Temporal Patterns of Woody Species Diversity in a Central Appalachian Forest From 1856 to 1997

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SCHULER, T. M. (Northeastern Research Station, US Forest Service, Parsons WV 26287) AND A. R. GILLESPIE (Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN 47907). Temporal patterns of woody species diversity in a central Appalachian forest from 1856 to 1997. 127:149–161. 2000.—This study examined the composition of woody species in a mixed mesophytic forest in the central Appalachian region with respect to both time and different disturbance regimes. Species composition and diversity were assessed from 1856 to 1997 on a tract of land that currently is part of the Fernow Experimental Forest in north-central West Virginia. Additionally, the effect of different silvicultural disturbances are described using inventory data from four silvicultural demonstration areas initiated in 1948. These areas included a commercial clearcut, diameter-limit harvesting, single-tree selection, and an area that has not been artificially manipulated since initial logging around the turn of the century (ca 1907). Witness tree data from early land surveys (1856 and 1915) conducted in the same watershed were used to gain some insight into species frequency prior to and after initial logging. A forest inventory conducted in 1922 provided a more detailed description of the vegetation in the vicinity of the post-1948 stand data. The Shannon-Weiner Diversity Index was calculated based on species importance values for all time periods and management activities. Detrended correspondence analysis was used to assess differences in composition related to time and management activity. Data from old-growth (1856), early second-growth (1915 and 1922), and more mature second-growth stands were well separated in ordination space. A decline in species diversity from a high in 1922 to a low in 1997 appears to be driving this separation. Diversity declined primarily due to a reduction in evenness, which was significantly correlated with increasing importance of *Acer saccharum*. Relative *A. saccharum* importance is increasing in both the overstory and understory for all disturbance regimes. The increasing dominance of this species with time, regardless of stand age or disturbance regime evaluated, may be unprecedented and suggests new silvicultural techniques are needed to maintain the diversity of central Appalachian forests.

Key words: *Acer saccharum, Quercus rubra*, West Virginia, forest vegetation, diversity.

Temporal change in floristic composition is common in most ecosystems (Kimmins 1987). The rate and direction of change is affected by both internal and external factors. Internally derived changes are caused by plants and their interactions (Spurr and Barnes 1980). Changes are also caused by events external to the plant community such as outbreaks of wildfire and cutting of forests by humans (Oliver and Larson 1996). Stand level silvicultural manipulation is an example of a planned external factor that can significantly influence species composition and di-

versity (Smith et al. 1997). Historically, silvicultural practices often sought to control composition to increase production of one or more desirable species. More recently, silvicultural objectives have included the retention of species diversity (Society of American Foresters 1991). Diverse stands are considered more desirable, in part, because they may be more resilient to perturbation (McNaughton 1977). While this theory continues to be evaluated (May 1974; Perry 1994; Hooper and Vitousek 1997; Wardle et al. 1997), empirical support for the theory has been presented (Tilman and Downing 1994; Naeem et al. 1995).

To evaluate temporal species composition change in forested ecosystems, chronosequences of stands have often been used (Peet and Loucks 1977; Finegan 1984; Roberts and Christensen 1988). However, such chronosequences can introduce variability from numerous factors including physical site characteristics and disturbance histories. To avoid composition differences related to unaccounted for spatial environmental gradients, Goebel and Hix (1996)

compared old-growth and second-growth forests located on the same ecological landtype in southeastern Ohio. However, Elliott et al. (1997) assert that the least ambiguous method of evaluating temporal change is to reassess species composition through time on a single site (i.e., long-term monitoring). Opportunities to utilize this approach are limited in forest ecosystems because the time scale of interest is one of decades and centuries (Parker and Swank 1982; Hornbeck et al. 1987; Smith and Miller 1987; Elliott et al. 1997; Spetich and Parker 1998). Long-term monitoring efforts have examined the role of disturbance and recovery on species composition changes through multiple decades, but have not yet addressed species composition changes spanning old-growth, early second-growth, and late second-growth stages in the eastern broadleaf forest of the United States.

In this research, changes in composition and diversity of woody species were examined over 131 years, a period that spans old-growth, early second-growth, late second-growth, and managed forest conditions. First, we compare woody vegetation from prior to initial logging to current conditions with respect to species composition, richness, evenness, and diversity. Second, we assess the effect of different silvicultural practices implemented in 1948 on diversity of woody species in managed second-growth stands.

Methods. STUDY AREA. Data for this study were collected on the Fernow Experimental Forest (39.03°N, 79.67°W) in north-central West Virginia, USA, located in the Allegheny Mountains Section of the Central Appalachian Broadleaf Forest (M221B) (McNab and Avers 1994). The land type association has been designated as the Allegheny Front Sideslopes (Ba10) (DeMeo et al. 1995) and the vegetation is classified as mixed mesophytic (Braun 1950). Characteristic species include but are not limited to *Quercus rubra, Liriodendron tulipifera, Prunus serotina, Acer saccharum, Carya cordiformis, Betula lenta, A. rubrum,* and *Fagus grandifolia.* The topography is mountainous; elevations range from 534 to 1,113 m above sea level. Mean annual precipitation is ca. 143 cm and is distributed evenly throughout the year (Pan et al. 1997). The growing season is approximately from May through October with an average frost-free period of 145 days.

The Elklick watershed (which later became the Fernow) was initially logged between 1903 and 1911 (Trimble 1977) during the railroad log-

ging era (Fansler 1962). During this period, many trees were left uncut due to insufficient size, poor form, or because the species was considered undesirable (e.g., *A. saccharum, F. grandifolia, Betula* spp., and *Carya* spp.). The federal government purchased the land in 1915 and began forest and watershed research in 1933. Since 1915, fire has not been recorded and grazing has been prohibited. Chestnut blight caused by *Cryphonectria parasitica,* first noted in West Virginia as early as 1909 (Brooks 1911), resulted in a 25-percent reduction in the volume of standing timber on the Fernow during the 1930s (Weitzman 1949).

Slopes ranging from 20 to 50 percent cover most of the Experimental Forest. Soils are predominantly from the Belmont and Calvin series. Belmont soils are derived from shale, sandstone, and interbedded limestone, and represent one of the most productive forest soils in the region (USDA Soil Conservation Service 1967). Typical *Q. rubra* growth on this soil type will reach 25 m in the first 50 years of development (Yawney 1964). The Calvin soil series develops both above and below the Belmont series, and is well drained and moderately permeable. Calvin soils lack a limestone parent material; consequently, these soils are more acidic than the Belmont soils.

Data from 1948 and later were obtained from inventories of a silvicultural research and demonstration unit nominally referred to as Compartment 8 (10.12 ha). This compartment is within a single ecological landtype (ELT) which integrates soil (Belmont), landform (midslope), slope (15–35%), aspect (W), and potential vegetation (*A. saccharum—Q. rubra,* dry phase) (ELT's for the Fernow were recently completed by the staff of the Monongahela National Forest). Two attributes made Compartment 8 especially suitable for this study. First, field notes from a recently discovered 1922 forest inventory indicate that data were collected in the same vicinity as Compartment 8 with the same aspect, slope position, and elevation. The 1922 inventory, in which all trees >2.54 cm dbh were tallied on about 2.43 ha, provided the first detailed data on species composition and forest stand structure for this watershed. Second, Compartment 8 represents the longest continuous record of woody species dynamics on the Fernow and includes a range of silvicultural disturbances originally designed to demonstrate different management intensity levels.

Silvicultural treatments of Compartment 8

Table 1. Summary of Compartment 8 management activities since 1948.

Unit #	Date	Management
8A	1948	Commercial clearcut (dbh > 12.7 cm)
8B	1948, 1968, 1988	Diameter-limit (dbh > 40.6 cm)
8C	1948, 1958, 1968, 1978, 1988	Single-tree selection (Q = 1.3, maximum dbh = 81.3 cm, and residual basal area $\cong$ 15 m² ha⁻¹ for dbh > 27.9 cm)
8E		None

represent a gradient of harvest intensity and include a commercial clearcut, diameter-limit harvesting, and single-tree selection (Table 1). All treatment areas are of equal size (2.06 ha). A contiguous area that has not been harvested since about 1907 (8E) also was included in the study. The commercial clearcut (8A) removed all stems larger than 12.7 cm dbh following the 1948 growing season. Culls were not treated and no site preparation followed harvesting activities. It should be noted that this treatment did not meet the definition of a true clearcut (i.e., the removal of all influence from residual stems on the next cohort). The diameter-limit harvest (8B) removed all trees larger than 40.6 cm dbh in 1948, 1968, and 1988. Residual basal area after logging in 8B ranged from 9 to 12 m² ha⁻¹ in trees larger than 12.7 cm dbh. The single-tree selection unit (8C) was harvested following the growing seasons of 1948, 1958, 1968, 1978, and 1988. The silvicultural guidelines for 8C include a Q factor of 1.3 (which defines the desired ratio of trees in subsequently smaller diameter classes), a maximum dbh of 81.3 cm, and a residual basal area following each harvest of 14.9 m² ha⁻¹ for trees greater than 27.9 cm dbh.

DATA COLLECTION. To assess temporal changes in composition and to reflect data collection procedures, we divided stems into two broad categories for analysis: understory stems (dbh $\geq$ 2.54 cm and <12.7 cm) and overstory stems (dbh $\geq$ 12.7 cm). By this definition, all overstory stems within each managed compartment have been individually tallied since 1948 using 5.08-cm dbh classes. All data presented here represent measurements before each treatment if one coincided with the measurement period. Initial measurements in 8E were taken in 1958. With the exception of the 1948 survey, understory-sized stems were sampled from 50 temporary 0.00405-ha regeneration plots within each treatment; the plots were remeasured every 10 years after establishment. In 1948 saplings were simply tallied in dbh categories from 2.54 to 5.08 cm and from 5.08 to 12.70 cm.

Witness tree data from early metes and bounds land surveys conducted in 1856 and 1915 on the Elklick Watershed were used to extend the temporal scale of this study. The 1856 survey provides some insight into species composition prior to initial logging and the 1915 survey does the same for the post-logging environment of the Elklick watershed. It should be noted that even though we refer to the 1856 survey data as old-growth, we simply mean the pre-logged forest conditions at that time and do not mean to imply "climax" conditions (e.g., Whittaker 1975) or specific functional or structural attributes associated with old-growth (Oliver and Larson 1996). Although early land surveys are a valuable source of early vegetation characteristics, they must be interpreted with caution, due to possible misidentification of trees, sampling biases, or fraud (Whitney 1994). Moreover, in a comparison of land survey data with modern forest inventory data, we expect there to be sample differences due to differences in data acquisition procedures and landforms sampled. However, these early metes and bounds land survey data allowed us to determine if trends observed in Compartment 8 after 1948 could be observed prior to 1948 using the only available data source.

DATA ANALYSIS. The Shannon-Weiner Diversity Index (H′) (Whittaker 1972) was calculated based on species importance value (IV) for all time periods and management activities (H′ = $-\Sigma p_i \ \ell n \ p_i$, where p_i is equal to the proportional importance of the ith species). This index of diversity is independent of sample size (Magurran 1988), which was important for this study. IV's were calculated for each species in each stand as the mean of relative density (stems) and relative dominance as expressed by basal area. Because tree size was not recorded in 1856, comparisons that included the 1856 witness trees were based on relative frequency of stems alone for all time periods.

Because communities can change without affecting measures of diversity, detrended corre-

Table 2. Relative importance values based on stem frequency of selected overstory species from the Fernow Experimental Forest in West Virginia (n = number of trees at each observation period). Observations from selected years are combined and demonstrate the effect of time rather than post-1948 silvicultural treatments.

Species	1856	1915	1922	1948	1968	1997
Fagus grandifolia	29.9	23.6	8.7	4.6	2.0	2.0
Castanea dentata	8.3	15.1	5.5			
Quercus rubra	6.5	5.7	6.3	6.9	7.9	6.3
Liriodendron tulipifera	3.6	4.9	1.7	23.3	29.0	24.8
Prunus serotina		1.1	1.5	6.2	4.2	3.3
Robinia pseudoacacia		0.7	0.8	14.4	9.8	7.2
Acer saccharum	3.4	8.8	14.5	17.3	20.1	37.9
Tilia americana	9.0	0.9	10.3	2.3	4.3	4.9
Fraxinus americana		7.7	5.5	4.4	5.6	3.5
Carya sp.	3.6	6.9	10.4	14.4	8.8	3.5
other species	35.7	24.6	34.8	6.2	8.1	6.5
Richness	20	19	22	16	22	21
n	86	96	673	1865	2937	2554

spondence analysis (DCA) was used to assess potential differences in composition related to time and management activity. An indirect gradient analysis, DCA often is used to study species distributions along spatial gradients (Palmer 1993). Here it was used to assess changes in species composition along temporal and disturbance gradients (Foster and Zebyrk 1993). Summary statistics from the DCA analysis include the eigenvalues of each DCA axis and post-procedure derived coefficients of determination. In the case of DCA, coefficients of determination are calculated indirectly after the ordination and simply represent the correlations between the ordination distances and the distances in the original unreduced space (McCune and Mefford 1997). To interpret the ordination, relationships were developed between the ordination scores and the individual variables used to construct the ordination using a non-parametric ranking procedure known as the Mann-Kendall test which is not dependent on a linear association (Kendall 1975). All relevant variables were also compared graphically to ordination axes as well and characteristics of the distribution were noted.

A covariance model was used to evaluate the temporal rate of change in A. saccharum IV among different silvicultural groups. The usual assumption of homogeneity of regression coefficients was posed as a null hypothesis and tested (Steel and Torrie 1980). Slope differences among silvicultural groups were evaluated using an interaction term in the covariance model (Littell 1991).

Results. OVERSTORY. Thirty-five species of woody plants were identified throughout the period from 1856 to 1997. Only B. lenta, F. gran-difolia, A. saccharum, and Tilia americana were present in all samples. Overstory species composition was conspicuously affected by elimination of Castanea dentata. Castanea IV (based on relative density of stems) fell from almost 16% in 1915 to about 3% in 1922 to virtual extirpation by 1948. A small presence of Q. alba was detected by all sampling strategies from 1856 through 1948, but this species too is no longer present in Compartment 8. Elimination of Q. alba from the overstory after 1948 resulted from timber harvesting in the commercial clearcut and single-tree selection areas. Disturbance-dependent Populus grandidentata was present in 1956 and 1968 but no longer is found in the study area. Cornus florida met the specified criteria to be included as an overstory tree in 1968 and 1988 but was not recorded in 1997. Although Juglans cinerea and Ulmus rubra were not major components of the study area or surrounding forest in the past, those individuals present are also on the verge of extirpation from the study area, possibly due to well-known pathogens (Gibbs 1978; Ostry et al. 1994).

Several species emerged on the site through time. Shade-intolerant P. pensylvanica and Sassafras albidum were not present in 1948, but were present in 1968 after the commercial clearcut. Shade-tolerant Magnolia fraseri was first recorded in the diameter-limit area in 1968, and Tsuga canadensis emerged as a small overstory stem in the single-tree selection area in 1988. Because of the loss of some species and the emergence of others, species richness has not changed notably throughout the analysis period (Table 2). However, species composition has been dynamic and it was possible to quantify these changes.
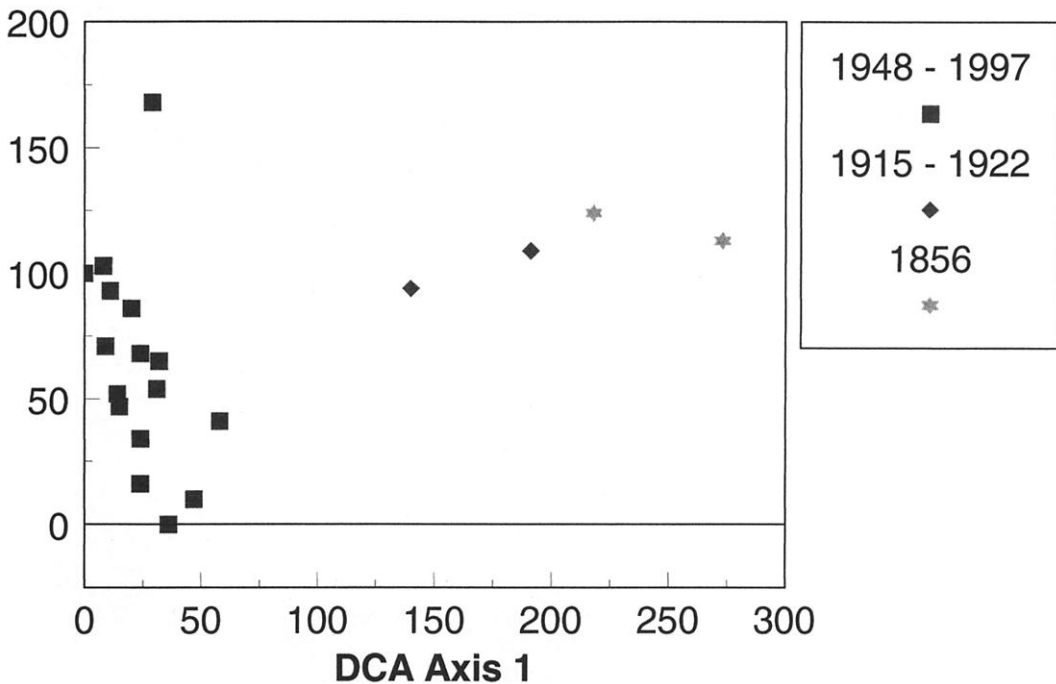
DCA Axis 2

Fig. 1.   Detrended correspondence analysis of woody overstory species from the Fernow Experimental Forest stratified by measurement period. Results are based on relative frequency of stems only for all time periods since the 1856 survey data did not include tree size.

Overstory plots were well separated in the ordination space of the DCA. The first ordination axis (eigenvalue = 0.5412, r^2 = 0.379) appears to exhibit a temporal continuum from managed conditions (i.e., post − 1948) to early second growth (i.e., 1915 and 1922) to old-growth (i.e., 1856) as axis values increase (Fig. 1). This apparent relationship may be confounded by differences in data acquisition noted earlier. However, the close relative proximity of the 1915 and the 1922 species composition in the ordination suggests otherwise, given the differences in data acquisition between these two time periods. DCA axis 1 scores were strongly affected by a positive correlation with *C. dentata* according to the Mann-Kendall test (τ = 0.555) and negative correlations with shade-intolerant species such as *L. tulipifera* (τ = −0.695), *Robinia pseudoacacia* (τ = −0.642), and *P. serotina* (τ = −0.526). Ordination scores from the second axis (eigenvalue = 0.1724, cumulative r^2 = 0.610) were negatively correlated with increasing importance of *A. saccharum* (τ = −0.884) and year of observation (τ = −0.759) when this variable was evaluated from a secondary matrix for in-

terpretation purposes. The third axis explained little of the variability in the ordination (eigenvalue = 0.0260, cumulative r^2 = 0.734) but did appear to generally correspond to increasing importance of some shade-tolerant species as axis values increased.

To assess the effect of the different silvicultural options described earlier, we excluded the data prior to 1948 and reexamined the data for separation using IV's based on relative density and relative basal area (Fig. 2). The first axis of the ordination (eigenvalue = 0.1974; r^2 = 0.620) was strongly influenced by a negative correlation with *L. tulipifera* (τ = −0.550) and *R. pseudoacacia* (τ = −0.633), and the second axis (eigenvalue = 0.0222; cumulative r^2 = 0.684) was negatively correlated with the year of observation (τ = −0.688) evaluated from a secondary matrix. Nut producers such as *Q. rubra* (τ = 0.183) and *F. grandifolia* (τ = 0.450) are positively correlated with the second axis suggesting that the importance of these species has declined since 1948. Graphically, it is evident that the diameter-limit (8B) and the single-tree selection (8C) areas have become more homogenous with
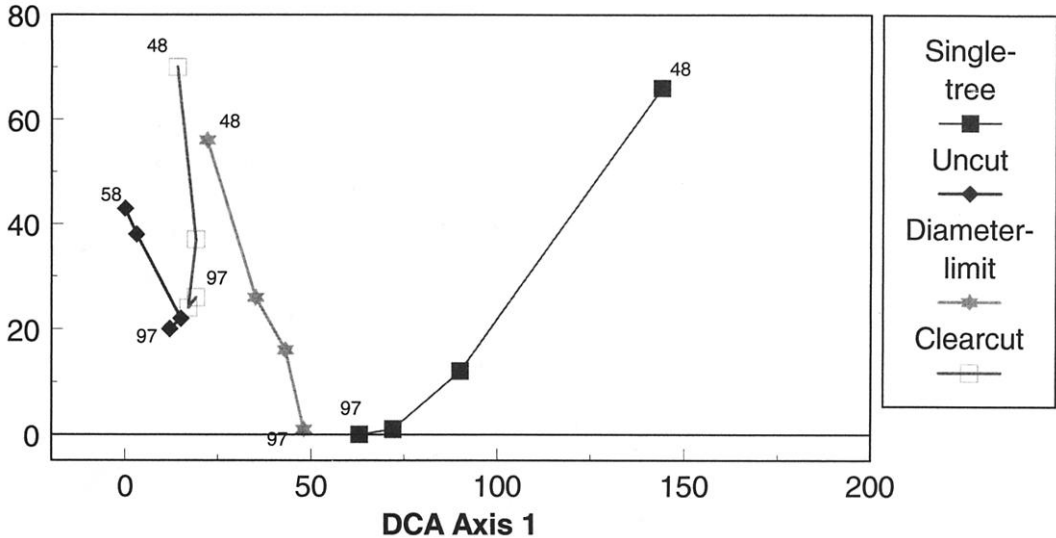
Fig. 2. Detrended correspondence analysis of second-growth overstory species composition from the Fernow Experimental Forest (Compartment 8 and vicinity) stratified by silvicultural treatment. Results are based on IV which combines relative frequency and relative basal area of individual species.

respect to species composition in the last five decades (Fig. 2). This might be expected based on similar disturbance regimes, but it should be noted that 8B and 8C are contiguous. This indicates similarity in site characteristics as well. The species composition of the uncut area (8E) and the clearcut (8A) have also become more homogeneous (Fig. 2). It is noteworthy that subcompartment 8A lies between 8E and 8B and has diverged from 8B and converged with 8E in the ordination.

Estimates of overstory diversity (based on relative density alone) show significant variability prior to 1900 (Fig. 3A) which may reflect inadequate sample sizes (Table 2) or inadequate data acquisition procedures given our objectives. However, during the last 80 to 100 years, diversity has consistently declined largely because of a precipitous drop in evenness (Fig. 3B). The decline in evenness among species is most strongly associated with increases in *A. saccharum* (Fig. 4A). *A. saccharum*'s IV has risen steadily since 1856 and there is no indication from these results that this trend is abating (Fig. 4B).

To further evaluate the importance of *A. saccharum* since 1948, we examined the changes in this species IV's (based on relative density and basal area combined) by management history using covariance analysis. *A. saccharum* IV was

strongly correlated with year of observation (p = 0.0001) and silvicultural option (p = 0.0010). All subcompartments appeared to have some increase in *A. saccharum* IV during the last five decades including the uncut area (8E) (p = 0.0593). As such, we compared the rates of change in *A. saccharum* IV for each treatment with 8E. There was no evidence that 8E and the clearcut options differed in the rate of *A. saccharum* increase (p = 0.8469). The rate of increase for this species also did not differ between the diameter-limit (8B) and single-tree selection (8C) areas (p = 0.4425), but the rate of *A. saccharum* increase for both 8B and 8C was greater than that observed in 8E (p = 0.0595 and 0.0170, respectively). Data from similar treatments were combined to produce equations describing the rates of increase for *A. saccharum* (Table 3). In the single-tree and diameter-limit areas, *A. saccharum* IV increased at more than twice the rate as in the clearcut or uncut units over the past 50 years of observation.

UNDERSTORY. Thirty species of woody plants were identified throughout the period from 1922 to 1997. Only *A. saccharum* was present in all subcompartments at each time period (including the 1922 survey). *C. dentata* had a minor presence in the understory in 1922 (<1% IV), but has not been recorded since. *Q. rubra* was pres-
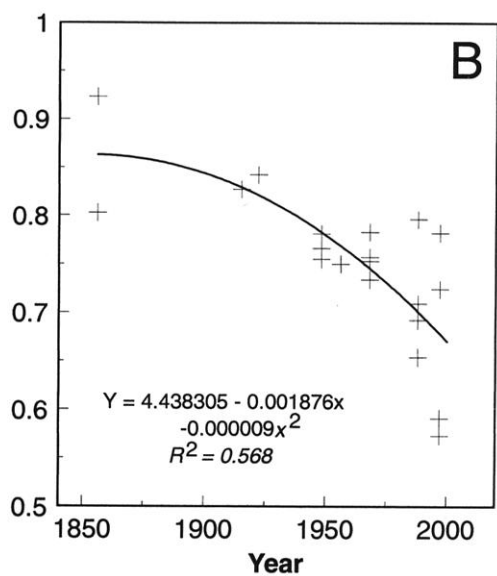
Diversity (H')
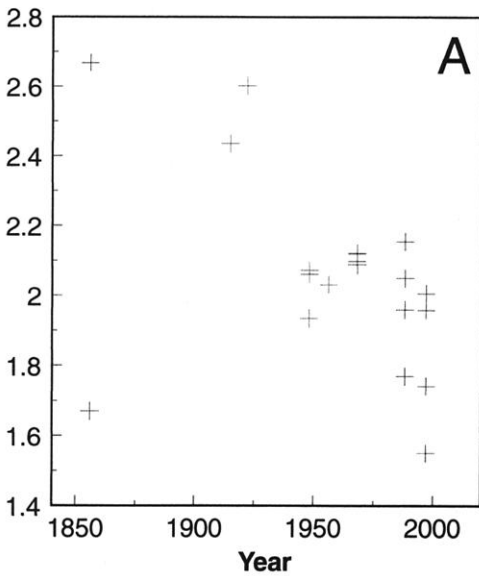
Evenness

Fig. 3. Diversity (A) and evenness (B) of stands within the Fernow Experimental Forest with respect to the year of observation. Results are based on relative frequency of stems for all time periods since the 1856 survey data did not include tree size. Quadratic response coefficient derived from a standardized independent variable, i.e., $x_i = x_i - \bar{x}$.
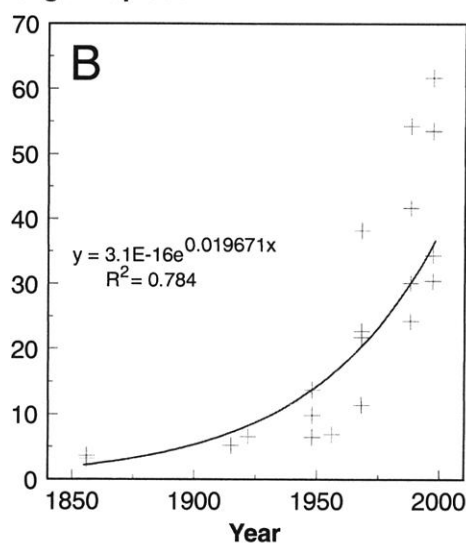
Evenness
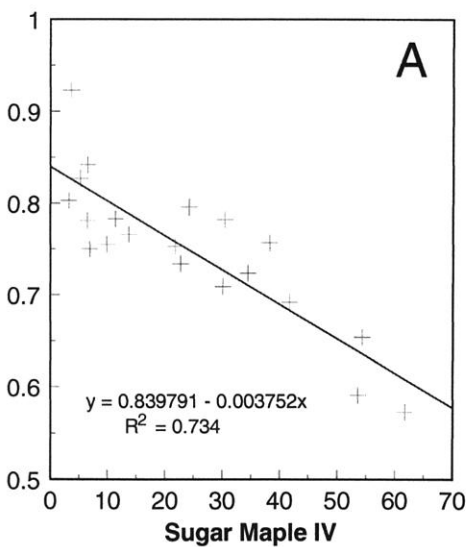
Sugar Maple IV

Fig. 4. A: The apparent relationship between decreasing evenness and increasing *Acer saccharum* IV; B: *Acer saccharum* IV as a function of the year of observation appears to be increasing exponentially. Results for both A and B are based on relative frequency of stems only for all time periods since the 1856 survey data did not include tree size.

Table 3. Equations describing overstory *Acer saccharum* IV (based on stems and basal area) as a function of the year of observation (x) between 1948 and 1997 (ST = single-tree selection, DL = diameter limit, CC = clearcut, NC = uncut). Management options were combined when statistical differences were not evident.

Management	Equation	r^2	SE
ST and DL	$y = 0.672(x) - 1294.704$	0.838	6.465
CC and NC	$y = 0.246(x) - 466.759$	0.704	3.246

ent in all subcompartments except 8B in 1948 but was no longer an understory constituent in 1997. *J. cinerea* and *J. nigra* were present but rare during the early monitoring of Compartment 8, although neither species has been recorded since 1978. In contrast, *P. serotina* abundance increased in all subcompartments following silvicultural manipulation. *A. saccharum* trends observed in the overstory are even more pronounced in the understory. Moreover, overall species composition has changed dynamically with time and it was possible to quantify these changes using ordination techniques.

DCA axis 1 (eigenvalue = 0.2836, r^2 = 0.671) was negatively correlated with year of observation ($\tau = -0.431$). Moreover, all silvicultural treatments but the diameter-limit area had their lowest axis 1 values in 1997 (Fig. 5). The first axis was well correlated with H' ($\tau = 0.648$), reflecting a general trend in declining H' since 1922 (no understory observations prior to 1922). Axis 1 values were also negatively cor-

related with *A. saccharum* IV ($\tau = -0.410$). The second ordination axis does not reflect a temporal trend but is highly correlated with increasing *F. grandifolia* IV ($\tau = 0.625$). For example, the greatest change in the second axis values followed the commercial clearcut in 1948 which decreased *F. grandifolia* relative IV from about 12% to less than 5%. Graphically, it appears that understory composition in the clearcut, diameter-limit, and single-tree selection areas are increasing in similarity, while the uncut stand remains more isolated from the others in the ordination. The third axis of the ordination did not add any additional interpretive value (eigenvalue = 0.0307).

Species richness in the understory was sensitive to perturbation (Fig. 6A) as expected. Richness was greatest during the inventory conducted in 1922 with 23 species, which was similar to the maximum value observed in the overstory stratum. However, prior to silvicultural treatment in 1948, species richness was lower in all sub-
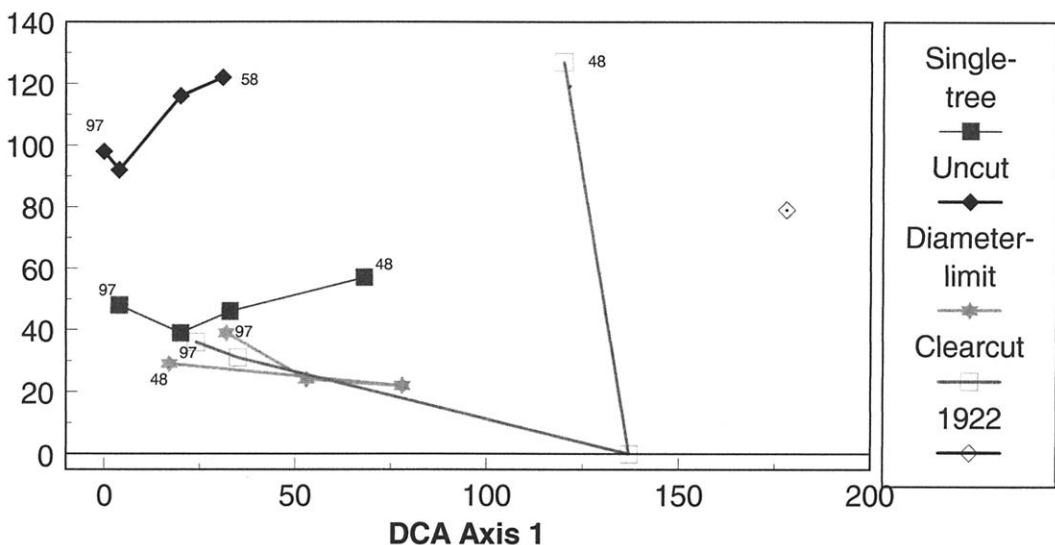

Fig. 5. Detrended correspondence analysis of second-growth understory species composition from the Fernow Experimental Forest (Compartment 8 and vicinity) stratified by silvicultural treatment. Results are based on IV's which combined relative frequency and relative basal area of individual species.
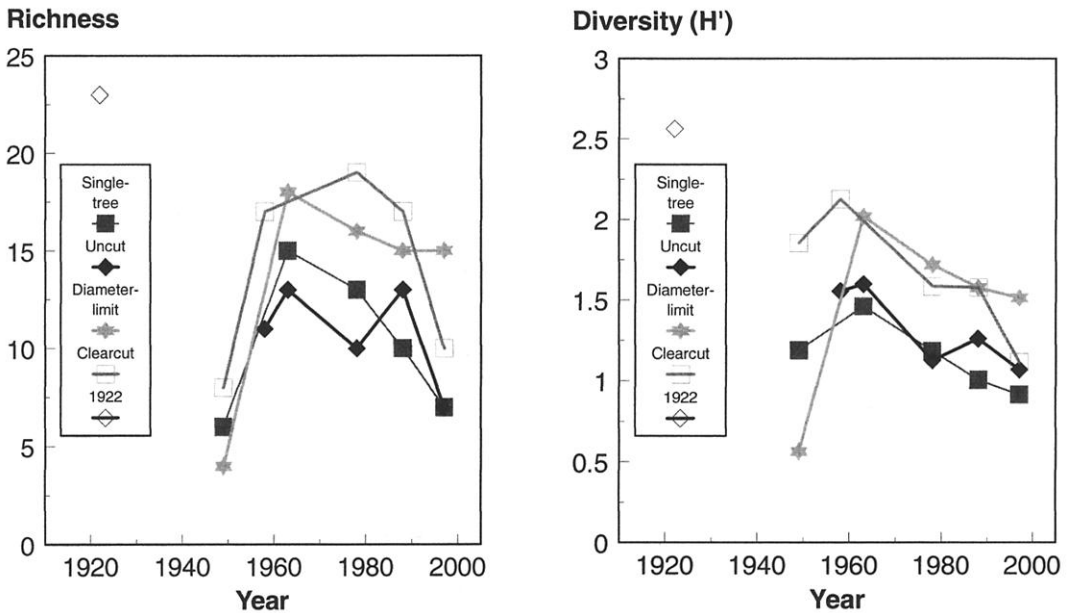
Fig. 6. Understory richness (A) and diversity (B) stratified by silvicultural treatment. Results are based on IV's which combined relative frequency and relative basal area of individual species.

compartments (maximum = 8 species) and totaled only 10 species when 8A, 8B, and 8C were combined. Richness increased to an average of 16.6 species for each subcompartment at the next measurement period in the wake of the imposed disturbances following the 1948 growing season. Understory richness continued to increase in the commercial clearcut unit until 1978, reaching a peak of 19 species. Species richness in the diameter-limit and single-tree selection areas declined between 1978 and 1997. Understory diversity reflects the change in richness (Fig. 6B). Understory H′ was lowest in the control, clearcut, and single-tree selection areas in 1997 due to both a reduction in richness as well as a decline in evenness.

As with the overstory, declines in evenness were highly correlated with the increasing importance of A. saccharum IV (r = −0.931, p < 0.001). A. saccharum IV's (based on relative density and relative basal area) exceeded 70% in both the clearcut and single-tree selection areas at the last remeasurement (Table 4) and A. saccharum IV has generally increased throughout the last five decades. However, this species was also the most abundant understory species in all but 8A following the 1948 growing season. At the first measurement period in subcompartment 8B, A. saccharum made up nearly 86% of understory IV. Other shade-tolerant species

such as F. grandifolia were also common (Table 4). Yet in contrast to the situation today, an abundance of shade-tolerant species in 1948 did not exclude the presence of understory Q. rubra. At that time, understory Q. rubra IV constituted about 12% (148 stems ha^{-1} 2.54 to 5.08 cm dbh) in 8A and 18% (296 stems ha^{-1}) in 8C.

Discussion. Old-growth, early second-growth, and managed forest stands exhibited distinct composition characteristics in this research. In old-growth, forest species composition was more evenly distributed, with substantial densities of individuals from the Fagaceae family. Shortly after initial logging, second-growth forests comprised substantial densities of shade-intolerant species such as R. pseudoacacia, P. serotina, and L. tulipifera, although shade-tolerant species retained a substantial presence. Current forests are increasingly dominated by shade-tolerant species such as A. saccharum with a concomitant decline in diversity. Vascular plant diversity is expected to decline during the mid-aggradation phase as defined by Bormann and Likens (1979) as species are eliminated by competitive exclusion (Oliver and Larson 1996). Other factors affecting woody plant diversity in this study include local extirpation of species due to exotic disease (e.g., chestnut blight) and silvicultural practices that selectively

Table 4. Understory importance values of *Acer saccharum* (Acsa), *Quercus rubra* (Quru), *Fagus grandifolia* (Fagr), and *Betula lenta* (Bele) in Compartment 8, Fernow Experimental Forest, for selected sample years.

Subcompartment	Year	Acsa	Quru	Fagr	Bele
Commercial clearcut	1948	15.6	11.7	11.7	29.2
(8A)	1958	23.9	4.3	4.5	1.3
	1978	64.2	1.1	4.5	0.6
	1988	61.9	1.0	4.6	0.7
	1997	74.7	0.0	5.0	0.0
Diameter-limit	1948	85.8	0.0	0.0	4.7
(8B)	1963	40.3	2.0	5.1	0.7
	1978	56.2	1.2	4.1	1.8
	1988	59.9	0.0	7.0	1.7
	1997	62.6	0.0	8.0	1.2
Single-tree selection	1948	60.4	17.8	0.0	3.0
(8C)	1963	64.6	3.6	7.6	1.6
	1978	72.2	0.8	9.0	0.0
	1988	75.8	0.0	8.9	2.8
	1997	73.2	0.0	14.7	1.1
Uncut	1958	39.4	2.3	36.7	2.8
(8E)	1963	42.7	2.7	34.3	3.6
	1978	58.3	0.5	30.4	2.0
	1988	59.1	0.0	23.9	2.3
	1997	56.1	0.0	34.1	0.0

remove some species (e.g., *F. grandifolia* and *R. pseudoacacia*) and are ineffective at regenerating others (e.g., *Quercus rubra* and *Juglans nigra*). Since monitoring began in 1948, composition changes are least detectable in the second-growth stand that has not been harvested since approximately 1900 (8E). However, there is no evidence that species composition is returning to pre-1900 characteristics in any of the subcompartments evaluated.

The observed declines in H′ throughout this century were empirically related to reductions in evenness. These reductions were strongly related to the growing importance of *A. saccharum*, which was not unexpected. Trimble (1965) predicted that cove hardwood stands in the central Appalachians that were subjected to some type of selection cutting would eventually be composed of 50 to 75 % *A. saccharum*. However, in this study, increasing *A. saccharum* importance applied to all management scenarios, not just areas that were selectively harvested. Moreover, the level of *A. saccharum* importance in these forests may be unprecedented and not heretofore recognized. Early this century, Brooks (1911) estimated that *A. saccharum* accounted for about 10% of the species composition in the remaining old-growth hardwood forests in the vicinity of the Fernow. Additionally, pollen deposits from a nearby bog indicate *A. saccharum* never exceeded 20% of the forest community since the end of the Wisconsin glaciation about 17,000

years B.P. (Larabee 1986). Although our estimates of *A. saccharum* abundance from 1856 through 1948 reflected historical levels, more recent IV's for this species in the partially cut units exceed 40% in the overstory, with even greater abundance in the understory. This trend may exacerbate potential long-term forest health problems related to global climate change (Kattenberg et al. 1996). *A. saccharum* is near the southern extent of its range in West Virginia (Godman et al. 1990) and will be heavily stressed by a warming trend related to climatic change (Iverson and Prasad 1998).

In contrast to the increase in *A. saccharum* has been the decrease in *Quercus* species. Elsewhere in West Virginia, Abrams and McCay (1996) concluded levels of *Q. rubra* increased in importance following initial logging during the early 1900's. Our results do not exhibit a distinct trend regarding the level of *Q. rubra* abundance in the overstory between 1856 and 1997. However, the level of *Q. rubra* in the understory has clearly declined since 1948. Accordingly, the continued presence of *Q. rubra* in this research area will be temporary because late seral species replace it in small gaps and both early and late seral species replace it in larger openings. It is noteworthy that understory *Q. rubra* was sufficiently developed in 1948 to sustain the Quercus component of the stand following the commercial clearcut. Understory *Q. rubra* also had a significant presence in the single-

tree selection subcompartment in 1948. Yet, a decade later, understory *Q. rubra* was in decline in this study and similar understory *Quercus* characteristics were beginning to be noted regionally (Weitzman and Trimble 1957; Carvell and Tryon 1961).

The coexistence of abundant understory *F. grandifolia* and *A. saccharum* in conjunction with the more shade-intolerant *Q. rubra* in 1948 is perplexing. Was the coexistence of *Quercus* and more shade-tolerant species in 1948 simply a transition state between *Quercus* and late-seral species, or did *Q. rubra* formerly coexist in the understory with an abundance of shade-tolerant species? Fire has often been suggested as an important disturbance that is absent from both managed forests and forest preserves in much of the eastern United States and that favored retention of *Quercus* and the reduction of other species (Van Lear and Waldrop 1989; Abrams 1992; Abrams and Nowacki 1992). The discriminatory characteristics of fire as a disturbance mechanism to the forest floor, seedbank, floral and faunal communities, and their interactions are only beginning to be understood (Vose and Swank 1993). Brose and Van Lear (1998) found *Quercus* to be more competitive following fire due to more resilient sprouting characteristics compared to other upland species. Yet, as we noted, understory *Q. rubra* abundance in 1948 occurred simultaneously with abundant understory *A. saccharum* and *F. grandifolia*. The simultaneous occurrence of *Quercus* and more shade-tolerant species in 1948, if not an ephemeral state, suggests the scarcity of *Quercus* in the understory more recently may be functionally related to factors other than fire. Factors that could be contributing to a limited regeneration pool include acorn predation by insects (Galford et al. 1991) and vertebrates (Steiner 1995), and overbrowsing of small *Quercus* seedlings by deer (Inouye et al. 1994).

A secondary objective of this study was to assess the relationship between different silvicultural practices and species diversity. The results illustrate that partial harvesting is accelerating successional trends of dominance by more shade-tolerant species in the overstory. Partial harvesting elsewhere in the central Appalachians has had similar effects on species composition (Abrams and Downs 1990; Stapanian et al. 1997). However, over the past several centuries, perturbation of the canopy every 20 to 30 years may have been the historical disturbance regime for this forest type (Lorimer 1980; Nowacki and

Abrams 1997; Schuler 1998) and mimicking historical disturbance cycles is plausibly one way to maintain historical levels of diversity and species composition. Yet, the trends reported here demonstrate that overstory gaps alone created by techniques used in this study are not a diversifying force with respect to the composition of woody species in the central Appalachians at this scale.

Conclusion. This case study contributes to an understanding of species composition changes during a period that spans major land use changes in the central Appalachians. By incorporating data from long-term monitoring and historical documentation, we were able to expand the temporal scale of inference regarding composition changes. None of the disturbance regimes evaluated appear to be effective at creating conditions that favor the development of understory *Q. rubra* or alter the increasing dominance of *A. saccharum*. Thus, defining the factors that maintain diversity, and maintain the variability of historical composition remains a vital research interest.

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