CORRELATIONS AMONG STAND AGES AND FOREST STRATA IN MIXED-OAK FORESTS OF SOUTHEASTERN OHIO

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Abstract: Many models of landscape ecosystem development, as well as of forest stand dynamics, are based upon spatial and temporal changes in the species composition and structure of various forest strata. However, few document the interrelationships among forest strata, or the response of different strata to alterations of natural disturbance regimes. To examine how relationships among forest strata varied with stand age, we sampled a chronosequence (five age classes) of 21 second-growth (70 to 149 years old) and old-growth (≥ 150 years old) mixed-oak stands from a single ecosystem type within the ecological classification system framework for the Wayne National Forest. All woody stems were measured by dbh and species, and classified into these strata by lifeform: (1) canopy (dominant, codominant, and intermediate crown classes); (2) saplings (stems < 10 cm dbh, but > 1.37 m tall with canopy potential); (3) subcanopy (stems < 10 cm dbh, but > 1.37 m tall without canopy potential); and (4) seedlings (stems < 1.37 m tall with canopy potential). Canonical correspondence analysis (CCA) was used to summarize the compositional variation in each strata by age class. Canonical correlation analysis was then used to examine the interrelatedness among forest strata using CCA axis scores. CCA ordinations revealed several trends, primarily that site differences and stand age were important factors constraining the development of various forest strata. Although there was no significant correlation between the canopy and sapling strata, there was strong correlation between the canopy and seedling strata, as well as between the sapling and seedling strata. These canopy, sapling, and seedling strata also were strongly correlated with their canonical variables, suggesting that each is responding to similar gradients. We suggest that the natural disturbance regimes of the study area have been altered, and as a result, the compositions of the mixed-oak stands in southeastern Ohio are responding to these modifications. Whereas a primary landform effect regulating landscape ecosystem and stand development prior to European settlement was likely the spatial pattern of surface fires, the effect of landform on the frequency and spatial geometry of these surface fires has diminished with fire suppression efforts.

INTRODUCTION

Models of landscape ecosystem development are predicated on a hierarchical structure, with the upper levels of the hierarchy constraining the lower levels (Figure 1). At broad continental scales, climatic and large-scale physiographic variation mediate the development of regional landscapes (Bailey 1996). Within these regional landscapes, differences in geology and physiography, as expressed by landforms, reflect the differences in the type of geologic surface deposits and depositional environments. Landforms, in turn, control the local microclimate, soil genesis, and local disturbance regimes (Rowe 1984, Host and others 1987, Bailey 1996, Goebel and others 1996). These constraints result in distinctive and repeatable patterns of vegetative composition, structure, and development (Barnes and others 1982, Hix and Lorimer 1991, Goebel and Hix 1996).

Swanson and others (1988) suggest that there are four major effects that landforms have on the patterns and processes of landscape ecosystem development. First, landforms (by their elevation, aspect, parent material, and slope steepness) influence the local climatic regimes and the levels of moisture, nutrients, and other materials that are available to landscape ecosystems. Second, landforms affect the flow of organisms, propogales such as seeds and sprouts, energy, and other materials (e.g., organic matter, water) through a landscape ecosystem. Third, landforms can influence the frequency and spatial pattern of non-geomorphic disturbances, such as fire, wind, and grazing, that are expressed through changes in the composition and structure of biotic communities. Finally, landforms constrain

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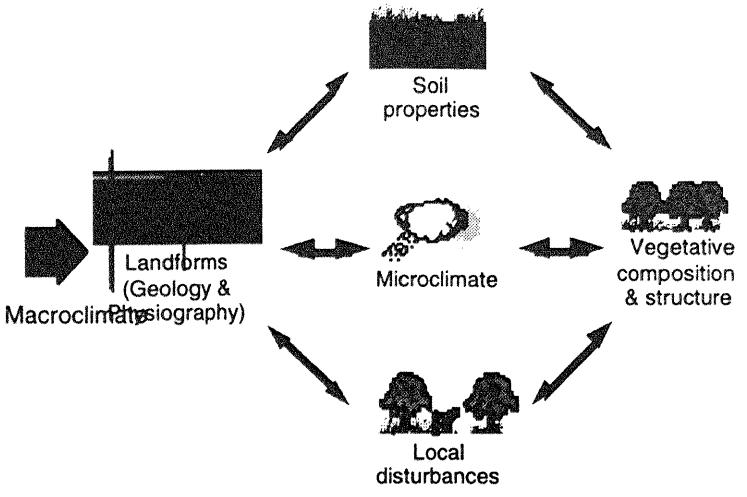

Figure 1. Hierarchical controls on landscape ecosystem development. The left side represents the upper levels of the hierarchy, while the right side represents the lower levels of the hierarchy. Modified from Bailey (1996) and Rowe (1984).

the spatial pattern and rate or frequency of geomorphic processes that alter biotic features and processes. When disturbance regimes are suppressed or altered, the interaction of these landform effects on ecosystem development may influence strongly the persistence and geometry of the mosaic of landscape ecosystems (Swanson and others 1988).

Multifactor and hierarchical ecological classification systems that base the higher levels of the system on landforms, such as a recent classification developed for the Wayne National Forest (Hix and Pearcy 1996), provide a framework for separating and identifying landscape ecosystems (Barnes and others 1982, Bailey 1987). These hierarchical classification systems also provide an opportunity to examine the effects of landforms on the development of an individual landscape ecosystem type. By examining a single ecosystem type, the landform effects on environmental gradients and movement of materials (class 1 and 2 effects; Swanson and others 1988) are assumed to be constant, allowing for analysis of the landform effects on disturbance regimes (class 3 and 4 effects).

The objective of this study was to examine the landform effects on the successional mechanisms that may be controlling the later-stage development of south-facing, upper to middle slope, second-growth and old-growth forest ecosystems in southeastern Ohio. Analysis of the development mechanisms were accomplished by: (*i*) quantifying the relationships between various strata and stand age on a single ecosystem type through the use of a chronosequence, and (*ii*) determining whether the various forest strata were highly correlated on a single ecosystem type, thus providing information on the inter-stratal relationships among various stand ages. Our hypothesis is that highly correlated strata on a single ecosystem type are responding to the same environmental conditions (class 1 and 2 effects), and thus any compositional differences are most likely responding to differences in stand age and (or) disturbance patterns (class 3 and 4 effects).

STUDY AREA

The current study was conducted on public and private lands located in southeastern Ohio (Figure 2) within the Western Hocking Plateau Subsection (221Ef) of the Southern Unglaciated Allegheny Plateau Section (221E) in the Eastern Broadleaf Forest Province (221; Keys and others 1995). The climate of the area is humid continental with relatively cold winters and warm summers. Mean daily temperatures are 0° C and 21° C , respectively (Lucht and others 1985). Precipitation averages 98 cm annually, of which half falls during the growing season (Lucht and others 1985).

The Western Hocking Plateau Subsection is a dissected plateau with moderate to steep slopes, narrow ridgetops, rock outcrops, and narrow stream valleys with elevations ranging from 195 to 322 m above sea level. Bedrock geology consists of inter-bedded sandstone, shale, siltstone, limestone, and coal (Rympa 1961, Keys and others 1995). In general, the forest soils are moderately acidic and were formed in colluvium (Keys and others 1995). Specifically, the dry upper to middle hillslopes (ecosystem type or ecological landtype phase (ELTP) 32) examined in the current study are south-facing, tend to be moderately to steeply sloping, and have moderately deep and well-drained soils with loamy over clayey textures (Hix and Pearcy 1996).

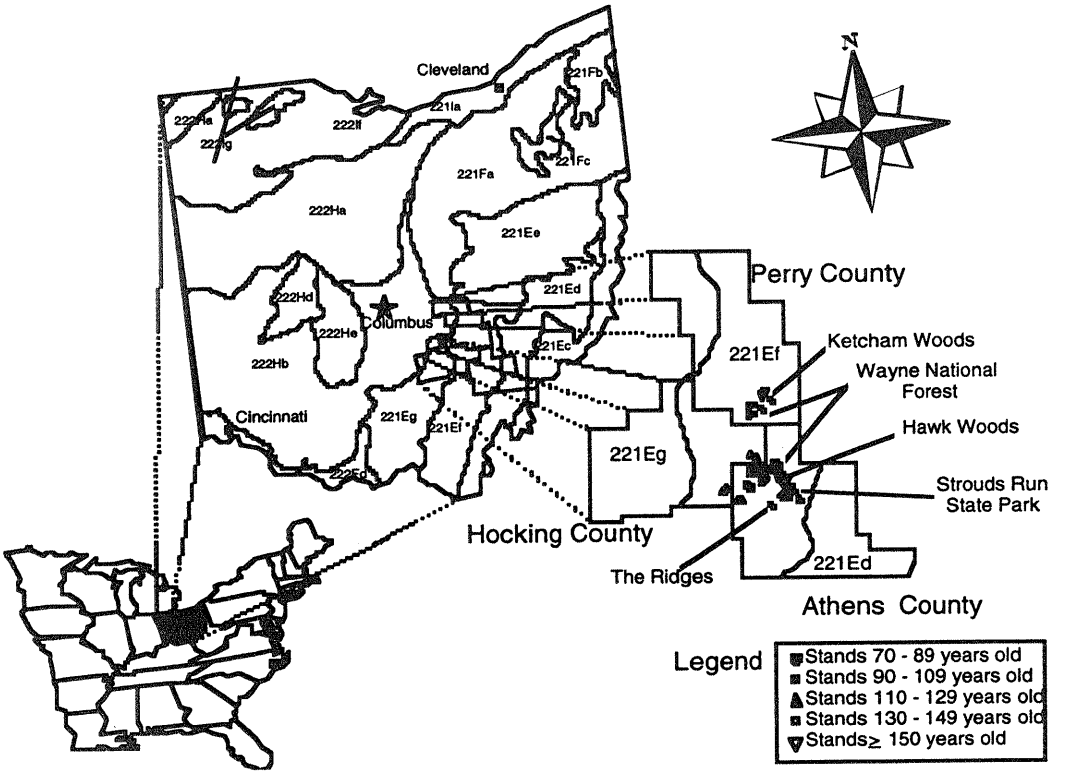

Figure 2. Location of second-growth and old-growth study areas within the Western Hocking Plateau Subsection (221Ef) of southeastern Ohio.

In southeastern Ohio, frequent burning is believed to have historically favored the more fire-resistant oaks, and eliminated understories of mesic species, such as American beech (*Fagus grandifolia* Ehrh.) and sugar maple (*Acer saccharum* Marsh.), resulting in a disturbance climax (Beatley 1959, Rympa 1969). Gordon (1969) suggested that the presettlement vegetation types of the study area were mixed-oak, mixed-mesophytic, and beech forests. However, the presettlement forests on south-facing ecosystem types in southeastern Ohio were most likely oak-hickory or mixed-oak forests (Cutler 1812, Boetticher 1929, Beatley 1959, Rypma 1961, Goebel and Hix 1996). The second-growth forests of southeastern Ohio have been heavily disturbed by agricultural conversion, timber harvesting, coal mining, and livestock grazing. Currently, oak-hickory and Appalachian mixed-hardwoods (Eyre 1980) that established after extensive clearcutting approximately 70 to 140 years ago are the dominant second-growth forest types of the study area (Ducey 1982).

The south-facing, upper to middle slopes examined in this study are dominated by white oak (*Quercus alba* L.). Canopy white oak importance has been shown to be significantly greater in older second-growth stands than younger second-growth stands (Goebel and Hix 1996). However, the canopies of old-growth ecosystems on similar south-facing, upper to middle slopes were dominated by mixed-oaks, including white oak, black oak (*Q. velutina* Lam.), chestnut oak (*Q. prinus* L.), and scarlet oak (*Q. coccinea* Muenchh.). Additionally, the sapling strata of both the second-growth and old-growth south-facing, upper to middle slopes were dominated by shade-tolerant species, such as red maple (*Acer rubrum* L.) and sugar maple, while the seedling strata of the older second-growth and the old-growth stands were comprised of shade mid-tolerant oak species (Goebel and Hix 1996).

METHODS

During the summers of 1993 and 1994, 21 forest stands were sampled on the Athens Unit of the Wayne National Forest and adjacent public and private property. The sampling design consisted of a sequence of stands of different ages (a chronosequence) at least 70 years old. The chronosequence included stands of the following five age classes: 70 - 89, 90 - 109, 110 - 129, 130 - 149, and ≥ 150 years old. Because old-growth forests are rare in southeastern Ohio and those present are generally believed to be less than 250 years old (Davis 1993, McCarthy 1995, Goebel and Hix 1996), the old-growth age class (≥ 150 years old) did not represent a specific age range (e.g., 150 - 169 years old). Rather, the old-growth age class provides a general comparison of the forest conditions at the time of European settlement. Specific details on the procedures used to verify the chronosequence can be found in Goebel and Hix (1996).

Within each identified stand, two plots were established randomly on a transect that bisected the area along the contour; the first plot located randomly between 20 and 30 meters from the stand boundary, and the second plot installed randomly at least 40 to 50 meters from the first plot. Each sample plot consisted of a set of two concentric, circular subplots (sizes = 500 m^2 and 100 m^2), and eight rectangular 1- by 2-m quadrats. The centers of the quadrats were located 2 m beyond the outside edge of the 100 m^2 subplot in eight directions (N, NE, E, SE, S, SW, W, NW). On each 500 m^2 plot the species, dbh (diameter at breast height, 1.37 m) and crown class (dominant, codominant, intermediate, or overtopped, c.f. Smith 1986) of all living trees > 10.0 cm dbh were recorded. Sapling and subcanopy individuals were measured by species and dbh on the 100 m^2 plots, while seedlings were counted by species on the 2 m^2 plots. Members of the sapling strata included those individuals ≤ 10.0 cm dbh but ≥ 1.37 m tall with canopy potential (Rheinhardt 1992), whereas subcanopy members were the same size but whose lifeform relegated them to understory or subcanopy positions. Seedlings were individual woody plants < 1.37 m in height with canopy potential. Scientific nomenclature follows Gleason and Cronquist (1991), and common names follow Little (1979).

Basal areas and densities of canopy trees, and densities of sapling and seedling species, were converted from a plot basis to per hectare basis. Relative density (percent) was calculated by summing the total density on a plot by species, dividing by the total density of all species on the plot, and multiplying by 100. Relative dominance (percent) of canopy species was similarly computed, substituting basal area for density. Importance values (IV, summation of relative density and relative dominance divided by 2) were calculated for canopy trees (dominant, codominant, and intermediate crown classes), while relative densities were calculated for each woody sapling, subcanopy, and seedling species.

Canonical correspondence analysis (CCA) was used to explore the variation in species composition among the various age groups and selected stand factors (CANOCO; ter Braak 1990). CCA was performed on four separate matrices: (*i*) canopy species, (*ii*) sapling species, (*iii*), subcanopy species, and (*iv*) seedling species. Monte Carlo permutation procedures were used to test the significance of each stand factor in each CCA (ter Braak 1990).

Canonical correlation analysis (COR; proc CANCORR; SAS 1989), a linear multivariate regression analysis that maximizes the correlation of two matrices, was used to measure the correspondence between pairs of datasets (Gittens 1985, Jongman and others 1995). An artifact of the regression analysis is that the number of species plus

the number of environmental factors must be smaller than the number of sampled stands (Jongman and others 1995). To account for this restriction, we used the CCA stand scores in the canonical correlation analysis of all possible ordination combinations ($n = 6$). COR generates three statistics that are instrumental in determining the correspondance between two datasets. These include: (*i*) the canonical correlation coefficient of each axis with each canonical variable; (*ii*) the percentage of variance extracted by the stand factors for each canonical variable; and, (*iii*) the redundancy, or proportion of the variation in a vegetative stratum (as summarized by CCA axes 1 and 2) accounted for by each canonical variable (Gittens 1985).

RESULTS

CCA Ordinations

The ordinations of all sample plots by strata illustrate the variation in woody species composition found in the second-growth and old-growth forest ecosystems on south-facing middle to upper slopes in southeastern Ohio. Although selected from a single ecosystem type, the stand factors combined only explain 64.6% of the variation in canopy IV along the first two canonical axes. The first canonical axis was not significantly correlated with stand age ($P = 0.16$), however, the first axis was positively associated with scarlet oak IV and shagbark hickory IV. The second CCA axis was positively associated with higher values of chestnut oak IV (Figure 3). These results confirmed that that the older, second-growth stands are characterized by higher IVs of longer-lived, and shade-tolerant white oak while the younger second-growth stands are comprised by shorter-lived, more shade-intolerant species (Table 2). Old-growth canopies were comprised of a mixture of oak species. While elevation was significantly correlated with the first axis ($P \leq 0.05$), the other stand factors were not strongly correlated with either canonical axis (Table 1), suggesting that the influence of the measured stand factors on canopy composition is minimal.

Whereas the canopy CCA was not highly constrained by stand age, the sapling CCA was significantly constrained by several stand factors, including stand age (Table 1). The sapling layers of most second-growth and old-growth stands were characterized by red maple (Table 2). However, sugar maple relative densities were highest in the 90 to 129 year old stands, while American beech saplings were more common in the old-growth stands (Table 2). The CCA triplot reveals that several stand factors significantly constrain the distribution of sapling species (Figure 3). Aspect, percentage of the distance to the ridgetop (PDR), percent slope, and stand age are all significantly correlated with the first CCA axis, while aspect and slope shape were significantly correlated ($P \leq 0.05$) with the second CCA axis (Table 1). This suggests that within a single ecosystem type, small differences in the measured stand factors may result in different sapling compositions. For example, older stands with steep, southwesterly slopes have higher relative densities of red maple and American beech.

Although the stand factors combined to explain 79.1% of the variation in subcanopy relative density (Table 1), stand age was not significantly correlated with either the first or second canonical axes ($P > 0.05$). Slope shape and aspect were both strongly correlated with both CCA axes ($P \leq 0.01$), suggesting that eastern hophornbeam (*Ostrya virginiana* (Mill.) K. Koch) relative density was higher on more xeric, southwesterly facing, convexed-shaped slopes, while serviceberry (*Amelanchier arborea* (Michx.f.) Fern.) and flowering dogwood (*Cornus florida* L.) relative densities were higher on more dry-mesic, southerly facing, concave-shaped slopes (Figure 3). Old-growth stands were centrally located along both the first and second CCA axes (Figure 3).

Table 1. Summary statistics of the canonical correspondence analyses for each strata.

	CCA Axis 1	CCA Axis 2
Canopy:		
Eigenvalue	0.20	0.15
Species-environment correlation	0.69	0.61
Cumulative % variance of species	7.70	13.40
Cumulative % variance of species-environment relation	37.10	64.60
Monte Carlo Permutation tests:		
Elevation	2.14 (0.04)[1]	0.70 (0.79)
Slope %	0.98 (0.55)	1.03 (0.46)
Aspect	1.25 (0.30)	1.03 (0.46)
PDR	0.86 (0.55)	0.81 (0.62)
Slope shape	1.35 (0.14)	1.28 (0.20)
Stand age	1.54 (0.16)	1.46 (0.20)
Sapling:		
Eigenvalue	0.28	0.18
Species-environment correlation	0.80	0.66
Cumulative % variance of species	9.90	16.10
Cumulative % variance of species-environment relation	38.70	63.00
Monte Carlo Permutation tests:		
Elevation	1.52 (0.11)	1.43 (0.16)
Slope %	1.47 (0.15)	1.45 (0.14)
Aspect	2.46 (0.03)	2.41 (0.03)
PDR	1.91 (0.02)	0.43 (0.96)
Slope shape	2.34 (0.03)	2.45 (0.03)
Stand age	2.03 (0.02)	1.15 (0.33)
Subcanopy:		
Eigenvalue	0.53	0.29
Species-environment correlation	0.83	0.76
Cumulative % variance of species	15.10	23.40
Cumulative % variance of species-environment relation	51.0	79.10
Monte Carlo Permutation tests:		
Elevation	0.38 (0.93)	0.30 (0.96)
Slope %	0.55 (0.76)	0.64 (0.73)
Aspect	3.88 (0.01)	4.20 (0.01)
PDR	0.95 (0.51)	0.82 (0.50)
Slope shape	4.46 (0.01)	4.03 (0.01)
Stand age	1.81 (0.08)	1.46 (0.18)
Seedling:		
Eigenvalue	0.29	0.14
Species-environment correlation	0.80	0.68
Cumulative % variance of species	11.10	16.50
Cumulative % variance of species-stand factor relation	44.70	66.70
Monte Carlo Permutation tests:		
Elevation	1.81 (0.04)	0.88 (0.55)
Slope %	0.72 (0.74)	0.37 (1.00)
Aspect	2.24 (0.01)	1.75 (0.06)
PDR	0.34 (0.99)	0.31 (1.00)
Slope shape	2.49 (0.02)	1.23 (0.21)
Stand age	2.72 (0.01)	1.71 (0.12)

[1] F-statistic and associated *P*-value for Monte Carlo permutation tests of stand factors with canonical axes.

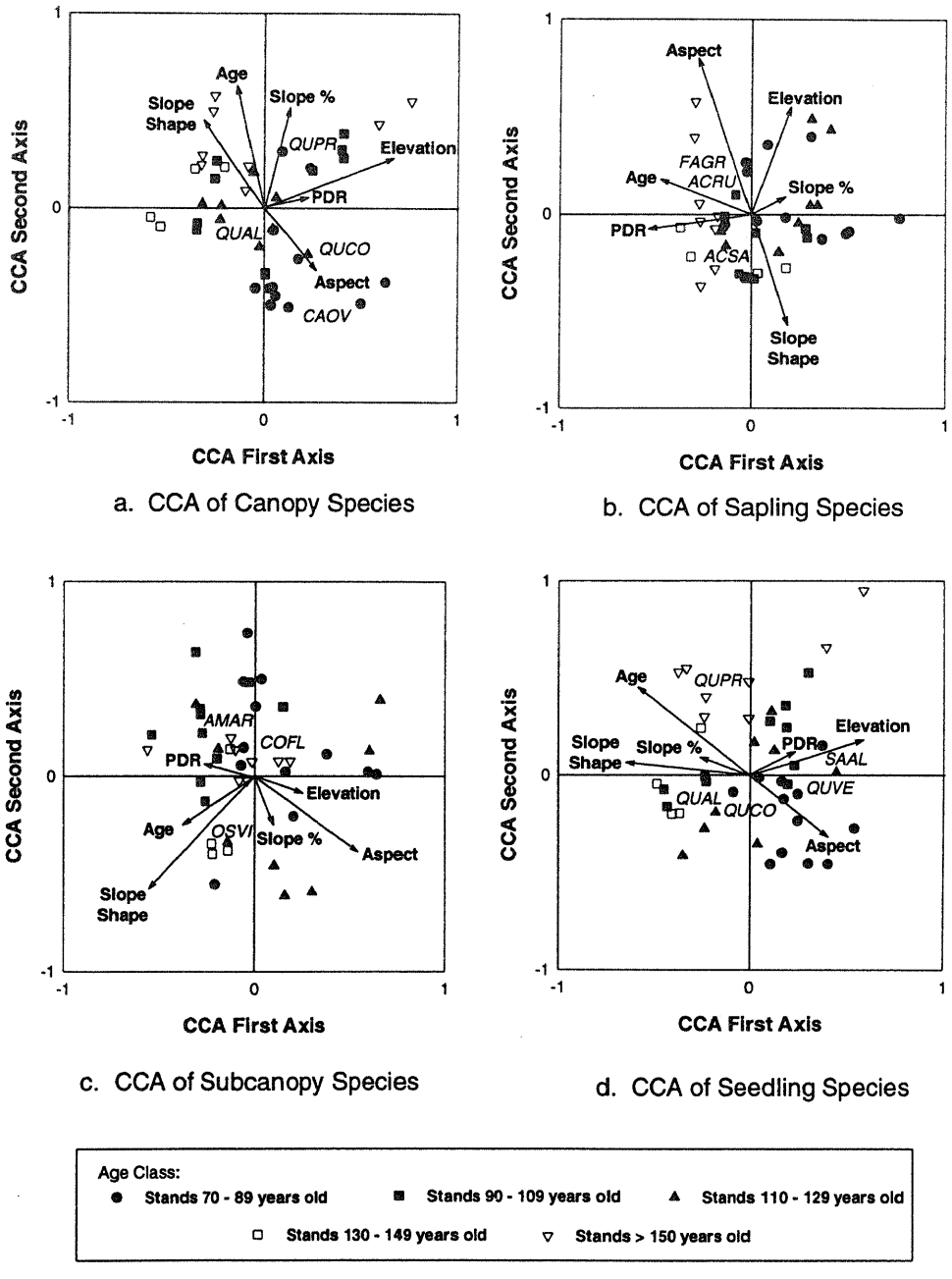

Figure 3. Canonical correspondence analyses (CCA) of canopy species (a), sapling species (b), subcanopy species (c), and seedling species (d) and stand factors.

Table 2. Importance values of selected canopy species, and relative densities of selected sapling, subcanopy, and seedling species by age class for second-growth and old-growth study sites in southeastern Ohio.

Species Name	Acronym	Age Class (yrs) 70 - 89	90 - 109	110 - 129	130 - 149	≥ 150
Number of plots (*n*)		12	10	8	4	8
Canopy Species:						
Acer rubrum	ACRU	0.4	0.9	1.7	0.0	0.0
A. saccharum	ACSA	1.5	6.8	3.3	0.0	0.0
Carya glabra	CAGL	0.7	5.6	0.8	0.0	0.0
Quercus alba	QUAL	35.5	54.7	67.0	86.1	46.5
Q. coccinea	QUCO	11.8	2.7	1.0	0.0	1.6
Q. prinus	QUPR	12.2	12.2	2.8	0.0	27.6
Q. rubra	QURU	9.8	3.0	0.0	3.8	6.1
Q. velutina	QUVE	16.2	8.5	13.8	3.0	13.9
Other[1]		11.9	5.6	9.6	7.1	4.3
Sapling Species:						
Acer rubrum	ACRU	45.9	33.8	27.1	33.9	29.7
A. saccharum	ACSA	6.4	44.2	47.8	18.0	27.8
Fagus grandifolia	FAGR	9.4	6.4	14.7	18.2	28.3
Nyssa sylvatica	NYSY	1.3	0.0	0.8	8.6	4.9
Quercus alba	QUAL	3.1	0.0	2.1	0.0	1.1
Q. coccinea	QUCO	4.9	0.0	0.0	0.0	0.0
Q. prinus	QUPR	6.1	0.0	0.0	0.0	0.0
Q. rubra	QURU	1.9	0.6	0.0	0.0	0.0
Q. velutina	QUVE	0.8	0.6	2.3	0.0	0.0
Other[2]		20.2	14.4	5.2	22.2	8.2
Subcanopy Species:						
Amelanchier arborea	AMAR	10.0	7.5	33.0	13.0	13.0
Carpinus caroliniana	CACA	6.4	6.3	1.3	8.6	0.0
Cornus florida	COFL	63.3	60.0	16.6	31.3	72.7
Ostrya virginiana	OSVI	8.5	15.9	27.7	46.7	6.5
Other[3]		11.8	10.3	21.4	0.4	7.8
Seedling Species:						
Acer rubrum	ACRU	16.8	12.4	17.1	8.3	21.7
A. saccharum	ACSA	4.6	11.0	8.3	3.3	9.7
Fagus grandifolia	FAGR	3.8	3.5	3.3	3.3	9.0
Quercus alba	QUAL	4.9	22.7	10.9	49.0	7.0
Q. coccinea	QUCO	2.5	0.0	0.0	0.0	1.1
Q. prinus	QUPR	3.4	5.2	0.6	0.0	9.0
Q. rubra	QURU	2.5	1.5	1.5	1.8	1.0
Q. velutina	QUVE	3.2	2.3	2.5	0.0	1.3
Sassafras albidum	SAAL	16.3	12.3	13.0	4.0	12.8
Other[4]		41.4	29.1	41.8	30.3	27.4

[1] *Carya cordiformis, C. lacinosa, C. ovata, C. tomentosa, Fraxinus pennsylvanica, Juglans nigra, Liriodendron tulipifera, Nyssa sylvatica,* and *Populus grandidentata.*

[2] *Aesculus octandra, Carya glabra, C. ovata, C. tomentosa, Diospryos virginiana, Fraxinus americana, F. pennsylvanica, Liriodendron tulipifera, Magnolia acuminata, Oxydendrum arboreum, Prunus serotina, Sassafras albidum,* and *Ulmus rubra.*

[3] *Asimina triloba, Cercis canadensis, Crataegus* spp., *Hamamelis virginiana, Lindera benzoin, Viburnum acerifolium,* and *V. prunifolium.*

[4] *Aesculus octandra, C. cordiformis, C. glabra, C. ovata, C. tomentosa, Cercis canadensis, Fraxinus americana, F. pennsylvanica, Liriodendron tulipifera, Magnolia acuminata, Nyssa sylvatica, Oxydendrum arboreum, Pinus strobus, Prunus serotina, Tilia americana,* and *Ulmus rubra.*

Finally, the seedling CCA revealed similar trends as the sapling CCA, with the stand factors explaining 66.7% of the variation in seedling composition (Table 1). In general, the seedling layers of the younger second-growth stands were comprised of scarlet oak, black oak, and sassafras (*Sassafras albidum* (Nutt.)), while those of the older second-growth stands were comprised of primarily of white oak (Table 2). The CCA triplot confirmed this trend, with stand age significantly, negatively associated with the first CCA axis ($P \leq 0.01$). Aspect was significantly and positively correlated with the first canonical axis, suggesting that the younger, more southerly facing slopes were associated with higher relative densities of scarlet oak and black oak seedlings ($P \leq 0.01$).

Canonical Correlations Among Forest Strata

The canonical correlation coefficients of the CCA axis scores varied considerably among the strata comparisons (Figure 4). The highest canonical correlations were between the canopy and seedling strata for both the first and second canonical axes ($P < 0.01$; $r = 0.63$ and 0.53, respectively), while the canonical correlations between the sapling strata and the seedling strata were also significant for both CCA axes ($P < 0.05$; $r = 0.50$ and $r = 0.30$, respectively). However, the canopy and sapling strata were not significantly correlated. Similarly, the subcanopy strata CCA axis scores were not significantly correlated with any of the other strata axis scores (Figure 4).

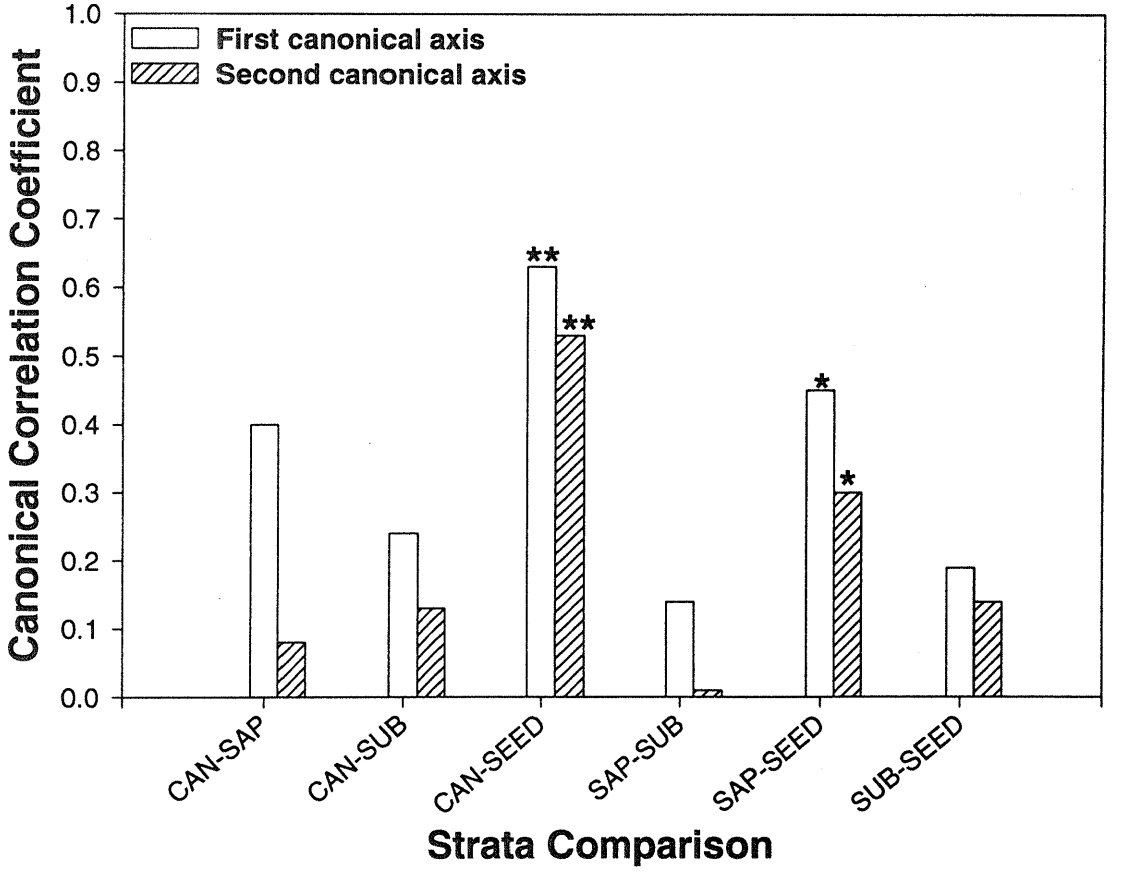

Figure 4. First and second axis canonical correlation coefficients of strata comparisons for second-growth and old-growth study areas in southeastern Ohio. CAN = canopy strata, SAP = sapling strata, SUB = subcanopy strata, and SEED = seedling strata. * = $P < 0.05$; ** = $P < 0.01$.

More detailed analysis of the significant canonical correlations revealed several interesting trends. The first and second axis scores of the canopy CCA and seedling CCA comparison were positively correlated with the their respective canonical variable (Table 3). Thus, the first and second axes of the canopy and seedling ordinations presumably represent the same gradients. As the canopy strata increased in white oak IV, the sapling strata also increased in white oak relative density. Because stand age is significantly correlated with the first CCA axis of the seedling ordination, the canonical correlation may represent the relationship between stand age and increasing importance of white oak in the canopy and seedling strata. The fact that the canopy and seedling strata are correlated is not surprising in that the correlation may reflect the strong influence of canopy trees on the composition of the seedling strata (e.g., local seed sources).

Similarly, the sapling strata and seedling strata were also significantly correlated (Figure 4). However, the relationships between the CCA axes were different than the canopy and seedling comparison. The first axis of the sapling ordination was weakly and negatively correlated with the first canonical variable, while strongly and negatively correlated with the second canonical variable (Table 4). Conversely, the seeding ordination was highly, positively correlated with the first and second canonical variables (Table 4). As a result, the second axis of the sapling CCA and the inverse of CCA axis 2 of the seedling ordination represent similar gradients. However, the variance extracted and redundancy values for both canonical variables are low, therefore caution should be exercised when interpreting these axes (Table 4).

DISCUSSION

Several studies that have shown that there are strong relationships among vegetational strata in response to environmental and disturbance gradients (Grigal and Arneman 1970, del Moral and Watson 1978, Bradfield and Scagel 1984, Gagnon and Bradfield 1986, Roberts and Christensen 1988). Our data suggests a similar trend. Canonical correlation analyses indicate that the canopy and seedling strata, as well as the sapling and seedling strata, are correlated and are responding to similar gradients. However, the results of this study also show that compositional changes are not strongly related to stand age in all cases, although there do appear to be some consistent trends among the various strata. First, the younger second-growth stands 70 - 119 years old are comprised of mixed-oak canopies, red maple saplings, and mixed-oak seedlings. However, the composition of all three strata are markedly different in the older second-growth stands. The older second-growth stands 110 - 149 years old are

Table 3. Canonical correlation comparison of canopy strata with seedling strata ordination (CCA) scores.

	CAN 1[1]	CAN 2
Correlation of Canopy CCA Scores with their canonical variable		
CCA Axis 1	0.94	0.33
CCA Axis 2	-0.45	0.89
Variance extracted (%)[2]	52.0	48.0
Redundancy (%)[3]	21.0	13.0
Correlation of Seedling CCA Scores with their canonical variable		
CCA Axis 1	0.99	0.11
CCA Axis 2	-0.01	0.99
Variance extracted (%)[2]	51.0	49.0
Redundancy (%)[3]	17.0	17.0

[1] Canonical variable.
[2] Proportion of the variance in the stand factors accounted for by the canonical variable.
[3] Proportion of variance in a vegetative stratum (as summarized by CCA axes 1 and 2) accounted for by the canonical variable.

Table 4. Canonical correlation comparison of sapling strata with seedling strata ordination (CCA) scores.

	CAN 1[1]	CAN 2
Correlation of Sapling CCA Scores with their canonical variable		
CCA Axis 1	-0.27	0.96
CCA Axis 2	0.88	0.46
Variance extracted (%)[2]	51.0	49.0
Redundancy (%)[3]	10.0	5.0
Correlation of Seedling CCA Scores with their canonical variable		
CCA Axis 1	0.85	0.52
CCA Axis 2	0.61	-0.79
Variance extracted (%)[2]	52.0	48.0
Redundancy (%)[3]	10.0	4.0

[1] Canonical variable.
[2] Proportion of the variance in the stand factors accounted for by the canonical variable.
[3] Proportion of variance in a vegetative stratum (as summarized by CCA axes 1 and 2) accounted for by thecanonical variable.

dominated by canopies of white oak, saplings of sugar maple, and seedlings of white oak and subcanopy species (e.g., eastern hophornbeam). Finally, the old-growth stands appear to be comprised of canopy layers of mixed-oaks, sapling layers dominated by both red maple and sugar maple, and seedling layers of mixed-oaks. Since all study areas were located on a single ecosystem type with similar environmental characteristics, the changes in the vegetative composition are probably the result of modifications in the disturbance regimes (e.g., fire, grazing) rather than changes in site conditions or stand age.

The multivariate analyses used to describe the relationships between strata along the chronosequence suggest that the mechanisms regulating the development of these mixed-oak forest ecosystems in southeastern Ohio have been modified. Prior to European settlement and the subsequent changes in the disturbance regimes of the study area (see Goebel and Hix 1996), the primary mechanism regulating stand dynamics was most likely a class 3 effect (Swanson and others 1988). On south-facing ecosystem types surface fires most likely damaged or killed many of the red and sugar maple saplings and seedlings (Beatley 1959, Rympa 1969, Runkle 1990, Abrams 1992), inhibiting the development of a shade tolerant understory. Similar development of more shade tolerant understories on xeric sites in response to landform effects on disturbance patterns have been observed in other regions (Ware and others 1993, Goebel and others 1996).

With the active fire suppression activities of the past 80 years, the mechanism most likely inhibiting the development of shade tolerant understory strata was removed from the landscape. This change resulted in the development of a dense layer of red maple and sugar maple sapling layer. In the absence of a class 3 effect, the mechanism currently regulating stand development on these south-facing slopes appears to be a class 1 effect (Swanson and others 1988). Because many of the correlations between forest strata were weak, these class 1 effects may influence the development of various strata at different rates, as proposed by McCune and Antos (1981). The lack of correspondence between the canopy and sapling layers (e.g., few oaks in the sapling strata) suggests that red maple and sugar maple have survived in the understory of the mixed-oak canopies, and have overtopped the oaks of the seedling layer. Harvesting activities also have been shown to further the development of a shade tolerant understory on dry-mesic sites (Abrams and Nowacki 1992). Once the primary factor inhibiting the development of these shade tolerant understories was removed from the system and these understories become dominated by shade tolerant species, any natural or anthropogenic canopy disturbance will likely shift the canopy composition towards more shade tolerant species.

Although relatively undisturbed since establishment, the mechanisms regulating stand development in the old-growth stands of this study have also been modified. The old-growth areas sampled have been forested since European settlement and appear to have been in compositional equilibrium (Goebel and Hix 1996), the old-growth forests are no longer in equilibrium (e.g., canopy species are replacing themselves). Human activities in the surrounding matrix of second-growth forests such as logging, agricultural conversion, mining, and urban development have modified the landscape disturbance regimes of these mixed-oak ecosystems, primarily the frequency and intensity of surface fires. Without these natural disturbances, both red and sugar maple dominate the sapling layer of the old-growth study areas and will most likely increase in canopy importance in the future. Similar trends have been documented throughout the eastern United States (Whitney and Somerlot 1985, Lorimer 1989, Abrams 1992, Abrams and Nowacki 1992, Goebel and Hix 1996). Although the old-growth forests in the study area meet many of the structural and functional definitions of old-growth forests (e.g., high species richness, uneven-aged structure, large canopy individuals, relatively undisturbed soils), they are not in steady state with regard to species composition and other ecosystem properties because they are still responding to modified disturbance regimes. As a result, these old-growth forests are probably best described as changing, or transitional old-growth (Runkle 1996).

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