Dynamic Fire Regimes and Forest Conditions Across Three Centuries in a Shortleaf Pine-Oak Forest in the Ouachita Mountains, Arkansas, USA

William T. Flatley,* Lillian M. Bragg,* and Don C. Bragg†

*Department of Geography, University of Central Arkansas, USA
†Southern Research Station, U.S. Department of Agriculture Forest Service, USA

In the interior highlands of the eastern United States, there is evidence that fire was frequent in some forests during the eighteenth and nineteenth centuries before declining drastically in the twentieth century. To better understand past fire regimes and how they shaped forest dynamics during periods of change, we conducted a dendroecological study at Lake Winona Research Natural Area (LWRNA), a 110-ha unlogged forest dominated by shortleaf pine (*Pinus echinata* Mill.) in the Ouachita Mountains of Arkansas. We used remnant wood and living tree cores to construct a multicentury record of fire occurrence and tree recruitment. Our results indicate the forest at LWRNA passed through multiple fire regime transitions that altered forest dynamics. During the protohistoric period (1701–1834), prior to widespread European American settlement (EAS), fire was frequent, but limited sample depth results in greater uncertainty regarding fire frequency and forest conditions. During EAS (1835–1929), fire was very frequent and tree establishment was dominated by shortleaf pine. After 1930, effective fire protection led to establishment shifting toward increasingly fire-intolerant hardwoods. Evidence of temporal variations in the fire regime, age structure, and contemporary composition broaden our understanding of reference conditions in this pine-oak forest and demonstrate that fire management could be used to restore a range of vegetation conditions from frequently burned pine- and oak-dominated woodlands to fire-excluded, closed-canopy mesophytic communities. *Key Words: dendrochronology, fire history, mesophication, Pinus echinata, Quercus alba.*

Fire often plays an important role in shaping vegetation pattern and ecosystem processes (Bond, Woodward, and Midgley 2005; Murphy and Bowman 2012). Increases or decreases in fire frequency can alter species composition, vegetation structure, and ecosystem function (Bowman et al. 2009). For example, increases can shift closed-canopy forest to woodlands or grasslands, whereas decreases can move forests toward denser structure and mesophytic composition (Nowacki and Abrams 2008; Murphy and Bowman 2012; Hanberry, Bragg, and Hutchinson 2018). In fire-prone ecosystems, managers and scientists often describe a historic range of variation in fire regime and vegetation characteristics to better characterize the fires that maintain a particular vegetation condition and guide their management for native species and ecosystem function (Swetnam, Allen, and Betancourt 1999). This can be challenging, though, because fire regimes are not static at any one location, but sensitive to temporal shifts in climate, vegetation, and human activity (Krawchuk et al. 2009; Bowman et al. 2011). Therefore, it is important to understand the factors that maintain and disrupt fire regimes, and how changes in fire regimes alter vegetation characteristics over time.

Climate and vegetation are the underlying drivers that shape fire regimes, but humans play an important role in modifying fire regimes in many temperate forests (e.g., Guyette, Muzika, and Dey 2002; Larson, Kipfmueller, and Johnson 2021). Globally, temperate forests have been altered by people through the addition or removal of ignitions, alteration of fuels, and subsequent changes to fire regimes (McWethy et al. 2013; Alexander et al. 2021). As an example, sediment-based pollen and charcoal remains have been interpreted as evidence that Native Americans used fire to manipulate and manage landscapes in the southeastern United States for millennia (Chapman et al. 1982; Delcourt and Delcourt 2004). Indeed, the wetter temperate forests like those found in the eastern United States might be particularly responsive to changes in ignitions because of rapid fuel production and abundant

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fire-sensitive species (McWethy et al. 2009; Kitzberger et al. 2012). It is difficult to directly link cause and effect at the coarse scale of sediment analysis (Swetnam, Allen, and Betancourt 1999), however, and this has spurred a continued debate over the role of humans and fire in shaping the eastern deciduous forest prior to reliable written records (Matlack 2013; Stambaugh et al. 2015).

The finer temporal and spatial scale of dendrochronology can tie vegetation change more directly to cultural change, land-use episodes, and fire regime disruptions (e.g., McEwan and McCarthy 2008; Larson, Kipfmueller, and Johnson 2021). Many temperate regions, however, lack information on past fire regimes and long-term forest dynamics because native ecosystems were often disrupted early and intensively by human activity (Whitney 1994; Margolis et al. 2022). For instance, researchers have been accumulating evidence of accelerating rates of burning or "waves of fire" that accompanied European American settlement (EAS) across portions of eastern North America during the 1700s and 1800s (Guyette, Spetich, and Stambaugh 2006; Stambaugh et al. 2018). This work has documented a substantial increase in fire frequency coinciding with initial EAS and it is likely that increasing fire frequency altered forest structure and species composition in these areas before the expansion of agricultural clearing or the industrial lumbering of the late nineteenth and early twentieth centuries. Yet, there is a lack of empirical data on the corresponding forest responses to this early fire regime variation(s), largely because stands of sufficient age are rare in the repeatedly cutover eastern United States. Only the most recent (past century or so) forest responses due to fire protection have been examined for most of this region (Harrod, White, and Harmon 1998; Aldrich et al. 2010).

Managers seeking to use frequent fire to manage habitat and species diversity across multiple scales need better information on the relationships between protohistoric forest conditions and the fire regimes that shaped them. For example, the national forests of the Interior Highlands (the western part of the EPA Ouachita-Appalachian Forests Level II ecoregion) of Arkansas, Missouri, and Oklahoma have made prescribed fire an integral part of their land management and ecosystem restoration plans. Unfortunately, to date the needed research on the relationship between fire history and forest composition in the Interior Highlands is limited. More fire history research has been conducted in the oak-shortleaf pine (*Pinus echinata* Mill.) forests of the Ozark Plateau (e.g., Guyette and Spetich 2003; Guyette, Spetich, and Stambaugh 2006). The nearby Ouachita Mountains might have been more fire-prone (Foti and Glenn 1991) and historically supported extensive fire-adapted shortleaf pine, but there has been very little fire regime work in these mountains (e.g., Johnson and Schnell 1985; Masters, Skeen, and Whitehead 1995).

To help address this shortcoming, we examined the fire regime and forest characteristics over multiple centuries in an unlogged, mature, shortleaf pine-dominated forest at Lake Winona Research Natural Area (LWRNA) in the Ouachita National Forest of Arkansas. Using a combination of dendroecological approaches and stand inventories, we assessed the historical fire regime and temporal trends in tree recruitment in this old stand. Our objective was to characterize long-term forest vegetation changes for LWRNA to help determine (1) the frequency and seasonality of past fires; (2) if fire frequency and seasonality at the LWRNA varied in response to land-use changes; and (3) if forest establishment and composition were altered by changes in the fire regime.

Methods

Study Area and Site History

Due to its tree age and largely unmanaged state over the past century, the LWRNA presents a rare opportunity to evaluate multiple lines of evidence to characterize variations in the fire regime and forest characteristics from protohistoric Native American periods into EAS and development to the present day. LWRNA encompasses 110 hectares of uncut timber in the Jessieville-Winona-Fourche Ranger District, Ouachita National Forest, Arkansas (34°48′ N, 92°56′ W; Figure 1). Annual precipitation averages 1,452 mm at Jessieville (20 km southwest) and mean monthly temperatures range between 5 °C and 27.7 °C (National Climatic Data Center 2012). Bounded on the east by the Alum Fork of the Saline River, LWRNA occupies a low ridge that is in a valley between larger mountains. Locally, the bedrock is made up mostly of sandstones and shales, with soils that are primarily Typic Hapludults. Our study

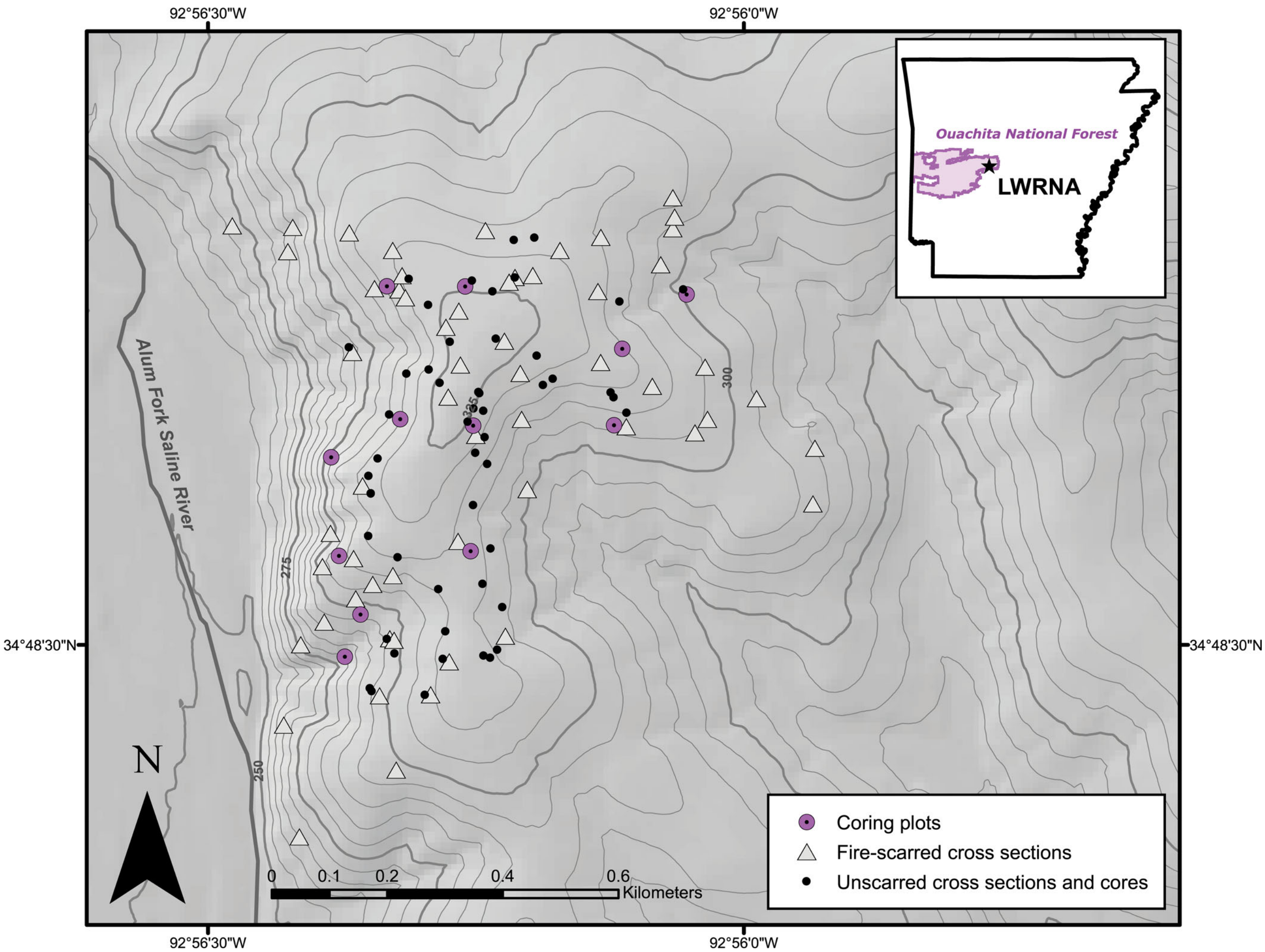

Figure 1. Study area at Lake Winona Research Natural Area (LWRNA), Ouachita National Forest, Arkansas. White circles are 0.05-ha circular coring plots, gray triangles are fire-scarred samples, and black dots are non-fire-scarred tree-ring samples collected outside of plots.

was conducted in the portion of LWRNA that was never logged and was minimally affected by a 24 December 1982 tornado that struck the southern part of this natural area.

Currently, the forests of LWRNA are classified as mixed pine-oak, with shortleaf pine and white oak (*Quercus alba* L.) dominating the overstory. During prehistoric times (especially before A.D. 1700), the Caddo Nation and their progenitors dominated most of the Ouachita Mountain region (Sabo 2001; Trubitt 2019). By the late 1700s and early 1800s, the Caddo had been displaced in this part of Arkansas by the Osage, Cherokee, and other eastern tribes and some of the first European American settlers (Trubitt 2019). Regardless of tribal affiliation, Native American land use was diffuse across most of this region, consisting primarily of hunting game, gathering edibles, and collecting other cultural resource materials from hilly upland sites such as the LWRNA (Trubitt 2019). One fairly universal practice of these early residents was the use of fire by Native American (and later European American) hunters, primarily to improve game habitat, hunting, and foraging (e.g., Dunbar 1809; Berry, Beasley, and Clements 2006). It is hard to judge the frequency of fire from these accounts, but it might have been common.

After Native Americans were removed from Arkansas in the early decades of the nineteenth century, EAS slowly began in the Ouachita Mountains, accelerating after the completion of public land surveys. These European American settlers were primarily subsistence agriculturists who cleared small farmsteads and pastured livestock in the open forests. After the Civil War, more arrived in the waning years of the 1800s in search of economic opportunities, cheap timber, and inexpensive land. Large-scale lumbering in the Ouachita Mountains accelerated during the first decades of the twentieth century (Smith 1986). To better protect an increasingly exploited and diminishing timber resource from overcutting and destructive wildfires, the Arkansas (later, Ouachita) National Forest was established in late 1907 (U.S. Forest Service 1909). Harvesting of the remaining virgin forests continued under federal control and effective fire control was not achieved across most of the region until after 1930 (Bruner 1930). Over the decades, the area that became the LWRNA managed to escape harvesting and other major natural disturbances, and the U.S. Forest Service established the natural area in 1975 (Fountain and Sweeney 1987).

Fire History Reconstruction

To reconstruct historical fire occurrence at LWRNA, we collected fire-scarred wood samples from living trees, snags, stumps, and logs with visible basal scars between 2017 and 2019. Fire scar samples were identified by a thorough survey of the old-growth portion of LWRNA. Sections were collected from the fire scar samples and their locations were recorded with Global Positioning System (GPS). In the laboratory, we surfaced the wood samples with progressively finer sandpaper, visually cross-dated the rings, scanned an image of the surfaced wood, and measured annual ring width using the program CooRecorder v9.3.1 (Speer 2010; Larsson 2018). COFECHA was used to statistically verify annual ring dates (Holmes 1983) before fire scars were assigned a calendar year and season of burn (Baisan and Swetnam 1990). We used FHAES software to graph and analyze fire dates (Brewer et al. 2016).

To characterize fire frequency, we calculated composite mean fire intervals (CMFIs), 25 percent filtered CMFIs, and the individual sample fire intervals (point intervals). Intervals were calculated for the period from 1701 to 1929, beginning with the first date with three samples and continuing through the date of the last major fire at the site (Stambaugh, Marschall, and Abadir 2020). For each interval type we calculated the mean interval, Weibull median interval, standard deviation, lower exceedance interval, and upper exceedance interval. We summarized fire seasonality based on the seasonality of fire years, rather than the seasonality of individual fire scars to ensure that fire years recording many scars (generally the more recent fires) would not have an outsized influence on the estimate of fire seasonality. Fire year seasonality was assigned based on the season of all scars recorded in a fire year. Three fire years included both dormant season scars and late growing season scars and we chose to classify these fire years as late growing season scars, as a mix of dormant and late growing season scars indicates that the fire was burning during a time in the fall when some trees were still growing. We then calculated the percentage of fire years in each season.

To assess whether there were temporal changes in the fire regime, we divided the record into three periods. Our protohistoric period was before 1835, when the area around Saline County began to experience a greater influx of settlers (Billingsley 1993). We defined the EAS period as 1835 to 1929, with the fire protection period starting in 1930, coincidental with the beginning of statewide fire prevention education and burn suppression efforts (Bruner 1930; Strausberg and Hough 1997). We calculated the same set of fire interval metrics for each of the periods. Differences in mean fire intervals between the protohistoric period and the EAS period were determined with a two-sample *t* test, where data are normally distributed with unequal variance (Sokal and Rohlf 2003). We used a chi-square test to assess whether there was a difference in the seasonality of fire years between the protohistoric and EAS periods. We used superposed epoch analysis (SEA) to investigate the relationship between fire occurrence and annual drought. We tested all fire years and 25 percent filtered fire years (Swetnam and Baisan 1996) against the Cook et al. (1999) tree-ring reconstruction of Palmer Drought Severity Index (PDSI), gridpoint 202. To assess whether there were any temporal changes in the fire–climate relationship we conducted additional separate SEA tests on fire years recorded during the protohistoric and EAS periods.

Forest Dynamics

To characterize past forest dynamics at LWRNA, we sampled twelve 0.05-ha circular forest plots randomly distributed across the 110-ha site (Figure 1).

In each plot we recorded the species and diameter of every living tree greater than 5 cm diameter at breast height (DBH) and collected two cores on opposite sides of the tree at 20 cm height. If either core was rotten, we collected an additional core higher up the stem (mean coring height for all cores = 23.8 cm). We recorded the species of all saplings (< 5 cm DBH, ≥ 1 m height) and tallied seedlings (< 1 m height) by species in a 10-m^2 circular subplot. Data collected within the plots were used to calculate basal area, tree density, sapling density, and seedling density for individual species. To increase the temporal depth of our record of forest dynamics, we additionally cored the five largest shortleaf pine trees that were visible from the center—but outside the boundary—for each overstory plot (M distance = 30.4 m, *SD* = 10.8 m). We also opportunistically collected thirty-three cross-sections across LWRNA from shortleaf pine stumps and logs that did not exhibit fire scars. These samples were used to construct the cross-section recruitment dates, but they were not included in any of the plot-level calculations of age structure, basal area, or tree density.

The shortleaf pine and oak cores were dated in the same manner as the fire scar samples and the ages of the remaining species were estimated with annual ring counts. If the pith was not visible but there was ring curvature, then a pith estimator was used to estimate the number of missing rings (Larsson 2018). If there was no clear ring curvature indicating the location of the pith, or the core was rotten or broken, then no pith date was assigned. Pith dates were grouped into decadal bins and plotted by species groups to characterize temporal changes in the number and composition of tree recruitment. We identified temporal variations in recruitment by calculating the percent change in the number of pith dates from one decade to the next ($\Delta_{est} = \frac{Est_{1860s} - Est_{1850s}}{Est_{1850s}} * 100$). Decadal recruitment pulses were any ten-year period in which the percent increase in pith dates was 100 percent or greater and more than five pith dates were recorded. We did not include the wood samples collected outside of the plots in our calculation of recruitment pulses or age structure diagrams because these were not systematically sampled. We created a separate plot of these cores and cross-sections (including the fire-scarred samples), however, to assess whether temporal patterns of pith dates from this sample matched those from within the plots.

Addressing Uncertainty in the Dendroecological Record

Tree rings are imperfect recorders of fire occurrence and forest change, and it is important to recognize the limitations in our data set. First, our study was conducted in a relatively small area (110 ha) and we cannot assume that the patterns and processes observed in the LWRNA are representative of the geography of the broader Ouachita Mountains. Second, low sample depth during the protohistoric period increases uncertainty in our reconstructions of early fire frequency and tree recruitment. Data from this period should be interpreted with this uncertainty in mind. Third, contemporary age structure is a record of trees that have persisted until the date of sampling, not a direct record of past establishment. To supplement the known limitations of this approach, other studies have measured snags, stumps, and downed trees to further characterize stand history (e.g., Oliver and Stephens 1977; Fulé et al. 2002). Unfortunately, at the LWRNA we found that of resinous shortleaf pine stumps and downed logs were the only dead wood that resisted decay sufficiently to be useful in reconstruction of past forest dynamics in this humid environment—a limited and biased sample. Hence, to address the limitations of any one data set, we combined multiple lines of contemporary physical evidence from fire scars, contemporary forest composition, and age structure with other forms of historical documentation to provide a more robust characterization of fire and forest dynamics over time.

Results

Fire Frequency and Seasonality

Fires were frequent at LWRNA for at least two centuries prior to the imposition of fire protection in the 1930s (Figure 2). We successfully cross-dated fifty-four of fifty-eight fire-scarred samples, with ring dates that spanned the years 1561 to 2019. The samples included 188 individual fire scars that recorded fourty-two separate fire years. The earliest fire scar dated to 1703 and the last fire was recorded at the site in 1943. The last major fire (scarred > 25 percent of the recording samples) occurred in 1923. During the period from 1701 to 1929, the filtered CMFI was 6.7 years with a range of two to twenty-five years (Table 1). The unfiltered CMFI

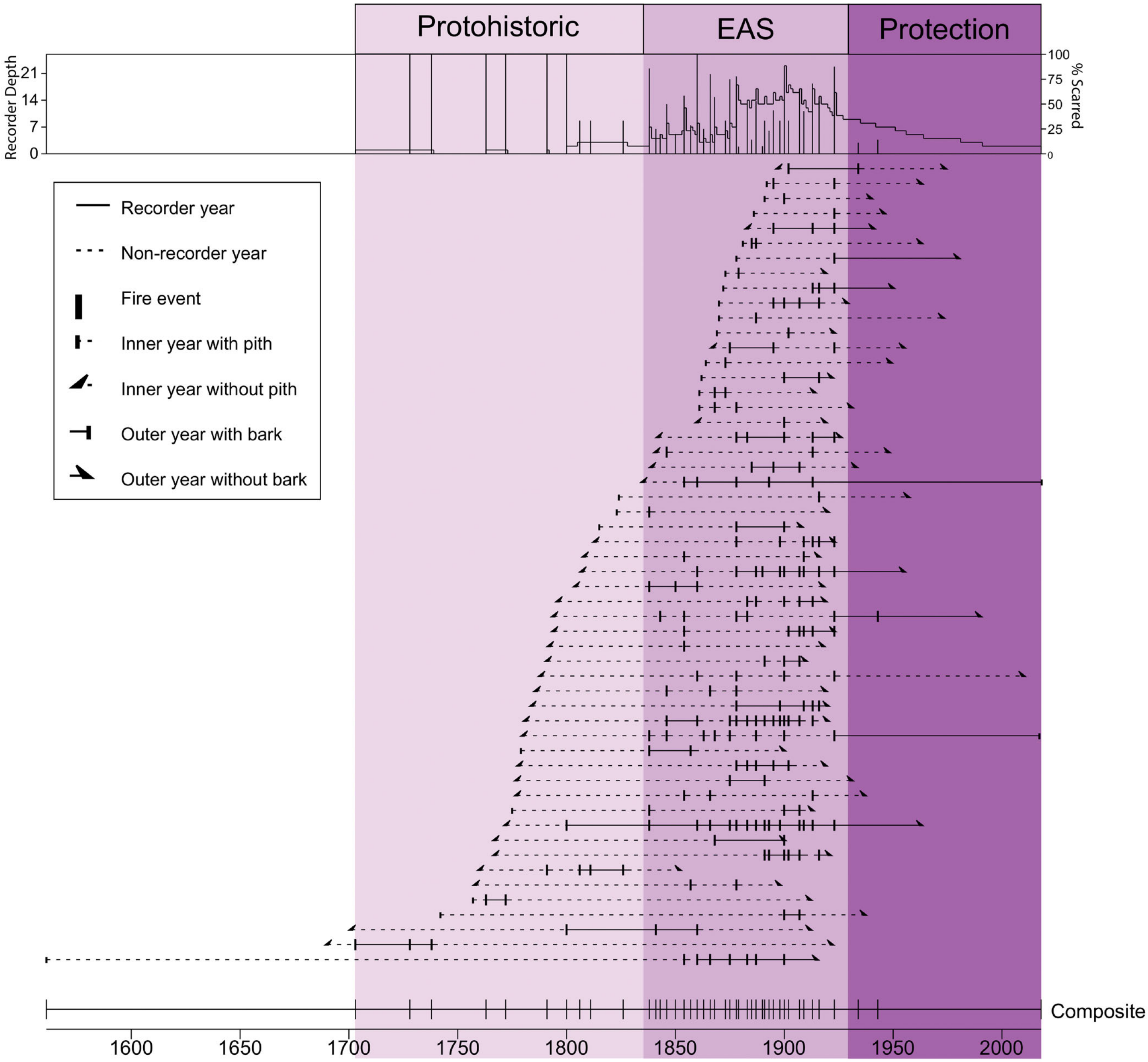

Figure 2. Fire chronology for Lake Winona Research Natural Area showing dates of fire scars for cross-dated wood sections. In the upper panel, the line shows the number of recording trees, and the histogram bars show the percentage of recording trees scarred. The horizontal line at the bottom represents the composite fire record, combining all fires that occurred at the site. Shading indicates the different land use periods: Protohistoric (1701–1834), European American settlement (EAS; 1835–1929), and (fire) protection (1930–2018).

Table 1. Fire interval metrics from 1701 to 1929

Fire interval type	Initial fire year	Mean fire return interval	Weibull median fire return interval	*SD*	Lower exceedance interval	Upper exceedance interval	Range	No. of intervals
Composite	1703	5.6	4.3	6.0	1.0	11.3	1–25	39
Filtered composite	1703	6.7	5.5	6.1	1.5	12.9	2–25	33
Point	1703	12.3	9.8	11.9	2.5	24.3	2–67	132

Table 2. Percent of fire years in each season determined according to the position of scars within the annual growth ring

	Dormant	Early	Late	Undetermined
All fires	73.8	4.8	16.7	4.8
Protohistoric (1701–1834)	70.0	0.0	20.0	10.0
European American settlement (1835–1929)	80.0	6.7	13.3	0.0

Table 3. Mean fire intervals (MFIs) during the different land-use periods

	Protohistoric period (1701–1834)	European American settlement period (1835–1929)	Fire protection period (1930–2018)
Composite MFI	13.7[a]	2.9[a]	42
Filtered composite MFI	13.7[b]	3.7[b]	—
Point MFI	19.1[c]	7.5[c]	42

Note: Values with same superscript are significantly different based on *t* test ($p < 0.05$). The filtered composite MFI was not calculated during the fire protection period because the 1934 and 1943 fires were recorded by only one tree each and therefore did not meet the threshold of scarring 25% of the recording samples.

was 5.6 years, and the individual sample fire interval was 12.3 years. We were able to determine the seasonality of 95.2 percent of the fire years, with the majority (73.8 percent) occurring in the dormant season (Table 2).

Temporal Changes in the Fire Record

The fire regime varied during the different land-use periods. Prior to 1835, fires were frequent at LWRNA, but all three mean fire intervals (*t* test, $p < 0.05$) were shorter during the EAS period compared to the protohistoric period (Table 3). In contrast, fire was infrequent during the fire protection period, with only two fires recorded, both occurring during the initial fifteen years and scarring a single tree, resulting in a CMFI of fourty-two years. The longest fire interval in the 300-year record is the current interval of seventy-six years. During the protohistoric period there was a higher proportion of late growing season fires ($\chi^2 = 12.7$, $p < 0.05$). Most fires, however, occurred in the dormant season, both before and after EAS (Table 2). None of the SEA tests identified a significant relationship between fire years and annual PDSI (see Figure S.1 in the Supplemental Materials). The protohistoric fires, though, did exhibit a nonsignificant trend of drier conditions in the year of the fire and the two preceding years.

Temporal Changes in Forest Dynamics

The non-fire-scarred cross-sections and cores collected at the site provide a multicentury record of tree establishment (Figure 3). We dated 719 cores and twenty cross-sections from a total of 340 trees. The rate and composition of tree recruitment shifted in response to temporal changes in the fire regime. Cohorts of recruitment occurred in the 1860s following EAS and then in the 1920s during the decade of the last major fire at the site. The species composition of recruits responded to changes in the fire regime as well. Our record of tree establishment was very limited during the protohistoric period, with only four living trees (three white oaks, one shortleaf pine) in the plots that predated EAS. Shortleaf pine recruitment dominated during the post-EAS period (84.9 percent shortleaf pine, 11.9 percent oaks, 3.2 percent non-oak hardwoods). Recruitment during the fire protection period was a mix of oaks and other hardwoods but very little pine (67.6 percent oaks, 31.3 percent non-oak hardwoods, 1.1 percent shortleaf). The cross-sections and cores collected outside of the plots were not a systematic sample of age structure, but this longer record of shortleaf pine recruitment included many trees that were established in the 1860s.

Current Forest Composition

The forest overstory at LWRNA is currently dominated by shortleaf pine, with a significant proportion of oak (Table 4). Shortleaf pine, which tend to

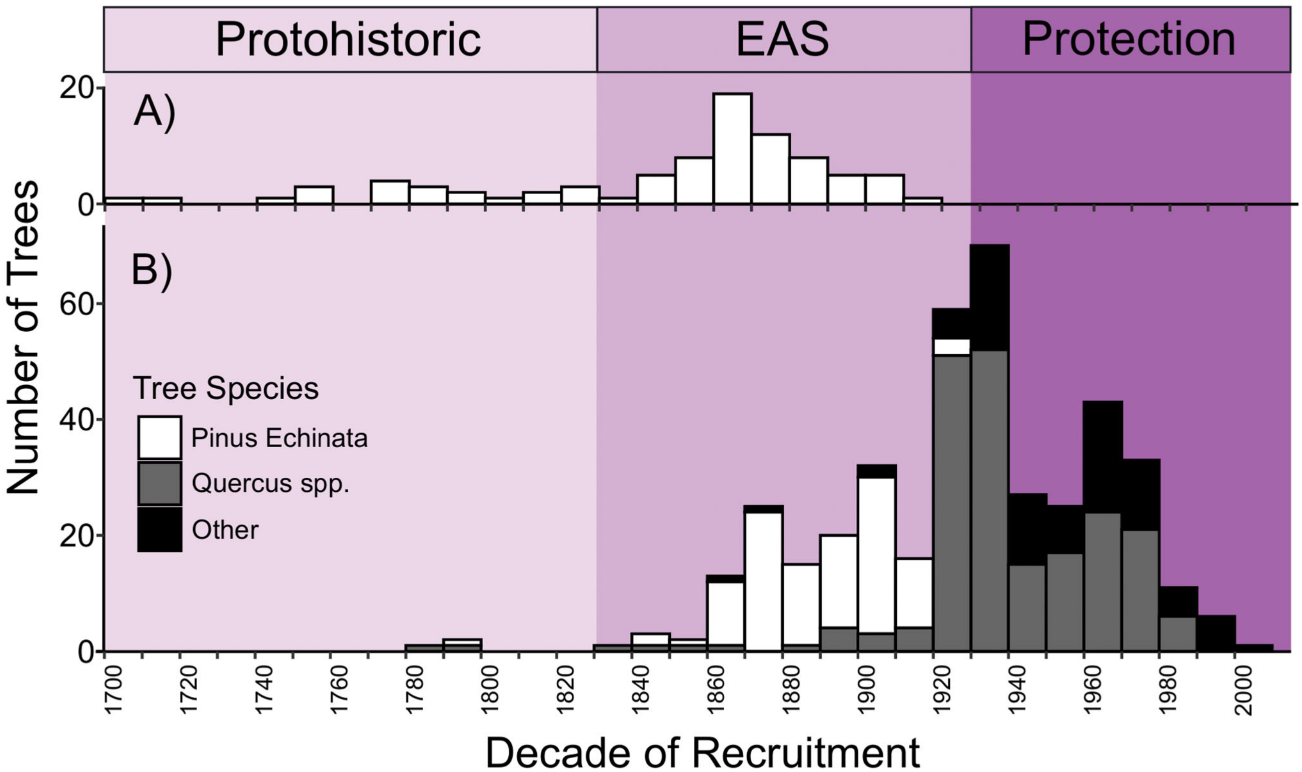

Figure 3. Decadal tree recruitment from (A) supplemental cores and cross-sections, and (B) forest sampling plots at Lake Winona Research Natural Area, Arkansas. *Note:* EAS = European American settlement.

be the largest and oldest trees, accounts for the most basal area in the forest—at over 20 m^2/ha (about 64 percent), and shortleaf has 2.5 times the basal area of the next most dominant taxa (white oaks). Although there are some large white oaks and there are more stems per hectare of this species than pine, these white oaks are generally in the smaller diameter classes. Combined, shortleaf pine and white oak contribute nearly 90 percent of the overstory basal area of this stand. This overwhelming overstory dominance of these two species, however, does not translate to the under- and midstories. Although white oak and shortleaf pine comprised about one fifth of the contemporary seedling and sapling layers, these strata were dominated by other hardwoods (Table 4). Not surprisingly in this now closed-canopy stand, more shade-tolerant (and less fire-tolerant) hardwood species such as blackgum (*Nyssa sylvatica* Marsh.), eastern hophornbeam (*Ostrya virginiana* (Mill.) K. Koch), red maple (*Acer rubrum* L.), hickories (*Carya* spp.), flowering dogwood (*Cornus florida* L.), and American holly (*Ilex opaca* Ait.) are common in the under- and midstories (Table 4).

Discussion

Forest Dynamics and Fire Regimes

Dendroecological studies that combine fire scars and age structure provide a depth of information on fire regimes and forest dynamics (Stambaugh, Marschall, and Guyette 2014; Flatley et al. 2015; Larson, Kipfmueller, and Johnson 2021; Lafon et al. 2022). A growing body of dendroecological work in the eastern United States (e.g., McEwan and McCarthy 2008; this study) provides evidence that historical increases and decreases in fire frequency shifted community composition and stand structure, thereby promoting widespread dominance of fire-resilient species and open forests during certain periods and less fire-tolerant species during periods of less frequent fire. In eastern North America, this might have been accomplished through the addition or removal of anthropogenic ignitions timed to coincide with periods when normally wet biomass is drier and available for burning (Lafon, Hoss, and Grissino-Mayer 2005). An increase in appropriately timed ignitions could promote more flammable

Table 4. Basal area and density of trees, saplings, and seedlings for different species in the contemporary forest

Common name	Scientific name	Basal area (m^2/ha)	Tree density (#/ha)	Sapling density (#/ha)	Seedling density (#/ha)
Shortleaf pine	*Pinus echinata* Mill.	20.4	201.7	0.0	333.3
White oak	*Quercus alba* L.	8.0	313.3	116.7	1833.3
Blackgum	*Nyssa sylvatica* Marsh.	1.0	91.7	113.3	250.0
Northern red oak	*Quercus rubra* L.	0.6	16.7	10.0	833.3
Post oak	*Quercus stellata* Wang.	0.5	31.7	6.7	0.0
Black oak	*Quercus velutina* Lam.	0.5	16.7	16.7	500.0
Red maple	*Acer rubrum* L.	0.4	43.3	126.7	3583.3
Blackjack oak	*Quercus marilandica* Muenchh.	0.2	10.0	3.3	0.0
Mockernut hickory	*Carya tomentosa* Nutt.	0.1	8.3	13.3	833.3
Eastern hophornbeam	*Ostrya virginiana* (Mill.) K. Koch	0.1	15.0	16.7	583.3
Bitternut hickory	*Carya cordiformis* (Wang.) K. Koch	0.1	8.3	3.3	83.3
Flowering dogwood	*Cornus florida* L.	$<$ 0.1	6.7	3.3	0.0
Serviceberry	*Amelanchier arborea* (Michx.f.) Fern	$<$ 0.1	8.3	0.0	166.7
Black cherry	*Prunus serotina* Ehrh.	$<$ 0.1	3.3	0.0	0.0
American holly	*Ilex opaca* Ait.	$<$ 0.1	1.7	16.7	1416.7
Southern red oak	*Quercus falcata* Michx.	$<$ 0.1	1.7	3.3	0.0
Farkleberry	*Vaccinium arboreum* Marsh.	$<$ 0.1	3.3	53.3	0.0
Mexican plum	*Prunus mexicana* S. Wats.	$<$ 0.1	1.7	0.0	0.0
	Total	31.9	783.3	503.3	10416.7

vegetation and contribute to low-density forests dominated by fire-tolerant species (Hanberry, Bragg, and Hutchinson 2018). The removal of ignitions and suppression of fires has led to increased forest density and the dominance of fire-intolerant species in the contemporary forest (Nowacki and Abrams 2008).

Our study is consistent with McWethy et al.'s (2013) conceptual framework that predicts wetter temperate ecosystems (e.g., the humid southeastern United States) are sensitive to human impacts on the fire regime. The fire scar, age structure, and stand composition evidence from LWRNA documents variations in the fire regime and variations in forest conditions (Figure 4). The nature and timing of the fire regime transitions and corresponding forest change provides strong evidence of the interaction between fire disturbance and forest conditions. George Featherstonhaugh, having witnessed a number of burned landscapes while traveling through Arkansas (including the Ouachita Mountains) during the early 1830s, described the traditional use of fire by Native Americans to "burn the cane and high grass in the upland forests, and which has somewhat thinned but has not destroyed them, as we see from the state of more open woods in Virginia, Tennessee, Kentucky, Indiana, Missouri, and Arkansas; where, now that the Indians have abandoned the country, the undergrowth is rapidly occupying the ground again" (Featherstonhaugh 1844, 168).

Fire Regimes

Protohistoric Fire Regime. The dendroecological record from LWRNA provides some evidence that fires were less frequent prior to EAS. If we missed fires during the early record, then our protohistoric CMFI (13.7 years) overestimates the length of the mean fire interval during this period. The fourteen-year protohistoric CMFI at LWRNA, however, is within the range of protohistoric fire intervals previously documented in the nearby Ozark Plateau region, which had a range of seven to twenty-two, removing outliers of forty and sixty years (Guyette and Spetich 2003; Guyette, Spetich, and Stambaugh 2006; Stambaugh and Guyette 2006). Stands in the Blue Ridge Mountains of Tennessee dominated by shortleaf pine had protohistoric CMFIs that ranged from 7.9 to 11.6 years (LaForest 2012); the Cumberland Plateau of Georgia, Tennessee, and Kentucky was 4.4 to 5.3 years (Stambaugh, Marschall, and Abadir 2020); and the Appalachian Plateau of Kentucky and Ohio was 6.6 to 8.4 years (Hutchinson et al. 2019).

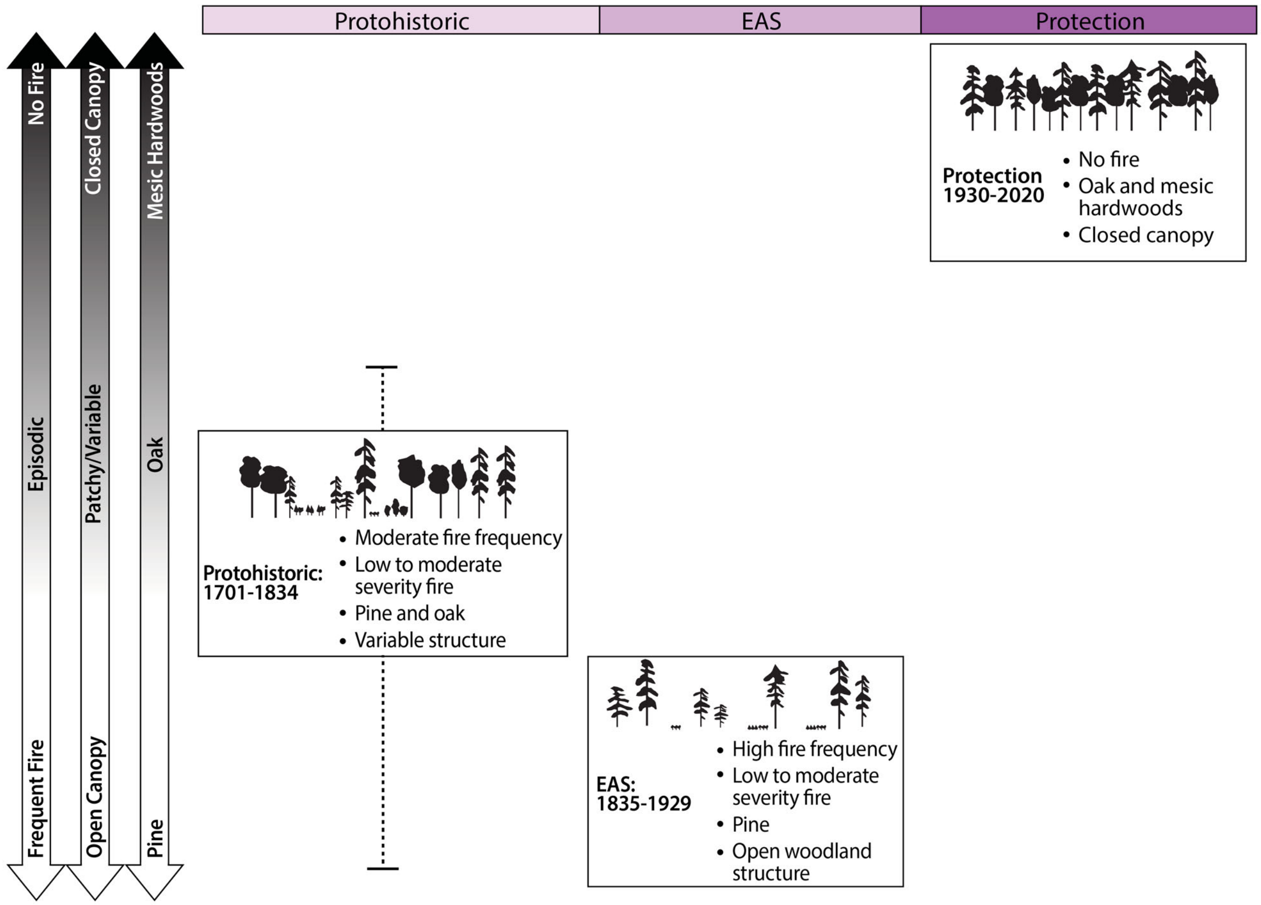

Figure 4. Conceptual diagram of temporal change in fire regime characteristics and forest dynamics. Fire-forest states during different time periods are illustrated and placed along a hypothesized spectrum of fire frequency, forest structure, and forest composition at Lake Winona Research Natural Area, Arkansas, during the last 300 years. The dotted lines illustrate uncertainty in our reconstruction of fire and forest dynamics during the Protohistoric period. *Note:* EAS = European American settlement.

In the Ouachita Mountains, previous information on protohistoric fire intervals is quite limited. Masters, Skeen, and Whitehead (1995) dated fire scars from the McCurtain County Wilderness Area in eastern Oklahoma that dated from 1800 to 1834, but did not specifically calculate a CMFI for this period. Johnson and Schnell (1985) calculated a protohistoric point mean fire interval of 7.25 years for a single tree at Hot Springs National Park. Less frequent fires at LWRNA might have been due to its location in the interior of the Ouachita Mountains (Guyette, Spetich, and Stambaugh 2006), human population dynamics (Guyette, Muzika, and Dey 2002), or different fire-use practices among the peoples inhabiting the area (Masters, Skeen, and Whitehead 1995).

During the protohistoric period there was a slightly higher proportion of late growing season burns. Contemporary lightning fires in the Ouachita Mountains occur most frequently in the months of August and September (Foti and Glenn 1991), which would manifest in the tree-ring record as late growing season fires. Most fires, however, occurred during the dormant season, a traditional season for anthropogenic burning in the Southeast (Fowler and Konopik 2007). For instance, William Dunbar, while in northern Louisiana, wrote of his experience while co-leading an expedition up the Ouachita River in 1804 and 1805, "This smokey [sic] or misty appearance which in our Country is common in the months of November and December is attributed to a common practize [sic] of the Indians and Hunters, of firing the woods, planes [sic] or savannahs; the flames often extending themselves for some hundred miles, before the fire is extinguished" (Berry, Beasley, and Clements 2006, 41). The fires noted by Dunbar and others (e.g., Stoddard 1812) might also reflect a transition toward a more frequent fire

Figure 5. Shortleaf pine-dominated stands in the Ouachita National Forest, illustrating stands with overwhelmingly pine overstories, relatively open (compared to modern) structures, and understories with a mix of grasses, forbs, hardwood saplings, and shrubs. (A) U.S. Forest Service negative 192041 taken by an unknown person in Yell County, Arkansas, in 1924. (B) U.S. Forest Service negative 255802 taken in Polk County, Arkansas, in 1931 by W. G. Wahlenberg.

regime that started in the latter decades of the protohistoric period in this region. During this period (mid-1700s onward), Native American tribes displaced from east of Arkansas began settling in this area and early European American hunters and traders arrived (Whayne, Arnold, and Whayne 1995; Sabo 2001). These groups have been documented elsewhere in eastern North America to apply fire more frequently than the tribes they replaced (e.g., Guyette, Muzika, and Dey 2002; Guyette and Spetich 2003; Stambaugh, Guyette, and Marschall 2013; Stambaugh et al. 2018; Hutchinson et al. 2019).

EAS Fire Regime. High fire frequency (3.7-year filtered CMFI) at LWRNA coincided with EAS in Saline County and the broader region (ADC 2020). By the 1840s, a doubling of the population of Saline County from about 2,000 to 4,000 persons corresponded with frequent burning at LWRNA. Many European American settlers in the hillier areas of the state were small-scale agriculturists, primarily pastoralists, who cleared little land but very frequently used fire to keep the forests open, grassy, and suitable for livestock grazing (Smith 1986; Strausberg and Hough 1997). The resulting open, pine-dominated, often grassy stands with limited woody understories are evident in many photographs of the Ouachitas from the EAS period (e.g., Figure 5).

There is limited documentation on fire frequency in the Ouachita Mountains during EAS, aside from anecdotes (e.g., Featherstonhaugh 1844; Foti and Glenn 1991; Berry, Beasley, and Clements 2006) and limited tree-ring surveys of other parts of the region (e.g., Johnson and Schnell 1985; Masters, Skeen, and Whitehead 1995). The 3.7 year filtered CMFI that we found at the LWRNA during EAS, however, is comparable to that found in shortleaf pine and shortleaf pine-oak forests on the Ozark Plateau during this period (Batek et al. 1999; Guyette, Spetich, and Stambaugh 2006). Studies in the Ridge and Valley region of Pennsylvania and the Cumberland Plateau in Tennessee found similarly frequent burning during early EAS (Stambaugh et al. 2018; Stambaugh, Marschall, and Abadir 2020). Productive forest growth and potential for year-round burning in the southeastern United States might make it particularly responsive to the addition or removal of ignitions during periods when lightning is not frequent. Climate appears to modulate a landscape's sensitivity to variation in anthropogenic ignitions. For example, in the drier southern Rockies and the Sierra Nevada, fuel production often limits fire frequency and increases in Native American ignitions can break up fuel continuity and decrease fire frequency at the landscape scale (Swetnam et al. 2016; Taylor et al. 2016). In wetter and colder locations like the Lake States and New England, shorter fire seasons and higher fuel moisture might have limited the spread of fire beyond areas adjacent to population centers and travel corridors (Oswald et al. 2020; Kipfmueller et al. 2021). The Ouachita Mountains might inhabit a climate space that is balanced between fuel production and fuel moisture limitations on fire frequency, providing frequent opportunities for ignitions and fire spread.

Fire Protection Regime. The last fire recorded at LWRNA occurred in 1943. Since that burn, the fire-free interval of seventy-six years is far greater than the upper exceedance interval or any of the other fire intervals in this stand's 300-year tree-ring record. This is the most pronounced variation in the fire regime at LWRNA. The near-complete cessation of fires after the first half of the twentieth century is a common pattern across fire history studies in the humid southeastern United States (Guyette, Spetich, and Stambaugh 2006; Lafon et al. 2017). The extent and duration of fire exclusion in these forests has altered landscape continuity, stand structure, species composition, and the ecology of fuels, likely increasing resistance to future fire occurrence and spread (Nowacki and Abrams 2008; Alexander et al. 2021).

Disturbances Other Than Fire. The mixed shortleaf pine-oak forests of the Ouachita Mountains experience numerous natural disturbances in addition to fire, including insect outbreaks, windstorms, ice storms, and major droughts (e.g., Turner 1935; Stevenson et al. 2016). Hence, it is likely that disturbance processes other than fire played some role in the forest changes we have documented in this stand (sensu McEwan, Dyer, and Pederson 2011). Interactions between disturbances might also have played a role; for example, insect outbreaks, ice storms, or windstorms preceding fires could have added to fuel loads, contributed to higher severity fires, and therefore accelerated forest change. We suggest, however, that nonfire canopy disturbances are unlikely to have driven the forest transition during EAS, as the changes in the rate and composition of tree recruitment persisted for sixty years (Figure 3) rather than a few years or a decade following a severe insect infestation or major storm. In this part of Arkansas, the 1830s and 1850s were two very dry decades (Stahle, Cleaveland, and Hehr 1985) and this might have initiated overstory mortality and favored the recruitment of drought-tolerant shortleaf pines. Again, though, it seems unlikely that drought alone triggered the compositional changes at LWRNA, as pine recruitment remained dominant and substantial during both wet and dry decades from 1860 to 1920, a period of frequent fires (Figure 2).

Forest change during the latter decades of the twentieth century provides further evidence of the central role that fire played in shaping the contemporary forests of LWRNA. Multiple large-scale disturbances (including a 1982 tornado, a pine beetle outbreak in the mid-1990s, and a major ice storm in 2000) have affected the site and likely accelerated the decline of the aging shortleaf pine canopy (Fountain and Sweeney 1987). These disturbances have not created conditions sufficient to bolster shortleaf pine recruitment into the tree or sapling layers (Table 4) in the LWRNA, however, which contrasts with both the protohistoric and EAS periods when fires were occurring. The decades-long removal of fire has pushed the forest into a fundamentally different condition from the forest conditions we reconstructed from the preceding 200 years. Therefore, we conclude that although nonfire disturbances or processes such as herbivory have substantially affected the old-growth forest of the LWRNA during the past several centuries, their overall influence has been less significant than both the frequent occurrence and long absence of fire.

Forest Dynamics

Protohistoric Forest Dynamics. The data available to characterize tree establishment during the protohistoric period are now too limited to infer composition at the site during this earliest part of the record. Previous studies, however, provide evidence that oak was abundant in this region during the protohistoric period. Although not an unbiased assessment, the General Land Office (GLO) surveyed witness trees in the LWRNA area recorded from 1821 to 1838[1] were 67.3 percent oak, 21.6 percent shortleaf pine, and 11.1 percent other species (Bragg 2004). GLO data from counties in the Ouachita Mountains just west of the LWRNA exhibited relative pine importance values that ranged from 24 to 55 percent, with the remainder dominated by oaks (Foti and Glenn 1991). Note that it is possible—even likely—that at least some of the surveyors preferentially selected oaks (or avoided pines) as witness trees, thereby skewing abundance patterns from the GLO records (Hanberry et al. 2012). Because of this, it is important to think of this historical source as reflective of a significant oak presence in the protohistoric period at the LWRNA, rather than an exact representation of actual abundance.

A combination of longer fire intervals and associated canopy gap would favor oaks over shortleaf pine or mesophytic hardwoods (Stambaugh, Guyette, and Dey 2007; Scheller et al. 2008; Izbicki et al. 2020; Zhao et al. 2021). The forests of the LWRNA prior to EAS might not have been sparsely treed savannas, but more of a closed woodland condition (sensu Hanberry, Bragg, and Hutchinson 2018). Although traits vary by taxa, oaks tend to be more shade-tolerant than pines and species such as white oak are prolific sprouters (when young) and seed producers with considerable potential longevities, and therefore could persist in landscapes where fire was infrequent enough to support accumulations of advanced regeneration capable of taking advantage of periodic canopy gaps (Arthur et al. 2012). Long-term research has shown that higher frequency fire in oak-dominated forests can prevent the development of advanced regeneration (e.g., Knapp, Stephan, and Hubbart 2015).

EAS Forest Dynamics. The high fire frequency during EAS aligned with periods of establishment indicative of a forest with open structure dominated by shortleaf pine (Table 3; Figures 2, 3, and 5). Evidence for compositional change during the EAS transition was found in the historical surveys conducted in the LWRNA area, which showed an increase in shortleaf pine witness trees from about 22 percent in the early 1830s to 73 percent of the trees by 1931 (Bragg 2004). Increasing fire frequency tends to shift regeneration from oak to shortleaf pine (Stambaugh, Guyette, and Dey 2007), as shortleaf pine is well adapted to frequent surface fire, with thick bark and the ability to resprout as a seedling or sapling following topkill (Fire Effects Information System 2021). Shortleaf pine also regenerates more successfully with high light levels, an open canopy, and bare mineral soil (Fire Effects Information System 2021)—all benefits of certain types of fire. For instance, more recent experience using mechanical overstory thinning to restore shortleaf pine-dominated forests on the Ouachita National Forest suggests that without sufficiently intense fires, sprouts from cut hardwoods can quickly dominate the woody regeneration, reducing the advantages of sprouting-capable shortleaf pine regeneration over seed-origin non-pine competitors (e.g., Sparks et al. 1998; Guldin 2019).

Fire Protection Forest Dynamics. The cessation of fires in the early twentieth century coincided with a shift from shortleaf pine-dominated recruitment toward oaks and other hardwoods (Figure 3). The loss of fire removed the primary mechanism regulating overstory density and understory conditions and this led to a dramatically altered forest composition across all strata. Recruitment of all tree species is now limited in this closed-canopy environment; for shade-intolerant species such as shortleaf pine, overstory recruitment over the past century has virtually disappeared. The small shortleaf pine seedlings currently found in our plots (Table 4) rarely move into sapling size classes and the under- and midstories of LWRNA are now dominated by increasingly shade-tolerant hardwood species. Until recent decades (Figure 3), oaks have been able to regenerate and have become increasingly important in the overstory. Similar to pine, though, oaks are absent from tree recruitment to the overstory in the most recent two decades of our record. Consequently, the current LWRNA overstory, although still largely shortleaf pines and white oaks, is transitioning toward other less pyrophytic species as attrition to the dominant trees continues to accumulate following small-scale, periodic losses to wind, ice, lightning, disease, and insects.

Although there are no plans to reintroduce fire to the LWRNA, it is unclear if such an effort would achieve the desired management goal of restoring an open, pine-dominated ecosystem after this long period of fire protection. Our results suggest that people were able to reduce forest density and favor shortleaf pine regeneration during the EAS transition through purposeful burning. At this stage, though, the reimplementation of fire in the LWRNA without concurrent decreases to overstory stocking (e.g., via thinnings or fire-induced mortality) will likely see little to no benefit because the low light levels reaching the forest floor will not encourage the development of continuous cover of fine herbaceous fuels needed to support these burns (Sparks et al. 1998; Guldin 2019; Bragg et al. 2020). Without those additional treatments, fire of low intensity or insufficient frequency is also unlikely to produce good shortleaf pine regeneration, as they will not suitably prepare the seedbed, reduce the amount of competing understory vegetation, or open the canopy enough to facilitate new seedling recruitment (e.g., Elliott and Vose 2005; Olson and Olson 2016; Jin et al. 2018; Robertson, Hermann, and Staller 2021).

Conclusions

This case study complements others (e.g., Guyette, Spetich, and Stambaugh 2006) with comparable fire and forest dynamics in eastern North America, particularly in the Interior Highlands of Missouri and Arkansas. Evidence of fire waves in other regions suggests that forests in many portions of the eastern United States underwent similar changes during recent centuries. We also note that shortleaf pine-oak forests appear to be highly resilient to very frequent fire (three- to eight-year intervals), which they experienced during the EAS period and perhaps during earlier periods. Additional studies examining multi-century fire history and forest dynamics would help determine if the patterns we found during the last three centuries at LWRNA are typical across the Ouachita region and more broadly across shortleaf pine-oak forests in the southeastern United States.

The fire and forest history we have documented for the LWRNA argues against using any one specific time period as a static reference condition when attempting to restore historical forests in the Ouachita Mountains because fire regimes and forest conditions have been highly dynamic for at least the last three centuries. The dendroecological record indicates that prescriptions at either end of the historical range of variation in fire intervals at LWRNA could produce exceedingly different stand structure, composition, and habitat. Even still, our dendroecological record at LWRNA could help design management objectives in how it might encourage the treatment of comparable stands along a broader fire frequency gradient from open, frequently burned shortleaf pine woodlands to fire-protected mesic forest structure and composition (and all points in between), rather than trying to implement a single option for stand conditions.

Note

1. Although most GLO surveys were about the time of our 1835 initiation of EAS, these witness trees would have been in place for decades to centuries already and reflect forest dynamics of the protohistoric period.

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ORCID

William T. Flatley http://orcid.org/0000-0002-6189-0065
Don C. Bragg http://orcid.org/0000-0002-5207-8606

Supplemental Materials

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WILLIAM T. FLATLEY is an Associate Professor in the Department of Geography, University of Central Arkansas, Conway, AR 72035. E-mail: wflatley@uca.edu. His research interests include forest disturbance, dendroecology, historical ecology, fire ecology, forest ecology, and biogeography.

LILLIAN M. BRAGG is a graduate with a BS in environmental science from the Department of Geography, University of Central Arkansas, Conway, AR 72035. E-mail: lillianmcdaniel2@gmail.com. Her research interests include dendrochronology, fire ecology, and forest ecosystem management.

DON C. BRAGG is a Research Forester and Project Leader with the U.S. Department of Agriculture Forest Service's Southern Research Station, Monticello, AR 71655. E-mail: Don.C.Bragg@usda.gov. His research interests include southern pine silviculture, old growth, restoration ecology, fire ecology, and historical ecology.