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VEGETATION PATTERNS ON A SOUTHERN APPALACHIAN WATERSHED[1]

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Abstract. The vegetation on a relatively undisturbed hardwood forest watershed at Coweeta Hydrologic Laboratory, Franklin, North Carolina was sampled, and estimates of density, basal area, and above-ground biomass were computed. These vegetational parameters and five topographic variables (elevation, aspect, slope angle, distance from stream channel, and distance from water divide) were used to analyze site-species relationships on the watershed. The primary analytical techniques used were correlation analysis and principal components ordination. Major changes in the vegetation since the introduction of chestnut blight were also examined.

The vegetation on the watershed was found to be dominated by oaks, though considerable change had occurred in the vegetation composition since the appearance of chestnut blight. Total basal area on the watershed was 25.6 m^2/ha and the total above-ground biomass was 139, 900 kg/ha. Significant correlations were found between 13 major species and one or more of the topographic variables. The ordination results revealed species groupings related to the correlation results. Distance from the stream, distance from the water divide and elevation, which produce a soil moisture gradient, were the important topographic factors determining species distribution at Coweeta.

Key words: Appalachians; biomass; correlation; moisture gradient; ordination; species distribution; vegetation; watershed.

INTRODUCTION

Vegetation has been classified or described in accordance with two major philosophies, the discontinuous and continuous concepts. The discontinuous concept, the more traditional approach, provides a description that enables one to discuss a gross vegetational unit. However, it is poorly suited to one interested in the dynamics of the vegetation. Gleason's (1926) individualistic concept provides a framework for examining a plant community in greater detail with the dynamics of the community in mind. This approach is generally termed gradient analysis (Whittaker 1967).

The primary objective of this study was to sample the vegetation on a hardwood forest watershed at Coweeta Hydrologic Laboratory, Franklin, North Carolina, to obtain data conducive to gradient analysis. Our major interest was in relating distribution patterns of the major species to topographic gradients within the watershed. In addition to analyzing site-species relationships, we examined several compositional aspects of the vegetation on the watershed. Of special interest were the above-ground standing crop biomass of plants on the watershed and vegetation changes since the introduction of chestnut blight, caused by *Endothia parasitica* (Murr.) P.

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DESCRIPTION OF THE WATERSHED

The watershed is located in the Coweeta Basin, which is managed by the U.S. Forest Service Coweeta Hydrologic Laboratory about 10 miles south of Franklin, North Carolina. Coweeta Basin is in the Nantahala Mountains, a part of the Blue Ridge province in the southern Appalachians. This watershed serves as the control hardwood forest for the Eastern Deciduous Forest Biome IBP research efforts at Coweeta. The mean annual temperature on the watershed is 13°C and the mean annual precipitation is 180 cm (Kovner 1955). The prevailing winds are from the southwest and high intensity storms are frequent throughout the growing season. October has the lowest and March the highest mean monthly rainfall. The soils, sandy loams and sandy clay loams, are of the Porter series; the bedrock is granite, mica schists, and gneisses. The horizontal area of the watershed is 12.46 ha and the average slope of the land is 53% (28°). From the weir pond to the top of the watershed there is a range in elevation of 267 m, from 726 m to 993 m above sea level. The main drainage is south to north with a channel length of 290 m and a channel gradient of 18.9% (Kovner 1955).

The only major disturbances known to have occurred in the study area are logging, which ceased in 1923, and the chestnut blight, which appeared in the southern Appalachians around 1925 (Kovner 1955, Woods and Shanks 1957). The former prominence of chestnut (*Castanea dentata* (Marshall)

TABLE 1. Regression coefficients used to estimate above-ground standing biomass. The equations are of the form $\log_{10} Y = A + B \log_{10} X$, with Y = oven dry weight and X = dbh in cm except for hardwoods < 2.5 cm dbh for which X = diameter at ground level in cm

Species	Plant component	A	B	r	Source of data
Hardwoods ⩾ 2.5 cm dbh	Leaves (kg)	–1.5799	1.7719	.94	Sollins and Anderson 1971[a]
	Branches (kg)	–1.4472	2.2350	.96	Sollins and Anderson 1971[a]
	Stem (kg)	–1.0382	2.3885	.98	Sollins and Anderson 1971[a]
Hardwoods < 2.5 cm dbh	Leaves (kg)	–1.8789	2.1716	.96	Sollins and Anderson 1971[a]
	Stems (kg)	–1.3620	2.7172	.98	Sollins and Anderson 1971[a]
Kalmia latifolia	Leaves (g)	0.9332	2.0744	.84	Monk et al. 1971[b]
	Stems (g)	2.1533	2.0017	.97	Monk et al. 1971[b]
Rhododendron maximum	Leaves (g)	1.7711	2.0164	.93	R. H. Whittaker (unpubl.)[c]
	Branches (g)	2.1077	2.1334	.99	R. H. Whittaker (unpubl.)[c]
	Stem (g)	1.5504	2.7122	.95	R. H. Whittaker (unpubl.)[c]
Pinus rigida	Total (g)	2.0171	2.3373	.99	Whittaker and Woodwell 1968[d]
	Branches (g)	1.1100	2.5516	.99	Whittaker and Woodwell 1968[d]
	Stem (g)	1.8758	2.3261	.99	Whittaker and Woodwell 1968[d]
Tsuga canadensis	Leaves (kg)	–0.947	1.395	.99	W. Santee (unpubl.)[b]
	Branches (kg)	–1.044	2.080	.99	W. Santee (unpubl.)[b]
	Stem (kg)	–1.089	2.342	.99	W. Santee (unpubl.)[b]

[a] Plants harvested throughout Southeastern U.S. Equations based only on species found at Coweeta.
[b] Plants harvested at Coweeta.
[c] Plants harvested in the Great Smoky Mountains. Dr. Whittaker generously provided these data.
[d] Equations based on trees in Brookhaven Forest, New York.

Borkh.) on the watershed is obvious from the many sprouts and decaying logs.

METHODS

Estimating vegetational and topographic parameters

To obtain representative samples of the vegetation and of points along topographic gradients, we positioned sample plots on the watershed in a systematic manner (Kershaw 1966, Kulow 1966). A grid was superimposed upon a topographic map of the watershed, and 25 plots (25 × 50 m) were located where the grid lines intersected. The plots were oriented with the long axes perpendicular to the slope. LaFrance (1972) showed that with artificial populations, rectangular plots arranged perpendicular to the gradient are more efficient in extracting species groupings in ordination analysis than are rectangular plots parallel to the gradient. Within the 25 × 50 m plots all stems ⩾ 2.5 cm dbh were tallied by species and diameter. In two nested 5 × 5 m plots positioned in opposite corners of each 25 × 50 m plot, one in an upslope corner and the other in a downslope corner, all stems < 2.5 cm dbh and ⩾ .3 m tall were tallied by species and diameter at ground level. Herbs, seedlings, and woody plants < .3 m tall were harvested in six nested 1-m² plots within each 25 × 50 m plot. The 1-m² plots were positioned in each of the four corners of the 25 × 50 m plot and the inside corner of each of the 5 × 5 m plots. Care was taken to avoid trampling the corners when the plots were marked with string. The seedlings and woody plants < .3 m tall were separated by species, oven dried, and weighed. The herbaceous plants were also dried and weighed but were not separated by species. The total area sampled represented approximately 25% of the area of the watershed.

The data collected from the sample plots were used to calculate density, basal area, and standing crop biomass. The biomass estimates of herbs and stems < .3 m tall were based on the harvested material from the 1-m² plots. Biomass estimates of the remaining size classes of trees were obtained by the use of regression equations developed from harvest data from a variety of sources (Table 1). The use of regression equations in predicting biomass is well described in the literature (Shanks and Clebsch 1962, Ovington et al. 1967, Satoo 1970, Young 1971).

Five topographic parameters were determined on each plot. We determined slope aspect with a compass and calculated the mean slope angle by averaging five Suunto clinometer readings per plot. Aspect was converted to a relative moisture value. A scale from 1 to 16 was used, with SSW (1) the driest aspect and NNE (16) the wettest. The scale was derived from slope aspect-moisture regimes suggested by Whittaker for the Great Smoky Mountains of

TABLE 2. Composition of woody vegetation on watershed. Species arranged in order of contribution to percent basal area. Only species with ⩾ 0.1 m^2/ha basal area and ⩾ 20 stems/ha are listed. Estimates of the above-ground standing biomass are based on sample plot data and regression equations (Table 1)

Species	Basal area m^2/ha	Relative basal area %	Density no. stems/ha	Relative density %	Leaf wt. kg/ha	Branch wt. kg/ha	Stem wt. kg/ha	Total dry wt. kg/ha
Quercus prinus	5.5	21.3	190.8	6.3	845.9	5761.8	25,785.8	32,393.5
Acer rubrum	2.4	9.3	181.8	6.0	403.6	2301.5	9763.4	12,468.5
Quercus coccinea	2.0	7.9	44.5	1.5	300.1	2171.9	9763.4	12,235.4
Rhododendron maximum	1.9	7.4	887.0	29.2	1531.9	3301.8	4202.4	9036.1
Quercus rubra	1.7	6.8	21.4	0.7	320.8	2005.2	9460.6	11,786.6
Liriodendron tulipifera	1.6	6.4	53.7	1.8	251.0	1765.5	8051.5	10,068.0
Carya glabra	1.3	5.1	70.4	2.3	212.0	1332.6	5785.3	7329.9
Kalmia latifolia	1.3	5.1	890.9	29.3	269.2	—	3038.4	3307.6
Quercus velutina	1.2	4.8	30.1	1.0	186.8	1299.0	5827.5	7313.3
Oxydendrum arboreum	1.1	4.4	75.5	2.5	200.8	1021.5	4102.9	5325.2
Nyssa sylvatica	1.0	3.7	70.0	2.3	162.0	911.5	3818.7	4892.2
Cornus florida	0.8	3.2	182.7	6.0	175.5	644.6	2410.6	3230.7
Betula lutea	0.7	2.7	62.1	2.0	126.7	612.2	2425.4	3164.3
Tsuga canadensis	0.4	1.4	41.0	1.3	91.7	543.8	1161.1	1796.5
Hamamelis virginiana	0.2	0.7	71.4	2.3	45.3	120.3	446.3	611.9
Others (27 spp.)	2.5	10.0	171.0	5.2	492.2	2478.2	11,806.0	14,940.2
Totals	25.6	100.0	3044.3	100.0	5615.4	26,271.4	108,013.1	139,899.9

Tennessee and North Carolina, the Santa Catalina Mountains of Arizona, and the Siskiyou Mountains of Oregon and California (Whittaker 1956, 1960, Whittaker and Niering 1965). The scale is as follows:

NNE 16, NE 15, N 14, ENE 13, NNW 12, E 11, NW 10, ESE 9, WNW 8, SE 7, W 6, SSE 5, WSW 4, S 3, SW 2, SSW 1

Elevation, distance from the stream channel, and distance from the water divide were obtained from a topographic map of the watershed.

Analytical procedures

General distribution maps of the major species were developed from basal areas on the 25 × 50 m plots. These patterns provided a gross look at site-species relationships on the watershed. We used a gradient analysis approach to elucidate statistically some of these relationships.

Forward stepwise multiple regression (IBM Fortran IV program) was tried as a technique to find significant relationships between the vegetational parameters and topographic gradients. The independent variables were the topographic parameters measured on each plot, i.e., elevation, slope angle, aspect moisture value, distance from the stream channel, and distance from the water divide. The analysis was conducted with absolute density then absolute basal area as the dependent variable. Several significant equations were obtained with as many as three significant independent variables associated with a vegetational parameter and with a coefficient of determination (R^2) as high as .72. However, the resulting regression equations were not especially useful in interpreting plant distributions and the results were complicated by the fact that not all the topographic variables are independent. Elevation is significantly correlated with distance from the stream channel ($r = .40$, $P < .05$) and distance from the water divide ($r = -.68$, $P < .01$). Therefore, bivariate linear correlation coefficients were computed and these results were more useful in the interpretation of site-species relationships. Correlation analysis of site-species relationships is justifiable where relatively narrow topographic gradients exist, such as on the small watershed utilized for this study. Over wider gradients the site-species relationships would be more strongly curvilinear and correlation analysis would be inappropriate. Correlation results obtained with biomass were similar to those obtained with absolute basal area since one parameter is calculated from the other and they are highly correlated. Therefore, correlation results dealing with biomass will not be reported here. The primary limitation of correlation analysis is that causal relationships cannot be inferred from significant correlations.

A principal components ordination of the major species was conducted to derive their spatial relationships and to relate the extracted factors to significant topographic parameters. The variates used in the ordination were absolute basal areas per plot of the 15 major species. The IBM Fortran IV computer program used to do the ordination was written by Goldstein and Grigal (1971). Solution for the principal components was from the correlation matrix.

RESULTS

Vegetational composition of the watershed

Ecological dominants as defined by Odum (1971) are those species exerting a controlling influence on the nature or function of a community by virtue of their numbers, size, production, or other activities. Dominance in the plant community may be based on several measures of species importance. Of the vegetational parameters estimated in this study, basal area and biomass are probably better measures of species importance in the community than is density. Basal area and biomass are measures of size and bulk; thus, they probably represent the utilization of resources by a species better than do numbers of individuals (Oosting 1956, Whittaker 1970). The dominant species on the watershed with respect to relative basal area were the oaks, which made up 42.7% of the total basal area (Table 2). The oaks were followed in importance by red maple (*Acer rubrum* L.) with 9.3% and the hickories with 8.5% of the basal area. The oaks, red maple, and hickories constituted only 9.6%, 6%, and 3.2% respectively of the total number of stems ⩾ 2.5 cm dbh on the watershed. Two ericaceous species, mountain laurel (*Kalmia latifolia* L.) and rhododendron (*Rhododendron maximum* L.), accounted for 58.5% of the stems ⩾ 2.5 cm dbh. The large difference between the ordering of species based on relative basal area and that based on relative density can be explained by the distribution of trees among size classes. There were about 191 stems ⩾ 2.5 cm dbh/ha of chestnut oak (*Quercus prinus* L.) and 89 of those were ⩾ 10 cm dbh. There were 1,778 stems ⩾ 2.5 cm dbh/ha of mountain laurel and rhododendron but only 30 of those were ⩾ 10 cm dbh.

On a total watershed basis, the overstory was dominated by the oaks, of which chestnut oak was the most prominent, followed in importance measured by relative basal area by scarlet oak (*Quercus coccinea* Muenchh.), red oak (*Quercus rubra* L.), and black oak (*Quercus velutina* Lam.). The hickories occurred as codominants in the overstory with pignut hickory (*Carya glabra* (Miller) Sweet), mockernut hickory (*Carya tomentosa* (Poiret) Nuttall), and red hickory (*Carya ovalis* (Wang.) Sargent) comprising 5.1%, 2.2%, and 1.3% respectively of the total basal area on the watershed. Red maple was also an important codominant in the overstory. The most important understory species were mountain laurel and rhododendron, followed in relative basal area by dogwood (*Cornus florida* L.) and witch hazel (*Hammamelis virginiana* L.). The herb layer was relatively sparse, with ferns composing much of the ground vegetation.

Above-ground standing crop biomass

There was little difference between the rank order of species based on percent contribution to total above-ground biomass and that based on percent contribution to basal area. The oaks contributed 47.8% to above-ground biomass, followed by hickories with 9.5% and red maple with 8.9% (Table 2). The biomass of herbaceous plants was 55.5 kg/ha. The biomass of rhododendron leaves was strikingly greater than that of any other species: its leaves had almost twice the biomass of chestnut oak leaves. This estimate is not significantly different from McGinty's (1972) estimate, so we are confident it is realistic. The primary reasons for this large standing biomass are that rhododendron leaves are retained 6–8 yr and individual leaves increase in biomass until their fifth growing season at Coweeta (McGinty 1972). Whittaker and Garfine (1962) reported an increase in dry weight per leaf until the third growing season in the Great Smoky Mountains.

TABLE 3. Changes in composition of vegetation since 1934. *Kalmia latifolia* and *Rhododendron maximum* are not included. The red oaks include *Quercus rubra, Q. coccinea,* and *Q. velutina*. The white oaks include *Quercus prinus* and *Q. alba*. The hickories include *Carya tomentosa, C. glabra,* and *C. ovalis*

	Percent basal area			
Species	1934[a]	1941[a]	1953[a]	1970
Castanea dentata	31.1	22.1	0.9	0.1
White oaks	13.5	14.3	18.3	26.6
Red oaks	25.2	30.0	34.7	22.2
Acer rubrum	2.6	2.9	4.6	10.6
Hickories	4.4	6.3	8.5	9.8
Liriodendron tulipifera	0.2	0.6	2.5	7.3
Oxydendrum arboreum	2.3	2.5	4.3	5.6
Nyssa sylvatica	7.4	7.1	5.2	4.3
Cornus florida	3.4	3.9	5.4	3.7
Hamamelis virginiana	0.4	—	0.7	0.8
Others (25 spp.)	9.5	10.5	14.9	9.0
Totals	100.0	100.0	100.0	100.0

[a] Based on U.S. Forest Service cruises (Kovner, 1955).

Vegetation changes since the introduction of chestnut blight

The vegetation on the watershed has changed considerably since the appearance of chestnut blight in the area. The total basal area was reduced from 24.8 m^2/ha in 1934 to 21.6 m^2/ha in 1953 (Kovner 1955). The total basal area in 1970 was 25.6 m^2/ha, suggesting that replacement species had filled the gaps left in the overstory. The 21.6 m^2/ha in 1953 probably does not represent a minimum basal area after the introduction of the blight into the Coweeta site. Chestnut had been reduced from 31.1% of the basal area in 1934 (7.79 m^2/ha) to 0.1% in 1970 (0.01 m^2/ha) (Table 3). Woods and Shanks (1957, 1959) found that the species most commonly replacing chestnut in the Great Smoky Mountains were chestnut oak, red oak, red maple, and hemlock (*Tsuga canadensis* (L.) Carr.). Nelson (1955) found on another watershed at Coweeta that chestnut was being replaced primarily by species codominant

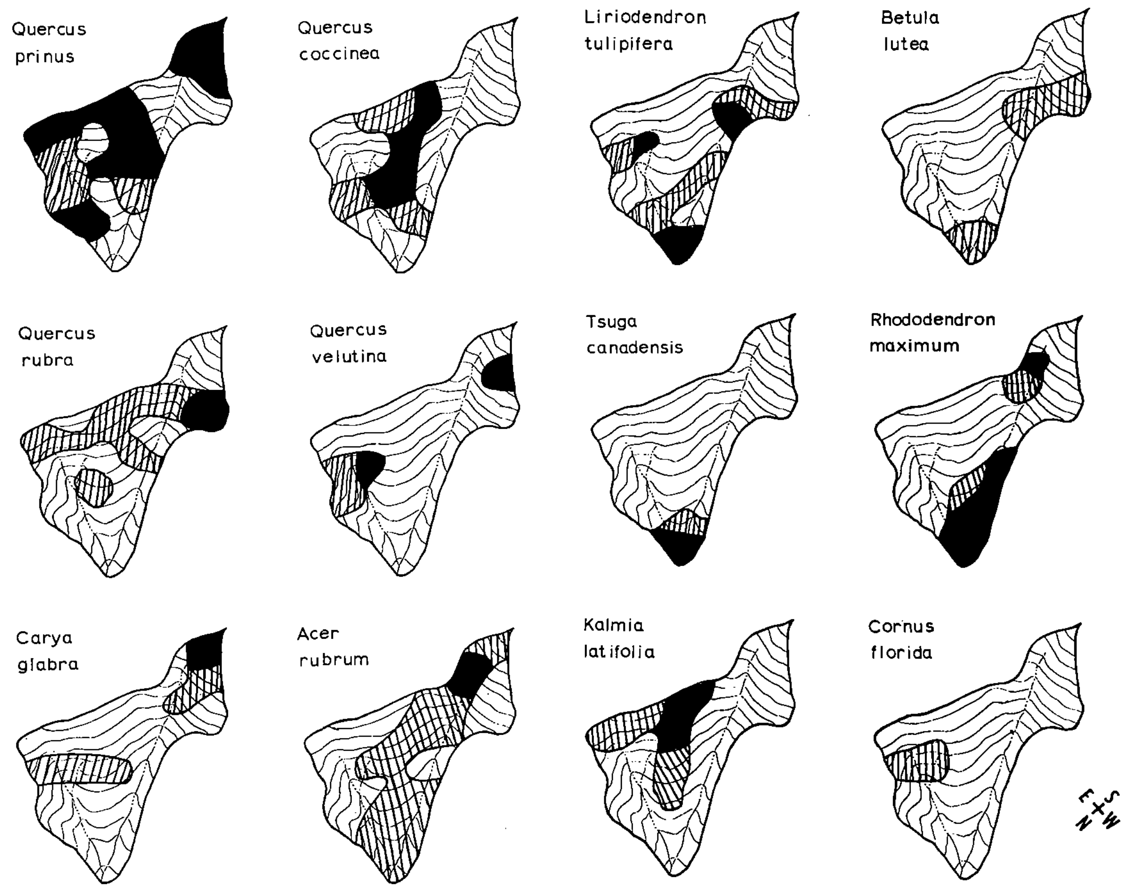

FIG. 1. Species distribution patterns based on absolute basal area. Solid shading = > 5 m^2/ha, slashed = 2–5 m^2/ha, remaining area = < 2 m^2/ha. *Quercus prinus* was the most abundant overstory dominant. Co-dominant overstory species included *Q. rubra, Q. coccinea, Q. velutina, Carya glabra, Acer rubrum, Liriodendron tulipifera, Betula lutea,* and *Tsuga canadensis.* The most important understory species were *Rhododendron maximum, Kalmia latifolia,* and *Cornus florida.*

with chestnut and secondarily by subordinate species, especially tulip poplar (*Liriodendron tulipifera* L.). Species that had increased in relative basal area since 1934 on the Coweeta watershed were the white oaks (including chestnut oak), red maple, the hickories, tulip poplar, and sourwood (*Oxydendrum arboreum* (L.) DC.). Witch hazel and dogwood stayed about the same and blackgum (*Nyssa sylvatica* Marshall) decreased in relative basal area. Rhododendron and mountain laurel were not included in Table 3 because these species were not included in the earlier Forest Service cruises. According to McGinty (1972) this may be because these two species were not present at that time or occurred very infrequently. Most of the rhododendron and mountain laurel on the watershed are about the same age; their time of establishment dates back to the opening of the overstory by the death of chestnut. The largest change next to the decline of chestnut was the increase and subsequent decrease in the percentage of red oaks. McCormick and Platt (1970) found on a south-facing slope in Virginia that northern red oak initially increased after the loss of chestnut but was subsequently replaced by hickory. They postulated that as chestnut died and the canopy opened up, conditions became drier, and more xeric species, such as hickories, replaced northern red oak, which was in the southern limit of its range. They found red oak persisting on north-facing slopes, which had few chestnut trees on them before the blight.

Site-species relationships

The distribution maps based on absolute basal areas of the major overstory species reveal some of the general patterns on the watershed (Fig. 1). The oaks and pignut hickory were distributed primarily high on the slope away from the stream. Red maple was distributed over most of the watershed. In two areas, at the base and near the stream halfway up the NW-facing slope, the composition of the over-

TABLE 4. Correlation coefficients (r) of basal area and density (stems ⩾ 2.5 cm dbh) correlated with topographic variables. Only significant values are included. *P* (.05), *r* = .40; *P* (.01), *r* = .45

	Basal area (dependent variable)				Density (dependent variable)			
Species	Elevation	Aspect	Distance from stream channel	Distance from water divide	Elevation	Aspect	Distance from stream channel	Distance from water divide
Quercus prinus	.56		.55	–.65			.62	–.44
Quercus coccinea			.65				.67	
Carya glabra							.43	
Liriodendron tulipifera			–.55	.44			–.58	
Betula lutea			–.40	.44				.53
Tsuga canadensis	–.45			.69	–.47			.70
Acer rubrum		.42			.50		.42	
Oxydendrum arboreum			.49				.44	
Kalmia latifolia			.75				.73	
Rhododendron maximum		.60			–.47	.61		.44
Cornus florida	–.47		–.61		–.45		–.58	
Nyssa sylvatica		.42			.49		.59	–.43
Hamamelis virginiana	–.63			.40	–.56			
All species		.57	.50		–.43		.40	

story was atypical. Instead of being composed of oaks or hickories, much of the overstory consisted of tulip poplar, hemlock, and birch (*Betula lutea* Michaux f.). The patterns of understory species are striking (Fig. 1) and were readily seen in the field. Rhododendron was distributed primarily on the lower NE-facing slopes and areas near the stream, mountain laurel occurred near the ridges, and dogwood was concentrated mostly in an area near the stream. The understory species had very distinct distributions and were virtually exclusive of each other in a given area.

Correlation analysis was used to correlate the distributions of the major species with topographic gradients. No significant correlations were obtained between any of the major species and slope angle, nor were any significant correlations found relating site to red oak or black oak. However, out of the 15 major species analyzed, 13 were significantly correlated to one or more of the other topographic variables, i.e., elevation, aspect moisture value, distance from the stream channel, and distance from the water divide (Table 4).

Absolute basal area of chestnut oak and absolute densities of red maple and blackgum were positively correlated with elevation. Basal areas of hemlock, dogwood, and witch hazel and densities of these three species and rhododendron were negatively correlated with elevation. Positively correlated with aspect moisture value were the absolute basal areas of rhododendron, red maple, and blackgum and the absolute density of rhododendron. There were no species negatively correlated with aspect moisture value. The basal areas of chestnut oak, scarlet oak, sourwood, and mountain laurel were positively correlated with distance from the stream channel, as were densities of these four species and pignut hickory, red maple, and blackgum. Negatively correlated with distance from the stream channel were basal areas of tulip poplar, birch and dogwood and densities of tulip poplar and dogwood. Positively correlated with distance from the water divide were basal areas of tulip poplar, hemlock, witch hazel, and birch and densities of hemlock, birch, and rhododendron. Basal area of chestnut oak and densities of chestnut oak and black gum were negatively correlated with distance from the water divide.

Principal components ordination

To further elucidate site-species relationships on the watershed, we used principal components ordination to depict the spatial relationships of the major species. We then related the significant site-species correlations to these spatial patterns. Goldstein and Grigal (1972) have suggested that rigorous statistical interpretations of an ordination of ecological data are not usually possible. Therefore, the discussion of our principal components results will be primarily qualitative.

The major problem with principal components ordination is the difficulty in determining what factors are represented by the components. Some of the extracted components are difficult to recognize as particular factors, and some are actually artifacts of the analysis. Understanding the extracted factors usually requires information from other sources (Whittaker 1967). Our approach was to group on the ordination plot the species with basal area significantly correlated with each of the topographic gradients. Those species positively correlated to each gradient formed one group and those negatively correlated formed another group. This approach sought to find groups arranged in the ordination in such a way as to impart some meaning to the axes or components and to strengthen the interpretation of site-species relationships as determined by the correlation analysis.

The results of the first two components of the species ordination (Fig. 2) account for 55% of the total variation. This is quite high compared to the stand ordination results of Grigal and Goldstein (1971). The cumulative percent variations accounted for by the first six components for Grigal and Goldstein's data were 17%, 28%, 39%, 49%, 58%, and 67%. Those for the species ordination in this study were 38%, 55%, 68%, 78%, 86%, and 91%.

The species significantly correlated with distance from the stream and distance from the water divide on the basis of basal area are grouped in Fig. 2A. Those species positively correlated with distance from the divide include tulip poplar, birch, hemlock, and witch hazel. These species increase in basal area as the distance from the ridges increases, thus occupying moist sites. Overlapping this group is the group of species negatively correlated with distance from the stream; these include tulip poplar, birch, and dogwood. Thus those species occupying moist sites based on these two topographic gradients are grouped together in the ordination and are at one extreme of the ordination plot. At the other extreme are the species occupying the drier sites based on these two topographic gradients. The one species negatively correlated with distance from the divide was chestnut oak. Those species positively correlated with distance from the stream were chestnut oak, scarlet oak, mountain laurel, and sourwood. The two groups of species occupying the more moist sites are both located at one extreme of the arbitrary moisture gradient while the two groups occupying drier sites are at the other extreme. Thus, the spatial arrangement of most species on the watershed as depicted by the ordination seems to align regularly with these two topographic gradients which probably produce a moisture gradient.

The species grouped in Fig. 2B are significantly correlated with aspect moisture value and elevation. There were no species negatively correlated with aspect moisture value. Those positively correlated with aspect moisture value, thus occupying more moist sites, were rhododendron, red maple, and blackgum. However, red maple had been observed widely distributed over the watershed, and blackgum was found on upper slopes and ridges. Also, densities of red maple and blackgum were positively correlated with elevation and distance from the stream channel, and blackgum density was negatively correlated with distance from the water divide (Table 4). Therefore, we are less than satisfied with the manner in which aspect was quantified in the analysis. A relative moisture scale for aspect may be inappropriate for Coweeta. A measurement of solar radiation with respect to slope aspect would probably be a better quantification of this parameter. The only species positively correlated with elevation was chestnut oak, which is at one extreme of the gradient. Dogwood, hemlock, and witch hazel were negatively correlated with elevation, thus occupying the moist base of the watershed. Again, the groups associated with moist sites based on these two topographic gradients are located together at one extreme of the ordination plot, and chestnut oak is at the other extreme.

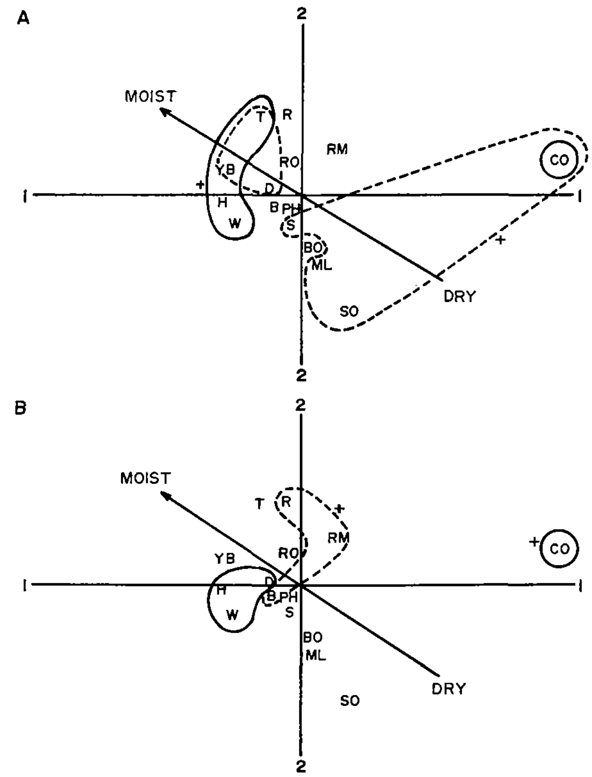

FIG. 2. Plot of species on the plane of the first two principal components. (A) The solid lines group species significantly correlated with distance from the water divide; the dashed lines group species correlated with distance from the stream. (B) The solid lines group species significantly correlated with elevation; the dashed line groups species correlated with aspect. A+ indicates that the group is positively correlated. The moisture gradient is arbitrarily sketched in. Species codes: CO = chestnut oak, RM = red maple, SO = scarlet oak, R = rhododendron, RO = red oak, T = tulip poplar, PH = pignut hickory, ML = mountain laurel, BO = black oak, S = sourwood, B = blackgum, D = dogwood, YB = yellow birch, H = hemlock, and W = witch hazel.

TABLE 5. Above-ground standing biomass of all strata in several hardwood forest stands similar in composition to that at Coweeta

Species	Location	Biomass kg/ha	Source
Temperate oak—average		166,000	Ovington 1965
Temperate oak—maximum		432,000	Ovington 1965
Chestnut oak	Great Smoky Mts.	420,000	Whittaker 1966
Oak–Hickory	Great Smoky Mts.	370,000	Whittaker 1966
Chestnut oak	Oak Ridge, TN	126,000	Sollins 1972
Oak–Hickory	Oak Ridge, TN	130,000	Sollins 1972
Oak–Hickory	Georgia piedmont	145,000	Monk et al. 1970
Oak–Hickory (predominantly chestnut oak)	Coweeta	139,900	present study

DISCUSSION

Above-ground standing crop biomass

Standing crop biomass is a necessary parameter for developing biomass or carbon models of an ecosystem and is useful for comparing one system with another. The total above-ground standing crop biomass of other hardwood forest stands in the southeastern United States is comparable to the estimate of above-ground biomass on the hardwood forest watershed at Coweeta (Table 5). Our biomass estimate of 139,900 kg/ha does not differ greatly from the estimates for stands at Oak Ridge, Tennessee (126,000 and 130,000 kg/ha), and on the Georgia piedmont (145,000 kg/ha). Ovington (1965) estimated the average above-ground biomass of a temperate oak forest to be 166,000 kg/ha. Whittaker's (1966) biomass estimates of chestnut oak and oak–hickory stands in the Great Smoky Mountains (420,000 and 370,000 kg/ha) are about three times the biomass estimate at Coweeta. Whittaker's estimates approach Ovington's maximum biomass for a temperate oak forest (432,000 kg/ha). Biomass is probably much greater in the Great Smoky Mountains than at Coweeta because of the greater age of the forest stands, as Coweeta was logged until 1923.

Leaf litterfall is commonly taken as a measure of stand leaf biomass. Our estimate of leaf biomass on the hardwood forest watershed exceeded measured leaf litterfall by 19.7% (Cromack 1972). Leaf biomass estimates obtained by regression equations based on harvest data were reported by Sollins (1972) to exceed measured leaf litterfall on 22 hardwood stands in the southeastern United States by about 10%. Litter trap estimates of litterfall should underestimate leaf standing biomass because several organic losses occur in the leaves prior to leaf fall. These losses include insect grazing, leaching and translocation of carbohydrates and mineral nutrients, and microbial decomposition in the leaf while still on the tree (Cromack 1972). A more important reason for our study, is that rhododendron leaves, which comprise 27.3% of the total leaf biomass on the Coweeta watershed, are retained on the trees for several years, thus contributing only a fraction of their biomass to annual leaf fall. Sollins (1972) concurs that leaf litterfall measurement may not be a valid absolute measure of stand leaf biomass.

Site-species relationships

The correlation results obtained with absolute density and with absolute basal area differed notably. These differences can probably be explained by the distribution of size classes along the gradients. A greater number of stems at one end of a gradient may represent less basal area than a few stems at the other end of the gradient if those few stems are in the larger size classes. Analysis of absolute density of stems < 2.5 cm dbh showed a positive correlation of total stems with elevation ($r = .57$, $P < .01$). However, the total stems $\geqslant 2.5$ cm dbh were negatively correlated with elevation (Table 4). A possible explanation is that there is a greater mortality of seedlings at lower elevations than at higher elevations (Racine 1969).

Site-species relationships have been successfully analyzed by correlation and regression techniques in several other studies. Mowbray and Oosting (1968) studied vegetation gradients in the Long Spur branch of the Thompson River gorge near Highlands, North Carolina. They calculated simple linear and curvilinear regression equations relating species importance values to several environmental factors. Highly significant correlation coefficients were obtained, but these results cannot be compared with ours since different variables were used. Mowbray and Oosting also charted the distribution of major species in relation to slope position. Seven major species were common to their study area and the study area at Coweeta, and the species distribution patterns were comparable in the two areas. Chestnut oak, scarlet oak, and sourwood were more important from midslope to top slope on north-facing aspects. Tulip poplar and witch hazel were found primarily on the lower slope. Dogwood was on midslope positions and red maple was widely distributed over the entire slope.

Site-species relationships were examined on Wilson Mountain at the southern end of the Cumberland Mountain section of the Appalachian Plateau province in Tennessee by Thor et al. (1969). They computed simple linear and multiple regression equations relating several site factors to species density. Three of the site variables comparable to factors used in the Coweeta study were slope direction (aspect), percent slope, and slope position (percentage of the distance from the ridge to the bottom of the slope). There were no similarities in the correlation results of the two studies, with six species common to the analyses. Thor et al. also made general observations on species distributions and slope position. There were similarities and dissimilarities among their observations, those of Mowbray and Oosting, and those made at Coweeta. Scarlet oak, black oak, sourwood, and blackgum were more dense near the ridges. Dogwood attained maximum density in the draws and red maple was widely distributed. Chestnut oak and northern red oak were observed at maximum densities in the draws, in contrast to maximums on the ridges at Coweeta. Tulip poplar was more dense in the draws but was reproducing more on the ridges. Reproduction of tulip poplar on the ridges was not observed at Coweeta.

In studies conducted at Hubbard Brook Forest, New Hampshire (Bormann et al. 1970, Siccama et al. 1970), significant linear and curvilinear regression equations were computed relating elevation to tree basal area, and slope and aspect to herb cover. No major species at Hubbard Brook were common to Coweeta.

The use of topographic variables in gradient analysis such as in the studies conducted by Thor et al. (1969), Bormann et al. (1970), and Siccama et al. (1970) and in the present study does not facilitate the correlation of species distributions with other, more biologically significant environmental variables. However, general relationships can be inferred between environment and species distributions from the microenvironmental trends that exist on the topographic gradients.

Soil moisture seems to be the most important environmental gradient coinciding with the topographic gradients used in this study, although other environmental factors are certainly involved. Site conditions are drier at increasing distances from the stream as water drains from the higher slopes to lower slopes and the stream. Likewise, site conditions are more moist at increasing distances from the water divide as precipitation runs off near the divide and both run-off and seepage are received lower on the slopes (Hewlett and Hibbert 1963). An increase in elevation is usually accompanied by an increase in precipitation (Dils 1957, Kovner 1957) and decreases in temperature (Spurr 1964) and evapotranspiration (Dils 1957, Kovner 1957), thus creating more moist conditions. However, over the elevations encountered in this study the slope position effect negates the increase in moisture normally produced by these trends. Upper slope positions are drier than lower slope positions (Mowbray and Oosting 1968) primarily because the total amount of moisture drained and the rate of drainage increase with elevation above the outflow (Hewlett and Hibbert 1963). Higher evaporation rates have also been reported for upper slope positions (Cooper 1961). South-facing slopes are usually drier than north-facing slopes, and west-facing slopes are usually drier than east-facing slopes because the south and west slopes receive more solar radiation than do north and east slopes (Mowbray and Oosting 1968). On the basis of these environmental trends, species positively correlated with either elevation or distance from the stream channel would be more prominent on dry sites, and species negatively correlated with either of these two gradients would predominate on moist sites. Species positively correlated with aspect moisture value or distance from the water divide would predominate on moist sites, and species negatively correlated would be found primarily on dry sites. However, correlations relating species distributions to these general trends should be interpreted cautiously. Keever (1973) has recently shown that relationships which might appear obvious, such as chestnut oak occupying dry sites because it is prominent on ridges, can be misleading. She found in southern Pennsylvania that the ridge tops were sometimes more moist than other habitats in the region.

The principal components ordination analysis in the present study derived spatial arrangements of species as determined by extracted factors, i.e., the first two principal components. If a group of species was significantly correlated with a realistic factor, the group should have been separated out in the ordination. The groups of species correlated with the topographic gradients in the present study separated out reasonably well in the ordination plots. Distance from the stream channel, distance from the water divide, and elevation, all of which represent measures of slope position, appear to be the important topographic gradients determining species distributions at Coweeta. These topographic gradients are complexes of several environmental factors, but soil moisture is probably the most important.

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Literature Cited

Bormann, F. H., T. G. Siccama, G. E. Likens, and R. H. Whittaker. 1970. The Hubbard Brook ecosystem study: Composition and dynamics of the tree stratum. Ecol. Monogr. **40**:373–388.

Cooper, A. W. 1961. Relationship between plant life-forms and microclimate in southeastern Michigan. Ecol. Monogr. **31**:21–59.

Cromack, K. 1972. Litter production and litter decomposition in a mixed hardwood watershed and in a white pine watershed at Coweeta hydrologic station, N.C. Ph.D. Thesis, Univ. Georgia. 137 p.

Dils, R. E. 1957. A guide to the Coweeta Hydrologic Laboratory. SE Forest Exp. Sta., Forest Service, U.S. Dep. Agric. 40 p.

Gleason, H. A. 1926. The individualistic concept of the plant association. Bull. Torr. Bot. Club **53**:7–26.

Goldstein, R. A., and D. F. Grigal. 1972. Computer programs for the ordination and classification of ecosystems. Ecolog. Sci. Div. Publ. No. 417, ORNL-IBP-71-10. 125 p.

Grigal, D. F., and R. A. Goldstein. 1971. An integrated ordination—classification analysis of an intensively sampled oak-hickory forest. J. Ecol. **59**:481–492.

Hewlett, J. D., and A. R. Hibbert. 1963. Moisture and energy conditions within a sloping soil mass during drainage. J. Geophys. Res. **68**:1081–1087.

Keever, C. 1973. Distribution of major forest species in southeastern Pennsylvania. Ecol. Monogr. **43**:303–327.

Kershaw, K. A. 1966. Quantitative and dynamic ecology. American Elsevier Publ. Co., New York. 183 p.

Kovner, J. L. 1955. Changes in streamflow and vegetation characteristics of a southern Appalachian mountain watershed. Ph.D. Thesis. State Univ. New York. 245 p.

———. 1957. Evapotranspiration in forest stands of the southern Appalachian Mountains. Ga. Acad. Sci. Bull. **15**:80–85.

Kulow, D. L. 1966. Comparison of forest sampling design. J. Ecol. **64**:469–474.

LaFrance, C. R. 1972. Sampling and ordination characteristics of computer-simulated individualistic communities. Ecology **53**:387–397.

McCormick, F., and R. Platt. 1970. A half century of succession in an Appalachian forest following chestnut blight. ASB Bull. **17**:54.

McGinty, D. T. 1972. The ecological roles of *Kalmia latifolia* and *Rhododendron maximum* in the hardwood forest at Coweeta. Masters Thesis. Univ. Georgia. 81 p.

Monk, C. D., G. I. Child, and S. A. Nicholson. 1970. Biomass, litter and leaf surface area estimates of an oak–hickory forest. Oikos **21**:138–141.

Monk, C. D., F. P. Day, and W. T. Swank. 1971. Dry weight of tree and shrub species from the Coweeta Hydrologic Laboratory, Franklin, N.C., p. 26–27. *In* P. Sollins and R. M. Anderson [ed.], Dry weight and other data for trees and woody shrubs of the southeastern U.S. Ecolog. Sci. Div. Publ. No. 407, ORNL-IBP-71-6.

Mowbray, T. B., and H. J. Oosting. 1968. Vegetation gradients in relation to environment and phenology in a southern Blue Ridge gorge. Ecol. Monogr. **38**: 309–344.

Nelson, T. C. 1955. Chestnut replacement in the Southern highlands. Ecology **36**:352–353.

Odum, E. P. 1971. Fundamentals of ecology. W. B. Saunders Co., Philadelphia. 574 p.

Oosting, H. J. 1956. The study of plant communities. W. H. Freeman Co., San Francisco. 440 p.

Ovington, J. D. 1965. Organic production, turnover and mineral cycling in woodlands. Biol. Rev. **40**: 295–336.

Ovington, J. D., W. G. Forrest, and J. S. Armstrong. 1967. Tree biomass estimation, p. 4–31. *In* H. E. Young [ed.], Symposium on primary productivity and mineral cycling in natural ecosystems. College of Life Sciences and Agriculture, Univ. Maine at Orono.

Racine, C. H. 1969. Tree reproduction in relation to vegetational and environmental gradients on slopes in the southern Blue Ridge. Ph.D. Thesis. Duke Univ. Durham, N.C. 192 p.

Satoo, T. 1970. A synthesis of studies by the harvest method, p. 55–72. *In* D. E. Richle [ed.], Analysis of temperate forest ecosystems. Springer-Verlag, N.Y.

Shanks, R. E., and E. E. C. Clebsch. 1962. Computer programs for estimation of forest stand weight and mineral pool. Ecology **43**:339–341.

Siccama, T. G., F. H. Bormann, and G. E. Likens. 1970. The Hubbard Brook ecosystem study: Productivity, nutrients, and phytosociology of the herbaceous layer. Ecol. Monogr. **40**:389–402.

Sollins, P. 1972. Organic matter budget and model for a southern Appalachian *Liriodendron* forest. Ph.D. Thesis. Univ. Tennessee, Knoxville. 150 p.

Sollins, P., and R. M. Anderson [ed.]. 1971. Dry-weight and other data for trees and woody shrubs of the southeastern U.S. Ecolog. Sci. Div. Publ. No. 407, ORNL-IBP-71-6. 80 p.

Spurr, S. H. 1964. Forest ecology. Ronald Press, New York. 352 p.

Thor, E., H. R. DeSelm, and W. H. Martin. 1969. Natural reproduction on upland sites in the Cumberland Mountains of Tennessee. J. Tenn. Acad. Sci. **44**:96–100.

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecol. Monogr. **26**:1–80.

———. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monogr. **30**:279–338.

———. 1966. Forest dimensions and production in the Great Smoky Mountains. Ecology **47**:103–121.

———. 1967. Gradient analysis of vegetation. Biol. Rev. **42**:207–264.

———. 1970. Communities and ecosystems. Collier-Macmillan Ltd., London. 158 p.

Whittaker, R. H., and V. Garfine. 1962. Leaf characteristics and chlorophyll in relation to exposure and production in *Rhododendron maximum*. Ecology **43**: 120–125.

Whittaker, R. H., and W. A. Niering. 1965. Vegetation of the Santa Catalina Mountains, Arizona: A gradient analysis of the south slope. Ecology **46**: 429–452.

Whittaker, R. H., and G. M. Woodwell. 1968. Dimension and production relations of trees and shrubs in the Brookhaven Forest, New York. J. Ecol. **56**: 1–25.

Woods, F. W., and R. E. Shanks. 1957. Replacement of chestnut in the Great Smoky Mountains of Tennessee and North Carolina. J. For. **55**:11.

Woods, F. W., and R. E. Shanks. 1959. Natural replacement of chestnut by other species. Ecology **40**: 349–361.

Young, H. E. [ed.]. 1971. Forest biomass studies. Life Sci. Agric. Exp. Stat., Univ. Maine at Orono, Misc. Publ. No. 132. 205 p.