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Understory Tree Characteristics and Disturbance History of a Central Appalachian Forest Prior to Old-Growth Harvesting

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Abstract

To better understand the dynamics of red oak regeneration, we evaluated the composition of understory woody species and recruitment characteristics of a mixed mesophytic forest in the central Appalachian region at the time of old-growth logging. We also evaluated canopy disturbance history during both the old-growth and second-growth periods. Three possible modes of oak recruitment are proposed: isolated, episodic, and continuous. Patterns of stemwood radial growth were used to evaluate the frequency of disturbance. Levels of change in red oak radial growth were greatest from 1906 to 1911, an indication of major disturbance. Oak regeneration in all sampled areas that developed into second-growth forest was dominated by seedling-size individuals recruited from 1902 to 1910. However, there also was evidence that red oak, white ash, and bitternut hickory were developing into larger size classes before 1900, and that recruitment and development was related to periodic canopy disturbance. The stand-wide median canopy disturbance interval was 30.83 years between 1797 and 1983. Second-growth oak forests on mesic sites may represent the reproductive potential of an abundance of existing seedlings in the understory prior to harvesting rather than older and larger advanced regeneration.

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Introduction

Pollen evidence has established the importance of oak as a major forest constituent for thousands of years during the Holocene in the central Appalachians and elsewhere in the eastern hardwood region (Kapp and Gooding 1964; Watts 1979; Larabee 1986; Delcourt and Delcourt 1987). However, for the past 40 years, most efforts to regenerate oaks on mesic sites have been unsuccessful (Weitzman and Trimble 1957; Carvell and Tryon 1961; McGee 1975; Lorimer 1984; Schuler and Miller 1995). Yet logging of old-growth forests often resulted in the retention and possibly the enhancement of the oak component in the newly established stands (Potzger and Friesner 1934).

Research has shown that successful regeneration of northern red oak (*Quercus rubra* L.) on mesic sites is enhanced by the establishment of oak seedlings of sufficient size and number before overstory removal (Carvell and Tryon 1961; Sander and others 1976). Loftis (1990) found that large oak seedlings have a greater probability of survival than smaller seedlings following overstory removal. However, it is not known whether second-growth oak forests are the result of the reproductive potential of abundant small seedlings, fewer larger individuals, or both. Delineating the size and age-class structure of understory oak just before old-growth harvesting provides insight into this question and helps define prior disturbance regimes that potentially led to this condition.

Three possible modes of oak recruitment are proposed: isolated, episodic, and continuous. A short period of recruitment that results in a single cohort with a narrow age distribution suggests that conditions suitable for the establishment and development of oak seedlings were isolated. Such periods of recruitment may have been related to unusual disturbance events. A longer period of recruitment (50 to 100 years) that results in an all-age understory suggests that conditions for oak regeneration were relatively continuous. These conditions would require lower levels of stocking, perhaps more frequent disturbances to maintain such levels, and perhaps regular acorn crops. Episodic recruitment that results in two or more distinct oak cohorts suggests that conditions for regeneration were discrete periods with a favorable environment. This also suggests a disturbance history of multiple events with a relatively rapid recovery to a predisturbance state.

To assess modes of oak recruitment, we evaluated the age, size-class structure, and species composition of an old-growth forest understory (around 1900) using the overstory of a contemporary second-growth forest that was initially logged around the turn of the century. Stand reconstruction required establishing the date of old-growth harvesting by dendroecological analysis and then using the year of harvesting to reconstruct the age and size-class structure of the understory at that time. It was anticipated that the oak component would predate a new cohort of shade-intolerant species established after initial logging. New oak seedlings that germinate at the time an older stand is clearcut often fail to compete with sprouts and faster growing species such as yellow-poplar (*Liriodendron tulipifera* L.) (Beck 1970; Sander and Clark 1971). Oaks rely on advance reproduction and dominance probability increases with initial stem size (Loftis 1990). The characteristics of a preharvest oak component prior to initial logging provides insight into the size and abundance of advanced oak regeneration that are required to compete with other species following a major disturbance, and tests the three possible modes of oak recruitment described. We also investigated the history of canopy disturbance using older understory components in the old-growth forest that survived initial logging. The objective was to gain insight into the disturbance pattern prior to old-growth harvesting and how that might have influenced oak recruitment.

Methods

Study Area

This study was conducted on the 1,900-ha Fernow Experimental Forest (39.03^0 N, 79.67^0 W) within the Monongahela National Forest in north-central West Virginia. The ecological landtype of the Fernow, which is administered by the USDA Forest Service's Northeastern Research Station, is referred to as the Allegheny Mountains of the Central Appalachian Broadleaf Forest (McNab and Avers 1994). The draft landtype association is the Allegheny Front Sideslopes (DeMeo and others 1995) and is representative of more than 40,000 ha on the Monongahela National Forest alone. The vegetation of the Fernow ranges from mixed mesophytic to northern hardwoods at higher elevations (Braun 1950). Mesic site overstories often include northern red oak, yellow-poplar, black cherry (*Prunus serotina* Ehrh.), sugar maple (*Acer saccharum* Marsh.), white ash (*Fraxinus americana* L.), and basswood (*Tilia americana* L.). Shade-tolerant understories often consist of American beech (*Fagus grandifolia* Ehrh.), sugar maple, striped maple (*Acer pensylvanica* L.), and serviceberry (*Amelanchier arborea* (Michx. f.) Fern.). The topography of the surrounding area is mountainous with elevations on the Fernow ranging from about 530 to 1,115 m above sea level. Mean annual precipitation is about 143 cm and is distributed evenly throughout the year (Pan and others 1997). The average growing season is 145 days (May to October).

The Elklick watershed (which later became the Fernow) was initially logged between 1903 and 1911 (Trimble 1977) during the railroad logging era (Fansler 1962). Skidding was done with horses and log slides to a temporary standard-gauge railroad. During this period of forest exploitation, many trees were left due to insufficient size or poor form, or because the species was considered undesirable (e.g., sugar maple and American beech).

Field Data

In 1994, as part of a long-term silvicultural study on the Fernow, 18 openings (0.162 ha each) were created by harvesting all merchantable stems within these openings in a 28-ha research unit known as Compartment 18A&B. At the same time, three openings were selected for dendroecological analysis. These openings were distributed from the lower (793 m) to the upper boundary of Compartment 18B (915 m) and are referred to as plots 37, 51, and 55, respectively. Sample units were selected based on the abundance of oak coupled with the presence of what appeared to be old-growth residual sugar maples. Sample selection was based on our desire to investigate the possibility of a correlation between disturbance, as indicated by patterns of stemwood radial growth of existing trees and oak recruitment. The analysis reflects only a portion of the heterogeneity of the stand, but it was the intent of this study to examine the developmental history of the portions of the stand that led to oak dominance. Individual-tree measurements including species and diameter were recorded for all stems larger than 12.7 cm in diameter at breast height (d.b.h.) in each opening. The NED/SIPS computer program was used to summarize the data (Simpson and others 1995), including a measure of relative density (Stout and others 1987).

Disks for dendroecological analysis were cut from each tree at stump height, approximately 10 cm above the ground line on the uphill side of the tree, and labeled by opening and species. Minimum tree size for collection and analysis was 12.7 cm d.b.h. On the basis of field inspection, it was determined that smaller stems were too young to explain the dominance of overstory oak. The number of stems per opening used for analysis was 47, 81, and 42 for plots 37, 51, and 55, respectively. All disks were prepared for ring-width measurements by sanding the surface of the disk with up to 800-grit sandpaper so that the rings could be seen under magnification. Ring width was measured with a Velmex measuring stage calibrated to 0.01 mm in conjunction with PJK6DOS® software to record tree-ring measurement files. Measurement direction was from the bark to the pith using a cross-slope radius to avoid tension wood characteristics often found on the uphill side of angiosperms. Most oaks were measured along two radii; other species generally were measured along one. Following crossdating of tree-ring measurements using marker years based on consistently narrow years (e.g., 1988), a program called COFECHA® (Grissino-Mayer and others 1997) was used to statistically validate the crossdating of ring-measurement series for individual species.

Data Analysis

Patterns of stemwood radial growth were used to evaluate the frequency of disturbance (Lorimer and Frelich 1989). Distinguishing releases from climatic effects was based on the period of release. Drought effects in eastern mesic forests have been shown to last only for several years (McIntyre and Schnur 1936; Cook and Jacoby 1977). Release events were defined as changes in growth with respect to subsequent 10-year growth periods (McCarthy and Bailey 1996; Nowacki and Abrams 1997), and were calculated using established methodology (Eqn. 1):

$$\%GC = \left(\frac{(M_2 - M_1)}{M_1} \right) * 100 \qquad (1)$$

where %GC is percent growth change from preceding to superseding 10-year radial means, M_1 is the preceding 10-year mean radial growth (exclusive of the current year), and M_2 is the superseding 10-year mean radial growth (inclusive of the current year).

Established criteria regarding magnitude of %GC were used to further screen out undesired responses such as droughts or other climatic factors (Lorimer and Frelich 1989; Abrams and others 1995; McCarthy and Bailey 1996). A major release was defined as an increase in growth greater than 99 percent. A moderate release was an increase in growth of 50 to 99 percent. Duration of release was also variable and an important consideration in the analysis, but specific temporal criteria were not employed to classify responses into discrete categories. Rather, duration of response was used graphically to determine the response characteristics of known disturbances, which was then used as a guide to evaluate the character of unknown disturbances.

Minor releases were also used and were defined as changes in growth rate greater than 25 percent but less than 50 percent that displayed graphical peaks in %GC. Nowacki and Abrams (1997) found that a change in percent growth of about 25 percent was useful in central Pennsylvania to demarcate significant growth changes of overstory trees because of their inability to respond as robustly as understory trees following a disturbance. Mean northern red oak %GC was used in part to identify the date of old-growth logging. Red oak was used for this purpose because of its abundance throughout the stand and because it is notably responsive to disturbance (Minckler 1957; Kurtz and others 1981; Orwig and Abrams 1995).

Disks also were inspected for evidence of fire or any other distinguishing characteristics that might provide insight into the past disturbance history. Recruitment dates for all individuals and species groups were evaluated as potential indicators of past disturbances (McClaran and Bartolome 1989). Although historical documentation provides dates of initial timber harvests for the watershed as a whole, the year of harvesting at the spatial scale of the individual plots was of interest. The time of old-growth harvesting was established from shade-intolerant species establishment dates, significant and sustained differences in %GC, logging damage to residual trees, and historical documentation.

Disturbance frequency was evaluated graphically and statistically using the distribution of moderate or greater %GC's. Distributions of this nature often are positively skewed and overestimate the interval length assuming a normal distribution (Baker 1992) and are more appropriately described by measures of central tendency such as the Weibull distribution (Sutherland 1997). Central tendencies of the Weibull are expressed as exceedance probabilities (i.e., the 0.5 exceedance probability is the 50th percentile of the distribution). The FHX2® program was designed in part to evaluate goodness of fit between fire interval data and normal and Weibull distributions using the one-sample Kolmogorov-Smirnov (K-S) test (Grissino-Mayer 1995). Here it was used to evaluate the distribution of disturbance

Table 1.—Total basal area ($m^2 ha^{-1}$), percent species composition (based on total basal area), and tree density (ha^{-1}) in sampled forest areas used for dendroecological analysis after the 1994 growing season (d.b.h. > 12.7 cm)

Item	All species	Red oak	Sugar maple	Black cherry	Basswood	Yellow-poplar	Red maple	Other
Basal area	48.01	21.40	9.74	5.56	4.55	2.14	1.72	2.92
Species composition	100	44.6	20.3	11.6	9.5	4.5	3.6	5.9
Tree density	425	91	168	30	69	7	17	42

intervals. It may be that disturbances are serially correlated within a stand. Such correlations, if they exist, might produce p-values that are too low, and underestimate interval length. As a result, the associated p-values from the K-S test should be interpreted as relative measures rather than absolute values.

Stand-wide disturbance frequency was modeled and defined as concurrent moderate or greater %GC's on two or more trees. The disturbance caused by chestnut decline was detected but we chose not to use it to calculate stand-wide disturbance frequency because of its unique character, which is more dispersed in time. Chestnut blight, first noted in West Virginia as early as 1909 (Brooks 1911), resulted in a 25-percent reduction in the volume of standing timber on the Fernow during the 1930's (Weitzman 1949). Thus, our standwide disturbance frequencies are more representative of canopy gap characteristics created by storm damage or logging operations rather than disease outbreaks.

Results

The second-growth forest patches selected for analysis had a total density of 425 stems ha^{-1} and a basal area of 47.98 $m^2 ha^{-1}$ for stems larger than 12.7 cm d.b.h. following the 1994 growing season. Northern red oak, sugar maple, black cherry, and basswood accounted for 86 percent of the basal area (Table 1). Relative stand density calculated as a percentage of full site occupancy was 153 percent of the average maximum stocking expected in undisturbed stands of similar size and species composition. The medial d.b.h. was 59.4 cm for northern red oak, 41.9 cm for sugar maple, 52.1 cm for black cherry, and 33.5 cm for basswood. The aggregate diameter distribution approximated a reverse J shape, though the shape of the distribution was heavily dependent on abundant sugar maple in the smaller size classes (Fig. 1). Moreover, in contrast to the reverse J shape of the overall sample, the northern red oak population displayed a unimodal size-class distribution typical of even-aged cohorts (Fig. 1).

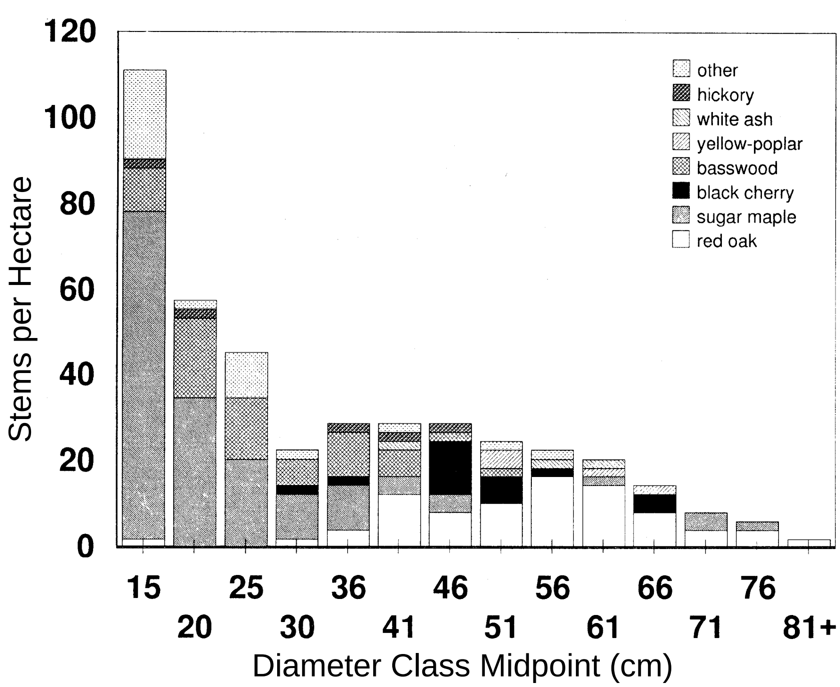

Figure 1.—Diameter-class distribution in 1994 by d.b.h. midpoint interval in a second-growth forest, Compartment 18A/B, Fernow Experimental Forest, West Virginia.

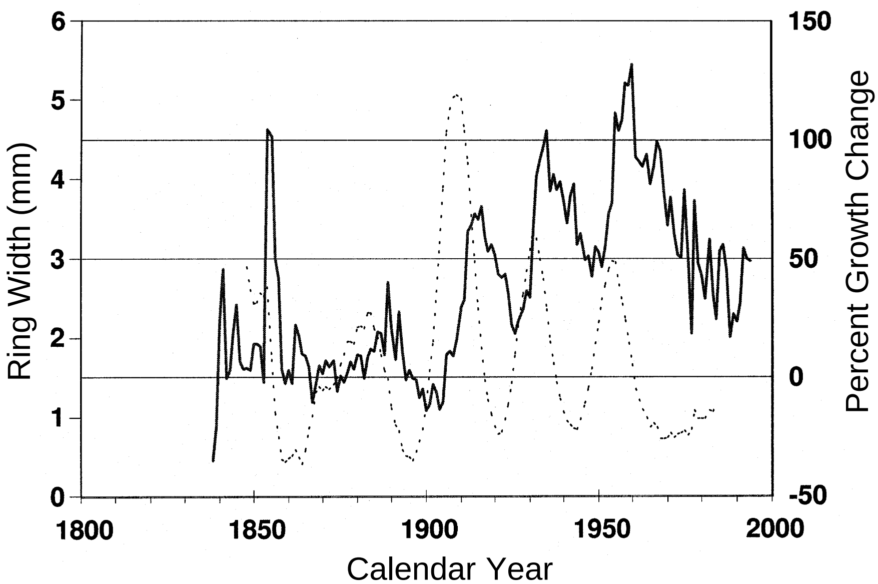

Figure 2.—Radial ring width (solid line) and percent growth change (dashed line) chronologies of 70 northern red oak series from Compartment 18A/B, Fernow Experimental Forest, WV.

Date of Old-Growth Logging

The mean ring-width chronology for northern red oak included 41 trees and 70 ring-width series (29 red oaks were measured along two radii) totaling 6,471 rings. During the 157 years evaluated for red oak (1838 to 1994), the highest %GC was recorded from 1906 to 1911, exceeding 100 percent for the 6-year period (Fig. 2). In 1908, %GC peaked at more than 121 percent, though the mean red oak ring width in 1907 was slightly greater. Growth releases of this nature are indicative of major canopy disturbances.

Additional evidence of a disturbance during the period identified by %GC analysis was obtained from a white ash sapling (55fr03). In 1906, the tree was 9 cm in d.i.b. (diameter inside bark at stump height, about 10 cm above the ground line). About one-fourth of the xylem tissue formed during that year was damaged. The outer cellular structure of the remaining xylem tissue was rough and appeared to be the result of a mechanical abrasion after the onset of seasonal xylem formation. Scar tissue that formed during the 1907 growing season was intact, as was the xylem tissue formed in 1905. Thus, the tree was damaged during the period bounded by the summer of 1906 and the onset of growth in 1907.

Black cherry and yellow-poplar were the only shade-intolerant species in the three openings selected for dendroecological analysis. The emergence of yellow-poplar was first noted in 1908 in plot 37 with subsequent recruitment from 1910 to 1912 (Fig. 3a). Black cherry recruitment ranged from 1905 to 1916 on plot 37 (Fig. 3a), but only became evident in 1908 on plots 51 and 55 (Fig. 3b,c). Black cherry was the only shade-intolerant species in these two plots.

We concluded that old-growth harvesting at the sample locations likely occurred between the middle of the 1906 growing season and the onset of growth in 1907. Using this period, it was possible to quantify the age and size-class structure of the surviving understory of the old-growth forest at that time.

Size and Age of Oak Regeneration

Oak regeneration in all sampled areas (n = 41) that developed into the second-growth forest overstory was dominated (90.2 percent) by seedling-size individuals recruited from 1902 to 1910 (recruitment peaked in 1906, Fig. 3d). The mean d.i.b. of oak stems present following the 1906 growing season was 0.7 cm and the distribution of sizes did not deviate from normality (p = 0.3995) when excluding four significantly older and larger stems established before 1900 (Fig. 4). The even-age structure of oak suggested by the overstory size-class distribution (Fig. 1) was reflected by the unimodal age-class (Fig. 3d) and size-class distributions of the sampled trees (Fig. 4).

The three sampled plots were similar in that the dominant age class of all species was a cohort established from 1900 to 1909 (Fig. 3a,b,c). This cohort included as many as 10 different species, though it was dominated by northern red oak. Sugar maple was the principal shade-tolerant species in all three areas and was established in conjunction with shade-intolerant species following the 1906-07 logging date. However, unlike the shade-intolerant species, recruitment of sugar maple, basswood, and other shade-tolerant species continued for several more decades, and presumably continued in the smaller size classes until the 1994 harvest. Sugar maple and American basswood have accounted for more than 80 percent (based on number of stems) of all new recruitment since 1920.

Disturbance History

The second objective of this study was to use the old-growth understory to evaluate disturbance history using age cohorting and frequency of moderate or greater %GC's.

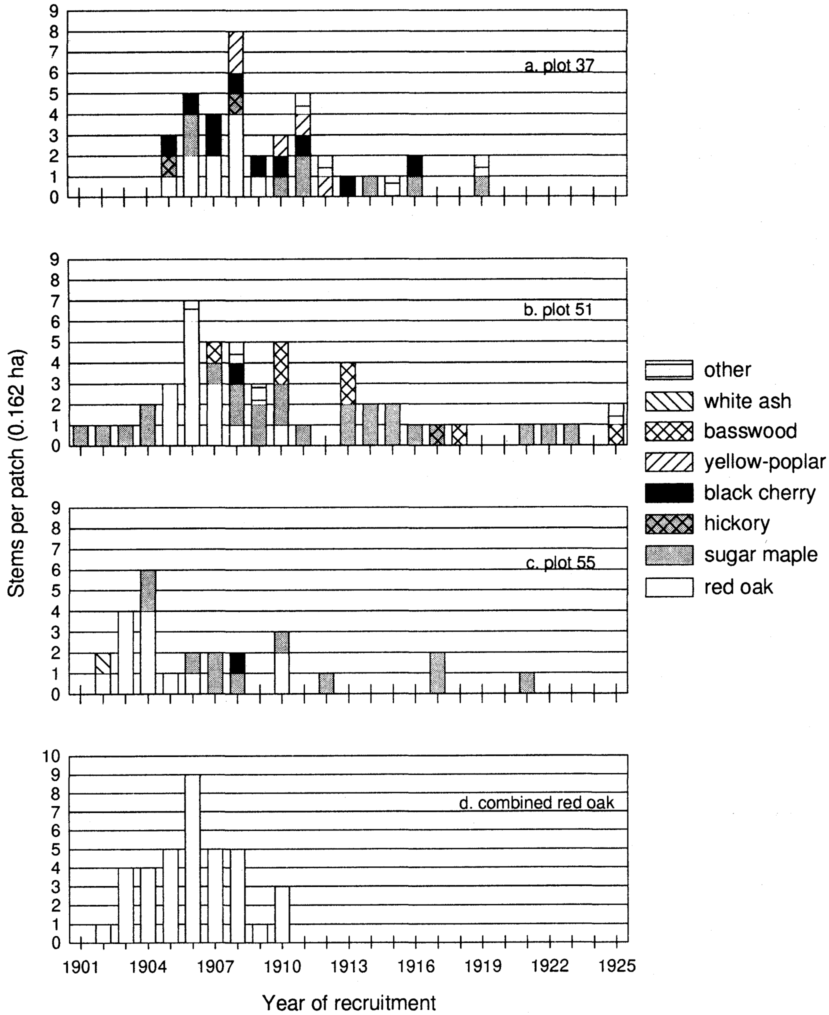

Figure 3.—Recruitment characteristics from 1901 to 1925 in Compartment 18A/B, Fernow Experimental Forest, a: foot slope, b: lower-middle slope, c: upper-middle slope, d: combined red oak age-class distribution.

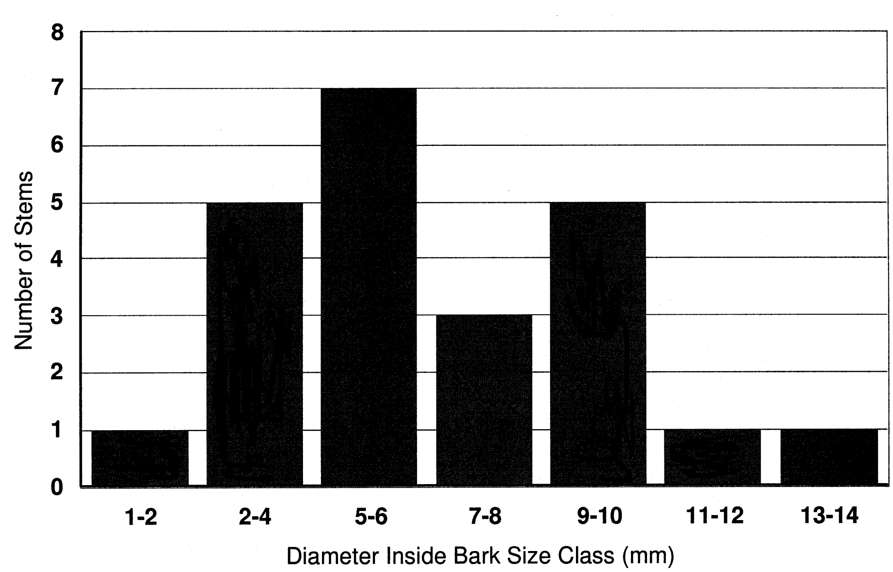

Figure 4.—Northern red oak seedling diameter-class distribution by d.i.b. midpoint interval after the 1906 growing season (n = 23). Red oak stems established before 1900 (n = 4) and after 1906 (n = 14) are not represented.

Older understory northern red oak (i.e., established before 1900) were recruited in 1838, 1858, 1876, and 1890 and were 23.3, 22.0, 8.8, and 2.1 cm in d.i.b., respectively, at the time of old-growth logging. Development of these individuals followed the same general pattern characterized by initial slow radial growth (i.e., < 2.0 mm yr^{-1}) for 10 to 20 years after recruitment followed by a rapid increase in growth that eventually declined before the dramatic growth increase in 1906 (Fig. 5). The oldest individual tree of this group (55qu04) demonstrated two distinct periods of release before old-growth logging; the youngest (51qu14) was released for the first time by the disturbance caused by logging. All of the older advanced oak regeneration established before 1900 responded to old-growth logging with unprecedented increases in radial growth (Fig. 5).

White ash and bitternut hickory also were in the old-growth understory for at least 5 decades before initial logging. In plot 55, white ash was recruited in 1861 and 1875 and was 10.9 and 9.3 cm d.i.b. following the 1906 growing season. This size indicates that both individuals were larger sapling-size trees prior to harvesting. Reflecting understory oak dynamics, white ash recruitment dates coincided closely with oak recruitment years and both individuals (55fr03 and 55fr02) were released between 1884 and 1885 (Fig. 6). The timing of understory white ash release on plot 55 corresponded closely with understory oak release in the same location (Fig. 2).

Of the limited number of hickories sampled (n = 6), those established before 1900 (n = 3) had periods of extremely slow growth (i.e., <0.5 mm yr^{-1}). They produced indistinct ring structures that made cross-dating difficult. Moreover, due to the presence of heartwood decay, it was not possible to establish the recruitment date of two of the three hickories recruited before 1900 (51ca01 and 51ca02). However, it was clear that this species was developing in the understory prior to old-growth harvesting (Fig. 7). Understory hickory on plot 51 was 8.1, 8.0, and 2.9 cm in d.i.b. following the 1906 growing season (d.i.b. was established at 2.4 m above the ground line for 51ca01 and 51ca02 due to heart rot). Major %GC's for 51ca01 and 51ca02 were evident in conjunction with old-growth logging (i.e., 1906-07), though distinct release events prior to that time were not apparent (Fig. 7).

Throughout the sampled area, the oldest remaining trees were sugar maples that ranged in d.i.b. from 5.7 to 37.3 cm following the 1906 growing season (Fig. 8). Establishment dates ranged from 1728 to 1787, making these trees about 120 to 179 years old in 1906. Sugar maple chronologies demonstrated extended periods of slow radial growth (<1.0 mm yr^{-1}). This is best illustrated by 51ac02, which was recruited in 1772. It experienced three moderate or greater %GC's during the 19th century, though radial growth

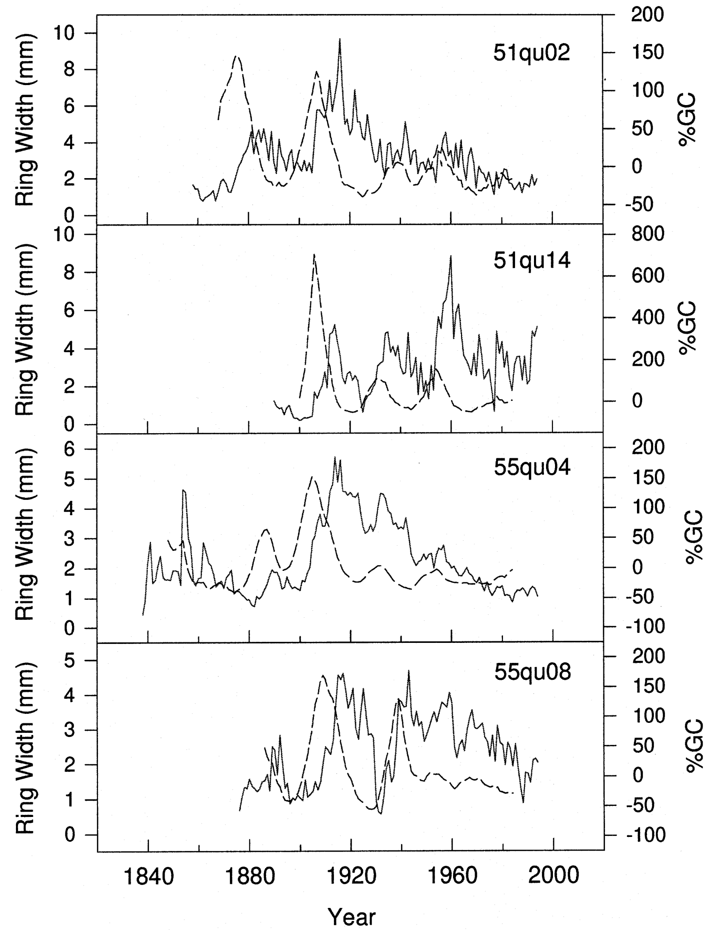

Figure 5.—Red oak radial increment (solid line) and percent growth change (dashed line) with establishment dates before 1900 in a second-growth forest initially logged in 1906-07.

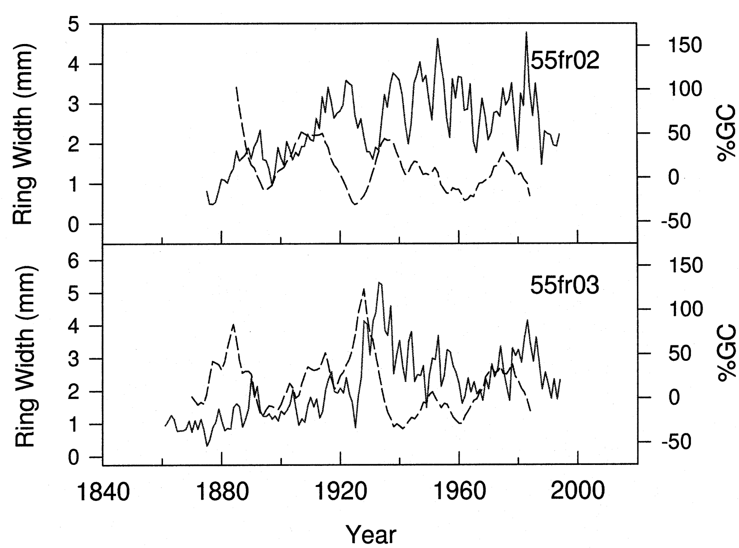

Figure 6.—White ash radial increment (solid line) and percent growth change (dashed line) established before 1900 in a second-growth forest initially logged in 1906-07.

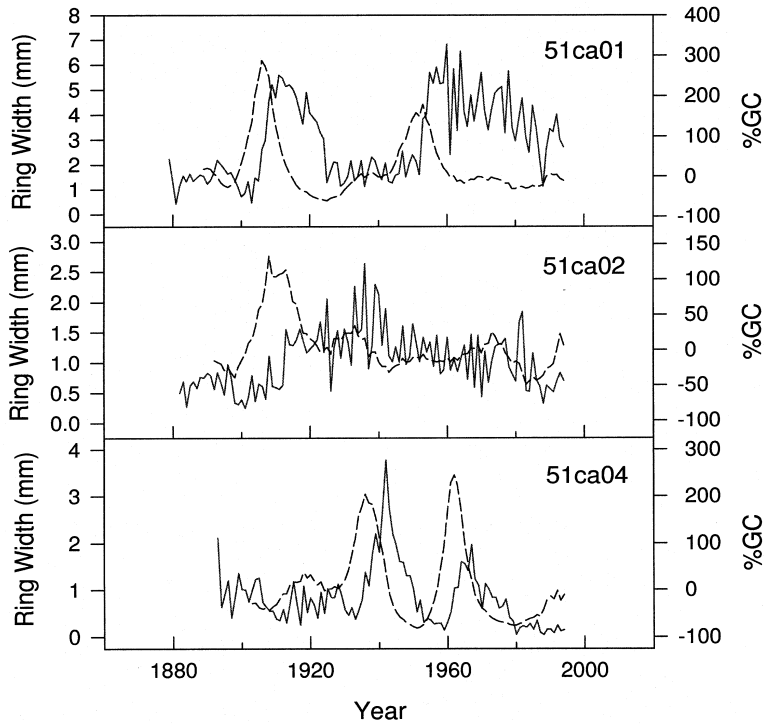

Figure 7.—Bitternut hickory radial increment (solid line) and percent growth change (dashed line) with establishment dates before 1900 in a second-growth forest initially logged in 1906-07.

did not exceed 2.0 mm yr^{-1} until after 1906 (Fig. 8). Consequently, even though this individual tree was approximately 135 years old at the time of initial logging, it was only 5.7 cm in d.i.b. The remaining three sugar maples with establishment dates before 1800 experienced a series of moderate or greater %GC's that resulted in sustained growth rates greater than 2.0 mm yr^{-1} prior to old-growth logging (Fig. 8).

There was considerable dendroecological evidence of stand-wide disturbances during both the old-growth and second-growth periods. Most recently, a stand-wide disturbance pattern was graphically evident in association with a stand-wide light thinning conducted between October 1952 and July 1953 (Figs. 2 and 9). Harvesting activities in October 1984 also were reflected by growth increases in plots 51 and 55. In 1984, plot 55 was adjacent to a 0.162-ha harvest opening and plot 51 was bisected by a skid road. The disturbance pattern is characterized by periods of increased growth rates and close association of peaks in those changes (Fig. 9). The indirect effects of American chestnut decline in the 1920's and 1930's also were detected. The growth response varied more temporally compared to the thinning response (Fig. 9). Throughout the 3 centuries sampled, old-growth logging was the most prominent and defined disturbance (Figs. 2 and 9).

These disturbance signatures from known events make the interpretation of unknown disturbances more plausible. For instance, the peak of the response does not always correlate among trees given a common disturbance event such as occurred in 1906 and 1952. However, the broad band of increased growth rates (i.e.,

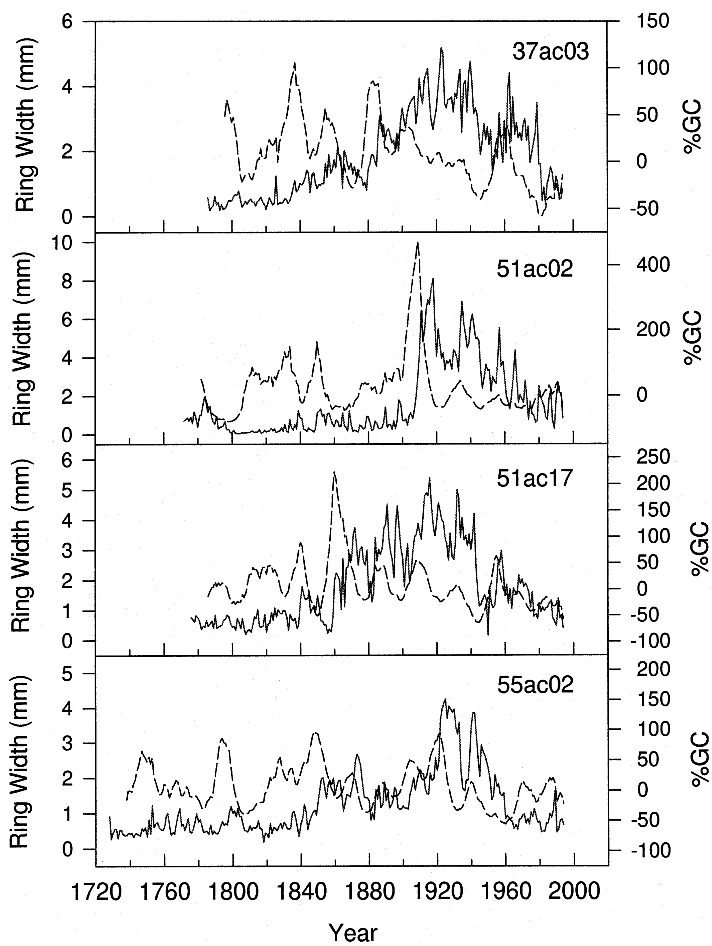

Figure 8.—Sugar maple radial increment (solid line) and percent growth change (dashed line) with establishment dates before 1800 in a second-growth forest initially logged in 1906-07.

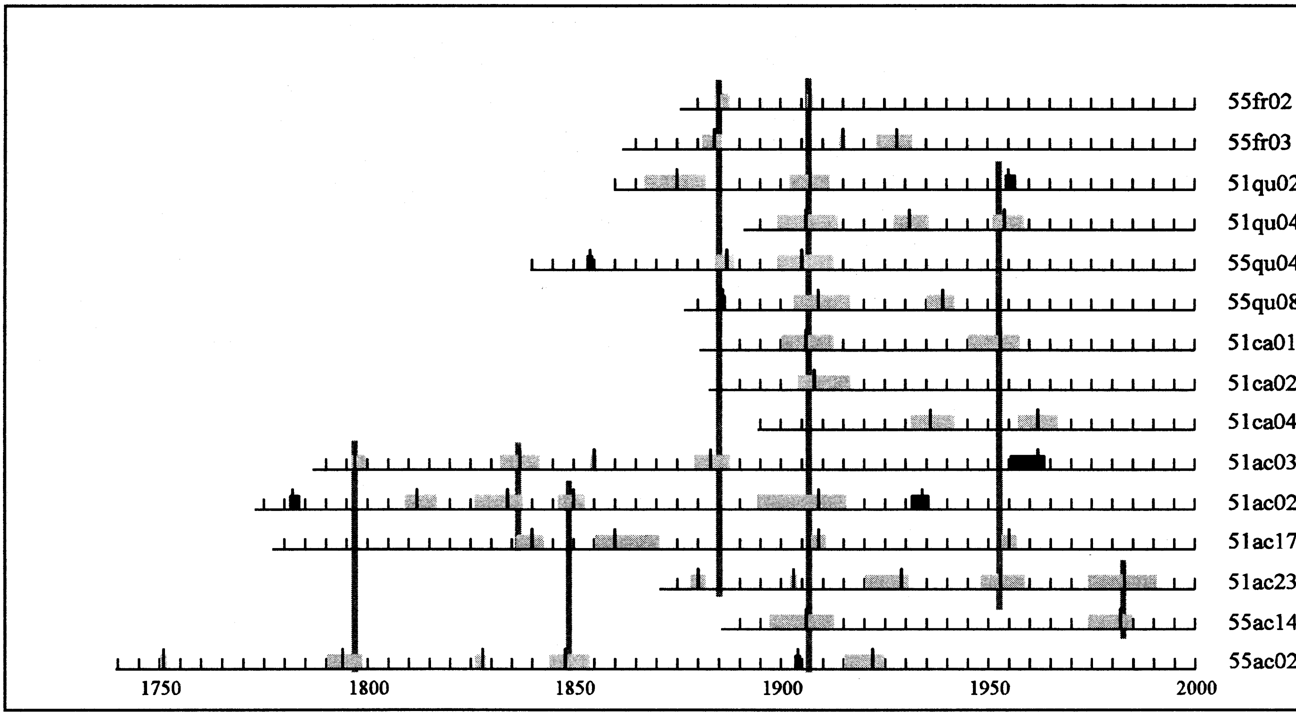

Figure 9.—Disturbance chronologies from Compartment 18A/B, Fernow Experimental Forest, West Virginia. Each horizontal line represents the disturbance history of one tree (qu = red oak, fr = white ash, ca = bitternut hickory, ac = sugar maple). Stand-wide canopy gap disturbances are identified graphically in 1983, 1954, 1907, 1885, 1849, 1837, and 1797 as indicated by vertical lines that span multiple chronologies. Gray zone indicates %GC > 50 percent, black zone indicates %GC > 25 percent, short vertical line in %GC indicates peak year of response.

Table 2.—Disturbance intervals (years) as measured by %GC on the Fernow Experimental Forest, Compartment 18A/B from 1728 to 1994 (<< = significantly short interval, >> = significantly long interval)

Exceedance probability	Stand-wide disturbance interval[a]
0.875	17.94<<
0.750	23.09
0.500[b]	30.83
0.250	38.73
0.125	44.25>>
Mean interval	31.00
Total intervals	6

[a]p > di = exp(-(di/34.78)**3.04), where di = disturbance interval.
[b]Weibull median.

> 50 percent) do correlate. Prior to old-growth harvesting, such stand-wide disturbance signals were identified in 1797, 1837, 1849, and 1885 (Fig. 9). Individual-tree growth peaks (Fig. 9) and peaks in %GC analysis for combined red oak (Fig. 2) correspond closely for disturbances in 1849, 1885, 1906, 1952, and 1984.

The distribution of stand-wide disturbance intervals using both the Weibull function (K-S d = 0.139, p = 0.9998) and a normal distribution (K-S d = 0.301, p = 0.6469) described the data adequately. The median Weibull disturbance interval for stand-wide events was 30.83 years from 1797 to 1983. Stand-wide disturbance intervals less than 18 years and more than about 44 years were unusual based on threshold level exceedance probabilities (Table 2). There was no statistical evidence of temporal changes with respect to whole-stand disturbances (K-S d = 0.500, p = 0.925) when old-growth and second-growth periods were compared with this technique.

Discussion

The results suggested two modes of oak recruitment into the canopy layer. First, the second-growth oak component was predominantly the result of an isolated period of recruitment that arose from the disturbance associated with logging of the old-growth forest in 1906-07. The above-ground age-class structure of this oak cohort was unimodal and reflected the diameter-class structure of the second-growth oak overstory. There was little evidence that the oak component of the second-growth forest was dependent on the presence of sapling-size or larger advanced regeneration at the time of initial logging. Peak recruitment coincided with logging activities in 1906. Seedlings of preharvest origin contributed somewhat more than postharvest origin seedlings to the newly established oak cohort, though not significantly so. However, estimates of the age and density of advanced regeneration based on recruitment date alone may be conservative. Oaks recruited after 1906 may have been of sprout origin from existing seedlings or stumps or had not yet reached sample height. Many oak seedlings are damaged during logging and form a new terminal shoot. In the southern Appalachians, about half of the existing understory oak seedlings resprouted following a clearcut (Loftis 1990). Therefore, our finding that 38 percent of the oak stems reached sample height after 1906 are consistent with results observed more recently and simply may account for stems of sprout origin.

In reconstructing past understory dynamics, it is helpful to understand whether oak regeneration originated from abundant small seedlings or less abundant, larger individuals. Our results suggest that both abundance and size were more favorable in 1906 than conditions typically found today. We estimate there were about 9,000 seedlings ha^{-1} in 1906 to achieve the survivorship observed in 1994 (Appendix). This estimate was partially based on a mean d.i.b. of 0.7 cm and the associated dominance probability 20 years after clearcutting (Loftis 1990). The estimate also incorporates the survival rate of northern red oak in a 20-year-old stand projected 70 years using NED/SIPS and NE-TWIGS (Simpson and others 1995). Oak seedling density seldom exceeds 2,400 stems ha^{-1} in the understory of present day mesic forests and often is substantially less (Schuler and Miller 1995; Clatterbuck and others 1999). Contributing factors to modern understory oak characteristics are high deer herbivory of acorns and young seedlings (Steiner and Joyce 1999) and the presence of dense understories of shade-tolerant species, which may be limiting both oak longevity and development in the understory (Lorimer and others 1994). Control of shade-tolerant understories is feasible and increases both understory oak survival and seedling growth (Loftis 1988; Lorimer and others 1994). However, herbivory of acorns may be limiting initial oak seedling densities today compared to past conditions, increasing the importance of silvicultural intervention to sustain oak's presence in the understory. However, reliance on fewer but larger seedlings to achieve oak regeneration goals requires longer planning horizons and is difficult to implement on mesic sites.

In contrast to the predominant mode of recruitment of the second-growth forest, the red oak established before 1900 appeared to result from periodic recruitment. Although the data were limited, red oak establishment prior to 1900 occurred under less than free-to-grow conditions based on initial radial growth rates of less than 2 mm yr^{-1}. Following establishment, red oak persistence in the understory and midstory appeared to be functionally related to periodic canopy disturbance. A pattern of periodic recruitment and release could have led to an uneven age-class structure of red oak in the overstory before 1906. The correlation between age and size of red oak established before 1900 suggests that upper canopy recruitment was occurring during the 19th century even in the absence of major disturbances.

The stand-wide disturbance interval of about 31 years with even greater frequency of smaller events indicates the potential for developing an uneven-age stand structure and is consistent with the distribution of understory red oak, white ash, and hickory before 1900 and the continued recruitment of shade-tolerant species in the 20th century. Our estimate of a stand-wide disturbance frequency generally reflects previous estimates of partial canopy disturbance frequencies in the central Appalachians (Lorimer 1980; Nowacki and Abrams 1997; Ruffner and Abrams 1998). Such disturbances frequently influenced oak recruitment in both mesic (McCarthy and Bailey 1996) and more xeric (Ruffner and Abrams 1998) oak-dominated old-growth forests. However, the effect of such disturbances no longer facilitates oak establishment or development and it is widely recognized that eastern hardwood forests are increasingly dominated by shade-tolerant species (Carvell and Tryon 1961; Parker and others 1985; Smith and Miller 1987) and that the rate of change is increased by small-scale canopy disturbances (Schuler 1998). Our findings do not isolate a limiting factor related to poor oak competitiveness following overstory removal, but they do suggest that oak recruitment is not limited by the frequency of canopy gaps.

The apparent ability of oak to regenerate in small gaps before1900 in this case study has implications for silvicultural attempts to regenerate mesic site oak forests. The even-age condition of most second-growth forests has been in part the impetus for the use of even-age silviculture to regenerate oak stands. Yet, the even-aged cohort that comprised the sampled second-growth forest developed in the understory of an old-growth, possibly uneven-aged forest. Apparently, oak can attain upper canopy strata through the variability associated with past disturbance patterns once a competitive oak understory is established. Identifying the factors that lead to a competitive oak understory is of prime importance. Several aspects of stand development in the central Appalachians have been altered significantly in modern forests and include overbrowsing by white-tailed deer (Marquis 1981; Inouye and others 1994), changes in fire frequency (Whitney 1987; Crow 1988; Delcourt and Delcourt 1997; Sutherland 1997), and the extirpation of American chestnut. A better understanding of these aspects of forest development may lead to greater success in maintaining the oak component in both harvested and unharvested stands.

In this study, dendroecological data have been used to derive past understory tree characteristics in a mixed mesophytic forest nearly 90 years ago. As is true of all sources of past ecological information, each has own limitations and merits (Whitney 1994). Old-growth forests are particularly suited for retrospective studies because of the relatively minimal influence of modern anthropogenic influences on them compared to second-growth forests. The virtual absence of expansive tracts of old-growth forests in the eastern United States limits this possibility (Parker 1989), but even if sufficient old-growth forests were available for study, the factors that favored the current overstory species composition have been altered significantly (Abrams 1992). However, second-growth forests can be substituted to determine past old-growth understory characteristics. The sudden and widespread release of the understory associated with old-growth logging preserved substantial information related to species composition, age distribution, and size-class structure of the understory at the time of the release. Of course, differential species mortality and the reduction in stem density by two orders of magnitude make the interpretation of such data critical. Vertical stem analysis could be added to the procedures used in this study to provide additional insight into understory dynamics both before and after old-growth logging.

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Appendix

Given the following:

- Mean diameter inside bark (d.i.b.) of oak stems after 1906 = 0.7 cm,

- Dominance probability (*D*) 20 years after clearcutting for given mean d.i.b. = 0.02 (Loftis 1990); (d.i.b. not adjusted for basal diameter, which may inflate estimate of stem density),

- Stems/ha recruited from 1902 to 1911 = 75.85 (assumes post-1906 stems were sprout origin and were present prior to 1907),

- Survival rate (*S*) of oak stems from age 20 to age 90 = 0.42 (from NED/SIPS using NE-TWIGS to make projection; starting conditions based on 20-year-old oak stand from Fernow Experimental Forest, Compartment 8A in 1968),

Then oak seedling density can be estimated as the following:

- Oak seedlings present in 1906 = 1/*D* * 1/*S* * 75.85 = 9,029/ha.

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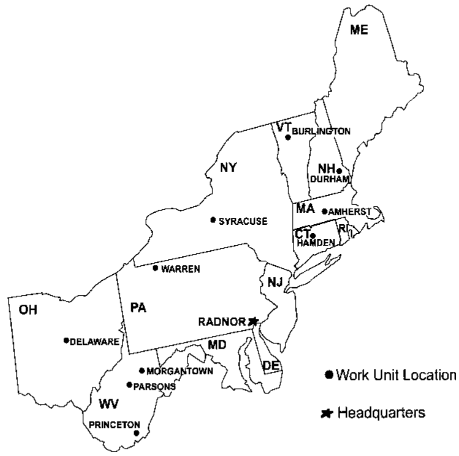
To better understand the dynamics of red oak regeneration, we evaluated the composition of understory woody species and recruitment characteristics of a mixed mesophytic forest in the central Appalachian region at the time of old-growth logging. We also evaluated canopy disturbance history during both the old-growth and second-growth periods. Stemwood radial growth patterns were used to evaluate the frequency of disturbance. Levels of red oak radial growth change were greatest from 1906 to 1911, which is indicative of a major disturbance. The oak regeneration in all sampled areas that developed into the second-growth forest was dominated by seedling-size individuals that were recruited from 1902 to 1910. The stand-wide median canopy disturbance interval was 30.83 years between 1797 and 1983.

Keywords: oak regeneration, disturbance, dendroecology, West Virginia



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