THE HISTORIC FIRE REGIME ON THE EDGE OF THE PRAIRIE: A CASE STUDY FROM THE CROSS TIMBERS OF OKLAHOMA

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ABSTRACT

Changes in the historical disturbance regime because of Anglo-American settlement and forced removal of Native Americans have altered vegetation composition and structure of forests, particularly in mesic ecosystems. However, xeric forests have gone largely unstudied, even though they may contain some of the largest tracts of remnant old-growth forests in eastern North America. Using dendrochronological techniques, we reconstructed fire, drought, and vegetation dynamics of an old-growth forest in the Cross Timbers region of Oklahoma. We tested predictions that fires would 1) be influenced by topography, 2) have decreased in frequency since Anglo-American settlement, 3) increase in frequency during drought events, and 4) be followed by pulses of hardwood recruitment. Support for our first prediction included higher fire frequency on the most southwest-facing aspect. We found no evidence to support prediction 2; fires became more frequent following Native American and Anglo-American movement into the area. Our third and fourth predictions were both supported; large-scale fire events occurred following periods of prolonged drought and 57–100% of oak (*Quercus*) recruitment followed a fire event. In contrast, eastern redcedar (*Juniperus virginiana*), an invasive native species, recruited during fire-free periods. Our results indicate that the sequence of drought followed by fire is an important process in long-term maintenance of forest conditions in this oak ecosystem. We attribute the increase in fire frequency after settlement to increasing local anthropogenic ignitions. The local effect of settlement on the fire regime (i.e., increased fire frequency) seems to contrast with the regional effects of settlement (i.e., decreased fire frequency).

keywords: Anglo-American settlement, Cross Timbers, drought, fire regime, oak recruitment, Oklahoma, stand dynamics.

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INTRODUCTION

Fire has influenced vegetation patterns of forests in eastern North America for millennia (Clark et al. 1996, Delcourt and Delcourt 1998, Bonnicksen 2000). Removal of Native Americans and the onset of Anglo-American settlement have led to changes in the fire regime in many eastern North American forests (Cutter and Guyette 1994, McClenahen and Houston 1998, Ruffner and Abrams 2002). The early days of settlement often brought a temporary increase in fire frequency due to population pressures related to land use (Ruffner and Abrams 2002). However, by the early 1900s, fire frequency was largely reduced from presettlement levels, contributing to a decreased oak (*Quercus*) component, particularly on mesic sites where competition from fire-sensitive species is intense (Abrams et al. 1995, Delcourt and Delcourt 1998).

In xeric oak woodlands and savannahs, reductions in fire frequency have led to an increase of invasive plant species, changes in stand structure, and decrease in spatial heterogeneity across the landscape (Jenkins and Rebertus 1994, Bóo et al. 1997, Heikens 1999, Fuhlendorf and Engle 2004). However, few studies have linked the changes in fire frequency to human population changes and to subsequent effects on vegetation response in these ecosystems. Studies that have

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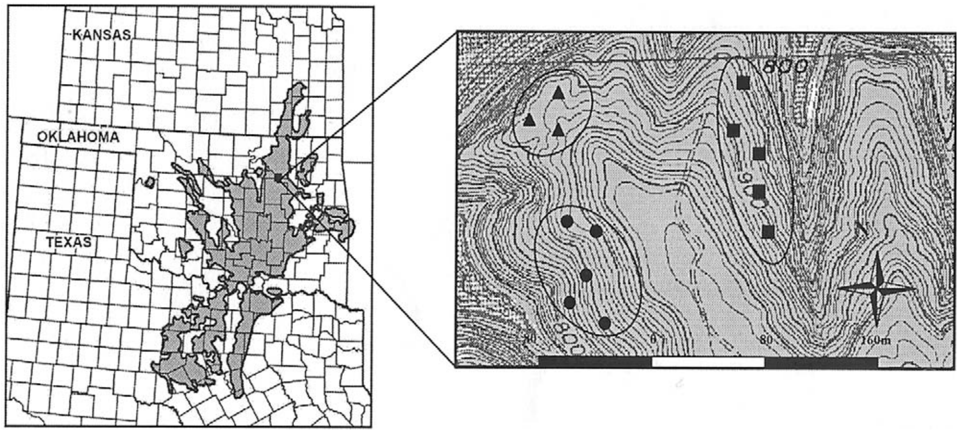

Fig. 1. The Cross Timbers region (adapted from Küchler 1964) with approximate location of Keystone Ancient Forest Preserve (inset) and location of plots in each stand (● = Southwestern slope stand; ■ = Northeastern slope stand; ▲ = Bench stand). Copyright 2005 by Natural Areas Association. From *Natural Areas Journal,* by S.L. Clark, S.W. Hallgren, D.W. Stahle, and T. Lynch, "Characteristics of the Keystone Ancient Forest Preserve, an old-growth forest in the Cross Timbers of Oklahoma." Reprinted by permission of Natural Areas Association.

reconstructed fire history in xeric oak ecosystems have generally been confined to the Ozarks (Guyette and Cutter 1991, Cutter and Guyette 1994, Guyette et al. 2002). These studies have found that fire frequency was generally reduced following Anglo-American settlement and was highest during occupation by the original Native American habitants.

The Cross Timbers region of Oklahoma has gone largely unstudied, but is an important region from a biological and historical perspective (Stahle and Hehr 1984, Therrell and Stahle 1998, Hoagland et al. 1999). The region was occupied by Osage Indians from the 1700s until the 1830s, when bands of Cherokee, Creek, Seminole, Choctaw, and Chickasaw tribes were forced to leave their homes to the southeast to occupy the new Indian Territory in present-day Oklahoma (Wyckoff 1984). Although many explorations took place in the 1800s (Foreman 1947, Albert and Wyckoff 1984), the Cross Timbers was largely unoccupied by Anglo-Americans until 1889 when settlement became legal (Wyckoff 1984).

In this study, we examine how topography, changes in human demographics, and climate influenced the fire regime of an old-growth oak forest in the Cross Timbers region of Oklahoma. Our specific objectives were to 1) reconstruct the fire history of this site through dendrochronological dating of fire scars, 2) examine the effects of topography and climate on fire occurrence and spread, and 3) determine the relationship between tree recruitment patterns and fire events. We had four research hypotheses: 1) fire frequency would be influenced by topography, 2) fire frequency has decreased since Anglo-American settlement, 3) fire events were more likely to occur during periods of prolonged drought, and 4) fire promoted oak recruitment.

STUDY AREA

The study area was part of The Nature Conservancy's Keystone Ancient Forest Preserve (KAFP). The KAFP lies in the northern Cross Timbers region (Küchler 1964), approximately 32 km west of Tulsa, Oklahoma, in southern Osage County at the confluence of the Cimarron and Arkansas rivers (Figure 1). The region is characterized as a mosaic of xeric oak woodlands, savannas, and prairie openings scattered throughout approximately 4.8 million ha, with nearly half of its area in Oklahoma (Küchler 1964, Hoagland et al. 1999). Average annual precipitation is 101 cm, and average winter and summer temperatures are 3° and 26°C, respectively (Oklahoma Climatological Survey 2002). The KAFP has been characterized as old growth because of the presence of post oak (*Quercus stellata*) and eastern redcedar (*Juniperus virginiana*) trees greater than 300 and 500 y old, respectively, and the absence of anthropogenic disturbances (Therrell and Stahle 1998). Elevation ranges from 251 to 304 m; topography is moderately to steeply sloping with underlying bedrock of shale and sandstone. Soils are a Niotaze–Darnell complex, with a sandy loam surface layer (Bourlier et al. 1979).

Previous research indicated that topography was the primary factor in identifying distinct forest vegetation communities (Roe 1998). Thus, we delineated three stands based on aspect and elevation. The 11-ha Southwestern slope stand was located on the steep upper slopes (slope = 17%) with a southwestern aspect. The 14-ha Northeastern slope stand was located on steep lower slopes (slope = 20%) with a northeastern aspect and had the lowest elevation. The 5-ha Bench stand was located on relatively level terrain (slope = 6%) just north of the main ridgetop.

METHODS

Field Sampling

We randomly placed three to five 55 × 55-m plots within each stand (Figure 1), and we randomly sampled 98 saplings (>1 m height, <10 cm diameter at breast height) from five species for age structure analysis. We obtained cores or cross sections within 10 cm of the root collar. The number of saplings selected within a species was consistent with species' relative densities (Clark et al. 2005). By sampling smaller trees at the base, we could examine recruitment response to recent fire events at a near-annual resolution (Villalba and Veblen 1997); all cores and cross sections either hit pith or were estimated to be within 1 or 2 y of pith.

Fire scars from dead tree cross sections were used to reconstruct the fire history of the KAFP. We obtained 11, 8, and 8 cross sections from dead tree logs or snags within the Southwestern slope, Northeastern slope, and Bench stands, respectively. We also obtained 2 cross sections along the main ridgeline, just outside of the designated stands' boundaries. For downed logs, cross sections were taken as close to the log's base as possible (<30 cm from base) to improve chances of detecting injury from fire (Guyette and Cutter 1991, Smith and Sutherland 1999). We similarly obtained wedges from the base of standing snags. To provide a fire history of most recent fire events, we documented fire scars on sapling cross sections. We analyzed 13, 3, and 2 saplings that contained fire scars from the Southwestern slope, Northeastern slope, and Bench stands, respectively. Including dead trees and saplings, we collected 46 samples for the fire scar analysis from post oak (n = 23), blackjack oak (*Q. marilandica*; n = 10), black hickory (*Carya texana*; n = 9), and Shumard's oak (*Q. shumardii*; n = 4).

Dendrochronological Techniques

Sapling and dead tree samples were dried and sanded with progressively finer grades of sandpaper (100–400 grit) and cross-dated using a regional post oak chronology available in the International Tree-Ring Data Bank (ITRDB) (NOAA 2004). Cross-dating provides confidence that samples were dated to the exact calendar year (Douglass 1941, Stokes and Smiley 1996). Cross-section and sapling tree-ring widths were measured to the nearest 0.001 mm with a Velmex stage micrometer. Portions of cores containing rot were not measured. Many cross sections exhibited eccentric ring growth and were measured along the radius that was intermediate in ring width. We were neither able to cross-date nor to measure eastern redcedar samples because of occurrence of missing rings and false rings, and ages of these trees should be considered ring counts and not exact ages (Schweingruber 1988).

We identified fire scars on the dead tree samples and dated them to an exact calendar year. Fire scars are defined as wounds resulting from cambial death due to excessive heating or scorching (Smith and Sutherland 1999). All fire scars were associated with abnormal vessel formation and production of callus tissue, i.e., undifferentiated cells that contain little lignin (Smith and Sutherland 1999), which resulted in wide growth rings in the year of fire and sometimes several years following the fire. Fire scars from two known and documented fire events at the KAFP in 1994 and 1996 were also used as reference for identifying fire scars in previous years. Fire scars sometimes produced woundwood ribs at the margins of the fire scar (Smith and Sutherland 1999), particularly if the fire injured a large portion of the tree's circumference. However, fires sometimes caused relatively localized injury and did not cause formation of woundwood ribs. Fire scars generally occurred during the dormant season that spans two calendar years (i.e., after the end of the previous year's growing season). The fire scars were assigned the year in which the tree first showed a wounding response to the fire (i.e., the year containing the earlywood immediately following the fire scar).

Fire Scar Analysis

Fire scar analysis was conducted using FHX2 software (Grissino-Mayer 2001). Years were assigned as recorder or null years, and only recorder years are included in the analysis. Recorder years include the time period from the first year the tree recorded a fire to the year of the tree's outer ring. Once a tree is scarred, it becomes more susceptible to injury by subsequent fires and years between two fire events are, therefore, considered recorder years. Years from the inner ring to the first fire event were considered null years because proof of fire events were not being recorded, even though the tree may have been experiencing fire during this time. Null years included prolonged periods (>100 y) between two fire events; if the tree completely healed the wound from the previous fire event, proof of fire history information does not exist and was therefore not included in the sample (Grissino-Mayer 2001). Null years also included rings that were unreadable due to rot or because fire burned off portions of the wood.

We performed fire scar analyses for each stand and across stands; separate analyses were also conducted for all fire events, and for moderate-scale fires, defined as fires that scarred ≥25% of sample trees. We calculated the fire return interval for each stand and across stands, defined as the number of years between two consecutive fire events and is a measure of fire frequency. We determined the fire return interval data were not normally distributed according to a Kolmogorov–Smirnov test for goodness of fit ($P < 0.05$). We therefore used the median fire return interval as an indicator of fire frequency, which is a better descriptor of the central tendency of a data set than the mean when the data are not normally distributed.

We calculated a fire index to determine how fire effects have changed through time (Guyette and Cutter 1991). The index compensates for the effects of sampling size bias; generally, sample size will increase with more recent fire history, and number of fire scars detected will increase with increasing sample size. We calculated the index by dividing the number of fire scars in each 10-y time interval by the number of trees in the record for the same interval.

We performed temporal change analysis to determine if fire frequency has changed because of the movement of displaced Native Americans into the region and the onset of legal Anglo-American settlement. A t-test was used to determine differences in the mean fire return interval and the percentage of trees scarred between a control period and two test periods. The control period was from 1772 to 1830 and represents time from the beginning of the tree-ring chronology to the beginning of Native American movement into the area from their native homelands to the east. The first test period was from 1830 to 1889 and represents the time period of occupation by displaced Native Americans until legal Anglo-American settlement. The second test period was from 1889 to 2002 and represents the time period from legal Anglo-American settlement to the end of the tree-ring chronology. The data were first transformed to the standard normal distribution to apply the *t*-test. A probability value of 0.05 was chosen to indicate significance.

Analysis of Climatic Effects

Annual instrumental Palmer drought severity indices (PDSIs) from 1900 to 2002 and annual reconstructed PDSIs for 1770 to 1899 were obtained by averaging data from grid points 178, 178, 193, and 194 available from the NOAA Paleoclimatology Program, the National Geophysical Data Center, and the National Climatic Data Center (http://www.ncdc.noaa.gov/paleo/pdsi.html; Cook et al. 2004). Monthly PDSI values from 1895 to 2002 were obtained using data from the National Climatic Data Center for Oklahoma, Division 5 (NOAA 2004). The PDSI ranges from −4 (extreme drought) to +4 (extreme wet) and represents several environmental variables that affect tree growth, including drought duration, soil water-holding capacity, temperature, and precipitation (Palmer 1965). We adjusted the annual reconstructed values by multiplying by the ratio of the two variances:

$$rPDSI \times \left(\frac{\sigma_{iPDSI}}{\sigma_{rPDSI}}\right) = adjPDSI,$$

where *rPDSI* = the annual reconstructed value, *iPDSI* = annual instrumental value, and *adjPDSI* = the annual adjusted reconstructed value.

We conducted a superposed epoch analysis using Program EVENT (Holmes and Swetnam 1994) to determine if drought occurred prior to and during a dated fire event. The EVENT program computes average values for an independent variable during a window of time surrounding an event year (i.e., in this study, an event year was a year of a fire) and compares average values of the independent variable to randomly generated predicted values. The predicted values represent 1,000 random simulations generated for each event. A departure value is then calculated for each year in the event window that represents the actual value minus the predicted value. A statistically significant departure value is detected when the actual value is greater than or less than the 95% confidence limits (based on a normal distribution) of the predicted value.

We conducted the analysis for two types of fire events: a moderate-scale fire, defined as fires that scarred ≥25% of sample trees; and a large-scale fire, defined as a fire that scarred at least 50% of sample trees or a fire that burned in all three stands. The latter type of fire event would represent only the most widespread fires at the study site. We conducted the analysis for annual PDSI values from 1770 to 2002 using the reconstructed and instrumental values as described above. We also conducted the analysis for each season within a year by averaging monthly PDSI values from the current year as follows: January–March for winter, April–June for spring, July–September for summer, and October–December for fall. The analysis for seasonal PDSI values could only be conducted for years after 1895 when instrumental data were available.

Table 1. Median fire return interval (FRI) with coefficient of variation (CV) within and across stands for all fire events and for moderate-scale fires at the Keystone Ancient Forest Preserve (KAFP), Oklahoma.

Variable	Stand			KAFP
	Southwestern slope	Northeastern slope	Bench	
All fires				
FRI	2.5	6.0	3.5	2.0
CV	0.9	1.1	1.7	0.9
Minimum interval	1.0	1.0	1.0	1.0
Maximum interval	18.0	45.0	62.0	15.0
Moderate-scale fires				
FRI	4.0	6.0	4.5	7.0
CV	0.9	1.1	1.4	1.2
Minimum interval	1.0	1.0	1.0	1.0
Maximum interval	20.0	45.0	62.0	49.0

RESULTS

Topoedaphic and Temporal Patterns of Fire Frequency

The median fire return interval from 1772 to 2002 for all fire events was 2.0 and was 7.0 for moderate-scale fires (Table 1). Approximately 40% of fires scarred only one tree. Fires occurred most frequently in the Southwestern slope stand and least frequently in the Northeastern slope stand. The Bench stand had the longest single fire-free interval (62 y). A total of 77 fires were recorded, with total number of fires and sample size increasing over the length of the chronology (Figure 2). We documented 24 moderate-scale fire events and 8 large-scale fire events (Table 2).

The fire index value increased slightly over the last 150 y and was lowest during the 1830s, with no fires reported during that decade (Figure 3). The fire return interval for all fire events did not change significantly with the onset of Native American displacement into the area according to the temporal change analysis (Table 3). However, the fire return interval was significantly shorter following Anglo-American settlement compared with the control period. Conversely, moderate-scale fire return interval increased from 4.9 during the control period to 15.0 following Anglo-American settlement, but this difference was not significant. The temporal change analysis performed on percentage of trees scarred differed from fire return interval analysis. The percentage of trees scarred for all fire events was significantly lower during the two test pe-

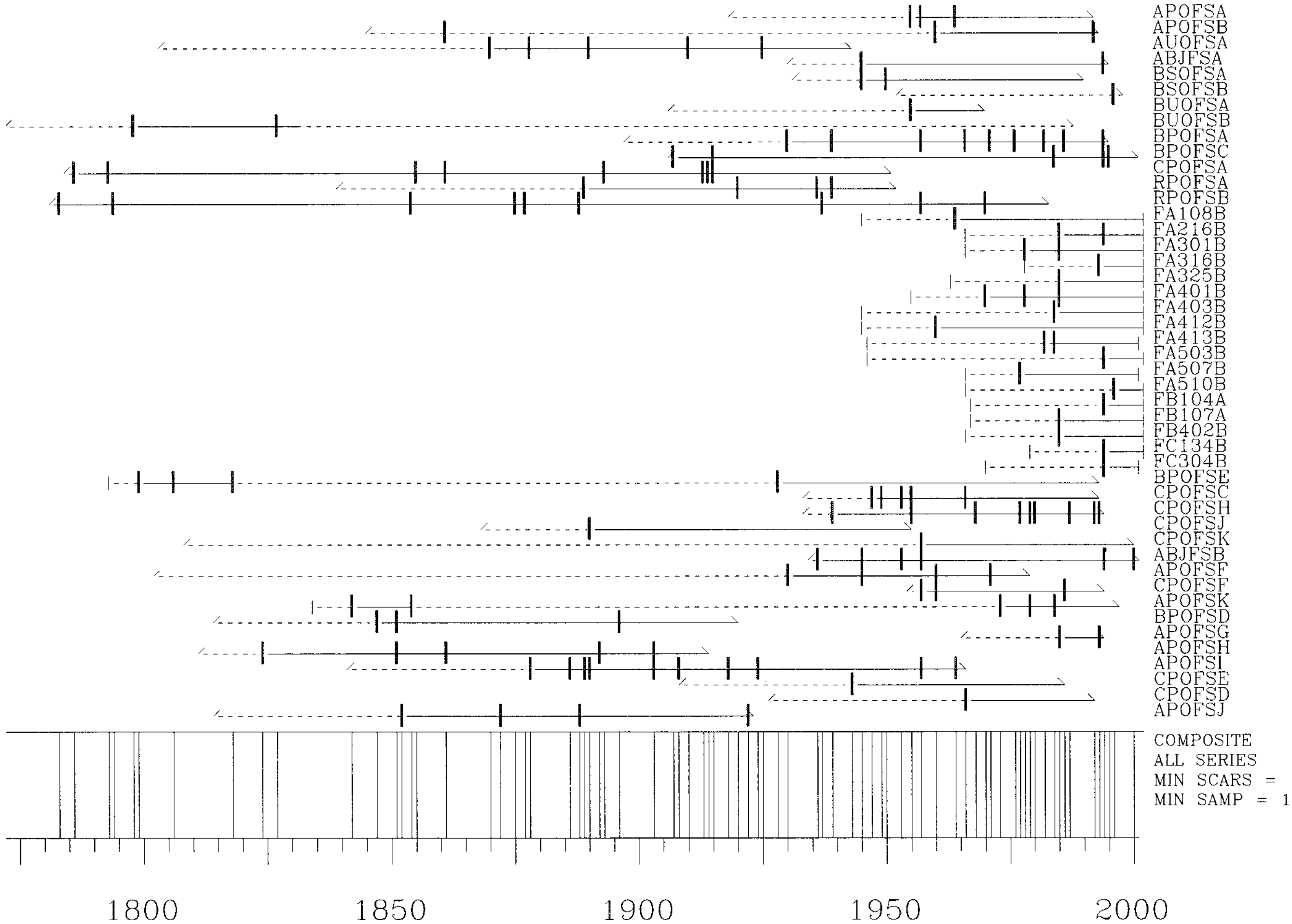

Fig. 2. Fire chronology from 1772 to 2002. Horizontal lines represent individual sample trees (author's nomenclature) and vertical dashes represent fire events; dashed horizontal line represents period not included in analysis and solid horizontal line represents period included in fire analysis. Bottom bar is master fire chronology for all samples in the Keystone Ancient Forest Preserve, Oklahoma.

riods of Native American displacement and Anglo-American settlement compared with the control period. However, no differences were detected for moderate-scale fire events.

Effects of Climate

Neither moderate-scale nor large-scale fire events were related to annual PSDI values, but fire did appear to be dependent on drought during a particular season. The superposed epoch analysis indicated that summer and fall PDSI values preceding a dated fire event were

Table 2. Moderate-scale and large-scale fire events at the Keystone Ancient Forest Preserve, Oklahoma.

Moderate-scale fire			Large-scale fire
1783	1824	1889	1783
1786	1827	1890	1786
1793	1842	1939	1793
1794	1851	1945	1794
1798	1854	1955	1861
1799	1861	1957	1955
1806	1878	1985	1957
1818	1888	1994	1994

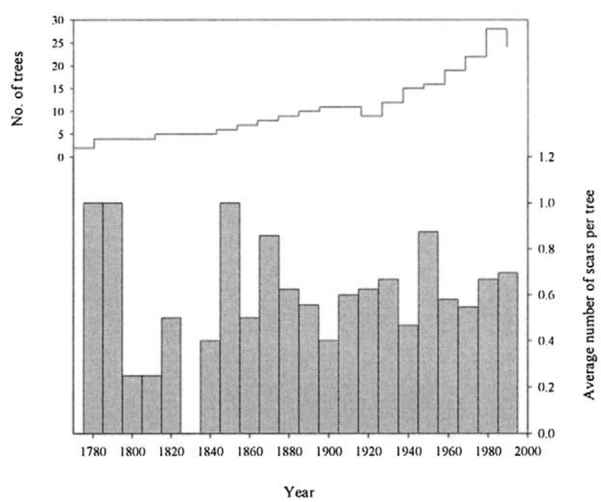

Fig. 3. Fire index values (number of scars per tree) per 10-y interval, Keystone Ancient Forest Preserve, Oklahoma. The top graph represents sample size used in our analysis.

Table 3. Comparison in differences in fire return interval and percent trees scarred (standard error in parentheses) between control time period (1772–1830), and displaced Native American period (1830–1889) and Anglo-American settlement test period (1889–2002).

Variable	Control period (1772–1830)	Test period (1830–1889)	Test period (1889–2002)
Fire return interval			
All fires	4.9 (1.2)	3.4 (0.7)	2.1[a] (0.2)
Moderate-scale fires	4.9 (1.2)	7.8 (2.3)	15.0 (6.6)
Percent trees scarred			
All fires	40.8 (7.5)	24.5[a] (2.6)	14.2[a] (1.2)
Moderate-scale fires	40.8 (7.5)	32.9 (3.5)	31.4 (2.6)

[a] *t*-test with control period was significant ($P < 0.05$).

contributing factors in the occurrence of large-scale fires (Figure 4). Moderate-scale fire events showed the same trend as large-scale fires, but departure from normal PDSI values was not significant.

Recruitment Dynamics

Recruitment pulse of hardwood species predominately occurred following fire events in each stand (Figure 5). Sapling recruitment for the four hardwood species occurred within 2 y following a fire 61–90% of the time, depending on stand. This pattern was greater than expected by chance alone, given the length of the sapling age structure. Fire appeared to have the most effect on recruitment in the Northeastern slope stand and the least effect in the Bench stand. A large recruitment pulse followed the 1945 and 1964 fires in the Southwestern slope stand and followed 1966 in the Northeastern slope and Bench stands. Recruitment response to fire was similar among species, except for eastern redcedar. While some saplings were able to withstand fire, the majority of eastern redcedar recruited during prolonged fire-free periods (>15 y), particularly in the Bench stand, where it had the highest abundance and was increasing in density.

DISCUSSION

Differences across the Topoedaphic Gradient

We found support for our first hypothesis that fire frequency was influenced by topography. However, inferences from our results are speculative due to the lack of replication of different stands. Landscape has been shown to have a strong local effect on a fire regime, due to effects on insolation and fuel moisture (Bergeron 1991). The Southwestern slope and Bench stands would have the highest levels of insolation, due to reduced canopy cover and southerly exposure (Clark et al. 2005) and would therefore have the highest probability of fire ignition and spread (Pyne et al. 1996), as our results support. In contrast, the Northeastern slope stand would have the highest levels of fuel moisture and less probability of fire. A drainage to the east (Figure 1) may also serve as a natural firebreak.

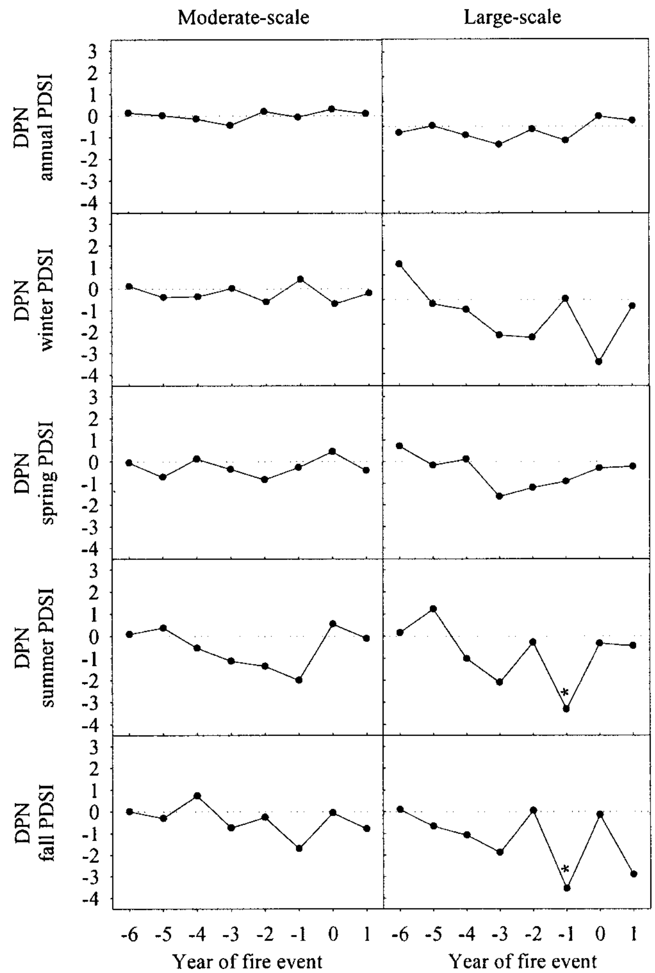

Fig. 4. Departure from long-term normal (DPN) Palmer drought severity index (PDSI) for fire event (year 0) and years surrounding fire event for annual and seasonal PDSI values and for moderate- and large-scale fire events, Keystone Ancient Forest Preserve, Oklahoma. Asterisks indicate years in which departure from normal PSDI was significant ($P < 0.05$).

Temporal Changes in the Fire Regime

We did not find support for our second hypothesis that fire frequency has decreased since Anglo-American settlement. Fire frequency increased after Anglo-American settlement, differing from numerous studies conducted in oak forests throughout the midwestern and eastern United States (Guyette and Cutter 1991, Cutter and Guyette 1994, Abrams et al. 1997, Orwig et al. 2001, Shumway et al. 2001). The fire return interval at the KAFP was shorter than those reported in Missouri Ozark forests (Guyette and Cutter 1991, Cutter and Guyette 1994, Batek et al. 1999) and in oak gallery forests of northeastern Kansas (Abrams 1985) of similar or larger size. The lack of significant change in fire frequency with the period of Native American displacement is attributed to the fact that the actual influx of Native Americans during this time at this particular site was relatively low (Wyckoff 1984). Human populations did not increase dramatically until after the Osage Indian lands were allotted after statehood in 1907, coinciding with the first oil explorations in

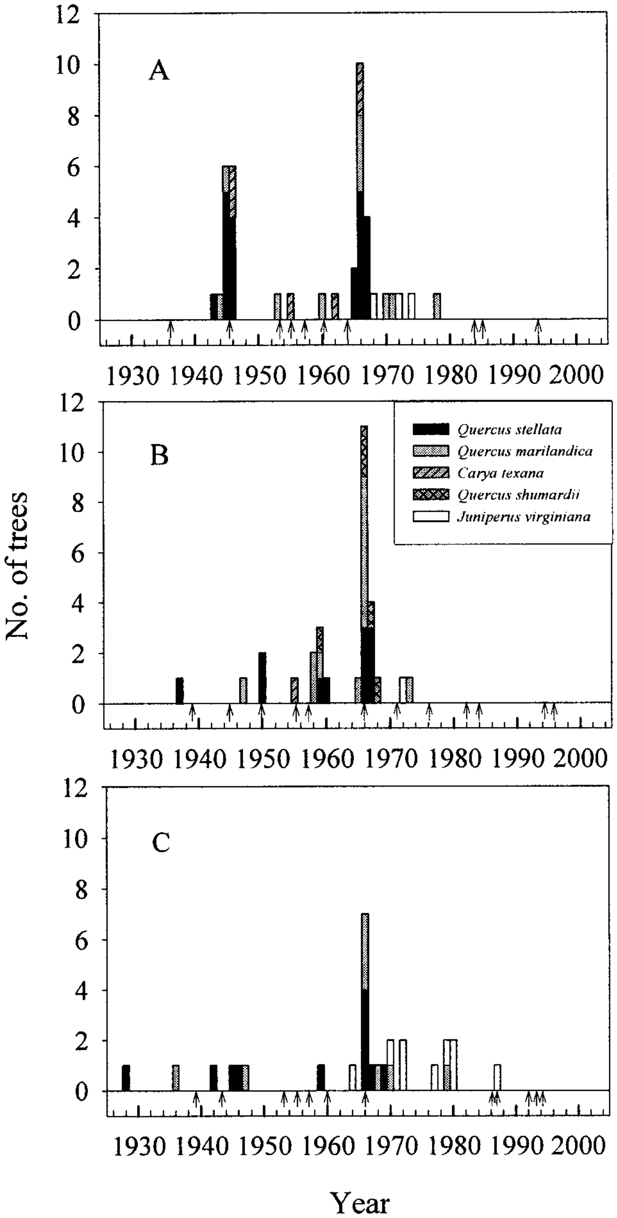

Fig. 5. Age structure of saplings in the (A) Southwestern slope, (B) Northeastern slope, and (C) Bench stands, Keystone Ancient Forest Preserve, Oklahoma. Arrows represent moderate-scale fire events.

the area that continue to the present day. The potential for anthropogenic ignitions increases as human population density increases, as supported by our results (Guyette and Cutter 1991, Guyette et al. 2002). Additionally, construction of a major highway in the mid-1900s and the frequent use of fire by local farmers to clear fields may have contributed to the increase of fire frequency during the past 100 y.

Sample size bias may be artificially increasing fire frequency. As sample size increases over time, the possibility of finding fire scars also increases, thereby biasing our results. This potential bias is also supported by the fact that the percentage of trees scarred decreased over time. However, other studies also had similar potential for bias due to sample size (Guyette and Cutter 1991) and did not show an increase in fire frequency, giving some support to an actual increase in ignition because of increased human population pressure.

The fire return interval for moderate-scale events would have increased if we had included null years prior to the first fire event and periods between two prolonged fire events in the analysis. Although some suggest these periods represent real fire-free intervals (Baker and Ehle 2001), years in which fire history information is not known should not be included in the analysis because no scientific information is available for that time period.

Drought Influences on Fire

We found support for our third hypothesis that climatic conditions affect fire frequency, but only for large-scale fire events. We speculate that while ignition of fire is likely independent of climate, the ability of fire to spread across the landscape may be partially dependent on climatic conditions, particular during the previous summer and fall. This can best be seen with the droughts of the late 1850s and mid-1950s, when PDSI levels remained below normal for several consecutive years (data not shown). Consequently, large-scale fires occurred (Table 2) and fire index values were high (Figure 3) during both of these periods.

The analysis of seasonal effects on fire in the Cross Timbers is lacking in many studies and may help explain the conflicting results among past studies, even within the same climatic region. Fire was not related to drought in the Missouri Ozarks (Cutter and Guyette 1994), but a relationship was found in a nearby post oak savanna (Guyette and Cutter 1991). These previous studies did not examine seasonal effects of climate on fire, which was shown to be important in this study.

Oak species are particularly sensitive to climate, producing narrow rings (Stahle and Hehr 1984) and exhibiting high mortality during severe droughts (Rice and Penfound 1959, Jenkins and Pallardy 1995, Olano and Palmer 2003). Changes in fuel moisture and availability related to drought could be affecting fire spread. Drought increases fine fuel loads due to death of live plant material and reduces fuel moisture in large fuels (Pyne et al. 1996). Thus, fuel unavailable to burn during normal climate conditions becomes available during dry periods, facilitating fire spread and intensity (Engle et al. 1989, Bidwell and Engle 1991, Pyne et al. 1996).

Sapling Recruitment Response to Fire

We found evidence to support our fourth prediction that fire promoted oak recruitment into the sapling layer. Our results support theories that oaks exhibit a "bottleneck" effect, whereby recruitment from seedlings to saplings is encouraged by periodic disturbances (Johnson 1992, 1993; Johnson et al. 2002). Evidence of the bottleneck effect in this forest is also supported by previous studies at the KAFP that showed seedling populations were high (approximately 6,000–13,000 trees ha^{-1}), while sapling populations were comparatively low (approximately 1,500–2,000 trees ha^{-1}) (Clark et al. 2005). Adaptations such as thick bark and deep rooting provide oaks with resistance to fire (Hengst and Dawson 1994, Abrams 1996), whereas fire promotes prolific sprouting of oaks, particularly in the more xerophytic species (Penfound 1968, Crow et al. 1994, Johnson et al. 2002, Clark and Hallgren 2004). Black hickory was also encouraged by fire in this forest, indicating that this species may have similar adaptations and recruitment dynamics as the oak species.

In contrast to hardwood species, fire restricted the establishment of eastern redcedar, a species that has been invasive in prairie and glade communities throughout the Midwest (Bragg and Hubert 1976, Engle et al. 1996). This species appeared to recruit under fire-free conditions and would likely increase in these stands in the absence of fire (Beilmann and Brenner 1951). Sapling population structure suggests that this species is increasing in the Bench stand, with no recruitment prior to 1964. This finding is further substantiated by the fact that large overstory species were relatively rare in this stand (Roe 1998, Clark et al. 2005).

CONCLUSIONS

On a local scale, Native American displacement and Anglo-American settlement had a positive effect on fire frequency and oak recruitment, in contrast to findings from the majority of dendroecological studies in eastern North America. On a regional scale, Anglo-American settlement has increased eastern redcedar invasion due to the seed rain from surrounding invaded fields and prairies (Engle et al. 1996). Fire appeared to limit the early establishment of eastern redcedar, a species that can negatively affect oak recruitment due to shading and competition for water (Ormsbee et al. 1976; Wittwer 1985; Engle et al. 1987, 1996; Oswald et al. 1996), but once established, this species was able to resist fire.

Despite changes in human demographics, drought is the underlying force of this ecosystem; fire frequency of large-scale fires increased after drought, which helps promote sprouting of hardwood species through top-kill of live saplings. Drought can also directly cause mortality of mature trees (Rice and Penfound 1959, McGee 1984, Olano and Palmer 2003) and thus directly create or maintain canopy gaps suitable for seedling recruitment.

Stand dynamic processes of this forest include interactions among human demographics, climate, and fire. The management of old-growth upland oak forests should include a burning regime that incorporates drought and local human impacts in the decision-making process. A special management consideration may be removal of invasive species, such as eastern redcedar, particularly where invasion is favored by specific site conditions. Although fire-history information and analysis in this study was limited by the number of trees sampled and recording fire history, our results can provide a building block in understanding the stand dynamics of xeric oak forests in the Cross Timbers. This information will become increasingly important as society simultaneously demands and threatens forest conservation.

LITERATURE CITED

Abrams, M.D. 1985. Fire history of oak gallery forests in a northeast Kansas tallgrass prairie. American Midland Naturalist 114:188–191.

Abrams, M.D. 1996. Distribution, historical development and ecophysiological attributes of oak species in the eastern United States. Annales des Sciences Forestières 53:487–512.

Abrams, M.D., D.A. Orwig, and T.E. Demeo. 1995. Dendroecological analysis of successional dynamics for a presettlement-origin white-pine–mixed-oak forest in the southern Appalachians, USA. Journal of Ecology 83:123–133.

Abrams, M.D., D.A. Orwig, and M.J. Dockry. 1997. Dendroecology and successional status of two contrasting old-growth oak forests in the Blue Ridge Mountains, U.S.A. Canadian Journal of Forest Research 27:994–1002.

Albert, L.E., and D.G. Wyckoff. 1984. Oklahoma environments: past and present. Pages 12–43 *in* R.A. Bell (ed.). Prehistory of Oklahoma. Academic Press, New York.

Baker, W.L., and D. Ehle. 2001. Uncertainty in surface-fire history: the case of ponderosa pine forests in the western United States. Canadian Journal of Forest Research 31:1205–1226.

Batek, M.J., A.J. Rebertus, W.A. Schroeder, T.L. Haithcoat, E. Compass, and R.P. Guyette. 1999. Reconstruction of early-nineteenth-century vegetation and fire regimes in the Missouri Ozarks. Journal of Biogeography 26:397–412.

Beilmann, A.P., and L.G. Brenner. 1951. The recent intrusion of forests in the Ozarks. Annals of the Missouri Botanical Garden 38:261–282.

Bergeron, Y. 1991. The influence of island and mainland lakeshore landscapes on boreal forest fire regimes. Ecology 72:1980–1992.

Bidwell, T.G., and D.M. Engle. 1991. Behavior of headfires and backfires on tallgrass prairie. Fire and the environment: ecological and cultural perspectives. Pages 344–350 *in* S.C. Norton and T.A. Waldrop (eds.). Fire and the environment: ecological and cultural perspectives; Proceedings of an international symposium. General Technical Report SE-69, U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station, Asheville, NC.

Bonnicksen, T. 2000. America's ancient forests: from the Ice Age to the Age of Discovery. John Wiley and Sons, New York.

Bóo, R.M., D.V. Peláez, S.C. Bunting, M.D. Mayor, and O.R. Elías. 1997. Effect of fire on woody species in central semi-arid Argentina. Journal of Arid Environments 35:87–94.

Bourlier, B.G., J.D. Nichols, W.J. Ringwald, P.J. Workman, and S. Clemmons. 1979. Soil survey of Osage County, Oklahoma. National Cooperative Soil Survey, Washington, D.C.

Bragg, T.B., and L.C. Hubert. 1976. Woody plant invasion of unburned Kansas bluestem prairie. Journal of Range Management 29:19–24.

Clark, J.S., P.D. Royall, and C. Chumbley. 1996. The role of fire during climate change in an eastern deciduous forest at Devil's Bathtub, New York. Ecology 77:2148–2166.

Clark, S.L., and S.W. Hallgren. 2004. Dynamics of oak (*Quercus marilandica* and *Q. stellata*) reproduction in an old-growth Cross Timbers forest. Southeastern Naturalist 2:559–574.

Clark, S.L., S.W. Hallgren, D.W. Stahle, and T. Lynch. 2005. Characteristics of the Keystone Ancient Forest Preserve, an old-growth forest in the Cross Timbers of Oklahoma. Natural Areas Journal 25:165–175.

Cook, E.R., C.A. Woodhouse, C.M. Eakin, D.M. Meko, and D.W. Stahle. 2004. Long-term aridity changes in the western United States. Science 306:1015–1018.

Crow, T.R., W.C. Johnson, and C.S. Adkisson. 1994. Fire and recruitment of *Quercus* in a postagricultural field. American Midland Naturalist 131:84–97.

Cutter, B.E., and R.P. Guyette. 1994. Fire frequency on an oak–hickory ridgetop in the Missouri Ozarks. American Midland Naturalist 132:393–398.

Delcourt, P.A., and H.R. Delcourt. 1998. The influence of prehistoric human-set fires on oak–chestnut forests in the southern Appalachians. Castanea 63:337–345.

Douglass, A.E. 1941. Crossdating in dendrochronology. Journal of Forestry 39:825–831.

Engle, D.M., T.G. Bidwell, A.L. Ewing, and J.R. Williams. 1989. A technique for quantifying fire behavior in grassland fire ecology studies. Southwestern Naturalist 34:79–84.

Engle, D.M., T.G. Bidwell, and M.E. Moseley. 1996. Invasion of Oklahoma rangelands and forests by eastern redcedar and Ashe juniper. Circular E-947, Oklahoma Cooperative Extension Service, Oklahoma State University, Stillwater.

Engle, D.M., J.F. Stritzke, and P.L. Claypool. 1987. Herbage standing crop around eastern redcedar trees. Journal of Range Management 40:237–239.

Foreman, C.T. 1947. The Cross Timbers. The Star Printery, Muskogee, OK.

Fuhlendorf, S.D., and D.M. Engle. 2004. Application of the fire–grazing interaction to restore a shifting mosaic on tallgrass prairie. Journal of Applied Ecology 41:604–614.

Grissino-Mayer, H.D. 2001. FHX2—software for analyzing temporal and spatial patterns in fire regimes from tree rings. Tree-Ring Research 57:115–124.

Guyette, R.P., and B.E. Cutter. 1991. Tree-ring analysis of fire history of a post-oak savanna in the Missouri Ozarks. Natural Areas Journal 11:93–99.

Guyette, R.P., R.M. Muzika, and D.C. Dey. 2002. Dynamics of an anthropogenic fire regime. Ecosystems 5:472–486.

Hengst, G.E., and J.O. Dawson 1994. Bark properties and fire resistance of selected trees species from the central hardwood region of North America. Canadian Journal of Forest Research 24:688–696.

Heikens, A.L. 1999. Savanna, barrens, and glade communities of the Ozark Plateaus Province. Pages 220–230 *in* R.C. Anderson, J. Fralish, and J. Baskin (eds.). Savannas, barrens, and rock outcrop plant communities of North America. Cambridge University Press, Cambridge, United Kingdom.

Hoagland, B.W., I.H. Butler, and F.L. Johnson. 1999. The Cross Timbers. Pages 231–245 *in* R.C. Anderson, J. Fralish, and J. Baskin (eds.). Savannas, barrens, and rock outcrop plant communities of North America. Cambridge University Press, Cambridge, United Kingdom.

Holmes, R.L., and T. Swetnam. 1994. Program EVENT, superposed epoch analysis. Version 6.02P. Dendrochronology Program Library, University of Tennessee, Knoxville. http://web.utk.edu/~grissino/software.htm#2 [accessed 21 Apr 2006].

Jenkins, S.E., and S.G. Pallardy. 1995. The influence of drought on red oak group species growth and mortality in the Missouri Ozarks. Canadian Journal of Forest Research 25: 1119–1127.

Jenkins, S.E., and A.J. Rebertus. 1994. Spatial demography of an oak savanna in the Ozarks. Pages 107–111 *in* J.S. Fralish, R.C. Anderson, J.E. Ebinger, and R. Szafoni (eds.). Proceedings of the North American Conference on Barrens and Savannas. Illinois State University, Normal.

Johnson, P.S. 1992. Oak overstory/reproduction relations in two xeric ecosystems in Michigan. Forest Ecology and Management 48:233–248.

Johnson, P.S. 1993. Perspectives on the ecology and silviculture of oak-dominated forests in the central and eastern states. General Technical Report NC-153, U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, MN.

Johnson, P.S., S.R. Shifley, and R. Rogers. 2002. The ecology and silviculture of oaks. CABI Publishing, New York.

Küchler, A.W. 1964. Potential natural vegetation of the coterminous United States. Special Publication No. 36, American Geographical Society, New York.

McClenahen, J.R., and D.B. Houston. 1998. Comparative age structure of a relict prairie transition forest and indigenous forest in southeastern Ohio, USA. Forest Ecology and Management 112:31–40.

McGee, C.E. 1984. Heavy mortality and succession in a virgin mixed mesophytic forest. Research Paper SO-209, U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC.

NOAA [National Oceanic and Atmospheric Administration]. 2004. Contributors of the International Tree-Ring Data Bank. IGBP PAGES/World Data Center for Paleoclimatology, NOAA/NGDC Paleoclimatology Program, Boulder, CO. http://www.ngdc.noaa.gov/paleo/treering.html [accessed 22 Sep 2005].

Oklahoma Climatological Survey. 2002. Climatological information for Osage County, OK. http://lwf.ncdc.noaa.gov/oa/ncdc.html [accessed 1 Jun 2002].

Olano, J.M., and M.W. Palmer. 2003. Stand dynamics of an Appalachian old-growth forest during a severe drought episode. Forest Ecology and Management 174:139–148.

Ormsbee, P., F.A. Bazzaz, and W.R. Boggess. 1976. Physiological ecology of *Juniperus virginiana* in oldfields. Oecologia 23:75–82.

Orwig, D.A., C.V. Cogbill, D.R. Foster, and J.F. O'Keefe. 2001. Variations in old-growth structure and definitions: forest dynamics on Wachusett Mountain, Massachusetts. Ecological Applications 11:437–452.

Oswald, B.P., L. Zhang, T.H. Green, and K.E. Ward. 1996. Differences in species composition and stand characteristics of mixed upland hardwood forests of north Alabama as reflected by the presence of eastern redcedar (*Juniperus virginiana* L.). Journal of Sustainable Forestry 3:75–100.

Palmer, W.C. 1965. Meteorological drought. Research Paper 45, U.S. Department of Commerce, Weather Bureau, Washington, D.C.

Penfound, W.T. 1968. Influence of wildfire in the Wichita Mountain Wildlife Refuge, Oklahoma. Ecology 49:1003–1006.

Pyne, S.J., P.L. Andrews, and R.D. Laven. 1996. Introduction to wildland fire. Second edition. John Wiley and Sons, New York.

Rice, E.L., and W.T. Penfound. 1959. The upland forests of Oklahoma. Ecology 40:593–608.

Roe, S.A. 1998. The vegetation of a tract of ancient cross timbers in Osage County, Oklahoma. M.S. Thesis, Oklahoma State University, Stillwater.

Ruffner, C.M., and M.D. Abrams. 2002. Dendrochronological investigation of disturbance history for a Native American site in northwestern Pennsylvania. Journal of the Torrey Botanical Society 129:251–260.

Schweingruber, F.H. 1988. Tree rings: basics and applications of dendrochronology. D. Reidel Publishing, Boston, MA.

Shumway, D.L., M.D. Abrams, and C.M. Ruffner. 2001. A 400-year history of fire and oak recruitment in an old-growth forest in western Maryland, U.S.A. Canadian Journal of Forest Research 31:1437–1443.

Smith, K.T., and E.K. Sutherland. 1999. Fire scar formation and compartmentalization in oak. Canadian Journal of Forest Research 29:166–171.

Stahle, D.W., and J.G. Hehr. 1984. Dendroclimatic relationships of post oak across a precipitation gradient in the southcentral United States. Annals of the Association of American Geographers 74:561–573.

Stokes, M.A., and T.L. Smiley. 1996. An introduction to tree-ring dating. University of Arizona Press, Tucson.

Therrell, M.D., and D.W. Stahle. 1998. A predictive model to

locate ancient forests in the Cross Timbers of Osage County, Oklahoma. Journal of Biogeography 25:847–854.
Villalba, R., and T.T. Veblen. 1997. Regional patterns of tree population age structures in northern Patagonia: climatic and disturbance influences. Journal of Ecology 85:113–124.
Wittwer, R.F. 1985. Biology of eastern red cedar. Pages 9–16 *in* R.E. Witter and D.M. Engle (eds.). Eastern red cedar in Oklahoma. Publication E-849, Cooperative Extension Service, Oklahoma State University, Stillwater.
Wyckoff, D.G. 1984. The Cross Timbers: an ecotone in historic perspective. Pages 1–20 *in* P.L. Kawecki and D.G. Wyckoff (eds.). Contributions to the Cross Timbers prehistory. Oklahoma Archeological Survey No. 12, University of Oklahoma, Norman.