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BIOMASS, ANNUAL NET PRIMARY PRODUCTION, AND DYNAMICS OF SIX MINERAL ELEMENTS IN A POST OAK-BLACKJACK FOREST

A DISSERTATION

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BY

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BIOMASS, ANNUAL NET PRIMARY PRODUCTION, AND DYNAMICS OF SIX MINERAL ELEMENTS IN A POST OAK - BLACKJACK FOREST

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DISSERTATION COMMITTEE

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BIOMASS, ANNUAL NET PRIMARY PRODUCTION, AND DYNAMICS OF SIX MINERAL ELEMENTS IN A POST OAK-BLACKJACK FOREST

ABSTRACT

Dimension analysis was used to estimate biomass and annual net primary production for a post oak-blackjack forest in central Oklahoma. Time-series of concentrations of six mineral elements in various plant tissues were determined and used with biomass and production estimates to determine the annual cycle of N, P, K, Ca, Mg, and Mn in the forest. Total accumulation of organic material in the stand is 245000 kg/ha, of which 1.6% is leaves, 26.4% live branches, 5.9% dead branches, 44.8% trunks, 15.9% roots, 0.6% understory, and 4.4% litter. Annual net primary production is 14900 kg/ha, distributed as follows: 32.0% leaves, 28.0% twigs and branches, 24.9% trunks, 15.1% roots, and 2.0% understory. The biomass contains 1157 kg/ha N, 101 kg/ha P, 1258 kg/ha K, 4549 kg/ha Ca, 311 kg/ha Mg, and 124 kg/ha Mn. Curves are shown for seasonal variation of mineral concentrations in twigs and leaves. High values for true increment of biomass and for retention of mineral elements indicate that the stand has not reached a steady state, which is confirmed by observations of stand structure.

INTRODUCTION

This paper represents a continuation of the series of investigations in the deciduous forest border initiated at the University of Oklahoma in 1953 (Rice and Penfound 1955). Rice and Penfound (1959) conducted an extensive quantitative analysis of the Oklahoma upland forests, in which they investigated species distribution and importance and characterized the major upland forest types of the state. Comparative microclimate studies in forests were done by Rice (1960, 1962). Buck (1964) investigated the effect of soil types, geological formations, and topography on the distribution of forest vegetation in the Wichita Mountains. Rice (1965) studied the relationships between floodplain forests and various edaphic factors. Species behavior and species diversity in the upland forests of the state were investigated by Risser and Rice (1971a, 1971b). Adams and Risser (1971a, 1971b) investigated the phytosociology of corticolous lichens in upland forests. Johnson and Risser (1972) determined the distribution of major upland tree species in relation to gradients of soil moisture and soil chemical properties. A correlation analysis of rainfall with annual ring width for post oak and blackjack was done by Johnson and Risser (1973).

The purpose of the present study was to determine biomass, primary production and mineral budgets for several important elements in a representative Oklahoma upland forest stand. Since post oak and blackjack account for approximately 70% of the total basal area in the upland forests of Oklahoma (Rice and Penfound 1959), a stand composed almost entirely of these two species and located in the central part of the state was chosen for study.

About 4,170,000 ha (24% of the land area) of Oklahoma is in forest (Phillips, Gibbs, and Mattoon 1959), which constitutes a major natural resource for the state. An understanding of ecosystem function is essential for efficient management and utilization of these forest resources. Results of this study and others will be used in construction of a dynamic, mechanistic simulation model of the post oak-blackjack forest ecosystem in order to gain a better understanding of the flow of energy and materials through the system. The only work done so far toward characterizing a total ecosystem in Oklahoma has been in the tall-grass prairie (Sheedy 1971; Sheedy, Johnson and Risser 1973; Risser and Kennedy 1972).

Elsewhere, several ecosystem studies have been done in recent years and many more are presently being conducted. No attempt is made here to review the extensive literature, but a number of the studies will be referred to in the results and discussion section.

STUDY AREA

Field sampling was done in the University of Oklahoma's Lake Thunderbird Research Area 17 km east of Norman, Oklahoma. The climate of the area is classified by Trewartha (1968) as subtropical humid. Mean annual precipitation is 86.2 cm and mean annual temperature is 16.1 C. Topography of the area is gently rolling and the soil (see Table 2 for textural analysis) is a sandy red-yellow podzolic developed from sandstone.

The vegetation of the area is similar to that described by Dyksterhuis (1948) in the Western Cross Timbers of Texas. Woody vegetation is dense on lower slopes and along ravines, but is open and savannah-like on upper slopes and ridgetops. Sampling for this study was confined to the lower slopes.

Overstory vegetation on the lower slopes consists almost entirely of post oak (*Quercus stellata* Wang.) and blackjack (*Q. marilandica* Muench.) with a few black oak (*Q. velutina* Lam.) and hickory (*Carya texana* Buckl.). The understory consists mostly of small oaks, dogwood (*Cornus drummondii* Meyer), and redbud (*Cercis canadensis* L.). Herbaceous vegetation is sparse but consists of many species. A species list is given in Table 1 and a quantitative analysis of the woody vegetation is given in Table 3.

An area 40 x 50 m (0.2 ha) was selected to be representative of the lower slope (forest type) vegetation and was divided into 20 10 x 10 m (0.01 ha) squares identified by numbered stakes at each corner. This area was used for intensive and repetitive sampling throughout the time of the investigation.

Table 1. List of Species from Study Plot.

Acalypha virginica L.	Lechea villosa Ell.
Ambrosia artemisiifolia L.	Morus rubra L.
Andropogon ternarius Michx.	Oxalis violacea L.
Aristida longespica Poir.	Panicum praecocius Hitchc. & Chase
Ascyrum hypericoides L.	Panicum ravenelii Scribn. & Merr.
Baptisia leucophaea Nutt.	Panicum sphaerocarpon Ell.
Carex muhlenbergii Schkuhr.	Passiflora lutea L.
Carya texana Buckl.	Penstemon laxiflorus Pennell
Cassia nictitans L.	Quercus marilandica Muench.
Cercis canadensis L.	Quercus prinoides Willd.
Clitoria mariana L.	Quercus stellata Wang.
Cornus drummondii Meyer	Quercus velutina Lam.
Desmodium paniculatum (L.) DC.	Rhus glabra L.
Eragrostis capillaris (L.) Nees	Rhus radicans L.
Eragrostis spectabilis (Pursh.) Steud.	Rhynchosia latifolia Nutt.
Erigeron strigosus Muhl. ex Willd.	Spermolepis inermis (Nutt.) Math. & Const.
Euphorbia geyeri Engelm.	Symphoricarpos orbiculatus Moench.
Festuca octoflora Walt.	Vitis riparia Michx.
Lechea tenuifolia Michx.	Vitis vulpina L.

Table 2. Textural analysis of soil.

Depth	% sand	% silt	% clay
0-15 cm	77	11	12
30-45 cm	60	9	31

Table 3. Analysis of woody vegetation larger than 2.5 cm DBH.

	post oak	blackjack	other
Relative basal area	54.1	44.5	1.4
Relative density	65.2	27.9	6.9
Relative frequency	38.8	40.8	20.4
Importance percentage[1]	52.7	37.7	9.6

[1]Importance percentage = $\sum_{1}^{N} \frac{(\text{Rel. BA} + \text{Rel. Den} + \text{Rel. Freq.})}{3}$

Where N is the number of species.

FIELD SAMPLING

On each sample date (Table 4), either 10 or 20 samples of each item were collected, using a stratified random sampling design. If 10 samples were taken, alternate squares were used and if 20 samples were taken all squares were used. Samples within a particular square were taken as close as possible to a point determined at random before going into the field.

Twigs and Leaves. At approximately two-week intervals during the growing season, five twigs with leaves at different levels in the canopy were removed from each of 20 post oak and 20 blackjack trees. Leaves and first-year twigs were separated in the field to prevent movement of materials prior to laboratory analysis. At approximately one-month intervals during the winter, live twigs were sampled in the same manner.

Litter, Soil, and Understory Vegetation. At four to six-week intervals, understory vegetation (arbitrarily defined as any plant with a DBH of less than 2.5 cm) was clipped at ground level from 10 quarter-square meter quadrats. Litter was collected down to the mineral soil and three soil cores were taken at 0-15 cm and 30-45 cm from the same quadrat.

Litterfall. Ten litter traps were distributed in the plot according to a stratified random design. The traps were square, screen-bottom wooden boxes one square meter in

Table 4. Sample dates of material collected for analysis.

Date	Leaves	Twigs	L.F.[1]	Clip	Lit.	Soil	T.F.[2]	S.F.[3]	L.A.[4]
8-15-70	x	x							
8-30-70	x	x							
9-19-70	x	x	x	x	x	x			
10-3-70	x	x	x						
10-25-70	x	x	x	x	x	x			
11-8-70	x	x	x						
11-22-70			x						
11-26-70		x	x	x	x	x			
12-6-70		x	x						
1-17-71			x	x	x	x	x		
1-30-71		x	x						
2-20-71		x	x	x	x	x	x		
3-13-71		x	x				x		
4-3-71		x	x						
4-18-71	x	x	x				x		x
4-25-71	x	x	x	x	x	x	x		x

Table 4. Continued

Date	Leaves	Twigs	L.F.[1]	Clip	Lit	Soil	T.F.[2]	S.F.[3]	L.A.[4]
5-8-71	x	x	x				x		x
5-23-71	x	x					x	x	x
5-29-71				x	x	x	x	x	
6-4-71	x	x					x	x	x
6-26-71	x	x					x	x	x
7-17-71	x	x	x	x	x	x	x	x	x
8-8-71	x	x					x	x	x
8-22-71	x	x					x	x	x
9-12-71	x	x							x
9-26-71			x	x	x	x	x	x	x
10-6-71	x	x	x				x	x	x
10-24-71	x	x	x						x
10-31-71			x				x	x	x
11-14-71			x						

[1] Litterfall

[2] Throughfall

[3] Stemflow

[4] Leaf area and weight

area. They were placed on the ground on 3 x 3 m polyethylene sheets to reduce contamination by soil splash and were emptied at intervals depending on the rate of litterfall.

Throughfall and Stemflow. Ten throughfall traps were placed in the stand according to a stratified random design. Each trap consisted of a 10 cm diameter polyethylene funnel, fitted with a cover of wire screen and a glass wool plug to keep out insects and debris, inserted into a 2 liter polyethylene bottle and secured with tape. The traps were supported at a level of one meter above the ground to prevent contamination by soil splash. An identical trap and a standard rain gauge were placed in an open area 100 m from the study area for calibration and to collect rain water and dry fallout. Five trees of each species were fitted with polyurethane stemflow collectors (Likens and Eaton 1970). As soon as possible after each rain, total volume of water in each throughfall and stemflow collector was recorded, a 200 ml aliquot was removed and placed in a glass bottle to which had been added 1 ml of a saturated solution of iodine in methanol, and the collector was emptied and dried.

Leaf Area and Weight. At intervals of 1-4 weeks (depending on growth rates) during the growing season of 1971, 75-100 leaves of the two major species were collected at random locations and at several canopy levels in the stand for determination of mean area and dry weight of individual leaves.

Roots. Once during the study (September 20, 1970) 20 root samples were taken according to a stratified random design. Samples were collected by driving a sharpened post hole digger, which cuts an area of 173 cm^2, into the ground in 15 cm increments to 60 cm. The soil cores were air dried, crumbled, and the large roots were removed by hand and brushed free of soil. The sample was then crushed (but not ground) and the small roots were removed by passing the sample through a 2mm sieve and then a 0.5mm sieve. Gravel was removed by hand from the remaining fibrous mass of small roots and as much of the remaining soil as possible was removed by washing with benzene. Roots were not washed with water since this would remove appreciable amounts of minerals, particularly potassium, whereas these compounds are only slightly soluble in benzene.

At irregular intervals during the study, samples of trunk wood, bark, and branches were collected for chemical analysis. All material for chemical analysis was dried for 48 hr at 65 C, ground to pass a 0.5mm sieve, and stored in airtight containers.

Biomass. Tree and shrub biomass was estimated by a method similar to that used by Whittaker and Woodwell (1968). In June 1972, a complete census of all live stems larger than 2.5 cm DBH (diameter at a height of 130 cm) was made for each of the twenty 0.01 ha squares. Each stem was identified as to species and its DBH was measured. In an area adjacent to the study plot and similar in vegetational composition to it, five post oak and five blackjack trees were selected to cover the size range of those in the study plot. Each tree was cut at ground level and the DBH and height were recorded. The basal diameter of each branch was recorded. The basal diameter of each branch was recorded and five representative branches from each tree were taken to the laboratory for further measurement. Branches were removed and the trunk was cut into segments of convenient size for handling. The basal diameter, mid-diameter, length, bark thickness, sapwood thickness, heartwood diameter, and weight were recorded for each segment and a basal disk was cut from each, weighed, and taken to the laboratory for dry weight determination. Total weight of dead branches was measured for each tree.

For each of the representative branches, total dry weight, number and dry weight of leaves, dry weight and number of 1-, 2-, and 3-year twigs, weight of dead twigs, weight of material older than three years, and age were determined. Polynomial regression equations were derived for each of these variables with basal diameter and used to estimate the value of each variable for each sample tree.

Dry weight of each trunk segment was calculated from its wet weight and the percent dry weight of its basal disk. Weight proportions of bark and wood were estimated from volume and density measurements. Estimates were summed to give total weight, bark weight, and wood weight for each sample trunk.

Polynomial regression equations were derived for weight of trunk bark, weight of trunk wood, tree height, number and weight of 1-, 2-, and 3-year twigs, weight of live branch material older than three years, and weight of dead wood for both post oak and blackjack using DBH as the independent variable.

The regression equations derived above and the results from the plot census were used to estimate aboveground biomass for all stems larger than 2.5 cm DBH on the study plot. Total basal area of all other woody species larger than 2.5 cm was small in relation to that of the two dominants (Table 3). The minor species were lumped together and the equations for post oak were used for calculation of their biomass. Results of quadrat sampling were used to estimate the biomass of stems less than 2.5 cm DBH. Belowground biomass was estimated by treating the core samples as quadrats and converting the mean value to a per ha basis.

Primary Production. Annual production of trunk wood for the sample trees was estimated from a formula given by Whittaker and Woodwell (1968):

$$\Delta W = W\ (2ri - i^2)/r^2 \qquad (1)$$

where:

ΔW = dry weight of annual wood increment

W = wood dry weight

r = wood radius at middle of log

i = mean annual radial increment of wood

This formula is based on the assumption that trunk wood is a cylinder with radius equal to the radius of the midpoint of the trunk. Results were used to derive a polynomial regression equation for trunk wood growth with DBH. A correction of 1.2 was applied to compensate for variation of annual increment with height (Whittaker 1966).

Annual production of trunk bark was based on the assumption that yearly bark increment is a thin-walled hollow cylinder as long as the trunk and with inside radius equal to the mid-radius of the log. The equation derived from this assumption is:

$$\Delta B = dh\ (2ri + i^2) \qquad (2)$$

where:

ΔB = dry weight of yearly bark increment

d = bark density

h = length of log

r = wood radius at middle of log

i = mean annual radial increment of bark

This equation was used to estimate bark production of the sample trees and polynomial regression equations were derived with DBH for estimation of stand values.

Methods given by Whittaker and Woodwell (1968) were used for estimation of branch growth. First, logarithmic regressions of branch weight with age were derived for the two major species:

$$\log L = a + b\ (\log A) \qquad (3)$$

where:

L = branch weight

A = age of branch

a and b are regression coefficients

Then the annual increment of branch biomass for each of the sample branches was estimated from:

$$\Delta L = bL/A \qquad (4)$$

where:

ΔL = annual increment of branch weight

b, L, and A are from Eq. 3

Polynomial regressions were then derived for ΔL with basal diameter and used to estimate total branch weight on the sample trees. Finally, the sum of branch weight increments on each sample tree was used to derive polynomial regressions with DBH for the two major species, which were used to estimate branch wood increment for the stand.

Leaf production was estimated from numbers of leaves (see above) and maximum average leaf weight. Since all trees in the stand are deciduous, leaf production was assumed to be the maximum standing crop of leaves.

Root production was estimated from the simple allometric relation (Nihlgard 1972):

$$\Delta R = R\Delta X/X \qquad (5)$$

where:

ΔR = root production

R = root biomass

ΔX = total [redacted]duction

X = tot[redacted]iomass

Other methods for [redacted]uction exist (Kira and Ogawa 1968), [redacted] case because of the difficulty in [redacted]

Biomass of r[redacted]s was very small and quite variable on the [redacted]therefore no attempt was made to estimate production.

Total basal area of all other woody species was small in relation to that of the two dominants (Table 3). The minor species were lumped together and the equations for post oak were used in calculation of their production.

Production of understory vegetation was estimated as the difference between maximum and minimum standing crop of vegetation less than 2.5 cm DBH.

(see above) and maximum average leaf weight. Since all trees in the stand are deciduous, leaf production was assumed to be the maximum standing crop of leaves.

Root production was estimated from the simple allometric relation (Nihlgard 1972):

$$\Delta R = R\Delta X/X \qquad (5)$$

where:

ΔR = root production

R = root biomass

ΔX = total aboveground production

X = total aboveground live biomass

Other methods for estimation of root production exist (Kira and Ogawa 1968), but were not used in this case because of the difficulty in sampling roots.

Biomass of reproductive structures was very small and quite variable on the sample trees, therefore no attempt was made to estimate production.

Total basal area of all other woody species was small in relation to that of the two dominants (Table 3). The minor species were lumped together and the equations for post oak were used in calculation of their production.

Production of understory vegetation was estimated as the difference between maximum and minimum standing crop of vegetation less than 2.5 cm DBH.

Leaf Area and Weight. Collections of leaves for area and weight measurement were first air-dried in a plant press and the area of each was measured with a Hayashi Denko AAM-5 photoelectric planimeter. The leaves were then dried 48 hr at 65 C and each was weighed on an analytical balance to the nearest mg.

Chemical Analysis. Calcium, magnesium, potassium, manganese, phosphorus, and nitrogen were determined for leaves, twigs, fruit, wood, bark, roots, litterfall, litter, soil, material clipped from quadrats, throughfall, stemflow, and rainwater.

Ca, Mg, K, and Mn were determined with a Perkin-Elmer Model 303 atomic absorption spectrophotometer using standard procedures supplied by the manufacturer. Plant material was digested in a perchloric-nitric acid mixture and soil minerals were extracted with 1% EDTA. Strontium (1500 mg/l) was added before determination of Ca and Mg.

Phosphorus was determined with the Fiske-Subbarow method (Fiske and Subbarow 1925) using perchloric acid digestion. Nitrogen was determined with a modified Kjeldahl method (Rice 1964).

RESULTS AND DISCUSSION

Biomass and Production

Results of dimension analysis for biomass are given in Table 5 and for net primary production in Table 6. A biomass-production compartment model is shown in Figure 1.

Biomass. Total biomass (Table 5), including litter and dead branches, is approximately 245000 kg/ha. This is comparable to the range of 100000-500000 kg/ha given by Rodin and Bazilevich (1967) for a broad range of temperate deciduous forests. Approximately 50% of the biomass in the stand is in the tree trunks and another 29% is in live branches for a total of 79% aboveground perennial parts. The roots account for about 18% and the leaves for about 2% of the live biomass. According to Rodin and Bazilevich (1967), perennial aboveground parts usually make up 60-85%, roots 15-35%, and leaves 1.5-3% of the live biomass in a temperate deciduous forest. Dead branches account for 5.8% of the organic matter, which is primarily because branches remain on blackjack for many years after they die.

Net primary production. The net primary production of the stand (Table 6) is about 14900 kg/ha/yr which is within the range of 3600-20000 kg/ha/yr given by Rodin and Bazilevich (1967) for temperate deciduous forests, but is higher than the values 7000-12000 kg/ha/yr given for typical mature deciduous forests. Net primary production in this

Table 5. Dry weight of organic material in a post oak - blackjack stand. Units are kg/ha.

Component	Post oak	Blackjack	Stand	% of total	% of live
Leaves	3472	1287	4759	1.59	2.17
Current twigs	201	133	334	0.14	0.15
Live branches	55042	9521	64563	26.39	29.40
Dead branches	7270	7040	14310	5.85	
Trunks	83464	26038	109502	44.76	49.87
Roots			39000	15.94	17.76
Understory			1411	0.58	0.64
Litter			10767	4.40	
Total			244646		
Total live			219569		

Table 6. Dry weight of net annual primary production in a post oak - blackjack stand. Units are kg/ha/yr.

Component	Post oak	Blackjack	Stand	% of total	% of aboveground
Leaves	3472	1287	4759	32.04	37.72
Current twigs	201	133	334	2.25	2.65
Branches	2967	861	3828	25.77	30.34
Trunks	2100	1594	3694	24.87	29.28
Roots			2240	15.07	
Understory			300	2.02	2.38
Total			14855		

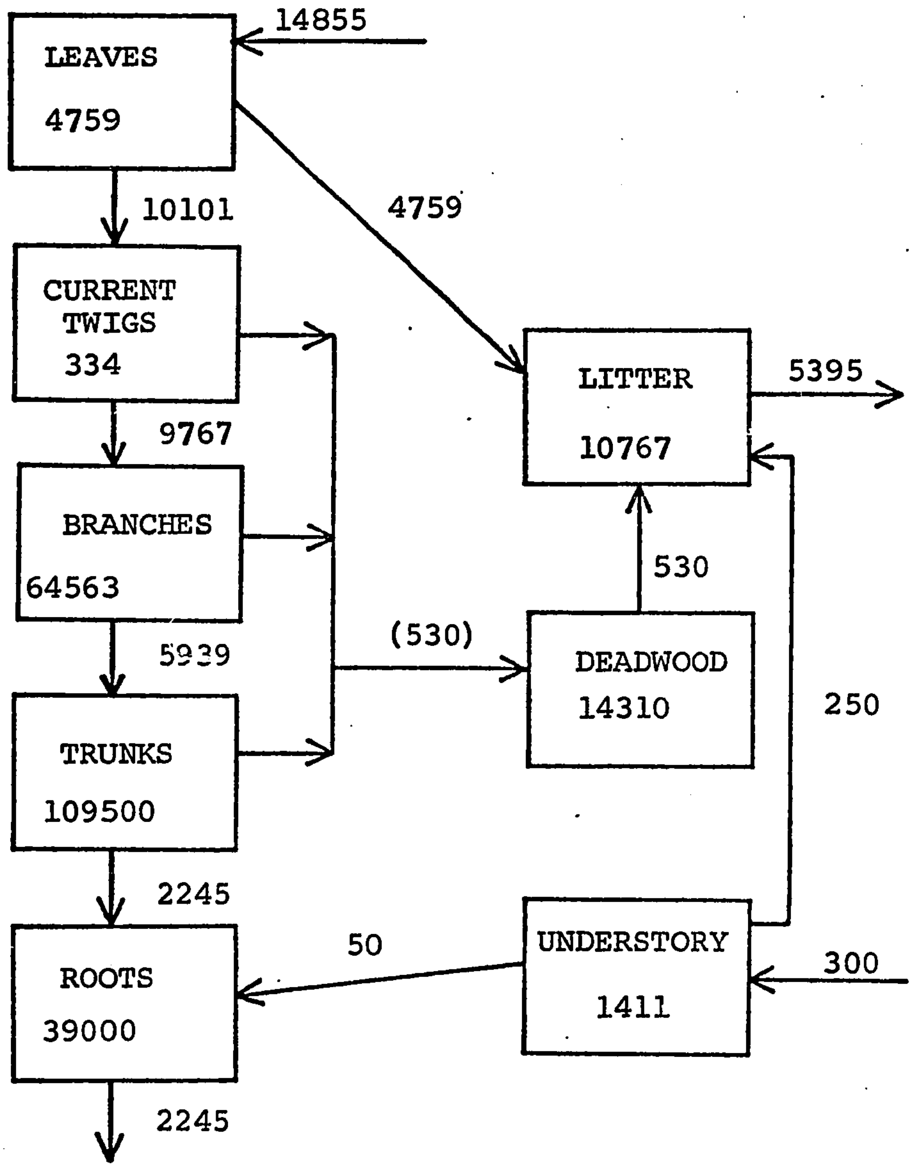

Figure 1. Compartment model showing distribution of dry weight of biomass and net primary production in a post oak - blackjack stand. Units are kg/ha for compartments and kg/ha/yr for flows between compartments.

stand is very similar to that for two Belgian oak forests (Duvigneaud and Denaeyer-De Smet 1970). The stand in this study is not mature and is farther south than most of the forests discussed by Rodin and Bazilevich (1967). Immature stands often have a net primary production more than twice as great as mature stands and the general trend in net primary production is higher toward the south. Net primary production in subtropical and tropical forests is often as high as 25000-32000 kg/ha/yr. The annual aboveground net primary production predicted for the stand, based on climatological data for the area (Rosenzweig 1968), is 9360 kg/ha/yr. The value of 12600 kg/ha/yr estimated from dimension analysis of the stand is within the 5% confidence interval of Rosenzweig's equation. The stand might be expected to be more productive than the mean for the area because of favorable moisture relations, since it is near the bottom of a slope which has 100-300 cm of sandy permeable soil over a relatively impermeable bedrock.

Distribution of the annual aboveground net primary production is: 38% leaves, 33% branches and current twigs, and 29% trunks. Values given by Satoo (1970) for the distribution of aboveground net primary production in Japanese deciduous forests are: leaves 25-41%, branches 10-25%, and trunks 34-64%. Nihlgard (1972) found the following distribution of aboveground production in a beech forest: 25% leaves + current twigs, 40% branches, and 31% trunks.

Relative variations in annual radial increment of a trunk wood (annual rings) can probably be used as an approximation to the relative variations in annual net primary production. In a tree-ring study in the same area for the 80-year period 1892-1971, the yearly average ring width for 7 post oak trees varied from 58 to 164% of the 80-year mean and the yearly average ring width for 7 blackjack trees varied from 56 to 148% of the 80-year mean, while standard deviation of the yearly averages from the 80-year mean was 20% for both species. Ring widths for both species were correlated with rainfall and previous growth rates (Johnson and Risser 1973).

The production efficiency (net primary production divided by leaf area or leaf weight) for post oak in the stand is 0.258 kg/m^{2}leaf/yr (2.83 kg/kg leaf/yr) and for blackjack it is 0.427 kg/m^{2}leaf/yr (3.29 kg/kg leaf/yr). For the stand as a whole, production efficiency is 0.299 kg/m^{2}leaf/yr (3.02 kg/kg leaf/yr). These values are somewhat higher than the 0.145 kg/m^{2}leaf/yr for Betula maximowicziana and 2.43 kg/kg leaf/yr for Fagus crenata in Japan (Satoo 1970) and are close to the value of 2.91 kg/kg leaf/yr for Betula verrucosa in England (Ovington and Madgwick 1959).

Figure 1 shows a compartment model summarizing the distribution of biomass and net primary production in the stand. The measured amount of dead wood in the litterfall

(530 kg/ha/yr) may be an underestimate of the actual amount. The litterfall sampling procedure was found to be statistically adequate for leaf fall (allowable error = ± 10% of mean, 80% confidence interval) but not for twig and branch fall. The observed branch and twig litterfall was 9.8% of the total. Data given by Nihlgard (1972) indicate that 19.1% of the annual litterfall in a beech forest was twigs and branches, while Sykes and Bunce (1970) found that 26.5% of the annual litterfall in a mixed woodland was made up of twigs and branches.

The values given in Figure 1 and Tables 5 and 6 represent a number of different time periods. The biomass values for current twigs, branches, trunks, and standing dead wood are estimates based on data from 10 trees sampled in June 1972. The value for roots is based on a group of 20 samples taken in September 1970. The value for leaves is based on an estimate of numbers of leaves from the June 1972 sample combined with results of a study of the changes in mean leaf area and weight conducted through the growing season of 1971. The value shown is the maximum leaf biomass, which would coincide with the peak leaf area index (Figure 2) in early June. Litter biomass in Figure 1 is the mean of all samples taken between August 1970 and November 1971, while the biomass given for the understory is the mean for the growing season of 1971.

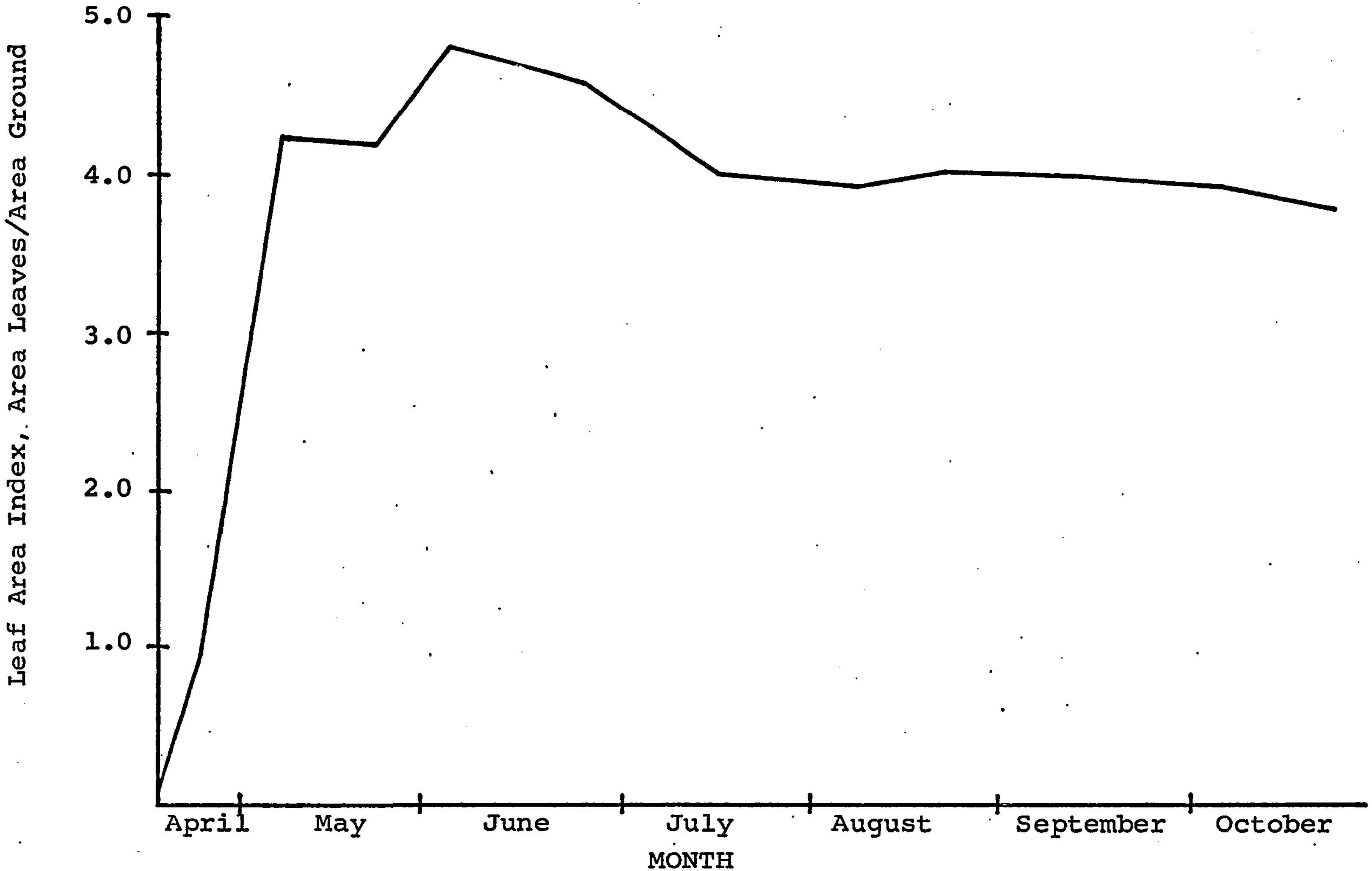

Figure 2. Changes in leaf area index of a post oak - blackjack forest during one growing season. Values plotted are total L.A.I. for all vegetation larger than 2.5 cm DBH.

The net primary production values for leaves and current twigs are the same as the values for biomass. Ages of sample branches used in estimating branch production ranged from 10 to 56 years. The mean annual increments of trunk wood are the mean ring widths of the post oak and blackjack sample trees and cover a period of up to 80 years. Bark increment was measured on 5 samples of each species, covering periods of 9 to 22 years.

Leaf Area Index. A curve showing changes in leaf area index (LAI) over a growing season is shown in Figure 2. Points on the curve were calculated from numbers of post oak and blackjack leaves estimated from the June 1972 sample and mean area/leaf for each species determined at 12 points in the 1971 growing season. Calculations were corrected for leaf litterfall during the growing season.

LAI for the stand went rapidly from 0 at the time of bud break in mid-April to 4.2 in early May, increased more slowly to a peak of 4.8 in early June, then decreased slowly to 3.8 at the end of the growing season in late October. Other investigators have reported leaf area indices of 2-5.5 for Japanese deciduous forests (Satoo 1970), 3.4 for a Swedish beech forest (Nihlgard 1972), 3.5 for an oak-hickory forest in the southeastern United States (Monk, Child, and Nicholson 1970), 3.6 for an alder-birch woodland in England (Hughes 1971) and 6.77 for an oak forest in Belgium (Duvigneaud and Denaeyer-

DeSmet 1970). The curve is similar to one presented by Satoo (1970) for a young stand of *Ulmus parvifolia*.

Litter Dynamics. Figure 3 shows a 14-month sequence of observed litterfall rates for the stand. Maximum litterfall rates (greater than 50 kg/ha/day) were observed for about a month after the first killing frost, which occurred in early November in both years. Many leaves of both species and especially of blackjack remain attached and continue to fall throughout the winter. Litterfall rates reached a secondary peak in late March and early April just before the beginning of the growing season. Branch and twig litterfall also reached a peak in March and April. Litterfall from mid-April through May consisted mostly of bud scales and flowers. The rate reached a minimum of about 1 kg/ha/day in June and July, when material collected consisted mostly of insect frass. Leaf fall began to be noticeable in late July and continued to increase through October. The litterfall characteristics for this stand are probably not typical for most deciduous forests because of the lag in leaf fall after frost. A probably more typical litterfall curve is given by Reiners and Reiners (1970) in which most of the yearly litterfall occurs within a few weeks after the first killing frost.

Measured litterfall from the overstory is 5136 kg/ha/yr and the amount estimated for the understory is 250 kg/ha/yr,

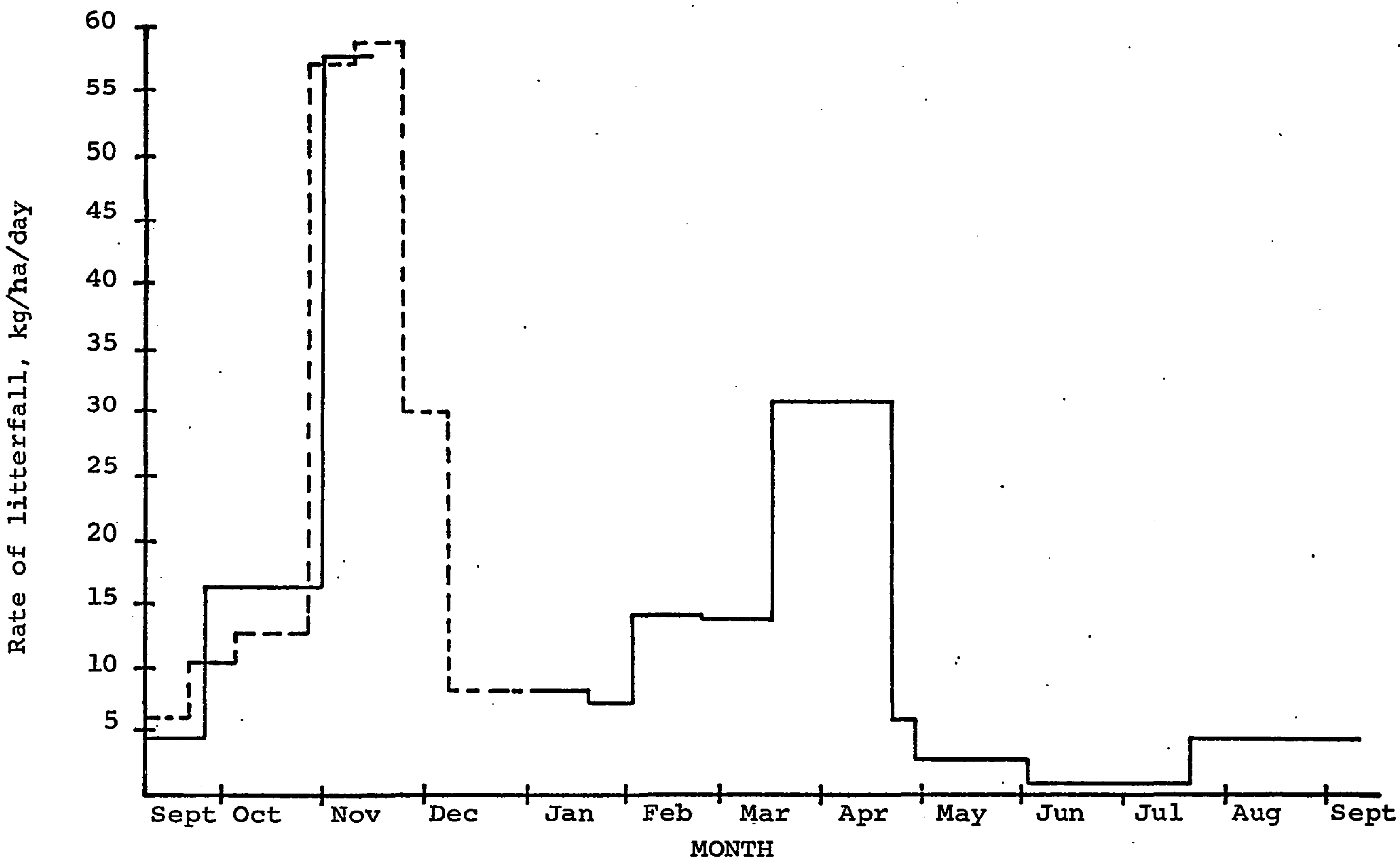

Figure 3. Litterfall rates in a post oak - blackjack forest. 1970 - dashed line; 1971 - solid line.

for a total of 5386 kg/ha/yr. Subtracting the understory portion and the woody portion leaves approximately 4600 kg/ha/yr to be accounted for by leaves, bark, flowers, bud scales, etc. Since estimated leaf production was 4760 kg/ha/yr, there is a discrepancy of 160 kg/ha/yr or more which must be accounted for by errors in methodology. Litter decomposition between collection dates and the failure to measure microlitter are probable sources of error. Understory litterfall is also probably underestimated, since the procedure of estimating litterfall by the difference between maximum and minimum standing crop underestimates litterfall in grasslands by 20-50%.

Figure 4 shows changes in the amount of litter on the ground through a period of one year. The amount increases during the fall, decreases through the winter, and reaches another peak in early spring as might be expected from litterfall rates (Figure 3). However, the magnitude of the winter decrease is much greater than would be expected from observed decay rates, so part of the decrease is probably due to sampling error. The decrease in litter between February and April is real and is due to a ground fire which occurred in late March.

A simple mathematical model using observed decay rates and litterfall rates gives the results shown as a dashed line in Figure 4. The model is based on the equation:

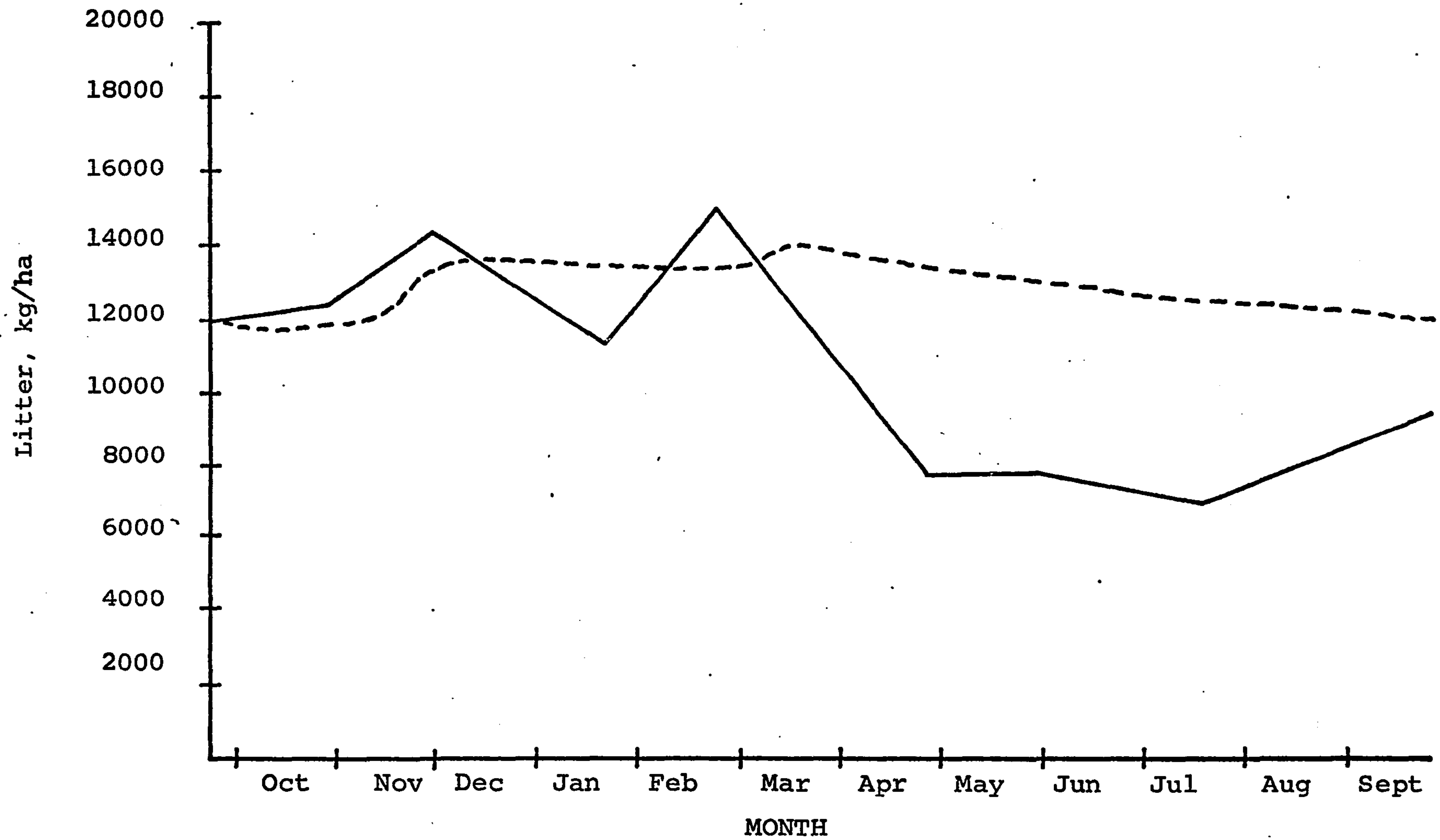

Figure 4. Changes in litter accumulation during one year in a post oak - blackjack forest. Solid line = observed data. Dashed line = model-generated values, using observed rates of litterfall and litter decay.

$$X_{t+\Delta t} = X_t + (F - RX_t)\,\Delta t$$

where:

t = time, days

X = litter, kg/ha

F = observed litterfall at time t, kg/ha/day

R = observed litter decay rate at time t, kg/kg

The model results return to approximately 12000 kg/ha in September even after iteration through several yearly cycles, which might lead to the conclusion that litterfall was not underestimated as stated earlier. However, there is evidence that ground fires occur every 3-5 years in the stand, so that litter may build up faster than it decays for several years and then be reduced by fire. An accurate representation of litter dynamics in the stand would probably require several years of observation.

Mineral Content and Yearly Flows

Figures 5 through 10 show the mineral content and net yearly flows between the various components of the stand for the elements N, P, K, Ca, Mg, and Mn. Except as noted below, the values shown in Figures 5 through 10 are calculated from the biomass and net primary production data given in Tables 5 and 6 and the corresponding concentrations of mineral elements.

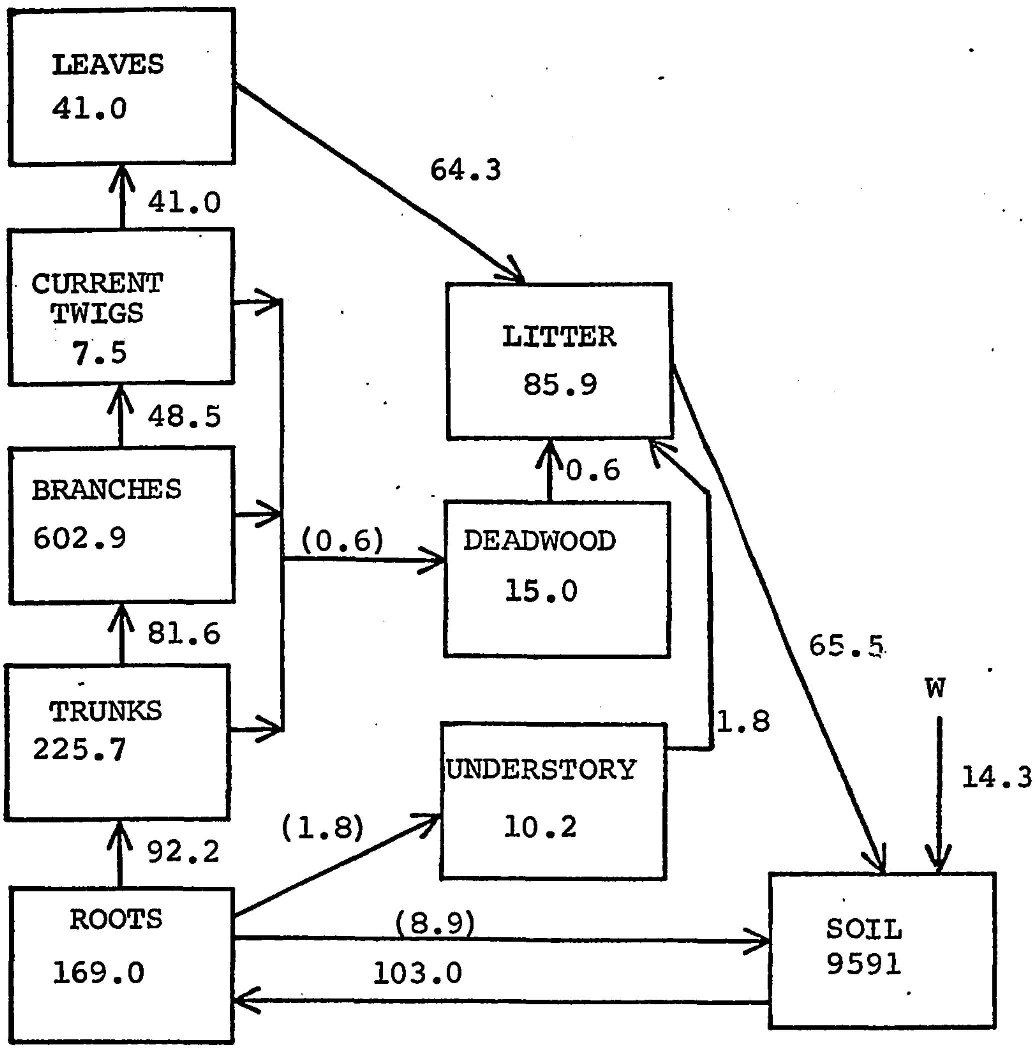

Figure 5. Distribution of nitrogen among the components of a post oak - blackjack stand. Units are kg/ha for compartments and kg/ha/yr for flows.

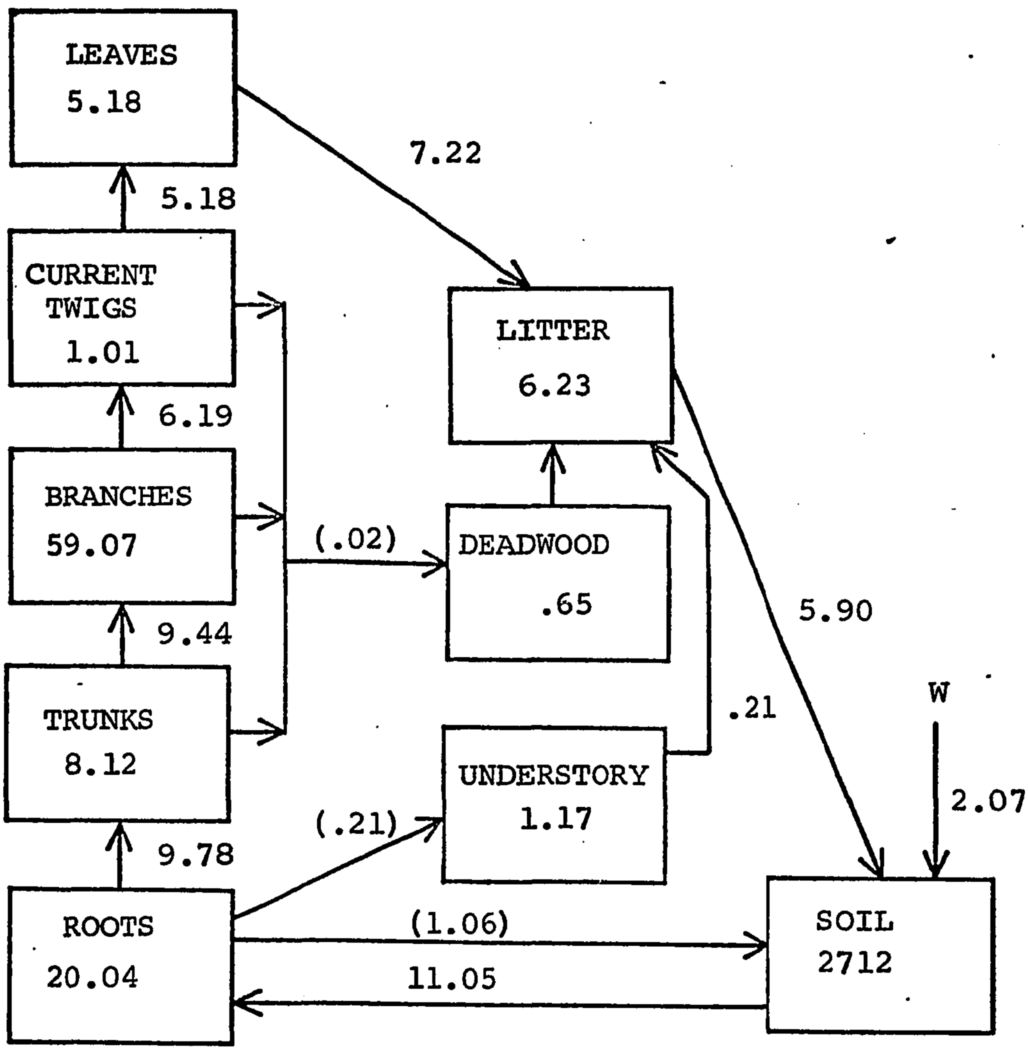

Figure 6. Distribution of phosphorus among the components of a post oak - blackjack stand. Units are kg/ha for compartments and kg/ha/yr for flows.

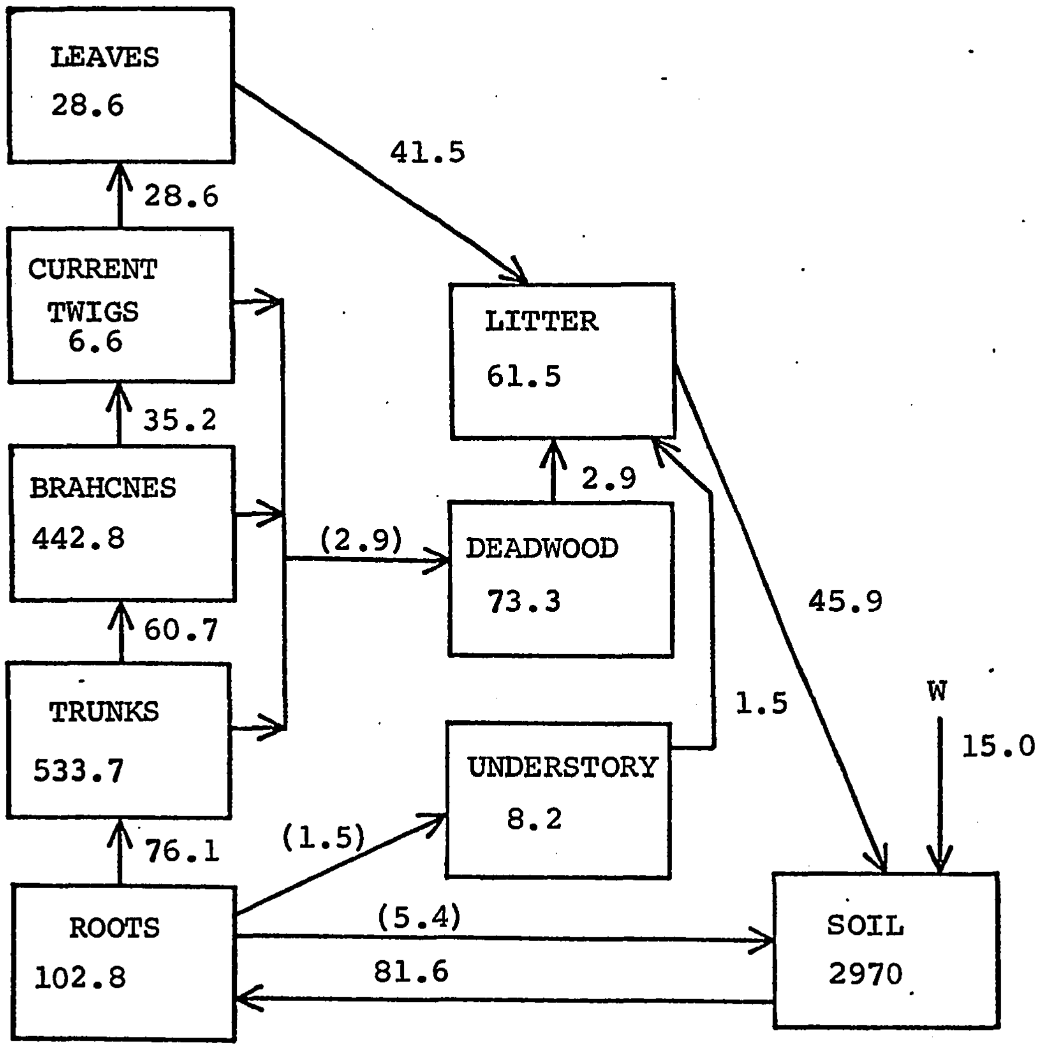

Figure 7. Distribution of potassium among the components of a post oak - blackjack stand. Units are kg/ha for compartments and kg/ha/yr for flows.

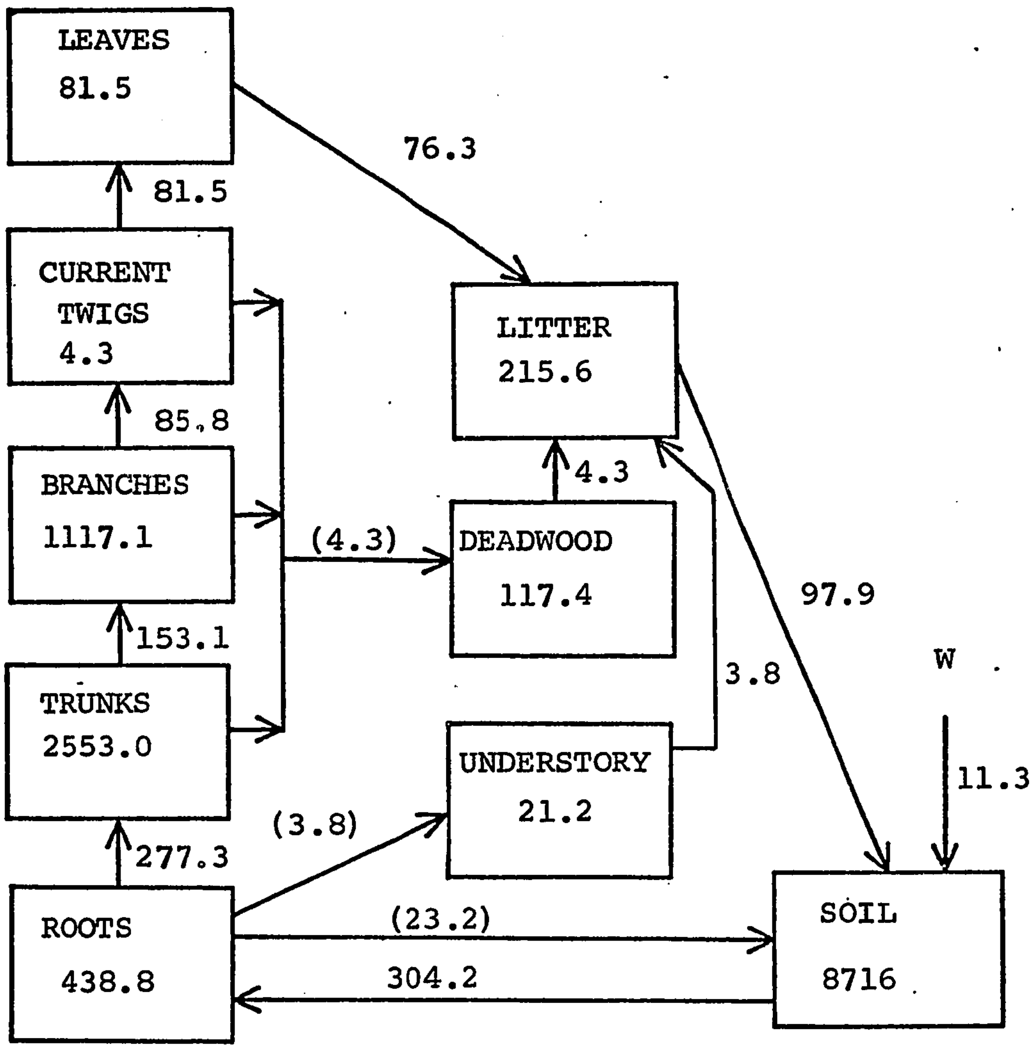

Figure 8. Distribution of calcium among the components of a post oak - blackjack forest stand. Units are kg/ha for compartments and kg/ha/yr for flows.

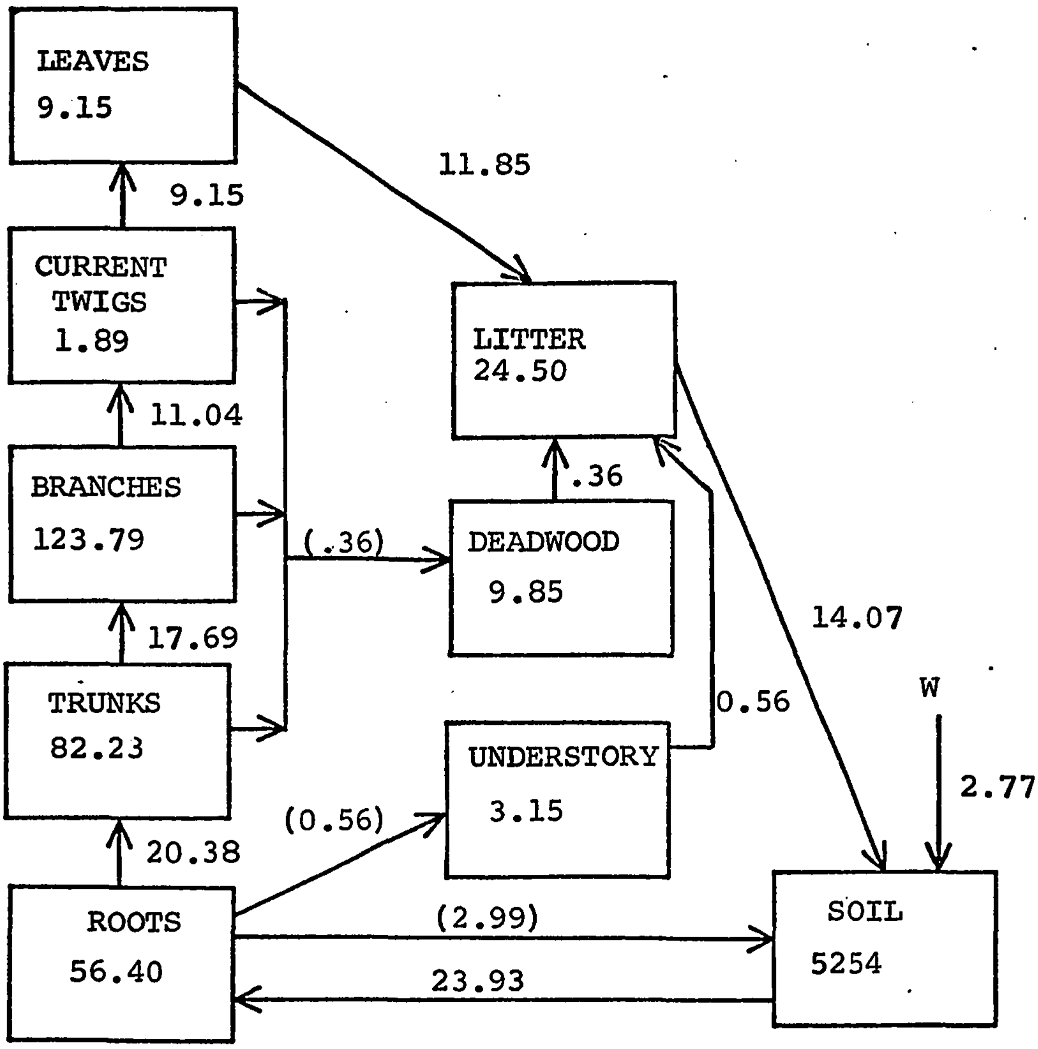

Figure 9. Distribution of magnesium among the components of a post oak - blackjack forest stand. Units are kg/ha for compartments and kg/ha/yr for flows.

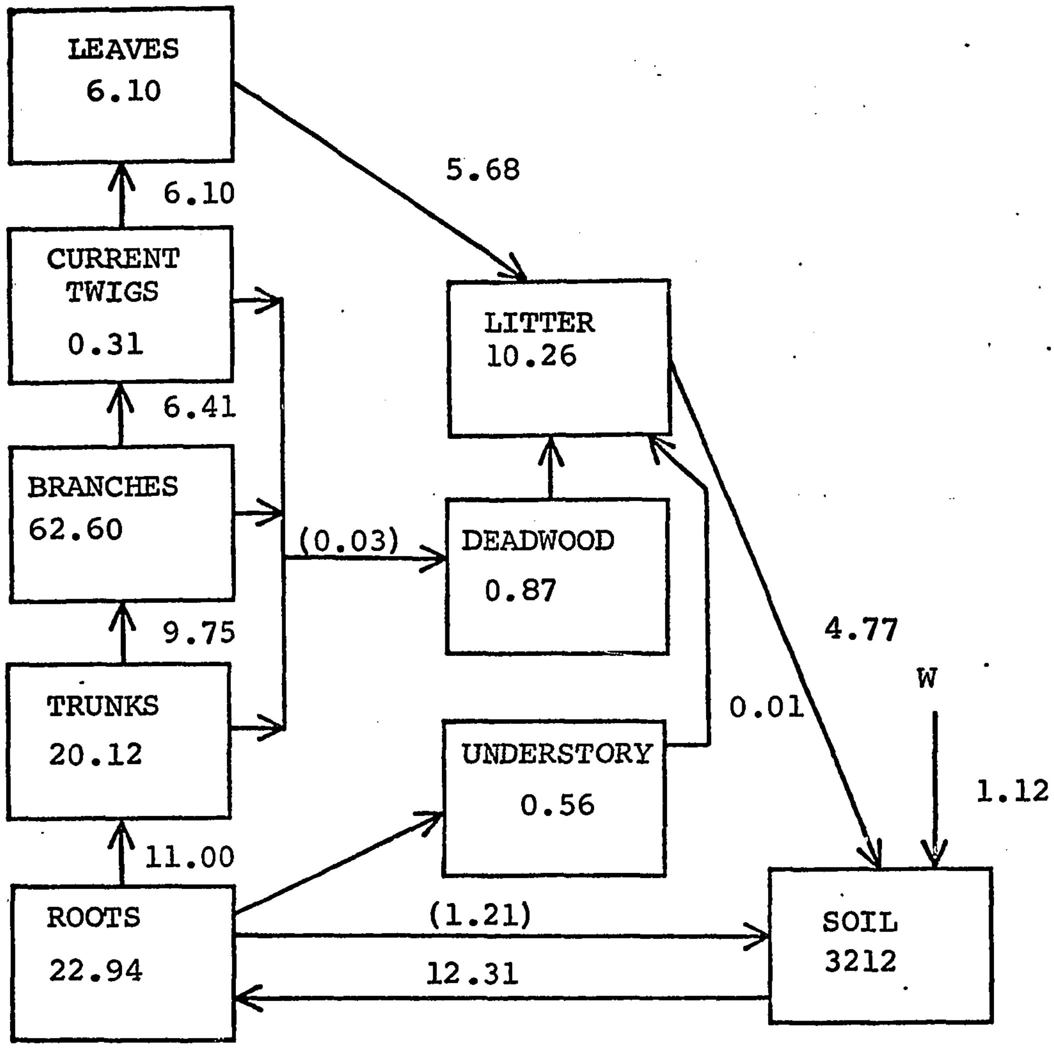

Figure 10. Distribution of manganese among the components of a post oak - blackjack forest stand. Units are kg/ha for compartments and kg/ha/yr for flows.

The flow from leaves to litter for each element was calculated as follows: (1) the amount in leaf fall after frost was assumed to be the amount present in leaves at the last sampling date (biomass of leaves of each species at 30 October times the concentration of the element in leaves at that date); (2) the amount of leaf litterfall and caterpillar feces before frost was calculated as the product of the difference between leaf biomass at 6 June and 30 October, and the mean concentration of the element in leaves between the two dates; (3) the amount given is the sum of (1) and (2).

The flow from litter to soil was taken to be the sum of the loss by decay of litter and the rapid loss by leaching which occurs soon after the litter falls. The loss of an element by litter decay was calculated as the yearly loss of organic material by decay times the mean concentration of that element in the litter. The loss by rapid leaching was estimated by collecting a bulk sample of unfallen leaves soon after frost and before rainfall occurred. The bulk sample was divided into 8 subsamples, four of which were analyzed for mineral content. The other four were leached for 48 hours with distilled water, dried, and analyzed for mineral content. Losses were: 43% of the N, 41% of the P, 48% of the K, 12% of the Ca, 31% of the Mg, and 7% of the Mn. The amount of an element in leaf litterfall times the fraction lost in the leaching experiment was used as an approximation to the amount which would be rapidly lost by leaching.

The methods used in calculation of flow of minerals into and out of the litter component are crude approximations, but except in the case of P and Ca there is a fair agreement between input and output. In the case of Ca, the discrepancy may have resulted from not including bark litterfall in the input calculation.

The values given for soil are based on mean concentrations of the elements over a 1-year period in the 0-15 cm and 30-45 cm soil levels, soil bulk density at 0 and 30 cm, and an estimated soil depth of 300 cm. The amounts of N and P in the soil component are totals, while the amounts given for K, Ca, Mg, and Mn are the EDTA-extractable fraction. Therefore, the amounts of N and P available for uptake by plants are much less than the values given (Donahue 1965), while the amounts given for the other elements are approximately the amounts available to plants (Fried and Broeshart 1967).

Table 7 is a summary of yearly amounts in the mineral cycle and the amounts of the six elements contained in the non-soil organic matter. Uptake of an element is the sum of the products of net primary production of the individual components of the system times the corresponding concentrations of that element. Return is the sum of the amounts of the element returned to the soil by throughfall, stemflow, and decay of roots and litter. Retention is the difference between uptake and return. Import is the amount of the element in yearly precipitation and dry fallout. Accumulation is the amount of the element present in the biomass, dead wood, and litter.

Mineral Content of Biomass. Ranges of accumulation given for deciduous forests by Rodin and Bazilevich (1967), Nihlgard (1972), and by Duvigneaud and Denaeyer-DeSmet (1970) are: (kg/ha) 530-1200 for N, 40-100 for P, 340-1400 for K, 650-2240 for Ca, 100-300 for Mg, and 10-125 for Mn. Values determined for N, P, K, and Mn in the present study (Table 7) are near the upper limits given in the literature, while the value for Mg is slightly higher than the highest given and the Ca accumulation is more than twice as high as the highest given.

The extreme value for calcium accumulation is due entirely to the concentrations of this element in the bark. The bark of most deciduous tree species has 1.5-2% Ca (Rodin and Bazilevich 1967) and up to 3.4% in European oaks (Duvigneaud and Denaeyer-DeSmet 1970), while concentration of Ca in the bark of trees in this stand is 9.0% for post oak and 3.7% for blackjack. The concentration of Ca in other tissues of the two species (Table 9) is not unusual.

Mineral Cycling. Ranges of mineral uptake for temperate deciduous forests (Duvigneaud and Denaeyer-DeSmet 1970 ; Nihlgard 1972) are: (kg/ha/yr) 92-204 for N; 7-15 for P;

Table 7. Uptake, retention, return, import, and accumulation of 6 mineral elements in a post oak - blackjack forest.

Element	Uptake kg/ha/yr	Retention kg/ha/yr	Return kg/ha/yr	Import kg/ha/yr	Accumulation kg/ha
N	103.0	17.0	86.0	3.9	1157
P	11.05	1.54	9.51	1.07	101
K	81.6	19.2	62.4	4.0	1258
Ca	304.2	188.4	115.8	3.9	4549
Mg	23.93	6.26	17.67	0.86	311
Mn	12.31	5.26	7.05	1.09	124

43-99 for K; 49-201 for Ca; and 11-24 for Mg. Values determined for the same elements in the post oak-blackjack forest (Table 7) fall within the ranges given, except for Ca which is incorporated into bark production in large amounts. The amounts of the six mineral elements imported with precipitation (Table 7) and removed from the canopy by throughfall and stemflow (Table 8) are similar to values given by other investigators (Rodin and Bazilevich 1967; Nihlgard 1970; Duvigneaud and Denaeyer-DeSmet 1970; Reiners 1972).

The nutrient cycle in the post oak-blackjack forest seems to be similar (except for Ca) to nutrient cycles in the European oak forests discussed by Duvigneaud and Denaeyer-DeSmet (1970). The same authors state that the nutrient requirements of oak forests are much greater than those of other temperate forest ecosystems, and are similar to the nutrient requirements of agricultural crops.

Concentrations of Mineral Elements

Table 9 is a list of concentrations of N, P, K, Ca, Mg, and Mn in the post oak - blackjack forest. The concentrations shown for each component are the means of all samples of that component over a 15 month period.

Except for Ca, the highest concentrations of the mineral elements are generally found in the leaves, followed by current twigs, small branches, large branches and trunks. For Ca, higher concentrations are found in branches and twigs than in leaves, while the highest concentration is in the bark and the lowest is in the wood. Concentration

Table 8. Amounts of N, P, K, Ca, Mg, and Mn removed from the canopy by throughfall and stemflow in a post oak - blackjack forest. Units are kg/ha/yr.

Element	Throughfall	Stemflow	Total Removed
N	10.3	0.1	10.4
P	0.87	0.13	1.00
K	10.9	0.1	11.0
Ca	8.1	0.1	8.2
Mg	1.89	0.02	1.91
Mn	0.03	0.01	0.04

gradients between tissues are different for each element. For example, within post oak the highest and lowest concentrations differ by a factor of 12.4 for N, 26.2 for P, 1.9 for K, 10.0 for Ca, 3.7 for Mg, and 19.5 for Mn.

In general, the mineral content of the tissues and organs of blackjack is lower than that of the corresponding tissues and organs of post oak. N and P are consistently higher in post oak, by 11-45% for N and 6-53% for P. K is slightly higher in twigs and small branches of post oak, but 12-19% lower in leaves, large branches, and trunks. Ca concentration is essentially the same in twigs and small branches of both species, but is 28-73% higher in leaves, large branches, and trunks in post oak leaves, post oak twigs, and blackjack leaves, but is considerably lower in blackjack twigs. Mg concentrations are higher for post oak than for blackjack in small branches but higher for blackjack than for post oak in large branches and trunks. The pattern of Mn concentrations is the same as for Mg.

The understory component is made up of grasses, forbs, shrubs, and small tree saplings and has intermediate concentrations of mineral elements as would be expected for a mixture of tissues. The roots have rather low concentrations of the mineral elements measured in this study. No attempt was made to separate the roots into living and dead portions, so the concentrations of minerals in the living portion of the

Table 9. Mean concentrations of 6 mineral elements in various components of a post oak-blackjack forest. Units are µg/g dry weight.

Component	N	P	K	Ca	Mg	Mn
Post oak leaves	15402	1441	8865	14300	2316	1098
" " current twigs	9456	1240	7304	20849	2359	1114
" " smallest branches	8874	907	6211	19300	1998	975
" " large branches and trunks	2120	77	4667	25912	741	167
" " bark	5470	160	4643	90213	1139	587
" " wood	1240	55	4673	8995	636	57
Blackjack leaves	13786	995	9921	11175	2325	1050
" current twigs	8385	1052	6458	19860	1654	636
" smallest branches	7136	690	5794	20143	1278	585
" large branches and trunks	1868	65	5539	14986	783	236
" bark	4830	151	5420	37207	900	733
" wood	855	36	5580	7388	743	66
Understory	7306	796	6250	14724	2110	405
Roots	4330	514	2636	11251	1446	588
Litterfall	7902	698	5479	16754	2662	938
Litter	5357	467	4393	14346	1697	1013
Soil, 0-15 cm depth	429	88	62	325	104	108
Soil, 30-45 cm depth	189	51	50	149	74	83

roots would be expected to be somewhat higher than those listed for roots in Table 9.

Seasonal Changes in Mineral Concentrations

Figures 11 through 16 show the changes in N, P, K, Ca, Mg, and Mn for leaves and current twigs of post oak over a 15 month period. Although absolute values of concentrations were different, the relative changes in blackjack were very similar to those shown for post oak.

The period of observation was from 15 August 1970 through 30 October 1971. The graphs show noticeable differences between the mineral concentrations of leaves near the ends of the two growing seasons. There was a noticeable yellowing of leaves in the stand for 3-4 weeks before frost in 1970, while the leaves in 1971 remained green until frost. No explanation for the differences has been found.

Nitrogen (Figure 11) in leaves decreases through the growing season from about 2.2% in May to around 1.5% in September. In 1970, N in leaves decreased rapidly through October to about 0.9%, while in 1971 it remained at 1.4%. N in twigs decreases from 3.1% in April to about 0.6% in September, increases slightly until the end of the growing season, and remains constant at about 0.8% through the winter.

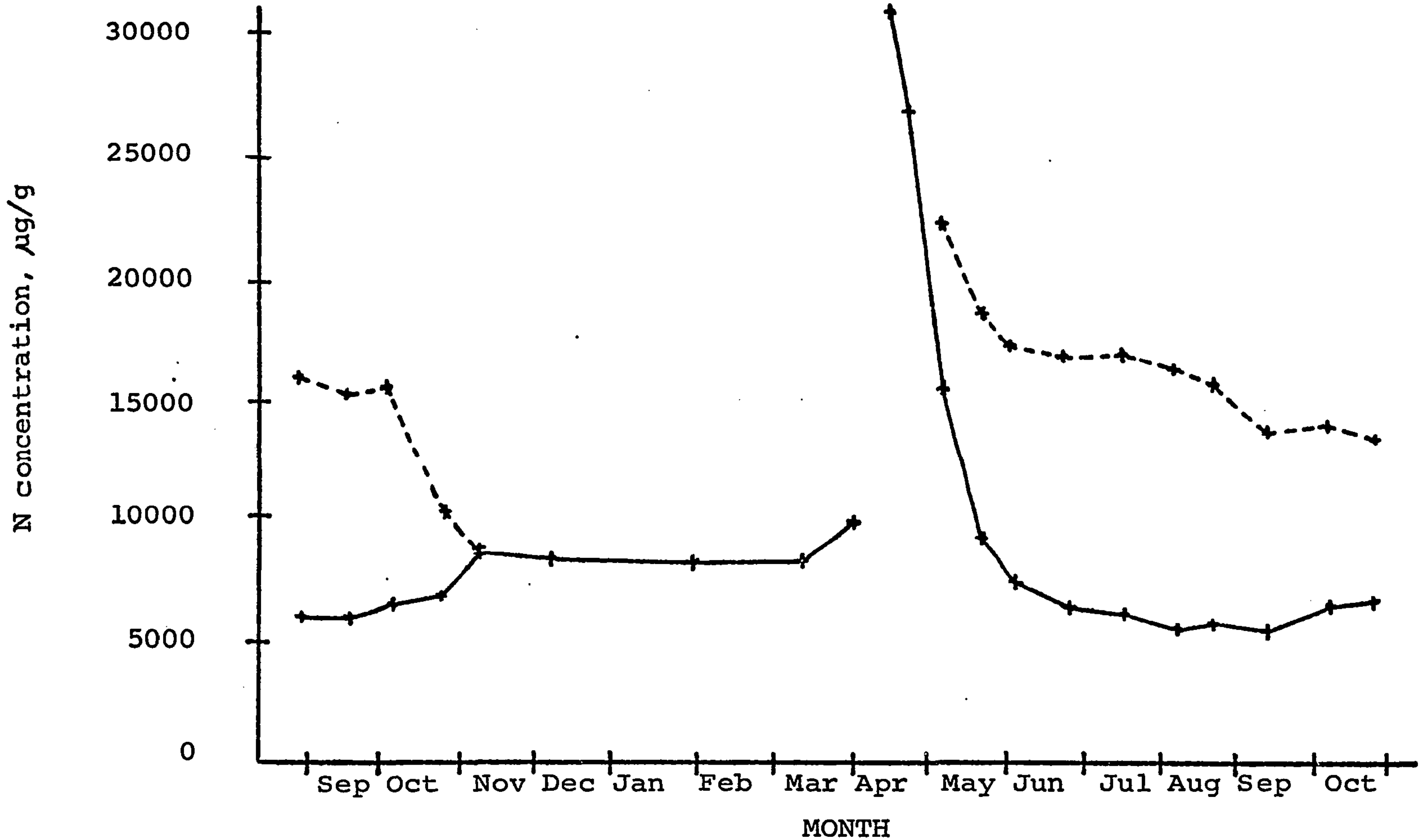

Figure 11. Seasonal changes of nitrogen concentration in current twigs (solid line) and leaves (dashed line) of post oak.

Phosphorus (Figure 12) in leaves decreased from about 0.2% in May 1971 to 0.1% in June, then increased to almost 0.2% by the end of the season, while in 1970 it decreased during October. P in twigs decreases from 0.4% in early spring to less than 0.1% at the end of September and remains constant through the winter.

Potassium (Figure 13) shows considerable variability in concentration in the leaves and at times in the twigs, but both concentrations have a general downward trend through the growing season with little change in concentration in the twigs through the winter. K reached a somewhat lower concentration in leaves at the end of the 1970 season (0.5%) than at the end of the 1971 season (0.8%).

Calcium (Figure 14) in leaves increases from about 0.6% in early spring to around 1.5-1.7% in midsummer. In 1970 it continued to increase and reached a concentration of 1.9% by the end of the growing season, while in 1971 it remained constant from July through September and dropped to 1.4% at the end of the season. The same pattern was observed in blackjack leaves. Ca concentrations in twigs are quite variable, but the pattern seems to be a decrease from about 2.2% in mid-April to 1.2% at the end of May, then an increase to 2.5% in July, and then to remain more or less constant through the rest of the year.

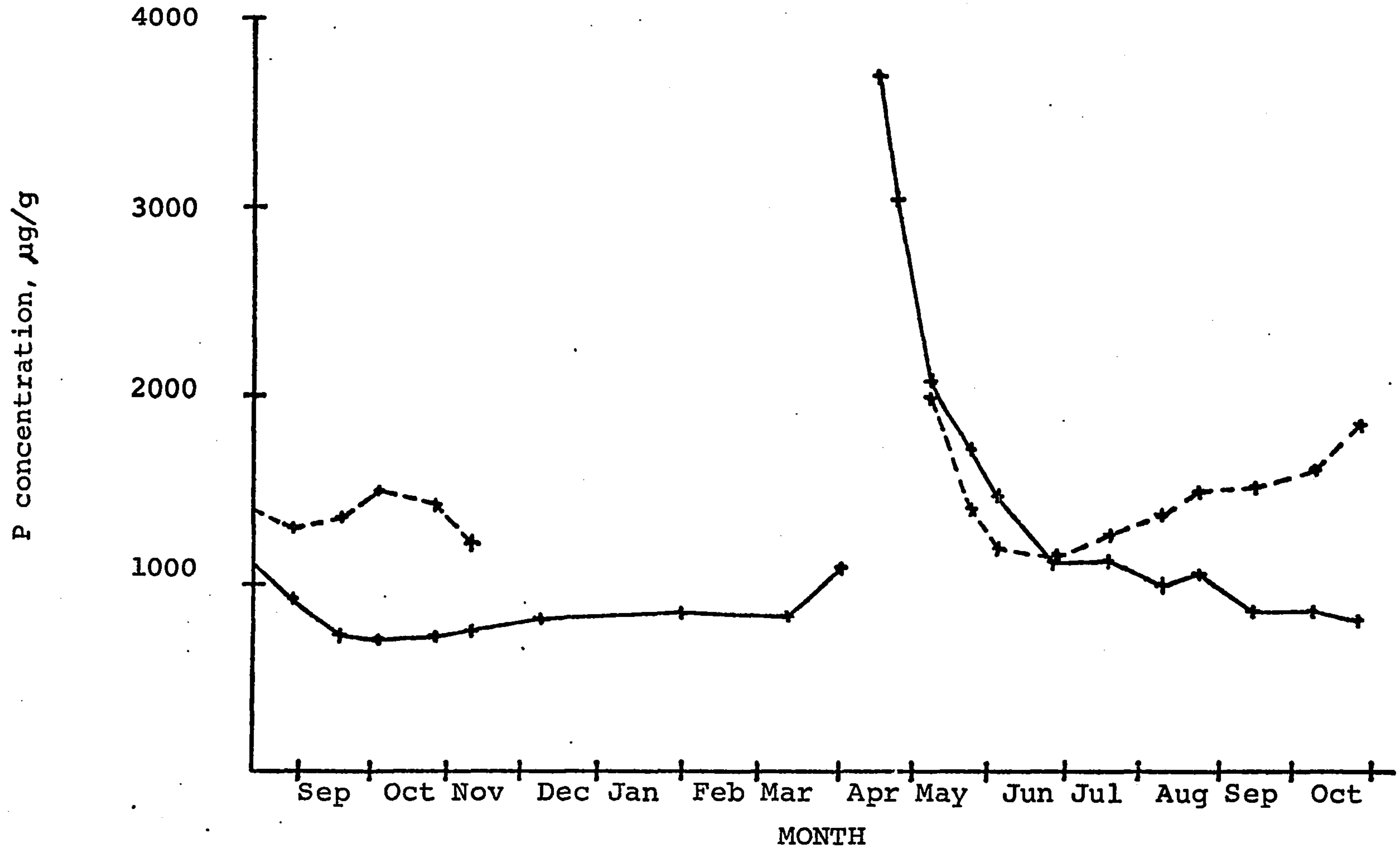

Figure 12. Seasonal changes of phosphorus concentration in current twigs (solid line) and leaves (dashed line) of post oak.

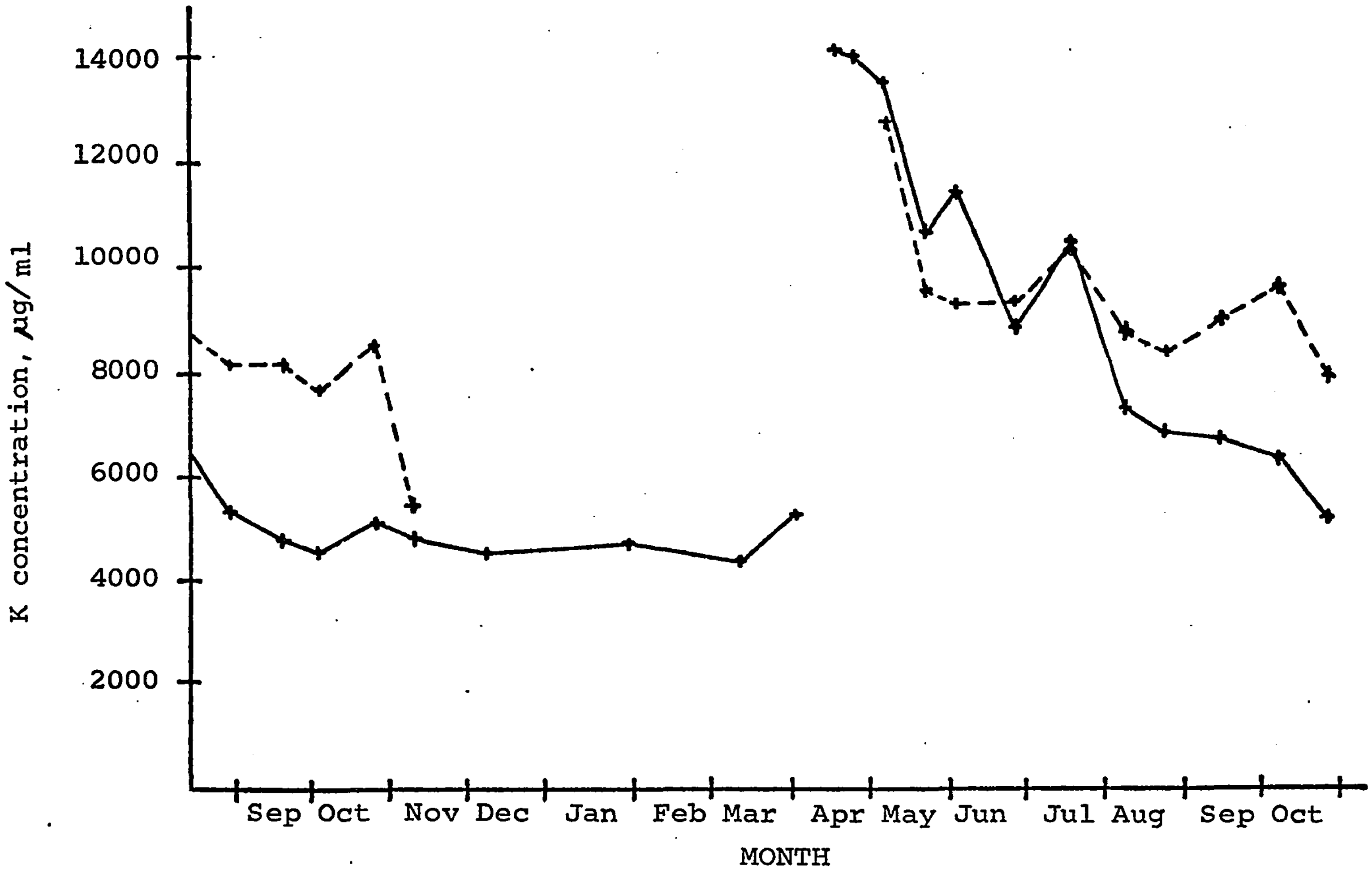

Figure 13. Seasonal changes of potassium concentration in current twigs (solid line) and leaves (dashed line) of post oak.

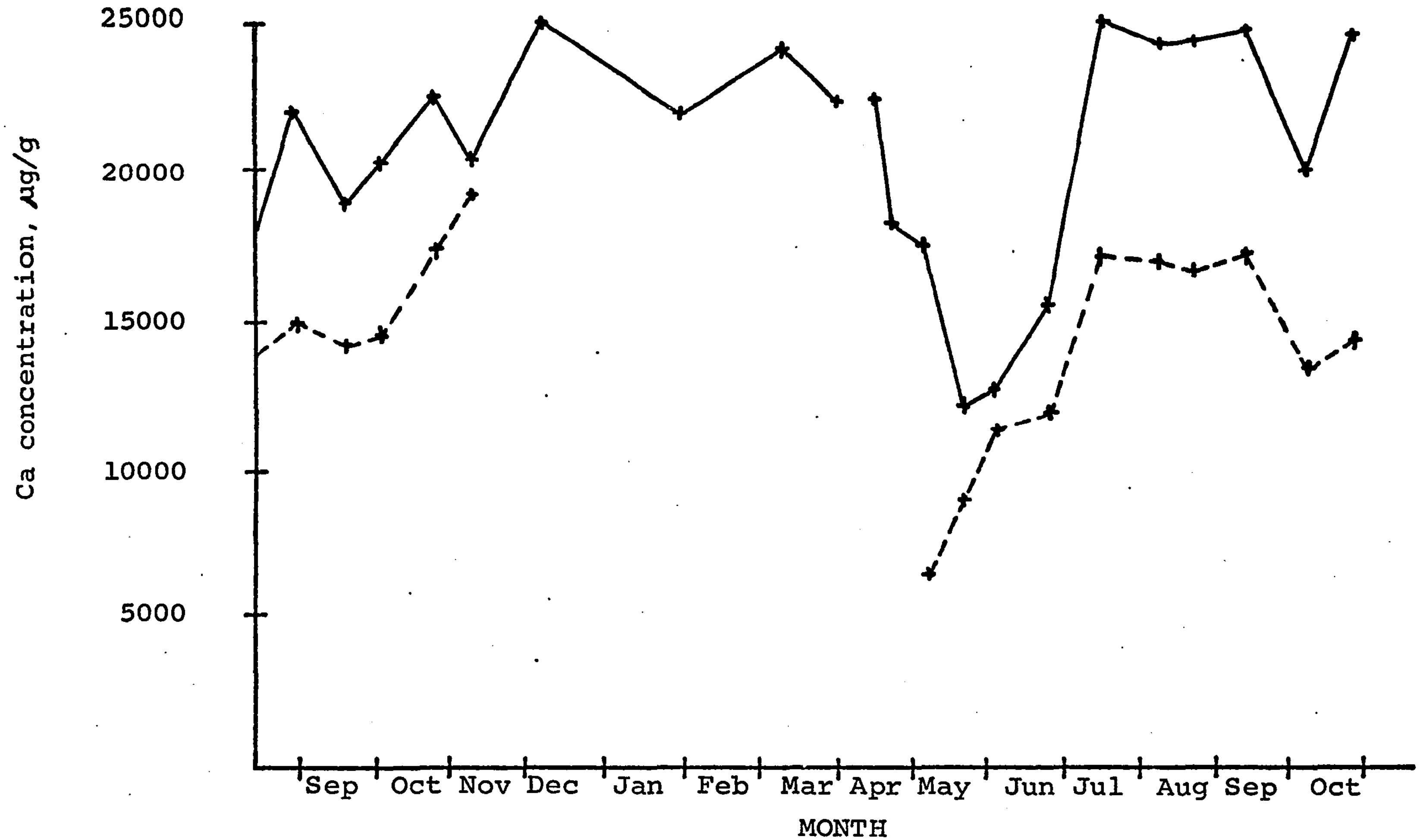

Figure 14. Seasonal changes of calcium concentration in current twigs (solid line) and leaves (dashed line) of post oak.

Magnesium (Figure 15) concentrations in both leaves and twigs decreases from the beginning of the growing season to early fall. In the 1970 season, concentrations continued to decrease slightly until frost. In the 1971 season, concentrations in both twigs and leaves increased considerably from late September to the end of October. The same pattern was observed for Mg in blackjack.

Manganese concentrations (Figure 16) in both leaves and twigs seem to increase steadily from about 0.05% at the beginning of the growing season to about 0.13% by early fall and then to remain constant to the end of the season. Variability in the data prevents detection of any definite difference between years.

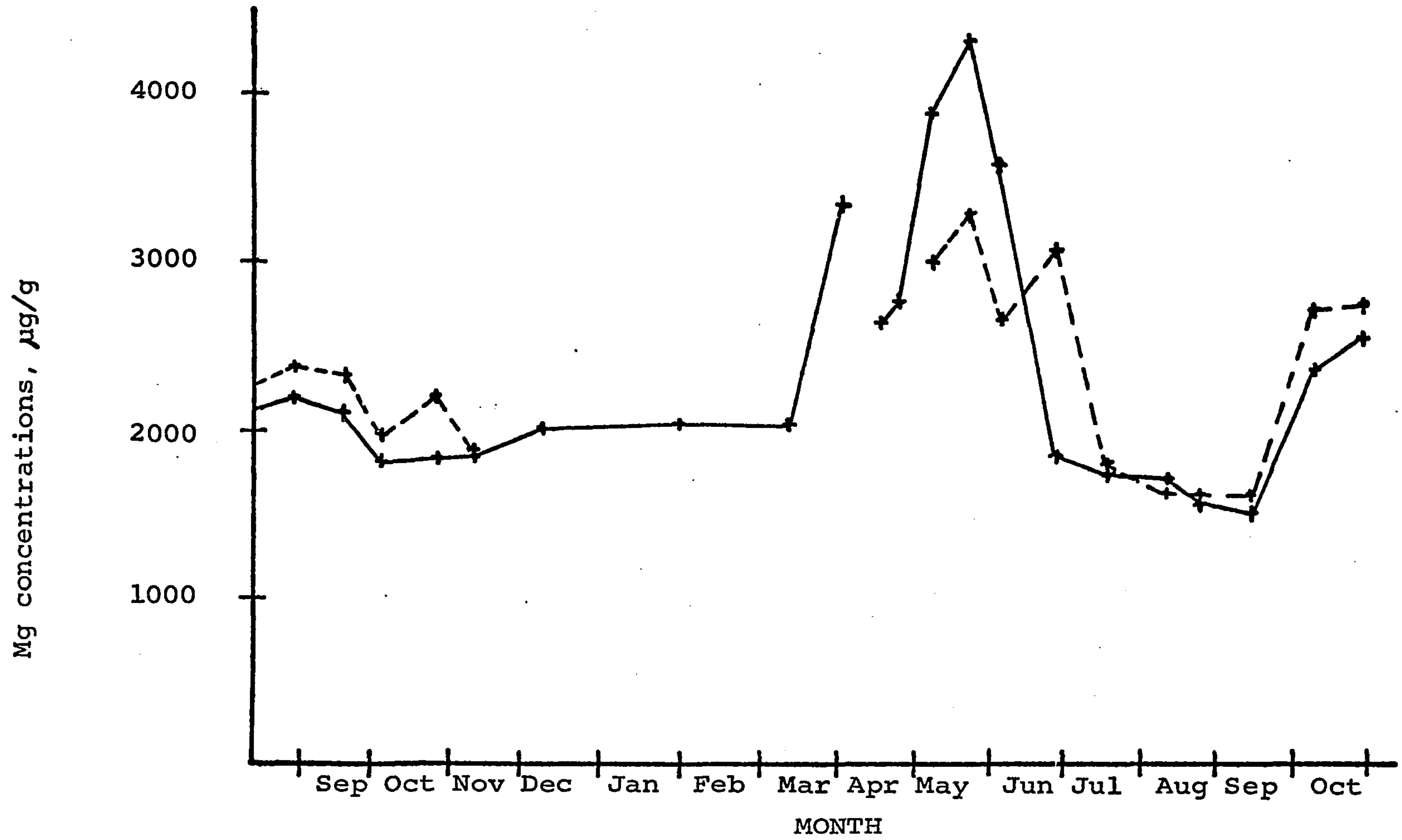

Figure 15. Seasonal changes of magnesium concentration in current twigs (solid line) and leaves (dashed line) of post oak.

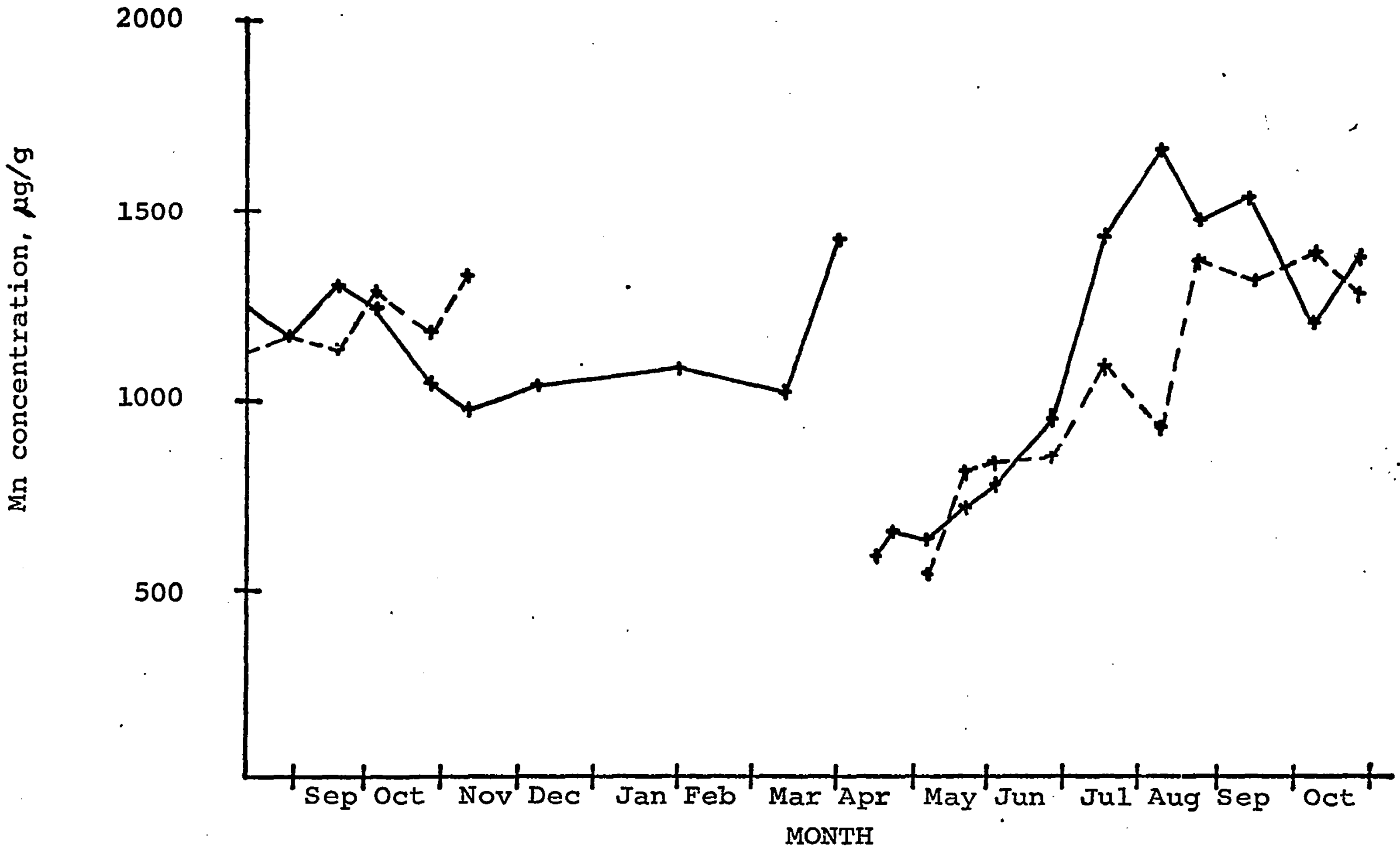

Figure 16. Seasonal changes of manganese concentration in current twigs (solid line) and leaves (dashed line) of post oak.

CONCLUSIONS

The stand consists of a few very old trees in a dense thicket of young trees and saplings, having been converted from a savannah to a forest during the past 80 years (Johnson and Risser, unpublished data). The stand is still in a phase of rapid growth, as shown by the high values for true increment of biomass and retention of mineral elements. An accurate prediction of biomass for the stand at equilibrium is not possible with present data, but by assuming that biomass is proportional to basal area an estimate can be made. The basal area of the stand is 18 m^2/ha and the biomass is about 220000 kg/ha. Upland forest stands in the area rarely exceed a basal area of 25 m^2/ha (Rice and Penfound 1959), so a steady-state biomass for the stand of much greater than 300000 kg/ha is unlikely. Annual net primary production in the stand can be expected to decrease as the stand matures (Rodin and Bazilevich 1967).

Mineral concentrations and the yearly mineral cycle for the elements considered in this study for the post oak - blackjack forest resemble those of the European oak forests, except for Ca. The unusual Ca uptake and retention in the stand is due to the high concentrations in post oak bark.

Some factors which need further study in the post oak - blackjack forest are: (1) litter dynamics, of which yearly variations in litterfall and litter decay, rate of branch and twig fall, and the role of fire have not been adequately investigated in this study; (2) variations from year to year in the seasonal cycle of mineral concentrations in plant tissues, examples of which were observed in this study but which remain unexplained; and (3) the high concentrations of Ca in post oak bark, which may be related to the fire tolerance of the species.

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