CANOPY DISTURBANCE INTERVALS, EARLY GROWTH RATES, AND CANOPY ACCESSION TRENDS OF OAK-DOMINATED OLD-GROWTH FORESTS

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ABSTRACT.—Using a radial growth averaging technique, changes in growth rates of overstory oaks were used to quantify canopy disturbance events at five old-growth sites. On average, at least one canopy disturbance occurred on these sites every 3 years; larger multiple-tree disturbances occurred every 17 years. Although there was some variation by site and by historical period, there has been little significant change in canopy disturbance rates for the 300-year period examined. A review of tree-ring chronologies yielded three growth strategies. For these oaks,

a) the likelihood of originating in a large opening and achieving overstory status before canopy closure is about the same as the probability of requiring a major release, either from
b) a smaller gap that closed, or
c) from the understory.

Half of the cored trees established individually, and 30 percent attained overstory status individually, members of no identifiable larger cohort. For trees that required a major canopy release, residence time in the understory averaged 89, 54, and 50 years for white oak, red oak, and black oak, respectively. These long-term understory residences averages suggest that the abundance of shade tolerant understory species was considerably less before 1900. These results are consistent with presettlement survey tree-tallies, the absence of shade tolerant species in the oldest cohorts, and fact that virtually no oak canopy recruitment after 1900 occurred after an extended period of below-average growth in the understory.

Concerns for oak regeneration in the eastern United States go back as early as the early 1900s. Clark (1993) notes that Hawley's text, *Practice of Silviculture* (Hawley 1946), described a successful 1902 shelterwood cut that favored oak, and concluded that there must have been a shortage of advance oak in that stand. By the 1950s, forestry literature included accounts that detailed problems with regenerating oak on sites where it had been historically dominant. Difficulties were most pronounced on better sites and regional in scope. The earliest accounts considered 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 and others 1985).

To solve this problem, a variety of forms of stand manipulation targeting overstory light levels, understory light levels, and inter-species competition have been attempted. More recently, 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). Key components of this understanding are determinations both of the natural disturbance regime at the time of stand initiation (Oliver and Larson 1996) and the historical range of variability of disturbances over the life of the stand (Aplet 2000).

This study uses dendroecological and community sampling techniques to characterize stand-level dynamics of five oak-dominated, old-growth stands in Ohio, Pennsylvania, and West Virginia. We have two objectives. First, what is the historic rate of canopy disturbance and tree release of the five old-growth stands? Intervals

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between years when at least one canopy disturbance occurred, and intervals between years when larger disturbances occurred were examined over the entire tree-ring chronology of each stand. Disturbance intervals were also compared for several historical periods. The second objective focuses on individual tree dynamics. Early oak growth rates and the presence or absence of a major crown release were used to determine modes of oak establishment and canopy recruitment, and by inference, the understory light environment in which trees originated.

STUDY AREAS AND METHODS

Five oak-dominated old-growth stands were selected for study. These include one stand in Belmont County, OH (Collins Woods), one in Washington County, PA (Wrights Woods), and three in central West Virginia (Watter Smith State Park, Harrison County; Murphy Tract, Ritchie County; and Horners Woods, Lewis County). Two 0.45 ha (60 x 75 m) study plots were established at each site and subdivided into twenty 15 x 15 m subplots, with the exception of Watter Smith State Park, which had a single study plot.

A 100-percent inventory of overstory (dbh ≥ 15 cm) and understory (2.5 cm ≤ dbh < 15 cm) stems was made, and importance values (IV) were calculated for each canopy stratum by averaging relative abundance (stems ha^{-1}), relative basal area (BA ha^{-1}), and relative frequency. Importance values are reported as site averages.

At the minimum, the largest tree in each 15 x 15 m subplot was cored at breast height. An average of 34 trees was cored at each 0.45 ha plot (N_{total} = 314), of which 176 were oaks. Cores were cross-dated by matching unique patterns of narrow and wide rings, and measured under a dissecting microscope to the nearest 0.001 mm in conjunction with J2X® software. Tree-ring dating was validated using the program COFECHA (Grissino-Mayer and others 1997), and the two cores for each tree were then averaged to yield a mean chronology for the tree.

DATA ANALYSIS

Canopy disturbances were identified empirically by an abrupt and sustained increase in tree-ring width, using the decadal averaging technique of Nowacki and Abrams (1997):
percent GC = $[(M_2 - M_1)/M_1]*100$ percent,
where percent GC = percent growth change,
M_1 = preceding 10-year mean radial growth (inclusive of the disturbance year), and
M_2 = subsequent 10-year mean (exclusive of the disturbance year) (Nowacki and Abrams 1997).

Three levels of canopy disturbance/crown release were recognized, using the criteria of Lorimer and Frelich (1989) and Schuler and Fajvan (1999):
1) major releases were defined as events when percent GC ≥ 100 percent;
2) moderate releases were classified as those with a percent GC of 50 to 99 percent; and
3) small releases resulted in percent GC of 25 to 49 percent.

Major releases correspond to overhead releases of smaller, overtopped saplings and pole-sized trees in canopy openings. Small and moderate releases apply to gap-associated growth increases caused by increased sidelight to trees already in the overstory.

Canopy Disturbance Intervals

Two types of canopy disturbance intervals were investigated:
1) single-tree event intervals, or the time period between those years when at least one canopy disturbance-crown release occurred in the study site, and
2) multiple-tree event intervals—the time period between years when two or more non-adjacent trees underwent a release.

Years in which at least one disturbance occurred were readily identified. For multiple-tree disturbances, a histograph of all events at each site was compiled, and peaks of the curve identified disturbance years. Because sample size varied with time, we used only trees ≥ 150 years old in the disturbance analysis.

The percent GC technique, as defined, assumes that there is a 1-year lag between the disturbance event and release-response. However, a precise correlation does not always exist between peak percent 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 may also 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 percent GC, disturbance events were initially assigned a 3-year window (peak percent GC-year ±1 year), and these data were the input for each site's disturbance histograph. Using a 3-year window for disturbance year potentially inflates the disturbance frequency by a factor of three; thus a single year was assigned to each disturbance based on the peaks of the curve.

We used the FHX2® (Grissino-Mayer 1997) program to determine the frequency of single-tree and multiple-tree disturbances. Weibull median disturbance intervals were first calculated for the entire tree-ring chronology for each site, and then means of different historical time periods were compared to detect within-site changes over time. Disturbance intervals for three time periods were compared based on a general assessment of human impacts and a variable fire regime (Nowacki and Abrams 1997). The presettlement period is defined as years before 1800. The settlement period (1800-1899) corresponds to the period during which extensive land clearing for agriculture, forest harvesting, and associated slash fire occurred. The modern era (after 1900) is distinguished primarily by fire suppression, the introduction of exotic pests and disease (e.g., chestnut blight and gypsy moth), and a dramatic increase in the white-tailed deer population.

Canopy Accession Trends

Three growth trends were identified based on juvenile growth rates (at dbh), overall growth pattern, and the presence/absence of a major crown release (percent GC ≥ 100 percent).

Gap origin

The absence of a major crown release distinguishes this trend (fig. 1a). Trees with average juvenile growth followed by a slightly increasing trend, or trees with above-average initial growth and a flat or slightly declining trend were considered to be direct overstory recruits in high-light conditions (Lorimer and others 1988, Lorimer and Frelich 1989, Frelich and Graumlich 1994, Nowacki and Abrams 1997).

Gap origin-gap release

Radial growth during the first 25 years for these trees was similar to a) above. However, growth was subsequently reduced by canopy closure from above, and then resumed pre-suppression rates after a major release and overstory accession (fig. 1b).

Understory origin-gap release

Initial growth for these trees was at least 50 percent less than the site average (0.5-0.8 mm yr^{-1}), and these trees were considered to have originated in a low light, understory position. Following one, or occasionally, two major releases, growth showed a large increase and no further evidence of overstory suppression (fig. 1c). For trees categorized as gap origin-gap release or understory origin-gap release, dbh (inside bark, dib) at the time of final major release and understory residence time (age at overstory accession minus year of earliest ring) were evaluated by species and by site.

RESULTS

Table 1 summarizes present stand composition of the five stands. Oaks occupied, at minimum, a codominant position in the overstory stratum. However, oaks were virtually absent from the understory (2.5 cm ≤ dbh < 10 cm), and oak seedlings (stems > 1 m tall, dbh < 2.5 cm)

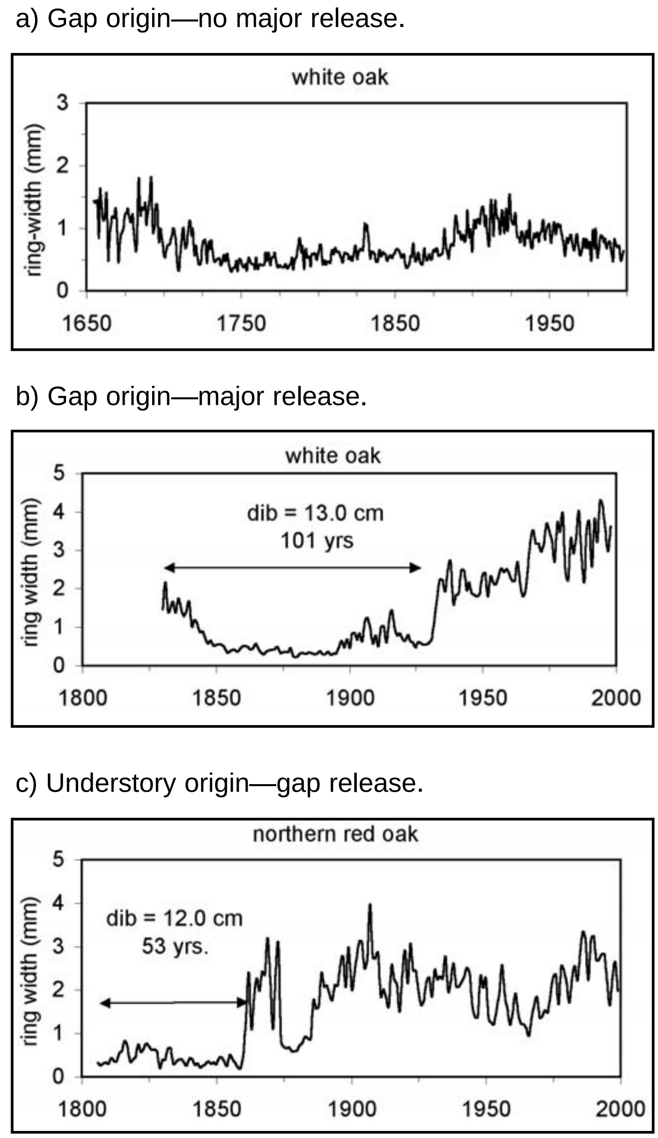

Figure 1.—*Examples of suggested classification of tree-origin and growth trends of canopy oak trees based on early growth rates and presence/absence of a major crown release (percent growth change ≥ 100 percent).*

were present at only one site. Two trends characterized the age structure and oak recruitment at these sites. At Collins Woods and Wrights Woods, establishment of oaks was limited to the period 1650-1875. White oaks (*Quercus alba* L.) were the oldest trees, however the most recent recruitment of this species occurred in 1850; northern red oaks (*Q. rubra* L.) first recruited between 1750-1800 and continued until 1850 at Wrights Woods, and 1875 at Collins Woods.

Both sites showed large ingrowth of shade tolerant tree species in the 1800s, as well as pioneer species such as yellow-poplar (*Liriodendron tulipifera* L.), pignut hickory (*Carya glabra* Mill.), American elm (*Ulmus americana* L), and black cherry (*Prunus serotina* Ehrh.) (table 1). At Watter Smith, Murphy Tract, and Horners Woods, white oak and chestnut oak (*Q. prinus* L.) were the oldest trees, and red oak and black oak (*Q. velutina* Lam.) were recruited beginning in the early 1800s. These sites also showed gradual ingrowth of both shade tolerant and pioneer species in the 1800s, however, in contrast to Collins Woods and Wrights Woods, recruitment of oak species continued during this period.

The oldest trees at Wrights Woods, Watter Smith, and Murphy Tract date to well-defined time periods that suggest these stands initiated in the aftermath of a stand-initiating disturbance. The absence of clearly defined cohorts among the oldest trees at Collins Woods and Horners preclude a reliable estimate of stand origin. Here, the small number of old trees and wider age ranges make it difficult to determine if they are survivors of a large disturbance-initiated cohort, or remnants of a smaller cohort in a stand that has been uneven-aged for centuries. At all sites, shade tolerant species such as sugar maple (*Acer saccharum* Marsh.) and American beech (*Fagus grandifolia* L.) were absent from the oldest cohorts.

Canopy Disturbance Intervals

Table 2 summarizes median disturbance intervals for single- and multiple-tree events for each site. Similarity over time was the most significant finding. Single-tree disturbances occurred about every 3 years, while larger,

Table 1.—*Importance values (IV) for major overstory tree (dbh ≥ 15 cm dbh), and understory tree (2.5 cm ≤ dbh < 15 cm) strata at five oak-dominated old-growth study sites. IV = (relative basal area + relative abundance + relative frequency)/3*

Species	Collins Woods (OH)	Wrights Woods (PA)	Watter Smith (WV)	Murphy Tract (WV)	Horners Woods (WV)
Overstory tree					
red maple	7.4	15.2	13.7	14.9	12.4
sugar maple	34.0	49.0	9.6	0.8	10.7
hickory	2.0	--	8.0	4.0	10.2
Am. beech	21.6	--	12.2	14.4	18.4
yellow-poplar	7.9	--	1.9	--	3.6
black cherry	0.6	10.7	--	--	--
white oak	9.8	15.1	13.7	28.5	10.2
chestnut oak	--	--	4.0	5.0	7.2
northern red oak	7.9	4.8	16.2	6.7	0.6
black oak	--	--	6.9	12.6	16.9
Understory tree					
red maple	3.2	9.2	11.1	30.5	9.3
sugar maple	73.2	79.4	15.2	2.8	37.5
hickory	4.7	1.4	1.9	2.3	2.2
Am. beech	9.2	--	25.0	26.4	31.3
white ash	1.5	--	0.5	0.4	0.9
eastern hophornbeam	6.7	1.2	24.2	0.8	4.0
sourwood			1.0	11.7	2.2
white oak	--	--	--	4.1	--
scarlet oak	--	--	--	0.4	--
chestnut oak	--	--	--	0.6	1.0

multiple-tree disturbances occurred every 17 years. A historical comparison of disturbance intervals revealed a few differences by site. However, even when statistically significant, most differences were small, within the ± 1 year margin of error of the radial growth averaging method, and not ecologically meaningful. There was a slight decline in single-tree disturbance intervals between the presettlement (1700-1800) and settlement (1801-1900) periods, and a slight increase during the modern period (1901-1990, table 2a).

Because the single-tree disturbance frequency is strongly correlated with number of sample trees, increasing sample depth accounts for a portion of these changes. On average, the interval between multiple-tree events slightly increased from an all-site average of 14 years in the presettlement era, to 18 years in the modern period (table 2b). However, the magnitudes of most changes were relatively small, and none were statistically significant.

Canopy Accession Trends

Tree origin and mode of canopy accession were classified as either

a) gap origin-no release,
b) gap origin-gap release, or
c) understory origin-gap release (table 3, see fig. 1 for examples).

For all trees, the likelihood of originating in a large opening and achieving overstory status before canopy closure (N = 85), is about the same as the probability of requiring a major release, either from the understory (N = 66) or from a smaller gap that closed (N = 22).

White oak and red oak best exemplified this trend, with almost the same number of trees requiring at least one release from above (N = 47 and 16, respectively) as those that did not show a major release (46 and 13, respectively). Chestnut oak was more likely to have originated in the shaded understory before release, consistent with its reputation as the slowest grower of these four species (Burns and Honkala 1990). In contrast, a higher proportion

Table 2.—*Median and mean disturbance intervals for five oak-dominated old-growth study sites. Shown are single-tree events and multiple-tree events for the entire chronology, and for three historical periods. Means with different letters are statistically different (F-test for unequal variances).*

Site	Median	-- Means --		
	1700-1990	1700-1800	1801-1900	1901-1990
Single-tree events				
Wrights Woods (PA)	3.0	6.6a	3.1b	3.5ab
Murphy Tract (WV)	2.2	3.1ab	2.3a	4.2b
Horners Woods (WV)	2.8	7.1a	3.0b	2.4b
Watter Smith St. Park (WV)	3.4	5.4a	3.3a	4.6a
Collins Woods (OH)	3.8	6.3a	4.4b	3.8b
Multiple-tree events				
Wrights Woods (PA)	20.7	17.0a	17.3a	18.8a
Murphy Tract (WV)	14.2	12.3a	12.0a	22.3a
Horners Woods (WV)	14.8	17.0a	14.4a	15.8a
Watter Smith St.Park (WV)	15.9	13.2a	18.0a	19.1a
Collins Woods (OH)	14.9	14.0a	13.2a	15.2a

Table 3.—*Summary of growth trends and origin of canopy oak trees based on early growth rates and identification of major release events (GC percent ≥ 100 percent) using radial growth averaging (N = 176). Values represent sums from five study sites.*

Origin-growth trend type	Species			
	white oak	chestnut oak	red oak	black oak
Gap origin-no release	46	3	13	23
Understory origin-gap release	34	9	12	11
Gap origin-gap release	13	2	4	3

of black oaks were successful in using gaps to attain overstory status without being overtopped and then released.

Understory residence time and dib at overstory accession for trees that survived being overtopped are shown in table 4. White oak averaged 89 years before reaching the overstory at an average dib of 15.3 cm. Red oak and black oak attained overstory status sooner (51 and 50 years, respectively) and at smaller diameters (11.8 and 11.0 cm, respectively). Variability of understory residence time was very high. For example, at Murphy Tract, understory residence time for white oak varied from 20 to 215 years.

DISCUSSION

Canopy disturbance rates of the oak-dominated stands of this study are remarkably consistent across a broad geographical area and a 300-year time period. Small scale disturbances occur, on average, every 3 years, while larger events involving more than one tree occur on a 17 year interval. The similarity of canopy disturbance rates was not unexpected. 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). These landscape-scale factors, in turn, constrain disturbance rates to a fairly narrow and predictable range of values (Runkle 1985).

Canopy Disturbance and Recruitment

The tree-ring record suggests three modes of oak recruitment that correspond to three levels of canopy disturbance:

a) recruitment in large openings after a large stand-initiating disturbance;
b) episodic recruitment in canopy gaps that either remain open long enough for stems to reach the overstory without being overtopped from above, or which undergo a repeat disturbance and second release; and
c) continuous establishment in the understory and overstory recruitment after gap release.

Murphy Tract, Wrights Woods, and Watter Smith State Park originated after large stand-initiating disturbances. Growth trends of these trees were distinguished by the absences of overstory suppression and major crown releases. The absence of shade tolerant tree species in the disturbance-initiated cohort suggests that either some type of disturbance eliminated them (i.e., fire), or they were present but in small numbers.

Oaks were also recruited via smaller canopy disturbances involving two or more trees that occurred, on average, every 17 years. These trees also reached overstory position 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 multi-cohort age structure. Large multiple-tree gaps were identified, however two-tree gaps were most common. Oaks were also found that had initiated in the understory under less than free-to-grow conditions. Here early growth rates were consistently less than 1 mm yr^{-1}.

Understory Shade and Recruitment

The length of time these oaks survived in the understory varied by their relative shade tolerance. White oaks, the most tolerant of the four oak species of this study, required on average, 90 years to reach the overstory. Long understory residence time for white oak is consistent with previously published work on this species. Seedlings, saplings, and pole-sized trees may persist for 60 to 90 years under a closed canopy (Minckler 1957, McGee and Bivens 1984), and are therefore in place when canopy gaps occur. Red oak and black oak are generally considered less tolerant of shade than white oak (Burns

Table 4.—*Mean understory residence time (MRT) and dbh (inside bark) at canopy accession for four oak species (N = 89) at five oak-dominated old-growth study sites. Trees included are those classified as gap origin-gap release, and understory origin-gap release.*

	Species			
	white oak	chestnut oak	red oak	black oak
Mean understory residence time (± SE, years)	89±48	38±20	54±24	50±25
DBH (inside bark) at canopy accession (± SE, cm)	13.3±8.3	6.2±5.0	11.7±6.9	10.0±6.8
Number of trees	47	12	16	14

and Honkala 1990), but the percentage of these species that initiated in understory shade (41 and 30 percent, respectively) were comparable to white oak (37 percent, table 3).

The 50-year average understory residence times of red oak and black oak in this study exceed most current estimations of these species' ability to survive heavy shade. Like white oak, seedlings of red oak and black oak readily resprout after dieback, and roots may be 30 years older than stems (Merz and Boyce 1956, Johnson 1994). However, red oak seedlings demonstrate a negative carbon balance under a heavy canopy, and seedlings often die once acorn reserves are depleted (Lorimer 1993). Current experience suggests that survival of aboveground portions of seedlings and sprouts, particularly on better sites, is often very low. In an experiment that removed tall understory vegetation (> 1.5 m), 5-year survival of planted white oak and red oak seedlings was 93 percent compared to only 27 percent survival on control plots (Lorimer and others 1994).

Numerous other studies show that understory light levels are critical for survival and growth of oaks (Carvell and Tryon 1961, Loach 1970), but particularly for red oak, because of this species lower drought and shade tolerance (McGee 1968, Larsen and Johnson 1998). However, while increasing understory light increases oak seedling growth, competing species such as beech, sugar maple, red maple, and black cherry also benefit. The latter two species may, in fact, gain an advantage over oaks due to greater morphological and physiological plasticity, and the ability to respond more rapidly to changing conditions (Gottschalk 1994, Abrams 1998). Therefore, unless a reduction in the level of understory competition accompanies an increase in light to the understory, the temporary advantage available to oaks may be lost.

In the stands of this study, the existence of numerous and variable-sized oak cohorts suggest that they were historically maintained by a unique combination of large and small disturbances, high understory light levels, and low levels of understory competition. However, beginning in the 1800s, conditions changed. Oak replacement largely ceased during the last 150 to 200 years at Wrights Woods and Collins Woods. At Wrights Woods, the youngest white oak and red oak date to 1805 and 1852, respectively. At the remaining three study sites, oak replacement continued through the 1800s and early 1900s, but current understory (seedling-sapling) levels are either low or virtually absent. The disturbance interval analysis suggests no appreciable change in the creation-rate of canopy gaps. Thus, the primary change must lie with the level of understory light and inter-species competition. There are several lines of evidence to support this hypothesis. Early land surveys attest to forests dominated by oak species (Rentch 2001). Presettlement-era dominance of upland forests in this region by species more shade tolerant than oak was uncommon outside of mesic and protected environments (Russell 1980, Abrams 1992, Lorimer and others 1994, Nowacki and Abrams 1997).

The species composition of the oldest surviving trees does strongly suggest low levels of shade tolerant species in the understory of pre-settlement forests. Sugar maple and beech are potentially as long-lived as white oak (Burns and Honkala 1990), and seed sources of sugar maple, red maple, and beech were surely present. The canopy disturbance regime described in this study—frequent, small, repeat canopy gaps—should facilitate the presence of shade tolerants in the old-growth cohorts (Runkle 1985, Canham 1990). Nevertheless, none of the study sites had these species in the oldest cohorts. The oldest sugar maples and beech generally date to the 1850s, and as late as 1890 at Wrights Woods. At Collins Woods and Wrights Woods, the earliest establishment of shade tolerant species, 1850 to 1900, was concurrent with the cessation of oak establishment.

The change in understory composition signaled by the recruitment of shade tolerant species in the mid-late 1800s is paralleled by a change in the frequency of oak modes of canopy accession. Figure 2 shows a chronology of oak recruitment by historical period. Before 1900, oaks utilized gap origin-no release and understory origin-gap release strategies in roughly equal proportions. After 1900, 10 of 14 (71 percent) oaks were established in large openings and underwent no overstory suppression. In contrast, only one white oak now in the overstory established in understory shade, and three white oaks originated in a gap and survived being overtopped. These results are influenced by a smaller number of cored trees representing the post-1900 time period, however these trees generally comprise a 100 percent inventory of oaks in 15 cm or greater size-classes.

Evidence from the old-growth oak forests of this study suggests that, for a time, they utilized a relatively constant canopy disturbance rate to replace themselves in kind. Low levels of shade

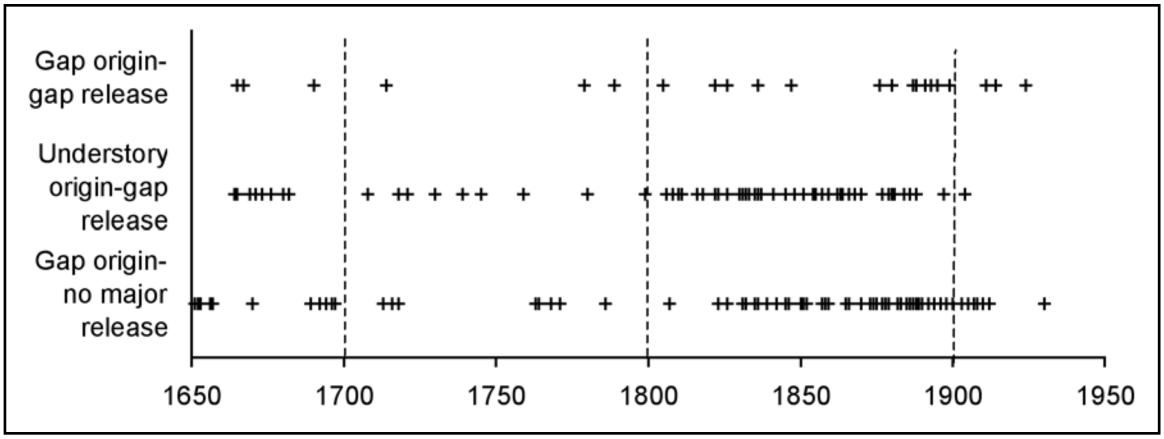

Figure 2.—*Chronology of oak tree-origin by mode of canopy accession for five oak-dominated old growth study sites.*

tolerant species in presettlement land surveys, their absence from the old-growth cohorts, their ingrowth in the mid-1800s, and the concurrent decline of oak establishment as understory species, all suggest substantial changes in the understory species composition over the time period reviewed.

The consequence of understory change was an increase in understory shade, a decline in oak sapling abundance, and a decline in the pool of oak stems that could utilize canopy openings to retain these species share of the canopy. The results of this study support Lorimer's (1993) hypothesis that the principal bottleneck is more a function of the physiological limitations placed on oak advanced regeneration by dense low overstory shade than low levels of oak germination.

CONCLUSION

Because of their antiquity, the old-growth forests of this study provide a valuable source of long-term data on individual tree and stand dynamics of oak forests of this region. These data, in turn, may contribute to a better understanding of the ecological foundations of the oak regeneration problem. Although there was variation by site and by historical period, there have been no significant changes in canopy disturbance rates for the 300-year period reviewed.

Using a variety of growth strategies and canopy opening-sizes, oak components have been maintained in a relatively stable, uneven aged condition. However, current sparseness of sapling-size oak advance regeneration suggests that the future oak composition is in question, particularly on better sites. Oaks' ability to persist in the understory for long periods of time constitutes the key difference between the past and present condition of these stands. Average understory residence times suggest that past understory light levels and the competitive environment allowed oak seedlings and saplings to survive until release. Although there is some historical precedence for these values, few contemporary second-growth forests contain surviving understory oaks of this age, particularly red oak.

These 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 this system's manipulation of overstory density, understory light levels, and the level of understory competition is consistent with factors that this study has 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 more tolerant species. Yet the variety of growth strategies exhibited by these old trees, and the age structures of these stands suggest that continuous "natural" cultural treatments were in fact an integral component of the historic disturbance regimes of these forests, and the key to establishment and survival of a competitive oak understory, and eventual accession to the overstory.

Changes in the historic fire regime best account for the changes in stand composition and structure suggested by this study. No other form of surface-level disturbance discriminates in favor of oak species and against maple, beech, and other typical understory competitors. Most of the long-term fire chronologies are for areas at the periphery of the Central Hardwood region. These studies suggest a relatively frequent recurrence of low intensity surface fires during presettlement and settlement times; the few studies of oak dominated forests in the study area confirm this. Additional fire chronologies of older forests are a needed area of research. In addition, stem reconstructions of trees that initiated in understory shade would be useful in verifying height growth patterns proposed by this study.

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