PATTERNS OF WOODY SPECIES COMPOSITION ON THE FERNOW EXPERIMENTAL FOREST AND ADJACENT PORTIONS OF THE OTTER CREEK WILDERNESS AREA

R.M. Muzika
University of Missouri; Columbia MO 65211
S.L. Stephenson
Dept. of Biology, Fairmont State College; Fairmont, WV 26554
H.S. Adams
Dabney Lancaster Community College; Clifton Forge, VA 24422
D.M. Lawrence
Lamont-Doherty Earth Observatory; Palisades, NY 10964
G.W. Miller
USDA Forest Service; Parsons, WV 26287

ABSTRACT.—Quantitative data on the composition and structure of the overstory tree (stems ≥10cm dbh) and understory tree strata (≥2.5 but <10 cm dbh) were obtained from 105 - 0.1 ha plots in the Allegheny Plateau of West Virginia. Fifteen species occurred as the leading dominant in at least one plot for the overstory, but *Quercus rubra* (northern red oak) was the overall dominant and had the greatest importance value in 25 of the 105 plots. *Acer saccharum* (sugar maple), *Fagus grandifolia* (beech), and *Acer rubrum* (red maple) were the usual dominants in the understory. Ordination analysis using detrended correspondence analysis (DCA) with data for both structural layers indicated that species importance values along the first axis seemed to be most closely related to a moisture complex-gradient, whereas positions along the second axis appeared to be related to an elevation complex-gradient. Canonical Correspondence Analysis (CCA) results of the overstory data suggested that soil characteristics relate in a more meaningful way to vegetation patterns than do physiographic characteristics. TWINSPAN analysis of the overstory data delineated eight forest types, which were named on the basis of their dominant tree species. Forest types represented by the greatest number of plots were red oak / sugar maple (39 plots), yellow-poplar (*Liriodendron tulipifera*) / sugar maple / Fraser magnolia (*Magnolia fraseri*) (27 plots), red maple / red oak (15 plots), and chestnut oak (*Quercus prinus*) / red maple / red oak (14 plots).

KEYWORDS: Ordination, detrended correspondence analysis, vegetation analysis, canonical correspondence analysis, TWINSPAN, mixed oak forest.

Despite decades of research, understanding the factors responsible for controlling vegetation distribution and composition remains a pursuit of plant ecologists and biogeographers. Some portions of the *Quercus* spp. (oak) dominated forests of the Mid-Appalachians have been studied, but because of a broad topographically heterogenous and diverse landscape, unique and understudied communities are present in many areas. *Castanea dentata* (American chestnut) was once a dominant or codominant tree in many oak communities until eliminated by the blight fungus (*Cryphonectria parasitica*) early in this century. Although it would seem that various species of oak, especially *Q.rubra* (northern red oak) and *Q. prinus* (chestnut oak) have increased in importance in areas where American chestnut once dominated (*e.g.*, Adams and Stephenson, 1983; Stephenson *et al.*, 1991; Agrawal and Stephenson, 1995; Rhoades, 1995), generalities concerning successional patterns in the Appalachian oak forest are inconclusive (Stephenson *et al.*, 1993). Many factors affect the direction of succession, including topographic features, past disturbances, and underlying substrate. Whether oak forests truly represent climax communities (Keever 1973), or are successional in nature is generally uncertain (Abrams, 1992; Rhoades, 1995).

Dramatic shifts in species composition in many forests of the eastern United States are likely to occur over the next few decades, in part because of a noted loss of *Quercus* spp. (oak). From both an ecological and economic perspective, a fundamental knowledge of plant / site relationships can contribute to a better understanding of likely successional patterns and future forest composition. The objectives of this paper are to (1) describe current composition of forest communities found in the Fernow Experimental Forest and adjacent portions of nearby Otter Creek Wilderness Area, and (2) provide information concerning the relationship of important environmental factors to patterns of composition within the tree component of these communities, and to relate these to the biogeography of the communities.

STUDY AREA

The Fernow Experimental Forest (39°03 N, 79°41 W) is located in Tucker County, in eastern-central West Virginia, which is within the Allegheny Mountain physiographic province of the southern Appalachian Mountains (Fenneman 1938). Elevations in the Fernow range from 533 to 1112 m, with slopes typically ranging from 10 to 60 percent. Soils are predominantly loams and silt loams of the Calvin and Berks-Muskingham series (Typic Dystrochrepts). These soils originate from acid shales and sandstones on the western half of the Forest and from sandstones, shales, and limestones on the eastern half of the Forest. Average soil depth is about 1 m, and average soil pH is about 4.5 (Helvey and Kochenderfer, 1991). A rainy, cool climate is typical on the Fernow; precipitation averages 145 cm per year, and is evenly distributed throughout the year. Mean annual temperature is about 9°C, and the length of the growing season is approximately 145 days (U. S. Department of Agriculture, Forest Service, 1987).

At the lowest elevations, the original forests of the general study area consisted mainly of hardwoods, with an admixture of *Tsuga canadensis* (eastern hemlock) along stream bottoms and on north slopes. Forests at the higher elevations were dominated by *Picea rubens* (red spruce) and hemlock (Core, 1966). Small patches of pure spruce occurred on the tops of the mountains. Braun (1950) placed this portion of West Virginia in the Allegheny Mountain Section of the Mixed Mesophytic Forest Region.

The pattern of cutting and regeneration on the Fernow is similar to that found throughout much of the central Appalachians. Logging removed the most valuable species. Undesirable trees of poor form and unmarketable species were left. Forest fires burned repeatedly over the area, and chestnut blight eliminated 10,440 m^3 of American chestnut in the 1930s (Weitzman, 1949), representing approximately 25 percent of the volume of the Experimental Forest,

Present-day forest types and conditions on the Fernow reflect the site qualities and past history of the area. *Quercus* spp.(oaks) are the most common species and are found on all sites along with *Fagus grandifolia* (American beech) and *Betula lenta* (sweet birch). High productivity sites in coves and on north slopes support primarily northern red oak, *Acer saccharum* (sugar maple), *Liriodendron tulipifera* (yellow poplar), *Prunus serotina* (black cherry), *Fraxinus americana* (white ash), *Tilia americana* (basswood), *Magnolia acuminata* (cucumbertree), and beech. Sites of moderate productivity on south and east slopes usually support oak stands composed of red oak, *Quercus alba* (white oak), chestnut oak, and *Quercus coccinea* (scarlet oak). *Acer rubrum* (red maple), sweet birch, *Nyssa sylvatica* (blackgum), *Sassafras albidum* (sassafras), and *Oxydendrum arboreum* (sourwood) are also commonly found on such sites. *Robinia pseudoacacia* (black locust), sweet birch, and *Magnolia fraseri* (Fraser magnolia) are consistent but generally minor components of the forest on all sites.

MATERIALS AND METHODS

Study Area and Field Methods

Quantitative data on topographic variables and composition and structure of all strata of vegetation were collected from 105 - 0.1 ha plots located in the Fernow Experimental Forest and adjacent portions of the Otter Creek Wilderness Area. A series of nested quadrats (Adams and Stephenson, 1989) was used to sample vegetation in each plot. Potential study sites were located on USGS 7.5 minute quadrangle maps and then established as closely as possible in the field, using benchmarks and other obvious topographic features as reference points. Criteria for selection of the units of vegetation (plots) actually sampled were that: (1) the vegetation be relatively homogeneous both floristically and structurally; (2) the topography of the area be uniform; and (3) there be no obvious evidence of major disturbance (*e.g.*, logging, fire, windthrow) during the lifetime of the trees sampled.

In each plot, diameters at breast height (1.37 m above ground level and hereafter referred to as dbh) of all live stems of overstory (≥10 cm dbh) and understory (≥ 2.5 but < 10 cm dbh) were recorded by species in a single 20 m by 50 m (0.1 ha) quadrat. Quadrats were typically placed with their long axes parallel to the contour of the slope. Saplings of tree species (stems <2.5 cm dbh but ≥1.0 m tall) were tallied by species in these same quadrats. Seedling (stems < 1 m tall) were counted by species in four 25 m^2 quadrats nested within each larger quadrat at four equidistant points on the 50 m tape used to establish the long axis of the 0.1 ha quadrat.

Soil samples were collected from the upper 10 cm at four or more locations in each plot, mixed thoroughly, and placed in plastic bags. In the laboratory, these were oven-dried and passed through a 1.0 cm sieve to remove gravel. Analysis of pH and percent organic matter, along with content (in parts per million) for phosphoric acid, calcium, magnesium, potassium, zinc, nitrate nitrogen, manganese, copper, aluminum, iron, boron, and total soluble salts were conducted by the Soil Testing Laboratory at Virginia Polytechnic Institute and State University, using procedures outlined by Donohue and Friedericks (1984).

Topographic features recorded for each plot included slope position (*e.g.*, lower slope, upper slope, ridgetop), inclination (percent), aspect (degrees), and elevation (m). Slope inclination and aspect were recorded at several locations within each plot. Elevation was determined using two digital aneroid altimeters. The center of each plot was permanently marked with a metal stake and its location determined by means of a portable global positioning system.

Vegetation Data Analysis

Quadrat data were used to calculate relative basal area and relative density values separately for overstory trees and understory trees. Only relative density values were calculated for saplings, seedlings, and shrubs. For each plot, species importance value indices for overstory and understory trees were calculated as one-half the sum of relative basal area and relative density.

Ordination of vegetation in the 105 plots was performed by Detrended Correspondence Analysis using the Cornell Ecology Program DECORANA (Hill, 1979; Hill and Gauch, 1980). Ordination is predicated on the concept of continuous variation in composition of vegetation (Greig-Smith, 1964). This method of ordination was chosen because it has been shown to be effective in a number of other studies (Gauch, 1982). The ordination was computed using importance value indices of trees in plots as inputs. Two-dimensional ordinations were derived with and without rare species downweighted.

In addition, two-way indicator species analysis (TWINSPAN) (Hill, 1979) was used for initial characterization (classification) of the vegetation. This is a polythetic divisive classification and may furnish some preliminary information about species groups. These groupings can then be used as a means of stratifying further sampling, specifically such parameters as tree growth data.

As noted, several environmental and physical variables were measured during the field data collection and thus incorporated in vegetation analysis. Canonical correspondence analysis (CCA) was used as a means of relating environmental (physiographic) variables to the abundance and occurrence of plant species. Ter Braak (1986) developed CCA as an approximation of canonical Gaussian ordination, but using species data in addition to environmental data. Thus, this technique combines direct gradient analysis with regular ordination. CCA selects the linear combination of environment variables that maximizes the dispersion of species scores. Results of the analysis can be used to identify patterns in the vegetation community and to assess and the extent of the control of specific environmental variables.

RESULTS

Overstory

Based on importance values, red oak was the most abundant and common overstory tree, with yellow-poplar, sugar maple, and red maple also consistently important. Red oak ranked first in terms of importance value in 25 of the 105 plots and yellow poplar had the highest importance value in 22 plots (Table 1). For the most part, the high importance values of both red oak and yellow-poplar were due to high basal area values, whereas the relatively high importance values of sugar maple and red maple were due to high density values. Although many species were represented in the overstory of the plots we sampled, dominance in this stratum was controlled by only a few species.

Indirect gradient analysis, specifically detrended correspondence analysis (DCA), was used to explore the possible influence of underlying environmental gradients on the pattern of vegetation. The separation of species on the ordination suggests that complex gradients related to moisture, topographic position and elevation control the pattern of overstory vegetation (Fig. 1).

Table 1.—*Rank frequency of species abundance, based on importance value, of overstory tree species, in 105 plots on the Fernow Experimental Forest.*

Overstory	Rank				
species	1	2	3	4	5
Red oak	25	16	24	9	7
Yellow-poplar	22	3	6	8	2
Sugar maple	15	23	14	12	5
Red maple	11	22	14	9	7
Chestnut oak	9	6	4	10	3
Beech	5	9	11	6	16
Black cherry	5	5	12	3	5
Basswood	3	7	5	4	4
Fraser magnolia	2	1	0	1	3
Hemlock	2	1	1	4	5
White oak	2	1	3	4	2
Yellow birch	1	3	0	3	4
Red spruce	1	0	0	0	0
Black birch	1	2	4	11	12
Black oak	1	0	0	0	1

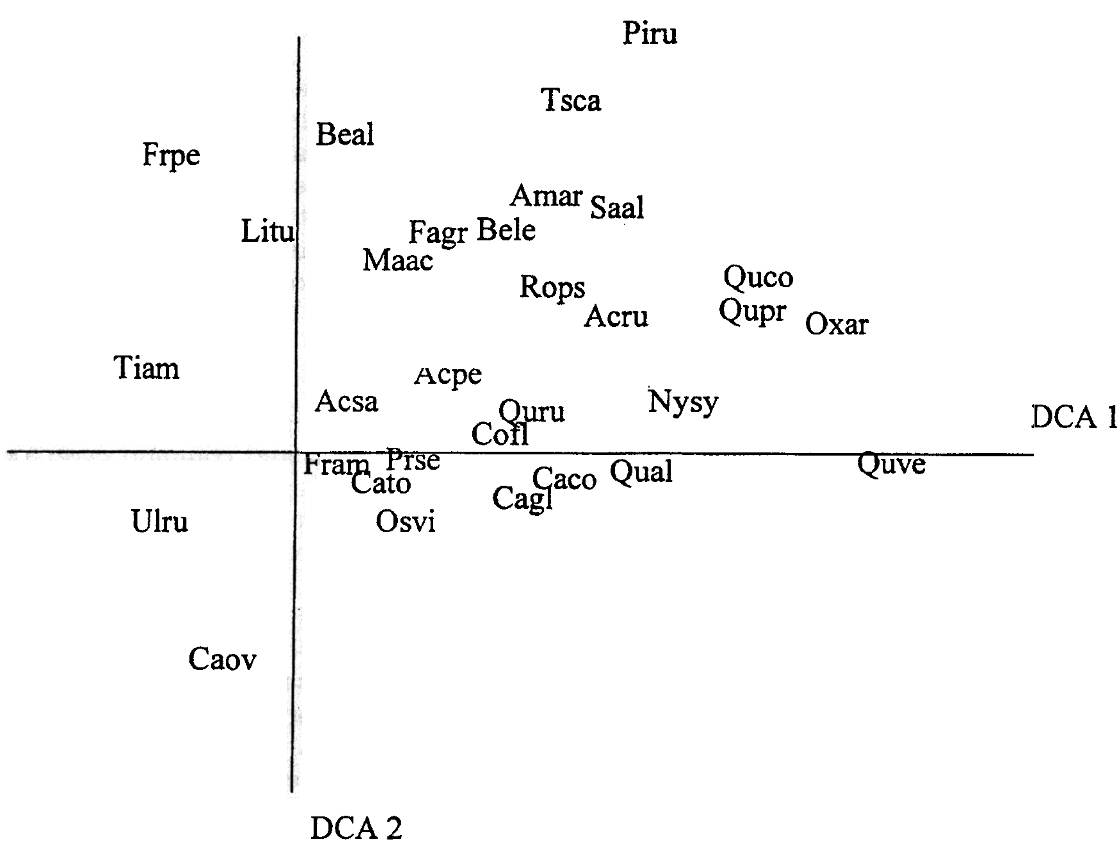

Figure 1.—DCA ordination of plots based on importance values of overstory species. Codes for species are: Acpe- *Acer pensylvanica* (striped maple), Acru - *Acer rubrum*, Acsa - *Acer saccharum*, Beal - *Betula allegheniensis*, Bele - *Betula lenta*, Caco - *Carya cordiformis* (bitternut hickory); Cagl - *Carya glabra* (pignut hickory); Caov - *Carya ovata* (shagbark hickory); Cato - *Carya tomentosa* (mockernut hickory); Cofl - *Cornus florida* (flowering dogwood); Fagr - *Fagus grandifolia*, Fram - *Fraxinus americana*; Frpe - *Fraxinus pensylvanica;* Litu - *Liriodendron tulipifera*; Maac - *Magnolia acuminata;* Mafr - *Magnolia fraseri;* Nysy - *Nyssa sylvatica;* Osvi - *Ostrya virginiana;* Oxar - Oxydendron arborea; Piru - *Picea rubra*; Prpe - *Prunus pensylvanica*; Prse - *Prunus serotina*; Qual - *Quercus alba;* Quco - *Quercus coccinea;* Qupr - *Quercus prinus;* Quru - *Quercus rubra;* Quve - *Quercus velutina;* Rops - *Robinia pseudoacacia;* Saal - *Sassafras albidum;* Tiam - *Tilia americana;* Tsca - *Tsuga canadensis;* Ulru-*Ulmus rubra.*

The positions of species along the first axis range from characteristic moist site species such as *Fraxinus pensylvanica* (green ash), *Ulmus rubra* (slippery elm), and basswood to species characteristic of more xeric conditions (e.g. scarlet oak, chestnut oak, and sourwood). The second axis appears to reflect elevational differences, with high elevation species, such as red spruce and *Betula allegheniensis* (yellow birch), separating out near the high end of the axis. The first two axes account for 90% of the variation in this data set.

Understory

For comparative purposes, the understory species listed in Table 2 are arranged in an order identical to that used in the overstory table (Table 1), and it is obvious that the species abundance in the understory differed dramatically from the overstory. The understory was dominated by sugar maple, American beech and red maple (Table 2.). An ordination (DCA) of the understory (based on importance values) indicates that the complex gradients influencing the pattern of understory vegetation are similar to those of the overstory (Fig. 2). Specifically, a strong moisture-complex gradient and an elevation-complex gradient appear to have a great deal to do with the composition of the understory as well as that of the overstory. Slight differences in the understory data set include the addition of *Ilex montana* (mountain holly), a high elevation species not found in the overstory. This species has a relatively high value on the second ordination axis, confirming the relationship of elevation to this axis.

Table 2.—*Rank frequency of species abundance, based on importance value, of understory tree species, in 105 plots on the Fernow Experimental Forest.*

Understory	Rank				
species	1	2	3	4	5
Red oak	1	0	0	3	2
Yellow-poplar	0	0	0	0	0
Sugar maple	44	21	9	3	3
Red maple	14	15	7	6	9
Chestnut oak	0	0	1	1	2
Beech	31	29	11	6	5
Black cherry	0	1	4	1	0
Basswood	0	2	10	3	2
Fraser magnolia	0	0	3	6	4
Hemlock	2	4	1	1	1
White oak	0		0	2	0
Yellow birch	1	2	6	6	4
Red spruce	1	1	1	1	0
Black birch	1	0	5	7	4
Black oak	0	0	0	0	0

Twinspan analysis

Twinspan (two-way indicator species analysis) assists in deriving a classification scheme for a given set of data. Using importance values, the TWINSPAN analysis yielded 27 groups. Based on the number of plots associated with each group, we considered eight of these groups to be ecologically meaningful and valid. Each group appears to have one or two dominant species associated with it (Table 3). The most significant of these eight groups are likely groups 2, 4, 5 and 6, because of the number of associated plots (14, 15, 39, 27 plots, respectively). The characteristics of the forest types represented by these four groups are summarized in Table 4. Although group 1 appears to be a distinct red spruce group, based on average importance values, only one plot is associated with that group. Group 3 is clearly a white oak group, but only three plots were associated with this group.

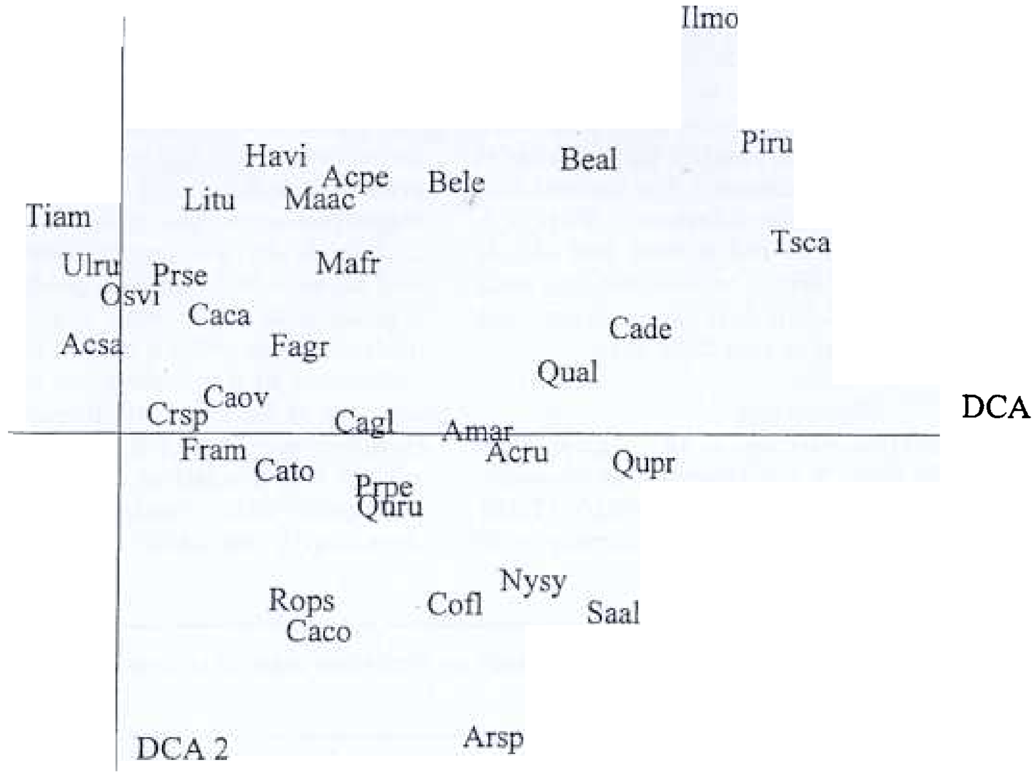

Figure 2.—DCA ordination of plots based on importance values of understory species. See Figure 1 for species codes. Additional species present only in the understory : Arsp - *Aralia spinosa* (Hercules' club) ; Caca - *Carpinus caroliniana* (muscle wood); Cade - *Castanea dentata;* Ilmo - *Ilex montana* and Havi - *Hamamelis virginiana,*

Table 3.—*Relative importance values of major species by TWINSPAN grouping. The highest importance values for each group is indicated in boldface type.*

Species	Twinspan Group							
	1	2	3	4	5	6	7	8
Red spruce	**63.19**	-	-	-	-	-	1.15	21.57
Chestnut oak	35.49	**31.23**	19.06	14.69	3.51	2.85	-	-
Red maple	31.26	25.52	3.40	**24.74**	11.56	3.54	15.81	19.15
Red oak	8.65	18.45	15.27	23.16	**27.20**	10.13	4.31	
Scarlet oak	7.77	3.71	-	-	-	-	-	-
Pignut hickory	3.35	-	6.34	2.34	3.15	2.96	-	-
Hemlock	2.47	3.52	2.76	4.13	4.65	4.80	31.63	**31.18**
Yellow birch	0.86	-	-	1.46	8.78	6.49	14.87	22.58
Beech	0.80	2.28	2.98	7.03	15.13	8.22	17.28	
Sugar maple	-	15.82	19.48	10.39	18.22	21.62	2.26	
Yellow-poplar	-	11.65	-	11.07	12.73	**30.94**	-	
Black oak	-	11.37	-	7.01	-	-	-	
Sourwood	-	9.96	-	2.32	1.14	-	-	
White oak	-	6.44	**26.34**	6.93	5.46	1.86	-	
Bitternut hickory	-	5.67	4.90	-	4.02	3.21	-	-
Black cherry	-	3.07	-	7.29	17.57	8.70	**31.89**	5.22
White ash	-	-	4.66	3.20	5.07	4.54	--	-
Fraser magnolia	-	-	-	6.51	9.73	16.05	-	1.19
Basswood	-	-	-	-	6.29	14.10		
Shagbark hickory	-	-	4.02	-	7.51	5.54		

Table 4.—*Summary data on the four major forest types identified on the Fernow Experimental Forest.*

FOREST TYPE	Elevation range	mean	Aspect (°)	Slope (%)	Position
Red oak / Sugar maple	591 - 1180 m	860 m	8 - 333	0 - 33	Mid to Upper Side Slopes
Yellow-polar / Sugar maple	548 - 884 m	681 m	5 - 359	12 - 36	Lower Side Slopes
Red oak / Red maple	582 - 823 m	734 m	121 - 349	11 - 26	Upper Slopes
Chestnut oak / Red maple	591 - 820 m	746 m	138 -310	9 - 27	Mid to Upper Side Slopes

Canonical Correspondence Analysis

Canonical correspondence analysis (CCA) provides information about the influence of particular environmental variables on the pattern of vegetation. Among the environmental variables we used were data from soil chemical characteristics determined for samples collected in each plot (Table 5). These environmental variables and the strength of the correlation of each variable with vegetation are presented in Table 6.

The CCA graph (Figure 3) suggests a relationship between some environmental variables and tree species, but generally the correspondence is not strong. In the quadrant influenced by elevation and density, red spruce and yellow birch have been removed because of their high values on the second axis. *Amelanchier arborea* (service berry) and *Prunus pensylvanica* (fire cherry) appear to be the only other species that correspond positively with elevation and density.

Table 5.—*Soil chemical characteristics for the 105 plots sampled in the present study.*

PARAMETER	MEAN	RANGE
pH	4.1	3.1 - 5.8
Ca (ppm)	368.0	46.6 - 2210.0
Mg (ppm)	41.2	18.8 - 197.9
P (ppm)	5.3	0.3 - 16.8
K (ppm)	53.9	20.0 - 158.5
Mn (ppm)	134.8	5.2 - 556.8
Zn (ppm)	3.8	1.5 - 14.0
Fe (ppm)	58.4	6.4 - 158.8
Al (ppm)	351.4	69.2 - 764.0
Cu (ppm)	0.4	0.1 - 0.6
B (ppm)	0.2	< 0.1 - 1.1
N (ppm)	6.13	3.0 - 43.0

Table 6.—Correlation matrix of environmental variables and CCA axis eigenvalues.

	Axis one	Axis two	Axis three	Axis four
Eigenvalue	.9186	.8216	.7634	.6670
Elevation	.2279	.2904	.2825	.0226
Aspect	-.3438	.1036	.0323	-.0162
% Slope	-.1902	-.1166	-.2310	-.0296
Slope position	.2913	.0146	.1854	.1106
TRMI*	-.4205	.1126	-.0747	-.1011
Basal area / ha	-.1083	.0984	.0624	.0054
Density / ha	.3889	.1699	-.0133	.0432
Ca	-.4531	.1041	-.1560	.0971
Mg	-.4376	.1158	-.1822	.0657
P	-.2318	.3535	-.0822	.0589
K	-.4514	.1074	-.1360	.1208
Mn	-.4915	.0301	.0172	.0666
Zn	-.2223	.1966	-.0672	.1457
Fe	.4270	-.1445	.1188	-.0425
Al	.1075	-.3328	.1818	.0656
Cu	-.0413	-.1016	.1340	-.0798
B	-.4716	.0827	-.1302	.1203
pH	-.5752	-.0171	-.0847	.0685
N	-.3102	.1595	-.0182	.-0204
Soluble Salts	.0233	.2722	-.1184	.0447

*TRMI : Topographic Relative Moisture Index, which is a combined estimator of slope position, elevation and aspect (Parker 1982)

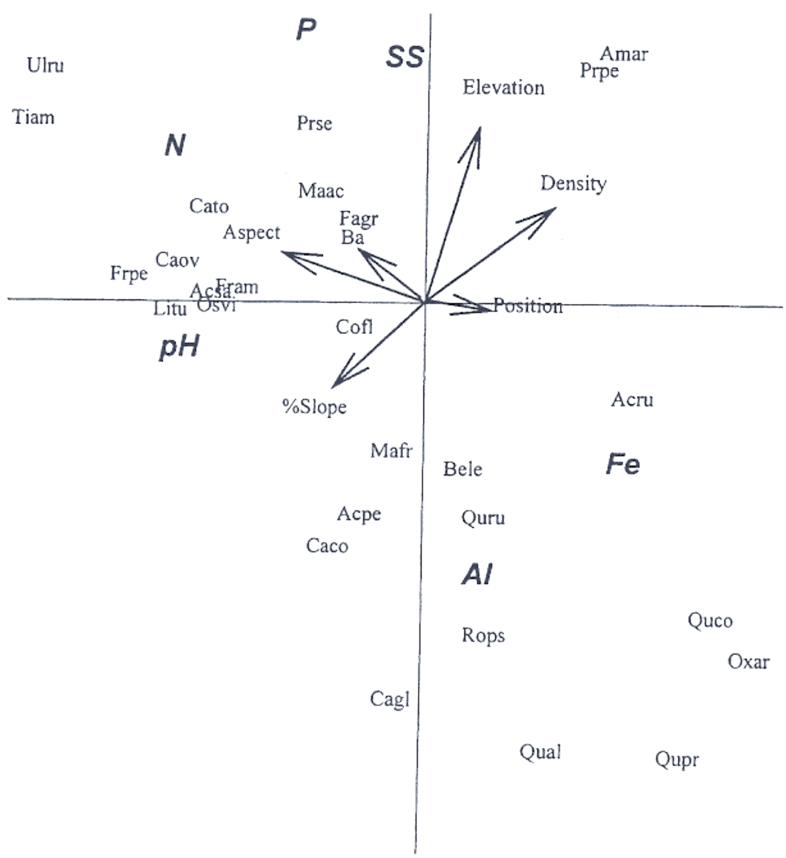

Figure 3.—CCA ordination computed with overstory data; the first axis is horizontal and the second vertical. Arrows indicate the strength of the association between the variables and species. Soil variables are indicated by bold type. Tree species abbreviations are the same as those used in Figures 1 and 2. Environmental variables appear in Table 6.

DISCUSSION

Based on the overstory and the understory data presented in Tables 1 and 2, it is clear that dramatic shifts in species composition are taking place on these forests. Specifically, the dominant species are represented infrequently in the understory. Nearly all of the overstory species were present in the understory, but their relative importance in the two strata varied markedly. Despite a dominant oak overstory on much of the Fernow Experimental Forest and adjacent portions of Otter Creek Wilderness, the regenerating species composition suggests that oak will constitute a minor role in the future forest. This loss of oak has been noted numerous times in forests of the East and Midwest, so its decline in the Appalachians is not unexpected.

A major concern, however, is which species will likely replace the oak. Throughout much of the East, red maple appears to become a dominant in forests that have lost significant portions of the oak component. Muzika and Twery (1995) found that Appalachian Plateau forests may be dominated by black cherry when the overstory oaks have been eliminated by a major disturbance. Following the loss of chestnut in Allegheny Mountains of western Pennsylvania, black cherry and red maple become dominant (Mackey and Sevec, 1973). Natural successional processes in the absence of a major disturbance will likely not produce a single cohort of early successional species. The relatively undisturbed forest conditions in the Fernow Experimental Forest and adjacent portions of Otter Creek Wilderness appear to favor shade-tolerant species, more characteristic of late successional stages. Specifically, beech and sugar maple dominate the understory and red maple is widespread. Shade intolerant species such as yellow poplar are rarely present in the understory. The presence of beech and sugar maple, as well as some representation of basswood in the understory (Table 2) suggest a northern hardwood component in these forests, quite distinct from ridge and valley forests, and appreciably different from the mixed oak forest which has dominated the landscape for the past century.

Ordination of both the overstory and the understory data indicates that comparable factors are responsible for species occurrence along major environmental gradients. That these large scale environmental factors are important for individual species and groups of species is evident from some of the classifications derived from TWINSPAN. Many of the categories require validation, refinement, and collection of more data. For example, a red spruce forest type is certainly a biological reality, but such a species grouping was represented in the overstory on only a single plot. Red spruce was slightly more widespread in the understory than the overstory, suggesting an increase in importance of this species in later successional stages of these forests. Sampling scheme may present a bias in data collection in that the selection of areas undisturbed in the past 50 years may limit an adequate representation of current vegetation / site relationships. Furthermore, information in Table 4 indicates that upper and mid slopes were likely oversampled, but that ridgetops and footslopes may have been undersampled.

Soil variables are more important than environmental or physiographic variables in determining patterns of species composition and abundance. For example, the first CCA axis (represented as the abscissa in Fig. 3) is characterized by pH and manganese (negatively), as well as density and slope position (positively). The direction of the correlation score is not as important as the direction of the trajectory indicated on Fig. 3. As such, species with negative scores on the first axis, (e.g. green ash, shagbark hickory, and some "northern hardwood" species) are associated with increasing pH and increasing amounts of manganese. Physiographically, these species are associated with greater aspects and greater basal area. The latter variable is closely related to the distribution of beech; presumably, beech tends to have the greatest basal areas, because of the deliberate avoidance of this species by loggers (Trimble, 1977).

The second axis is controlled by elevation and the soil nutrients Al and P. All oak species fall within the quadrant characterized by Al and Fe, but no physiographic characters seem to be associated with the corresponding species. Other species grouped with oaks appear to be xeric (e.g., sourwood) or opportunistic early successional species, such as red maple. It seems likely that the occurrence of all of the species seemingly associated with oaks may have more to do with disturbance history than with the environmental variables that we measured.

In summary, the results of the present study appear to provide evidence that major changes are occurring in forest communities of the mid-Appalachians, even in the absence of dramatic disturbance. While species shifts are not always obvious, the relative contributions and abundance of species between overstory and understory strata suggest a sugar maple-beech forest will likely replace the oak dominated forest that presently exists. It is likely that certain disturbances that preferentially influence oaks, e.g., defoliation by *Lymantria dispar* L. (gypsy moth), or logging activity, will cause an acceleration in the transition to a sugar maple - beech forest.

LITERATURE CITED

ABRAMS, M. D. 1992. Fire and development of oak forests. Bioscience 42: 346-353.

ADAMS, H. S. AND S. L. STEPHENSON. 1983. A description of the vegetation on the south slopes of Peters Mountain, southwestern Virginia. Bull. Torrey Bot. Club 110: 18-22.

ADAMS, H. S. AND S. L. STEPHENSON. 1989. Old-growth red spruce communities in the mid-Appalachians. Vegetatio 85: 45-56.

AGRAWAL, A. AND S. L. STEPHENSON. 1995. Recent successional changes in a former chestnut-dominated forest in southwestern Virginia. Castanea 60: 107-113.

BRAUN, E. L. 1950. Deciduous forests of eastern North America. Blakiston Co., Philadelphia, Pennsylvania. 596 pp.

CORE, E.L. 1966. Vegetation of West Virginia. McClain Printing Company, Parsons, West Virginia,

DONOHUE, S. J. AND J. B. FRIEDERICKS. 1984. Laboratory procedures of the soil testing and plant analysis laboratory at Virginia Polytechnic Institute and State University. Va. Cooperative Extension Serv. Publ. 452-881. 30 p.

FENNEMAN, N. M. 1938. Physiography of the eastern United States. McGraw-Hill Book Co., N. Y.

GAUCH, H. G., JR. 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge. 298 p.

GREIG-SMITH, P. 1964. Quantitative plant ecology (2nd ed.). Butterworths and Co., London and Washington. 256 p.

HELVEY J.D. AND J.N. KOCHENDERFER. 1991. Time trends in selected chemical characteristics of streamflow from anundisturbed watershed in West Virginia. Pages 429-437 *in* Rennie, P.J. and G. Robitaille. eds. Effects of acid rain of forest resources: Proceedings of the conference. Forestry Canada, Ottawa.

HILL, M. O. 1979. DECORANA—a Fortran program for detrended correspondence analysis and reciprocal averaging. Cornell University, Ithaca, NY. 52 p.

HILL, M. O. AND H. G. GAUCH, JR. 1980. Detrended correspondence analysis: An improved ordination technique. Vegetatio 42: 47-58.

KEEVER, C. 1973. Distribution of major forest species in southwestern Pennsylvania. Ecological Monographs 43: 303-327.

MACKEY, H. E. JR. AND SEVEC, N. 1973. The present composition of a former oak-chestnut forest in the Allegheny mountains of western Pennsylvania. Ecology 54(4): 915-919.

MUZIKA, R.M. AND M.J. TWERY. 1995. Regeneration in defoliated and thinned hardwood stands of north-central West Virginia. P.326-340. in Gottschalk, K.W. and S.L.C. Fosbroke eds. Proceedings of the Tenth Central hardwoods Conference. USDA Forest Service General Technical Report GTR NE-197.

PARKER, A.J. 1982. The topographic relative moisture index: an approach to soil moisture assessment in mountain terrain. Physical Geography 3:160-168.

RHOADES, R. W. 1995. Succession in a mature oak forest in southwest Virginia. Castanea 60: 98-106.

STEPHENSON, S. L., H. S. ADAMS, AND M. L. LIPFORD. 1991. The present distribution of chestnut in the upland forest communities of Virginia. Bulletin of the Torrey Botanical Club 118: 24-32.

STEPHENSON, S. L., A. N. ASH, AND D. F. STAUFFER. 1993. Appalachian oak forest. P. 255-330. in Martin, W. H., S. G. Boyce, and A. C. Esternacht eds. Biodiversity of the southeastern United States: Upland terrestrial communities. John Wiley and Sons, Inc., New York. 373 pp.

TER BRAAK, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167-1179.

TRIMBLE, G.R. 1977. A history of the Fernow Experimental Forest and the Parsons Timber and Watershed Laboratory. USDA Forest Service General Technical Report NE-28. 46 pp

USDA FOREST SERVICE. 1987. Forest Research: Fernow Experimental Forest. Northeastern Forest Experiment Station NE-INF-75-87.

WEITZMAN, S. 1949. The Fernow Experimental Forest. USDA Forest Service Northeastern Forest Experiment Station, Upper Darby, PA

Proceedings of the

APPALACHIAN BIOGEOGRAPHY

SYMPOSIUM

Held June 25-29 1995 at the Donaldson Brown Center
Virginia Polytechnic Institute and State University
Blacksburg, VA

Supported in Part by the Virginia Academy of Science

Edited by Ralph P. Eckerlin

Virginia Museum of Natural History
Special Publication Number 7
1999