

Changes in Older and Younger Woods in West-Central Ohio¹

JAMES R. RUNKLE, LISA A. FAIRBANKS, KEELAN H. ARMSTRONG, TIMOTHY S. CAMPBELL, AND AMANDA L. ESPENSCHIED-REILLY, Department of Biological Sciences, Wright State University, Dayton, OH 45435

ABSTRACT. This study examines changes in two forest stands in the *Quercus-Acer saccharum* forest region of west central Ohio: an old-growth stand changing from *Quercus*-dominated to *Acer saccharum*-dominated and a stand established following agricultural abandonment about 1950. Both stands are in the Wright State University woods. Permanent plots were sampled in 1980 (younger stand only), 1982 (older stand only), 1993, and 2000. The older stand had more small, fewer intermediate, and more large stems than the younger stand. The plot in the new stand showed a bell-shaped distribution with most stems established shortly after land abandonment. Mortality decreased and growth increased with stem size for both stands. *Acer saccharum* in all sizes and large *Quercus* dominated the older stand. The younger stand was dominated by *Robinia pseudo-acacia* with *Acer saccharum* also important. In the older plots small stems generally were clustered, intermediate-sized stems randomly distributed, and the largest stems regularly distributed. In the younger plot small stems were aggregated while larger ones were randomly distributed. *Quercus* regenerated well until the late 1800s, singly or in small groups, but few stems have become established since 1900. *Quercus* may need fires or grazing to regenerate successfully. Both stands are changing to increased dominance by *Acer saccharum* and other shade-tolerant species as they lose species (*Robinia pseudo-acacia* in the younger stand, *Quercus* in the older stand) more successful under past than present conditions.

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INTRODUCTION

In much of the Midwest the last two centuries of changing land management practices have been characterized partly by a decrease in oaks (*Quercus*), affecting first their regeneration and later their importance in the canopy (Whitney and Somerlot 1985; Lorimer 1993; Walters and McCarthy 1997; McCarthy and others 2001). Other species, such as sugar maple (*Acer saccharum*), have waxed as the oaks have waned. This change in species dominance has occurred even in stands which fit many of the definitions of old growth (Runkle 1996), such as no history of large-scale logging and the presence of old trees and both standing and fallen coarse woody debris. Few studies have quantified the rates and directions of changes in those stands.

Other understudied aspects of forest dynamics are the speed and direction of changes in mid-successional forests. Ohio has gone from 12% forested in 1940 to 30% forested in 1990 (Griffith and others 1993). Therefore over 18% of the land area of Ohio in 1991 was composed of forests <50 yr old. Understanding the dynamics of those forests is thus important for understanding the natural and economic environment of Ohio, both at present and in the future. One unresolved question is whether changes in older and mid-successional forests are leading to the same or to different types of vegetation in the future.

The goals of this study are: 1) to describe the species composition and structure of an old-growth (never clear-cut) woods dominated by sugar maple and oaks sampled in 1982, 1993, and 2000; 2) to describe the species composition and structure of a stand that was

released from agriculture about 1950 and sampled in 1980, 1993, and 2000; 3) to document changes in structure in both those stands; 4) to determine changes in species composition of the older stand, especially for oak and maple; 5) to determine the historical pattern of oak regeneration in that stand; and 6) to determine whether the two stands might eventually have similar vegetation if current trends persist.

METHODS

Sites and Vegetation Sampling

The study site is located in the Wright State University's (WSU) campus woods. Wright State University is located in Bath Township, Greene County, OH (39°47' N, 84°3'W). The climate of Greene County is considered continental (Miller 1969). Mean annual precipitation from 1971 to 2000 was 102 cm, with a mean January temperature of -2° C and a mean July temperature of 23° C (US Weather Service 2003). The study area soils are Miamian silt-loams (Garner and others 1978). Braun (1950) included Greene County within the beech-maple (*Fagus-Acer*) forest region. Gordon (1969) classified the area of the WSU woods as an oak-maple forest. An earlier publication on the WSU woods (DeMars and Runkle 1992) explored relationships among the ground layer vegetation, soil factors, topographic position, and stand age. Aerial photographs from the USGS for 1940, 1949, 1956, 1950, and 1968 were used to document stand ages.

Three plots were established within the WSU woods. The Chiles plot (39°46.964'N, 84°3.408'W) was established in 1982 (Chiles 1985). It is a 0.39 ha transect made up of 39 contiguous 10 × 10-m squares. The transect runs along an upland area with an arm extending perpendicular to the main transect down slope to a

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stream. In 1982 the diameter at breast height (1.4 m) and species for all living stems ≥ 2.0 -cm dbh were recorded, and each stem was tagged for future identification. Although sugar maple dominated all parts of the topographic gradient, the areas nearest the stream had significantly higher basal areas of hackberry (*Celtis occidentalis*), Ohio buckeye (*Aesculus glabra*), black cherry (*Prunus serotina*), and bush honeysuckle (*Lonicera maackii*) (Chiles 1985). The lower sections also had relatively high values for soil moisture, potassium, calcium, and magnesium (Chiles 1985; DeMars and Runkle 1992). These plots were resampled in 1993 (Campbell 1995) and 2000. The fate (living, dead) and dbh were measured for previously measured stems. New stems ≥ 2.0 -cm dbh were recorded. In addition, in 1993 and 2000 all stems ≥ 1.0 m in height were measured for subplots 14-23.

The Old and New Woods plots (referred to in this paper as OLD and NEW, respectively) are both 0.5 ha (50 m \times 100 m) and were established in 1989-1990 by students in an ecology course under the direction of the first author (J.R.R.). The students recorded all stems ≥ 1.0 m high for dbh, species, and height, noted if the tree was dead or alive, and marked each with an identification number and tag. The OLD plot never has been completely clear-cut but probably has had selective cutting and livestock grazing (Hagan 1987; DeMars and Runkle 1992). The NEW plot was an agricultural field abandoned about 1950. We resampled the plots in 1993 (Campbell 1995) and 2000: data from those two resamples are presented here. Both plots are close together on a flat upper section of the woods (OLD at 39°47.002'N, 84°3.272'W; NEW at 39°47.133'N, 84°3.208'W). Bush honeysuckle was not sampled in the NEW plot because its abundance made it difficult to identify individuals.

In the Chiles plot the location of each stem was estimated to the nearest meter on both the x and y coordinates. In the NEW and OLD plots in 1993 stem locations were measured with the Sonin Combo Pro electronic distance-measuring device.

The main comparisons of this study are between the NEW plot and the two plots in the older woods (Chiles and OLD plots). The Chiles plot covers a wider range of topographic positions than the OLD plot and adds a longer time component to the comparisons.

In 1980, contiguous plots were established along transect lines 50 m apart throughout the WSU woods. Stems ≥ 9.0 cm dbh were recorded for plots 5.0 m long (along the transect) and 8.0 m wide. Stems ≥ 0.5 m high and < 9.0 cm dbh were recorded for plots 5.0 m long (along the transect) and 4.0 m wide. For comparison with the NEW plot, we selected 21 of those plots, located near the NEW plot and in the same general type and age of forest.

Historical Patterns of Oak Regeneration

Dendrological techniques were used to determine the historical patterns of establishment for white oak (*Quercus alba*), sugar maple, and white ash (*Fraxinus americana*) (Hagan 1987). We selected 76 white oaks,

scattered throughout the older woods, for aging in 1986. We also aged the four nearest canopy neighbors of each of the selected white oaks. Because our initial emphasis was on white oak establishment we did not repeat the process using other species as central trees. Increment cores were taken from all five trees, as close to their bases as possible. A second core was taken if the first did not approach the center of the tree. Cores were dried, mounted, and sanded. Some cores were excluded from the analysis because of heart rot, breaks, insect damage, and other factors. We dated 167 cores in total. Cross dating was used to reduce errors in estimating establishment dates. Narrow rings were noted for most trees in years 1874, 1911, 1914, 1936, 1940, 1941, 1954, and 1977. Sometimes the age of the tree was estimated if the core did not go through its center. We measured yearly increment growth on 112 of the dated cores using an increment-measuring bench (Swetnam and others 1985).

Analytical Methods

Size distributions of stems were compared using the Kolomogorov-Smirnov two-sample test for large samples (Sokal and Rohlf 1995). Comparisons were made between distributions in 1993 and 2000 for all three plots and among the three plots for the year 2000.

Growth was compared for the NEW and OLD plots using analysis of variance followed by Tukey's procedure (GLM procedure from SAS 1995). Significant ($P \leq 0.05$) variation was determined among five dbh size classes for each plot and between the two plots for each size class.

Mortality was calculated using the fraction of stems that died in the sampling intervals (1993-2000 and, for the Chiles plot, 1982-1993). Mortality rates were calculated as a constant percent per year (Runkle 1990; Sheil and others 1995):

$$M = 100 * [1 - (S/N)^{1/t}]$$

where M = annual mortality (% of stems/yr), S = the number of surviving stems in the second survey, N = the number of stems in the first survey, and t = the number of years between surveys. Significant differences between mortality rates were calculated using the chi-square test comparing ratios of initial number of stems to surviving number.

Pattern analysis in the NEW and OLD plots was calculated using the Clark-Evans plant-to-plant index (Clark and Evans 1954). The Clark-Evans index is the ratio of the average actual distance from each plant to its nearest neighbor divided by the distance expected if all stems were randomly distributed. A value less than one indicates that stems are clumped. A value greater than one indicates that stems are regularly distributed. Significance can be tested using the Z-distribution for the normal curve. A problem with using this index in a plot is that many stems will have nearest neighbors outside the plot. In order to compensate for this edge bias, we used the developed empirically derived formulas of Donnelly (1978), setting plot area = 5000 m² and edge length = 300 m. Significance was set as $\alpha = 0.05$.

RESULTS

Vegetation Structure, Composition, and Changes

All three plots had similar basal areas of about 30 m²/ha in 2000 (Table 1). Basal area increased in the Chiles and NEW plots for each sample interval and decreased in the OLD plot. Net changes in the old plots were <1.0%/yr; those in the NEW plot were 1.4%/yr from 1993 to 2000 and higher, earlier.

TABLE 1

Changes in basal area over time for the three plots based on stems ≥25 cm dbh.

Plot	Basal area (m ² /ha)			Annual Net Change (%)	
	1982	1993	2000	82-93	93-00
Chiles	27.6	29.7	30.5	0.66	0.38
OLD	-	32.0	30.5	-	-0.68
NEW	14.3*	27.0	29.8	5.01*	1.42

*Based on a site sampled near the NEW plot in 1980.

Size structure of the plots varied with plot and with sample year (Fig. 1). Stem size distributions differed significantly ($P \leq 0.05$) between samples for each of the three plots individually. Each plot had more small stems in 1993 than in 2000. Stem size distributions also differed significantly between each pair of plots in 2000. The largest absolute difference in size distributions was between the NEW plot and the two older plots, with the latter having a larger fraction of small stems. Stem totals were 1064 in 1993 and 904 in 2000 for the Chiles plot, 2720 in 1993 and 1999 in 2000 for the OLD plot, and 699 in 1993 and 558 in 2000 for the NEW plot.

Mortality rates generally decreased with increased stem size (Fig. 2). Stems <2.0 cm suffered a high mortality of 6-8%/yr in all three plots. Mortality rates varied significantly with stem size if the smallest size class (stems <2.0 cm dbh) was included but not if it was omitted for the two older plots. Mortality in the NEW plot did not vary significantly with stem size even including the smallest size class, although the trend was in

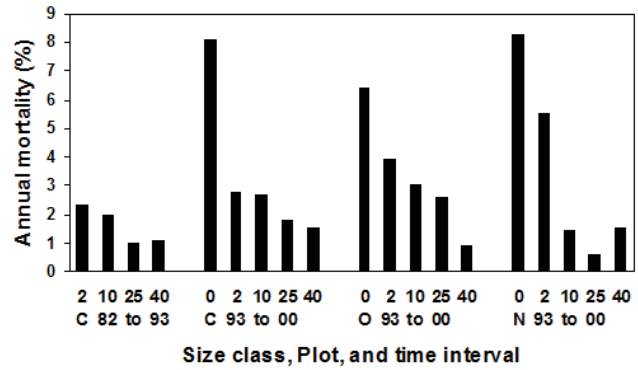


FIGURE 2. Annual mortality (%) as a function of stem size for the three plots and two time intervals. Plot-intervals are coded C82-93 for Chiles plot from 1982-1993, C93-00 for Chiles 1993-2000, O93-00 for OLD 1993-2000, and N93-00 for NEW 1993-2000. Size classes are coded with the smallest dbh (cm) included in that size class.

the same direction as for the older plots ($P = 0.06$). Canopy stem mortality was only about 1.0%/yr for all three sites and both time periods. Mortality rates for a given stem size did not vary significantly among the three plots from 1993 to 2000.

Growth rates increased with stem size (Fig. 3). The highest growth rates were in the NEW plot for stems ≥25 cm. Growth was significantly different between the OLD and NEW plots for the two largest size classes but not for the three smallest size classes. For the NEW plot the two largest size classes grew similarly to each other and significantly greater than smaller size classes. The two smallest size classes also were similar to each other and significantly smaller than the other size classes. Growth for stems 10-25 cm dbh was significantly different than growth for the other size classes. For the OLD plot growth for each size class was significantly different than growth for each other size class except that growth rates for sizes 10-25 and 25-40 cm dbh did not differ significantly from each other.

Sugar maple dominated the smaller size classes (<25 cm dbh, usually in the understory) in all plots for all time periods except for the youngest (NEW, 1980) (Table 2), consisting 60-80% of stems <2.0 cm and 48-79% of stems 2.0-25 cm. Further, its relative density of stems 2.0-25 cm dbh increased over time for all three

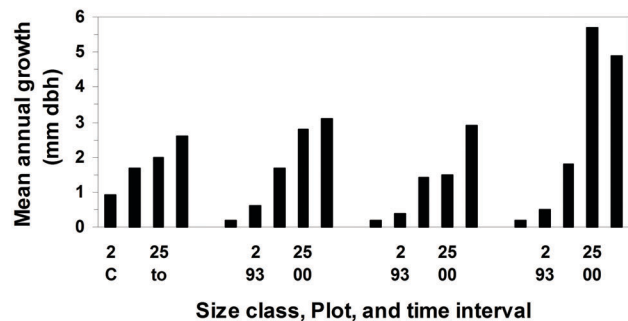


FIGURE 3. Mean growth (mm dbh) as a function of stem size for the three plots and two time intervals. Plot-intervals and size classes are coded as in Figure 2.

FIGURE 1. Cumulative dbh distributions of stems for the three plots in 1993 and 2000. Stems >40 cm dbh were not included in order to accentuate differences in smaller stems.

TABLE 2

Relative density (%) of understory stems for different plot-year combinations. Columns identify plot-year combinations: C = Chiles, O = OLD, N = NEW, 80 = 1980, 82 = 1982, 93 = 1993, and 00 = 2000. Species are listed if at least one value is $\geq 5\%$.

Species*	Stems <2.0 cm dbh							Stems 2.0-25 cm							
	C93	C00	O93	O00	N80	N93	N00	C82	C93	C00	O93	O00	N80	N93	N00
<i>Acer saccharum</i>	61	60	81	80	39	71	77	50	48	56	50	63	62	75	79
<i>Aesculus glabra</i>	10	15	5	6	0	0	0	29	30	27	19	17	2	0	0
<i>Celtis occidentalis</i>	1	1	3	1	0	0	0	5	1	4	14	5	11	0	0
<i>Fraxinus americana</i>	5	0	5	2	29	0	0	3	2	1	7	3	8	8	6
<i>Fraxinus quadrangulata</i>	15	15	3	3	16	0	0	3	9	7	2	2	0	0	0
<i>Lindera benzoin</i>	5	7	0	0	0	0	0	2	1	1	0	0	0	0	0
<i>Lonicera maackii</i>	0	1	1	5	0	-	-	1	1	1	1	3	0	0	0
<i>Prunus serotina</i>	0	0	0	0	4	9	6	3	2	2	2	1	2	1	1
<i>Acer negundo</i>	0	0	0	0	0	13	13	0	0	0	0	0	0	0	0
<i>Robinia pseudo-acacia</i>	0	0	0	0	8	0	0	0	0	0	0	0	9	11	10

*Other species found on plots were *Acer negundo* (NEW), *Acer rubrum* (OLD, NEW), *Asimina triloba* (Chiles), *Carpinus caroliniana* (Chiles), *Carya cordiformis* (Chiles, OLD), *Cercis canadensis* (NEW), *Cornus florida* (Chiles), *Gleditsia triacanthos* (NEW), *Juglans nigra* (Chiles), *Ostrya virginiana* (Chiles, OLD), *Ulmus americana* (Chiles, OLD, NEW), *Ulmus rubra* (OLD, NEW), and *Viburnum prunifolium* (Chiles, OLD).

plots. Ohio buckeye had relatively high densities for both understory size classes in the older plots. Hackberry and blue ash (*Fraxinus quadrangulata*) also were important in the older plots. In the NEW plot, box elder (*Acer negundo*) had relatively high densities of stems <2.0 cm, and black locust had relatively high densities of stems 2.0-25 cm. White ash decreased in relative density for both understory size classes for all three plots from 1993-2000. The area near the NEW stand in 1980 had relatively more small black locust (*Robinia pseudo-acacia*) and white ash and relatively less sugar maple than in 1993. No small oaks were found in any of the plots.

Species composition of stems ≥ 25 cm (usually present in the canopy) varied greatly with stand age (Table 3). Sugar maple dominated the older stands with relative densities of 58-71% and relative basal areas of 46-64% for each plot-date combination. White ash had the second highest relative density for the Chiles plots although was less important in the OLD plot. Oaks (white = *Q. alba*, red = *Q. rubra*, and chinkapin = *Q. muehlenbergii*) were important in both older plots, making up 20-37% of the basal area. Composition did not change greatly over the time span of this study. Black locust dominated the NEW plot with 44-45% of both relative density and relative dominance in both samples. From 1993-2000 sugar maple and white ash increased in importance in the NEW plot while black cherry, cottonwood (*Populus deltoides*), and American elm (*Ulmus americana*) decreased. In 1980 in the area near the NEW plot almost all stems ≥ 25 cm dbh were black locust.

Sugar maple showed the J-size-class distribution in the older plots typical of species regenerating well (Fig. 4). Some other species in the older plots, for

example, buckeye and white ash, showed similar size-class distributions, although their densities of larger stems were too low to indicate clearly that they are replacing themselves in the stand. In contrast the oaks were found only as large stems. Species in the NEW plot, for example, sugar maple, white ash, and black locust, showed more bell-shaped distributions resulting from the even-aged cohort that established following field abandonment. Sugar maple had some small stems, indicating that it was able to reproduce to at least some degree. Black locust had no small stems, indicating that its reproduction success would be limited to the one post-disturbance cohort.

The OLD and NEW plots had different species dispersion patterns (Table 4). The main pattern in the OLD plot was for small stems to be aggregated both for all species together and for the main species individually. Intermediately-sized stems were randomly dispersed. Larger stems (all species and sugar maple by itself) were evenly distributed. In the NEW plot small stems were aggregated while larger stems were randomly distributed.

Historical Patterns of Oak Regeneration

White oak was uneven aged with a mean establishment date of 1839. Regeneration occurred in the 1700s (under Native American land use) and steadily through most of the 1800s (under pioneer and settler land use) (Fig. 5). All successful oak regeneration in the 1900s occurred in one section of the woods that appeared more open (due to grazing?) than the rest of the woods in a 1940 aerial photograph. Sugar maple also was uneven aged, although younger, with a mean establishment date of 1889. Its regeneration increased greatly in the late 1800s and has continued to be high through the

TABLE 3

Changes in species importance values for the three plots over time for stems ≥ 25 cm dbh. Column headings as in Table 2.

Species	Relative density								Relative basal area							
	C82	C93	C00	O93	O00	N80	N93	N00	C82	C93	C00	O93	O00	N80	N93	N00
<i>Acer saccharum</i>	58	64	63	69	71	0	5	14	46	49	47	58	64	0	3	8
<i>Fraxinus americana</i>	8	7	7	1	2	0	20	23	14	14	16	1	1	0	16	23
<i>Quercus alba</i>	6	5	6	15	12	0	0	0	10	11	11	26	19	0	0	0
<i>Aesculus glabra</i>	6	4	4	0	0	0	0	0	6	5	5	0	0	0	0	0
<i>Quercus muehlenbergii</i>	6	5	4	3	3	0	0	0	6	6	4	5	5	0	0	0
<i>Ulmus rubra</i>	4	3	3	1	2	16	4	2	5	4	5	1	1	16	3	3
<i>Quercus rubra</i>	3	1	1	3	3	0	0	0	5	3	3	6	7	0	0	0
<i>Carya cordiformis</i>	3	1	1	4	5	0	0	0	2	1	1	2	2	0	0	0
<i>Prunus serotina</i>	1	1	1	0	0	0	11	7	2	2	2	0	0	0	12	10
<i>Robinia pseudo-acacia</i>	0	0	0	0	0	84	45	44	0	0	0	0	0	84	44	44
<i>Populus deltoides</i>	0	0	0	0	0	0	7	5	0	0	0	0	0	0	12	10
<i>Ulmus americana</i>	0	0	0	0	0	0	4	0	0	0	0	0	0	0	5	0
Other*	6	7	5	2	4	0	6	3	5	5	5	1	2	0	4	4

*Other species found on plots were *Celtis occidentalis* (Chiles, OLD), *Carya glabra* (Chiles), *Juglans nigra* (Chiles), *Acer rubrum* (OLD), *Gleditsia triacanthos* (NEW), and *Fraxinus quadrangulata* (NEW).

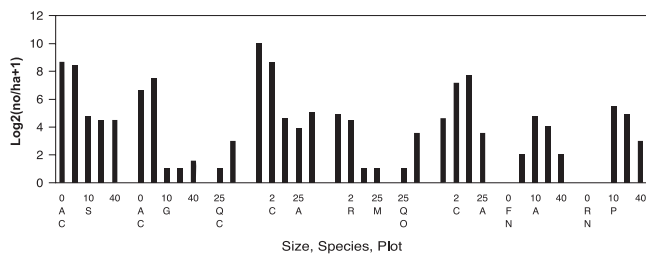


FIGURE 4. Size class distribution for selected species in 2000 for the three plots. Size classes are coded with their minimum dbh (cm). Species are coded using first two letters of genus and species from Table 2 except that QU = combined total for the three *Quercus* species. Plots are coded C = Chiles, O = OLD, and N = NEW.

present. White ash became established in low levels throughout the 1800s with a large increase in the late 1800s and the 1900s. White oak and sugar maple showed similar patterns of increment growth with an increase in the early 1900s and a decrease since about 1950 (Fig. 6). White ash grew more slowly than white oak and sugar maple in the early 1900s but more rapidly since 1960. Establishment dates of white oaks were compared with those of their nearest neighbors (Table 5). Most of the nearest neighbors established more than 20 yr before or after the central white oak.

DISCUSSION

Composition and Structure of Older Woods

Gordon (1969) classified the area now composing the

TABLE 4

The Clark-Evans index values (as %) for species and size classes for the Old Woods plot and New Woods plot. Values <100 imply clumping; values >100 imply regular distribution.

Location/Species	<1	1-10	10-25	≥ 25	all
Old Woods					
<i>A. saccharum</i>	88*	100	113	117*	103*
<i>A. glabra</i>	61*	63*	-	-	60*
<i>F. americana</i>	59*	87*	-	-	79*
<i>C. occidentalis</i>	85	94	-	-	92
<i>Q. alba</i> ^a	-	-	-	129	129
all species	91*	104*	111	120*	109*
New Woods					
<i>A. saccharum</i>	65	91*	100	-	101
<i>F. americana</i>	-	39*	83	81	77*
<i>P. serotina</i>	-	-	-	-	49*
<i>R. pseudoacacia</i>	-	-	75*	84	82*
<i>U. americana</i>	-	-	81	-	93
all species	63*	91*	104	102	99

^aOnly stems ≥ 25 cm dbh were abundant enough for index values. *P ≤ 0.05 .

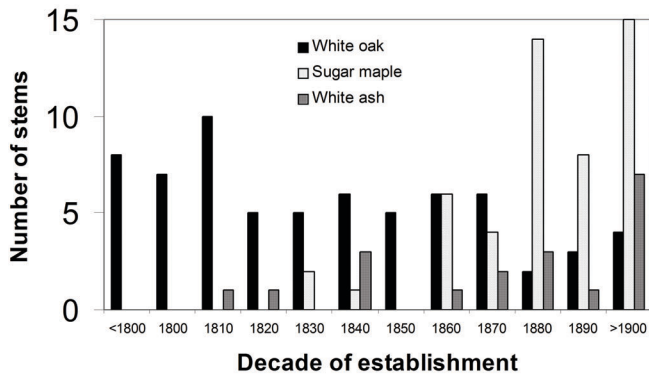


FIGURE 5. Establishment decades for white oak, sugar maple, and white ash.

Wright State University woods as in the oak-sugar maple forest type. His list of dominants is still an accurate description of the older woods studied: white oak, red oak, black walnut (*Juglans nigra*), sugar maple, white ash, slippery elm (*Ulmus rubra*), basswood (*Tilia americana*), black cherry, bitternut hickory (*Carya cordiformis*), and shagbark hickory (*C. ovata*). Gordon (1969) stated that few old stands of this type remain due to its extraordinary natural fertility for agriculture. Few studies of this forest type have been done in Ohio compared to forests in the beech-maple forest region (Vankat and others 1975; Kupfer and Runkle 1996; Fore and others 1997) and the mixed oak forest region (McCarthy and others 2001). The general high diversity of forest types in south-western Ohio also makes it impossible to compare our results too closely to other studies (Bell 1978). Tawawa Woods, located in the same county, has recently been studied (Lowell and others 2003; Silvius and others 2003). Its herbaceous flora is similar to that previously reported for the WSU woods (DeMars and Runkle 1992). Its tree composition also is similar although WSU has relatively more sugar maple, white ash, white oak, and chinkapin oak, whereas Tawawa Woods has more black cherry, tuliptree (*Liriodendron tulipifera*), beech (*Fagus grandifolia*), and sassafras (*Sassafras albidum*) than the WSU woods. The recent occurrence of a hurricane in Tawawa Woods may account for some of those species differences.

The basal area of the older woods (30 m²/ha) is similar to that from other mature woods in Ohio. Bell (1978) found a range of basal areas of 13-40 m²/ha

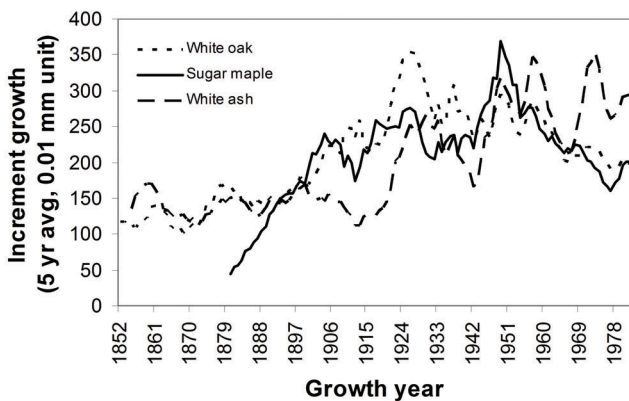


FIGURE 6. Increment growth for white oak, sugar maple, and white ash.

TABLE 5

Tree establishment patterns. The number of nearest neighbor trees whose ages are within 20 years of the age of the central white oak out of the total number of trees aged. A maximum of four nearest neighbors were aged for each central white oak; often, however, one or more of those trees could not be aged accurately.

No. of trees aged	Trees aged within 20 years of the central white oak				
	0	1	2	3	4
1	10	3	-	-	-
2	7	14	1	-	-
3	7	4	1	2	-
4	4	3	0	2	0

and a mean of 24 m²/ha for 54 sites in south central Ohio. Vankat and others (1977) found basal areas of 17-28 m²/ha for a southern Ohio site with relatively more oaks and less sugar maple than the WSU woods. McCarthy and others (2001) found basal areas of 31 and 35 m²/ha for an old growth forest in east central Ohio dominated by oaks and maples. Runkle and others (1984) found a basal area of 32 m²/ha for the old-growth beech-maple stand in Hueston Woods.

Structure and Composition of Younger Woods

Few studies of successional forests have been done in Ohio. Hoyer and others (1979) studied stands aged 3, 9, 25, 80 and >120 years located in southwestern Ohio. Their mid-successional stands were similar to ours in containing slippery elm, white ash, hackberry, sugar maple, and black cherry. They contained far less black locust, however. Ramey-Gassert and Runkle (1992) looked at 17 woodlots in the same county as the WSU woods and varying in disturbance history and species composition. Compared to their disturbed sites the WSU younger woods contained high amounts of black locust and cottonwood and average amounts of black cherry, white ash, and sugar maple.

The basal area of the younger woods is higher than that for successional stands in oak forests in south central Ohio of 22-25 m²/ha (Goebel and Hix 1997; Williams and Heiligmann 2003). It is similar to the basal areas found by Ramey-Gassert and Runkle (1992), which ranged 17-37 m²/ha and were not correlated with stand disturbance history or species composition.

The younger WSU woods are unusual among Ohio published studies in their high dominance by black locust. In Ohio, black locust is found only in the southern counties, mostly on moist, rich, loamy soils or those of limestone origin (Burns and Honkala 1990). Boring and Swank (1984) found it to dominate clearcut oak forests in North Carolina, consisting 71% of the stand basal area for stands aged 4 yr and 51-56% basal area for stands 17 and 38 yr. Black locust grows very rapidly in such stands for 10-30 yr then its growth slows rapidly. It has a relatively short lifespan.

Demography of Stems and Stand Changes

Runkle (2000) summarized basal area growth rates from the literature for old-growth stands sampled at least twice. The Chiles plot showed normal basal area increases of 0.4-0.7%/yr. The decrease in the OLD plot is unusual. It possibly is due merely to chance acting on small sample size but also could be a sign that the forest is undergoing reorganization to a new state with fewer oaks. The rapid increases in basal area in the NEW plot are substantially higher than those shown by old-growth stands, not surprisingly.

This study found mortality to decrease and growth rates to increase as stem size increased. These results agree well with the literature (Parker and others 1985; Runkle 1990, 2000; Forrester and Runkle 2000; Wyckoff and Clark 2002). Exceptions in the literature include beech, where beech bark disease causes increased mortality rates of larger stems (Runkle 1990; Forrester and others 2003). Several studies also find mortality to increase in the very largest stem sizes. The present study had too few of those largest stems for this trend to be tested.

Changes in Species Composition of Older Woods: Oak Versus Maple

Oaks dominated much of the eastern United States when the dominant human influence was by Native Americans. Oaks continued to regenerate successfully under the influence of pioneers and settlers in the 1800s in the Midwest (Hagan 1987; Crow 1988; Lorimer 1993; Johnson 1994). Red oak may have increased during that time due to human-promoted activities such as grazing and fire (Crow 1988; Loftis 1990b). However, oak regeneration decreased in the 1900s through much of its range in the eastern United States (Whitney and Somerlot 1985; McGee 1986; McGee and Loftis 1993; Lorimer 1993; Sander and Graney 1993; Lorimer and others 1994; Goebel and Hix 1997; Walters and McCarthy 1997; McCarthy and others 2001). This decrease is particularly striking on better quality sites where shade-tolerant saplings and shrubs have proliferated (Ramey-Gassert and Runkle 1992; McGee and Loftis 1993; Lorimer 1993; Sander and Graney 1993; Lorimer and others 1994; Johnson 1994; Stanturf and others 1997; Abrams 1998; Silvius and others 2003).

Oaks, although often identified as of intermediate or low shade tolerance (Baker 1949), can not be stimulated to regenerate merely by cutting openings in the canopy (Sander and Clark 1971; Crow 1988; Hodges and Gardiner 1993; Marquis and Twery 1993). Oaks are not an important component of younger stands establishing after land abandonment from agriculture (Whitney and Somerlot 1985), despite the open conditions thought to be favorable to shade intolerant species. Oak seedlings do respond to increases in light by increased growth (Crow 1988, 1992; Hodges and Gardiner 1993; Johnson 1994). However, merely cutting a canopy opening on good sites releases the advance regeneration of shade tolerant species more than oaks. Indeed, one way to increase oak regeneration has been to use herbicides against shade-tolerant competitors

(Crow 1992; Hodges and Gardiner 1993; Johnson 1993, 1994). The key to successful oak regeneration is to establish a high density of oak saplings before canopy openings are created (Sander and others 1984; Loftis 1990a; Ward 1992). Lorimer and others (1994) found that removal of small canopy trees and understory stems increased the survival, height, and density of both planted and naturally occurring red oak. These studies indicate that competition with understory saplings is a key factor affecting oak regeneration.

Several factors might have reduced this competition in previous centuries, thereby promoting oak regeneration. Ground fires were more common before modern fire suppression techniques were developed. Fires keep overall sapling and shrub levels low, reducing competition. Oaks are physiologically and morphologically more fire resistant than their competitors (Crow 1988; Abrams 1992; Lorimer 1993; Van Lear and Watt 1993; Miller 1993; Lorimer and others 1994; Johnson 1994; Kruger and Reich 1997a,b; Abrams and Seischab 1997; Laatsch and Anderson 2000). Several authors find single fires to have little lasting impact and hypothesize that a series of fires is necessary to regenerate oaks. Higher past grazing levels also may have favored oaks (Crow 1988, 1992; Lorimer 1993; Smith 1993; Johnson 1994).

Farmers in Greene County in the 1800s often owned several disjunct properties. They owned a variety of livestock at least some of which were allowed to range in their woodlots. The land now consisting of the WSU woods had been owned by several different individuals and was broken into different parcels. One particular change in ownership for the parcel containing most of the older woods occurred near the time when oak regeneration began to decline and regeneration by sugar maple and white ash began to increase. Isaac Mays, in a will of 1880, gave two sons "the right to pass over the Rockafield farm so that they can get to their timberland." He thus identified the woods as intact but used for some harvest of forest products, presumably timber. This will indicates that he separated the woods from the land where his sons had their main farm, suggesting that access to and use of that woods decreased. Further, after his wife died in 1886 the land was held in a trust from 1886 to 1907 and presumably was little used during that time. The great increase in sugar maple and white ash establishment at that time is similar to increases after livestock grazing has stopped in woodlots (Den Uyl and others 1938). Before the 1880s, oaks in the WSU woods regenerated regularly (Fig. 6) and either singly or in small openings (Table 5). They do not regenerate well following agricultural abandonment (the NEW plot). They are not reproducing well in the Chiles or OLD plots at present. Current weather conditions seem generally favorable to oak, leading to faster growth than in the 1800s (Fig. 6; Rubino and McCarthy 2000). These results suggest that disturbance of the understory, such as by fires or grazing, is necessary to decrease the density of competitors and allow oak to regenerate successfully.

Convergence?

The forests of both the NEW plot and the Chiles and OLD plots are changing in composition. In the NEW plot the change in vegetation appears to be driven by successional changes, as species adapted to open conditions following agricultural abandonment are unable to reproduce in the understory. In the older plots, changes in land management practices that affect the understory appear to be changing species establishment success rates. In both stands the change in dominance occurs slowly, requiring a tree generation for the dominants established in different conditions to disappear from the stand. In the NEW plot this process requires about a century for black locust to die off; in the older plots it requires perhaps two to three centuries for the oaks to be gone. Both older and younger plots seem to be converging to strong dominance by sugar maple, suggesting that eventually (perhaps two centuries from now), given no more major changes in conditions (unlikely), the two stands may converge to a similar composition.

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