NET PRIMARY PRODUCTION AND PHENOLOGY ON A SOUTHERN APPALACHIAN WATERSHED[1]

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ABSTRACT

Net primary production (NPP) is an important function of plant communities which has not often been examined seasonally in a forested ecosystem. The major objective of the study was to measure above-ground NPP seasonally and relate it to phenological activity on a hardwood forest watershed at Coweeta Hydrologic Laboratory, North Carolina. NPP was estimated as the increase in biomass, estimated from regression equations on diameter. Diameter increases were measured by vernier tree bands. Phenological observations were made on bud break, leaf emergence, flowering, mature fruit, leaf senescence, and leaf fall. The species studied intensively were *Acer rubrum, Quercus prinus, Carya glabra, Cornus florida*, and *Liriodendron tulipifera*. *Liriodendron* was found to be the most productive species per individual, but *Quercus prinus* was the most productive per unit ground area. The total watershed estimate of aboveground NPP was 8,754 kg ha^{-1} yr^{-1} and included 47.9% leaves, 33.2% wood, 7.8% bark, 4.8% reproductive tissues, 4.2% loss to consumers, and 2.1% twigs. Increases in leaf biomass were most rapid in the spring, but woody tissue production peaked in June and continued through August. Since leaf production peaked in the spring, the plants' photosynthetic machinery was activated early in the growing season to support woody tissue production, which followed the period of rapid leaf growth, and reproductive activity. Flowering occurred during the leaf expansion period except for *Acer rubrum*, which flowered before leaf emergence. Fruit maturation occurred during late summer to early fall, when there were no additional biomass increases. *Acer rubrum* was an exception as its fruit matured during the period of leaf expansion.

NET PRIMARY PRODUCTION (NPP) is a measure of community vitality and is greatest when optimal environmental conditions prevail. Thus, primary productivity may be used as an indicator of an ecosystem's potential for storage of nutrients and energy. NPP also provides a useful value for comparisons between ecosystems.

Seasonal dynamics of communities or ecosystems are extremely important but are often ignored. Primary objectives of the present study were to measure aboveground NPP on a seasonal basis for a hardwood forest watershed at Coweeta Hydrologic Laboratory, North Carolina, associate NPP with phenological stages, and obtain total aboveground NPP estimates. The study concentrated on five major tree species, *Quercus prinus* L., *Acer rubrum* L., *Carya glabra* (Miller) Sweet, *Cornus florida* L., and *Liriodendron tulipifera* L. Other species on the watershed were studied in less detail.

MATERIALS AND METHODS—*Description of study area*—Coweeta Hydrologic Laboratory managed by the Forest Service, USDA, is located in southwestern North Carolina in the Nantahala Mountains in the Blue Ridge province of the Southern Appalachians. From 1909 to 1923 controlled selective logging took place in the Coweeta area; in 1924 the region became part of the Nantahala National Forest (Dils, 1957). The only major disturbance known to have occurred since then was the die-off of *Castanea dentata* (Marshall) Bockh. as the result of chestnut blight which reached the area around 1925 (Kovner, 1955).

The present study was conducted on the hardwood forest watershed which served as the control watershed for the IBP-Eastern Deciduous Forest Biome research effort at Coweeta. The horizontal area of the watershed is 12.46 ha and the average slope of the land is 53%. Predominant slope aspect is NW and elevation ranges from 721 m to 1,006 m above sea level. Bedrock is Carolina gneiss and the soils are classified as Porter loam. Mean annual temperature on the

TABLE 1. *Mean annual diameter increments (cm) of 14 woody species. Increments determined from cores represent averages of 10 years' growth in three cores from each sample tree. Increments determined from tree bands are based on 1973 readings. Error terms are ±1 SE*

Species	Annual increment (Tree bands)	N	Annual increment (Increment cores)	N
Quercus prinus	.294 ± .037	9	.248 ± .006	259
Liriodendron tulipifera	.522 ± .082	9	.348 ± .012	228
Acer rubrum	.340 ± .059	10	.212 ± .008	296
Carya glabra	.209 ± .055	7	.164 ± .006	205
Cornus florida	.120 ± 0	2	.098 ± .002	210
Oxydendrum arboreum	.156 ± .012	4	.130 ± .004	120
Acer pensylvanicum	.112	1	.120 ± .008	30
Betula lutea	.227 ± .055	5	.194 ± .008	150
Nyssa sylvatica	.213 ± .093	3	.166 ± .006	90
Magnolia fraseri	.486	1	.250 ± .010	60
Quercus velutina	.261 ± .097	3	.240 ± .014	110
Quercus coccinea	.338 ± .018	3	.286 ± .006	89
Quercus alba	.313	1	.220 ± .016	59
Robinia pseudo-acacia	.168	1	.182 ± .010	30

watershed is 13 C and mean annual precipitation is 1,813 mm (Johnson and Swank, 1973).

The overstory vegetation on the watershed was dominated by *Quercus prinus* L. Important co-dominants were *Q. coccinea* Muenchh., *Q. rubra* L., *Q. velutina* Lam., *Acer rubrum* L., *Carya* spp., and *Liriodendron tulipifera* L. Prominent under-story species were *Rhododendron maximum* L., *Kalmia latifolia* L., and *Cornus florida* L. A shrub layer dominated by *Vaccinium stamineum* L. was prominent over much of the watershed, even though the herb layer was relatively sparse. Total basal area on the watershed was 25.6 m²/ha and total aboveground biomass was 139,000 kg/ha in 1970 (Day and Monk, 1974). The forest seemed to be approaching maturity but probably had not peaked in total biomass at the time of the study (Day and Monk, 1974).

Sampling and analytical techniques—Net primary production is the amount of organic matter assimilated by a plant community minus the amount used up by respiration and is estimated by the equation NPP = B + L + G, where B is the increase in living biomass, L equals the loss of plant parts due to death and shedding, and G is the loss to consumers (Newbould, 1967). Commonly net primary production is underestimated because of a failure to consider losses to herbivores and shedding of plant parts such as reproductive structures (Ovington, 1963). The present study dealt only with increase in biomass; estimates of L and G used in the above equation were obtained by others at Coweeta. Both annual and seasonal increases in aboveground woody biomass were measured in the present study, but only annual values were measured for leaves. In-direct estimates of early season increases in leaf biomass were based on measurements of leaf area.

Aboveground production of woody tissues was estimated by calculating the increase in biomass from one time period to another. Aboveground woody biomass was calculated by regression equations of the form $\log_{10}$ WOODY DRY WT. = A + B $\log_{10}$ DBH (Day and Monk, 1974). The equations were developed from data reported by Sollins and Anderson (1971) for the southeastern U.S. Separate equations were used to estimate biomass of the boles and branches. Tree diameters used to calculate biomass were tallied in twenty-five 25 × 50 m inventory plots (Day and Monk, 1974). Woody biomass was calculated at the beginning of the growing season, mean diameter increments measured biweekly were added to the tree diameters, new biomass values were calculated, and the differences between values were taken as production. To satisfy the needs of a nutrient budget study (Day and Monk, 1977), bark and wood components were separated on the basis of values found in the literature (Whittaker, Cohen, and Olson, 1963; Whittaker and Wood-well, 1969; Young, 1971). Bark biomass was estimated as 27% of branch biomass and 17% of stem biomass. Diameter increments were measured for only 14 of the 42 woody species found on the watershed and for stems ≥2.5 cm dbh; consequently, only initial biomass values could be directly calculated for unmeasured stems. Production of unmeasured stems was estimated by assuming their biomass increase to be proportional to woody biomass increase of measured stems. Actual measurement of stem growth of all species would have been desirable but was im-practical. Based on Reiners' data from three Min-nesota forests (Reiners, 1972), twig production (current terminal growth) was assumed to be 25% of total branch production. Herbaceous plants were harvested in meter square plots, oven dried and weighed (Day and Monk, 1974).

Diameter increments were measured with

aluminum vernier tree bands (Liming, 1957). Bands are easily installed, do not injure the cambium which might cause unusual growth responses, and integrate uneven stem growth by measuring increases in circumference. Bands were placed on 69 trees during the winter of 1972. Trees were selected to represent a range of sizes and a variety of locations on the watershed. Forty-two trees included the five species of particular interest in this study and the other 27 trees included 11 other species. Bands were read either weekly or biweekly during the 1972 growing season and biweekly during the 1973 season. Readings were taken at approximately the same hour in the morning on each sample date to minimize the effects of diurnal diameter changes on data interpretation. In late October 1972, cores were taken from banded trees to measure the previous ten years of growth and validate the accuracy of the tree bands. Three cores were taken from each tree and the growth rings measured with a De Rouen dendrochronograph. Tree bands which registered diameter changes less than the mean annual increment minus one standard deviation (determined from cores) were discounted in the statistical analysis of the band data. The bands on these trees had probably not tightened on the stems. Most 1972 readings were discounted; consequently, only the 1973 data will be reported here. Bower and Blocker (1966) have suggested that bands should be installed one year before data are needed.

Total leaf biomass or annual production was estimated by regression equations of the form $\log_{10}$ LEAF DRY WT. $= A + B \log_{10}$ DBH (Day and Monk, 1974). However, leaf biomass increases very rapidly in early spring when leaves are still emerging and expanding. To quantify seasonal dynamics, early season leaf biomass must be determined. A crude estimate was obtained by the following technique. Ten to 20 leaves from each of 10 sample trees for each of the five species of interest, i.e., Quercus prinus, Acer rubrum, Carya glabra, Liriodendron tulipifera, and Cornus florida were taken from a variety of locations in the crowns at weekly intervals during early spring and biweekly through the summer of 1972. An optical planimeter (Gist and Swank, 1974) was used to measure the surface area of the sample leaves after first calibrating the planimeter with leaves of known area. The average surface area per leaf was calculated for each of the five species at each sample date and percent leaf expansion was determined. Percent leaf expansion was then considered to approximate the percentage of the annual leaf biomass present.

Since only the 1973 tree band data were used and leaf collections were made in 1972, woody production and leaf production were measured during different growing seasons. To estimate total seasonal production, leaf production and woody production were treated as if they were measured concomitantly. Initiation of growth and phenological development occurred about one week earlier in 1973 than in 1972; therefore, the 1972 sample dates were shifted back one week to align the leaf production data phenologically with the woody production data. Although Quercus prinus was observed to initiate leaf growth at about the same time both years on at least a few individuals, leaf development for most Quercus prinus trees still lagged about a week in 1972.

Phenological observations were made on the watershed on the five species of interest, either weekly or biweekly in 1972 and biweekly in 1973. The first date of observation was recorded for bud break, leaf emergence, flowering, mature fruit and leaf senescence. We observed variation of a week or more in the initiation time of phenological events among individuals of the same species. Leaf fall was recorded when the majority of leaves on all observed individuals of a given species had abscised.

RESULTS—Mean tree band increments exceeded mean growth increments determined from cores in all but two of the 14 species measured, and each of those species (Acer penyslvanicum and Robinia pseudo-acacia) had only one banded representative (Table 1). Species with the largest annual increments (fastest growers) were Liriodendron tulipifera (.522 cm) and Magnolia fraseri (.486 cm). Species with the smallest annual increments (slowest growers) were Acer pensylvanicum (.112 cm) and Cornus florida (.120 cm).

Diameter growth of the five species of particular interest through the 1973 growing season revealed logistic or S-shaped curves which commonly describe organismal and population growth patterns (Fig. 1A). Diameter growth began in late March with Quercus prinus and Carya glabra initially increasing in diameter more rapidly than the other species. Liriodendron tulipifera started last but surpassed the other species by mid-June. Most diameter growth occurred between early May and mid-July with the most rapid growth occurring during June. Liriodendron tulipifera continued rapid diameter growth until mid-August.

Leaf expansion, expressed as average surface area per leaf, occurred rapidly during the spring (Fig. 1B). Leaves of the five species studied had emerged from the bud by mid-April. Expansion was rapid and leaves were fully expanded by the last week of May or the first week of June. Cornus florida had the smallest surface area per leaf and Carya glabra, which has compound leaves, had the largest.

Phenological development was observed during the 1972 and 1973 growing seasons (Table 2). Bud break occurred about one week earlier in
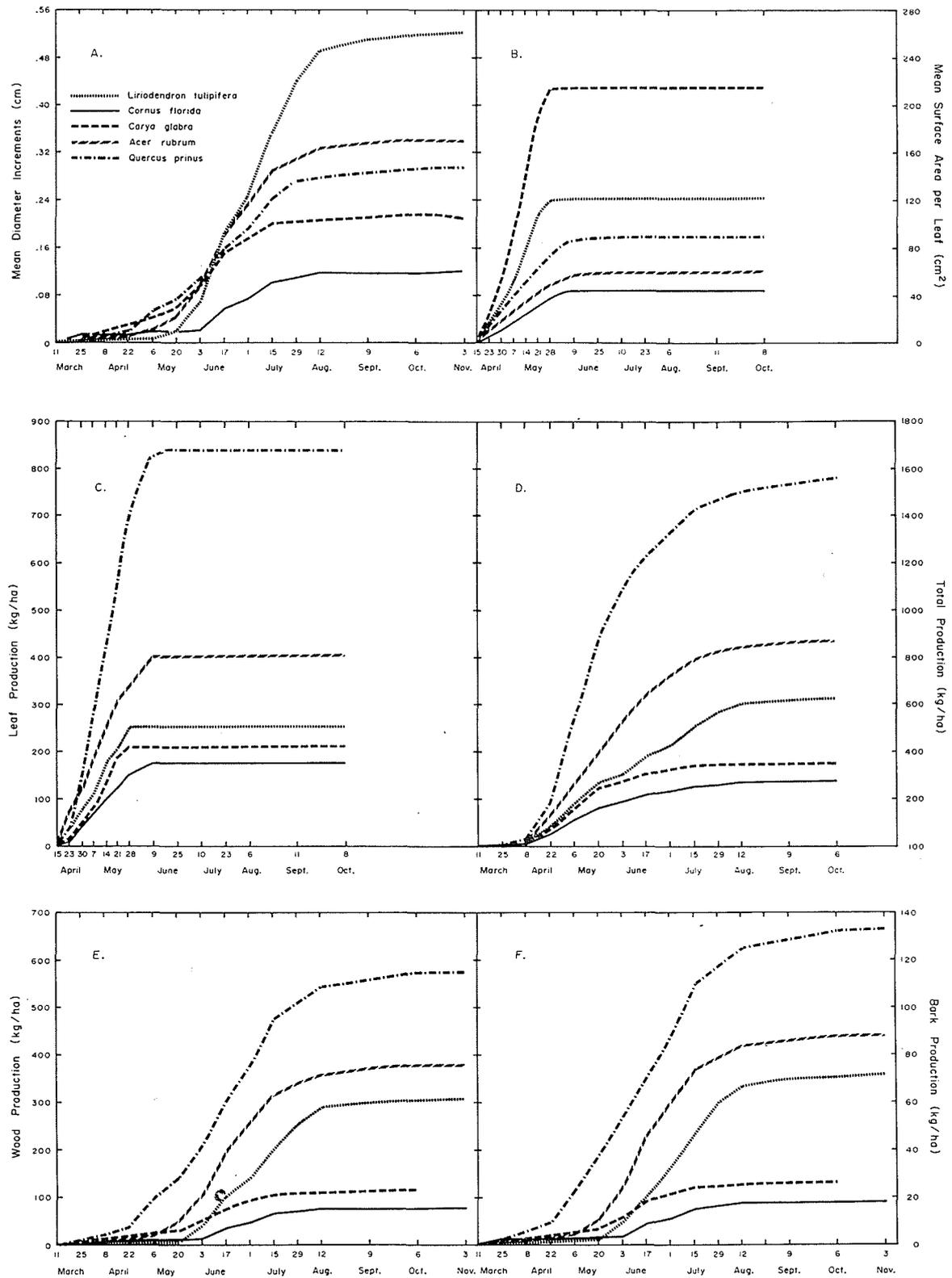
Fig. 1. Seasonal production of five prominent tree species on the hardwood forest watershed. (A) Diameter growth (cm) in 1973 measured by tree bands, (B) leaf expansion in 1972 expressed as mean surface area per leaf (cm²/leaf), and (C, D, E, F) leaf, total, wood and bark production estimated from increases in biomass (kg/ha). Note that the scales on the Y-axes differ.

TABLE 2. *Phenology of five prominent woody species on the hardwood forest watershed. Dates represent the first time a particular event was observed*

	Acer rubrum		Cornus florida		Quercus prinus		Liriodendron tulipifera		Carya glabra	
	1972	1973	1972	1973	1972	1973	1972	1973	1972	1973
Bud break[a]	April 9	March 25	April 9	March 25	April 15	April 8	April 9	March 25	April 15	April 8
Leaf emergence[b]	April 15	April 8	April 15	April 8	April 23	April 22	April 15	April 8	April 30	April 22
Flower[c]	March 16	March 11	April 15	April 22	April 23	May 6	May 14	May 20		May 20
Abortion of immature fruit[d]	April 15	April 8	May 21		July 10				July 10	July 1
Mature fruit[e]		May 6	Oct. 8	Oct. 6		Sept. 9		Oct. 6		Sept. 9
Leaf senescence[f]	Oct. 8	Oct. 6	Oct. 8	Oct. 6	Oct. 8	Nov. 3	Oct. 8	Oct. 6	Oct. 8	Oct. 6
Leaf fall[g]	Nov. 5	after Nov. 3	Nov. 5	after Nov. 3	Nov. 5	after Nov. 3	Nov. 5	after Nov. 3	Nov. 5	after Nov. 3

[a] Scales on foliage buds split open.
[b] First leaves open and recognizable.
[c] First flowers fully open.
[d] Fruits green.
[e] Fruit color changed from green to brown or red.
[f] Chlorophyll broken down in leaves resulting in color change to yellow or red.
[g] Majority of leaves on all observed individuals of a given species had abscised.

TABLE 3. *Annual aboveground net primary production on the hardwood forest watershed in kg/ha. Twig values represent current years terminal growth. Reproductive tissue data are incomplete*

Species	Bark	Wood	Twigs	Leaves	Reproductive tissues	Totals
Quercus prinus	124.1	552.0	32.0	845.9		1,554.0
Acer rubrum	81.3	359.6	22.2	403.6		866.7
Cornus florida	16.7	72.7	5.0	175.5		269.9
Carya glabra	24.6	109.5	6.1	212.0		352.2
Liriodendron tulipifera	66.5	294.3	18.1	251.0		629.9
Oxydendrum arboreum	19.6	86.3	5.5	200.8		312.2
Nyssa sylvatica	20.4	89.9	5.7	162.0		278.0
Quercus velutina	23.2	103.5	5.9	186.8		319.4
Quercus coccinea	46.3	206.2	11.9	300.1		564.5
Rhododendron maximum[a]	96.7	292.5	23.9	263.4	3.7	680.2
Kalmia latifolia[a]	24.1	124.2	9.4	129.4	1.3	288.4
other woody species	136.7	616.0	37.9	1,008.8		1,799.4
herbs				55.5		55.5
Totals	680.2	2,906.7	183.6	4,194.8	424.2[b]	8,389.5[b]

Loss to Consumers = 364.8 kg/ha[c]
Total NPP = 8,754.3 kg/ha

[a] Data from McGinty (1972).
[b] Includes 419.2 kg/ha oak reproductive tissues (Cromack, 1972).
[c] Calculated as 8% of leaf production at Coweeta (Crossley, pers. comm.).

1973 than in 1972 and the leaves fell later in 1973 than in 1972. *Acer rubrum* was the first to flower (in mid-March before the leaves were out) and produce fruit (early May), while *Liriodendron tulipifera* and *Carya glabra* were the last (mid-May). Aborted fruits of *Acer rubrum*, *Cornus florida*, *Quercus prinus*, and *Carya glabra* were observed on the ground prior to fruit maturation in 1972 and 1973.

Bark, wood, leaf and total aboveground net primary production were estimated by calculating increases in biomass (Fig. 1C, D, E, F). Total NPP of a given species on the watershed is a product of the species' rate of growth and the abundance or total standing crop biomass of that species on the watershed. Although *Liriodendron tulipifera* had the greatest growth rate, *Quercus prinus* was the most productive species on the watershed because of its large biomass.

Total aboveground NPP was estimated to be 8,754.3 kg ha⁻¹ yr⁻¹ (Table 3), or approximately 6% of the standing crop biomass. Accumulation of perennial biomass (wood production) was found to be 3,770.5 kg ha⁻¹ yr⁻¹. One source of underestimation of total NPP was the lack of complete information on production of reproductive structures; only flower and fruit production of *Rhododendron maximum*, *Kalmia latifolia*, and *Quercus prinus* were available. Losses to consumers were estimated as 8% of leaf production (Crossley, pers. comm.). Species contributing most to aboveground NPP were *Quercus prinus* (18.5%), *Acer rubrum* (10.3%), *Rhododendron maximum* (8.1%), *Liriodendron tulipifera* (7.5%) and *Quercus coccinea* (6.7%).

Rhododendron maximum, an evergreen species, contributed 22.5% of the total leaf biomass on the watershed but only 6.3% of total leaf production. Most current annual *Rhododendron* leaf biomass remains on the tree while a smaller quantity of older leaves falls to the forest floor. *Rhododendron* leaves may remain on the tree for up to seven years (McGinty, 1972).

Total aboveground NPP included 47.9% leaves, 33.2% wood, 7.8% bark, 4.8% reproductive structures, 4.2% loss to consumers and 2.1% twigs. However, the distribution of production among plant components differed among species. For example, leaf production was 65% of *Cornus florida* NPP but only 39.8% of *Liriodendron tulipifera* NPP. Although over half of the annual NPP (57%) is lost as litter and to consumers, perennial tissues accumulate over the years and produce a standing crop biomass many times greater than annual production. At Coweeta the portion of annual NPP that went to litter and consumers represented only 3.4% of the total standing crop biomass.

DISCUSSION—Mean annual diameter increments determined from tree bands exceeded mean increments determined from cores in part because the cores probably shrank after removal from the tree as the result of dehydration. Natural shrinkage of tree diameters also occurs during the winter months because of dehydration. Also, the initial diameter increases registered by tree bands in the spring are primarily the result of rehydration of the stem tissues, not cell division (Zimmermann and Brown, 1971). Monk (1959) has

TABLE 4. *Aboveground annual net primary production of several deciduous forest stands*

Species	Location	Total aboveground NPP kg ha⁻¹ yr⁻¹	Aboveground increment kg ha⁻¹ yr⁻¹	NPP (% of standing crop biomass)	Source
Quercus	Belgium	12,200	6,240	10	Duvigneaud and Denaeyer-DeSmet (1970)
Liriodendron tulipifera	Oak Ridge, Tenn.	11,700	2,920	10	Sollins (1972)
Liriodendron tulipifera	Oak Ridge, Tenn.	10,300	3,590	8	Sollins (1972)
Quercus prinus	Oak Ridge, Tenn.	12,500	3,890	10	Sollins (1972)
Quercus-Carya	Oak Ridge, Tenn.	11,100	3,130	9	Sollins (1972)
Quercus-Carya	Georgia piedmont	5,415	—	4	Monk, Child and Nicholson (1970)
Quercus	Minnesota	8,908	5,215	7	Reiners (1972)
Quercus-Carya	Great Smoky Mountains	12,030	—	3	Whittaker (1966)
Quercus prinus	Great Smoky Mountains	14,650	—	4	Whittaker (1966)
Liriodendron tulipifera	Great Smoky Mountains	24,080	—	11	Whittaker (1966)
Quercus rubra	Great Smoky Mountains	8,280	—	6	Whittaker (1966)
Quercus rubra Quercus alba	Great Smoky Mountains	5,680	—	6	Whittaker (1966)
Quercus-Carya (predominantly *Quercus prinus*)	Coweeta	8,754	3,771	6	present study

suggested that the question of whether diameter increases due to rehydration are part of growth is academic. In the present study initial diameter increases were included in the analysis as the rehydration of tissues was considered to be part of the seasonal development of the trees. Rehydration certainly results in an increase in tree volume and nutrient standing crop.

The most rapid radial growth occurred during June and about 95% of radial growth was complete by late August or early September. Radial growth of oaks and hickories was initiated more rapidly than growth of other deciduous species. Oaks and hickories are ring porous trees, which begin radial growth immediately throughout the tree in conjunction with bud activity. In diffuse porous trees, such as *Acer rubrum, Cornus florida,* and *Liriodendron tulipifera,* radial growth begins at the twigs and slowly moves down the tree (Wareing, 1951; Fraser, 1952; Zimmermann and Brown, 1971). Mowbray and Oosting (1968) observed that diffuse porous species grew faster than ring porous species even though diffuse porous trees started later. This was also observed at Coweeta. *Liriodendron tulipifera* had a con-

siderable lag phase after leaf expansion began but a rapid growth phase followed.

An examination of the time sequence of phenological events in relation to seasonal NPP rates suggested several strategies of plant development. The rate of accumulation and timing was inherently different among species. Leaf production peaked in the spring; thus, the plants' photosynthetic machinery was activated early in the growing season to support woody tissue production, which followed the period of rapid leaf growth, and reproductive activity. Flowering occurred during peak leaf production except for *Acer rubrum,* which flowered before leaf emergence. Fruit maturation occurred during late summer to early fall, when there were no additional biomass increases. *Acer rubrum* was again an exception as its fruit matured during peak leaf production. Early, rapid development of the photosynthetic tissues (leaves) is advantageous to the plants.

Total annual aboveground NPP at Coweeta was within the lower range of values reported in other temperate forest ecosystems (Table 4). Rodin and Bazilevich (1968) reported NPP

values for temperate forest stands all over the world in the range of 7,000 to 12,000 kg ha^{-1} yr^{-1}. Whittaker (1966) found the usual range of NPP values in the Great Smoky Mountains to be between 9,000 and 12,000 kg ha^{-1} yr^{-1} in climax forests. Most NPP values reported for forest systems have been determined by averaging five to ten years of growth. NPP at Coweeta was measured for one year only; thus, the study year may not have been typical. Some NPP values have been determined by dividing stand biomass by stand age; however, this method does not give an accurate estimate of annual production in the mature stand, as Rodin and Bazilevich (1968) have reported that net production decreases as the forest stand becomes older. An oak forest in Russia attained maximum productivity at 25 years (16,000 kg ha^{-1} yr^{-1}) but NPP was only 4,500 to 5,000 kg ha^{-1} yr^{-1} after 60 to 100 years. The NPP value reported on the Georgia piedmont by Monk, Child, and Nicholson (1970) was low (5,415 kg ha^{-1} yr^{-1}), but they report that it was an underestimate and actually probably exceeded 6,000 kg ha^{-1} yr^{-1}. The relatively low productivity estimates for the Coweeta forest may be attributed to the presence of unproductive areas characterized by very steep terrain and by a predominance of shrubby plants, primarily *Kalmia*. Total aboveground biomass on the watershed was fairly low. In terms of total aboveground net primary production and NPP as a percent of total standing crop biomass, the forest stand at Coweeta most closely resembled the Minnesota *Quercus* forest (Reiners, 1972) and the *Quercus rubra* stand in the Great Smoky Mountains (Whittaker, 1966). However, the aboveground biomass increment in the Minnesota *Quercus* forest exceeded that at Coweeta, and the stand at Coweeta had greater production of leaves and reproductive structures than the Minnesota stand (Reiners, 1972). This could be due to variation in species composition and age of the two forests.

Seasonal productivity data are useful in characterizing an ecosystem's dynamic nature for both energy and nutrient regimes and in making comparisons with other systems. Too often systems analysts concern themselves with annual budgets alone; consequently, seasonal dynamics are not considered in the resulting models and valuable information about the system is ignored. A study of vegetation nutrient dynamics was conducted on the Coweeta watershed (Day and Monk, 1977), and seasonal productivity data were invaluable in obtaining and evaluating results.

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