Spatial and Temporal Disturbance Characteristics of Oak-Dominated Old-Growth Stands in the Central Hardwood Forest Region

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ABSTRACT. Using a radial growth averaging technique, decadal-scale growth changes of 150- to 350-yr-old overstory oaks were used to identify canopy disturbance events in five old-growth stands, and canopy disturbance intervals were estimated using frequency analysis. Stem maps and tree-establishment and canopy-accession chronologies were then used to reconstruct the size of canopy openings. Between 1700 and 1990, median canopy disturbance interval was approximately 3 yr for each stand; larger disturbances involving two or more trees occurred about every 16 yr per stand. Based on age distribution of the oldest cohorts, three stands became established after a major disturbance, but the majority of multiple-tree disturbances were associated with gaps < 200 m^2 in area. Historic disturbance frequency and size distribution of canopy gaps suggest that the oak components of these stands persisted by utilizing a variety of growth strategies appropriate to large and small openings. The absence of significant changes in overstory disturbance frequencies further suggests that increases in the level of understory competition are responsible for the present-day decline in oak dominance. For. Sci. 49(5):778–789.

Key Words: Canopy disturbance, disturbance regime, radial growth averaging, stand development.

Forest disturbances kill forest organisms, alter the total amount of growing space available to plants in an area, and redistribute growing space among survivors and new individuals (Barnes et al. 1998, p. 409). In fact, it is the release of growing space, rather than the disturbance itself, that drives stand dynamics. Oliver and Larson (1996, p. 21–36) defined growing space as the sum of necessary resources—sunlight, water, nutrients, temperature, oxygen, and carbon dioxide—available to the individual organisms present. Growth continues until one or more of these components becomes limited (Smith 1996 pp. 31–32). In closed canopy, deciduous forests, light levels beneath intact canopies often are the limiting resource, averaging as little as 1 to 2% of full sunlight (Canham and Burbank 1994). Canopy disturbances that alter light availability are thus very influential in determining individual tree growth and survival, and often overshadow climatic factors (Phipps 1982, Pacala et al. 1994, Nowacki and Abrams 1997).

Over time, there is a fundamental compatibility between a species' presence and the prevailing disturbance regime. Disturbance regimes that create large openings tend to favor exploitative species: fast-growing, light-demanding pioneers that grow rapidly and mature early (Bormann and Likens 1979 p. 118–133, Runkle 1985). Smaller openings favor

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conservative species: long-lived, tolerant of shade, with the ability to exploit temporary canopy openings (Grime 1977, Bormann and Likens 1979, p. 118–133, Runkle 1985, Hicks 1998, p. 131–135). Plant species are found where their life history strategies are compatible with the prevailing disturbance regime (Grime 1977, Denslow 1980, 1985, Runkle 1990). Changes in species composition may be indicative of changes in the disturbance regime (e.g., see Sprugel 1991, Abrams 1998, Cowell 1998, Rooney et al. 2000).

Oak (*Quercus* L.) forests have a long history in the central hardwood forest region. Following the last glacial retreat, oaks began migrating north about 10,000 yr ago, and reached their current range 7000 yr ago (Davis 1981). Reconstructions of presettlement forest composition in this region provide evidence of oak dominance (Sears 1925, Leitner and Jackson 1981, Loeb 1987, Abrams and Downs 1990, Nowacki and Abrams 1992, Abrams and McCay 1996, Dyer 2001), and areas dominated by oak during this period tended to remain in oak whether or not they were logged by settlers (Lorimer et al. 1994). However, as early as the 1950s, reports of declines in oak regeneration on sites where they had been historically dominant began to appear in forestry literature. Declines were most pronounced on better sites, and the problem was regional in scope. Some of the earliest accounts concerned second-growth, managed stands (Weitzman and Trimble 1957, Carvell and Tryon 1961); however, a similar trend has been noted in old-growth preserves (McGee 1984, Parker et al. 1985). To increase oak regeneration, foresters have experimented with a variety of stand manipulations, targeting overstory light levels, understory light levels, and interspecific competition. Manipulative experiments have been supplemented by ecological studies that seek to understand, and then duplicate, the conditions that fostered oak stands in the first place (Schuler 1998).

Studies of disturbance regimes of eastern deciduous forests have traditionally focused either on canopy gap dynamics, or dendroecological reconstruction of past disturbances. Barden (1980, 1981), Runkle (1982, 1998), Cho and Boerner (1991) and others have identified gap makers and gap fillers, and have measured the frequency of gap formation and size, and gap closure rate by sampling along transects. Gap-sampling studies have described the disturbance regimes of relatively large sample areas. However, because it is difficult to interpret gaps older than 15 yr (Cho and Boerner 1991), the sampling period of this method is limited to relatively short periods.

This study uses a dendroecological approach to quantify spatial and temporal disturbance characteristics of five oak-dominated old-growth stands in the central hardwood forest region. Study objectives were: (1) estimate the historic rate of canopy disturbances for study stands using the tree-ring record of establishment and canopy release events; (2) compare canopy disturbance intervals for several historical periods; and (3) use plot stem-maps and tree establishment and release chronologies to reconstruct the size-distribution of openings created by past canopy disturbance events, and compare these to current gap distributions.

Study Areas and Data Collection Methods

Fifteen potential study sites in eastern Kentucky, western Pennsylvania, eastern Ohio, and central West Virginia were evaluated for more intensive study using four criteria: (1) the presence of large (dbh ≥ 75 cm), old (> 200 yr) oak trees; (2) the absence of evidence of widespread human disturbance (e.g., logging, grazing); (3) a minimum size of ~4 ha (i.e., large enough to maintain a buffer of at least 50 m from plot borders to the edge of the stand); and (4) a stand composition that is dominated by deciduous trees with dominant or codominant (Smith et al. 1996) oaks as a major component of the overstory. Five stands were selected: Collins Woods in Belmont County, Ohio; Wrights Woods in Washington County, Pennsylvania; and Watter Smith State Park, Murphy Tract, Horners Woods, in Harrison County, Ritchie County, and Lewis County, West Virginia, respectively (Figure 1). Size of the old-growth stands ranged from 5–22 ha; three of

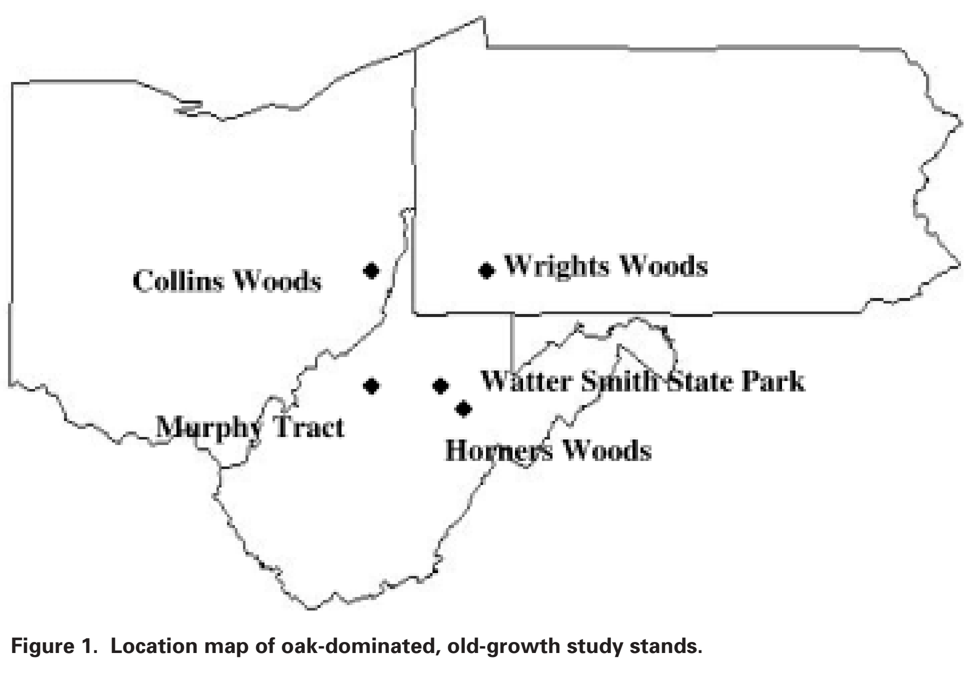

Figure 1. Location map of oak-dominated, old-growth study stands.

the stands were surrounded by larger but younger forested tracts. The five stands selected were all under some form of protection as old-growth preserves. Murphy Tract and Collins Woods are managed by The Nature Conservancy and Muskingham Watershed Conservancy District, respectively; Horners Woods and Watter Smith are part of a state wildlife management area and park, respectively; Wrights Woods has been owned by Wright's Chapel Methodist Church since 1823 (Higbee 1999).

Study plots (60 × 75 m, 0.45 ha) were subdivided into twenty 15 × 15 m subplots, and 100% inventories of overstory (dbh > 15 cm) and understory (2.5 cm ≤ dbh < 15 cm) stems were conducted. Two study plots were established in all stands except Watter Smith. In each plot, locations of all overstory and understory trees were mapped. Importance values (IV) were calculated for overstory and understory strata by averaging relative density, relative basal area, and relative frequency. In each 15 × 15 m subplot, two 2 × 2 m regeneration plots were established (total 160 m^2 $plot^{-1}$). Tree seedlings were tallied as either small (< 1 m tall), or large (≥ 1 m tall, < 2.5 cm dbh).

Current canopy gaps were evaluated using three criteria. First, only gaps that were formed by the death of at least one canopy tree were considered (Romme and Martin 1982). Second, the minimum gap size was 25 m^2, based on a range of 27–40 m^2 crown area for intermediate-class (the smallest tree that may create a canopy gap) canopy trees in the five study stands, and gap size distributions reported by Runkle (1990) and Busing and White (1997). Third, only gaps approximately 10 yr old or less were considered (Runkle 1982, Cho and Berner 1991). Older, partially closed gaps have canopies that are often indistinguishable from the canopy of surrounding border trees (Runkle 1992). For canopy gaps that met these three criteria, length (longest distance from gap edge to gap edge) and width (largest distance perpendicular to length) were measured, and gap area was calculated using the formula for an ellipse (Runkle 1982). When a gap occurred along the plot border, only that portion that fell within the 0.45 ha study plot was considered.

The largest tree in each subplot was cored at breast height. In addition, all overstory oaks in the subplot were cored. Two cores, approximately 180° apart, were extracted parallel to topographic contours. Sample cores were prepared using standard dendrochronological techniques (cf. Stokes and Smiley 1968). Cores were cross-dated by matching unique patterns of narrow and wide rings, and annual rings were measured with a Leica binocular microscope and Velmex measuring stage to the nearest 0.001 mm. Data output were recorded using J2X® software. Tree-ring dating was validated using the program COFECHA (Grissino-Mayer et al. 1997), and the two cores for each tree were then averaged to yield a mean chronology for the tree.

Data Analysis

Canopy Disturbance

Canopy disturbances were identified empirically by an abrupt increase in tree-ring width, using the decadal averaging technique proposed by Nowacki and Abrams (1997):

$$\%GC = [(M_2 - M_1)/M_1] * 100\% \qquad (1)$$

where $\%GC$ = percentage growth change, M_1 = preceding 10 yr mean radial growth (inclusive of the disturbance year), and M_2 = subsequent 10 yr mean radial growth (exclusive of the disturbance year) (Nowacki and Abrams 1997).

Three levels of crown release were recognized, based on the criteria of Lorimer and Frelich (1989), Nowacki and Abrams (1997), and Schuler and Fajvan (1999): (1) major releases were defined as events where $\%GC \geq 100$; these releases correspond to complete overhead releases of smaller, overtopped saplings and pole-sized trees in canopy openings; (2) moderate releases were classified as those with a $\%GC$ 50–99%; and (3) minor releases resulted in $\%GC$ of 25–49%. These apply to gap-associated growth increases caused by increased sidelight to trees already in the overstory; however, overtopped trees may show an increase of this magnitude when neighbors die from self-thinning processes. We did not apply specific temporal criteria to classify responses.

In a test of this methodology in an experimental forest with a known disturbance (thinning) history, Rentch et al. (2002) found that (1) the relationship between $\%GC$ and percent crown release was linear for northern red oak (*Quercus rubra* L.) and chestnut oak (*Q. prinus* L.); (2) peak $\%GC$ provided an accurate estimation of the disturbance year (± 1 year); and (3) the $\%GC$ 25 threshold was low enough to capture growth increases associated with increased sidelight from existing canopy trees, and high enough to filter out drought-induced growth reductions and subsequent recovery. Mean number of disturbances per tree were compared by species, stand, and tree age, using ANOVA (PROC-GLM, SAS Inst. 1998) and Fisher's L.S.D. test.

Canopy Disturbance Intervals

Two types of canopy disturbance intervals were investigated: (1) the time period between those years when at least one canopy disturbance/crown release occurred in the study stand, and (2) the time period between years when two or more nonadjacent trees underwent a release in the stand. Years in which at least one disturbance occurred were readily identified. For instances where more than one disturbance occurred per stand per year, a histograph of all events at each site was compiled, and years were identified graphically by the peaks of the curve.

There are three potential sources of ambiguity in this methodology. First, sample depth (the number of trees alive and represented by a tree-ring chronology) varied with time; i.e., more of the sample trees were alive in 1900 than in 1700. Thus, strict quantitative criteria for identifying multiple-tree gap disturbances could not be applied. For example, when only four trees were available for analysis of 1700s-era disturbances, requiring evidence from 50% of the sample trees was reasonable. However, when sample size increased to 30 trees in 1900, the 50% criterion would overlook less extensive disturbances (i.e., 10 trees out of 30) that should still qualify as a multiple-tree gap event. To minimize the effect of variable sample size, only trees ≥ 150 yr were included in canopy disturbance interval analysis.

Second, the %*GC* technique, as defined, assumes that there is a 1 yr lag between the disturbance event and release response. However, the response time may vary according to the precise timing of the disturbance event. For example, a disturbance in January (heavy snow, for example) may precede the growing season enough for a growth increase to occur in the same calendar year, while one in July (windthrow), after most of the radial growth is completed, would not be apparent until the following year. In addition, a precise correlation does not always exist between peak %*GC* as calculated, and the actual disturbance year (Schuler and Fajvan 1999). Differences in individual tree genetics and physiological condition before the disturbance, as well as species-level differences, affect the precise time of response (Lorimer and Frelich 1989, Schuler and Fajvan 1999). To account for the variability in timing of disturbance and peak %*GC*, disturbance events were initially assigned a 3 yr window (peak %*GC* year ±1 yr), and these data were the input for each stand's disturbance histograph. While using a 3 yr window for disturbance year potentially inflates the disturbance frequency by up to a factor of three, a single year was assigned to each multiple-tree gap disturbance based on the peaks of the histograph. This datum was input for the disturbance interval analysis.

We used the FHX2® program to evaluate the goodness of fit between disturbance interval data and normal and Weibull distributions (Grissino-Mayer 1997). The Weibull median is the measure of central tendency for this distribution, expressed as the 0.50 exceedance probability, corresponding to the 50th percentile of the distribution. The 0.125 and 0.875 exceedance probabilities provide a confidence interval, or thresholds of that median. FHX2® uses a Kilmogorov-Smirnov (*K-S*) test to determine whether the normal or the Weibull distribution provides a better statistical fit, expressed as a *d*-statistic.

To test for significant differences in return intervals between different temporal periods, FHX2® first transforms skewed, nonnormal data to a distribution that approaches normality using the third and fourth moments of the distribution (i.e., the skewness and kurtosis of the distribution which indicate the departure from normality), and then standardizes the data so the mean is zero and the standard deviation is one. Once transformed, mean disturbance intervals of different historical periods can be compared using a *t*-test, an *F* test, and a *K-S* test (Grissino-Mayer 1997). For trees ≥ 150 yr old, multiple-tree disturbance intervals were normally distributed (*K-S* test, *d*-statistic ≤ 0.12, $P = 0.15$), but the distribution of single-tree disturbance intervals was highly skewed (skewness >1), and the normal distribution did not provide an adequate model (*K-S* test *d*-statistic > 0.184, $P < 0.01$). Because the Weibull distribution is flexible enough to approximate the normal distribution (Grissino-Mayer 1997), we used the Weibull median as a measure of central tendency.

Mean disturbance intervals of three time periods were compared, based on a general assessment of human impacts and a variable fire regime (Nowacki and Abrams 1997). The presettlement era (before 1800) disturbance regime consists of a suite of natural disturbances such as ice and windstorms, drought, and insect infestations and disease, as well as natural and Native American fire. The settlement period (1800–1899) corresponds to the period during which extensive land clearing for agriculture and forest harvesting and associated fires occurred. The modern era (after 1900) is distinguished primarily by a fire suppression policy, the introduction of exotic pests and disease (e.g., chestnut blight and gypsy moth), and a dramatic increase in the white-tailed deer (*Odocoileus virginianus*) population.

Spatial Distribution of Tree Establishment and Release Events

For each study plot, maps were prepared showing cored-tree locations and establishment and canopy accession dates. Canopy accession was identified by a %*GC* ≥ 100%. In addition, for those tree species that require a gap for germination and/or survival and that are intolerant of shade (e.g. yellow-poplar, *Liriodendron tulipifera* L., and black cherry, *Prunus serotina* Ehrh.), establishment was considered to be synonymous with canopy accession (Lorimer and Frelich 1989). Cohorts were identified by similar establishment and/or release years, and the patch-size was estimated by the distance between trees of the same cohort. Cohorts were evaluated spatially, based on two general questions. First, were trees established and/or released individually, or in groups? Second, when multiple-tree gaps were identified, what was the relative patch size?

Our method provides an estimate of synchronous disturbance/release events and patch size, but may result in under- or over-estimates. We assumed that if two or more trees showed the same establishment or release year, it was caused by the same discrete event. However, if more than one disturbance occurred in a plot in the same year, an overestimation of patch size would result. Patch size could be underestimated when mortality removes some individuals with similar establishment/release years. Because some cohorts initiated after large disturbances, patch-size sometimes exceeded the area of a single 60×75 m plot. These cases were not included in this analysis, and thus true patch size may again be underestimated. Finally, because the margin of error of the radial growth averaging technique is ±1 yr, some trees may be grouped in the same disturbance patch when in fact they were separated in time by one year.

Results

Stand Composition and Structure

Oaks were present as dominant or codominant trees at all five study stands. At Collins Woods and Wrights Woods, the oak component was limited to a few very large, dominant trees. The IVs of sugar maple (*Acer saccharum* Marsh.) in Wrights Woods, or sugar maple, beech (*Fagus grandifolia* Ehrh.), and red maple (*Acer rubrum* L.) in Collins Woods, equaled or exceeded those for oaks in these stands due to high stem densities (Table 1). At Watter Smith, Horners Woods, and Murphy Tract, the oak component was more numerous and distributed among more species, size- and age-classes. Understory oaks (saplings and pole-size trees, 2.5 cm < dbh < 15 cm) were virtually absent in all five stands. Only at Murphy Tract, which had the greatest total overstory oak IV,

Table 1. Importance values (IV) for major (a) overstory tree (dbh ≥ 15 cm), (b) understory tree (2.5 cm ≤ dbh < 15 cm) species, and density for (c) large seedlings (dbh < 2.5 cm, height > 1 m) at five oak-dominated old-growth study stands. IV = (rel. basal area + rel. abundance + rel. frequency)/3. Seedlings are stem ha^{-1}.

Species	Collins Woods	Wrights Woods	Watter Smith	Murphy Tract	Horners Woods
(a) Overstory tree IV					
Acer rubrum	7.4	15.2	13.7	14.9	12.4
A. saccharum	34.0	49.0	9.6	0.8	10.7
Carya spp.	2.0	—	8.0	4.0	10.2
Fagus grandifolia	21.6	—	12.2	14.4	18.4
Liriodendron tulipifera	7.9	—	1.9	—	3.6
Prunus serotina	0.6	10.7	—	—	—
Quercus alba	9.8	15.1	13.7	28.5	10.2
Q. prinus	—	—	4.0	5.0	7.2
Q. rubra	7.9	4.8	16.2	6.7	0.6
Q. velutina	—	—	6.9	12.6	16.9
(b) Understory tree IV					
Acer rubrum	3.2	9.2	11.1	30.5	9.3
A. saccharum	73.2	79.4	15.2	2.8	37.5
Carya spp.	4.7	1.4	1.9	2.3	2.2
Fagus grandifolia	9.2	—	25.0	26.4	31.3
Fraxinus americana	1.5	—	0.5	0.4	0.9
Oxydendron arboreum	—	—	1.0	11.7	2.2
Quercus alba	—	—	—	4.1	—
Q. prinus	—	—	—	0.6	1.0
(c) Large seedlings ha^{-1}					
Acer rubrum	—	—	63	313	—
A. saccharum	1190	1276	250	—	250
Aesculus flava	—	—	125	—	—
Carya spp.	26	—	—	—	63
Fagus grandifolia	132	—	63	875	656
Fraxinus americana	159	94	250	125	125
Liriodendron tulipifera	—	—	63	—	—
Magnolia acuminata	—	—	—	—	31
Nyssa sylvatica	—	—	63	94	—
Oxydendron arboreum	—	—	—	125	281
Prunus serotina	26	31	63	—	—
Quercus alba	—	—	—	125	—
Q. rubra	—	125	—	—	—
Q. velutina	—	—	—	94	—
Ulmus spp.	26	63	63	—	—

did the understory oak IV approach a value of 5 (Table 1). Sugar maple and red maple were the most abundant species in the regeneration plots of all stands, averaging a total of 16,000 small seedlings ha^{-1} (height < 1 m, data not shown), and 668 large seedlings ha^{-1} (height > 1 m, dbh < 2.5 cm, Table 1). Oak advance regeneration was present at all stands except Collins Woods, but large oak seedlings (> 1 m tall) were found only at Wrights Woods and Murphy Tract, and even there, abundance was less than 125 stems ha^{-1}.

Two trends characterized the origins of these stands (Figure 2). The oldest trees at Murphy Tract, Wrights Woods, and Watter Smith date to well-defined time periods (i.e., 1650, 1665, and 1690, respectively) that suggest these stands originated in the aftermath of stand-initiating disturbances. Juvenile growth rates were above average, and tree growth trends exhibited no periods of extended suppression or subsequent overstory release. Each of the three stands also underwent a pause (60 to 100 yr) in new tree recruitment consistent with the stem exclusion and understory reinitiation stages of stand development (Oliver and Larson 1996, p. 152–157). At Collins Woods and Horners Woods, it is difficult to determine if the oldest trees are remnants of a previously larger disturbance-initiated cohort, or members of small cohorts that arose in the aftermath of smaller (1–2 tree) canopy openings. At all sites, shade tolerant tree species were absent from the oldest cohorts.

Oak establishment tended to be either temporarily fixed or continuous (Figure 2). At Collins Woods and Wrights Woods, establishment of oaks was limited to the period 1631–1877. White oaks (*Quercus alba* L.) were the oldest trees, and the most recent establishment of this species occurred in 1866 for Collins Woods and 1805 for Wrights Woods. Northern red oaks (*Q. rubra* L.) were established between 1750–1800 and continued until 1877 at Collins Woods, and 1852 at Wrights Woods. After 1850, both sites showed large ingrowth of shade-tolerant tree species (maples and American beech), species of intermediate shade tolerance (hickories, *Carya* Nutt. and, elms, *Ulmus* L.), as well as shade-intolerant species such as yellow-poplar, and black cherry.

In contrast to Collins Woods and Wrights Woods, recruitment of oak species was continuous at Watter Smith, Murphy Tract, and Horners Woods until about 1930. White oak and chestnut oak (*Q. prinus* L.) were the oldest trees in these stands, and red oak and black oak (*Q. velutina* Lam.) established later, beginning in the early 1800s. These stands also showed gradual ingrowth of both shade-tolerant and intolerant species in the 1800s.

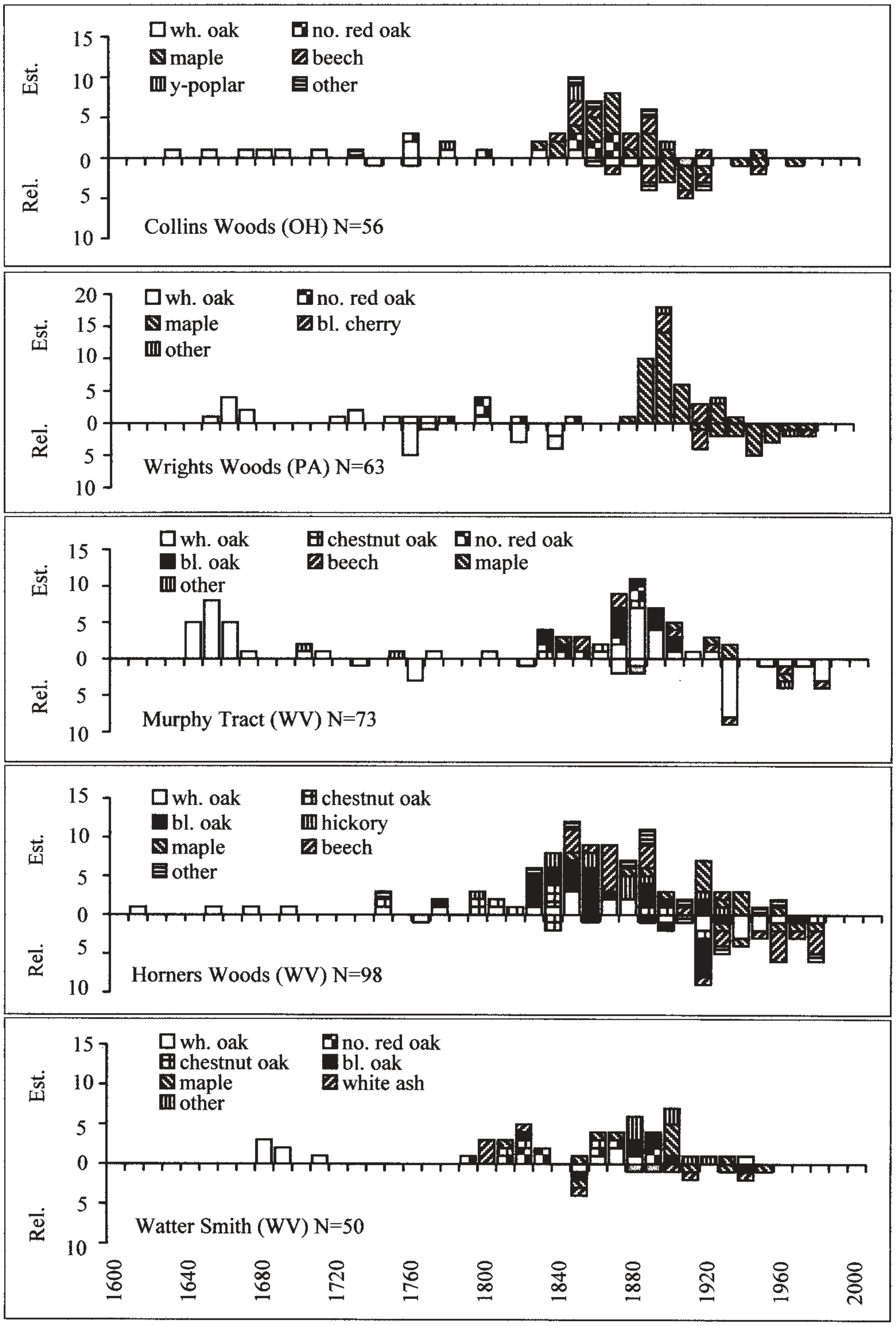

Figure 2. Tree establishment and major release (canopy accession, %*GC* ≥ 100%) events for five oak-dominated old-growth stands. Events are summed by decade. Establishment (Est.) events are above the X-axis, and canopy accession events (Rel.) are below the X-axis. N = number of sample trees. "Other" = American elm, slippery elm, sourwood, bitternut hickory, shagbark hickory, mockernut hickory, scarlet oak, black gum, cucumber tree, and black birch.

Canopy Disturbances

A total of 756 canopy disturbance events were identified from 177 overstory oak trees at the five study sites using the %*GC* technique. Sixty percent of the disturbances (459) produced minor releases (%*GC* = 25–49%), 26% (199) produced moderate releases (%*GC* = 50–99%), and 14% (101) were major releases involving overstory accession (%GC ≥ 100%). The average number of disturbance events per tree was 4.1. Older trees tended to show more releases than younger ones ($F = 103.9$, $P < 0.001$). For example, one white oak experienced 13 small releases over 347 yr. However, differences in the mean number of disturbances per tree were not significant when either stand or oak species were considered ($F = 1.09$, 0.22, respectively, $P > 0.05$).

Canopy Disturbance Intervals

Disturbance intervals were similar across the five study areas, despite variable sample sizes (Table 2). On average, at least one canopy disturbance occurred per stand every 3 yr (range 2.2–3.8 yr). For these stands, two or more canopy disturbances occurred approximately every 16 yr (range 14.2–20.7 yr, Table 2, Figure 3). The estimated maximum time interval between single-tree gap events and the minimum number of years between multiple-tree gap events were generally consistent with each other. For example, at Murphy Tract, it is unlikely that canopy disturbances involving at least one tree are more than 6.2 yr apart (exceedance probability = 0.125), or that disturbance events involving two or more trees occur, on average, less than 6.3 yr apart (exceedance probability = 0.875).

The historical comparison of disturbance intervals revealed a few differences among stands (Table 3, Figure 3). Between the presettlement (1700–1800) and settlement periods (1801–1900), the single-tree disturbance interval declined at Wrights Woods, Horners Woods, and Collins Woods ($P < 0.05$). With the exception of Murphy Tract, there were no significant changes between settlement and modern (1901–1990) periods, and even in this case, the magnitude of the increase was only 1.9 yr. Because the single-tree disturbance frequency is strongly correlated with number of sample trees, increasing sample size accounts for a portion of these changes. For multiple-tree gap disturbances, mean disturbance intervals for the three periods were not significantly different ($P > 0.05$, range 12.0–22.3 yr).

Spatial Distribution of Oak Cohorts

Plot maps and growth chronologies of live (in 1999) trees were used to estimate the spatial distribution of canopy disturbances and oak cohorts. For the five study stands, there was a total of 174 tree establishment events, and 87 major crown releases evenly divided between single-tree (127) and multiple-tree gap events (134). Thirty-four trees were established in the aftermath of stand initiating disturbances at Murphy Tract (23 trees, 1650), Watter Smith State Park (6, 1690), and Wrights Woods (5, 1665). The remainder of the multiple-tree gap events occurred in smaller patches whose size was estimated by the distance between trees of each cohort.

Table 4 shows the size-distribution of multiple-tree gaps and the number of trees involved. The smallest size-class ($\leq$ 100 m^2) is underrepresented because single-tree establishment and overstory-recruitment events could not be assigned a gap size. Most multiple-tree gap events involved cohorts of two trees in smaller patches ($\leq$ 200 m^2); nine of these events were gaps < 50 m^2. This trend is consistent with the distribution of current canopy gaps based on gaps $\leq$ 10 yr old. However, several larger old disturbances (> 1000 m^2) were identified from the %*GC* chronologies. For example, at Murphy Tract, three oaks and one red maple were established in 1900 in an opening that was at least 57 m wide (2552 m^2). This disturbance also released one 64-yr-old chestnut oak. At Wrights Woods, a tornado in 1848 (Higbee 1999) released four red oaks more than 50 m apart.

Discussion

Components of the Disturbance Regime

Characteristics of the disturbance regime of the oak-dominated stands of this study are consistent across a portion of the central hardwood forest region and the past 300 yr time period. Across these stands, canopy disturbances occurred, on average, every 3 yr, while larger events involving more than one tree occurred on an approximately 16 yr interval. These values are comparable to other estimates of the frequency of multiple-tree gap formation. For example, Lorimer (1980) estimated that disturbances of higher than average intensity occurred at 30 yr intervals in western North Carolina. In central Pennsylvania, Nowacki and Abrams (1997) estimated mean disturbance intervals of 21, 21, and 31 yr for the presettlement, settlement, and modern periods, respectively. However, as with our study, changes were not significant ($P > 0.05$). Comparing old-growth (before 1907) and second-growth periods in a central West Virginia forest, Schuler and Fajvan (1999) found no statistical evidence of temporal change in whole-stand disturbance frequency. Natural disturbance regimes are strongly correlated with broad geographic patterns of climate, topography, and soils, in the same way that these factors influence the vegetation of a region (Runkle 1990). Because landscape-scale factors change slowly and gradually (if at all), disturbance rates are con-

Table 2. Disturbance intervals (yr), 1700–1990, for five oak-dominated old-growth stands in Ohio, Pennsylvania, and West Virginia. Disturbances are defined by radial growth averaging, %GC ≥ 25%. Data are modeled with a two-parameter Weibull distribution. Data from one additional site in West Virginia shown for comparison.

Site	0.875 exceedance probability	0.500 Weibull median	0.125 exceedance probability	No. of trees > 150 yr old
(a) Single-tree gap events				
Wrights Woods (PA)	0.6	3.0	8.7	17
Murphy Tract (WV)	0.5	2.2	6.2	26
Horners Woods (WV)	0.6	2.8	7.3	24
Watter Smith State Park (WV)	0.8	3.4	8.9	14
Collins Woods (OH)	1.1	3.8	9.0	14
(b) Multiple-tree gap events				
Wrights Woods (PA)	11.6	20.7	30.4	17
Murphy Tract (WV)	6.3	14.2	24.5	26
Horners Woods (WV)	6.8	14.8	25.0	24
Watter Smith State Park (WV)	7.5	15.9	26.2	14
Collins Woods (OH)	5.8	14.9	27.7	14
Fernow Experiment Forest (WV)*	17.9	30.8	44.2	15

* Data from Schuler and Fajvan (1999). Minimum disturbance threshold set at %GC ≥ 50%. Time interval includes 1728–1994, all trees.

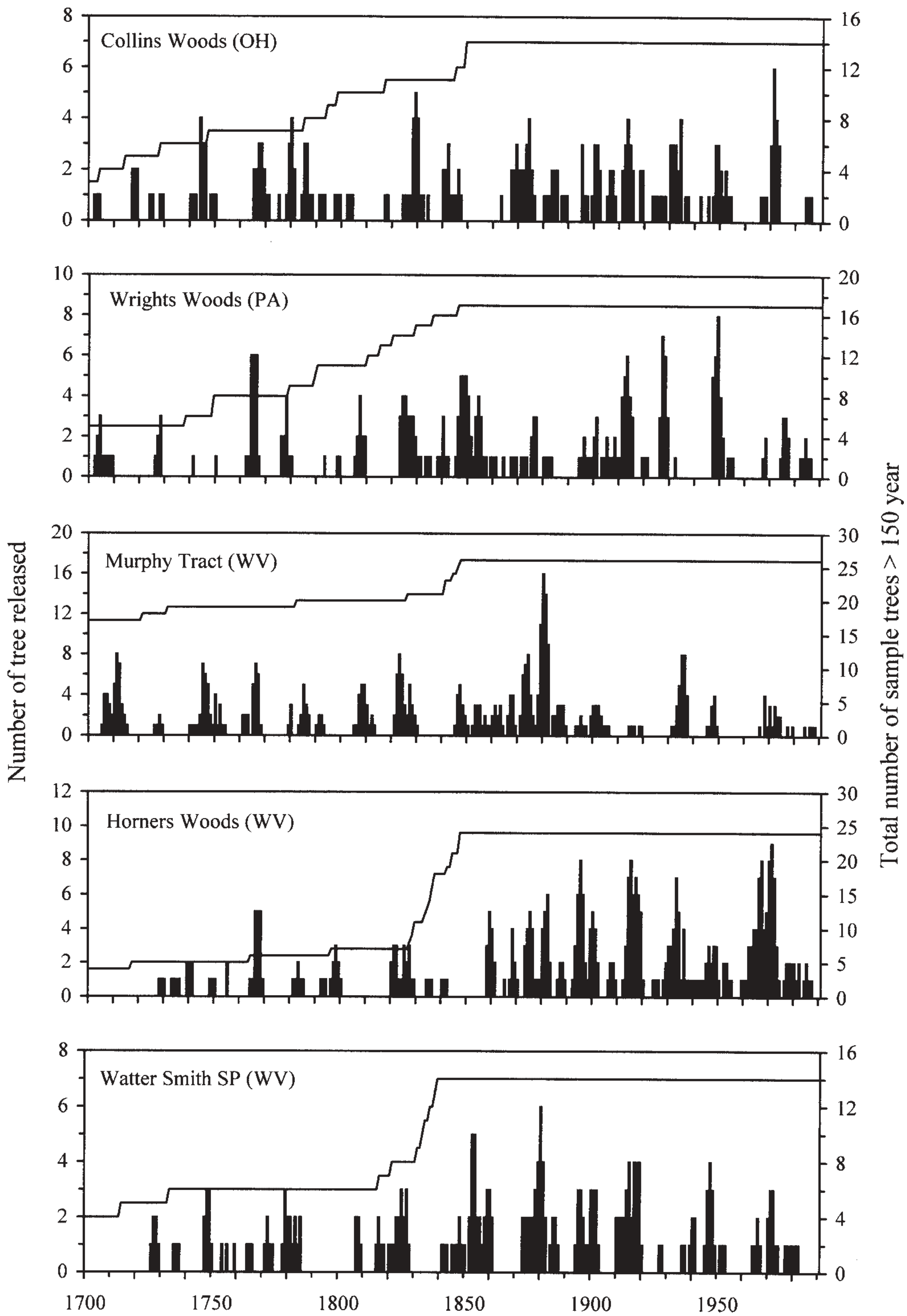

Figure 3. Histograph of canopy disturbance events in five oak-dominated old-growth stands in Ohio, Pennsylvania, and West Virginia. Disturbance events/tree releases defined by radial growth averaging (%*GC* ≥ 25). Each disturbance assigned a 3 yr window (peak %*GC* year ± 1 yr), and multiple tree gap events determined graphically from peaks of histograph. Sample depth indicated by solid line and right Y-axis.

strained to a fairly narrow and predictable range of values (Runkle 1985).

Disturbance frequencies have little value unless the sample unit is scaled. When estimating the occurrence of single-tree events, the sampling unit is "trees" that were at least 150 yr old; accordingly, there was a strong negative relationship between the disturbance interval and number of trees sampled (F = 16.5, P = 0.06, R^2_{adj} = 0.84). Theoretically, more intensive sampling would yield a smaller interval, limited only by the number of trees available that meet the minimum age requirement. However, for multiple-tree disturbances, estimated return interval and number of sample trees were largely independent of each other (F = 3.7, P = 0.19, R^2_{adj} = 0.40). Here, the disturbance interval is better considered a

Table 3. Disturbance intervals for three historical periods: 1700–1800, 1801–1900, 1901–1990, for five oak-dominated old-growth stands in Ohio, Pennsylvania, and West Virginia. Disturbances are defined by radial growth averaging, %GC ≥ 25%. Mean disturbance intervals are compared using *t*-tests for equal and unequal variances (α = 0.05). Data from three sites in Pennsylvania are shown for comparison.

	Mean disturbance interval (yr*)					
Site	Presettlement 1700–1800	*n*	Settlement 1801–1900	*n*	Modern 1901–1990	*n*
(a) Single tree gap events						
Wrights Woods (PA)	6.6a	11	3.1b	17	3.5ab	17
Murphy Tract (WV)	3.1ab	21	2.3a	26	4.2b	26
Horners Woods (WV)	7.1a	7	3.0b	24	2.4b	24
Watter Smith State Park (WV)	5.4a	6	3.3a	14	4.6a	14
Collins Woods (OH)	6.3a	10	4.4b	14	3.8b	14
(b) Multiple tree gap events						
Wrights Woods (PA)	17.0a	11	17.3a	17	18.8a	17
Murphy Tract (WV)	12.3a	21	12.0a	26	22.3a	26
Horners Woods (WV)	17.0a	7	14.4a	24	15.8a	24
Watter Smith State Park (WV)	13.2a	6	18.0a	14	19.1a	14
Collins Woods (OH)	14.0a	10	13.2a	14	15.2a	14
Bald Eagle Ridge (PA)†	17	6	16	6	27	6
Nittany Ridge (PA)†	21	11	21	11	27	11
Tussey Ridge (PA)†	24	8	25	8	40	8

* Means in the same row with different letters are significantly different.

† Data from Nowacki and Abrams (1997). Presettlement era: 1590–1774, Settlement era: 1775–1900. Multiple-tree disturbances defined as events when >25% of sample trees showd %GC > 25%. Disturbance intervals not significantly different based on ANOVA, α = 0.05.

stand variable, representative of a particular stand, with certain compositional, topographic, and disturbance characteristics. Stand, rather than tree, is the more ecologically meaningful dimension of scale.

The consistent temporal pattern of canopy disturbance intervals suggests that the causes of these disturbances have remained relatively constant as well. In forests of eastern North America, wind and fire are historically the most common agents of canopy disturbance (Runkle 1985, 1990). In the Ohio Valley and the Appalachian Plateau, a highly dissected topography with frequent natural firebreaks limits the size of potential fire compartments (Frost 1998). Lightning is an occasional ignition source, particularly during drought years (Ruffner and Abrams 1998), but low correlations between climate and fire frequency suggest most fires in this region are caused by humans (Sutherland 1997, Wade et al. 2000), with fire effects largely concentrated in the understory. Although there are few long-term fire chronologies for the mixed-oak forests of this study, there is a growing consensus that surface fire was a significant component of the disturbance regime and strongly correlated with Native American habitation and European land-use patterns (Abrams 1992, Delcourt and Delcourt 1997, Bonnicksen 2000). Prior to 1900, fire return intervals as low as 2 yr (McCarthy et al. 2001), 8 yr (Shumway et al. 2001) and 14 yr (Buell et al. 1954) have been reported for eastern deciduous forests. Since 1900, a fire suppression policy has greatly reduced fire frequency and the annual area burned (Wade et al. 2000).

In this study area, large wind events such as tornadoes occur but are relatively rare. For example, since 1885, four F2 and larger tornadoes (winds in excess of 182 km hr^{-1}) were recorded for both Belmont County, Ohio and Washington County, Pennsylvania (NWS 2001), and two for Harrison County, West Virginia (NWS 2001; NOAA 2001). However, our study and others indicate that smaller, less intense wind events account for most forest turnover (Barden 1981, Romme and Martin 1982, Runkle 1982, Clebsch and Busing 1989). High velocity, very localized, and short duration windstorms (microbursts) associated with thunderstorms account for 40–70% of severe weather events in the five study site counties (NCDC 2001). The likelihood of thunderstorm-associated winds in excess of 92 km hr^{-1} occurring at any location is approximately 2% between May 20–June 16, and July 18–August 12, in-

Table 4. Frequency of patch-size and number of trees involved/patch for synchronous establishment and major release events. Large, stand-initiating disturbances that exceed plot dimensions are not included.

		Multiple-tree patch size-class (m^2)				
Event type	Single-tree	<100	100–200	200–500	500–1000	>1000
		No. of patches				
Establishment	76	10	5	5	3	3
Major release	51	8	6	2	2	3
Total	127	18	11	7	5	6
		No. of trees				
Establishment	76	20	11	8	8	10
Major release	51	16	6	13	7	9
Total	127	36	17	21	15	19
		No. of canopy gaps—1999–2000				
Total	10	4	4	2	0	0

creasing to approximately 4% between June 17 and July 15 (adapted from NSSL 2001). These winds tend to create gaps during the growing season when trees are fully leafed out, soils are near saturation, and foliage is heavy with recent rain.

Disturbance agents such as heavy snow, ice storms, lightning, and insect and disease infestations also injure or kill trees and produce gaps. Snag densities and the volume of downed logs (dbh ≥ 15 cm, all stand average 3.2 m^2 ha^{-1} and 39.3 m^3 ha^{-1}, respectively) attest to the frequency of these events. Dominant trees are particularly vulnerable to snow, ice, and lightning (Carvell et al. 1957, Whitney and Johnson 1984), and their deaths create canopy openings consistent with those created by localized wind events. However, damage is less extensive for oaks because these species have wood that is resistant to breakage (Whitney and Johnson 1984, Rebertus et al. 1997) and extensive root systems (Gale and Grigal 1987, Abrams 1990) that resist uprooting.

Canopy Disturbance and Oak Recruitment

The reconstructed spatial distribution of cohorts suggests the following overall trends: (1) about one-half of the oaks were established as an individual tree and not as a member of an identifiable cohort; (2) 30% of the oaks attained overstory status individually; (3) more than half the multiple-tree gaps involved only two trees in relatively small openings (< 200 m^2); and (4) nearly 1 in 5 oaks are remnants of large stand-initiating events whose dimensions exceed the size of the study plot.

The species composition of the study stands is consistent with a disturbance regime characterized by frequent, small events and less frequent large events. Forests at Murphy Tract, Wrights Woods, and Watter Smith State Park originated after large stand-initiating disturbances. At each of these sites, the oldest cohort included trees from both sample plots. Growth trends of these trees were distinguished by the absence of overstory suppression and major crown releases.

Large (> 1000 m^2) canopy gaps were identified; however, most oaks recruited via smaller (≤ 200 m^2) canopy disturbances involving two or more trees that occurred, on average, every 16 yr. These trees also reached overstory positions without being overtopped. However, in contrast to the even-aged structure resulting from stand-initiating events, these disturbances resulted in a spatially and temporally dispersed multicohort age structure. This disturbance regime is also consistent with conditions that are favorable to the establishment of shade-tolerant species (Barden 1980, Runkle 1985, Canham 1990, Poulson and Platt 1996). The absence of species with shorter lifespans (e.g., red maple) from the older cohorts illustrates a limitation of reconstructions of stand history using live trees. Evidence is lost as trees die and decay. However, sugar maple and beech are as potentially long-lived as white oak (Burns and Honkala 1990, Hicks 1998 p. 137–169), and had they been present as advanced regeneration at the time of the stand initiating disturbances, some, presumably, would have survived to the present. However, none of the study sites had these species (or other shade-tolerant species) represented in the oldest cohorts.

Evidence from the old-growth stands of this study support Lorimer's hypotheses that (1) presettlement-era dominance of upland forests in this region by shade tolerant species was uncommon (Lorimer et al. 1994), and (2) the primary cause of contemporary oak establishment failure is the physiological limitation imposed by dense, low shade (Lorimer 1993). For these stands, early oak tree- and stand-replacement relied on relatively constant canopy disturbance rates, sufficient understory light levels for oak regeneration, and minor understory competition from shade tolerant species. However, oak replacement ceased at Wrights Woods and Collins Woods by the 1850s. Oak establishment continued until the early 1900s at the other three sites, but current oak sapling abundances are either very low or absent. During the mid-1800s, the successful establishment of shade-tolerant regeneration would have increased levels of understory shade, which contributed to a decline in oak sapling abundance, hence a decline in the pool of oak stems that could utilize canopy openings to gain overstory status. Changes in the understory fire regime best account for the changes in species composition and increases in the level of understory competition suggested by this study (Abrams 1992, Lorimer 1993, Brose et al. 2001). No other form of surface-level disturbance effectively discriminates in favor of oak species, and against mesophyptic competitors.

Conclusions

Because of their antiquity, the old-growth stands of this study provide a valuable source of long-term data on individual tree and stand dynamics of oak forests of this region. Our results have implications for the management of oak-dominated old-growth forests, as well as for oak silviculture in general. Most silvicultural prescriptions for oak forests propose even-aged management. The shelterwood system is currently preferred, and manipulation of overstory density and understory light levels under this system is consistent with factors that we have identified as crucial in the development of these old stands. The preference for even-aged systems is, in part, due to the even-aged condition of most second-growth forests, and the difficulty of using an uneven-aged selection system without continuous cultural treatments to control shade-tolerant species. Yet, the variety of growth strategies exhibited by these old trees, and the age structures of these stands, suggest that persistent human use of fire, coupled with the frequent creation of canopy openings of various sizes, were integral components of the historic disturbance regimes of these forests, and the key to establishment and survival of a competitive oak understory, and eventual accession of oaks into the overstory.

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