Effects of Rhododendron (Rhododendron maximum *L.) on Regeneration of Southern Appalachian Hardwoods*

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ABSTRACT. The long-term record of forest composition at the Coweeta Hydrologic Laboratory, North Carolina, was used to assess the change in tree regeneration patterns over a 34–38 year period, and to evaluate the impact of rhododendron on that change. Density-diameter distributions of dominant tree species were determined from 1934–35 and 1969–72 inventories of high density rhododendron (HR) and low density rhododendron (LR) plots. Oak and maple regeneration, which was abundant in 1934–35 due to past disturbance, decreased by 1969–72 as the canopy closed. Total tree regeneration was lower in HR plots than in LR plots and the magnitude of the difference increased with time. In 1969–72, regeneration of chestnut oak and white oak was depressed in HR plots, whereas that of red maple was not; scarlet oak and black oak regeneration was poor at all sites regardless of rhododendron. Hemlock was unique among canopy species in that its sapling density increased with time and abundance of rhododendron. FOREST SCI. 31:226–233.

ADDITIONAL KEY WORDS. Coweeta, density-diameter distribution, oak, red maple.

THIS PAPER IS PART of a long-term ecological study of past and present forest composition at the Coweeta Hydrologic Laboratory, Otto, North Carolina. The existence of hundreds of permanent plots at Coweeta, which were inventoried in 1934–35 and again in 1969–72, makes it possible to document long-term compositional changes and provides a basis for predicting future forest composition.

Preliminary observation of the oak-dominated forest of Watershed 2 at Coweeta revealed that forest areas on lower to middle slopes with and without rhododendron (*Rhododendron maximum* L.) understory were similar in canopy composition, but different in density-diameter distribution of dominant species. Hardwood sapling density appeared to be inversely related to rhododendron density. These observations suggest that: (1) current canopy trees became established at a time of low rhododendron density, (2) the density of rhododendron increased between the time of the first and second census, and (3) the regeneration of canopy species is being affected by rhododendron. Direct verification of a temporal change in the density of rhododendron in permanent plot sites is impossible because the species was not tallied in the 1934–35 inventory.

The extent of establishment and spread of rhododendron in the southern Appalachian forests during the past half century is an unsettled question. McGee and Smith (1967), in a study of rhododendron thickets at the Bent Creek Experimental Forest near Asheville, N.C., reported that most of them became established between 1897 and 1917, a period that parallels the cessation of fire and grazing disturbance in the region. McGinty (1972), in a study of the ecological role of rhododendron at Coweeta, determined the age of 30 specimens and concluded that the establishment of rhododendron thickets at Coweeta coincided with the opening of the canopy caused by the death of American chestnut trees. However, Johnson and Kovner (1956) reported specimens of rhododendron at Coweeta up to 9 inches DBH, which were 85 to 100 years old.

We suggest that the long history of burning of forests at Coweeta until the turn of the century (Williams 1954) prevented the establishment of rhododendron thickets over much of the area. Logging operations in the early twentieth century dramatically opened the canopy and stimulated the establishment and growth of understory species, including

rhododendron. A subsequent opening of the forest canopy in the 1930's by the death of American chestnut may have allowed both establishment of new rhododendron thickets in certain places and an overall stimulation of growth and vegetative propagation within established thickets.

This study was designed to assess the impact of rhododendron in the process of regeneration of dominant species in two forest types: (1) Chestnut Oak, where chestnut oak is the dominant species and white oak is uncommon, and (2) Mixed Oak, where scarlet, black, and white oak are dominant or codominant and where the latter species is common. Density-diameter distributions of dominant tree species were determined for high and low density rhododendron sites using data collected at two times, 34–38 years apart, in order to determine how their regeneration patterns have changed through time and to assess the impact of rhododendron in that change.

METHODS

Study Area.—The 1,626 ha (4,018 acre) Coweeta Basin is part of the Coweeta Hydrologic Laboratory, North Carolina, established in 1933 and administered by the U.S. Forest Service. The area (lat. N35°03', long. W83°27') lies in the Blue Ridge physiographic province with elevations from 679 to 1,592 m. Precipitation varies from 178 cm at lower elevations to over 250 cm on the upper slopes. Mean annual temperature is 13°C. Prior to the 1840's when white settlers moved into the Coweeta Basin, the area was occupied by Cherokee Indians. According to Williams (1954), both groups practiced light semiannual burning and grazing. Fall burning removed the fallen leaves, exposing acorns and nuts for cattle to forage. The purpose of the spring burning was to kill rhododendron, mountain-laurel, briars, and weeds and to improve the growth of grass. These practices continued until the turn of the century. Selective logging occurred between 1909 and 1923 (Iglich 1975). The U.S. Forest Service acquired the land in 1924 and since that time only experimental logging treatments in designated watersheds have occurred. The chestnut blight (*Endothia parasitica*) had spread to Coweeta during the 1920's (Iglich 1975) but had little effect prior to 1934 (U.S. Forest Service files). By 1941 most of the chestnuts over 15 cm DBH were probably dead (U.S. Forest Service Coweeta files).

Vegetation of the Coweeta Basin can be divided into four main forest types: Northern Hardwoods, Cove Hardwoods, Oak-Pine, and Oak-Chestnut (Phillips and Ragsdale, in prep.). Only plots from the latter forest type were used in this study. Prior to the chestnut blight in the late 1930's American chestnut (*Castanea dentata*) dominated the Oak-Chestnut forest type with various species of oaks as subdominants. These oaks have now attained dominance, with white oak (*Quercus alba* L.), black oak (*Q. velutina* Lam.) and scarlet oak (*Q. coccinea* Muenchh.) dominant at low elevations in a Mixed Oak subtype, and chestnut oak (*Q. prinus* L.) dominant at mid-elevations in a Chestnut Oak subtype. These subtypes correspond to the "mixed oak-hickory" and "chestnut oak" types of Cooper and Hardin (1971) for forests of the southern Blue Ridge Escarpment. Other important species include northern red oak (*Q. rubra* L.), red maple (*Acer rubrum* L.), and hickory (*Carya* spp. Nutt.).

Sampling.—During 1934 and 1935, thirteen cruise lines at 201 m (10 chain) intervals were established across the Coweeta Basin on a bearing of 330°. The lines were divided into 0.81 ha (0.2 acre) segments 20.1 m (1 chain) long and 40.2 m (2 chains) wide. Each of the 977 segments was permanently marked with stakes. Trees were tallied by species beginning with a 1.3–8.9 cm (0.5–3.5 inch) DBH class which was increased by 2.54 cm (1 inch) increments thereafter. During 1969 to 1972, the 403 permanent plots which occurred on control watersheds, undisturbed since 1934, were re-inventoried in the same way. Percent slope, aspect, elevation, and slope position (ridge, upper, middle, lower, and cove) were also recorded for each plot. Rhododendron (*Rhododendron maximum* L.) and mountain-laurel (*Kalmia latifolia* L.) were tallied only in the second inventory, using the procedures described above.

Analysis.—All plots on lower to middle slopes between 702–823 meters (Mixed Oak forest type—MO) and 885–1,006 meters (Chestnut Oak forest type—CO) were arranged according to the percent basal area of rhododendron. Elevations intermediate between these ranges were not used, to avoid ecotonal forest types. Those in which rhododendron had a 1969–72 relative basal area <2 percent were designated Low Rhododendron (LR; 24 plots for

MO, 32 plots for CO) while those with >15 percent rhododendron were designated High Rhododendron (HR; 20 plots for MO, 32 plots for CO). The remainder were not used in this study. Mean rhododendron densities for LR plots were 94 stems/ha (MO) and 101 stems/ha (CO), and for HR plots were 3,960 stems/ha (MO) and 4,163 stems/ha (CO).

Five dominant tree species were selected for examination of density-diameter distributions: chestnut oak, white oak, black oak, scarlet oak, and red maple. The criterion for inclusion was the occurrence as one of the three most dominant species (based on 1969–72 relative basal area) in >25 percent of the MO and/or CO plots. Eastern hemlock (*Tsuga canadensis* [L.] Carr.) was also included because of its common association with rhododendron.

For each species, eight density-diameter distributions were examined; 2 forest types (CO, MO) × 2 rhododendron abundance classes (LR, HR) × 2 inventories (1934–35, 1969–72). Diameter classes were 7.6 cm (3 inch) intervals, starting with 1.3–8.9 cm (0.5–3.5 inches). Comparisons between distributions allowed determination of the reproductive status of the populations, how they changed over a 34–38 year period, and correlations of the effect of rhododendron abundance with tree reproduction.

If differences in tree reproduction between HR and LR plots are to be attributed to the abundance of rhododendron, other potentially important factors must be ruled out. If the degree of canopy cover or understory cover differed in HR and LR plots, they would have experienced different amounts of canopy opening following the chestnut blight. To discern if these confounding effects were present, t-tests were used to test for significant differences between HR and LR plots in basal area of all trees, overstory trees >8.9 cm (3.5 inches) DBH, understory <8.9 cm DBH, and all chestnut trees. These tests were repeated for both forest types and both inventories. To determine the similarity in species composition between LR and HR plots, correlation coefficients (r) were calculated using (1) basal areas and (2) densities of the different tree species from the first inventory. Also, to determine the initial similarity in size structure, correlation coefficients were calculated using densities by 7.6 cm (3 inch) DBH classes from the first inventory. A t-test was used to test for differences in total density between LR and HR plots. To test for differences in tree reproduction at different rhododendron densities and over time, t-tests were used to compare tree sapling densities between LR and HR plots, as well as between years. In most of the above comparisons the variances were found to be homogeneous ($P > 0.05$). Where they were not, an approximate t-test assuming unequal variances was used (Sokal and Rohlf 1969).

RESULTS

No significant differences ($P > 0.05$) were found between HR and LR plots in any of the comparisons of total, overstory, understory, or chestnut basal areas (Table 1). Similarly, there were no significant ($P > 0.05$) differences between 1934–35 tree densities in HR and LR plots. 1934–35 species composition was very similar in HR and LR plots. Basal area correlations by species were 0.854 for the Mixed Oak type and 0.958 for the Chestnut Oak type ($P < 0.000005$). Density correlations by species were 0.821 and 0.907 ($P < 0.000005$). By size classes, density correlations were 1.000 for both forest types ($P < 0.000005$). Hence, in 1934–35 the HR and LR plots in each forest type were similar in basal area, density, species composition, and size structure. Mean densities of mountain-laurel, another major understory species, were found to be inversely related to rhododendron densities in HR and LR plots of both forest types in 1969–72 ($r^2 = 0.997$). Total densities of tree saplings (1.3–8.9 cm DBH) changed over time and between HR and LR plots (Table 2). Total tree sapling densities in HR plots were lower than those in LR plots in both forest types for both inventories. The differences were small and not statistically significant ($P > 0.05$) in 1934–35, but were much larger and highly significant ($P < 0.005$) in 1969–72. Likewise, there was a significant ($P < 0.05$) decrease in the number of tree saplings over time in LR and HR plots of both forest types. The decrease was greater and more significant in HR plots than LR plots.

Density-diameter distributions of the dominant species are shown for the Mixed Oak type in Figure 1 and for the Chestnut Oak type in Figure 2. Black oak distributions were very similar to those for scarlet oak and are thus not shown. All species in both LR and HR plots show a steep inverted J-shaped curve in 1934–35. All five species at Coweeta

TABLE 1. Mean basal area (m²/ha) of all trees and shrubs (Total), those over 8.9 cm DBH (Overstory), those under 8.9 cm DBH (Understory) and all chestnut. Confidence intervals are X̄ ± 2 S.E. There were no significant basal area differences (P > 0.05) in any of the categories between Low Rhododendron (LR) and High Rhododendron (HR) plots in either forest type.

Type and rhododendron density	1934–35 basal area (m²/ha)				1969–72 basal area (m²/ha)		
	Total	Overstory	Understory	Chestnut	Total	Overstory	Understory
Mixed Oak type							
LR	22.50	17.51	4.99	5.26	31.86	19.86	12.00
	±2.72	±2.72	±0.58	±2.14	±3.45	±2.46	±3.96
HR	22.21	17.14	5.07	7.79	34.92	22.54	12.38
	±2.74	±2.69	±1.60	±2.33	±3.75	±3.34	±2.23
Chestnut Oak type							
LR	26.56	20.92	5.64	9.27	34.01	22.61	11.40
	±2.80	±3.16	±1.38	±2.25	±3.78	±1.85	±4.24
HR	27.05	21.68	5.37	10.13	37.18	25.86	11.32
	±2.95	±3.34	±1.05	±2.16	±3.91	±3.74	±1.82

had concave log density vs. diameter curves and departed from the negative exponential model by an overabundance of the smallest (sapling) DBH class in 1934–35 in both LR and HR plots. In 1969–72 the number of saplings had decreased in every case. In some instances the density-diameter curves had flattened out and were no longer J-shaped, and the log density vs. diameter curves were convex denoting an underrepresentation of saplings. Red maple showed no such depression of reproduction. Chestnut oak showed depressed reproduction in HR plots in the Mixed Oak type but not in the Chestnut Oak type. White oak showed depressed reproduction in HR plots in both forest types. Scarlet oak exhibited depressed reproduction in all areas. Hemlock was the only tree species which showed an increase in sapling density from 1934–35 to 1969–72 (Table 3). This was particularly evident in the HR areas where it showed a concave log density-diameter distribution and seemed to be reproducing well. There was a general increase between 1934–35 and 1969–72 in the number of trees in larger DBH classes for all species examined.

TABLE 2. Total density (stems/ha) of tree saplings in the 1.3–8.9 cm DBH class. Shrubs and small tree species with no individuals >11.4 cm DBH were omitted. LR = Low Rhododendron, HR = High Rhododendron.

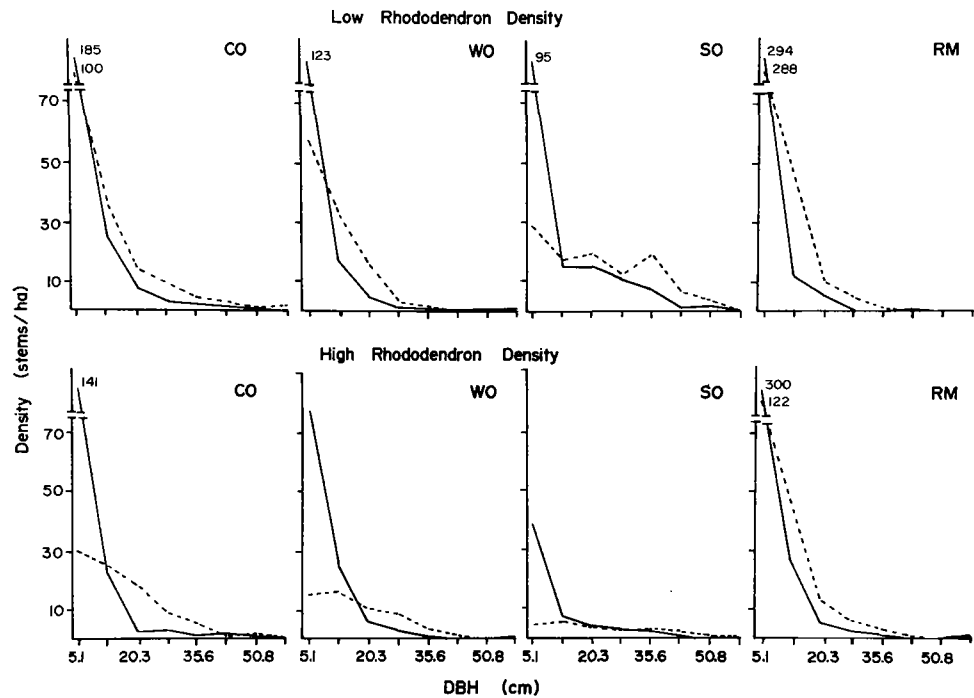| Type	LR	HR	Percent decrease	P
Mixed Oak type				
1934–35	2,324	2,257	3	>0.05
1969–72	1,566	793	49	<0.005
Percent decrease	33	65		
P	<0.005	<0.005		
Chestnut Oak type				
1934–35	2,657	2,343	12	>0.05
1969–72	1,198	660	45	<0.005
Percent decrease	55	72		
P	<0.0005	<0.0005		

FIGURE 1. Density-diameter distributions for Mixed Oak type plots of low and high rhododendron density. The solid lines represent the 1934–35 distribution; dotted lines are for 1969–72. CO = chestnut oak, WO = white oak, SO = scarlet oak, RM = red maple. Note that the vertical axis scale changes above 70 stems/ha.

DISCUSSION

The sapling size class for tree species at all sites was unusually large at the time of the 1934–35 census, probably because the canopy had been opened 10–25 years earlier by heavy logging. We attribute the significant decrease in tree sapling density at all sites over the next 34–38 years to increased sapling mortality caused by closure of the canopy and competition from understory species (Christensen 1977, Harcombe and Marks 1978). However, the greater decrease in number of saplings for HR than for LR sites was not caused by a difference in species composition, a differential increase in canopy or understory, or by differences in the loss of chestnut (Table 1), since the 1969–72 inventory showed that the two sites were comparable in these respects. We thus suggest that the differential decrease of saplings with time was due to an increase in density and basal area of rhododendron in sites where rhododendron was already established, which occurred in response to an opening of the canopy in the 1930's and 1940's by the death of American chestnut.

TABLE 3. Density (stems/ha) of hemlock saplings in the 1.3–8.9 cm DBH class. LR = Low Rhododendron, HR = High Rhododendron.

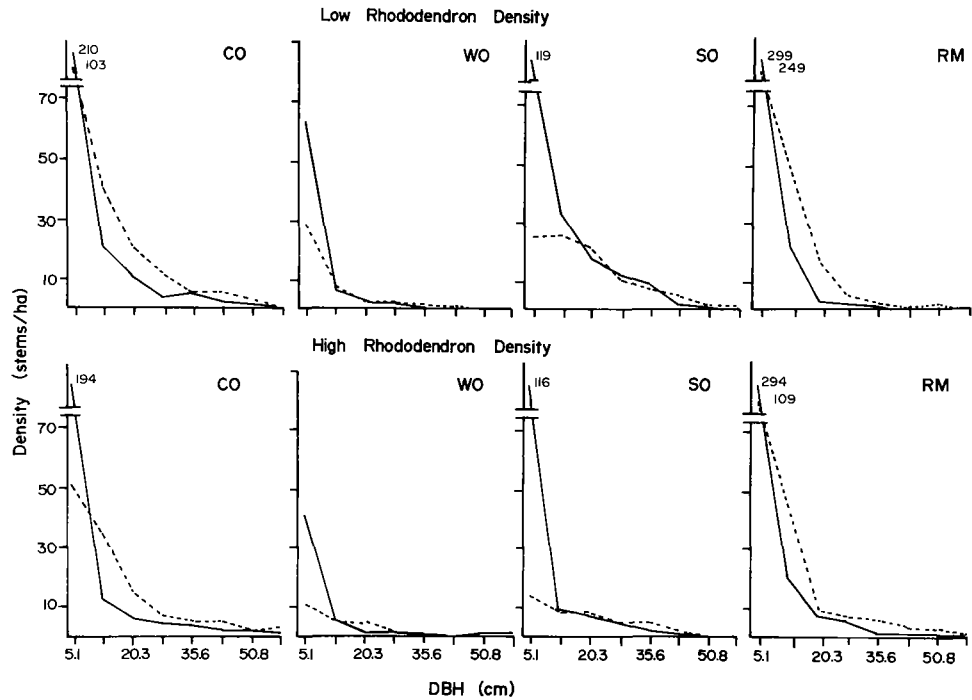| Inventory period	Mixed Oak type		Chestnut Oak type	
	LR	HR	LR	HR
1934–35	0.5	11.1	0.8	12.7
1969–72	73.1	134.1	3.1	113.1

FIGURE 2. Density-diameter distribution for Chestnut Oak type plots of low and high rhododendron density. The solid lines represent the 1934–35 distribution; dotted lines are for 1969–72. CO = chestnut oak, WO = white oak, SO = scarlet oak, RM = red maple. Note that the vertical axis scale changes above 70 stems/ha.

Mountain-laurel density tended to vary inversely with rhododendron density, and thus cannot explain the reduced hardwood regeneration in HR plots.

Woods and Shanks (1959), in a study of replacement of chestnut by other species in the Great Smoky Mountains, found that hemlock responded vigorously to release following the death of American chestnut by an increase in canopy height and diameter of formerly suppressed saplings, and in seedling recruitment. In our study, hemlock was the only canopy tree species with more saplings in 1969–72 than in 1934–35. Its high shade tolerance (Baker 1949, Harlow and others 1979) allows it to reproduce under canopies that inhibit the reproduction of other species. Hemlock may in part be responsible for a smaller sapling size class for other species. However, sapling loss by the five dominant species was far too great to be interpreted as a one-to-one substitution by hemlock. Woods and Shanks (1959) noted that rhododendron did not respond to release by the death of American chestnut, at least with respect to radial growth of stems. We contend that a more likely response of a rhododendron thicket to canopy opening would be increased stem density by layering.

In her study of forests near Highlands, North Carolina, Keever (1953) found that dominant species in the overstory were among the top five dominants in the understory. A classical characterization of size class distribution in an uneven-aged forest is the inverted J-shaped curve which results when density is plotted against diameter classes (Goodman 1930, Hough 1932). The authors recognize that density-diameter distributions may not adequately represent density-age distributions (Ross and others 1982). However, we are limited to the former, because past forest inventories of permanent plots at Coweeta did not include data on age of trees. This negative exponential curve may be converted to a straight line when plotted on semi-logarithmic paper (Meyer 1952). In such a distribution all diameter classes are represented, but the greatest numbers of individuals are in the smaller diameter classes.

In our study, red maple has an inverted J-shaped density-diameter distribution for both

HR and LR sites and this pattern does not change with time. Woods and Shanks (1959) suggest that the former oak-chestnut association in the Great Smoky Mountains is becoming an oak complex in which chestnut oak and red maple are likely to be dominant species. In the latest census of Coweeta forests, red maple was the most important species with respect to density and the third in importance with respect to basal area. Red maple appears to be a species with a wide ecological amplitude and on the basis of our studies, promises to be a major component of future forests at Coweeta if they remain undisturbed.

Chestnut oak has a density-diameter distribution pattern which indicates good regeneration at LR sites and at mid-altitudinal slopes where rhododendron is present. Chestnut oak is the canopy species with the greatest basal area for the Coweeta Basin as a whole. Our data indicate that chestnut oak will continue to dominate forests at Coweeta, but its importance may diminish with time at lower elevation sites where rhododendron is present.

White oak density-diameter distribution patterns showed good regeneration at LR sites, but in the presence of rhododendron within both Chestnut and Mixed Oak associations, smaller diameter classes were underrepresented. Its regeneration is clearly suppressed at HR sites. In the future, the importance of white oak will likely diminish in forest areas of high rhododendron density.

The density-diameter distribution data for black oak and scarlet oak are so similar that only the latter was included in this paper. Instead of an inverted J-shaped curve, scarlet oak had a relatively flat curve at all sites. This pattern suggests that population recruitment for this species within forests at Coweeta is episodic and probably dependent on some kind of disturbance, such as fire, logging, or chestnut blight. Our data indicate that without major disturbances, the importance of scarlet oak and black oak in the future composition of forests at Coweeta will diminish.

It is assumed that forest sites at Coweeta that have dense stands of rhododendron differ in a number of environmental factors from those where rhododendron is sparse. In the 1934–35 census, both sites were similar in basal area, density, size structure, and species composition. At the time of the 1969–72 census, 35 years later, the HR sites had a significantly smaller sapling class than the LR sites, which resulted in major deviations from the density-diameter distribution curves of dominant species found in the earlier census. Since these changes are so well correlated with 1969 rhododendron abundance and there is evidence in the literature that rhododendron increased in importance following disturbances earlier in the century (McGee and Smith 1967, McGinty 1972), we suggest that the changes were a result of differentially increased rhododendron abundance. This in turn may have been fostered by a combination of logging, the chestnut blight, and the cessation of burning. While the most parsimonious explanation, this hypothesis cannot be directly verified with our data since rhododendron was not tallied in the first census, nor can other environmental causes be completely ruled out. If our interpretation is correct, interference by rhododendron with the regeneration of dominant canopy species would be a major factor in altering forest composition at Coweeta.

LITERATURE CITED

BAKER, F. S. 1949. A revised tolerance table. J For 47:179–181.

CHRISTENSEN, N. L. 1977. Changes in structure, pattern and diversity associated with climax forest maturation in Piedmont, North Carolina. Am Midl Natur 97:176–188.

COOPER, A. W., and J. W. HARDIN. 1971. Floristics and vegetation of the gorges on the southern Blue Ridge escarpment. In The distributional history of the biota of the southern Appalachians. Part II. Flora (P. C. Holt, ed). Va Polytech Inst and State Univ, Res Div Monogr 2:291–330.

GOODMAN, R. B. 1930. Conditions essential to selective cutting in northern hardwoods and hemlock. J For 28:1070–1075.

HARCOMBE, P. A., and P. L. MARKS. 1978. Tree diameter distributions and replacement processes in southeast Texas forests. Forest Sci 24:153–166.

HARLOW, W. M., E. S. HARRAR, and F. M. WHITE. 1979. Textbook of dendrology, 6th ed. McGraw Hill, New York. 510 p.

HOUGH, A. F. 1932. Some diameter distributions in forest stands of northwestern Pennsylvania. Ecology 17:9–28.

IGLICH, E. M. 1975. Population age structures and dynamics of six hardwood species in a forested watershed ecosystem in the southern Appalachians. M S thesis, Univ Ga, Athens. 87 p.

JOHNSON, E. A., and J. L. KOVNER. 1956. Effect on streamflow of cutting a forest understory. Forest Sci 2:82–91.

KEEVER, C. 1953. Present composition of some stands of the former oak-hickory-chestnut forest of the southern Blue Ridge Mountains. Ecology 34:44–54.

McGEE, C. E., and R. C. SMITH. 1967. Undisturbed rhododendron thickets are not spreading. J For 65:334–336.

McGINTY, D. T. 1972. The ecological roles of *Kalmia latifolia* and *Rhododendron maximum* in the hardwood forest at Coweeta. M S thesis, Univ Ga, Athens. 81 p.

MEYER, H. A. 1952. Structure, growth and drain in balanced uneven-aged forests. J For 50:85–92.

ROSS, M. S., T. L. SHARIK, and D. W. SMITH. 1982. Age-structure relationships of tree species in an Appalachian oak forest in southwest Virginia. Torrey Bot Club Bull 109:287–298.

SOKAL, R. R., and F. J. ROHLF. 1969. Biometry. Freeman, San Francisco. 776 p.

WILLIAMS, J. G. 1954. A study of the effect of grazing upon changes in vegetation on a watershed in the southern Appalachian Mountains. M S thesis. Mich State Coll, East Lansing. 138 p.

WOODS, F. W., and P. E. SHANKS. 1959. Natural replacement of chestnut in the Great Smoky Mountain National Park. Ecology 40:349–361.