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**ACCUMULATION AND CYCLING OF CALCIUM
BY FLOWERING DOGWOOD TREES
(Thesis)**

W. A. Thomas

S. I. Auerbach and J. S. Olson

Submitted as a dissertation to the Faculty of the Graduate School of the University of Minnesota in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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AUGUST 1967

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I. INTRODUCTION

This is a study of the influence of flowering dogwood (Cornus florida L.) trees on the distribution of calcium in forest stands. The two primary objectives are to document the accumulation of calcium by various plant organs and to determine the rate of calcium circulation in the tree-soil system.

Chemical analyses of plants and soils were initiated in the 17th century in studies of agricultural productivity (Davies 1940). During the 19th century similar analyses were made in forest stands in studies concerned with productivity of forest tree species (Ebermayer 1876; Rennie 1955). Much of the emphasis was on calcium since it is the element removed in greatest quantity when tree crops are harvested. Recently, impetus for such studies has shifted from strictly practical considerations to basic understanding of the function of ecosystems and their components. Prime consideration has been given to cycling of nutrients by plants. Availability of radioisotopes has greatly facilitated these studies since they permit measurement of rates of movement of elements within ecosystems.

For several decades flowering dogwood has been acknowledged as a nutritionally beneficial species due to accumulation of calcium in its leaves and rapid decomposition of litter, thus releasing calcium for use by other species. There is an increasing awareness that so called "pure" stands are not biologically pure since they contain more than one species, and that the entire plant assemblage contributes to the nutrient economy

of the stand (Scott 1955). This study was undertaken to elucidate the cycling of calcium by flowering dogwood trees.

II. REVIEW OF THE LITERATURE

A. Concept of Element Cycling

Elements taken up by plants are subsequently released in one of several ways. Those that are lost from the plant may enter animal systems before being available for plant use again, or they may be made directly available for plant utilization. There are inputs of elements to the plant-soil system by, e.g., precipitation, dust, weathering of parent material, and losses due to, e.g., drainage waters and plant and animal harvests. These incomes and exports have been discussed by Ovington (1962, 1965).

Circulation of elements within the plant-soil system is exceedingly complex. Remezov (1959) classified nutrient cycles as subannual cycles, annual cycles, and those consisting of successive annual cycles. One characteristic of subannual cycles is that the same amount of nutrients can be taken up by plants and returned to soil many times during one year. Remezov stated that it is impossible to list all minor cycles and that, "The biological cycle of elements in a forest is a complicated polycyclic process depending on the combination of many factors." In spite of such complexity, nutrient cycling has received increased attention in the practical aspects of forest productivity (Ovington 1960). Bormann and Likens (1967) have stressed the value of combining studies of the plant-soil cycle and the geochemical cycle of weathering and erosion.

There are two principal methods for studying the cycling of nutrients. The first is to analyze forest stands along an age gradient and with periodic sampling to calculate the amount of nutrients returned to the soil per unit of material in the standing crop (Ovington 1959a; Ovington and Madgwick 1959a). Gross estimates of nutrient turnover by different species may be obtained with this method. The second method is to study small ecosystems over time and to calculate the flow of nutrients by intensive sampling. The latter approach is preferable for understanding mechanisms of the nutrient cycling process (Remezov 1959; Madgwick 1963). It is probable that the greatest understanding of nutrient cycling will be gained by a combination of the two approaches.

Auerbach (1965) summarized the needs for cycling studies and concluded that additional tracer investigations should be undertaken to measure cycles in various ecosystems. He cites Olson as stating, "To demonstrate and interpret the relative importance of rates of internal circulation vs rate of import-export (as part of a larger scale geochemical cycle) is one of the unifying problems of cycling studies."

B. Principal Pathways in Plant-Soil Nutrient Cycles

1. Litter

Litter is the most obvious and most intensively studied component of nutrient cycles. Although the amount of litter in similar stands and in the same stand from year to year is variable (Lutz and Chandler 1946; Kittredge 1948; Bray and Gorham 1964) and the amount of nutrients in leaves from the same position on a tree may vary among years (Plice

1944), it is evident that litter is the primary route of exchange of nutrients from plant to soil.

Return of nutrients to soil is variable among species and among sites due to many factors that influence the rate of organic matter decomposition (Lutz and Chandler 1946; Witkamp and van der Drift 1961). Rapid decomposition of litter in the tropics (Nye 1961) permits rapid growth of vegetation in spite of the low nutrient content of the soil and results in high turnover of available nutrients (Lutz and Chandler 1946; Richards 1957).

Correlation of calcium content of litter with its rate of decomposition has been of interest for many years. Broadfoot and Pierre (1939) studied decomposition of leaves from 19 tree species and reported a correlation coefficient of 0.59 ($P < 0.01$) between calcium content of the leaves and their decomposition during six months. Statistically significant correlations were also found between rate of decomposition and excess base, water-soluble organic matter, total nitrogen, and total ash of the leaves. Voigt (1965) conducted a similar experiment with leaves of six species but did not find a significant correlation between their calcium content and their rate of decomposition. Daubenmire and Prusso (1963) also reported no significant correlation between calcium content of forest tree leaves and their rate of decomposition. Remezov (1961) found that oak, ash, basswood, and hazelnut leaves lost 40 to 50% of their calcium in one year after abscission.

Coile (1933) thought that dogwood leaves should decompose more rapidly than pine and oak litter because of low hydrogen ion concentration

of dogwood leaves. He later considered effects of the carbon/nitrogen ratio and calcium content of the leaves (Coile 1937). Olson and Crossley (1963) found that loss of weight by decomposing dogwood leaves was greater than that of southern red oak (Quercus falcata) and virginia pine (Pinus virginiana). Decomposing dogwood leaves generally had larger arthropod populations than the other two species (Crossley and Hoglund 1962).

Using litter from a wide range of species in litter bags with holes of various diameters, Heath, Arnold, and Edwards (1966) demonstrated that different size-classes of soil-litter fauna had different effects on the decomposition of litter.

Although primary emphasis in the majority of studies of litter production and decomposition is on leaves, it should be remembered that there are many other components of litter. Carlisle, Brown, and White (1966), for example, presented data for eight components of litter. Ovington (1963) found that reproductive organs may account for a surprisingly large percentage of the total litter; he reported that in an aspen (Populus tremuloides) stand the catkins amounted to 26% of the weight and 23% of the calcium in leaves and emphasized that litter collections should include the total annual input to the forest floor. Wood may persist in humus for centuries (McFee and Stone 1966); factors affecting decomposition of wood and bark have lately received some attention (Allison and Murphy 1962). Ovington (1962) pointed out that different components of litter may decompose at different rates, thus influencing the nutrient cycle for varying periods of time.

2. Foliar leaching and absorption

Precipitation can remove nutrients from plant foliage (Stenlid 1958), but the importance of this process has not been understood until recently. Mina (1965) and Tukey and Tukey (1959) discussed the ecological significance of foliar leaching. Tukey and Mecklenburg (1964) demonstrated that nutrients can be removed from one plant by leaching and then taken up from the soil by other plants. Stenlid (1958) and Attiwill (1966) reviewed the literature on foliar leaching and the factors which may affect its efficiency. Attiwill's tabulation of some published values for nutrients removed by precipitation shows that they are removed (kg/ha/yr) in the order: $K > Ca > Na > Mg > P$.

Mecklenburg and Tukey (1964) found that the amount of calcium removed in foliar leachate depended upon the amount of calcium in the transpiration stream and that leaching increased the rate of transpiration and quantity of calcium absorbed by roots. They found that foliar leaching by a mist for four days removed up to 40% of the ^{45}Ca in leaves of bean plants growing in a solution containing ^{45}Ca . Mecklenburg, Tukey, and Morgan (1966) concluded that precipitation removed calcium from leaves by passive processes: (1) calcium exchange on cuticle and cell walls by hydrogen ions in the leaching solution; (2) diffusion of ions from the transpiration stream into the leaching solution, or (3) a combination of the two processes. This explains the frequent observation (Stenlid 1958; Attiwill 1966) that amount of precipitation has little effect on amount of nutrients removed and that dew or gentle rain is more effective in removing nutrients. Calcium is more easily leached

from mature leaves than from young ones since a greater percentage of the calcium in younger leaves is immobilized in the cells and cell walls.

Guttation is really part of the foliar leaching process since nutrients in guttation solution are removed by precipitation (Tukey, Wittwer, and Bukovac 1962; Ivanoff 1963). Calcium is commonly found in relatively high concentrations in guttated solutions (Stenlid 1958; Kramer 1959).

Leaves can also absorb nutrients through the cuticle (Tukey, Wittwer, and Bukovac 1961, 1962). These authors classified calcium as immobile after foliar absorption; it will move acropetally, but basipetal movement is negligible. It is possible for calcium to be removed from leaves by precipitation and then absorbed by leaves at lower positions. Damaged leaves may absorb or lose more nutrients than undamaged ones. Hewlett and Kramer (1963) found that discs cut from dogwood leaves absorbed much more water than entire leaves floating on water and that amount absorbed by the discs varied directly with the area of cut surface.

Tukey et al. (1952) reported that isotopes of K, P, and C were absorbed through bark of fruit trees and concluded that the old horticultural practice of applying mineral substances to trunks and branches of trees may be justified scientifically. Harley, Regeimbal, and Moon (1956) and Ticknor and Tukey (1957) found that absorption of material by bark was greatly enhanced by scraping the bark and concluded that absorption occurs primarily through imperfections in the bark.

3. Roots

Many small roots and root hairs on living trees die every year (Büsgen and Münch 1929), but this loss is extremely difficult to measure. Remezov (1959) cited work by Orlov in which he found that about 0.6 metric tons of roots less than 0.3 mm diameter died each year per hectare in a spruce stand; Remezov found this value to be 0.4 metric tons/ha/yr in an oak stand. The complete role of trees in nutrient cycling will not be understood until methods for measuring root production and loss are developed (Madgwick 1963).

Exudation of nutrients from roots (Stenlid 1958; Samtsevich 1965) and transfer of material between trees through root grafts (Graham and Bormann 1966) may have roles in the nutrient economy of plants. Ririe and Toth (1952) used the split-root technique to study transfer of calcium from roots of tomato plants to other roots of the same plant. They found little transfer of ^{45}Ca from roots immersed in a solution containing ^{45}Ca to roots of the same plant in nutrient solutions with various concentrations of calcium; there was still very little transfer of the radioisotope when calcium was completely omitted from the nutrient solutions. Woods and Brock (1964) found that ^{45}Ca was transferred within eight days from stumps of red maple (Acer rubrum) trees to other species. They did not attribute this movement to root grafts but to exudation from the roots followed by uptake by roots of other plants, aided perhaps by shared mycorrhizal fungi. They concluded that the movement was probably faster than that which may occur normally because of "back pressure" from roots due to dry soil and large amounts of water

supplied to the stumps.

4. Foliage consumption

Although the role of various animals, especially litter fauna, in cycling of minerals has been acknowledged for some time, there have been few investigations in which the amount of plant material consumed has been evaluated in the context of nutrient cycling.

Chandler (1939) suggested that there was a correlation between calcium content of tree leaves and preferences by foliage-feeding insects, although he was aware of many factors affecting palatability. Lyford (1943) found a correlation coefficient of 0.55 ($P < 0.01$) between calcium content of leaves of 21 species of forest trees and leaf area eaten by a milliped.

Bray (1961) found that from 3.2 to 15.0% (mean was 8.3%) of the leaf area of 10 tree species was removed by insects and suggested that leaves with higher calcium content were preferred by insects. Later work (Bray 1964) did not confirm this; in these samples the mean area removed was 7.7%. Rothacher, Blow, and Potts (1954) reported that leaf area removed by insects in an oak stand increased from 3.7% in May and June to 6.7% in September and October. Not all material removed is assimilated by insects. Grimshaw et al. (1958) reported that 12 g of Ca per hectare fell to the ground in caterpillar frass during 50 summer days in a pine plantation.

C. Trees as Nutrient Pumps

The fact that some species of forest trees contribute more nutrients to litter than do others may be important to the stand in several ways. The most commonly cited effect is on characteristics of humus; Lutz and Chandler (1946) list the specific effects of calcium in litter as neutralization of decomposition products, improvement of soil physical condition, and encouragement of active bacterial populations. Although leaves of hardwood trees often have such effects on conifer litter, generalizations must be avoided due to large differences in characteristics of litter of different species (Lutz and Chandler 1946).

Chandler (1939) suggested that trees in general may be important in keeping calcium in circulation to reduce loss in drainage waters. In tropical forests, where soil nutrients may be depleted by severe leaching, vegetation may be as important as soil in storing plant nutrients (Greenland and Kowal 1960). Beneficial effects of many tree species on soil and/or surrounding vegetation have been reported (Auten 1945; Walker 1953; Read and Walker 1950; Daubenmire 1953; Tarrant 1961; Tarrant and Miller 1963; Pogrebnyak 1960; Pokhiton 1958, 1960; Samoylova 1962). Zinke (1962) stressed the pattern of influence of individual trees on soil conditions in a forest stand.

Although the beneficial effects of understory species has been argued since the 1880's (Dengler 1944), they are commonly looked upon with disfavor in forestry since they may compete with the crop trees for water and nutrients, shade the soil surface, increase the supply of fuel

for fire, serve as alternate hosts of diseases, etc. There is some evidence that this opinion is changing (Youngberg 1965). The nutrient content of lesser vegetation may be a considerable portion of that in the entire stand. For example, Scott (1955) found that 17.5% of the litter in several different stands was contributed by understory species, and Madgwick (1965) found 37% of total leaf weight and calcium content in the leaves of understory plants in an ash (Fraxinus excelsior) stand.

Rennie (1955) observed that although some species are considered favorable because of the nutrient content of their leaves, they may be immobilizing large quantities of nutrients in nonfoliar tissues, making the overall effect less advantageous than anticipated. He found that three times as much calcium was returned to soil in litter as was removed from circulation by immobilization; although this may appear favorable, it also means that within a short time in the life of the species a large quantity of calcium will be in woody tissue. From these considerations he concluded that "soil improving" species may be justified in forest stands only if they are not harvested, and thus removed from the site, and if they have high foliar:woody organ ratios.

Wittich (1952) and Rennie (1955) pointed out that productivity of nutrient-poor soils cannot be increased by introduction of "soil improving" species. Rennie added, however, that it may be necessary in some cases to provide shade-tolerant shrubs to produce palatable food for mull-forming fauna. Ovington (1960) stated that it is doubtful from scientific and economic considerations that "soil improving" species can be used extensively to increase nutrient reserves in soil.

D. Calcium

Although not all roles of this essential element in higher plants are understood, it is known that it occurs as calcium pectate in the middle lamella of cell walls and is necessary for several biochemical processes (Nason and McElroy 1963). There is a common misconception that most calcium in plants is immobilized in cell walls. Bowen, Cawse, and Thick (1962) reported that calcium was present in the free ionic state in tomato leaves and that only 40% of the ^{45}Ca in plants five hours after placing their roots in a tagged solution was in the form of calcium pectate. Maier and Knezek (1966) grew tomato plants in a solution containing ^{45}Ca and found after eight weeks that 23% of the ^{45}Ca in leaves and 12% in the stem was water soluble. Calcium is found in other forms, the most common of which is calcium oxalate. Jane (1956) stated that calcium oxalate is commonly found in parenchyma of hardwood trees. Chandler (1937) reported that leaves of 10 of 12 forest tree species studied contained calcium oxalate and that in 8 of them all oxalates were in the form of calcium oxalate. Olsen (1948) found 65 to 70% of the calcium in Fagus sylvatica leaves in calcium oxalate crystals, 20% bound to other organic fractions, and 12% free in leaf sap.

Calcium is the most immobile of the essential elements (Bollard 1960) and is not readily redistributed in plants (Biddulph 1959). Older leaves on a plant may have large calcium reserves at the same time that younger leaves on the same plant exhibit a deficiency (Nason and McElroy 1963). Results of many experiments show that minerals move upward only

in xylem (Bollard 1960), and all evidence indicates that calcium is very immobile in phloem (Zimmermann 1960). Tukey, Wittwer, and Bukovac (1962) described a simple experiment showing that calcium transport displays polarity. They grafted terminal ends of lateral shoots from different tomato plants; the graft represented a region of reversed polarity. When ^{32}P was made available to roots of one plant, it moved out the branch and into the other plant, whereas calcium did not move across the graft against reversed polarity.

Amount of calcium in plants was formerly thought to be a direct function of calcium content of soil; for example, Beeson (1941) emphasized the concentration of calcium in soil with respect to amounts of calcium in agricultural plants. It is now recognized that some plants accumulate more calcium in their tissues than do others. Collander (1941) studied the mineral composition of plants grown in nutrient solutions and found that some species consistently had a greater concentration of certain cations while other species had high concentrations of other cations. Bard (1945) concluded that calcium content of a tree species was an inherent species characteristic which was relatively independent of calcium content of soil over a wide range of soil conditions. Although variations occur within species, it is clear that specific differences do exist and that within-species variation in nutrient content on the same site may be as great as that among individuals in widely separated regions (Lutz and Chandler 1946). Leyton (1948) concluded that, generally, soil type is only one of the factors which determine mineral composition of trees and, although there may be variation between sites for the same species, there are some

species that are characterized by high calcium content independent of site. This is probably applicable to most forest soils but not at extremely low concentrations of calcium (Ebermayer 1876; Wittich 1952). There is also evidence that other forest plants accumulate nutrients relatively independent of site (Gagnon, Lafond, and Amiot 1958). Although much is known about calcium behavior in soil (Wiklander 1958), there is much yet to be learned about biological cycling of calcium (Müller 1965).

There are many references which document the increasing amount of calcium in leaves of hardwood tree species during the growing season (Alway, Maki, and Methley 1934; Sampson and Samisch 1935; Mitchell 1936; Chandler 1939; Lutz and Chandler 1946; Olsen 1948; Tamm 1951; Stenlid 1958; Oland 1963; Smith 1962; Hoyle 1965; Guha and Mitchell 1965, 1966). In all of these reports and reviews the amount of calcium per leaf was reported to increase during the growing season, and in most cases it also increased when expressed as a percentage of dry weight. Calcium is not resorbed into woody tissues prior to leaf abscission as are several elements, notably N and K (Stenlid 1958; Biddulph 1959; Oland 1963). Although the amount of calcium in leaves may be expressed in several ways (Goodall and Gregory 1947), absolute amount of calcium per leaf is the most meaningful (Stenlid 1958) since calcium as percentage of dry weight is affected by leaf growth and changes in concentrations of other elements.

Garnaga (1955) placed fertilizer containing ^{45}Ca and ^{32}P under young apple trees and determined concentrations of the two isotopes after

40 days. He found that concentration of ^{45}Ca in roots was greater than that in stem and leaves but the opposite for ^{32}P . Rubin and Moiseichenko (1964) inoculated ^{45}Ca into roots and branches of apple and pear trees. They found that radiocalcium was retained in roots until buds opened and that ^{45}Ca in branches was concentrated near the site of inoculation.

Movement of calcium in the transpiration stream is not fully understood. Fischer (1958) stated that calcium movement could not be explained by mass flow alone. Biddulph, Nakayama, and Cory (1961) compared movement of ^{45}Ca and tritiated water in bean plants and found that xylem operated essentially as an exchange column for calcium. This was confirmed by additional work on the translocation of calcium in bean plants growing in nutrient solutions containing ^{45}Ca (Bell and Biddulph 1963). After various periods (0.75 to 6 hr.) plants were transferred to solutions containing stable calcium, strontium, and magnesium. These elements replaced ^{45}Ca in this decreasing order of efficiency, whereas potassium and water were ineffective in moving radiocalcium up the stem. Bell and Biddulph concluded that calcium movement in xylem occurred in two phases. (1) Calcium entered the transpiration stream, was bound on exchange sites, and then ascended by exchange with aid of the transpiration stream. (2) Calcium was removed from exchange sites to more immobile positions; these included ion utilization by metabolizing cells and deposition in calcium oxalate crystals. They further concluded that these processes occur at a slower rate when calcium is transferred from xylem to phloem because a greater percentage of the calcium is immobilized in phloem.

Emmert (1965) found this explanation adequate to interpret upward movement of strontium in bean plants. Morrison and Heine (1966) did not believe this explained movement of all polyvalent cations, and O'Leary (1965) interpreted results of additional experiments as indicating that the mass flow theory could not be entirely discarded as an explanation for calcium ascent in bean plants.

O'Leary (1965) found the $^{45}\text{Ca}/^{32}\text{P}$ ratio in foliage and stem of bean plants was lower when bases of derooted plants were placed in a solution containing these isotopes than when roots of intact plants were placed in the solution. This indicated that roots had a greater effect on movement of calcium in the stem than on phosphorous. Jacoby (1966) placed derooted and intact bean plants in nutrient solutions containing ^{45}Ca and acid fuchsin dye. Dye and ^{45}Ca were both widely distributed throughout intact plants, but in derooted plants ^{45}Ca was retained in the basal stem segment although dye was distributed throughout the plant. Other elements (K, Cl, and S) were also distributed throughout the entire plant when absorbed by derooted plants. Jacoby suggested that mobility of calcium in xylem vessels was increased by passage of calcium through roots and that calcium was bound to an organic compound during root penetration and then translocated as an organic calcium compound. The chemical form in which calcium occurs in xylem is not known (Bollard 1960).

Fraser and Mawson (1953) introduced ^{45}Ca into holes drilled in boles of a yellow birch (Betula lutea) and a white pine (Pinus strobus). The ^{45}Ca moved upward in xylem of the birch tree in a narrow dextral spiral. Some of the ^{45}Ca in the pine tree was in calcium oxalate crystals

in phloem (Fraser 1958). Ferrell and Johnson (1956) inoculated stems of western white pine trees with ^{45}Ca and reported that newly-formed buds one and two years after inoculation contained significant quantities of ^{45}Ca . They interpreted this as an indication of substantial movement of previously deposited calcium into new buds. Swanson (1957) suggested that some of this ^{45}Ca may have been previously leached from foliage and subsequently taken up by roots. Ferrell and Johnson corrected their counting rates for physical decay to the time of inoculation. This would greatly inflate their estimates of ^{45}Ca in buds since it is not valid to correct for decay to times prior to when samples are collected unless rate of radioisotope movement during the intervening time is known precisely (Perrault, Bazin, and Pages 1967).

Olson (in press) tagged a flowering dogwood tree simultaneously with ^{45}Ca , ^{85}Sr , and ^{42}K . Radiopotassium ascended about 5 m in less than four hours, but ^{85}Sr was not detected at that height after several weeks. He found that ^{45}Ca behavior was similar to that of ^{85}Sr .

E. Flowering Dogwood

Flowering dogwood is a common understory species in forests of eastern and southeastern United States, where it is present in many stages of succession (Billings 1938; Coile 1940; Oosting 1942; Bard 1952). Survival of this species is increased by its ability to attain maximum photosynthetic rate at low light intensity (Kramer and Decker 1944); a highly branched root system (Billings 1938) which is much more developed than that of loblolly pine (Kozlowski and Scholtes 1948), a common

dominant species; greater permeability of its roots to water compared with pine (Kramer 1946); mycorrhizal relationships (Kelly 1960); and reproduction by seeds, sprouting, and layerage. Dogwood trees have a long growing season compared to other species (Kozlowski and Ward 1957, 1961; Jackson 1952). Silvical characteristics of this species have been presented elsewhere (Fowells 1965).

Dogwood leaves have a high concentration of calcium compared to other tree species (Lutz and Chandler 1946). For this reason Coile (1937, 1940) stated that dogwood might be a beneficial species in forest stands. Metz (1952) recommended that species with high leaf calcium content, such as dogwood and redbud (Cercis canadensis), be encouraged in the understory of pine stands. Published values for calcium content of leaves at the end of the growing season are listed in Table 1. Average value is $3.2\% \pm 0.2$ (SE) on oven-dry weight basis. This value must be considered with caution since, as will be pointed out later, truly representative leaf samples for this species are difficult to obtain.

Hundley (1959) presented data for calcium content of flowering dogwood twigs (current annual growth) on four soils with various concentrations of exchangeable calcium (0.07 to 6.50 meq/100 g). Mean calcium content of twigs, calculated from his data, was $1.56\% \pm 0.11$ (SE); calcium concentration in twigs was not significantly correlated with exchangeable calcium in soil ($r^2 = 0.07$; $P > 0.05$).

The relatively small size of mature dogwood trees is an advantage in nutrient cycling experiments since mature or nearly-mature trees can be effectively handled as experimental units.

Table 1. Published values for calcium content of dogwood leaves

Percent Calcium ^a	Weight Basis	Reference
2.08	32 to 33 C	Lunt (1935)
2.20	Air-dry	Voigt (1965)
2.74	Air-dry	Broadfoot and Pierre (1939)
2.8	105 C	Thomas (present study)
3.03	Air-dry	Van Camp (1948)
3.38	90 C	Metz (1952)
3.4	Oven-dry	Coile (1937, 1940)
3.46	65 C	Bard (1945)
4.21	Air-dry	McHargue and Roy (1932)

^aAt time of leaf abscission

III. MATERIALS AND METHODS

Determination of calcium distribution in tree components involves rather straightforward procedures of tree harvesting and laboratory determination of calcium. It is much more difficult to trace pathways by which calcium circulates in a tree-soil system. Radioisotopes were used to estimate rates of calcium transfer between some components of the tree-soil system. Major pathways were studied individually, and results were combined with data for calcium content of tree components to determine relative importance of these pathways.

Two radioisotopes of calcium are suitable for use in biological studies. The most commonly used, ^{45}Ca , is a weak beta emitter (0.25 Mev) with a radiological half-life of 165 days. The low energy of the beta particles is a distinct disadvantage because of time required to prepare samples for counting. The other isotope, ^{47}Ca , is a gamma emitter (1.31 Mev), which has limited usefulness due to its short half-life (4.5 days). Both isotopes were used in this study.

Results of statistical tests of significance are reported at the 0.05 (*) or the 0.01 (**) level, and values are expressed as the mean ($\bar{X}$) plus or minus one standard error of the mean ($\pm$ SE). Values expressed as kg/ha may be converted to lb/acre by dividing by 1.12, and hectares may be converted to acres by dividing by 2.47.

A. Leaf Data

Areas of 200 dogwood leaves sampled in October, 1965, over a wide range of leaf size were determined (mean of two planimeter measurements

per leaf). A regression equation was computed to predict leaf area (cm^2 ; one surface) from the product of leaf length including petiole (cm) and width (cm) at the widest part of the leaf perpendicular to the long axis.

In September, 1966, number of leaves and branch diameter were obtained for 200 dogwood branches. Branches were collected from 25 trees in pine stand A (described later) and represented many crown positions. These data were used to construct a regression equation which equated leaf number with branch diameter.

Since dogwood trees produce new leaves during the entire growing season and leaves are lost due to insect damage, drought, and senescence toward the end of the season, it is necessary to correct leaf-number estimates obtained with the regression equation. Data for these correction factors were obtained by selecting one branch on each of 12 trees in pine stand A so that all crown positions were represented and counting the number of leaves on them the same day that routine leaf collections were made.

B. Laboratory Procedures

Plant materials for ^{45}Ca and stable calcium determinations were oven-dried at 105 C for 48 hours, weighed, and ashed in a muffle furnace overnight at 575 C. The entire sample was ashed if it weighed less than 20 g; larger samples were thoroughly mixed and 20-g subsamples were taken for ashing. Ashed samples were allowed to cool and were then moistened with distilled water and dissolved in 4 N HCl. This solution was then diluted to known volume with distilled water.

Stable calcium was determined in plant material essentially by the method of Cheng and Bray (1951). An aliquot of sample solution containing approximately 3 mg Ca was diluted to about 50 ml with distilled water, and pH was adjusted to between 11.5 and 12.0 with 10% (v/v) NaOH. Murexide powder (0.2 g in 40 g K_2SO_4) was added to the solution, and calcium was determined by titration with 0.01 M disodium ethylenediaminetetraacetate (EDTA, also known as Versene). Coefficient of variation for 10 replicate determinations of a sample of dogwood leaves was 1.56%, indicating exceptional reproducibility. Stable calcium in precipitation was determined on a Coleman Instruments, Inc., Model 21 flame photometer.

Exchangeable soil calcium was extracted from 25 g of air-dry soil which had been ground to pass a 2-mm mesh screen. Soil was washed into Buchner funnels with 50 ml of 1 N ammonium acetate (pH 7.0), and three additional 25-ml aliquots were added successively after the previous one had passed through the soil. Extracted calcium in the solutions was determined on the flame photometer by comparison with standards prepared from the extracting solution.

Calcium-45 in plant material was determined by slowly evaporating a 4-ml aliquot of solution in planchets on a hotplate and counting with a Beckman Instruments, Inc., Widebeta II planchet counting system. Coefficient of variation for 10 replicate determinations of ^{45}Ca in dogwood leaves was 1.80% which compares favorably with variation in stable calcium determinations. Foliar leachate and tree sap samples were filtered and counted in the same manner. Calcium-45 was extracted from soil samples, which had been ground to pass a 2-mm mesh screen, by shaking the soil

overnight in an excess of 1 N HCl; this solution was filtered and counted. This procedure was used since it was desired to extract all ^{45}Ca , not just that which was exchangeable. Standards were prepared using ^{45}Ca in solutions of the same normality as sample solutions.

Samples containing ^{47}Ca were counted in a Packard Instrument Co. Armac scintillation detector, Model 440. The detector threshold was adjusted so the weaker ^{47}Sc gamma rays (daughter product of ^{47}Ca) were not detected. All samples, control materials, and standards were of the same shape and density and were placed in the counting chamber to achieve identical geometry. Standards for leaf and bark material consisted of 10 pieces of sponge containing ^{47}Ca . Standards for tree stem segments were prepared by removing the bark cylinder and inserting small pieces of sponge containing ^{47}Ca into holes drilled in the xylem; bark was then replaced.

Counting data were corrected for machine efficiency, background radioactivity in control material, and physical decay. Self-absorption corrections were not necessary since standards were of the same volume, density, and geometry as the samples. Samples containing ^{45}Ca were counted for 20 minutes or 10^6 counts; those with ^{47}Ca were counted for 10 minutes or 10^6 counts. Sample counting data were not considered significant unless they were greater than background at 0.05 level (Jarrett 1946).

Soil and litter pH values were obtained with a Beckman Zeromatic pH meter. Soil samples were in a 1:1 soil:water paste, and litter samples were just covered with distilled water. All samples were allowed to equilibrate for one hour.

C. Site Descriptions

The Oak Ridge Reservation, Roane and Anderson Counties, Tennessee, is in the Ridge and Valley Province between the Cumberland Plateau and the Great Smoky Mountains and is in the Humid Mesothermal climatic region of Southeastern United States. Much of the reservation was used for agriculture prior to early 1940's when the area was acquired by the (now) Atomic Energy Commission. Vegetation of the area has been designated by Braun (1950) as Oak Chestnut Forest Region, Ridge and Valley Section. The area's geology, climate, and former land use have been described by DeSelm and Shanks (1963). Six sites on the reservation were used for all experiments and collections of experimental material.

Pine stand A is a loblolly pine (Pinus taeda L.) plantation on a cherty, medium textured, colluvial soil of the Minvale series. The site is uniformly smooth with a 2 to 5% slope and had been cultivated until about 1942. The litter layer was 8 cm deep. A distinct plow layer (A_1 horizon), 18 cm deep, is a brown to dark yellowish-brown, very friable silt loam with bulk density of 1.15 ± 0.02 g/cc ($N = 5$) and porosity of $46.0\% \pm 0.7$ ($N = 5$). Exchangeable calcium (meq/100 g) of this layer was 1.35 ± 0.05 ($N = 4$), and pH was 5.5 ± 0.05 ($N = 4$). The A_2 horizon extends from 18 to 23 cm and is a yellowish-brown silt loam. The B_1 is a yellowish-red silty clay loam extending to 41 cm; B_2 is a yellowish-red silty clay. Pines accounted for 99.3% of the basal area of $38 \text{ m}^2/\text{ha}$, and flowering dogwood accounted for the remainder. Most common ground species were trumpet-creeper, (Campsis radicans L.) and honeysuckle (Lonicera

japonica Thunb.). The pine trees were 18 years old in 1966.

Pine stand B is a loblolly pine plantation with a basal area of $44 \text{ m}^2/\text{ha}$ on shallow acid soil of the Litz series which is underlain by shale. The pine trees were 19 years old in 1966. The pH of the upper 20 cm of mineral soil was 5.1 ± 0.05 ($N = 4$). Dogwood trees were very common in the understory.

Pine stand C is also a plantation of loblolly pine; the trees were 19 years old in 1966. Soil is a colluvial member of the Leadvale series. Pines constituted 99.8% of the $42 \text{ m}^2/\text{ha}$ basal area. Trumpet-creeper and poison ivy (Toxicodendron radicans L.) were the most common ground species.

Yellow poplar stand A is a mixed-age yellow poplar stand on an alluvial soil of the well drained, highly fertile Emory series. The dominant species accounted for 93% of the basal area of $43 \text{ m}^2/\text{ha}$. The pH of the upper 20 cm of mineral soil was 5.5 ± 0.05 ($N = 4$).

Yellow poplar stand B is a mixed-age stand in which yellow poplar constituted 64% of the $17 \text{ m}^2/\text{ha}$ basal area; sweet gum (Liquidambar styraciflua L.) accounted for an additional 28%. The alluvial soil belongs to the Hamblen series. An understory of Alnus sp., with a canopy height of about 2 m, and a ground cover of honeysuckle were present.

The oak stand, on soil of the Litz series, had a basal area of $20 \text{ m}^2/\text{ha}$, of which 77% was white oak (Quercus alba L.). Oak and hickory (Carya sp.) reproduction dominated the ground cover.

D. Distribution of Weight and Calcium in Dogwood Trees

Ten dogwood trees were collected in pine stand B and ten in yellow poplar stand A in January, 1966. These trees represented the size range of dogwood trees in the understory canopy of each stand. All branches were included with the sampled trees; dead branches contributed a negligible amount ($< 1\%$) to tree weight since dogwood trees are efficient self-pruners. Roots were obtained when the soil was moist following several days of rain; they were first loosened with a truck-mounted power winch and then excavated with hand tools. Considerable effort was expended in collecting the root systems to insure that all roots with a diameter greater than several mm were included. Soil was washed from roots with cold water. These trees were sectioned into 11 components, and weight and calcium content of each component were determined separately. To evaluate effect of tree size on weight and calcium distribution, 10 seedlings were collected in each of the two stands in November 1966. Weight and calcium content were determined individually for leaves, tops, and roots.

All branch diameters less than 1 cm were measured on the 20 large trees, and number of leaves was estimated with the equation relating number of leaves to branch diameter. Weight and calcium content of leaves were estimated by using the mean values of the September and October samples collected in 1966. Leaves on small trees were counted in early September and many of them were collected when they fell from the trees. Total weight and calcium content of these leaves were corrected for the number of leaves that had fallen prior to sampling.

Four soil samples (each a composite of 10 soil cores taken to a depth of 20 cm) were collected in both stands and analyzed for exchangeable calcium.

E. Cycling of ^{45}Ca

1. Tree inoculation

Twelve dogwood trees in pine stand A were selected to represent the range of sapling sizes in the stand. Tree weights were estimated with a regression equation (based on data from the 20 trees collected in January) which related oven-dry weight of total nonfoliar components to the product of (a) tree diameter at ground level, (b) diameter 1 m above the ground, and (c) tree height. This equation was later recalculated to include data from eight tagged trees. Amount of ^{45}Ca inoculated in each tree, from 0.67 to 2.51 millicuries (mCi), was proportional to estimated weight of the tree (1 mCi per 2500 g). Inoculum was introduced directly to the transpiration stream since this is the most efficient method of distributing radioisotopes in a tree-soil system.

Trees were tagged by a trough technique (Auerbach, Olson, and Waller 1964). Troughs were about 1 dm above the ground and had a volume of from 20 to 40 cc. Troughs were filled with water, evenly-spaced chisel cuts (5 mm wide; 5 mm deep) into the stem were made under the water surface, and the isotope was added. After the troughs had emptied, they were refilled with water three times and then removed after all the solution had entered the transpiration stream. The inoculum was about 10 ml of $^{45}\text{CaCl}_2$ in HCl which was adjusted to pH 5 with NaOH. After the troughs were removed, they were soaked overnight

in 1 N HCl from which an aliquot was taken to estimate retention of ^{45}Ca by troughs. Trees were tagged on 4 May 1966 between 1150 and 1300 hours. Soil was moist, air temperature in the stand was 26 C, and the sky was clear. Uptake of solution was rapid; all troughs were emptied once within 20 minutes.

2. Throughfall collection

Three rain gauges were placed under each tagged tree (one under each 120° crown segment) and were rerandomized several times during the experiment as recommended by Wilm (1946). Gauges were constructed of polyethylene funnels (19.9 cm diameter) inserted in 1 liter polyethylene bottles. They were leveled by mounting on pieces of plywood which were firmly fastened with spikes to the soil. Four gauges were placed under pine canopy only, three under an untagged dogwood tree, and one in a large opening about 50 m from the tagged trees. Precipitation samples from these gauges were used as controls for stable calcium under dogwoods, ^{45}Ca under tagged trees, and throughfall estimation under tagged trees, respectively.

Volume of precipitation in all gauges was measured and sampled after every continuous period of precipitation. Calcium-45 was measured in all samples, and stable calcium was determined in a composite sample of precipitation under each tree (weighted by volume in each gauge).

3. Stemflow collection

Tagged trees were stratified into four estimated weight classes, and one from each class was randomly selected for stemflow collections. After the trough used for tagging was removed, a new trough was

constructed 3 dm above the ground to intercept stemflow. These troughs were 1 cm wide around the stem and slanted so stemflow would be collected in 4 liter polyethylene bottles connected with plastic tubing to the troughs. A similar collector was placed on the control tree. Stemflow volume was measured and sampled whenever precipitation samples were collected.

4. Crown area estimation

Azimuths and distances from stem to prominent points on the crown circumference of the tagged trees were measured in July. An average of 10 such measurements were made per tree and were plotted on graph paper. Lines were drawn between points corresponding to the shape of crown edge, and the resulting area was planimetered.

5. Leaf collection

Fifty leaves from each tagged tree were collected monthly by removing two leaves from each of 25 branches. All 50 leaves were included in one sample which was oven-dried, weighed, and analyzed for ^{45}Ca and stable calcium. The same branches were used for all collections and were selected to represent the entire crown. This method was checked in September by taking an additional sample from each tree by collecting one leaf from 50 different crown positions. Mean values of the two samples were not significantly different ($P > 0.05$) for either leaf weight or ^{45}Ca content. Two large polyethylene tubs were placed under each crown to collect premature leaf fall in the event of prolonged dry periods. Although there were several dry periods during the summer, the number of leaves in the tubs ($< 5/\text{tree}/\text{month}$) did not justify collection.

6. Tree harvesting

On 4 November, six months after tree inoculation, the eight trees not used for stemflow collection were harvested, and weight, ^{45}Ca , and stable calcium were determined for each of four components (stem, branches, roots > 4 cm diameter, roots < 4 cm diameter). All leaves had fallen before trees were harvested; number of leaves on each tree was estimated by the regression equation of leaf number on branch diameter.

7. Insect damage

On each leaf sampling date 400 leaves were randomly selected from a total of 40 branches on adjacent untagged trees. Lengths and widths of these leaves were used to estimate their areas with the regression equation. A transparent grid with 1 mm^2 squares was laid on each leaf, and the area of missing portions was measured. Where a portion of leaf margin was missing, the leaf margin was drawn, and the missing area was estimated. As Bray (1961) noted, this was easy to do after handling several leaves. Weight, ^{45}Ca , and stable calcium losses from tagged leaves were estimated by using data for the distribution of these in leaves.

IV. RESULTS AND DISCUSSION

A. Leaf Data

The regression equation for leaf area (Fig. 1) was used to estimate leaf area throughout the study unless otherwise indicated. Regression equation for number of leaves on branches is shown in Fig. 2, and seasonal trend in leaf number is in Table 2. Number of leaves per branch increased from May to June and then decreased although new leaves were produced throughout the growing season. The fact that leaf fall exceeded new leaf production can be attributed to three causes. (1) Due to drought-sensitivity of the species some of the larger leaves withered and fell during periods in which there was no detectable precipitation for at least two weeks (26 May - 16 June; 16 June - 3 July; 15 July - 30 July; 31 August - 18 September). (2) Leaves heavily damaged by insects fell before undamaged leaves of the same size. On 4 August threads were tied to petioles of 20 heavily damaged and 20 undamaged leaves of about equal size on the same branches. After two weeks all healthy leaves, but only 11 damaged ones, were still on the branches. (3) The date of leaf senescence and abscission ranged from late August to late October.

B. Distribution of Weight and Calcium in Trees

Mensurational data for the 28 larger harvested trees are in Table 3, and data for the seedlings are in Table 4. Several conclusions can be made concerning the distributions of tree sizes (Table 5). (1) The 20 larger trees were significantly ($P < 0.01$) larger than the smaller

Fig. 1. Regression (forced through origin) of leaf area on leaf dimensions.
 $N = 200$; $r^2 = 0.999$ ($P < 0.01$).

Fig. 2. Relationship of branch diameter and leaf number. Data collected in September. $N = 200$; $r^2 = 0.959$ ($P < 0.01$).

Table 2. Trend in leaf numbers during 1966 growing season^a

Date	Percent of Previous Month's Leaf Number	Percent of May Leaf Number
4 May		100.0
5 June	108.4 $\pm$ 2.8 (**)	108.4 $\pm$ 2.8 (**)
5 July	99.2 $\pm$ 0.9 (NS)	107.7 $\pm$ 3.3 (*)
4 August	97.8 $\pm$ 1.0 (*)	105.4 $\pm$ 3.6 (NS)
5 September	98.0 $\pm$ 1.6 (NS)	103.0 $\pm$ 3.1 (NS)
5 October	42.8 $\pm$ 10.0 (**)	46.2 $\pm$ 11.3 (**)

^aMean $\pm$ SE; N = 12 branches. Mean number of leaves per branch on 4 May was 211 (Range: 124 to 405). Levels of significance refer to comparisons of monthly values with 100.

Table 3. Data for large dogwood trees

Tree Number ^a	Age (Years)	Diameter ^b (cm)		Height (m)	Dry Weight ^c (g)		Calcium (g)		Leaf Number ^e
		0 m	1 m		Top ^d	Root	Top ^d	Root	
1	13	3.4	2.0	2.9	841	288	7.0	1.3	2047
2	17	4.8	2.7	4.1	1758	582	13.0	2.2	4139
3	16	4.0	2.6	3.7	1087	356	9.8	1.4	1334
4	14	4.7	2.6	4.4	1871	677	14.1	2.9	3549
5	14	5.1	3.3	4.6	2378	985	17.7	3.5	5017
6	16	5.3	3.4	4.5	2610	871	20.2	3.3	4223
7	10	3.6	2.0	3.5	904	433	8.1	2.0	2713
8	13	3.7	2.5	3.4	1173	336	10.3	1.4	3189
9	16	4.2	2.6	3.9	1699	469	13.9	2.2	4118
10	12	2.5	1.6	3.0	457	123	3.6	0.5	968
11	18	4.2	2.9	4.2	1625	467	13.6	1.7	2212
12	14	3.2	1.5	2.7	461	150	3.5	0.6	887
13	9	2.1	1.1	2.4	219	81	1.9	0.3	504
14	28	5.2	3.6	4.6	2699	737	23.0	3.2	3617
15	27	4.6	3.0	4.6	1729	611	13.7	2.6	2156
16	15	3.9	2.7	3.5	1109	413	11.2	1.6	2427
17	15	4.5	2.8	3.5	1277	478	10.3	1.7	2436
18	17	4.5	2.7	3.6	1455	537	12.8	2.2	2648
19	17	4.8	3.0	4.0	1925	744	15.8	3.2	3614

Table 3, continued

Tree Number ^a	Age (Years)	Diameter ^b (cm)		Height (m)	Dry Weight ^c (g)		Calcium (g)		Leaf Number ^e
		0 m	1 m		Top ^d	Root	Top ^d	Root	
20	18	5.2	3.5	5.6	2497	723	18.6	2.8	2554
21	15	5.4	3.6	5.2	4305	883	49.3	4.9	6005
22	14	4.5	3.0	4.0	2378	470	21.9	2.9	4294
23	15	6.3	4.2	5.1	3884	994	38.7	10.0	5755
24	16	6.1	3.6	5.0	4082	1002	40.4	8.4	7352
25	15	7.1	4.5	5.2	6443	1430	57.6	11.2	7766
26	15	4.8	2.9	3.6	1963	324	15.7	2.2	2422
27	16	5.6	3.8	4.5	2639	588	27.0	5.7	3716
28	13	4.4	2.6	3.3	1757	372	14.0	2.4	2795

^aTrees 1-10 from pine stand B; 11-20 from yellow poplar stand A; 21-28 harvested tagged trees from pine stand A.

^bDiameters are at ground level and 1 meter above ground level.

^cOven-dry at 105 C.

^dWithout leaves

^eLeaf numbers are estimates of September values obtained with the regression equation in Fig. 2.

Table 4. Data for dogwood seedlings.

Tree Number ^a	Diameter at Ground Level (mm)	Height (cm)	Weight ^b (g)		Calcium (mg)		Leaf Number ^d
			Top ^c	Root	Top ^c	Root	
1	17	134	86.6	49.5	1119.8	501.4	308
2	7	42	4.7	3.2	66.8	35.1	26
3	9	71	10.4	5.0	179.4	39.0	72
4	21	145	129.6	60.6	1426.2	390.0	579
5	7	47	5.1	1.8	74.1	17.3	47
6	8	63	7.5	4.3	107.5	42.3	74
7	6	62	5.6	2.0	71.9	13.4	27
8	11	78	19.5	7.2	217.3	123.7	97
9	19	96	54.7	34.0	612.8	123.1	204
10	13	166	100.5	50.0	936.0	429.0	71
11	14	151	71.7	30.0	635.1	158.8	183
12	10	105	22.3	12.9	357.7	86.4	68
13	10	109	27.3	12.4	356.6	107.5	159
14	17	171	130.0	47.8	1520.9	395.6	400

Table 4, continued

Tree Number ^a	Diameter at Ground Level (mm)	Height (cm)	Weight ^b (g)		Calcium (mg)		Leaf Number ^d
			Top ^c	Root	Top ^c	Root	
15	8	70	10.6	4.8	167.1	51.2	71
16	4	36	2.2	0.9	36.8	16.0	22
17	6	48	5.7	4.8	94.7	53.5	31
18	8	72	12.6	7.3	235.1	79.1	30
19	7	71	10.6	4.7	156.0	39.6	75
20	7	70	10.8	6.3	187.2	57.9	86

^aTrees 1-10 from pine stand B; 11-20 from yellow poplar stand A.

^bOven-dry at 105 C.

^cWithout leaves.

^dLeaf numbers are actual counts during the first week of September.

Table 5. Size distribution of harvested experimental trees^a

Trees	N	Range (g)	Mean (g)	Standard Deviation
Small Trees				
Pine Stand	10	7 to 190	64	71
Yellow Poplar Stand	10	3 to 178	44	55
Both Stands	20	3 to 190	54	63
Large Trees				
Pine Stand	10	580 to 3481	1990	958
Yellow Poplar Stand	10	300 to 3436	1994	1014
Both Stands	20	300 to 3481	1992	960
Tagged Trees	8	2129 to 7873	4189	1943
All Large Trees	28	291 to 7873	2619	1628

^aValues are oven-dry weights of the tops (without leaves) plus roots.

trees; this permits valid comparisons of effect of tree size on their distribution of weight and calcium. (2) There were no significant differences ($P > 0.05$) in tree size between sites for either size class; this permits valid comparison of effect of site on calcium content of these trees.

1. Effect of size class

It can be concluded from the distribution of calcium in trees of each size class on both sites (Table 6) that there are no significant differences ($P > 0.05$) between sites in the distribution of calcium in either size class, but that attributes of seedlings are all significantly greater ($P < 0.01$) than those of larger trees. These conclusions support the warning by Gessel (1962) and Tamm (1964) that care must be exercised in extrapolating data from seedlings to larger trees since physiology of the tree may change with age.

2. Effect of calcium content of soil

Exchangeable calcium (meq/100 g air-dry soil; $N = 4$) in pine stand was 1.1 ± 0.1 , and in the yellow poplar stand it was 3.3 ± 0.2 . These are significantly different ($P < 0.01$), but calcium concentrations of dogwood trees were not significantly different ($P > 0.05$) between sites. This supports the contention that dogwood trees accumulate calcium in quantities independent of soil calcium over a wide range of concentrations.

3. Effects of Bark and Leaves

Weight and calcium distributions in dogwood trees (Table 7) were not the same due to different concentrations of calcium in various tree

Table 6. Weight and calcium content of dogwood trees (without leaves) of different size classes and from different sites ^a

	Large Trees			Small Trees		
	Pine Stand (N=10)	Poplar Stand (N=10)	t	Pine Stand (N=10)	Poplar Stand (N=10)	t
Root/Top Ratio						
Weight	0.35 ± 0.02	0.33 ± 0.04	0.45 (NS)	0.51 ± 0.04	0.43 ± 0.04	1.41 (NS)
Calcium	0.18 ± 0.01	0.16 ± 0.01	1.41 (NS)	0.36 ± 0.05	0.28 ± 0.03	1.37 (NS)
Percent Calcium						
Top	0.80 ± 0.02	0.83 ± 0.02	1.06 (NS)	1.13 ± 0.07	1.23 ± 0.09	0.88 (NS)
Root	0.40 ± 0.01	0.40 ± 0.03	0.00 (NS)	0.79 ± 0.11	0.79 ± 0.11	0.00 (NS)
Entire Tree	0.70 ± 0.02	0.72 ± 0.02	0.71 (NS)	1.02 ± 0.06	1.10 ± 0.08	0.80 (NS)

	Large Trees (N=20)	Small Trees (N=20)	t
Root/Top Ratio			
Weight	0.34 ± 0.01	0.48 ± 0.03	4.43 (**)
Calcium	0.17 ± 0.01	0.32 ± 0.03	4.74 (**)
Percent Calcium			
Top	0.81 ± 0.01	1.18 ± 0.06	6.08 (**)
Root	0.40 ± 0.01	0.79 ± 0.08	4.84 (**)
Entire Tree	0.71 ± 0.01	1.05 ± 0.05	6.67 (**)

^a Mean ± SE.

Table 7. Weight and calcium distribution in nonfoliar tree tissues^a

Component ^b	% Calcium	Percent of Total Tree		Percent of Top or Root	
		Weight	Calcium	Weight	Calcium
Top					
> 2 cm	0.80 ± 0.02	38.4 ± 2.4	42.4 ± 2.6	51.4 ± 3.0	49.4 ± 2.9
1 to 2 cm	0.57 ± 0.01	11.0 ± 1.7	8.8 ± 1.4	14.7 ± 2.3	10.2 ± 1.6
0.5 to 1 cm	0.57 ± 0.02	9.0 ± 0.6	7.2 ± 0.6	12.0 ± 0.8	8.4 ± 0.6
< 0.5 cm	1.21 ± 0.02	16.4 ± 0.8	27.3 ± 1.4	21.9 ± 1.1	32.0 ± 1.7
Root					
> 2 cm	0.33 ± 0.01	14.2 ± 0.5	6.6 ± 0.3	56.8 ± 1.8	47.2 ± 2.2
1 to 2 cm	0.47 ± 0.01	4.7 ± 0.5	3.1 ± 0.3	18.2 ± 1.6	21.5 ± 2.0
0.5 to 1 cm	0.50 ± 0.01	4.6 ± 0.4	3.2 ± 0.3	18.0 ± 1.4	21.9 ± 1.4
< 0.5 cm	0.55 ± 0.01	1.8 ± 0.3	1.4 ± 0.2	7.0 ± 1.1	9.4 ± 1.4

^aMean = SE; N = 20 except for root > 2 cm (N = 19).

^bSize classes refer to diameter ranges.

components. Much of this variation among components was attributable to bark (Table 8), which normally has a greater calcium concentration than wood (Ebermayer 1876; Rennie 1955; Stenlid 1958; Young and Guinn 1966). A greater proportion of tree calcium than of weight is in leaves (Table 9).

C. Cycling of ^{45}Ca

Essentially all of the ^{45}Ca entered the trees (only $0.1\% \pm 0.02$ of inoculum was retained by the trough).

1. Leaves

There were significant quantities ($0.214 \pm 0.018 \mu\text{Ci/leaf}$) of ^{45}Ca in all leaf samples collected on 5 June, one month after inoculation. Total amount of ^{45}Ca in tree foliage on each sampling date was determined as follows. Number of leaves on the trees was estimated with the regression equation in Fig. 2; monthly correction factors for leaf fall and new leaf production (Table 2) were applied to estimated leaf number (a small correction was also made for leaves removed during previous samplings). These data and the amounts of ^{45}Ca in leaves of individual trees were then used to calculate total amount of radiocalcium in foliage. Maximum amount was found on 5 June ($73\% \pm 6$ of total inoculum). Amount of ^{45}Ca in leaves (percentage of total or absolute amount) steadily decreased during the growing season due to radiological decay, foliar leaching, and leaf fall.

Estimated number of leaves that fell each month and their ^{45}Ca content were summed for the season (with appropriate radiological decay

Table 8. Bark contribution to weight and calcium content of stem and branches^a

Diameter Class	% Calcium ^b		Bark (% of wood + bark) ^b	
	Wood	Bark	Weight	Calcium
> 2 cm	0.12 ± 0.01	3.95 ± 0.10	17.8 ± 0.4	87.7 ± 0.5
1 to 2 cm	0.23 ± 0.01	2.50 ± 0.04	15.1 ± 0.4	66.1 ± 0.7
0.5 to 1 cm	0.22 ± 0.01	1.90 ± 0.07	21.2 ± 0.6	69.6 ± 1.4

^aMean ± SE; N = 19.

^bBark has a significantly higher concentration of calcium than does wood and a significantly greater percent of the total calcium than of weight (0.01 level for all 6 comparisons).

Table 9. Contribution of leaves to dogwood tree (top plus root)
weight and calcium content^a

	Tree Size Class		t
	Large	Small	
Percent of the Tree Weight in Leaves	16.6 ± 0.8	32.8 ± 2.1	7.07 (**)
Percent of the Tree Calcium in leaves	42.9 ± 1.5	51.6 ± 2.1	3.34 (**)

^aMean ± SE; N = 20.

corrections) to estimate amount of ^{45}Ca that was added to the forest floor in leaf litter. This amounted to $64.0\% \pm 1.4$ of total inoculum.

On 23 September ten small leaves were collected from tagged trees to determine if newly-formed leaves were receiving ^{45}Ca . Mean area of these leaves was $6.5 \pm 0.7 \text{ cm}^2$ (one surface). These leaves were treated as one sample; mean ^{45}Ca content was 78,400 dpm/leaf. This suggested that radiocalcium was still available from the transpiration stream since calcium is not transferred from older to younger leaves (Nason and McElroy 1963). On 28 September three samples of solution were extracted from the transpiration stream of twigs on tagged trees with a vacuum pump (1.83 kg/cm^2). All samples contained ^{45}Ca (70, 380 and 770 dpm/ml), indicating that ^{45}Ca was still present in the transpiration stream of the trees nearly 5 months after inoculation.

Distribution of ^{45}Ca in leaves as shown by autoradiograms (e.g., Fig. 3; leaf collected 15 July and exposed to Kodak No-Screen Medical X-Ray Film for 48 hr.) is characterized by apparent concentration of radiocalcium in petiole, midrib, and lateral veins. This has led some authors to conclude that leaf calcium is located primarily in veins. This apparent concentration of calcium may only be a result of veins being in closer contact with the film, thus allowing a greater percentage of the weak beta particles (per unit area) to affect the emulsion. To determine if this was the cause, leaves were permitted to absorb ^{47}Ca , a gamma emitter, through their petioles; autoradiograms of these leaves displayed the same pattern of radioisotope distribution as those containing ^{45}Ca . If their patterns were determined by proximity of veins

Fig. 3. Autoradiogram (positive print) of dogwood leaf containing ^{45}Ca . Enlarged 2.15 diameters. Holes caused by insects.

to emulsion, the two autoradiograms should not be similar.

Five samples of 10 leaves each were collected in August from tagged trees, and the leaves were sectioned into two components: (1) petiole, midrib, and lateral veins (hereafter referred to as veins), and (2) intervein area. All leaves were planimetered, and vein area was estimated with a dot-grid (mean of four counts per leaf). Separate components were weighed and analyzed for ^{45}Ca and stable calcium (Table 10). Veins accounted for only 7.6% of leaf area but 24.6% of the weight and 21.5% of the calcium in leaves. Although most of the weight and calcium are in the intervein area, there is a greater density of both in veins; this results in the characteristic appearance of autoradiograms. Fraser (1958) found that veins of leaves from yellow birch trees tagged with ^{45}Ca had a higher counting rate (per unit weight) than did intervein area.

Regression equations based on 20 randomly selected leaves (area from 3.73 to 75.90 cm^2 ; one surface) show that these relationships change with leaf size.

$$\text{Vein area (cm}^2\text{)} = 0.6308 + 0.0739 \text{ Leaf area (cm}^2\text{)}$$

$$F = 145.3 (**); r = 0.943; N = 20$$

$$\text{Vein area (\% of leaf area)} = 15.693 - 0.1203 \text{ Leaf area (cm}^2\text{)}$$

$$F = 69.6 (**); r = -0.891; N = 20.$$

As leaf area increases, area occupied by veins also increases; however, vein area as percentage of leaf area decreases as size of leaf increases.

Apparent ^{45}Ca distribution in leaves as indicated by autoradiograms

Table 10. Distribution of area, weight, and calcium in dogwood leaves^a

	Mean	SE	t
Veins, % of Leaf Area	7.58	0.01	
Veins, % of Leaf Weight	24.63	0.36	5.85 (**)
Veins, % of Leaf Calcium	21.46	0.40	0.84 (NS)
Veins, % of Leaf ⁴⁵ Ca	20.23	1.41	
Veins, % Calcium	2.41	0.06	5.29 (**)
Intervein Area, % Calcium	2.88	0.07	
Entire Leaf, % Calcium	2.76	0.06	
Veins, mg/cm ²	12.49	0.47	18.88 (**)
Intervein Area, mg/cm ²	3.14	0.15	
Entire Leaf, mg/cm ²	3.85	0.17	
Veins, mg Ca/cm ²	0.30	0.01	33.20 (**)
Intervein Area, mg Ca/cm ²	0.09	0.01	
Entire Leaf, mg Ca/cm ²	0.11	0.01	

^aN = 5 with each a mean of 10 leaves.

can be altered (from no apparent radioactivity to uniform distribution of radioisotope throughout) by varying film exposure time and developing procedures.

2. Foliar leaching

Arrangement of rain gauges, stemflow collector, and litter baskets under a tagged tree is shown in Fig. 4. Precipitation samples were collected 15 times during the season. All 36 throughfall samples under the tagged trees contained ^{45}Ca after each period of precipitation. Total amount of ^{45}Ca removed from crowns was calculated from sample concentrations and crown areas. These areas (m^2 of ground surface) for the 12 tagged trees (1 to 12, respectively) were 7.0, 6.5, 7.4, 4.2, 9.0, 6.8, 9.2, 4.9, 2.8, 6.8, 5.5, and 9.9.

It is not possible to calculate the percentage of ^{45}Ca in crowns that was removed by precipitation since foliage samples were not collected immediately before each period of precipitation. A mean of 8.2% of maximum ^{45}Ca levels in foliage (June) was removed during the entire growing season in foliar leachates; this was $6.0\% \pm 0.9$ of the total inoculum.

Removal of calcium from leaves by dew was demonstrated by collecting dew with absorbent paper from the upper surfaces of 20 leaves on tagged trees in the early morning of 3 October. Total ^{45}Ca removed was 3600 dpm (180 dpm/leaf; 5 dpm/ cm^2 of leaf); this was 0.2% of total ^{45}Ca in those leaves.

Fig. 4. View under a tagged tree. Meter stick in foreground.

3. Stemflow

All stemflow samples from tagged trees contained ^{45}Ca but at greatly lower concentrations than throughfall. Total amount of precipitation which passed through crowns (throughfall plus stemflow) during the entire growing season was calculated for the four trees with stemflow collectors. Although volume of stemflow was appreciable (normally between 100 and 3500 ml depending upon the tree and amount of precipitation), it accounted for only $0.20\% \pm 0.01$ of the total volume and $0.17\% \pm 0.02$ of the total ^{45}Ca ($N = 60$; $P > 0.05$).

Stemflow was collected five times during the winter after all leaves had fallen. All 20 samples had statistically significant quantities of ^{45}Ca although at much lower concentrations (even after allowance for physical decay) than when leaves were on the trees.

4. Calcium- 45 transfer to ground vegetation

Three species of ground vegetation were sampled on 15 October under crowns of tagged trees and were analyzed for ^{45}Ca . Each sample consisted of the entire aboveground portion of three plants of the same species; individuals were collected under different trees. Results (mean dpm/g oven-dry; $N = 3$) for the three species were: trumpet-creeper 3500, greenbrier (Smilax sp.) 14,200, and honeysuckle 82,100. Low concentration of radiocalcium in trumpet-creeper may be due to early defoliation of these plants whereas the other plants still had leaves. Pubescence on honeysuckle leaves probably enabled them to more efficiently trap nutrients than greenbrier.

Calcium- 45 in these plants was probably from foliar leachate that was absorbed by their leaves, although some of it may have entered by roots in the litter. Transfer of calcium by this method is of only minor importance in this experiment due to the paucity of ground vegetation.

5. Calcium- 45 in Litter and Soil

On 12 October, during leaf abscission, two litter and soil samples were collected under each tagged tree and were analyzed for ^{45}Ca . Dogwood leaves were excluded from litter samples so that the primary source of ^{45}Ca was foliar leachate. Soil samples were taken to a depth of 6 cm (soil at greater depths did not contain ^{45}Ca). Of total ^{45}Ca found in all 24 profile samples, $87.8\% \pm 1.4$ was in litter. Although more of this ^{45}Ca will move into soil with additional leaching by precipitation, a large percentage of the radiocalcium in the tree-soil system will be in litter due to the contribution by dogwood leaves. Riekerk and Gessel (1965) reported that ^{45}Ca moved at a slower rate through the forest floor of Douglas fir (Pseudotsuga menziesii) stand than did ^{32}P or ^{86}Rb .

6. Leaching of ^{45}Ca from Senescent Leaves

Five samples of five green (undamaged) leaves each and similar samples of yellow (senescent) leaves were collected on 1 October from tagged trees. Mean area of the 25 green leaves ($35.8 \pm 2.2 \text{ cm}^2$) was not significantly different ($P > 0.05$) than that of yellow ones (37.7 ± 2.2). The ten separate samples were immersed in 200 ml of precipitation for 20 hours, after which an aliquot was taken for counting; residual ^{45}Ca

in the leaves was also determined. Percentage of ^{45}Ca removed by this leaching was significantly greater ($P < 0.01$) for yellow leaves (40.6 ± 2.5) than for green ones (18.6 ± 3.4).

These losses may be higher than would be obtained with intact leaves; Stenlid (1958) stated that in many cases material lost from excised leaves is greater than that lost from normal plants. Greater loss from senescent leaves was probably due to increased permeability to water caused by breakdown of cuticle. Tukey and Morgan (1963) found that slightly damaged squash (Curcubita pepo) leaves lost more calcium by leaching than did undamaged leaves. They lightly brushed both leaf surfaces to break epidermal hairs and soaked damaged and normal leaves in distilled water for 48 hours. They found that 65% of ^{45}Ca in brushed leaves was leached, but that only 22% was lost from normal ones.

It was impossible to ascertain if ^{45}Ca loss from foliage of tagged trees increased as leaves became senescent since precipitation intensities before and during senescence were not comparable.

7. Insect damage

Leaf damage due to insects (Table 11) was almost entirely in intervein areas. Weight and calcium losses were estimated with data on their distribution in leaves (Table 10); similar calculations were used to estimate that $3.0\% \pm 0.1$ of total inoculum was lost from leaves due to insect damage during the entire growing season. These estimates are subject to error since the size of holes in leaves may increase during the season, resulting in an overestimate of area removed when sampled at later dates. In addition, these estimates are only for damage due to

Table 11. Insect damage to leaves^a

Date (1966)	Leaves with Holes (%)	Percent Lost ^b		
		Area	Weight	Calcium
4 May	18	0.06	0.04	0.04
5 June	39	1.0	0.7	0.8
5 July	46	1.1	0.8	0.9
4 August	69	1.5	1.1	1.2
5 September	74	1.5	1.1	1.2
5 October	92	1.8	1.3	1.4

^aN = 400 for each sampling date.

^bLosses during the growing season to the date of sampling.

foliage-feeding insects that leave visible evidence of their activity. The autoradiogram (Fig. 3) shows typical insect damage and some evidence that ^{45}Ca may have been used for cell repair on the periphery of the smaller hole. A similar observation was made by Fraser (1958).

8. Calcium- 45 in harvested trees

Radiocalcium was distributed almost entirely in the aboveground portions of tagged trees six months after inoculation (Table 12). It is not clear how ^{45}Ca entered roots, but it probably entered from the stem since there was more found in larger roots than in smaller ones and because so little ^{45}Ca was available in litter and soil for root absorption. This does not refute the concept of polarity for calcium movement in plants since radiocalcium was placed in trees so close to the roots that it could have diffused downward in bark (as opposed to translocation in vessels). All data in Table 12 include both xylem and bark.

Xylem and bark of 10 stem segments were analyzed separately for ^{45}Ca ; segments were from various heights on harvested trees. Xylem accounted for $85.8\% \pm 0.6$ of stem weight and $93.4\% \pm 0.9$ of ^{45}Ca in the stem. Concentration of radiocalcium ($^{45}\text{Ca/g}$ oven-dry) in xylem was 3.1 ± 0.6 times that in bark. Percentage of ^{45}Ca in xylem was significantly greater ($P < 0.01$) than percentage of weight in xylem, and concentration of ^{45}Ca in xylem was significantly greater ($P < 0.01$) than that in bark.

The nonuniform distribution of radiocalcium in the trees serves as a reminder that radioisotopes cannot be used to estimate distribution of materials in a system unless the radioisotope and the material are known

Table 12. Distribution of weight, calcium, and ^{45}Ca in nonfoliar components of trees
six months after inoculation^a

Component	Percent of Total Found			$\mu\text{Ci/g}$ Oven-dry Weight	$\mu\text{Ci/g}$ Calcium
	Weight	Calcium	^{45}Ca		
Stem	46.0 $\pm$ 1.7	39.0 $\pm$ 2.5	40.0 $\pm$ 2.6	0.043 $\pm$ 0.006	5.45 $\pm$ 0.58
Branches	36.3 $\pm$ 1.6	46.2 $\pm$ 3.7	56.7 $\pm$ 2.7	0.076 $\pm$ 0.009	6.65 $\pm$ 0.78
Roots > 4 cm	5.7 $\pm$ 0.4	4.2 $\pm$ 0.5	2.7 $\pm$ 0.7	0.020 $\pm$ 0.004	2.92 $\pm$ 0.56
Roots < 4 cm	12.0 $\pm$ 0.7	10.6 $\pm$ 1.2	0.6 $\pm$ 0.1	0.002 $\pm$ 0.001	0.31 $\pm$ 0.07
Top	82.3 $\pm$ 0.7	85.2 $\pm$ 1.3	96.7 $\pm$ 0.8	0.057 $\pm$ 0.007	6.02 $\pm$ 0.64
Roots	17.7 $\pm$ 0.7	14.8 $\pm$ 1.3	3.3 $\pm$ 0.8	0.009 $\pm$ 0.002	1.11 $\pm$ 0.20
Entire Tree				0.049 $\pm$ 0.006	5.28 $\pm$ 0.53

^aMean $\pm$ SE; N = 8.

to be in equilibrium.

A stem segment (xylem and bark) within 2 cm above and below the chisel cuts used for inoculation were analyzed for each harvested tagged tree to determine ^{45}Ca retention near the site of inoculation. Concentration of radiocalcium (dpm/g oven-dry) in these segments was 5.8 times that in the rest of the stem. However, the ^{45}Ca retained there was only $0.8\% \pm 0.1$ of total inoculum.

9. Calcium- 45 in dogwood club galls

A midge (*Mycodiplosis alternata* Felt) causes characteristic galls on smaller branches of flowering dogwood trees. All galls on harvested trees (30 to 120 per tree) were removed, and samples were analyzed separately for ^{45}Ca and stable calcium to determine if they affected the distribution of calcium in branches. An additional 10 samples of 25 galls each were analyzed, and twigs (< 4 mm diameter) 3 cm on either side of the galls were analyzed separately. Calcium and ^{45}Ca concentrations in galls were significantly greater than average concentrations for all branches (Table 13). These differences, however, were due to dilution of total-branch concentrations by larger branches which had lower calcium and ^{45}Ca values. Twigs which supported galls actually had significantly greater calcium and ^{45}Ca concentrations than the galls (Table 13).

Midge eggs are deposited in dogwood twigs in early summer; larvae leave the galls in late summer and over-winter in soil (Felt and Bromley 1939). The ^{45}Ca content of galls would probably have been greater if trees had been tagged several weeks later, when galls were being formed,

Table 13. Calcium and ^{45}Ca in dogwood club galls

	Mean	SE	t
<u>Total Branches</u> ^a			
% Calcium			
Galls	1.49	0.08	3.16 (**)
Branches	1.16	0.07	
μCi/g Oven-dry Weight			
Galls	0.127	0.016	2.78 (*)
Branches	0.076	0.009	
μCi/g Calcium			
Galls	8.52	1.10	1.57 (NS)
Branches	6.38	0.81	
% of the Branches in the Galls			
Weight	1.28	0.27	0.84 (NS)
Calcium	1.67	0.38	
<u>Twigs Only</u> ^b			
% Calcium			
Galls	1.49	0.03	3.45 (**)
Twigs	1.70	0.04	
Twigs/Galls			
dpm/g Oven-dry Weight	1.26	0.05	5.20 (**)
dpm/mg Calcium	1.10	0.04	2.50 (*)

^a_N = 8.^b_N = 10.

since 73% of the ^{45}Ca was already in leaves one month after inoculation. All galls had exit holes when they were collected; however, it was not possible to determine if the galls had been formed in 1966 or in previous years.

10. Elution of ^{45}Ca from wood

Stem segments were collected at various heights from tagged trees; bark was removed, and xylem was ground in a Wiley Mill to pass a 0.5-mm mesh screen. Wood was thoroughly mixed, and a 10-g (air-dry) portion was placed in a glass column with sintered glass filter at one end. The column of wood was 2 cm in diameter and 6 cm high. Calcium-45 was eluted with ten 25-ml fractions of distilled water followed by ten 25-ml fractions of 1 N HCl (Fig. 5). The pH of water fractions was 5.3 and that of HCl fractions was 0.5. Only $11.6\% \pm 1.0$ ($N = 4$) of total ^{45}Ca in wood was water soluble; elutions with water followed by HCl removed $63.6\% \pm 2.5$ ($N = 4$).

Brown (1964) eluted ^{137}Cs from small branches of tagged yellow poplar trees. He found that 83 to 89% of the ^{137}Cs was removed by water and that 1 N HCl eluted most of the remaining radiocesium. This is an interesting comparison of the solubilities of an alkaline earth and an alkali metal in trees.

11. Radiation dose received by apical meristems

Radiological dose received by tissues of nonuniform configuration and containing varying amounts of radioisotope during the course of an experiment can only be approximated. Taylor (1966) predicted from

Fig. 5. Extraction of ^{45}Ca from wood six months after inoculation. Points are means of 4 replications; 2 SE too small to be shown at most points.

interphase chromosome volume that flowering dogwood meristems were most sensitive to radiation in June, the month when they probably contained the greatest amount of ^{45}Ca . Concentration of radiocalcium in apical meristems of the 12 tagged trees in early June was $0.20 \pm 0.04 \mu\text{Ci/g}$.

A dose of 74 ± 15 rads during the entire experiment to these tissues was estimated with equation 92a in Loevinger, Holt, and Hine (1956), which estimates dose received by tissue from a decaying radioisotope; correction was made for beta particle energy not absorbed by tissue (Parmley, Jenson, and Mays 1962). This estimate is based on three assumptions: (1) there was no import or export of ^{45}Ca from meristems after the date they were assayed for radiocalcium; (2) radioisotope was uniformly distributed in the tissue; and (3) the apical meristems were cylinders. None of these assumptions are fully met since: (1) there was probably some change in ^{45}Ca concentration (other than that due to physical decay); (2) isotope was not uniformly distributed (revealed by autoradiograms); and (3) meristems are not perfect cylinders. With these qualifications, the estimated decreasing chronic dose over the experimental period (mean of less than 1 rad/day) is about two orders of magnitude less than that required to cause slight growth inhibition in a species with the seasonal interphase chromosome volume of flowering dogwood (Sparrow 1964).

12. Summary of ^{45}Ca cycling

Estimated amount of ^{45}Ca accounted for when the experiment ended was $106\% \pm 5$ of inoculum remaining after correction for radiological decay. This is well within limits of sampling error for a weak beta

emitter in a tree-soil system for six months. Distribution of radiocalcium in the tree-soil system is shown in Table 14. Amounts of radiocalcium transferred between components (Fig. 6) were estimated by applying sample data to known pathways of calcium transfer between components.

The large percentage of total inoculum lost from the 12 tagged trees during the first growing season (73%: litter $64.0\% \pm 1.4$; foliar leachate $6.0\% \pm 0.9$; insect damage 3.0%) was due to rapid transport of ^{45}Ca to leaves within one month after inoculation ($73\% \pm 6$ of total inoculum). These losses are much greater than those of cesium, an alkali metal, from trees because cesium moves basipetally as well as acropetally after inoculation and since a large percentage of foliar cesium returns to woody tissue before leaf fall. Witherspoon (1964) found that only 40% of ^{134}Cs inoculated in white oak trees in April reached leaves by June; Waller and Olson (1967) reported that this value was 27% for ^{137}Cs inoculated in yellow poplar trees in May. Waller and Olson pointed out that alkaline earths should be transferred more rapidly than alkali metals to the forest floor (via leaf fall and foliar leaching) but that alkali metals would be expected to make a greater contribution to soil directly through roots.

D. Seasonal Trend in Leaf Weight and Calcium Content

Weight and calcium content of leaves generally increased throughout the growing season (Table 15), with the greatest increase in both occurring between the May and June sampling dates. Because percentage

Table 14. Radiocalcium in tree-soil system six months
after inoculation

	% of Inoculum Found ^a
Remaining in Tree	
Stem	10.8 ± 1.1
Branches	15.3 ± 1.5
Roots > 4 cm	0.7 ± 0.2
Roots < 4 cm	0.2 ± 0.03
Transferred to Litter and Soil	
Leaf Fall	64.0 ± 1.4
Foliar Leachate	6.0 ± 0.9
Stem Flow	0.01 ± 0.01
Lost (?) from the Tree-Soil System ^b	
Insect Damage	3.0 ± 0.1

^aMean ± SE; N = 8.

^bSome of this amount was probably contributed to litter under the trees.

Fig. 6. Diagram of ⁴⁵Ca movement in stem-inoculated dogwood trees. Numbers not in parentheses represent maximum percentage of inoculum in the component during the growing season. Numbers in parentheses are percentages of inoculum found after leaf abscission.

Table 15. Trends in leaf weight and calcium content during the growing season^a

	Oven-dry Weight (mg)	Calcium (mg)	Percent Calcium	⁴⁵ Ca (μ Ci)
4 May	35.48 $\pm$ 3.27 (**)	1.06 $\pm$ 0.09 (**)	2.99 $\pm$ 0.04 (*)	-
5 June	120.08 $\pm$ 5.51	2.91 $\pm$ 0.12	2.42 $\pm$ 0.06 (*)	0.214 $\pm$ 0.018 (**)
5 July	117.22 $\pm$ 4.84	3.21 $\pm$ 0.14	2.74 $\pm$ 0.08 (*)	0.143 $\pm$ 0.005 (**)
4 August	116.53 $\pm$ 4.40	3.43 $\pm$ 0.13 (*)	2.94 $\pm$ 0.07	0.127 $\pm$ 0.008 (**)
5 September	137.47 $\pm$ 4.57	3.89 $\pm$ 0.13	2.83 $\pm$ 0.06	0.112 $\pm$ 0.007
5 October	138.72 $\pm$ 5.78	3.83 $\pm$ 0.17	2.76 $\pm$ 0.08	0.107 $\pm$ 0.006

^a Individual leaf value $\pm$ SE; N = 12, each a mean of 50 leaves. Significant changes in monthly values are indicated.

increase in weight between May and June greatly exceeded that of calcium, percentage calcium in leaves decreased significantly. Percentage calcium increase during the next two months was greater than percentage weight increase so percentage calcium significantly increased. These trends are shown in Fig. 7. Seasonal values for foliage of the eight harvested tagged trees (Table 16) were calculated as explained for ^{45}Ca burden in leaves.

Percentage calcium in leaves at time of abscission (mean of September and October, 1966, values) was 2.8 ± 0.07 . Ash content of leaves collected in October, 1965, (four samples with 20 leaves in each) was $8.1\% \pm 0.4$ of oven-dry weight; ash was $41.7\% \pm 1.4$ calcium. It is not possible to determine if high calcium content of leaves resulted from luxury consumption since leaves of different sizes and ages were included in all samples.

E. Difficulties in Leaf Sampling

As previously mentioned, flowering dogwood trees produce new leaves throughout the growing season. This causes difficulty in obtaining adequate samples due to the range in leaf size at any one time during the growing season (Fig. 8). Ratio of area of largest to smallest leaf in the monthly sample of 400 leaves increased from May (79.2) to June (384.6) and then decreased to 45.7 in October. This decrease is due to reduction in rate of new leaf production at the end of the season and to falling of larger leaves before smaller ones. Monthly coefficients of variation of leaf area were all in the range of 50 to 65%.

Fig. 7. Leaf weight and calcium content during 1966 growing season. Mean individual leaf value ± 2 SE; N = 12, with each a mean of 50 leaves.

Table 16. Total foliage data during 1966 growing season

	Large Tree Number							
	21	22	23	24	25	26	27	28
<u>Number of Leaves</u> ^a								
May	5885	4205	5640	7205	7611	2374	3642	2739
June	6335	4530	6072	7756	8193	2555	3920	2949
July	6281	4492	6020	7690	8123	2533	3887	2924
August	6143	4393	5887	7521	7945	2473	3801	2859
September	6005	4294	5755	7352	7766	2422	3716	2795
October	1265	904	1212	1548	1636	510	783	589
<u>Calcium in Leaves (g)</u> ^b								
May	6.24	4.46	5.98	7.64	8.07	2.52	3.86	2.90
June	16.60	13.18	21.50	21.25	24.25	7.90	10.04	6.25
July	17.21	15.09	20.59	21.53	29.32	10.13	11.00	7.72
August	13.06	14.80	22.90	27.15	31.94	10.08	12.12	7.72
September	22.22	17.48	23.25	29.48	34.95	10.34	13.27	8.55
October	4.80	4.06	4.62	5.99	6.45	1.94	3.72	1.66
<u>Weight of Leaves (g)</u> ^b								
May	208.8	149.3	200.1	255.6	270.0	81.2	129.2	97.2
June	762.7	515.5	890.2	901.2	978.2	321.4	353.6	278.4
July	708.5	581.3	830.8	785.9	1088.5	330.3	412.0	257.3
August	673.3	452.5	783.0	940.1	1112.3	328.6	380.0	284.2

Table 16, continued

	Large Tree Number							
	21	22	23	24	25	26	27	28
September	819.1	561.7	851.7	1085.2	1248.8	356.5	442.2	346.0
October	189.0	139.2	173.6	236.2	229.7	62.6	130.8	70.3
<u>Area of Leaves (one side in m²)^c</u>								
May	7.87	5.63	7.55	9.64	10.18	3.18	4.87	3.66
June	19.08	13.64	18.29	23.36	24.68	7.70	11.81	8.88
July	24.46	17.50	23.45	29.95	31.64	9.87	15.14	11.39
August	17.70	12.66	16.96	21.67	22.89	7.14	10.95	8.24
September	22.75	16.27	21.80	27.85	29.42	9.18	14.08	10.59
October	4.04	2.89	3.87	4.94	5.22	1.63	2.50	1.88

^a Number of leaves estimated with equation in Fig. 2 and the monthly correction factors in Table 2.

^b Weight and calcium values of leaves from the individual trees each month were used to estimate total foliage values.

^c The mean leaf area estimated with equation in Fig. 1 based on a sample of 400 leaves each month was used to calculate the total foliage area.

Fig. 8. Leaf area distribution during 1966 growing season. Leaf expansion began in late April. Mean $\pm$ SE; N = 400 leaves each month.

To further demonstrate variability in leaf characteristics, the three smallest and three largest leaves were collected from three branches on tagged trees in late August. Largest leaves had significantly greater area, weight, and calcium content, but smallest leaves had significantly higher percentage calcium (Table 17). Lack of a significant difference between ^{45}Ca contents was due to extreme variation among the largest leaves.

Calcium- 45 content of leaves of equal size was variable among branches. Coefficient of variation for dpm/leaf of 10 leaves of the same size on 10 different branches of a tagged tree 20 days after inoculation was 94%. This variability will be discussed in the section concerning the transpiration stream in dogwood trees.

F. Calcium in Throughfall Under Trees

Stable calcium in throughfall under tagged dogwood trees was analyzed after each precipitation period (Table 18). Fourteen of the 15 mean concentrations (mg Ca/m^2 under crowns) of calcium were significantly greater ($P < 0.01$) under loblolly pine and dogwood than under loblolly pine without dogwood. Calcium in samples ranged from about 1 to about 5 ppm.

As in the case of ^{45}Ca in foliar leachate samples, it is not possible to calculate percentage of calcium in the foliage that was removed by precipitation. However, the total amount removed during the entire season by foliar leaching expressed as a percentage of maximum amount in foliage during the season can serve as an indication of

Table 17. Effect of leaf size on several leaf attributes^a

Attribute	Smallest Leaves	Largest Leaves	t
Area (cm ²)	4.68 ± 1.41	71.23 ± 8.38	7.84 (**)
Weight (mg)	25.57 ± 7.28	298.87 ± 34.92	7.66 (**)
Calcium (mg)	0.81 ± 0.26	7.53 ± 1.05	6.20 (*)
Calcium (%)	3.09 ± 0.12	2.42 ± 0.15	-3.48 (*)
⁴⁵ Ca (10 ⁴ dpm)	6.04 ± 1.71	124.89 ± 53.89	2.20 (NS)

^aMean ± SE; N = 3 with 3 leaves in each sample.

Table 18. Precipitation throughfall and calcium in foliar leachates

Date (1966)	Precipitation in Open (cm)	Throughfall (% of Open) ^a N=36	Calcium Leached From Pine Alone (mg/m ²)	Calcium Leached From Pine + Dogwood (mg/m ²) ^a N=12
13 May	2.0	68.5 ± 2.1	24.2	37.0 ± 1.1
16 May	1.7	62.2 ± 2.8	7.5	12.6 ± 0.6
21 May	4.1	77.8 ± 1.7	26.1	24.7 ± 1.4
26 May	1.1	69.2 ± 2.5	27.1	38.2 ± 1.3
16 June	4.6	59.0 ± 1.6	48.0	68.0 ± 3.6
3 July	3.4	56.9 ± 2.4	52.1	68.0 ± 2.7
6 July	3.0	64.4 ± 2.6	21.5	26.0 ± 2.1
15 July	2.2	57.8 ± 1.9	31.2	46.3 ± 2.5
30 July	4.9	60.4 ± 3.9	40.9	65.3 ± 4.1
6 August	5.8	72.5 ± 2.8	27.9	38.7 ± 1.9
11 August	8.8	79.1 ± 2.7	30.6	44.0 ± 4.8
19 August	3.6	60.1 ± 2.5	21.1	37.1 ± 2.3
31 August	3.4	56.2 ± 2.5	77.5	89.8 ± 4.2
18 September	9.4	68.0 ± 3.3	98.9	157.3 ± 7.5
1 October	3.9	64.4 ± 2.4	29.6	73.2 ± 6.3

^a Mean ± SE.

importance of foliar leaching. In this study $9.8\% \pm 1.3$ of the maximum amount of calcium in leaves (September value) was removed by precipitation. This is comparable with removal of maximum leaf ^{45}Ca by foliar leaching (8.2%).

Total amount of calcium removed from foliage by precipitation during the growing season was 5.64 kg/ha under pine canopy alone and 8.26 kg/ha when the precipitation also passed through dogwood crowns. Amount of calcium in leachate reaching the forest floor under dogwood trees during the growing season was $8.4\% \pm 0.8$ of the total Ca in foliar leachate plus litter fall.

Stemflow samples were not analyzed for stable calcium since stemflow accounted for such a small proportion of the precipitation that passed through the crown ($0.2\% \pm 0.01$). Helvey and Patric (1965) stated that stemflow constitutes a very small amount of the precipitation reaching the forest floor and that it is difficult to accurately measure stemflow; if the collection trough is too wide it will intercept throughfall and if it is too narrow it will not include stemflow that drips from bark at greater heights.

Mina (1965) reported that calcium was the cation found in greatest concentration in stemflow but that it accounted for a very small amount of the total calcium reaching the forest floor. He concluded that the annual amount of stemflow cannot substantially alter soil concentration under trees but it may have some effect over many years.

Helvey and Patric (1965) reviewed the literature on throughfall and stemflow in deciduous forests in eastern United States and computed

regression equations for mean amounts of throughfall and stemflow during growing and dormant seasons. Their equation for throughfall during the growing season is

$$\Sigma T = 0.901(\Sigma P) - 0.031(n),$$

where ΣT is throughfall during the season, ΣP is seasonal precipitation in the open, and n is number of storms. Using this equation and data in Table 18 ($\Sigma P = 61.9$ cm and $n = 15$), the predicted throughfall under the dogwoods was 55.3 cm. The average measured amount was 41.3 cm. This is rather close agreement considering the variables which affect throughfall. Throughfall may be less than predicted since some precipitation was intercepted by the pine canopy before reaching dogwood crowns.

Foliage data (Table 16) were used to calculate monthly area and calcium content of leaves per m^2 of ground under tree crowns. These values were fairly uniform from 5 June to 5 September. Means of the 32 values for this period were $2.43 \pm 0.14 m^2$ of leaves (one surface)/ m^2 of ground surface and $2.40 \pm 0.14 mg Ca/m^2$ under the eight trees.

Regression equations were calculated for calcium in precipitation under crowns based on several precipitation variables which may have an effect on composition of foliar leachate. Amount of precipitation in the open or under crowns did not have a significant effect on amount of calcium in leachate (Table 19). Time interval between storms, however, did account for a significant amount of the variation in amounts of calcium removed. Combination of factors did not increase the reliability of these estimates. Reliability of the equations would

Table 19. Effect of some precipitation variables on calcium in foliar leachate^a

X Variable		Y Intercept ^b	Regression		F	r ²
			Slope	(b ± SE)		
X ₁	Precipitation in open (cm)	13.551	0.260	1.079	0.058 (NS)	0.008
X ₂	Precipitation under dogwoods (cm)	14.878	-0.061	1.225	0.002 (NS)	< 0.001
X ₃	Days since last precipitation	6.741	0.739	0.238	9.593 (*)	0.578
X ₄	(X ₁) x (X ₃)	7.470	0.156	0.051	9.222 (*)	0.569
X ₅	(X ₂) x (X ₃)	7.995	0.231	0.053	6.193 (*)	0.469
Log ₁₀ X ₁		0.982	0.243	0.413	0.300 (NS)	0.041
Log ₁₀ X ₂		1.092	0.093	0.363	0.065 (NS)	0.009
Log ₁₀ X ₃		0.457	0.694	0.157	19.594 (**)	0.737

^aOnly nine precipitation collections included (midsummer when the calcium content of the leaves per m² of ground under the tree crowns was uniform). Y = mean of 8 determinations; X₂ = mean of 36 measurements.

^bY = Calcium (mg) in foliar leachate/m² ground area under dogwood crowns corrected for that under the pine canopy. Log₁₀ Y used when the X variables were log₁₀ values.

probably be increased if precipitation intensity (rainfall amount/unit of time) were included in them since this variable has a profound influence on removal of elements from foliage (Stenlid 1958; Attiwill 1966).

G. Absorption of Calcium by Aboveground Portions of Trees

1. Leaves

Seven intact dogwood leaves (area: 1.21 to 21.03 cm²) on a small tree were immersed for one hour in a solution of precipitation and ⁴⁷CaCl₂. Solution pH was 6.5, and its activity was 28,000 dpm/ml. After removal from solution, leaves were rinsed in running tap water for one hour and assayed for ⁴⁷Ca. All leaves were radioactive. They were then swirled in 1 N HCl for three minutes and recounted to insure that all adsorbed ⁴⁷Ca was removed. The HCl treatment caused about 80% of the leaf surface to lose green coloration. Leaves were then soaked in 1 N HCl for 30 minutes and recounted. Total ⁴⁷Ca found in the seven leaves after the three treatments was 627,000 dpm, 104,600 dpm, and 27,700 dpm, respectively. Even after the severe HCl treatment there was still ⁴⁷Ca in leaves, which is evidence that ⁴⁷Ca absorption occurred. Coefficient of correlation between activity and leaf area for the seven leaves after the water rinse was 0.977 (P < 0.01).

2. Bark

One vigorous horizontal branch (1 cm in diameter and not visibly scarred or fissured) was selected on each of five untagged trees in March, May, and July. Bark thickness was about 0.5 mm on all 15

branches. About 5 g of cotton gauze was wrapped around 5 cm of each branch, enclosed in plastic film, and sealed at the ends with tape. A hole was made in the plastic covering, and 25 ml of ^{45}Ca solution (pH 6.0; 80,000 dpm/ml) was pipetted onto the gauze. Gauze retained all of the solution and was still moist after seven days when branches were sampled at 8-cm intervals on both sides of the assembly. No evidence of ^{45}Ca absorption and subsequent movement was found. This does not dispute the possibility of calcium absorption through damaged bark (leaf scars, fissures, etc.).

H. Exudation of Calcium by Roots

Three dogwood trees 50 to 70 cm in height and 3 to 5 mm in diameter at ground level were brought to the laboratory in July, and their roots washed free of soil. Half of the intact roots of each plant were placed in Hoagland solution and the other half in Hoagland solution containing ^{45}Ca (5000 dpm/ml). Volume of solution (pH 6.7; 26 to 27 C) in each container was maintained at 200 ml throughout the experiment. Untagged solution was assayed for ^{45}Ca at 24-hr intervals for 12 days; there was no evidence of calcium exudation from untagged roots. After 12 days the tagged solution was replaced with 20% Hoagland solution. This solution did not contain detectable quantities of ^{45}Ca after two days, indicating that tagged roots did not exude ^{45}Ca .

The still-vigorous trees were sectioned into four components after 14 days, and ^{45}Ca in each component was determined as percentage of total plant radiocalcium:

leaves	4.4 ± 1.9
stem and branches	53.6 ± 6.5
tagged roots	41.1 ± 6.8
untagged roots	0.9 ± 0.8

These results and those of Ririe and Toth (1952), which indicated that roots do not exude calcium, are in conflict with those of Fedorovskii (1958); he found that ^{45}Ca was transferred from tagged roots of corn plants to untagged roots and was then excreted into the surrounding soil. These contradictory results may be due to the root medium since soil microorganisms have been reported to increase exudation of material from roots (Ivanov 1965).

I. Translocation of Calcium in Layered Plants

Three dogwood shoots (50 to 80 cm in height) produced by natural layerage were selected for study in July. Litter above the adventitious roots was removed, and 200 ml of ^{45}Ca solution (50,000 dpm/ml) were poured on the soil around each root system; litter was then replaced. Plants were collected 24 days later and sectioned into three components for ^{45}Ca assay: adventitious roots, the adventitious shoot with its leaves, and a section of the layered branch toward the parent tree. Radiocalcium was found in both adventitious plant parts but not in the branch toward the parent tree.

Of total activity found (over 10,000 dpm in each plant), $12.9\% \pm 2.0$ ($N = 3$) was in the new shoot including leaves and $87.1\% \pm 2.0$ was in adventitious roots. Apparently, ^{45}Ca was translocated from roots to

the adventitious shoot via the layered branch but it was not translocated in that branch against polarity toward the parent tree.

J. Root Grafts

Six root grafts were found while excavating root systems of the 28 larger trees. Each of these self-grafts consisted of a lateral root (1 to 2 cm in diameter) grafted to another lateral root of the same size on the same tree. Microscopic examination of two of these grafts showed that tissues of the two roots had grown together. Root grafts in Cornus have not been previously reported (Graham and Bormann 1966).

Root systems of ten dogwood trees, each growing within 2 m of another dogwood, were excavated in a search for intraspecific root grafts. Only one such graft was found. Lateral roots 4 cm in diameter were grafted between trees 6 and 8 cm dbh (16 and 21 years old, respectively). Vessels in the roots were joined, and both roots had five growth rings in common at the graft union. Functional root grafts could enable trees to obtain nutrients that had been absorbed by other trees.

K. Pattern of Dye Ascent in Dogwood Trees

Information on water movement in trees has been accumulating for many years (Kozlowski 1961; Zimmermann 1964), but interest in the pattern of ascent in the transpiration stream has been more recent (Greenidge 1955; Vité and Rudinsky 1959; Rudinsky and Vité 1959; Kozlowski and Winget 1963).

Twenty-two dogwood trees (2 to 7 cm dbh and from 10 to 26 years old) were stem-inoculated during the growing season with 0.5% acid fuchsin dye. Several days after inoculation their bark was removed, and the pattern of dye ascent was observed (Fig. 9). Dye was confined to xylem and ascended dextrally in a narrow channel traversing about 90° of stem circumference every meter. This pattern was remarkably uniform within and among trees. Only variation in this pattern was near the base of several large branches; orientation of tissues was apparently altered there since the pattern of ascent was not uniform and in several cases ascended to the left for one or two centimeters. Maximum tangential spread of dye streaks (to about twice the width of chisel cuts used to intercept the transpiration stream) was attained within one meter above the site of inoculation. Dye moved basipetally in approximately the same pattern as it moved acropetally. Roots of one tree were excavated, and dye was found one meter out one of the lateral roots. As expected, dye was not translocated in heartwood even when it was injected there.

This pattern of ascent has been described by Rudinsky and Vité (1959) and Vité and Rudinsky (1959) as "sectorial winding," which they describe as a stream that ascends in a sector up the stem while winding around the stem axis.

Dye moved into tree branches only where branch bases were located in the relatively narrow channel of xylem containing dye. This caused nonuniform distribution of dye in tree canopies.

Fig. 9. Transpiration stream in dogwood stem showing dextral spiraling. Stem cross-sections at 0.5 m intervals above and below site of inoculation (arrow). Dye pattern in exposed xylem on left and in radial section on right. Variation in amount of dye which entered branches, resulting from their position in respect to dye stream, shown by three cross-sections in foreground.

L. Rate of Dye and ^{47}Ca Ascent in Dogwood Trees

Nine dogwood trees in pine stand A were tagged simultaneously with 0.5% acid fuchsin dye and 0.1 mCi of ^{47}Ca . All trees were naturally pruned to a height of 2 m. Two troughs were constructed on each stem; one (1 dm above ground) was used for dye, and the other (2 dm above ground) was used for ^{47}Ca . Dye was introduced to the transpiration stream by one chisel incision; three incisions were used for ^{47}Ca . To avoid confounding the experiment, incisions were located so the dye pattern would not overlap that of ^{47}Ca .

Thin strips of bark (4 mm), perpendicular to stem axis, were removed at 0.5, 1.0, 1.5, and 2.0 m above the trough used for dye. Length of the strip depended upon stem size but never exceeded 10% of stem circumference. Strips were located with the assumption that dye would ascend dextrally $90^\circ/\text{m}$. Dye velocity was obtained by observing the time required for dye to reach the various heights.

Bark from the entire stem circumference between 1 and 1.25 m above the trough used for ^{47}Ca was removed from two trees prior to inoculation to determine if phloem had significant role in upward movement of calcium.

Trees were inoculated on 23 August 1966 between 1100 and 1200 hours. Air temperature in the stand was 23 to 25 C; relative humidity was 70 to 74%; and soil was near field capacity. Time required for inoculum to enter the transpiration stream varied greatly; uptake was slower when the sun was obscured by clouds than when trees were in

direct sunlight, but all troughs emptied within three hours.

Rate of dye ascent was extremely variable within and among trees; for example, in one tree dye ascended 1 m in 7 minutes but required 21 minutes to reach 2 m. Twenty-four observations of rate of dye ascent were made. Calculated velocity (2.75 ± 0.32 m/hr) is within the range commonly found in trees (Kramer 1959). Attempts to follow ^{47}Ca ascent with a portable detector were unsuccessful due to slow ascent and high background readings caused by the 1.31 Mev gamma rays of ^{47}Ca in the trough.

Dye was apparent in some leaves of all trees on the morning following tagging. Fifty leaves representing the entire crown were collected from each tree every day until trees were harvested. Radioactivity in these samples did not significantly exceed that in control leaves.

Trees were harvested four, five, or seven days after inoculation. Stems were cut into 25-cm segments to a height of 3 m above the trough used for ^{47}Ca . Bark from these sections was removed, and amount of ^{47}Ca in xylem and in bark was determined (Table 20).

Regression equations for height to which ^{47}Ca ascended in xylem and in bark based on days between inoculation and harvest did not account for enough variability to be considered significant ($P > 0.05$). A regression equation for percentage of ^{47}Ca in bark based on days between inoculation and harvest was statistically significant ($F = 59.3$; $r = 0.96$; $P < 0.01$), indicating that 92% of variation in percentage of ^{47}Ca in bark was accounted for by number of days the trees were intact after inoculation. Calcium-47 content in xylem and bark decreased

Table 20. Calcium-47 ascent in dogwood trees

	Tree Number								
	1	2	3	4	5	6	7	8	9
Age (years)	18	10	15	17	15	15	12	16	17
DBH (cm)	4.4	2.4	4.7	4.3	4.1	4.5	3.4	4.7	4.7
Height (m)	7.0	4.7	6.0	5.7	5.9	5.9	5.6	7.0	6.3
Elapsed Time (days)	5	5	5	5	7	4	7	7	4
<u>⁴⁷Ca Ascended (m)</u>									
Xylem	3.0	2.0	2.75	2.75	3.0	2.75	3.0	3.0	3.0
Bark	3.0	1.0	1.25	1.0	3.0	1.25	2.75	3.0	1.75
<u>% of ⁴⁷Ca in Bark^a</u>									
Mean	14.8	18.2	18.3	19.9	31.2	8.7	27.6	18.9 (24.1) ^b	25.4 (6.2) ^b
SE	1.9	3.8	3.1	8.8	2.6	2.7	2.8	2.7 (4.3)	1.5 (2.4)
<u>Correlation of ⁴⁷Ca in Xylem and Bark</u>									
(r) ^{a,c}	0.850	0.957	0.906	0.896	0.950	0.981	0.934	0.969	0.999

^aN for % of ⁴⁷Ca in the bark and for correlation coefficients is the number of 25 cm segments in which significant quantities of radiocalcium were found.

^bTrees 8 and 9 had phloem removed between 1.00 and 1.25 m above site of inoculation. Numbers not in parentheses = below phloem block; numbers in parentheses = above phloem block.

^cAll correlation coefficients are significant at the 0.05 or 0.01 level.

rather uniformly with increasing height in the stem (Table 21).

Apparently, ^{47}Ca ascended in the xylem, and radiocalcium which was transferred to phloem was immobilized. Height to which ^{47}Ca ascended was probably a function of uptake rate; it was not possible to test this since times required for inocula to enter the transpiration stream were not recorded. Rate of dye ascent cannot be used as an independent variable for predicting the height to which ^{47}Ca ascended because of variability in within-tree observations and because dye apparently moved with water in the transpiration stream whereas calcium did not.

M. Weight and Calcium Content of Inflorescences and Fruits

Seven collections of inflorescences were made between 22 February and 5 May, and two additional collections were made in autumn after new flower buds had formed. Five fruit collections were made between 9 June and 6 October. Inflorescences included receptacle, peduncle, and bracts; fruits included receptacle, peduncle, and pericarps. All collections were made in 1966 from at least 40 branches on 10 trees in pine stand B. Collections consisted of four samples with 25 inflorescences or fruits in each ($N = 4$).

Maximum values for inflorescences were attained on 26 April when 100 of them were calculated to weigh 15.00 ± 0.24 g and contain 368.4 ± 18.2 mg Ca; maximum fruit values occurred on 2 September when 100 weighed 60.36 ± 1.56 g and contained 1012.3 ± 50.7 mg Ca. Distributions of weight and calcium in inflorescences and fruits are shown in Table 22.

Table 21. Calcium-47 in successive stem segments compared
to basal segment

25-cm Segment	Stem		Xylem		Bark	
	N	$\bar{X} \pm SE$	N	$\bar{X} \pm SE$	N	$\bar{X} \pm SE$
1 ^a	7	1.00	7	1.00	7	1.00
2	7	0.47 $\pm$ 0.04	7	0.47 $\pm$ 0.06	7	0.60 $\pm$ 0.05
3	7	0.28 $\pm$ 0.04	7	0.29 $\pm$ 0.05	7	0.33 $\pm$ 0.08
4	7	0.20 $\pm$ 0.04	7	0.24 $\pm$ 0.06	7	0.17 $\pm$ 0.06
5	7	0.14 $\pm$ 0.04	7	0.16 $\pm$ 0.05	5	0.16 $\pm$ 0.08
6	7	0.09 $\pm$ 0.03	7	0.11 $\pm$ 0.04	3	0.14 $\pm$ 0.03
7	7	0.07 $\pm$ 0.03	7	0.08 $\pm$ 0.03	3	0.13 $\pm$ 0.04
8	7	0.06 $\pm$ 0.02	7	0.07 $\pm$ 0.03	3	0.07 $\pm$ 0.03
9	6	0.04 $\pm$ 0.02	6	0.05 $\pm$ 0.02	3	0.07 $\pm$ 0.04
10	6	0.03 $\pm$ 0.01	6	0.03 $\pm$ 0.01	3	0.04 $\pm$ 0.02
11	6	0.02 $\pm$ 0.01	6	0.02 $\pm$ 0.01	3	0.03 $\pm$ 0.02
12	3	0.02 $\pm$ 0.01	3	0.03 $\pm$ 0.02	2	0.01 $\pm$ 0.00

^a Basal segment.

Table 22. Distribution of weight and calcium in inflorescences and fruits

	Percent of Total ^a	
	Weight	Calcium
Inflorescences		
Receptacle	33.2 ± 2.0	46.6 ± 0.8
Bracts	56.4 ± 1.9	37.4 ± 0.4
Peduncle	10.4 ± 0.3	16.0 ± 0.4
Fruits		
Receptacle + Peduncle	9.0 ± 0.2	11.8 ± 0.4
Pericarp	91.0 ± 0.2	88.2 ± 0.4
Pericarp		
Endocarp	53.8 ± 0.4	88.6 ± 0.5
Exocarp	46.2 ± 0.4	11.4 ± 0.5

^aMean ± SE; N = 4 with 25 in each sample. Values for fully developed organs.

Decrease in weight and calcium content of inflorescences in early May (Fig. 10) was due to abscission of bracts, the large showy parts of the inflorescence. Decrease in fruit weight and calcium content in September resulted from abscission of the larger ripe pericarps. Number of pericarps on each receptacle decreased during the season from 5.3 ± 0.2 on 9 June to 3.8 ± 0.2 on 6 October ($N = 100$); the range for all collections was from 1 to 10. Receptacles without fertilized flowers fall from the tree (Morse 1907). Since there were many dogwood trees in pine stand B, it is likely that most flowers were fertilized and most pericarps were fully developed (Davis 1927).

N. Contribution of Inflorescences and Fruits to Calcium Cycling

Formation of inflorescences may affect the amount of calcium in litter. Miller and Hurst (1957) found that variation in calcium content of beech (Nothofagus truncata) litter was related to the flowering cycle of trees. Although dogwood trees in the understory do not commonly produce large numbers of inflorescences (Shank 1938), it is of interest to estimate the maximum influence of inflorescences and fruits on weight and calcium distribution in trees and the maximum contribution of these organs to litter.

Five trees growing in the open that had as many inflorescences as any other trees in the area with the same size crown were harvested on 5 May 1966, and their leaves and inflorescences were counted. Trees ranged in dbh from 3.0 to 6.2 cm and from 4.0 to 6.2 m in height. Inflorescences (from 203 to 1111 per tree) accounted for $11.9\% \pm 0.4$

Fig. 10. Weight and calcium content of 100 inflorescences and fruits during 1966.

of the total number of inflorescences and leaves.

Total weight and calcium content of inflorescences and leaves were calculated, and weight and calcium content of the remainder of the tree were estimated with equations in Fig. 15. Weight and calcium content of leaves and fruits at time of abscission were calculated by correcting the May leaf-number with data in Table 2 and by assuming that all inflorescences produced five pericarps.

It can be seen (Table 23) that these organs make a sizeable contribution to weight and calcium of the entire tree and to total litter produced.

O. Litter Decomposition

Dogwood leaf, bract, seed, and twig decomposition were studied by placing the material in litter bags and determining loss of weight and calcium through time. Litter bags (25 x 25 cm) were made of nylon net with holes 2 mm in diameter. Material was placed in bags so that it rested on the forest floor in a natural position. Oven-dry weight and calcium content were determined for control samples. Three rain gauges were placed with the litter bags in all experiments; gauges were emptied after every period of continuous precipitation and were rerandomized three times during the experiment. All bags were covered with naturally-fallen litter within two weeks after placement in the field. Advantages and limitations of the litter-bag method have been discussed by Witkamp and Olson (1963).

Table 23. Contribution of dogwood inflorescences and fruits
to weight and calcium content of trees and litter^a

	Weight	Calcium
Inflorescences		
% of Total Tree	1.1 ± 0.1	3.3 ± 0.2
% of Leaves + Inflorescences	29.5 ± 0.9	28.9 ± 0.9
Bracts		
% of Total Tree	0.6 ± 0.1	1.2 ± 0.1
% of Leaves + Inflorescences	16.6 ± 0.5	10.8 ± 0.3
Fruits		
% of Total Tree	5.3 ± 0.6	8.0 ± 0.4
% of Leaves + Fruits	36.2 ± 1.0	25.6 ± 0.8
Percent of Total Added to Litter		
Bracts	3.6 ± 0.1	2.9 ± 0.1
Fruits	34.9 ± 0.9	24.9 ± 0.8
Leaves	61.5 ± 1.0	72.2 ± 0.9

^aMean ± SE; N = 5. Values when organs fully developed.

1. Leaves

Senescent leaves, just prior to abscission, were collected in October from 10 trees; they were then air-dried and thoroughly mixed. About 30 leaves with an air-dry weight of 5 g were placed in each of 78 litter bags. Twenty-six bags were placed in each of three stands (pine stand C, yellow poplar stand B, and the oak stand) on 10 November 1965. Two bags from each stand were randomly selected at four-week intervals for one year, and weight and calcium content of the leaves were determined.

Weight and calcium loss from leaves (Table 24) was very rapid. It is evident (Fig. 11) that weight and calcium losses had three distinct rates during the year: (1) rapid loss during the first four weeks; (2) gradual loss between four and twenty weeks (December to first of April); (3) more rapid loss during the remainder of the year.

Regression equations for weight and calcium loss through time in each stand for the 4 to 20 week and 20 to 52 week periods were calculated. Regression slopes (Table 25) were compared with the homogeneity of regression test (Steel and Torrie 1960) to determine if there were significant differences in loss rates (Table 26). These data can be summarized as follows:

(1) There were no significant differences between rates of weight or calcium loss among stands during the December to April period. Likewise, rates of weight and calcium loss were not significantly different in any stand during this period.

(2) There were significant differences in rate of weight loss

Table 24. Logwood leaf decomposition in three forest stands

Weeks ^a	Pine Stand			Oak Stand			Yellow Poplar Stand		
	% Remaining ^b		Cumulative Precipitation (cm)	% Remaining ^b		Cumulative Precipitation (cm)	% Remaining ^b		Cumulative Precipitation (cm)
	Weight	Calcium		Weight	Calcium		Weight	Calcium	
4	83.5	76.7	3.8	79.6	74.7	4.0	81.1	76.9	4.8
8	83.9	77.4	8.0	75.9	71.2	9.1	78.5	75.2	10.7
12	76.1	75.6	11.5	78.8	72.8	12.9	79.9	75.8	15.2
16	78.8	71.5	20.0	78.8	68.2	22.8	73.4	72.5	27.2
20	76.5	73.4	23.6	77.4	71.5	27.1	76.3	73.2	31.4
24	67.7	61.5	30.0	72.1	69.6	34.5	68.4	67.0	39.2
28	55.5	61.9	41.0	64.6	58.5	46.1	51.6	53.2	52.1
32	56.3	52.4	44.3	55.6	52.3	49.7	54.0	59.4	55.9
36	48.0	47.7	49.8	50.9	56.7	56.1	41.6	48.7	63.0
40	42.1	40.6	66.0	41.1	46.7	72.4	26.1	35.0	80.2
44	42.1	44.0	70.0	36.3	38.0	76.0	21.5	27.5	85.2
48	27.8	22.0	82.0	30.9	34.6	89.7	14.1	16.9	99.0
52	28.9	29.8	90.7	28.5	28.8	100.6	5.5	8.9	109.9

^aWeek 0 = 10 November 1965.^bMean of 2 samples.

Fig. 11. Decomposition of dogwood leaves. Mean of two samples for each point. Week 0 = 10 November 1965.

Table 25. Weight and calcium loss rates during leaf decomposition^a

	Time Period (Weeks After Abscission)	
	4 to 20 (N=10)	20 to 52 (N=18)
Pine Stand		
Weight Loss	0.48 ± 0.18	1.55 ± 0.10
Calcium Loss	0.30 ± 0.11	1.38 ± 0.16
Oak Stand		
Weight Loss	0.04 ± 0.18	1.63 ± 0.08
Calcium Loss	0.23 ± 0.25	1.35 ± 0.13
Yellow Poplar Stand		
Weight Loss	0.36 ± 0.19	2.16 ± 0.16
Calcium Loss	0.22 ± 0.24	2.01 ± 0.21

^aWeekly loss (%) ± SE determined by regression analysis. Week 0 = 10 November 1965.

Table 26. Tests of homogeneity of regression slopes
for leaf decomposition

Comparison	t value	
Between Stands (4 to 20 Weeks)		
Weight Loss		
Pine versus Oak	1.47 _L	(NS)
Pine versus Poplar	0.41	(NS)
Oak versus Poplar	-0.03	(NS)
Calcium		
Pine versus Oak	0.18	(NS)
Pine versus Poplar	0.23	(NS)
Oak versus Poplar	0.03	(NS)
Between Stands (20 to 52 Weeks)		
Weight Loss		
Pine versus Oak	-1.99	(. *)
Pine versus Poplar	-9.80	(**)
Oak versus Poplar	-8.61	(**)
Calcium		
Pine versus Oak	0.54	(NS)
Pine versus Poplar	-8.06	(**)
Oak versus Poplar	-8.84	(**)
Between Weight and Calcium		
4 to 20 Weeks		
Pine Stand	0.56	(NS)
Oak Stand	-0.54	(NS)
Poplar Stand	0.40	(NS)
20 to 52 Weeks		
Pine Stand	3.24	(**)
Oak Stand	6.14	(**)
Poplar Stand	1.75	(*)

Table 26, continued

Comparison	t value	
Between Time Periods		
Weight: 4 to 20 versus 20 to 52 Weeks		
Pine Stand	7.40	(**)
Oak Stand	5.27	(**)
Poplar Stand	8.96	(**)
Calcium: 4 to 20 versus 20 to 52 Weeks		
Pine Stand	5.07	(**)
Oak Stand	8.19	(**)
Poplar Stand	6.66	(**)

in each stand between the December to April and April to November periods. Rate of calcium loss was also significantly different between these periods in all three stands. In all cases loss rate during the latter period was significantly greater than that during winter.

(3) During the April to November period loss rates for weight and calcium were significantly greater in the yellow poplar stand than in the pine and oak stands. Weight, but not calcium, loss rate during this period was significantly greater in the oak stand than in the pine stand.

(4) During the April to November period rate of weight loss was significantly greater than rate of calcium loss in all stands.

Calcium loss ($24.3\% \pm 1.8$) in the six bags during the first four weeks was significantly greater ($P < 0.01$) than weight loss ($18.9\% \pm 1.21$). Initial losses were presumably due to leaching of water-soluble material from leaves. Broadfoot and Pierre (1939) found that 20% of the air-dry weight of dogwood leaves was water soluble. Further losses during winter are probably due to leaching, disintegration, and activities of litter fauna and microflora. Losses during this period were primarily from intervein areas, which contain more calcium than the veins (Table 10).

A combination of disintegration and increased activity of litter biota accounted for greater losses during the summer months. Loss of leaf veins during this period resulted in percentage weight loss being greater than percentage calcium loss since veins had a lower percentage calcium than the intervein area. The uniform rate of weight and calcium

loss continued into autumn and winter due to leaching of the small, broken pieces of leaves.

Differences in loss rates among stands can be partially explained by site description data. Less canopy cover in the yellow poplar stand resulted in more precipitation reaching litter there than in the other two stands. The pH of litter in June varied among stands (pine 5.8, oak 6.3, poplar 6.8). More favorable conditions for litter biota during summer in the yellow poplar stand could account for the more rapid rate of litter decomposition. Similarly, the oak stand probably had greater populations of litter biota than the pine stand.

Mean loss rates of weight and calcium were calculated with data from all three stands:

<u>Weeks</u>	<u>Weekly Percent Loss</u>	
	<u>Weight</u>	<u>Calcium</u>
0 to 4	4.73	6.07
4 to 20	0.28	0.25
20 to 52	1.78	1.58

Mean weight loss in one year was calculated to be 80.3%, and the calcium loss was 78.8%. About 35 weeks were required for 50% reduction in weight and calcium content of leaves. Seasonal trends in dogwood leaf decomposition (Fig. 11) are similar to those reported for dogwood by Olson and Crossley (1963); however, they found less first-year weight losses (approximately 50% in pine stand and 56% in oak stand). Lunt (1935) reported that dogwood leaves lost about 12% of their weight and 5% of their calcium during seven weeks after abscission. Effect of decomposition during one year can be seen in Fig. 12.

Fig. 12. Dogwood leaves in nylon bag compared with condition after one year of decomposition. Litter on left from pine stand, on right from oak stand, and on bottom from yellow poplar stand. Scale = 15 cm.

2. Bracts

Deciduous parts of the inflorescence, the four bracts, were collected from 200 inflorescences in early May; the bracts had started to wither and some had fallen. Ten litter bags were prepared by placing 7 g fresh weight (43 to 45 bracts) in each bag, which were placed under dogwood trees in pine stand B on 3 May 1966. Two bags were randomly selected every week for weight and calcium determinations.

3. Fruits

Fruits collected from 12 trees in late September were air-dried for one week. One hundred pericarps (endocarp plus exocarp) weighing 17 g were placed in each of four litter bags. An additional bag was prepared with 100 receptacles plus peduncles. Bags were placed under dogwood trees in pine stand B on 17 October 1966. One bag containing pericarps was collected every four weeks, and weight and calcium content of pericarps were determined. The bag containing receptacles and peduncles was collected with the last pericarp sample.

4. Twigs

Living twigs (< 3 mm diameter and 12 cm long, with bark thickness of 0.4 mm) were collected from dogwood trees in September and were air-dried for eight weeks to simulate the condition of naturally-fallen twigs. It was necessary to obtain material in this manner since dead twigs in litter or on trees had been subjected to some weathering, making it very difficult to obtain similar samples and controls. Ten

grams (34 to 36 twigs) were put in each of 12 litter bags and placed in pine stand C on 10 November 1965. Three samples were collected every 13 weeks.

Decomposition of bracts, fruits, and twigs (Table 27) proceeded at considerably different rates (Fig. 13). Weight loss from bracts and pericarps exceeded calcium loss. This can be explained for pericarps by the differences in composition of endocarp and exocarp (Table 22). The exposed exocarp contains 46% of pericarp weight but only 11% of the calcium. Although endocarp was partially exposed on about 10% of the pericarps after four weeks, it probably lost very little weight or calcium due to its density. More rapid decomposition of receptacles plus peduncles compared to pericarps is probably not too significant in terms of nutrient cycling since they account for such a small percentage of fruit weight (9%) and calcium (12%).

Decomposition data for twigs are interesting, not only because they permit comparison between woody and foliar tissues, but because calcium loss exceeded weight loss (although not significantly different for any sampling date, $P > 0.05$). This was due to high percentage of calcium in bark compared to the entire twig. Bark was starting to peel after 13 weeks; it was practically all decomposed after one year, leaving only xylem.

P. Effect of Dogwood Leaves on Decomposition of Loblolly Pine Needles

It is commonly accepted that addition of hardwood leaves increases rate of decomposition of conifer litter, which normally decomposes at a

Table 27. Dogwood bract, fruit, and twig decomposition

	Weeks	% Remaining		Cumulative Precipitation (cm)
		Weight	Calcium	
Bracts ^a	1	93.8	97.9	2.5
	2	60.6	76.7	5.1
	3	53.1	70.6	5.3
	4	47.7	71.4	6.0
	5	46.3	71.4	6.0
Fruits ^b (Pericarps)	4	85.5	96.0	9.4
	8	81.2	97.4	14.8
	12	83.6	96.7	21.0
	16	79.7	95.2	27.4
(Receptacles + Peduncles)	16	67.1	89.2	27.4
Twigs ^c	13	90.0 ± 0.4	82.8 ± 6.5	13.2
	26	82.7 ± 0.7	76.5 ± 3.2	35.5
	39	76.7 ± 0.8	74.9 ± 3.9	63.4
	52	66.3 ± 1.4	65.9 ± 1.3	90.7

^aMean of 2 samples for each collection.

^bSingle sample for each collection.

^cMean ± SE; N = 3 for each collection.

Fig. 13. Decomposition of dogwood bracts, pericarps, and twigs. Mean of two samples for bracts, single sample for pericarps, and mean of three samples for twigs at each sampling date.

slower rate (Lutz and Chandler 1946). Remezov (1961) found that mixing leaves that decompose rapidly (hazelnut, ash, and basswood) with those that decompose at a slower rate (oak and aspen) increased rate of decomposition of the latter. An experiment was performed to determine the magnitude of the effect, if any, of dogwood leaves on loblolly pine needle decomposition.

Brown needles were collected from lower branches of loblolly pine trees; they were air-dried, and 20 g (600 to 700 needles) were placed in each of 52 litter bags (35 x 35 cm; 2-mm mesh). Air-dried dogwood leaves (5 g; 29 to 31 leaves) were mixed with needles in half of the bags. All bags were placed in pine stand B on 10 November 1965. Two bags with pine needles alone and two with added dogwood leaves were collected every four weeks for one year, and weight loss of the needles was determined. Weight loss of dogwood leaves was determined separately.

Results (Fig. 14) show that addition of dogwood leaves did not increase the decomposition rate of pine needles. Weight loss of dogwood leaves mixed with needles was very similar to that of dogwood leaves alone as determined in litter decomposition experiments. Fragments of dogwood leaves which adhered to needles during decomposition were carefully removed so they would not affect measured weight of the needles.

Regression equations for weight loss through time of pine needles with and without added dogwood leaves (Table 28) are not significantly different ($P > 0.05$). First-year weight loss of needles (about 44%)

Fig. 14. Decomposition of loblolly pine needles with and without dogwood leaves.

Week 0 = 10 November 1965.

Table 28. Equations for weight loss of decomposing loblolly pine needles

Sample	Regression Equation ^a	SE of b	F	r ²
Needles not mixed with dogwood leaves	% Weight lost = 0.837 (Weeks)	0.015	3251. (**)	0.992
Needles mixed with dogwood leaves	% Weight lost = 0.845 (Weeks)	0.016	2768. (**)	0.991

^aRegression forced through the origin; N = 26.

was much less than that for dogwood leaves (about 80%, as determined in separate experiments).

Q. Effect of Dogwood Trees on Soil Calcium

Soil samples were taken under five dogwood trees in pine stand A to determine if the trees had a detectable effect on calcium content of soil. Four samples of mineral soil (each a composite of 10 soil cores to a depth of 10 cm) were taken under each tree, and four similar samples were taken in the stand in areas not under dogwood trees. Trees ranged in dbh from 3.7 to 5.1 cm and in age from 15 to 18 years.

Amount of exchangeable calcium in soil was significantly greater under dogwood trees than in the rest of the stand (Table 29). This effect probably extends some distance from under the crowns; observations made during leaf abscission indicated that most of the leaves were added to litter in an area twice the diameter of the crown. Enrichment of upper soil with calcium is a result of the "pumping" action of dogwood trees, thereby reducing the amount of calcium lost from mineral soil by percolation.

R. Weight and Calcium Content of a Loblolly Pine Plantation

Calcium content of dogwood trees would be more meaningful if it were known what percentages of weight and calcium in an entire stand were in dogwood trees. Total aboveground weight and calcium content of pine stand A were estimated for the time just prior to dogwood leaf

Table 29. Effect of dogwood trees on soil calcium

Sample	Exchangeable Calcium (meq/100 g oven-dry soil) ^a
Soil not under dogwood trees	1.35 ± 0.05
Soil under dogwood trees	
Tree A	1.81 ± 0.04
Tree B	1.96 ± 0.07
Tree C	2.24 ± 0.13
Tree D	2.40 ± 0.10
Tree E	2.95 ± 0.16

^aMean ± SE; N = 4. Mineral soil sampled to depth of 10 cm. Exchangeable calcium concentrations under dogwood trees were all significantly greater ($P < 0.01$) than the concentration in soil not under dogwood trees.

abscission. Madgwick (1963) recommended that such estimates be made during the dormant season or late in the growing season since nutrient content of the stand is most uniform then.

Ovington and Madgwick (1959b) described three techniques for estimating total weight and nutrient content of a tree species in a stand. (1) Trees of mean diameter are assumed to be of mean weight and nutrient composition, so that values for a tree with mean diameter can be multiplied by number of trees in the stand. (2) Trees can be placed in diameter classes, and weight and nutrient composition of a tree with mean diameter in each class can be used to estimate values for all trees in that class. (3) Regression equations for weight and nutrient content can be used to estimate these values for individual trees. They compared estimates of weight in a pine (Pinus sylvestris) plantation obtained by each of these methods and found that estimates based on method (1) were consistently low and that those with methods (2) and (3) were in general agreement. They stated that method (1) was clearly inferior to other methods because a tree of average diameter is not average in other respects, and that method (2) is somewhat inferior for the same reason and because it may not adequately account for larger trees outside the sampled diameter range.

Methods used to estimate stand values follow:

Litter. Twenty randomly-located samples (1 m^2) of the entire litter layer and ground vegetation were collected in October. Oven-dry weight of these samples was $4500 \pm 170 \text{ g/m}^2$ ($N = 20$), and calcium content was $17.1 \pm 0.4 \text{ g/m}^2$ ($N = 20$).

Dogwood trees. Diameters of dogwood trees on 10 plots with a total area of 0.5 ha were recorded, and aboveground weight and calcium content of the trees were estimated with regression equations (Table 32). There were an estimated 286 dogwood trees/ha.

Pine trees. Diameters of pine trees on 10 plots totaling 0.25 ha were measured, and five trees covering the range of diameters were harvested in October. Aboveground material was placed in three diameter classes (> 5 cm, 1-5 cm, and < 1 cm); all classes included bark and xylem, and the smaller class also included needles. Fresh weights were determined with field scales for each class, and five large samples of each class (representing all stem heights and crown positions) were taken for oven-dry weight and calcium determinations (Tables 30 and 31). Mean calcium value for entire aboveground portions (0.14%) agrees very well with that of 0.13% calculated from data published by Metz and Wells (1965) for 10 loblolly pine trees. Regression equations (Table 32) were used to estimate weight and calcium content of pine trees in the stand.

Total aboveground weight and calcium content of the pine plantation and the contributions of pine, dogwood, and litter were calculated (Table 33). Dogwood trees accounted for only 0.2% of aboveground weight of the stand but 1.8% of the calcium. Additional calculations, based on the assumption that dogwood trees had 100% canopy cover in the plantation, showed that dogwood trees would account for 1.3% of the weight and 9.8% of the calcium. These latter calculations were based on data from the eight tagged trees that were harvested. These trees

Table 30. Total aboveground weight and calcium content of
loblolly pine trees

	Tree Number				
	1	2	3	4	5
DBH (cm)	7.3	10.7	13.4	16.6	21.4
Height (m)	10.9	13.0	13.6	15.3	15.2
Oven-dry Weight (kg)	10.92	26.62	40.66	75.95	143.37
Calcium (g)	16.3	35.6	51.3	96.8	218.6
Calcium (%)	0.15	0.13	0.13	0.13	0.15

Table 31. Weight and calcium content of aboveground components
of loblolly pine trees^a

Component (Diameter Class)	% Calcium	Percent of Aboveground Tree	
		Weight	Calcium
> 5 cm	0.08 ± 0.004	73.4 ± 2.6	41.7 ± 3.0
1 to 5 cm	0.24 ± 0.03	14.7 ± 1.7	25.6 ± 2.1
< 1 cm ^b	0.38 ± 0.04	11.9 ± 1.0	32.7 ± 1.8
Total Tree	0.14 ± 0.01		

^aMean ± SE; N = 5.

^bIncludes needles.

Table 32. Regression equations for estimating aboveground weight and calcium content
of the loblolly pine plantation

Y Variable (Log ₁₀)	X Variable (Log ₁₀)	Y Intercept	Regression Slope (b)	N	F	r ²
Dogwood Trees With Leaves						
Oven-dry Weight (g)	Diameter (cm) at 1 m	2.371	2.147	28	293.(**)	0.919
Calcium (g)	Diameter (cm) at 1 m	0.485	2.098	28	189.(**)	0.879
Pine Trees						
Oven-dry Weight (g)	DEH (cm)	-1.050	2.397	5	786.(**)	0.996
Calcium (g)	DEH (cm)	-0.890	2.378	5	153.(**)	0.891

Table 33. Aboveground weight and calcium content of 18-year-old
loblolly pine plantation^a

Component	Oven-Dry Weight (kg/ha)	Calcium (kg/ha)	Percent of Total	
			Weight	Calcium
Dogwood Trees with Leaves	1,030	12.5	0.2	1.8
Pine Trees	382,940	525.0	89.3	74.1
Litter	45,020	170.6	10.5	24.1
Total	428,990	708.1		

^a Immediately before abscission of dogwood leaves.

had 572 ± 61 g oven-dry weight and 7.6 ± 0.8 g Ca in aboveground parts in September per m^2 of ground under crowns. As Ovington (1958) pointed out, a large amount of calcium in litter of conifer stands (24% of total aboveground calcium in this case) is temporarily removed from the active nutrient cycle.

S. Prediction of Dogwood Tree Characteristics

Total weight and calcium content of dogwood trees can be estimated with regression equations using any of several independent variables (Table 34). It is seen by comparing the F and r^2 values that very little additional confidence can be placed in equations with a combination of independent variables; this is due to correlations between these variables (Table 35). Since there is also little to be gained by using squared values of independent variables, final equations for weight and calcium content of trees without leaves (Fig. 15) do not include squared terms. Lack of significant correlations between tree age and weight or calcium content (perhaps due to the small range in age of the sampled trees) precludes use of regression equations for predicting tree weight and calcium content at different ages.

Mean amounts immobilized per year in nonfoliar tissues of the 28 larger trees were 168 ± 20 g oven-dry weight and 1.4 ± 0.2 g Ca. Number of leaves on dogwood trees may be estimated using an index of tree size, but not tree age, as the independent variable (Table 36).

Prediction of root/top ratios by mensurational values were generally unsuccessful. Ratios (with and without leaves for weight

Table 34. Regression equations for dogwood tree (top plus root) weight and calcium content^a

Y Variable (Log ₁₀)	X Variable ^b (Log ₁₀)	Without Leaves				With Leaves ^c			
		Y Intercept	Regression Slope (b)	F	r ²	Y Intercept	Regression Slope (b)	F	r ²
Oven-Dry Weight (g)	D ₁	2.376	2.174	386	0.937	2.482	2.107	314	0.924
	D ₁ H	1.950	1.334	415	0.941	2.070	1.292	325	0.926
	D ₀ H	1.466	1.502	577	0.957	1.600	1.455	432	0.943
	D ₀ D ₁ H	1.813	0.903	705	0.964	1.936	0.875	501	0.951
	D ₁ ²	2.378	1.085	388	0.937	2.484	1.052	316	0.924
	D ₁ ² H	2.106	0.831	456	0.946	2.221	0.805	354	0.932
	D ₀ ² D ₁ ² H	1.896	0.519	742	0.966	2.016	0.503	529	0.953
Calcium (g)	D ₁	0.176	2.367	291	0.918	0.482	2.172	198	0.884
	D ₁ E	-0.278	1.443	262	0.910	0.103	1.297	180	0.874
	D ₀ E	-0.790	1.515	280	0.915	-0.365	1.458	204	0.887
	D ₀ D ₁ H	-0.425	0.976	353	0.931	-0.034	0.880	233	0.900
	D ₁ ²	0.178	1.181	291	0.918	0.484	1.084	199	0.884

Table 34, continued

Y Variable (Log ₁₀)	X Variable ^b (Log ₁₀)	Without Leaves				With Leaves ^c			
		Y Intercept	Regression Slope (b)	F	r ²	Y Intercept	Regression Slope (b)	F	r ²
	D ₁ ² H	-0.113	0.901	295	0.919	0.218	0.826	197	0.884
	D ₀ ² D ₁ ² H	-0.034	0.562	380	0.936	0.006	0.517	251	0.906

^aN = 28. All F values are significant (P < 0.01).

^bD₀ is stem diameter (cm) at ground level; D₁ is diameter (cm) at 1 m; H is tree height (m).

^cWhen calcium content of foliage at maximum (September).

Table 35. Correlations between dogwood tree variables

Variables	N	Coefficient of Correlation (r)	Coefficient of Determination (r ²)	t
Height Diameter at ground level	55	0.820	0.672	10.42 (**)
Height Diameter at 1 m	55	0.855	0.731	11.99 (**)
Diameter at 1 m Diameter at ground level	55	0.960	0.922	25.00 (**)
Age Diameter at ground level	28	0.378	0.143	2.08 (*)
Age Diameter at 1 m	28	0.446	0.120	2.54 (*)
Age Height	28	0.474	0.225	2.74 (*)
Age Weight (without leaves)	28	0.008	< 0.001	0.04 (NS)
Age Calcium content (without leaves)	28	0.164	0.027	0.85 (NS)
Age Root/top ratio (weight, without leaves)	28	-0.106	0.011	0.54 (NS)
Age Root/top ratio (calcium, without leaves)	28	-0.130	0.017	0.67 (NS)
Age % of tree weight in leaves	28	-0.582	0.338	3.64 (**)
Age % of tree calcium in leaves	28	-0.486	0.236	2.84 (**)

Fig. 15. Equations for weight and calcium content of nonfoliar organs (top plus root) of dogwood trees. D_0 = diameter (cm) at ground level; D_1 = diameter (cm) at 1 m; H = height (m). $N = 28$; $r^2 = 0.964$ ($P < 0.01$) for weight and 0.931 ($P < 0.01$) for calcium.

Table 36. Regression equations for number of leaves on dogwood trees^a

X Variable ^b	Y Intercept ^c	Regression Slope (b ± SE)	F	r ²
Tree age (yrs)	2671.	44.7 ± 88.6	0.26 (NS)	0.010
D ₀ D ₁ H	994.	39.4 ± 5.0	51.08 (**)	0.701
Log ₁₀ (age)	2.42	0.88 ± 0.51	2.98 (NS)	0.103
Log ₁₀ (D ₀ D ₁ H)	2.25	0.72 ± 0.08	86.18 (**)	0.768

^aN = 28.

^bD₀ = diameter (cm) at ground level; D₁ = diameter (cm) at 1 m; H = height (m).

^cY = number of leaves on trees as estimated with equation in Fig. 2. Log₁₀Y used when X variables were log₁₀ values.

and calcium) for the 28 large trees were estimated using the mensurational value $D_0 D_1 H$. Similar estimates were made for the 20 seedlings using height and (height x diameter at ground level) as independent variables. Equations were calculated using nontransformed data and then with $\log_{10}$ values of the variables. None of the 16 equations for seedlings and only three of eight for the larger trees were significant.

$$(1) \text{ Root/top ratio (calcium, without leaves) } = 0.1476 - 0.0004 (D_0 D_1 H)$$

$$F = 4.80 (*); r = 0.395; N = 28$$

$$(2) \text{ Root/top ratio (calcium, with leaves) } = 0.0710 + 0.0004 (D_0 D_1 H)$$

$$F = 19.71 (**); r = 0.656; N = 28$$

Prediction (2) using $\log_{10}$ values was also significant but is not shown here since it is less reliable than the one shown ($F = 12.75$). D_0 is stem diameter (cm) at ground level; D_1 is stem diameter (cm) at 1 m; H is tree height (m).

The root/top ratio generally decreases with age and increasing size of plants (Bray 1963; Monk 1966). Lack of significant correlation between age and root/top ratios (Table 35) may be due to the narrow range of tree ages (Table 3). However, root/top ratios of the 28 larger trees is significantly different than those of the 20 seedlings (Table 6). These data probably apply only to understory trees since distribution of weight within trees is dependent upon the degree of shading (Kramer 1956).

T. Calcium Turnover by Dogwood Trees

The "calcium pumping efficiency" of trees may be defined as the amount of calcium lost from the tree by leaf fall expressed as a

percentage of calcium in nonfoliar organs. This measure of calcium turnover by the 28 larger trees is $71\% \pm 4$. Thus, nonfoliar tissues (the "pump") transport to leaves the equivalent of 71% of the "pump's" calcium which is subsequently released as litter. This value is greater if calcium in foliar leachate and other litter material are also considered.

Generally, most trees "pump" large quantities of calcium, returning about 55 to 95% of their annual calcium uptake to the forest floor in leaf fall (Ebermayer 1876; Dengler 1944; Remezov, Bykova, and Smirnova 1955; P'Yavchenko 1960; Hartmann 1963; Miller 1963; Ovington 1965). Turnover rates vary due to differences among species and among age classes within a species. Conifers usually return a smaller percentage of their annual uptake than do broadleaf species, and 20 to 50-year-old trees generally have higher turnover rates than trees of other ages.

Concentration of calcium in leaves significantly alters the distribution of calcium in dogwood trees (Table 37). Since seedlings have a greater percentage of their total calcium in leaves, their "calcium pumping efficiency" ($114\% \pm 9$) is significantly greater ($P < 0.01$) than that of larger trees ($71\% \pm 4$).

Table 37. Effect of leaves on weight and calcium
distribution in dogwood trees^a

	Without Leaves	With Leaves	t
Root/Top Ratio			
Weight	0.30 ± 0.01	0.24 ± 0.01	4.2 (**)
Calcium	0.17 ± 0.01	0.09 ± 0.01	5.7 (**)
% in Top			
Weight	76.8 ± 0.8	80.6 ± 0.7	3.6 (**)
Calcium	85.5 ± 0.5	91.4 ± 0.4	9.7 (**)
% Calcium			
Top	0.86 ± 0.02	1.24 ± 0.02	13.4 (**)
Roots	0.51 ± 0.04	0.51 ± 0.04	
Tree	0.77 ± 0.02	1.10 ± 0.02	11.7 (**)

^aMean ± SE; N = 28 larger trees.

V. SUMMARY AND CONCLUSIONS

Distribution of calcium in flowering dogwood trees and major pathways of calcium circulation in the tree-soil system were studied to evaluate the function of this common understory species in the cycling of an essential element.

Calcium concentrations (percentage of dry weight) and root/top ratios (weight and calcium) of dogwood trees from sites with significantly different concentrations of exchangeable soil calcium were not significantly different. Calcium concentration and root/top ratios were significantly greater for seedlings than for larger trees, and seedlings returned a greater percentage of total tree calcium to the forest floor in leaves than did the larger trees.

Calcium content per leaf increased during the growing season; leaf calcium was 2.8% of dry weight just before abscission, when leaves contained 17% of weight and 43% of calcium in the entire tree. Variation in calcium content (absolute or percentage of dry weight) among leaves of various sizes caused difficulties in obtaining valid mean values since dogwood trees produced new leaves throughout the growing season.

Inflorescences and fruits may account for a large fraction of annual contribution to litter by trees growing in the open (38% of weight and 28% of calcium). Decomposition rates of leaves, twigs, inflorescence bracts, and fruits are different. Rate of leaf decomposition varies among seasons and among sites with a mean weight and

calcium loss of about 80% within one year after abscission. Addition of dogwood leaves to loblolly pine litter did not increase rate of pine needle decomposition.

Twelve dogwood trees were stem-tagged with ^{45}Ca in early May and studied until leaf abscission six months later. One month after inoculation 73% of the inoculum was in leaves. After leaf fall only 27% of the inoculum was in woody tissues (stem 11%, branches 15%, roots 1%). Losses (as percentage of inoculum) were by leaf fall (64%); foliar leaching (6%), stemflow ($\ll 1\%$), and insect damage (3%). Calculated amount of radiocalcium in the tree-soil system after leaf fall, $106\% \pm 5$ of the inoculum, was well within limits of sampling error. Only 12% of the ^{45}Ca removed from trees by precipitation had reached the soil by the end of the experiment; some of the remainder was in ground vegetation, but most of it was in the litter layer. Dogwood club galls did not significantly alter the distribution of weight, calcium, or ^{45}Ca in the trees.

The estimated radiological dose received by the apical meristems (less than 100 rads during the entire experiment) was not sufficient to affect tree growth.

Transpiration stream in dogwood stems spirals dextrally. Ascent of ^{47}Ca in trees was much slower than that of dye, which was probably due to electrostatic retention of calcium ions in the xylem. Only 12% of ^{45}Ca in tree stems was water-soluble six months after inoculation.

Precipitation during the growing season removed 10% of the maximum amount of calcium in leaves; this was equivalent to 8% of total

calcium contributed to litter by foliar leachate and leaf fall. Foliar leachate under dogwood trees had higher concentrations of calcium than that under pine trees alone. Amount of calcium in foliar leachate under dogwoods was significantly related to the number of days since the previous period of precipitation. Calcium was more easily leached from senescent leaves than from vigorous ones. Foliar absorption permits entry of calcium into dogwood trees, but negative results were obtained in experiments with bark absorption.

There was no evidence from laboratory experiments that calcium was exuded from roots. There may be underground transfer of calcium by intraspecific root grafts, which were shown to occur between dogwood trees.

Dogwood trees accounted for 0.2% of the weight and 1.8% of the calcium in the aboveground portion of an 18-year-old loblolly pine plantation in which pine accounted for 99.3% of the basal area and dogwood density was 286 trees/ha.

To be most effective as a "nutrient pump," a plant should redistribute nutrients from lower to upper layers of the soil where a greater proportion of them may be utilized by other plants (with emphasis on the most important, ecologically or economically, species in the stand). This is accomplished by absorbing nutrients deep in the soil and depositing large quantities of them (compared to immobilization in woody tissue) on the forest floor in leaves that decompose rapidly. Not all these criteria are met by flowering dogwood. Since it is shallow-rooted, dogwood competes in pine stands with the equally

shallow-rooted pine trees for water and nutrients. Accumulation of calcium in dogwood leaves accounted for the high "calcium pumping efficiency" of 71% (calcium lost from the tree by leaf fall as percentage of calcium in nonfoliar organs). Mineral soil under dogwoods had significantly greater concentrations of exchangeable calcium than did soil not under dogwood trees. Dogwood is probably most beneficial in limiting movement of nutrients (particularly calcium) through the soil profile, thus keeping them in the rooting zone of other species.

Although emphasis in this study was on nutritional aspects of calcium cycling, movement of ^{45}Ca may be of interest following peaceful uses of nuclear detonations (James and Fleming 1966) since it is produced in soil and water by neutron activation (Klement 1959). In addition, since strontium behavior is similar to that of calcium in geochemical (Day 1963) and biological (Wasserman 1963; Aleksakhin and Ravikovich 1966; Russell 1966; Bollard and Butler 1966) systems, results of this study may contribute to the understanding of ^{90}Sr circulation in forests.

The only generalization which can be made concerning the estimated calcium budget in forest stands (Ovington 1959b; Miller 1963; Aleksakhin and Ravikovich 1966) is that large quantities of calcium are transferred among many compartments during a single growing season. More specific statements must await the completion of additional investigations in contrasting forest types.

Research in forest fertilization (Stoeckeler and Arneman 1960; Mustanoja and Leaf 1965) will be better directed, and results of such

programs predicted with greater accuracy, when circulation patterns of essential elements in forests are more thoroughly understood.

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