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RESEARCH ARTICLE

Fire Frequency Affects Structure and Composition of Xeric Forests of Eastern Oklahoma

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ABSTRACT: Since European settlement, changes in the fire regime of eastern deciduous forests of North America have led to changes in biological diversity and stand structure. These changes may be attenuated in xeric forests at the western limit of the eastern deciduous forest where woody plant species richness is low, and dominance high, due to the rigorous biotic and physical environment. Effects of fire frequency on woody plant species richness and stand structure were studied in a xeric, oak-dominated (*Quercus* spp.) old-growth forest in eastern Oklahoma where prescribed burning had been conducted over 20 years at frequencies ranging from zero to five fires per decade. Regeneration (stem height < 1.4 m) cover was not affected by fire frequency. Increasing fire frequency had a strong negative effect on species richness of saplings and shrubs (stem dbh < 5 cm) but no significant effect on small tree (stems 5 cm < dbh < 10 cm) and large tree (stems dbh > 10 cm) species richness. While oak sapling density was not affected by fire frequency, the density of non-oak saplings and shrubs was very high at zero and one fire per decade and strongly reduced by fire frequencies of two or more per decade. Although 20 years of treatment may not have been sufficient to show fire frequency effects on canopy trees, the effect on species composition of saplings was strong and may have long-term consequences for forest canopy composition. These results suggest that, without at least two fires per decade, tree species richness of these forests will increase and oak dominance will diminish.

Index terms: forest dynamics, mesophication, Oklahoma, prescribed fire, *Quercus stellata*

INTRODUCTION

The vegetation of the south-central United States, locally called the Cross Timbers, is characterized as a mosaic of tallgrass prairie, oak woodland, and oak forest covering almost five million ha from southeastern Kansas across Oklahoma to north-central Texas (Bruner 1931; Dyksterhuis 1948; Rice and Penfound 1959; Kuchler 1964; Therrell and Stahle 1998). It is a zone of transition where eastern forest and western prairie species meet at the limits of their natural ranges under conditions of physical and biotic stress (Curtis 1959; Weaver 1968; Fralish 2002; Williams et al. 2009). The resulting communities are determined by the interactions of fire, grazing, climate, soil, and plant adaptations (Abrams 1986, 1992; Bond et al. 2005).

The Cross Timbers and adjacent xeric eastern forests, dominated by post oak (*Quercus stellata* Wangehn.) and blackjack oak (*Quercus marilandica* Münchh.), are considered to be relatively species-poor due to the rigorous physical environment and strong dominance of these two species (Rice and Penfound 1959; Risser and Rice 1971; Dooley and Collins 1984). The fire frequency for hardwood forests in this region was one to five fires per decade prior to European settlement (Cutter and Guyette 1994; Brown and Smith 2000; Stambaugh and Guyette 2006; Clark et al. 2007) and most fires occurred in the dormant season (ca. 97% according to Stambaugh et al. 2009). This high frequency of fire was likely anthropogenic in origin, used by aboriginal people to increase desired plant species for food or game (Guyette and Cutter 1991; Pyne 1997; Guyette et al. 2002; Stambaugh et al. 2009). In the last century, land development and industrialization have often led to the removal of fire from the landscape (Pyne 1996, 1997), leading to large changes in species composition and stand density (Rice and Penfound 1959; Johnson and Risser 1975; Abrams 1986; Chapman et al. 2006; DeSantis et al. 2010). Because these fire-suppressed forest communities are subject to invasive species, reduced biological diversity, and more damaging fires due to fuel buildup, there is strong interest in reintroducing fire to the landscape to reverse these trends. Unfortunately, there is little information to guide application of prescribed fire to a landscape that has been under an altered fire regime since European settlement.

The overall goal of this study was to provide new knowledge about the effects of fire on forest composition and structure in the forest-prairie transition zone with focus on the eastern hardwood forests of Oklahoma. Specifically, we sought to determine the effects of fire frequency on forest stand structure and woody plant species richness. We measured the effects of over 20 years of prescribed fire of different frequencies on tree and shrub species composition and structure.

METHODS

Study Area

The study was conducted on the Okmulgee Game Management Area (OGMA), a portion of the Okmulgee Wildlife Management Area, managed by the Oklahoma Department of Wildlife Conservation. The 2400 ha OGMA is located approximately 55 km south of Tulsa, Oklahoma. The climate is humid subtropical with a mean annual temperature of 16.1 °C and mean daytime highs of 33.9 °C in July to mean lows of -3.9 °C in January. The area receives approximately 111 cm of precipitation annually; however, precipitation can be highly variable with a range of 54.5 cm to 156.2 cm (Oklahoma Climatological Survey 2005).

The study was limited to sites on the Hector-Endsaw complex soil (Lithic Dystrudept), which represented approximately 75% of the OGMA. This soil type was characterized as well-drained, non-arable, shallow stony fine sandy loam with bedrock at a depth of about 30 cm on hill or mountain topography of 5% to 30% slopes (Sparwasser et al. 1968).

The OGMA is on the western limit of the Central Hardwood Forest ecoregion (Fralish 2002). It is primarily forested and classified as the *Quercus stellata* – *Quercus marilandica* type (Duck and Fletcher 1945), locally referred to as the Cross Timbers forest. The U.S. Department of Agriculture Major Land Resource Areas (MLRA) has classified this forest as the East and Central Farming and Forest Region, Arkansas Valley and Ridges N-118B (USDA, NRCS 2006). Historically, the topography and soil type of the upland sites in the OGMA limited the conversion of the forest to agriculture, leaving much of the oak forest relatively undisturbed. The Okmulgee Wildlife Management Area may contain one of the largest continuous tracts of protected old-growth Cross Timbers forests remaining (Stahle 2007). The growth rates of upland oak species are low on upland xeric sites; however, large individuals of *Q. stellata* are not uncommon throughout the management area. The location of this site on the western periphery of the Central Hardwood Forest allowed for a unique opportunity to study the effects of fire in an oak forest landscape where extremes of drought and temperature are common.

The OGMA has been subjected to prescribed fire since the late 1980s. There was no record of fire occurrence prior to the beginning of prescribed fire, although wildfires may have burned some parts of the OGMA. The OGMA was divided into units ranging from approximately 100 to 600 ha, and each unit was burned on its own schedule. Some wildfires occurred during this period and were included in the count, contributing to a range of fire frequencies from zero to five fires per decade. All wild and prescribed fires occurred in February and March and were carefully documented (Table 1). Prescribed fires were set when relative humidity ranged from 30% to 50%, temperature was < 27 °C, and winds were < 25 kph, conditions considered ideal by managers for prescribed fire containment (Weir 2009). All fires were low-intensity surface fires.

Sampling Design

Eight treatment units were selected for study based primarily on their breadth of fire frequencies. Twenty 100 m^2 plots were randomly located within each unit using the random point tool in ArcCatalog (ESRI 2007; Figure 1). Plots within 10 m of clearings, including roads, rights-of-way, firebreaks, and wildlife food plots, were excluded. We used a Trimble (Sunnyvale, CA) Geo XT GPS unit with the Wide Area Augmentation System (WAAS) for sub-meter accuracy to locate each of the plots. Once a plot point was located, one of four compass directions, southwest, southeast, northwest, or northeast, was selected at random for orientation of the square plot, and the four sides of the plot were laid out with a compass in the cardinal directions. Within each 100-m^2 plot, we measured the diameter of all woody plant stems at breast height (dbh at 1.4 m above ground). Large trees were ≥ 10 cm dbh, small trees were ≥ 5 cm and < 10 cm dbh, and saplings and shrubs were < 5 cm dbh and > 1.4 m tall. We distinguished tree species from shrub species by defining trees as capable of obtaining canopy height of 10 m and dbh of 5 cm (Little 2002). Regeneration cover (tree and shrub seedlings and sprouts < 1.4 m tall) was visually estimated by species in four 1-m^2 sub-plots nested within each corner of the 100-m^2 plots using the Braun-Blanquet cover scale (Kent and Coker 1992). Nomenclature for woody plant species follows USDA, NRCS (2010).

Data Analysis

The experimental unit for analysis was the burn unit. Stem density and basal area (m^2 ha^{-1}) were calculated by species for each of the 100 m^2 plots which were used as observations for analysis. All statistical tests were conducted on burn unit mean values. Regression analysis was used to determine the relation of seedling and sprout cover, basal area of trees, and density of saplings, small, and large trees to fire frequency and time since last fire using SPSS Statistics (SPSS 2008). Only treatments experiencing fire were included in time since last fire analysis resulting in a limited range of zero to three years since last fire ($n = 7$). Regeneration cover values from nested sub-plots were square-root transformed prior to analysis. In order to summarize and illustrate community variation, we conducted principal components analysis (PCA) on each of these three classifications of square-root transformed woody stem densities in CANOCO version 4.5 (ter Braak and Šmilauer 2002; Lepš and Šmilauer 2003). All statistical tests were conducted at $P \leq 0.05$.

RESULTS

Regeneration

We tallied 22 tree and nine shrub species as woody plant regeneration and, with the exception of two species, neither fire frequency nor time since last fire showed a measurable effect on species presence/absence or foliar cover (Table 2). *Crataegus crus-gali* L. and *Quercus rubra* L. increased in cover with increased fire frequency. Total woody plant regeneration cover ranged

Table 1. Year and month of prescribed fires by burn units, Okmulgee Game Management Area, Okmulgee, Oklahoma.

	Burn Unit							
Year	1	2	3	4	6	7	10	13
2008				Mar	Mar			
2007	Feb	Feb						
2006								
2005			Feb	Feb		Feb	Mar	
2004		Mar		Mar				
2003	Mar						Mar	
2002				Feb	Feb			
2001	Mar			Feb			Mar	
2000	Feb	Feb	Mar					
1999	Feb							
1998	Feb							
1997	Feb		Feb		Feb			
1996						Feb	Feb	
1995	Feb							
1994		Mar		Mar			Mar	
1993	Mar				Mar			
1992		Feb		Feb			Feb	
1991			Feb					
1990								
1989	Feb							
1988								
Fires	10	5	4	7	4	2	6	0
per Decade	5.0	2.5	2.0	3.5	2.0	1.0	3.0	0.0
Since Last	1	1	3	0	0	3	3	20+

from 30% to 49% and was not affected by fire frequency, but increased with time since last fire ($r^2 = 0.679$, $P = 0.023$). Mean plot species richness of woody regeneration ranged from 5.2 to 7.1 species and was not related to fire frequency or time since last fire ($P > 0.10$).

Saplings and Shrubs

Twenty tree and four shrub species occurred in the sapling and shrub size classes, respectively (Table 2). Only two species showed an effect of fire frequency or time since last fire on stem density: *Rhus glabra* L. density increased with time since last fire; and *Vaccinium arboreum* Marsh. density decreased with increased fire frequency. Total sapling and shrub density varied greatly, ranging from 1465 stems ha^{-1} in the non-burned forest to 230 stems ha^{-1} in the forest that was burned five times per decade. While fire frequency had a strong negative influence on sapling and shrub density, there was no effect of time since last fire ($P > 0.10$). Oak sapling density ranged from 310 to 45 stems ha^{-1} with no clear relationship to fire frequency; however, non-oak species had a strong negative response to fire frequency (Figure 2). Plot and treatment richness of saplings and shrubs both decreased with increased fire frequency (Figure 3).

The shrub and sapling tree species strongly associated with low fire frequencies included *Vaccinium arboreum*, *Ulmus alata* Michx., *Prunus mexicana* Wats., and *Carya texana* Buckl. (Figure 4). Axis 1 of the PCA generally reflected the fire frequency of the treatment units and explained 55.2% of the variability in species data. Sample scores for treatments with fires more frequent than one per decade were clustered closely on the first axis, suggesting that the species composition of saplings in these treatments may not be strongly affected by fire frequencies within this range.

Trees

Eleven species occurred in the large-tree stratum and 10 species in the small-tree stratum across burn units (Table 2). *Quercus stellata* was strongly dominant (71% of total basal area), followed by the co-dominant *Q. marilandica* and *Carya texana* (9% and 8% of total basal area, respectively). Large and small tree densities showed no relation to fire frequency (Figure 3). Tree species richness was not related to fire frequency at both the plot and treatment level. Ordination by PCA did not show a particular pattern in the placement of species or treatment units by fire frequency (data not shown).

Stand Structure

Stand-level diameter distributions including all tree species suggested a strong effect of fire frequency (Figure 5). Diameter distributions reflected a reverse-J shape curve for zero and one fire per decade; the smallest diameter class, 2 cm, had the largest number of stems per ha and as diameter class increased, stem density dropped sharply at first and more slowly later. At two or more fires per decade, stem density in the smallest diameter class decreased by 70% to 90% from that found at zero and one fire per decade; thus, the diameter distribution was no longer a reverse-J shape curve. Stem density of trees tended to be greater in the 6-cm diameter class for most fire frequencies of two or more fires per

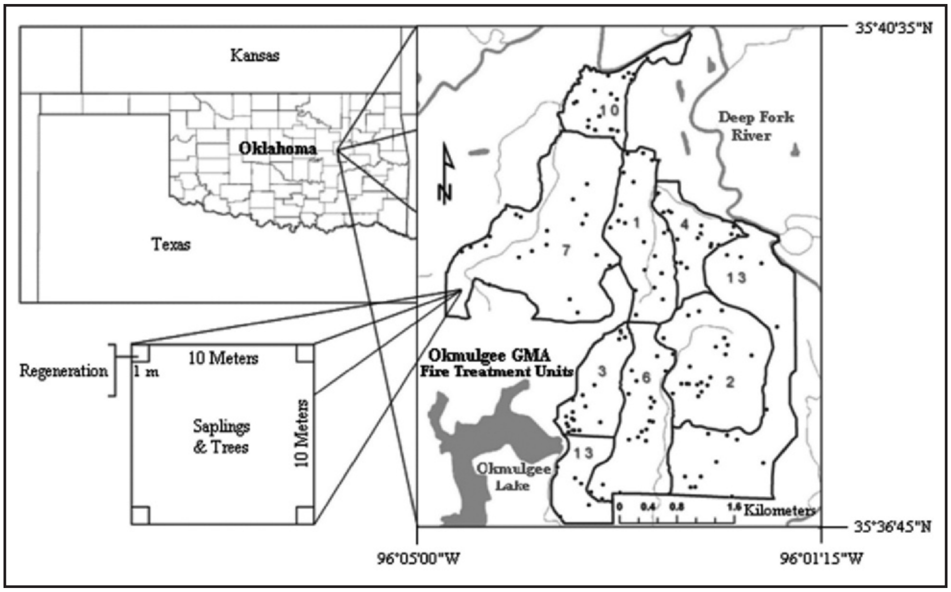

Figure 1. Location of the Okmulgee Game Management Area, Okmulgee, Oklahoma, and 20 sample plots within each of eight treatment units.

decade. In contrast, the diameter distributions for oak species were not strongly affected by fire frequency; they lacked a reverse-J shape curve and maximum stem density occurred between the 10 to 18 cm diameter classes.

DISCUSSION

The major finding of our study was the profound effect of infrequent low-intensity fires on species composition and stand structure of xeric forests in the transition zone between the southern Great Plains and the Central Hardwood Forest. Where fire had been absent for over 20 years, the sapling layer had 14 species and a density over 900 stems/ha^{-1}, and a frequency of two fires per decade was sufficient to reduce species richness by nearly 60% and stem density by 80%. The species eliminated or reduced by fire were mainly mesophytic species intolerant of fire and tolerant of shade including *Ulmus alata*, *Prunus mexicana,* and *Vaccinium arboreum*, providing evidence that "mesophication," as proposed for more mesic eastern deciduous forests, may also occur in the much drier and relatively species-poor western forests (Nowacki and Abrams 2008). This is an important finding, as there was doubt that fire-intolerant species would eventually succeed oak species in the absence of fire, largely because of the droughty conditions and lack of replacement species (Abrams 1992, 2003).

Over 15 relatively minor tree species occurred in the sapling and tree size classes that appeared to be intolerant of fire and capable of increasing at low fire frequencies in addition to the abundant *Ulmus alata* and *Carya texana*. In the future, these species could be expected to increase in density at low fire frequencies as understory saplings replace the dominant trees in the larger size classes. Species from these genera have been found to increase in other oak forests in the absence of fire or anthropogenic disturbance (Dorney and Dorney 1989; McClain et al. 1993; Abrams 1996; Rentch and Hicks 2005). The lack of abundance in the current canopy is likely due to the fire-free or infrequent-fire period not being sufficient for the species to grow into the canopy. Recruitment into the larger diameter classes requires mortality in those classes and growth of the smaller trees. The oak and hickory trees that dominate the current canopy are 100 to more than 300 years of age (Clark et al. 2005; DeSantis et al. 2010). Although we do not know growth rates for most of the tree species, recent estimates showed growth from one 4-cm diameter class to the next would require 14 to 15 years for *Q. marilandica* and *Q. stellata* to reach canopy status (Clark and Hallgren 2004). If the abundant fire-intolerant trees in the 2-cm and 6-cm dbh classes were able to grow into canopy gaps at that rate, their presence in the larger classes would likely not be apparent for another 15 to 20 years.

Oaks are considered to be fire-adapted species; they produce a large root system early in life and are capable of persistent resprouting after top-kill (Abrams 1996; Clark and Hallgren 2003). As early successional, shade-intolerant, and fire-tolerant species, oaks are believed to benefit from fire (Abrams 2003; McDonald et al. 2003; Clark et al. 2007). The two dominant oaks in these stands, *Q. stellata* and *Q. marilandica*, are well known to be moderately resistant to top kill from fire and to root-sprout well after fire (Penfound 1963; Powell and Lowry 1980). Despite these adaptations that favor oak dominance when fire is common, we observed a deficiency of oak stems in the small diameter classes at high fire frequencies, and the diameter distribution did not assume the reverse-J shape of an all-aged stand. It is possible that frequent fires stimulated sprouting of the oaks but the bottleneck caused by slow growth under a closed canopy and droughty conditions prevented their growth into the sapling at high fire frequencies (Rice and Penfound 1959; Abrams 1992; Russell and Fowler 2002). Also, frequent fire can kill the same sprouts that an earlier fire stimulated (Abrams 1996; Clark and Hallgren 2003). Other researchers have commonly found that oak seedlings and sprouts accumulate in high densities as regeneration over decades, but only recruit into the canopy after disturbance creates a favorable gap (Johnson et al. 2002).

On the other hand, why did oak species not show the dramatic increases in sapling density at low fire frequencies seen for the other more mesophytic species? Low fire frequencies may have resulted in restricted oak sapling production due to reduced fire-stimulated sprouting and increased competition from the high density of additional fire-sensitive species that grew there. The shade-tolerant, fire-sensitive species found to thrive at low fire frequencies may have reduced the understory light enough to impede oak development (Loftis 1990; Lorimer et al. 1994).

Table 2. Tree and shrub species in regeneration, sapling/shrub, and combined small and large tree classes (x). Significant linear increase (+) or decrease (-) in cover for regeneration and density for saplings/shrubs with years since last fire (YSLF) or fires per decade (FPD) are indicated (P < 0.05). Tree density was not affected by fire (P < 0.05). Nomenclature for woody plant species and PLANTS symbols follows USDA, NRCS (2010).

Tree	PLANTS	Regeneration			Saplings			Trees
Species	Symbol	X	YSLF	FPD	X	YSLF	FPD	X
Acer saccharinum L.	ACSA2	x						
Carya alba (L.) Nutt.	CAAL27	x			x			x
Carya texana Buckley	CATE9	x			x			x
Celtis laevigata Willd.	CELA	x			x			x
Celtis occidentalis L.	CEOC	x			x			x
Cercis canadensis L.	CECA4	x			x			
Crataegus crus-galli L.	CRCR2	x	+		x			
Crataegus engelmannii Sarg.	CREN				x			
Crataegus viridis L.	CRVI2	x			x			
Diospyros virginiana L.	DIVI5	x			x			
Fraxinus americana L.	FRAM2	x			x			x
Gleditsia triacanthos L.	GLTR	x						
Gymnocladus dioicus (L.) K. Koch	GYDI	x						
Juniperus virginiana L.	JUVI				x			
Morus rubra L.	MORU2							x
Platanus occidentalis L.	PLOC	x						
Prunus mexicana S. Watson	PRME	x			x			x
Prunus serotina Ehrh.	PRSE2	x			x			
Quercus marilandica Münchh.	QUMA3	x			x			x
Quercus muehlenbergii Engelm.	QUMU	x						
Quercus rubra L.	QURU	x	+		x			x
Quercus stellata Wangenh.	QUST	x			x			x
Quercus velutina Lam.	QUVE	x			x			x
Sideroxylon lanuginosum Michx.	SILA20	x			x			x
Ulmus alata Michx.	ULAL	x			x			x
Viburnum rufidulum Raf.	VIRU				x			
Shrub	PLANTS	Regeneration			Shrubs			
Species	Symbol	X	YSLF	FPD	X	YSLF	FPD	
Cephalanthus occidentalis L.	CEOC2	x			x			
Ilex decidua Walter	ILDE	x			x			
Rhus aromatica Aiton	RHAR4	x						
Rhus copallina L.	RHCO	x						
Rhus glabra L.	RHGL	x			x	+		
Rosa L. spp.	ROSA5	x						
Rubus L. spp.	RUBUS	x						
Symphoricarpos orbiculatus Moench	SYOR	x						
Vaccinium arboreum Marsh.	VAAR	x			x		-	

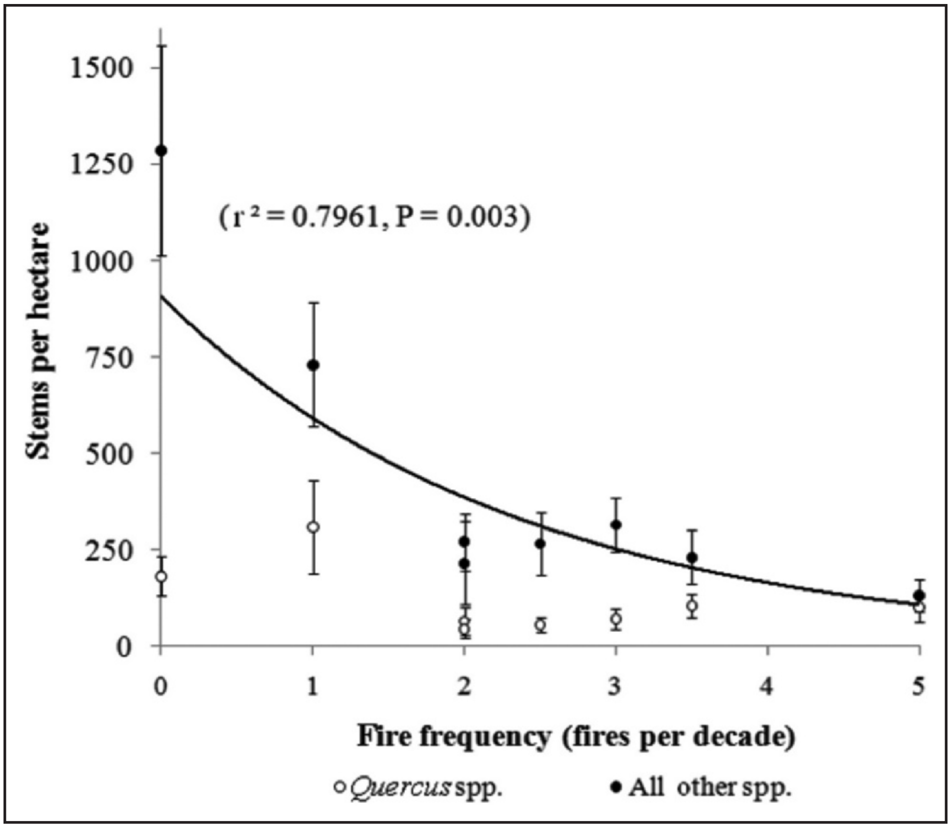

Figure 2. Effect of fire frequency on sapling density of oak (Quercus) spp. and non-oak tree and shrub species. Solid line indicates significant exponential regression. Error bars represent standard error of the treatment unit mean (n = 20).

We found that the abundant cover of oak and hickory regeneration from seedlings and sprouts was not affected by winter burns over the range in frequency of zero to five per decade. This is consistent with findings from earlier research that found only very intense burning could control oaks. Southern red oak (*Q. falcata* Michx.), post oak (*Q. stellata*), water oak (*Q. nigra* L.), willow oak (*Q. phellos* L.), and hickory (*Carya* Nutt. spp.) saplings were not suppressed after 30 years of periodic winter and summer burning and annual winter burning in a mesic pine-grass forest (Waldrop et al. 1992). In contrast, these same hardwood species declined sharply under annual summer burning over the same period. Research showed winter burns controlled how large hardwood sprouts will grow but only summer burns controlled the number of sprouts (Waldrop et al. 1992; Komarek 1974).

Scientists acknowledge the decline of oak forests within much of their pre-colonial range (Abrams 2003; Hart et al. 2008; Kabrick et al. 2008). There is strong evidence of conversion of oak forests to more shade-tolerant or mesic forest species through "mesophication" (Nowacki and Abrams 2008). In general, shade-tolerant, fire-sensitive species eventually succeed oak species following fire suppression; however, on xeric sites, such as the upland forests of eastern Oklahoma, oak may not be replaced by late successional species (Abrams 1992, 2003; Nowacki and Abrams 2008). These forests are considered to be relatively species-poor due to the rigorous environment and strong dominance of *Q. stellata* and *Q. marilandica* (Risser and Rice 1971; Dooley and Collins 1984). Results of our study suggested that mesophication is possible in these forests and the process can begin within 20 to 30 years.

As the primary mast-producing species in the region, oaks are a valuable resource for wildlife (McShea and Healy 2002). Fire-intolerant species such as eastern redcedar (*Juniperus virginiana* L.) and elm (*Ulmus* L. spp.) provide valuable cover, but not the important food resources needed by game species. Thus, regeneration of oak species is a key concern at OGMA where maintenance of biodiversity and quality wildlife habitat are management goals. Prescribed fire is recommended as a management tool to reduce competition by fire-intolerant tree species and promote oak regeneration (Van Lear et al. 2000; McShea and Healy 2002). In as few as five years, prescribed fire altered small tree species composition in Missouri oak forests (Blake and Schuette 2000). Over twenty years of prescribed fire reduced both the stem density and basal area of oak forests in Missouri and Minnesota, creating open woodland or savanna-like conditions dominated by larger oak individuals (Huddle and Pallardy 1996; Peterson and Reich 2001). The results of our study suggest that mesophication can occur when fire is excluded, but as few as two low intensity winter burns per decade can reverse the process. It is worth noting that the fire frequency found to control sapling density of non-oak species in our study was very close to the estimated fire frequency for Cross Timbers forests for the periods prior to European settlement (Clark et al. 2007; Stambaugh et al. 2009; and R.D. DeSantis, doctoral candidate, Oklahoma State University, pers. comm.).

While the primary factor limiting recruitment and growth of non-oak species at our study site in eastern Oklahoma may be climatic, fire regimes likely play an important role in oak dominance. It appears that non-oak species in the sapling size classes can be controlled by fire at a frequency as low as two per decade. More complete understanding of the effects of fire frequency in these forests would benefit from studies of annual burning, growing season burning, and fire treatments exceeding 20 years.

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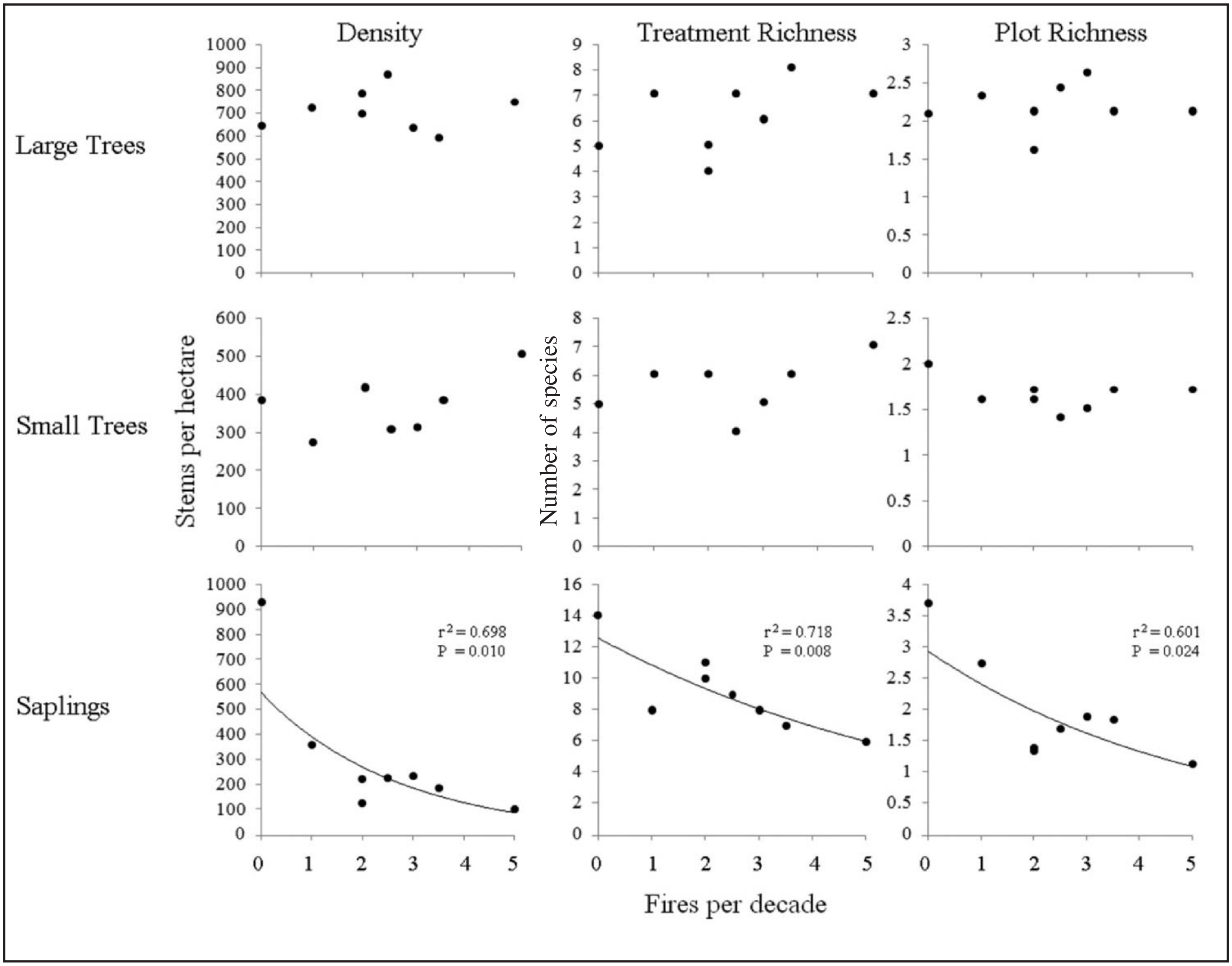

Figure 3. Fire frequency effects on density, treatment unit richness, and mean plot tree species richness of tree species. Solid lines indicate significant relationships with fire frequency using an exponential model.

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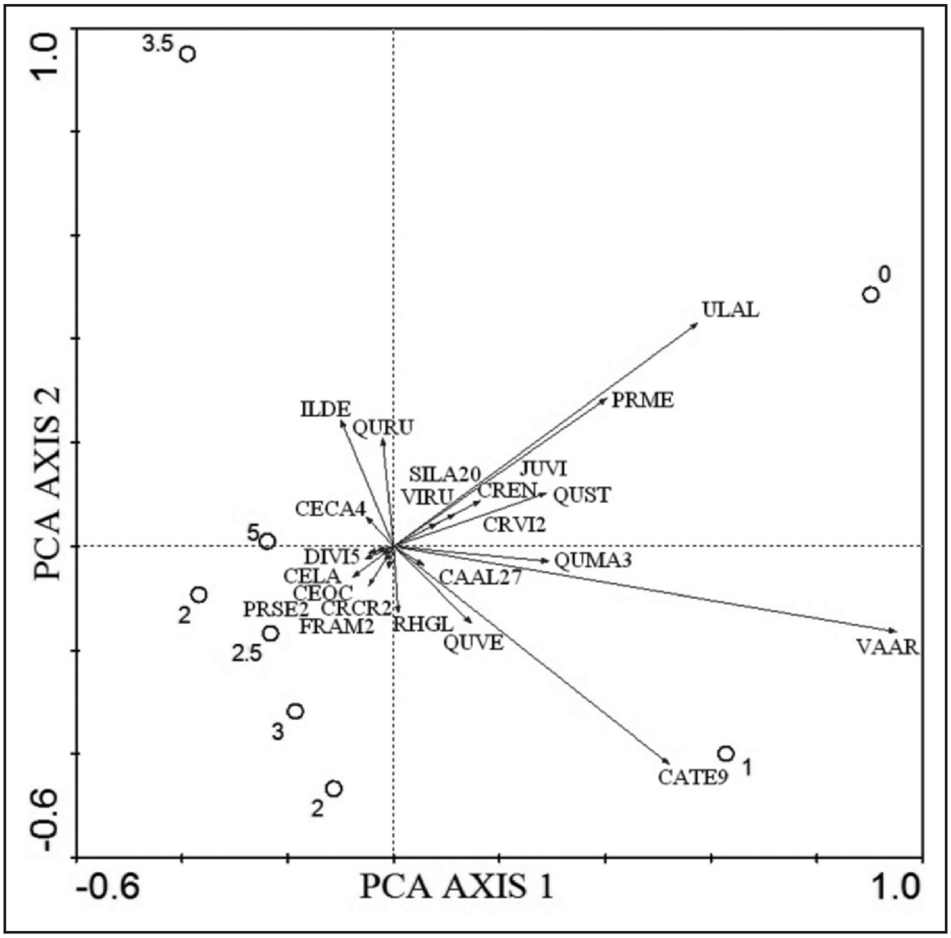

Figure 4. Principal components analysis of stem densities of saplings within the OGMA treatments. Treatment samples are represented by circles and number corresponds to the fire frequency (fires per decade) of the treatment. Eigenvalues for axis one is 0.552 and axis two is 0.186. Species that that were only sampled once, throughout the study, were removed from the PCA figure. References to species symbols occur in Table 2.

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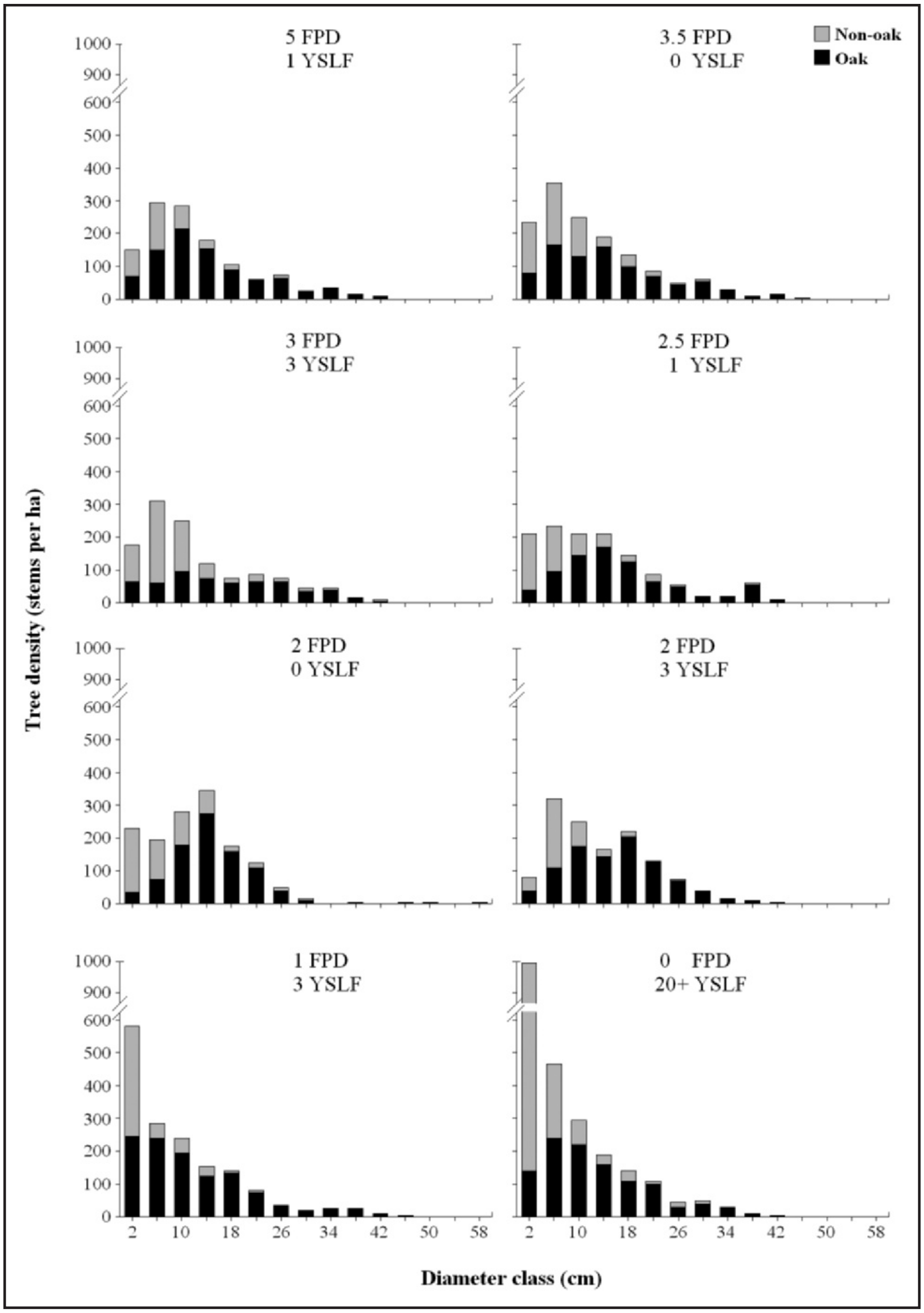

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