INFLUENCE OF OAKS ON THE ACCUMULATION OF CALCIUM IN FORESTS[1]/

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Abstract.--Forests of the Illinois Ozarks, which are oak-dominated but which also contain numerous other hardwood species, were studied to determine the degree to which the presence and types of oaks affect calcium storage in the overstory. Large differences in the amounts and distribution of calcium in hardwood tissues were found both within trees and among tree species. Stem bark which formed about 20% of the biomass is a major sink for calcium in these forests and contains up to 82% of the total calcium in some oaks. In contrast, bole wood forms about 70% of tree biomass but contains 10% or less of the calcium in several oak species. Black and white oak each form about 30% of the basal area of these forests and contain 36% and 42%, respectively, of the above-ground calcium mass. White oaks are major Ca sinks because they have very high bole bark Ca contents and have high total biomass. Red oaks are major Ca sinks because of high total biomass. Because of these accumulations, the total calcium mass in the overstory in these forests varies markedly and proportionally to the abundance of oaks. Comparison of calcium mass to biomass ratios reported for a variety of other temperate forests substantiates this effect of oaks on calcium storage.

Keywords: biomass, Illinois, mixed-hardwoods, temperate forests

INTRODUCTION

Oaks are widely distributed, major components of many forests types throughout the temperate zone (Braun 1950, Fowells 1965, Eyre 1968, Eyre 1980). Nutrient cycling studies have shown that oaks are generally rich in nutrients and that some species accrue exceptionally high levels of calcium (Ca) in certain tissues. Duvigneaud and Denaeyer-DeSmet (1970) found that Rennie's extrapolations, which indicated relatively large mineral masses especially Ca for old deciduous forests, agreed quite well with their measurements in Belgian oak forests. They concluded that the temperate deciduous oak ecosystem may be distinguished by its nutrient cycle.

The possible effects on soil reserves from accumulations of large amounts of Ca by trees is of concern in managed forests (Boyle and EK, 1972; Weetman and Weber, 1972; Johnson et al. 1982). Some species such as dogwood accumulate large amounts of Ca in foliage (Thomas 1969) which, assuming minimal or no retranslation, return a large proportion of uptake to soil through annual restitution. In contrast, oaks which sequester much of their Ca in perennial tissues effectively withdraw it from the annual nutrient cycle for many years.

Oaks (Bockheim et al. 1984) and other deciduous species (Alban 1982) which have a high affinity for Ca can cause substantial redistribution from soils to biomass. This makes Ca more susceptible to removal from oak-dominated ecosystems by harvesting than nutrients which accumulate in foliage. Johnson et al. (1982), who studied this problem, concluded that excessive Ca removal would result from whole-tree harvesting on sites with low Ca reserves. They recommended dormant season harvesting to conserve foliage Ca. Recent work by Bockheim et al. (1984) also raised the concern that excessive removal of Ca from some soil horizons by uptake

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by oaks may exacerbate the sensitivity of soils to atmospheric deposition.

Substantial differences occur among species in the amounts and storage locations of Ca within deciduous species (Rodin and Bazilevich 1967, Duvigneaud and Denaeyer-DeSmet 1970, Johnson and Risser 1974, Alban et al. 1978, Jones 1980). Because of the affinity of oaks for Ca, their abundance and distribution are likely to be major factors in determining the quantity, distribution, and cycling of Ca in mixed hardwood stands such as occur in the Ozark Hills in Illinois. The current study was undertaken in these forests to establish the comparative roles of oaks and several other hardwood species in calcium storage and distribution in these forests.

STUDY AREA

Forests at two locations within the unglaciated Ozark Hills of southwestern Illinois were studied. This Division as defined by Schwegman (1973) has a maximum elevation of 340 m, local relief of up to 60 m, and very steep, wooded slopes (Harris et al. 1977). Upland soils are predominantly Typic Paleudalfs and Typic Hapludalfs. Soils on uneroded ridges have formed in loess $\geq$6 m deep and are well supplied with plant nutrients, except N (Fehrenbacher et al. 1967). Soils on steep slopes may have cherty contents of 85-90% within the profile and only medium fertility. Precipitation averages 120 cm per year, albeit local summer droughts may occur, and the mean frost free period exceeds 200 days per year (Page 1949).

Species composition, basal area and density (table 1) are typical for early mature and mature forests in this region. Oak and hickory species predominate in upland forests, although many arboreal species are present (36 in the study areas). These forests include the salient characteristics described by Braun (1950) for forests of the Western Mesophytic Forest Region.

Twelve tree species were sampled for nutrient concentrations in five tissues (foliage, branch wood and bark, and bole wood and bark) between late August and mid-October, 1978. For abundant species, a total of 20 dominant or codominant trees per species were sampled from or near randomly distributed permanent plots established during previous mineral cycling studies. For species which were abundant at only one of the locations, ten trees each were sampled. Samples were collected only from branches occupying the lower one-third of the canopy. Branch canopy position, although statistically significant, usually accounted for four percent or less of the total variation of foliar nutrient concentrations (Jones et al. 1980); resources subsequently were allocated to

Table 1.--Vegetational characteristics and major species at two study sites in southwestern Illinois. Data are from Rosson (1981).

Structure and Composition	Alexander County Site	Union County Site
Stand Basal area[1/] ($m^2 \cdot ha^{-1}$)	21.9	24.2
Stand Density[1/]	748	868
	---------- % of Stand BA----------	
Acer saccharum	2	3
Carya glabra	4	5
Carya ovalis	4	3
Carya ovata	2	<1
Fagus grandifolia	<1	2
Fraxinus spp.[2/]	2	<1
Liquidambar styraciflua	<1	3
Liriodendron tulipifera	2	2
Quercus alba	29	28
Quercus rubra	8	6
Quercus stellata	2	<1
Quercus velutina	30	27
Sassafras albidum	2	3
Other Species[3/]		

[1/] Including stems $\geq$ 27.9 cm dbh.
[2/] Includes both *F. americana* and *F. pennsylvanica*.
[3/] Other species include: *Acer rubrum*, *Amelanchier arborea*, *Carpinus caroliniana*, *Carya cordiformis*, *C. texana*, *C. tomentosa*, *Cercis canadensis*, *Cornus florida*, *Diospyros virginiana*, *Juglans nigra*, *Magnolia acuminata*, *Morus rubra*, *Nyssa sylvatica*, *Ostrya virginiana*, *Platanus occidentalis*, *Prunus serotina*, *Quercus coccinea*, *Q. muehlenbergii*, *Rhus typhina*, *Tilia americana*, *Ulmus alata*, *U. americana*, *U. rubra*.

increase the number of species sampled, which accounted for 75 percent or more of the variance in nutrient concentrations (Jones et al. 1980). Foliage and branch tissues were obtained from branches harvested from sample trees; bole wood samples were collected by increment borer at dbh; bole bark was collected by removing sections from the bole at the same level.

Samples were oven-dried at 70 degrees C. and ground with a Wiley Mill to pass a 2 mm mesh screen. Oven-dried samples (0.5-0.7 g), weighed to the nearest 0.1 mg, were digested using nitric-perchloric acid (Smith 1953). Calcium concentrations were measured by atomic absorption spectrophotometry using a nitrous oxide flame. A 5% lanthanum solution was added to all samples to reduce interferences associated with Ca determinations (Perkin-Elmer 1973).

Biomass pools were calculated using equations developed by the allometric method for each species (Stortz 1975, Myers et al. 1976, Raisanen 1977). The equations are of the nonlinear form:

$$\text{Weight (kg)} = b_0 \cdot D^{b1} \cdot H^{b2}$$ where

b_0, b_1, b_2 are constants, D is diameter at breast height (137 cm), and H is total tree height. The equations were developed for trees $\geq$ 15 cm dbh which was the minimum diameter for trees included in this study. Scientific nomenclature follows Mohlenbrock (1975).

RESULTS

Tissue Concentrations

Calcium concentrations given in Table 2 varied considerably among both species and tissues. Members of the white oak group which are abundant in these forests (table 1) had relatively high Ca concentrations for most tissues (table 2). Red oaks (Quercus rubra and Q. velutina) of similar abundance had markedly lower Ca concentrations in bole bark.

Table 2.--Mean Calcium concentrations (mg. g^{-1}) in tissues of twelve hardwood species in southwestern Illinois.

Species	Foliage	-- Branch --- Bark	Wood	---- Bole ---- Bark	Wood
Acer sacchaum[1/]	15.4	25.9	2.5	27.6	1.88
Carya glabra[2/]	18.9	32.8	3.3	24.7	1.60
Carya ovata[2/]	19.3	41.9	3.6	30.1	2.10
Fagus grandifolia[1/]	8.0	22.4	1.7	25.9	1.37
Fraxinus spp.[1/]	18.3	11.5	1.2	30.9	0.97
Liquidambar styraciflua[1/]	13.2	29.1	1.3	23.2	1.27
Liriodendron tulipifera[2/]	21.5	11.5	1.0	9.0	0.79
Quercus alba[2/]	12.7	27.7	3.9	66.1	1.15
Quercus rubra[2/]	11.7	24.8	4.7	21.6	0.86
Quercus stellata[1/]	8.1	27.2	3.6	83.4	2.13
Quercus velutina[2/]	8.7	26.5	4.8	31.7	1.16
Sassafras albidum[2/]	12.7	4.9	1.1	3.6	0.36

[1/]Species sampled at one location; N size = 10 trees.
[2/]Species sampled at two locations; N size = 20 trees.

Concentrations of Ca were highest in bark of all species except Liriodendron tulipifera and Sassafras albidum, where in each case foliage concentrations were greater. Bole bark accumulated relatively high concentrations of Ca in all species except S. albidum and Liriodendron tulipifera. Especially apparent was the large accumulation of Ca in stem bark of Q. stellata and Q. alba. These are 163 and 109 percent higher than the next highest concentration which is in Q. velutina. However, for these species, branch bark concentrations were not appreciably greater than most other species and were less than some. The relatively low foliage concentrations of Ca were also in marked contrast to high bark concentrations and to concentrations in foliage of several other species. In these forests hickories also accumulated Ca in certain tissues, especially foliage and branch bark.

Biomass

Total biomass, which includes complete tree minus stump (≈30 cm) and roots, but includes leaves and branches was 155-160 t · ha^{-1}. Neither biomass nor tissue concentration differences were significant ($P \leq .10$) between locations. Biomass of individual species ranged from 3 to 63 t. (fig. 1), and its relative distribution among species as illustrated for one study site generally followed the same pattern of basal area (table 1). Q. velutina contained the largest proportion of biomass followed in decreasing order by Q. alba, Q. rubra, Carya glabra, C. ovata, Liriodendron tulipifera and Fraxinus spp. Biomass distribution among tissues for each of the species was bole wood >>>> bole bark >> branch wood > branch bark > foliage, except Fraxinus spp. which had more branch wood than bole bark. Distribution of biomass among tissues for all species was: 60-77% in bole wood, 13-20% in bole bark, 5-18% in branch wood, 1-7% in branch bark and 0.6-3% in foliage.

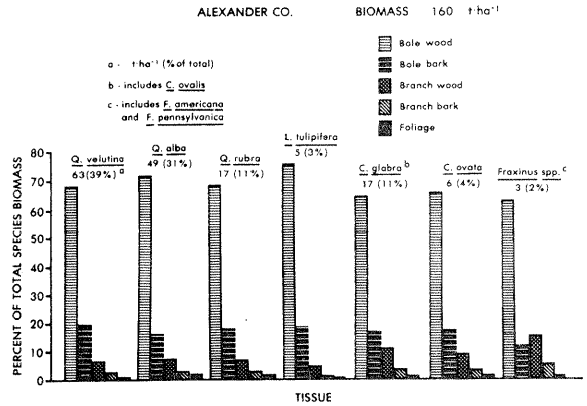

Figure 1.--The distribution of biomass among major tree species and tissues within species in upland oak forests in southwestern Illinois.

Calcium Standing Crop

The total Ca standing crop averaged 1431 and 1445 kg . ha^{-1} at the two sites. The typical distribution of Ca standing crops in decreasing order by species as illustrated by one site was: Q. alba, Q. velutina, Carya glabra, Q. rubra, C. ovata, Liriodendron tulipifera and Fraxinus spp. (fig. 2). Estimates for Q. stellata are not included because separate allometric biomass equations are not currently available. The decreasing importance of each tissue as a Ca reservoir followed the order of: bole bark >>>>> branch bark ≈ bole wood > foliage ≈ branch wood (fig. 2). Bole bark of all species was an important reservoir for Ca, but was particularly important for storage in Quercus alba and Q. velutina. Proportions of total Ca storage in bole bark varied from a low of 58% in both Carya species to a high of 82% in Q. alba. Relative Ca storage among tissues ranged from 58-82% in bole bark, 7-26% in bole wood, 6-17% in branch bark, 2-6% in branch wood and 2-6% in foliage, depending on the species.

DISCUSSION

Calcium Concentrations

Concentrations of Ca in bole bark determined in this study for Q. stellata and Q. alba compare

well with the values of 90.2 mg . g^{-1} reported by Johnson and Risser (1974) for Q. stellata in Oklahoma. Calcium concentrations were 30.0 mg . g^{-1} and 43.1 mg . g^{-1}, for outer and inner bark,

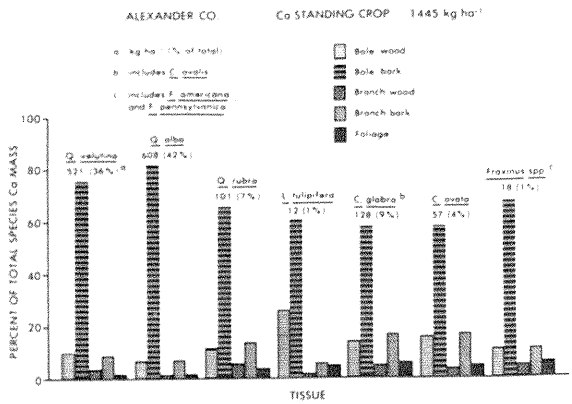

Figure 2.--The distribution of calcium among major tree species and tissues within tree species in upland oak forests in southwestern Illinois.

respectively, for red oak species in the Delta region of Louisiana (Choong et al. 1976), and 32-34 mg . g^{-1} in Belgium Oak Woods (Duvigneaud and Denaeyer-DeSmet 1970). But in an oak-pine forest in the eastern United States, concentrations in Q. alba and Q. coccinea were much lower, 25.0 and 13.4 mg . g^{-1}, respectively (Woodwell et al. 1975).

Several factors may be related to high concentrations of Ca in bark including contamination by airborne particulates, soil nutrient status, and physiological attributes. Deposition of dust contributes significant amounts of nutrients including Ca to these forests (Weaver, unpublished data), and undoubtedly some surface dust contamination of bark occurs. However, the large differences between Ca concentrations in bark among the various species suggest a physiological basis.

Oak bole bark Ca concentrations may be an important indicator of soil Ca status with luxury consumption by the trees increasing proportionally to soil Ca availability, as suggested from several studies. For example, the Oklahoma post oak-blackjack oak forest studied by Johnson and Risser (1970) is growing on a limestone soil. Calcium nodules are present in the solum at the southern Illinois sites (Harris, cited in Luvall 1976) and at the Wavreille forest in Belgium (Duvigneaud and Denaeyer-DeSmet 1970). Although no information is known for the soils at delta site in Louisiana (Choong et al. 1976), periodic nutrient flushes from flooding may occur in this region. The oak-pine forest soil at Brookhaven is known to be droughty, acidic and nutrient poor (Reiners 1965). These reports indicate that soil nutrient status influence differential uptake and storage of Ca in oaks.

Species in the white oak group (Leucobalanus), Q. alba and Q. stellata in this study and Q. stellata in the Oklahoma study have greater Ca concentrations in bole bark than species of the red oak group (Erythrobalanus). This seems to indicate different accumulation rates and physiological attributes between the two subgenera.

The large difference between branch and bole bark concentrations shows that large amounts of Ca are irreversibly accumulated in the bole bark of the white oaks. Initial accumulation of large amounts of Ca in bark tissues of Q. alba and Q. stellata could be associated with retranslocation. Calcium retranslocation has been demonstrated in Q. prinus (Ostman and Weaver 1982) and perhaps occurs in other members of the Leucobalanus. However, a mechanism for phloem transport which involves the movement of Ca released from phytin (Sutcliff 1976) and active transport would function only in living components of the bark (Zimmermann and Brown 1971). As phloem and perhaps other bark tissues undergo senescence, Ca would become irreversibly sequestered. Similar processes may occur in branch bark tissues, but the much larger ratio of non-living and senescent to physiologically active tissue in boles would account for their higher Ca concentrations. The development of such a mechanism involving retranslocation would indicate substantial physiological differences among oaks and its occurrence should be investigated.

Biomass and Calcium Pools

Mean total above ground biomass for the seven species is at the lower limits (150 to 300 t · ha^{-1}) (Rodin and Bazilevich 1967) for deciduous and broad-leaved forests, but it is generally about average for other oak and oak-hickory forests (Duvigneaud and Denaeyer-DeSmet 1970, Monk et al. 1970, Art and Marks 1971, Rolfe et al. 1978). Biomass of the Illinois stands is underestimated because only seven species were measured and stems $\leq$ 15 cm dbh were not included. Total above ground biomass of these stands is estimated to be 200 t · ha^{-1}.

Calcium standing crop values are within ranges of other studies in oak and oak-hickory forests (Duvigneaud and Denaeyer-DeSmet 1970, Rochow 1975, Rolfe et al. 1978, Henderson et al. 1978). Johnson and Risser (1974) reported higher biomass estimates and Ca pools which were three times greater than this study. Their large Ca pools are a combination of high Ca concentrations in Q. stellata stem bark and the occurrence of 77% of the stand biomass in this species and the inclusion of smaller size classes in measurements.

Species composition of the forest is an important factor determining nutrient mass and distribution because species accumulate nutrients differentially within tissues. For example, in these forests the mass of Ca is closely related to the abundance of oak species, especially members of the white oak group, due to the concurrence of high Ca concentration and large biomass for the same tissue. Conversely, hickories contain lesser amounts of the Ca because they accumulate Ca in tissues with small biomass. The three oak species contain most of the biomass (83%) and Ca (85%).

It is evident in Figures 1 and 2 that the biomass distribution within a species is dissimilar to the pattern of calcium storage. The important factor is the reversal in importance of wood and bark. Woody tissues which comprise most of the biomass have low calcium contents, while bark tissues (especially bole bark) contain such great concentrations that they contain a disproportionally large amount of total tree Ca. Similar relationships exist for other studies of oak and oak-hickory forests cited in this study and for non-oak species (Alban et al. 1978 and Lambert et al. 1980). Therefore the importance of bark cannot be overlooked as an essential Ca pool in a variety of forest types.

Oak forests accumulate large amounts of Ca, a concept reflected by this study, which shows the importance of oaks in storing Ca and identifies bole bark as the principal sink in the forest biota studied. Table 3 shows how oak composition, abundance and species differences affect Ca storage in various forest types. The Ca/biomass values are ratios of Ca to biomass in kg . ha^{-1} multiplied by 1000 to provide easily comparable values for different forests. Ratios are generally higher for forest types with oak present. The Brookhaven oak-pine forest is a good example of the influence of oaks on the Ca storage of a forest. Pine forest Ca/biomass ratios are generally near one, but the presence of oaks, especially Q. alba increases the ratio to 5.1 or more. Intermediate ratios for northern hardwoods, aspen and spruce reflect their relatively high Ca content in bark. Conversely, the pines tend to have more Ca in wood than bark, but the levels are low in comparison to oaks and many other hardwoods.

SUMMARY AND CONCLUSIONS

The affinity of species of the white oak group for Ca is substantiated by this study. Concentrations in tissues of red oak species are not notably higher than for many non-oak species, but total Ca accumulation is large because these species are a large proportion of total forest biomass. Further, the distribution of Ca among various tissues is an important factor in determining its total mass in forest stands. For oaks (and many other species), bole bark is the major Ca sink. Many past studies have included bole bark tissue with wood when determining Ca pools which obscures the significance of this tissue as a Ca sink. In this study, Q. alba bole bark contained 82% of the white oak Ca pool, but bole wood contained only 7%. This shows the importance of bole bark which represents only 16% of the biomass in Q. alba. Non-oak species are less important Ca sinks in these forests because their total biomass is relatively small and highest Ca concentrations often occur in tissue with limited total biomass.

Table 3.--Comparison of Ca: biomass ratios [a/] for forest types.

Forest Type	Location	Ca/Biomass x 1000	Source
Post Oak-Blackjack Oak	Oklahoma	20.1	Johnson & Risser 1974
Oak-Hickory	Illinois Ozarks	9.0	Weaver & Jones (this study)
Oak-Hickory	Shawnee Hills, Illinois	8.3	Rolfe et al. 1978
Oak-Hickory	Walker Branch ORNL, TN	8.0	Henderson et al. 1978
Oak-Hickory	Coweeta Hydrologic Laboratory, NC	6.0	Henderson et al. 1978
Oak-Hornbeam-Beech	Belgium	5.6	Duvigneaud and Denaeger
Oak-pine	Brookhaven National Lab. NY	5.1	Woodwell et al. 1975
Oak-Hickory	Central Missouri	4.9	DeSmet 1970 Rochow 1975
Oak-Ash	Belgium	3.5	Duvigneaud and Denaeger DeSmet 1970
Northern Hardwoods	Hubbard Brook Expt Forest, NH	6.7	Whittaker et al. 1979
Aspen	Minnesota	5.1	Alban et al. 1978
White spruce	Minnesota	4.8	Alban et al. 1978
Jack pine	Minnesota	1.4	Alban et al. 1978
Jack pine	Canada	1.2	Foster & Morrison 1976
Red pine	Minnesota	1.1	Alban et al. 1978
Loblolly pine	North Carolina	1.0	Switzer & Nelson 1972
Douglas fir	H. J. Andrews Watershed, WA	1.0	Henderson et al. 1978

a/Ca: biomass ratio = (stand Ca kg . ha^{-1}/stand biomass kg. ha^{-1}) X 1000.

Our results indicate that return of bark to sites sensitive to Ca removal would be more effective than dormant season harvest in offsetting the losses from harvesting oak forests. Additionally, any factors such as selective removal of oaks, regeneration harvesting, fire, other perturbations or natural stand development which alter the proportional composition of white oaks and biomass distribution among tissues will effect concomitant changes in ecosystem Ca storage.

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