year. Rodin and Bazilevich (1967) found nitrogen concentrations in deciduous leaves to be roughly twice those in conifer leaves.

Although the actual nitrogen content varied (due to leaf weight differences) among species, all deciduous species exhibited similar patterns as the year progressed (Figure 5):

1. There was an increase in nitrogen content during the period of most rapid growth (May).
2. The nitrogen content leveled off in June and remained rather constant until the last of August.

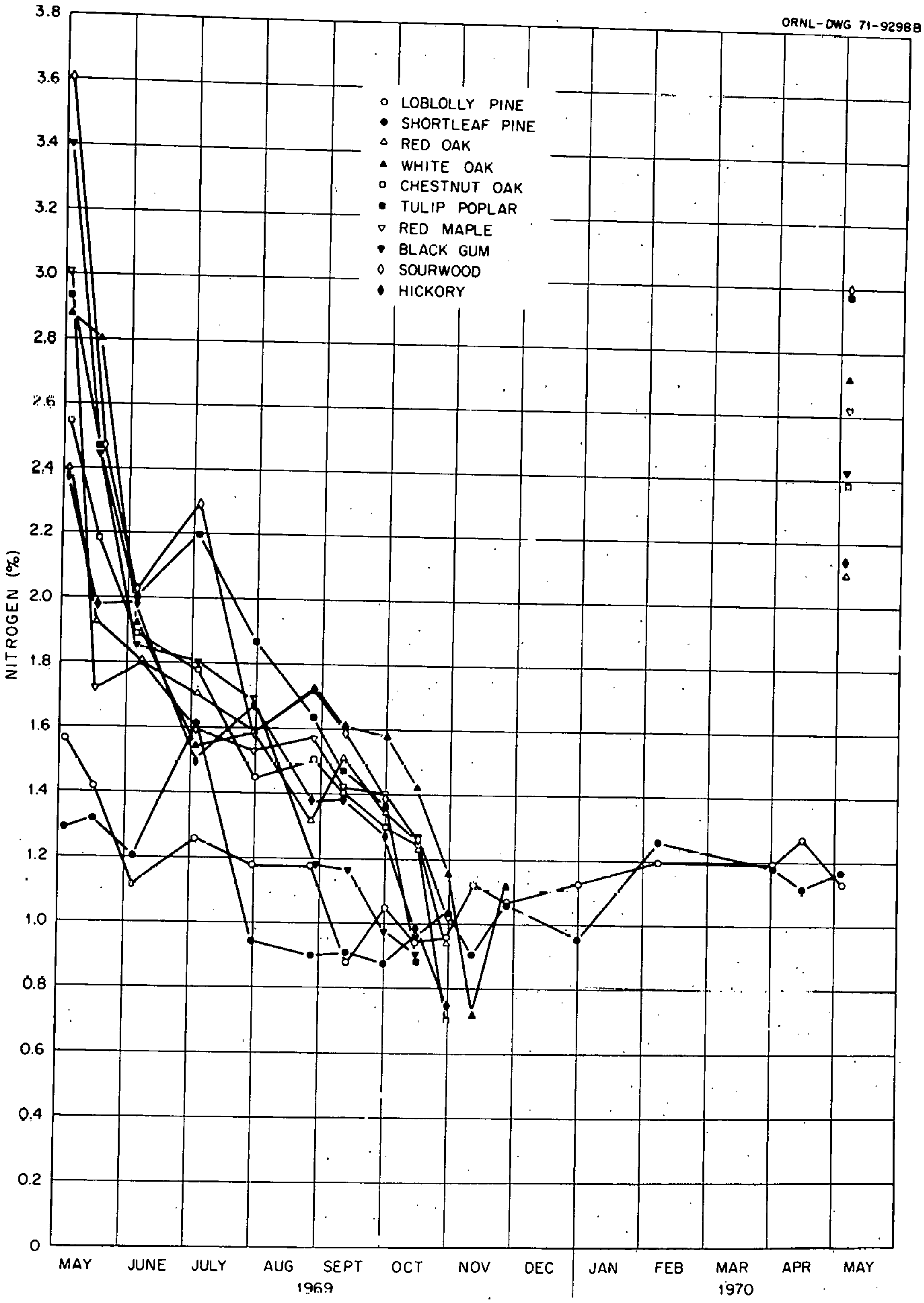

Figure 4. Seasonal patterns of nitrogen concentrations (% dry weight) in leaves of major tree species on Walker Branch Watershed.

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COLLECTION NO.	1	2	3	4	5	6	7	8	9	10
	MAY 2	MAY 16	JUNE 4	JULY 2	JULY 29	AUG 26	SEPT 13	SEPT 30	OCT 15	OCT 29
o LOBLOLLY PINE	59.8	50.3	54.7	44.6	43.8	37.1	26.2	38.0	28.6	33.8
● SHORTLEAF PINE	16.8	22.4	17.1	29.3	10.3	11.8	9.2	9.4	10.6	11.4
△ RED OAK	208.0	212.0	248.0	245.0	245.0	204.0	196.0	230.0	220.0	151.0
▲ WHITE OAK	90.1	171.0	149.0	113.0	124.0	137.0	146.0	126.0	123.0	109.0
□ CHESTNUT OAK	143.0	235.0	236.0	222.0	199.0	207.0	232.0	178.0	182.0	100.0
■ TULIP POPLAR	169.0	228.0	210.0	226.0	213.0	186.0	157.0	135.0	129.0	
▽ RED MAPLE	85.5	78.3	92.3	79.4	79.9	79.0	89.9	73.6	64.3	25.2
▼ BLACK GUM	65.8	95.8	111.0	102.0	88.6	63.2	60.5	54.0	30.7	
◊ SOURWOOD	23.6	57.3	101.0	109.0	84.5	77.9	71.2	48.4	46.4	
♦ HICKORY	72.9	85.1	122.0	89.4	108.0	88.3	82.7	83.0	57.8	33.4

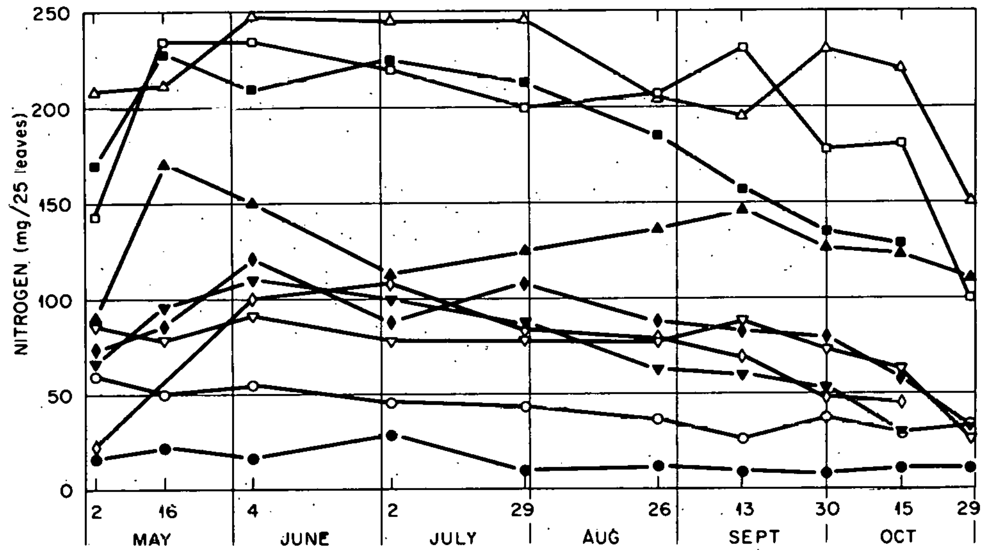

Figure 5. The amounts of nitrogen in leaves of major tree species on Walker Branch Watershed.

3. The nitrogen content decreased from September through defoliation.

Both coniferous species exhibited a trend of decreasing nitrogen with time. The nitrogen content in conifer foliage at nearly every collection was less than the nitrogen content in leaves of all deciduous species.

Calcium. Other investigators (Alway et al. 1934, Rodin and Bazilevich 1967, Gagnon et al. 1958, Chandler 1939) found that calcium concentrations in leaves increase as the season progress (Figure 6). Calcium is a structural constituent of cell walls and, therefore, is not diluted by growth; it must be supplied to the foliage throughout the season. Tulip poplar and hickory leaves had higher calcium concentrations than did the leaves of other deciduous species.

Chandler (1939) determined the calcium concentrations in leaves of six species that were examined in this study just prior to leaf fall (Table 5). The calcium concentrations in white oak, red oak, and chestnut oak leaves were similar, but tulip poplar and hickory leaf values were higher in Chandler's study and red maple concentrations were higher in this study.

The deciduous leaves had higher calcium concentrations than did conifer foliage at nearly all collection dates. There was an increase in calcium concentrations in conifer leaves in June and July followed by a sharp decrease in August and September. Loblolly pine leaves exhibited another increase during fall and winter with a decrease again in early spring.

The total calcium content in foliage of all deciduous species studied increased as leaf development progressed (Figure 7). Some species

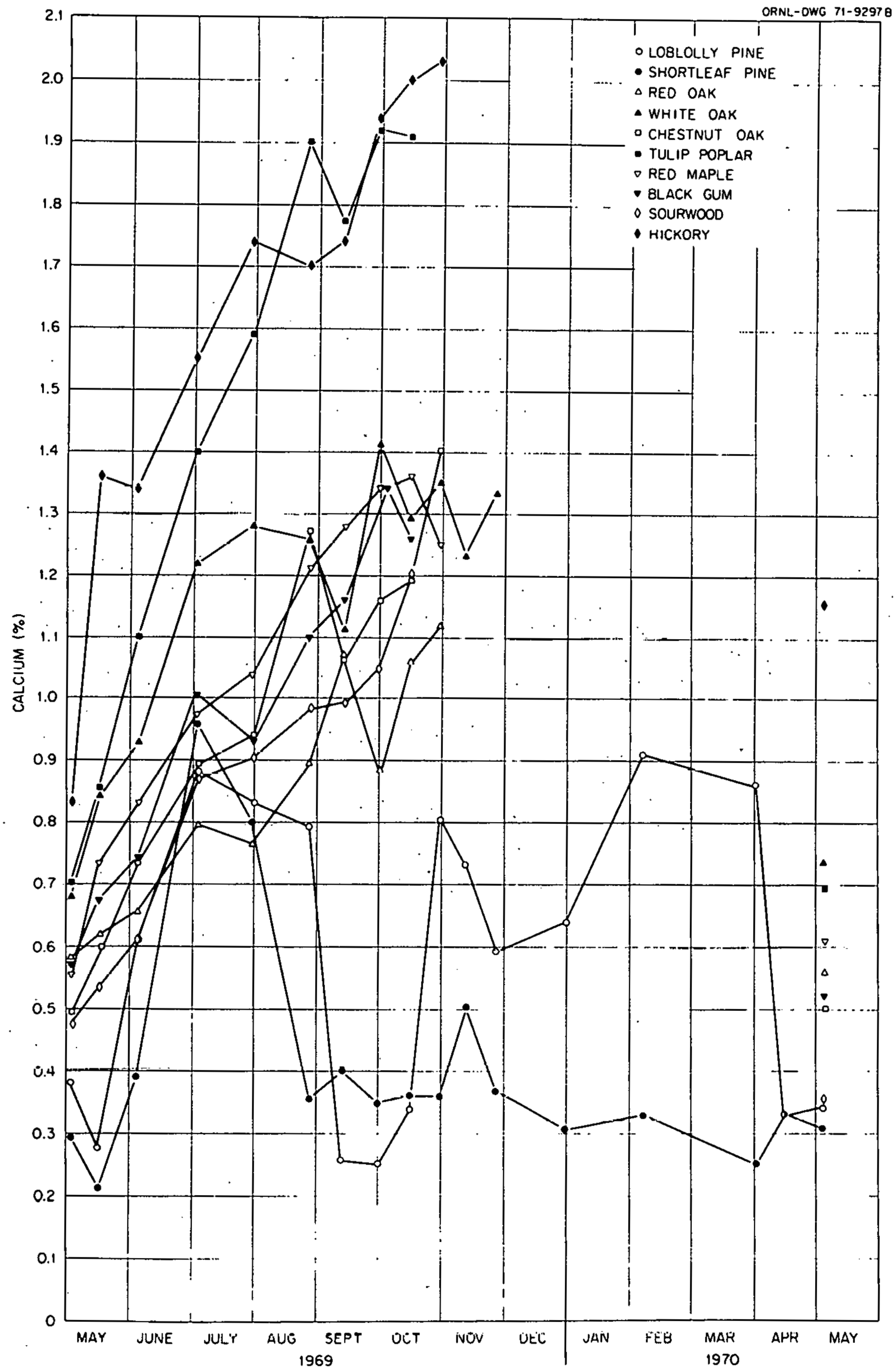

Figure 6. Seasonal patterns of calcium concentrations (% dry weight) in leaves of major tree species on Walker Branch Watershed.

Table 5. A comparison of calcium values in foliage from six deciduous species

Species	Chandler's 1939 Average (% oven dry wt.)	Walker Branch Watershed 1969-1970 Average (% oven dry wt.)
Tulip Poplar	3.24	1.92
Mockernut Hickory	2.62	2.04
White Oak	1.36	1.41
Red Oak	1.21	1.12
Chestnut Oak	1.20	1.40
Red Maple	0.91	1.36

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COLLECTION NO.	1	2	3	4	5	6	7	8	9	10
	MAY 2	MAY 16	JUNE 4	JULY 2	JULY 29	AUG 26	SEPT 13	SEPT 30	OCT 15	OCT 29
○ LOBLOLLY PINE	14.5	9.8	29.4	31.3	30.9	25.0	7.6	9.1	10.1	28.3
● SHORTLEAF PINE	3.8	3.8	5.5	17.5	8.7	4.7	4.0	3.7	3.4	4.0
△ RED OAK	50.3	67.7	89.5	114.0	118.0	137.0	139.0	151.0	185.0	179.0
▲ WHITE OAK	21.2	51.6	71.6	88.6	100.0	99.7	101.0	112.0	112.0	127.0
□ CHESTNUT OAK	27.7	64.9	91.7	112.0	129.0	174.0	176.0	159.0	173.0	199.0
■ TULIP POPLAR	41.3	78.6	116.0	144.0	181.0	215.0	189.0	190.0	166.0	
▽ RED MAPLE	15.9	33.3	42.3	48.3	54.3	60.9	81.0	70.5	69.4	30.9
▼ BLACK GUM	11.1	26.5	44.4	56.9	49.2	59.0	60.0	73.8	42.5	
◊ SOURWOOD	3.1	12.4	30.5	41.8	48.5	44.6	44.4	36.5	44.2	
♦ HICKORY	25.3	58.5	82.0	92.4	112.0	109.0	104.0	123.0	130.0	91.9

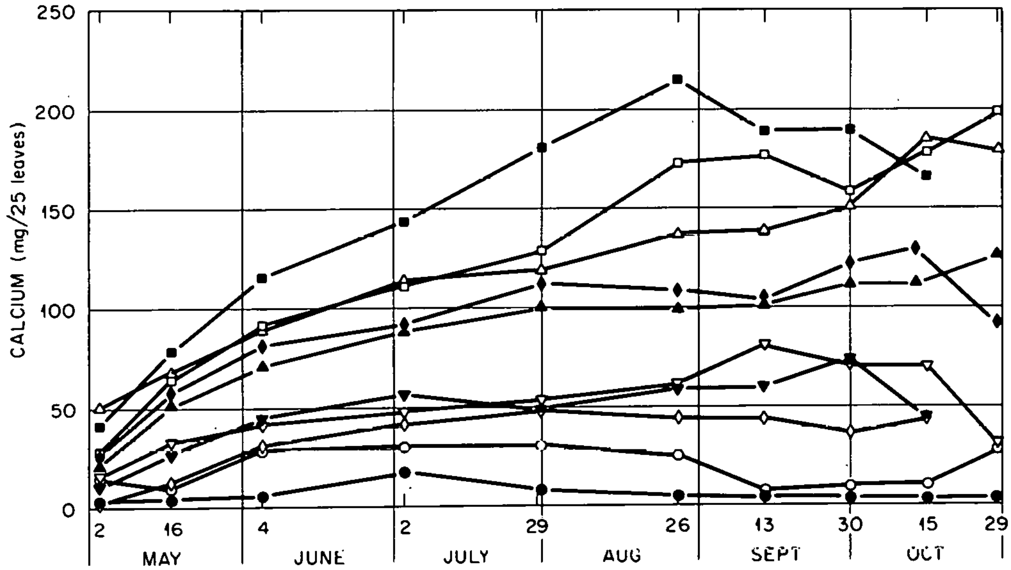


Figure 7. The amounts of calcium in leaves of major species on Walker Branch Watershed.

(tulip poplar, chestnut oak, red oak, hickory, and white oak) added great amounts of calcium while others (black gum, red maple, and sourwood) added lesser amounts. There was a slight decrease in calcium content before leaf fall in tulip poplar, red oak, hickory, red maple, and black gum associated with a weight loss in leaves prior to abscission.

Magnesium. All species showed fluctuations in magnesium concentrations throughout the season (Figure 8). Magnesium concentrations in red oak leaves (0.59-0.99%) increased during the development, while red maple leaves (0.23-0.22%) showed no change through the season. Alway et al. (1934) showed a similar trend for red oak (increases from 0.38 to 0.61%). Red oak leaves had higher magnesium concentrations than leaves of other deciduous species at all collections. In most collections white oak and tulip poplar leaves contained the next highest concentrations. Deciduous leaves of sourwood, red maple, and chestnut oaks had the lowest magnesium concentrations. Conifers (loblolly and shortleaf pine) had lower concentration than deciduous species at nearly every collection.

With the exception of red oak and tulip poplar, magnesium content of deciduous leaves increased from May through June and then remained relatively constant throughout the remainder of the season (Figure 9.). Magnesium contents in red oak, and to a lesser extent tulip poplar, continued to increase through the summer before declining slightly in autumn.

Sodium. The sodium concentrations (Figure 10) in the ten species studied ranged from 0.01 to 0.06%. The sodium values for all species were quite variable and may have been due to contamination during sample collection and preparation for analysis. Guha and Mitchell (1965) found the sodium concentration in red oak leaves to range from 0.02 to 0.30%,

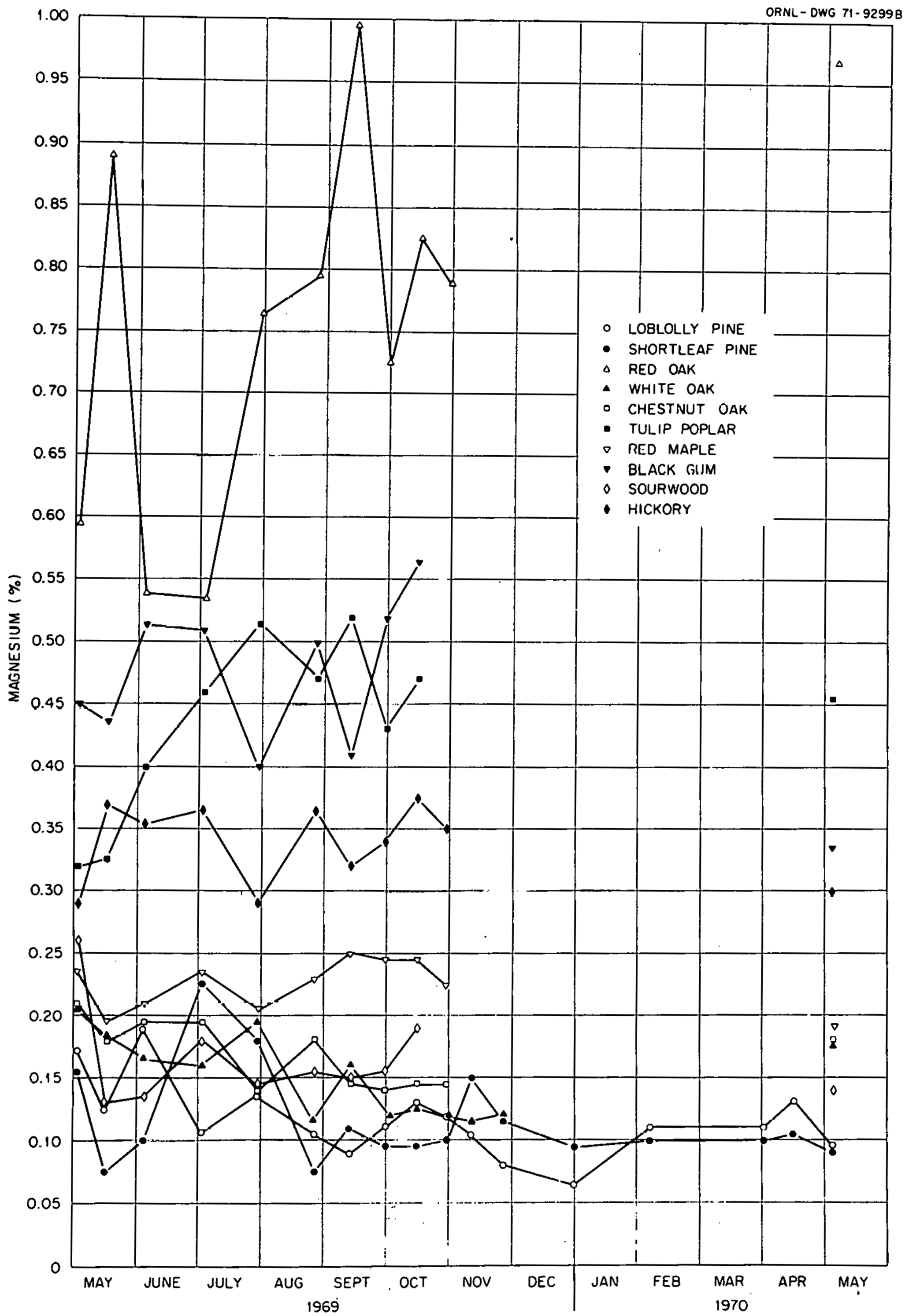


Figure 8. Seasonal patterns of magnesium concentrations (% dry weight) in leaves of major tree species on Walker Branch Watershed.

ORNL-DWG 73-2381

COLLECTION NO.	1	2	3	4	5	6	7	8	9	10
	MAY 2	MAY 16	JUNE 4	JULY 2	JULY 29	AUG 26	SEPT 13	SEPT 30	OCT 15	OCT 29
○ LOBLOLLY PINE	6.60	4.41	9.12	3.92	5.02	3.22	2.72	4.00	3.94	4.26
● SHORTLEAF PINE	2.03	1.26	1.41	4.17	1.97	0.97	1.09	0.98	0.87	1.10
△ RED OAK	51.65	97.40	73.65	76.50	117.98	123.24	143.57	123.63	143.91	126.74
▲ WHITE OAK	6.43	11.19	12.65	11.54	15.23	9.16	14.62	9.40	11.02	11.33
□ CHESTNUT OAK	11.84	19.80	24.56	24.20	19.43	24.95	24.32	18.80	21.09	20.75
■ TULIP POPLAR	18.56	29.94	41.99	47.21	58.50	53.02	55.34	42.36	40.77	
▽ RED MAPLE	6.70	8.93	10.79	11.59	10.65	11.44	15.70	12.76	12.44	
▼ BLACK GUM	8.66	17.05	30.75	28.70	21.08	26.73	21.12	28.59	19.08	
◊ SOURWOOD	1.71	2.96	6.66	8.51	7.87	6.97	6.77	5.33	7.19	
♦ HICKORY	8.83	15.87	21.72	21.60	18.73	23.41	18.93	21.53	24.55	15.54

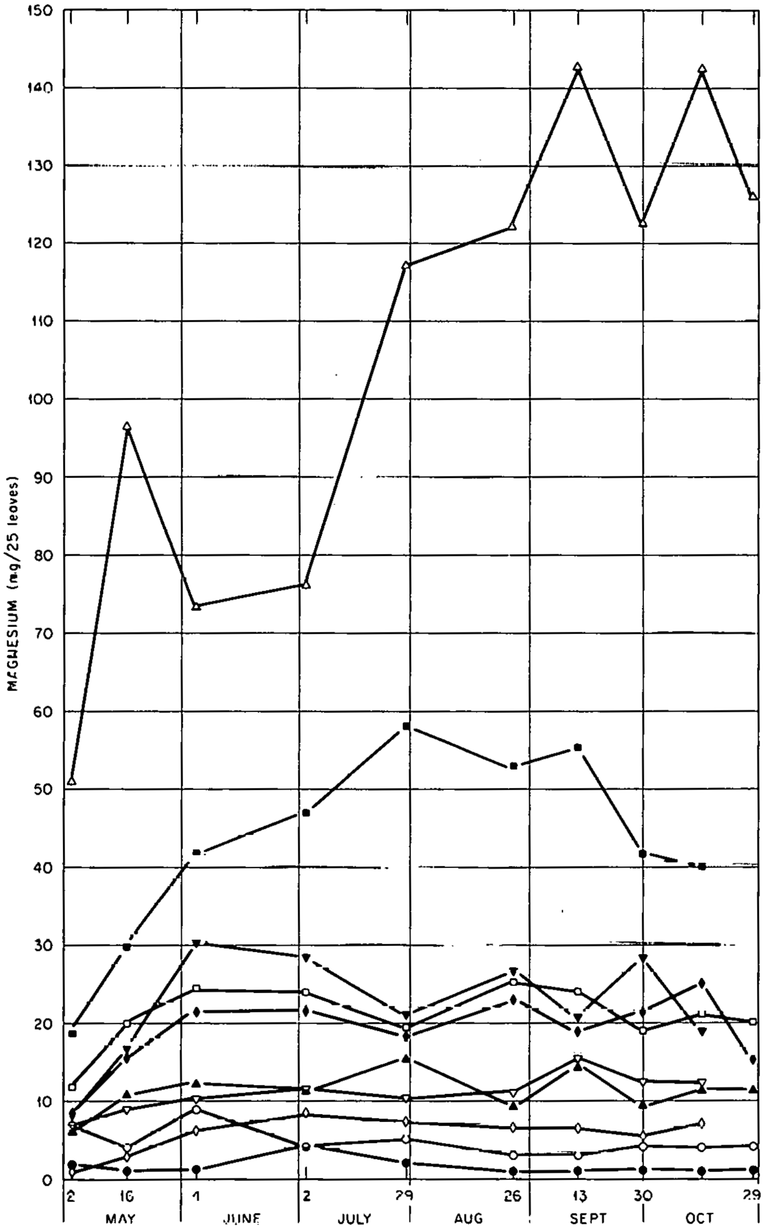


Figure 9. The amounts of magnesium in leaves of major tree species on Walker Branch Watershed.

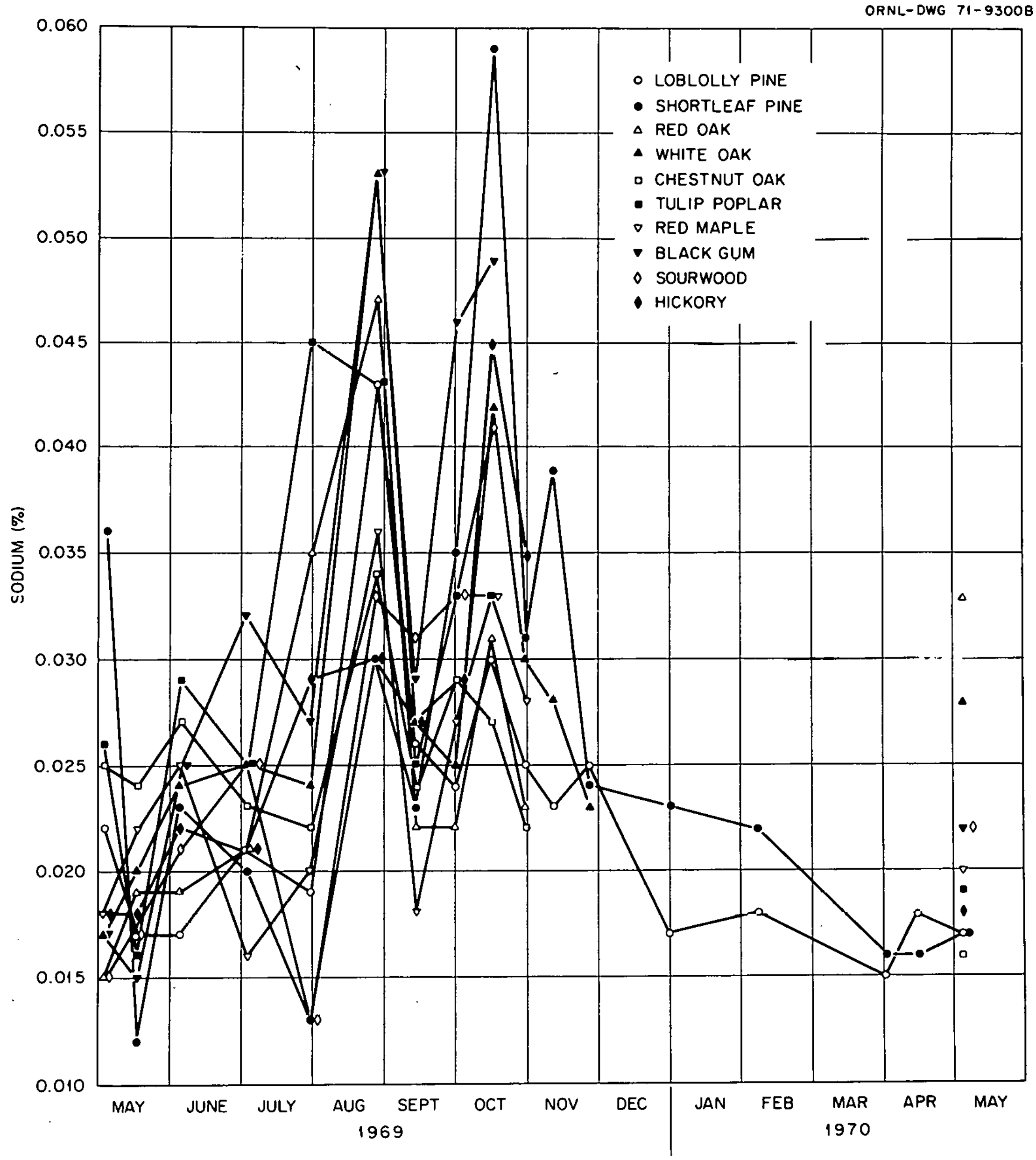


Figure 10. Seasonal patterns of sodium concentrations (% dry weight) in leaves of major tree species on Walker Branch Watershed.

higher than the range in this study. The sodium concentration in most species had two peaks, one in August and one in October. Sodium concentrations did not differ among coniferous and deciduous species.

The sodium content in leaves of the deciduous species increased, although erratically, until the sixth (August 26) collection when a decrease occurred (Figure 11). There was another peak just prior to abscission. Leaves of red oak, chestnut oak, white oak, tulip poplar, hickory, and black gum in the last collection (October 29) decreased in sodium content while leaves of sourwood and red maple increased slightly. The conifer leaves contained a rather constant amount of sodium at all collection, with loblolly pine leaves varying more than the shortleaf pine leaves.

<u>Potassium</u>. Potassium concentrations in foliage (Figure 12) were more variable than concentrations of other elements studied except sodium. Potassium concentrations in leaves of deciduous species decreased initially. Hickory and tulip poplar leaves were exceptions in that concentrations rose and then declined sharply after the second (May 16) collection. Potassium concentrations in tulip poplar, red oak, chestnut oak, and red maple leaves decreased until abscission. Concentrations fluctuated somewhat in white oak, hickory, and black gum and values of the first collection were higher than the last. After an initial decline of potassium concentration in sourwood foliage there was an increase up to the time of abscission. Mitchell (1936) found various deciduous leaf potassium concentrations to vary among species: 0.56 to 1.66%. Kornev (1959) reported concentrations to vary from 0.31 to 1.37%; concentrations in this study were 0.29 to 1.60% and agree with their results.

ORNL-DWG 73-2380

COLLECTION NO.	1	2	3	4	5	6	7	8	9	10
	MAY 2	MAY 16	JUNE 4	JULY 2	JULY 29	AUG 26	SEPT 13	SEPT 30	OCT 15	OCT 29
○ LOBLOLLY PINE	0.85	0.61	0.82	0.75	0.74	1.35	0.55	0.88	0.91	0.88
● SHORTLEAF PINE	0.47	0.20	0.33	0.36	0.14	0.39	0.23	0.37	0.56	0.35
△ RED OAK	1.31	2.06	2.66	2.94	5.38	7.19	2.88	3.66	5.47	3.63
▲ WHITE OAK	0.52	1.23	1.87	1.84	1.91	4.20	2.48	2.00	3.63	2.82
□ CHESTNUT OAK	1.40	2.54	3.38	2.92	2.94	4.70	4.02	3.91	3.90	3.10
■ TULIP POPLAR	1.47	1.47	3.06	2.53	5.14	4.92	2.70	3.30	2.82	
▽ RED MAPLE	0.51	0.98	1.26	0.79	1.03	1.81	1.15	1.40	1.70	
▼ BLACK GUM	0.33	0.60	1.47	1.82	1.41	2.82	1.52	2.51	1.65	
◊ SOURWOOD	0.10	0.35	1.06	1.20	0.71	1.48	1.38	1.15	1.50	
♦ HICKORY	0.54	0.77	1.36	1.24	1.84	1.89	1.58	1.85	2.96	1.55

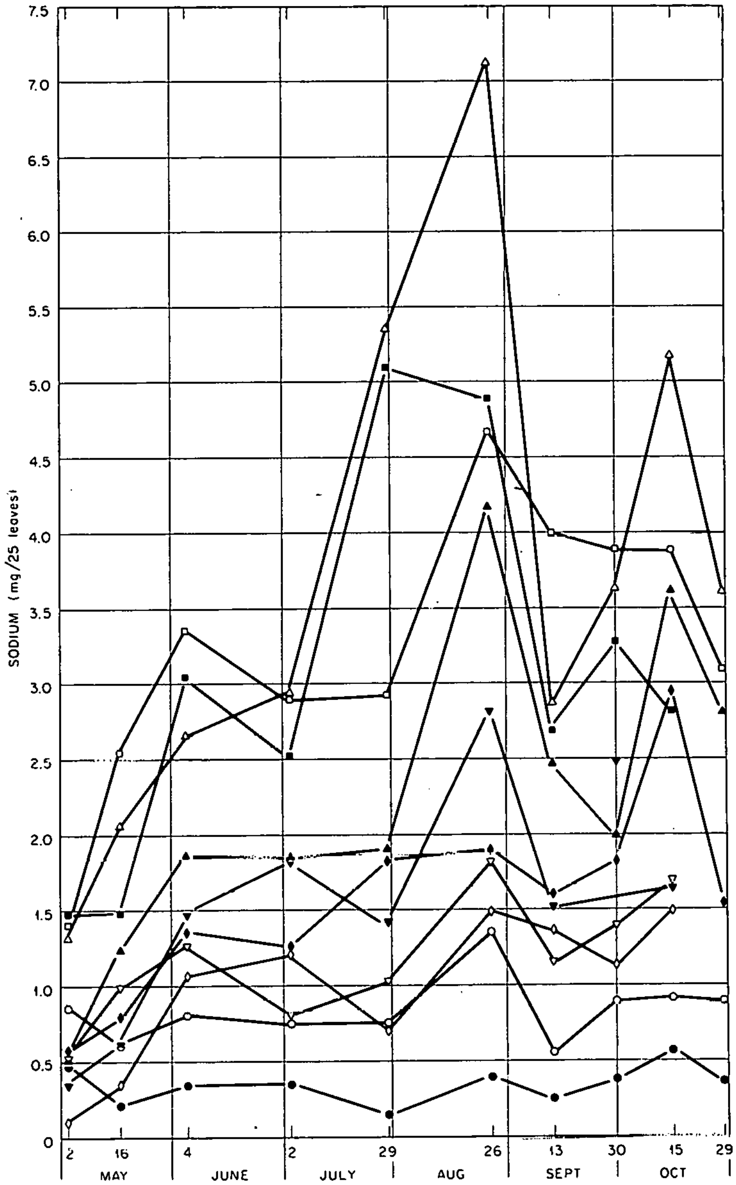


Figure 11. The amounts of sodium in leaves of major tree species on Walker Branch Watershed.

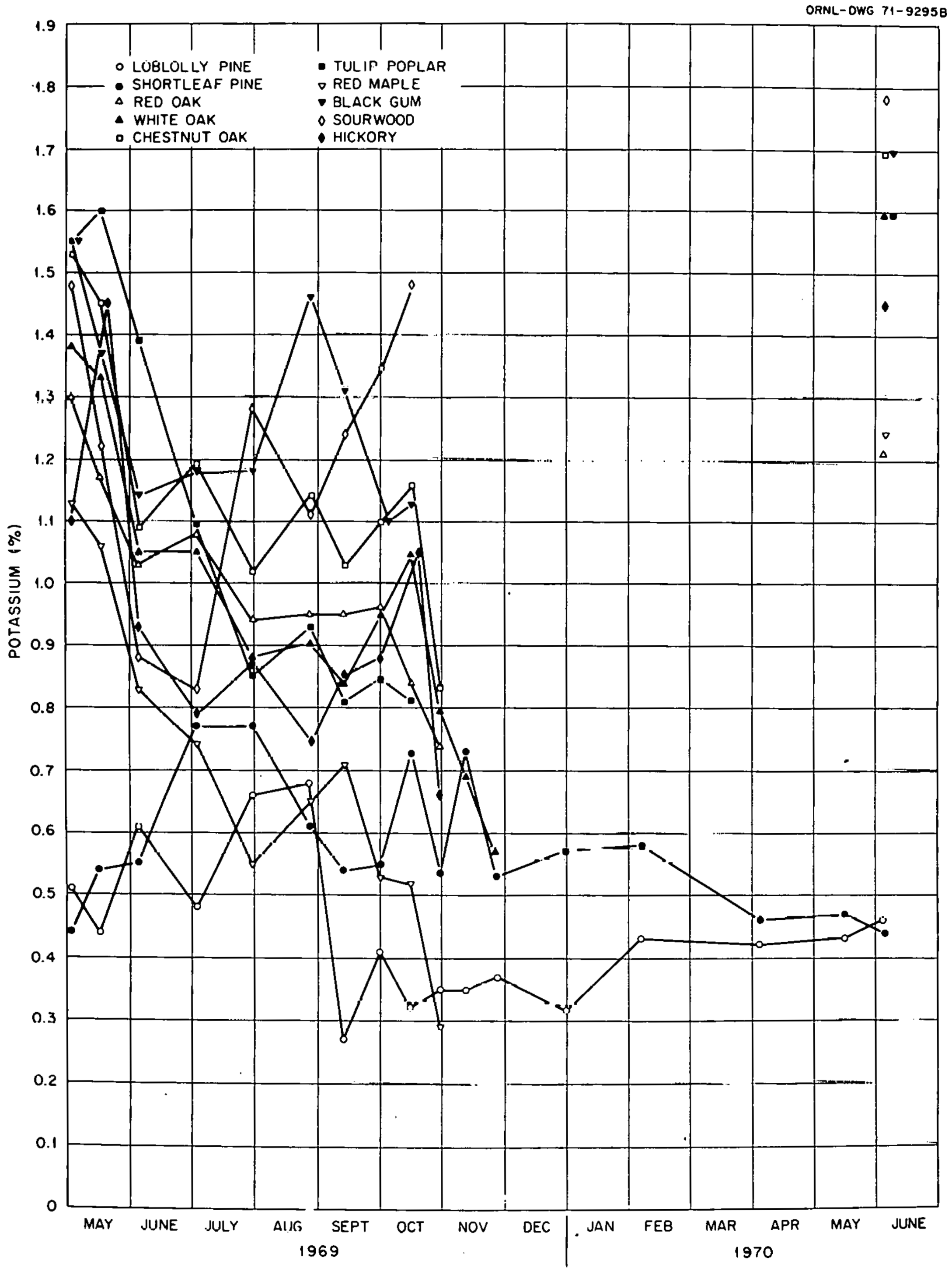


Figure 12. Seasonal patterns of potassium concentrations (% dry weight) in leaves of major tree species on Walker Branch Watershed.

Potassium concentrations in leaves of the two pine species remained constant throughout the year. Conifer foliage contained smaller concentrations than did the deciduous foliage.

Although the total potassium content in leaves varied among species, most followed the same general pattern (Figure 13):

1. There was a sharp increase in potassium content during spring (May 16 collection).
2. There was a leveling off in potassium content until early autumn (September 13 and September 30 collections).

The decrease in potassium content was due primarily to a decrease in percentage concentration and not due to the leaf weight loss before defoliation. Tulip poplar was the one species that differed from the other deciduous species in potassium content. After an initial increase in potassium content at the second (May 16) collection there was a constant decrease until leaf abscission.

Phosphorus. Like nitrogen, the concentrations of phosphorus (Figure 14) in deciduous leaves generally decreased with leaf development. The deciduous species showed early concentration differences, but those differences diminished as the season progressed. Phosphorus concentrations in conifer foliage were lower than those in the deciduous foliage early in the season but as the season advanced the conifer foliage had phosphorus concentrations nearly equal to the concentrations of the deciduous foliage. Guha and Mitchell (1965) reported that phosphorus concentrations decreased from 0.54% in spring to 0.12% in fall in sycamore (*Platanus occidentalis* L.) to range from 0.37% in spring to 0.08% in fall. for the ten species studied on Walker Branch Watershed the highest concentration

ORNL-DWG 72-1199

COLLECTION NO.	1	2	3	4	5	6	7	8	9	10
	MAY 2	MAY 16	JUNE 4	JULY 2	JULY 29	AUG 26	SEPT 13	SEPT 30	OCT 15	OCT 29
○ LOBLOLLY PINE	19.5	15.7	29.6	17.0	24.9	21.5	7.9	14.9	9.7	12.4
● SHORTLEAF PINE	5.7	9.1	7.8	14.1	8.4	8.0	5.4	5.8	6.9	5.9
△ RED OAK	11.3	12.8	14.1	15.5	14.5	14.7	12.3	16.4	14.7	11.8
▲ WHITE OAK	43.2	81.3	75.8	76.2	69.7	71.3	76.2	75.9	91.2	74.3
□ CHESTNUT OAK	85.5	156.0	136.0	148.0	140.0	157.0	171.0	150.0	168.0	119.0
■ TULIP POPLAR	89.3	148.0	146.0	112.0	97.2	106.0	86.2	83.7	70.1	
▽ RED MAPLE	32.1	48.2	42.4	37.0	28.9	32.7	44.6	28.0	26.6	7.2
▼ BLACK GUM	29.9	53.6	68.1	66.4	61.8	78.3	67.7	60.6	38.1	
◊ SOURWOOD	9.7	28.3	44.1	39.8	60.5	50.3	55.5	47.0	54.5	
♦ HICKORY	33.6	62.4	56.8	47.3	56.0	47.9	50.6	55.6	68.4	29.5

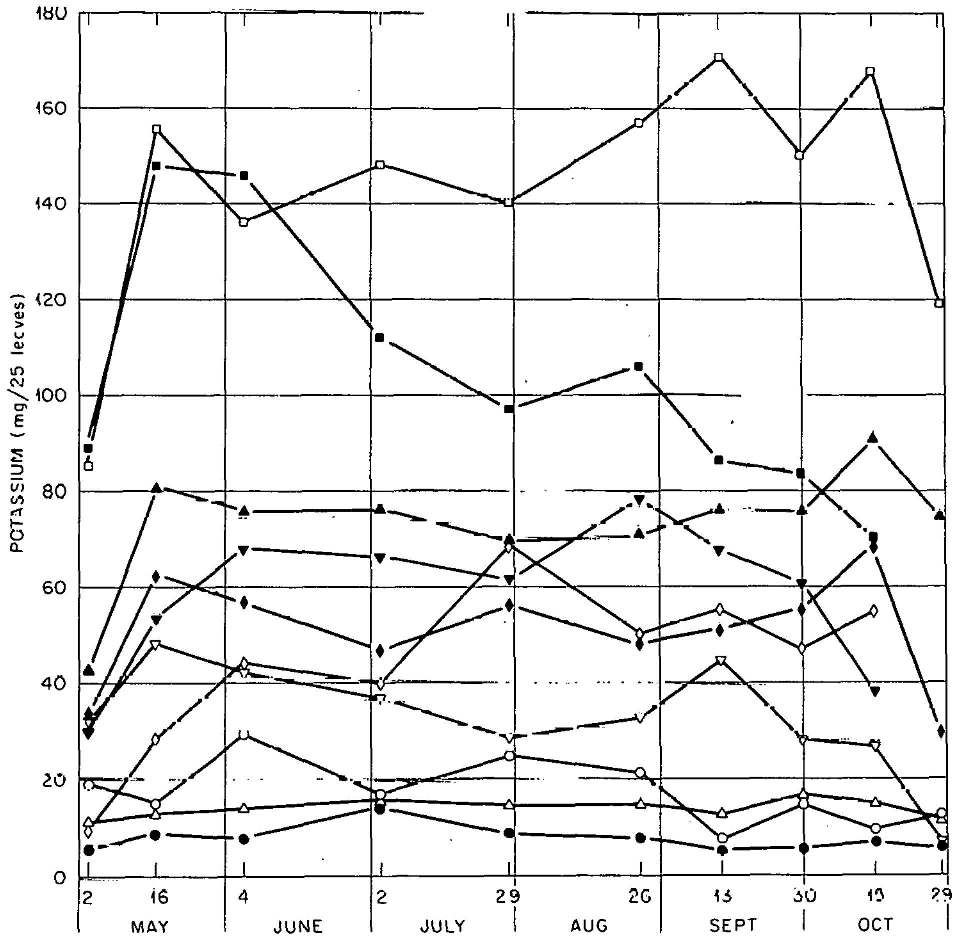


Figure 13. The amounts of potassium in leaves of major tree species on Walker Branch Watershed.

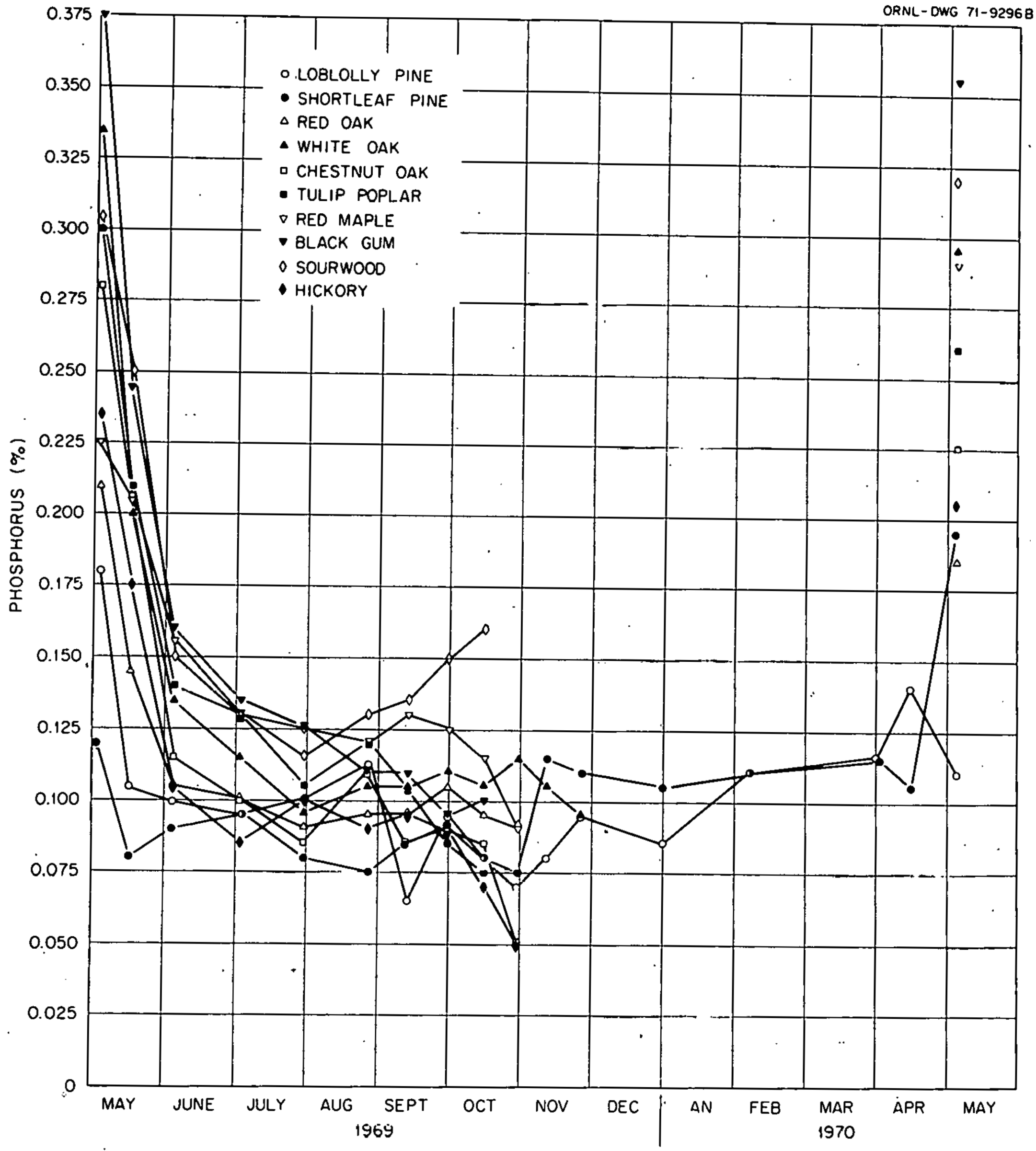


Figure 14. Seasonal patterns of phosphorus concentrations (% dry weight) in leaves of major tree species on Walker Branch Watershed.

was 0.37% in spring and ranged to the lowest concentration of 0.05% in fall before abscission.

The phosphorus content in foliage is illustrated in Figure 15. Leaves of all deciduous species except white oak contained more phosphorus during spring than during fall. Most deciduous species (red oak being the exception) increased in phosphorus content during spring (May 16 or June 4 collection) and then decreased until abscission.

Seasonal Variation in Litterfall Mass

Total litterfall. Total litterfall dry weight ranged from 443 to 492 g/m^2 among the four forest types on Walker Branch Watershed (Figure 16). Pine stands produced the most litterfall followed in decreasing amounts by oak-hickory, pine-oak-hickory, and mesophytic hardwood stands but differences between forest types were not significant. These values are similar to the values reported for deciduous forest stands in South Carolina (455-630 g/m^2) by Metz (1952) but less than litterfall in tropical forests (900-1200 g/m^2) and more than values for Sierra stands (90-336 g/m^2) (Jenney, Gessel, and Bingham 1949).

Of the total litterfall, 77 to 82% occurred as leaf fall while the remainder was branches (8 to 11%) and reproductive parts (8 to 14%). Bray and Gorham (1964) found an average of 27 to 31% of the total litterfall fell as non-leaf litter when they summarized data from various forests throughout the world.

Leaf fall. Leaf fall ranged from 342 g/m^2 in the mesophytic hardwood, 377 g/m^2 in the pine-oak-hickory, 389 g/m^2 in the pine, and 398 g/m^2 in the oak-hickory forest. Differences in annual leaf fall totals between forest types were not significant. Rodin and Bazilevich (1967) reported

ORNL-DWG 72-1197

COLLECTION NO.	1	2	3	4	5	6	7	8	9	10
	MAY 2	MAY 16	JUNE 4	JULY 2	JULY 29	AUG 26	SEPT 13	SEPT 30	OCT 15	OCT 29
○ LOBLOLLY PINE	6.8	3.7	4.7	3.3	3.7	3.5	1.9	3.5	2.4	2.4
● SHORTLEAF PINE	1.6	1.4	1.3	1.7	0.9	1.0	0.9	0.9	0.7	0.8
△ RED OAK	18.4	16.1	14.6	13.9	14.2	14.8	12.3	17.6	16.8	14.2
▲ WHITE OAK	10.4	12.2	10.3	8.3	7.7	8.1	9.4	8.9	9.2	10.8
□ CHESTNUT OAK	15.5	22.1	14.2	12.6	11.4	14.8	14.2	12.3	12.5	7.0
■ TULIP POPLAR	17.2	19.4	14.9	13.3	12.1	13.5	11.4	8.6	6.3	
▽ RED MAPLE	6.3	9.3	8.0	6.6	6.6	5.9	8.2	6.5	5.8	2.3
▼ BLACK GUM	7.3	9.6	9.6	7.4	6.5	5.8	5.6	5.3	3.3	
◊ SOURWOOD	2.0	5.8	7.5	6.3	6.3	6.0	6.0	5.2	5.9	
♦ HICKORY	7.2	7.6	6.4	5.2	6.6	5.6	5.5	5.7	4.7	2.2

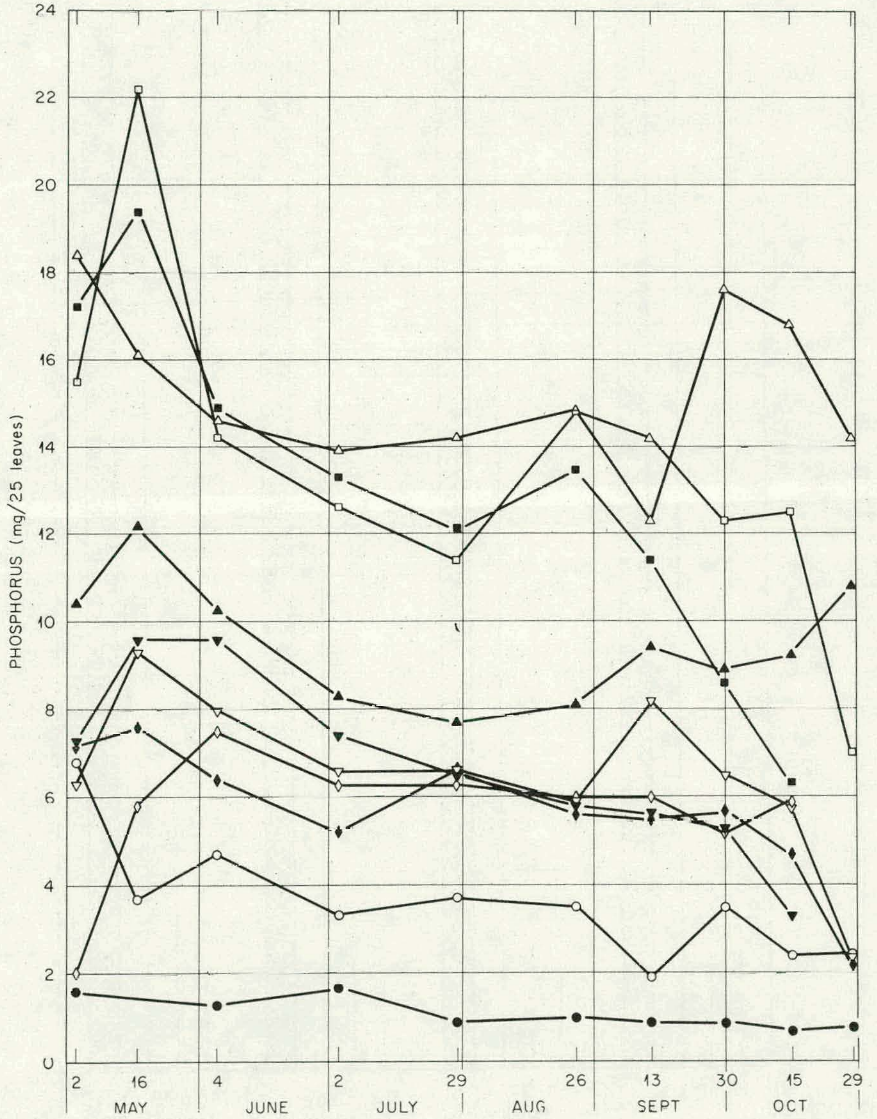


Figure 15. The amounts of phosphorus in leaves of major tree species on Walker Branch Watershed.

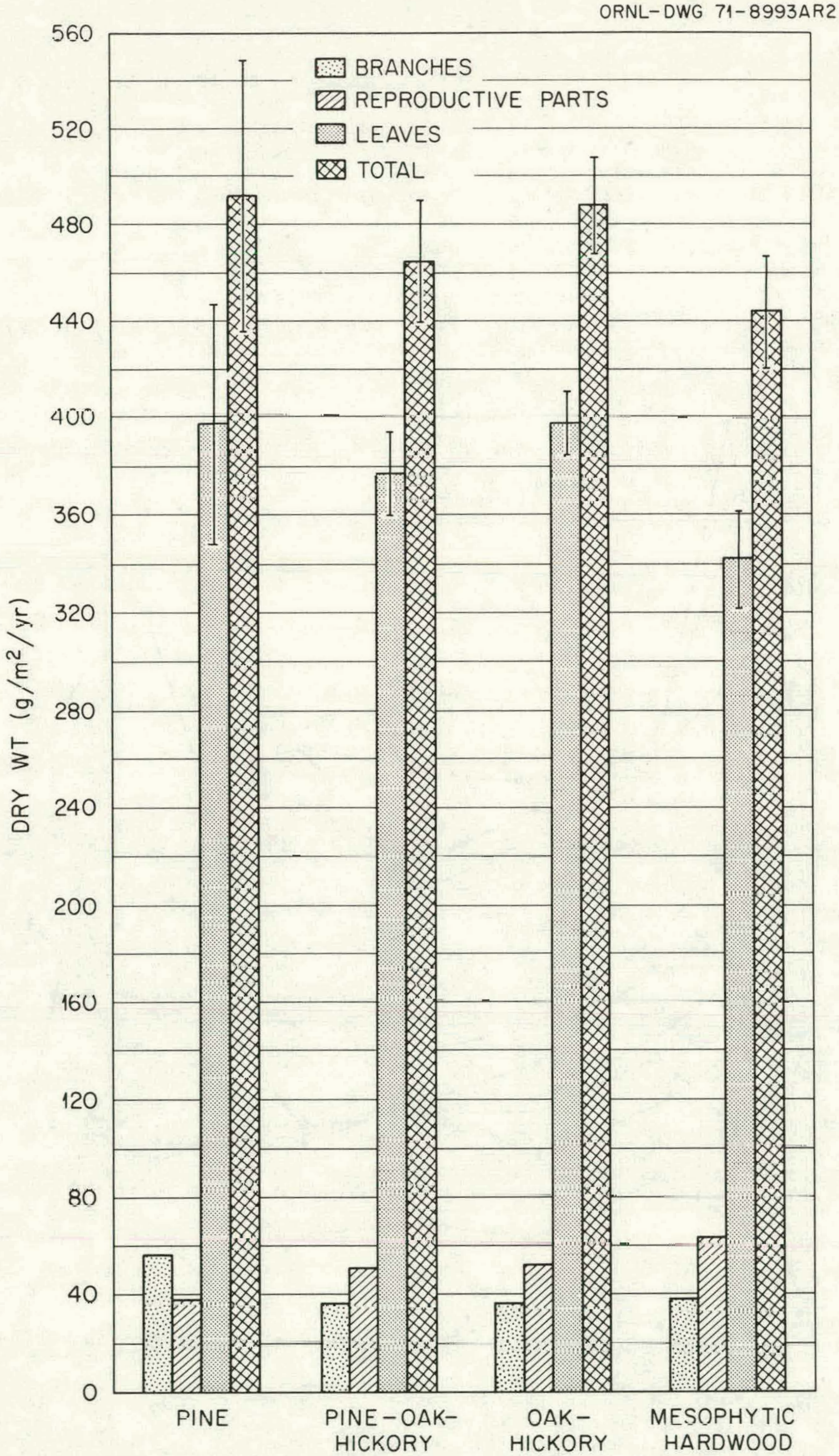


Figure 16. Annual total litterfall summarized by components for the four forest types on Walker Branch Watershed with standard errors for the leaf component and for total litterfall for each forest type indicated.

annual leaf fall in deciduous forests to be fairly constant in different regions, amounting to 300-400 g/m^2.

The leaf component of oak-hickory forests contributed 82% of total litterfall. Leaves of the pine and pine-oak-hickory forests accounted for 81% and mesophytic hardwood leaves accounted to 77% of total litterfall. Rates of leaf fall were greatest during autumn in all forest types (Figure 17). Peak leaf fall in pine stands extended over a four week period, whereas, leaf fall in the other forest types occurred over a shorter interval.

Branch fall. Branch fall was greatest in the pine forest (56 g/m^2), followed in decreasing order by mesophytic hardwood (38 g/m^2), pine-oak-hickory (37 g/m^2), and oak-hickory (37 g/m^2). Differences, however, were not significant (Figure 16). Branch fall accounted for from 8 to 11% of the total litterfall. The rate of fall of branches and bark in the litter traps (Figure 18) was much more variable than the rate of fall of leaves. Seasonal patterns were evident. Nye (1961) found branch fall over a small area to be very erratic and difficult to measure, since it could be influenced greatly by the fall of even a single large branch or tree. Such factors as wind and age of stand affect the time as well as the amount of fall.

Reproductive parts fall. Input of reproductive parts on an annual basis (Figure 16) was greatest in the mesophytic hardwood forest (63 g/m^2) and least in the pine forest (38 g/m^2). Reproductive parts input in the oak-hickory and pine-oak-hickory forests had intermediate amounts (52 g/m^2 and 51 g/m^2, respectively). Differences in annual reproductive parts fall between the forests were not significant. The rate of fall of reproductive parts (Figure 19) was similar for all forest types,

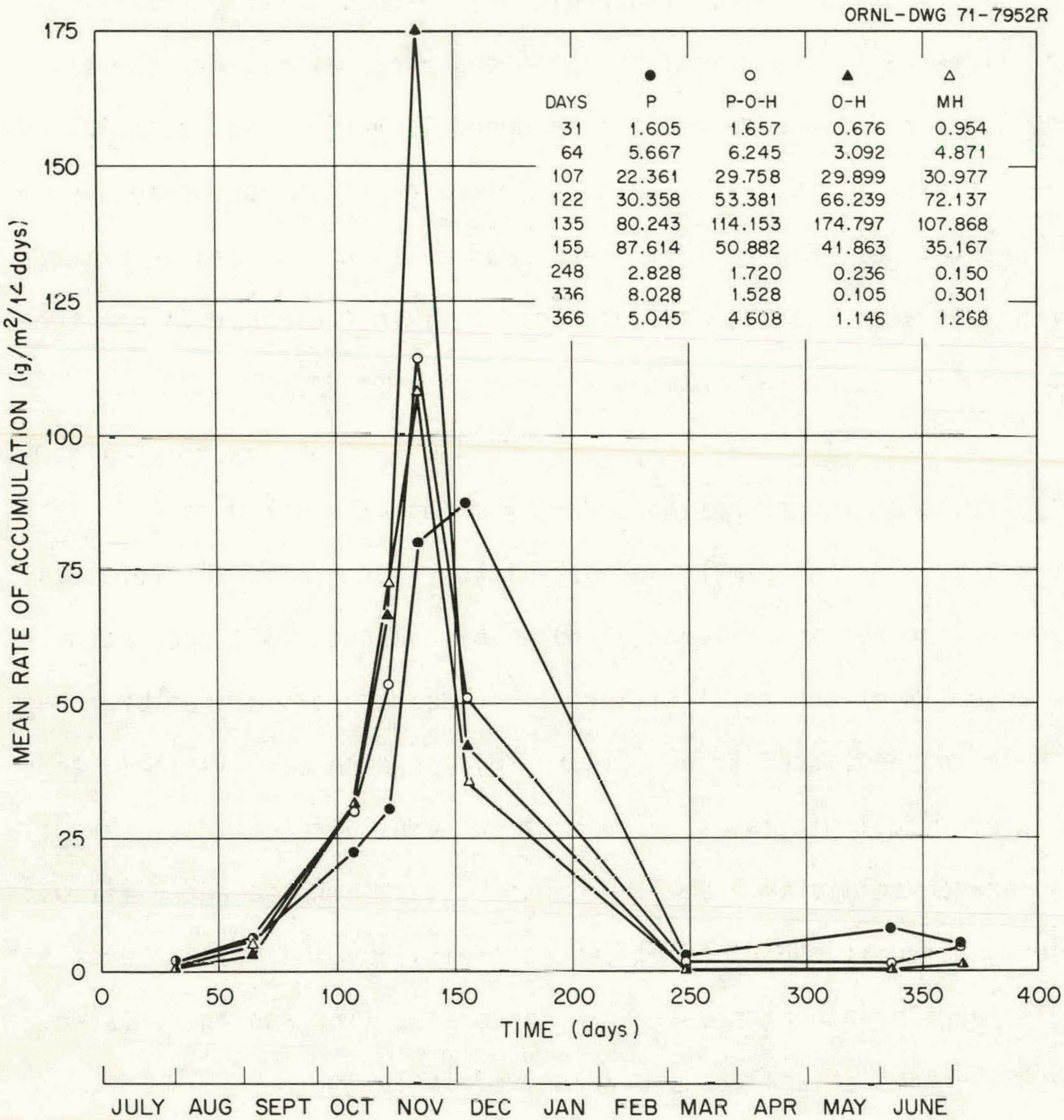


Figure 17. Seasonal patterns of dry weight in leaf litterfall in four forest types on Walker Branch Watershed.

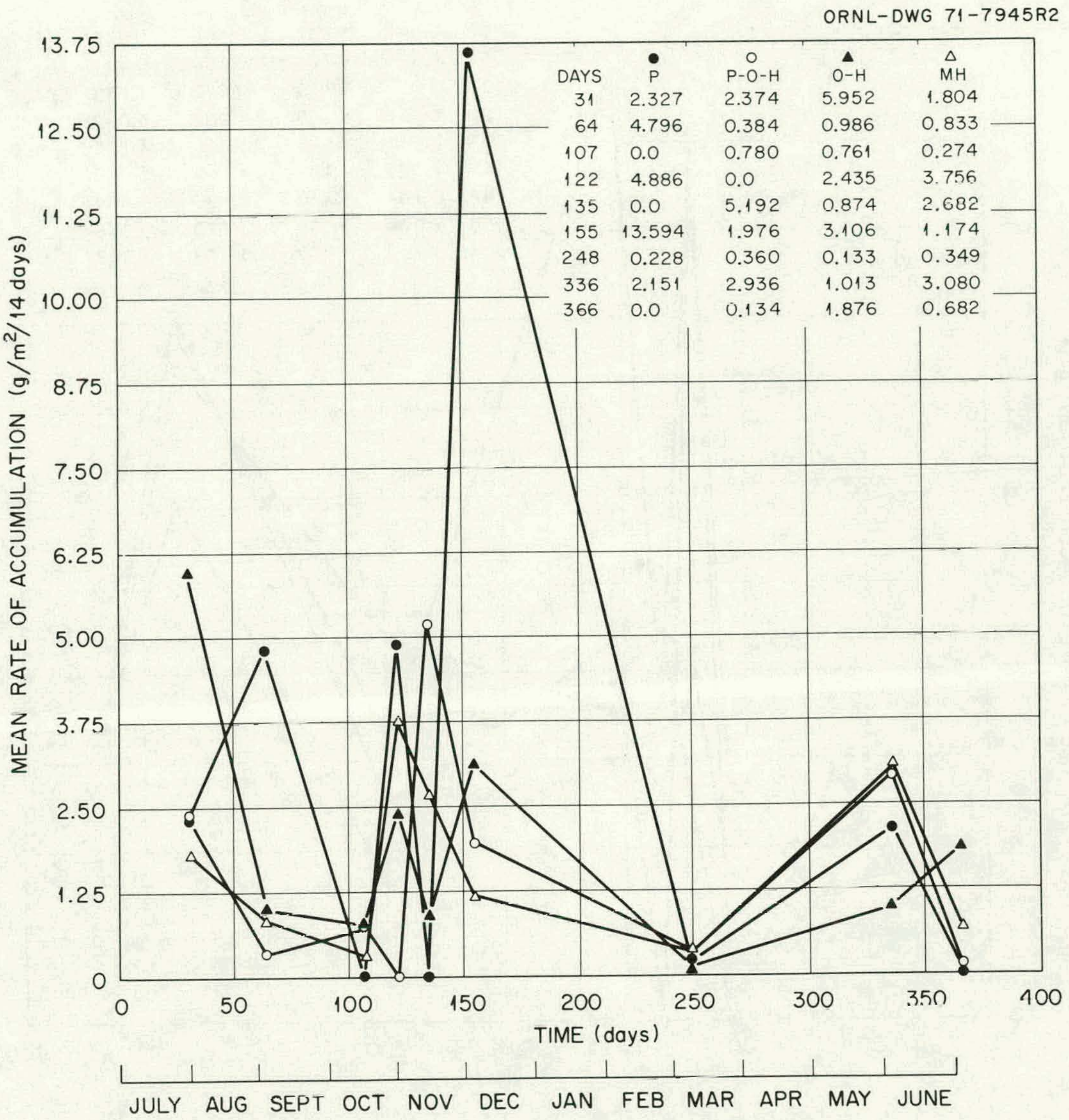
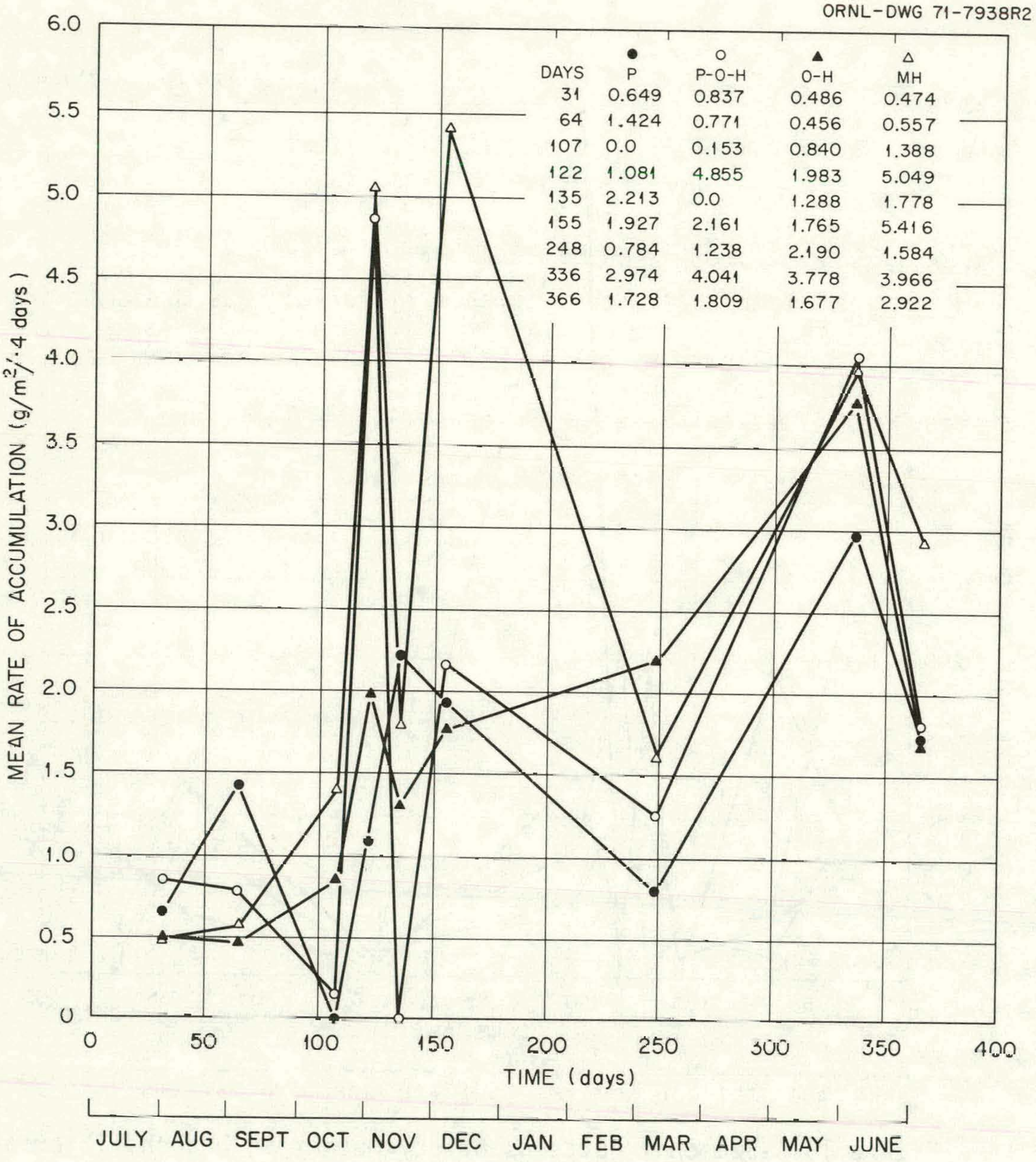


Figure 18. Seasonal patterns of dry weight in branch litterfall in four forest types on Walker Branch Watershed.



DAYS	● P	○ P-O-H	▲ O-H	△ MH
31	0.649	0.837	0.486	0.474
64	1.424	0.771	0.456	0.557
107	0.0	0.153	0.840	1.388
122	1.081	4.855	1.983	5.049
135	2.213	0.0	1.288	1.778
155	1.927	2.161	1.765	5.416
248	0.784	1.238	2.190	1.584
336	2.974	4.041	3.778	3.966
366	1.728	1.809	1.677	2.922

Figure 19. Seasonal patterns of dry weight in reproductive parts litterfall in four forest types on Walker Branch Watershed.

especially in late spring when reproductive parts play important roles in litterfall. The importance of reproductive parts to litterfall during the spring can be seen more fully when the absolute amount (wt./day x number of days) is considered rather than the relative rates expressed as g/14 days collection period.

Seasonal Variation of Nutrients in Litterfall

Nitrogen. Total nitrogen return in litterfall was greatest in pine (3.75 g/m^2), followed by oak-hickory, mesophytic hardwood, and pine-oak-hickory forests (3.65, 3.62, and 3.41 g/m^2) (Figure 20). However, forest type differences were not statistically significant. Carlisle et al. (1966) found a similar annual nitrogen return (4.11 g/m^2) in a Quercus petraea forest. Of the total nitrogen return in this study, leaf fall accounted for 75 to 81% of total litterfall input.

Nitrogen concentrations in leaf fall of all four forest types generally decreased as the season progressed from spring through fall and winter (Figure 21). There was then an increase in May of the following year. The nitrogen concentrations in leaf fall from pine stands on Walker Branch Watershed ranged from 0.56 to 1.09%. Lutz and Chandler (1946) also studied conifer and deciduous leaf litter and found the nitrogen concentrations to range from 0.58 to 1.25% and 0.51 to 1.01%, respectively. Deciduous stands in this study had nitrogen concentrations ranging from 0.59 to 1.52%. Annual nitrogen return in leaf fall was similar in all forest types, and differences ranging from 2.70 g/m^2 in mesophytic hardwood to 3.04 g/m^2 in pine (Figure 20) were not significant. Even though the concentration of nitrogen decreased with the approach of autumn the greatest amount of nitrogen in leaf fall was transferred to the

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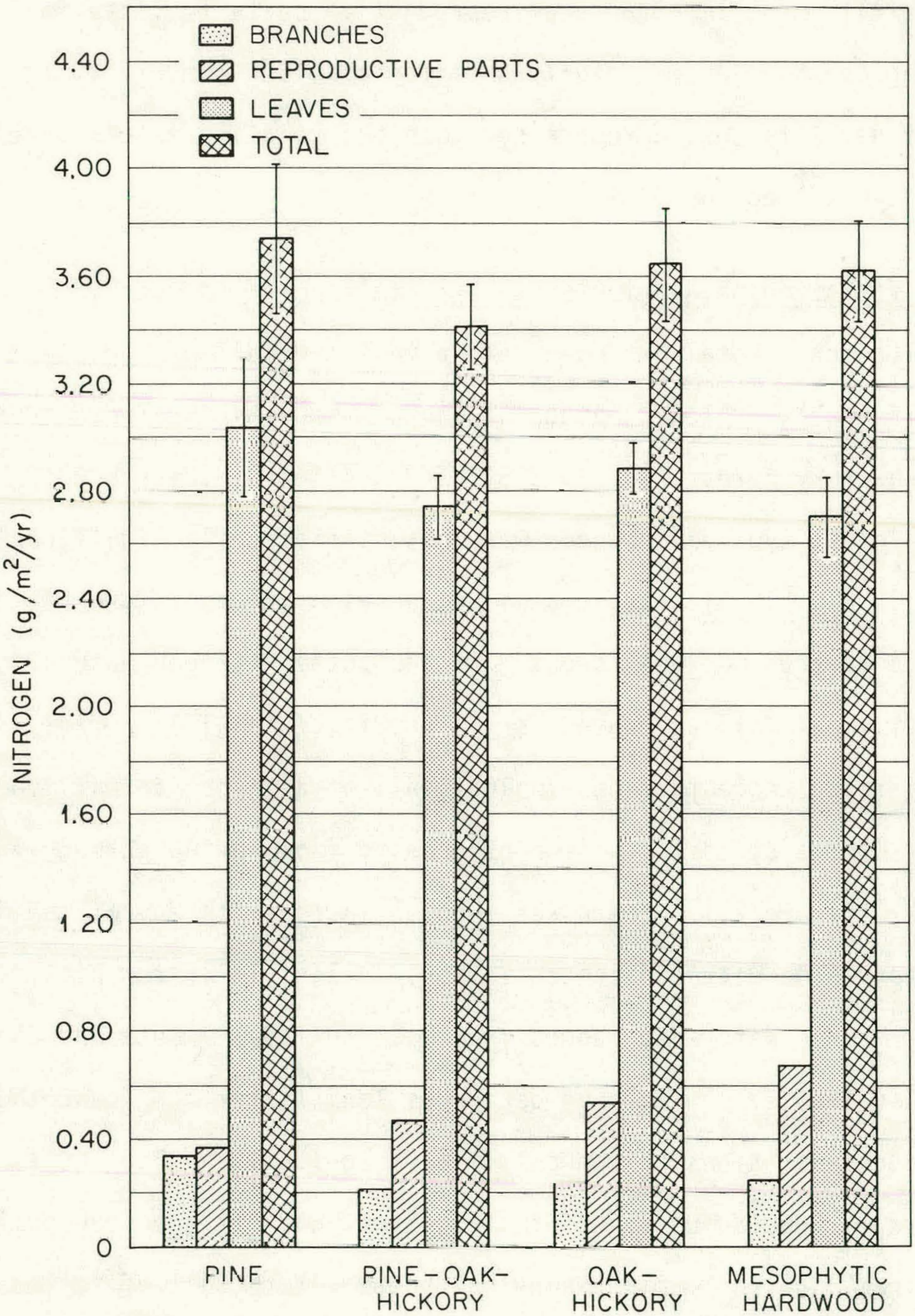


Figure 20. Annual return of nitrogen in litterfall components in four forest types on Walker Branch Watershed with standard errors for the leaf component and for total litterfall for each forest type indicated.

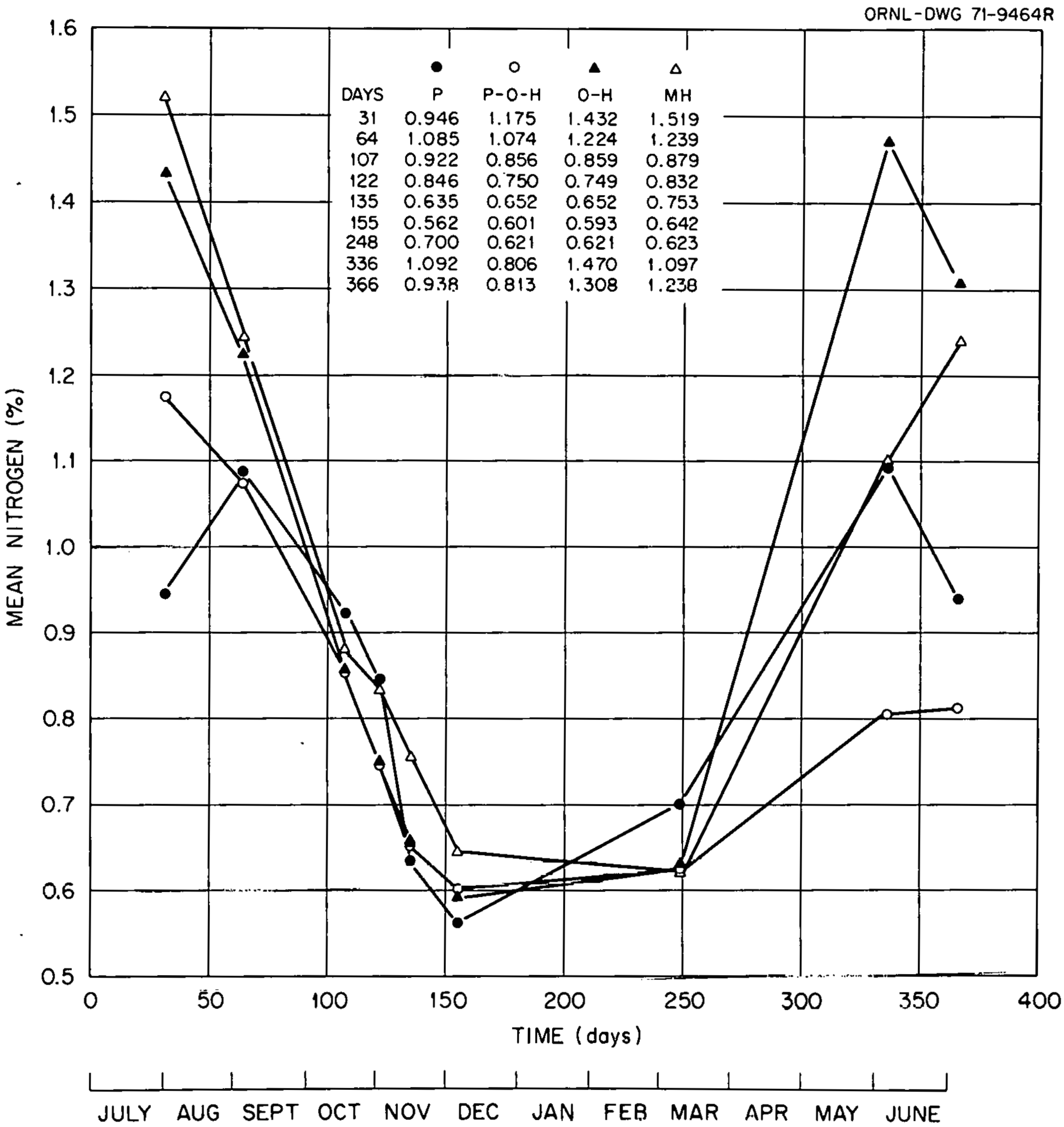


Figure 21. Seasonal patterns of nitrogen concentrations (% dry weight) in leaf litterfall in four forest types on Walker Branch Watershed.

forest floor during autumn due to the greater weight of leaves that fell during that period (Figure 22). The transfer rate of each nutrient is dependent upon the weight of each component of litterfall as well as the concentration of the nutrient. Therefore, the rate may follow the dry weight pattern of litterfall, especially if nutrient concentrations are low. Differences in the seasonal rate of transfer of nitrogen in the leaf fall between forest types were primarily due to weight differences in litterfall.

Nitrogen concentrations in branches remained relatively constant throughout the season (Figure 23). No apparent differences existed between forest types and concentrations were generally measured in a relatively narrow range from 0.50 to 0.75%. The annual nitrogen input to the forest floor as branch fall did not differ significantly among forest types, and ranged from 0.21 g/m^2 in pine-oak-hickory to 0.34 g/m^2 in pine (Figure 20). The seasonal pattern of nitrogen returning to the forest floor in branches (Figure 24) followed weight patterns closely but no consistent pattern among the forest types was observed.

Nitrogen concentrations in reproductive parts generally followed the same pattern in all four forest types. Highest concentrations occurred in the spring and then decreased through fall and remained low in winter. The concentrations of nitrogen in the reproductive parts showed similar patterns and magnitudes as leaf fall (Figure 25).

The annual input of nitrogen to the forest floor in the reproductive parts (Figure 20) was greatest in the mesophytic hardwood forest (0.68 g/m^2), least in the pine forest (0.37 g/m^2), while pine-oak-hickory (0.46 g/m^2) and oak-hickory (0.53 g/m^2) forests had intermediate amounts. The seasonal pattern of nitrogen transfer via reproductive parts (Figure 26)

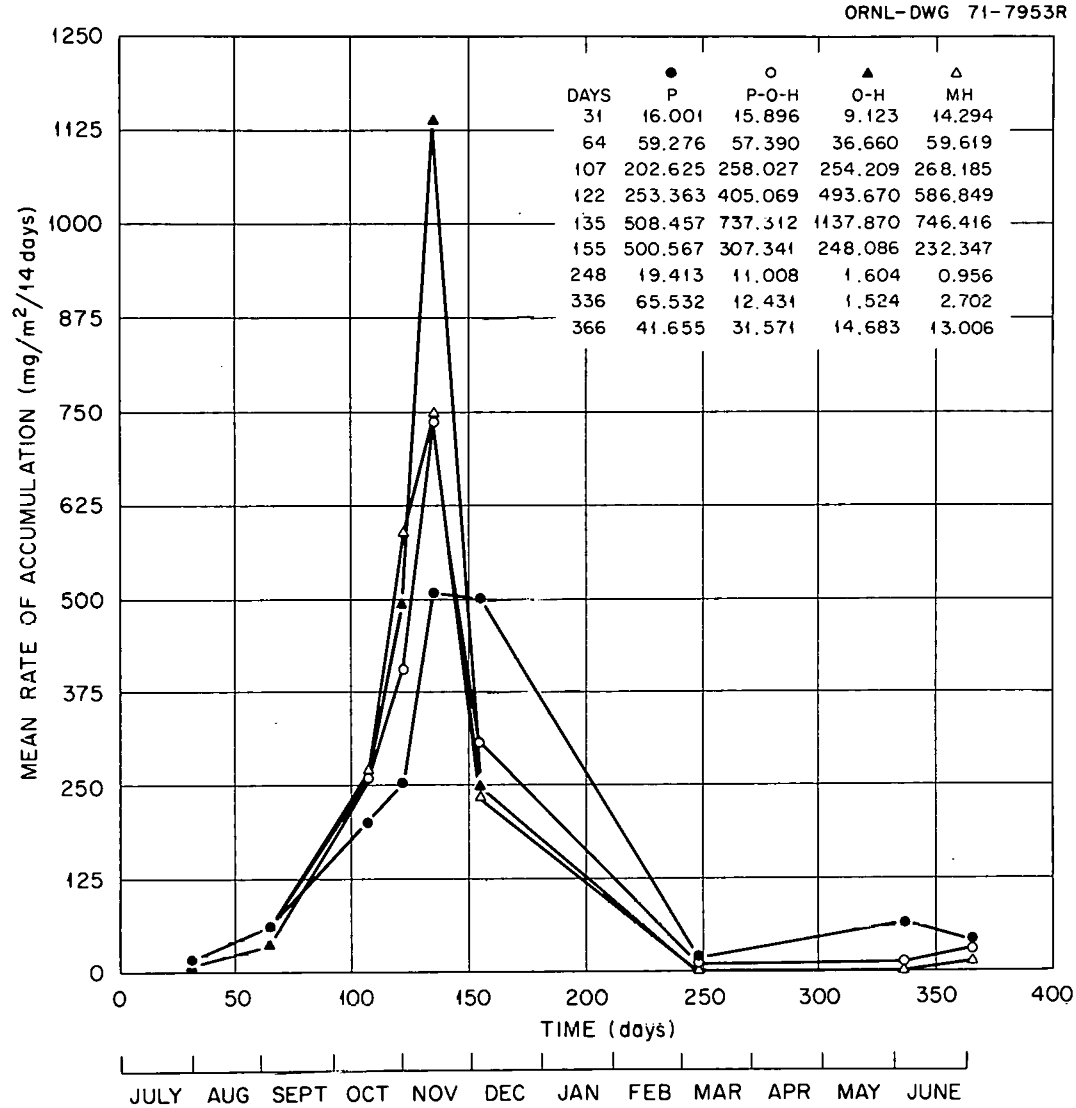
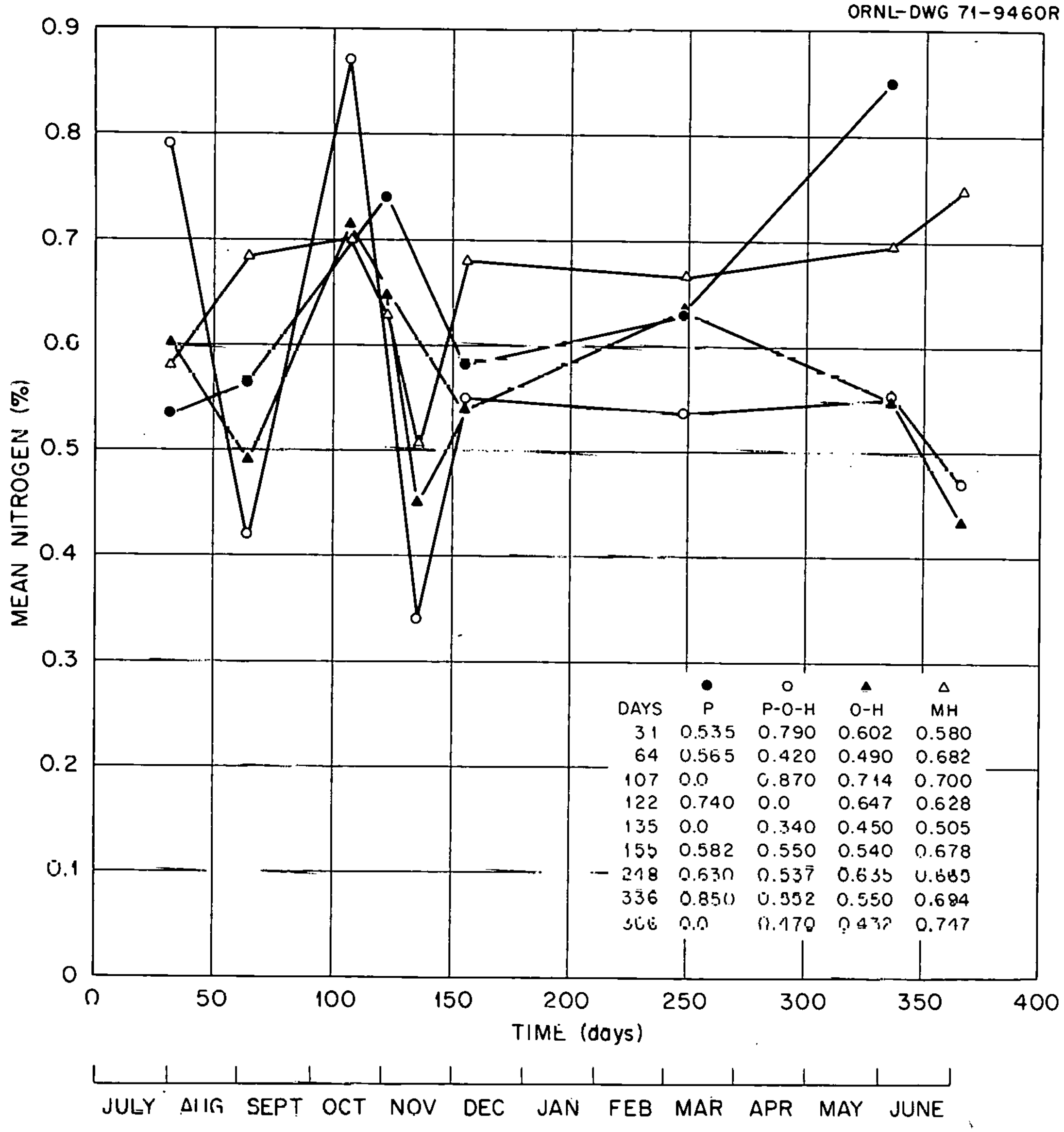


Figure 22. Seasonal rate of return of nitrogen to the forest floor in leaf litterfall in four forest types on Walker Branch Watershed.



DAYS	● P	○ P-O-H	▲ O-H	△ MH
31	0.535	0.790	0.602	0.580
64	0.565	0.420	0.490	0.682
107	0.0	0.870	0.714	0.700
122	0.740	0.0	0.647	0.628
135	0.0	0.340	0.450	0.505
155	0.582	0.550	0.540	0.678
248	0.630	0.537	0.635	0.685
336	0.850	0.552	0.550	0.694
366	0.0	0.470	0.432	0.747

Figure 23. Seasonal patterns of nitrogen concentrations (% dry weight) in branch litterfall in four forest types on Walker Branch Watershed.

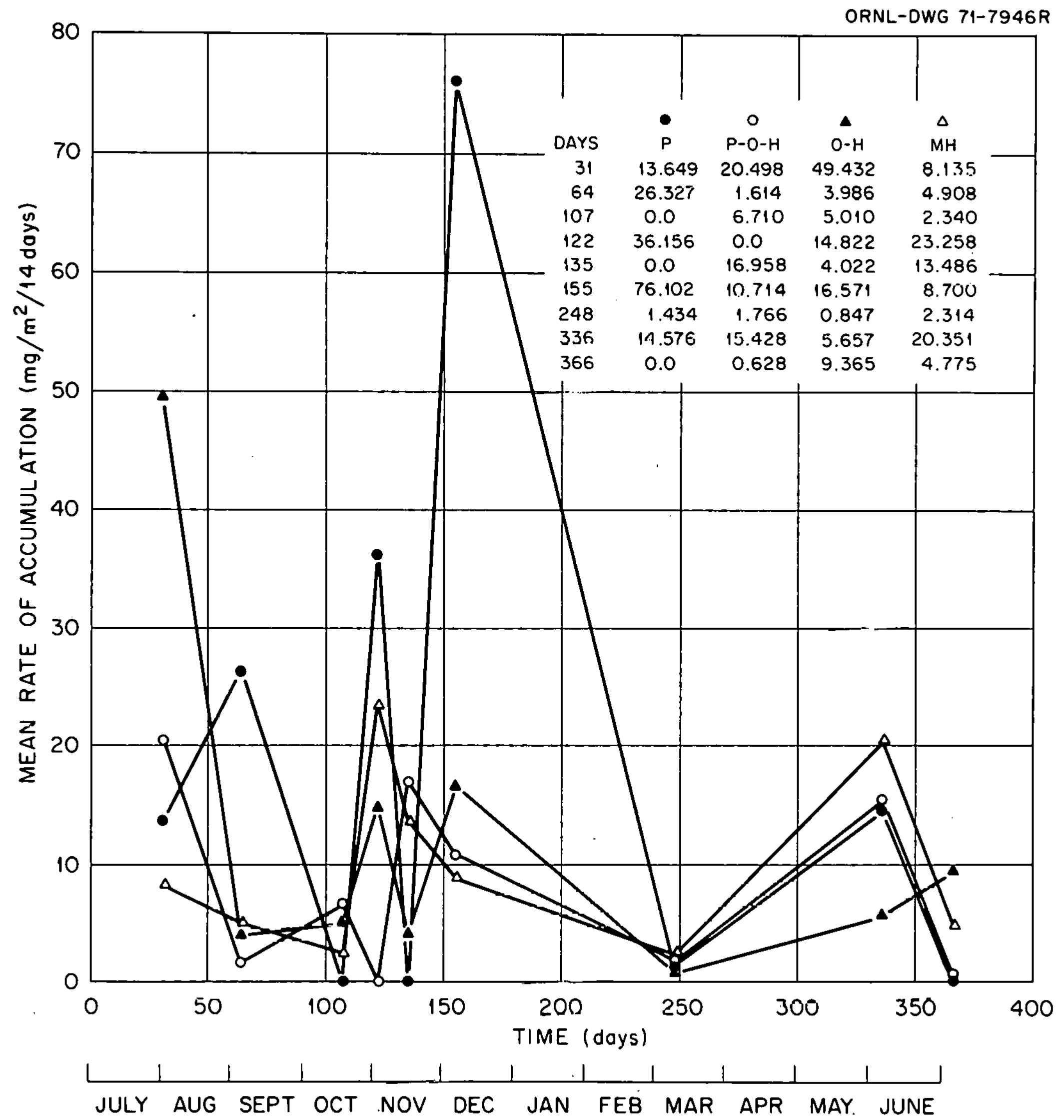
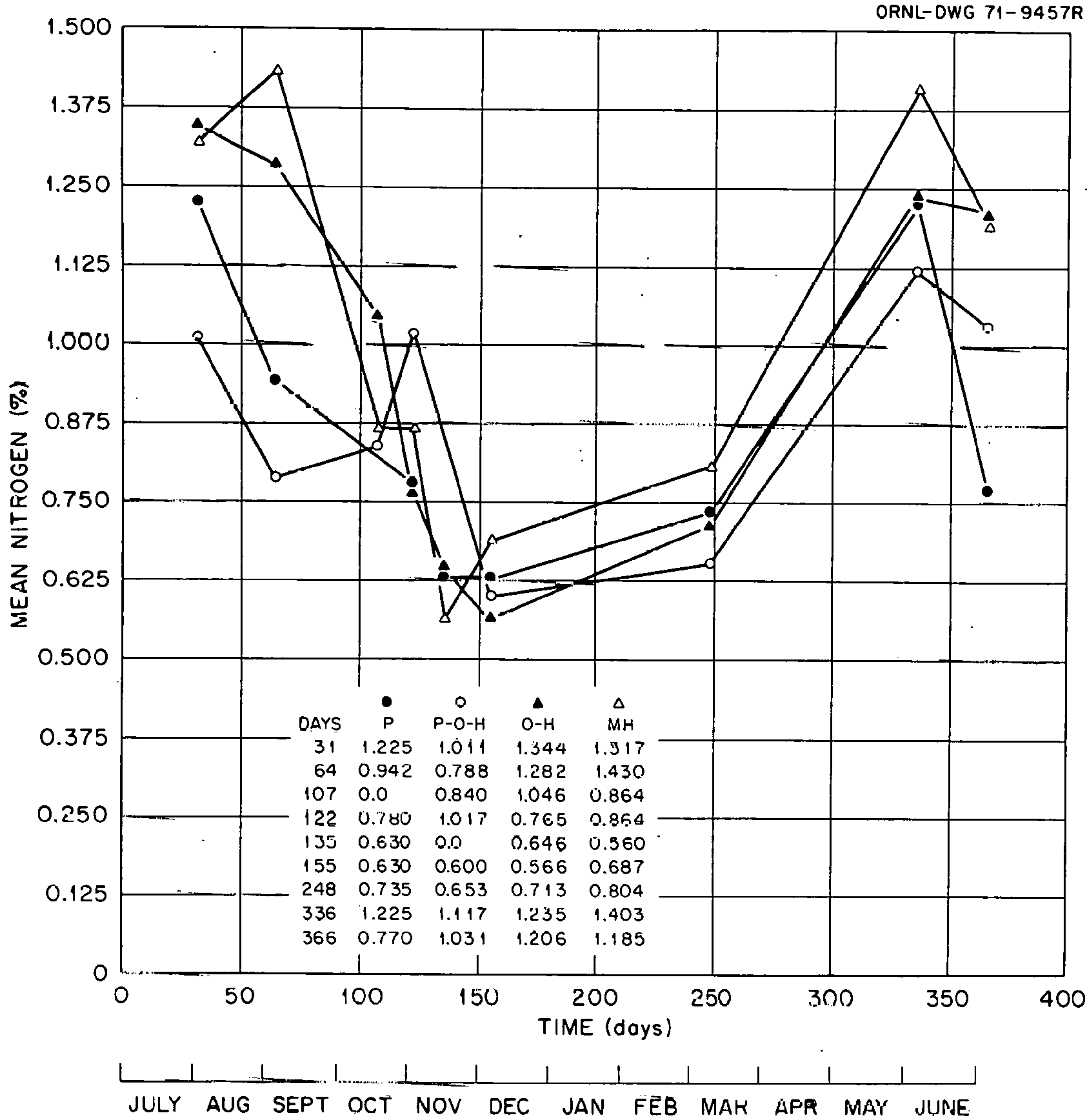


Figure 24. Seasonal rate of return of nitrogen to the forest floor in branch litterfall in four forest types on Walker Branch Watershed.



DAYS	● P	○ P-O-H	▲ O-H	△ MH
31	1.225	1.011	1.344	1.317
64	0.942	0.788	1.282	1.430
107	0.0	0.840	1.046	0.864
122	0.780	1.017	0.765	0.864
135	0.630	0.0	0.646	0.560
155	0.630	0.600	0.566	0.687
248	0.735	0.653	0.713	0.804
336	1.225	1.117	1.235	1.403
366	0.770	1.031	1.206	1.185

Figure 25. Seasonal patterns of nitrogen concentrations (% dry weight) in reproductive parts litterfall in four forest types on Walker Branch Watershed.

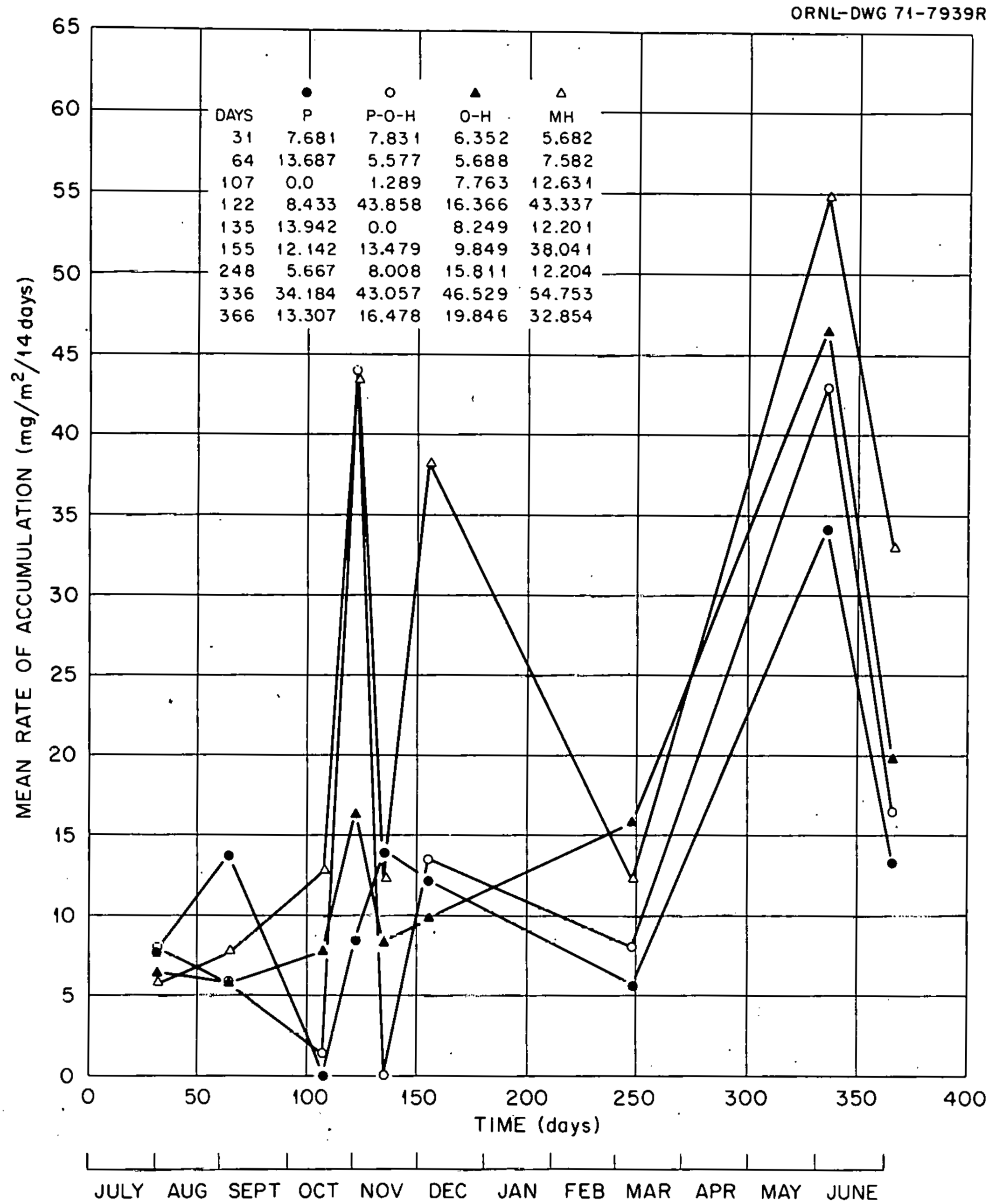


Figure 26. Seasonal rate of return of nitrogen to the forest floor in reproductive parts litterfall in four forest types on Walker Branch Watershed.

showed peaks in fall and late spring. The spring peak is especially important as it occurred over an 88 day period. Thus, most of the return of reproductive parts occurred during spring. With few exceptions, the pattern of rate of litterfall was the same in all forest types.

Calcium. The total amount of calcium that returned in all litter components was greatest in the mesophytic hardwood (5.83 g/m^2) forest, least in the pine-oak-hickory (4.50 g/m^2), and intermediate in the pine (5.10 g/m^2) and oak-hickory (4.91 g/m^2) forests (Figure 27). The total amount of calcium in the mesophytic hardwood forest varied significantly from the total amounts of calcium in the other forest types.

Calcium concentrations in leaf litterfall followed similar patterns in all forest types with time (Figure 28). The general trend was for calcium concentrations to generally increase through the growing season until autumnal leaf fall, after which concentrations decreased until the next growing season.

The greatest amount of calcium that returned annually in leaf fall was in the mesophytic hardwood (4.58 g/m^2) and least in the pine-oak-hickory (3.82 g/m^2) forest (Figure 27). The pine (4.11 g/m^2) and oak-hickory (3.86 g/m^2) forests had intermediate amounts. The leaf contribution did show statistical differences between the forest types. The mesophytic hardwood forest leaf calcium content varied significantly from the pine-oak-hickory and the oak-hickory forests but did not vary significantly from the oak-hickory hardwood forest.

The seasonal rate of transfer of calcium to the forest floor is shown in Figure 29. The oak-hickory forest transferred most calcium at peak leaf fall (November 12). Leaves of the pine-oak-hickory and

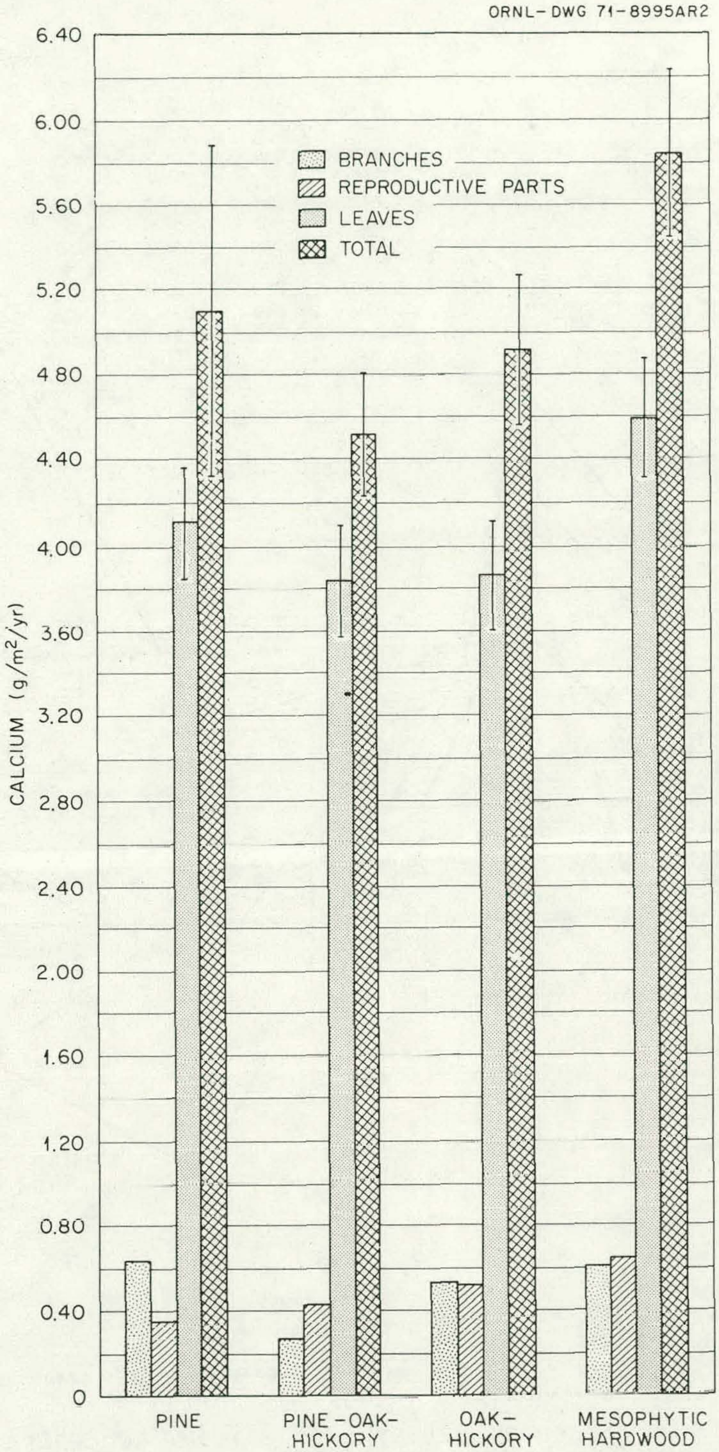


Figure 27. Annual return of calcium in litterfall components in four forest types on Walker Branch Watershed with standard errors for the leaf component and for total litterfall for each forest type indicated.

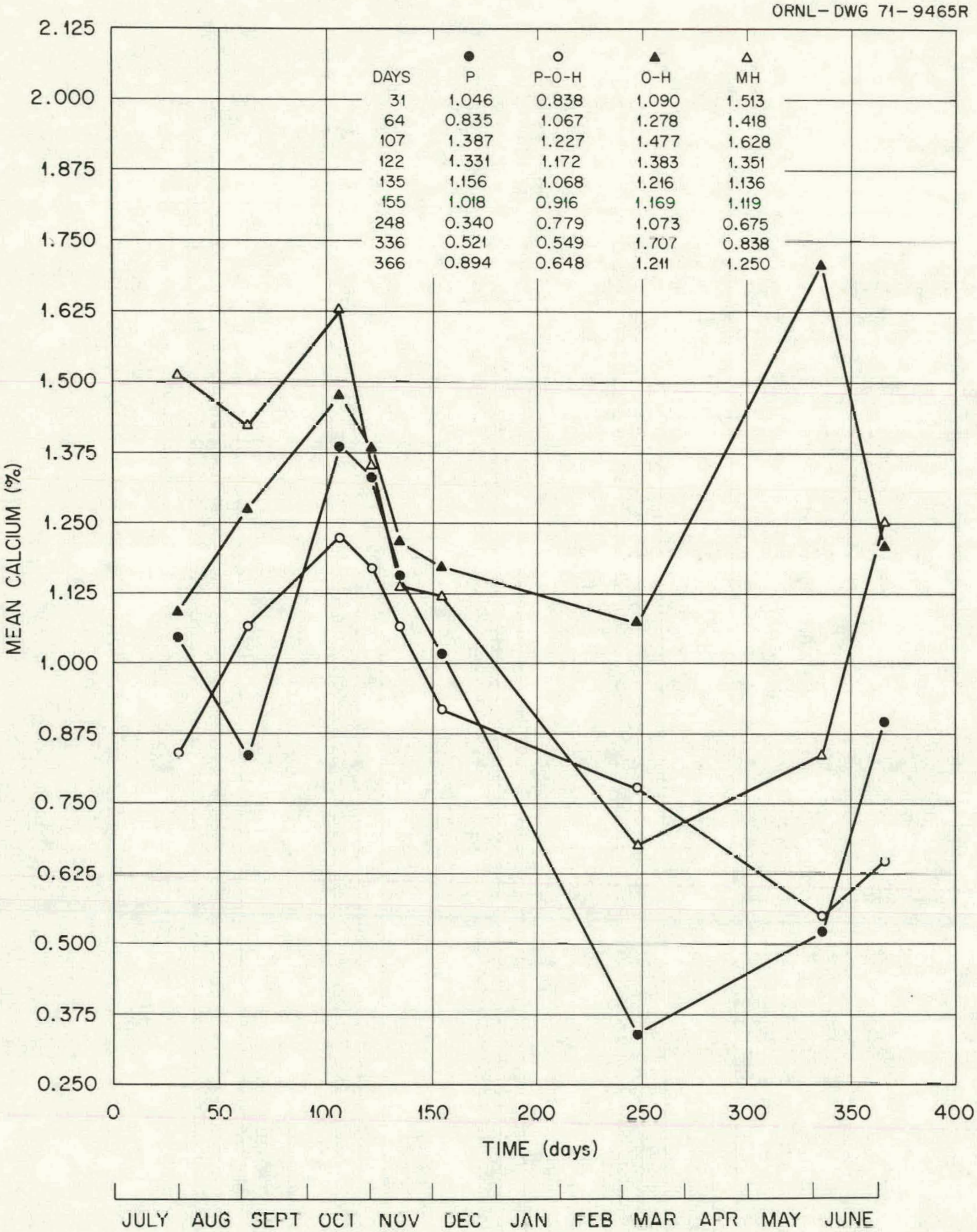


Figure 28. Seasonal patterns of calcium concentrations (% dry weight) in leaf litterfall in four forest types on Walker Branch Watershed.

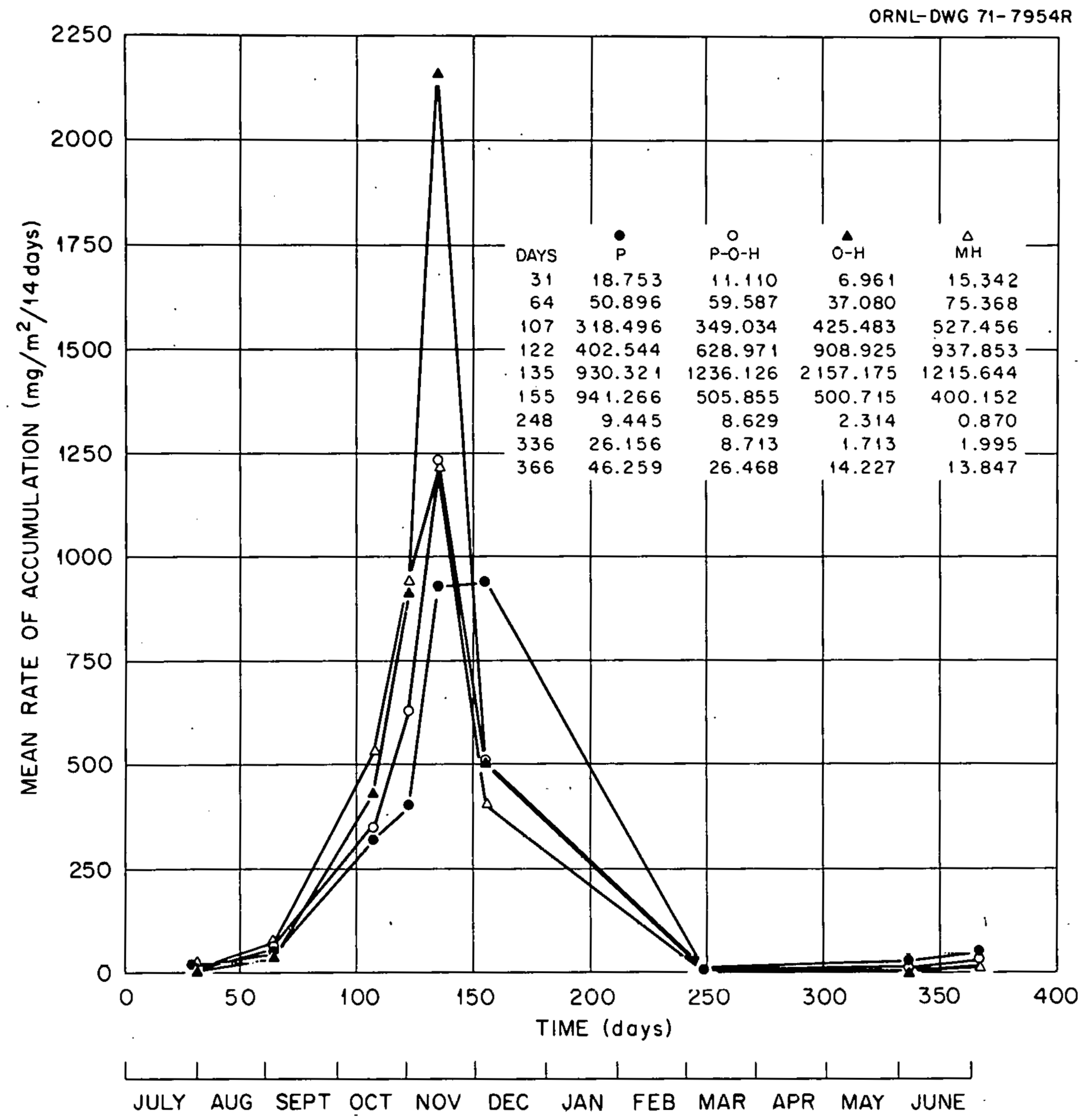


Figure 29. Seasonal rate of return of calcium to the forest floor in leaf litterfall in four forest types on Walker Branch Watershed.

mesophytic hardwood forests transferred nearly equal amounts of calcium, although those values were significantly lower than the oak-hickory value. There was a broader peak for leaf fall in the pine forest and its major transfer of calcium was, therefore, over an extended time period.

Branches of pine (0.64 g/m^2) and mesophytic hardwood (0.61 g/m^2) forests returned the most calcium to the forest floor annually while oak-hickory (0.53 g/m^2) and pine-oak-hickory (0.26 g/m^2) forest branches returned lesser amounts (Figure 27).

Calcium concentrations in branches (Figure 30) were generally higher than those in leaves (Figure 28). There was no discernable pattern, however, in the branch calcium concentrations among the various forest types.

The major input of calcium (Figure 31) to the forest floor was by pine forest branches at the late fall collection (December 2). The other three forest types contributed lesser amounts of calcium with major peaks during the fall. Again, it should be pointed out that the age of stand and weather conditions could alter the amount of branch litter falling to the forest floor.

As one might expect, the pine forest (0.35 g/m^2) contributed the least amount of calcium in the reproductive parts component to the forest floor annually (Figure 27). Pine-oak-hickory (0.42 g/m^2), oak-hickory (0.52 g/m^2), and mesophytic hardwood (0.64 g/m^2) forests contributed increasing amounts, respectively. The calcium concentrations (Figure 32) in reproductive parts in all forest types followed the same general trend with time, with the pine forest varying most. Calcium concentrations in the reproductive parts varied less during the year than they did in leaves (Figure 28) or in branches (Figure 30).

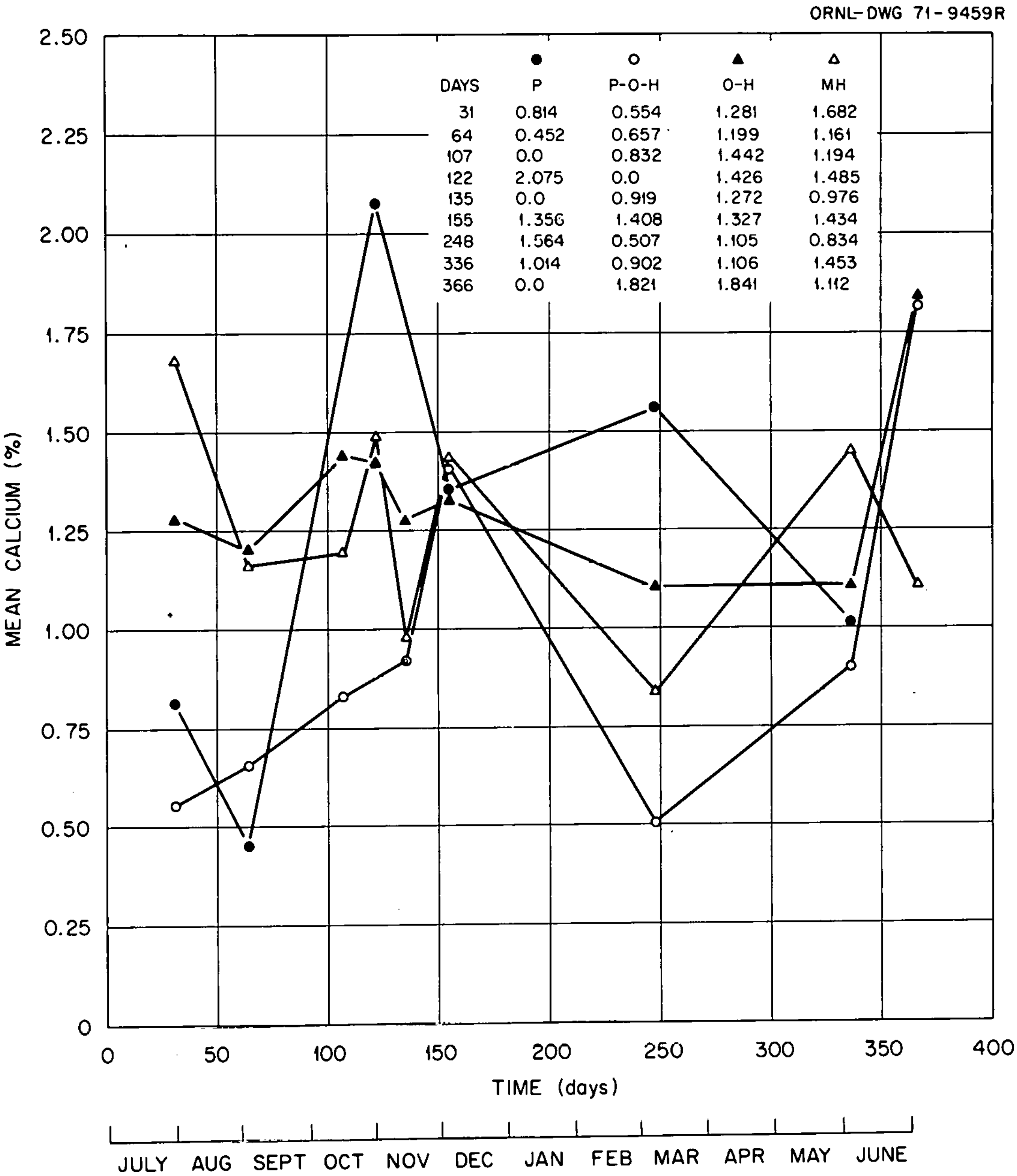


Figure 30. Seasonal patterns of calcium concentration (% dry weight) in branch litterfall in four forest types on Walker Branch Watershed.

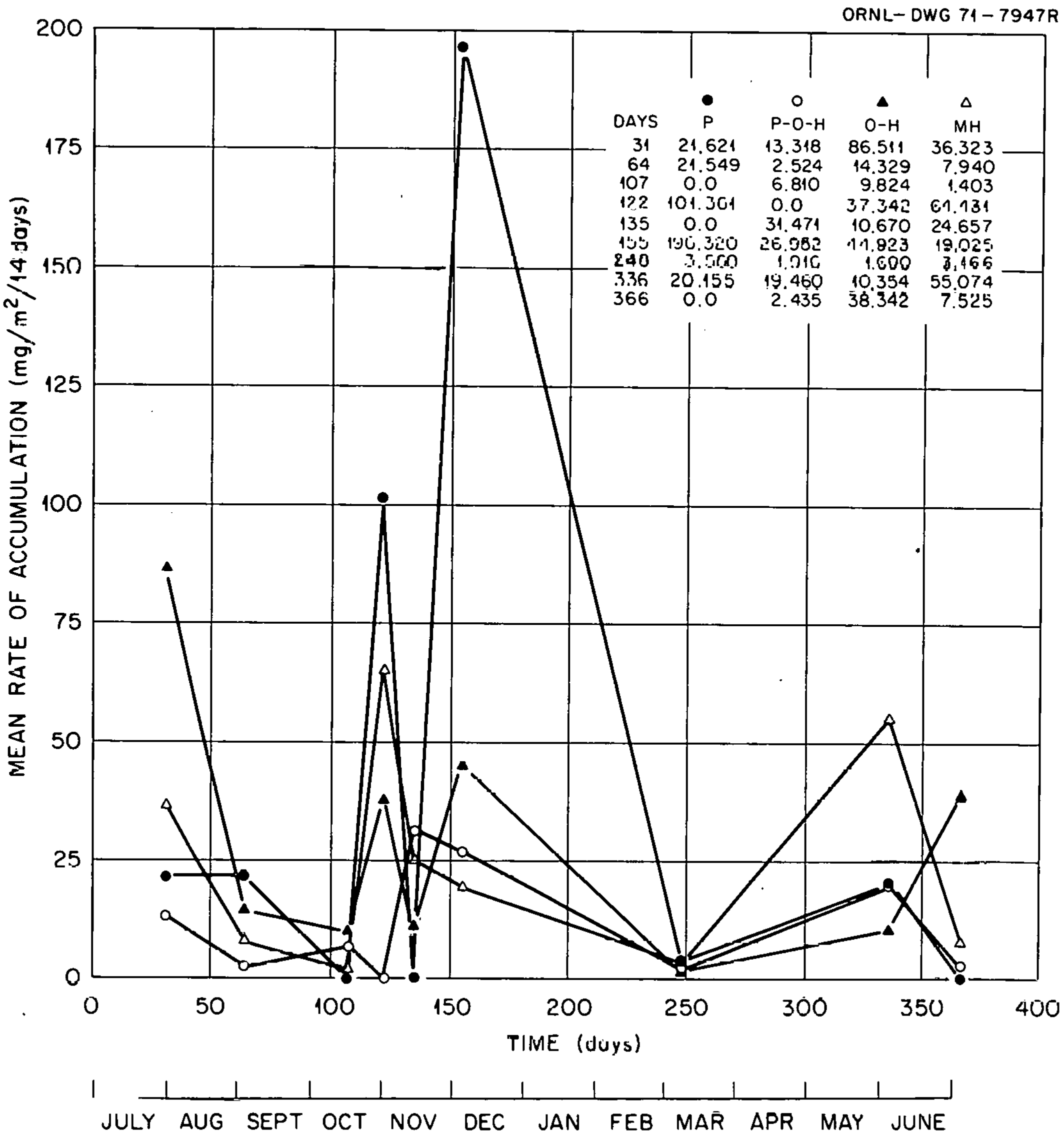
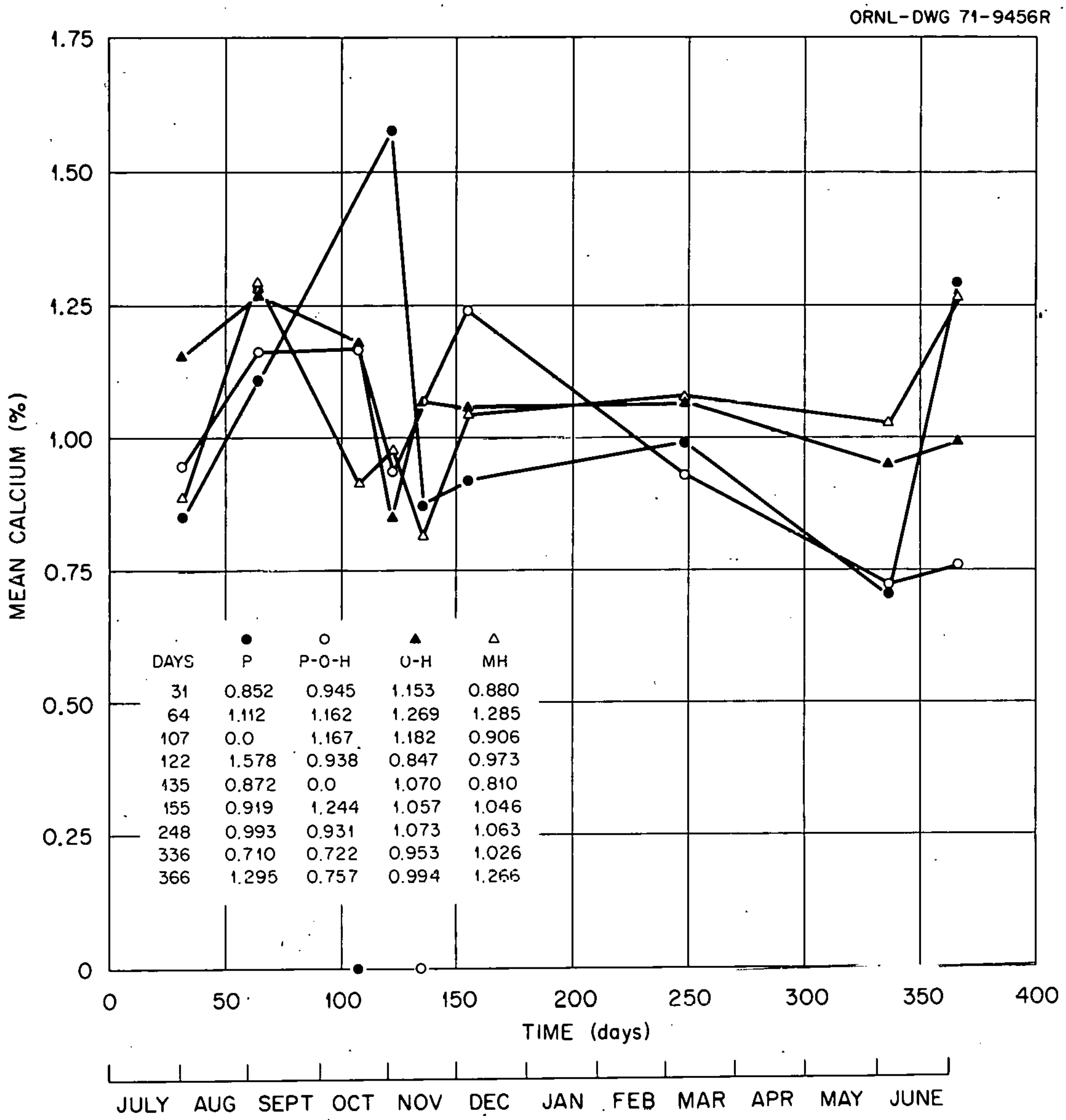


Figure 31. Seasonal rate of return of calcium to the forest floor in branch litterfall in four forest types on Walker Branch Watershed.



DAYS	● P	○ P-O-H	▲ O-H	△ MH
31	0.852	0.945	1.153	0.880
64	1.112	1.162	1.269	1.285
107	0.0	1.167	1.182	0.906
122	1.578	0.938	0.847	0.973
135	0.872	0.0	1.070	0.810
155	0.919	1.244	1.057	1.046
248	0.993	0.931	1.073	1.063
336	0.710	0.722	0.953	1.026
366	1.295	0.757	0.994	1.266

Figure 32. Seasonal patterns of calcium concentrations (% dry weight) in reproductive parts litterfall in four forest types on Walker Branch Watershed.

The amount of calcium transferred to the forest floor via the reproductive parts component (Figure 33) was greatest during autumn (October 30 and December 2 collections), especially in the pine-oak-hickory and mesophytic hardwood forests. The summer period (June 1) contributed a large amount of calcium because that is one of the times when most of the reproductive parts fell.

Magnesium. Total magnesium return in all litterfall components annually (Figure 34) was greatest in the oak-hickory forest (0.87 mg/m^2) with decreasing amounts returned by the mesophytic hardwood (0.83 mg/m^2), pine (0.76 mg/m^2), and the pine-oak-hickory (0.75 mg/m^2) forests, respectively, differences were insignificant.

Although differences among forests were insignificant, leaves (Figure 34) in the oak-hickory (770 mg/m^2) forest contributed the most magnesium to the forest floor annually, with the mesophytic hardwood forest (710 mg/m^2) leaves returning the second greatest amount. Leaves of the pine-oak-hickory (680 mg/m^2) and pine (670 mg/m^2) forests returned the least amount of magnesium annually.

Leaf concentration values (Figure 35) in all forest types were high (.187-.300%) during July, August, and September but dropped after the October 30 collection and reached lowest values (.063-.088%) during winter (March 5). Values for all forests then rose by the spring (June 1) collection (.136-.255%).

All forests (Figure 36) transferred most magnesium in leaf litter to the forest floor at the autumn collection (November 12), with the oak-hickory forest (292 mg/m^2) having the highest value. The pine forest exhibited a broader peak for leaf dry weight transfer (Figure 17, p. 40). This indicates that the length of time for major magnesium transfer by pine

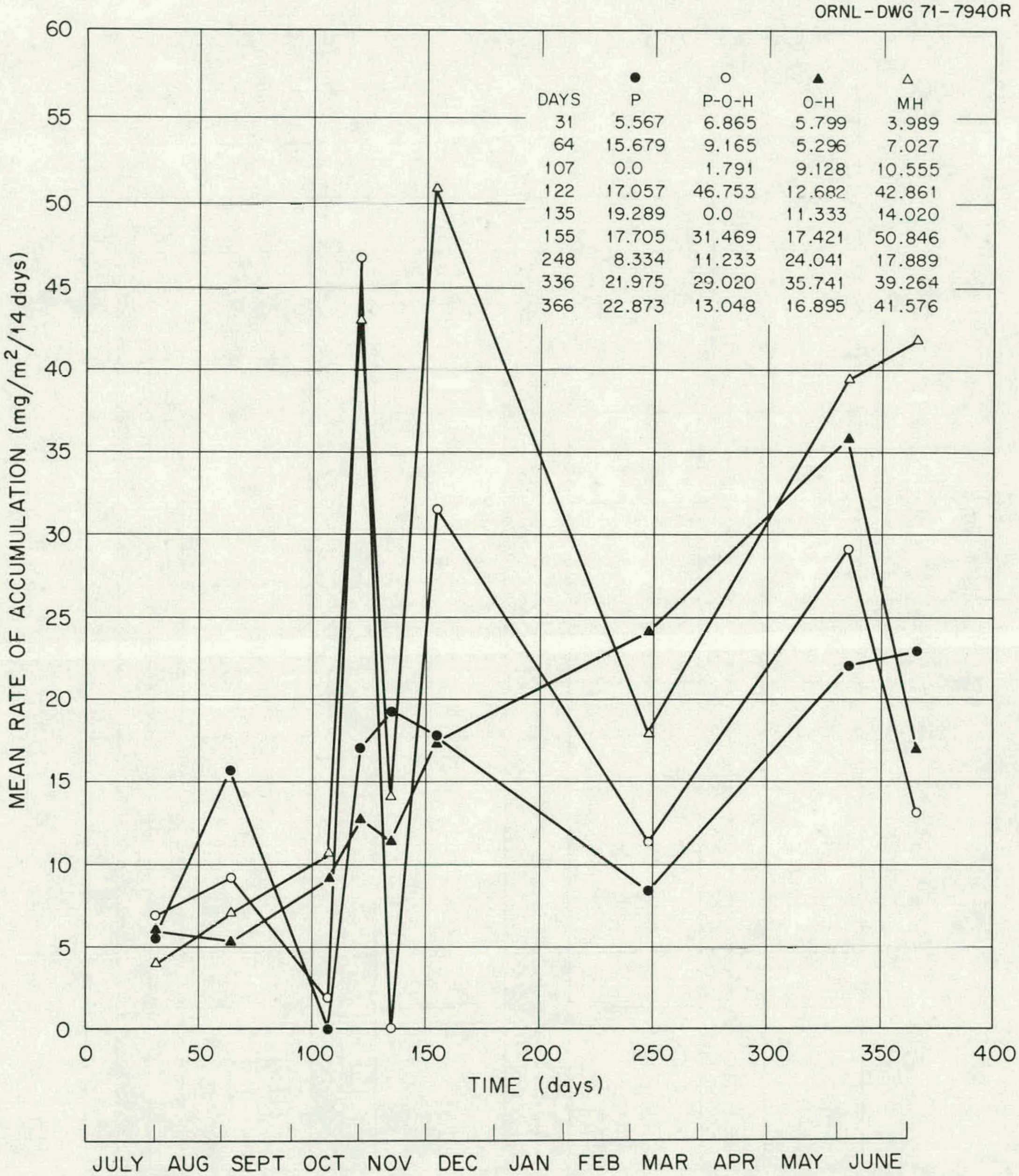


Figure 33. Seasonal rate of return of calcium to the forest floor in reproductive parts litterfall in four forest types on Walker Branch Watershed.

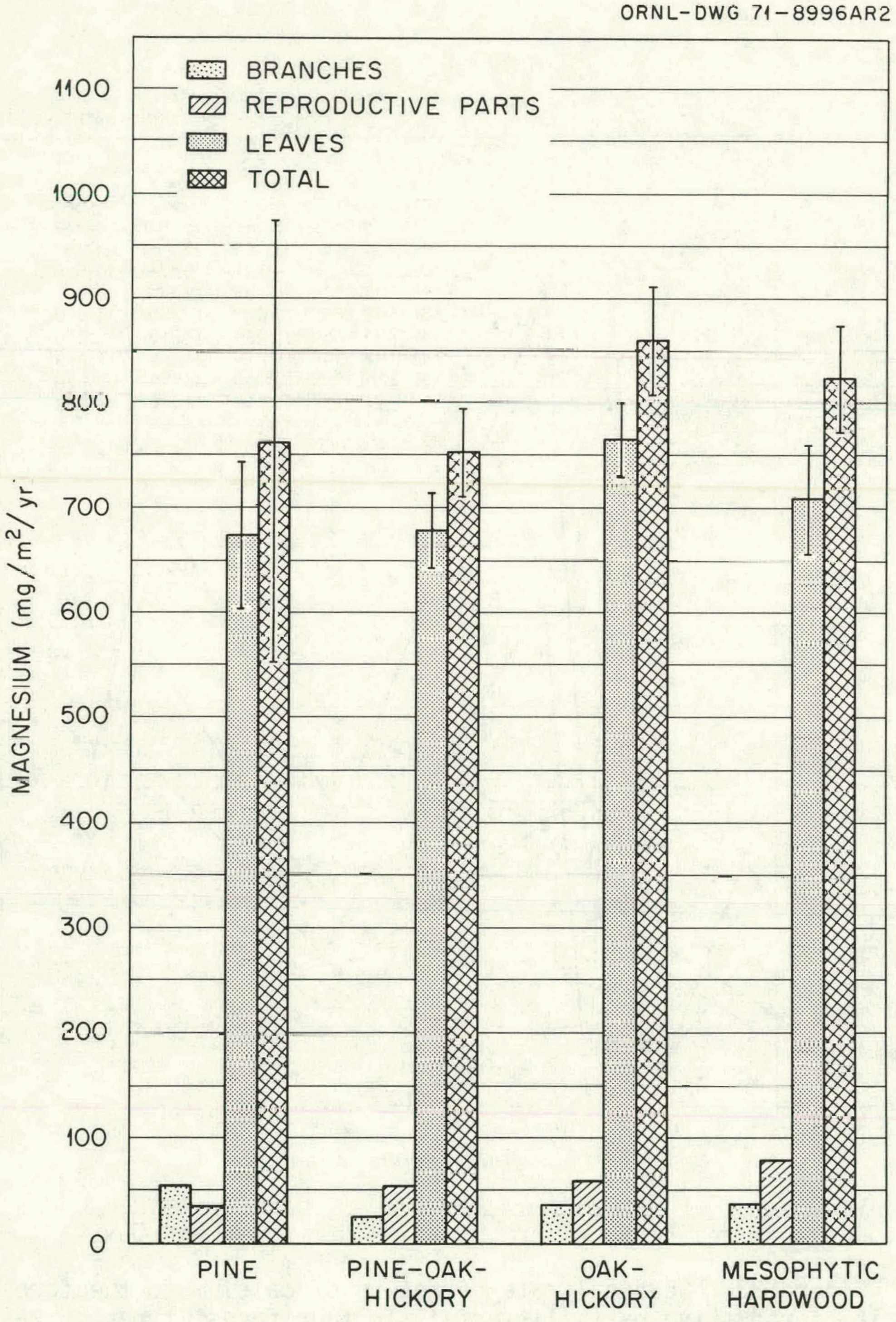


Figure 34. Annual return of magnesium in litterfall components in four forest types on Walker Branch Watershed with standard errors for the leaf component and for total litterfall for each forest type indicated.

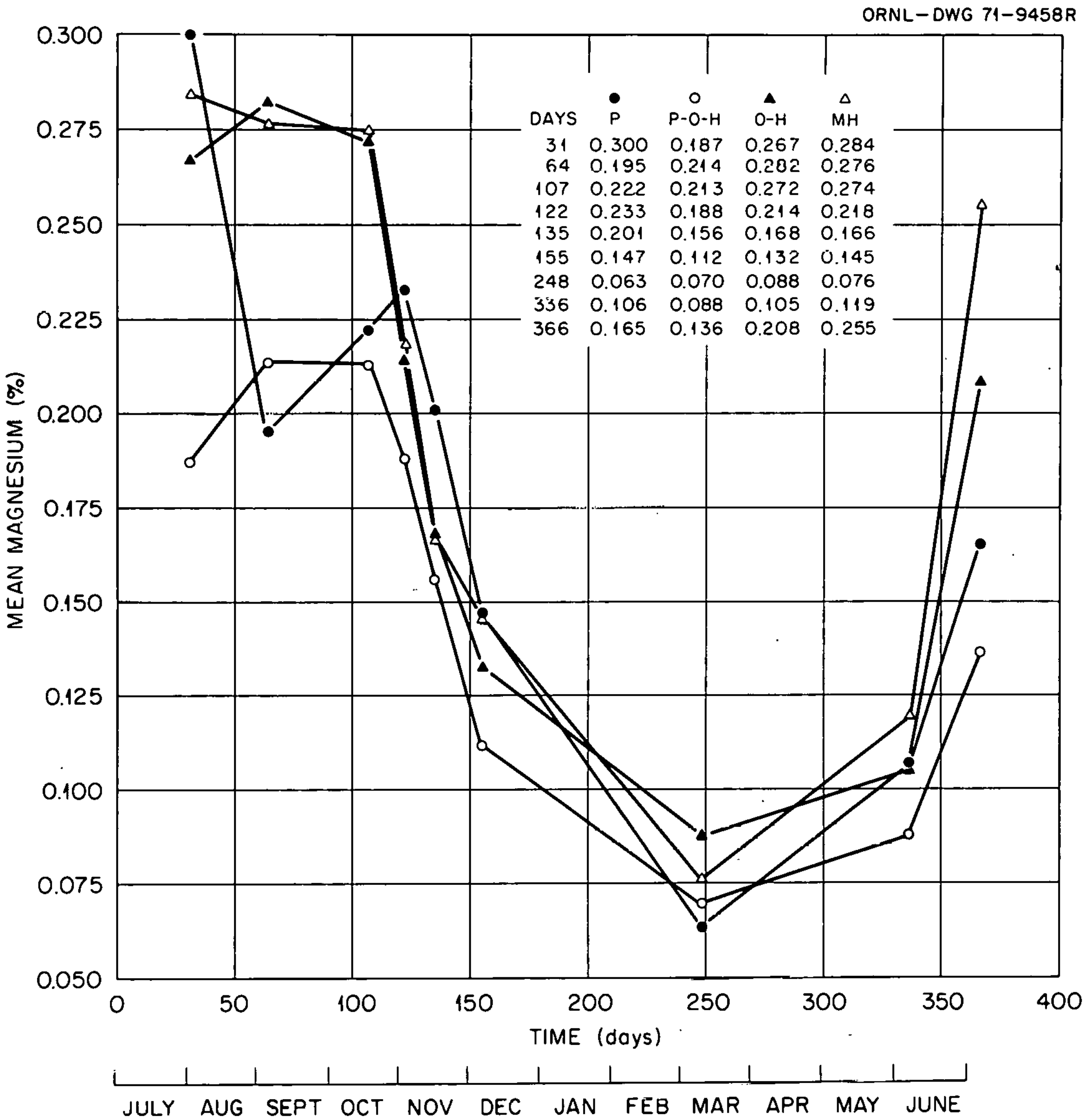


Figure 35. Seasonal patterns of magnesium concentrations (% dry weight) in leaf litterfall in four forest types on Walker Branch Watershed.

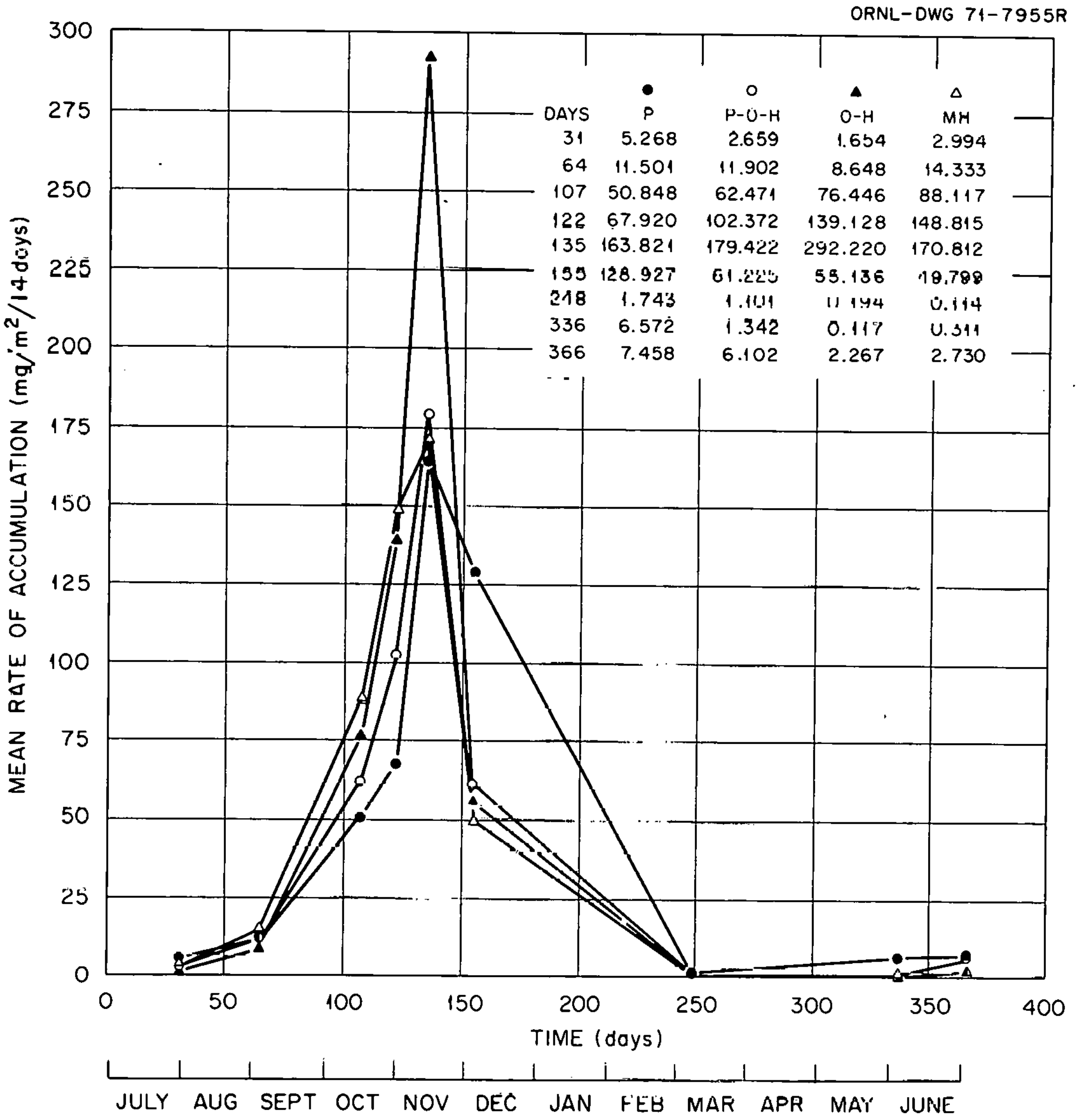


Figure 36. Seasonal rate of return of magnesium to the forest floor in leaf litterfall in four forest types on Walker Branch Watershed.

leaf litterfall was of longer duration than for magnesium transfer of the leaf litterfall by the other three forest types, thereby following the pattern of leaf litterfall.

Only about five percent of the total amount of magnesium in all components of litterfall was returned annually to the forest floor in branches (Figure 34). Pine forest (50 mg/m^2) branches contributed the most, followed by the mesophytic hardwood (40 mg/m^2), oak-hickory (40 mg/m^2), and pine-oak-hickory (20 mg/m^2) forest branches, respectively.

Magnesium concentrations in branches (Figure 37) generally decreased from early summer (0.103-0.177%) through winter (0.030-0.063%) after which it increased in all (0.053-0.105%) but the pine-oak-hickory forest which remained low (0.038%).

With one exception branches transferred insignificant amounts of magnesium to the forest floor in comparison with magnesium transfer via leaves in all forests (Figure 38). The exception was the magnesium transfer rate at the late autumn collection (December 2) in the pine forest when a significant amount of branch biomass was collected in that forest.

The total amount of magnesium (Figure 34) that returned to the forest floor annually in reproductive parts increased, although slightly, from pine (40 mg/m^2) to pine-oak-hickory (50 mg/m^2) to oak-hickory (60 mg/m^2) to mesophytic hardwood forests (80 mg/m^2).

All forest types (Figure 39) had higher magnesium concentrations in the reproductive parts component in summer and early fall (.132-.214%) than in winter (.058-.073%) which had the lowest concentrations.

The greatest rate of transfer of magnesium in the reproductive parts component (Figure 40) begain after the autumn collection (October

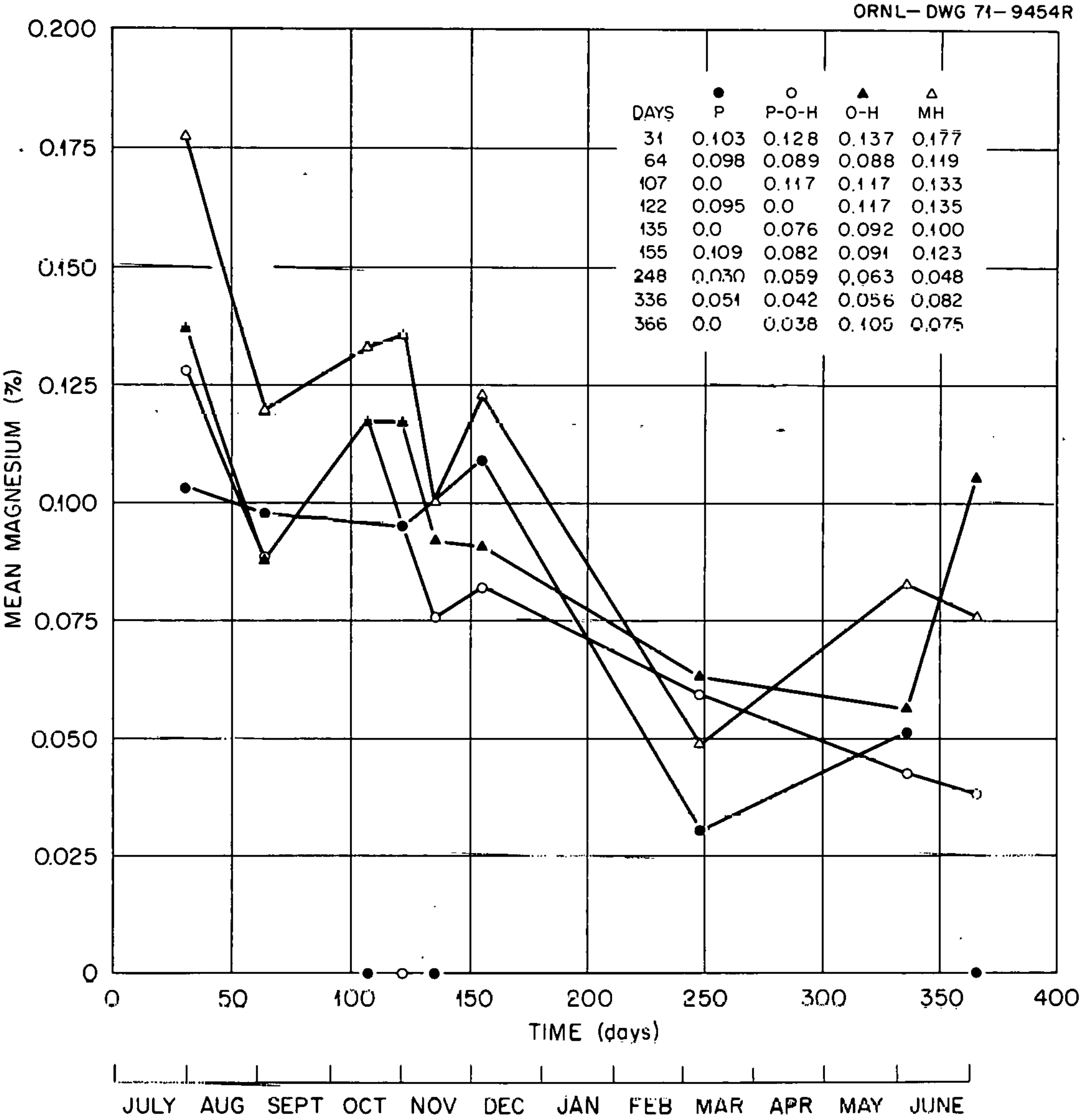


Figure 37. Seasonal patterns of magnesium concentrations (% dry weight) in branch litterfall in four forest types on Walker Branch Watershed.

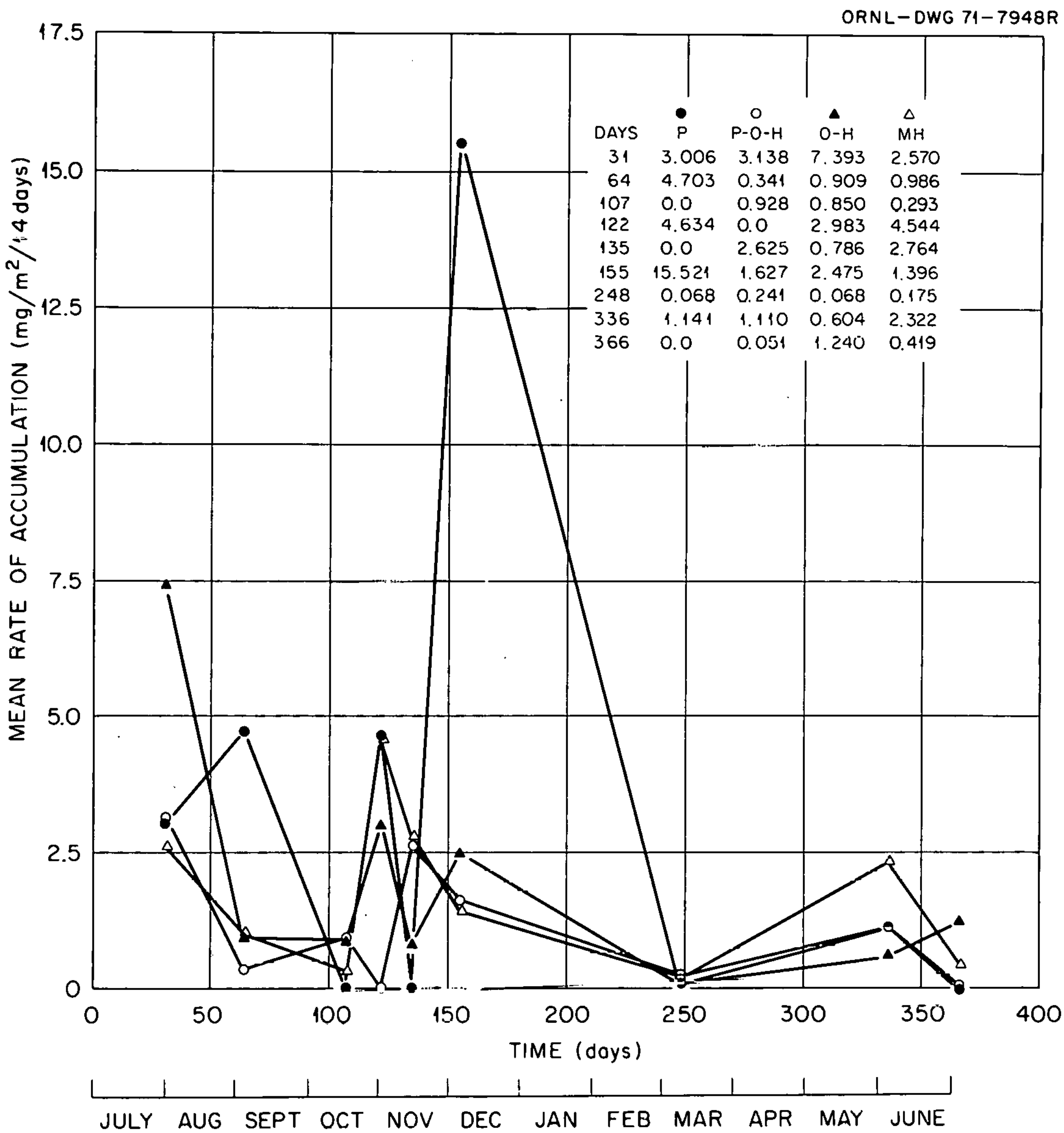


Figure 38. Seasonal rate of return of magnesium to the forest floor in branch litterfall in four forest types on Walker Branch Watershed.

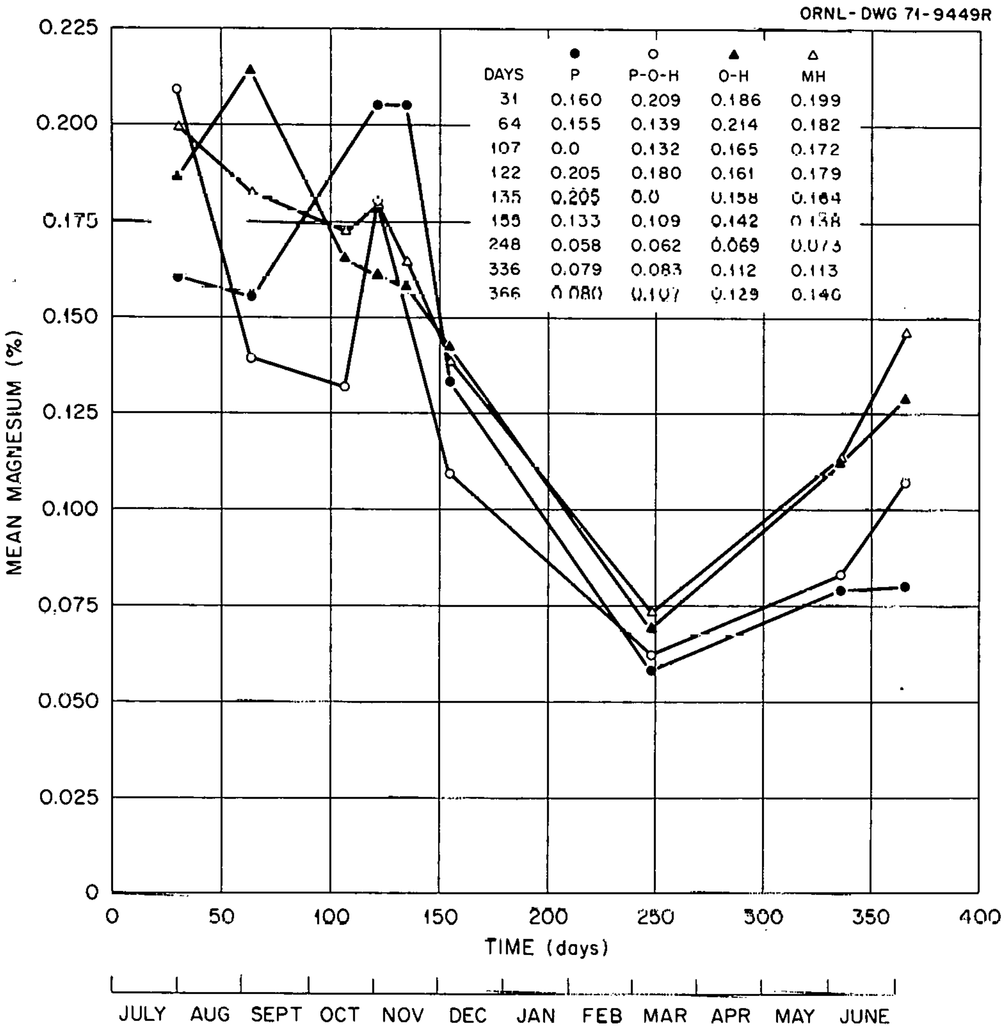


Figure 39. Seasonal patterns of magnesium concentrations (% dry weight) in reproductive parts litterfall in four forest types on Walker Branch Watershed.

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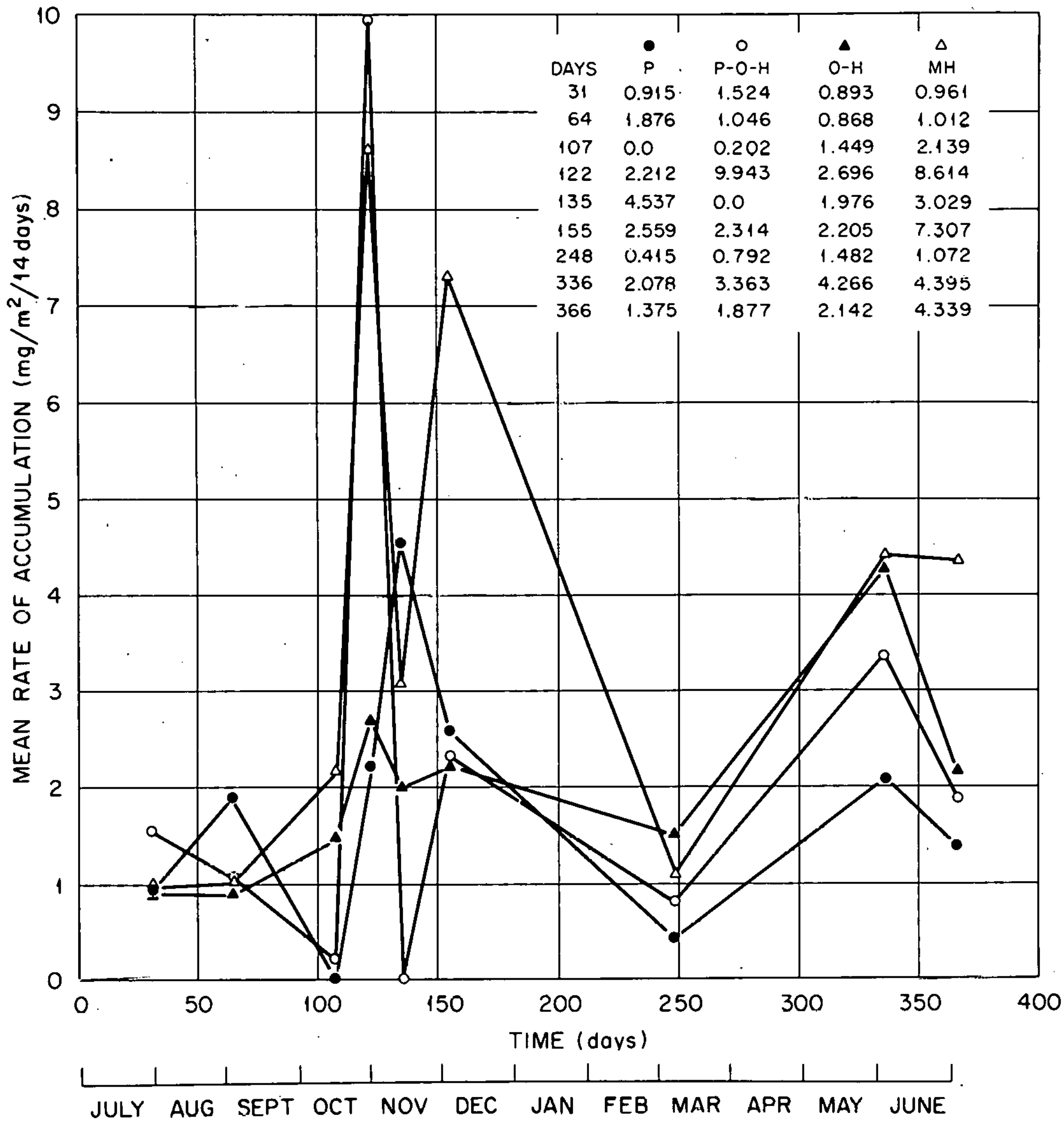


DAYS	● P	○ P-O-H	▲ O-H	△ MH
31	0.915	1.524	0.893	0.961
64	1.876	1.046	0.868	1.012
107	0.0	0.202	1.449	2.139
122	2.212	9.943	2.696	8.614
135	4.537	0.0	1.976	3.029
155	2.559	2.314	2.205	7.307
248	0.415	0.792	1.482	1.072
336	2.078	3.363	4.266	4.395
366	1.375	1.877	2.142	4.339

Figure 40. Seasonal rate of return of magnesium to the forest floor in reproductive parts litterfall in four forest types on Walker Branch Watershed.

15) and was greatest in the pine-oak-hickory (9.9 mg/m^2) and mesophytic hardwood (8.6 mg/m^2) forests, respectively. The decrease in the rate of transfer of magnesium was evidenced after the late autumn collection (December 2) in all forests. The second most pronounced period of magnesium transfer in all forests (2.1-4.4 mg/m^2) was in the June 1 collection and was due to fruiting bodies falling to the forest floor at that time.

Sodium. The oak-hickory and mesophytic hardwood forests returned the largest amounts of sodium (90 mg/m^2) in total litterfall on an annual basis (Figure 41). The pine and pine-oak-hickory (80 mg/m^2) forest litterfall components were next and contributed equal amounts annually. Differences between forest types were not statistically significant.

The sodium concentrations in the leaf litterfall component in all forests were small and the range was narrow (0.012-0.034%) for the entire year (Figure 42). Generally, all forests leaves had the same concentration pattern as the season progressed.

The total sodium content in leaf litterfall for the year was greatest in the oak-hickory (72 mg/m^2) and least in the pine and pine-oak-hickory (both with 64 mg/m^2) forests while the mesophytic hardwood (65 mg/m^2) forest content was intermediate (Figure 41). Values between the forest types were not statistically significant.

Pine-oak-hickory and oak-hickory forest leaves transferred the major portion of sodium during a two week period in autumn while pine and mesophytic hardwood leaves transferred most sodium over a four week period during autumn (Figure 43). This transfer rate was expected on the basis of the leaf litterfall biomass transfer rate (Figure 17, p. 40).

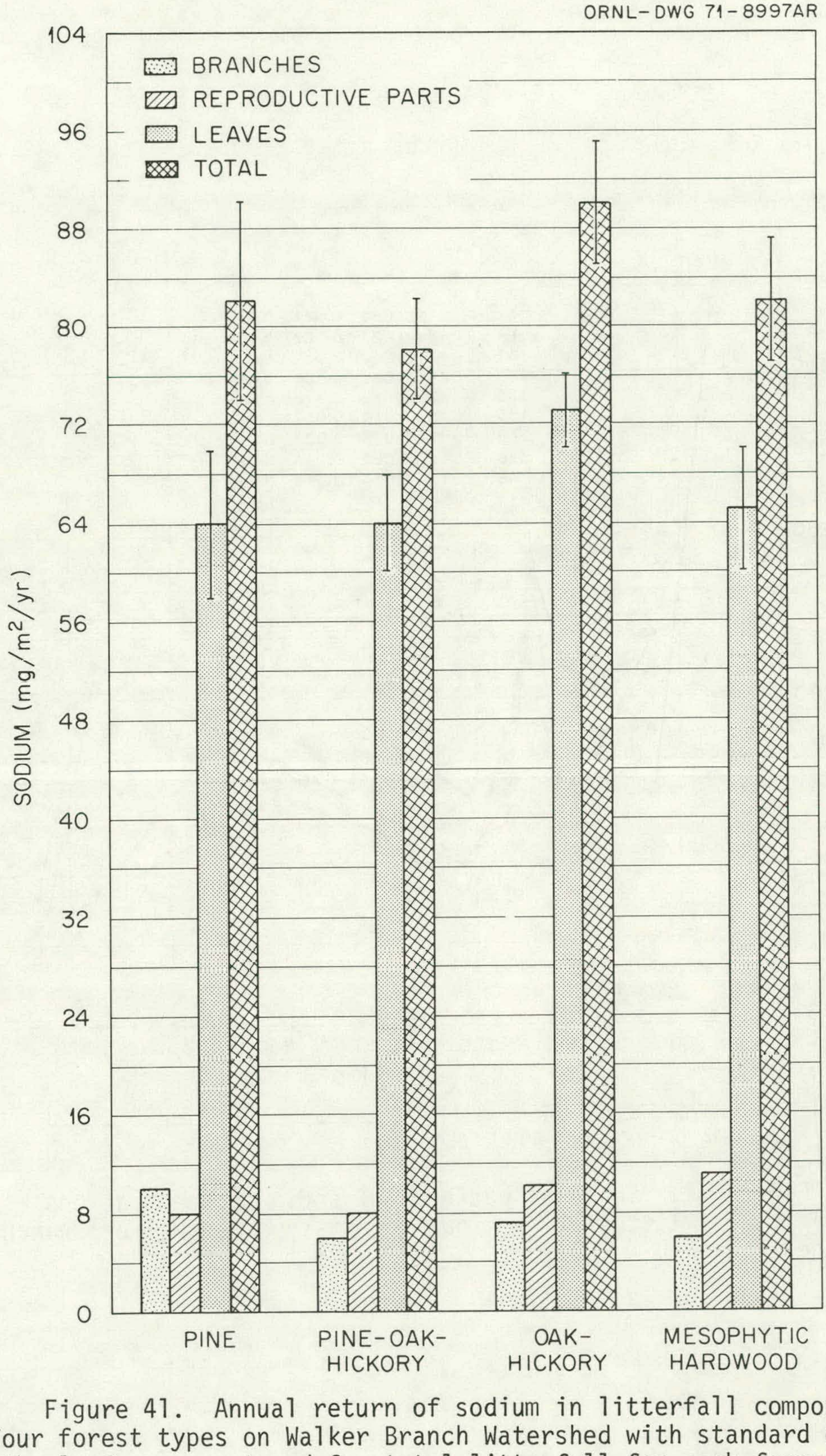


Figure 41. Annual return of sodium in litterfall components in four forest types on Walker Branch Watershed with standard errors for the leaf component and for total litterfall for each forest type indicated.

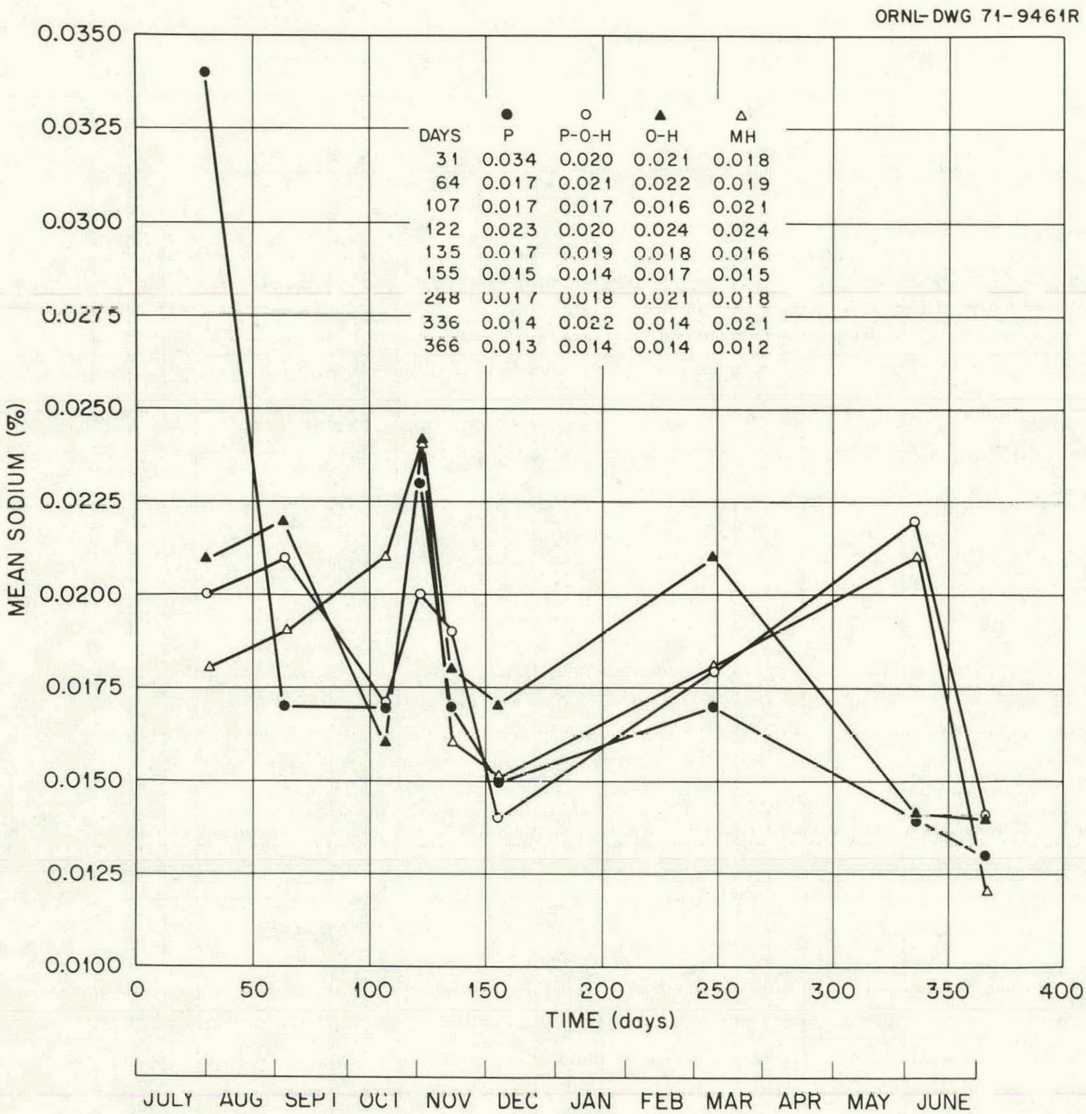


Figure 42. Seasonal patterns of sodium concentrations (% dry weight) in leaf litterfall in four forest types on Walker Branch Watershed.

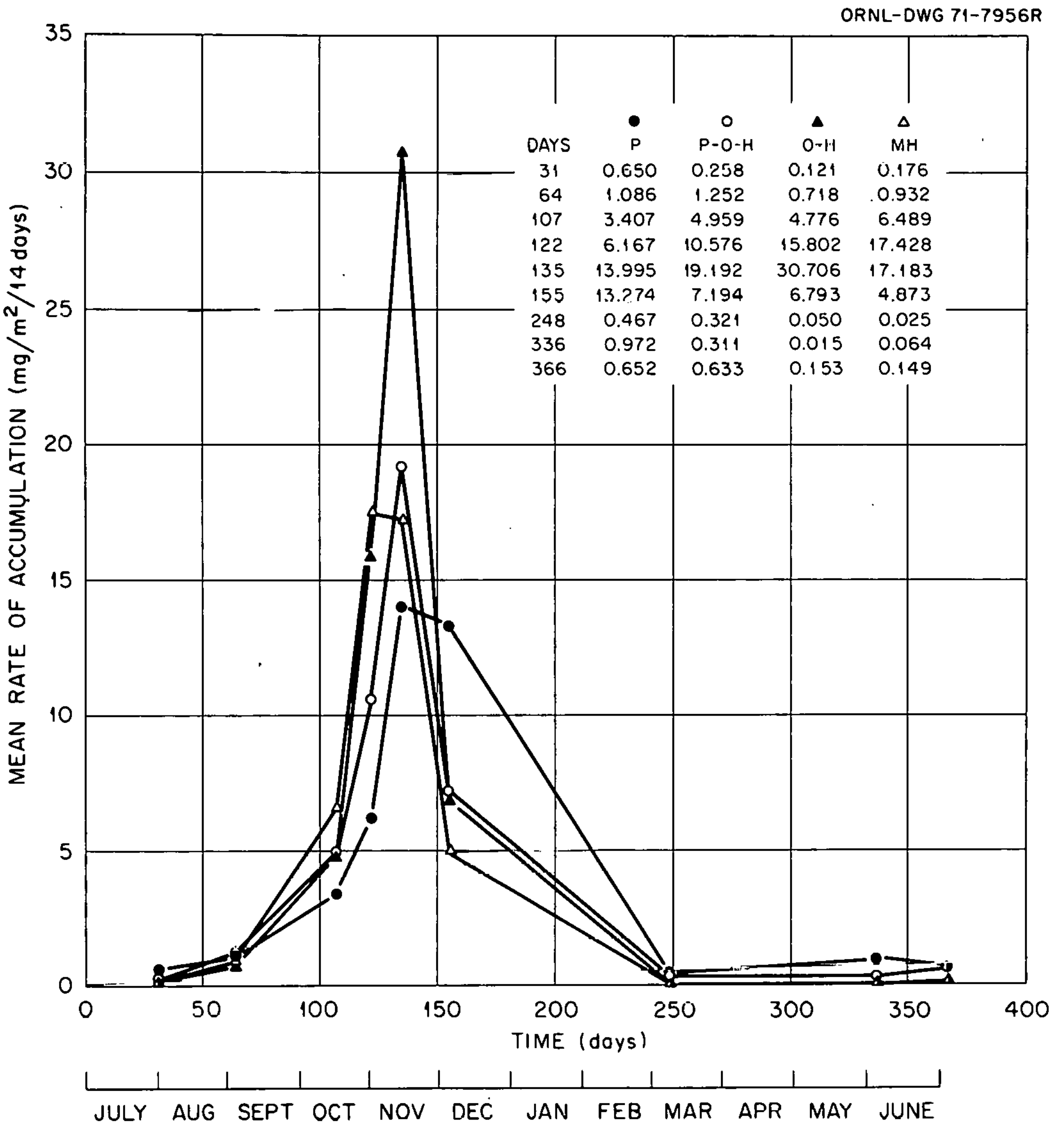


Figure 43. Seasonal rate of return of sodium to the forest floor in leaf litterfall in four forest types on Walker Branch Watershed.

The oak-hickory (31 $mg/m^2/14$ days) forest had the highest single value, while pine-oak-hickory (19 $mg/m^2/14$ days), mesophytic hardwood (17 $mg/m^2/14$ days), and pine (13 $mg/m^2/14$ days) leaves had decreasing values, respectively.

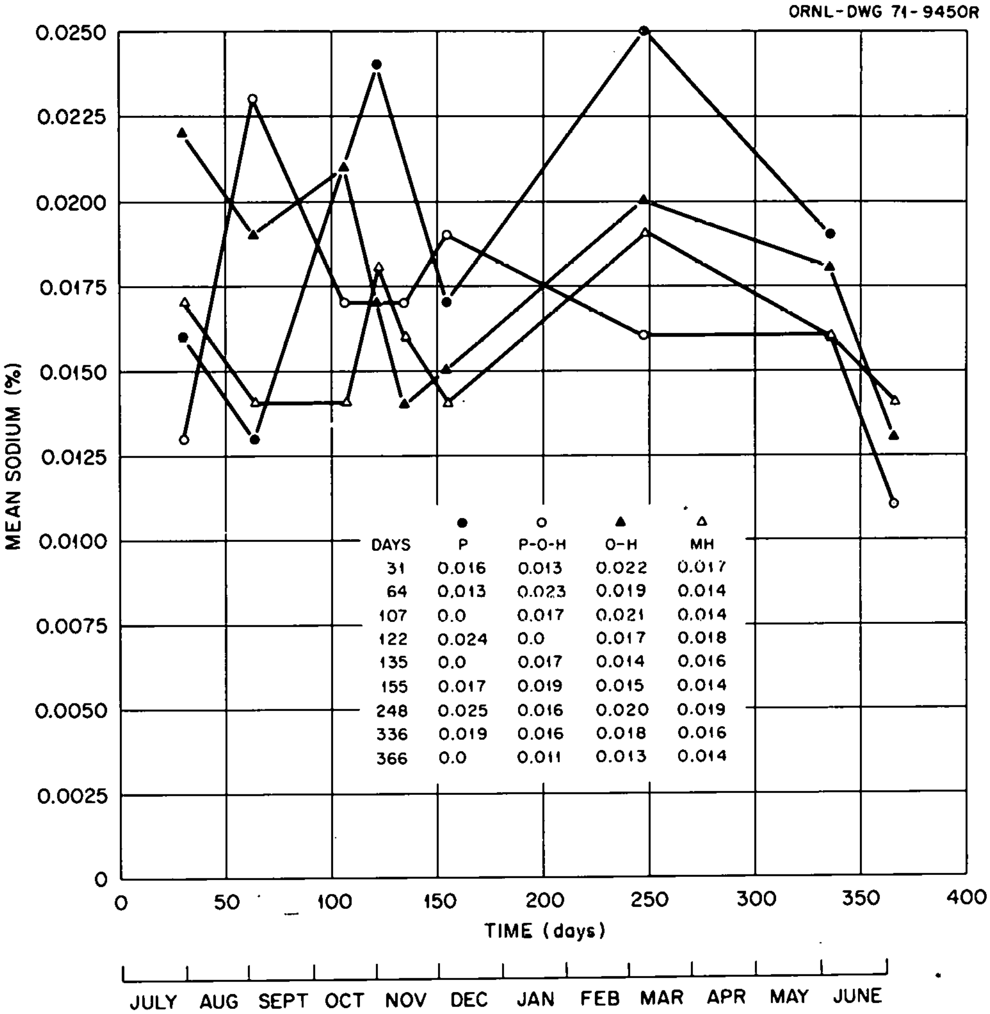
Pine forest branches (10 mg/m^2) were the largest contributors of sodium to the forest floor for the year (Figure 41). The oak-hickory (7 mg/m^2) forest branches returned the next largest amount of sodium to the forest floor. The pine-oak-hickory (6 mg/m^2) and mesophytic hardwood (6 mg/m^2) branches had equal amounts of sodium and returned the least amount.

The sodium concentrations in branches of all forest types followed no pattern (Figure 44). Concentrations were low and fluctuated over a narrow range. The concentration range in branches was similar with leaf concentrations in nearly all collections in all forest types.

There were no consistent differences in sodium transfer in branches among the forest types (Figure 45). Fall and early spring were the two major periods when most sodium was transferred in all forest types.

The mesophytic hardwood (11 mg/m^2) forest reproductive parts returned the greatest amount of sodium to the forest floor annually (Figure 41). The oak-hickory (10 mg/m^2) reproductive parts component returned the next greatest amount of sodium while pine (8 mg/m^2) and pine-oak-hickory (8 mg/m^2) forest reproductive parts had equal amounts and returned the least sodium for the year.

The sodium concentration in the reproductive parts component of litterfall (Figure 46) had, with the exception of the winter (March 5) collection in the pine forest, a range of values comparable to those in leaves (Figure 42) and in branches (Figure 44). The high sodium



DAYS	● P	○ P-O-H	▲ O-H	△ MH
31	0.016	0.013	0.022	0.017
64	0.013	0.023	0.019	0.014
107	0.0	0.017	0.021	0.014
122	0.024	0.0	0.017	0.018
135	0.0	0.017	0.014	0.016
155	0.017	0.019	0.015	0.014
248	0.025	0.016	0.020	0.019
336	0.019	0.016	0.018	0.016
366	0.0	0.011	0.013	0.014

Figure 44. Seasonal patterns of sodium concentrations (% dry weight) in branch litterfall in four forest types on Walker Branch Watershed.

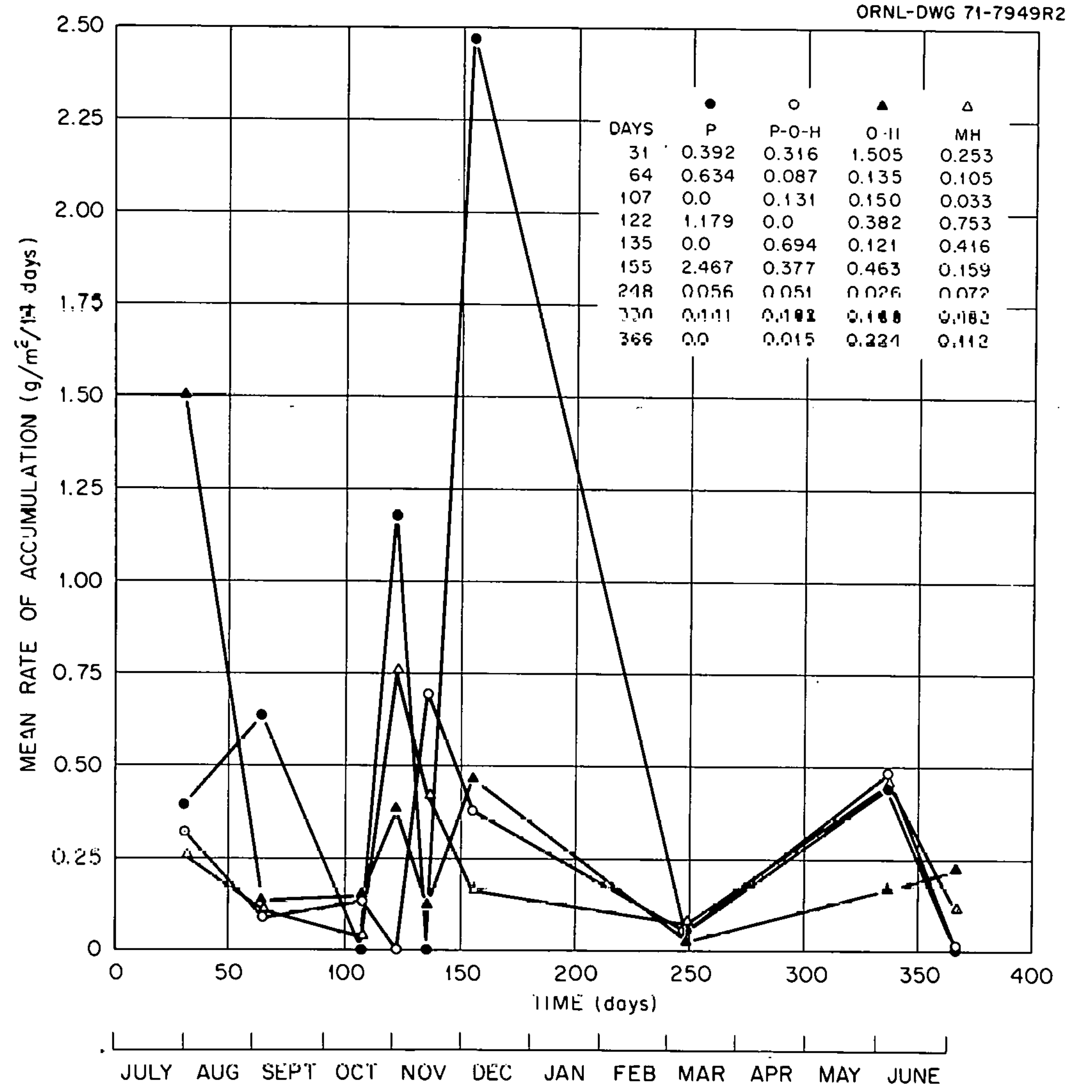


Figure 45. Seasonal rate of return of sodium to the forest floor in branch litterfall in four forest types on Walker Branch Watershed.

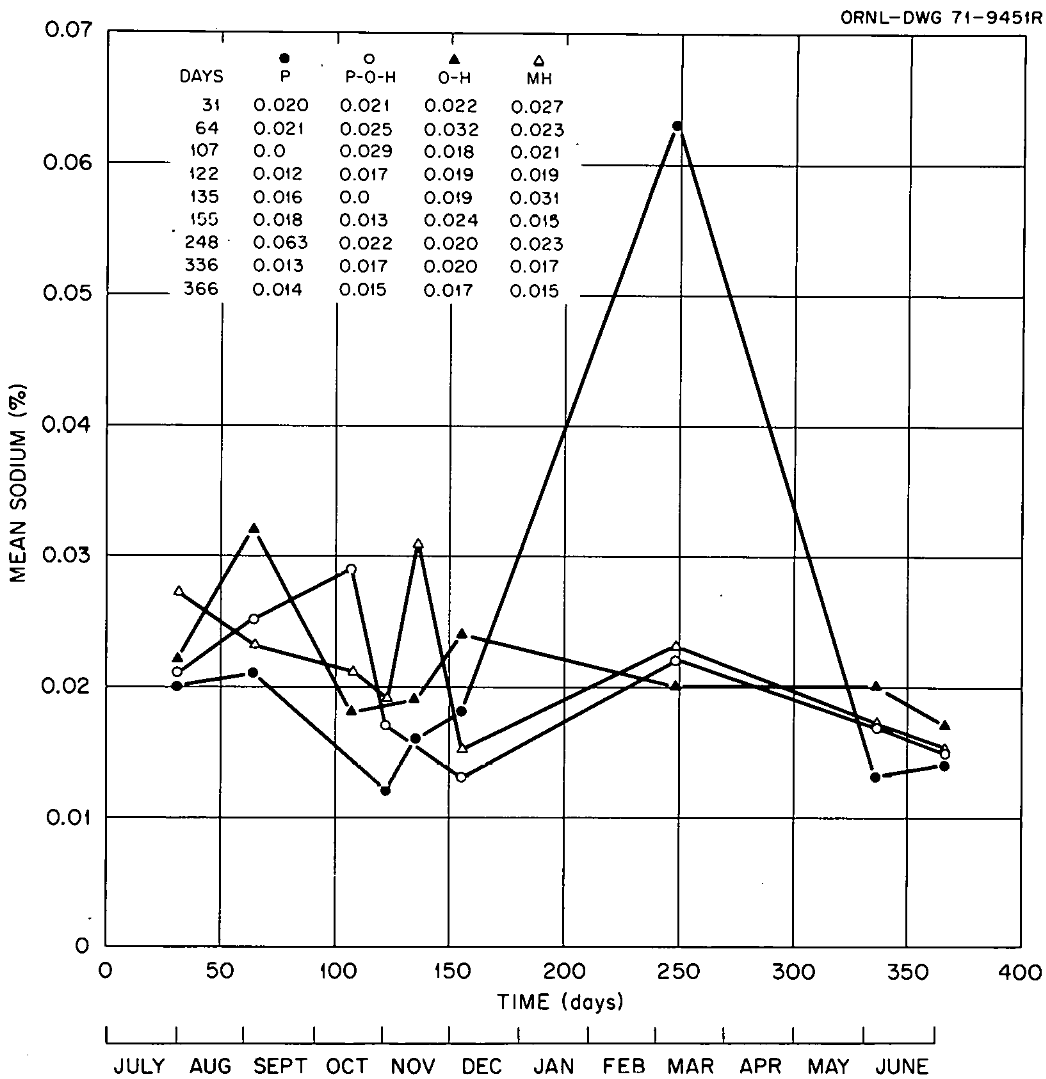


Figure 46. Seasonal patterns of sodium concentrations (% dry weight) in reproductive parts litterfall in four forest types on Walker Branch Watershed.

concentration in the pine forest reproductive parts at the March 5 collection may have been because an insect or insect frass was ground with the reproductive parts component.

Fall and spring were periods when most sodium was transferred from the canopy to the forest floor in the reproductive parts (Figure 47) in all forests. Reproductive parts from the mesophytic hardwood forest transferred the greatest amount of sodium in fall, while the oak-hickory forest reproductive parts component transferred most sodium during spring.

Potassium. The total amount of potassium in all components of litterfall for the year (Figure 48) was greatest in the oak-hickory (2.0 g/m^2) forest. The second greatest amount was in the mesophytic hardwoods (1.9 g/m^2) with the pine-oak-hickory (1.6 g/m^2) and pine (1.4 g/m^2) having lesser amounts, respectively. The potassium content in total litterfall in the pine forest was statistically lower than the oak-hickory and the mesophytic hardwood forests.

The annual summary (Figure 48) indicates that the oak-hickory (1.8 g/m^2) forest leaf litter was the main contributor of potassium. The mesophytic hardwood (1.6 g/m^2) forest leaf litter contributed the second greatest amount, while the pine-oak-hickory (1.5 g/m^2) and pine (1.3 g/m^2) forest leaf litter contributed lesser amounts of potassium, respectively. Leaf litter did show significant differences. The pine forest leaf litter varied statistically from the oak-hickory and the mesophytic hardwood forests. Potassium leaches from leaves easily and rainfall alters the amount of potassium in leaf litter if the amount, intensity, or time of precipitation differs.

The potassium leaf concentration pattern (Figure 49) between the four forest types varied during spring and summer but did not change

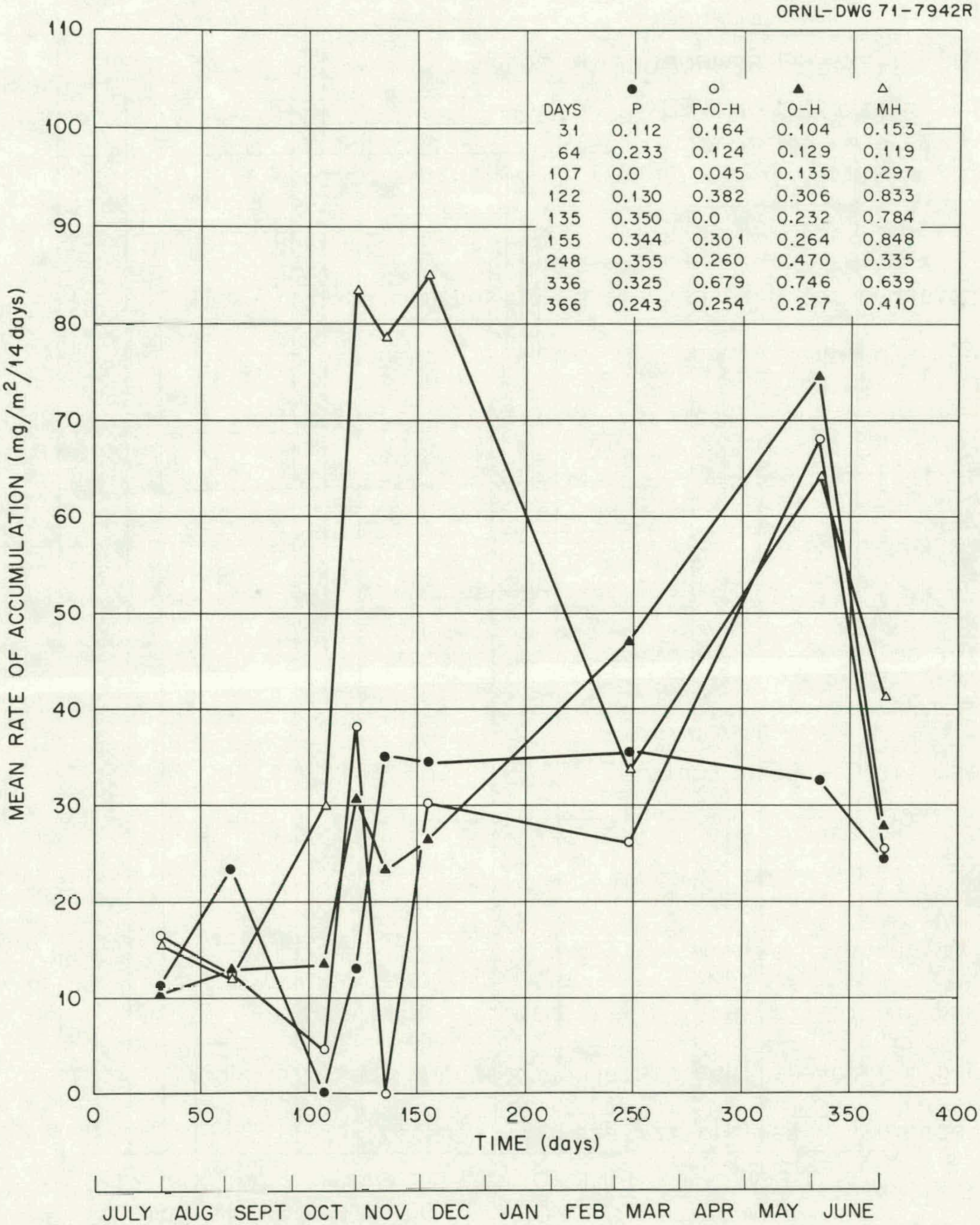


Figure 47. Seasonal rate of return of sodium to the forest floor in reproductive parts litterfall in four forest types on Walker Branch Watershed.

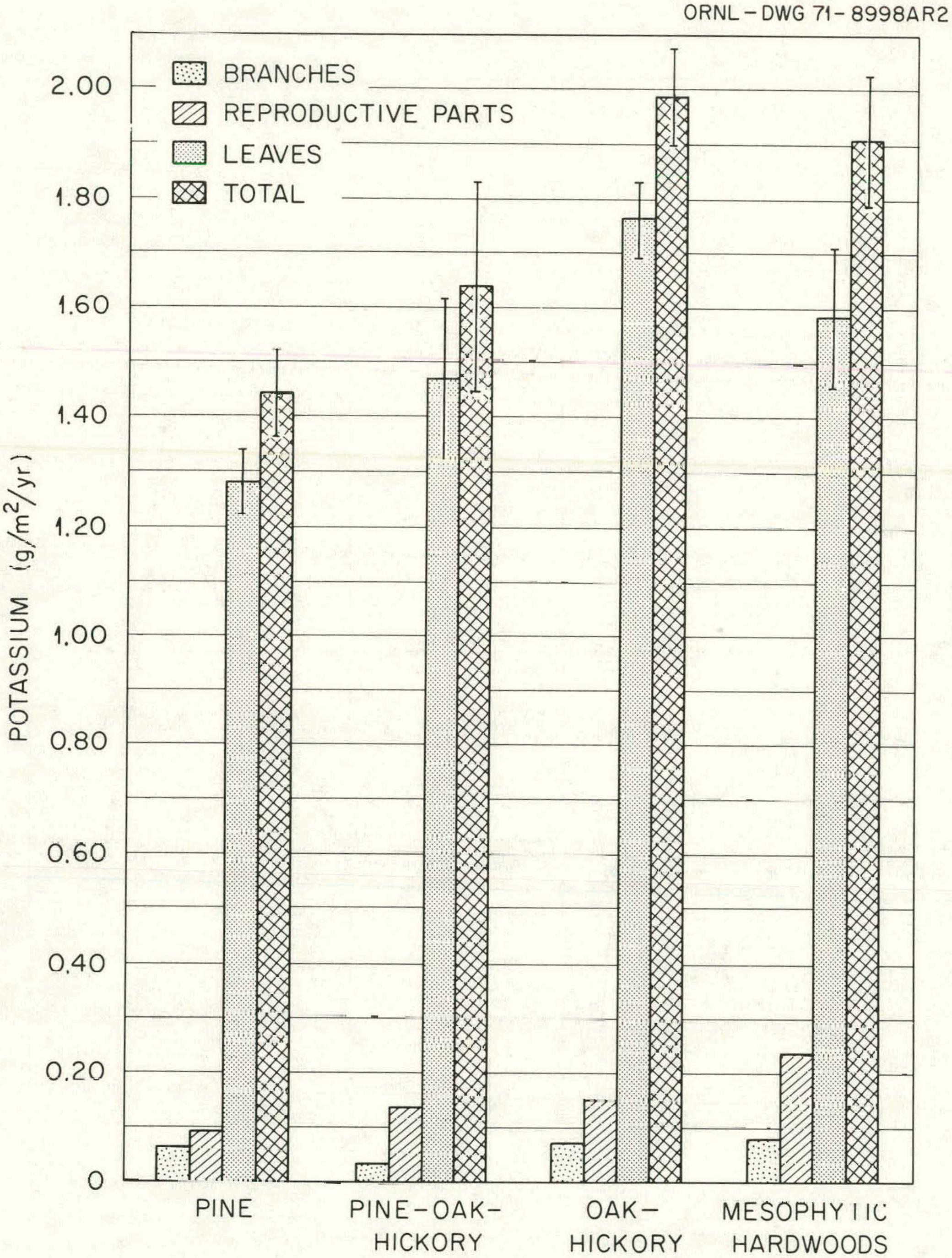


Figure 48. Annual return of potassium in litterfall components in four forest types on Walker Branch Watershed with standard errors for the leaf component and for total litterfall for each forest type indicated.

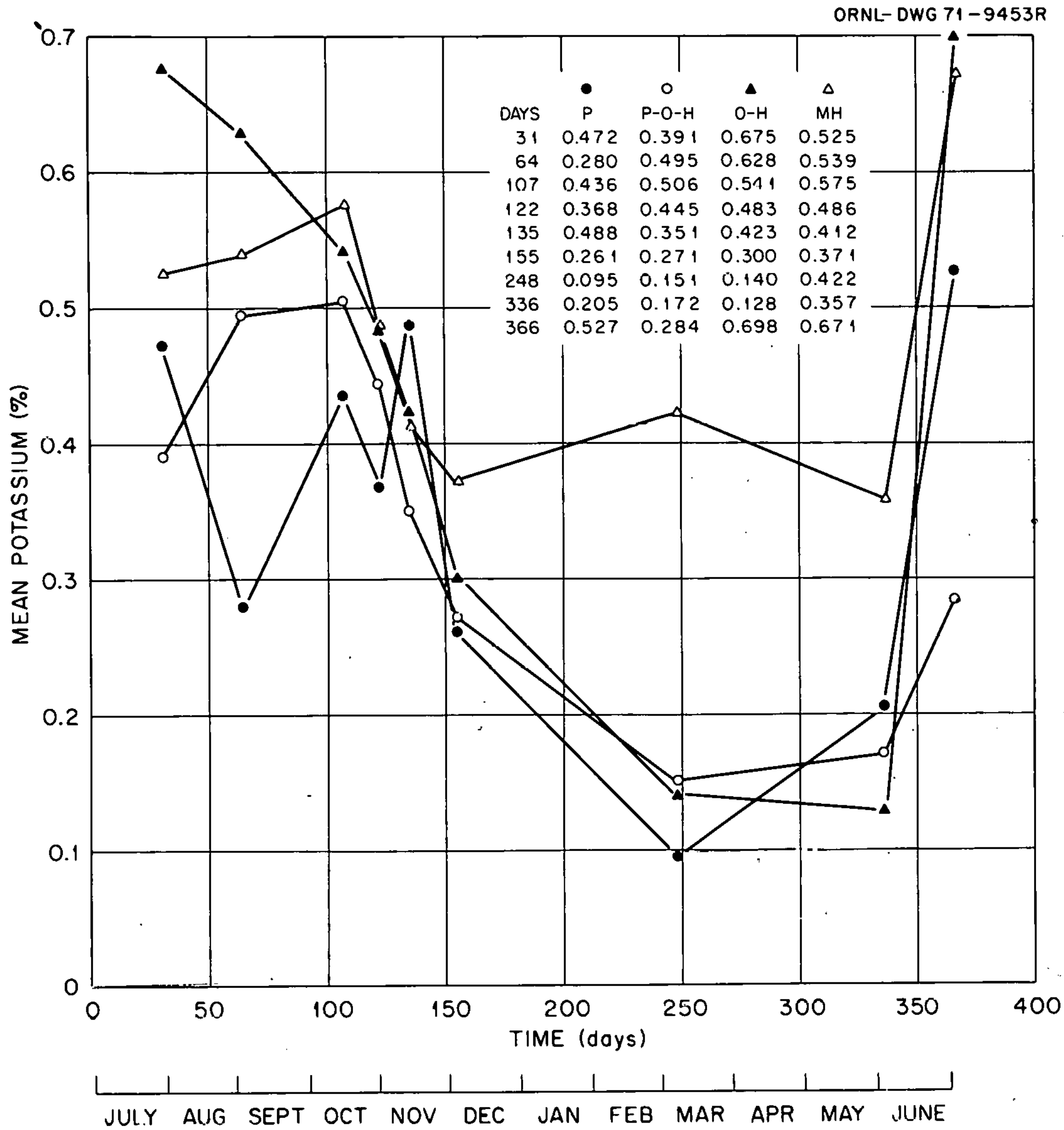


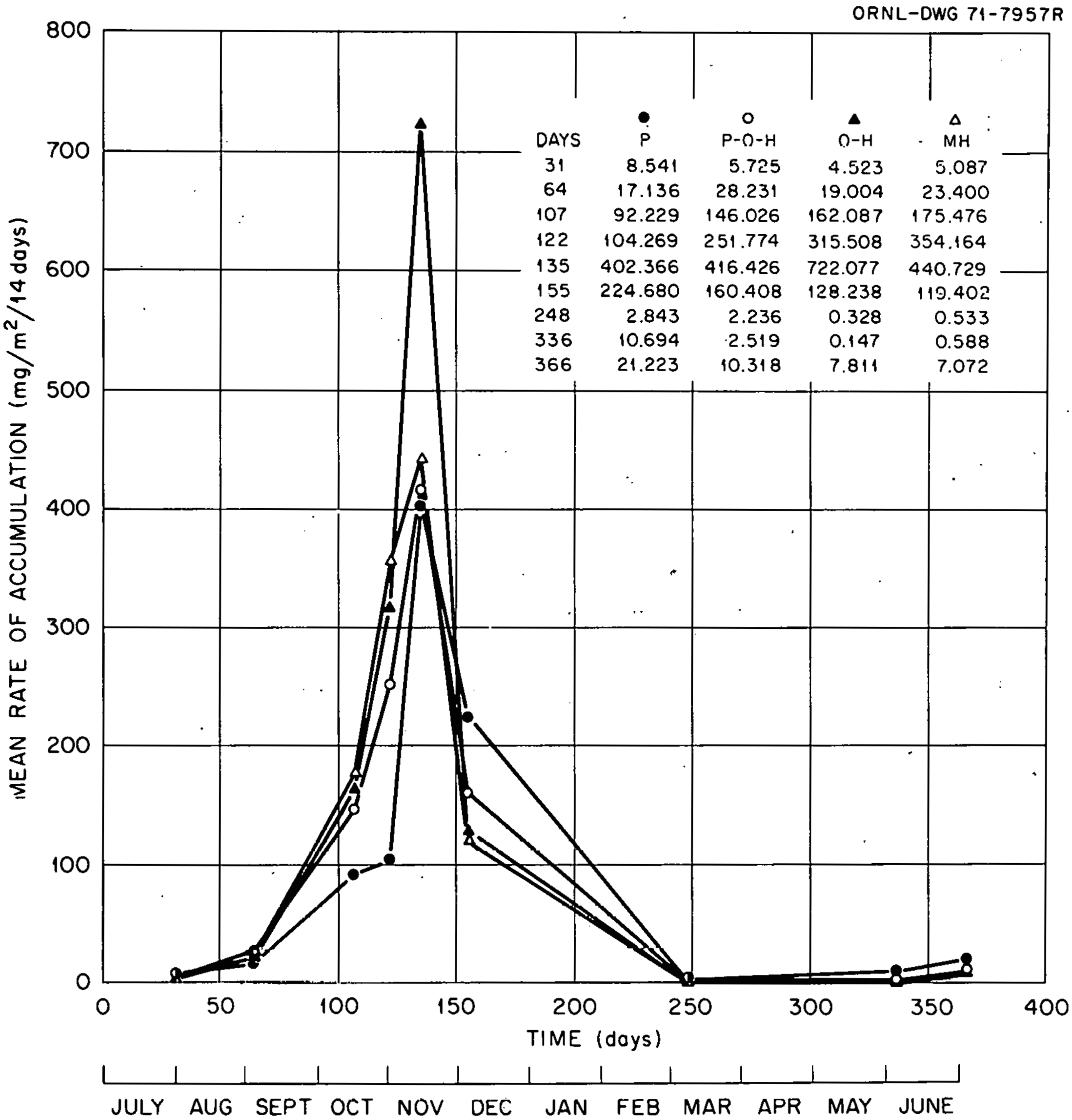
Figure 49. Seasonal patterns of potassium concentrations (% dry weight) in leaf litterfall in four forest types on Walker Branch Watershed.

during fall. The range of concentrations during spring (0.17-0.70%) and summer (0.28-0.63%) among the forests was greater than the fall (0.26-0.37). The largest transfer of potassium in leaf litter to the forest floor was autumnal collection in all forest types (Figure 50). The oak-hickory (0.72 g/m^2/14 days) forest transferred the largest amount of potassium at that collection due mostly to the larger leaf litter weight input in the oak-hickory forest and not because of higher percentage concentrations than the other three forest types. Nearly equal amounts of potassium in leaves were transferred to the forest floor at that collection in the pine (0.40 g/m^2/14 days), pine-oak-hickory (0.42 g/m^2/14 days), and mesophytic hardwood (0.44 g/m^2/14 days) forests.

The total amount of potassium (Figure 48) that returned by branch litterfall for the year was least in the pine-oak-hickory (30 mg/m^2) forest and greatest in the mesophytic hardwood (80 mg/m^2 forest). Pine (60 mg/m^2) and oak-hickory (70 mg/m^2) forest branches had intermediate amounts.

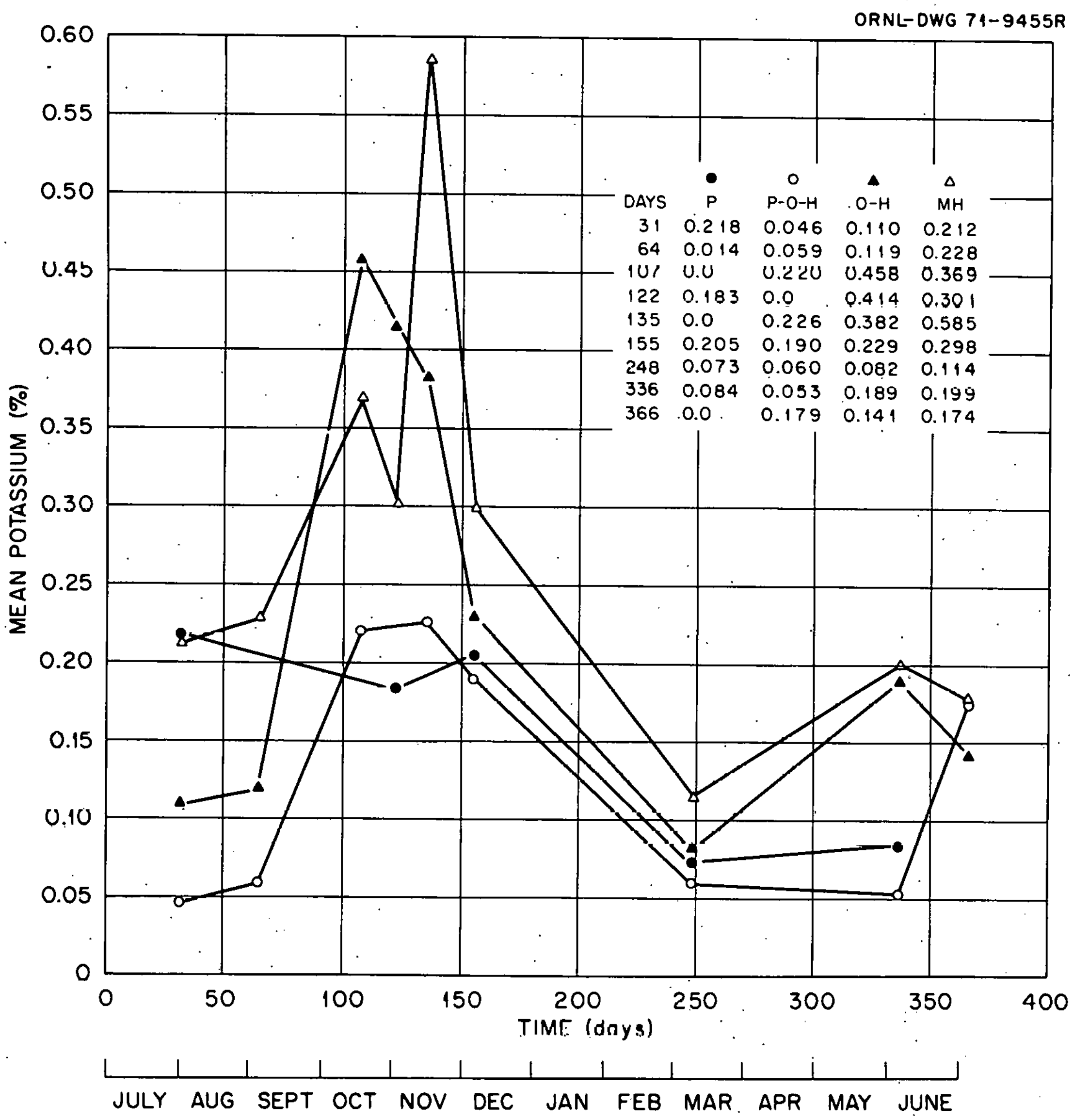
The potassium concentrations in the branch component of litterfall are illustrated in Figure 51. There was an increase in potassium concentrations from summer to autumn in the pine-oak-hickory (0.05-0.23%), oak-hickory (0.11-0.46%), and mesophytic hardwood (0.21-0.59%) forests. Pine forest branches did not show this increase (0.22-0.18%). Potassium concentrations in branches of all forest types are low and followed the same trend in the winter (March 5) collection (pine, 0.07%; pine-oak-hickory, 0.06%; oak-hickory, 0.08%; mesophytic hardwood, 0.11%).

As Figure 52 indicates, most potassium in branch litter moved to the forest floor in the autumn in all forest types. The pine forest branches (20.5 mg/m^2/14 days) returned the most potassium to the forest



DAYS	● P	○ P-O-H	▲ O-H	△ MH
31	8.541	5.725	4.523	5.087
64	17.136	28.231	19.004	23.400
107	92.229	146.026	162.087	175.476
122	104.269	251.774	315.508	354.164
135	402.366	416.426	722.077	440.729
155	224.680	160.408	128.238	119.402
248	2.843	2.236	0.328	0.533
336	10.694	2.519	0.147	0.588
366	21.223	10.318	7.811	7.072

Figure 50. Seasonal rate of return of potassium to the forest floor in leaf litterfall in four forest types on Walker Branch Watershed.



DAYS	● P	○ P-O-H	▲ O-H	△ MH
31	0.218	0.046	0.110	0.212
64	0.014	0.059	0.119	0.228
107	0.0	0.220	0.458	0.369
122	0.183	0.0	0.414	0.301
135	0.0	0.226	0.382	0.585
155	0.205	0.190	0.229	0.298
248	0.073	0.060	0.082	0.114
336	0.084	0.053	0.189	0.199
366	0.0	0.179	0.141	0.174

Figure 51. Seasonal patterns of potassium concentrations (% dry weight) in branch litterfall in four forest types on Walker Branch Watershed.

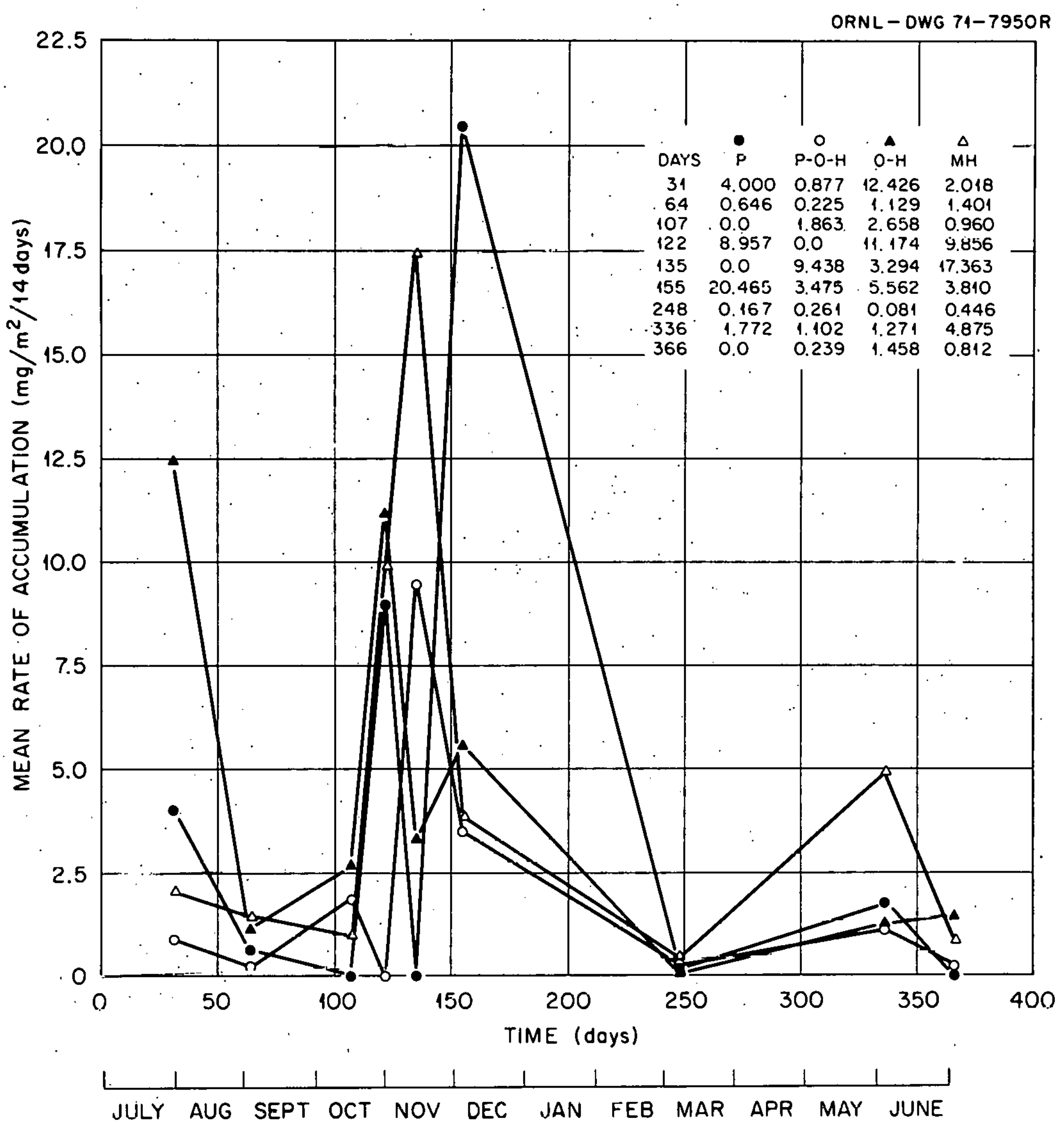


Figure 52. Seasonal rate of return of potassium to the forest floor in branch litterfall in four forest types on Walker Branch Watershed.

floor. The pine forest also returned more potassium later in the season than the other forest types. The least amount of potassium (0.08-0.45 mg/m^2/14 days) moved to the forest floor in the winter (March 5) collection in all four forest types.

The annual totals of potassium returning to the forest floor in reproductive parts are shown in Figure 48, p. 80. Reproductive parts of the mesophytic hardwood (240 mg/m^2) forest contributed the greatest amount of potassium to the forest floor. Reproductive parts of the oak-hickory (150 mg/m^2) forest contributed the second greatest amount, followed by the pine-oak-hickory (140 mg/m^2) and pine (100 mg/m^2) reproductive parts, respectively.

Potassium concentrations were highest in the reproductive parts component of litterfall in all four forest types in the autumn (Figure 53). The highest concentrations during that time were from a low of 0.629% in the oak-hickory forest to a high of 1.69% in the pine-oak-hickory forest. Late winter (March 5) had the lowest potassium concentrations in reproductive parts in all forest types (0.09-0.22%).

The potassium transfer rate through reproductive parts (Figure 54) was greatest during fall with a smaller but noticable increase during early summer (July 2). Again, the transfer rate was influenced mainly by the mass of reproductive parts that fell during this time.

Phosphorus. The greatest annual total amounts of phosphorus in total litterfall (Figure 55) were in the oak-hickory (274 mg/m^2) and mesophytic hardwood (272 mg/m^2) forests. The pine (251 mg/m^2) forest had the next highest amount, while all components of pine-oak-hickory (246 mg/m^2) forest contributed the least amount of phosphorus to the forest

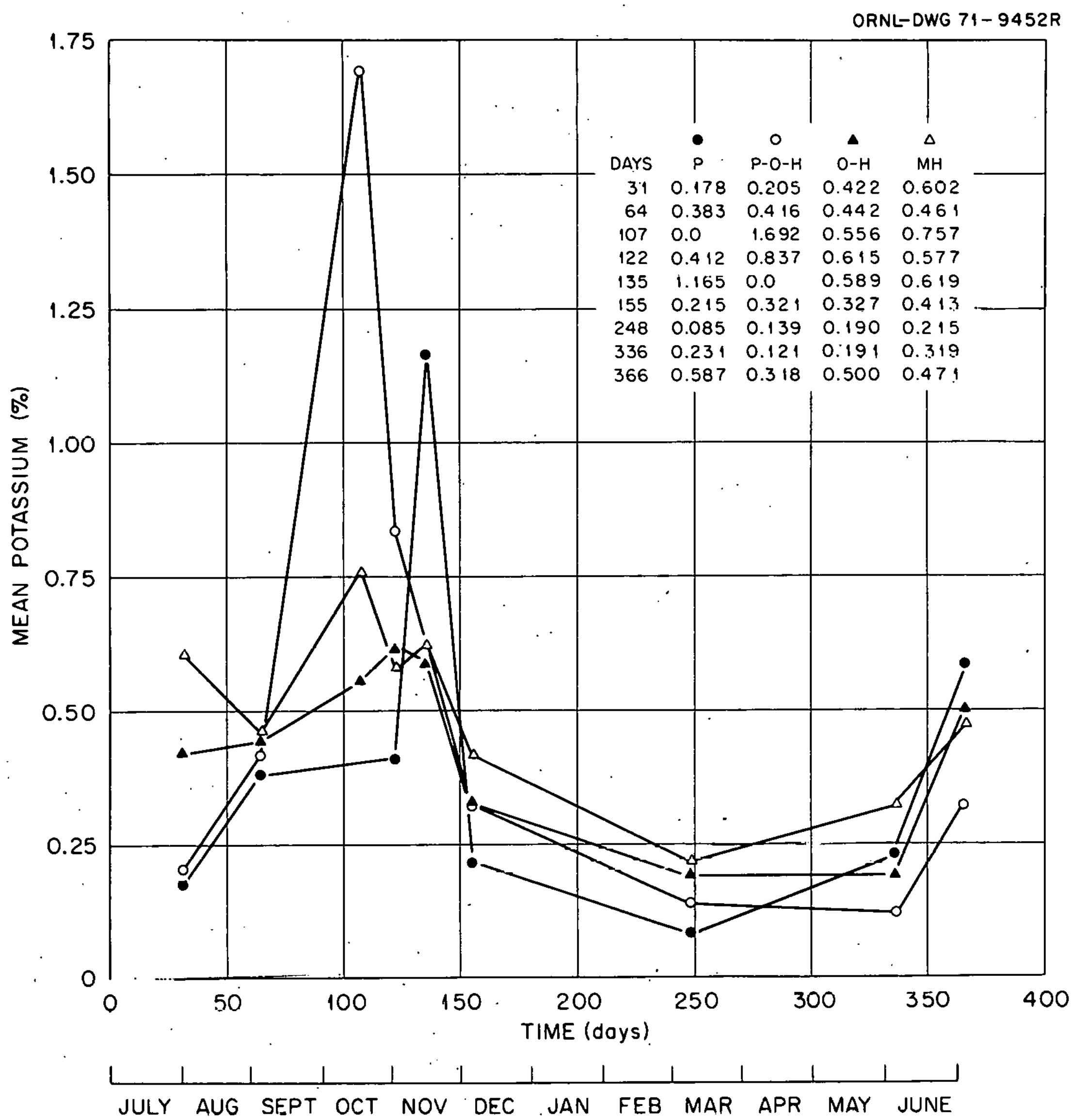


Figure 53. Seasonal patterns of potassium concentrations (% dry weight) in reproductive parts litterfall in four forest types on Walker Branch Watershed.

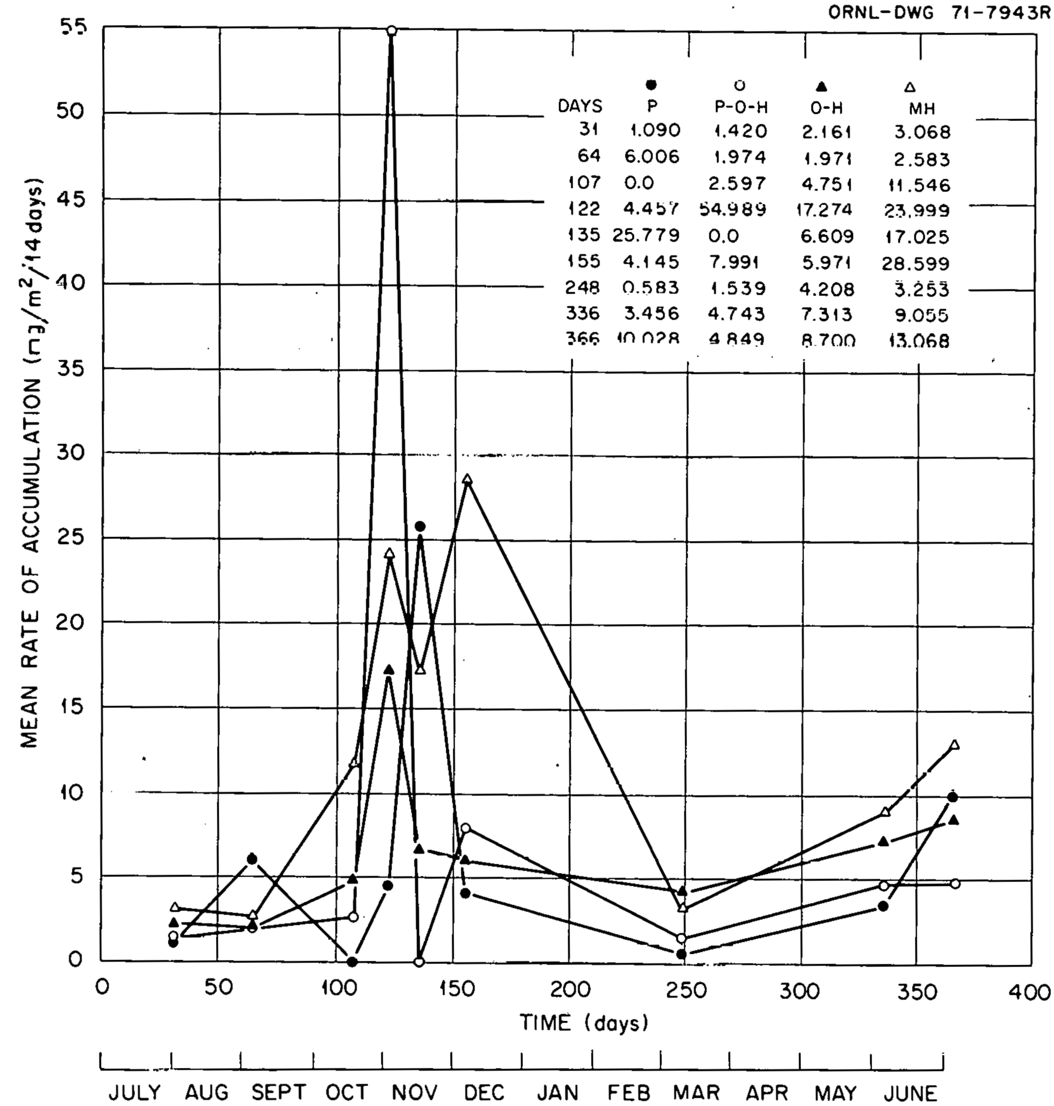


Figure 54. Seasonal rate of return of potassium to the forest floor in reproductive parts litterfall in four forest types on Walker Branch Watershed.

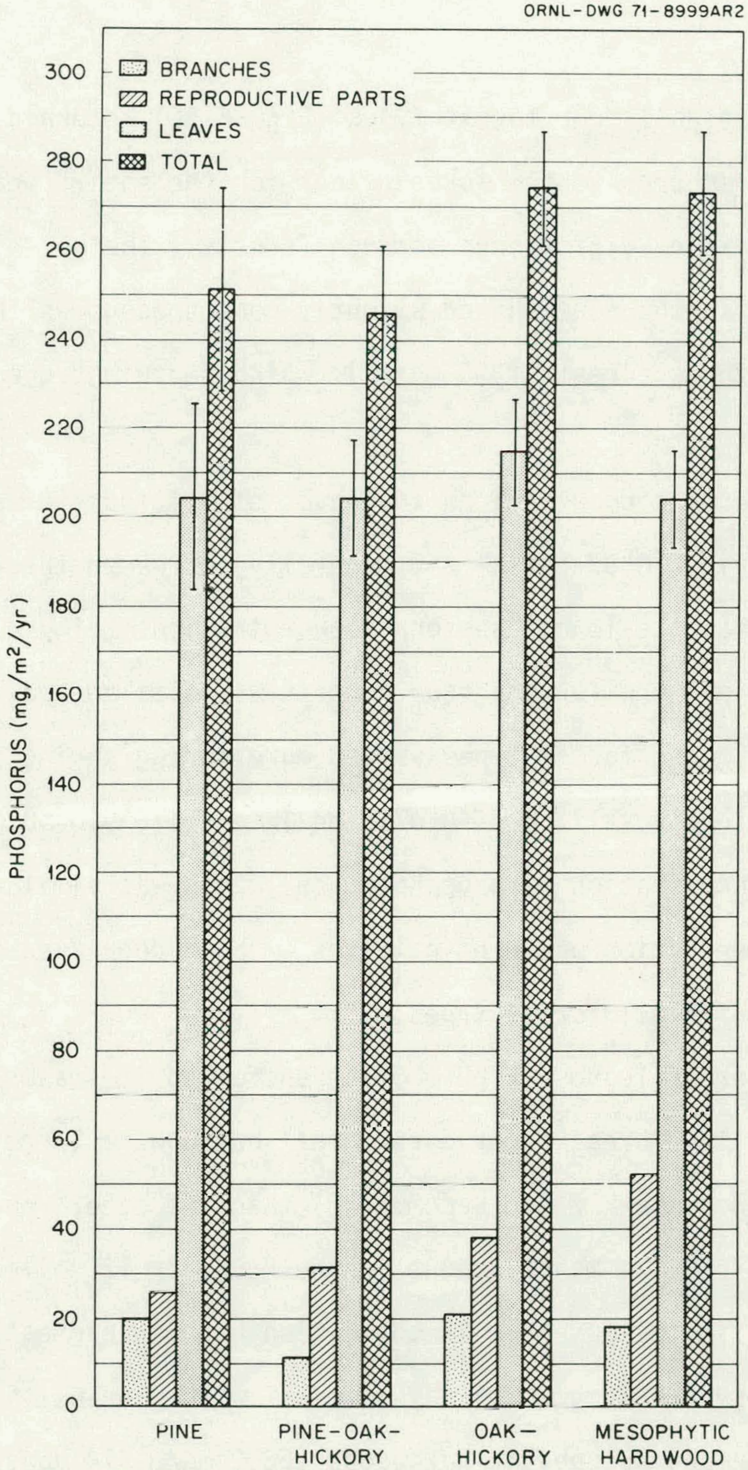


Figure 55. Annual return of phosphorus in litterfall components in four forest types on Walker Branch Watershed with standard errors for the leaf component and for total litterfall for each forest type indicated.

floor for the year. Variations between forest types were not stastically significant.

Leaves of all four forest types (Figure 55) returned almost equal amounts of phosphorus to the forest floor for the entire year. There were no significant differences between forests. The oak-hickory (215 mg/m^2) forest leaves contributed slightly more phosphorus than leaves of the other three forests (205 mg/m^2), which contributed essentially equally amounts.

Phosphorus concentrations in leaves of all four forest types were highest in spring (0.07-0.11%) and generally decreased through fall (0.04-0.05%) which had the lowest seasonal concentrations (Figure 56). The concentration pattern for the four forests was similar and the concentration range among forest types varied more during spring (0.07-0.10%) than in fall (early fall, 0.06-0.07% and late fall, 0.04-0.05%). The pattern of concentration of phosphorus in leaves was similar to the nitrogen concentration pattern in leaves -- both decreased from spring through autumn in all forest types.

Pine forest leaves (Figure 57) transferred its major portion of phosphorus to the forest floor during fall but over a longer and later time period (November 12 and December 2) than the other three forests which transferred its major amount in the November 12 collection. The transfer rate in the November 12 collection had its highest value in the oak-hickory (89.7 mg/m^2/14 days) forest with pine-oak-hickory (54.4 mg/m^2/14 days) and mesophytic hardwoods (53.2 mg/m^2/14 days) values being lower and nearly equal. The pine values in the November 12 and December 2 collections were 36.7 and 37.6 mg/m^2/14 days, respectively.

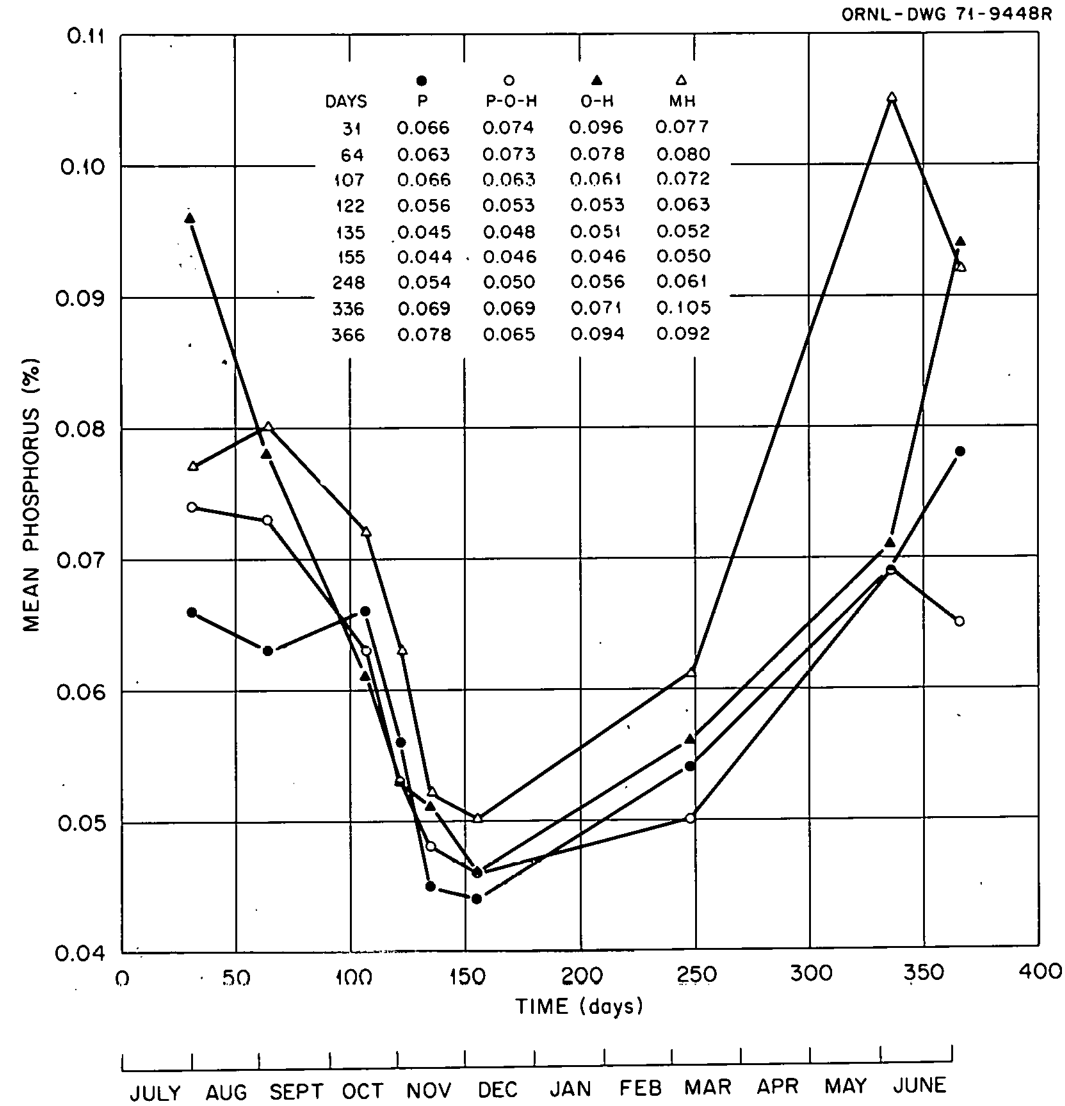


Figure 56. Seasonal patterns of phosphorus concentrations (% dry weight) in leaf litterfall in four forest types on Walker Branch Watershed.

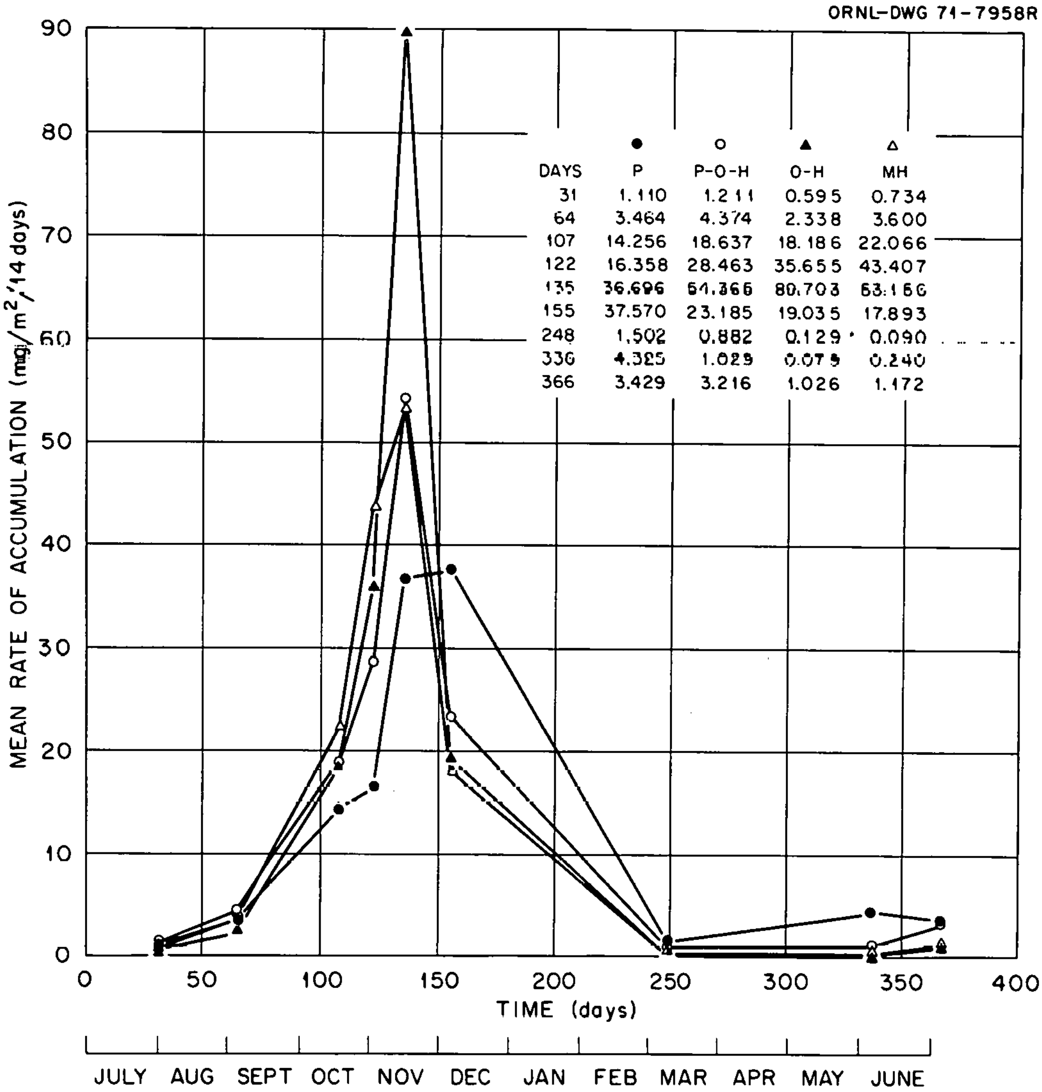


Figure 57. Seasonal rate of return of phosphorus to the forest floor in leaf litterfall in four forest types on Walker Branch Watershed.

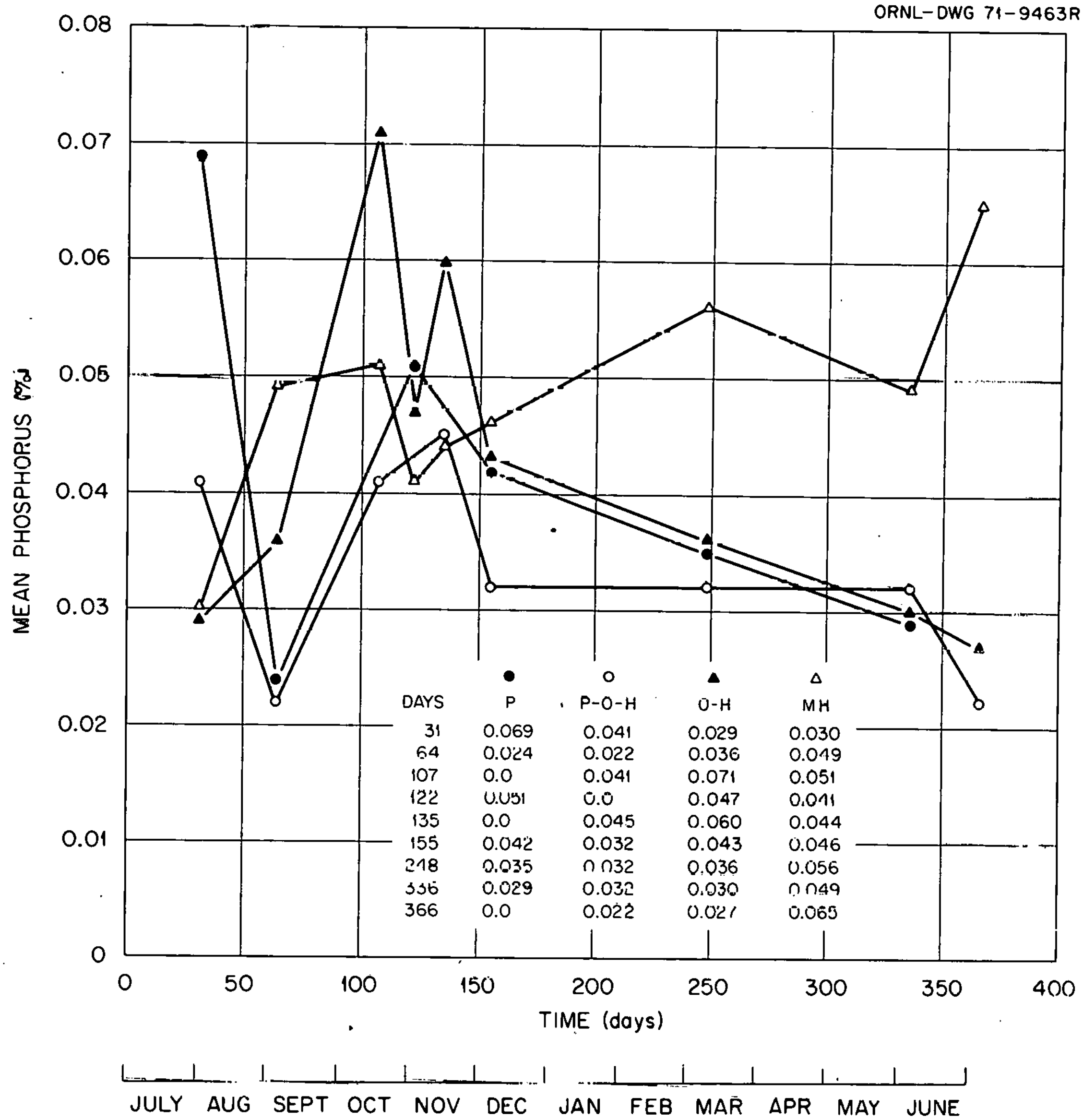
The yearly input of phosphorus to the forest floor by the deposition of branches is illustrated in Figure 55, p. 89. The total amount of phosphorus contributed by branches in the four forests was low and variations were slight. The oak-hickory forest branches contributed the highest amount (21 mg/m^2). The pine (20 mg/m^2), mesophytic hardwood (19 mg/m^2), and pine-oak-hickory (11 mg/m^2) forest branches contributed decreasing amounts of phosphorus, respectively.

Phosphorus concentrations in branches during the year are shown in Figure 58. There was no distinct pattern in phosphorus concentrations between branches of all four forests at almost every collection period.

The transfer rate of phosphorus from branches to the forest floor in the four forest types is shown in Figure 59. The pine (5.5 mg/m^2/14 days) forest had the highest transfer rate and that rate was observed in the late autumn collection (December 2). The pine (2.5 mg/m^2/14 days) forest exhibited a second but smaller value in the October 30 collection. The pine-oak-hickory, oak-hickory, and mesophytic hardwood forest branches had their highest transfer rates during fall and late spring. The lowest values were found in the late winter collection (.04-.21 gm/m^2/14 days).

The reproductive parts component of litterfall contributed annually more phosphorus than did branches in all forest types (Figure 55, p. 89). Reproductive parts of the mesophytic hardwood (52 mg/m^2) forest contributed the most phosphorus to the forest floor for the entire year. The oak-hickory (38 mg/m^2), pine-oak-hickory (31 mg/m^2), and pine (26 mg/m^2) forest reproductive parts contributed decreasing amounts, respectively.

The phosphorus concentrations (Figure 60) in the reproductive parts component for the four forests generally followed the same pattern as the season progressed. Late fall (December 2) and late winter (March



DAYS	● P	○ P-O-H	▲ O-H	△ MH
31	0.069	0.041	0.029	0.030
64	0.024	0.022	0.036	0.049
107	0.0	0.041	0.071	0.051
122	0.051	0.0	0.047	0.041
135	0.0	0.045	0.060	0.044
155	0.042	0.032	0.043	0.046
248	0.035	0.032	0.036	0.056
336	0.029	0.032	0.030	0.049
366	0.0	0.022	0.027	0.065

Figure 58. Seasonal patterns of phosphorus concentrations (% dry weight) in branch litterfall in four forest types on Walker Branch Watershed.

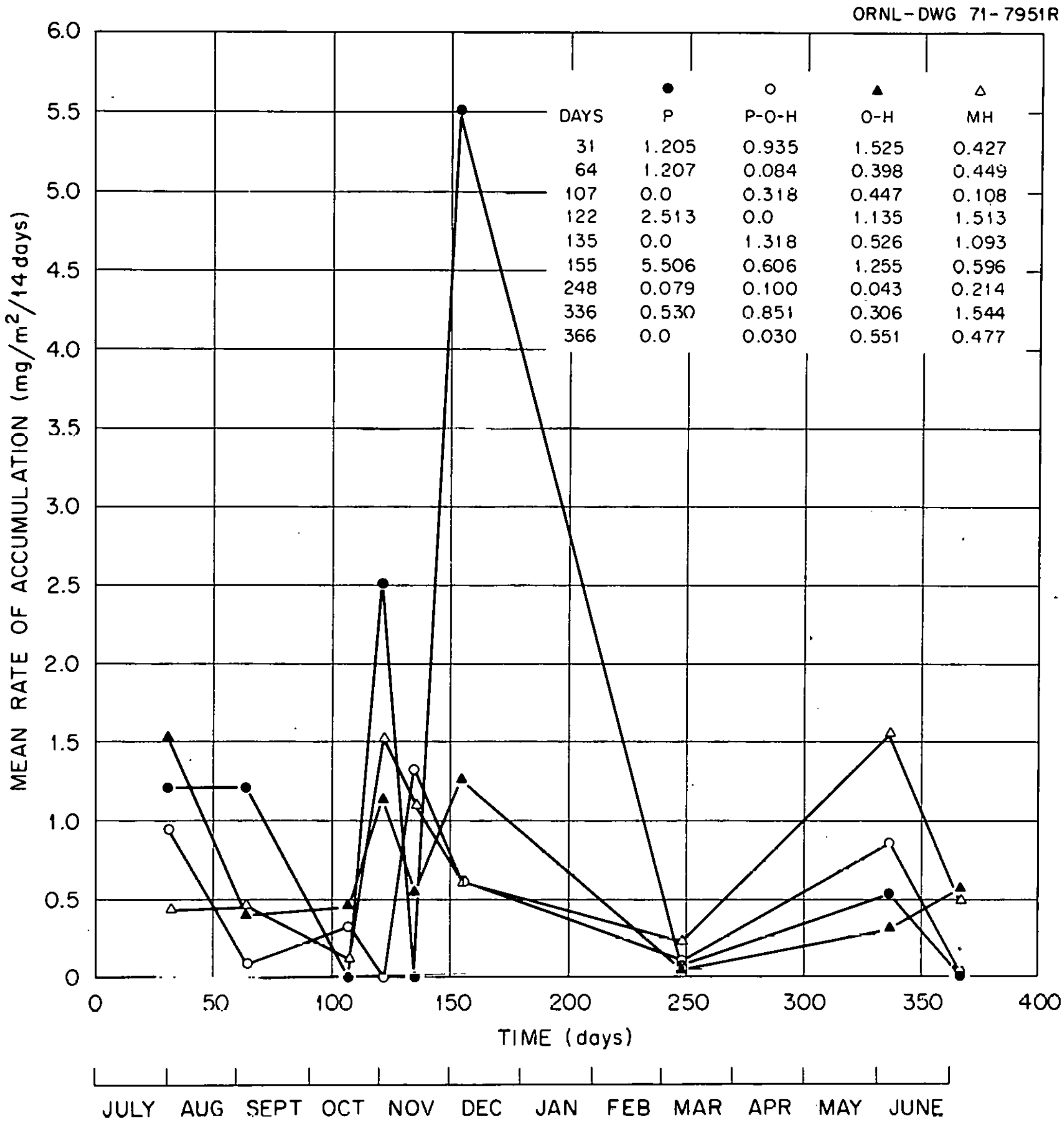


Figure 59. Seasonal rate of return of phosphorus to the forest floor in branch litterfall in four forest types on Walker Branch Watershed.

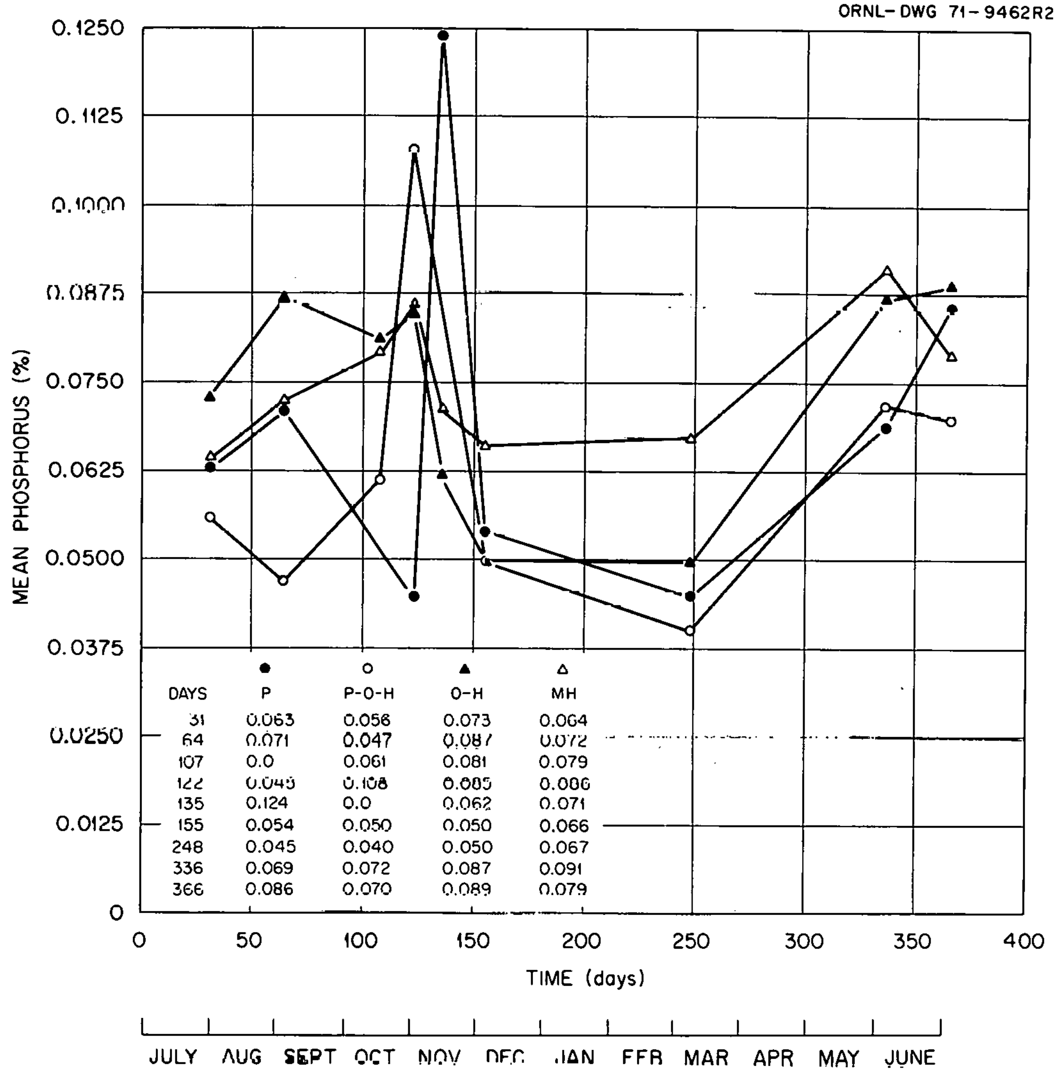


Figure 60. Seasonal patterns of phosphorus concentrations (% dry weight) in reproductive parts litterfall in four forest types on Walker Branch Watershed.

5) had the lowest concentrations while early fall and spring had higher concentrations. The pine (0.12%) forest reproductive parts component in the November 12 collection had the highest single value.

The reproductive parts of pine, pine-oak-hickory, and mesophytic hardwood forests transferred most phosphorus during two periods - fall and spring, while the oak-hickory reproductive parts transferred most phosphorus during spring (Figure 61). Summer and winter were periods of least phosphorus transfer in reproductive parts in all forest types.

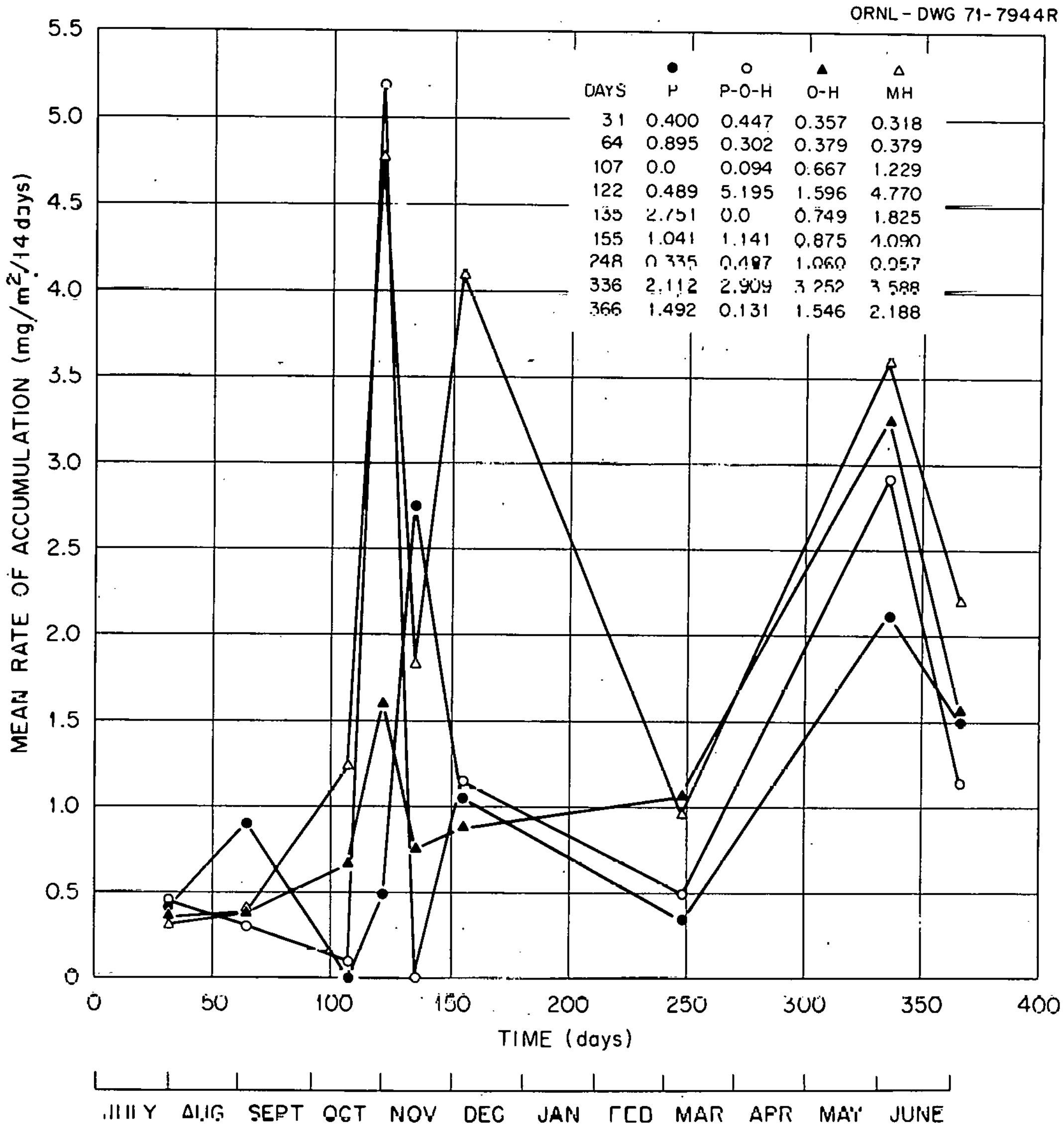


Figure 61. Seasonal rate of return of phosphorus to the forest floor in reproductive parts litterfall in four forest types on Walker Branch Watershed.

CHAPTER IV

DISCUSSION

Seasonal Trends in Deciduous Foliage

Nutrient concentrations and dry weight. Living deciduous leaves of most species increased in dry weight from leaf emergence through spring, when a peak dry weight generally occurred. Although there was variation among species, leaves of most species studied generally had decreasing concentrations of nitrogen and increasing concentrations of calcium through growth. With minor exceptions, magnesium concentrations remained rather constant through the year, while potassium and sodium were variable without a pattern.

Nutrient content. The nutrient content of leaves from the eight deciduous species revealed a seasonal trend. During the period of most rapid growth (May and June) there was an increase in nitrogen, magnesium, sodium, and potassium content to a peak value in July. The calcium and phosphorus contents also increased during this period of initial growth, but the calcium content continued to increase afterward while phosphorus decreased. During autumn, when leaves began to senesce, all nutrient contents decreased variably among species. Calcium decreased the least amount just prior to abscission.

Rank of nutrient concentration. By examining the seasonal data, a ranking of nutrient concentrations between spring (onset of foliage) and autumn (leaf fall) periods can be determined. In most cases these two time periods represent yearly extremes in concentration values. Spring values were N > K > Ca > Mg > P > Na. Autumn values were Ca >

N > K > Mg > P > Na. The one nutrient which changed in position in the rank order between spring and fall was calcium.

There are several reasons why calcium could change in position in the rank order as the season progresses. Potassium is more readily leached than calcium, especially in the fall (Edwards and Shanks 1972). Unlike potassium, calcium does not translocate readily from the leaves in autumn (Williams 1955). For the same reason, calcium exceeded nitrogen in rank order. Calcium also tended to accumulate in foliage while nitrogen did not. Calcium concentrations exceeded those of nitrogen in the fall because the exceptionally high nitrogen values in foliage early in the season were diluted as leaf expansion proceeded, rendering low and continuously decreasing nitrogen concentrations from June on.

Seasonal Trends in Conifer Foliage

Compared to changes in the nutrient status of deciduous conifer foliage, nutrient content changed little during the growing season. The dry weight of the two species of conifer foliage was not different in early May and the end of October. This consistency reflects the fact that the needles which were sampled were not newly initiated but were generally second and third year growth. Early season changes characteristic of recently formed, rapidly expanding leaves were, for the most part, not observed. Additional nutrient variability was thereby introduced since several years' needles were represented. For example, during the season of maximum leaf fall, it was possible that senescing needles and those which would remain for another season were both sampled, thus obscuring seasonal trends due to possible nutrient loss during senescence. Factors contributing to lack of sensitivity of the data include low content and concentration for all nutrients, thus increasing the chance of errors and the fact that needles of different ages may have different nutrient concentrations. Due to the above circumstances no conclusions concerning seasonal nutrient trends are justified, except for the fact that most were quite constant through the year.

Seasonal Trends in Litterfall

Rank of nutrient concentrations. The seasonal trends for nutrients in each component of litterfall and in total litterfall and the seasonal rank of nutrient concentrations are illustrated in Table 6. Values from the October 29, 1969 and June 1, 1970 litterfall collections were used for seasonal comparisons, since these dates coincide with the live leaf study. Foliage from both studies will be compared later.

The March 5, 1970 collection, the last litter trap collection prior to June 1, 1970, was made to collect the remainder of the winter's litterfall. The June 1, 1970 collection was designed to collect the initial spring litterfall material.

Nitrogen and phosphorus concentrations in the leaf litterfall decreased from spring to fall while calcium, magnesium, sodium, and potassium concentrations increased. The rank of nutrient concentrations in the leaf component in the spring was N > Ca > K > Mg > P > Na. Autumn rank was Ca > N > K > Mg > P > Na. The seasonal change in rank of nutrient concentrations was calcium with nitrogen, the reasons probably being that calcium neither leaches nor is translocated very readily and it tends to accumulate in foliage while nitrogen, having a high concentration in spring, is diluted by leaf expansion and development.

All six nutrients increased in percentage concentrations in the branch litterfall from spring to autumn. The rank of nutrient concentrations for both spring and fall was Ca > N > K > Mg > P > Na.

Table 6. Seasonal nutrient concentrations and rank of nutrient concentrations in litterfall components and in total litterfall

	Percentage Concentration of Litterfall Components											
	Leaf[a]			Branch[b]			Reproductive Parts[c]			Total[d]		
Nutrient	June 1	October 30	Increase Decrease Constant	June 1	October 30	Increase Decrease Constant	June 1	October 30	Increase Decrease Constant	June 1	October 30	Increase Decrease Constant
N	1.12	0.80	D	0.66	0.67	I	1.25	0.86	D	1.01	0.77	D
Ca	0.90	1.30	I	1.12	1.66	I	0.85	1.11	I	1.00	1.37	I
Mg	0.11	0.21	I	0.06	0.12	I	0.10	0.18	I	0.09	0.17	I
Na	0.02	0.02	I	0.02	0.02	I	0.02	0.02	C	0.02	0.02	I
K	0.22	0.45	I	0.13	0.30	I	0.22	0.61	I	0.19	0.45	I
P	0.08	0.06	D	0.04	0.05	I	0.08	0.08	C	0.07	0.06	D

[a]Leaf - Spring: N > Ca > K > Mg > P > Na; Autumn: Ca > N > K > Mg > P > Na.

[b]Branch - Spring: Ca > N > K > Mg > P > Na; Autumn: Ca > N > K > Mg > P > Na.

[c]Reproductive Parts - Spring: N > Ca > K > Mg > P > Na; Autumn: Ca > N > K > Mg > P > Na.

[d]Total - Spring: N > Ca > K > Mg > P > Na; Autumn: Ca > N > K > Mg > P > Na.

Nitrogen concentration decreased in the reproductive parts while calcium, magnesium, and potassium concentrations increased as the seasons progressed. The sodium and phosphorus concentrations remained constant. The rank of nutrient concentrations for spring and autumn was the same as the ranking of the leaf litterfall nutrients.

Nutrient concentration patterns or trends and the rank of the nutrients in the two seasons were the same in the leaf litterfall and total litterfall.

Seasonal Comparison of Live Leaf Concentration Values with Leaf Litterfall Concentration Values

Leaf litterfall concentration values and live leaf concentration values in spring and autumn are summarized in Table 7. The values shown for the live leaves are from the May 1 and October 24 collections. The values shown for the leaf litterfall study are from the June 1 and October 30 collections. Although the May 1 live leaf collection and June 1 leaf litterfall collection are 1 month apart, material collected on June 1 included material that fell during May and, therefore, the data are comparable.

Live leaf concentration values are averages of the eight deciduous species studied. Because of the biased sampling technique used on the pines, no conifer values were used. The leaf litterfall concentration values are therefore an average of only three forest types, omitting the pine forest. The high spring calcium concentration, 1.03% in the leaf litterfall, is a consequence of a significantly higher value in the oak-hickory forest.

Nitrogen and phosphorus concentrations decreased as the seasons progressed in both live leaves and leaf litterfall, while calcium and

Table 7. Seasonal nutrient concentrations and rank of nutrient concentrations* in live leaves and in leaf litterfall

Nutrient	Percentage Concentration			
	Live Leaf May 1	Leaf Litterfall June 1	Live Leaf October 29	Leaf Litterfall October 30
N	2.90	1.12	0.95	0.78
Ca	0.61	1.03	1.45	1.30
Mg	0.32	0.10	0.36	0.21
Na	0.02	0.02	0.03	0.02
K	1.23	0.22	0.84	0.47
P	0.28	0.08	0.09	0.06

*Rank of nutrient concentration:

Live Leaf - Spring: N > K > Ca > Mg > P > Na; Autumn: Ca > N > K > Mg > P > Na.

Leaf Litterfall - Spring: N > Ca > K > Mg > P > Na; Autumn: Ca > N > K > Mg > P > Na.

magnesium concentrations increased (sodium increased slightly). The potassium concentration decreased in the live leaves, but increased in the leaf litterfall. That discrepency is probably a result of the very low June 1 leaf litterfall concentration value, therefore increasing the chances of leaching due to the time lag between litter trap collections.

Table 7 also shows the seasonal rank of nutrient concentration in live leaves and leaf litterfall. The ranking of the nutrients in the two comparisons was the same in the autumn. In the spring, calcium ranked above potassium in leaf litterfall but below it in living leaves. This change is probably due to translocation or leaching of potassium that occurred in leaf litterfall while calcium was cumulative, did not translocate, and leached little.

Seasonal Foliage Nutrient Dynamics

Calcium. Since calcium is not translocated from leaves (Chandler 1939), an understanding of its seasonal dynamics is easier. Newly emerged leaves contain minimum amounts and concentrations of calcium. There was generally a sharp increase in both of these parameters thru May, during which time leaf dry weight was also increasing rapidly. Thus, during the earliest portions of the growing season there was a rapid accumulation of calcium in the leaves, most probably due to translocation from lower parts of the tree. With minor exceptions, both content and concentration continued to increase fairly rapidly during June. At that time, most species (except red and chestnut oak) showed no increase or a slight to moderate decrease in dry weight. This was probably due to canopy leaching since almost five inches of rain fell during that period. Thus, due to that decrease in dry weight and apparent lack of leaching of calcium as compared with other components of leaf biomass, the rise in concentration of calcium was considerably greater than that of content. Edwards and Shanks (personal communication) found low levels of calcium leaching during that period.

Resumption of dry weight increase for most species took place in July. The exception was in black gum, which continued to decrease in dry weight thru July. Those increases in dry weight for the seven other deciduous species were closely paralleled by increases in both concentration and content of calcium. Besides black gum, whose decrease in dry weight was reflected in a drop in concentration and content of calcium, the only exception to the previously mentioned trend was in red oak, where a decrease in concentration was accompanied by a slight increase in total content. Thus, not only did calcium content keep up with dry weight increase in most species but, as can be seen by the continuing increase in concentration, it was actually accumulating at a faster rate than was dry matter. The increase in calcium content during that time may have been facilitated by the relatively low (6.0 cm.) rainfall during that period.

The rapid increase in dry weight was again interrupted during August when trends generally varied from either a slight to moderate decrease (sourwood in the latter case) to a slight increase in dry weight values compared to those of July. Since a large amount of rain fell during that period (15 cm.) canopy leaching may have also been a factor in the dry weight pattern. However, during that time, six of the eight deciduous species showed increases in concentrations of calcium, while five of the eight showed substantial increases in total calcium content. Thus, again, while dry weight was not increasing or was actually decreasing, concentration and content of calcium were increasing. Sourwood, which showed the largest decrease in dry weight, also showed a slight decrease in overall content of calcium, but, as can be seen by the increasing concentration of calcium in the sourwood leaves, the decrease in calcium content was much less than the dry weight loss. On the other hand, hickory and white oak were exceptions to the general pattern and leaching could be a factor for values in those two species.

From the beginning of September to the end of the leaf season, trends were different among the species studied, possibly reflecting different phenological sequences (e.g., time of senescence). Sourwood and tulip poplar, which senesce early, declined in dry weight (which began in August) through the remainder of the season. Unlike tulip poplar, which exhibited a decreasing total content of calcium with a constant concentration, (thus showing that calcium was lost in proportion to the other dry weight components) the calcium concentration of sourwood increased continuously while the content remained constant. In sourwood calcium was not lost in proportion to dry weight of living leaves. Hickory, black gum, and red maple (except for one high value for the later) continued their constant levels of dry weight through September with a subsequent sharp decline during October. For those species, the period of constant dry weight was accompanied by increasing concentrations and somewhat higher contents of calcium, suggesting that calcium increases were partly compensating for the loss of foliar weight due to decreases of other nutrients. For black gum and red maple, the period of abrupt decrease in dry weight was accompanied by decreases in both concentration and content of calcium, the former to a much lesser extent than the latter. This suggests that for black gum and red maple calcium decreased more quickly than dry weight. Hickory, on the other hand, showed the opposite trend by an increase in concentration of calcium during autumn (with a corresponding decline in total content). Thus, for hickory, total calcium was lost from leaves less rapidly than dry weight.

The oaks (chestnut, red, and white) showed little tendency to decline in overall calcium content through October. Except for a small decline in red oak at the end of October, the total content of calcium was still increasing in white and chestnut oak leaves.

The divergent behavior exhibited by tulip poplar compared to the oaks and hickory as to their calcium content during the late summer-early fall period can be used to explain different results obtained in throughfall studies at ORNL. Edwards and Shanks (1972 and personal communication) measured throughfall in a forest which had approximately 80% of its basal area in tulip poplar. Their results showed an overwhelming proportion of the yearly canopy leaching of calcium during September-October. Their results coincide well with data from this study, which show that the calcium was lost in proportion to dry weight (which is appreciable) during that time. Since calcium is not translocated from the leaves, (Chandler 1959) its loss can only be explained by canopy leaching. Henderson and Todd (1972) observed that late summer-early fall canopy leaching of calcium was not exceptionally greater than during the rest of the growing season, even in the mixed mesophytic stands. Since tulip poplar comprises a much smaller percentage (18%) of the basal area of the stands on the Watershed than in the forest studied by Edwards and Shanks, less canopy leaching by the oak and hickory foliage should occur on the watershed.

Phosphorus and nitrogen. Phosphorus and nitrogen exhibited somewhat similar trends in concentration and content in leaves during the growing season, especially during early spring. Both nutrients are highly mobile in plants (Williams 1955) and are generally regarded as being in limited supply in most ecosystems.

During May, the period of rapid leaf expansion, both nutrients exhibited extensive decreases in concentration in all species studied. Phosphorus concentration declined by 50%, while the nitrogen concentration declined somewhat less. A comparison of total content helps explain the less drastic decline in nitrogen concentration levels. There was a general rise in total content of both nitrogen and phosphorus between May 2 and May 16, indicating that there was an overall accumulation via translocation during the period, even though phosphorus and nitrogen were not increasing in content as fast as dry weight. Thus, in contrast to calcium, phosphorus and nitrogen translocated through the season. The exceptions were red oak, which remained constant in content of nitrogen and decreased in phosphorus content, and red maple, which exhibited a general increase in phosphorus content but declined slightly in nitrogen content.

The nitrogen and phosphorus concentration trends between the May 16 and June 4 collections were dissimilar, with nitrogen content continuing to increase or at least remaining constant. The exceptions were tulip poplar and white oak, the former showing recovery of that loss in total content at the July 2 collection. Phosphorus content, on the other hand, declined significantly in six species, remained constant in black gum, and increased in sourwood (with subsequent significant declines at the July 29 sampling). Thus, phosphorus was lost from leaves during that time either by translocation to other plant parts or via leaching, or both.

Most studies (Tamm 1951, Olsen 1948, Henderson and Todd 1972) have found that leaching of nitrogen to be of relatively minor importance and thus this process can be disregarded as a factor influencing nitrogen content and concentration in foliage. Results of phosphorus leaching were more variable, with most literature values ranging from 5 to 15%. The spring peak in phosphorus throughfall seen by Carlisle et al. (1966) coincides with observations by Henderson and Todd (1972) and Edwards (personal communication) on Walker Branch Watershed and a Liriodendeon forest, at ORNL. Edwards' data also show a peak in the late summer-early fall while other studies do not. This difference may be due to differential behavior of phosphorus in different species. Tulip poplar, which makes up 80% of the basal area in the Liriodendron forest, exhibited the most pronounced loss of almost all nutrients in the present study, with distinct periods of net loss interrupted by an increase during August. What is probably occurring in the case of phosphorus are high rates of leaching that began abruptly in May as the leaves with high concentration were beginning growth, after which there was a continual process of less intense leaching through June or July, depending on the species. The effect of leaching is probably magnified by translocation of phosphorus from the leaves to other plant parts. Generally the phosphorus content increased or remained the same in mid-summer, possibly due to continued transport to the canopy and lack of leaching due to low levels of phosphorus in the leaves at that time. Except for white oak and sourwood, (which retained leaves after October 29) all other species showed a late summer-early fall decline in phosphorus content. All species except sourwood exhibited a decline in concentration during the fall after variable behavior during mid-summer. The leaching of phosphorus during senescence contributed appreciably to the decline in phosphorus content. A large part of this September-October nutrient loss probably occurred via translocation, as noted in other studies (Carlisle et al. 1966, Alway et al. 1934, Guha and Mitchell 1965, and Rodin and Bazilevich 1967). Similar phenomena probably occurred in the case of nitrogen, which also showed declines in content during late summer-early fall for all species. Edwards (personal communication) observed a small peak for nitrogen leaching in May and a larger peak in September-October, with canopy interception occurring during at least one sampling period each season. Similar results were obtained by Carlisle et al. (1966). Thus, the trend for nitrogen is quite similar to that of phosphorus, with variable behavior during the mid-summer period due to a combination of leaching, canopy interception and translocation, and overall losses during the fall due to leaching and translocation. The biggest difference in the behavior of the two nutrients was from late May to July, when phosphorus contents declined much more than those of nitrogen. The difference was most likely due to differential leaching patterns, with nitrogen showing only slight tendencies to decline in content during that time. Because of differential leaching, nitrogen concentrations declined less during the late spring-early summer period, due to the decrease or lack of increase in leaf dry weight and leaf nitrogen content during the interval.

Potassium. Like phosphorus and nitrogen, potassium was rapidly accumulated during early spring (May) in the newly-formed leaves, when concentrations were generally highest. In two species, tulip poplar and hickory, potassium was accumulated at a faster rate than dry weight, giving increased concentrations during the first sampling interval (May 2 to 16). The other species showed decreasing concentrations. All species showed decreasing concentrations during the second interval (May 16 to June 4). For three species the lower concentrations can be attributed to dry weight increases exceeding actual increases in potassium content, while for the others there were decreases in the total content accompanying increases in dry weight.

Potassium was leached in great quantities (Henderson and Todd 1972) from most vegetation, and there is substantial evidence (Edwards and Shanks 1972) that there was rapid translocation to the leaves throughout the growing season to replenish the leaching loss. The ready availability of potassium in most soils and its high degree of mobility within plants probably influenced its rapid translocation. Early season leaching of potassium is probably responsible for the late May drop in potassium content and partially responsible for the drop in concentration. Sourwood and black gum, the two species that increased substantially in potassium content during the May 16 - June 4 interval, are understory species. It seems possible that they did not lose potassium because the rainwater reaching their leaves already had a substantial amount of potassium in it. It is widely accepted that healthy leaves are capable of taking up nutrients from as well as releasing them to incident precipitation.

After June 4, trends among the different species became more variable. Generally, there was no pattern of continual loss of potassium through mid-summer, except for tulip poplar, which continued the June 4 decline at an accelerated rate through June and July and then at a lesser rate for the rest of the season. Most other species, while exhibiting oscillations during the growing season, maintained or reached element content levels as high as or higher than that of mid-May before exhibiting a sharp drop in concentration and content during the late summer-early fall. Sourwood was the only species which showed no such decline. These data tend to support the conclusion that much of the potassium in tree leaves is held in excess of plant needs ("luxury consumption"), and the excess is readily removed by rainwater. If potassium were less readily leached, its seasonal pattern would probably be similar to that of calcium. Attiwill (1966), Chandler (1939), and Carlisle et al. (1966) found potassium to translocate readily just prior to abscission.

Magnesium. The seasonal behavior of magnesium in foliage has been shown in the literature to be quite variable, depending on the individual species (Guha and Mitchell 1965). In the present study, most species showed an increase in total content during the period of rapid leaf growth, and that has been confirmed by results from this study. Depending on whether the accumulation was greater or less than the accumulation of dry weight during the same period, there was either an increase or a decrease in concentrations.

From early June to mid-summer, two trends were apparent. Overall increases were seen in total magnesium content and concentration of magnesium in red oak and tulip poplar, while relatively constant values of total content were recorded in the other species. Because dry weight changes were more variable than changes in magnesium content, concentration values for these species were somewhat variable, but they, too, oscillated around a constant mean.

September and October again showed several distinct trends in magnesium behavior. Red oak, although again quite variable, increased in magnesium content, while tulip poplar, hickory, and black gum decreased in content. The rest remained relatively constant. However, due to decreases in dry weight during October, the decreases in contents noted above were much less severe when expressed on a concentration basis, with sourwood showing an overall concentration rise.

The behavior of tulip poplar can be explained on the basis of throughfall leaching. Edwards (personal communication) reported substantial amounts of magnesium leaching (up to 40%) in the Liriodendron forest, with peak values during the late summer and fall. Losses during senescence in tulip poplar in our study were on the order of 25% of peak summer values. Translocation could have been a factor, since magnesium can move out of leaves and into the rest of the plant, but this is probably of minimal importance, since magnesium is readily available in the soils at Oak Ridge.

Throughfall data from the three deciduous forest types (Henderson, personal communication) on Walker Branch Watershed showed less distinct seasonal trends and somewhat less magnesium leaching than in the tulip poplar forest, and that is shown in magnesium behavior of the other species in this study. For example, there was a general lack of pronounced autumnal decline in magnesium content of most species, indicating lack of translocation or leaching at that time. Henderson and Todd (1972) found highest throughfall inputs during late summer and early fall to occur in the mesophytic hardwood stands, the forest type were Liriodendron makes its greatest basal area contribution.

Sodium. Sodium values were extremely variable both for total leaf content and leaf concentration through the season, with three overall peaks and declines exhibited by most species. When analyzed seasonally, the trend was for lowest content and concentration early in the season and rising continually through the season. Throughfall values for sodium in the literative are generally low (less than 5% leaching, Edwards personal communication) found canopy leaching to be about 6% leaching in the Liriodendron forest at ORNL. Thus, throughfall input can generally be disregarded as being of any real significance in causing changes in sodium content in foliage in this study. Guha and Mitchell (1965) found several distinct peaks for sodium for all species they studied. In their case, just as in the present study, the peaks for different species are fairly well synchronized. Their study demonstrated increases in sodium content and concentration at the end of the growing season (during senescence) with no subsequent decline. Although considerable variation in sodium concentrations were observed in the present study, the variability of the data does not justify the conclusion that leaching of translocation was occurring to any great degree. Almost all species showed two sodium concentration peaks and those peaks suggest at least two possibilities. One possibility is adsorption of atmospheric sources of sodium on the leaves, while another possibility is contamination during handling of the samples. Sodium occurred in such low concentrations in the foliage of the vegetation on Walker Branch Watershed (0.02-0.05% units) that contamination by either source is possible. The suggested trend, that of gradually increasing concentrations and contents through the season, becomes more possible when these possibilities are considered.

Comparisons of Annual Totals of Litter Components

Total elemental content and dry weight. The annual totals of dry weights and total elemental contents in each component of litterfall in each of the four forest types are summarized in Table 8. Leaves comprised the majority of litterfall in all forest types (77-82%). Reproductive parts constituted the second greatest amount (11-14%) with the exception

Table 8. Dry weight and elemental content of litterfall components by forest types

Component	Mean of Dry Weight (g/m^2) by Forest Types							
	P	%	P-O-H	%	O-H	%	MH	%
Annual Dry Weight Litterfall								
Leaves	389	81	377	81	398	82	342	77
Branches	56	11	37	8	37	8	38	9
Reproductive Parts	38	8	51	11	52	10	63	14
Total	492		465		488		443	
Elemental Content								
Nitrogen								
Leaves	3.04	81	2.74	80	2.88	79	2.70	75
Branches	0.34	9	0.21	6	0.24	7	0.24	7
Reproductive Parts	0.37	10	0.46	14	0.53	14	0.68	18
Total	3.75		3.41		3.65		3.62	
Calcium								
Leaves	4.11	81	3.82	85	3.86	80	4.58	79
Branches	0.64	13	0.26	6	0.53	10	0.61	10
Reproductive Parts	0.35	6	0.42	9	0.52	10	0.64	11
Total	5.10		4.50		4.91		5.83	
Magnesium								
Leaves	0.67	88	0.68	91	0.77	89	0.71	85
Branches	0.05	6	0.02	2	0.04	4	0.04	5
Reproductive Parts	0.04	6	0.05	7	0.06	7	0.08	10
Total	0.76		0.75		0.87		0.83	
Sodium								
Leaves	0.06	76	0.06	76	0.07	78	0.07	78
Branches	0.01	12	0.01	12	0.01	11	0.01	11
Reproductive Parts	0.01	12	0.01	12	0.01	11	0.01	11
Total	0.08		0.08		0.09		0.09	
Potassium								
Leaves	1.28	89	1.47	90	1.76	89	1.59	83
Branches	0.06	4	0.03	1	0.07	3	0.08	4
Reproductive Parts	0.10	7	0.14	9	0.15	8	0.24	13
Total	1.44		1.64		1.98		1.91	
Phosphorus								
Leaves	0.20	80	0.20	83	0.21	78	0.20	74
Branches	0.02	8	0.01	4	0.02	7	0.02	7
Reproductive Parts	0.03	12	0.03	13	0.04	15	0.05	19
Total	0.25		0.24		0.27		0.27	

of the pine forest (8%) while branches, again with the exception of the pine forest (11%), contributed the least (8-9%).

In considering the six nutrients studied in this paper, leaves contained 74 to 91% of the total nutrient content of litterfall in each of the forest types. With the exception of the calcium (13%) and magnesium (7%) content in branches of the pine forest, the elemental content of reproductive parts was equal to or greater than the elemental content of branches in all forest types.

Table 9 ranks forest types according to the contribution of biomass and nutrient content in each litterfall component. The nutrient content and biomass of leaf litterfall in the four forests varied more than the content and biomass of reproductive parts and of branch litterfall, which did not differ from each other.

The differences in amounts of nutrients in leaf litterfall in the four forests can be accounted for by discussing each nutrient individually. Although the oak-hickory forest was higher in total biomass than the pine forest, the amount of nitrogen (g/m^2) was higher in the matter. That is probably due to the time period of leaf fall which was longer in the pine forest (smaller but much broader peak) than in the oak-hickory forest (sharp peak).

Although the mesophytic hardwood forest contributed the least amount of leaf biomass, the calcium content (g/m^2) was greatest in that forest because of the high calcium content in tulip poplar (Figure 7, p. 25), the dominant overstory species of the mesophytic hardwood forest. The mesophytic forest also contributed the highest concentration of calcium during peak leaf fall (Figure 27, p. 53).

Table 9. Ranking of the four forest types by total annual contribution of biomass and nutrients in litterfall components

Biomass	Nitrogen	Calcium	Magnesium	Sodium	Potassium	Phosphorus
Leaves						
O-H	P	MH	O-H	O-H=MH	O-H	O-H
P	O-H	P	MH		MH	P=P-O-H=MH
P-O-H	P-O-H	O-H	P-O-H	P=P-O-H	P-O-H	
MH	MH	P-O-H	P		P	
Branches						
P	P	P	P	P=O-H=P-O-H=MH	MH	P=O-H=MH
MH	MH=O-H	MH	O-H=MH		O-H	
P-O-H		O-H			P	
O-H	P-O-H	P-O-H	P-O-H		P-O-H	P-O-H
Reproductive Parts						
MH	MH	MH	MH	P=P-O-H=O-H=MH	MH	MH
O-H	O-H	O-H	O-H		O-H	O-H
P-O-H	P-O-H	P-O-H	P-O-H		P-O-H	P=P-O-H
P	P	P	P		P	
Total						
P	P	MH	O-H	O-H=MH	O-H	O-H=MH
O-H	O-H	P	MH		MH	
P-O-H	MH	O-H	P	P=P-O-H	P-O-H	P
MH	P-O-H	P-O-H	P-O-H		P	P-O-H

(↑ Increase — printed beside each of the four blocks: Leaves, Branches, Reproductive Parts, Total)

The magnesium, potassium, and phosphorus contents (g/m^2) in leaves were highest in the oak-hickory forest (highest producer of biomass). The sodium contents (g/m^2) in the oak-hickory and mesophytic hardwood forests were equal. The sodium range in leaves was very low and very slight differences in values (Table 9) are observed.

The annual leaf litterfall nutrient content with respect to rank of forest types exhibited other, more minor variations. Those variations may be explained from the data on nutrient concentrations and nutrient content in the live leaf study and the leaf biomass, percent concentration, and mean rate of accumulation in the litter trap study.

Significance of nutrient litterfall input with other sources. The input of major nutrients to the forest floor via litterfall versus atmospheric (wetfall and dryfall) and leaching inputs in a very important and significant contribution. Atmospheric and leaching input values on Walker Branch Watershed taken from Swank and Henderson (1975) are used with litterfall input found in the present study to calculate total nutrient input to the forest floor (Table 10). Potassium is the only nutrient that litterfall did not contribute at least 50% of total input. Of the total input canopy leaching contributed 48% of the total potassium input, atmospheric input, 7%, and litterfall, 45%.

Rank of nutrient content of litterfall components. The rank order of the annual total of dry weight and of each of the six elements investigated in each component of litterfall is shown in Tables 11 through 14. The ranking for the leaf (Table 11), branch (Table 12), and total litterfall (Table 14) components in each forest type was Ca > N > K > Mg > P > Na and the average values for nutrients in the four forest types are in the tables. The ranking for the reproductive parts component (Table 13)

Table 10. Comparisons of the significance of the elemental content in litterfall input (Kg/ha/yr) to the forest floor with other sources of input on Walker Branch Watershed

Nutrient	Total Input	Litterfall		Atmospheric		Leaching	
		Input	%	Input	%	Input	%
Nitrogen	53.5	36.1	68	13.0	24	4.4	8
Calcium	80.9	50.9	63	15.7	19	14.3	18
Magnesium	13.6	8.0	59	3.1	23	2.5	18
Potassium	39.2	17.4	45	2.9	7	18.9	48
Phosphorus	3.5	2.6	73	0.6	17	0.3	9

Table 11. Amounts ($g/m^2/yr$) of elements in annual leaf litterfall in the four forest types on Walker Branch Watershed

Forest Type	Ca	>	N	>	K	>	Mg	>	P	>	Na	Dry Weight
1 Pine	4.11		3.04		1.28		0.67		0.20		0.06	398
2 Pine-Oak-Hickory	3.82		2.74		1.47		0.68		0.20		0.06	377
3 Oak-Hickory	3.86		2.88		1.76		0.77		0.21		0.07	398
4 Mesophytic Hardwood	4.58		2.70		1.59		0.71		0.20		0.07	342
Average	4.09		2.84		1.52		0.71		0.20		0.07	378

Table 12. Amounts ($g/m^2/yr$) of elements in annual branch litterfall in the four forest types on Walker Branch Watershed

Forest Type	Ca >	N >	K >	Mg >	P >	Na	Dry Weight
1 Pine	0.64	0.34	0.06	0.05	0.02	0.01	56
2 Pine-Oak-Hickory	0.26	0.21	0.03	0.02	0.01	0.01	34
3 Oak-Hickory	0.53	0.24	0.07	0.04	0.02	0.01	37
4 Mesophytic Hardwood	0.61	0.24	0.08	0.04	0.02	0.01	38
Average	0.51	0.26	0.06	0.04	0.02	0.01	41

Table 13. Amounts ($g/m^2/yr$) of elements in annual reproductive parts litterfall in the four forest types on Walker Branch Watershed

Forest Type	N	>	Ca	>	K	>	Mg	>	P	>	Na	Dry Weight
1 Pine	0.37		0.35		0.10		0.04		0.03		0.01	38
2 Pine-Oak-Hickory	0.46		0.42		0.14		0.05		0.03		0.01	51
3 Oak-Hickory	0.53		0.52		0.15		0.06		0.04		0.01	52
4 Mesophytic Hardwood	0.68		0.64		0.24		0.08		0.05		0.01	63
Average	0.51		0.48		0.16		0.06		0.04		0.01	51

Table 14. Amounts ($g/m^2/yr$) of elements in annual litterfall in the four forest types on Walker Branch Watershed

Forest Type	Ca	>	N	>	K	>	Mg	>	P	>	Na	Dry Weight
1 Pine	5.10		3.75		1.44		0.76		0.25		0.08	492
2 Pine-Oak-Hickory	4.50		3.41		1.64		0.75		0.24		0.08	465
3 Oak-Hickory	4.91		3.65		1.98		0.87		0.27		0.09	488
4 Mesophytic Hardwood	5.83		3.62		1.91		0.83		0.27		0.09	444
Average	5.09		3.61		1.74		0.80		0.26		0.09	472

in each forest type was N > Ca > K > Mg > P > Na and the average values for the forest types are in Table 13. The only variation in the ranking then, is the change of position between nitrogen and calcium in the reproductive parts component.

Elemental content and dry weight on total area of each forest type and on entire watershed. The dry weights and elemental content in each component of litterfall for the year for the total area of each forest as well as for the entire watershed are shown in Table 15. Numbers used in this table were rounded off to the nearest unit while the percentage values were taken from the actual numbers. The dry weight of leaves for the entire watershed constituted 81% of the total litterfall with reproductive parts (11%) and branches (8%) accounting for the remainder.

Leaves contained 78 to 88% of the total amount of any of the six nutrients studied. Reproductive parts contained the same amount of calcium (10%) and sodium (11%) as branches but greater amounts of nitrogen, magnesium, potassium, and phosphorus.

Canonical analysis. Canonical analysis (Seal 1968) was applied to the total weight and total content of the six nutrients in each component of litterfall and in total litterfall for the year in each forest type to test for differences between the four forest types. Canonical analysis reduces the seven (six nutrients plus dry weight) measurements which may be dependent to two measurements which are independent and these two factors are plotted on a two-dimensional graph. A 95% confidence circle is drawn around the points for each forest type. Overlapping of circles means that forest types do not differ significantly from one another.

As shown in Figure 62(a), leaves of the pine and pine-oak-hickory forest types were not significantly different from each other but leaves

Table 15. Extrapolation, using the area of each forest type, of annual transfers of dry matter and mineral content in litterfall components on Walker Branch Watershed

Component	P (6.88ha)	P-O-H (14.16ha)	O-H (57.87ha)	MH (18.62ha)	Entire Watershed (97.53ha)	%
Annual Dry Weight Litterfall						
Leaves	27,400	53,300	230,600	63,700	375,000	81
Branches	3,900	5,300	21,400	7,100	37,700	8
Reproductive Parts	2,600	7,200	30,400	11,800	51,000	11
Total	33,900	65,800	282,400	82,600	463,700	
Mineral Content						
Nitrogen						
Leaves	209	388	1,667	503	2,767	78
Branches	23	30	139	45	237	7
Reproductive Parts	25	65	307	127	524	5
Total	258	483	2,112	674	3,527	
Calcium						
Leaves	283	541	2,234	853	3,910	80
Branches	44	37	307	114	501	10
Reproductive Parts	24	59	301	119	504	10
Total	351	637	2,841	1,086	4,915	
Magnesium						
Leaves	46	96	446	132	720	88
Branches	3	3	23	7	37	5
Reproductive Parts	3	7	35	15	59	7
Total	52	106	503	155	817	
Sodium						
Leaves	4	9	41	13	66	78
Branches	1	1	6	2	10	11
Reproductive Parts	1	1	6	2	10	11
Total	6	11	53	17	86	
Potassium						
Leaves	88	208	1,019	296	1,611	88
Branches	4	4	41	15	64	3
Reproductive Parts	7	20	87	45	158	9
Total	99	232	1,146	356	1,833	
Phosphorus						
Leaves	14	28	122	37	201	78
Branches	1	1	12	4	18	7
Reproductive Parts	2	4	23	9	39	15
Total	17	33	156	50	258	

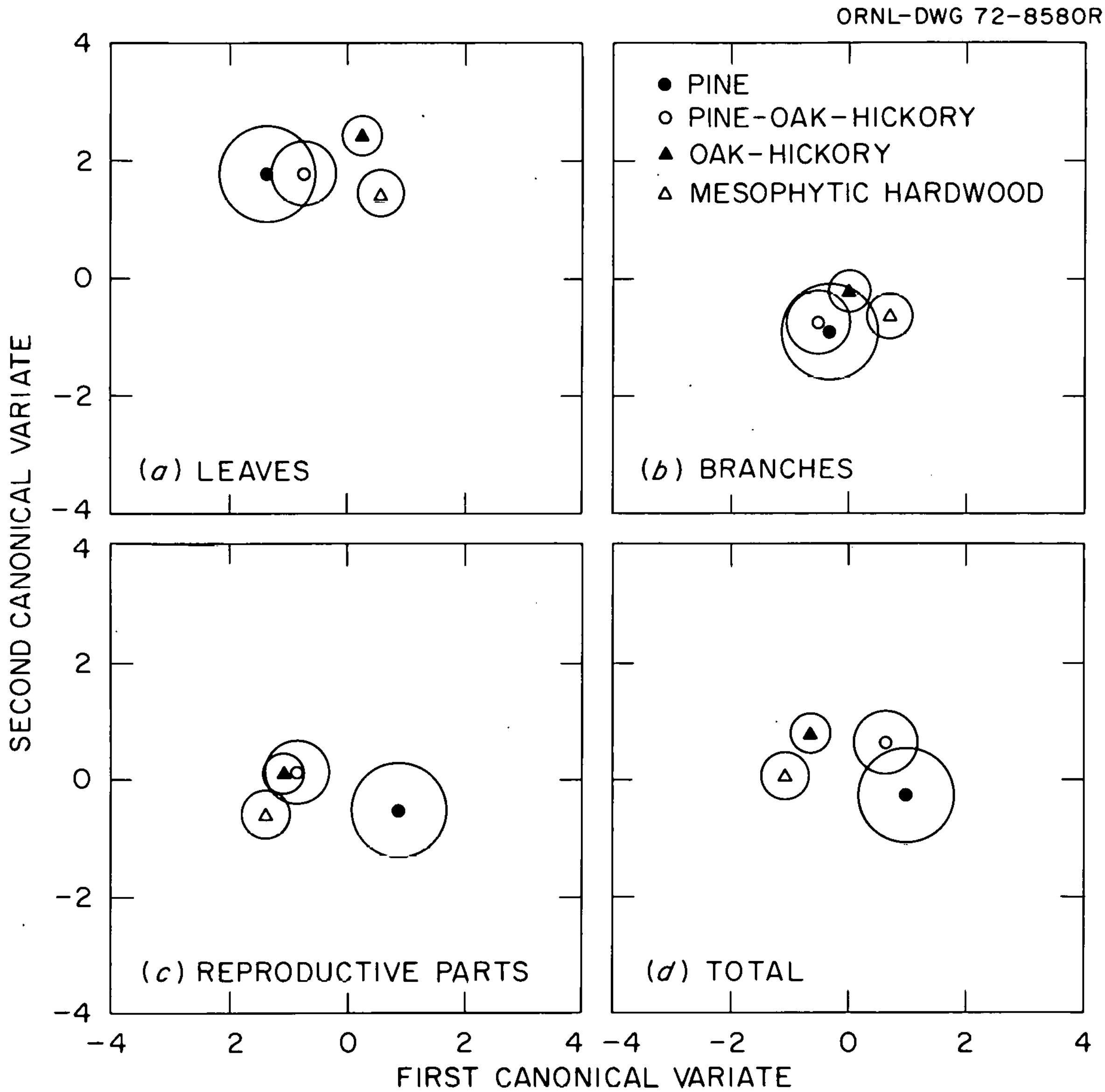


Figure 62. Mean canonical points for each component of litterfall and for total litterfall with 95% confidence circles.

from the oak-hickory and mesophytic hardwoods did differ significantly from each other and also from leaves of pine and pine-oak-hickory forests.

The branch component of litterfall is shown in Figure 62(b). Branches of the pine, pine-oak-hickory, and oak-hickory forest types did not appear to differ significantly, but there is a slight indication that mesophytic hardwood branches differed from branches of the pine-oak-hickory and oak-hickory forests.

Figure 62(c) illustrates the results of the canonical analysis for reproductive parts. Pine reproductive parts differed significantly from those of the other three forest types, which did not differ significantly from each other.

Results of the canonical analysis of total litter from leaves, branches and reproductive parts are plotted in Figure 62(d). Pine and pine-oak-hickory did not significantly differ from each other, but did differ significantly from oak-hickory and mesophytic hardwood, which also differed significantly from each other.

CHAPTER V

SUMMARY

1. The rank of nutrient concentrations in leaf litter during spring was N > Ca > K > Mg > P > Na while in fall it was Ca > N > K > Mg > P > Na. The concentration of nutrients in the reproductive parts component of litterfall during spring followed this pattern: N > Ca > K > Mg > P > Na. Autumn ranking was Ca > N > K > Mg > P > Na. The spring and autumn nutrient importance in branches was Ca > N > K > Mg > P > Na. The rank of nutrient concentration in combined litterfall during spring was N > Ca > K > Mg > P > Na. Fall ranking was Ca > N > K > Mg > P > Na.

2. Litterfall biomass averaged 492 $g/m^2/yr$ in the pine forest, 465 g/m^2 in the pine-oak-hickory forest, 488 g/m^2 in the oak-hickory forest, 444 $g/m^2/yr$ in the mesophytic hardwood forest. Seasonal peaks in litterfall inputs were: autumn for the leaf component, spring and autumn for reproductive parts, while the branch input was distributed erratically throughout the year. This ranking did not differ among forest types. For the watershed as a whole (97.5 ha), the litterfall biomass values were (in kg); leaves 3.75×10^5, branches 3.77×10^4, reproductive parts 5.20×10^4, and total litterfall 4.65×10^5.

3. The majority of litterfall biomass in all four forest types was made up of leaves (77-85%). Reproductive parts contributed 8-14% while branches contributed 8-11%. Leaves constituted 81% of the dry weight of litterfall on the whole watershed, reproductive parts accounted for 11%, and branches accounted for 8%.

4. A canonical analysis technique performed on the litterfall biomass and nutrient content data for the four forest types revealed that at

least one forest type differed significantly from the rest for each litterfall component and total litterfall.

5. The producers of leaf foliage biomass were, in decreasing rank on an annual basis: red oak, chestnut oak, tulip poplar, white oak, hickory, red maple, black gum, sourwood, loblolly pine, and shortleaf pine. Foliage of the deciduous species increased sharply in dry weight during early development and then gradually increased or leveled off. Prior to abscission all deciduous species lost weight. The conifer foliage showed no seasonal increase in dry weight because only mature leaves were collected.

6. The rank of nutrient concentration in spring foliage was N > K > Ca > Mg > P > Na. Autumn nutrient concentration order was Ca > N > K > Mg > P > Na. The nitrogen and phosphorus concentrations decreased as the growing season progressed while calcium increased with development. Magnesium concentrations remained constant, while potassium and sodium concentrations were variable from onset until defoliation.

7. Foliage of deciduous species increased in calcium content until abscission while the nitrogen, magnesium, sodium, and potassium content increased initially (during the period of most rapid growth) and then leveled off. The phosphorus content increased initially, also, but decreased thereafter. During fall, when leaves began to abscise, all nutrient content decreased, with calcium decreasing the least.

8. Foliage nutrient dynamics can be seen as a function of leaf biomass changes as well as such factors as differential canopy leaching, physiological age and condition of the leaf and translocation to and from the leaf. Thus, foliage biomass and nutrient dynamics, just as those of

litterfall, were mediated by environmental conditions, especially with regard to the hydrologic cycle.

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