A MULTI-CENTURY ANALYSIS OF DISTURBANCE DYNAMICS IN PINE-OAK FORESTS OF THE MISSOURI OZARK HIGHLANDS

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Abstract.—Using dendrochronology and growth release approaches, we analyzed the disturbance history of shortleaf pine (*Pinus echinata* Mich.) white oak (*Quercus alba* L.) forests in the Missouri Ozark Highlands. The objectives of this study were to (1) identify growth release events using living and remnant shortleaf pine and white oak, (2) analyze the temporal variation of canopy disturbances, (3) examine how topographic variation affects disturbance, and (4) note growth releases that occur during and subsequent to selected drought events. These data were used to more fully understand the contribution of disturbance types and the effects of changing disturbance regimes on the structure of the Ozark pine-oak forests. Comparisons were made among trees within a stand and between stands at two study sites to contrast the frequency and magnitude of canopy disturbance. Differences in the dynamics of historic disturbance events between stands were reflected in temporal variation of establishment for both shortleaf pine and white oak. Topography affected both the frequency and synchronicity of disturbance events and therefore contributed to heterogeneous forest structure within a limited spatial extent. Releases of varying magnitude appear to occur during and subsequent to prolonged drought events that likely reflect partial canopy dieback or tree mortality that is either directly or indirectly caused by drought conditions. These data suggest wide ranging temporal and spatial variation in canopy disturbance events over the 400 years of analysis.

INTRODUCTION

The presettlement forest communities of the Missouri Ozarks ranged from closed canopy forests of hardwoods, namely oaks (*Quercus*), to open oak woodlands and pine (*Pinus echinata* Mill.) savannas with a continuum of forest community types. Although many of the controlling factors for vegetation included physical site attributes such as soil, parent material, and topography, the type and frequency of disturbance also influenced vegetation composition and structure, particularly in the wide ranging intermediate types, generally referred to as pine-oak forests.

The general objective of this research was to address the historical disturbance dynamics of shortleaf pine-oak communities in the Ozark Highlands of Missouri and to contrast the historical structure of pine-hardwood forests with current forest composition and dynamics to understand long-term changes in forest ecosystems of the lower Midwest. Little is known about the variation in disturbance type in the Ozark Highlands. Previous disturbance research in the Missouri Ozarks clearly identified the importance of fire in determining forest structure and composition.

Fire regime, however, is strongly influenced by topography and human activity (Guyette et al. 2002, 2003). Although fire may have been the dominant form of disturbance in homogeneous landscapes, e.g., plains and plateaus, many topographically complex areas experienced very little fire over many centuries (Guyette et al. 2007).

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Little is known about the frequency and magnitude of other disturbance events such as wind. Rebertus and Burns (1997) examined the importance of gaps in woodland and savanna—communities where the frequency of fires overrides the importance of gaps. We hypothesize that in closed canopy forests, where fire occurs with varying frequency, wind-driven gap dynamics can control recruitment and ultimately stand composition and structure. We also hypothesize that the importance of gap dynamics varies with topographic position.

In this paper we aim to reveal the importance of disturbance that results in gap formation in Ozark forests. Specifically, we document the disturbance patterns associated with long temporal scales by using dendroecological methods and quantifying release events in growth of shortleaf pine and white oak. The objectives of this study were to (1) identify growth release events using remnant shortleaf pine and overstory shortleaf pine and white oak, (2) analyze the temporal variation of canopy disturbances among sites, (3) examine how topographic variation affects disturbance, and (4) note growth releases that occur during and subsequent to selected drought events.

STUDY SITES

Study sites were located at Pioneer Forest, LLC (L-A-D Foundation, St. Louis, MO), which uses single-tree selection for timber management. Pioneer Forest is a privately owned forest of nearly 65,000 ha located across six counties in the Missouri Ozark Highlands (Iffrig et al. 2004). We selected two sites at Pioneer Forest in Shannon County, MO: Mill Hollow/Current River Natural Area (MH/CRNA) (approximately 37°24' N, 91°26' W) and Randolph Tract/Woods Hole (RT/WH) (approximately 37°25' N, 91°38'W). Both sites are located in the Current River watershed and contain the three components for our study:

1) remnant shortleaf pine
2) dominant and codominant shortleaf pine and white oak >30 cm diameter at breast height (d.b.h.)
3) opposing slopes (south-facing vs. north-facing) along the same ridge

Mill Hollow includes a forested area of approximately 165 ha and is a generally south-facing slope ($\bar{x}$ =180.56° S) located on the east side of the Current River. Canopy dominant and codominant tree species in MH include scarlet oak (*Quercus coccinea* Muenchh.), white oak, and shortleaf pine. The Current River Natural Area is a forest of approximately 4 ha along a north-facing slope ($\bar{x}$=337.38° NNW) located on the same ridge as MH. Canopy dominant and codominant species in CRNA include white oak, black oak (*Quercus velutina* Lam.), and northern red oak (*Quercus rubra* L.). Elevations in MH/CRNA range from 1,100 m along the ridge top to 725 m at the lower slope positions. Randolph Tract/Woods Hole, a forest of approximately 497 ha on a generally SSW-facing slope ($\bar{x}$ =202.73°) located on the west side of the Current River, contains dominant and codominant white oak, shortleaf pine, black gum (*Nyssa sylvatica* Marsh.), and hickory (*Carya* spp.). Elevation transitions in RT/WH from 1,000 m at the upper slope positions to 650 m adjacent to the Current River.

METHODS

Sampling at MH and RT/WH occurred during the summers of 2009 and 2010. Belt transects (50 m x 100 m) were placed at upper slope and ridge top positions that were oriented with the slope contour at MH (15 transects) and RT/WH (18 transects). Within each belt transect, basal increment cores (one per tree) were sampled from shortleaf pine and white oak trees that were ≥30 cm d.b.h. Increment cores were sampled parallel with the slope contour to minimize the effect of reaction wood on the upper and lower portions of the stem. Remnant shortleaf pine stumps and natural snags were identified within each belt transect and cross-sections were sampled at ground level using a chainsaw. Universal Transverse Mercator coordinates (zone 15N) were collected for all increment cores and cross-sections using a handheld Garmin GPS (Olathe, KS). Tree-ring measurements for previously sampled white oak cores from CRNA were accessed via the International Tree-Ring Database (National Climatic Data Center 2009a-d).

Increment cores and cross-sections were sanded with progressively finer sandpaper (up to 1,200 grit) to differentiate smaller tree-rings (Stokes and Smiley 1996). Tree-ring width measurements to the nearest 0.01 mm for all samples were taken using a Velmex measuring stage (Velmex, Inc., Bloomfield, NY) and binocular microscope. Standard visual cross dating procedures (Yamaguchi 1991) and the COFECHA quality control program (Grissino-Mayer 2001, Holmes 1983) were used to cross date and verify the appropriate calendar year for each tree-ring.

We applied the percent growth change analysis (Nowacki and Abrams 1997) using 10-year running means to identify growth releases (a proxy for canopy disturbance) for each sample's tree-ring width chronology. The percent growth change (PGC) is determined by:

$$PGC = \frac{\bar{x}_2 - \bar{x}_1}{\bar{x}_1} x\ 100 \qquad (1)$$

where $\bar{x}_1$ indicates the prior mean radial growth rate and $\bar{x}_2$ represents the subsequent mean radial growth rate. We categorized growth release events as minor (≥25 percent but < 50 percent), moderate (≥50 percent but <100 percent), and major (≥100 percent) to identify differences in patterns and the magnitude of release events given the limited availability of previous research on historic canopy disturbance in the Missouri Ozarks.

We compared periods of growth releases in shortleaf pine and white oak to periods of prolonged drought at the two sites to determine if trees were exhibiting a response following a stress. We calculated the mean reconstructed Palmer Drought Severity Indices (PDSI, Palmer 1965) for two stations in southern Missouri (Station 210: 37°5' N, 90°0' W; and Station 201: 37°5' N, 92°5' W) to identify historic prolonged droughts given that our sites were nearly equal distance between the two stations. We defined a prolonged drought as one in which the mean PDSI was <-2.0 for 2 or more consecutive years. In addition, we also compared prolonged drought events to growth release events with the potential of growth releases occurring during and up to 5 years following the end of a drought. However, we differ from others (Rubino and McCarthy 2000) in that we identified consecutive years of drought in which the mean PDSI ≤-2.0. The results were nine drought events between 1700 and 2000 with $\bar{x}$ ≤-2.0 and lasting for at least 2 years (Table 1). Pinpointing those releases that occurred following a drought allowed us to infer releases that occurred at times other than drought that may indicate other types of canopy disturbance (ice storms, logging, windstorms, defoliation events).

Table 1.—Comparison of known drought years from mean reconstructed PDSI to the number of shortleaf pine and white oak combined releases across MH/CRNA and RT/WH; percentage of samples that released is based on the total number of shortleaf pine and white oak samples from both study sites during and up to 5 years following the drought period

Drought years (mean PDSI)	Number of shortleaf pine releases	Number of white oak releases	Percentage of samples that released (%)
1703-1705 (-2.091)	3	2	21.7
1734-1738 (-2.372)	3	7	19.6
1771-1774 (-2.329)	13	13	35.6
1799-1801 (-3.525)	10	3	15.9
1834-1835 (-3.210)	3	1	4.2
1838-1839 (-3.156)	17	5	22.7
1855-1860 (-2.124)	9	17	25.7
1952-1954 (-2.692)	17	24	22.2
1963-1964 (-2.359)	5	9	6.1

RESULTS

Growth Release Analysis

Increment cores and remnant wood of shortleaf pine (n = 52) and increment cores of white oak (n = 49) were collected from MH, and 55 white oak ring-width chronologies were used from CRNA (National Climatic Data Center 2009a-d) to analyze for growth releases. Ring-width measurements and cross-dating resulted in a 339-year ring-width chronology for shortleaf pine (1670-2009) and a 172-year ring-width chronology for white oak (1836-2008) from MH. A 404-year ring-width chronology (1588-1992) was used for growth release analysis from CRNA. A total of 60 shortleaf pine and 56 white oak increment cores were sampled from RT/WH, resulting in a 244-year ring-width chronology for shortleaf pine (1765-2009) and a 214-year ring-width chronology for white oak (1795-2009).

Mill Hollow/Current River NA

Mill Hollow trees experienced a total of 223 release events (n_{pine} = 166; $n_{white\ oak}$ = 57) from 1670 to 2009. The greatest number of releases in MH were moderate (>50 percent but <100 percent) (n = 83). Taking into account all categories of releases, there were historic synchronous shortleaf pine releases in MH based on the percentage of samples that released during the timeframe 1754-1760 (45 percent of samples), 1773-1776 (46 percent), 1800-1810 (81 percent), and 1840-1845 (80 percent). A large contemporary release occurred in MH shortleaf pine in 1985-1990 (88 percent). Thirty-six percent of white oak in MH experienced a release during the same time period (1980-1990) as the contemporary shortleaf pine. The earliest growth release in MH was in 1706.

White oak at CRNA had a total of 216 release events across the respective ring-width chronologies. In comparison to MH, the greatest number of releases for white oak at CRNA were minor (>25 percent but <50 percent) (n =114). White oak in CRNA experienced synchronous releases in 1730-1740 (51 percent of samples) and 1775-1785 (46 percent). The earliest detected release from CRNA was in 1611 (Fig. 1).

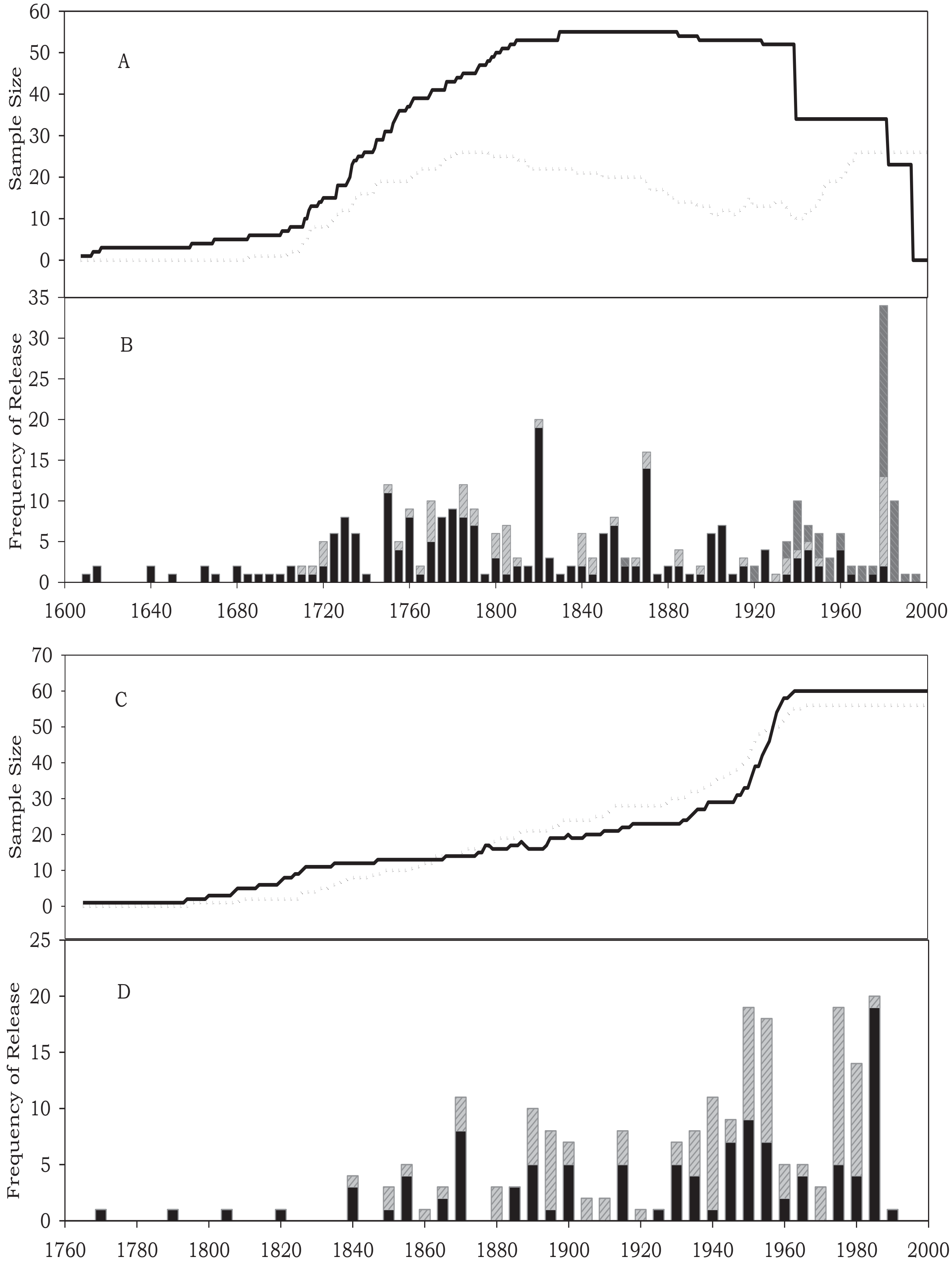

Figure 1.—Frequency of growth releases in MH/CRNA (1588-2009) and RT/WH (1765-2009). (A) Sample size from MH/CRNA. Black = CRNA; Dotted = MH. (B) Number of releases every 5 years in MH/CRNA. Black bars = CRNA white oak; Light gray = MH pine; Dark gray = MH white oak. (C) Sample size from RT/WH. Black line = shortleaf pine; Dotted line = white oak. (D) Number of releases every 5 years at RT/WH. Black bars = shortleaf pine; Dark gray = white oak. Note differences in scale.

All but one remnant shortleaf pine exhibited at least one growth release in 1670-1935, but 38 percent of living shortleaf pine ($\bar{x}_{age}$=71.3 years, S.E. = 4.2) in MH did not exhibit a growth release in 1899-2009. Approximately 60 percent of white oak ($\bar{x}_{age}$=67.0 years, S.E. = 3.5) in MH did not exhibit a growth release in 1836-2009. White oak samples from CRNA also had a large number of trees that did not release (29 percent) in 1588-1992.

A comparison of MH and CRNA is appropriate given that these two sites were on the same ridge but opposite slope positions. One notable release event occurred concurrently on both slopes from 1773 to 1785. Releases in CRNA were more commonly minor events; releases of shortleaf pine and white oak in MH were more commonly moderate to major releases based on our release categories.

Randolph Tract/Woods Hole

The tree-ring record of shortleaf pine in RT/WH revealed 109 growth release events with the earliest occurring in 1775. White oak in RT/WH experienced 105 growth release events; the first detected release occurred in 1842 (Fig. 1). Fifty-three percent of shortleaf pine and 18 percent of white oak demonstrated a synchronous release during 1872 to 1875. From 1947 to 1957, 40 percent of shortleaf pine and 28 percent of white oak released. The distribution of releases based on category (minor, moderate, major) were evenly distributed for shortleaf pine; white oak in RT/WH experienced more moderate releases (n = 40).

Comparison of Droughts and Growth Releases

We calculated the mean reconstructed PDSI (1588-2003) to compare growth releases to known periods of drought (Fig. 2). We identified years in which mean PDSI values were ≤-2.0, and there were negative PDSI values immediately before and after the year in which the reconstructed PDSI value was ≤-2.0. Due to the limited sample size during the 1600s, we restricted our analysis to the period 1700 to 2000.Using known drought years, we identified growth releases that were coincident with or immediately subsequent to the last year of identified drought (Table 1). As the sample size increases, we found that some release events corresponded during and subsequent to the identified drought period (Fig. 2).

Most release events during the identified prolonged drought periods were minor or moderate in growth response across both sites. However, two of the periods of drought (1771-1774; 1952-1954) had 10 and 18, respectively, releases that were categorized as major events (≥100 percent release). In addition, 14 of the major releases during the 1952-1954 drought period occurred at RT/WH. Of the major releases during the 1771-1774 drought period, all occurred in MH/CRNA.

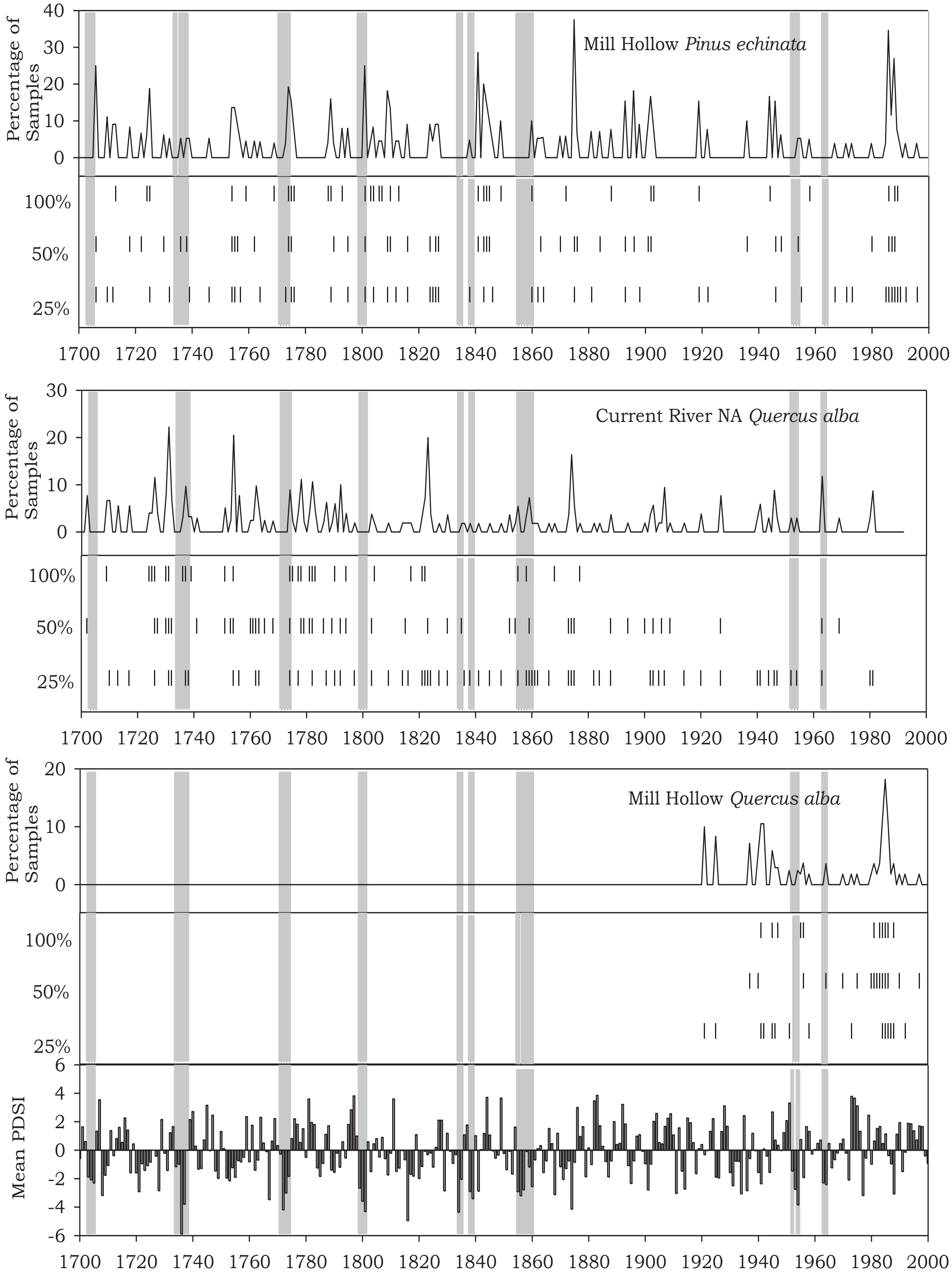

Figure 2.—The frequency and date of release events by species and site with the identification of prolonged drought (mean reconstructed PDSI). Vertical dashes represent the date of an identified release based on the percent increase in growth rate (25 percent = >25 percent but < 50 percent; 50 percent = >50 percent but <100 percent; 100 percent = >100 percent). The percentage of samples that released per year is shown. The gray shaded area represents the identified prolonged drought events ($\bar{x}$ = <-2.000). Note differences in the length of chronologies between MH/CRNA and RT/WH. (Figure 2 continued on page 57.)

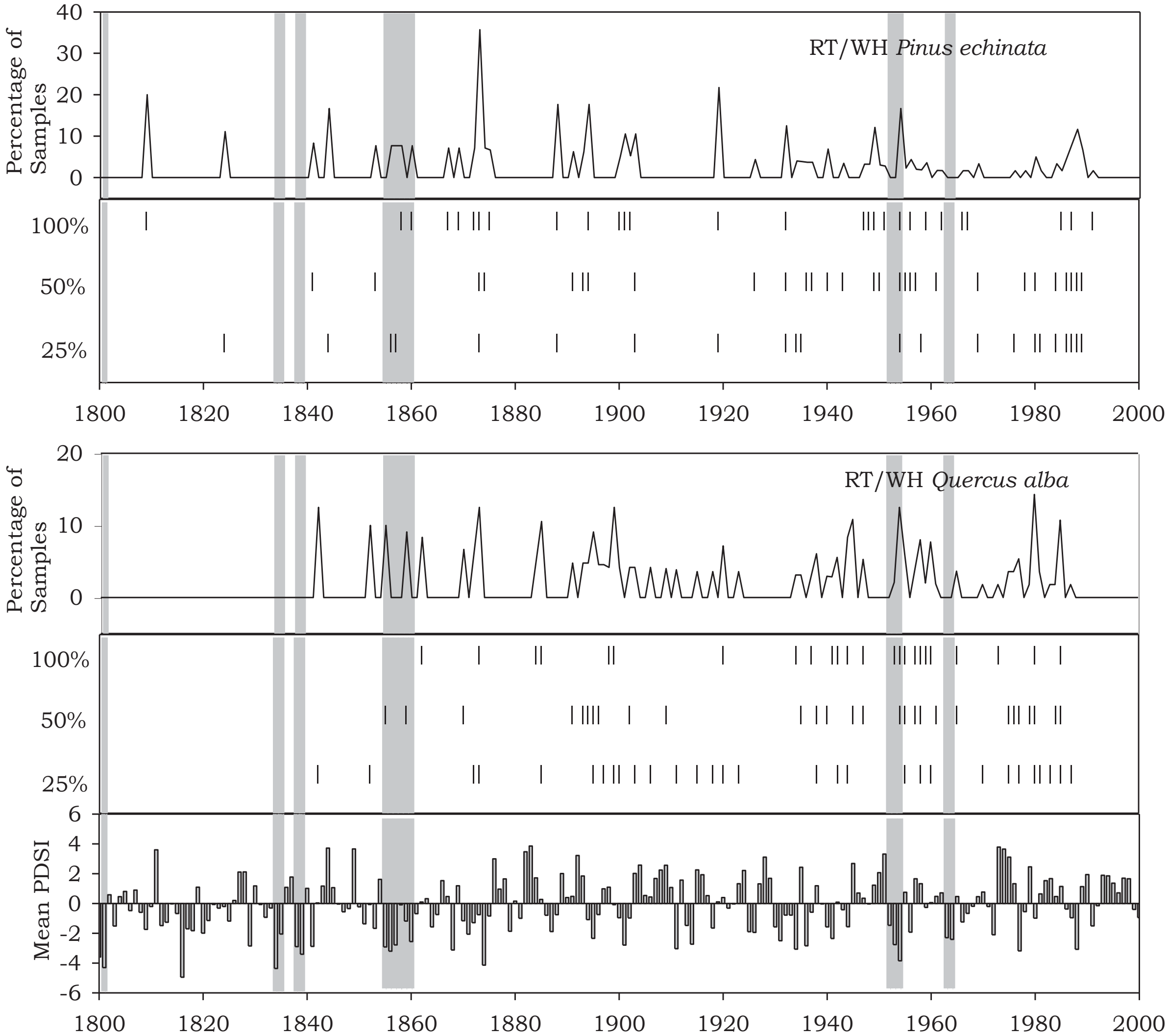

Figure 2.—continued from page 56.

DISCUSSION

Disturbance History

To facilitate an interpretation of the disturbance history of our study sites, we divided the analysis of growth releases into three centuries that encompass the temporal range of our dataset. Each century demonstrates variability in the frequency and magnitude of disturbance. The discussion of disturbance history focuses on the period 1700 to 2000 because of the limited sample size before 1700.

1700 – 1800

During this century, Mill Hollow shortleaf pine had 52 release events and white oak in CRNA had 90 releases with most of the releases concentrated during 1770-1800 (42 percent of all releases). The oldest shortleaf pine sample from RT/WH also released during the late 18th century. Our data suggest that some of the releases from 1770 to 1780 may have been associated with a drought (Table 1). However, in a study of historic anthropogenic fire regimes in the Missouri Ozarks, Guyette et al. (2002) indicated a potential increase in eastern Native American activity as tribes were displaced to the west and into the Missouri Ozarks during this time period. A study of the historic culture of the Current River watershed, where our two study sites are located, suggests the presence of Native American tribes adjacent to the Current and Jacks Fork Rivers (Stevens 1991). The concentrated release events may be attributable to these tribes using the forest resource along the Current River watershed.

1800 – 1900

The number of detected releases increased in MH/CRNA during this century (144 release events). One would expect an increased likelihood of detecting release events as sample size increases, but sample size in MH/CRNA decreased in 1799-1899 from 77 to 66. A total of 51 release events were detected in RT/WH. Most of the historic release data for RT/WH were concentrated during this century.

Patterns emerge from the release data for our two study sites during the19th century (Fig. 1). A large number of shortleaf pine samples (n=18) from MH indicate a major release in 1800-1809. However, during this same period, only four white oaks from CRNA exhibited a release. A small number of shortleaf pine samples released during and immediately subsequent to a drought from MH and RT/WH (Table 1). In addition, fire scar data indicate a fire during 1800 (King, unpublished data). Based on GPS point data, releases during 1800-1810 cover approximately 0.8 km at the upper slope position in MH. Our data suggest a volatile time in terms of disturbance in Mill Hollow during the late 18th and early 19th century.

Another group of major releases in MH appears during the 1840s, and then at least one shortleaf pine released every decade from 1850 to 1900. A small number of white oak samples from CRNA show major releases in 1845-1860. Several Euro-American settlements had already been established before 1850 north and south of the present-day study sites (Stevens 1991). The growth releases likely reflect the moderate clearing of the forest associated with these settlements. Most release events in white oak from CRNA were minor to moderate in growth, likely indicating that these trees had attained canopy status by 1860 to 1900. The minor and moderate releases in CRNA white oak may reflect canopy dieback of neighboring trees. In addition, only two major releases were detected in CRNA white oak during the middle and late 19th century.

Release events in RT/WH indicate an increase in the number of growth releases between 1865 and 1900 for both white oak and shortleaf pine, particularly during the last 20 years of the 19th century (Fig. 1) which may be attributable to the influx of the logging industry and Euro-American population during that time (Stevens 1991).

1900 – 2000

Evidence from these data indicates a limited number of shortleaf pine samples that date to the early 20th century (Fig. 1), particularly in MH. High fire frequencies during the late 19th and early 20th century, along with livestock disturbance (Guyette et al. 2002, 2003), may have contributed to the decreased establishment of shortleaf pine during this period. This is supported by the lagged establishment of the current shortleaf pine cohort ($\bar{x}_{age}$=71.3 years, S.E. = 4.2).

A large release event appeared to occur during the 1945-1955 period in RT/WH. During that period, a small number of releases occurred in MH but are noticeably absent in CRNA. Before Pioneer Forest took over ownership, the forest in the study sites was managed for white oak staves. Lands were sold to Pioneer Forest in the early 1950s (Iffrig et al. 2004). These releases, particularly in RT/WH, may reflect harvesting by previous owners.

Few trees at both sites released between 1960 and 1980. Individual tree releases that did occur during this time may reflect responses to small gap formations in the canopy. Release events appeared to occur at both sites in shortleaf pine and white oak between 1980 and 1990, possibly associated with harvests by Pioneer Forest.

Drought and Release Events

Some release events at both study sites appear to be associated with periods of drought. However, generally few trees during and subsequent to the droughts had a growth release. Our data indicate that the magnitude of historic releases during and subsequent to the identified prolonged droughts ranged widely from minor to major releases. Minor releases may reflect partial crown dieback, or in the case of major releases, the death of an adjacent overstory tree. Regardless, releases during and subsequent to droughts tended to result in few trees demonstrating a release. It is possible that releases that occurred during a prolonged drought period may not be due to the drought conditions. However, releases that occurred a few years following the drought (2-6 years) may be related to reduced growth during the period of drought (Orwig and Abrams 1997). Rubino and McCarthy (2000), in their drought analysis of white oak, determined that white oak exhibited a growth decline up to 5 years following a severe drought (PDSI = -5.23). Within our identified drought periods were 4 years in which PDSI < -4.0 (1736, 1772, 1801, 1834). The result was the detection of growth releases during and subsequent to the drought periods that may be directly or indirectly attributable to drought events in the Missouri Ozarks.

Given the relative proximity of both study sites, we can assume that prolonged drought conditions had a similar effect on shortleaf pine and white oak. By taking into account drought as a contributing disturbance to a forest, it may be possible to infer causation of growth releases when there is limited availability of historical documentation. A contemporary example from our study is the prolonged drought during 1952 to 1954 in which there are differences in the number of growth releases between MH/CRNA and RT/WH (Fig. 2). There are two potential explanations for this variation. One explanation may be the occurrence of at least one management harvest at RT/WH during this period, which may reflect the large number of release events subsequent to the prolonged drought, yet we do not identify the same degree of release at MH/CRNA. Secondly, a large mortality event may have contributed to release events. However, we cannot infer causation of the disturbance at the tree level given the potential of multiple disturbances (harvest, mortality, drought) occurring at the same time. If there is a lag between the disturbance and growth release (D'Amato and Orwig 2008, Jones et al. 2009), it is possible the disturbance (timber harvest) occurred just before the drought.

CONCLUSIONS

Both sites indicate periods of synchronous release events, likely indicating large gap formations due to anthropogenic influence or a natural disturbance such as windstorms. There are also indications of responses to small gap formation in which an individual tree was released during a decade throughout the disturbance chronologies from both sites. The only exception was during the 1980s in which a large number of trees revealed a release, which we hypothesize to be related to management harvests at the two sites. Throughout the last 400 years, these two sites have exhibited periods of high frequency canopy disturbance. However, each site revealed differences in the timing of large-scale canopy disturbance, particularly before 1900. Subsequent to 1900, both sites exhibit similar patterns of release culminating in a large number of releases during the 1940s through the 1950s and the 1980s, suggesting the development of timber management. Prolonged drought events may have contributed to lagged growth releases in some of the trees at the two sites. We encourage further analysis of drought in forests to better evaluate causation of historic disturbance when there is limited historical documentation to validate disturbance type.

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