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Long-term patterns in vegetation-site relationships in a southern Appalachian forest[1]

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ELLIOTT, K. J., J. M. VOSE, W. T. SWANK, AND P. V. BOLSTAD. Long-term patterns in vegetation-site relationships in a southern Appalachian forest. J. Torrey Bot. Soc. 126:320–334. 1999.—We used permanent plot inventories from 1969–1973 and 1988–1993 to describe forest species distribution patterns of the Coweeta Hydrologic Laboratory, a 2,185 ha basin in western North Carolina, USA. We used canonical correspondence analysis to explore the vegetation-site patterns for the 1970s and 1990s inventories combined. Site variables were determined by direct measurements or calculated by digital geographical information system mapping methods. Site variables were percent slope, elevation, terrain shape, precipitation, modified azimuth, soil organic matter content, soil depth, soil clay content, depth of A-horizon, potential solar radiation, and mean temperature during the growing season. Fifty percent of the variation in the vegetation distribution was explained by the site variables used in the canonical correspondence analysis. Soil organic matter, terrain shape, and elevation were the variables most strongly related to vegetation distribution. Species associated with convex terrain (upper slopes and ridges), such as *Pinus rigida, Quercus coccinea,* and *Quercus velutina,* decreased in abundance from the 1970s to the 1990s; species associated with soils having high organic matter content and deep A-horizons, such as *Liriodendron tulipifera, Rhododendron maximum,* and *Tsuga canadensis* increased in abundance. Individual species responded differently to site gradients. For example, *Acer rubrum, Quercus prinus, Oxydendrum arboreum,* and *Nyssa sylvatica* were located in the center of the ordination space (i.e., their occurrence was not related to any of the site variables), which suggests that these species are habitat generalists.

Key words: canonical correspondence analysis; species-environment relationships; Coweeta Hydrologic Laboratory.

The Southern Appalachians harbor a diverse flora as a result of the combined influences of physiography, site environmental conditions, prior species composition, adaptive life history strategies of species, and disturbance history. Elevation and topography have been shown to strongly influence vegetation patterns (Whittaker 1956, 1967; Day and Monk 1974; Golden 1980; Day et al. 1988). For example, Whittaker (1956) related the vegetation patterns of the Great Smoky Mountains National Park to an elevation gradient and a topographic gradient that he attributed to soil moisture. Day & Monk (1974) described the distribution of species over the highly varied topography in the Coweeta Basin, western North Carolina, as a predictable mosaic that is related to a moisture gradient. In these earlier studies (e.g., Whittaker 1956; Day and Monk 1974), it was commonly implied that hillslope gradients reflected available soil moisture because no direct measurements of soil moisture were taken. More recently, Yeakley (1993) found that soil water-holding capacity (water storage) and local topography (water drainage) explained much of the variance in soil moisture along a hillslope at Coweeta.

Natural disturbances such as drought, insects and disease, fire, and windthrow can contribute to changes in forest species composition and structure through time (Pickett and White 1985). The southern Appalachians have experienced two large-scale, natural disturbance events in the decades between 1970 to 1990. Dogwood anthracnose, caused by *Discula destructiva* Redlin., is a serious threat to native flowering dogwood (*Cornus florida* L.) in the eastern United States (Redlin 1991). Dogwood anthracnose was found to extend throughout the northeast (Hibben and Daughtrey 1988) and down the Appalachian mountain range into northern Alabama and Georgia by the late 1970s (Anderson 1991). A major drought was recorded from 1985–88 in the Coweeta Basin (Swift, et al. 1989). It was the most severe drought on record in terms of

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duration and accumulated precipitation deficit. Total precipitation for 1986, the peak of the drought, was 123.9 cm, 39% below normal (Swift et al., 1989). Clinton et al. (1993) showed an increase in canopy gap formation due to tree mortality in the Coweeta Basin during the 1985–88 drought. In addition, significant mortality of *Pinus rigida* occurred due to a combination of drought and subsequent attack by the southern pine beetle (*Dendroctonus frontalis* Zimmerman) (Smith 1991).

We describe the relationships among vegetation and a number of site environmental variables in the Coweeta Basin to understand the distribution of species along a complex environmental gradient and describe how this vegetation distribution changes through time. Forests within the Coweeta Basin have a complex mix of species and vegetation types that are at best fuzzy constructs with broadly overlapping borders (Bolstad et al., 1998). Transitions between the different community types are considered gradual (Whittaker 1956; Day and Monk 1974) and thought to reflect gradients in species distribution rather than distinct communities. However, Day et al. (1988) described four broad community types (northern hardwoods, cove hardwoods, oak—formerly chestnut, and oak-pine) that occur across elevation and topographic positions within Coweeta, and these descriptions have been used in several studies to discuss changes in composition and diversity of communities following forest management practices (e.g., Boring et al. 1988; Elliott et al. 1997).

The objectives of our study were to: (1) examine the change in vegetation over approximately 20 years (1969–1973 inventory versus 1988–1993 inventory) in a southern mixed deciduous forest, (2) investigate the association between the vegetation and the abiotic and physical site variables that determine the pattern of species distribution, and (3) determine how well community classifications can be discriminated using site variables.

Methods. SITE DESCRIPTION. Coweeta Hydrologic Laboratory is a research site of the USDA Forest Service, Southern Research Station. It is located in the Nantahala Mountain Range of western North Carolina, USA, within the Blue Ridge Physiographic Province, near the southern end of the Appalachian Mountain chain (latitude 35°03′ N, longitude 83°25′ W). The 2,185 ha basin consists of two adjacent, east-facing, bowl-shaped basins. Ball Creek and Shope Fork are fourth-order streams draining the Coweeta Basin. They join to form Coweeta Creek, which flows 7 km east to the Little Tennessee River. Elevations range from 675 to 1592 m. Steep slopes range from 30 to over 100 percent. Soils are deep sandy loams and are underlain by folded schist and gneiss. The relief has a major influence on hydrologic, climatic, and vegetation characteristics. Streams flow throughout the year, fed by approximately 2,000 mm of precipitation per year, most of which is rain. Mean annual temperature is 12.6 °C and ranges from an average of 11.7 °C in winter to 21.6 °C in summer. Frequent rain, more than 130 storms distributed throughout the year, sustains high evapotranspiration rates and a humid climate (Swift, et al. 1988). Vegetation is southern mixed deciduous forest. The principal overstory species are of the genera *Quercus, Carya,* and *Liriodendron.* There are scattered groups of *Pinus rigida* and *Tsuga canadensis.* Evergreen shrubs (*Rhododendron* and *Kalmia*) combined with *Cornus, Robinia, Acer,* and *Betula* form a dense understory cover (Day et al. 1988). Nomenclature follows Brown and Kirkman (1990).

Two soil orders are found within Coweeta, immature Inceptisols and older developed Ultisols. The Inceptisols include Umbric Dystrochrepts of the Cashiers series found on steep, rocky faces at high elevations of northern or southern aspect; Typic Dystrochrepts represented by the Chandler gravelly loam series, found on south-facing slopes underlain by the Tullulah Falls formation, and by the Cleveland-Chestnut complex, found on windswept, rock outcrops; and Typic Haplumbrepts represented by the Plott fine sandy loam series and Cullasaja-Tuckasegee complex, formed in colluvium in long narrow areas associated with hollows and coves. The Ultisols include Typic Hapludults, represented by the Cowee-Evard gravelly loam series found on strongly sloping to very steep ridges and sideslopes and by the Fannin sandy loam series found on gently sloping sideslopes, and Humic Hapludults, represented by Trimont gravelly loams found on cool, steep, north-facing slopes (Thomas 1996).

DISTURBANCE HISTORY PRIOR TO THE 1970S. Prior to 1842, the Coweeta Basin was occupied by the Cherokee Indians, who practiced semiannual burning to improve forage for livestock (Douglass and Hoover 1988). Between 1842 and 1900, European settlers continued the practice of light semiannual burning and grazing. The For-

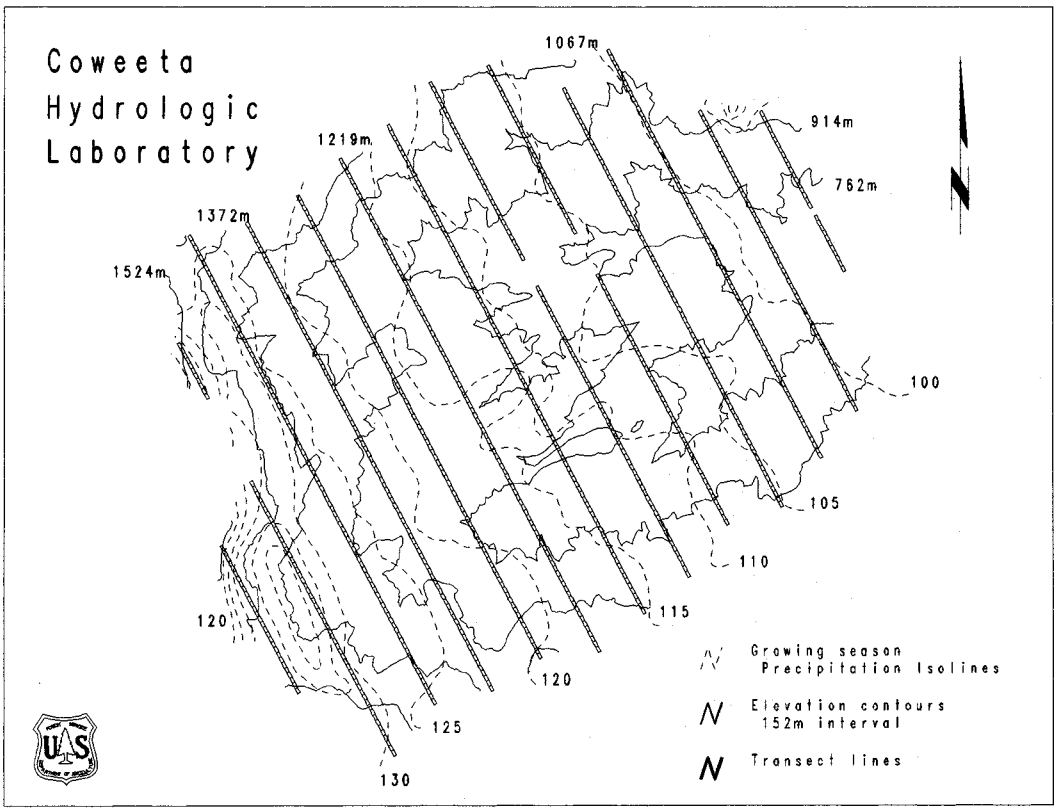

Fig. 1. Map of Coweeta Basin with permanent plot transects and growing season precipitation isohytehal lines (values are percentage of base station precipitation).

est Service purchased the basin in 1918, but rights to timber over 15 inches at the stump were reserved for the J.A. Porter Logging Company. Logging began in 1919, and selective but heavy cutting continued until 1923. In 1923, the Forest Service took over administration of the basin. Chestnut blight {*Endothia parasitica* (Murr.) P.} was first noted in Coweeta in the early 1920s. *Castanea dentata* comprised about 30% of the basal area in the watershed and most individuals in the basin were infected with the chestnut blight fungus by 1930 (Woods and Shanks 1959).

VEGETATION SURVEYS. Permanent plots were used to study changes in vegetation patterns after 20 yrs in forests at Coweeta (Fig. 1); 403 permanent plots were inventoried during 1969–1973, and 297 permanent plots were inventoried during 1988–1993. Only data from the same 283 permanent plots that were inventoried in both the 1970s and 1990s were used in our analyses. Permanent 0.08 ha (20 m × 40 m) plots were established along 13 parallel, approximately north-south transects (330°) at 200 m intervals spanning the Coweeta Basin. Plots were located in reference watersheds, which have been without human disturbance since 1923 (Douglass and Hoover 1988). Trees >1.3 cm dbh were tallied by species in 2.5 cm diameter classes in each plot. For all species and for both inventories, we calculated frequency, relative frequency (the frequency of a given species as a proportion of the sum of the frequencies for all species), density (number of stems per hectare), relative density (number of stems of a given species as a proportion of total number of stems of all species), basal area (m^2/ha), relative basal area (basal area of a given species as a proportion of total basal area of all species), and importance value (IV; {relative frequency + relative density + relative basal area}/3).

SITE VARIABLES. Site variables used in our analyses included percent slope, elevation, modified azimuth, terrain shape, soil depth, depth of A-horizon, soil clay content, soil organic matter content, mean temperature during the growing

Table 1. Explanatory environmental variables used in Canonical Correspondence Analysis.

Variable	Unit	Range	Comments
Topography			
Slope	%	0–100	Measured by compass during the 1970s survey
Aspect	degrees	0–360	Measured by compass during the 1970s survey
Elevation	meters	675–1600	Measured by altimeter during the 1970s survey.
Modified azimuth		0–180	Recalculated from aspect (360° scale) on a linear 0–180 scale, following Dargie's (1984) heat index calculation. NNE 40° was given the value 0 least xeric, SSW 220° was given the value 180 most xeric.
Terrain shape		0–10,000	GIS mapping method; unitless value for each ground position. 0—highest concavity, deep coves to 10,000—highest convexity, narrow, well-defined ridges.
Soil variables			
Soil depth	cm	43–168	GIS mapping method; overlaying soils map (Thomas's (1996) Soil Survey of Macon County, North Carolina) onto permanent vegetation plots map. Values were derived from soil series descriptions, first order soil survey completed in 1985 by the Natural Resources Conservation Service.
A-horizon depth	cm	10–43	
Clay content	%	5–27	
Organic matter content	%	5–20	
Available water capacity	cm	0.04–0.10	
Atmospheric			
Mean growth season temperature (Apr.–Sept.)	°C	16.8–22.0	GIS mapping method; mean temperature during the growing season using a temperature prediction model (Bolstad et al.)
Mean growing season precipitation (Apr.–Sept.)	mm	235–330	GIS mapping method; estimated on the basis on long-term data and isohytehal maps that provide weighting factors (Swift 1968)
Potential solar radiation	%	12–131	GIS mapping method; estimated using an algorithm for calculating potential solar radiation on mountain slopes (Swift & Knoerr 1973; Swift 1976).

season, growing season precipitation, and potential solar radiation (Table 1). Values of site variables were determined by direct measurements or calculated by digital geographical information system (GIS) mapping methods. During the 1970s survey, percent slope, aspect, elevation, and slope position (ridge, upper slope, middle slope, lower slope, cove) were recorded for each plot. Terrain shape, mean temperature, and potential solar radiation were derived using a GIS (ARC/INFO™). (The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.) Soils data for individual plots were obtained from a first-order soil survey completed in 1985 by the Natural Resources Conservation Service (Thomas 1996). This soil survey map was overlain onto the permanent vegetation plots map using a GIS (ARC/INFO™). Maximum values for percent soil organic matter content, percent clay content, soil water content, soil depth, and depth of A-horizon were derived from soil series descriptions and used in our analyses (Table 1).

Previous research at Coweeta has shown that the above site variables modify the local environment. Plot soil moisture is a function of precipitation (input), terrain shape (water drainage), and soil characteristics (water holding capacity) (Yeakley 1993). Availability of soil nutrients is a complex function of soil characteristics in-

cluding organic matter content, clay content, soil depth, and A-horizon depth, terrain shape (downslope movement of nutrients with water drainage), and soil temperature and moisture (Knoepp and Swank 1997a, 1997b). Temperature is a function of elevation, terrain shape (e.g., ridge, middle slope, or cove bottom), aspect (e.g., south-facing slope or north-facing slope), and percent slope. Potential solar radiation, adjusted for solar declination (latitude), at any plot is influenced by the slope inclination and aspect, shading by adjacent hills, and cloud cover (Swift and Knoerr 1973).

Digital terrain shape was determined by taking a scaled 9-celled zero-sum difference, centric minus the weighted average of perimeter cells (Burrough 1986; McNab 1989) using a GIS (ARC/INFO™). This yielded a unitless value for each ground position. Calculated values for terrain shape were rescaled linearly, where the range −2 to +2 was rescaled from 0 (highest concavity—deep coves) to 10,000 (highest convexity—narrow, well-defined ridges).

For each plot, mean temperature during the growing season was calculated by means of a temperature prediction model (Bolstad et al. 1998). Temperatures decreased with elevation at mean rates of 7 °C/km (maximum temperature) and 3 °C/km (minimum temperature). Mean growing season precipitation for each plot was estimated on the basis of long-term data and isohytehal maps that provide weighting factors (Swift 1968). Precipitation generally increases with elevation (about 5% per 100 m) along the east-west axis of the Coweeta valley but changes little with elevation on north- and south-facing side slopes (Fig. 1). The pattern is fairly regular except near ridge-lines where gage catch is consistently lower than at sites immediately downslope. Monthly mean precipitation amounts for the upper and lower elevations show a consistent difference in all seasons. Solar radiation on mountain slopes was estimated using an algorithm for calculating potential radiation (Swift and Knoerr 1973; Swift 1976). This algorithm estimates solar radiation within 10% of measured radiation values when slope inclination and aspect and a variable to adjust for topography are included.

DATA ANALYSIS. Vegetation data from the 1970s permanent plot inventory were classified into community types by means of cluster analysis. We compared the centroid method, average linkage, and Ward's minimum variance method (PROC CLUSTER, SAS 1987) to distinguish forest community types. These three methods produced similar results and the pseudo F and t^2 statistics were used to indicate the number of useful clusters. The community classification was stopped at seven groups as additional variance, explained by subsequent divisions, was low and caused the division of particular communities into small ($n<3$) groups. We followed the CLUSTER procedure with PROC FASTCLUS (SAS 1987) using the centroid method and setting maximum number of clusters at seven. The clustering was done on the basis of Euclidean distances computed from basal areas of individual species. PROC FASTCLUS identified the species that were most useful in distinguishing forest community types. Discriminant analysis (PROC DISCRIM, SAS 1987) was then used to derive sets of linear combinations of site variables that provided the greatest contrasts between the community groups. The discriminant analysis identified the site variables that were significant in distinguishing the groups and determined the percentage of plots classified correctly based on the site variables.

To explore the vegetation-site patterns for the 1970s and 1990s inventories, we used direct gradient analysis (CCA, canonical correspondence analysis, Gauch 1982; ter Braak 1986, 1988). CANOCO version 3.12 (ter Braak 1990a, 1990b) was used for all ordination analyses.

Site variables were standardized to zero-mean and unit-variance before the analysis. This standardization removes arbitrariness in the units of measurement and allows comparisons of canonical coefficients without influencing other aspects of the analysis (CANOCO, ter Braak 1988). The joint plot of species and environmental (site) variables is a biplot (ter Braak 1983), chosen because of its ability to provide least squares approximations of weighted averages. The measure of goodness-of-fit [$100 * (\lambda_1 + \lambda_2) \div$ (sum of all eigenvalues); where λ_1 is the first eigenvalue and λ_2 is the second eigenvalue] is the percent variance of the weighted-averages that the two-dimensional ordination could explain. The signs and relative magnitudes of the intraset correlations (correlations between individual environmental variables and the first two environmental axes) and the standardized canonical coefficients, formed the basis for estimating the relative importance of each environmental variable in the overall community composition. In the resulting ordination graph, plot points indicate species and arrows indicate

Table 2. Leading dominant wood species ordered by sequence of maximum importance value in 1969–1973. Columns are frequency (Freq; percentage of total plots sampled {n = 283}), basal area (BA; m^2/ha), density (stems/ha), and importance value (IV = [relative frequency + relative basal area + relative density]/3) in 1969–1973 and 1988–1993.

Species	1969–1973				1988–1993			
	Freq	BA	Density	IV	Freq	BA	Density	IV
*Kalmia latifolia**	77	1.45	2871	18.8	68	0.27	1553	14.0
*Rhododendron maximum**	81	0.74	1366	9.9	83	0.29	1088	10.7
Quercus prinus	90	5.18	172	9.0	89	5.88	158	9.9
Acer rubrum	100	2.53	285	6.6	99	3.89	277	8.8
Quercus coccinea	67	3.06	77	5.5	59	2.44	52	4.5
Carya spp.	86	1.63	135	4.4	80	1.65	95	4.4
*Cornus florida**	83	0.84	257	4.1	75	0.71	173	3.8
Nyssa sylvatica	88	1.04	96	3.5	83	1.19	99	3.9
Quercus rubra	61	1.61	30	3.3	53	2.03	34	3.8
Liriodendron tulipifera	55	1.45	63	3.2	55	1.95	68	4.0
Oxydendrum arboreum	80	1.00	78	3.2	81	1.39	74	3.9
Quercus velutina	63	1.35	29	3.0	41	0.97	21	2.2
*Castanea dentata**	80	0.36	144	2.8	61	0.23	61	2.1
Robinia pseudoacacia	64	0.67	26	2.2	59	0.67	27	2.2
Betula lenta	46	0.64	49	2.0	47	0.82	41	2.3
Quercus alba	41	0.82	29	2.0	32	0.80	17	1.7
Tsuga canadensis	42	0.60	57	1.9	49	0.93	62	2.6
Pinus rigida	24	0.90	23	1.7	19	0.46	12	1.0
Totals		27.4	6186			28.3	4210	

Note: Other minor species with an IV < 1.5 in either year: *Acer pensylvanicum**, *Acer saccharum, Aesculus octandra, Alder* spp.*, *Amelanchier arborea, Betula alleghaniensis, Calycanthus floridus**, *Castanea pumila**, *Clethra acuminata**, *Magnolia fraseri, Quercus falcata, Prunus serotina, Pyrularia pubera**, *Rhododendron calendulaceum**, *Sassafrass albidum, Symplocus tinctoria**, *Tilia americana,* and *Vaccinium stamineum**.

* Understory species.

environmental variables. The length of each arrow represents the rate of change in the weighted average as inferred from the biplot, showing how much the species distributions differ along that environmental variable. The most important environmental variables are those with the longest arrows.

For each site variable, the direction of the arrow reflects the eigenvalues of the axes and the intraset correlations of that site variable with the axes. Each arrow represents a direction or axis in the diagram, realized by visually extending the arrow in both directions. The position of each species on the environmental axis can be determined by extending a perpendicular line from the plot point to the environmental axis. The endpoints of the perpendicular line indicate the relative position of the centers of the species distributions along the environmental axis; they indicate the relative value of each species' weighted average with respect to that particular environmental axis.

We used basal area as the quantitative variable for species abundance in the CCA ordination analyses. We used a joint ordination of both data sets (1970s and 1990s) to demonstrate how each permanent plot had moved in ordination space through time and vegetation type. Joint ordination of both data sets provided similar results as separate analysis of each data set (i.e., species-site relationships were similar and eigenvalues were only slightly lower for the individual analyses), while providing an efficient display of the position of all plots along the ordination axes. Significance of site variables was tested by using each site variable in turn as the only constraining variable in CCA followed by an unrestricted Monte Carlo test (ter Braak 1990b). Monte Carlo permutations were applied to CCA analyses to determine if the strength of species sorting along the environmental variables was greater than would be expected by chance (ter Braak 1988; Crowley 1992). Eleven site variables were significant at the $p \leq 0.01$ level. Finally, we used forward selection of the eleven site variables in CCA followed by an unrestricted Monte Carlo test. With CCA, the sum of canonical eigenvalues indicates the amount of variation explained by the site variables supplied (ter Braak 1988). Two plots, which had vegetation described as northern hardwoods, were excluded from all final analyses because they had extreme axes scores and would have exaggerated the length of the ordination axes.

Table 3. Average basal area of the species that significantly ($r^2 \geq 0.15$, $p < 0.0001$) contributed to clustering of groups using inventory data from 1969–1973. Average basal area of species in these groups in 1988–1993.

Species	r^2	Average basal area (m^2/ha) I	II	III	IV	V	VI	VII
Cluster groups; 1969–1973 plots								
Q. prinus	0.68	2.09	12.88	2.80	0.88	5.23	4.14	3.82
L. tulipifera	0.66	2.16	0.25	0.81	11.03	2.50	0.38	0.12
Q. coccinea	0.64	0.33	2.63	2.82	0.07	0.24	11.48	5.63
P. rigida	0.64	0.03	0.14	0.30	0.00	0.00	0.53	6.30
Q. rubra	0.62	2.26	1.34	0.46	1.50	8.96	0.29	0.23
K. latifolia	0.52	0.22	1.46	1.00	<0.01	0.04	1.82	5.69
T. canadensis	0.36	3.12	0.08	0.14	0.66	0.09	0.01	0.04
B. lenta	0.31	2.01	0.16	0.29	1.85	0.72	0.03	0.03
Carya spp.	0.19	1.33	0.95	1.93	3.28	4.16	1.40	0.43
C. florida	0.17	0.73	0.55	1.19	0.66	1.75	0.87	0.17
R. maximum	0.16	1.48	0.72	0.68	0.52	0.98	0.21	0.11
Q. alba	0.15	0.64	0.28	1.94	0.14	0.00	0.71	0.22
Total basal area (SE)	0.49	25.0 (0.9)	29.9 (0.8)	24.4 (0.6)	30.8 (1.3)	33.9 (1.2)	28.0 (1.1)	28.0 (1.0)
Cluster groups; 1988–1993 plots								
Q. prinus		3.14	12.90	4.01	1.98	5.79	4.87	4.02
L. tulipifera		3.61	0.24	1.13	13.27	3.20	0.55	0.04
Q. coccinea		0.27	2.17	2.80	0.39	0.03	7.02	4.50
P. rigida		0.07	0.13	0.21	0.00	0.00	0.33	2.86
Q. rubra		2.70	1.45	1.25	3.12	9.16	0.38	0.44
K. latifolia		0.04	0.35	0.24	0.00	<0.01	0.39	1.26
T. canadensis		4.43	0.21	0.29	1.20	0.27	0.02	0.07
B. lenta		3.06	0.21	0.52	1.86	1.05	0.07	0.06
Carya spp.		1.38	0.94	2.21	3.02	3.46	1.24	0.52
C. florida		0.49	0.44	1.06	0.52	1.44	0.86	0.17
R. maximum		0.83	0.33	0.48	0.37	0.33	0.06	0.12
Q. alba		0.53	0.34	1.83	0.24	0.00	0.69	0.26
Total basal area (SE)		30.5 (1.3)	30.1 (1.0)	27.7 (0.8)	35.1 (2.2)	34.0 (1.8)	25.2 (1.2)	25.3 (0.9)
Number of plots per group (percentage of total)		45 (16%)	61 (22%)	83 (30%)	15 (5%)	21 (7%)	23 (8%)	33 (12%)

Results. Forty-two woody species were identified in the vegetation inventories of the Coweeta Basin. Of these, 18 were considered understory taxa (shrub or small-tree growth forms that rarely enter the overstory canopy) and the remaining 24 were overstory taxa (Table 2). *Quercus prinus* had the highest basal area and occurred frequently in the 1970s and 1990s (Table 2). *Kalmia latifolia* and *Rhododendron maximum,* both understory taxa, had the highest importance values in both sample periods because of their high densities (5–10 times greater than that of any other species). Species that occurred in at least 80% of the plots in both inventories were *R. maximum, Q. prinus, Acer rubrum, Carya* spp., *Nyssa sylvatica,* and *Oxydendrum arboreum.* Among the oaks, *Q. prinus* and *Quercus rubra* increased in importance from the 1970s to 1990s, while *Quercus coccinea, Quercus velutina,* and *Quercus alba* decreased in frequency, density, and importance. The importance value of *A. rubrum,* a species ubiquitous in the Coweeta Basin, increased from the 1970s to the 1990s because all measures of its relative abundance increased. In contrast, *Pinus rigida* decreased in importance because of a decrease in all measures of its abundance.

COMMUNITY CLASSIFICATION. Twelve woody species significantly contributed to discriminating among the seven cluster groups for the 1970s inventory data (Table 3). The overall coefficient of determination for the clustering of woody species was only 0.49. Group I, described as a mesic, hemlock-poplar (*Tsuga canadensis-Liriodendron tulipifera*) community, was dominated by *Tsuga canadensis, A. rubrum,* and *Liriodendron tulipifera* and had a large component of *Q. prinus* and *Betula lenta* (Table 3). This group was found at low elevations with deep soils, high organic matter content, and deep coves (lowest terrain shape). Group II, which is described as a dry, chestnut oak (*Q. prinus*) dominated community by Schafale and Weakley (1990), occurred at middle elevations on upper slopes (high terrain shape) where soils contained

low soil organic matter and had a shallow A-horizon (Table 3). Group III, a mixed deciduous community, included *A. rubrum, Q. prinus, Q. coccinea, Carya* spp., *Q. velutina,* and *Q. alba*; it occurred at low elevations and mid-slope positions. Group IV, which is described as a cove hardwood community by Schafale and Weakley (1990), was dominated by *L. tulipifera*; it occurred on low elevation sites with low terrain shape (coves) and deep soils with high organic matter content. Group V, a mesic, mixed-oak community, was dominated by *Q. rubra* and had a large component of *Q. prinus* and *Carya* spp.; it occurred at mid-slope positions (moderately high terrain shape) and moderately high elevations. Group VI, a dry-to-xeric, mixed-oak community, was dominated by *Q. coccinea* and also had a large component of *Q. prinus*; it occurred at low elevations on upper slopes to ridges with shallow soils that contained little organic matter and high soil clay content. Group VII, an oak-pine community which corresponds to Schafale and Weakley's (1990) xeric pine-oak heath type, was dominated by *Pinus rigida, Q. coccinea, K. latifolia,* and *Q. prinus.* This group occurred on low elevation ridges with shallow soils that contained little organic matter content.

In the 1990s inventory, the same permanent plots were placed in the cluster groups as described in the 1970s analyses (Table 3). Plots in two of the community groups (Group VI and VII) had a decrease in average basal area over the 20 yr period. In Group VI, there was a substantial decline in *Q. coccinea*; and, in Group VII, there was a substantial decline in *Q. coccinea* and *P. rigida* (Table 3). Vegetation groups IV, V, and VI had low frequencies with fewer than 10% of the plots in any of these groups (Table 3). Group III occurred on almost 30% of the plots.

Eleven site variables significantly contributed to discriminating among groups (Table 4). Soil organic matter content, terrain shape, depth of A-horizon, elevation, soil clay content, and potential solar radiation explained the most variation ($r^2 \geq 0.10$) among the community groups (Table 4). All site variables combined explained 45% of the variation among the community groups in the 1970s. The communities were correctly classified from 22% to 67% of the time based on site variables (Table 5).

VEGETATION-SITE PATTERNS. The results from the CCA suggested that there was a gradient in woody species distribution across the Coweeta

Table 4. Average values (SE) of site variables that significantly ($p \leq 0.001$) contributed to discriminating among cluster groups. Cluster groups based on analysis of 1969–1973 inventory.

Site variables	r^2	I	II	III	IV	V	VI	VII
Soil OM (%)	0.20	13.9 (0.8)	9.0 (0.6)	8.4 (0.6)	12.0 (1.5)	9.1 (1.2)	6.4 (0.8)	6.2 (0.5)
Terrain shape	0.20	4675 (79)	5279 (73)	5021 (68)	4715 (113)	4980 (140)	5341 (93)	5591 (90)
A-horizon (cm)	0.17	28 (1.9)	19 (1.4)	19 (1.2)	28 (3.6)	20 (2.6)	14 (1.4)	13 (0.8)
Elevation (m)	0.12	912 (23)	965 (14)	876 (11)	933 (23)	1010 (28)	909 (16)	900 (14)
Clay content (%)	0.12	25 (1.1)	26 (1.0)	30 (0.8)	25 (1.9)	28 (1.7)	33 (1.2)	31 (1.2)
Solar radiation (%)	0.11	82 (4)	94 (3)	94 (3)	86 (7)	82 (5)	105 (5)	103 (4)
Precipitation (cm)	0.09	273 (3)	272 (3)	263 (2)	274 (5)	278 (5)	258 (3)	264 (2)
Modified azimuth	0.08	111 (6)	91 (5)	92 (5)	99 (14)	116 (10)	72 (9)	76 (7)
Temperature (°C)	0.07	19.6 (0.1)	19.7 (0.1)	20.0 (0.1)	19.4 (0.2)	19.2 (0.3)	20.2 (0.1)	20.3 (0.2)
Soil depth (cm)	0.06	140 (4)	125 (4)	124 (3)	132 (8)	128 (6)	117 (5)	120 (4)
Percent slope	0.04	50 (3)	58 (2)	50 (2)	51 (5)	53 (3)	48 (3)	53 (3)
Total r^2	0.45							

Table 5. Discriminant analysis of clustered vegetation groups for the 1969–1973 vegetation inventory. Percentage of plots correctly classified into cluster groups based on site variables.

Predicted vegetation by site variables	Vegetation classified by cluster analysis							Number of plots per group
	Mesic, hemlock-poplar	Dry, chestnut oak	Mixed deciduous	Cove hardwood	Mesic, mixed-oak	Dry to xeric, mixed-oak	Xeric, oak-pine	
				1969–1973				
Mesic, hemlock-poplar	**17**	5	4	14	4	1	0	45
	38%	11%	9%	31%	9%	2%	0%	
Dry, chestnut oak	4	**15**	3	9	10	10	10	61
	6%	**25%**	5%	15%	16%	16%	16%	
Mixed deciduous	9	7	**18**	13	8	17	11	83
	11%	8%	**22%**	16%	10%	20%	13%	
Cove hardwood	1	0	2	**10**	0	2	0	15
	7%	0%	13%	**67%**	0%	13%	0%	
Mesic, mixed-oak	1	1	2	4	**10**	3	0	21
	5%	5%	10%	19%	**48%**	14%	0%	
Dry to xeric, mixed-oak	1	0	3	1	2	**14**	2	23
	4%	0%	13%	4%	9%	**61%**	9%	
Xeric, oak-pine	1	4	4	0	2	5	**17**	33
	3%	12%	12%	0%	6%	15%	**52%**	

Note: Percentages correctly classified in each group are in bold.

Basin. The eigenvalues were 0.231 for CCA1 and 0.143 for CCA2 (Fig. 2) and the sum of all canonical eigenvalues was 0.501 (i.e., 50% of the variation in the species distribution was explained by the eleven site variables). The species-site correlations were high (68.0% for CCA1 and 66.5% for CCA2): soil organic matter content, A-horizon depth, and terrain shape were highly correlated with CCA1; and elevation, terrain shape, and precipitation were highly correlated with CCA2 (Fig 2). Soil organic matter content, elevation, and terrain shape explained 33% of the variation in the species distribution, much more than any of the other variables. A-horizon depth was highly correlated with CCA1 but explained only an additional 1% of the variation more than explained by soil organic matter content alone. Potential solar radiation and mean growing season temperature explained an additional 8% of the variation.

In the CCA ordination diagram (Fig. 2), species at the low end of CCA1 (steep terrain, soil low in organic matter, and high solar radiation) were *P. rigida, K. latifolia, Castanea pumila, Q. coccinea,* and *Symplocos tinctoria.* Species at the high end of CCA1 (coves, high soil organic matter, and deep A-horizon) were *L. tulipifera, B. lenta,* and *T. canadensis.* Species at the low end of CCA2 (low elevation and low terrain) were *T. canadensis* and *Fagus grandifolia.* Species at the high end of CCA2 (high elevation and high precipitation) were *Prunus serotina* and *Acer saccharum.*

The CCA ordination diagram (Fig. 3) showed distinct separation among some communities, however, there was overlap among others. Group VII, the xeric oak-pine community, was located at the far left along CCA1 with high terrain shape, high soil clay content and south- to southwest-facing slopes with high solar radiation. Group IV, cove hardwood, was located at the lower right along CCA1 with high soil organic matter content and deep A-horizon. Group V, mesic, mixed-oak, was positioned at the high end of CCA2, with high elevation and precipitation. Group III, mixed-deciduous, was distributed along the entire length of CCA2 and the center of CCA1. Community boundaries overlapped, but Group IV was clearly distinct from Groups II, VI, and VII. Group III was a transition community extending from the boundary of Group VII (the negative end of the gradient) to the boundaries of Groups I and IV (the positive end of the gradient).

Although there was considerable variation in terms of how sample plots moved in ordination space, on average three of the seven vegetation communities moved in ordination space through time (Fig. 3). The xeric, oak-pine (Group VII) and dry, mixed-oak (Group VI) types moved towards the center of the ordination (Fig. 3). By the 1990s, many of the sample plots in Group VI or VII moved to the right along CCA1 and some plots in Group VI moved down along CCA2 (Fig. 4). Some of the plots in Group IV moved up along CCA2 (Fig 4). The other four

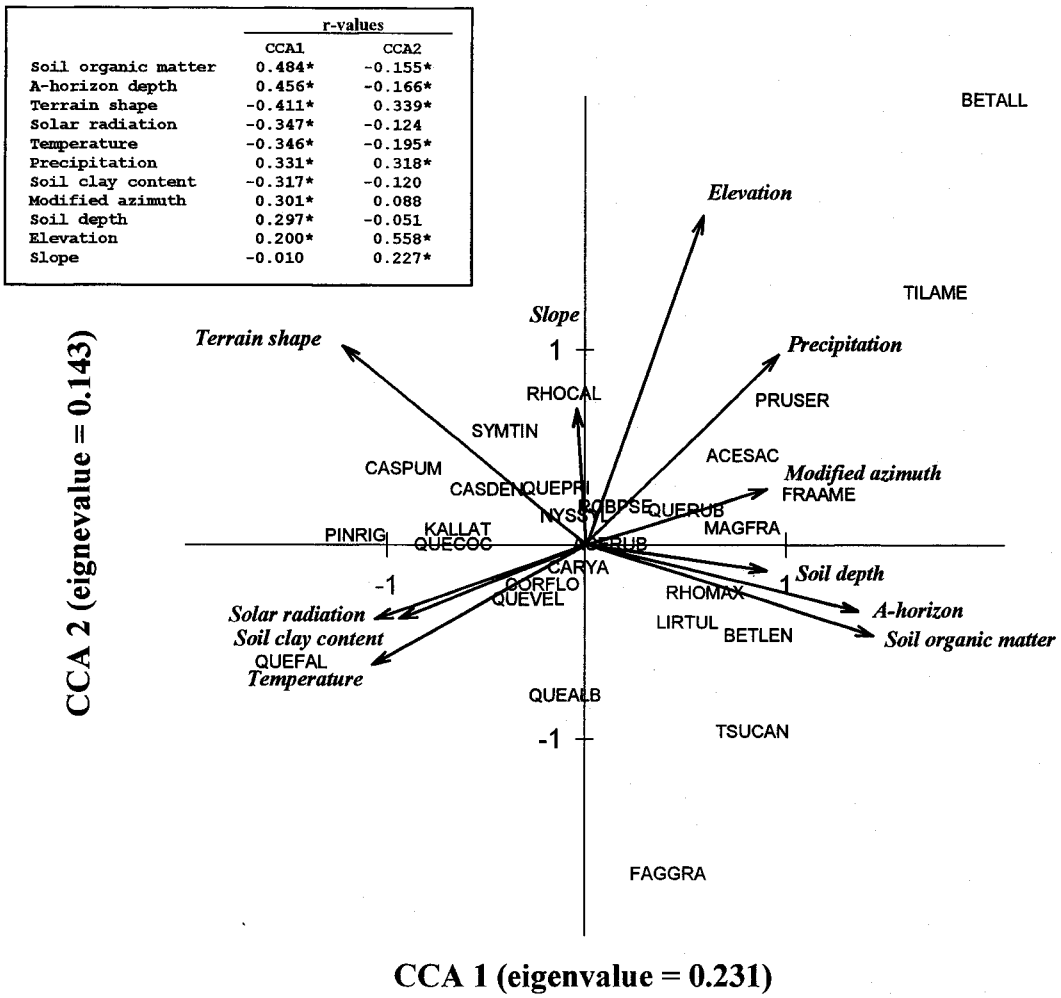

Fig. 2. Coweeta Basin vegetation data from 1969–1973 and 1988–1993 inventories combined; canonical correspondence analysis (CCA) ordination diagram of species scores and site environmental variables. Species codes: ACESAC = *Acer saccharum*; ACERUB = *Acer rubrum*; ACEPEN = *Acer pensylvanicum*; AESOCT = *Aesculus octandra*; AMEARB = *Amelanchier arborea*; BETALL = *Betula alleghaniensis*; BETLEN = *Betula lenta*; CALFLO = *Calycanthus floridus*; CARSPP = *Carya* spp.; CASDEN = *Castanea dentata*; CASPUM = *Castanea pumila*; CORFLO = *Cornus florida*; FAGGRA = *Fagus grandifolia*; FRAAME = *Fraxinus americana*; KALLAT = *Kalmia latifolia*; LIRTUL = *Liriodendron tulipifera*; MAGACU = *Magnolia acuminata*; MAGFRA = *Magnolia fraseri*; NYSSYL = *Nyssa sylvatica*; PINRIG = *Pinus rigida*; PRUSER = *Prunus serotina*; QUEALB = *Quercus alba*; QUECOC = *Quercus coccinea*; QUEFAL = *Quercus falcata*; QUEPRI = *Quercus prinus*; QUERUB = *Quercus rubra*; QUEVEL = *Quercus velutina*; RHOCAL = *Rhododendron calendulaceum*; RHOMAX = *Rhododendron maximum*; ROBPSE = *Robinia pseudoacacia*; SYMTIN = *Symplocus tinctoria*; TSUCAN = *Tsuga canadensis*; TILAME = *Tilia americana.* Site environmental variables with a significant correlation coefficient ($p \leq 0.05$) are denoted by an asterisk.

communities had little or no change over the 20 yr period.

Discussion. The mature forests of the Coweeta Basin appear to be approaching the end of the aggradation phase of succession (sensu Bormann and Likens 1979); density has decreased by 32% over the 20-yr period between inventories and there has been a concomitant increase of only 3% in basal area. The two most abundant understory taxa, *K. latifolia* and *R. maximum,* differed in their vegetation dynamics over time. *Kalmia latifolia* decreased in importance; all measures of its abundance were lower in the 1990s than the 1970s. In contrast, *R. maximum* increased in importance as a result of its increase in relative frequency and relative density. *Acer rubrum,* which is ubiquitous in the Coweeta ba-

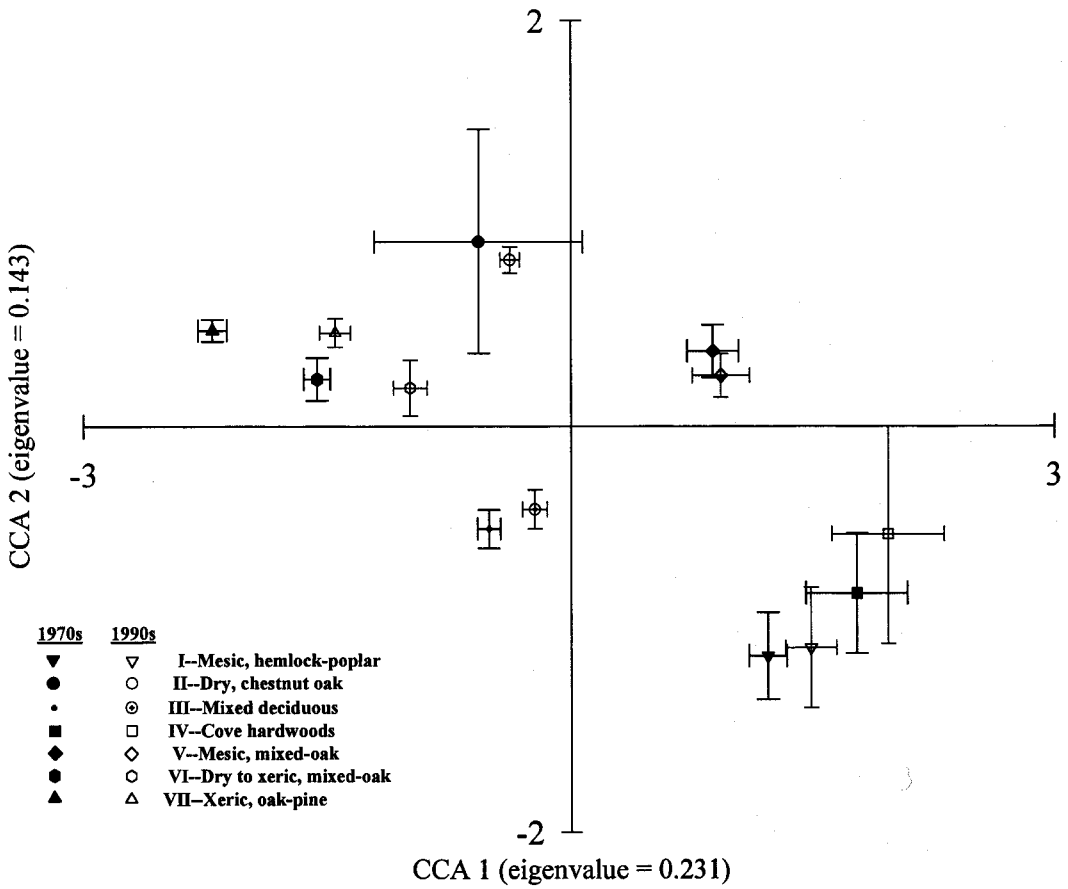

Fig. 3. Coweeta Basin vegetation-site joint ordination for data from 1969–1973 and 1988–1993 inventories: canonical correspondence analysis (CCA) ordination diagram of mean values of sample scores (with standard error bars) coded by vegetation groups determined from cluster analysis; filled symbols represent mean values from the 1970s inventory and open symbols represent mean values from the 1990s inventory.

sin, occurred in at least 99% of the plots in both inventories and increased in importance over the last 20 yrs. Two of the oak species, *Q. prinus* and *Q. rubra,* increased in importance, while the importance values of the other three oaks decreased. *Liriodendron tulipifera,* a dominant species in the cove hardwood community and abundant in three others, also increased in importance. *Cornus florida* declined in importance with a decrease in frequency and density. *Pinus rigida,* a dominant species in the oak-pine community in the 1970s, declined in importance as a result of mortality induced by drought and insect attack in the 1980s (Smith 1991).

Although community types can be distinguished within the Coweeta Basin, their boundaries overlap when plotted in ordination space. These plant communities are typically diverse and are distributed in a mosaic over the highly varied topography in relation to gradients in moisture (Yeakley 1993) and nutrients (Leopold and Parker 1985). However, some communities could be distinguished from others. For example, the xeric oak-pine and dry mixed-oak communities clearly differ from the mesic hemlock-poplar or cove hardwood communities. However, a large proportion of the plots (almost 30%) were occupied by a mixed-deciduous community dominated by *Acer rubrum.* This community is transitional or intermediate between communities that occupy sites characterized by extremes of elevation and terrain shape. Many of the sample plots from the 1970s inventory had moved a significant distance in ordination space by the 1990s. For example, a large proportion of plots in the oak-pine or the dry, mixed-oak communities had moved towards the center of the ordination space.

Only 50% of the variation in the vegetation distribution of the Coweeta Basin was explained

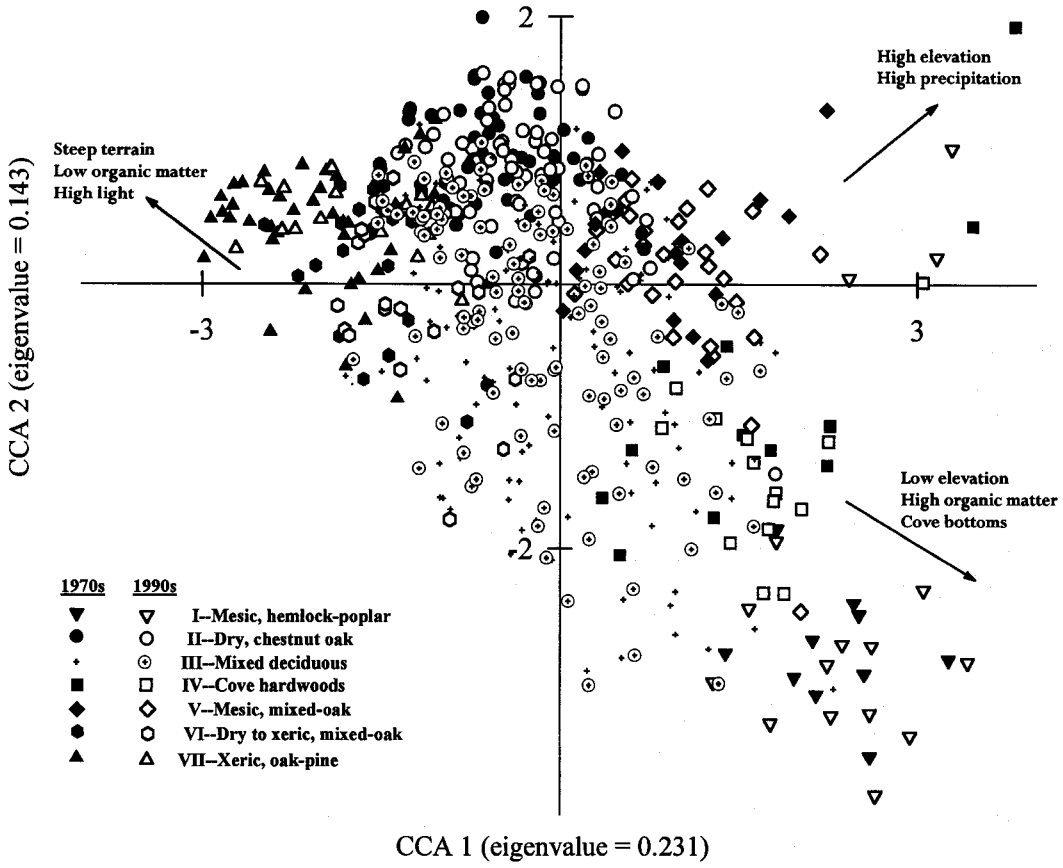

Fig. 4. Canonical correspondence analysis of sample scores of individual plots (samples) in ordination space from 1969–1973 to 1988–1993. Samples are coded by vegetation groups determined from cluster analysis as in Fig 3.

by the site variables used in the CCA ordination. Soil organic matter content, elevation, and terrain shape explained more variation than any of the other variables. Species that usually occur on high terrain (upper slopes, ridges), such as *P. rigida, K. latifolia,* and *Q. coccinea,* decreased in IV; whereas species associated with high organic matter content and deep A-horizons, such as *L. tulipifera, R. maximum,* and *T. canadensis,* increased in importance. Bolstad et al. (1998) observed that occurrence of some species (e.g., *Q. velutina, Robinia pseudoacacia, B. alleghaniensis,* and *Acer saccharum*) was weakly related to terrain shape, while occurrence of others (e.g., *L. tulipifera, Q. prinus, T. canadensis, P. rigida*) was strongly related to it. Our findings regarding terrain shape are consistent with these observations. For example, in our study, *T. canadensis* and *L. tulipifera* were most abundant at low terrain while *P. rigida* and *Q. coccinea* were most abundant at high terrain.

Soil variables have often explained much of the variation in vegetation distribution (Grigal and Arneman 1970; Peet and Loucks 1977; Golden 1980; Muller 1982; Leopold and Parker 1985; Roberts and Richardson 1985; Roberts and Christensen 1988; Jeglum and He 1995; Taft et al. 1995; McDonald et al. 1996). Leopold and Parker (1985) found that soil variables measured in each plot (e.g., pH, Ca, organic matter) were important in describing the vegetation distribution in a small watershed in the Coweeta Basin. Soil pH, organic carbon, Ca, Mg, base saturation, and soil moisture were significantly higher in the plots occupied by cove hardwood than in the plots occupied by mixed-oak (mid-slope) or oak-pine (upper-slope and ridge) communities. In addition, the occurrence of some species was more highly correlated with soil variables than was occurrence of others (Leopold 1984). For example, *L. tulipifera* was significantly ($p \leq 0.01$) and positively related to soil pH ($r =$

0.84), total nitrogen (r = 0.72), calcium (r = 0.87), magnesium (r = 0.74), base saturation (r = 0.83), and soil moisture (r = 0.71), whereas *Q. prinus, Q. coccinea,* and *K. latifolia* were negatively related to the same variables. The soil variables used in our study were taken from a soil series map of Coweeta and thus were coarse grained, but they were significantly related to the first axes of the CCA. We also found that occurrence of some species was related to soil variables but that other species occurred across the gradient of site variables. For example, *A. rubrum* was located in the center of the ordination space, suggesting that its occurrence was not related to the extremes of the site variables used. Other species that were located in the center of the ordination space and increased in importance between 1970 and 1990 were *Q. prinus, Oxydendrum arboreum,* and *Nyssa sylvatica.* These species may be habitat generalists, occurring across the entire range of environmental conditions in the Coweeta Basin, or they may be specialists on intermediate sites. However, since *A. rubrum* occurred in at least 99% of the plots in either inventory, it may be considered a habitat generalist.

The composition and structure of forest ecosystems are usually influenced by climatic, edaphic, and physiographic variation within local landscapes (Roberts and Christensen 1988; Nowacki et al. 1990). Some of the variation in species distribution patterns was not explainable by site variables. Disturbance may explain additional variation in species distribution in the Coweeta Basin. Natural disturbance and past land-use history are important factors in the development of forest stands (Lorimer 1977; Runkle 1982; Christensen 1989; Foster 1992; Orwig and Abrams 1994). Although only data from permanent plots undisturbed by humans in the past 70+ yrs were used in our analyses, natural disturbances such as drought, insect damage, and localized windfall, as well as land use prior to 1923, may have contributed to the current distribution of species. Thus, disturbances interacting with physical gradients and stand condition may have substantially shaped the vegetation pattern we observed. Moreover, plot-specific quantification of disturbance history would probably contribute to a better understanding of vegetation patterns and their response to environmental changes. For example, both localized windfall or drought induced mortality could create single tree or multiple tree gaps large enough to provide regeneration sites for early successional species (Clinton et al. 1994). However, these two types of disturbance are quite different in terms of their distribution of kind and number of new microsites for regeneration. Drought induced mortality, where trees die standing, results in a relatively lack of forest floor disturbance, whereas tree blowdown openings create pit and mound topography with exposed mineral soil. These types of disturbance may or may not be widespread, but could be detected at the individual plot level.

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