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A Multivariate Analysis of Forest Communities in the Western Great Smoky Mountains National Park

RAGAN M. CALLAWAY[1] and EDWARD E. C. CLEBSCH
Graduate Program in Ecology, University of Tennessee, Knoxville 37996

and

PETER S. WHITE
Uplands Field Research Laboratory, Great Smoky Mountains National Park, Gatlinburg, Tennessee 37738

ABSTRACT: An integrated sequence of multivariate techniques was applied to the vegetation of the western Great Smoky Mountains National Park. Included in the sequence were hierarchial classification, detrended correspondence analysis and multiple discriminant analysis. Based on the importance of landform in previous research, a system of topographical quantification was developed and also used in the classification.

Elevation and the topographical index, termed protection, were the most important variables associated with the 12 classified forest types. Drainage area, another topographic measurement, soil *p*H and water-holding capacity were also significant in the vegetation analysis. Logging and farming disturbances prior to the formation of the national park were probable causal factors for some forest types.

INTRODUCTION

The Great Smoky Mountains of Tennessee and North Carolina have been a focal point of vegetation analysis since 1930 (Cain, 1930). Because the Smoky Mountains provide elevation-related temperature and precipitation gradients, complex topographical patterns, and a rich woody-species composition, they have been used repeatedly in studies of the relationships of plants to the environment and within communities.

Whittaker (1956) identified species associations throughout the Great Smoky Mountains National Park (GRSM) and defined their positions on a moisture complex-gradient. He concluded that the interaction of elevation, topographic shape and slope aspect determined the vegetation present at a given site. Golden (1974, 1981) approached the problem of vegetation distribution in the central GRSM with an integrated sequence of multivariate techniques (cluster analysis and similarity sorting, discriminant analysis, reciprocal averaging, ordination and canonical correlation) using quantitative environmental variables. He found the overwhelming importance of topography and elevation as described by Whittaker was also indicated by his data and analyses. Soils data collected by Golden (1981) indicated that the *p*H of the A horizon and the percent clay in the B horizon were also important correlative factors.

The major purposes of this paper are (1) to develop a method for quantifying topographic shape in the Smoky Mountains; (2) to provide an integrated multivariate analysis, including the topographic index, of the western Great Smoky Mountains, and (3) to examine stands disturbed by prepark logging and agriculture. Neither Whittaker (1956) nor Golden (1981) satisfactorily quantified topographic shape, which they cited as being important. Whittaker (1956) assigned a sequential order to land shapes and assumed that the order represented moisture characteristics. Golden (1981) measured the position of stands on slopes and the slope aspect but did not include slope shape. We have constructed an index of topographic shape and included it in our vegetation analysis. Most of the study area was on three major topographic features in the western

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[1]Present address: Department of Biological Sciences, University of California, Santa Barbara, CA 93106.

GRSM (Davis, Leadbetter and Gregory ridges) which had not been included in any previous vegetation analyses. The plots ranged from 300-1800 m in elevation. The spruce-fir forests of Whittaker (1956) and Golden (1981) are not present in the western GRSM. This study also extended the data base from the undisturbed stands of Whittaker (1956) and Golden (1981) to include forests that had been disturbed by logging and farming, thus permitting a comparison between disturbed and undisturbed stands. It should be pointed out that the chestnut blight (*Endothia parasitica*) has affected almost all forest communities in the GRSM.

METHODS

Vegetation distribution. — Data from 154 permanent 20 x 50 m (0.1 ha) plots previously established by the National Park Service were used to assess vegetation distribution. These plots had been established with the intent to represent all combinations of elevational, topographic and successional gradients (Bratton, 1978). Plots had been placed so as to not overlap obviously different topographic conditions. Woody plants over 1.0 cm in diam were recorded by 1.0-cm classes. The units of species importance used throughout the analysis were total m^2 of basal area per ha.

Environmental variables. — A soil pit excavated to the top of the C horizon was established on each plot. Depth of organic matter, thickness of A horizon, B horizon, and total unconsolidated soil were noted. Samples were removed from the A and B horizons for texture and *p*H analysis, and the percent volume of large stones in the pit was recorded. All soil samples were analyzed for particle size using the Bouyoucos (1963) hydrometer technique and size classes were recorded to the nearest 1%. Water-holding capacity of the A and B horizons was calculated using texture tables by Longwell *et. al.* (1963), A and B horizon thickness, and percent volume stone.

Slope aspect, distance from the plot to surface water, degree of disturbance, nature of parent material, and percent slope were recorded. Slope aspect was transformed by the Beers *et al.* (1966) method. This technique transforms the clockwise increase of azimuth value into a linear sequence from 0.00 (SW aspect) to 2.00 (NE aspect). Topographical type was derived subjectively from maps and in the field (*cf.*, Whittaker, 1956) with types categorized as mesic flat, ravine, cove, protected slope, xeric flat, open slope, gap and ridge.

An index of site protection was constructed on a scale of 0-100, 0 indicating a plot with no nearby landforms of greater elevation, and 100 being the plot measured as having the most surrounding land of higher elevation. The variable was labeled "protection" because it did not measure downslope topography, its meaningfulness being limited to the surrounding "protecting" topography. The index was developed by calculating the ratios of the heights of surrounding landforms to the distances of those landforms from the plot. To selectively sample the protection of a given plot, eight fixed azimuths were plotted from each plot center at 0, 45, 90, 135, 180, 225, 270 and 315 degrees on topographical maps. The equation

$$\text{protection} = \frac{\sum_{i=1}^{8}\left[\dfrac{ER_i - EP}{D_i}\right]}{8}$$

where ER = elevation of the "protecting" landform, EP = elevation of the plot and D = distance from the plot to the protecting landform, was applied to each plot. Calculations were made for each azimuth and averaged for the plot protection value. In order to remain consistent with the Beers *et al.* (1966) transformation's weighing of northern aspects the 135, 180 and 225 degree azimuths were subjectively weighted by a factor of

1.5. This weighting resulted in slightly higher values for plots with higher landforms to the S.

A planimeter and gridform were used on topographical maps to measure the catchment area from which runoff rainfall and snowmelt could drain into the plot. This value ranged from 1000 m^2 (the area of a plot) to an area of greater than 100 ha.

Data analysis. —A sequence of multivariate procedures (*after* Golden, 1981) was used to examine the relationships among the forest types. All species were included in all analyses.

Two-way indicator species analysis. —TWINSPAN, a hierarchical classification program, was used to initially identify forest types (Hill, 1979b). The function of TWINSPAN is basically to make repeated dichotomies until the sample-units are placed in a hierarchy ranging from the total collection of sample-units to individual sample-units. From this hierarchy meaningful units of vegetation, or forest types, must be selected. Hill (1979b) summarizes the process as (1) the primary ordination (reciprocal averaging) to obtain an initial dichotomy; (2) the refined ordination, derived from indicator species prominent in the primary ordination, and (3) the indicator ordination. Once a classification hierarchy was obtained, the forest types were chosen through a series of comparisons of DECORANA sample-unit groupings, examination of the original data and consideration of previous work. Ultimately, the decisions were subjective and were not restricted to a single level of the hierarchy.

Detrended correspondence analysis. —The precision of the forest type groups obtained from the previous analysis was examined by indirect ordination analysis. The computer program written by M. O. Hill (1979a) was used to execute the procedure. The major advantages of detrended correspondence analysis (DCA) is the avoidance of the "arch effect" (Gauch *et al.*, 1977) and the "horseshoe effect" (Kendall, 1971) common to reciprocal averaging by not permitting systematic relationships between the primary and secondary axes. Another major fault attributed to reciprocal averaging is the distortion of relative distances between samples on its axes (Hill and Gauch, 1980; Gauch, 1982). DCA summarizes the species composition of samples in various segments of the gradient and develops an arrangement such that equal differences in species composition correspond to equal differences along the gradient (Hill and Gauch, 1980). The techniques of replacing orthogonalization with detrending and standardizing the units of within-samples variance characterize the method of DCA. Environmental causes of vegetation distribution were investigated by regression and correlation analyses of the indirect ordinates.

Stepwise discriminant analysis. —Discriminant analysis distinguishes between groups of observations on the basis of a set of discriminating variables which are expected to differ among the various groups. This is done by forming linear combinations of the discriminating predictor variables that differ significantly in their group means (Tatsuoka, 1971; Nie *et al.*, 1975). From previously defined groups (forest types in this case), sets of discriminant functions are derived stepwise from their linear combinations of input variables (environmental variables in this case) that present the greatest contrast between the groups (Golden, 1981; Anderson, 1958).

An important use of discriminant analysis is its classification power. After discriminant functions are calculated, they in turn may be used to re-evaluate the groups (forest types) from which they were derived. This classification process may be used to consider the quality and success of other classification techniques. If a low percentage of groups has been properly classified, then the original selected variables are poor discriminators by virtue of their commonness among groups (Nie *et al.*, 1975). In this study discriminant analysis was used to measure the success of the TWINSPAN classification by using environmental variables to establish discriminant functions.

RESULTS

Twelve forest types were chosen from the TWINSPAN hierarchical classification program by a process including comparisons of DECORANA sample groupings, examination of the original data and consideration of previous work. These forest types were: white oak-white pine (*Quercus alba, Pinus strobus*), scarlet oak-yellow pine (*Q. coccinea, P. pungens, P. rigida*), chestnut oak (*Q. prinus*), northern red oak-silverbell (*Q. rubra, Halesia carolina*), hemlock-silverbell-beech (*Tsuga canadensis, H. carolina, Fagus grandifolia*), yellow poplar (or tulip poplar) (*Liriodendron tulipifera*), hemlock-yellow poplar (*Tsuga canadensis, Liriodendron tulipifera*), basswood-buckeye (*Tilia heterophylla, Aesculus octandra*), northern red oak (*Q. rubra*), yellow birch-buckeye (*Betula alleghaniensis, Aesculus octandra*) and beech (*Fagus grandifolia*) (Fig. 1, Table 1).

Of the four axes provided by DECORANA two were the most significant and their ordination scores were tested by linear regression and correlation with all of the environmental variables. The distribution of forest types on the primary axis was best explained by elevation change in the regression analysis, yielding an r^2 value of 0.53 (significant at $P<0.001$). The primary axis also accounted for more variation in the species distributions than the other axis, evidenced by an eigenvalue of 0.773 for the primary axis and an eigenvalue of 0.457 for the secondary axis. The secondary axis was significantly negatively correlated with protection, with $r^2 = -0.49$ ($P<0.001$).

Beech, yellow birch-buckeye, northern red oak, chestnut oak and yellow pine forest types were clearly separated on the first and second DCA ordinates (Fig. 2). Cove forests overlapped considerably on the ordination. Yellow poplar and hemlock-yellow poplar types occupied similar positions on the first two axes. This overlap is corroborated by the similarity of direct measurements of elevation, protection and soil textures for the two types (Table 2).

Environmental variables were used as data for a discriminant analysis on forest type groups. The resulting functions and their associated coefficients were used to describe the relationships of the types environmentally and to rank the relative importance of the

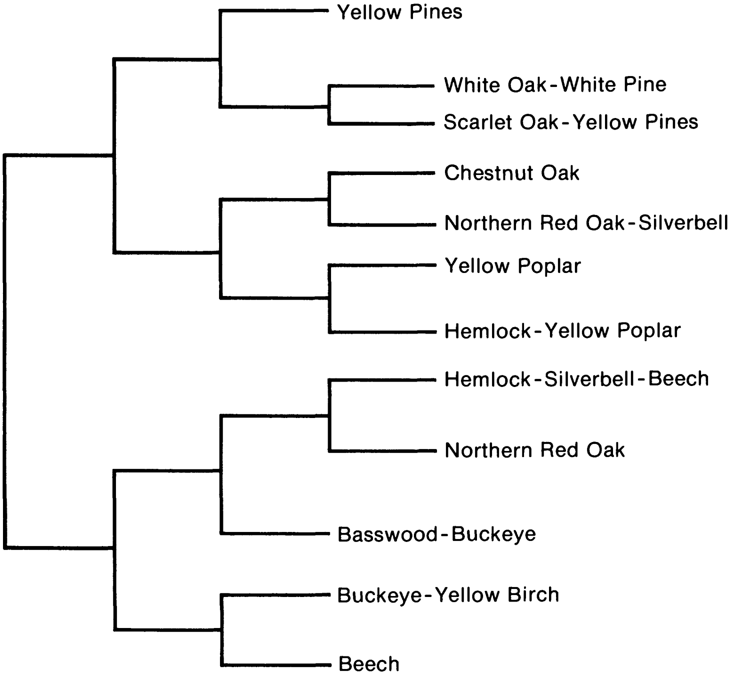

Fig. 1.—Dendrogram of TWINSPAN hierarchy of forest types from the western GRSM

TABLE 1.—Tree species average basal area (m²/ha) in 12 forest community types. The order of types follows increasing elevation

Species		YP	WO-WP	SO-YP	CO	NRO-Sil	H-SIL-Beech	TP	H-TP	B-B	NRO	YB-B	Bee
	n =	12	11	7	26	12	9	11	9	6	11	13	6
Pinus virginiana		14.6	1.9	3.7									
P. rigida		9.3	0.6	6.0									
P. strobus		4.4	6.0		1.6			0.4	.05				
P. pungens		0.1		5.0									
Quercus coccinea			0.8	3.7	0.4								
Q. alba			10.4		0.3	0.4		0.1			0.5		
Q. velutina			1.3		0.8	0.2							
Carya glabra		0.2	0.3		0.5				0.4				
Oxydendrum arboreum		1.6	2.5	0.7	1.3	0.6		0.8	0.7				
Nyssa sylvatica			0.4	1.3	1.8	0.2			0.2				
Robinia pseudoacacia					0.3	0.9		0.8					
Q. prinus				5.4	9.1	1.4		0.1	0.1				
Acer rubrum		1.6	2.0	2.3	3.4	4.6	3.1	2.8	3.9	0.7	2.1		
Magnolia fraseri						0.5	2.8	0.1	0.7				
Quercus rubra					2.0	12.1	1.6	1.1	0.3	0.3	20.0		
Liriodendron tulipifera		3.4			2.0	1.1	0.2	18.8	8.9	2.3	0.1		
Betula lenta					0.1	1.2	0.7	0.9	2.4		0.1		
Fraxinus americana						0.1		0.4	0.2	3.1	0.4		
Halesia carolina						3.4	5.1	2.0	1.5	5.1	0.8		
Magnolia acuminata						0.6		0.2		0.6	0.1		
Prunus serotina							2.3	0.9			0.4	0.3	
Tsuga canadensis						0.3	9.2	0.7	15.8	1.8		0.3	
Tilia heterophylla							0.7	0.9	0.7	5.6		0.1	
A. saccharum						0.3	0.2	0.4	0.7	1.6	1.1	1.7	0.5
C. cordiformis								0.5		2.5			
Aesculus octandra								0.7	0.1	7.8	1.5	8.0	3.3
B. alleghaniensis							1.4		0.9	1.7	1.9	8.5	1.2
Fagus grandifolia							5.5				0.2	7.8	24.7

variables for determining the presence of specific forest types. Scarlet oak-yellow pine, basswood-buckeye, and beech forest types were all classified correctly by the TWINSPAN program as evaluated by discriminant analysis and the environmental variables (Table 3). The major classification problems encountered were with the pine-dominated forest types, all of which were abundant on exceptionally dry sites. TWINSPAN misclassification occurred more frequently for forests which had experienced human disturbance, including hemlock-silverbell-beech and yellow poplar. Discriminant analysis of the environmental variables correctly classified 74.8% of all of the forest types.

Although five discriminant functions were significant at $P<0.001$, the first two accounted for 76.4% of the total variability attributable to the environmental variables measured. Although the stands were graphed on only the first two discriminant functions, the classification matrix was determined by using all of the calculated functions.

In the first discriminant function elevation was the predominant discriminating variable (Table 4). In contrast to the strong relationship of landform to the second DCA axis, the second discriminant function was more determined by the *p*H of the A horizon and the water-holding capacities of the A and B horizons. Protection is highly correlated with soil *p*H and water-holding capacity, however, and protection remained prominent in the second function as well as the third, fourth and fifth discriminant functions.

As in the DECORANA graph, the elevation-topographic moisture trend was evident, originating with the xeric yellow pine forest at the low elevation, low *p*H, exposed topography corner of the discriminant function graph (Fig. 3). The trend is apparent at the other extreme in the beech forests at high elevations, and the three cove forest types, basswood-buckeye, hemlock-yellow poplar, and yellow poplar at the high *p*H, protected topography end of the second function. As in the DECORANA graph, the hemlock-yellow poplar and the yellow poplar centroids were closely grouped, indicating either a high degree of habitat overlap or the lack of a discriminating variable for these types.

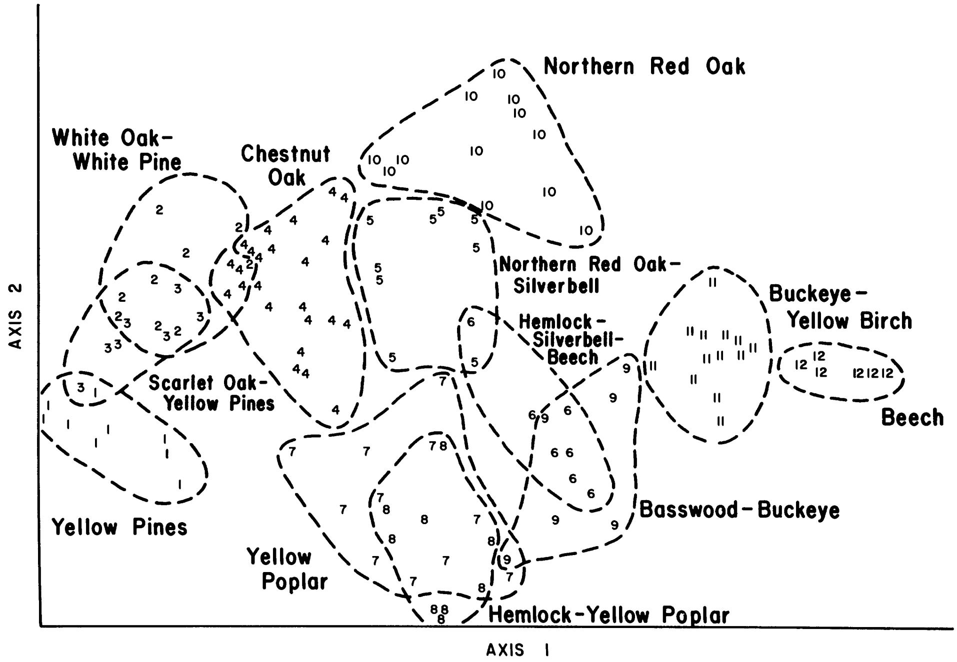

Fig. 2.—Distribution of samples on first and second DECORANA ordination axes

TABLE 2.—Environmental characteristics (mean ± standard error) for forest community types

	Yellow pine	White oak-white pine	Scarlet oak-yellow pine	Chestnut oak	N. red oak-silverbell	Hemlock-sil-beech
Elevation (m)	572 ± 16	587 ± 16	841 ± 73	874 ± 39	1113 ± 44	1201 ± 86
Protection	0.15 ± 0.01	0.15 ± 0.01	0.13 ± 0.02	0.21 ± 0.02	0.24 ± 0.02	0.24 ± 0.03
Drainage area (ha)	0.75 ± 0.28	0.78 ± 0.11	0.23 ± 0.04	1.08 ± 0.02	1.64 ± 0.38	1.54 ± 0.31
Total soil depth (cm)	70.3 ± 4.9	66.7 ± 4.4	61.1 ± 7.1	67.8 ± 3.0	79.8 ± 3.0	80.1 ± 2.1
% Clay in A	27.3 ± 2.2	27.0 ± 1.7	25.3 ± 2.7	18.4 ± 1.9	13.8 ± 1.7	19.7 ± 1.7
% Silt in A	49.2 ± 2.6	51.5 ± 2.6	51.6 ± 2.6	54.5 ± 2.2	49.5 ± 3.8	47.2 ± 1.7
% Sand in A	23.4 ± 3.0	21.5 ± 2.3	23.3 ± 2.1	27.6 ± 1.7	36.1 ± 2.6	33.2 ± 2.5
% Clay in B	30.7 ± 2.9	32.5 ± 1.9	31.2 ± 1.6	22.2 ± 2.3	17.7 ± 2.4	21.7 ± 1.6
% Silt in B	48.8 ± 2.8	47.7 ± 2.9	48.9 ± 3.4	54.5 ± 2.8	51.5 ± 4.5	49.3 ± 1.9
% Sand in B	20.6 ± 2.6	19.6 ± 3.5	19.3 ± 2.4	23.5 ± 1.8	30.6 ± 3.0	29.0 ± 2.1
*p*H of A	5.1 ± 0.1	5.0 ± 0.04	4.6 ± 0.8	5.0 ± 0.04	5.1 ± 0.05	4.9 ± 0.07
*p*H of B	5.2 ± 0.1	5.2 ± 0.04	4.9 ± 0.8	5.1 ± 0.04	5.2 ± 0.06	5.2 ± 0.08
Water-holding capacity (cm)	7.4 ± 0.9	5.4 ± 0.7	4.8 ± 1.2	7.0 ± 0.8	12.1 ± 1.0	9.3 ± 0.8

TABLE 2.—(Continued)

	Yellow poplar	Hemlock-yel. poplar	Basswood-buckeye	Northern red oak	Buckeye-yel. birch	Beech
Elevation (m)	711 ± 56	705 ± 54	897 ± 24	1369 ± 24	1386 ± 26	1575 ± 49
Protection	0.29 ± 0.03	0.33 ± 0.02	0.38 ± 0.01	0.09 ± 0.02	0.18 ± 0.03	0.10 ± 0.01
Drainage Area (ha)	3.82 ± 1.01	5.26 ± 1.27	6.13 ± 1.4	0.38 ± 0.10	1.80 ± 0.64	0.50 ± 0.16
Total soil depth (cm)	78.8 ± 2.3	80.1 ± 2.4	80.7 ± 2.8	73.4 ± 4.1	71.0 ± 4.1	50.0 ± 5.1
% Clay in A	17.3 ± 2.1	18.0 ± 2.1	15.0 ± 1.6	8.7 ± 1.0	11.7 ± 1.5	11.0 ± 1.7
% Silt in A	44.3 ± 2.2	42.3 ± 1.9	41.4 ± 1.2	63.5 ± 3.0	57.3 ± 2.9	56.3 ± 2.7
% Sand in A	39.3 ± 2.6	39.9 ± 3.4	43.6 ± 2.2	27.6 ± 3.0	30.8 ± 2.9	32.5 ± 1.5
% Clay in B	20.1 ± 2.0	19.3 ± 2.1	16.2 ± 2.0	8.1 ± 1.6	11.8 ± 2.1	12.3 ± 2.1
% Silt in B	43.0 ± 2.1	43.6 ± 2.5	47.2 ± 1.5	64.3 ± 3.4	58.9 ± 3.6	57.7 ± 3.1
% Sand in B	37.0 ± 2.8	37.1 ± 3.9	36.6 ± 2.6	27.5 ± 3.6	29.3 ± 3.3	30.2 ± 1.4
*p*H of A	5.3 ± 0.09	5.0 ± 0.05	5.3 ± 0.07	4.7 ± 0.06	4.8 ± 0.05	4.4 ± 0.09
*p*H of B	5.3 ± 0.07	5.2 ± 0.06	5.5 ± 0.09	4.9 ± 0.03	5.0 ± 0.05	4.7 ± 0.09
Water-holding capacity (cm)	7.9 ± 1.2	7.2 ± 1.4	11.2 ± 2.8	8.3 ± 1.0	8.2 ± 0.8	5.7 ± 1.3

TABLE 3.—Matrix of classification success from discriminant analysis of forest types using environmental variables*

Actual groups	Predicted group membership											
	YP	WO-WP	SO-YP	CO	NRO-S	H-S-B	TP	H-TP	B-B	NRO	YB-B	B
Yellow pine	60.0	20.0	20.0									
White oak-white pine	30.0	50.0	10.0	10.0								
Scarlet oak-yellow pine			100.0									
Chestnut oak		7.7	3.8	80.8	7.7							
Northern red oak-silverbell				18.8	72.7	8.5						
Hemlock-silverbell-beech					11.1	66.7	11.1	11.1				
Tulip poplar		9.1			18.2		54.5	9.1	9.1			
Hemlock-yellow poplar				22.2	11.1			66.7				
Basswood-buckeye									100.0			
Northern red oak						12.5				87.5		
Yellow birch-buckeye										9.1	81.8	9.1
Beech												100.0

* Percent of grouped forest types correctly classified: 74.8%

DISCUSSION

High-elevation forest types.—The spruce-fir association is absent from the western end of the GRSM where these samples were taken. The three major forest types above 1300 m were northern red oak, buckeye-yellow birch and beech. These stands were environmentally distinct from one another on the basis of elevation and protection (Table 2). The high-elevation oak stands reported by Whittaker (1956) and absent from Golden's (1981) study area were represented by the northern red oak type, often composed of over 90% *Quercus rubra* canopy coverage (Table 1). The densest of the *Q. rubra* stands were located along the apex of the state line ridge crest from approximately 1350-1550 m elevation. *Quercus rubra* was associated in this study with both dry site species and mesic species, both on ridges and in deep coves. This range of distribution has been reported by others (Whittaker, 1956; Golden, 1981; Blackman and Ware, 1982). Blackman and Ware found that the distribution of *Q. rubra* and the more xeric *Q. prinus* overlapped extensively on a soil moisture gradient. This complexity was apparent in the present study. Beech stands, also reported by Whittaker (1956), Golden (1981), Cain (1937) and Russell (1953), were sampled at higher elevations than any other forest type. Previous studies have cited ice accumulation, wind funneling, and limited seed dispersal as causal factors for the presence of these stands (Cain, 1937; Russell, 1953; Whittaker, 1956). It has been proposed that, in the northern parts of its range, *Fagus grandifolia* is not usually found on soils where the surface layers are often dry (Harlow and Harrar, 1969). This relationship appears to be true in this study. Although the high-elevation stands existed on very shallow soils with low water-holding capacities, rainfall during the growing season was very consistent regardless of precipitation at lower elevations (Stephens, 1969). Buckeye-yellow birch forests were normally found at the same elevations as northern red oak types but on more protected topography. Duncan's multiple range analysis of the means of protection and drainage area for the two types showed them to be significantly different. In general, buckeye-yellow birch stands became fre-

TABLE 4.—Standardized coefficients of environmental variables

	Discriminant function 1	Discriminant function 2
Elevation	-1.00	-0.39
Protection	-0.01	0.28
Topographical type	-0.33	-0.24
Drainage area	-0.03	0.36
Slope aspect	-0.23	0.24
Distance to water	0.15	-0.07
Disturbance class	-0.23	-0.24
Parent material	0.44	-0.42
Silt in A horizon	0.38	-0.07
Clay in B horizon	0.40	-0.22
Depth of A horizon	0.18	0.09
*p*H of A horizon	0.10	0.62
Depth of O horizon	0.35	-0.05
Total soil depth	0.27	-0.25
Total water-holding capacity	-0.02	0.49
Percentage of variation explained	53.1	23.3

quent in coves and ravines from 1200-1300 m, and as the elevation (temperature-moisture) gradient increased, the forest type extended onto more exposed sites.

Cove forest types.—Species common to the cove forest of the western GRSM are consistent with results reported by Cain (1943), Whittaker (1956) and Golden (1981), although the elevations at which dominant species shift are somewhat different. From approximately 500-800 m, topography with high protection values was dominated by mixtures of *Quercus prinus*, *Liriodendron tulipifera* and *Tsuga canadensis*. At the top of that altitudinal range the latter two species dominate with combinations of *Tilia heterophylla, Halesia carolinia* and *Aesculus octandra*. From ca. 800-1000 m, *T. heterophylla* and *A. octandra* predominate with mixtures of *T. canadensis, Fraxinus americana* and *Halesia carolina*. Above 1000 m *Betula alleghaniensis* and *A. octandra* codominate the coves with the above-mentioned species, but in steadily decreasing percentages. This was also reported by Whittaker (1956) and Golden (1981), but the transitions occurred at lower elevations in the western GRSM. Golden (1981) also reported *Tsuga canadensis* as a more dominant cove species in his study area than it was in the western Smokies.

Pine and oak forest types.—Stands dominated by *Pinus virginiana* were recognized by Whittaker (1956) but absent from Golden's (1981) data. As was the case for *P. rigida*-dominated types, these stands were found only in disturbed areas with low protection values. This old-field and xeric correlation was corroborated by Harmon (1980) and Kuykendall (1978). In similar environmental conditions, but generally on a limestone substrate, *Quercus alba* and *P. strobus* were dominants as the white oak-white pine forest type. *Quercus prinus* was a common member of the low elevation coves, but as elevation increased the species spread onto more exposed topography. Above 1000 m *Q. prinus* was rarely observed. Pine forests codominated by *Q. coccinea* were sampled from 500-1000 m on the most xeric topography measured. Golden (1974) considered the oak-pine communities ecotonal and samples of the scarlet oak-yellow pine basically correspond with his evaluation.

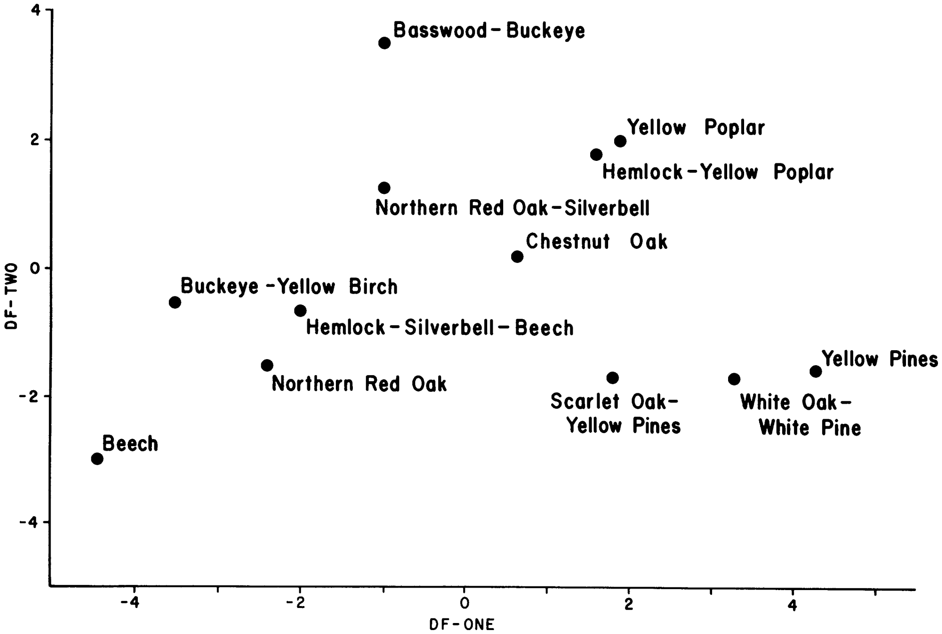

Fig. 3.—Centroids of forest community types along the first two discriminant functions (DF) based on environmental variables

As in preceding studies, forest types overlapped considerably in species composition and habitat (Whittaker, 1956; Golden, 1974, 1981). This continuity of forest types was in part due to the continuity of the predominant environmental variable, elevation. Elevation, in turn, is actually an environmental complex including temperature and moisture. This complexity is apparent in community relationships throughout the Smoky Mountains. For example, the three high-elevation forest types are composed primarily of species found at lower elevations only in protected cove and ravine topography. *Aesculus octandra, Quercus rubra*, *Betula alleghaniensis*, *Acer saccharum* and *Fagus grandifolia* dominated at the higher elevation under different topographic conditions, but as elevation decreased these species almost exclusively occupied sheltered topography. Although all of the above species followed this basic pattern, the communities in which they were found changed with elevation. In other words, entire communities did not move with changing elevation and topography. For example, *Aesculus octandra* was associated with *B. alleghaniensis* in highly exposed ridgetop plots but at lower elevations its primary associate was *Tilia heterophylla* in deep concave topography. *Quercus rubra* was another prime example of this community sharing. *Quercus rubra* was common on the most exposed ridges measured at high elevations (in almost pure stands), in protected cove positions with *Liriodendron tulipifera, Halesia carolina* and *Tilia heterophylla,* and with *Q. prinus* in dry southerly positions. This conflicts with the traditional assumption that *Q. rubra* is an essentially mesic or submesic species (Whittaker, 1956; Mowbray, 1966; Golden, 1974). This finding is substantiated by a study of *Q. rubra* and its association with *Q. prinus* (Blackman and Ware, 1982). Stands of *Q. rubra* could not be correlated with moisture conditions, and samples occurred at both extremes of a soil moisture gradient.

Although the continuity of elevation and topography resulted in highly overlapping community distributions, some forest types were relatively distinct on the DECORANA axes (Fig. 1). Beech, northern red oak-silverbell, northern red oak, buckeye-yellow birch, and the yellow pines forest types were clearly separated. It is questionable, however, whether this distinctness is a result of environmental control or is an artifact of the location of plots so that the overlap is not sampled.

Changes of land shape have been considered by previous researchers as a dominant condition influencing vegetation distribution in the Smokies, but they were not quantified. Thus the importance of land shape was measured in fragmented pieces, such as distance from ridgetop, slope length, distance from valley bottom and other similar measurements. Protection, although not measuring all aspects of topography, proved to be a significant step towards quantifying land shapes, and thus toward understanding vegetation distribution. As for elevation, protection is most likely a complex variable including relationships to isolation, drainage, soil particle movement, temperature and wind. We assumed that the most influential aspects of topography are products of the landforms at higher elevations than the plot. Although this assumption may be true, it is undoubtedly incomplete. Slope shape at elevations lower than the plot is partially responsible for air flow, water drainage and soil particle movement. Despite the problems inherent in the variable, protection, it has proven useful in this study, and it has proven highly significant for prediction of forest productivity (Callaway, 1983).

The complexity of the variable, protection, was apparent in the results of the discriminant analysis. Although protection was an important variable in four of the five functions, it was replaced by the *p*H of the A horizon and the total water-holding capacity of the soil as the most important variable in the second discriminant function. Both of these variables are highly correlated with protection. It is likely that topographic shape is partially responsible for the soil conditions at a given site. Thus it is possible that elements of the environmental complex inherent in landform are being measured. Golden (1981) measured variation in soil *p*H with topographic change and, as in this study, found the *p*H of the A horizon was a major variable correlated with vegetation distribution.

Human disturbance appeared to be an important factor in the distribution of

Smoky Mountains vegetation but was very difficult to quantify. All of the yellow pine and white oak-white pine plots had been disturbed by farming or logging, as were high percentages of the yellow poplar and hemlock-silverbell-beech forests. In the case of the first two there are no undisturbed areas of similar habitat with which to compare them. Because of the lack of comparative vegetation with no or little human disturbance, this study can determine little about the influence of disturbance on the yellow pine and white oak-white pine forest types. Alternatively, the abundance of undisturbed sites similar to those of yellow poplar and hemlock-silverbell-beech indicate that other communities may be more common without the influence of human disturbance. Of the six yellow poplar plots that overlapped most with hemlock-yellow poplar forest types (numbers 7 and 8 in Fig. 2) five were disturbed. This indicates that human disturbance is influential in the development of yellow poplar forest types from what potentially would be hemlock-yellow poplar. A similar situation can be observed with the hemlock-silverbell-beech forest type. Almost 80% of these plots were disturbed and the forest type overlaps highly with both the basswood-buckeye forest type and the northern red oak-silverbell forest type (Fig. 2). This indicates that the hemlock-silverbell-beech forest type may be a product of human disturbance and without disturbance the community composition would be different. Conversely, human disturbance may convert sites supporting hemlock-yellow poplar to yellow poplar forest types, and sites supporting basswood-buckeye and northern red oak-silverbell communities into different groups of species better classified as hemlock-silverbell-beech communities.

Human disturbance has been cited as influential to other forest types in the Smokies. Harmon (1980) found that yellow pines increased their coverage in fire-disturbed sites. Forest composition in the GRSM has also been changed by the widespread loss of the dominant *Castanea dentata.* Former chestnut-dominated stands now show increased cover of *Quercus prinus, Q. rubra* and *Acer rubrum* (Woods and Shanks, 1959). Golden (1981) found that the inclusion of dead *Castanea dentata* remains was the most significant environmental variable entered in his stepwise multiple discriminant analysis. He attributed the significance to the opening of the canopy, which encouraged the growth of specific shade-intolerant species, in turn establishing specific forest types. In previous studies, as well as in this one, disturbance worked synergistically with topography, soil characteristics and elevation to determine vegetation distribution in the Smoky Mountains. Because there has been some disturbance in all communities of the GRSM, vegetation results show some degree of increased variation.

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