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PHENODYNAMICS OF PRODUCTION AND CHEMICAL POOLS IN MAYAPPLE AND FLOWERING DOGWOOD

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1. INTRODUCTION AND LITERATURE REVIEW

Phenology has been described as the observation of life phases of plants and animals in their environment throughout the year. Among plants, these life cycle phases include germination, leaf development, flowering time, fruiting time, seed dispersal, senescence, and leaf fall. While these events are determined by the genetics of the species, the onset of a phase is often controlled by some environmental factor (Daubenmire 1959). Certain phenological events appear to respond to moisture, light, or temperature thresholds and consequently are manifested with some regularity corresponding to seasons.

Associated with the phenodynamics of species or communities are changes in biomass and productivity. Such quantitative changes reflect an influence of meteorology on primary production, particularly in agricultural systems, and offer similar aids to the analyses of natural ecosystems such as deserts, grasslands, and forests. Because of these seasonal influences, the period during which a particular event occurs can be predicted providing that basic meteorological information is available. The capability to accurately predict phenological events has been utilized by climatologists and agrometeorologists to select optimum seeding dates (Hopkins 1938), and in the planning of other agricultural practices, particularly in Europe (Molga 1962, Schnelle 1955). Further applications of phenological considerations have been utilized in crop pest control to maximize production (Hopp 1969, Wallin 1967, Woods 1969). In terms of economic investment, quantitative phenology (phenometry) has been successfully applied to predicting harvest dates and the scheduling of agricultural practices to ensure both quality and an even flow of produce to food processors (Bomalaski 1948, Brown 1952, Katz 1952, Newman 1967, Seaton 1955). In defining the beginning, duration, and end of seasons, it has been stated that phenological records are better indices to the bioclimatic character of local areas than recordings made by mechanical instruments (Hopkins 1918, 1938). This suggests that specific plants and selected phenological events might be useful as indicators on which to key major land management practices and productivity studies (Caprio 1966, Lieth 1971).

As pointed out by Lieth (1970), there are two approaches to studying phenological events: descriptive and analytical. Both methods have been used in floristic and ecological studies. Descriptive studies have relied mainly on morphology and constitute the majority of investigations. The analytical approach is not a new concept, but it is receiving renewed interest for future productivity studies.

An appeal was made for scientists to orient their research related to phenology as part of the United States' contribution to the International Biological Programme (IBP). Such unified efforts would provide a better understanding of biological phenomena (Bliss 1967). Lieth (1970) pointed out the value of phenological considerations in productivity research because previous studies with harvest at the end of the growing season only yielded an estimate of net production. Productivity studies with phenological considerations, as proposed within the IBP, would lead to a more accurate analysis of ecosystems.

Because microclimate (Jackson 1966, Brown 1952) can strongly influence phenologic events, the most useful information would consist of observations taken from habitats having well defined boundaries. Some phenological observations, particularly date of first flowering, have been incidental to a major study (Stevens 1917), while others merely reflect a personal interest (Hulbert 1963, Taylor 1969). Lieth (1970, 1971) has demonstrated the importance of phenology to mineral cycling and elemental storage pools, primary production, and eventually predictive models (Lieth and Radford 1971).

The standing crop biomass of plants represents a pool of mineral elements available for subannual and annual chemical cycles among established plant communities and provides for storage and the potential release of elements necessary for the revegetation of sites following perturbations (e.g., fire). Many elements are permanent constituents of plants (e.g., protoplasm and cell walls) and are not easily mobilized or translocated to other plant parts. In this study only the essential elements, carbon, nitrogen, sulfur, potassium, calcium, magnesium, and phosphorus, are considered. With the exception of carbon, all of these elements enter the plant from the soil. Carbon is obtained from water or atmospheric gases. Sulfur may enter the leaves as SO_2 when the gas is present in the atmosphere, while there is no reliable evidence that plants can utilize gaseous nitrogen from atmosphere. Each of the mineral elements impart important influences on plant growth and metabolism. Their concentration and abundance is strongly related to seasonality within species and the different life stages.

Sulfur is distributed throughout plant cells and is a part of the amino acids, cystine, cysteine, and methionine; thus, it contributes to plant proteins. This element is usually absorbed by roots as the SO_4^{--} ion, but often becomes toxic as SO_2 from fossil fuel combustion. During the phenophases of fruit development and seed ripening, sulfur may accumulate in those tissues and organs while being depleted from the leaves.

Plant calcium is largely in the foliage and is relatively immobile and not easily redistributed in other plant tissues as it is permanently fixed in the cell walls as a calcium salt. As leaves develop and expand, calcium concentration increases becoming greatest in the older mature leaves. Calcium is important to nondifferentiated cells as mitosis is altered or inhibited in the absence of this element.

A considerable fraction of the phosphorus burden in a plant is located in the fruits and seeds, accumulating during the life stages of fruit and seed development. Phosphorus is generally absorbed by plants as the $H_2PO_4^-$ ion. A major role of phosphorus is in plant processes such as phosphorylation and high energy phosphate bonding. Phosphorus is easily redistributed in plants, especially from older leaves to developing leaves or fruits when the external availability is deficient.

Potassium concentrations are greatest in developing buds and leaves, but decrease in mature foliage, fruits, and seeds. The exact role of potassium in plant metabolism is not known, but it is generally thought to be catalytic. As noted by Attiwill (1966), potassium is the nutrient most easily leached by precipitation. Potassium contained in throughfall indicated that 10% of the maximum foliar content was removed by rainfall (Thomas et al., 1967). The protein content of potassium deficient plants is low, suggesting that potassium is involved in the synthesis of proteins.

Magnesium is the only mineral constituent of the chlorophyll molecule, and consequently a majority of the plant magnesium is present in chlorophyll-bearing components (leaves, stems, floral appendages, etc.). This element is easily transferred from older plant organs to the newly developing ones. It is associated with phosphate metabolism and affects the respiratory processes.

All physiological reactions typical of living cells are influenced by the physical and chemical properties of proteins (16 to 18% nitrogen). Nitrogen is absorbed from the soil as nitrates, nitrites, organic nitrogen compounds, and ammonium salts. The latter is probably the most readily available form to plants.

Among land plants the atmosphere is the major source of CO_2. Carbon dioxide is returned to the atmosphere from plant and animal respiration, combustion of fossil fuels, volcanoes, mineral springs, and the oceans. Since the beginning of the industrial revolution, atmospheric CO_2 has increased in concentration nearly 17% (Lemon 1983) and is expected to increase at the rate of 1.5 ppm per year if fossil fuel utilization and worldwide deforestation remains unaltered. Plants are always CO_2 limited for photosynthesis such that they respond positively to increasing CO_2 concentrations. The hypothesis that increasing CO_2 enhances forest and tree growth poses an interesting concept. If net production increases from elevated CO_2, it must be in the form of increased photosynthates, which in part, are indirectly utilized in the synthesis of new wood (xylem). Experimental plant fumigations at elevated CO_2 atmospheres have shown that flowering phenology has been influenced by increased CO_2 mobilization, while enhanced wood formation has been documented by Doyle (1986).

The objective of this study is to provide an understanding of the seasonality of biomass production and chemical storage among selected forest species as an aid to the analysis and management of a forest ecosystem model. The specific goals to accomplish the objectives included

1. the construction of phenological calendars to be superimposed on the civil calendar, such that the seasons of the year are not marked by calendar dates but rather by dated groups of phenological events;
2. to develop a capability to predict onset of the generative phase (flowering) from heat unit summation methods;
3. to illustrate the role of phenology to biomass production and chemical storage in two indicator species, mayapple and flowering dogwood; and
4. to develop the capability to predict aboveground and below ground standing crop biomass in dogwood.

2. THE OAK RIDGE SITE OF IBP

The phenological observations reported are from the Oak Ridge IBP site in Roane County in eastern Tennessee (approximately 84°18′W longitude and 35°54′N latitude) on lands acquired in 1942 by the federal government. Since acquisition as farmlands, most of the forests on the Department of Energy's (DOE) Oak Ridge Reservation (ORR) have remained relatively undisturbed except for some recent forest management practices (Curlin 1965). Approximately 15,175 ha, now mostly forest, have long been utilized as sites for ecological research (Auerbach et al., 1964). Access to the area is denied to the general public and the reservation affords maximum protection for long-range ecological studies. Communities, populations, or individual species selected for phenological observations can provide data year after year (Taylor 1969).

The general area was formerly classified as an oak-chestnut association (Braun 1950) within the Ridge and Valley Physiographic Province (Fenneman 1938). As individual chestnut trees were eliminated by the chestnut blight, suppressed or codominant species (oaks and hickories) replaced them as major canopy components (Woods and Shanks 1959). Tulip- or yellow-poplar (Liriodendron tulipifera L.) is abundant near the base of ridge and slope habitats in secondary communities. A tulip-poplar-dominated forest ecosystem has been the subject of numerous experiments (Auerbach et al., 1964; Olson 1965, Peters et al., 1969; Reichle et al., 1972; Waller and Olson 1967). Data presented here are indicative of the phenodynamics within the major forest association (oak-hickory) and certain subcommunities (including escaped or naturalized species) as influenced by meteorological parameters. Phenological observations, where complemented with quantitative analyses, can reveal the importance of short-term phenological events to functional processes within the forest ecosystem.

3. METHODS

The phenological records summarize observations for individual plants or populations of plants (annuals) within species between 1963 and 1970. All observations are limited to Roane and Anderson Counties within the DOE ORR. While major emphasis is on the generative phase (flowering) for most species, several species common to the mesic slope forest were selected for detailed observations. Life cycle events observed in detail were intended to provide records of the following events (phenophases):

1. initiation of vegetative growth (bud swelling);
2. vegetative growth (photosynthetic period);
3. onset of floral development;
4. flowering (generative phase);
5. fruiting, unripe seeds and fruits;
6. ripe fruits and seed dispersal; and
7. senescence (color change in leaves).

The objectives of these observations are intended to provide insight as to the arrival of spring, definition of the growing season (photosynthetic period), and initiation of fall dormancy. These data, in turn, are valuable to correlate with changes in functional processes such as photosynthesis and respiration.

In addition, the short-term phenological events represent mineral input into nutrient (element) pools and subsequently affect or contribute to the mineral cycle within the ecosystem. The latter consideration was studied in detail for a single tree species, dogwood (Cornus florida L.), important to the understory layer of the oak-hickory forest association, and a herbaceous layer species, mayapple (Podophyllum peltatum L.), selected to illustrate the values of short-term phenological considerations to estimates of productivity and nutrient pools through growth analysis. Mayapple has been suggested as a potential indicator species for phenological networks throughout the eastern deciduous forest.

Mayapple is a component of the herbaceous layer of a lower slope forest dominated by tulip-poplar with Christmas fern [Polystichum acrostichoides (Michx.) Schoot.] and wild hydrangea (Hydrangea arborescens L.) constituting approximately 80% of the total biomass of the herbaceous layer (Cristofolini 1970). The study site is located on the lower slope of Copper Ridge with a north-facing exposure. The area is a series of sinkhole depressions on dolomitic limestone. Classified as Emory silt loam, the well-drained soil is a dark reddish-brown in color, with the A and B horizons extending to a depth of 90 cm or more. Reaction is medium (5.6 to 6.0) to strongly acid (5.1 to 5.5) in all horizons. A grid system was established in a forest ecosystem on the north slope of Copper Ridge of the reservation (Auerbach et al., 1964) to study mayapple populations. The grid encompassed an area of 2 ha and consisted of 200 permanent reference plots (100 m^2 each). Biomass, productivity, and chemical pools were determined from dimensional (stems, leaves, flowers, fruits, etc.) and chemical analyses at each of the phenophases previously identified. Harvest plots (0.01 ha) were randomly selected from the grid in such a way that mayapple colonies appeared in at least 21 plots. This would permit replication (3) of harvest plots during each of the several phenophases and thus reduce sample variability. Within each plot selected for harvest, plant density was determined. At each harvest period 20 plants were collected, and partitioned according to leaves, stems, roots (rhizomes), flowers, and fruits. Following gravimetric analyses, samples were ground in a Wiley mill using a 20 mesh screen and prepared for elemental analysis by atomic absorption spectrophotometry (K, Ca, Mg) using standard procedures (ORNL 1973) and hydrogenation and element-selective detection procedures for P, C, N, and S (Horton et al., 1973).

A shortleaf pine plantation in an extension of Bethel Valley south of Chestnut Ridge was harvested in 1970. The stand was 0.9 km from New Zion Cemetery on an azimuth of S35°W and covered an area of 6.6 ha. The soil of this site is strongly acid in reaction (5.1 to 5.5), with low organic matter and plant mineral content. Classified as a Clarksville cherty silt loam, derived from cherty dolomitic limestone, a distinct plow layer exists to 18 cm as evidence of cultivation prior to government acquisition of the land in 1942. The present surface horizon (A and E) extends to 25 cm, the B horizon to 45 cm, and the recent development (since 1942) of an A horizon to 5 cm deep. Twenty-one undamaged, mature dogwood trees were selected for later harvest. Each tree was numbered and three were randomly harvested at each of seven life stages (phenophases) in 1971. Each tree was harvested at ground level and partitioned into bole, branches, and roots for fresh weight determinations in the field. Roots were removed in a method similar to that described by Thomas et al., (1967). Trees with leaves, flower buds, flowers or fruits were bagged and taken into the laboratory for counting and fresh weight measurements. All samples were oven dried at

100°C to a constant weight. After dry weights were determined, subsamples were ground in a Wiley mill using a 20 mesh screen and archived for later analytical analyses as described above.

4. PHENOLOGY OF FLOWERING WITHIN AN OAK-HICKORY FOREST ASSOCIATION

Vegetative growth of some plants diminishes with the advent of flowering. Among selected species (indicators), the dates of first flowering reported by regional networks of observers form the basis of maps portraying the arrival of the growing seasons and offering guides to agricultural practices (Caprio 1966, Lieth and Radford 1971). Records of dates of first flowering for major species at the Oak Ridge site have been observed since 1963 (Taylor 1969). These records are summarized in a phenogram (Figure 1) illustrating the mean date of first flower between 1963 and 1970. The figure shows that phenological development can be examined for particular communities or for various taxa. An early peak in the number of species flowering, followed by a decline and a subsequent increase in early summer, has been widely observed (Harper 1906).

The first major peak (Week 16) is composed of woodland species, mainly herbaceous, while the second or early summer peak (Week 23) is dominated by species indigenous to thickets, roadsides, or openings within the forest. By week 16 fully 50% of the spring, early summer species have flowered (Figure 2).

The transmission of incident radiation to ground level is reduced 40% following the spring peak in flowering, corresponding to 75% leaf emergence of the dominant canopy species of lower slope forests (Figure 3). At the time of total leaf emergence (Week 24) light transmission is reduced to 11%. These data are comparable to results in agricultural experiments (Yocum et al., 1964).

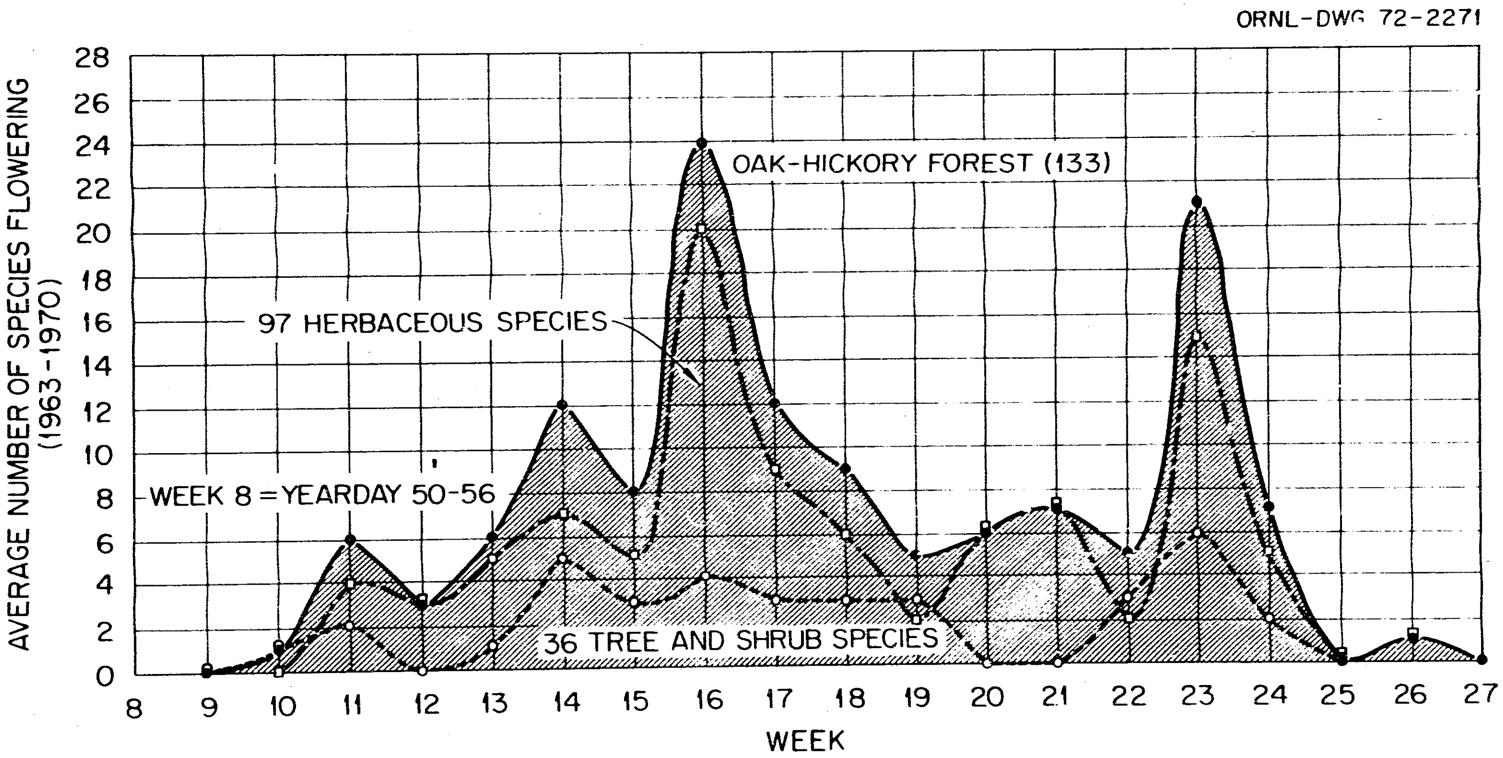


Figure 1. Phenogram of the oak-hickory forest association depicting flowering seasons of moist and dry habitats, distinguished by spring and early summer floras. Data represent mean date of first flower between 1963 and 1970. Richness of the understory is noted by the number of herbaceous species observed. Number in parenthesis indicates the total number of species observed.

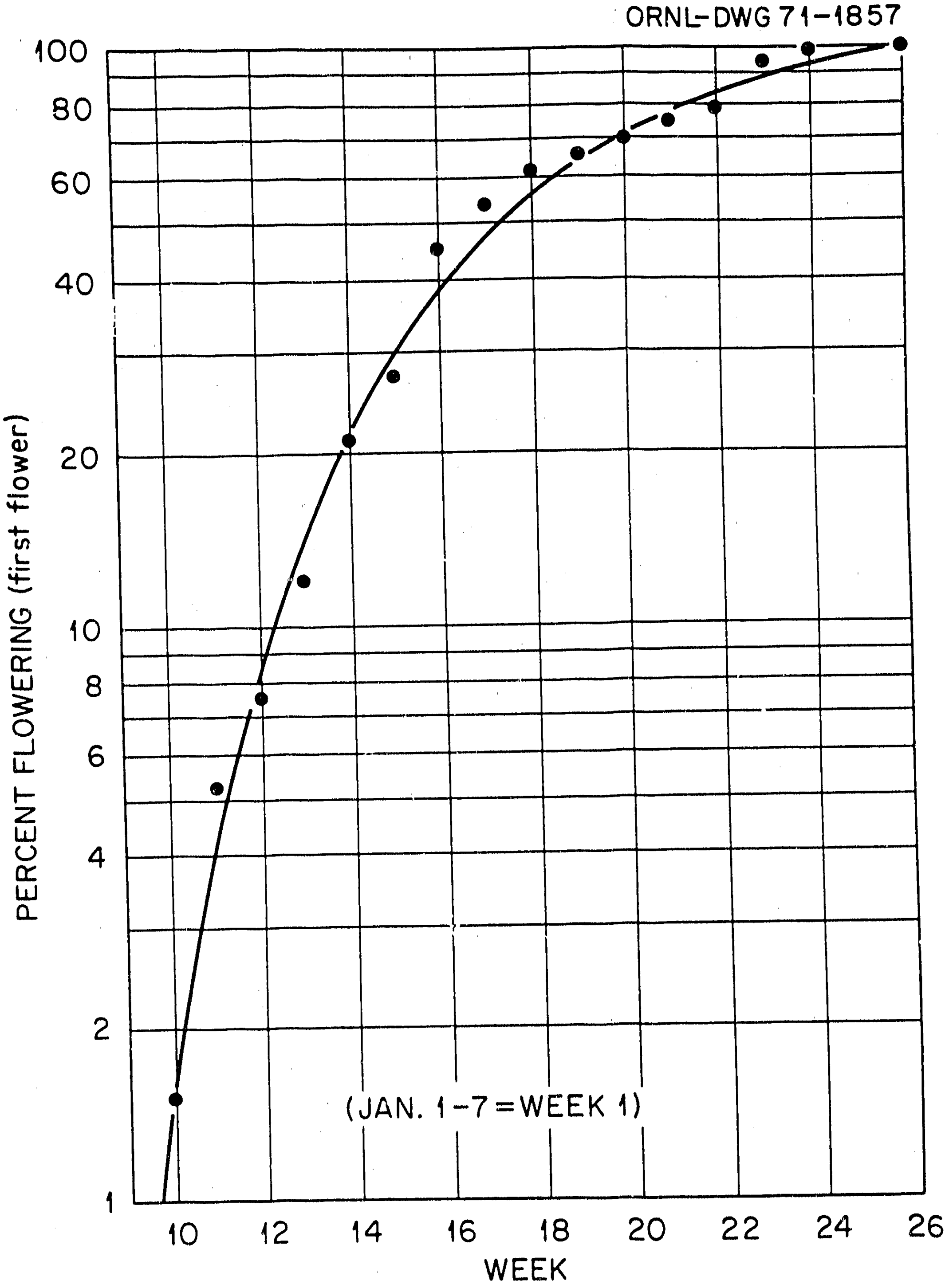


Figure 2. Progression of the spring flowering season as noted by the percent taxa flowering.

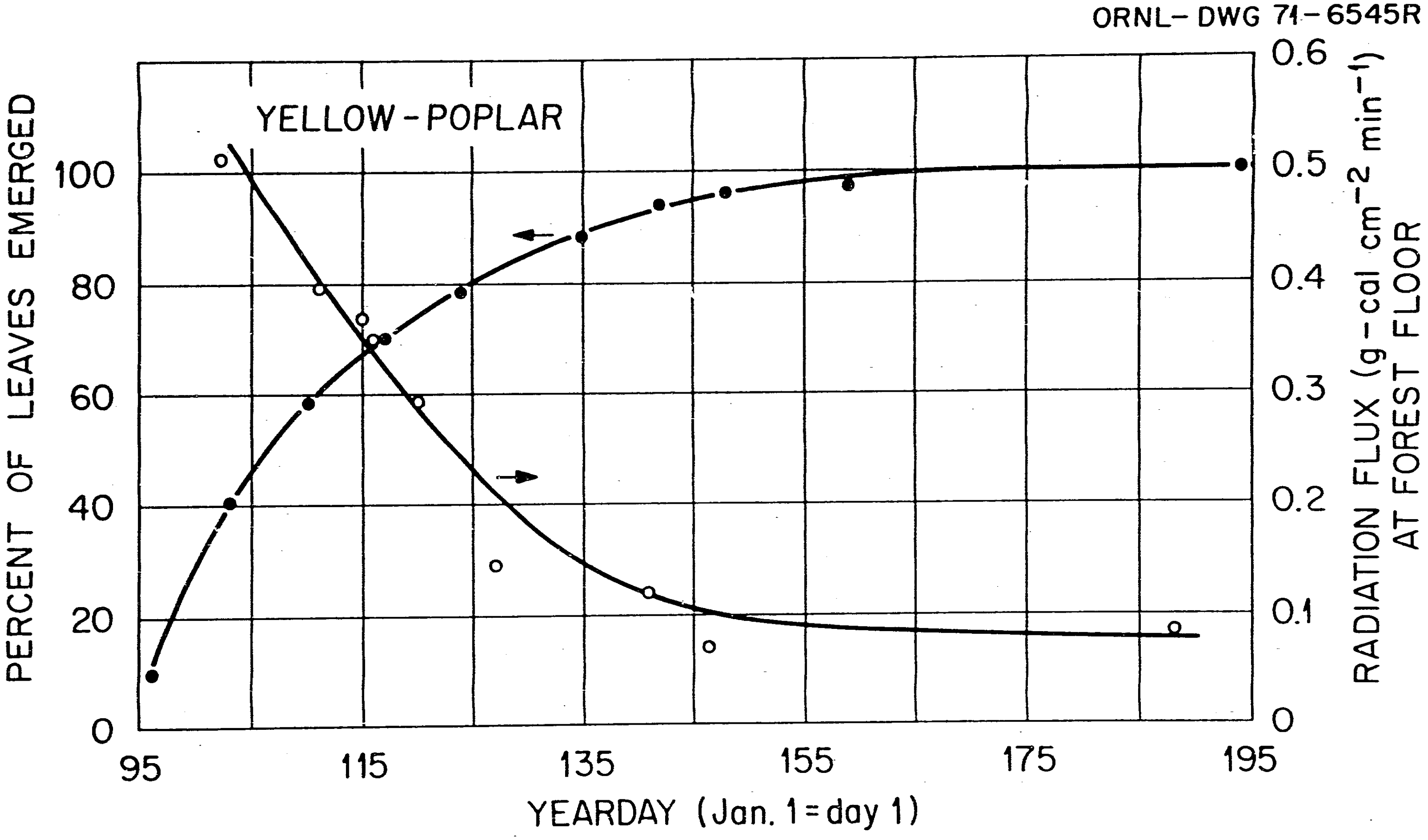


Figure 3. Cumulative percentage of maximum leaf emergence for <u>Liriodendron tulipifera</u> during the 1970 growing season and concomitant light extinction on the forest floor.

The second peak flowering season (Week 23) occurs after the canopy has closed. However, this floristic component in the development of the forest ecosystem is composed of species found in more open habitats (roadsides and forest edges) where light transmission is not so significantly reduced. Early canopy development by dominant tree species and subsequent reduction in light transmission to the forest floor might alter the photosynthetic efficiency of understory species. Consequently, the completion of the life cycle phases might result in reduced propagules (seeds), jeopardizing the continued existence of certain species within the ground layer.

4.1 INFLUENCE OF METEOROLOGICAL FACTORS

Variability in date of first flower within a species (Figure 4) is due, in part, to variation in one or more meteorological parameters. Mean monthly temperatures during early 1970 were below the monthly mean values for the 10-year period between 1961 and 1970 (Figure 5) but were generally higher during the remainder of the year.

The relationship between the thermal environment and the phase of development of certain plant species has been utilized by agriculturists with varying success to characterize the developmental phases of plants from trends in the thermal environment (Baker and Brooks 1944, Bomalaski 1948, Brown 1952, Hopkins 1938, Katz 1952, Newman et al., 1967, Reaumur 1935, Seaton 1955). In thermal summation techniques (degree-days or heat units), threshold temperatures have been utilized to predict plant development within homogeneous systems such as corn (Scott 1946) and peas (Katz 1952). The development of the heat unit concept and subsequent modifications have been discussed in detail by Wang (1960).

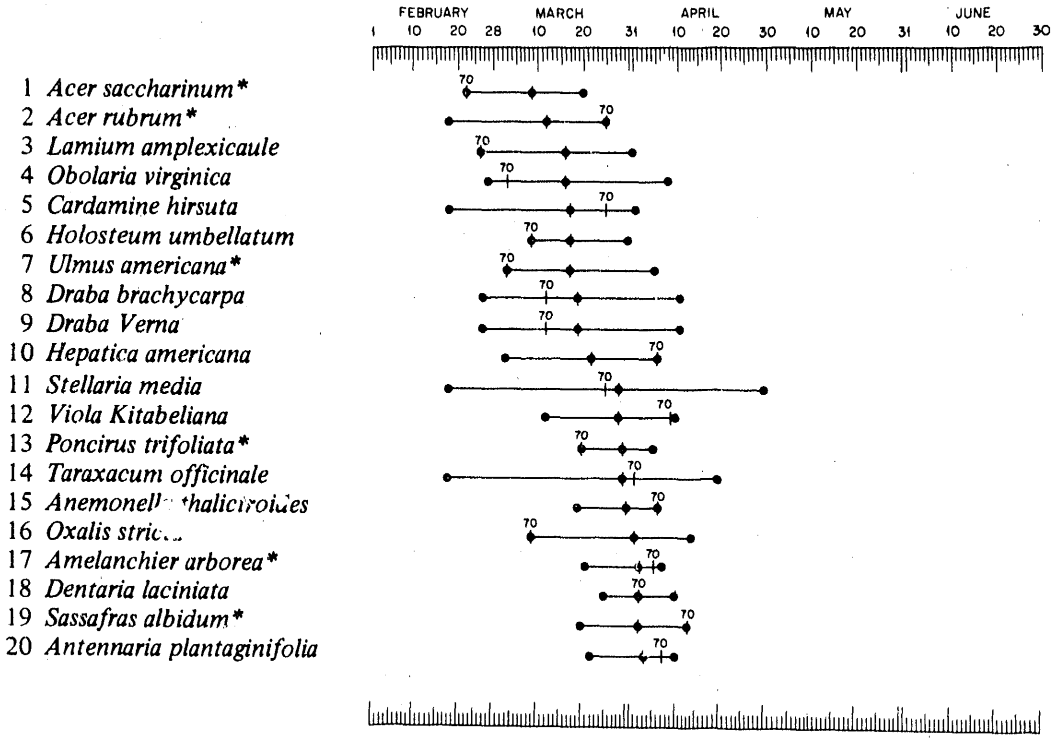


Figure 4. Flowering period of species on the Oak Ridge Reservation between 1963 and 1970 arranged chronologically by date of first flower (Nomenclature after Fernald 1950). Species number corresponds to data points in Figure 8.

●—● = Range in date of first flower.
-⊕- = Average date of first flower.
70 = Date of first flower during 1970 season.
* = Denotes woody species.

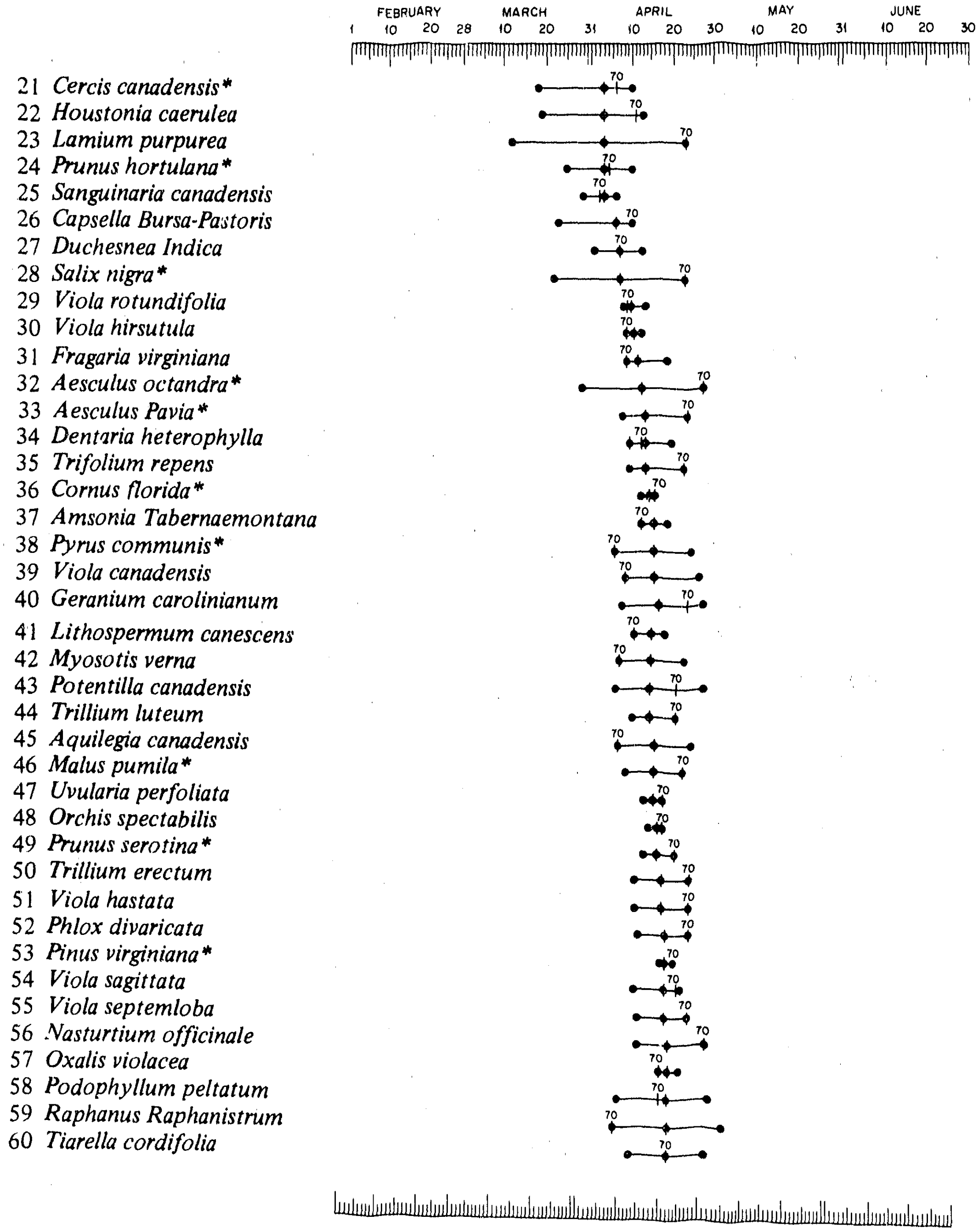
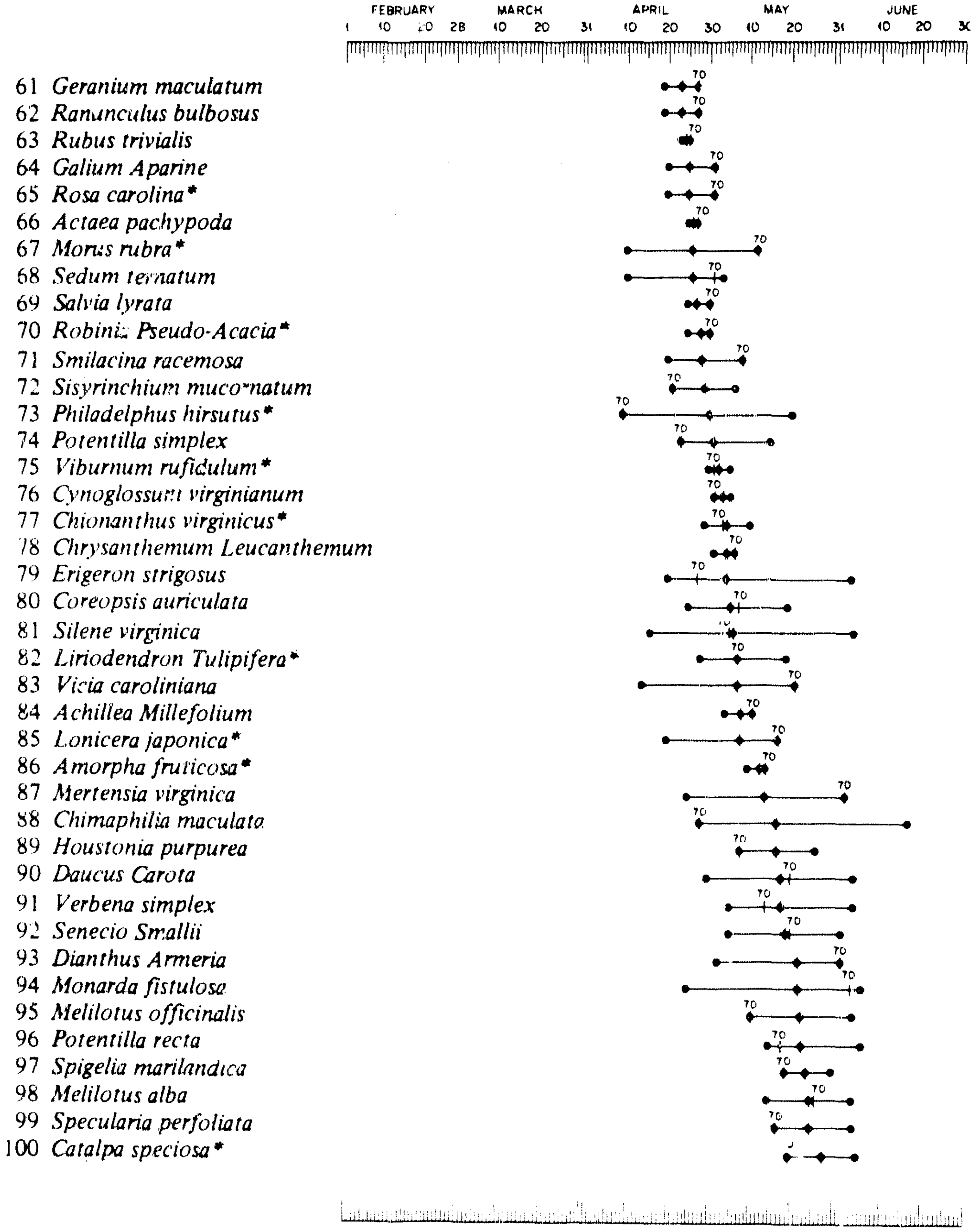


Figure 4. (Continued)



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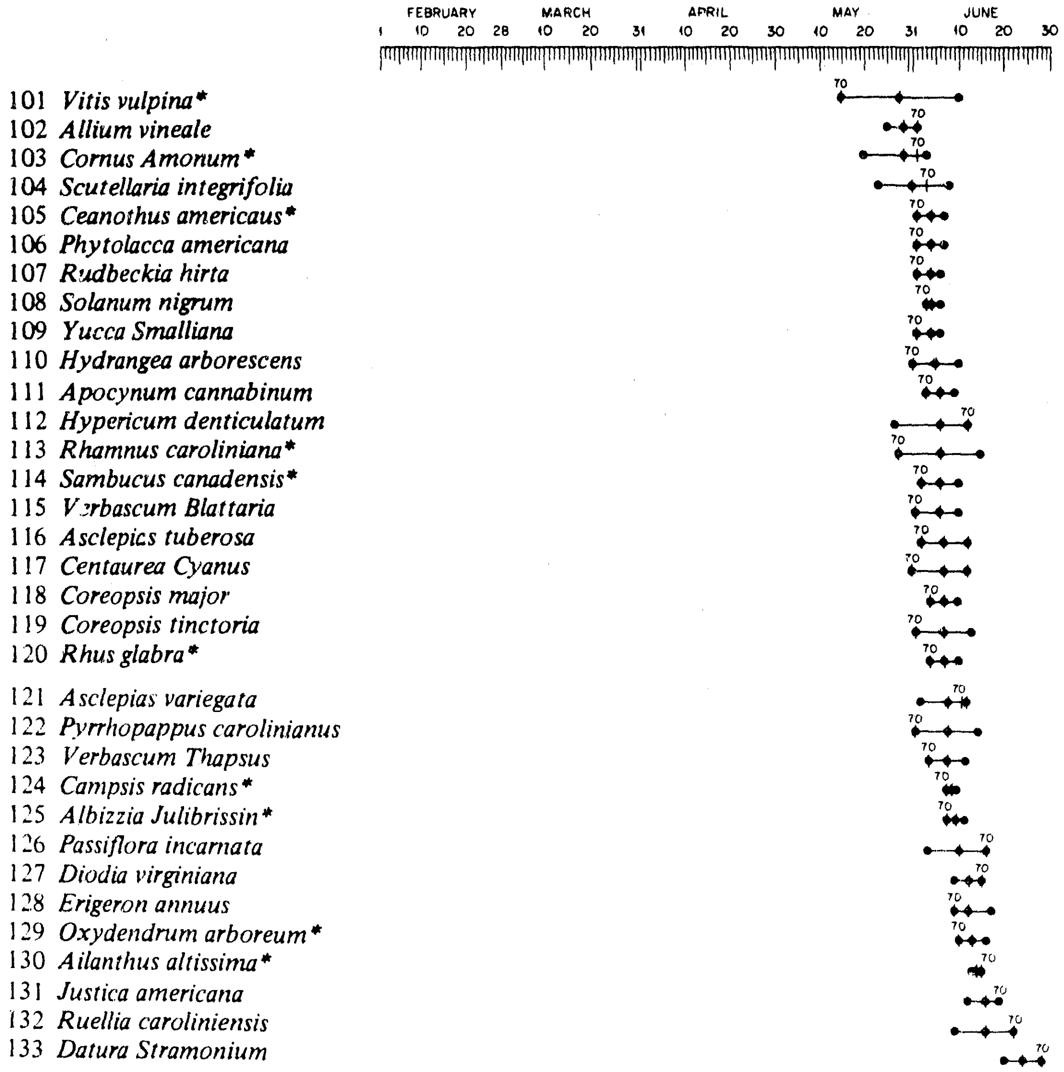

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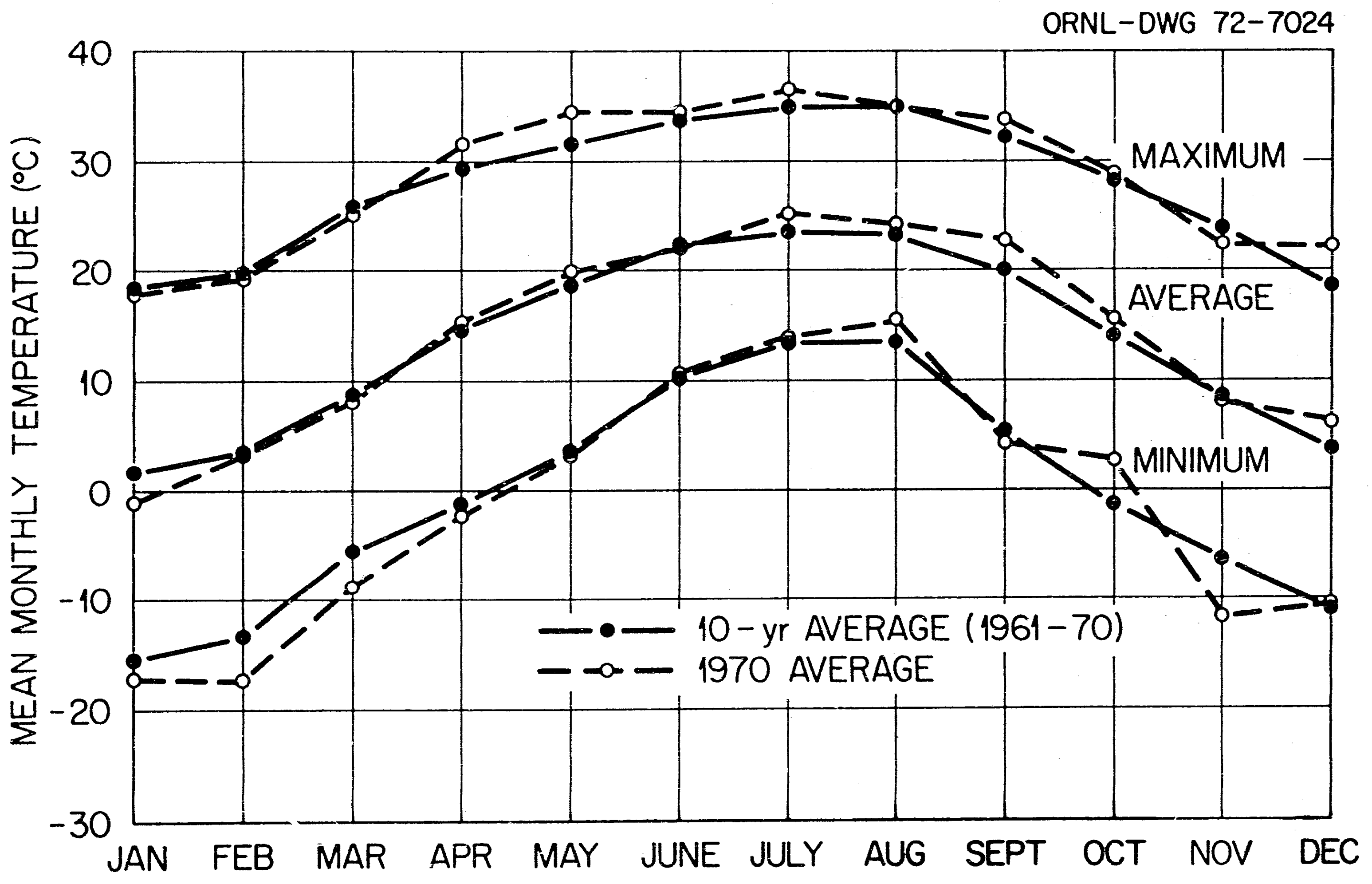

Figure 5. **Monthly temperature averages (maximum, mean, and minimum) for the 10-year period (1961-1970)** as compared with averages for 1970.

Thermal considerations have been shown to be important to the phenological development within managed forests or natural ecosystems (Jackson 1966). Temperature summations or degree-days have been used to depict differences in thermal environments between successive years (Bomalaski 1948). Within the heterogeneous structure of a forest ecosystem, a common temperature threshold has little validity for analytical techniques because not all species respond equally to the same temperature regimes.

If a diagram depicting flowering within the oak-hickory forest during 1970 were superimposed upon the phenogram illustrating mean date of flowering between 1963 and 1970 (Figure 1), the early spring peak would be advanced by seven days, to Week 15, whereas the early summer flora would be delayed seven days, to Week 24. Monthly average temperatures (Figure 5) for 1970, compared for these periods, offer little explanation for the variability. However, characterizing the thermal environment by the summation of daily mean temperature (Figure 6) shows that the thermal climate at Yearday 112 (Week 16), the mean peak flowering period between 1963 and 1970, is attained nine days earlier in 1970. This suggests that the advancement in flowering during the spring of 1970 was strongly related to the thermal climate within the forest ecosystem. Likewise, the temperature sum during 1970 for the early summer component was also attained earlier (by 14 days) than the same temperature sum during the mean peak flowering period between 1963 and 1970 (Yearday 161). Flowering was delayed seven days in 1970, which suggests that other factors were more important than temperature or that optimum thermal regimes were exceeded, thus inhibiting the initiation of flowering.

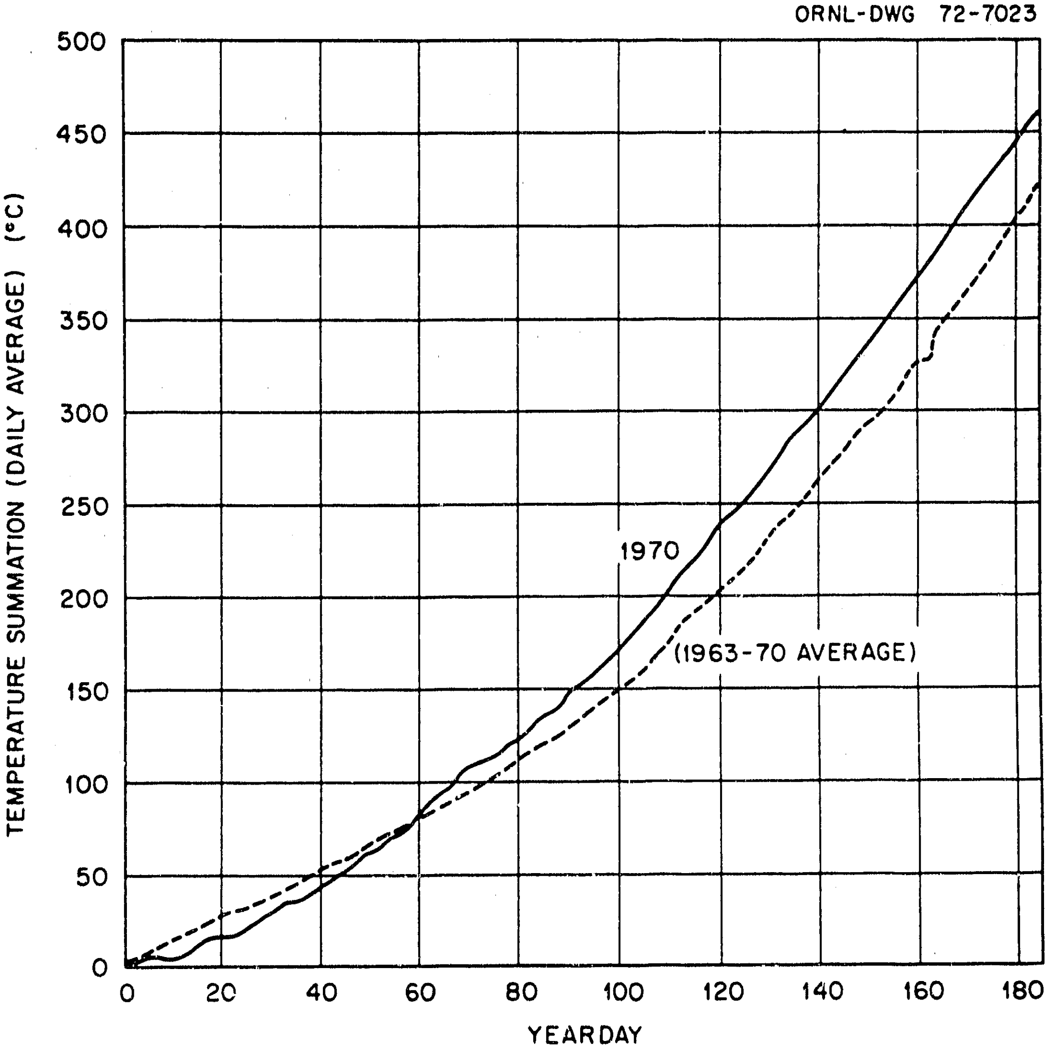

Figure 6. Comparison of the thermal environment within the oak-hickory forest association between 1963 and 1970 by temperature summations of the mean daily temperature.

The early summer flora (Week 23) includes species indigenous to more open, dry habitats where moisture may have been a limiting factor during 1970. There was a moisture deficit (approximately 10%) in comparison with the 10-year mean. During the first half of 1970, four of six months received below normal precipitation (Figure 7). Especially noticeable was the deficit in May which was probably critical for plant species occupying drier sites. This deficit occurred prior to the early summer peak in number of species flowering and could be responsible for the delay in flowering season noted previously.

The relationship between the temperature sum and date of first flower (Yearday) provides significant predictability between species (Figure 8). Silver and red maple are the first species to begin reproductive phases, at a period when the mean daily air temperature is approximately 10°C. The significant correlation ($r^2 = 0.99$) suggests that observations of mean date of first flower (Figure 4) spanning several years are sufficient to estimate advent of the reproductive phase between many species. Thermal or temperature summations (Figure 6) utilizing the mean daily temperatures would provide a more precise estimate of flowering date from temperature summations (TS) such

$$TS_i = \sum_{k=1}^{i} adt_k \qquad (1)$$

that where adt_k is the average daily temperature, $\left[\frac{\text{sum of mean hourly temperatures}}{N}\right]$. Since the correlation between species is highly significant, the predicted date of first flower

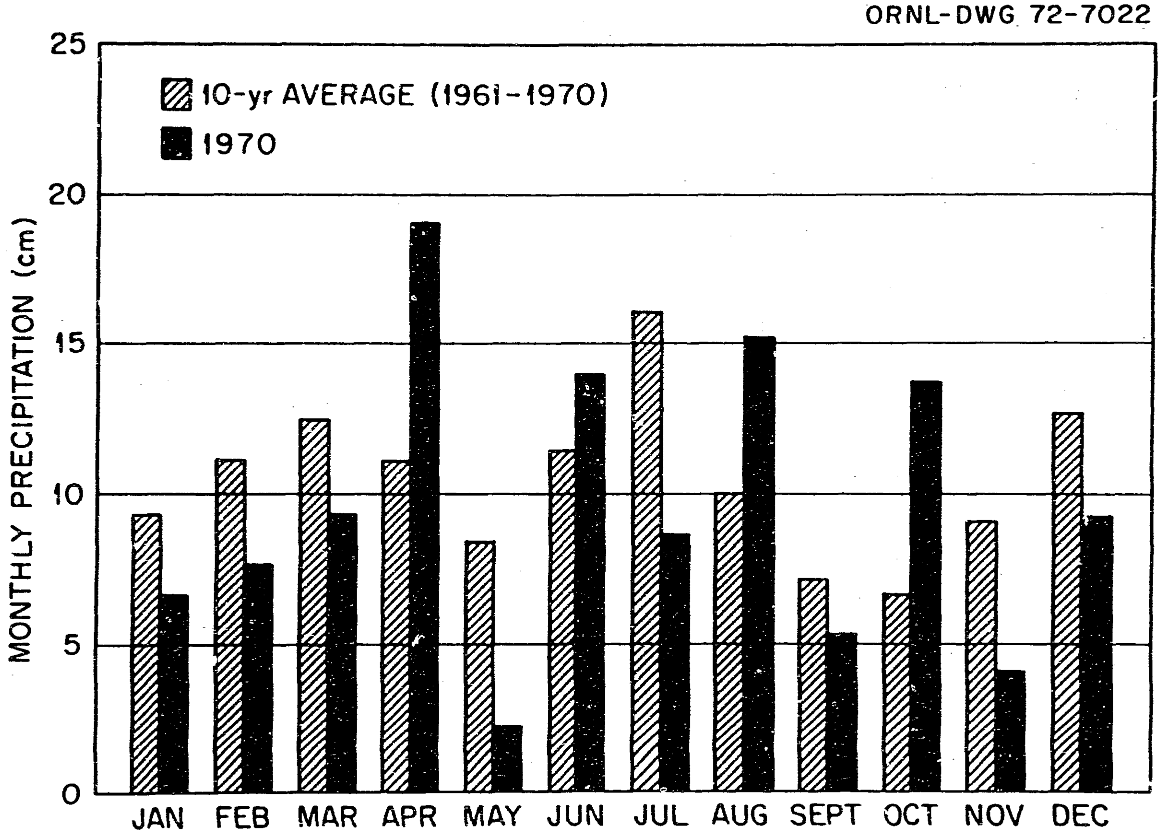

Figure 7. Comparison of total precipitation during 1970 with the expected quantity based on 10-year average between 1961-1970. A deficit exists for 8 of the 12 months during 1970. Note particularly the deficit preceding the early summer flora (May).

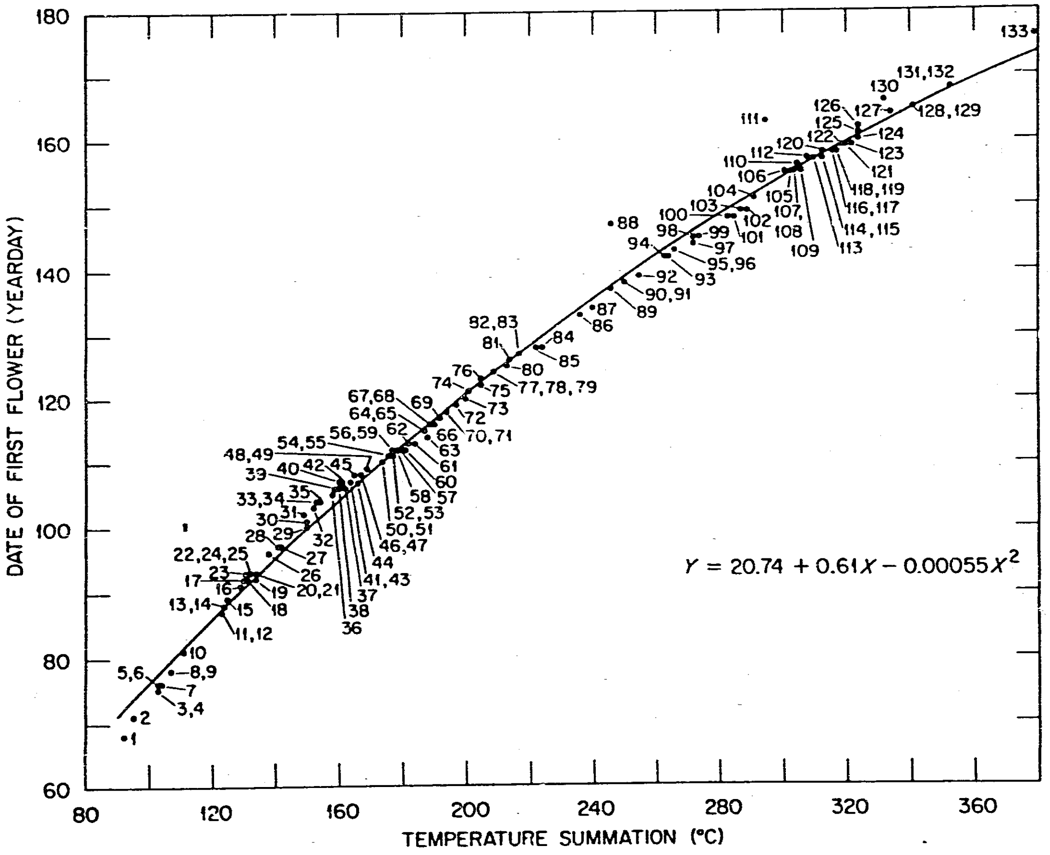

Figure 8. Relationship between mean date of first flower and mean temperature summation (1963-1970). Numbers correspond to species numbers in Figure 4. Each number also represents a species identified in the Appendix.

(Yearday) may indicate minimum or threshold thermal regimes necessary to initiate the productive phase (Figure 8).

Moisture, light, and temperature interactions are all known to enhance or delay timing of certain phenological events (Daubenmire 1959). Departure from normal environmental conditions can alter the appearance of various phenological events within forest ecosystems as indicated by the response of flowering to differences in temperature and moisture. Deviations in micrometeorological parameters, in turn, influence dynamic characteristics of ecosystems (e.g., availability of food base to secondary producers, pollination, and rates of accumulation and turnover of standing crop).

4.2 RELATIONSHIP OF EVENTS WITHIN SPECIES

In addition to responses to environmental factors in determining the growing season, it is essential to know how each phenological event within a season is related to each adjacent phase, especially for studies for productivity. Within the eastern deciduous forest biome, 10 species were selected for detailed observations for the construction of phenological spectra (Figure 9). Those selected represent the first woody species to initiate growth (red maple), the dominant canopy species of slope forests (yellow-poplar) and selected shrubs and herbaceous species within areas under intensive study. Particularly noticeable (Figure 9) is the almost simultaneous development of the reproductive phase of shrub species most characteristic of local forest ecosystems (dogwood, redbud, and shadbush or serviceberry). This series of phenological events precedes canopy development of one of the codominant canopy species (yellow-poplar).

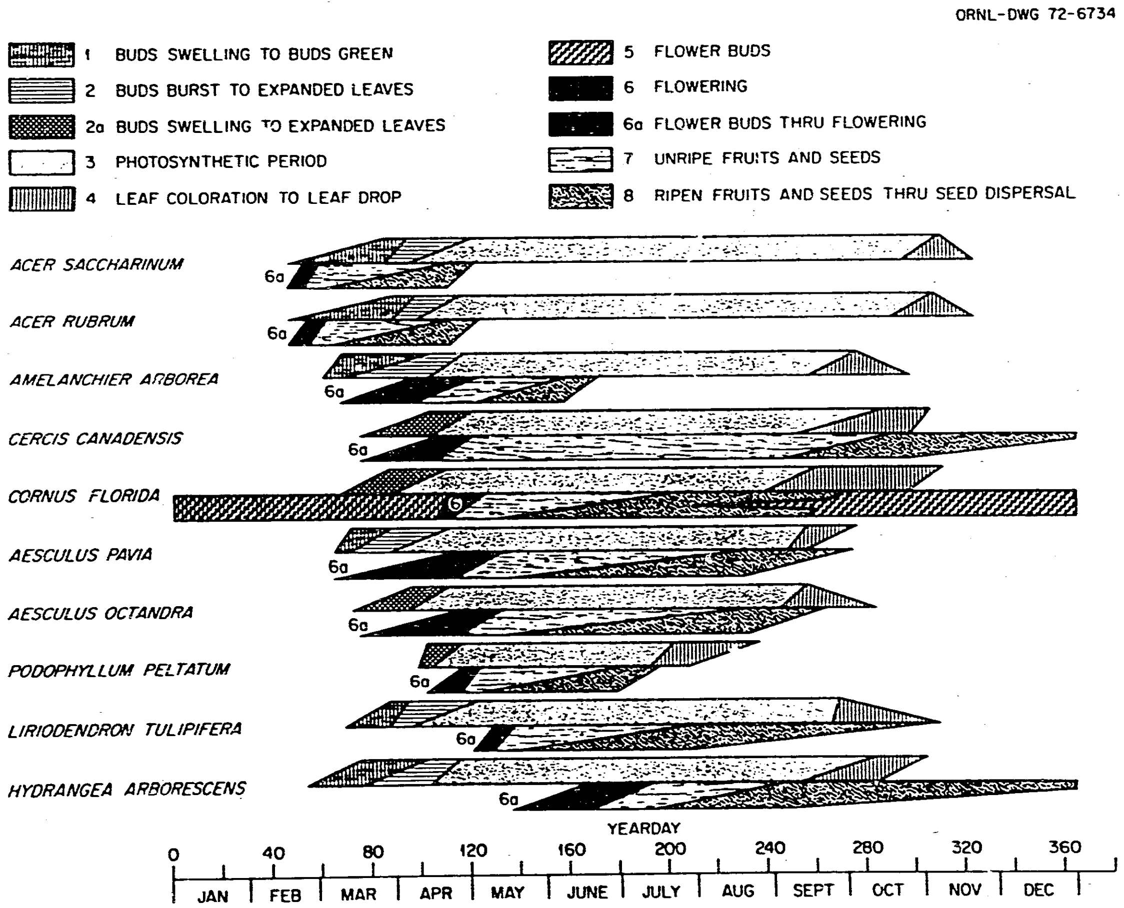

Figure 9. Phenological spectra of species characteristic of secondary forest communities dominated by Liriodendron tulipifera within the oak-hickory association. These spectra indicate the relationships of phenological events within species and compare events between species and delineate the growing season.

5. RELATIONSHIP OF PHENOLOGY TO PRODUCTION AND CHEMICAL POOLS AS ILLUSTRATED BY MAYAPPLE (*Podophyllum peltatum* L.) AND DOGWOOD (*Cornus florida* L.)

An important ecological consideration in the classification of forest types or associations is the presence or absence of binding genera or species (Braun 1950), especially within the herbaceous layer. Although this stratum of the forest contributes little biomass to the total primary production of the ecosystem, it may well provide insight into the interactions between individual species of communities and their environment (Kubicek 1970). The importance of some phenological events to the total productivity of single species (Kreh 1965) suggests that each component within a community could be analyzed in a similar manner. Such studies of growth analysis would permit the construction of more precise models of production within communities or ecosystems.

Particularly noticeable (Figure 9) is the almost simultaneous development of the reproductive phase of shrub species most characteristic of the forest ecosystem (dogwood, redbud, and shadbush or serviceberry). This series of phenological events precedes canopy development of one of the codominant species (yellow-poplar). Within the eastern deciduous forest biome 10 species were selected for detailed observations for the construction of phenological spectra (Figure 9). Those selected represent the first species of the slope forests (yellow-poplar), and selected shrubs and herbaceous species within areas under intensive study.

Within the mesic yellow-poplar dominated slope forest at Oak Ridge, biomass and productivity of the herbaceous layer have been estimated by indirect (allometric) methods (Christofolini 1970). Data were obtained during one growing season and revealed no relationship to phenological development and environmental interactions. By comparison, the herbaceous layer within an oak-hornbeam forest in Europe was evaluated phenodynamically (Kubicek 1970) during two growing seasons, and variations in monthly production were directly related to climatic conditions. Such analyses provide explanations for variations in total productivity within communities from one season to the next.

Growth analysis and chemistry data are presented for a single herbaceous layer species (Podophyllum peltatum L.) and a common understory tree (Cornus florida L.) at the Oak Ridge site to exemplify the role of phenology in studies of the net productivity. Mayapple is used as an example because of its social occurrence and rapid phenological development in the spring. As one of the most conspicuous herbaceous species to initiate spring growth within the eastern deciduous forest, mayapple is a potential indicator species for regional studies. Dogwood was selected because of its landscape and horticultural importance, and as a relatively small tree it can be effectively handled as an experimental unit in biomass and chemical cycling experiments.

5.1 GROWTH ANALYSIS STUDY OF MAYAPPLE

During the first three years of growth, the nonreproductive mayapple plants manifest a vertical shoot growth (Figure 10) with developmental forms distinct from older reproductive plants (Holm 1899). Older plants annually produce a single leaf from underground horizontal shoots (Figure 10). Plants within mature mayapple colonies or populations

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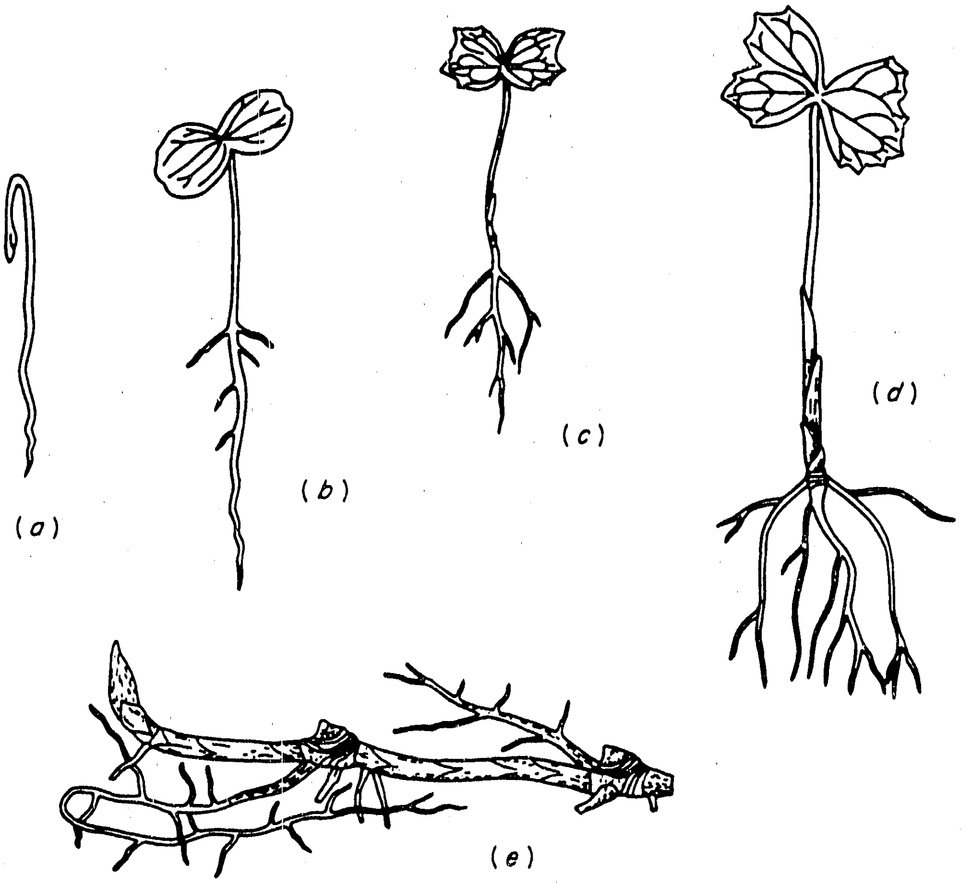

Figure 10. Little stages of mayapple plants during the period of vertical shoot growth: a = germination, b = first-year plant with cotyledonary leaves, c = second-year seedlings, d = third-year plant depicting final vertical growth of the shoot, e = horizontal shoot (rhizome) and roots developed from a lateral bud of a three-year-old plant, illustrating an additional three years' growth including the terminal bud. (Modified from Holm, 1989)

exhibit an almost simultaneous response in phenological development. The phenophases of individual plants are depicted in Figure 11. The time from leaf emergence through the litter to date of first flowering is approximately three weeks. Fruiting and germination success are frequently low, often with 100% of all flowers failing to set fruit (Sohn and Policansky 1977). Distinct populations or colonies of mayapple occur frequently within slope or mesic (northerly exposed) forests. Within the "Liriodendron forest study area," mayapple is best established in social units on low, moist sites. Being partially clonal with moderate longevity, the perennial populations vary in area, appearing elliptical to circular in shape. Colony size among 21 populations averaged 21.04 m^2, ranging from 0.7 to 176.6 m^2. Plant density within this array varied from 10 to 683 with an average of 167 plants per population.

Regression analysis of computed area to number of plants permits an estimate of population density ($r^2 = 0.88$), providing that the area of the clone is known (Figure 12). The resulting equation, $\log_{10}Y = 1.12 \times 0.85 (\log_{10}X)$, assumes the configuration of the population to be circular. Colony area (X) is computed from diameter measurements of the population. Within the broad definition of the oak-hickory association, density per square meter is less than 1, whereas the density within the average colony or population is approximately $8/m^2$. Excavation of the rhizome system of a colony revealed that the average age of viable underground shoots was six years with obvious decay of older segments and that the population had increased in radial growth at the rate of 10 cm per year (Figure 13). This particular population had therefore

Figure 11. Phenophases of aboveground plant structures from the underground horizontal shoot. (a) Leaf emergence through the litter, (b) unfolding of leaves, (c) leaf expansion of nonflowering plant, (d) leaflet expansion and flower bud of reproductive plant, (e) a plant in flower.

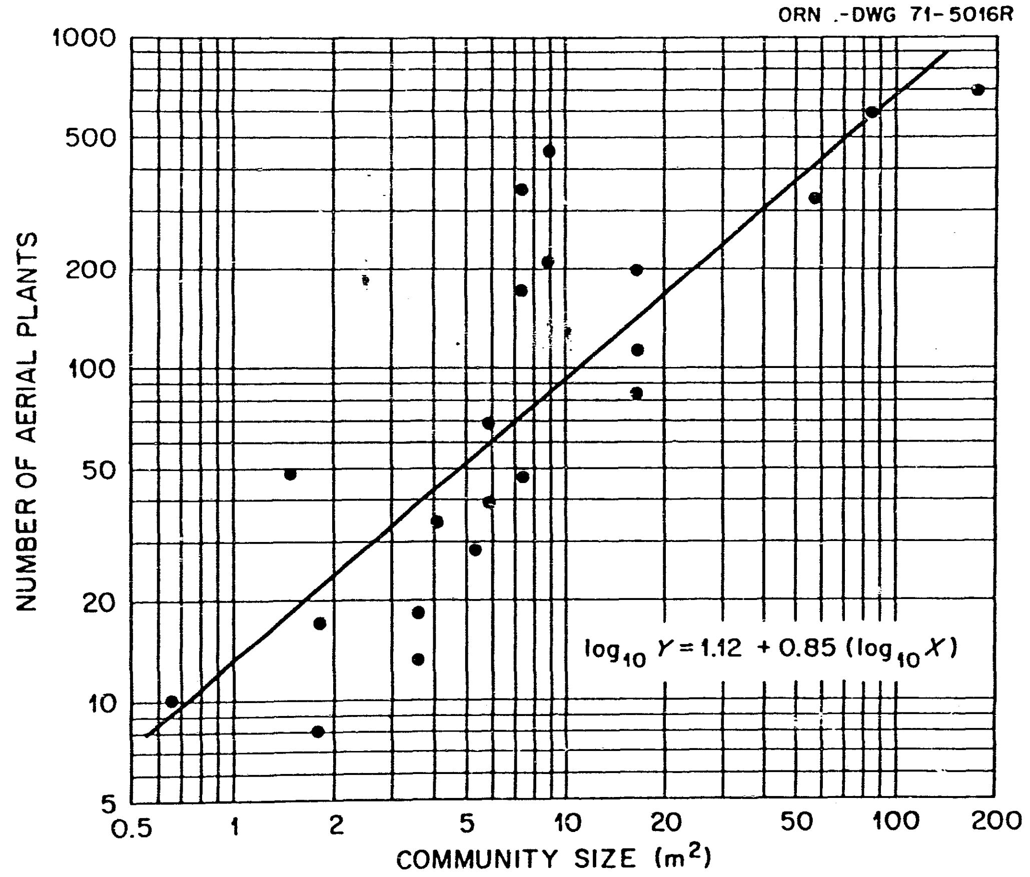

Figure 12. Relationship between the number of plants and population size. Data points represent populations from 0.66 to 176.6 m^2, containing from 10 to 683 plants. The average colony was 21.04 m^2, while the mean number of plants (aerial leaves) was 167.24.

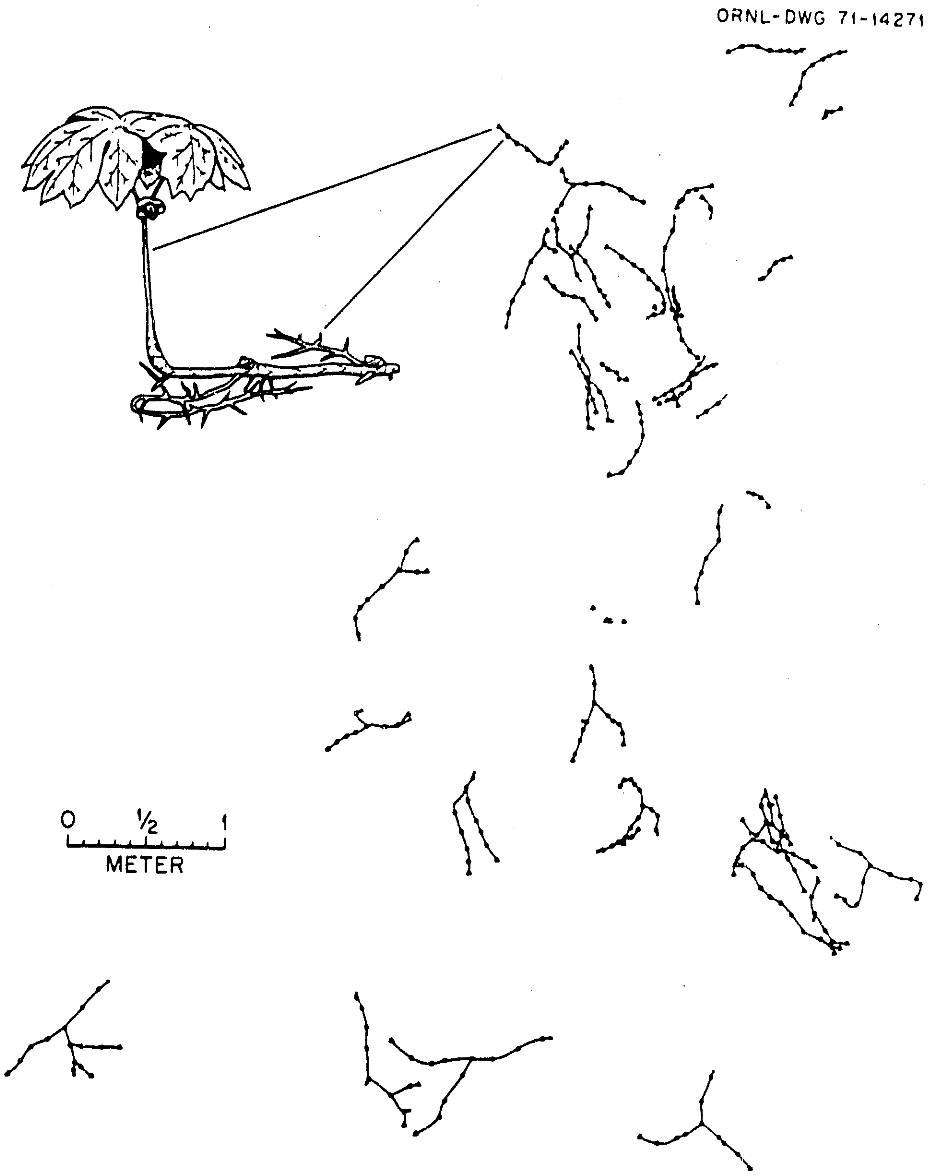

Figure 13. Network of a viable rhizome system. The dots along the rhizome represent leaf scars, while the triangles identify a terminal bud. Drawing insert illustrates a rhizome section with two leaf scars and a terminal sexual plant. Raised leaf scars indicate the plant was sexual at the previous season, whereas a concave scar indicates the plant was asexual.

occupied the site for approximately 45 years. Phenodynamic studies of specific populations spanning many years could provide data depicting the impact of seasonal or annual climatic variations on production.

Beginning with leaf emergence (Yearday 99), 20 plants were harvested at each of seven life phases from three randomly selected plots. Plants were compartmentalized into leaf, stem, flower, or fruit, and rhizome-root for biomass estimates. Estimates of rhizome-root biomass during the leaf emergence phase (Yearday 99-102) were included in standing crop, such that subsequent estimates would reflect changes throughout the life cycle. Biomass increased for each component with the progression of phenological development (Figure 14), reaching maximum dry weights during the phase of unripe seeds and fruits, prior to the onset of senescence (Yearday 162). At that time, rhizome-root (1970 increment) showed an increase of 21% in dry weight above the standing crop estimate at leaf emergence. Leaf and aboveground stem (petiole) accounted for 57% of total dry weight, whereas unripe fruits and seeds represented 17%. The underground rhizome system grew terminally, producing an overwintering apical bud (Figure 10e). The 1971 underground shoot was initiated during the reproductive phase (Yeardays 116-123), and showed an increase of 4% in dry weight prior to senescence of aerial parts. At the onset of senescence (Yearday 162), leaves began to change color, followed by leaf and fruit drop and subsequent decreases in dry weight. Seeds are distributed by insects and small mammals feeding on ripe fruits. Further increases in the increment to the underground shoot system (1971) were accompanied by decreases in dry weight of the previous season's growth (1970), indicating that the rhizome functions as a storage organ for

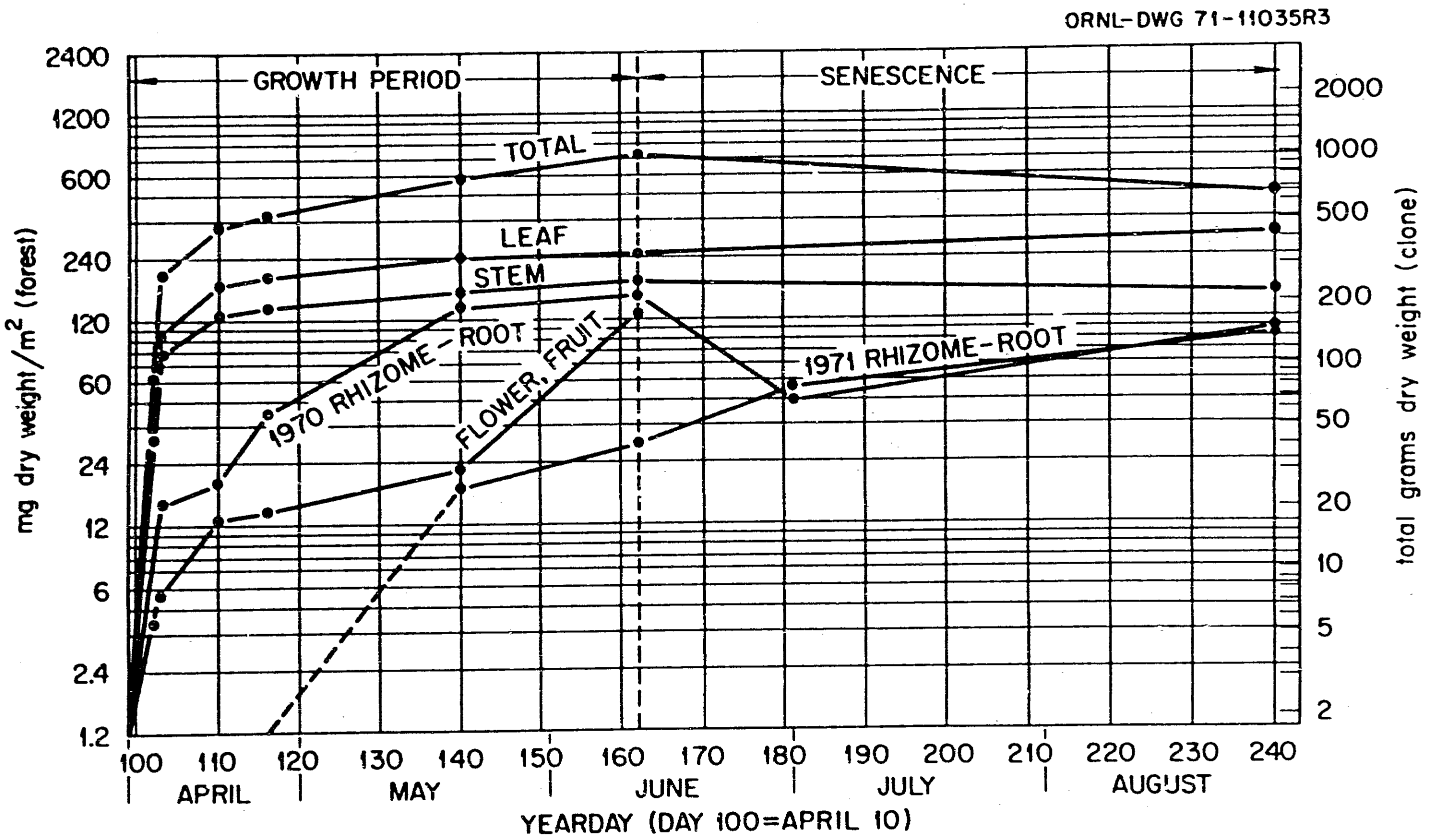

Figure 14. Biomass in mayapple, partitioned into obvious components. Phenophases correspond to the following time intervals: Yeardays 99-102 (leaf emergence), 102-103 (leaves expanding), 99-116 (flower buds), 116-123 (flowering), 123-178 (unripe seeds and fruits), 178-196 (ripe seeds and fruits), 196-240 (leaf drop and seed dispersal). The vegetative growth phase is between yearday 99 and 162. Color change of leaves begins on yearday 162 and terminates with total leaf drop, day 240.

subsequent growth processes. By the end of the growth period (Yearday 240), each increment in rhizome-root (1970 and 1971) accounted for 25% of the biomass, with the other 50% consisting of fallen aerial parts (leaf, fruit, and seeds). Biomass per unit area within the oak-hickory forest is summarized in Fig. 14 where plant density is <1/m^2 or on the basis of the average mayapple colony within the "Liriodendron forest study site" (plant density is 8/m^2).

Productivity estimates per unit area or average colony within the intensive study area (Figure 15), reflect growth in excess of the standing crop of rhizome-root (1970) at leaf emergence. Productivity is maximum during the reproductive (flowering) phase, Yeardays 103-116, decreasing rapidly through fruit development and leaf coloration phases. The decrease in production between Yeardays 163 and 181 represents a loss due to the consumption of ripe fruits by animals and insects. As indicated in biomass data, unripe fruits and seeds account for as much as 17% of the total dry weight. The phenological spectrum above the productivity curve in Figure 15 illustrates the relationship of various events to changes in productivity.

5.2 CHEMICAL POOLS IN MAYAPPLE POPULATIONS AS A FUNCTION OF SEASONALITY

Elements contained in plant materials, whether standing dead or standing live biomass, represent a considerable pool of nutrients in reserve for potential utilization by plants. Plant materials may be returned to the plant-soil system through fragmentation, mechanical harvesting, or leaf fall at autumnal senescence. Following decomposition processes, the elements may enter the soil matrix for later uptake or be available immediately for growth processes. Some

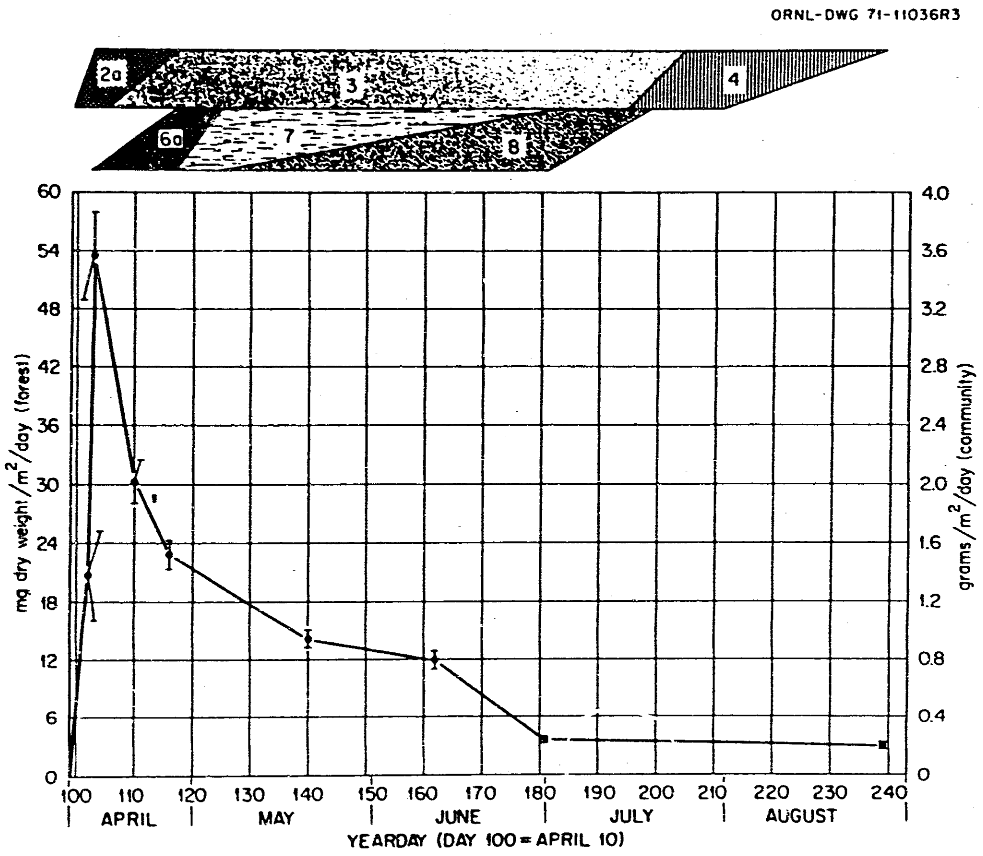

Figure 15. Seasonality in productivity by mayapple, Podophyllum peltatum. As indicated by the spectral strip above the curve (numbers represent the same phenophases as identified in Fig. 9), productivity is maximum during the reproductive phase. Reduced productivity by fruit consumption of small mammals and insects coincides with the period of ripe fruits and seeds to seed dispersal. Brackets denote ± 1 S.E.

elements may be readily available as the result of leaching following precipitation events, removal by dew, guttation or contained in the excrement of primary consumers. Attiwill (1966) suggests that elements removed by precipitation are in the order: K > Ca > Na > Mg > P. Litter is the primary path of exchange of elements from plants to the soil. The rate of return of elements to the soil varies between species due to many factors controlling decomposition.

Seasonal nutrient dynamic studies of _Solidago_ indicated that leaves and inflorescences were major sinks for K, Mg, N, and P (Abrahamson and McCrea 1985). Similar allocation patterns were observed in mayapple. Reallocation of nutrients within these taxa reduces the amount of nutrients required from the soil and suggest the species may have a broad site tolerance.

Although herbaceous plants represent minor contributions to the total elemental pool in forest ecosystems, they probably are more valuable as early inputs of nutrients to meet the demands of late season species because of their rather rapid turnover. Such is the example of mayapple with a life cycle of 138 days (emergence to litter) from mid-April to the end of August. Canopy-sized trees are more important in the long-term nutrient cycle, while understory species such as mayapple are important in the annual nutrient cycle (Day 1973). The productivity and standing crop biomass data previously discussed are combined with elemental data (K, Ca, Mg, P, C, N, S) to exemplify the short-term inputs related to phenological events. The average area of mayapple colonies among the 21 colonies in the 2 ha study area is 21 ± 9 m^2 with an average of 167 ± 42 plants. That is a plant density of $8/m^2$. If one considers the total 2 ha study area, plant density is 3512 or 0.2 $m/^2$.

Mayapple generally establishes growth in sink areas, or in cool, mesic sites and is not randomly distributed over the total forest area. The elemental pool from a population is probably available only in the immediate area of the population and not the total forest. For that reason the chemical data are presented in the context of the average population (8 plants/m^2) and not the total study site. The biomass and productivity data depicted in Figs. 14 and 15 reflect the forest area and the average mayapple colony.

Because of budget restrictions, chemical analyses were not provided for each plant component or for every life cycle event. Some analyses were conducted on replicate samples, whereas most sample determinations were not replicated. The chemical data are normalized to the average mayapple population in the 2 ha study area. The nutrient reserve (pool) is calculated as the product of the elemental concentration and the ratio of the average standing crop biomass to the area of the average population within the study area. The average standing crop biomass is depicted in Figure 14.

5.2.1 Potassium

Potassium is an element common to all plant tissues. While its exact metabolic function to plant processes is not known, it is generally observed that uptake by roots and accumulation by developing foliage is strongly influenced by the life cycle events (Table 1). Beginning with leaf budding (Yearday 116) to the onset of senescence (Yearday 162), there is a rapid uptake of potassium by the root (rhizome system) from 0.06 g/m^2 to 0.13 g/m^2, an increase of 53% in potassium reserves.

Table 1. Elemental concentrations (mg/g) and chemical pools (g/m^2) of average mayapple populations during the periods of leaf bud to leaf drop (YEARDAYS 116 to 240).

	K		Ca		Mg		P		C		N		S	
	mg/g	g/m^2	mg/g	g/m^2	mg/g	g/m^2	mg/g	g/m^2	%	g/m^2	%	g/m^2	%	g/m^2
Phenophase/Yearday 2a, 6a / 116 (April)														
Leaves[a]	34.1	0.45	3.4	0.05	1.7	0.02	6.4	0.09	42.2[c]±8.8	5.63	0.4±0.1	0.05	0.4±0.1	0.05
Flowers	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Flowers/ Fruits	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Stems[a]	55.9	0.51	5.3	0.05	1.3	0.01	3.8	0.03	32.9[d]±1.9	2.98	0.4±0.1	0.04	0.2±0.1	<0.01
Roots[a]	26.2	0.06	7.1	0.02	2.3	0.01	3.2	0.01[c]	34.5 ±2.3	0.82	0.6±0.1	0.01	0.2±0.1	<0.01

2a Leaf budding to expanded leaves
6a Flower buds to flowering
[a] n = 1
[b] n = 2
[c] n = 3
[d] n = 4

Table 1. (Continued)

	K		Ca		Mg		P		C		N		S	
	mg/g	g/m^2	mg/g	g/m^2	mg/g	g/m^2	mg/g	g/m^2	%	g/m^2	%	g/m^2	%	g/m^2
Phenophase/Yearday 3,7,8 / 140 (May)														
Leaves[a]	32.7	0.50	13.9	0.21	2.7	0.04	1.4	0.02	52.4[a]	7.98	0.3	0.05	0.5	0.08
Flowers	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Flowers/ Fruits	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Stems[a]	37.1	0.42	11.6	0.13	0.7	0.01	1.2	0.01	28.5[a]	3.26	0.5	0.06	0.1	0.01
Roots[a]	12.9	0.12	4.7	0.05	1.2	0.01	2.2	0.02	--	--	--	--	--	--

3 Photosynthetic period
7 Unripen fruit
8 Ripen fruit to seed dispersal
[a] n = 1

Table 1. (Continued)

	K		Ca		Mg		P		C		N		S	
	mg/g	g/m^2	mg/g	g/m^2	mg/g	g/m^2	mg/g	g/m^2	%	g/m^2	%	g/m^2	%	g/m^2
Phenophase/Yearday 3,7,8 / 162 (June)														
Leaves	--	--	--	--	--	--	--	--	42.3^b±1.9	8.58	0.3±0.3	0.06	0.3±0.1	0.06
Flowers	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Flowers/ Fruits^a	24.1	0.21	2.6	0.02	1.2	0.01	2.3	0.02	32.9^a	2.89	0.6	0.05	0.2	0.02
Stems^a	37.1	0.49	11.6	0.15	0.7	0.01	1.2	0.02	30.9^a	4.12	0.6	0.08	0.1	0.01
Roots^a	12.9	0.13	4.7	0.05	1.2	0.01	2.2	0.02	40.4^b±0.1	4.04	0.3±0.3	0.03	0.2±0.1	0.02

3 Photosynthetic period
7 Unripen fruit
8 Ripen fruit to seed dispersal
[a] n = 1
[b] n = 2

Table 1. (Continued)

	K		Ca		Mg		P		C		N		S	
	mg/g	g/m²	mg/g	g/m²	mg/g	g/m²	mg/g	g/m²	%	g/m²	%	g/m²	%	g/m²
Phenophase/Yearday 4 / 240 (August)														
Leaves[a]	16.8	0.34	23.1	0.47	2.7	0.05	1.1	0.02	48.5[a]	9.8	0.5	0.10	0.2	0.04
Flowers	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Flowers/ Fruits	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Stems[a]	20.0	0.14	22.7	0.15	1.0	0.01	0.5	<0.01	30.6[a]	2.07	0.6	0.04	0.1	0.01
Roots[a]	12.9	0.09	4.9	0.03	1.2	0.01	2.4	0.02	41.1[a]±4.8	2.74	0.9±0.1	0.06	0.2±0.1	0.01

4 Leaf coloration to leaf fall

[a] n = 1

[b] n = 2

Coincident with the increased potassium uptake by rhizomes is a nearly constant reserve in maturing foliage up to leaf coloration (Yearday 240). The range in foliar potassium storage varies from 0.50 g/m^2 (Yearday 140) to 0.34 g/m^2 at Yearday 240. This 32% decrease in the elemental pool corresponds to a 40% decrease in active uptake by rhizomes. While uptake mechanisms probably maintain foliar concentrations during the photosynthetic period, the decrease at the onset of senescence (Yearday 160) to leaf fall (Yearday 240) is also related to losses by precipitation leaching. Stems show a similar equilibrium in potassium pool reserves from leaf budding to senescence, ranging from 0.51 g/m^2 to 0.49 g/m^2 (Yeardays 116 to 162). Following onset of senescence to leaf fall (Yearday 240) the stem reserves decrease from 0.49 to 0.14 g/m^2. This represents a loss of 70%. The mayapple rhizomes remain viable up to 10 years (Figure 13) with the possibility that the potassium remobilizes and moves baseptally from the above ground storage compartments through the rhizome network to the soil medium. This phenomenon was observed in the transport of a related alkali metal (cesium) by Witherspoon (1964). Beginning with spring leaf budding, this element is available again for transfer to the rhizome with rapid uptake and distribution to developing above ground storage compartments (leaves, stems, fruits, etc.).

5.2.2 Calcium

Calcium is generally thought to be immobile in plant foliage and bound to cell walls and the middle lamella in the form of a calcium salt. At the onset of spring growth (Yearday 116) the calcium concentrations in developing leaves and stems were 3.4 and 5.3 mg/g, respectively. Normalizing these concentrations to the average mayapple colony in the study area indicates a calcium reserve of 0.05 g/m^2 within colonies. With leaf and stem development calcium pools rapidly increase throughout the phenological season (Table 1), attaining maximum concentrations of 23.1 and 22.7 mg/g for leaves and stems at Yearday 240. Calcium reserves within the population colony increased by a factor of 9.4 between Yearday 116 and leaf fall at Yearday 240. The increase in stem calcium was three-fold (0.05 to 0.15 g/m^2). At leaf fall (Yearday 240), calcium pools were maximum with no evidence of leaching or remobilization to other plant parts. Uptake by rhizomes is maximum at Yearday 140 (period of fruit ripening to seed dispersal) and maintains a constant concentration (4.7 mg/g) throughout the growth period. Calcium pools associated with rhizomes indicate reserves of 0.03 to 0.05 g/m^2. The return of calcium to the soil and succeeding plant species from decomposing litter is subject to normal decomposition and mineralization processes.

5.2.3 Magnesium

Magnesium, a component of every chlorophyll molecule, is essential to the photosynthetic process. Consequently, magnesium is present in all chlorophyll-bearing plant parts (leaves, stems, flowers, fruits, etc.) and is readily transferred from storage compartments or from soil/root uptake pathways. At the onset (Yearday 116) of leaf budding (Figure 11a,b), foliar magnesium concentration was 1.7 mg/g. This represents a reserve in the average mayapple colony of 0.02 g/m^2 (Table 1). The maximum concentration was in the rhizomes (2.3 mg/g), decreasing as the season progressed (Table 1). Foliar magnesium storage continued to increase throughout the life cycle, reaching a maximum reserve of 0.05 g/m^2 at Yearday 240. Concentrations decreased (Table 1) with the periods of unripen fruit through seed dispersal. Elemental reserves among stems and rhizomes remained constant (0.01 g/m^2) throughout the season. There was no increase among rhizomes at senescence, indicating no mobilization of the element. The concentration data suggest that root uptake diminishes with the onset of flowering and fruiting.

5.2.4 Phosphorus

Phosphorus is usually available for plant processes in the form of the $H_2PO_4^-$ ion through root uptake. By the time the young mayapple had emerged (Yearday 116) through the litter layer (Figure 11a,b), considerable phosphorus had already been transferred to and was accumulated by the foliage (Table 1). Phosphorus concentration was maximum (6.4 mg/g) at that time and decreased as the growth period progressed. Phosphorus is moved from one plant part to another compartment where the element is deficient. Phosphorus often is transferred to developing fruits. Reserves were maximum (0.09 g/m^2) during the period of rapid leaf expansion and development and showed a 4.5-fold decrease in storage (0.02 g/m^2) by leaf fall (Yearday 240). An increase in root phosphorus concentrations at Yeardays 140 and 162 (Table 1) indicate active uptake by the rhizomes. Stem phosphorus was maximum at leaf development (Yearday 116), but rapidly decreased.

5.2.5 Carbon

Among mayapple compartments (leaves, stems, roots, etc.), carbon comprised from 29 to 50% of the plant materials (Table 1) depending on the particular phenophase. At plant emergence (Figure 11a,b), leaves contained 42.2%, stems 32.9%, and roots 34.5% carbon. Normalized to the average colony in this study, the compartments represented 5.63, 2.98, and 0.82 g/m^2 of carbon reserves. Root carbon decreased as the season progressed, probably associated with losses due to respiration. Stem carbon remained rather constant (29 to 32%) throughout the growing season, most likely bound to structural components (e.g., xylem). As the growth period continued, the carbon reserves continued to increase, reaching a maximum storage of 9.8 g/m^2 (Table 1) at the period from leaf color change to leaf fall (Yearday 240). The standing crop carbon pool is ultimately available to primary and secondary consumers. Primary consumers include insects and small animals. Fruits are consumed by numerous insects, and it is reported that the ripened fruit is the favorite diet of the dry land terrapins (box turtles), although this has never been documented.

5.2.6 Nitrogen

Nitrogen is absorbed by plants as nitrates, nitrites, organic nitrogen compounds, and ammonium salts. Nitrogen is a major component (~20%) of proteins, such that plants utilize this element in combination with photosynthates to form proteins. Beginning with leaf budding, the mayapple population continued to fix nitrogen, increasing in storage from 0.05 to 0.10 g/m^2 from Yeardays 116 to 240 (Table 1). This two-fold increase represents a 50% increase in reserves. During senescence nitrogen may increase in roots and stems. Nitrogen reserves in roots (rhizomes) increased by a factor of five (80%) from leaf budding to leaf fall. Stem nitrogen increased with seasonality, reaching maximum reserves (0.08 g/m^2) at the period of unripen fruit to seed dispersal (Table 1).

5.2.7 Sulfur

Sulfur is also a component of protein synthesis in plants. The element is usually absorbed by roots as the SO_4^{--} ion. Sulfur is also available to foliar contributions in the form of SO_2 from the atmosphere. Among the mayapple populations, foliar sulfur reserves increased to a maximum storage of 0.08 g/m^2 at the time of fruit development (Yearday 140), decreasing to 0.04 g/m^2 at leaf fall (Yearday 240). Table 1 summarizes the changes in sulfur content and storage throughout the growth period. The decrease in foliar sulfur at Yearday 140 may represent allocations to flower and fruit development. Because flowers and fruits are rapidly eaten by animals, very few are ever present to maturity. Therefore, no measurements of concentration were possible. Stem sulfur remained constant throughout the growth period (Table 1) whereas roots exhibited active uptake until the onset of senescence (Table 1). The maximum reserve at that time was 0.02 g/m^2. Although sulfur from fossil fuel combustion often becomes toxic to plants, atmospheric SO_2 may constitute a fertilizer effect in regions of sulfur-poor soils.

5.3 GROWTH ANALYSIS OF DOGWOOD AS A FUNCTION OF SEASONALITY

Twenty-one dogwood trees were harvested in an 18-year-old planted shortleaf pine plantation similar in soils and stand composition (stocking density) to the loblolly stand described by Thomas et al. (1967). The nutrient pools are estimated from the average dry weight of each compartment (bole, root, leaves, etc.), the specific elemental concentration, and a stand stocking density of 286 trees/hectare. The density is assumed from the empirical data of Thomas et al. (1967) from a planted loblolly pine plantation of similar age, soils, and exposure. The stand described by Thomas et al. (1967) was also 18 years old. The 21 trees were randomly numbered and assigned to the seven different phenophases identified in Figure 9 and Table 2.

Dogwood is probably the most important understory species within the eastern deciduous forest formation (Braun 1950). Because of its affinity to accumulate calcium in foliage and floral parts, dogwood has been termed a beneficial species in forest management practices (Coile 1940 and Metz 1956), whereas Rennie (1955) argues that such a species competes with crop trees for water and nutrients, shades the soil surface, increases fuel for fire potential, and serves as host for diseases. While some species may store elements in their foliage, they may also immobilize large quantities of the specific element by accumulations and slow turnover and release by nonfoliar parts (bole, branches, roots, etc.) (Rennie 1955).

The mensuration data among the 21 dogwood trees harvested is summarized in Table 2. Average age among the sample population ranged from 13.33 ± 0.33 years for trees harvested in March to 23.67 ± 1.33

Table 2. Mensuration data by Phenophase/Yearday[a].

	2a,5/85 (March)	3,6/113 (April)	3,7,8/190 (July)	3,4,5,8/243 (August)	4,5,8/265 (September)	4,5/295 (October)	5/342 (December)
Age (years)	13.33±0.33	19.33±0.33	15.00±0.58	23.67±1.33	16.00±4.36	17.67±0.67	20.67±0.88
Diameter base (cm)	9.50±0.95	11.33±0.91	10.25±1.88	6.07±0.23	7.33±0.56	7.25±0.75	8.73±0.90
Diameter breast height (cm)	5.10±0.78	6.50±0.76	5.50±0.76	3.93±0.18	4.37±0.52	4.23±0.54	5.10±0.55
Diameter base crown (cm)	4.73±0.72	5.92±0.85	5.98±0.53	3.33±0.35	4.60±0.38	4.73±0.54	4.80±0.67
Bark thickness (mm)	4.67±0.33	4.50±0.29	4.67±0.67	2.83±0.17	3.00±0.58	3.00±0.58	4.33±0.33
Height (m)	5.13±0.12	5.80±0.29	5.70±0.32	4.93±0.26	4.03±0.38	4.54±0.61	6.00±0.45
Crown width (m)	4.07±0.43	3.33±0.17	4.00±0.29	2.57±0.18	3.27±0.39	3.00±0.40	3.23±1.00
Crown depth (m)	3.77±0.15	4.07±0.35	3.87±0.42	2.10±0.49	2.53±0.41	3.02±0.40	2.88±0.51

[a] Data are means±1SE of three replicate trees each harvest period.

2a	Buds swelling to expanded leaves
3	Photosynthetic period
4	Leaf coloration to leaf drop
5	Flower buds
6	Flowering
7	Unripe fruits and seeds
8	Ripe fruits and seeds through seed dispersal

years for trees harvested in August. Since the shortleaf pine plantation was 18 years old at the time of dogwood harvesting, many of the dogwoods were young seedlings prior to establishment of the plantation. Diameter breast height (dbh) among the sample population ranged from 3.93 ± 0.18 cm to 6.50 ± 0.76 cm. Trees ranged in total height from 4.03 ± 0.38 m to 6.00 ± 0.45 m. Another important measurement was the diameter of each tree at ground level. The smallest (6.07 ± 0.23 cm) were harvested in August, while the largest (11.33 ± 0.91 cm) were harvested in April.

The aboveground biomass (bole and branches) was strongly correlated ($P < 0.01$) with dbh. The resultant model, $Y = -3.32 + 2.092 X$, gave a correlation coefficient of 0.85 (Figure 16a).

The below ground biomass is more difficult to measure since roots must be washed free of soil and small stones. Small rootlets are usually lost during washing procedures, such that estimates of root biomass are considered conservative. Diameter at the base of the tree identified a significant relationship ($P < 0.01$) with the below ground biomass when resolved with a linear model. The resultant equation, $Y = -0.75 + 0.34 X$, had a correlation coefficient of 0.77 (Figure 16b). This equation should prove valuable for estimating below ground biomass (roots) among dogwood trees in future studies.

The standing crop biomass (kg/ha) for wood and foliage was compared with data summarized by Day (1973) for the U.S. Forest Service's Coweeta Hydrologic Laboratory in southwestern North Carolina.

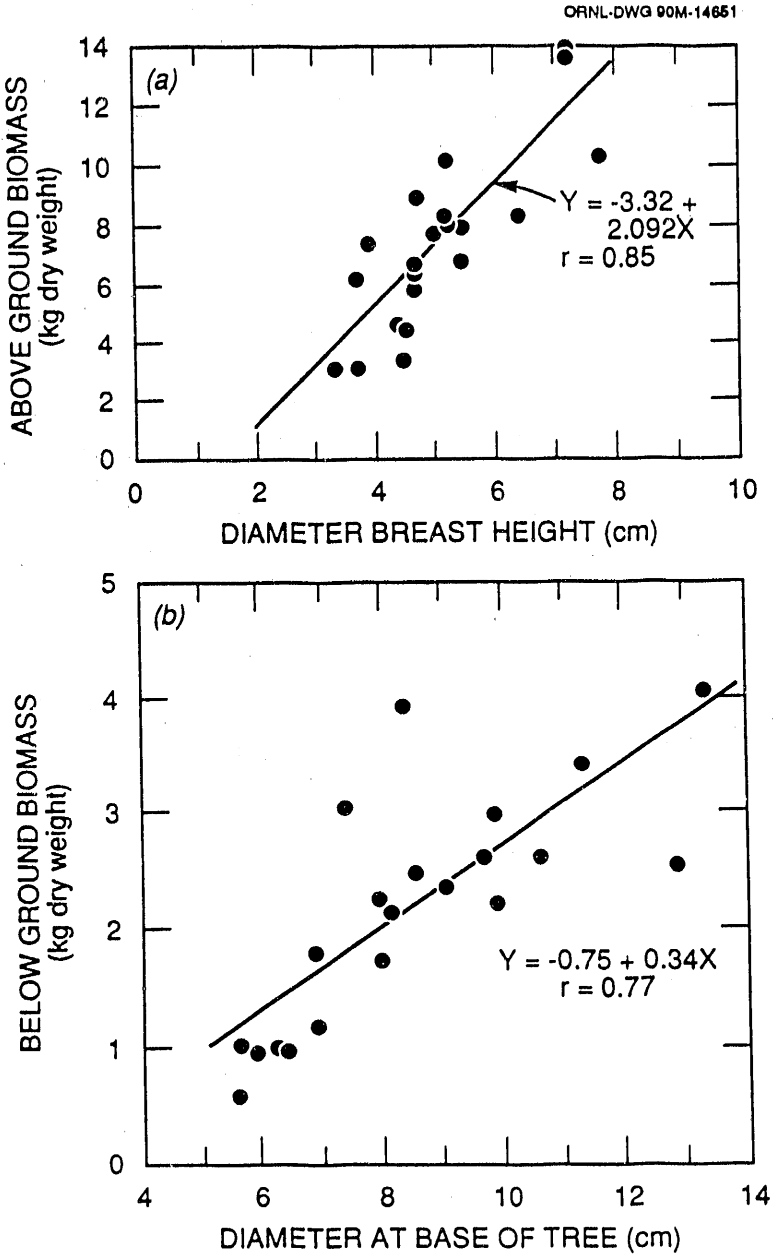

Figure 16. Correlations between aboveground biomass and diameter breast height (a), and belowground biomass and diameter at the base of the tree (b).

Elevation and mean annual temperature at Coweeta differs significantly from the Oak Ridge IBP site.

Standing crop biomass is the product of the average weight of the tree or tree component and the density of the site (trees/ha). Density (286 trees/ha) for the Oak Ridge stand is assumed from data presented by Thomas et al. (1967). Harvest periods and phenophases at both sites are similar.

The partitioning of biomass among the trees studied during the various phenophases is summarized in Table 3. These data reflect the means of three replicate trees for each harvest period.

Day and McGinty (1975) concluded that standing crop biomass at the Coweeta site was primarily in the wood (2466 kg/ha). Maximum standing crop biomass for wood at Oak Ridge was calculated (standing crop biomass x stocking density) to be 2808 kg/ha for bole and branches combined in the July harvest (Table 3). Leaves during the same period were estimated to account for 480 kg/ha. While Oak Ridge data were not partitioned for bark, Day and McGinty (1975) determined the standing crop biomass of this compartment to be 584 kg/ha. Flowers were present only during April with an estimated standing crop biomass of 14.3 kg/ha.

In comparison to Coweeta data, dogwood standing crop biomass (kg/ha) is 20% less for wood (bole and branches) in March. During the months of April through July, biomass at Oak Ridge is approximately the same as observed at Coweeta (Day 1973), but is reduced rapidly through the remainder of the study. This is probably a function of smaller trees available for harvest. Total standing crop of leaves among trees at Oak Ridge is greater by a factor of 2 to 3 in comparison to Coweeta.

Table 3. Partitioning of biomass (kg±1SE) by components.[a]

	Phenophase/Yearday						
	2a,5/85 (March)	3,6/113 (April)	3,7,8/190 (July)	3,4,5,8/243 (August)	4,5,8/265 (September)	4,5/295 (October)	5/342 (December)
Bole	4.47±0.22	5.98±0.30	5.93±1.44	2.88±0.27	3.26±0.94	3.86±1.02	5.12±0.86
Branch	2.35±0.32	3.82±0.84	3.89±1.88	1.01±0.14	1.62±0.26	2.34±0.44	3.04±0.47
Root	3.33±0.43	2.50±0.13	2.86±0.66	0.88±0.13	2.10±0.59	1.68±0.35	2.12±0.50
Leaves	--	0.13±0.01	1.68±0.77	0.32±0.04	0.52±0.12	1.05±0.09	--
Flower Buds	0.05±0.02	--	--	0.002±0.0004	0.02±0.01	0.04±0.03	0.03±0.01
Flowers	--	0.05±0.01	--	--	--	--	--
Fruit	--	--	0.18±0.09	0.09±0.05	0.03±0.01	0.02±0.01	--
Total	10.20±0.99	12.48±0.69	14.54±4.84	5.18±0.63	7.55±1.93	8.99±2.02	10.3±1.84

[a] Three replicate trees were sampled each harvest period.

2a	Buds swelling to expanded leaves
3	Photosynthetic period
4	Leaf coloration to leaf drop
5	Flower buds
6	Flowering
7	Unripe fruits and seeds
8	Ripe fruits and seeds through seed dispersal

This is likely the result of the shortleaf pine overstory being removed at Oak Ridge and more radiant energy available for leaf formation throughout the season.

Additional seasonal influences in standing crop biomass are presented in Table 4. These data are concerned with the generative (flowering) and photosynthetic phase of plant development. No leaves were present in the March harvest, but by Yearday 113 (April) leafing had occurred and the average number of leaves for 19-year-old trees was 7192 ± 2021 (n=3). Flower buds were present from buds set the previous year with an average of 508 ± 131 buds at Yearday 85 (March). As depicted in Table 4, flowering occurred by Yearday 113 (April) with an average of 349 ± 50 flowers. No floral buds were present until new bud set was evident in August (Yearday 243). Flowers were present only during the month of April. Fruit development began in July (Yearday 190) with an average of 525 ± 300 unripen fruits. This period reflected a maximum period of fruit formation as fruits decreased in numbers from August to October. Young developing fruit provide food for birds and squirrels as they ripen. By Yearday 342 (December) no leaves or fruits remained; only the next year's flower buds were present.

In a comparison of phenological events, development of life stage events were remarkably similar in timing between Coweeta and Oak Ridge for the same periods of years. Day (1973) indicates bud-break at Coweeta between March 25 and April 9 between 1973 and 1974. This compares with March 12, 1971 (Figure 9) at Oak Ridge. First flowering was observed at Coweeta between April 15 and 22, compared to April 21 at Oak Ridge. The period of mature or ripen fruits present began October 2

Table 4. Average number (±1SE) of leaves, flower buds, flowers, and fruits by Phenophase/Yearday. Three replicate trees were sampled each harvest period.

	2a,5/85 (March)	3,6/113 (April)	3,7,8/190 (July)	3,4,5,8/243 (August)	4,5,8/265 (September)	4,5/295 (October)	5/342 (December)
Leaves	--	7192±2021	12762±5229	2775±383	3733±954	1054±878	--
Flower Buds	508±131	--	--	101±12	657±371	825±602	222±119
Flowers	--	349±50	--	--	--	--	--
Fruit	--	--	525±300	164±37	52±15	40±24	--

2a Buds swelling to expanded leaves
3 Photosynthetic period
4 Leaf coloration to leaf drop
5 Flower buds
6 Flowering
7 Unripe fruits and seeds
8 Ripe fruits and seeds through seed dispersal

at Oak Ridge in contrast to October 6-8 at Coweeta. Senescence and leaf fall are similar at both sites, with the latter occurring between November 3-5 at Coweeta and beginning November 8 at Oak Ridge.

5.4 CHEMICAL POOLS IN DOGWOOD AS A FUNCTION OF SEASONALITY

Chemical storage in mayapple represents short-term, annual reserves because of a short turnover rate. Short-term storage compartments are also present in tree species (leaves and flowers), but the majority of chemical pools among trees represent long-term (years) reserves in woody compartments (bole, branch, and roots). The rates of decay among plant materials are functions of site factors (xeric vs mesic), condition of the canopy (open vs closed), time of year when senescence or tree mortality occurs, and the activity of ground fauna and microflora. As a calciphyte with calcium bound to cell walls, one would expect weight and calcium losses to be similar. Thomas et al. (1967) reported the percent loss of foliar calcium as similar to that for weight loss, with the initial losses due to water-soluble materials. Information on turnover rates of foliage exists in the literature, but very little data are available for wood decay. Turnover of dogwood foliage on the ORR followed an exponential decay curve with rapid initial weight loss (5% per week) during the first month (beginning November 10), followed by a much slower loss (2%) during the last half of the study (Thomas et al., 1967). Only 20% of foliar materials remained after one year.

Unpublished data from a wood decay study at Oak Ridge using 10 cm diameter boles indicated a turnover rate from four to five years for hickory and yellow-poplar and seven years for chestnut oak (Todd 1990).

Information concerning turnover in dogwood stems was obtained from the Southeastern Forest Experiment Station in Asheville, North Carolina. Fallen trees were decayed by five years depending on the time of the year when tree mortality occurred. Disintegration followed an exponential decay curve with the outer sapwood decomposing rapidly and the heartwood at a much slower rate (Anderson 1990). The concentrations of four essential elements (potassium, calcium, magnesium, and phosphorus) were determined in the various storage compartments in dogwood at seven distinct phenophases (Tables 5-11). Day and McGinty (1975) reported the storage of the same elements in dogwood at Coweeta. Their data do not illustrate the effect of seasonality on nutrient pool dynamics or provide any insight for storage in flowers or fruits. Potassium reserves in wood was 4.4 kg/ha in comparison to 0.04 kg/ha in twigs and 2.5 kg/ha in leaves. Data from the Oak Ridge site indicate a wood (bole) potassium concentration of 1.6 kg/ha (Table 5) at a time prior to leaf emergence and expansion (Yearday 85).

5.4.1 Potassium

As an alkali, metal potassium moves with the transpiration stream. Potassium generally shows rapid uptake and distribution in developing foliage. Root reserves throughout the growing season ranged from a minimum of 1.11 kg/ha in October (Table 10) to a maximum of 2.05 kg/ha in July (Table 7). Branch data are inclusive of twigs and are higher in concentrations than wood concentrations by factors of 3 to 5 (Tables 7-11). Potassium storage among the branch compartment was greatest, 3.62 kg/ha, during the period of fruit development (July) as

Table 5. Elemental concentrations and chemical pools among dogwood components during the periods of buds swelling to expanded leaves and flower buds swelling.

	Phenophase/Yearday 2a,5/85 (March)							
	K		Ca		Mg		P	
	mg/g	Kg/ha	mg/g	Kg/ha	mg/g	Kg/ha	mg/g	Kg/g
Bole	1.21	1.55	3.51	4.49	0.39	0.50	0.18	0.23
Branch	--	--	--	--	--	--	--	--
Roots	2.08	1.98	5.57	5.30	0.62	0.59	0.35	0.33
Leaves	--	--	--	--	--	--	--	--
Flower Buds	11.31	0.16	28.86	0.41	2.48	0.04	2.78	0.04
Flowers	--	--	--	--	--	--	--	--
Fruit	--	--	--	--	--	--	--	--

2a Buds swelling to expanded leaves
5 Flower buds

Table 6. Elemental concentrations and chemical pools among dogwood components during the photosynthetic period through flowering.

	Phenophase/Yearday 3,6/115 (April)							
	K		Ca		Mg		P	
	mg/g	Kg/ha	mg/g	Kg/ha	mg/g	Kg/ha	mg/g	Kg/g
Bole	1.21	1.94	3.51	6.00	0.39	0.67	0.18	0.31
Branch	--	--	--	--	--	--	--	--
Roots	2.08	1.49	5.57	3.98	0.62	0.44	0.35	0.25
Leaves	11.87	0.44	33.09	1.23	3.85	0.14	4.54	0.14
Flower Buds	--	--	--	--	--	--	--	--
Flowers	11.64	0.14	22.05	0.32	1.91	0.03	2.75	0.04
Fruit	--	--	--	--	--	--	--	--

3 Photosynthetic period
6 Flowering

Table 7. Elemental concentrations and chemical pools among dogwood components during the periods of photosyntheses, unripe fruits, and seeds through ripe fruits and seed dispersal.

	Phenophase/Yearday 3,7,8/190 (July)							
	K		Ca		Mg		P	
	mg/g	Kg/ha	mg/g	Kg/ha	mg/g	Kg/ha	mg/g	Kg/g
Bole	1.18	2.00	5.68	9.63	0.44	0.75	0.19	0.32
Branch	3.25	3.62	9.06	10.08	0.98	1.09	0.38	0.42
Roots	2.51	2.05	8.01	6.55	0.88	0.72	0.44	0.36
Leaves	10.64	5.11	21.84	10.49	3.19	1.53	1.39	0.67
Flower Buds	--	--	--	--	--	--	--	--
Flowers	--	--	--	--	--	--	--	--
Fruit	11.95	0.62	20.07	1.03	2.69	0.14	1.78	0.09

3 Photosynthetic period
7 Unripe fruits and seeds
8 Ripe fruits and seeds through seed dispersal

Table 8. Elemental concentrations and chemical pools among dogwood components during the periods of photosyntheses to leaf drop and ripe fruits and seeds through seed dispersal.

	Phenophase/Yearday 3,4,5,8/243 (August)							
	K		Ca		Mg		P	
	mg/g	Kg/ha	mg/g	Kg/ha	mg/g	Kg/ha	mg/g	Kg/g
Bole	1.18	0.94	5.68	4.68	0.44	0.36	0.19	0.16
Branch	3.25	0.94	9.06	2.62	0.98	0.23	0.38	0.11
Roots	2.51	1.60	8.01	2.20	0.88	0.22	0.44	0.11
Leaves	6.36	0.58	30.00	2.75	2.59	0.24	1.70	0.16
Flower Buds	--	--	--	--	--	--	--	--
Flowers	--	--	--	--	--	--	--	--
Fruit	11.95	0.31	20.07	0.52	2.69	0.07	1.78	0.05

3	Photosynthetic period
4	Leaf coloration to leaf drop
5	Flower buds
8	Ripe fruits and seeds through seed dispersal

Table 9. Elemental concentrations and chemical pools among dogwood components during periods of leaf coloration to leaf fall, formation of next year's floral buds, and ripe fruits to seed dispersal.

	Phenophase/Yearday 4,5,8/265 (September)							
	K		Ca		Mg		P	
	mg/g	Kg/ha	mg/g	Kg/ha	mg/g	Kg/ha	mg/g	Kg/g
Bole	--	--	--	--	--	--	--	--
Branch	6.36	2.95	30.00	13.90	2.59	1.20	1.70	0.79
Roots	--	--	--	--	--	--	--	--
Leaves	--	--	--	--	--	--	--	--
Flower Buds	10.51	0.06	33.85	0.19	2.84	0.02	2.40	0.01
Flowers	--	--	--	--	--	--	--	--
Fruit	11.95	0.10	20.07	0.17	2.69	0.02	1.78	0.02

4 Leaf coloration to leaf drop
5 Flower buds
8 Ripe fruits and seeds through seed dispersal

Table 10. Elemental concentrations and chemical pools among dogwood components during periods of leaf coloration to leaf drop and flower buds present.

	Phenophase/Yearday 4,5/295 (October)							
	K		Ca		Mg		P	
	mg/g	Kg/ha	mg/g	Kg/ha	mg/g	Kg/ha	mg/g	Kg/g
Bole	1.21	1.13	5.44	5.07	0.34	0.32	0.20	0.19
Branch	3.04	1.41	9.77	4.53	0.29	0.13	0.46	0.21
Roots	1.85	1.11	3.88	2.33	0.47	0.28	0.44	0.26
Leaves	--	--	--	--	--	--	--	--
Flower Buds	10.51	0.06	33.85	0.19	2.84	0.02	2.40	0.01
Flowers	--	--	--	--	--	--	--	--
Fruit	11.95	0.10	20.07	0.17	2.69	0.02	1.78	0.02

4 Leaf coloration to leaf drop
5 Flower buds

Table 11. Elemental concentrations and chemical pools among dogwood components during the period of flower buds present.

	Phenophase/Yearday 5/342 (December)							
	K		Ca		Mg		P	
	mg/g	Kg/ha	mg/g	Kg/ha	mg/g	Kg/ha	mg/g	Kg/g
Bole	1.21	1.77	5.44	7.97	0.34	0.50	0.20	0.29
Branch	3.04	2.64	9.77	0.49	0.29	0.25	0.46	0.40
Roots	1.85	1.12	3.88	2.35	0.47	0.28	0.44	0.27
Leaves	--	--	--	--	--	--	--	--
Flower Buds	10.51	0.09	33.85	0.29	2.84	0.02	2.40	0.02
Flowers	--	--	--	--	--	--	--	--
Fruit	--	--	--	--	--	--	--	--

5 Flower buds

shown in Table 8. The designation of twigs as used by Day and McGinty (1975) probably is not synonymous with use of branches in this study. Their study focused on the very small diameter twig materials, whereas the Oak Ridge site branch data included everything arising from the bole axis to the leaf. Their potassium pool is noted as 5.0 kg/ha. The uptake and distribution of potassium by foliage is reported in their data (2.5 kg/ha), but without an indication of phenophase. Their estimate of standing crop foliage was 175.5 kg/ha.

During April (Table 6) the canopy was developing with an average foliage biomass (Table 3) of 0.13 ± 0.01 kg (n=3) or 37.2 kg/ha. Leaves contained 11.87 mg/g potassium or 0.44 kg/ha, indicating the canopy was not fully developed. By July (Table 3) the average tree foliage was 1.68 ± 0.77 kg, or 480.5 kg/ha. A potassium concentration of 10.64 mg/g translates to 5.11 kg/ha (Table 7). Flower buds, flowers, and fruits showed maximum concentrations of 10.51 to 11.95 mg/g potassium (Tables 5-11), but minimal reserves due to insignificant standing crop biomass (Table 3).

5.4.2 Calcium

Calcium storage increases rapidly in developing leaves and stems. Foliar calcium reserves are maximum in developed foliage, where it is bound to the cell walls and middle lamella. Day and McGinty (1975) reported a calcium pool of 2.7 kg/ha in wood among Coweeta samples. Data from the Oak Ridge site in March was considerably higher calcium, 4.5 kg/ha (Table 5), than of Coweeta. Roots provided a storage of 5.30 kg/ha, while the flower buds formed during the 1970 season contained a reserve of 0.41 kg/ha. Flower bud calcium concentration was

28.86 mg/g, but the low standing crop biomass (14 kg/ha) was insignificant compared to the total tree standing crop. In March no leaves were present on trees at Oak Ridge. The average tree foliage (0.13 kg) in April (Table 4) was normalized to the site stem density (286) to yield a standing crop biomass estimate of 37.18 kg/ha. At a calcium concentration of 33.09 mg/g (Table 7), the calcium storage is estimated to be 1.23 kg/ha. This is in contrast to data reported by Day (1973), 4.0 kg/ha. Branch calcium ranged from 9.1 mg/g to 30 mg/g in July (Table 7) and September (Table 9), respectively. Maximum calcium reserve in branches was 13.9 kg/ha during the period of leaf coloration to leaf fall (Table 9). Flowers were present only during April (Table 6) with a concentration of 22.05 mg/g and a storage reserve of 0.32 kg/ha. The maximum storage in September foliage supports the concept that calcium is transported to developing leaves and bound to cell walls or middle lamella. Calcium content in fruits was greatest in August, 0.52 kg/ha (Table 8).

5.4.3 Magnesium

Magnesium is the only plant nutrient constituent of the chlorophyll molecule. Wood and twig contents from the Coweeta data (Day and McGinty 1975) were 1.0 and 0.01 kg/ha, respectively. Wood data from the Oak Ridge site ranged from a minimum of 0.32 kg/ha (Table 10) in October to a maximum of 0.75 kg/ha (Table 7) during July. Magnesium storage in branches ranged from a minimum of 0.23 kg/ha in August (Table 8) to a maximum of 1.20 kg/ha in September (Table 9). Foliar magnesium was greatest (1.53 kg/ha) in July (Table 7) in comparison to 0.7 kg/ha as an annual average for Coweeta. A magnesium pool was present (although minimal) in flowers (Table 6) during April (0.03 kg/ha). Fruit magnesium was minimal throughout the growing season with a maximum of 0.14 kg/ha during the period of fruit ripening (Table 7).

5.4.4 Phosphorus

Wood phosphorus pools remained relatively constant throughout the growing season (0.16 to 0.32 kg/ha), suggesting a steady uptake from soil. Data from Coweeta indicated a similar storage of 0.3 kg/ha (Day and McGinty 1975). Root phosphorus (0.11 to 0.36 kg/ha) (Tables 5-11) suggests a constant transport from soil to roots, with distribution to above ground storage compartments. Foliage phosphorus is greatest in July during the period of fruit development (Table 7). Flowers account for a storage pool of 0.04 kg/ha in April (Table 6). Fruit phosphorus concentration is greatest (1.78 mg/g) during the months of fruit development (Tables 7-10), but total reserves are minimal due to the low standing crop of fruits as the result of consumption by primary consumers (e.g., squirrels, bluejay, grosbeaks, and waxwings). Maximum phosphorus reserves (0.09 kg/ha) in fruits are evident during early fruit development during July (Table 7).

6. SUMMARY

Plants manifest changes in life stage events during various climatic and meteorological regimes. Observations in this study focused on the generative phases (flowering) of individual plants and colonies of plants as indicators of productivity. Mayapple was chosen as a study species to exemplify short-term nutrient pools, in which the colonies responded in almost total synchrony to phenological changes. The decomposition and mineralization of plant materials in mayapple (turnover rate) is relatively short, such that elemental inputs to plant/soil systems are complete within annual nutrient cycles. Because of the almost total synchrony of phenophase development in mayapple populations, this taxon is proposed as an ideal species on which to key developmental strategies within the southeastern deciduous forest formation.

Dogwood is a major understory species of the southeastern deciduous forest formation. Its nutrient reserves depict long-term (years) pools, primarily stored in the woody (bole or branch) compartments. Concentration data and storage reserves among dogwoods were similar to quantities determined at Coweeta, another southern Appalachian forest watershed (Day 1973 and Day and McGinty 1975). Data for dogwood are supportive to previous studies (Thomas et al., 1967), and offer additional insights on the responses of standing crop biomass and nutrient pools to life stage (phenophase) development.

Phenological calendars were constructed for silver and red maples, serviceberry, red bud, flowering dogwood, painted buckeye, yellow buckeye, mayapple, yellow-poplar, and hydrangea. These calendars are valuable to superimpose on the civil calendar, such that the seasons of the year are not marked by calendar date but by dated groups of phenological events.

A significant correlation ($P < 0.01$) was observed between average date of first flowering and heat unit summations using a second degree polynomial model. Application of the model permits the capability to predict onset of flowering among 133 plant species.

Additional correlations were established between diameter at breast height and aboveground biomass for mature dogwood trees and diameter at ground level and the below ground biomass. These models permit predictions of standing crop biomass for dogwood boles, branches, and twigs and roots.

Plant density among mayapple colonies can be estimated ($P < 0.01$) from the linear correlation with diameter of the colony.

Standing crop biomass or standing crop present at any given time should not be confused with productivity. Primary productivity is the rate at which energy is stored by photosynthetic or chemosynthetic activity of producer organisms (green plants) in the form of organic substances which can be used as food materials. Good estimates of net primary production (rate of organic matter storage less respiration losses) may be obtained from standing crop biomass providing the organisms are large and the living materials were accumulated over relatively long periods of time. Thus, net primary production of dogwood can be estimated from the standing crop biomass by normalizing the data over the number of days of active growth during the photosynthetic period (growing season) and the number of growing seasons (years) the trees have lived (Tables 2 and 3).

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APPENDIX

Alphabetic listing of species. Species numbers correspond to data points on Figure 8 and define the period of flowering depicted in Figure 4. The asterisk denotes the species as woody.

APPENDIX

Species	Common Name	Species Number
*Acer rubrum L.	Red Maple	2
*Acer saccharinum L.	Silver Maple	1
Achillea millefolium L.	Common Yarrow	84
Actaea pachypoda Ell.	Doll's-Eyes	66
*Aesculus octandra Marsh.	Yellow Buckeye	32
*Aesculus pavia L.	Red Buckeye	33
*Ailanthus altissima (Mill.) Swingle	Tree-of-Heaven	130
*Albizzia julibrissin Durazzini	Mimosa	125
Allium vineale L.	Field Garlic	102
*Amelanchier arborea (Michy. f.) Fern.	Serviceberry	17
*Amorpha fruticosa L.	False Indigo	86
Amsonia tabernaemontana Walt.	Dogbane	37
Anemonella thalictroides (L.) Spach	Rue-Anemone	15
Antennaria plantaginifolia (L.) Hook	Pussy's-Toes	20
Apocynum cannabinum L.	Indian Hemp	111
Aquilegia canadensis L.	Wild Columbine	45
Asclepias tuberosa L.	Butterfly-Weed	116
Asclepias variegata L.	Pleurisy-Root	121

APPENDIX (Continued)

Species	Common Name	Species Number
*Campsis radicans (L.) Seem.	Trumpet-Vine	124
Capsella brusa-pastoris (L.) Medic	Shepherd's-Pouch	26
Cardamine hirsuta L.	Bitter Cress	5
*Catalpa speciosa Warder	Catalpa	100
*Ceanothus americanus L.	New Jersey Tea	105
Centaurea cyanus L.	Bachelor's-Button	117
*Cercis canadensis L.	Redbud	21
Chimaphilia maculata (L.) Pursh	Pipsissewa	88
*Chionanthus virginicus L.	Old-Man's-Beard	77
Chrysanthemum leucanthemum L.	Ox-Eye-Daisy	78
Coreopsis auriculata L.	Tickseed	80
Coreopsis major Walt.	Tickseed	118
*Cornus amomum Mill.	Red Willow	103
Cornus florida L.	Flowering Dogwood	36
Cynoglossum virginianum L.	Hound's-tongue	76
Datura stramonium L.	Jimsonweed	133
Daucus carota L.	Queen Anne's-Lace	90
Dentaria heterophylla Nutt	Toothwort	34
Dentaria laciniata Muhl.	Toothwort	18
Dianthus armeria L.	Deptford Pink	93
Diodia virginiana L.	Buttonweed	127

APPENDIX (Continued)

Species	Common Name	Species Number
Draba brachycarpa Nutt.	Whitlow-Grass	8
Draba verna L.	Whitlow-Grass	9
Duchesnea indica (Andr.) Focke	Indian Strawberry	27
Erigeron annuus (L.) Pers.	Daisy-Fleabane	128
Erigeron strigosus Muhl.	White-top	79
Fragaria virginiana Duchesne	Strawberry	31
Galium aparine L.	Goosegrass	64
Geranium carolinianum L.	Carolina Geranium	40
Geranium maculatum L.	Wood Geranium	61
Hepatica americana (DC.) Ker	Liverleaf	10
Holosteum umbellatum L.	Jagged Chickweed	6
Houstonia caerulea L.	Bluets	22
Houstonia purpurea L.	Purple Bluets	89
Hydrangea arborescens L.	Wild Hydrangea	110
Hypericum denticulatum Walt.	Coppery St. John's Wort	112
Justica americana (L.) Vahl	Water-Willow	137
Lamium amplexicaule L.	Henbit	3
Lamium purpurea L.	Purple Dead-Nettle	23
*Liriodendron tulipifera L.	Yellow-Poplar	82
Lithospermum canescens (Michx.) Lehm.	Puccoon	41
*Lonicera japonica Thumb.	Japanese Honeysuckle	85

APPENDIX (Continued)

Species	Common Name	Species Number
*Malus pumila Mill.	Wild Apple	46
Melilotus alba Desr.	White Sweet Clover	98
Melilotus officinalis (L.) Lam.	Yellow Sweet Clover	95
Mertensia virginica (L.) Pers.	Bluebells	87
Monarda fistulosa L.	Wild Bergamot	94
*Morus rubra L.	Red Mulberry	67
Myosotis verna Nutt.	Scorpion-Grass	42
Nasturtium officinale R. Br.	Watercress	56
Obolaria virginica L.	Pennywort	4
Orchis spectabilis L.	Showy Orchid	48
Oxalis stricta L.	Sorrel	16
Oxalis violacea L.	Violet Wood-Sorrel	57
*Oxydendrum arboreum (L.) D.C.	Sourwood	129
Passiflora incarnata L.	Apricot-Vine	126
*Philadelphus hirsutus Nutt.	Mock-Orange	73
Phlox divaricata L.	Phlox	52
Phytolacca americana L.	Poke Weed	106
*Pinus virginiana Mill.	Virginia Pine	53
Podophyllum peltatum L.	May Apple	58
*Poncirus trifoliata (L.) Raf.	Trifoliate Orange	13
Potentilla canadensis L.	Cinquefoil	43
Potentilla recta L.	Rough-Fruited Cinquefoil	96

APPENDIX (Continued)

Species	Common Name	Species Number
Potentilla simplex Michx.	Old-Field Cinquefoil	74
*Prunus hortulana Bailey	Wild-Goose-Plumb	24
*Prunus serotina Ehrh.	Black Cherry	49
Pyrrhopappus carolinianus (Walt.) D.C.	False Dandelion	122
*Pyrus communis L.	Common Pear	38
Ranunculus bulbosus L.	Bulbous Crowfoot	62
Raphanus raphanistrum L.	Wild Radish	59
*Rhamnus caroliniana Walt.	Carolina Buckthorn	113
*Rhus glabra L.	Smooth Sumac	120
*Robinia pseudo-acacia L.	Black Locust	70
*Rosa carolina L.	Carolina Rose	65
Rubus trivialis Michx.	Southern Dewberry	63
Rudbeckia hirta L.	Black-Eyed Susan	107
Ruellia caroliniensis (Walt.) Steud.	Ruellia	132
*Salix nigra Marsh.	Black Willow	28
Salvia lyrata L.	Lyre-Leafed Sage	69
*Sambucus canadensis L.	Common Elderberry	114
Sanguinaria canadensis L.	Bloodroot	25
*Sassafras albidum (Nutt.) Nees	Sassafras	19
Scutellaria integrifolia L.	Skullcap	104
Sedum ternatum Michx.	Stonecrop	68

APPENDIX (Continued)

Species	Common Name	Species Number
<u>Senecio</u> <u>smallii</u> Britt.	Goundsel	92
<u>Silene</u> <u>virginica</u> L.	Fire-Pink	81
<u>Sisyrinchium</u> <u>mucronatum</u> Michx.	Blue-Eyed Grass	72
<u>Smilacina</u> <u>racemosa</u> (L.) Desf.	False Soloman's-Seal	71
<u>Solanum</u> <u>nigrum</u> L.	Nightshade	108
<u>Specularia</u> <u>perfoliata</u> (L.) A. DC.	Venus's Looking-Glass	99
<u>Spigelia</u> <u>marilandica</u> L.	Indian-Pink	97
<u>Stellaria</u> <u>media</u> L.	Common Chickweed	11
<u>Taraxacum</u> <u>officinale</u> Weber	Common Dandelion	14
<u>Tiarella</u> <u>cordifolia</u> L.	Foanflower	60
<u>Trifolium</u> <u>repens</u> L.	White Clover	35
<u>Trillium</u> <u>erectum</u> L.	Purple Trillium	50
<u>Trillium</u> <u>luteum</u> (Muhl.) Harbison	Yellow Trillium	44
*<u>Ulmus</u> <u>americana</u> L.	American Elm	7
<u>Uvularia</u> <u>perfoliata</u> L.	Bellwort	47
<u>Verbascum</u> <u>blattaria</u> L.	Moth-Mullein	115
<u>Verbascum</u> <u>thapsus</u> L.	Common Mullein	123
<u>Verbena</u> <u>simplex</u> Lehm.	Vervain	91
*<u>Viburnum</u> <u>rufidulum</u> Raf.	Southern Black-Haw	75
<u>Vicia</u> <u>caroliniana</u> Walt.	Wood-Vetch	83
<u>Viola</u> <u>canadensis</u> L.	Canada-Violet	39

APPENDIX (Continued)

Species	Common Name	Species Number
Viola hastata Michx.	Halberd-Leaved Yellow Violet	51
Viola hirsutula Brainerd	Violet	30
Viola kitaibeliana R. & R.	Field-Pansy	12
Viola rotundifolia Michx.	Early Yellow Violet	29
Viola sagittata Ait.	Arrow-Leaved Violet	54
Viola septemloba LeConte	Seven-Lobed Violet	55
*Vitis vulpina L.	Fox Grape	101
Yucca smalliana Fern.	Yucca	109

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