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Forest Ecology and Management 184 (2003) 285–297

Forest Ecology and Management

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Oak establishment and canopy accession strategies in five old-growth stands in the central hardwood forest region

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Received 15 December 2002; received in revised form 11 February 2003; accepted 1 April 2003

Abstract

Using a radial growth averaging technique, decadal-scale changes in growth rates of overstory oaks were used to identify canopy accession events at five old-growth sites. A review of tree-ring chronologies yielded three growth strategies: (1) one-half of the oaks originated in a large opening and achieved overstory status before canopy closure; (2) 38% originated in a smaller opening and required a second gap event to attain overstory status; and (3) 13% achieved overstory status after an extended period of very low growth in understory shade and one or two subsequent gap releases. For trees that required a major canopy release, understory residence times averaged 89, 54, 50 and 38 years for white oak, northern red oak, black oak, and chestnut oak, respectively. Average diameters (inside bark) at canopy accession were 13.3, 11.7, 10.0, and 6.2 cm for the four oak species, respectively. Although there is some historical precedence for these values, few contemporary second-growth forests contain understory oaks of this age, particularly red oak. These long understory residence times suggest that the level of understory shade, and by inference, the abundance of shade tolerant understory species, was considerably less before 1900.

Keywords: Canopy accession; Canopy release; Oaks; Radial growth averaging; Central hardwood forest

1. Introduction

Following the most recent glacial maximum, oaks (*Quercus* spp.) became a dominant tree genus in eastern North American deciduous forests (Watts, 1979; Davis, 1981). Pollen records suggest that oaks were also dominant in eastern deciduous forests when first settled by Euro-Americans (Russell, 1980; Larabee, 1986; Delcourt and Delcourt, 1997). These findings are consistent with early written descriptions of forest composition (Michaux, 1853; Braun, 1950; Spurr, 1951), as well as reconstructions of presettlement forest composition from early land surveys in Ohio (Sears, 1925; Dyer, 2001), southwestern Pennsylvania (Abrams and Downs, 1990), eastern West Virginia (Abrams and McCay, 1996), and New Jersey and New York (Russell, 1980; Loeb, 1987).

In the last 50 years, the declining dominance of canopy oaks and understory oak recruits has become acute on all but the driest and below average sites (SI $<$ 18 m, Lorimer, 1993). This trend is true both for second-growth, managed stands (Weitzman and Trimble, 1957; Carvell and Tryon, 1961), as well as old-growth preserves (McGee, 1984; Parker et al., 1985). Understory failure of oak regeneration is all the more important because canopy replacement of oaks in kind

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0378-1127/$ – see front matter
doi:10.1016/S0378-1127(03)00155-5

is heavily dependent on the accumulation of advance reproduction beneath the parent stand (Carvell and Tryon, 1961; Larsen and Johnson, 1998).

Because 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 the disturbance regime have been proposed as contributing to declines in oak dominance in eastern forests (Abrams, 1992; Nowacki and Abrams, 1997). Disturbances initiate, or renew, a process of species replacement that is dependent on the species present, their competitive potential and growth strategies, and the amount of growing space released by the disturbance. However, oaks are not readily characterized by their disturbance regime (Runkle, 1990), and do not fit well into standard ideas of succession (Abrams, 1992). Oaks are generally classified as mid-successional species of intermediate shade tolerance (Burns and Honkala, 1990), yet there is compelling evidence that oaks dominated many eastern presettlement forests (Sears, 1925; Russell, 1980; Abrams, 1992; Bonnicksen, 2000). The presettlement oak–hickory forest was considered climax by Braun (1950), and there is little indication in the early literature of conversion of oak forests to other species, even after logging by early settlers (Lorimer et al., 1994). Dominance of eastern upland forests in the oak–chestnut region by species more shade tolerant than oak was uncommon outside the more mesic and protected environments (Abrams and Downs, 1990; Nowacki and Abrams, 1992; Lorimer et al., 1994).

The purpose of this study was to examine canopy accession strategies of overstory oaks in five eastern old-growth stands. We reviewed tree-ring chronologies over a 350-year period and identified stand-level disturbances and canopy accession events using a decadal radial growth averaging technique (Nowacki and Abrams, 1997; Rentch et al., 2002). Diameter and age at time of overstory recruitment were determined in order to describe species growth strategies. We also classified trees by modes of establishment and early growth rates to characterize the understory environment in which these trees originated.

2. Study area and data collection methods

Five study stands were selected using four criteria: (1) the presence of oak trees that were larger than 75 cm dbh and older than 200 years; (2) a low level of identifiable human disturbance, for example logging or grazing; (3) minimum size of approximately 4 ha, large enough to maintain a buffer of at least 50 m between plot borders to the edge of the stand; and (4) stand composition that is dominated by deciduous trees with dominant or codominant (Smith et al., 1997) oaks as a major component of the overstory. Study stands sampled include: Collins Woods (Belmont County, Ohio), Wrights Woods (Washington County, Pennsylvania), Watter Smith State Park (Harrison County, West Virginia), Murphy Tract (Ritchie County, West Virginia), and Horners Woods (Lewis County, West Virginia).

Two 0.45 ha (60 m $\times$ 75 m) study plots were established at each stand, with the exception of Watter Smith, where only one plot was established. Each study plot was subdivided into twenty 15 m $\times$ 15 m subplots, and 100% inventories of overstory (dbh $\geq$ 15 cm) and understory (2.5 cm $>$ dbh $<$ 15 cm) stems were conducted. Species 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 (maximum = 100). In each 15 m $\times$ 15 m subplot, two 2 m $\times$ 2 m regeneration plots were established (total 160 m^2). Tree seedlings were tallied as either small (<1 m tall), or large ($\geq$1 m tall, <2.5 cm dbh). Only large tree seedling data are reported in this study.

Regardless of species, the largest tree in each subplot was cored at breast height. In addition, all overstory oaks in the subplot were also cored. Two cores, 180° apart, were extracted parallel to topographic contours. Samples were cross-dated by matching patterns of narrow and wide rings, and measured under a dissecting microscope to the nearest 0.001 mm in conjunction with J2X® software (VoorTech Consulting, 2000). 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.

3. Data analysis

3.1. Canopy disturbance

For each sample tree, we calculated a disturbance chronology by applying the radial growth averaging technique (Nowacki and Abrams, 1997) to the tree's entire raw ring-width series. Canopy disturbances were identified empirically by an abrupt increase in tree-ring width, using the decadal averaging technique:

$$\%GC_i = \left[\frac{M_2 - M_1}{M_1}\right] \times 100 \quad (1)$$

where %GC is the percentage growth change for year$_i$, M_1 the preceding 10-year mean radial growth (inclusive of the disturbance year), and M_2 the subsequent 10-year mean radial growth (exclusive of the disturbance year). Thus, each year's radial growth was evaluated with respect to the means of the previous 10 years and the subsequent 10 years. This radial growth averaging method was tested in a thinned, second-growth mixed oak forest in West Virginia (Rentch et al., 2002). Results indicated that: (1) the technique provided a fairly accurate estimation of the disturbance year, with a precision of ±1 year; (2) there was an approximate 1:1 relationship

Table 1
Importance values (IV) for major: (a) overstory tree (dbh > 15 cm), (b) understory tree (2.5 cm < dbh < 15 cm), and (c) density (stems ha^{-1}) for large regeneration (dbh < 2.5 cm, height > 1 m) at five oak-dominated old-growth study stands[a]

Species	Collins Woods	Wrights Woods	Watter Smith	Murphy Tract	Horners Woods
(a) Overstory tree (IV)					
Red maple	7	15	14	15	12
Sugar maple	34	49	10	1	11
Hickory	2	–	8	4	10
American beech	22	–	12	14	18
Yellow-poplar	8	–	2	–	4
Black cherry	1	11	–	–	–
White oak	10	15	14	28	10
Chestnut oak	–	–	4	5	7
Northern red oak	8	5	16	7	1
Black oak	–	–	7	13	17
(b) Understory tree (IV)					
Red maple	3	9	11	31	9
Sugar maple	73	79	15	3	37
Hickory	5	1	2	2	2
American beech	9	–	25	26	31
White ash	2	–	1	0	1
Sourwood	–	–	1	12	2
White oak	–	–	–	4	–
Chestnut oak	–	–	–	1	1
(c) Large regeneration (stems ha^{-1})					
Red maple	–	–	63	313	–
Sugar maple	1190	1276	250	–	250
Buckeye	–	–	125	–	–
Hickory	26	–	–	–	63
American beech	132	–	63	875	656
White ash	159	94	250	125	125
Yellow-poplar	–	–	63	–	–
Cucumber tree	–	–	–	–	31
Black gum	–	–	63	94	–
Sourwood	–	–	–	125	281
Black cherry	26	31	63	–	–
White oak	–	–	–	125	–
Northern red oak	–	100	–	–	–
Black oak	–	–	–	94	–
Elm	26	63	63	–	–

[a] With the exception of Watter Smith, values are means of two 0.45 ha study plots.

between %GC and %crown release (%CR), and (3) the magnitude of %GC is strongly correlated with disturbance severity.

Canopy accession events were delineated from smaller crown releases by the magnitude of growth change. Minor to moderate releases (%GC, 25–99) corresponded to gap-caused growth increases associated with increased sidelight to trees already in the overstory. Canopy accession events were defined as major releases when $\%GC \geq 100$, following the criteria of Lorimer and Frelich (1989), Nowacki and Abrams (1997), and Schuler and Fajvan (1999). These release events corresponded to overhead releases of smaller, overtopped saplings and pole-sized trees in canopy openings.

4. Results

4.1. 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 IV 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, 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 929 large seedlings ha^{-1}. However, large oak advance regeneration was present only at Wrights Woods and Murphy Tract, and abundance was less than 125 stems ha^{-1} (Fig. 1).

Two trends characterized the origins and disturbance histories of these sites (Fig. 2). The first trend was represented by Murphy Tract, Wrights Woods, and Watter Smith. There, the oldest trees dated to rather well defined time periods (i.e., 1650, 1665, and 1690, respectively) suggesting that these stands originated in the aftermath of stand-initiating disturbances. Juvenile growth rates for the oldest cohort were above-average and tree growth trends exhibited no periods of

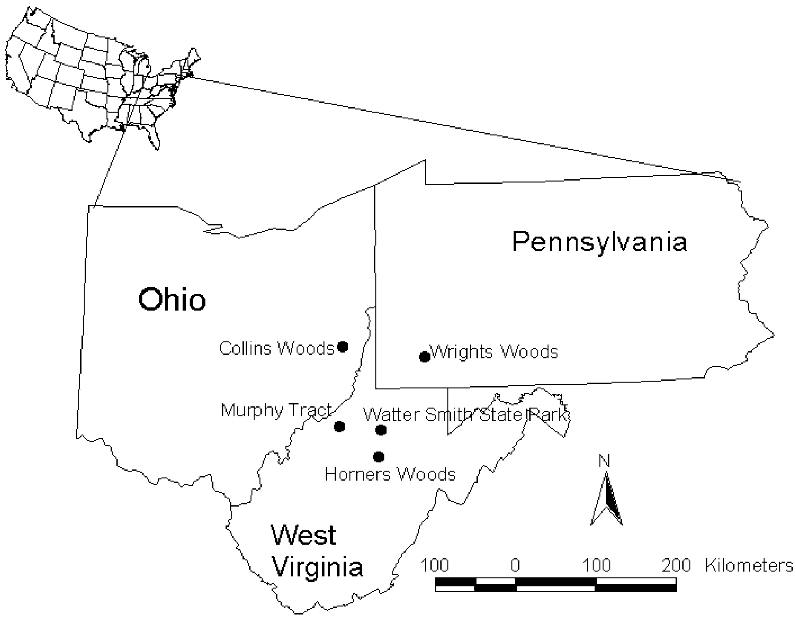

Fig. 1. Location map of five oak-dominated, old-growth study stands.

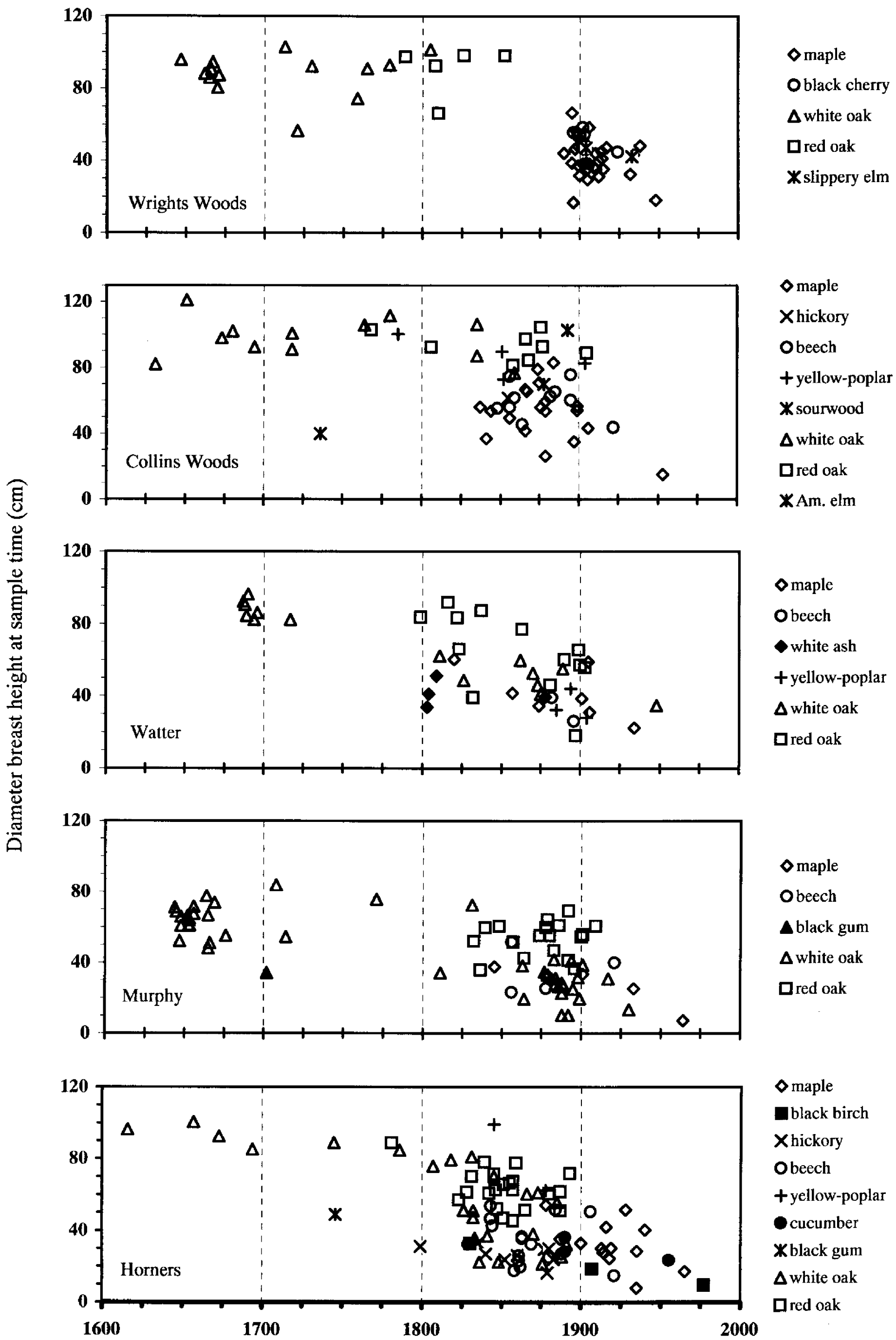

Fig. 2. Diameter (cm) versus age (at dbh) for cored overstory trees at five study stands. Data are pooled from two 0.45 ha study plots, except for Watter Smith (one study plot). Wrights Woods, Watter Smith, and Murphy Tract originated in the aftermath of stand-initiating disturbances. The origins of Collins Woods and Horners Woods are less identifiable.

extended suppression or subsequent overstory release. Each of these three sites also underwent a pause (60–100 years) in new tree recruitment consistent with the stem exclusion and understory reinitiation stages of stand development (Oliver and Larson, 1996). The second trend was exhibited by Collins Woods and Horners Woods. There, it was difficult to determine if the oldest trees were remnants of a once larger disturbance-initiated cohort or members of small cohorts that arose in the aftermath of smaller (one to two trees) canopy openings. At all sites, the absence of shade tolerant tree species from the oldest cohorts suggests that oaks were historically dominant.

4.2. Oak establishment

Oak establishment tended to be either fixed in time or continuous (Fig. 2). At Collins Woods and Wrights Woods, 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 and 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) as well shade intolerant species

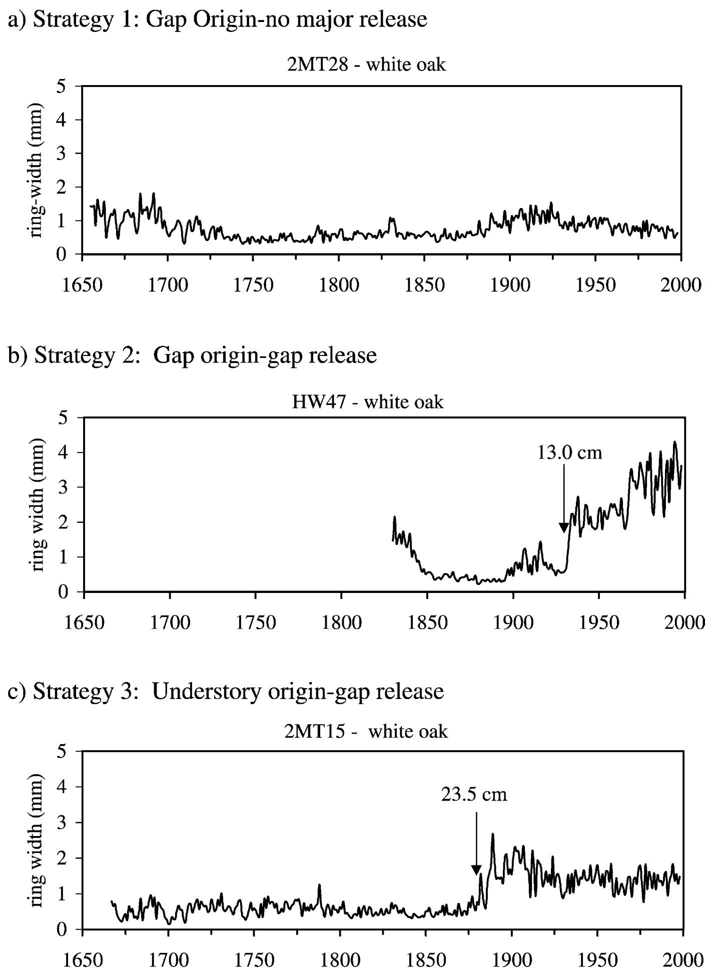

Fig. 3. Individual tree radial growth patterns classified according to tree-origin and canopy accession strategies. Strategies are based on early growth rates and presence/absence of a major crown release (percent growth change $\geq$ 100%). Trees are labeled according to stand: MT, Murphy Tract; HW, Horners Woods.

such as yellow-poplar (*Liriodendron tulipifera* L.), hickories (*Carya* spp.), elms (*Ulmus* spp.), and black cherry (*Prunus serotina* Ehrh.).

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

4.3. Early growth rates and canopy accession trends

For sample oaks, three canopy accession strategies were identified based on juvenile growth rates (at dbh), overall growth patterns, and the presence or absence of a major crown release (%GC $\geq$ 100%, see Fig. 3):

(a) Strategy 1: Gap origin—no major release. The absence of a major crown release distinguishes this trend. 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 (Fig. 3a) were considered to be direct overstory recruits in high-light conditions (Lorimer et al., 1988; Lorimer and Frelich, 1989; Frelich and Graumlich, 1994; Nowacki and Abrams, 1997).

(b) Strategy 2: Gap origin—gap release. Radial growth during the first 50 years for these trees was similar to Strategy 1. However, growth was subsequently reduced by canopy closure from above, and then resumed pre-suppression rates after a major release and overstory accession (Fig. 3b).

(c) Strategy 3: Understory origin—gap release. Initial growth for these trees averaged 0.5–0.8 mm per year, less than one-half the site average, and these trees were considered to have originated in a low-light, understory position. Following one, or occasionally, two major releases and overstory accession, growth showed a large increase and no further overstory suppression (Fig. 3c).

Half the oaks ($N = 85$) originated in a large opening and achieved overstory status before canopy closure (Strategy 1); 38% ($N = 66$) originated in a smaller opening and required a second gap opportunity to attain overstory status (Strategy 2); 13% ($N = 22$) initiated as advance regeneration and achieved overstory status after an extended period of very low growth in understory shade (Strategy 3, Table 2). For white oak and red oak, almost the same proportion of trees required at least one release from above ($N = 47$ and 16, respectively) as those that did not show a large release (46 and 13, respectively). Chestnut oak was approximately 30% 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 (62%) of black oaks were successful in using gaps to attain overstory status without being overtopped.

Mean understory residence time (MRT) and dbh inside bark (dib) at overstory accession for overtopped trees are shown in Table 3. Variability of understory residence time was very high. For example, at Wrights Woods and Murphy Tract, the range of understory residence time for white oak was 20–215 years. White oak averaged 89 years before reaching the overstory at an average dib of 13.3 cm. Red oak and black oak

Table 2
Summary of frequencies of oak canopy accession strategies based on early growth rates and identification of major release events (percent growth change $\geq$ 100), using radial growth averaging

Origin—growth strategy	White oak	Chestnut oak	Number of red oak	Black oak	Total
Gap origin—no release	46	3	13	23	85
Gap origin—gap release	13	2	4	3	22
Understory origin—gap release	34	9	12	11	66
Total	93	14	29	37	

Table 3
MRT[a] and dib at canopy accession for four oak species ($N = 88$)[b]

Species	N	MRT (±S.E.)	dib at accession (±S.E.)
White oak	47	89 ± 48	13.3 ± 8.3
Chestnut oak	12	38 ± 20	6.2 ± 5.0
Northern red oak	16	54 ± 24	11.7 ± 6.9
Black oak	14	50 ± 25	10.0 ± 6.8

[a] MRT defined as time between initial establishment (earliest ring) and canopy accession (percent growth change ≥ 100%). Trees that initiate in gaps with no major releases (canopy accession strategy 1) are not included.

[b] Trees included are those classified gap origin—gap release (canopy accession strategy 2), and understory origin—gap release (canopy accession strategy 3).

attained overstory status sooner (54 and 50 years, respectively) and at smaller diameters (11.7 and 10.0 cm, respectively, see Fig. 4 for examples).

Only 13 of the 173 oaks examined showed more than one major crown release. In contrast, sugar maple and beech may require two to five repeat gap events before final overstory accession (Canham, 1990; Yetter and Runkle, 1986). While setting a 100% GC as evidence of overstory recruitment was somewhat conservative, the fact than so few oaks showed more than one release of this magnitude validates this definition. For white oaks that showed more than one major release ($N = 9$), average MRT and dib were 111 years and 17.8 cm, respectively.

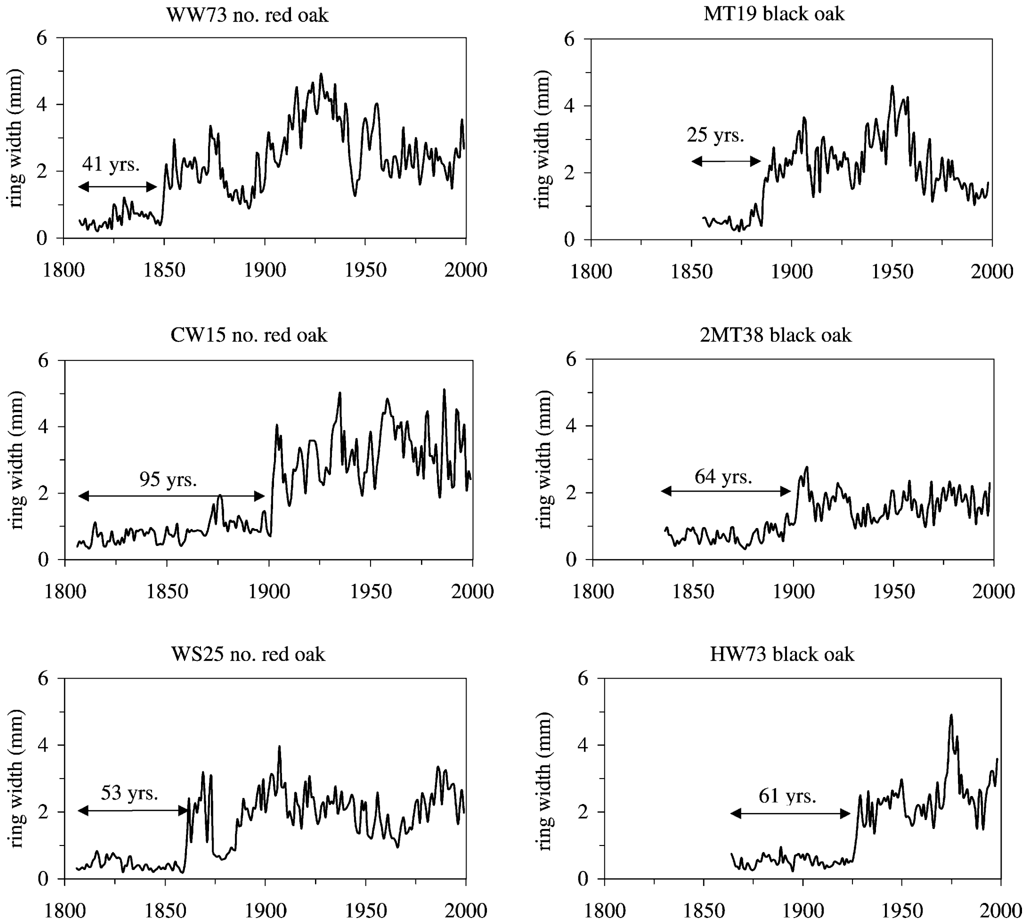

Fig. 4. Examples of northern red oaks and black oaks that initiated in the understory and survived for an extended period until overhead release and canopy accession (canopy accession strategy 3). Arrows indicate understory residence time (years) prior to final overhead release (percent growth change ≥ 100%). Trees are labeled according to stand: WW, Wrights Woods; MT, Murphy Tract; CW, Collins Woods; WS, Watter Smith State Park; HW, Horners Woods.

5. Discussion

5.1. Canopy disturbance and oak recruitment

The tree-ring record suggests three modes of oak establishment and canopy recruitment: (a) establishment/release in large, multiple-tree openings after a 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 temporarily close followed by a repeat disturbance and release; and (c) continuous establishment, extended period of low annual growth in the understory, and subsequent overstory recruitment by means of either (a) or (b).

The oldest cohorts at Murphy Tract, Wrights Woods, and Watter Smith State Park originated after large stand-initiating disturbances. Growth trends of these trees were distinguished by the absence of overstory suppression and major crown releases. In addition, the absence of shade tolerant tree species from the oldest cohorts (i.e., trees that were alive in 1999) suggests that either the disturbance eliminated them or they were present, but in small numbers and at a competitive disadvantage with oaks. At all five study sites, oaks also were recruited via smaller canopy gap disturbances involving two or more trees that occurred, on average, every 16 years (Rentch et al., in press). These oaks also reached an overstory position without being overtopped. However, these gap disturbances resulted in a spatially and temporally dispersed multi-cohort age structure. Large (>1000 m^2) multiple-tree gaps were identified; however, two-tree gaps ($\leq$200 m^2) were most common.

Oaks that initiated in the understory in less than free-to-grow conditions showed growth rates that were consistently less than 1 mm per year. Tree 2MT15 (Fig. 3c) is an extreme example of this pattern. Between its earliest ring (1667) and canopy accession (1881), this tree had an average growth rate of 0.54 mm per year. The standard deviation during this time period was 0.12 mm, suggesting that low-light levels influenced radial growth more than variation in annual moisture and temperature.

5.2. Oak overstory recruitment and understory shade

Literature on shade tolerance of white oak seedlings (Burns and Honkala, 1990), saplings, and pole-sized trees (Minckler, 1957, 1967; Schlesinger, 1978; McGee and Bivens, 1984; Graney, 1987) document their potential for survival for up to 60–90 years under a closed canopy, and is consistent with the understory residence times found in this study. However, the 50-year average understory residence times of red oak and black oak in this study exceeded most current estimates of these species' ability to survive heavy shade. Red oak and black oak are generally considered less tolerant of shade than white oak (Burns and Honkala, 1990), but the percentage of these species that initiated in understory shade (41 and 30%, respectively) were comparable to white oak (37%, Table 2). Like white oak, seedlings of red and black oaks readily resprout after dieback, and roots may be 30 years older than stems (Merz and Boyce, 1956; Johnson, 1994). However, current experience suggests that survival of aboveground portions of seedlings and sprouts, except on drier and below average sites (Lorimer, 1993), is often very low. Red oak seedlings demonstrate a negative carbon balance under a heavy canopy, and often die once acorn reserves are depleted (Lorimer, 1993). Johnson (1994) reported that 8-year seedling survival of red oak was as low as 20% when the subcanopy was intact. However, in an experiment that removed all understory vegetation >1.5 m tall, 5-year survival of planted white oak and red oak seedlings was 93% compared to only 27% survival on control plots (Lorimer et al., 1994). Net height decreased on the control plots because of dieback, but increased 50–96% on the understory-removal plots.

Numerous other studies show that understory light levels are critical for survival and growth of all oaks (Carvell and Tryon, 1961; Loach, 1970), but particularly for red oak, because of this species lower drought and shade tolerance (McGee, 1968; Phares, 1971; 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 may 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, if an increase in light reaching the forest floor is not accompanied by a reduction in competing species, the temporary advantage available to oaks may be lost.

The canopy disturbance regime described in this study—large, infrequent stand-initiating disturbances, and frequent, small, repeat canopy gaps—should facilitate the presence of shade tolerant species in the old-growth cohorts (Barden, 1980, 1981; Runkle, 1985; Canham, 1990; Poulson and Platt, 1996). However, none of these sites had these species in the oldest cohort. 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 (1850–1900) was concurrent with the cessation of oak establishment.

Two reasons may account for the absence of non-oaks in the oldest cohorts. First, they may have recruited and died. Red maple and hickories at Murphy Tract are currently present in the overstory, yet neither is as long-lived as white oak (Iverson et al., 1999), and had they been a component of the initial stand, they would not necessarily be present today. The absence of overstory sugar maple and beech suggests the second dynamic. As seedlings and saplings, these species are highly susceptible to damage, topkill, and mortality from low intensity surface fires (Burns and Honkala, 1990; Iverson et al., 1999). In contrast, oak acorns germinate well on mineral soil after low intensity surface fires (Iverson et al., 1999). Oak seedlings sprout readily after fire topkill (Barnes and Van Lear, 1998; Huddle and Pallardy, 1999), and larger trees are relatively fire resistant because of thick, deeply furrowed bark (Burns and Honkala, 1990; Abrams, 1992; Smith and Sutherland, 1999). Oaks not only survive fire, they also benefit from the removal of tall understory shade (Lorimer et al., 1994). The dominance of oak in presettlement-era forests can be attributed, in part, to the frequency of surface fires set by native Americans (Bromley, 1935; Day, 1953; Buell et al., 1954; Abrams, 1992; Bonnicksen, 2000). Settlers continued this practice through the 1800s (Van Lear and Waldrop, 1989; Abrams, 1992; Sutherland, 1997).

Although few in number, fire chronologies for mixed oak forests that are similar to those of this study generally support the oak–fire hypothesis (Abrams, 1992). McCarthy et al. (2001) found a median fire interval of 2.0 years between 1624 and 1997 in Dysart Woods, Ohio, less than 10 km from Collins Woods. Most occurred during the settlement period (i.e., after 1780) and none occurred after 1881. These data coincide with our oak establishment data from Collins Woods. In western Maryland, Shumway et al. (2001) found that fire was a persistent disturbance before 1930, occurring at a median interval 7.6 years between 1616 and 1959, and that the recruitment of red maple and black birch increased since fire suppression. In managed, second-growth stands, recent research indicates that shelterwood-burn techniques provide the most effective combination of overstory (canopy gaps) and understory (reduction of low shade) disturbance that facilitates oak success (Brose et al., 1999; Van Lear et al., 2000).

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. Low levels of shade tolerant species in presettlement land surveys (Rentch, 2001), 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 changes in understory composition 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.

5.3. Management implications

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. Using a variety of growth strategies and canopy opening-sizes, oak components have been maintained in a relatively stable, multi-aged condition. However, the current sparseness of sapling-size oak advance regeneration suggest that the future oak composition is in question, particularly on better quality 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 of 89 and 54 years for white oak and red oak, respectively, 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 overstory disturbance combined with understory fire 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 sugar maple, beech, and other typical understory competitors. Most of the long-term fire chronologies are for areas at the periphery of the central hardwood forest 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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