Fifty years of partial harvesting in a mixed mesophytic forest: composition and productivity

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Abstract: Long-term silvicultural trials contribute to sustainable forest management by providing a better scientific understanding of how forest ecosystems respond to periodic timber harvesting. In this study, species composition, diversity, and net periodic growth of tree species in a mixed mesophytic forest in the central Appalachians were evaluated after about a half century of management. Three partial cutting practices on 18 research compartments and on 3 unmanaged reference compartments were evaluated (1951–2001) on 280 ha. Single-tree selection, diameter-limit harvesting, and timber harvesting in 0.162-ha patches were assessed on three northern red oak site index$_{50}$ (SI) classes: 24, 21, and 18. Shannon–Weiner's diversity index (H') declined from the first (1951–1959) to last (1987–2001) measurements and was related to both SI (P = 0.004) and treatment (P = 0.009). Sugar maple (*Acer saccharum* Marsh.) and red maple (*Acer rubrum* L.) were the two most abundant species in recent years (1987–2001); in contrast, in initial inventories (1951–1959), northern red oak (*Quercus rubra* L.) and chestnut oak (*Quercus prinus* L.) were most abundant. Net periodic annual increment (PAI) of merchantable trees (DBH ≥12.7 cm) was related to both SI (P = 0.004) and treatment (P = 0.003). Mean PAI ranged from 4.6 $m^3 \cdot ha^{-1} \cdot year^{-1}$ for single-tree selection to 2.5 $m^3 \cdot ha^{-1} \cdot year^{-1}$ for unmanaged reference areas across all SI classes. The decline of oak species suggests that only intensive and specific forest management focused on maintaining oak species can obtain historical levels of diversity.

Résumé : Les expériences sylvicoles à long terme contribuent à l'aménagement forestier durable en procurant une meilleure compréhension scientifique de la façon dont les écosystèmes forestiers réagissent à une récolte périodique de matière ligneuse. Dans cet article, la composition en espèces, la diversité et la croissance périodique nette des espèces arborescentes dans une forêt mésique mixte de la zone centrale des Appalaches ont été évaluées après un demi-siècle d'aménagement. Trois méthodes de coupe partielle dans 18 compartiments expérimentaux et trois compartiments témoins non aménagés ont été évalués (1951–2001) sur une superficie de 280 ha. La coupe de jardinage par pied d'arbre, la coupe à diamètre limite et la coupe par trouées de 0,162 ha ont été évaluées pour trois classes d'indice$_{50}$ de station du chêne rouge : 24, 21 et 18. L'indice de diversité de Shannon–Weiner (H') a diminué du premier (1951–1959) au dernier (1987–2001) inventaire et était relié à la fois à l'indice de station (P = 0,004) et au traitement (P = 0,009). L'érable à sucre (*Acer saccharum* Marsh.) et l'érable rouge (*Acer rubrum* L.) étaient les deux espèces les plus abondantes au cours des dernières années (1987–2001), alors que le chêne rouge (*Quercu rubra* L.) et le chêne châtaignier (*Querca prinus* L.) étaient les espèces les plus abondantes lors des premiers inventaires (1951–1959). L'accroissement périodique net des tiges marchandes (dhp ≥ 12,7 cm) était relié à la fois à l'indice de station (P = 0,004) et au traitement (P = 0,003). L'accroissement périodique moyen pour l'ensemble des catégories d'indice de station variait de 4,6 $m^3 \cdot ha^{-1} \cdot an^{-1}$ dans le cas du jardinage par pied d'arbre à 2,5 $m^3 \cdot ha^{-1} \cdot an^{-1}$ dans les compartiments témoins non aménagés. La disparition des espèces de chênes montre que seul un aménagement forestier intensif et spécifique qui met l'accent sur le maintien des espèces de chênes peut atteindre des niveaux historiques de diversité.

[Traduit par la Rédaction]

Introduction

Partial harvesting is currently the dominant form of timber harvesting in central Appalachian forests (Fajvan et al. 1998). Most of the owners of nonindustrial private forest land who choose partial cutting are motivated more by the desire to harvest commercially valuable timber than by the desire to develop the future stand through silvicultural planning (Nyland 1992). Selective cutting that removes only large-diameter trees, often called diameter-limit harvesting, is thought to degrade product yields through time (Nyland 1996). However, partial harvesting allows the landowner to maintain a continuous forest cover. In the central Appalachians, single-tree selection (Lamson and Smith 1991) and the more common diameter-limit harvesting (Fajvan et al. 1998) favor a preponderance of shade-tolerant species (Smith and Miller 1987; Schuler and Gillespie 2000). This often results in less oak (*Quercus* L.), yellow-poplar (*Liriodendron tulipifera* L.), and black cherry (*Prunus serotina* Ehrh.) and more maple (*Acer* L.), American beech (*Fagus grandifolia* Ehrh.), and American basswood (*Tilia americana* L.). Oaks are important commercially for sawtimber and veneer, and the associated hard mast production provides an important winter food source for a multitude of species (Wentworth et al. 1992; Wolff 1996). Shade-intolerant black cherry is important to many landowners because it has the greatest commercial value of any species in the region.

Received 5 March 2003. Accepted 17 October 2003. Published on the NRC Research Press Web site at http://cjfr.nrc.ca on 5 May 2004.

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doi: 10.1139/X03-262

Yellow-poplar is also a shade-intolerant, fast-growing species but often has commercial values less than those of oaks, black cherry, and sugar maple (*Acer saccharum* Marsh.). In addition to changes in commercial value of species associated with partial harvesting, associated declines in merchantable wood yield have been predicted because shade-tolerant trees often have slower growth rates (Trimble 1967; Smith and Debald 1975), although the extent of such declines has not been documented. Moreover, sustainable forest management as defined by the Montreal Process (Montreal Process Criterion and Indicators 1998) includes the maintenance of forest productive capacity and the conservation of biological diversity. A reduction in either forest productivity or some aspect of biological diversity associated with some forms of partial harvesting practices may be inconsistent with sustainable forest management.

Changes in species composition and possible associated changes in forest productivity after timber harvesting also have important implications with respect to management options available to individual owners in subsequent timber harvesting operations and to regional forest industries that rely on selected species for specific markets and products. In addition, a decline in oaks and other species that produce hard mast could adversely affect populations of certain wildlife species. A dramatic example of such a decline is the virtual extirpation of American chestnut (*Castanea dentata* (Marsh.) Borkh.) in the early 1900s, as a result of chestnut blight (Weitzman 1949). In the absence of chestnut, oaks are a critical winter food source for numerous wildlife game species, small mammals, and nongame birds (Wentworth et al. 1992; Wolff 1996; McShea 2000). Changes in species composition also suggest potential changes in species diversity, which has statutory and ecological implications. For example, the *National Forest Management Act* of 1976 directs the USDA Forest Service to maintain the diversity of tree species present at the onset of management activities. Especially diverse stands are of particular interest because they may be more resilient to some forms of perturbation (McNaughton 1977) and better able to adapt to the severe climatic changes predicted for the 21st century (Iverson and Prasad 1998).

To better understand partial harvesting and its impacts on forest stand dynamics, three partial cutting practices, in conjunction with the monitoring of three unmanaged reference stands, were applied experimentally and monitored for 50 years (1951–2001) on the Fernow Experimental Forest, in West Virginia. Single-tree selection that used carefully defined goals for residual stand structure, diameter-limit harvesting that lacked a residual stand structure goal, and timber harvesting in small patches (0.162 ha) were used to assess the long-term effects of these harvesting and (or) regeneration systems. In this study, the number of patches harvested at each cutting cycle within each compartment was regulated by area control. The long-term objective was to achieve a balanced age-class distribution in the compartment.

Using portions of this experimental framework, past analyses have addressed numerous forest management concerns, including residual tree quality following partial cutting (Trimble and Smith 1970; Smith et al. 1994), composition of natural regeneration (Smith and Miller 1987; Miller et al. 1995), forest economics (Miller 1991, 1993), growth and yield (Trimble 1961, 1970), and forest management effects on water yield (Troendle 1979). My objective was to use the experimental design as intended by the original investigators to assess treatment-, site-, and time-related effects on species composition and forest productivity, including the potential interaction between species composition and productivity through time. I hypothesized that as species composition became more dominated by shade-tolerant species, productivity would decline.

Table 1. Number and area of research compartments used to assess alternative silvicultural systems, by treatment and SI.

	SI (no. of compartments/area in ha)[a]			
Treatment	24	21	18	Total
Diameter-limit harvesting	2/44	2/35	2/16	6/95
Single-tree selection	2/42	2/22	2/9	6/73
Patch cutting	2/24	2/26	2/23	6/73
Reference (unmanaged)	1/28	1/5	1/5	3/38
Total	7/138	7/89	7/53	21/280

[a] Northern red oak SI (m) at base age 50 years. SI, site index$_{50}$.

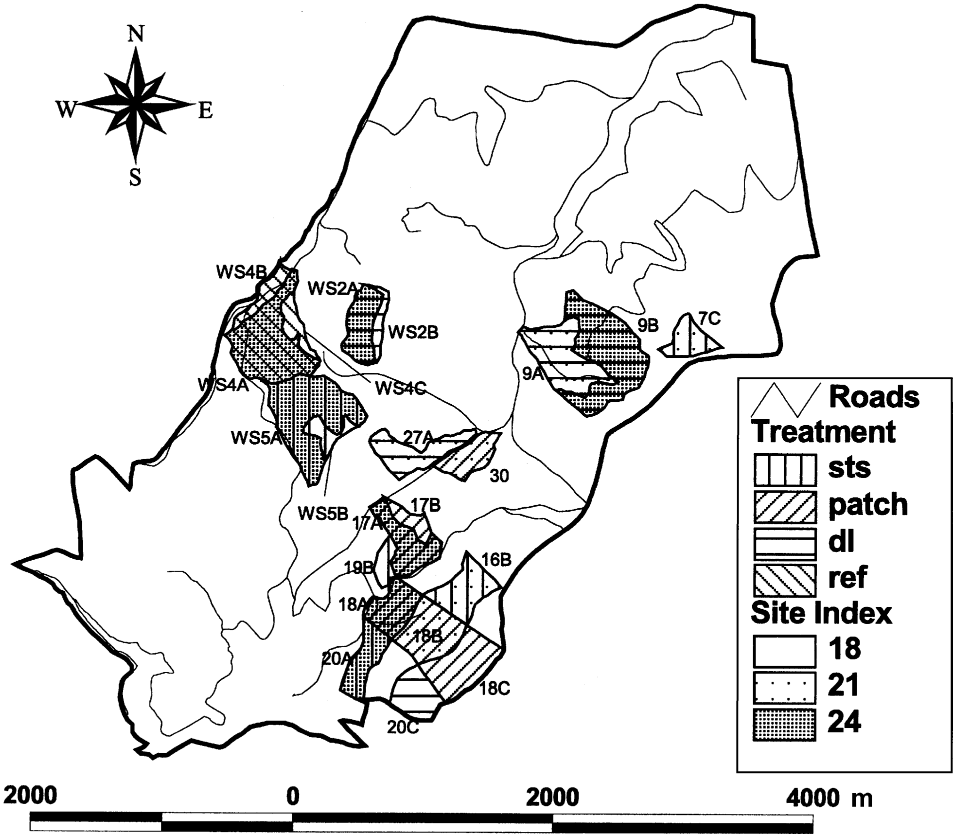
Materials and methods

Study area

This study was conducted on the Fernow Experimental Forest (39.03°N, 79.67°W) within the Monongahela National Forest. Elevations on the Fernow range from about 530 to 1115 m above sea level. The average growing season is 145 days (May–October), and the mean annual precipitation is about 1430 mm, which is distributed evenly throughout the year (Pan et al. 1997). The ecological land type of the Fernow is referred to as the Allegheny Mountains of the Central Appalachian Broadleaf Forest (McNab and Avers 1994). This study encompasses 21 management units or compartments on 280 ha (Table 1, Fig. 1). These units were selected because they were representative of many sites throughout the Appalachian Plateau as defined by Braun (1950), including the Allegheny Mountains of northern West Virginia, western Maryland, and central Pennsylvania; the unglaciated Allegheny Plateau of western West Virginia, western Pennsylvania, and southwestern Ohio; and the Cumberland Mountains of eastern Kentucky. Of the several forest types in the region, the white oak – black oak group and the red oak – sugar maple group as defined by Smith (1995) approximate the range of forest types and potential productivity of sites found on the Fernow. In this study, site quality is divided into three classes as determined by northern red oak site index$_{50}$ (SI): 24 (22.5 m = SI < 25.5 m), 21 (19.5 m = SI < 22.5 m), and 18 (16.5 m = SI < 19.5 m). The oak SI of Schnur (1937) was determined for each compartment by field sampling, using the equation developed by Trimble and Weitzman (1956).

The tract of land that later became the Fernow Experimental Forest was logged initially between 1903 and 1911 (Trimble 1977), during the railroad logging era. During this period, some trees were left uncut because of their insufficient size or poor form or because the species was considered undesirable. The federal government purchased the land in 1915 and began forest and watershed research in 1933.

Fig. 1. Locations of study compartments in the Fernow Experimental Forest by SI class and treatment. Note: dl, diameter-limit harvesting; patch, patch cutting; ref, unmanaged reference stands; SI, site index$_{50}$; sts, single-tree selection.



When this study was initiated, in 1950, stands were predominantly even aged and 38–45 years old, with variable densities of old-growth residual trees. Species composition was complex (Table A1) and varied with site (aspect, slope position, soil characteristics) and disturbance history, but it has generally been described as mixed mesophytic (Braun 1950), with northern red oak (*Quercus rubra* L.) and sugar maple more common on the relatively mesic sites, such as coves and north-facing slopes; and chestnut oak (*Quercus prinus* L.) and red maple (*Acer rubrum* L.) more common on the relatively xeric sites, such as ridge tops and south-facing slopes. Soils of the Fernow are predominantly of the Belmont and Calvin series (Losche and Beverage 1967). The Belmont soils are derived from Greenbrier Limestone, along with some sandstones and shales. The Calvin soils are derived from sandstone and shale and are more acidic and less fertile than the Belmont soils. Both are well-drained, medium-textured loams and silt loams, with an average depth of about 1 m. Understory vegetation is species rich and is dependent on site and disturbance history (Gilliam et al. 1995). Chestnut blight caused by *Cryphonectria parasitica* (Murr.) Barr, first noted in West Virginia as early as 1909, resulted in a 25% reduction in the volume of standing timber on the Fernow during the 1930s (Weitzman 1949).

Data collection

Field inventories were conducted for all trees more than 12.7 cm in diameter at breast height (DBH) by 5.08-cm classes and species before the first cut and usually just before each management intervention cycle (e.g., 10, 15, or 20 years thereafter) (Table 2). Smaller trees were not sampled systematically, because natural regeneration was not a formal study objective. Also, it was assumed that ingrowth into the smallest diameter class would eventually characterize the successful tree regeneration. Each tree was recorded as merchantable, cull (unmerchantable), or dead. Most cull material was cut during the first or second stand intervention and is no longer prominent in the managed compartments. The first inventories and assigned treatments were started in 1951 (Tables 1 and 2). The first phase of inventories and (or) treatments was completed by 1959 on all 21 compartments. Since the study was initiated the compartments assigned to this study have been manipulated according to the guidelines of the study only. All marked trees were tallied at each intervention, and residual stand structure following logging was calculated from the initial or recruise information less the species and diameter of trees removed. Logging crews made separate tallies of all trees not marked for cut that were damaged and cut during timber harvesting. Cubic volume estimates used in this analysis were developed from local volume tables derived from sites throughout the Fernow. In the 1950s, volume tables were constructed for each compartment. In 1971, the original data were used to revise the cubic volume tables for SI and species. The cubic volume of each tree ≥12.7 cm in DBH to a minimum top diameter of 10.2 cm was determined, and all volumes presented in this study are based on the 1971 revisions. Periodically, and most recently in 2002, volume tables were checked for validity; they continue to serve as useful estimators of actual tree volume. Because cubic volume in English

Table 2. Characteristics of silvicultural treatments and compartments used on the Fernow Experimental Forest.

(*a*) Single-tree selection.

SI[a]	Cutting cycle (years)	RBA[b] ($m^2 \cdot ha^{-1}$)	LDT[c] (cm)	*q*	Compartment
24	10	14.9	81.3	1.3	ws5a, 20a
21	10	11.5	66.0	1.3	7c, 16b
18	15	8.0	50.8	1.3	ws5b, 19b

(*b*) Diameter-limit harvesting.

SI	Cutting cycle (years)	Harvest DBH[d] (cm)	Compartment
24	15	43.2	ws2a, 17a
21	15	43.2	27a, 9a
18	20	43.2	ws2b, 20c

(*c*) Patch cutting.

SI	Cutting cycle (years)	Rotation age	Compartment
24	10	65	18a, 17a
21	10	75	30, 18b
18	15	85	17c, 18c

(*d*) Unmanaged.

SI	Compartment
24	ws4a
21	ws4b
18	ws4c

Note: See Fig. 1 for location of compartment; Table 1, for area of compartments. DBH, diameter at breast height; LDT, largest diameter-class tree; *q* factor, see explanation in text; RBA, residual basal area; SI, site index_{50}.

[a] Red oak SI (m) at base age 50 years.

[b] Desired RBA of trees with DBH ≥28 cm.

[c] LDT to retain in the residual stand structure (e.g., 81.3 represents the center of a 5.08-cm DBH class).

[d] Trees with DBH ≥43.2 cm are harvested at each cutting cycle.

units was used originally, a simple mathematical conversion to metric units was possible. Net periodic annual increment (PAI) of merchantable trees (DBH ≥12.7 cm) was computed as the difference in ending and initial merchantable volumes, plus harvest volume, divided by the number of years within the cutting and (or) inventory cycle. Dead trees are not usually merchantable and were not included in the productivity estimates.

Silvicultural treatments

Guidelines for each treatment and SI combination are described in Table 2. Each treatment was adjusted for the range of site quality present on the Fernow. For example, cutting cycles for the patch cutting treatment were longer on lower quality sites (Table 2). The criteria used are reasonable approximations of what has been recommended or used for the range of sites involved, but they have not been tested for optimality.

The *q* factor for the single-tree selection (Table 2) refers to one aspect of residual stand structure following a harvest operation. A *q* of 1.3 means that each consecutively smaller 5.08-cm DBH class contains 1.3 times more stems than the preceding class for the range of size classes managed. Trees with a DBH of less than 28 cm were not treated according to a desired residual stand structure, because they could not be sold as sawlogs and had little monetary value as pulpwood. In the 1950s, during the study's inception, managing trees smaller than 28 cm in DBH had little potential to be adopted operationally, and the original investigators chose to constrain their experimental treatments accordingly. Subsequent research has shown little difference in productivity and only minimal influence on species composition between stands managed with single-tree selection to a minimum DBH of 28 cm and stands managed to a minimum DBH of about 13 cm (Smith and Miller 1987). Ideally, residual stand structures managed in this manner will have a reverse J-shaped size-class distribution. The history and use of such an approach to uneven-age management is described in Nyland (1996).

Patch cutting in circular openings (0.162 ha) was regulated by area control. Rotation age divided by the length of the cutting cycle determined the number of harvests in a rotation. The area of the compartment divided by the number of harvests in a rotation determined the total area of harvest at each cutting cycle. In addition, the total area harvested at each cutting cycle divided by patch opening size determined the approximate number of patches harvested at each cutting cycle. The original investigators believed that the size of patch openings used was sufficient to encourage the establishment of shade-intolerant species (Tryon and Trimble 1969).

Additional treatments in the diameter-limit compartments were minimal. At each cutting cycle, in addition to trees above the specified DBH (Table 2), all cull trees or trees of extremely low quality and high-risk trees were marked for cutting. As cull trees are not merchantable, they were not included in the PAI estimates reported.

Data analysis

The Shannon–Weiner diversity index (H') (Whittaker 1972) and Pielou's evenness index (J') (Pielou 1969) were calculated on the basis of species relative density (species stem density / total stem density for DBH ≥12.7 cm) for all periods and management scenarios. This index is largely independent of sample size (Magurran 1988), which for this study was important for dealing with compartments of unequal size. Relative stem density alone was used for ordinations and calculations involving H', J' because population and community dynamics were of primary interest. Basal area alone or combined with relative stem density could mask the importance of emerging overstory populations where dominant overstory species are no longer being recruited in smaller size classes.

Because communities can change without affecting measures of diversity, i.e., one species replaces another, we also assessed species composition through time, using an ordination technique called nonmetric multidimensional scaling (NMS) (McCune and Mefford 1999). An iterative procedure that is particularly appropriate for ecological applications (Clarke 1993), NMS was conducted using the Sorensen distance measure with 60 runs of real data and 50 runs of randomized data (maximum of 200 iterations for each run) for a Monte Carlo test of significance. Following a finding that the results probably were not due to chance ($P = 0.020$), a three-dimensional solution was chosen for the final iterative ordination; the best ending point in the preliminary analysis was used as the starting point in the final run. Coefficients of determination (R^2) for each ordination axis were calculated as a proportion of the variation explained in the reduced matrix relative to that in the original matrix. Unlike other ordination techniques, NMS axis order does not correlate with the relative strength of the axis.

Univariate analysis of variance was used to discern differences in mean PAI related to treatments and SI. Both treatment and site classification were considered fixed effects. Model adequacy was evaluated using graphical and statistical techniques, including the Shapiro–Wilkes statistic, which tests the expected normality of the error component. Residuals were also plotted against both the predicted values and the independent variables to verify the assumption of constant variance. PAI means for each SI class and silvicultural treatment were plotted to expose significant interactions.

Repeated measures analyses were used to evaluate changes in productivity and diversity through time. Because management–measurement cycles differed somewhat across treatments (Table 2), the effects of time on PAI were evaluated separately for each treatment. To achieve adequate replication for a repeated measures analysis, data from SI classes 21 and 24 were combined after preliminary analysis indicated no significant differences in overall productivity, similar species composition, and equal cutting cycles (SI 18 cutting cycles were longer). Greater experimental replication may have permitted statistical differentiation between SI 21 and SI 24 compartments. Therefore, the results of the combined repeated measures analysis of these two SI classes should be interpreted with this mind. For patch cutting and single-tree selection, only compartments with five inventory cycles (40 years total) were used. This provided four repeated estimates of productivity ($n = 3$ compartments for each silvicultural treatment with five inventory cycles). For diameter-limit cutting, only compartments with four inventory cycles (45 years total) were used. This provided three repeated estimates of productivity ($n = 3$ compartments). Data from SI 18 compartments were not evaluated, because of insufficient replication for a repeated measures analysis. Temporal changes in measures of diversity (H', J', and species richness) from the initial to the most recent conditions were evaluated by repeated measure analysis, but somewhat differently than for PAI. Results from all compartments were combined using the first and last calculations of diversity. Site index$_{50}$ (height of the tallest trees at age 50), silvicultural treatment, time, and all potential interactions were considered fixed effects. To eliminate different inventory cycles and numbers of inventories, only the first (1951–1959) and most recent (1987–2001) inventories were used.

Results

Species composition and diversity

Thirty-two species of trees were identified during inventory dates in the period 1951–2001 within the study area (Table A1). During the most recent inventories, sugar maple and red maple were the two most abundant species, as measured by relative density. This was a notable change from the initial inventories, when northern red oak and chestnut oak were the most abundant species. Northern red oak and chestnut oak declined to the third and eighth most abundant species, respectively. Apart from the maples, only American beech and black birch (*Betula lenta* L.) increased in importance: they represented at least 5% of overall relative density at the most recent inventory dates. All other species declined or were minor components of species composition.

There have been significant changes in compartment-level measures of diversity throughout this study, according to the first and last inventories. These changes were related to both SI and silvicultural treatment. In the repeated measures analysis of H', both time × SI ($P = 0.004$) and time × treatment ($P = 0.009$) interactions were significant. Unmanaged reference and single-tree selection compartments were most notable with respect to declining diversity, and both differed significantly from initial conditions (Fig. 2*a*). Regardless of treatment, SI classes 21 and 24 were more diverse than SI 18 compartments when the study was initiated. However, through time, these classes (SI 21 and SI 24) have declined in diversity, while SI 18 has not (Fig. 2*b*). As a result, H' no longer differs across SI classes when compared using the Tukey–Kramer mean comparison procedure. The time × treatment interaction was also significant ($P = 0.005$) when species richness was assessed, and this partially explains the reduction in H'. In the unmanaged reference areas, species richness declined significantly ($P = 0.020$, with the Tukey–Kramer mean comparison procedure) from a mean of 21.33 during the first inventory cycle to 19.0 most recently. In the analysis of evenness through time, J' was significantly related to the time × SI interaction ($P = 0.016$). Evenness did not change appreciably on SI 18 compartments ($P = 0.635$), but it did decline on SI 21 ($P = 0.001$) and SI 24 ($P < 0.001$). Consequently, the decline in H' was due to the reduction in evenness for these SI classes.

Additional understanding of how overstory communities have changed through time was reflected in the NMS ordination. The proportion of variance explained in the final three-dimensional ordination was 23.7% for axis 1, 28.9% for axis 2, and 40.3% for axis 3 (cumulative $R^2 = 92.9\%$), indicating compartments were well separated in species space of the ordination. The first-ordination axis represented temporal change and was negatively correlated with the year of inventory ($r = -0.545$) when assessed from a secondary matrix. Northern red oak, white oak (*Quercus alba* L.), chestnut oak, and scarlet oak (*Quercus coccinea* Muenchh.) were positively correlated with axis 1 (i.e., they were less abundant through time) (Table 3). Conversely, sugar maple, yellow birch (*Betula alleghaniensis* Britton), black birch, and American beech were all negatively correlated with axis 1 (i.e., they were more abundant through time). Compartments along the second-ordination axis represented a gradient of species associations related to moisture and were negatively correlated with abundance of mesic species, such as sugar maple, black cherry, and yellow-poplar, and positively correlated with more xeric-tolerant species, such as red maple and chestnut oak (Table 3). Compartment SI had a strong negative correlation with NMS axis 2 ($r = -0.755$) when evaluated from a secondary matrix (Fig. 3). The third-ordination axis was positively correlated with H' ($r = 0.399$) and negatively correlated with SI ($r = -0.438$) and PAI ($r = -0.327$)

Fig. 2. Mean Shannon–Weiner diversity index (*H′*) stratified by treatment (*a*) and SI class (*b*). Vertical lines represent ±1 SE. Mean *H′* declined significantly through time (α = 0.05) for sts and ref treatments and SI 21 and SI 24 (evaluated using the Tukey–Krammer adjustment for multiple comparisons). Note: dl, diameter-limit harvesting; patch, patch cutting; ref, unmanaged reference stands; SI, site index$_{50}$; sts, single-tree selection.

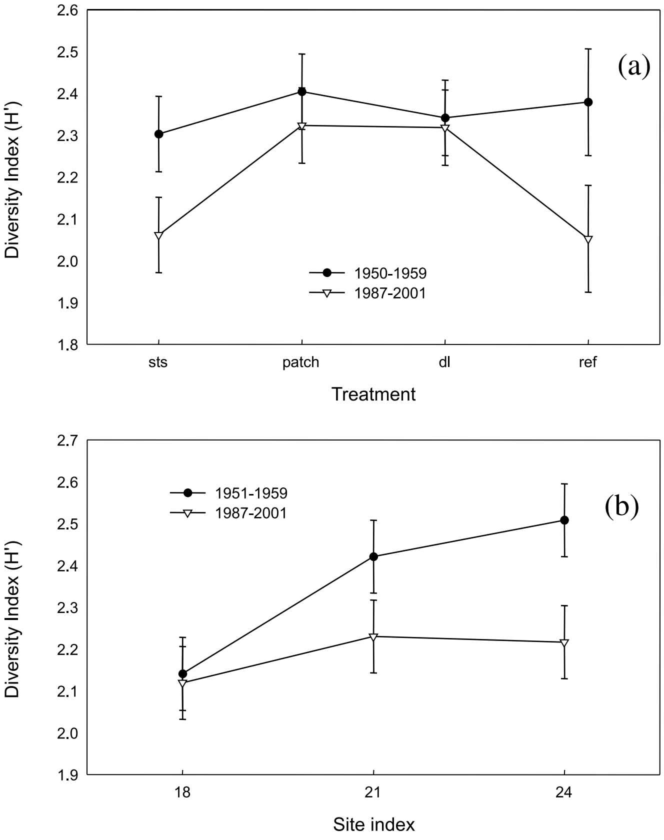


Table 3. Correlation matrix of relative stem density and final scores of the nonmetric multidimensional scaling ordination for each species.

Species	Axis 1	Axis 2	Axis 3
Picea rubra	–0.005	0.131	–0.109
Tsuga canadensis	–0.380	–0.163	0.260
Populus grandidentata	0.343	0.192	0.206
Juglans cinerea	0.196	–0.451	–0.289
Juglans nigra	–0.118	–0.280	–0.050
Carya cordiformis	0.152	–0.579	–0.534
Carya ovata	0.015	–0.269	–0.342
Ostrya virginiana	–0.364	–0.286	–0.550
Betula lenta	–0.315	–0.270	0.410
Betula alleghaniensis	–0.448	–0.324	0.304
Fagus grandifolia	–0.366	–0.042	0.348
Quercus alba	0.707	0.513	0.357
Quercus prinus	0.746	0.633	0.604
Quercus rubra	0.556	0.343	–0.314
Quercus coccinea	0.330	0.487	0.198
Quercus velutina	–0.005	0.004	0.010
Ulmus rubra	–0.190	–0.403	–0.288
Magnolia acuminata	–0.161	0.147	0.434
Magnolia fraseri	–0.203	0.336	0.444
Lirodendron tulipifera	–0.377	–0.694	0.123
Sassafras albidum	0.338	0.327	0.596
Amelanchier arborea	0.114	0.462	0.596
Prunus pensylvanica	–0.240	0.066	–0.213
Prunus serotina	–0.093	–0.597	–0.682
Robinia pseudoacacia	0.411	–0.262	0.274
Acer saccharum	–0.596	–0.462	–0.816
Acer rubrum	0.033	0.807	0.346
Tilia americana	–0.365	–0.457	–0.514
Nyssa sylvatica	0.606	0.389	0.662
Cornus florida	0.234	–0.019	0.077
Oxydendrum arboreum	0.293	0.449	0.542
Fraxinus americana	–0.246	–0.613	–0.741

when evaluated from a secondary matrix, somewhat reflecting earlier results that showed that SI 18 compartments had the lowest initial diversity characteristics. Axis 3 also juxtaposes diversity (*H′*) with productivity.

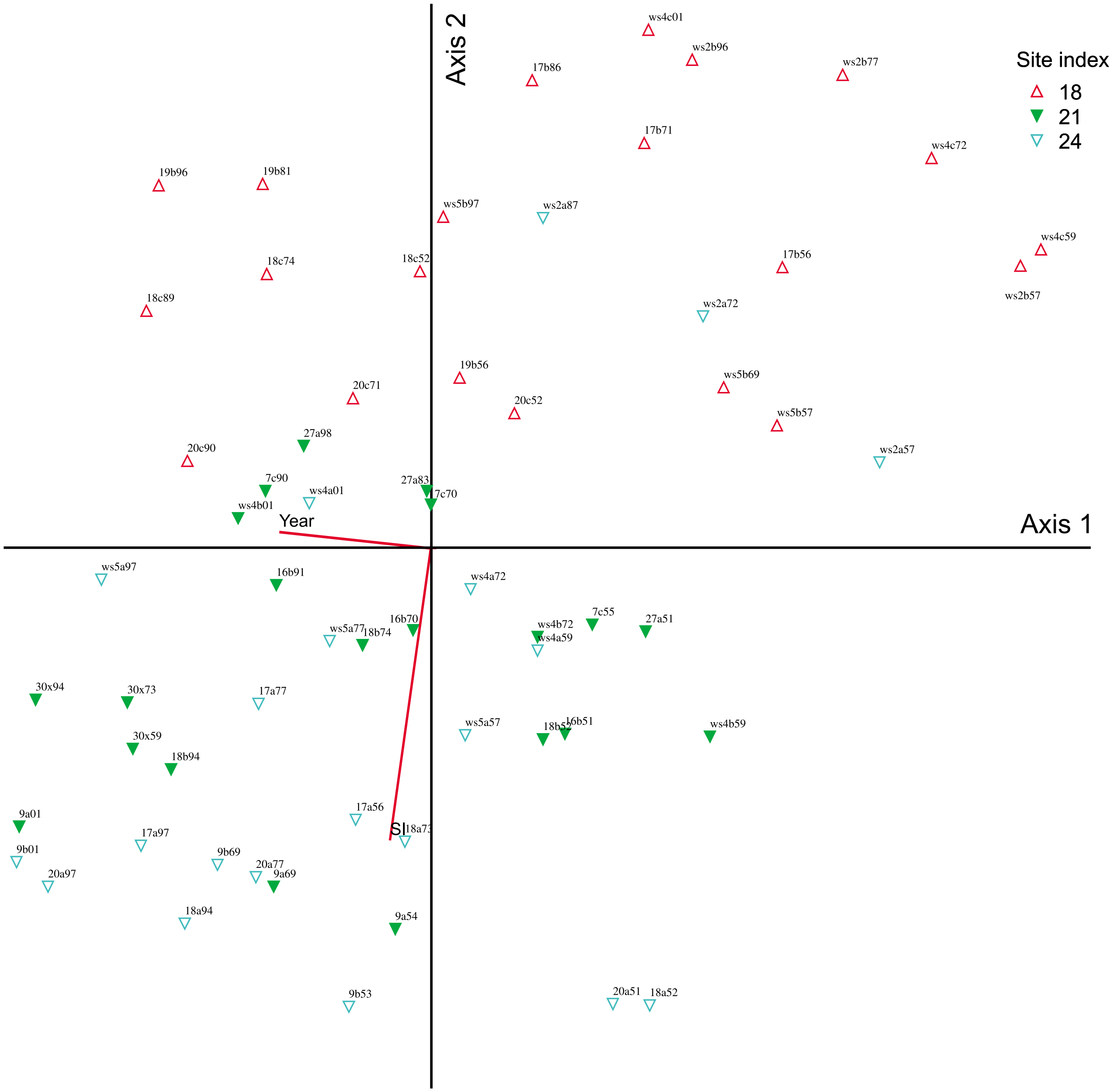
The temporal trend in the ordination is a consistent movement of virtually all compartments toward the lower left quadrant of the first- and third-ordination axes (Fig. 4). This trend was not visibly related to the imposed treatment (Fig. 4). Even after 50 years of manipulation, SI rather than treatment appears to be the critical factor with regard to species composition, as illustrated by the spatial arrangement of the compartments in species space when SI is used as a grouping variable (Fig. 3). Compartments with an SI of 18 had the highest axis-2 scores and were spatially distinct from the others in the ordination. The exception was compartment ws2a (SI 24), which occupies the entire eastern half of a small watershed from the stream channel to a broad ridgeline. Portions of ws2a near the ridgeline are more xeric than other SI 24 compartments, possibly accounting for this inconsistency.

Productivity

The model predicting overall PAI (mean PAI during study duration) from site and treatment was highly significant ($P < 0.001$). PAI was related to both SI ($P = 0.034$) and silvicultural treatment ($P < 0.001$). The unmanaged reference compartments had the lowest productivity and were significantly different from the managed compartments (Table 4). The type of treatment was not significant in terms of productivity, given the variation within treatments. However, overall PAI was about 80% greater in stands managed with single-tree selection than in the unmanaged areas for all SI combined. PAI was significantly different (α = 0.05) for SI 24 and SI 18, but neither differed from SI 21 (Table 4).

Changes in PAI through time were evaluated by combining the data from SI 21 and SI 24 to achieve adequate replication, following the similarities documented earlier with respect to species composition and mean PAI during the past 50 years. A change in PAI was significant with respect to time for the diameter-limit treatment only ($P = 0.047$). There was not a significant quadratic term, indicating a linear response through time (Fig. 5). Mean periodic increment for the diameter-limit compartments increased from 4.3 $m^3 \cdot ha^{-1} \cdot year^{-1}$ during the first 15-year period to 4.8 $m^3 \cdot ha^{-1} \cdot year^{-1}$ during the third 15-year period. In contrast, declining trends for the other treatments are suggested graphically, but they were not significant in the repeated measures analysis ($P_{[sts]} = 0.602$,

Fig. 3. Nonmetric multidimensional scaling ordination (axes 1 and 2) of research compartments grouped by SI class. Points are identified by compartment number and year of observation. Vectors radiating from the center of the ordination graph indicate the correlation of SI with axis 2 (r = –0.755); and year of observation, with axis 1 (r = –0.545). Species correlations with axis scores are in Table 3. Note: SI, site index$_{50}$.

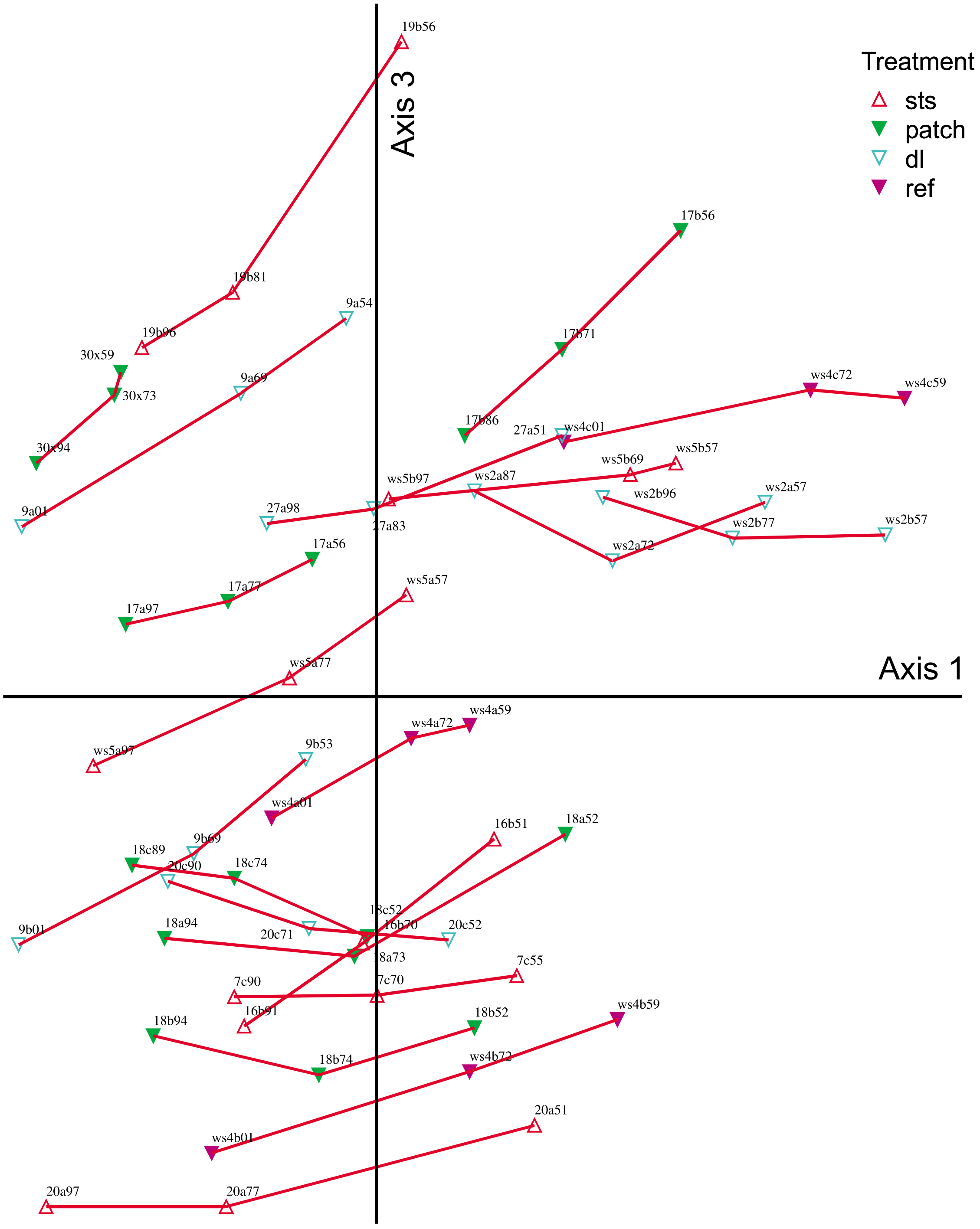


$P_{[\text{patch}]}$ = 0.143, $P_{[\text{ref}]}$ = 0.149, where sts refers to single-tree selection; patch refers to patch cutting; and ref refers to unmanaged reference stands).

Discussion

In this study, temporal shifts in species composition corroborate local and regional forest trends, which indicate a decline in all oaks and hickories (*Carya* Nutt. spp.) and an increase in red and sugar maples (Parker et al. 1985; Abrams and Downs 1990; Schuler and Gillespie 2000). This trend is often accompanied by a concomitant decline in diversity. In terms of forest management options, this decline in oak and sympatric species has been partially offset for several decades because of abundant oaks in smaller size classes that were recruited into the commercial classes as canopy dominants were harvested periodically. For example, before treatment began in 1954, there were more than 350 red and chestnut oaks in the 15-cm DBH class alone in compartment 9a (one compartment of the diameter-limit treatment). By 2001, there were fewer than 50 oak stems in the same size class, or about 2 oaks·ha^{-1}. Based on the probability of virtually no new recruitment and the expected diameter growth rate of about 5 cm·decade^{-1} (Lamson and Smith 1991), all of the remaining oak will be harvested in about 50–60 years, according to the 43-cm DBH diameter-limit protocol used in this study. Smaller minimum diameters (e.g., 30 cm), often used in commercial logging operations, would shorten this

Fig. 4. Nonmetric multidimensional scaling ordination (axes 1 and 3) of research compartments stratified by treatment. Points are identified by compartment number and year of observation. Temporal changes are indicated by lines connecting repeat observations. Species correlations with axis scores are in Table 3. Note: dl, diameter-limit; patch, patch cutting; ref, unmanaged reference stands; sts, single-tree selection.



period to about 30 years. Significant declines in oak yield and acorn production would occur during this period. Restoring oaks in stands without an oak seed source would be costly and likely require artificial regeneration.

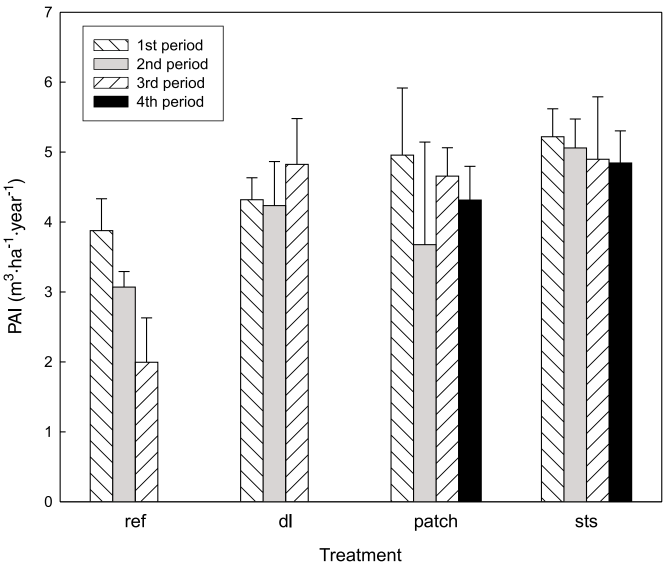
According to current trends, future forest composition would be more analogous to the beech–maple–basswood type (Tyrrell et al. 1998), which is generally located in the northern third of the eastern United States and southern regions of eastern Canada. However, at a time when global warming is expected to shift species distributions to the north, problems related to forest health could emerge to alter patterns that have been occurring during the past 50 years. For example, sugar maple is expected to decline in West Virginia if this region experiences the expected warming trend (Iverson and Prasad 1998), and new invasive forest pathogens will shape future forests in ways not reflected in

Table 4. Cubic volume net PAI of merchantable trees (DBH ≥12.7 cm).

Treatment and SI category	Mean PAI ($m^3 \cdot ha^{-1} \cdot year^{-1}$)	*N*
Single-tree selection	4.55a	6
Diameter-limit harvesting	4.28a	6
Patch cutting	4.00a	6
Reference (unmanaged)	2.52b	3
SI 24	4.46a	7
SI 21	3.98ab	7
SI 18	3.64b	7

Note: Treatment means from about 1951 to 2001 for each treatment and SI class. Means separated (α = 0.05) using the Duncan mean comparison procedure and designated by lower case letters. DBH, diameter at breast height; PAI, periodic annual increment; SI, site index$_{50}$.

Fig. 5. Mean cubic volume net PAI of merchantable trees (DBH 12.7 cm) (vertical lines = 1 SE) by measurement cycle and treatment category (northern red oak classes SI 21 and SI 24). Compartments 27a, 9a, and 9b included in dl; 16b, ws5a, and 20a included in sts; ws4a and ws4b included in ref; and 30, 18a, and 18b included in patch. Measurement cycles differed by treatment and were as follows: 10 years for sts and patch; 15 years for dl; and 10, 20 and 40 years after the initial inventories for the reference compartments. Note: DBH, diameter at breast height; dl, diameter-limit harvesting; PAI, periodic annual increment; patch, patch cutting; ref, unmanaged reference stands; sts, single-tree selection.



this study. Beech bark disease, caused by an exotic beech scale (*Cryptococcus fagisuga* Lind.) and nectria fungi (*Nectria coccinea* var. *faginata* Lohm., Wats., & Ayers and *Nectria galligena* Bres.) association (Houston and O'Brien 1983), is beginning to cause overstory mortality of American beech in the immediate vicinity of the Fernow Experimental Forest. Thus, a transition to a beech–maple–basswood forest probably will lack overstory beech and associated production of hard mast. The expected future composition represents a significant change from the previous mixed mesophytic forest type, which included hard mast from oaks, hickories, beech, and—at one time—American chestnut, as well as other species of lesser importance, e.g., black walnut (*Juglans nigra* L.) and butternut (*Juglans cinerea* L.). As stated earlier, mast-producing species are a critical food source for many wildlife species, particularly in the winter (Wolff 1996; McShea 2000). Eastern hemlock (*Tsuga canadensis* (L.) Carr.) is also expected to be affected by new forest pathogens. A minor component of the study area but long present, eastern hemlock may be functionally extirpated because of the exotic hemlock woolly adelgid (*Adelges tsugae* Annand), which has spread to the Allegheny Mountains (USDA Forest Service 2002). Eastern hemlock is considered a constituent of late successional forest in the region (Smith 1995) and is often found in ecologically important riparian corridors.

A conversion in forest type from mixed mesophytic to beech–maple–basswood, even absent forest health problems, would be unprecedented during Middle to Late Holocene in the central Appalachians. Such a change could not be attributed to successional change only. Extensive pollen studies have revealed patterns of persistence of mesic oak communities in the eastern hardwood forests for several thousand years (Delcourt and Delcourt 1987). Holocene vegetation dynamics determined from pollen analysis reveal dramatic changes in species composition during the period 17 000 – 8 000 years BP as the global climate warmed. However, for the last 8000 years, upland forests in the Allegheny Mountains have been dominated by oak, birch, and chestnut (Larabee 1986). During the last 2000 years and before European settlement, oak made up about 60% of the forest composition in the central Appalachians (Delcourt and Delcourt 1987). During this time, Native American use of fire may have created conditions suitable for oak to compete successfully with both early and late seral species (Whitney 1994; Delcourt and Delcourt 1997). Following settlement, oaks and other mid-seral species may have been further enhanced by repeated partial cuttings, fires, and the decline of American chestnut (Whitney 1987; Crow 1988; Abrams et al. 1995). A recent dendroecological study found that oak, using growth strategies appropriate to both large and small openings (<200 m^2), became established in remnant old-growth forests in the central Appalachians until recruitment ceased in the early 20th century (Rentch et al., 2003).

If diverse stands are a management objective for statutory or ecological reasons, this study demonstrated that stand-level diversity is declining in forests managed with single-tree selection and diameter-limit harvesting. However, there is no evidence that these practices are accelerating this process relative to unmanaged stands. In this study, unmanaged and single-tree selection compartments exhibited the greatest decline in diversity (H') as shade-tolerant species increased in relative density. Perhaps only the patch cut compartments would provide canopy gaps large enough to avoid the trend of increasing dominance of shade-tolerant species. In earlier work focusing on the species composition of the patches, shade-intolerant yellow-poplar, black cherry, and black locust (*Robinia pseudoacacia* L.) were able to compete with shade-tolerant species in the patch openings two decades after the patches were created (Miller et al. 1995). These results also demonstrated that light was adequate for oak development. However, unless understory density is controlled before harvesting, to increase the size of oak seedlings, oaks will not persist in stands harvested in small patches, variably sized groups, or clearcuts (Smith 1995). This is important in the mixed-oak forest types of the region because the recovery of diversity following a large disturbance without the suite of oak species seems improbable. Elliott and Swank (1994) documented a slight increase in H' (based on stem density for DBH >5.0 cm) after a 1939 clearcut in a southern Appalachian mixed-oak forest, but a subsequent clearcut resulted in a decline in diversity. Earlier work on the Fernow documented a temporary increase in H' after a 1948–1949 clearcut, followed by a decline three decades later, with near elimination of oak in the smaller size classes (Schuler and Gillespie 2000). Diversity is expected to be high after a large disturbance, decline as a stand matures, and recover during the transition to the old-growth stage (Oliver and Larson 1996). However, regional old-growth forests are experiencing the same lack of oak replacement evident in this study, often with a concomitant increase in dominance of one or two shade-tolerant species (Parker et al. 1985; Abrams and Downs 1990; McCarthy and Bailey 1996). The regional decline of oak species suggests that only intensive and specific forest management focused on maintaining oak species can maintain historical levels of diversity.

During the past half century in this study, overall PAI has not yet differed significantly among managed compartments (single-tree selection, diameter-limit harvesting, and patch cutting), although all demonstrated higher productivity than the unmanaged reference compartments. Differences in productivity between managed and unmanaged compartments were expected, as the rate of growth generally declines as stands age and growing space becomes more limited (Smith 1986). The unmanaged reference compartments clearly exhibit this expected trend graphically (Fig. 5), but a repeated measures analysis did not reveal a significant temporal trend. However, given that this pattern follows robust patterns of stand dynamics, it is reasonable to assume that the observed trend is valid and reflects ecological principles of forest growth.

The long-term framework of this study provides an unusual opportunity to evaluate the effects of repeated harvesting and (or) silvicultural treatments to changes in productivity. The expectation was that after about a half century of experimental stand interventions, changes in species composition might be beginning to negatively affect productivity. Mean PAI has generally declined for both the single-tree selection and the patch cut treatments (Fig. 5), but given the low number of replications and the variability of the treatments the trends were not significant, as indicated by a repeated measures analysis. Lamson and Smith (1991) speculated that converting Appalachian hardwood stands to shade-tolerant species would reduce periodic growth by at least 10% because such species often have slower radial growth than shade-intolerant ones. In contrast to this expectation, especially after the persistent, increasing abundance of shade-tolerant species was documented, PAI has increased in the diameter-limit compartments (red oak SI_{50} of 21 and 24), most recently to about 4.8 $m^3 \cdot ha^{-1} \cdot year^{-1}$, equaling the recent productivity of the single-tree selection compartments. These results are not totally understood but may be related to the inadvertent effect of the diameter-limit treatment on residual stocking. Early in the study, in two of the three compartments used for the diameter-limit repeated measures analysis (9b and 27a), residual stocking levels were less than full after the initial harvests, according to even-aged guidelines (Gingrich 1967). Stands that are not fully stocked are expected to be less productive because the residual trees cannot fully utilize the growing space. Residual stocking following subsequent harvests in the diameter-limit compartments happened to meet full stocking criteria, and subsequent productivity estimates were similar to those for the single-tree selection compartments. During the last treatment cycle, PAI did not differ between the single-tree selection and the diameter-limit treatments. Guidelines for residual stocking in the single-tree selection compartments have generally been met throughout the study, but a transition period was required for some compartments to obtain the desired number of stems in the larger size classes. Additional harvest cycles are needed to test the apparent convergence of the diameter-limit and single-tree selection treatments in terms of productivity and to evaluate the potential temporal trends associated with these practices (Fig. 5). Developing optimal stocking guides for stands managed with single-tree selection was not part of this study, and guidelines have not been published elsewhere. However, optimal stocking in stands managed with uneven-aged silviculture may differ from desired stocking levels from stands managed using even-aged silvicultural techniques, such as intermediate thinnings. Research is needed to develop optimal stocking for uneven-aged management practices and to determine whether even-aged management guidelines are acceptable.

Average annual productivity in even-aged stands is expected to be about 4.5 $m^3 \cdot ha^{-1} \cdot year^{-1}$, assuming a 65-year rotation and northern red oak SI_{50} of 24 (Smith 1995). Mean PAI in the patch cut compartments during the last management cycle was 4.3 $m^3 \cdot ha^{-1} \cdot year^{-1}$, similar to the expected growth rate of even-aged stands. Moreover, excluding the unmanaged reference compartments, all of the treatments used in this study approximate productivity levels expected from even-aged management. This suggests that at current levels of production (if sustainable), uneven-aged management can be accomplished without sacrificing productivity relative to that of even-aged silvicultural systems. This is not to say that diameter-limit harvesting represents uneven-aged silviculture or is an acceptable alternative to sound silvicultural practices. Previous work has shown that monetary values of such stands are often substantially less than potential values (Lamson and Miller 1982; Hassler et al. 1999; Fajvan et al. 2002). Diameter-limit cuts often remove faster growing species, such as yellow-poplar, black cherry, and northern red oak, as second-growth stands mature and leave shade-tolerant species of lesser economic value, such as red maple and American beech (Fajvan et al. 1998). In practice, diameter-limit cutting usually removes commercially valuable timber and leaves the rest, with no consideration of the future stand values or uses. Residual shade-tolerant species are often damaged and frequently worth a small fraction of what was removed (Miller and Kochenderfer 1998). Yet despite associated silvicultural problems, diameter-limit cutting remains the dominant timber harvesting practice in the central Appalachians (Fajvan et al. 1998). Woodland owners continue to prefer this method because it often maximizes short-term cash flow and is easy to apply (Miller 1993). A diameter-limit technique that incorporates economic guidelines, controls residual stem quality, and manages residual stocking has been suggested as a less complicated alternative to single-tree selection (Miller and Smith 1993). However, no known treatment can avoid problematic changes in species composition associated with this type of management.

Sustainable forest management includes maintaining long-term forest productivity by balancing wood removals with what is determined to be sustainable (Montreal Process Criterion and Indicators 1998). Determination of what has been removed is straightforward, but estimating potential long-term forest productivity is complex (Powers et al. 1994). Potential threats to sustainable forest productivity in the central Appalachians include long-term acidic deposition and the impacts of repeated harvesting on nutrient depletion (Adams et al. 2000). In some cases, the effects of timber harvesting have been assessed indirectly by measuring soil nutrients before and after management activity (Hendrickson et al. 1989; Kraske and Fernandez 1993), but the results are influenced by the addition of new biomass to the forest floor, which can increase soil nutrient availability in the short term (Knoepp and Swank 1997). Chronic acidic deposition can also reduce site productivity by reducing soil base cation availability (Adams 1999). The unmanaged reference stands in this study have been monitored intensively for the effects of acid deposition. Signs of nitrogen saturation have been reported, but the effects on periodic growth are unknown (Adams 1999). Current growth rates are less in these unmanaged reference stands than in managed areas, but presumably this difference is primarily related to stocking and increasing stand age and reflects the difficulty of assessing long-term potential productivity. By ultimately achieving stability with respect to stocking and composition, long-term silvicultural trials provide opportunities to periodically measure productivity and assess long-term trends in a changing environment. Through these assessments, determination of the level of sustainable forest production may be possible.

Acknowledgements

I gratefully acknowledge the efforts of G.R. Trimble (deceased), who worked on the initial design and implementation of this study over a half century ago, and H.C. Smith (retired) and G.W. Miller (Northeastern Research Station, Morgantown, W. Va.) for their combined efforts in managing this study for three decades. I also thank R. Rosier and R. Hovatter for many years of data collection, F. Wood and L. Plaugher for database management, and R. Poling, S. Hockman, and M. Owens for conscientious logging in many of the managed compartments. K. Elliott, B. Leak, S. Duke, two anonymous reviewers, and an associate editor provided helpful comments on earlier versions of the manuscript.

References

Abrams, M.D., and Downs, J.A. 1990. Successional replacement of old-growth white oak by mixed mesophytic hardwoods in southwestern Pennsylvania. Can. J. For. Res. **20**: 1864–1870.

Abrams, M.D., Orwig, D.A., and DeMeo, T.E. 1995. Dendroecological analysis of successional dynamics for a presettlement-origin white pine – mixed oak forest in the southern Appalachians, USA. J. Ecol. **83**: 133–143.

Adams, M.B. 1999. Acidic deposition and sustainable forest management in the central Appalachians, USA. For. Ecol. Manage. **122**: 17–28.

Adams, M.B., Burger, J.A., Jenkins, A.B., and Zelazny, L. 2000. Impact of harvesting and atmospheric pollution on nutrient depletion of eastern hardwood forests. For. Ecol. Manage. **138**: 301–319.

Braun, E.L. 1950. Deciduous forests of eastern North America. Blakiston Co., Philadelphia, Pa.

Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. **18**: 117–143.

Crow, T.R. 1988. Reproductive mode and mechanisms for self-replacement of northern red oak (*Quercus rubra*): a review. For. Sci. **34**: 19–40.

Delcourt, H.R., and Delcourt, P.A. 1997. Pre-Columbian Native American use of fire on the southern Appalachian landscapes. Conserv. Biol. **11**: 1010–1014.

Delcourt, P.A., and Delcourt, H.R. 1987. Long-term forest dynamics of the temperate zone. Springer-Verlag, New York.

Elliott, K.J., and Swank, W.T. 1994. Changes in tree species diversity after successive clearcuts in the southern Appalachians. Vegetatio, **115**: 11–18.

Fajvan, M.A., Grushecky, S.T., and Hassler, C.C. 1998. The effects of harvesting practices on West Virginia wood supply. J. For. **96**: 33–39.

Fajvan, M.A., Knipling, K.E., and Tift, B.D. 2002. Damage to Appalachian hardwoods from diameter-limit harvesting and shelterwood establishment cutting. North. J. Appl. For. **19**: 80–87.

Gilliam, F.S., Turrill, N.L., and Adams, M.B. 1995. Herbaceous-layer and overstory species in clear-cut and mature central Appalachian hardwood forests. Ecol. Appl. **5**(4): 947–955.

Gingrich, S.F. 1967. Measuring and evaluating stocking and stand density in upland hardwood forests in the central states. For. Sci. **13**: 38–53.

Hassler, C.C., Grushecky, S.T., and Fajvan, M.A. 1999. An assessment of stand damage following timber harvests in West Virginia. North. J. Appl. For. **6**: 191–196.

Hendrickson, O.Q., Chatarpaul, L., and Burgess, D. 1989. Nutrient cycling following whole-tree and conventional harvest in northern mixed forest. Can. J. For. Res. **19**: 725–735.

Houston, D.R., and O’Brien, J.T. 1983. Beech bark disease. USDA For. Serv. For. Insect Dis. Leafl. 75.

Husch, B., Miller, C.I., and Beers, T.W. 1972. Forest mensuration. 2nd ed. Ronald Press, New York.

Iverson, L.R., and Prasad, A.M. 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. Ecol. Monogr. **68**: 465–485.

Knoepp, J.D., and Swank, W.T. 1997. Long-term effects of commercial sawlog harvest on soil cation concentrations. For. Ecol. Manage. **93**: 1–7.

Kraske, C.R., and Fernandez, I.J. 1993. Biogeochemical responses of a forest watershed to both clearcut harvesting and papermill sludge application. J. Environ. Qual. **22**: 776–786.

Lamson, N.I., and Miller, G.W. 1982. Logging damage to dominant and codominant residual stems in thinned West Virginia cherry–maple stands. *In* Proceedings, 4th Central Hardwood Forest Conference. *Edited by* Robert N. Muller. University of Kentucky, Department of Forestry, Lexington, Ky. pp. 32–38.

Lamson, N.I., and Smith, H.C. 1991. Stand development and yields of Appalachian hardwood stands managed with single-tree selection for at least 30 years. USDA For. Serv. Res. Pap. NE-655.

Larabee, P.A. 1986. Late-Quaternary vegetational and geomorphic history of the Allegheny Plateau at Big Run Bog, Tucker County, West Virginia. M.S. thesis, University of Tennessee, Knoxville, Tenn.

Losche, C.K., and Beverage, W.W. 1967. Soil survey of Tucker County and part of Northern Randolph County, West Virginia. USDA Soil Conservation Service and Forest Service, Washington, D.C.

Magurran, A.E. 1988. Ecological diversity and its measure. Princeton University Press, Princeton, N.J.

McCarthy, B.C., and Bailey, D.R. 1996. Composition, structure, and disturbance history of Crabtree Woods: an old-growth forest of western Maryland. Bull. Torrey Bot. Club, **123**: 350–365.

McCune, B., and Mefford, M.J. 1999. PC-ORD. Multivariate analysis of ecological data. Version 4.0 [computer program]. MjM Software, Gleneden Beach, Ore.

McNab, W.H., and Avers, P.E. 1994. Ecological subregions of the United States: section descriptions. USDA For. Serv. Admin. Publ. WO-WSA5.

McNaughton, S.J. 1977. Diversity and stability of ecological communities: a comment on the role of empiricism in ecology. Am. Nat. **111**: 515–525.

McShea, W. J. 2000. The influence of acorn crops on annual variation in rodent and bird populations. Ecology, **81**: 228–238.

Miller, G.W. 1991. Practicing uneven-age management: does it pay? Some economic considerations. *In* Proceedings: Uneven-Aged Management of Hardwoods in the Northeast. *Edited by* M.C. Vodak. Rutgers University, New Brunswick, N.J. pp. 47–59.

Miller, G.W. 1993. Financial aspects of partial cutting practices in central Appalachian hardwoods. USDA For. Serv. Res. Pap. NE-673.

Miller, G.W., and Kochenderfer, J.N. 1998. Maintaining species diversity in the central Appalachians. J. For. **96**: 28–33.

Miller, G.W., and Smith, H.C. 1993. A practical alternative to single-tree selection? North. J. Appl. For. **10**: 32–38.

Miller, G.W., Schuler, T.M., and Smith, H.C. 1995. Method for applying group selection in central Appalachian hardwoods. USDA For. Serv. Res. Pap. NE-696.

Montreal Process Criterion and Indicators. 1998. The Montreal Process [online]. Available from http://www.mpci.org/criteria_e.html [accessed 29 Aug 2002].

Nyland, R.D. 1992. Exploitation and greed in eastern hardwood forests. J. For. **90**: 33–37.

Nyland, R.D. 1996. Silviculture: concepts and applications. McGraw-Hill, New York.

Oliver, C.D., and Larson, B.C. 1996. Forest stand dynamics. John Wiley & Sons, New York.

Pan, C., Tajchman, S.J., and Kochenderfer, J.N. 1997. Dendroclimatological analysis of major forest species of the central Appalachians. For. Ecol. Manage. **98**: 77–87.

Parker, G.R., Leopold, D.J., and Eichenberger, J.K. 1985. Tree dynamics in an old-growth, deciduous forest. For. Ecol. Manage. **11**: 31–57.

Pielou, E.C. 1969. An introduction to mathematical ecology. John Wiley & Sons, New York.

Powers, R.F., Mead, D.J., Burger, J.A., and Ritchie, M.V. 1994. Designing long-term site productivity experiments. *In* Impacts of forest harvesting on long-term site productivity. *Edited by* W.J. Dyck, D.W. Cole, and N.B. Comerford. Chapman & Hall, New York. pp. 247–286.

Rentch, J.S., Fajvan, M.A., and Hicks, R.R., Jr. 2003. Oak establishment and canopy accession strategies in five old-growth stands in the central hardwood forest region. For. Ecol. Manage. **184**: 285–297.

Schuler, T.M., and Gillespie, A.R. 2000. Temporal patterns of woody species diversity in a central Appalachian forest from 1856 to 1997. J. Torrey Bot. Soc. **127**: 149–161.

Smith, D.M. 1986. The practice of silviculture. John Wiley & Sons, New York.

Smith, D.W. 1995. The southern Appalachian hardwood region. *In* Regional silviculture of the United States. 3rd ed. *Edited by* John W. Barrett. John Wiley & Sons, New York. pp. 173–225.

Smith, H.C. 1980. An evaluation of four uneven-aged cutting practices in central Appalachian hardwoods. South. J. Appl. For. **4**: 193–200.

Smith, H.C., and Debald, P.S. 1975. Economics of even-aged and uneven-aged silviculture and management in eastern hardwoods. *In* Proceedings of a Symposium on Uneven-Aged Silviculture and Management in the Eastern United States. USDA For. Serv. Gen. Tech. Rep. WO-24. pp. 121–137.

Smith, H.C., and Miller, G.W. 1987. Managing Appalachian hardwood stands using four regeneration practices: 34 year results. North. J. Appl. For. **4**: 180–185.

Smith, H.C., Miller, G.W., and Schuler, T.M. 1994. Closure of logging wounds after 10 years. USDA For. Serv. Res. Pap. NE-692.

Trimble, G.R., Jr. 1961. Managing mountain hardwoods: a ten-year appraisal. USDA For. Serv. Northeast. For. Exp. Stn., Stn. Pap. 143.

Trimble, G.R., Jr. 1967. Diameter increase in second-growth Appalachian hardwood stands: a comparison of species. USDA For. Serv. Res. Note NE-75.

Trimble, G.R., Jr. 1970. 20 years of intensive uneven-aged management: effect on growth, yield, and species composition in two hardwood stands in West Virginia. USDA For. Serv. Res. Pap. NE-154.

Trimble, G.R., Jr. 1977. A history of the Fernow Experimental Forest and the Parsons Timber and Watershed Laboratory. USDA For. Serv. Gen. Tech. Rep. NE-28.

Trimble, G.R., Jr., and Smith, H.C. 1970. Sprouting of dormant buds on border trees. USDA For. Serv. Res. Pap. NE-179.

Trimble, G.R., Jr., and Weitzman, S. 1956. Site index studies of upland oaks in the northern Appalachians. For. Sci. **2**: 162–173.

Troendle, C.A. 1979. Hydrologic impacts of silvicultural activities. Proc. Am. Soc. Civ. Eng. **105**: 57–70.

Tryon, E.H., and Trimble, G.R., Jr. 1969. Effect of distance from stand border on height of hardwood reproduction in openings. Proc. W. Va. Acad. Sci. **41**: 113–125.

Tyrrell, L.E., Nowacki, G.J., Crow, T.R., Buckley, D.S., Nauertz, E.A., Niese, J.N., Rollinger, J.L., and Zasada, J.C. 1998. Information about old growth for selected forest type groups in the eastern United States. USDA For. Serv. Gen. Tech. Rep. NC-197.

USDA Forest Service. 2002. Hemlock woolly adelgid [online]. Available from http://www.fs.fed.us/na/morgantown/fhp/hwa/infestations.htm [accessed 28 Aug 2002].

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

Wentworth, J.M., Johnson, A.S., Hale, P.E., and Kammermeyer, K.E. 1992. Relationships of acorn abundance and deer herd characteristics in the southern Appalachians. South. J. Appl. For. **16**: 5–8.

Whitney, G.G. 1987. An ecological history of the Great Lakes forest of Michigan. J. Ecol. **75**: 667–689.

Whitney, G.G. 1994. From coastal wilderness to fruited plain: a history of environmental change in temperate North America, 1500 to the present. Cambridge University Press, Cambridge, U.K.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. Taxon, **21**: 213–251.

Wolff, J.O. 1996. Population fluctuations of mast-eating rodents are correlated with production of acorns. J. Mammol. **77**: 850–856.

Appendix A

Table A1. Relative stem density and current rank of woody overstory species from most recent, middle, and oldest inventory dates.

Species	Current rank	1987–2001	1970–1981	1951–1959
Acer saccharum	1.000	0.197	0.131	0.069
Acer rubrum	2.000	0.161	0.122	0.078
Quercus rubra	3.000	0.136	0.180	0.198
Fagus grandifolia	4.000	0.070	0.048	0.044
Betual lenta	5.000	0.065	0.062	0.060
Quercus prinus	6.000	0.059	0.077	0.082
Liriodendron tulipifera	7.000	0.055	0.052	0.059
Prunus serotina	8.000	0.047	0.054	0.079
Tilia americana	9.000	0.043	0.042	0.038
Magnolia fraseri	10.000	0.025	0.027	0.031
Magnolia acuminate	11.000	0.021	0.026	0.026
Fraxinus americana	12.000	0.021	0.030	0.032
Quercus alba	13.000	0.014	0.018	0.019
Betula alleghaniensis	14.000	0.012	0.012	0.012
Tsuga canadensis	15.000	0.009	0.004	0.001
Carya cordiformis	16.000	0.009	0.018	0.030
Robinia pseudoacacia	17.000	0.008	0.016	0.047
Oxydendrum arboretum	18.000	0.007	0.013	0.013
Oystrya virginiana	19.000	0.007	0.005	0.003
Amelanchier arborea	20.000	0.006	0.006	0.003
Sassafras albidum	21.000	0.005	0.026	0.048
Prunus pensylvanica	22.000	0.005	0.004	0.000
Nyssa sylvatica	23.000	0.005	0.007	0.011
Quercus coccinea	24.000	0.005	0.006	0.000
Carya ovata	25.000	0.003	0.009	0.008
Ulmus rubra	26.000	0.002	0.001	0.002
Quercus velutina	27.000	0.000	0.001	0.000
Juglans cinerea	28.000	0.000	0.000	0.003
Populus grandidentata	29.000	0.000	0.001	0.003
Cornus florida	30.000	0.000	0.000	0.001
Juglans nigra	31.000	0.000	0.000	<0.001
Picea rubra	32.000	0.000	0.000	<0.001

Note: Observations are combined for all treatments to illustrate overall temporal trends (including unmanaged reference stands).