

FIRE AND VEGETATION DYNAMICS IN THE CROSS TIMBERS FORESTS OF SOUTH-CENTRAL NORTH AMERICA

Steve W. Hallgren, Ryan D. DeSantis, and Jesse A. Burton

Associate Professor (SWH), Department of Natural Resource Ecology and Management, Oklahoma State University, 008C Ag Hall, Stillwater, OK 74078; Postdoctoral Research Associate (RDD); Fire Ecologist (JAB). SWH is corresponding author: to contact, call 405-744-6805 or email at steve.hallgren@okstate.edu.

Abstract.—The vegetation of the Cross Timbers forests was maintained for thousands of years by fire; the historic fire return interval was likely 1 to 10 years. Fire suppression over the past century led to a doubling of stand basal area, increased diversity of tree species, reduced dominance of oak, and increased mesic species intolerant of fire. Dendrochronological studies suggested tree mortality from severe droughts opened stands and accelerated recruitment of eastern redcedar (*Juniperus virginiana* L.) where fire was suppressed. Without reintroduction of fire, Cross Timbers forests will become denser and more diverse with a less diverse understory of herbaceous species, and in many locations, eastern redcedar may become dominant. Research showed prescribed burning every 4 years was sufficient to control understory hardwoods and benefit herbaceous plant cover and diversity which increased with fire up to a burn interval of 2 years. Because low intensity surface fires characteristic of the region usually do not remove established trees, mechanical or chemical methods may be necessary to restore open forests and savannas. Further research is warranted to determine how restoring Cross Timbers forests and savannas to more open conditions will affect ecosystem services including carbon storage, water supply, biological diversity, and wildlife resources.

INTRODUCTION

The ecotone between the eastern deciduous forest and southern Great Plains is a patchwork of forest, savanna, and prairie. This vegetation type, known as the Cross Timbers (Fig. 1), is believed to have once covered nearly 8 million ha from southern Kansas to north-central Texas (Küchler 1964, Therrell and Stahle 1998). The forests of the Cross Timbers may contain some of the least disturbed primary forest in the eastern United States (Therrell and Stahle 1998). Large tracts of what appear to be old-growth forests are still found throughout the region where they have remained relatively undisturbed due to their location on poor shallow soils with rocky outcrops and steep slopes. These areas were rarely logged due to the timber having low commercial value, and they were rarely

cultivated for crops due to the poor soil. Many of these forests contain 200 to 400 year-old post oaks (*Quercus stellata* Wangehn.) and 500 year-old eastern redcedar (*Juniperus virginiana* L.).

The Cross Timbers provides ecosystem services to a regional population of over 7 million persons, and this number is expected to grow to over 17 million by 2040 (Texas Forest Service 2008). The capacity of the ecosystem to provide services is threatened by many factors including changes in land use, urbanization, pollution, overgrazing, global climate change, invasive species, and changes in the fire regime. A study of 143 Cross Timbers stands found that over the past 50 years, approximately 50 percent of the forest area was lost, mostly to agriculture (Stallings 2008).

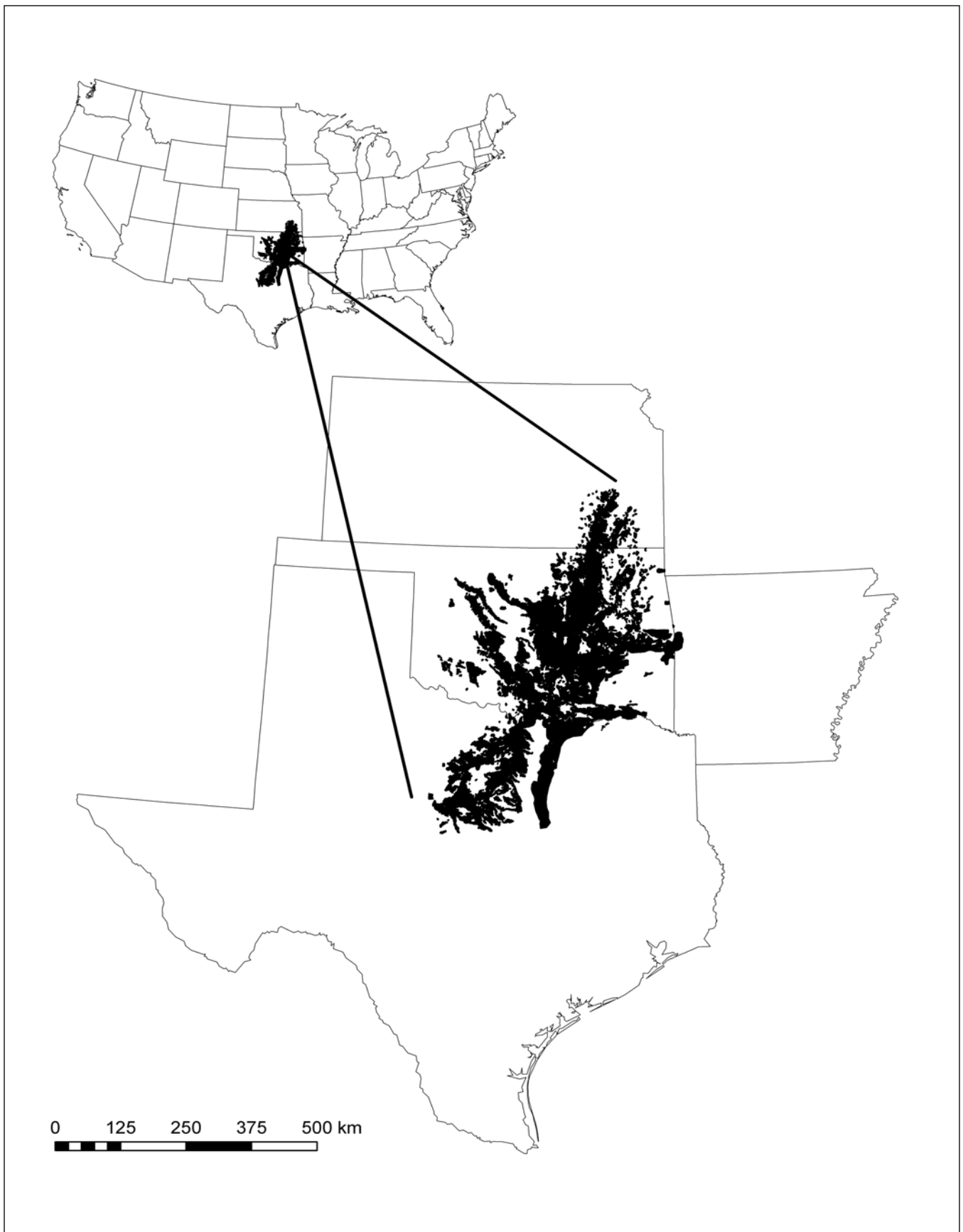


Figure 1.—Geographic extent of the Cross Timbers.

Encroachment by eastern redcedar due mainly to fire suppression has become one of the major threats to sustainable management in the region (Drake and Todd 2002). When eastern redcedar invades grasslands, it reduces plant species richness (Briggs and others 2002, Gehring and Bragg 1992, Linneman and Palmer 2006) and forage production for livestock and wildlife (Briggs and others 2002) and creates more dangerous fuel conditions for wildfire (Drake and Todd 2002). It seems likely eastern redcedar encroachment in the forest would have similar results, but research to confirm this assumption has not been done. There is strong interest in maintaining and restoring Cross Timbers forests to pre-Euro-American settlement (EAS) conditions, and prescribed fire is considered to be an important tool to achieve this objective. Unfortunately, there is relatively little research to provide guidance for prescribed burning of forests.

This paper presents the current knowledge of the role of fire in shaping the forest vegetation of the Cross Timbers. It describes an anthropogenic landscape where thousands of years of human fire created a vegetation type that is changing rapidly to more dense mesophytic forests due to fire suppression. This new trajectory cannot be altered without the reintroduction of fire and substantial mechanical reduction of woody vegetation. The success of Cross Timbers vegetation restoration will be measured by a return to and maintenance of the savanna, woodland, and open upland oak forests last observed at the beginning of Euro-American settlement.

PHYSICAL SETTING

Low elevation and low relief characterize the Cross Timbers Region. Elevation ranges from a low of approximately 150 m along the Red River to a high of 430 m in the Arbuckle Mountains and 755 m in the Wichita Mountains (Johnson 2006b). The rock outcrops are mainly horizontal or slightly dipping sandstones and shales of the Pennsylvanian, Permian, Cretaceous, and Tertiary age. Ridges are formed by the more resistant sandstones. Because most of the

surface rock is not very resistant to erosion, much of the area is low rolling hills and broad flat valleys, and the maximum relief rarely exceeds 180 m (Johnson 2006a).

The mean annual temperature decreases from 18 °C in the south to 13 °C in the north, and the mean annual rainfall increases from 600 mm in the west to 1010 mm in the east. Precipitation is well distributed throughout the year with a maximum in May. Wide swings in precipitation can result in severe droughts. The most remarkable recent droughts for the region occurred in the 1930s and 1950s. The summers are hot and the temperature can exceed 40 °C, and winters are generally mild, but when cold arctic air intrudes, the temperatures drop to -25 °C (Arndt 2011).

VEGETATION

The vegetation has undergone many changes during the Holocene. Pollen studies at a site near the east-central part of the Cross Timbers in Oklahoma suggested that as the climate changed following the last retreat of the glaciers, the initial vegetation was grassland that began to give way to oaks about 9000 years before present (YBP) (Bryant and Holloway 1985). For thousands of years the vegetation appeared to be oak savanna, and during mid postglacial times about 5000 YBP, the increase in oak dominance led to the development of oak woodlands. Pines arrived about 2100 YBP and an oak-hickory-pine forest finally developed approximately 1200 YBP, but pine never developed dominance and is restricted to isolated pockets and the eastern edge of the Cross Timbers forests. Charcoal was present indicating fire was an important disturbance force since at least 5000 YBP (Albert 1981).

Forest canopy vegetation is dominated by post oak and blackjack oak (*Quercus marilandica* Muenchh.) and subdominant species include black hickory (*Carya texana* Buckl.) and black oak (*Q. velutina* Lam.) (Ewing and others 1984, Rice and Penfound 1959). The overstory trees are small in stature; the

top of the canopy is usually between 12 and 14 m (Fig. 2). Closed stands can attain a basal area of 23 to 27 m²/ha with 1400 to 1800 trees/ha and an average stand diameter at breast height (d.b.h.) of 14 to 17 cm (Karki 2007). The understory shrubs include poison ivy (*Toxicodendron radicans* [L.] Kuntze), rough-leaf dogwood (*Cornus drummondii* Meyer), redbud (*Cercis canadensis* L.), and coralberry (*Symphoricarpos orbiculatus* Moench) (Ewing and others 1984). Common herbaceous plants in the forest understory and prairies include bluestems (*Schizachyrium scoparium* [Michx.] Nash and *Andropogon* spp. L.), Indiangrass (*Sorghastrum nutans* [L.] Nash), and rosette grasses (*Dichanthelium* spp. [Hitche. & Chase] Gould) (Ewing and others 1984, Tyrl and others 2002). The Cross Timbers ecotonal position contributes to its

high taxonomic diversity. A study of the The Nature Conservancy's Tallgrass Prairie Preserve found 763 species in 411 genera and 109 families (Palmer 2007). Over 1100 plant species were found at the Lyndon B. Johnson (LBJ) National Grasslands in north-central Texas (O'Kennon, pers. comm., Botanical Research Institute of Texas, 2009).

The dominant forces shaping the vegetation of the ecotone include soils, climate, and fire. The savannah and forest vegetation occur mostly on the coarse textured soils derived from sandstones or granites (Dwyer and Santelmann 1964, Rice and Penfound 1959). Grasslands occur predominantly on fine textured soil derived from shale and limestone. That means the climate is not a true grassland or



Figure 2.—Typical Oklahoma Cross Timbers forest in dormant season.

forest climate, because either vegetation type can be supported depending on the soil texture and its effects on water relations (Rice and Penfound 1959). The region-wide gradient of decreasing moisture from east to west is strongly manifested in the vegetation that decreases in stature and richness from east to west as the forests give way to savannas, and eventually to grasslands. Fire is a major force in shaping the vegetation mosaic.

FIRE

The potential vegetation of the region as mapped and defined by Küchler (1964) was assumed to support understory fires with a return interval of 0 to 10 years (Brown 2000). It is commonly held that fire suppression has effectively ended wildland fire as a force in shaping the ecosystems. However, recent evidence suggested fire suppression may not have been effective everywhere. Fire scar analysis found the mean fire interval (MFI) in some locations decreased after Euro-American Settlement (Allen and Palmer 2011, Clark and others 2007, DeSantis and others 2010b) or changed very little (Stambaugh and others 2009). This may indicate fire suppression has been spatially highly variable. It was shown for similar forest vegetation in Missouri that MFI declined soon after EAS because settlers learned to use fire for many of the same purposes as the Native Americans. MFI did not increase until there was a substantial increase in human population in the 20th century that brought an end to fire use and resulted in strong support for fire suppression to protect property (Guyette and others 2002). Perhaps variability in human population density

and land use across the Cross Timbers landscape has resulted in a patchwork of vegetation with very different MFIs.

Based on fire scar analysis of the dominant oaks that extends back to the early 18th century (Table 1), it seems likely most of the fires were human caused and occurred during the dormant season. From 80 to 97 percent of the fires were classified as occurring during the dormant season because the scars were located at the boundary between annual rings. A recent study determined the dormant season for cambial activity in post oak and blackjack oak was from mid-August to late March (Thapa, pers. comm., Oklahoma State University, 2010). This means scars during that period were caused by dormant season fires. Historical records of 418 dated fires in the Great Plains over the period 1535 to 1890 mentioned only one lightning fire. Lightning is abundant in the region, but most of it occurs with heavy rainfall which is not advantageous for igniting wildland fires. The most common reasons for Native Americans to set fires were for communication and warfare. In contrast, most fires started by settlers were accidental (Moore 1972). Approximately 60 percent of the fires occurred during the dormant season, mid-August to late March, and 40 percent were recorded during the growing season for the entire Great Plains and for the Cross Timbers Region. Another study of records of 590 fires in the Great Plains found 50 percent of the fires occurred in September and October, the dormant season (Gaskill 1906). These reports support the conclusion that although a substantial number of fires occurred during the growing season, slightly more than half of

Table 1.—Mean fire interval (MFI) and prevalence of dormant season fires for selected sites pre- and post-EAS (Euro-American settlement)

Location ¹	MFI (years)		Dormant season (percent)	Reference
	Pre-EAS	Post-EAS ²		
TGPP	3.4	1.3*	77	Allen and Palmer 2011
OWMA	4.0	2.0*	95	DeSantis and others 2010b
KAFP	4.9	2.1*	--	Clark and others 2005
WMWR	4.4	5.2	97	Stambaugh and others 2009

¹ TGPP = Tallgrass Prairie Preserve; OWMA = Okmulgee Wildlife Management Area; KAFP = Keystone Ancient Forest Preserve; and WMWR = Wichita Mountains Wildlife Refuge.

² * = Pre- and post-EAS MFI different at P=0.05.

fires occurred in the dormant season. There is some evidence that fires burn more frequently (Stambaugh and others 2009) or to a greater extent (Clark and others 2007) during periods of severe drought. But the link between fire frequency and extent and weather has not been established. Most often correlation analyses with drought indices show no relation to fire occurrence (Allen and Palmer 2011, Clark and others 2005, DeSantis and others 2010b, Stambaugh and others 2009).

STAND DEVELOPMENT

In addition to fire there are numerous natural disturbance forces acting on these forests including tornados, straight-line wind, drought, hail, and ice that kill or damage large branches, single trees, and small groups of trees (Clark 2003). Large-scale catastrophic disturbances are not common. Tornados, one of the few forces to create large disturbances, are rare (return interval ~2000 years [NOAA 2011]) relative to the lifespan of the major tree species (300 to 500 years [Therrell and Stahle 1998]). The fires typical of the region are low intensity, rarely kill individual trees >5 cm d.b.h. (Burton and others 2010), and are not stand replacing events. Although the canopy trees are considered to be relatively intolerant of shade, there is evidence of continuous replacement of canopy trees by growth of understory saplings into the canopy without gaps (Clark and others 2005, Karki 2007). There are also small gaps that facilitate growth of saplings into the canopy (Karki 2007). Research suggested gap-phase regeneration was the major type of canopy replacement in these xeric oak forests, as most trees had rapid growth from the pith indicating they started in a gap (Clark 2003).

Recent research found no evidence for change in overstory composition in Cross Timbers forests where gap-phase regeneration was occurring with frequent burning (Karki 2007). Although blackjack oak contributed a higher percentage of the gap makers than its proportion of the canopy, it and all the other species had replacement probabilities sufficient to

maintain their relative abundance in the canopy. In contrast, there was strong evidence for major changes in forest composition and density where fire had been suppressed. Remeasurement in the 2000s of plots first measured in the 1950s (Fig. 3) found basal area had doubled, oak dominance had declined, mesophytic and fire-intolerant species including eastern redcedar had increased, and tree species richness had increased (DeSantis and others 2010a). Dendrochronological studies showed a large increase in eastern redcedar recruitment beginning in the 1960s and declining oak recruitment in the 1970s (Fig. 4). There was strong evidence the combination of oak mortality from severe

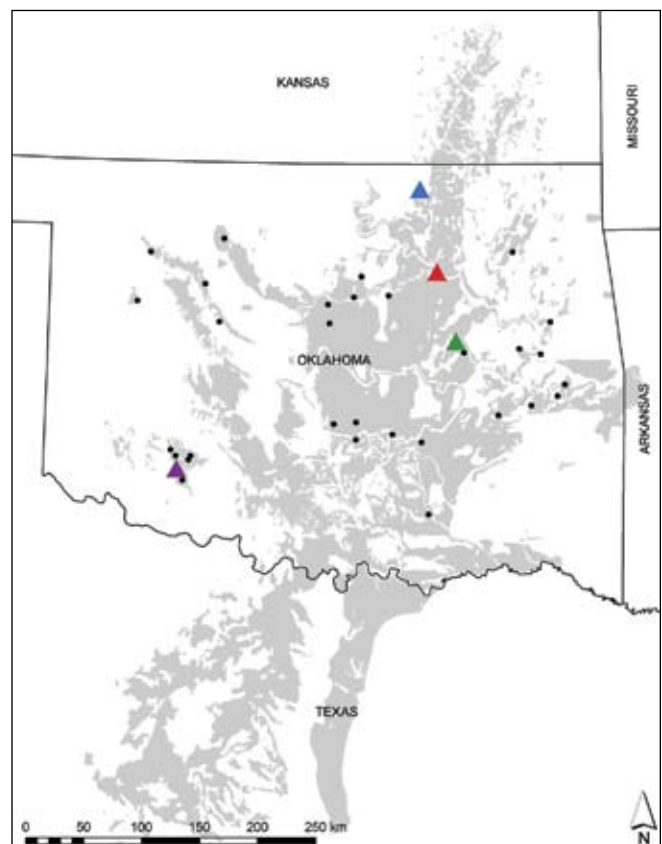


Figure 3.—Map of Cross Timbers with research sites. Black dots show locations of 30 forest stands measured by Rice and Penfound (1959) in the 1950s and again by DeSantis and others (2010a) in 2008 and 2009. Blue triangle = Tallgrass Prairie Preserve (Allen and Palmer 2011, Karki 2007); green triangle = Okmulgee Wildlife Management Area (Burton and others 2010, Burton and others 2011, DeSantis and Hallgren 2011, DeSantis and others 2010b, Karki 2007); red triangle = Keystone Ancient Forest Preserve (Clark and others 2005, Karki 2007); and purple triangle = Wichita Mountains National Wildlife Refuge (Stambaugh and others 2009). Adapted from Therrell and Stahle (1998).

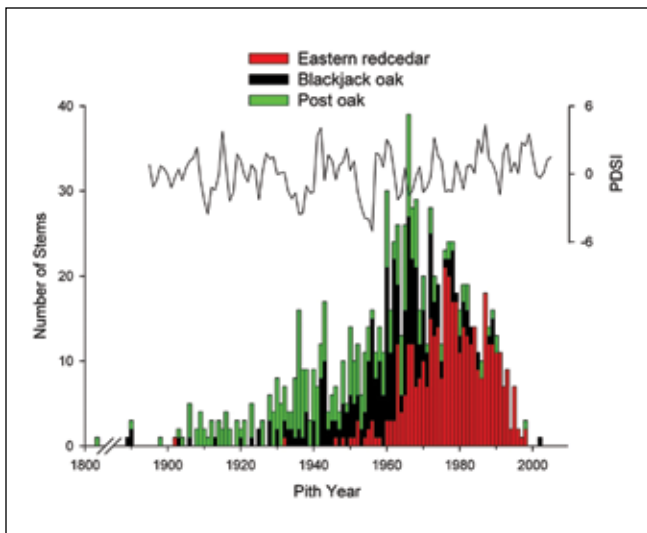


Figure 4.—Recruitment year for *Juniperus virginiana*, *Quercus marilandica*, and *Quercus stellata*, and instrumental Palmer Drought Severity Index (PDSI) in Cross Timbers forests of Oklahoma. Data represent sums of number of stems for three Oklahoma regions and average of regional PDSI (from DeSantis and others 2011).

droughts, mostly in the 1950s, and fire suppression were responsible for the changes (DeSantis and others 2011). The mortality of mainly blackjack oak from the 1950s drought (Rice and Penfound 1959) opened the stands for recruitment of new cohorts of forest tree regeneration. Fire suppression removed the control on eastern redcedar encroachment and ended the stimulation of oak sprouting. Eastern redcedar had always been a minor component in riparian zones and on ridges where fire burned infrequently. It is disseminated widely and effectively by birds (Holthuijzen and Sharik 1984, Holthuijzen and others 1986) and cannot tolerate fire when small (Engle and Stritzke 1995). It appeared suppression of fire may have contributed to eastern redcedar becoming widespread and may lead to its dominance in some forests.

Regeneration of the dominant oaks, post oak and blackjack oak, is highly adapted to fire. Although successful reproduction by seedlings is very rare (Backoulou 1998, Clark and Hallgren 2003, DeSantis and Hallgren 2011), both species sprout prolifically. A burn frequency of 1 in 10 years was found to produce the highest number of sprouts, up to 22,000 stems/

ha of both species combined. Mortality thinned the sprouts over time since the last burn. Apparently these oak species are capable of accumulating reproduction over time even without fire, as stands not burned for over 20 years were found to have sprout densities as high as 11,000 stems/ha. Although the average age of sprouts in nonburned stands was only 5.5 years and the height was only 40 cm, some of the sprouts were 20 years old (DeSantis and Hallgren 2011).

Regeneration in these post oak-blackjack oak forests can be characterized as auto-accumulating (Clark and Hallgren 2003, Johnson 1993). There can be four or more cohorts of reproduction that accumulate over at least 20 years. Most sprouts are from stumps and seedlings (d.b.h. <5 cm), and both species produce a substantial number of root sprouts (attachment to root >25 cm from proximal end). Post oak can produce 30 percent root sprouts, and blackjack oak around 20 percent (Clark and Hallgren 2003, DeSantis and Hallgren 2011). A recent study found high density sprouting 6 years after a fire where none of the reproduction dated before the fire, and many of the root systems of young plants were much older, up to 67 years. The height growth of both species is relatively slow due to low moisture and light in these closed xeric stands, attaining 6 to 10 cm per year over the first 6 years (Clark and Hallgren 2003, DeSantis and Hallgren 2011). This slow growth means the sprouts may not become large enough to resist even the low intensity burns until after many years.

Post oak and blackjack oak dominance of these forests is well documented. A study of Oklahoma's forests in the 1950s found them to be the most important species on a statewide basis by every ecological measure including presence, constance, frequency, density, and basal area (Rice and Penfound 1959). Species of secondary importance were black oak and black hickory in the eastern Cross Timbers. A remeasurement in the 2000s of 30 of the 208 original stands measured in the 1950s found post oak was still the most important canopy tree across the state, but blackjack oak had decreased in importance, and

the second most important species had changed to eastern redcedar in the west and central regions and black hickory in the east. The species shift was even greater in the saplings which reflect composition of the future canopy. The relative density of post oak and blackjack oak saplings dropped by nearly two-thirds across the Cross Timbers. The replacement species included eastern redcedar in the west and black hickory and winged elm (*Ulmus alata* Michx.) in the east (DeSantis and others 2010a).

PRESCRIBED FIRE

Taken together the vegetation type and climate suggest the Cross Timbers forests supported frequent low intensity fires pre-EAS. The fine fuels in the grasslands were easier to ignite than the oak leaf litter, so fires likely started there and burned into forests. When Native Americans were managing the landscape, fires occurred year-round. At present, there is very little information about fire effects on vegetation to help make decisions about prescribed fire. The most common type of prescribed fire is a low intensity dormant season burn (Fig. 5) (Weir 2011).

Prescribed fire both kills oak sprouts and stimulates sprouting. Although Cross Timbers forests produce abundant oak sprouts even without fire, infrequent prescribed burning (one fire per decade [FPD]) was found to increase the density of sprouts. Sprouts are susceptible to high mortality from burning, and because they are slow growing, it takes many years to become resistant to fires (DeSantis and Hallgren 2011). When oak sprouts grow above 1.4 m after 10 to 15 years, they begin to show resistance to burning, and trees >5 cm d.b.h. easily survive the low intensity dormant season fires commonly prescribed for Cross Timbers forests. In contrast, understory non-oak saplings and shrubs (>1.4 m tall and <5 cm d.b.h.) were strongly reduced by prescribed burning two or more times per decade, dropping from nearly 1,300 to 200 stems/ha (Fig. 6). Woody plant species richness was greatest when there were no burns in 20 years



Figure 5.—Low-intensity dormant season prescribed fire typical for Cross Timbers forests. Prescribed fire was set when relative humidity ranged from 30 to 50 percent, temperature was <27 °C, and winds were <25 kph. The forest was burned every 4 years.

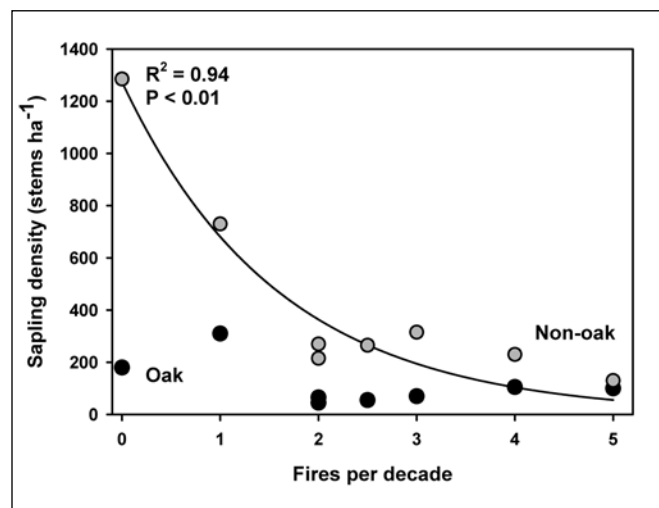


Figure 6.—Effect of fire frequency on sapling density of oak (*Quercus* spp.) and non-oak tree and shrub species (Burton and others 2010).

and dropped by 50 percent when fire frequency was increased to 5 FPD (12 vs. 6 species per treatment). Eventually, the small diameter non-oak saplings in the unburned stands may recruit into the larger size classes and change the overstory composition (Fig. 7). It appears that prescribed burning at two or more FPD may be effective in maintaining oak dominance in these stands (Burton and others 2010).

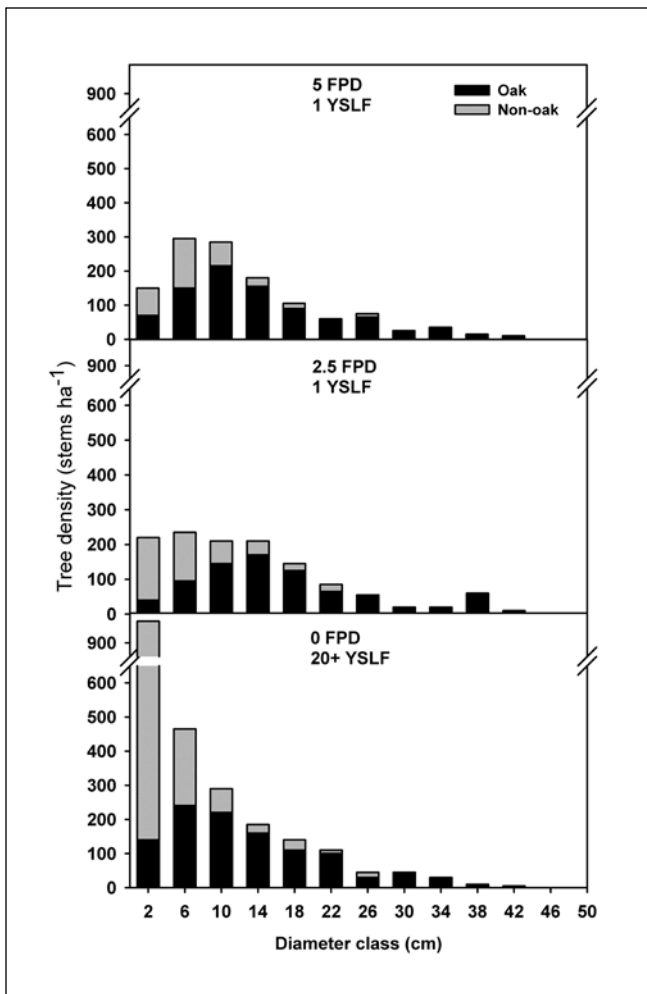


Figure 7.—Effect of fire frequency (fires per decade, FPD) and years since last fire (YSLF) on tree diameter distributions in terms of stems per ha by 4-cm diameter classes. Prescribed burning treatments were applied for 20 years (Burton and others 2010).

Despite the low light and strong competition for moisture and nutrients under the closed canopy of Cross Timbers forests, the herbaceous layer can be very responsive to prescribed burning (Fig. 8). This contrasts with the common belief that the understory herbaceous layer in oak forests will not respond to fire under a closed canopy (Franklin and others 2003, Harrington and Kathol 2009, Hutchinson and others 2005). In Cross Timbers forests with canopy closure of 88 to 96 percent, the understory <1.4 m tall was dominated by woody reproduction followed by forbs, C_3 graminoids, C_4 grasses, and legumes (Burton and others 2011). The cover of woody reproduction did not change with fire frequency, most likely due to its propensity to replace reproduction killed by fire with

more sprouts. Forb cover increased threefold and C_3 graminoid cover increased twofold over the range of 0 to 5 FPD. Both plant functional groups increased in richness over the same range of fire frequencies. Fire frequency did not affect the cover or richness of C_4 grasses likely due to the low light intensity under the full canopy. Biomass of combined C_4 and C_3 graminoids increased nearly fourfold from 0 to 5 FPD. The direct reduction in litter by burning may contribute to the increased herbaceous cover at high fire frequencies (Hiers and others 2007). In addition, the frequent fires reduced the density of non-oak shrubs and saplings thereby indirectly reducing litter production and reducing competition (Burton and others 2010).

RESTORATION OF CROSS TIMBERS VEGETATION

Research conducted nearly 40 years ago presented a likely scenario of changes in forest and savanna vegetation resulting from fire suppression in the Cross Timbers (Johnson and Risser 1975). The forest appeared to have been a savanna that had filled in with trees over 80 to 90 years to become a forest. Comparison of the size class distribution of trees in the forest with a contemporary savanna showed nearly identical numbers of trees in the large size classes and a much larger number of small trees in the forest. It appeared the small post oaks had recruited in the period 1910 to 1940 and the blackjack oaks in the period 1890 to 1920. As a consequence of recruitment of these two oak species, the basal area of the forest was double that of the savanna. These results were interpreted to show that when fire use ended and fire suppression began after EAS, oak encroachment changed the savanna to a forest.

The savanna can be kept open by fire because the high production of herbaceous fine fuels creates conditions for fires hot enough to reduce and kill woody plants (Johnson and Risser 1975). Once the savanna becomes a forest, the fuel type changes to tree leaf litter that produces a less intense fire, and the closed canopy



Figure 8.—Typical forests on the Okmulgee Wildlife Management Area, Oklahoma where prescribed burns have been conducted for over 20 years at the rate of 0, 1, 2.5, and 5 fires per decade (FPD).

prevents production of large quantities of fine fuels. As a consequence, fire intensity in the forest is too low to kill established trees, and fire alone cannot restore closed forest to open savanna. A likely force to thin forests to savanna density is severe drought, and the last century had two very severe droughts in the 1930s and 1950s; however, neither of these disrupted the conversion of savanna to forest. The severe drought of the 1950s, which was acknowledged to have killed many oaks (Rice and Penfound 1959), appeared to open the forest to encroachment by non-oak mesophytic and fire sensitive species because there was no fire to control their establishment and stimulate the oak sprouts (DeSantis and others 2011). The mortality suffered in the 1950s drought was more than

replaced over the next 50 years, and today these stands have twice the basal area they had then. The general belief is that without fire use in the Cross Timbers, woody encroachment will convert the grasslands to savannas, savannas to forests, and forests to denser and more diverse mesophytic forests.

Restoration of Cross Timbers vegetation to pre-EAS conditions will require treatments to reverse the encroachment of woody plants and increase grasslands and savannas and more open forests. Research has shown as few as two FPD can control the composition and structure of woody vegetation. When fire frequency is increased to five FPD, herbaceous plant diversity and grass biomass will strongly increase

even under a closed canopy (Burton and others 2010, Burton and others 2011). Although fire can maintain the open grassland, savanna, and woodland, it rarely kills established trees (Briggs and others 2005, Burton and others 2010, Engle and others 2006). Opening the forests and savannas will require treatments to first reduce tree density, and second to maintain the open condition long-term. Both mechanical removal plus frequent fire (Masters and others 1993) and chemical thinning plus frequent fire (Scifers and others 1981, Stritzke and others 1991) have been successful at reducing overstory tree density and stimulating herbaceous biomass production. Although the dormant season is the most common time for prescribed burning in the region (Weir 2011), research has shown growing season burning may be more effective in controlling woody plants which may be more susceptible to damage when actively growing (Engle and others 1996, Waldrop and others 1992).

The pre-EAS Cross Timbers region was an anthropogenic landscape with more grasslands, savannas, and open forests than found today. Restoring the current vegetation to that condition will require treatments to remove woody vegetation and prescribed fire to prevent its return. Successful restoration will result in an oak dominated forest with only a minor component of eastern redcedar and mesophytic tree species. The woody vegetation will be less diverse, and herbaceous vegetation will be more diverse and abundant. Further research is warranted to increase the understanding of the most effective tools for Cross Timbers forest restoration and to gain the confidence of land managers in their use. The knowledge of mechanical and chemical control of woody plants needs to be increased. The current understanding of effects of prescribed burning is based almost entirely on research with low intensity dormant season fire in rangelands. The effects of growing season prescribed burning are poorly understood, and managers are

reticent to employ it. Research on growing season prescribed burning has the potential to greatly increase the capability to restore Cross Timbers vegetation because its use will expand the window for prescribed burning and contribute to better control of woody plants (Weir 2011).

The woody encroachment of Cross Timbers plant communities over the past 100 years has changed more than the vegetation. Carbon storage, hydrologic cycles, biogeochemical cycles, and wildlife populations have also changed. Restoring the current landscape to pre-EAS vegetation may reverse these changes, and there is very little understanding of the consequences. Vegetation type and land use can have large effects on carbon storage. Forest lands can have much larger stocks of biomass carbon than grasslands, whereas grasslands can have larger stocks of soil organic carbon (SOC) (Jackson and others 2002, Post and Kwon 2000). Not only do grasslands allocate more net primary production (NPP) below ground, the distribution of carbon to the soil recalcitrant pools can be much higher in grasslands. The hydrologic and biogeochemical cycles are strongly affected by the type and density of vegetation (Huxman and others 2005, Wilcox and others 2006, Zhang and others 2001). Some wildlife benefit from the denser woody vegetation of a landscape without fire while others favor the vegetation produced by frequent fire, and landscape level species richness may be greatest where there is a patchwork of fire regimes (Engle and others 2008, Fuhlendorf and others 2006, Fuhlendorf and others 2009, Leslie and others 1996). Restoring the Cross Timbers to pre-EAS vegetation will require substantial efforts and major changes in land use. Intelligent and sustainable management of the Cross Timbers cannot be attained without more complete understanding of factors and forces controlling all its component resources and ecosystem services.

ACKNOWLEDGMENTS

The authors' research of the ancient Cross Timbers forests was inspired and encouraged by David Stahle, Distinguished Professor and Director, Tree-Ring Laboratory, University of Arkansas. Financial support was provided by the Oklahoma State University Department of Natural Resource Ecology & Management and the Oklahoma State University Cooperative Extension Service and Agricultural Experiment Station through a Division of Agricultural Sciences and Natural Resources Team Initiative Project grant and Centennial Scholarship. In addition, funding was provided by the Federal Aid Pittman-Robertson Wildlife Restoration Act under Project W-160-R of the Oklahoma Department of Wildlife Conservation and Oklahoma State University. The project was administered through the Oklahoma Cooperative Fish and Wildlife Research Unit (Oklahoma Department of Wildlife Conservation, Oklahoma State University, United States Geological Survey, United States Fish and Wildlife Service, and Wildlife Management Institute).

LITERATURE CITED

- Albert, L.E. 1981. **Ferndale Bog and Natural Lake: five thousand years of environmental change in southeastern Oklahoma.** Studies in Oklahoma's Past Number 7. Norman, OK: University of Oklahoma Archaeological Survey. 127 p.
- Allen, M.S.; Palmer, M.W. 2011. **Fire history of a prairie/forest boundary: more than 250 years of frequent fire in a North American tallgrass prairie.** Journal of Vegetation Science. 22: 436-444.
- Arndt, D. 2011. **Oklahoma's climate: an overview.** Oklahoma Climatological Survey. Available at: http://climate.mesonet.org/county_climate/Products/oklahoma_climate_overview.pdf.
- Backoulou, G. 1998. **Oak regeneration of the Cross-Timbers of Oklahoma.** Stillwater, OK: Oklahoma State University. 46 p. M.S. thesis.
- Briggs, J.M.; Hoch, G.A.; Johnson, L.C. 2002. **Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest.** Ecosystems. 5: 578-586.
- Briggs, J.M.; Knapp, A.K.; Blair, J.M.; Heisler, J.L.; Hoch, G.A.; Lett, M.S. 2005. **An ecosystem in transition: causes and consequences of the conversion of mesic grassland to shrubland.** BioScience. 55(3): 243-254.
- Brown, J.K. 2000. **Introduction to fire regimes.** In: Brown, J.K.; Smith, J.K., eds. Wildland fire in ecosystems: effects of fire on flora. Gen. Tech. Rep. RMRS-42, vol. 2. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 1-7.
- Bryant, V.M., Jr.; Holloway, R.G. 1985. **A late-Quaternary paleoenvironmental record of Texas: an overview of the pollen evidence.** In: Bryant, V.M., Jr.; Holloway, R., eds. Pollen records of Late-Quaternary North American settlements. Dallas, TX: American Association of Stratigraphic Palynologists: 39-70.
- Burton, J.A.; Hallgren, S.W.; Fuhlendorf, S.D.; Leslie, D.M., Jr. 2011. **Understory response to varying fire frequencies after 20 years of prescribed burning in an upland oak forest.** Plant Ecology. 212: 1513-1525.
- Burton, J.A.; Hallgren, S.W.; Palmer, M.W. 2010. **Fire frequency affects structure and composition of xeric forests of eastern Oklahoma.** Natural Areas Journal. 30: 370-379.
- Clark, S. 2003. **Stand dynamics of an old-growth forest in the Cross Timbers of Oklahoma.** Stillwater, OK: Oklahoma State University. 193 p. Ph.D. dissertation.
- Clark, S.L.; Hallgren, S.W. 2003. **Dynamics of oak (*Quercus marilandica* and *Q. stellata*) reproduction in an old-growth Cross Timbers forest.** Southeastern Naturalist. 2: 559-574.

- Clark, S.L.; Hallgren, S.W.; Engle, D.M.; Stahle, D.W. 2007. **The historic fire regime on the edge of the prairie: a case study from the Cross Timbers of Oklahoma.** In: Masters, R.E.; Galley, K.E.M., eds. Proceedings of the 23rd Tall Timbers fire ecology conference: fire in grassland and shrubland ecosystems. Tallahassee, FL: Tall Timbers Research Station: 40-49.
- Clark, S.; Hallgren, S.W.; Lynch, T.B.; Stahle, D.W. 2005. **Characteristics of the Keystone Ancient Forest Preserve, an old-growth forest in the Cross Timbers of Oklahoma.** Natural Areas Journal. 25: 165-175.
- DeSantis, R.D.; Hallgren, S.W. 2011. **Prescribed burning frequency affects post oak and blackjack oak regeneration.** Southern Journal of Applied Forestry. 35: 193-198.
- DeSantis, R.D.; Hallgren, S.W.; Lynch, T.B.; Burton, J.A.; Palmer, M.W. 2010a. **Long-term directional changes in upland *Quercus* forests throughout Oklahoma, USA.** Journal of Vegetation Science. 21: 606-615.
- DeSantis, R.D.; Hallgren, S.W.; Stahle, D.W. 2010b. **Fire regime of an upland oak forest in south-central North America.** Fire Ecology. 6: 45-61.
- DeSantis, R.D.; Hallgren, S.W.; Stahle, D.W. 2011. **Drought and fire suppression lead to rapid forest composition change in a forest-prairie ecotone.** Forest Ecology and Management. 261: 1833-1840.
- Drake, B.; Todd, P. 2002. **A strategy for control and utilization of invasive juniper species in Oklahoma.** Oklahoma City, OK: Oklahoma Department of Agriculture, Food and Forestry. 57 p.
- Dwyer, D.D.; Santelmann, P.W. 1964. **A comparison of post oak-blackjack oak communities on two major soil types in North Central Oklahoma.** B-626. Stillwater, OK: Oklahoma Agricultural Experiment Station. 15 p.
- Engle, D.M.; Bidwell, T.G.; Masters, R.E. 1996. **Restoring Cross Timbers ecosystems with fire.** Transactions of the 61st North American Wildlife and Natural Resources Conference. 61: 190-199.
- Engle, D.M.; Bodine, T.N.; Stritzke, J.F. 2006. **Woody plant community in the Cross Timbers over two decades of brush treatments.** Rangeland Ecology and Management. 59: 153-162.
- Engle, D.M.; Fuhlendorf, S.D.; Roper, A.; Leslie, D.M., Jr. 2008. **Invertebrate community response to a shifting mosaic of habitat.** Rangeland Ecology and Management. 61: 55-62.
- Engle, D.M.; Stritzke, J.F. 1995. **Fire behavior and fire effects on eastern redcedar in hardwood leaf litter fires.** International Journal of Wildland Fire. 5: 135-141.
- Ewing, A.L.; Stritzke, J.F.; Kulbeth, J.D. 1984. **Vegetation of the Cross Timbers Experimental Range, Payne County, Oklahoma.** Res. Rep. P-856. Stillwater, OK: Oklahoma Agricultural Experiment Station. 40 p.
- Franklin, S.B.; Robertson, P.A.; Fralish, J.S. 2003. **Prescribed burning effects on upland *Quercus* forest structure and function.** Forest Ecology and Management. 184: 315-335.
- Fuhlendorf, S.D.; Engle, D.M.; Kerby, J.; Hamilton, R. 2009. **Pyric-herbivory: re-wilding landscapes through re-coupling fire and grazing.** Conservation Biology. 23: 588-598.
- Fuhlendorf, S.D.; Harrell, W.C.; Engle, D.M.; Hamilton, R.G.; Davis, C.A.; Leslie, D.M., Jr. 2006. **Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing.** Ecological Applications. 16: 1706-1716.
- Gaskill, A. 1906. **Why prairies are treeless.** Proceedings of the Society of American Foresters. 1: 158-178.

- Gehring, J.L.; Bragg, T.B. 1992. **Changes in prairie vegetation under eastern redcedar (*Juniperus virginiana* L.) in an eastern Nebraska bluestem prairie.** American Midland Naturalist. 128: 209-217.
- Guyette, R.P.; Muzika, R.M.; Dey, D.C. 2002. **Dynamics of an anthropogenic fire regime.** Ecosystems. 5: 472-486.
- Harrington, G.W.; Kathol, E. 2009. **Responses of shrub midstory and herbaceous layers to managed grazing and fire in a North American savanna (oak woodland) and prairie landscape.** Restoration Ecology. 17: 234-244.
- Hiers, J.K.; O'Brien, J.J.; Will, R.E.; Mitchell, R.J. 2007. **Forest floor depth mediates understory vigor in xeric *Pinus palustris* ecosystems.** Ecological Applications. 17: 806-814.
- Holthuijzen, A.M.A.; Sharik, T.L. 1984. **Seed longevity and mechanisms of regeneration of eastern redcedar (*Juniperus virginiana*).** Bulletin of the Torrey Botanical Club. 111: 153-158.
- Holthuijzen, A.M.A.; Sharik, T.L.; Frazer, J.D. 1986. **Dispersal of eastern redcedar (*Juniperus virginiana*) into pastures: an overview.** Canadian Journal of Botany. 65: 1092-1095.
- Hutchinson, T.F.; Sutherland, E.K.; Yaussy, D.A. 2005. **Effects of repeated prescribed fires on the structure, composition, and regeneration of mixed-oak forests in Ohio.** Forest Ecology and Management. 218: 210-228.
- Huxman, T.E.; Wilcox, B.P.; Breshears, D.D.; Scott, R.L.; Snyder, K.L.; Small, E.E.; Hultine, K.; Pockman, W.T.; Jackson, R.B. 2005. **Ecophysiological implications of woody plant encroachment.** Ecology. 86: 308-319.
- Jackson, R.B.; Banner, J.L.; Jobbagy, E.G.; Pockman, W.T.; Wall, D.H. 2002. **Ecosystem carbon loss with woody plant invasion of grasslands.** Nature. 418: 623-626.
- Johnson, F.L.; Risser, P.G. 1975. **A quantitative comparison between an oak forest and an oak savanna in central Oklahoma.** Southwestern Naturalist. 20: 75-84.
- Johnson, K.S. 2006a. **Geomorphic provinces.** In: Goins, C.R.; Goble, D., eds. Historical atlas of Oklahoma. Norman, OK: University of Oklahoma Press: 4-5.
- Johnson, K.S. 2006b. **Topography and principal landforms.** In: Goins, C.R.; Goble, D., eds. Historical atlas of Oklahoma. Norman, OK: University of Oklahoma Press: 6-7.
- Johnson, P.S. 1993. **Perspectives on the ecology and silviculture of oak-dominated forests in the central and eastern states.** Gen. Tech. Rep. NC-153. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 34 p.
- Karki, L. 2007. **Tree fall gap dynamics in the Cross Timbers of Oklahoma.** Stillwater, OK: Oklahoma State University. 67 p. M.S. thesis.
- Küchler, A.W. 1964. **Potential natural vegetation of the conterminous United States: a map and manual.** Special Publication No. 36. New York: American Geographical Society. 116 p.
- Leslie, D.M., Jr.; Soper, R.B.; Lochmiller, R.L.; Engle, D.M. 1996. **Habitat use by white-tailed deer on Cross Timbers Rangeland following brush management.** Journal of Range Management. 49: 401-406.
- Linneman, J.S.; Palmer, M.W. 2006. **The effect of *Juniperus virginiana* on plant species composition in an Oklahoma grassland.** Community Ecology. 7: 235-244.
- Masters, R.E.; Lochmiller, R.L.; Engle, D.M. 1993. **Effects of timber harvest and prescribed fire on white-tailed deer forage production.** Wildlife Society Bulletin. 21: 401-411.

- Moore, C.T. 1972. **Man and fire in the central North American grassland 1535-1890: a documentary historical geography.** Los Angeles, CA: University of California, Los Angeles. 155 p. Ph.D. dissertation.
- NOAA. 2011. **National Weather Service storm prediction center, online severe weather climatology.** Available at <http://www.spc.noaa.gov/climo/online/rda/INX.html>. [Date accessed unknown].
- Palmer, M.W. 2007. **Vascular flora of the Tallgrass Prairie Preserve, Osage County, Oklahoma.** *Castanea*. 72: 235-246.
- Post, W.M.; Kwon, K.C. 2000. **Soil carbon sequestration and land-use change: processes and potential.** *Global Change Biology*. 6: 317-327.
- Rice, E.L.; Penfound, W.T. 1959. **The upland forests of Oklahoma.** *Ecology*. 40: 593-608.
- Scifres, C.J.; Stuth, J.W.; Bovey, R.W. 1981. **Control of oaks (*Quercus* spp.) and associated woody species on rangeland with tebuthiuron.** *Weed Science*. 29: 270-275.
- Stallings, C.V. 2008. **Analysis of land use, land cover change in the upland forests of Oklahoma: a comparison between the 1950s and 2000s.** Stillwater, OK: Oklahoma State University. 86 p. M.S. thesis.
- Stambaugh, M.C.; Guyette, R.P.; Godfrey, R.; McMurry, E.R.; Marschall, J.M. 2009. **Fire, drought, and human history near the western terminus of the Cross Timbers, Wichita Mountains, Oklahoma.** *Fire Ecology*. 5: 63-77.
- Stritzke, J.F.; Engle, D.M.; McCollum, F.T. 1991. **Vegetation management in the Cross Timbers: response of woody species to herbicides and burning.** *Weed Technology*. 5: 400-405.
- Texas Forest Service. 2008. **Texas statewide assessment of forest resources. A comprehensive analysis of forest-related conditions, trends, threats and opportunities.** College Station, TX: Texas Forest Service. 159 p.
- Therrell, M.D.; Stahle, D.W. 1998. **A predictive model to locate ancient forests in the Cross Timbers of Osage County, Oklahoma.** *Journal of Biogeography*. 25: 847-854.
- Tyrl, R.J.; Bidwell, T.G.; Masters, R.E. 2002. **Field guide to Oklahoma plants.** Stillwater, OK: Oklahoma State University. 515 p.
- Waldrop, T.A.; White, D.L.; Jones, S.M. 1992. **Fire regimes for pine-grassland communities in the southeastern United States.** *Forest Ecology and Management*. 47: 195-210.
- Weir, J.R. 2011. **Are weather and tradition reducing our ability to conduct prescribed burns?** *Rangelands*. 33: 25-30.
- Wilcox, B.P.; Owens, M.K.; Dugas, W.A.; Ueckert, D.N.; Hart, C.R. 2006. **Shrubs, streamflow, and the paradox of scale.** *Hydrological Processes*. 20: 3245-3259.
- Zhang, L.; Dawes, W.R.; Walker, G.R. 2001. **Response of mean annual evapotranspiration to vegetation changes at catchment scale.** *Water Resources Research*. 37(3): 701-708.

The content of this paper reflects the views of the author(s), who are responsible for the facts and accuracy of the information presented herein.