RESEARCH ARTICLE

•

Changes in Presettlement Forest Composition for Five Areas in the Central Hardwood Forest, 1784-1990

James S. Rentch[1]
Ray R. Hicks, Jr.[2]

Division of Forestry
West Virginia University
P. O. Box 6125
Morgantown, WV 26506

•

[1] Corresponding author:
jrentch2@wvu.edu
304-293-2941 Ext. 2480
[2] rhicks3@wvu.edu
304-293-2941 Ext. 2432

Natural Areas Journal 25:228–238

ABSTRACT: Witness tree tallies from early land surveys show that presettlement forests in eastern Ohio, southwestern Pennsylvania, and north central West Virginia were oak-dominated forests. *Quercus alba* was dominant by a large margin – at minimum, twice as abundant as *Q. velutina*, the second ranked species. *Acer saccharum* and *Fagus grandifolia* were among the top ten ranked species at each site; however, their importance value was consistently less than one-third the value for *Q. alba. Quercus rubra, Q. prinus, Castanea dentata*, and *A. rubrum* were relatively minor components of presettlement forests, rarely ranked among the 10 most abundant tree species. Where diameter-distribution data were available, results show that oaks were well distributed among all but the smallest size classes, suggesting that oak replacement was a stable feature of these forests. Multiple response permutation procedure-analysis of presettlement and modern U.S. Forest Service Forest Inventory analysis (FIA) data shows a clear separation by historical period. Modern inventories consistently show a significant decline in *Q. alba* abundance and a large increase for *A. rubrum*. Other early successional species such as *Prunus serotina, Liriodendron tulipifera*, and *Fraxinus americana* showed large increases, although this trend varied somewhat among the sites studied. The species composition of presettlement forests suggests a highly variable disturbance regime in which a variety of species with different life history strategies, disturbance tolerances, and growth requirements shared overstory position. Changes in species dominance over the time period reviewed suggest that 20th century reduction in fire frequency resulted in reduced oak abundance and accelerated recruitment of fire intolerant species.

Index terms: disturbance regimes, oaks, presettlement forest composition, witness tree tallies

INTRODUCTION

The nature of the eastern deciduous forest prior to European settlement has long intrigued forest historians and ecologists, and has a prominent place in popular culture. Popular belief held that the earliest settlers of eastern North America found everywhere an unbroken, primeval forest of gigantic proportions. Joseph Martin, (1835) in the Gazetteer of Virginia and the District of Columbia, thought the forest so vast that it could never be conquered, and "must remain for ever in its primitive forest." Lewis (1998) reports the remarks of a party of Virginians led by Thomas Jefferson's father, when they viewed Canaan Valley, West Virginia, from the top of Cabin Mountain in 1746: "Did not see a plain big enough for a man to lie on nor a horse to stand." In the 1850s, David Hunter Strother's (Porte Crayon) accounts and illustrations for popular magazines helped perpetuate the notion that western Virginia was exotic, threatening, and impenetrable. The 1908 report of the West Virginia Conservation Commission noted that when white men first came into the state "it was all forest except a few cliffs and rocky peaks, and two or three old fields where Indians had probably cultivated corn" (Maxwell 1908).

Paleo-Indians arrived in the upper Ohio Valley as early as 14,000 years ago, and the region was continually occupied and used thereafter until the first Europeans arrived in the 1600s (Yarnell 1998, Adovasio and Pedler 2000). Native American use of fire has been extensively documented both by early European visitors (Lederer and Talbot 1672) and contemporary researchers (Delcourt and Delcourt 1998, Bonnicksen 2000). Native Americans purportedly used fire to prepare land for agriculture, clear forests of understory vegetation and encourage grass, maintain a network of trails, and drive game. Fire frequency, in turn, influenced the species composition of presettlement forests. Before the advent of horticulture (2000 years ago), only 10% of the wood preserved as charcoal in archeological sites represents species favored by disturbed environments. After this period, the proportion of wood charcoal from early successional species such as pine (*Pinus* spp.), tulip-poplar (*Lirodendron tulipifera* L.), and cane [*Arundinaria gigantea* (Walt.) Muhl.], for example, steadily increased to a maximum of 50% (Chapman et al. 1982).

Native American use of fire to create openings for agriculture and to clear forests of understory vegetation is reflected in early descriptions of forest structure. Beverley (1971), writing in 1722, recounted early explorers' descriptions of the forests near the present-day West Virginia-Virginia border: "they found large level plains...and fine savannahs three or four miles wide." Seeking to entice settlers to his land along the Kanawha and Ohio Rivers, George Washington praised them as containing "most excellent meadows, many of which...are, in their present state, almost fit for the scythe" (Rice 1970). Bromley (1935) described the impact of Native American use of fire on forest structure in southern New England: "on one subject, all are in accord and that is the observation that the original forest was, in most places, extremely open and park like, due to the universal factor of fire, fostered by the original inhabitants." Maxwell (1910) cited a similar condition for precolonial forests of Virginia: "freedom from undergrowth was one of the most notable features of the original woods of Virginia." Delcourt and Delcourt (1998) concluded that Native American use of fire was a significant component of a total disturbance regime that resulted in a heterogeneous mosaic of different vegetation types, some of which included fire adapted species, and others of which included fire-intolerant species.

Contemporary evidence for the composition of the presettlement forest comes from three sources: (1) Pollen analysis has been used to chronicle changes in genus-level composition following the retreat of Pleistocene glaciers. These studies have reviewed both long-term trends over thousands of years (Watts 1979, Davis 1981, Delcourt and Delcourt 1987, Webb 1988), and the more recent historical era from presettlement to the present (Russell 1980). (2) Old-growth remnants that are representative of the presettlement forest have been extensively studied, using both living and dead stems (e.g., Henry and Swan 1974, Rentch et al. 2003a). One list of these studies contains 749 entries (Nowacki and Trianosky 1994). (3) In the East, early land surveys contain valuable information about forest composition before large-scale forest clearing. Because property was involved, surveys were intended to last, and thus to a certain extent, they are repeatable. Reconstructions of forest composition in Ohio (Sears 1925), northwest Pennsylvania (Lutz 1930), New England (Bromley 1935, Day 1953), and Michigan (Bourdo 1956) proved the utility of using early land surveys and witness tree records.

Reconstruction of the original forest composition and the dynamics of that forest are not entirely academic questions. Concern for the future of eastern oak (*Quercus* spp. L.) forests and management strategies for encouraging oak regeneration are based, in part, on evidence (or an assumption) that current forests were historically oak-dominated, and naturally maintained in the presettlement landscape. However, in some areas, particularly those around the periphery of the central hardwood forest region, oak stands are more recent and owe their origin to 50-100 years of influence by European settlers (Crow 1988, Lorimer 1993). Forest clearing in the mid-Atlantic region to produce charcoal for the early iron industry (Abrams 1992), succession of old-fields to pine and then to oak (Lorimer 1993), and fire suppression in the oak savannahs of the Midwest often created forests that were quite unlike those the first European arrivals saw. More recently, oak abundance has been augmented by elimination of American chestnut [*Castanea dentata* (Marsh.) Borkh.] as a canopy tree (Stephenson et al. 1993). Thus, what today appears "natural," may be quite temporary and recent (cf. Sprugel 1991).

The objective of this study was to use records of witness trees of early land surveys and property transfers to reconstruct county-level forest composition at the time of earliest European settlement. Results were then compared to modern data on composition from U.S. Forest Service Forest Inventory and Analysis (FIA) inventories. The bulk of the surveys used in this study were of public land, owned either by the Virginia colonial government (West Virginia and Pennsylvania) or by the Federal government (Ohio). These surveys, in the main, preceded large-scale European settlement and forest clearing (Loeb 1987). Thus, these records are a valuable database, and constitute one of the few quantitative sources of tree species composition and abundance over relatively large areas.

METHODS

Presettlement forest composition

Presettlement-era forest composition was derived from tallies of witness trees from property deeds, early metes and bounds warrant surveys, and township surveys for five areas in eastern Ohio, southwestern Pennsylvania, and north central West Virginia (Figure 1). The five areas examined were selected because today they contain remnant old-growth forests that were the subject of stand reconstruction and disturbance frequency analyses reported on in Rentch et al. (2003a, 2003b). The study areas occur in that portion of the central hardwood region defined by Braun (1950) as the Mixed Mesophytic forest association. This is the unglaciated Appalachian Plateau, lying west of the northern hardwood and oak-pine forests of the Allegheny Mountain and Ridge and Valley physiographic provinces, respectively, and east of the Western Mesophytic forests of western Ohio and central Kentucky. According to Bailey's (1995) classification of ecoregions of the United States, the study sites fall in the eastern forest (oceanic) province (221) of the Hot Continental Division, characterized by cold winters and warm summers, deeply dissected landforms, and winter deciduous vegetation. Precipitation averages 106 cm yr^{-1}, and is evenly distributed throughout the year. Bedrock under the study sites consists of sedimentary siltstones, shales, and sandstones – all of Pennsylvanian origin. Soils are generally Typic Hapludalfs, acidic, fine-loamy, mixed and well-drained soils of uplands, which are best suited for trees. The earliest settlement for all five study areas occurred between 1765 and 1788.

For Lewis County, West Virginia, property deeds covering the 3-year period 1817-1819 were reviewed. For Ritchie County and Harrison County, West Virginia, and Washington County, Pennsylvania, metes and bounds warrant surveys from Survey Book 1 of the respective counties were the data source for years 1784-1786. In Kirkwood Township, Belmont County, Ohio, witness trees were tallied from 1786 federal General Land Office (GLO) township surveys. We calculated importance values (IV) by species or species group (e.g., *Ulmus* spp.) as one-half the sum of relative frequency (based on number of surveys that mentioned a particular species) and relative abundance (the number

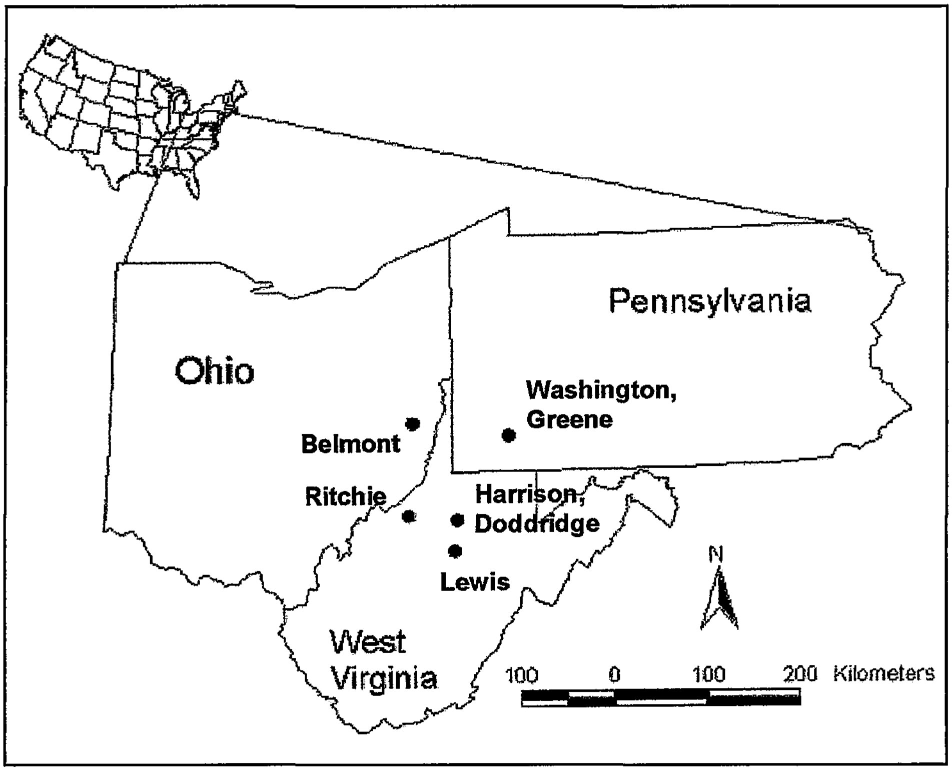


Figure 1. Location map of study areas.

of times a species was named).

Contemporary forest composition

Present-day forest composition was derived from the FIA database (U.S. Department of Agriculture 2001). Data were compiled by county. Because of the small number of FIA sample plots in Washington County, Pennsylvania, and Harrison County, West Virginia, we combined these two counties with adjacent counties, Greene County and Doddridge County, respectively, to increase sample size. We used Table 10 (live trees on timberland by species and diameter class) from the FIA database with two modifications. First, the physiographic class was limited to xeric, xeromesic, and mesic to eliminate wetter sites. Second, because of a bias against the smallest trees in the presettlement surveys (discussed below), only trees ≥ 12.7 cm dbh were used.

Because the FIA tree classification system focuses on commercial timber, some species richness information is lost. For example, the "other red oak" group includes black oak and scarlet oak, (*Quercus velutina* Lam., *Q. coccinea* Meunchh., respectively). "Soft maple" includes red maple and silver maple (*Acer rubrum* L., *A. saccharinum* L.). Other broader groupings include "other soft hardwood," "other hard hardwood," and "noncommercial." To compare presettlement and current forest composition, we reclassified presettlement witness tree tallies using the FIA classification system and relativized the data to an IV based on abundance by county:

$$\text{IV species}_n = \Sigma \text{ occurrences species}_n / \Sigma \text{ occurrences all species} * 100\%.$$

Data analysis

We used Analysis of Variance (ANOVA) of ranked data to compare species ranking between presettlement-era sites. This technique avoids problems associated with comparison of nonparametric, ordinal data. We then used multiple response permutations procedure (MRPP), available in PC-ORD® software (McCune and Mefford 1999), to check for similarity between species importance values of presettlement and contemporary forests. This procedure calculates two statistics. First, a weighted mean within-group distance in species space is calculated using Sorenson distance. The *T*-statistic is calculated as the ratio of the difference between the observed and expected mean distance and the standard deviation of the expected difference. This statistic describes the separation between groups; the more negative *T* is, the stronger the separation between groups. A *p*-value is used to evaluate the likelihood of achieving the observed difference (*T*) by chance. This procedure then calculates an *A* statistic that is an estimate of the within-group homogeneity, compared to random expectation. This statistic provides an estimate of the "effect size" that is independent of the sample size (McCune et al. 2002). When all plots are identical within groups, $A = 1$; if heterogeneity within groups equals expectation by chance, then $A = 0$. In community ecology, values for A are commonly <0.1 (McCune et al. 2002).

RESULTS

Presettlement forest composition and structure

Presettlement forests of the five study areas were very similar and consistently oak-dominated (Table 1). ANOVA revealed no significant differences of species rankings between sites ($F=0.187$, $p = 0.945$). White oak (*Quercus alba* L.) was the dominant tree by a large margin, twice as abundant as the second ranked species (average IV = 32.6). At four of the five sites, black oak was the second most abundant species, followed by hickories (*Carya* spp.), and the group, other hard hardwoods, which includes American chestnut, black birch (*Betula lenta* L.), black locust (*Robinia pseudoacacia* L.) and flowering dogwood (*Cornus florida* L.) (see Table 2). Yellow-poplar (*Liriodendron tulipifera* L.), American beech (*Fagus grandifolia* Ehrh.), and sugar maple (*Acer saccharum* Marsh.) were also among the top ten ranked species at each site; however, their importance was less than one-fourth the value for white oak. Red maple ranked 10th on average (IV = 3.0).

Surprisingly, northern red oak (select red oak, *Q. rubra* L.), chestnut oak (other white oak, *Q. prinus* L.), and American

Table 1. **Importance values (IV = (relative abundance + relative frequency)/2) of tree species cited as witness trees in early land surveys and deeds for five counties in eastern Ohio, southwestern Pennsylvania, and north central West Virginia.**

Name cited	Scientific name[1]	*Importance value (IV)* Belmont OH	Washington PA	Harrison WV	Ritchie WV	Lewis WV
boxelder	*Acer negundo*	--	--	--	--	0.3
maple	*Acer rubrum*	1.5	2.2	3.1	4.7	3.7
sugar tree	*Acer saccharum*	8.7	3.6	10.6	5.5	3.7
buckeye	*Aesculus flava*	1.9	0.5	0.5	0.7	1.1
serviceberry, sarvis	*Ameliancher arborea*	--	0.6	0.2	1.7	--
birch, burch	*Betula lenta, nigra*	2.5	--	1.1		0.3
iron wood	*Carpinus caroliniana*	--	1.2	--	1.2	--
hickory	*Carya spp.*	8.9	11.4	9.0	9.2	8.4
chestnut	*Castanea dentata*	3.4	0.5	2.4	1.7	1.5
red bud	*Cercis canadensis*	0.4	--	--	--	--
hoop ash	*Celtis occidentalis*	0.2	--	--	--	--
dogwood	*Cornus florida*	1.1	4.0	0.8	9.0	4.7
thorn tree	*Crataegus spp.*	--	0.7	--	--	--
beach, beech	*Fagus grandifolia*	5.5	1.1	8.3	5.5	14.8
ash	*Fraxinus americana*	1.1	2.1	1.1	0.7	2.3
white walnut	*Juglans cinera*	1.5	0.5	0.7	--	0.9
walnut, black walnut	*Juglans nigra*	2.5	1.7	3.1	1.4	0.4
poplar, white wood	*Liriodendron tulipifera*	2.8	3.6	4.1	9.7	7.5
cucumber tree	*Magnolia acuminata*	--	--	0.2	--	--
crab apple	*Malus spp.*	--	0.1	--	--	--
mulberry	*Morus rubra*	--	--	--	--	0.4
gum	*Nyssa sylvatica*	0.8	2.9	5.9	7.8	4.7
hophornbeam	*Ostrya virginia*	0.4	--	--		0.3
sourwood	*Oxydendron arboreum*	--	--	--	1.4	--
pine, jackpine	*Pinus rigida, virginiana*	1.5	0.5	0.8	0.7	0.3
white pine	*Pinus strobus*	--	0.2	--	--	--
sycamore, plane tree	*Platanus occidentalis*	--	0.8	--	--	1.2
cherry	*Prunus serotina*	0.2	0.8	--	0.3	0.3
white oak	*Quercus alba*	38.8	39.1	32.4	23.9	28.8
spanish oak[2]	*Quercus coccinea*	0.4	2.1	--	0.2	0.9
blackjack oak	*Quercus marylandica*	--	--	--	0.2	--
chestnut oak, rock oak	*Quercus prinus*	--	1.2	0.5	1.2	2.5

continued

Table 1. Importance values (IV = (relative abundance + relative frequency)/2) of tree species cited as witness trees in early land surveys and deeds for five counties in eastern Ohio, southwestern Pennsylvania, and north central West Virginia.

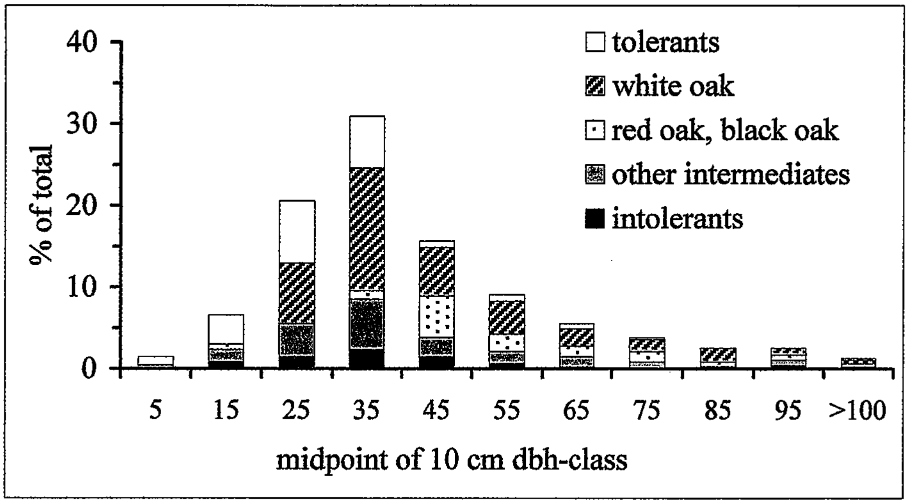
Name cited	Scientific name[1]	*Importance value (IV)*				
		Belmont OH	Washington PA	Harrison WV	Ritchie WV	Lewis WV
continued						
red oak	*Quercus rubra*	1.1	2.9	0.5	2.2	2.5
black oak, yellow oak	*Quercus velutina*	10.4	13.0	12.7	10.0	6.0
locust	*Robinia pseudoacacaia*	--	0.5	0.8	0.2	1.1
sassafras	*Sassafras albidum*	--	0.2	--	--	--
lynn, lyme, linden	*Tilia americana*	--	1.1	0.7	0.9	1.2
elm, hoop tree	*Ulmus americana, rubra*	4.4	1.1	0.7	--	0.5
Number of surveys		88	103	130	125	106
Species richness		23	29	23	24	27

[1] Some based on Peattie (1950).

[2] Also know as pin oak (*Q. palustris*, Loeb 1987) and southern red oak (*Q. falcata*, Peattie 1950).

chestnut were all relatively minor components of these forests. The highest county ranking for northern red oak occurred at Washington County, Pennsylvania, where it was seventh out of a total of 28 species (IV = 2.9). On average, the species was ranked 11th with an average IV of 1.8. American chestnut ranked among the top 10 species at only one location, and had an average rank of 13. Pines were generally not identified to species by land surveys and formed a relatively small component of these forests. Notably, eastern hemlock [*Tsuga canadensis* (L.) Carr.] did not appear in any of the surveys reviewed. The absence of hemlock is surprising since metes and bounds surveys often followed natural boundaries, such as streams, where this species frequently occur.

Some characteristics of the size structure of the Belmont County, Ohio, forest can be estimated using diameter records of corner and station trees from the township surveys (Figure 2). Oaks were well distributed among all but the smallest size classes; for example, 73% of the white oaks occurred in the 35-55 cm classes, while red oaks tended to be somewhat larger. The largest size classes (> 90 cm) contained white oak, black oak, black walnut (*Juglans nigra*), and American chestnut. Among the largest



Species code:
tolerants: dogwood, American beech, black gum, buckeye, sugar maple, red maple
intolerants: yellow-poplar, black cherry, butternut, black walnut
intermediates: hackberry, hickories, American chestnut, white ash, pines, elms

Figure 2. Diameter distribution of witness trees from township survey, Kirkwood Township, Belmont County, OH; 1786-1804.

Table 2. Comparison of species-group average importance values (IV) and ranking for presettlement and USDA Forest Service FIA data. Presettlement data are from witness tree records. FIA data are for trees > 12.7 cm dbh. A negative change in rank indicates an increase in relative ranking from presettlement to the present.

Species-group	Average for five areas.				
	IV-Pres	Rank	IV-FIA	Rank	Change in rank
select white oak[1]	32.6	1	7.3	5	4
other red oak[2]	11.2	2	3.8	8	6
hickory	9.4	3	9.4	3	0
other hard hardwoods[3]	7.1	4	3.5	9	5
American beech	7.0	5	2.8	14	9
sugar/black maple	6.4	6	7.2	6	0
yellow-poplar	5.5	7	9.4	3	-4
black gum	4.4	8	1.1	17	9
other soft hardwoods[4]	3.9	9	19.8	1	-8
red/silver maple	3.0	10	13.1	2	-8
select red oak[5]	1.8	11	3.1	12	1
black walnut	1.8	11	2.2	15	4
noncommercial species[6]	1.7	13	3.4	10	-3
ash	1.5	14	5.1	7	-7
other white oak[7]	1.1	15	2.9	13	-2
basswood	0.8	16	0.7	18	2
pine	0.8	16	3.3	11	-5
eastern hemlock	--	--	0.2	19	na
cottonwood/aspen	--	--	1.3	16	na

[1] Includes bur oak, chinkapin oak, swamp white oak, white oak.

[2] Includes black oak, blackjack oak, pin oak, scarlet oak, so. red oak.

[3] Includes American chestnut, black birch, black locust, flowering dogwood.

[4] Includes black cherry, boxelder, buckeye, butternut, cucumber tree, elm, hackberry, sassafras, sycamore.

[5] Includes northern red oak.

[6] Includes tree of heaven, hophornbeam, hawthorne, musclewood, pawpaw, pin cherry, red bud, serviceberry, sourwood, striped maple.

[7]includes chestnut oak, post oak

individual trees were a white oak, American chestnut, and buckeye (*Aesculus flava* Aiton.), each with an estimated diameter of 127 cm. In contrast, shade tolerant species such as maples and beech, and species intermediate in shade tolerance [e.g., hickories, white ash, (*Fraxinus americana* L.)] were concentrated in the 25-55 cm size classes and none were larger than 65 cm in diameter.

Comparison of presettlement-era and contemporary FIA forest composition

Multiple response permutation procedures analysis of species composition of presettlement and contemporary forest composition showed a clear separation by historical period. The *T*-statistic, representing separation between groups, was negative and significant ($T = -4.61$, $p < 0.003$). Average Sorenson percent similarity for presettlement and contemporary groups was 74.3% and 66.5%, respectively, and the *A*-statistic, representative of within-group agreement, was 0.25.

White oak and red maple IV's showed two of the larger differences between the two historical periods (Table 2). White oaks (select white oak) dropped from an average rank of 1st (average IV = 32.6) in presettlement forests to 5th (IV = 7.3) at present. Red maple (soft maple) showed the opposite trend, increasing from 10th in older forests to 2nd today. Because the FIA data used in this comparison are limited to stems > 12.7 cm dbh, the increased abundance of this species group is probably underrepresented. Northern red oak (select red oak group) declined slightly in overall ranking (11th to 12th), although its average importance value increased. Black oak (other red oak group) sharply declined from 2rd during presettlement to 8th today. Hickories and sugar maple showed little overall change importance value or rank. Beech showed a large decline, moving from 4th during presettlement time to 14th in 1989. Doubtless, this relative position will further decline as beech-bark disease complex moves into the study areas. In contrast, yellow-poplar showed a large increase in rank and its average IV nearly doubled.

The large group, "other soft hardwoods," showed one of the largest changes in ranking, moving from an average IV and rank of 3.9 and 9th, respectively, to 19.8 and 1st. This also illustrates the shortcomings of using the FIA species groupings to analyze species composition, because based on available FIA data alone, we were unable to determine which species were driving this change. According to species IV data from Iverson et al. (1999) based on all stems ≥ 2.54 cm dbh, the main component of "other soft hardwoods" is black cherry (*Prunus serotina* Ehrh.), with an average IV of 16.8.

DISCUSSION

Oak domination of presettlement forests

The presettlement forests of these five counties were consistently dominated by one tree species – white oak. This species ranked first by a large margin in all five areas examined, with an IV value more than twice that of the nearest competitor. The dominance of white oak is consistent with other studies that used witness trees to reconstruct original forest composition. White oak was the most common species in witness tree tallies of George Washington's 1748-1752 surveys across a variety of landforms in eastern West Virginia (Spurr 1951). Sears (1925) prepared a map of the natural vegetation of Ohio from the GLO survey notes, and classified Belmont County as oak-dominated, with white oak, black oak, and hickory the most common species. Similar results were found in Fayette County in southwestern Pennsylvania (Abrams and Downs 1990), the Nittany Valley of central Pennsylvania (Nowacki and Abrams 1992), the Ridge and Valley section of West Virginia (Abrams and McCay 1996), southern Illinois (Leitner and Jackson 1981), and east New Jersey and southeastern New York (Loeb 1987).

Early qualitative descriptions reinforce the results of witness tree tallies. White oak dominated presettlement forests in much of southwestern Pennsylvania, with much smaller components of beech and other mesophytic hardwoods, according to accounts by Michaux (1853) and Jenning (1927). In an 1854 description of the Great Kanawha Estate, a 100,000 acre uncut tract in central West Virginia, white oak was the most abundant species (Simpson, unpubl. data). Brooks (1910) estimated that white oak comprised 30% of the yet uncut hardwoods of West Virginia in 1910. Other oaks (chestnut oak, red oak, black oak, scarlet oak, etc.) together accounted for only 15%, along with yellow-poplar (18%), chestnut (12%), maple (5%), and beech (5%). Braun (1950) cites reports of original forest composition in northeastern Kentucky and southeastern Ohio, where white oak was dominant on the hillside plots, second to beech in the valley plots, and most abundant overall.

Forest disturbance and changes in species abundance

Species distributions in presettlement forests were influenced by the interaction of climate, soils, landform, and fire frequency (Sears 1925, Kline and Cottam 1979, Abrams 1992, Lorimer 1993, Abrams and McCay 1996, Ruffner and Abrams 1998). Since European settlement, major changes in regional species composition have been linked to forest clearing, chestnut blight, increased deer populations, and reduced fire frequency.

In this study, northern red oak and chestnut oak average IVs slightly increased between the two periods (Table 2). American chestnut was present in four of five study areas, but not abundant (Table 1). Northern red oak and chestnut oak have been cited as replacements for chestnut following blight (Stephenson et al. 1993, Abrams 2003), and the absence of larger increases may be due to low levels of American chestnut in these particular areas. Brooks' (1910) review of the original forest composition of West Virginia estimated chestnut comprised about 12% of the uncut forests, but does not give it much prominence for the three West Virginia counties in this study, and the witness tree tallies bear this out (average rank, 12th).

Other studies have also linked oak abundance to repeated harvesting during the 1800s and early 1900s (Crow 1988, Abrams 1992, Lorimer 1993). For the five counties of this study, forest clearing for agriculture and local use was probably largely completed before the onset of large-scale commercial logging operations that typified the economies of the Allegheny Plateau and eastern mountains of West Virginia at the turn of the century. In southwestern Pennsylvania and eastern Ohio, some intensive logging occurred in the early-mid 1800s in connection with charcoal production for iron foundries (Pearse 1876, McKelvey 1903). For the purposes of making charcoal, stem quality was of little importance, and thus forests were clearcut on 20-40 year rotations (Stout 1933, Ruffner and Abrams 1998). Fires often followed. Charcoal production peaked in the 1850s, when coke was substituted for charcoal (Moreland 1940), but the impact of this industry on forests was considerable. The coppice nature of the resultant forests favored species, such as red oak, that readily sprout from smaller stumps and that thrive in post-disturbance environments where light levels are high and competition is low.

In north central West Virginia, the production of cross ties for railroads, and later, timbers for mines, was spurred by the opening of the Baltimore & Ohio Railroad through the region in 1857. Brooks (1910) also reported stave mills and shingle mills in the region in the 1870s, as well as a large oak-export business. This region became the principal supplier for livestock for eastern markets in the antebellum era, and livestock grazing in forests and cutover lands and seasonal burning constituted additional disturbances to forests of the region. Farmers routinely burned the forest floor to reduce underbrush, curb parasites, and increase grasses for grazing (Lewis 1998). By 1910, Brooks described the forest condition of the region: "all of the forests remaining in the county have been culled, except for a few small boundaries," and "the percentage of cleared land is higher [than] farmer's woodlots."

In summary, the counties of this study did not experience the massive operations of the eastern mountains of West Virginia and elsewhere, where large band mills processed over one million board feet each day. Nevertheless, the pattern of extensive forest clearing, fires, and grazing of livestock occurred there, only over a somewhat longer time period; and, at least for a time, it was more in keeping with local economies.

Successional status of presettlement and contemporary forests

The successional status of the presettlement forests is suggested by the species composition and dominance trends from the witness tree data. Mid-successional species such as white oak, black oak, and hickories that have an intermediate-level tolerance to shade and competition comprised, at minimum, 48% of the trees in the five samples (Figure 3a). Based on the presettlement diameter distribution of Belmont County, Ohio, the only sample for which size data are available, these species were also well distributed in the medium-larger diameter classes (Figure 3c). Shade tolerant species, primarily sugar maple, beech, and buckeye, made up between 20-40% of the forest structure, and intolerant species were consistently around 10%. Red maple was a minor component, probably confined to streambed terraces and protected microenvironments (Lorimer et al. 1994, Abrams 1998). Individuals of both shade tolerant and shade intolerant groups also reached very large size and, by implication, great age. The Belmont County GLO surveys cite yellow-poplar and buckeye with diameters in excess of 100 cm.

The compositional trends and limited size distribution data of early forests provide, by inference, an indication of broad-scale disturbance patterns in the region. The disturbance regime and the turnover of growing space were such that a heterogeneous mosaic of different vegetation types coexisted (Delcourt and Delcourt 1998); shade intolerant species such as yellow-poplar and black walnut could become established in large gaps and reach overstory position before closure, while shade tolerant trees could persist in the understory and reach overstory position as smaller gaps were created. However, the dominance by oaks and other intermediate species suggest frequent surface fire as an additional dynamic. Fire return intervals have lengthened from a few years in presettlement and settlement eras (Sutherland 1997, Abrams 2000) to the longest fire-free intervals in the history of the central hardwood region (Wade et al. 2000). In the absence of recurring surface fire, large openings that were previously captured by oaks instead favor faster growing pioneer species and fire intolerant late successional species. The shade tolerance of red maple and black cherry seedlings also resulted in large accumulations of these species in the pool of advance regeneration, shading out oak seedlings (Lorimer 1984; Abrams 1992, 1998). Fire reduced understory competition, and enabled these species to survive high mortality as seedlings, recruit to sapling-size, and eventually dominate the lower-threshold size of the overstory (25-35 cm dbh). Finally, the presence of very large trees suggests that the rate of large, catastrophic disturbances was small enough to allow the longest lived trees of all shade tolerances (e.g., sugar maple, white oak, yellow-poplar) to grow to large size and, presumably, great age.

For current forests, the proportion of shade tolerant species is somewhat higher for two counties and slightly lower for three counties. However, the proportion of intolerants such as yellow-poplar and black cherry almost doubled; for two counties, shade intolerants increased threefold (Figure 3b). This steep decline in the contemporary abundance of intermediate-tolerance trees such as oak suggests that the previous disturbance regime that facilitated oak replacement is no longer present.

CONCLUSION

Based on witness tree data, the presettlement forests were primarily oak forests. White oak was dominant by a large margin; on average, black oak was the second most abundant species and, notably, much more important than northern red oak. Shade tolerant species, particularly red maple, were much less abundant than in current inventories. For the one area where size distribution data are available, the structure of this forest suggests a variable disturbance regime that allowed trees of all shade tolerances and growth strategies to occupy the overstory.

For the counties of this study, forest clearing was at least initially more closely tied to early settlement patterns and local economies. Although some intensive logging occurred in the study area in connection with the charcoal industry and the extension of the railroads, the processes of forest clearing for agriculture, fire, and grazing were well underway by the time the most intensive logging operations of the late 1800s occurred elsewhere in the region. Thus human disturbances began earlier, lasted longer, and varied in intensity; but their impact on forest composition was no less significant, and continued into the early 20th century when clearing of second growth forests, as well as invasive insects and disease, further altered forest composition and structure.

By the time of the most current forest inventories, significant shifts in species composition and dominance became evident. This change was marked by a significant increase in early successional species such as yellow-poplar, red maple, and black cherry that thrived in a high light environment where a combination of fire suppression, deer herbivory, and high levels of understory shade had reduced the potential for oak success.

ACKNOWLEDGMENT

This is Scientific Article No. 2920 of the West Virginia University Agricultural and Forestry Experiment Station, Morgantown, West Virginia.

James S. Rentch is a Research Assistant Professor in the Division of Forestry at West Virginia University. His research interests include disturbance dynamics of oak-dominated forest ecosystems and wetland ecology.

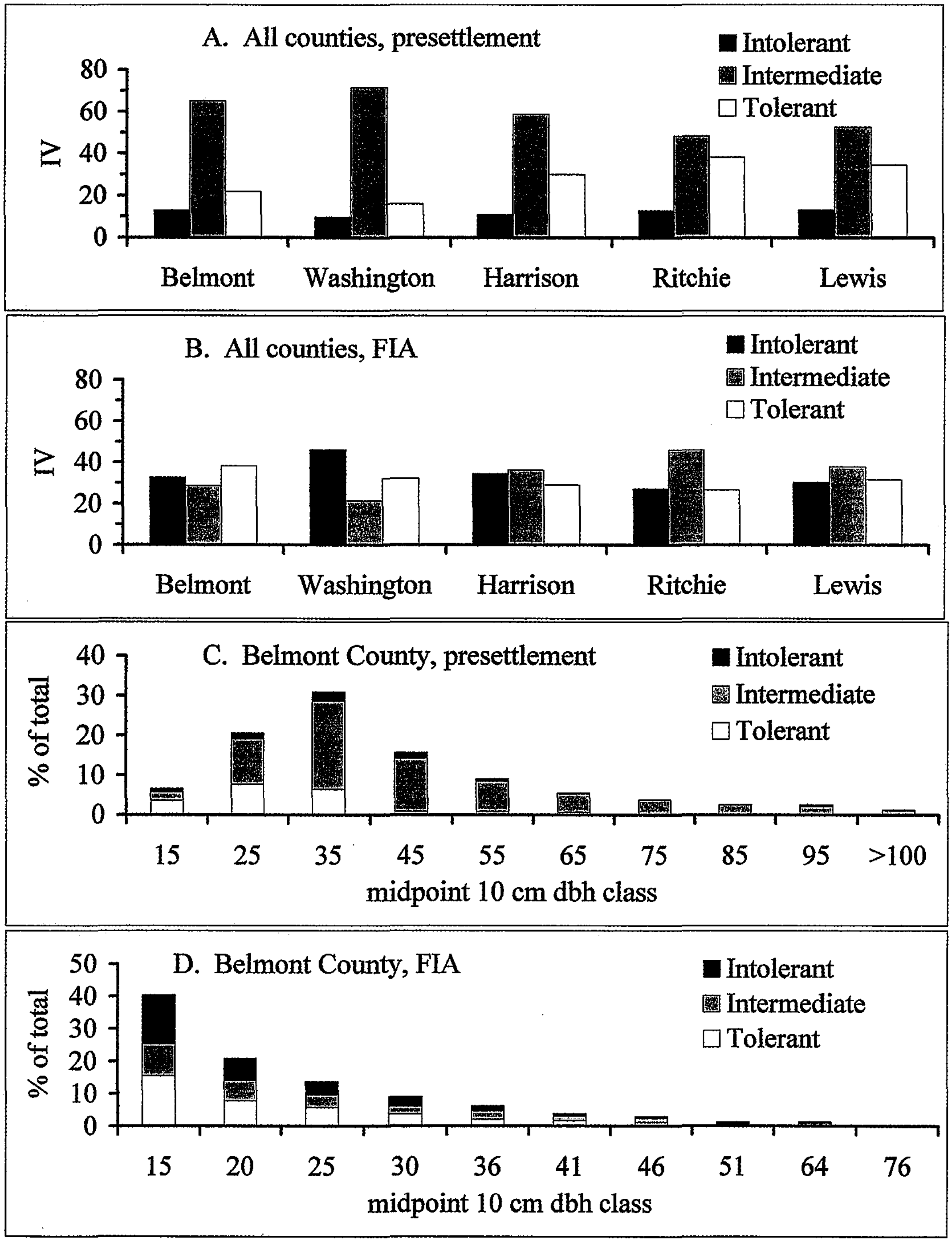


Figure 3. Comparison of importance values (A and B) and diameter distributions (C and D, Belmont County, OH, only) using witness tree tallies and FIA data. Data grouped by tolerance of shade and competition[1].

Ray R. Hicks, Jr., is Professor of Forest Ecology in the Division of Forestry at West Virginia University. He is author of the textbook, "Ecology and Management of Central Hardwood Forests."

LITERATURE CITED

Abrams, M.D. 1992. Fire and the development of oak forests. BioScience 42:346-353.

Abrams, M.D. 1998. The red maple paradox. BioScience 48:355-364.

Abrams, M.D. 2000. Fire and the ecological history of oak forests in the eastern United States. Pp. 46-55 *in* Yaussey, D.A., comp., Proceedings: Workshop on Fire, People, and the Central Hardwoods Landscape. General Technical report NE-247, U.S. Department of Agriculture, Forest Service, Newtown, Square, Pa.

Abrams, M.D. 2003. Where has all the white oak gone? BioScience 53:927-939.

Abrams, M.D., and J.A. Downs. 1990. Successional replacement of old-growth white oak by mixed mesophytic hardwoods in southwestern Pennsylvania. Canadian Journal of Forest Research 20:1864-1870.

Abrams, M.D., and D.M. McCay. 1996. Vegetation-site relationships of witness trees (1780-1856) in the presettlement forests of eastern West Virginia. Canadian Journal of Forest Research. 26:217-224.

Adovasio, J.M., and D.R. Pedlar. 2000. A long view of deep time at Meadowcroft Rockshelter. [no pagination available] *in* Proceedings, Current Archaeological Research in Pennsylvania and Related Areas, April 5-9, 2000, 65th Annual Meeting for the Society for American Archaeology, Philadelphia, Pa.

Bailey, R.G. (comp.) 1995. Description of the ecoregions of the United States. Miscellaneous Publication 1391, U.S. Department of Agriculture, Forest Service, Washington, D.C.

Beverley, R. 1971. The History and Present State of Virginia: a Selection. Bobbs-Merrill, Indianapolis, Ind.

Bonnicksen, T.M. 2000. America's Ancient Forests: From the Ice Age to the Age of Discovery. J. Wiley, New York.

Bourdo, E.A., Jr. 1956. A review of the General Land Office survey and of its use in quantitative studies of former forests. Ecology 37:754-768.

Braun, E.L. 1950. Deciduous Forests of Eastern North America. Blakiston, Philadelphia, Pa.

Bromley, S.W. 1935. The original forest types of southern New England. Ecological Monographs 5:61-89.

Brooks, A.B. 1910. Forestry and Wood Industries. Acme Pub. Co., Morgantown, W. Va.

Chapman, J, P.A. Delcourt, and P.A. Cridlebaugh. 1982. Man-land interactions: 10,000 years of American impact on native ecosystems in the Lower Little Tennessee River Valley, eastern Tennessee. Southeastern Archaeology 1:115-121.

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

Davis, M.B. 1981. Quaternary history and the stability of forest communities. Pp. 132-153 *in* D.C. West, H.H. Shugart, and D.B. Botkin, eds., Forest Succession. Springer-Verlag, New York.

Day, G.M. 1953. The Indian as an ecological factor in the northeastern forest. Ecology 34:329-346.

Delcourt, P.A., and H.R. Delcourt. 1987. Long-term Forest Dynamics of the Temperate Zone. Springer-Verlag, New York.

Delcourt, H.R., and P.A. Delcourt. 1998. Pre-Columbian native American use of fire on southern Appalachian landscapes. Conservation Biology 11:1010-1014.

Henry, J.D., and J.M.A. Swan. 1974. Reconstructing forest history from live and dead plant material—an approach to the study of forest succession in southwest New Hampshire. Ecology 55:772-783.

Iverson, L.R., A.M. Prasad, B.J. Hale, and E.K. Sutherland. 1999. An atlas of current and potential future distributions of common trees of the Eastern United States. General Technical Report NE-265, U.S. Department of Agriculture, Forest Service, Radnor, Pa. Available online <ww.fs.fed.us/ne/delaware/atlas>

Jenning, O.E. 1927. Classification of the plant societies of central and western Pennsylvania. Proceedings Pennsylvania Academy of Science 1:23-55.

Kline, V.M., and G. Cottam. 1979. Vegetation response to climate and fire in the Driftless Area of Wisconsin. Ecology 60:261-268.

Lederer, J., and W. Talbott. 1672. The Discoveries of John Lederer in Three Several Marches from Virginia, to the West of Carolina, and Other Parts of the Continent Begun in March, 1669 and Ended in September, 1670. Samuel Heyrick, London.

Leitner, L.A., and M.T. Jackson. 1981. Presettlement forests of the unglaciated portion of southern Illinois. American Midland Naturalist 105:290-304.

Lewis, R.L. 1998. Transforming the Appalachian Countryside: Railroads, Deforestation, and Social Change in West Virginia, 1880-1929. University of North Carolina Press, Chapel Hill.

Loeb, R.E. 1987. Pre-European settlement forest composition in east New Jersey and southeastern New York. American Midland Naturalist 118:414-423.

Lorimer, C.G. 1984. Development of the red maple understory in Northeastern oak forests. Forest Science 30:3-22.

Lorimer, C.G. 1993. Causes of the oak regeneration problem. Pp. 14-39 *in* D.L. Loftis and C.E. McGee, eds., Oak regeneration: serious problems, practical recommendations Research Paper NE-356, U.S. Department of Agriculture, Forest Service, Asheville, N.C.

Lorimer, C.G., J.W. Chapman, and W.D. Lambert. 1994. Tall understory vegetation as a factor in the poor development of oak seedlings beneath mature stands. Journal of Ecology 82:227-237.

Lutz, H.J. 1930. Original forest composition in northwestern Pennsylvania as indicated by early land survey notes. Journal of Forestry 28:1098-1103.

Martin, J.A. 1835. A New and Comprehensive Gazetteer of Virginia and the District of Columbia. J. Martin, Charlottesville, Va.

Maxwell, H. (chairman). 1908. Report of the West Virginia Conservation Commission. Tribune Printing Co., Charleston, W. Va.

Maxwell, H. 1910. The use and abuse of forests by the Virginia Indians. William and Mary College Quarterly Historical Magazine 19:73-103.

McCune, B., Grace, J.B., and Urban, D.L. 2002. Analysis of Ecological Communities. MjM Software Design, Glenedon Beach, Ore.

McCune, B., and Mefford, M.J. 1999. PCORD for Windows: Multivariate Analysis of Ecological Data. Version 4.0. MjM Software, Glenedon Beach, Ore.

McKelvey, A.T. (ed.). 1903. Centennial History of Belmont County Ohio and Representative Citizens. Biographical Publishing Company, Chicago, Ill.

Michaux, F.A. 1853. North American Silvan. Vol. 1. Robert P. Smith Publishing Company, Philadelphia, Pa.

Moreland, J.R. 1940. The early Cheat Mountain Iron Works. Monongalia Historical Society, Morgantown, W. Va.

Nowacki, G.J., and M.D. Abrams. 1992. Community, edaphic, and historical analysis of mixed oak forests of the Ridge and Valley Province in central Pennsylvania. Canadian Journal of Forest Research 22:790-800.

Nowacki, G.J., and P.A. Trianosky. 1994. Literature on old-growth forests of eastern North America. Natural Areas Journal 13:87-107.

Pearse, J.B. 1876. A Concise History of the Iron Manufacture of the American Colonies Up to the Revolution, and of Pennsylvania Until the Present Time. Allen, Lane & Scott, Philadelphia, Pa.

Peattie, D.C. 1950. A Natural History of Trees of Eastern and Central North America. Houghton Mifflin, Boston, Mass.

Rentch, J.S., M.A. Fajvan, and R.R. Hicks, Jr. 2003a. Oak establishment and canopy accession strategies in five old-growth stands in the central hardwood forest region. Forest Ecology and Management 184:285-297.

Rentch, J.S., M.A. Fajvan, and R.R. Hicks, Jr. 2003b. Spatial and temporal disturbance characteristics of oak-dominated old-growth stands in the central hardwood forest region. Forest Science 49:778-789.

Rice, O.K. 1970. The Allegheny Frontier: West Virginia Beginnings, 1730-1830. University of Kentucky Press, Lexington, Ky.

Ruffner, C.M., and M.D. Abrams. 1998. Relating land-use history and climate to the dendroecology of a 326-year old *Quercus prinus* talus slope forest. Canadian Journal of Forest Research 28:347-358.

Russell, E.W. 1980. Vegetational change in northern New Jersey from precolonization to the present: a palynological interpretation. Bulletin Torrey Botanical Club 107:432-446.

Sears, P.B. 1925. The natural vegetation of Ohio. Ohio Journal of Science 25:139-149.

Spurr, S.H. 1951. George Washington, surveyor and ecological observer. Ecology 32:544-549.

Sprugel, D.G. 1991. Disturbance, equilibrium, and environmental variability: what is 'natural' vegetation in a changing environment? Biological Conservation 58:1-18.

Stephenson, S.L., A.N. Ash, and D.F. Stauffer. 1993. Appalachian oak forests. Pp. 255-304 *in* W.H. Martin, S.G. Boyce, and A.C. Echternacht, eds., Biodiversity of the Southeastern United States: Upland Terrestrial Communities. J. Wiley, New York.

Stout, W. 1933. The charcoal iron industry of the Hanging Rock iron district: its influence on the early development of the Ohio Valley. Ohio State Archaeological and Historical Quarterly 42:72-104.

Sutherland, E.K. 1997. History of fire in a southern Ohio second-growth mixed oak forest. Pp. 172-183 *in* S.G. Pallardy, R.A. Cecich, H.G. Garrett, and P.S. Johnson, eds., Proceedings of the 11th Central Hardwood Forest Conference. General Technical Report NC-188, U.S. Department of Agriculture, Forest Service, St. Paul, Minn.

U.S. Department of Agriculture. 2001. Forest Inventory and analysis data base and retrieval system. U.S. Department of Agriculture, Forest Service, Washington, D.C. Available online <http://www.srsfia.usfs.msstate.edu>.

Wade, D.D., B.L. Brock, P.H. Brose, J.B. Grace, G.A. Hock, and W.A. Patterson III. 2000. Fire in eastern ecosystems. Pp. 53-96 *in* J.K. Brown, and J.K. Smith, eds., Wildland fire in ecosystems: effects of fire on flora. General Technical Report RMRS-42 Vol. 2, U.S. Department of Agriculture, Forest Service, Ogden, Utah.

Watts, W.A. 1979. Late Quaternary vegetation of central Appalachia and the New Jersey coastal plain. Ecological Monographs 49:427-469.

Webb, T., III. 1988. Glacial and holocene vegetation history: eastern North America. Pp. 385-414 *in* B. Huntley and T. Webb, eds., Vegetation History. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Yarnell, S.L. 1998. The southern Appalachians: a history of the landscape. General Technical Report SRS-18, U.S. Department of Agriculture, Forest Service, Asheville, N.C.