

FIRE FREQUENCY EFFECTS ON VEGETATION OF AN  
UPLAND OLD GROWTH FOREST IN EASTERN  
OKLAHOMA

By

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## INTRODUCTION

The thesis was written in two chapters. The first chapter “Fire Frequency Effects on Structure and Composition of Forest” was submitted to *Natural Areas Journal* for publication. This manuscript was coauthored with Stephen W. Hallgren and Michael W. Palmer. Both coauthors contributed to the development of the research questions, statistical analysis, and discussion of the manuscript. The manuscript is in the process of revision and some of the journal’s reviewer suggestions have been integrated into the thesis chapter. The second chapter “Fire Frequency Effects on Understory Plant Functional Groups and Diversity” will be submitted for publication in an appropriate scientific journal.

Humans have been utilizing fire for at least 1.9 million years (Wrangham et al. 1999). Their use of fire has likely altered and shaped many ecosystems since that time. Since the last glaciation 10,000 years ago, many of North America’s ecosystems have developed with the presence of anthropogenic fire. Much of the extant vegetation has resulted from not only geological and climatological constraints, but also fire restrictions (Axelrod 1985, Pyne 1997, Bond et al. 2005, Nelson et al. 2006, Bowman et al. 2009). Ecosystems such as the midwestern savannas of the United States may be entirely anthropogenic in origin (Guyette and Cutter 1991, McEwan and McCarthy 2008).

The aboriginal use of fire was interrupted with European settlement. Fire suppression became important for the protection of pioneers' property and their way of life. The exclusion of fire from this fire dependent ecosystem has now had a history of at least a century. More recently there are concerns that the ecosystems are changing due to fire suppression and would benefit from the reapplication of prescribed fire.

One of these ecosystems of concern is the ecotone of the southern Great Plains and Central Hardwood Forest. On a coarse scale this ecotone contained a mosaic of tallgrass prairie, savannas, bottomland hardwoods, and xeric oak forests prior to European settlement (Bruner 1931). The complex of oak forests and prairie is locally referred to as the Cross Timbers Forest. This Cross Timbers Forest is largely dominated by blackjack oak (*Quercus marilandica*), post oak (*Q. stellata*), and black hickory (*Carya texana*), with the first two being more prominent in the west and the latter two in the east where it intergrades into the oak/hickory forests of the Central Hardwood Forests (Rice and Penfound 1959, Fralish 2002, USDA NRCS 2006). In addition to soil properties and precipitation, fire likely had an important role in shaping this diverse mosaic of forests and prairie across Kansas, Oklahoma, and Texas (Johnson and Risser 1975, Engle et al. 1996). Since European settlement and removal of fire from the Cross Timbers landscape, these forests have experienced changes in tree density and species composition (Johnson and Risser 1975, Abrams 1986, DeSantis et al. 2009).

Recently land managers and biologists have begun reintroducing fire to restore historic conditions, improve wildlife habitat, suppress invasive species, and recover biodiversity in this ecoregion. In the 1980s many of the wildlife management areas administered by the Oklahoma Department of Wildlife Conservation established prescribed burning programs in order to reestablish historic plant communities and benefit game species' habitat. The growing interest in using fire to help manage fuels and create healthier ecosystems has been hindered by lack of knowledge of the fire regimes prior to European settlement and many unknowns relating the impacts on vegetation composition and structure following the return of fire to stands where burning has long been excluded.

Species-rich communities of vegetation have been found at intermediate intensities of disturbance resulting in a unimodal response of richness to disturbance intensity. "Intermediate Disturbance Hypothesis" is the phrase coined to name this relationship between species diversity and disturbance (Grime 1973, Connell 1978). The Intermediate Disturbance Hypothesis has been tested in a variety of conditions in order to predict the levels of disturbance that result in the highest species diversity with outcomes that suggest extensive and complex species and environmental interactions (Roxburgh et al. 2004). This hypothesis predicts that the highest species diversity will be at levels of disturbance that maintain opportunities for species that require disturbance for establishment, while minimizing the loss of species that are sensitive to the disturbance. Under low levels of disturbance, competitive or K-selected species will achieve dominance, excluding less competitive species. Levels of disturbance that are

too high will reduce the dominance of highly competitive species to more resistant and/or r-selected species (Grime 1973, Connell 1978, Huston 1979).

The “Most Frequent Fire Hypothesis” has been recently been described to explain understory diversity in forests of the southeastern United States (Glitzenstein et al. 2003). This hypothesis predicts that the highest vascular plant species diversity will occur at the highest fire frequency permitted by natural production of fuels. The Most Frequent Fire Hypothesis provides a basis for management strategies in southern longleaf pine forests (*Pinus palustris*) (Glitzenstein et al. 2003). A comparison of the Most Frequent Fire Hypothesis and the Intermediate Disturbance Hypothesis may provide insights concerning effects of disturbance intensity and frequency on biological diversity.

Increases in overstory heterogeneity caused by very frequent fire regimes may increase species diversity by amplifying resource heterogeneity. Higher diversities of understory species may occur in areas of broken canopy cover simply because of high plant resource heterogeneity, allowing grassland species to occur interspersed with forest species (Leach and Givnish 1999). Additionally, caution is necessary when interpreting richness or diversity indices, as an increase in diversity could simply be a result in an increase in plant density (Magurran 2003). Both the Intermediate Disturbance Hypothesis and Most Frequent Fire Hypothesis will be utilized to evaluate this study’s relevance to disturbance theory.

The overall objective of this project was to provide new knowledge about the effects of fire frequency on forest stand structure and composition that could be used to improve management prescriptions for xeric oak forests. Specific questions concerned the effects of fire frequency on woody plant size distribution and species richness of plant functional groups. The research was conducted on the Okmulgee Wildlife Management Area (OWMA) in east central Oklahoma. The OWMA encompasses a broad range of habitat types; from tallgrass prairie to bottomland hardwood timber. Of the over 4,000 hectares, 75 percent of the OWMA is relatively undisturbed upland hardwood forest. The OWMA has been subjected to prescribed burning to improve wildlife habitat and community diversity for over twenty years. It was broken into 15 different fire treatment units, all of which have a different fire history. I selected eight fire treatment units for this study based on similar time since last burn, topography, soils, forest cover, and differing fire frequencies. The fire frequencies of the selected treatments ranged from zero to five fires per decade.

## CHAPTER 1: FIRE FREQUENCY EFFECTS ON STRUCTURE AND COMPOSITION OF XERIC OAK FORESTS

### ABSTRACT

We investigated the effects of 20 years of dormant season fire over a range of frequencies on the composition and structure of woody plants in a xeric oak forest at the western limit of the eastern deciduous forest. Twenty 0.01 ha plots were randomly located in each of eight management units with fire frequencies ranging from zero to five per decade and the density of saplings and shrubs (height  $\geq 1.4$  m and dbh  $< 5$  cm), small trees ( $5 \text{ cm} \leq \text{dbh} < 10 \text{ cm}$ ) and large trees (dbh  $\geq 10 \text{ cm}$ ) was measured. The cover of woody regeneration (height  $< 1.4$  m) was measured on four  $1 \text{ m}^2$  sub-plots within each plot. Regeneration cover was not affected by fire frequency. Increasing fire frequency had a strong negative effect on species richness of saplings and shrubs and no effect on small and large tree species richness. While oak sapling density was not affected by fire frequency, the density of non-oak saplings and shrubs was strongly reduced by fire frequencies greater than two per decade. Consequently at high fire frequencies *Quercus stellata* and *Q. marilandica* saplings dominated and at low fire frequencies *Ulmus alata* and *Carya texana* saplings dominated. Although 20 years of treatment may not have been long enough to show fire frequency effects on canopy

trees, the effect on species composition of saplings was strong which may have long-term consequences for forest canopy composition. These results suggest that without at least two fires per decade the species richness of these forests will increase and oak dominance will diminish.

## **INTRODUCTION**

Prior to European settlement, the fire return interval was two to eight years in the upland oak (*Quercus* spp.) forests of the south-central United States (Cutter and Guyette 1994, Brown and Smith 2000, Stambaugh and Guyette 2006). This frequency of fire was likely anthropogenic in origin and used by aboriginal people to increase desired plant species for food or game (Guyette and Cutter 1991, Pyne 1997, Guyette et al. 2002). In the last century land development and industrialization has led to the removal of fire from the landscape (Pyne 1996, 1997). Since that time, many of these forests have experienced great changes in species composition and density (Rice and Penfound 1959, Desantis et al. 2009). Fire may be the important relation in these compositional changes in the upland forest.

Prescribed fire is recommended as a management tool to reduce competition by fire intolerant species and promote regeneration of oak species (Van Lear et al. 2000, McShea and Healy 2002). In as few as five years, prescribed fire can alter small tree composition in midwestern oak forests (Blake and Schuette 2000). Over twenty years of prescribed fire can reduce both the stem density and basal area of oak forests, creating



open woodland or savanna like conditions dominated by larger oak individuals (Huddle and Pallardy 1996, Peterson and Reich 2001). Long-term data, with a range of fire frequencies, would provide land managers with valuable information on the frequency of fire that is needed for maintaining oak dominance while not reducing oak regeneration.

One concern of ecologists today is the conversion of oak forests to more shade tolerant or mesic forest species, i.e. a “mesophication” of oak forests (Nowacki and Abrams 2008). Scientists acknowledge the decline of this genus within much of its pre-colonial range (Abrams 2003, Hart et al. 2008, Kabrick et al. 2008). As the primary mast producing species in the region, oak species are a valuable resource for wildlife species (McShea and Healy 2002). Fire intolerant species such as redcedar (*Juniperus virginiana* L.) and elm (*Ulmus* spp.) may provide value for cover; however, they do not provide the important food resources needed by game species. In general, intolerant species eventually succeed the oak species following fire suppression; however, on xeric sites, such as the upland forests of Oklahoma, oak might not be replaced by late successional species (Abrams 1992, 2003, Nowacki and Abrams 2008).

In this study, we addressed the effects of fire frequency on xeric old-growth oak forests of the Cross Timbers of Oklahoma, which is on the westernmost edge of the Central Hardwood Forest. We hypothesize that increasing fire frequency will suppress woody regeneration of fire intolerant saplings and shrubs, while having few effects on the trees and saplings of fire tolerant species.

## 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 2,400 hectare 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 annually (Oklahoma Climatological Survey 2005).

The study was limited to the Hector-Endsaw complex soil which represented approximately 75 percent 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 5-30 percent 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 was classified as the *Quercus stellata* Wangenh. – *Quercus marilandica* Muenchh. forest type (Duck and Fletcher 1945), locally referred to as the Cross Timbers forest. 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 study of effects of fire in an oak forest landscape where extremes of drought and temperature are common.

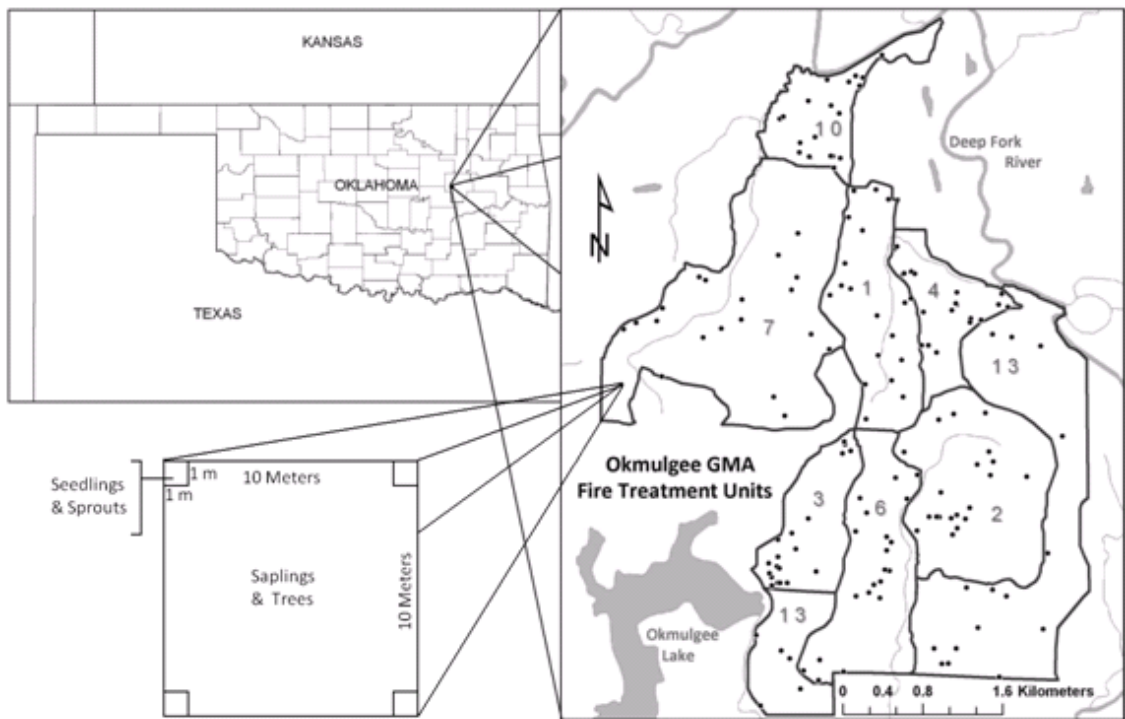
The OGMA has been subjected to prescribed fire since the late 1980s. There was no record of fire occurrence prior to the beginning of prescribed fire, although wild fires may have burned some parts of the OGMA. The OGMA was divided into units ranging from approximately 100 to 600 ha and each unit was burned on its own schedule. There were some wild fires during this period that were included in the count. This led to a range of fire frequencies among units from 0 to 5 fires per decade. All fires, both wild and prescribed, occurred during the dormant season in February and March of each year. They were all low intensity surface fires.

### Sampling Design

Eight treatment units were selected that ranged in size from 58 to 385 ha (Table 1). Twenty 100m<sup>2</sup> (0.01 hectare) plots were randomly located within each unit using the random point tool in ArcCatalog (ESRI 2007; Figure 1). No plots were allowed within 10 m of clearings including roads, rights of way, firebreaks, and wildlife food plots. We used a Trimble 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 the four directions, southwest, southeast, northwest or northeast, was

**Table 1 | Year and month of prescribed fires by units. \*Indicates arson set fire occurring outside of management prescriptions.**

Year	Burn Unit							
	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								
Total Fires	10	5	4	7	4	2	6	0
Fires per Decade	5.0	2.5	2.0	3.5	2.0	1.0	3.0	0.0
Years Since Last Fire	1	1	3	0	0	3	3	20+



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

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<sup>2</sup> plot, we measured the diameter of all woody plant stems at breast height (dbh, 1.4 m). Saplings and shrubs were > 1.4 m tall and < 5 cm dbh, small trees were ≥ 5 cm and < 10 cm dbh, and large trees were ≥ 10 cm dbh. Cover of tree and shrub seedlings and sprouts < 1.4 m tall was estimated by species in four 1 m<sup>2</sup> sub-plots nested within each corner of the 100m<sup>2</sup> plots. We visually estimated foliar cover within a modified square plot frame using the Braun-Blanquet cover scale (Kent and Coker 1992). Nomenclature for woody plant species follows the PLANTS database (USDA NRCS 2008).

### Data Analysis

The experimental unit was the burn unit and 20 sub-sample plots were taken within each one. Stem density and basal area (m<sup>2</sup> ha<sup>-1</sup>) at breast height were calculated for data from the 100m<sup>2</sup> plots. 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. 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).

## RESULTS

### Seedling and Sprout Cover

There was no relation between fire frequency and seedling and sprout cover for any species ( $P < 0.10$ , data not shown). The mean plot richness of seedling and sprout species ranged from 5.2 to 7.1 and was not significantly related to fire frequency or time since last fire ( $P < 0.10$ ). Twenty-two tree and ten shrub species less than 1.4 m in height were found throughout the treatment units (Appendix I).

### Saplings & Shrubs

Sapling density of all species varied greatly, from 1,465 stems  $\text{ha}^{-1}$  in the non-burned unit to 230 stems  $\text{ha}^{-1}$  in the most frequently burned treatment unit (Table 2, Appendix IV). Oak saplings ranged in density from 310 to 45 stems  $\text{ha}^{-1}$  with no clear relationship with fire frequency; however, non-oak species had a strong negative response to fire frequency (Figure 2). Total treatment and mean plot richness of saplings and shrubs both decreased with increased fire frequency (Figure 3). The sapling tree species most highly associated with lower fire frequencies were *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. The fire treatment units greater than one fire per decade were located close to one another on the first axis. PCA also showed the treatment with a fire frequency of three and a half fires per decade differed from the other treatments on axis 2 (Figure 5).

**Table 2 | Basal area, density, richness, and mean plot richness of the surveyed treatments at the Okmulgee Game Management Area. \* Indicates a significant regression with fire frequency (P < 0.05).**

	Treatment Unit	13	7	3	6	2	10	4	1
	Fire Frequency (fires/decade)	0	1	2	2	2.5	3	3.5	5
	Mean Basal Area (m <sup>2</sup> /ha)	25.2	22.3	25.8	24.6	27.3	23.9	26.7	22.7
Saplings/ Shrubs (< 5 cm dbh)	*Stem Density (Stems/ha)	1465	1040	280	315	320	385	335	230
	*Treatment Richness (Sp./Treatment)	15	9	12	10	11	10	7	6
	* $\bar{x}$ Plot Richness (Sp./100m <sup>2</sup> )	3.7	2.8	1.3	1.4	1.7	1.9	1.9	1.2
	Stem Density (Stems/ha)	385	270	410	415	305	310	380	500
Small Trees (≥ 5 < 10 cm dbh)	Treatment Richness (Sp./Treatment)	5	6	6	6	4	5	6	7
	$\bar{x}$ Plot Richness (Sp./100m <sup>2</sup> )	2	1.6	1.7	1.6	1.4	1.5	1.7	1.7
	Stem Density (Stems/ha)	645	715	775	690	860	630	585	740
Large Trees (≥ 10 cm dbh)	Treatment Richness (Sp./Treatment)	5	7	4	5	7	6	8	7
	$\bar{x}$ Plot Richness (Sp./100m <sup>2</sup> )	2.1	2.3	1.6	2.1	2.4	2.6	2.1	2.1



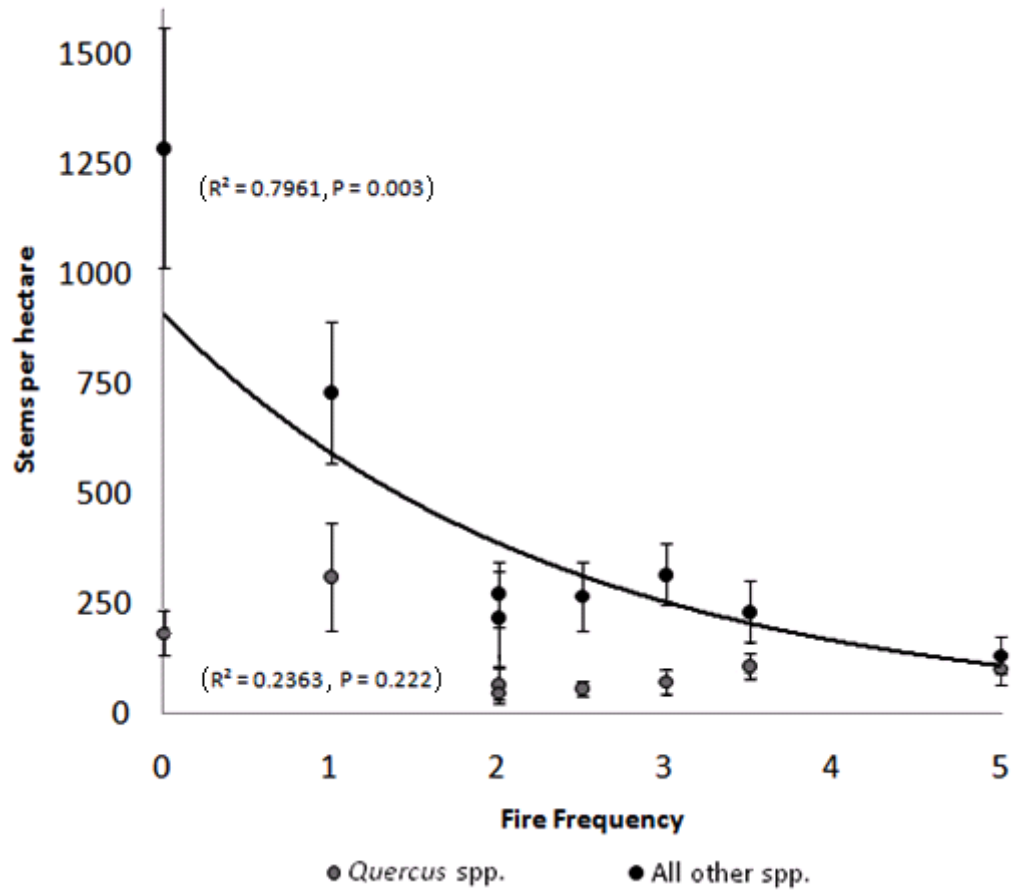
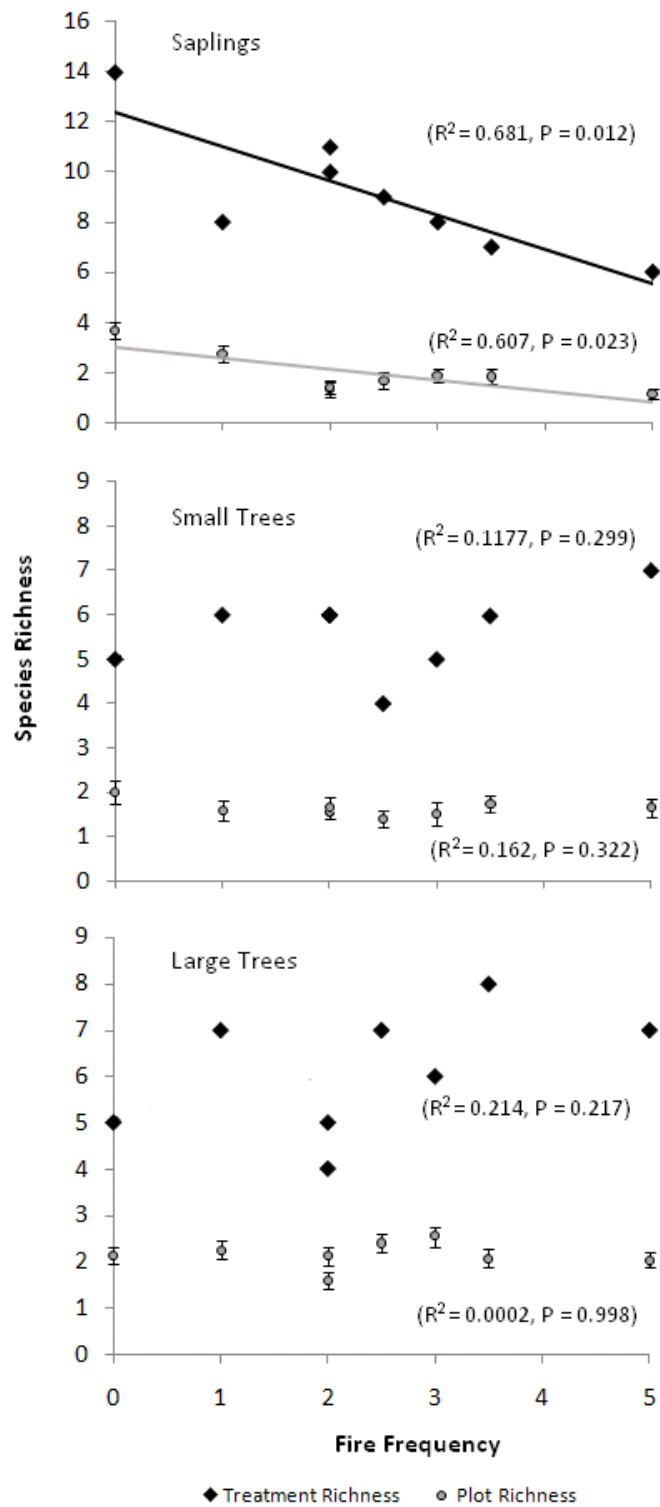
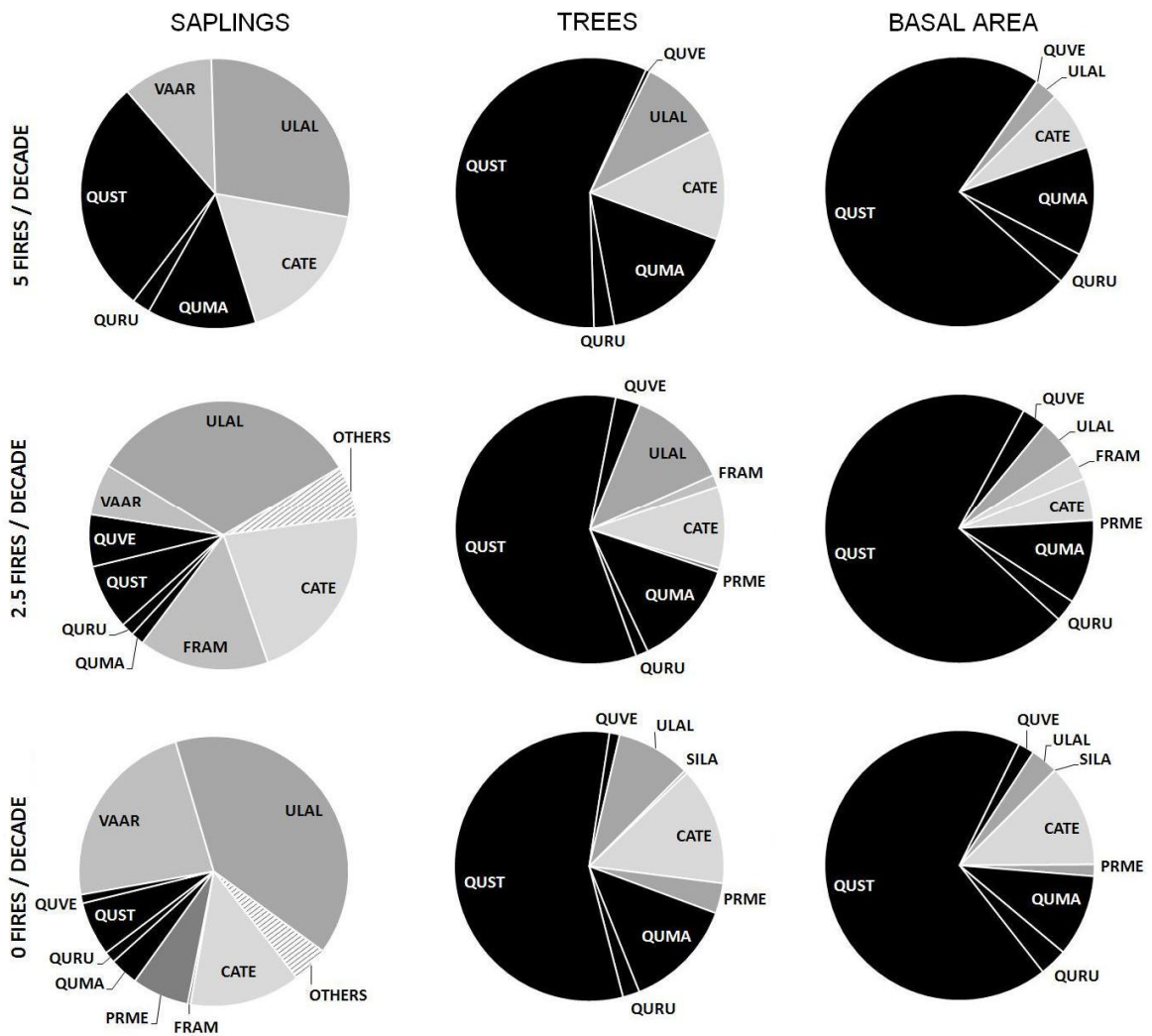


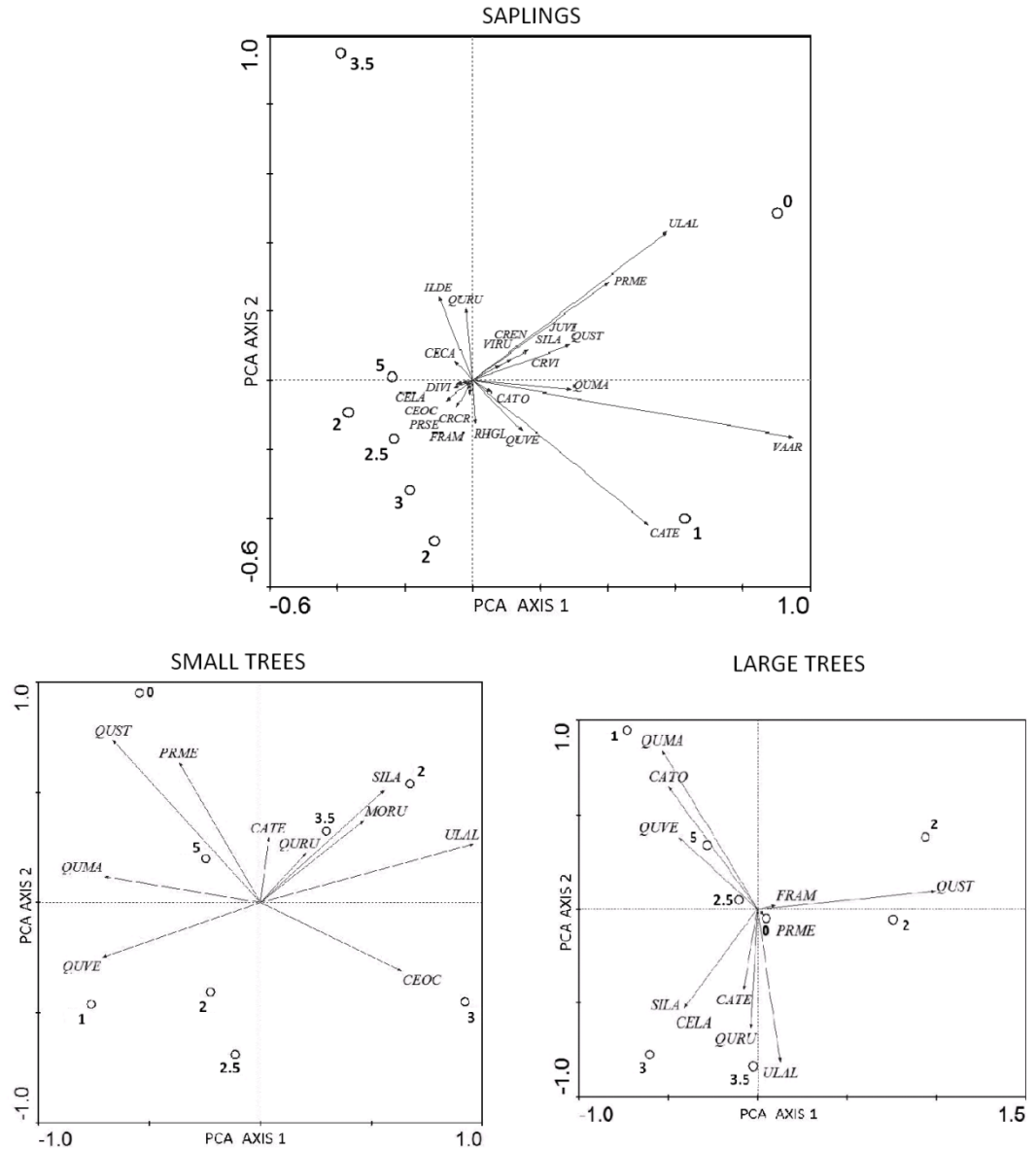
Figure 2 | Effect of fire frequency on sapling density of oak (*Quercus*) spp. and non-oak tree and shrub species. Error bars represent standard error. Solid line indicates significant exponential regression.



**Figure 3 | Effect of fire frequency on total plot richness and mean plot tree species richness. Error bars represent standard error. Solid lines indicate significant linear relations.**



**Figure 4 | Stem density of species of saplings and shrubs (< 5 cm dbh), trees ( $\geq$  5 cm dbh), and Basal Area of Trees ( $\geq$  5 cm dbh) in three treatment units. Woody species include; CATE – *Carya texana*, FRAM – *Fraxinus americana*, PRME – *Prunus mexicana*, QUMA – *Quercus marilandica*, QURU – *Q. rubra*, QUST – *Q. stellata*, QUVE – *Q. velutina*, SILA – *Sideroxylon lanuginosum*, ULAL – *Ulmus alata*, VAAR – *Vaccinium arboreum*. Other saplings for 2.5 fires per decade include; CELA – *Celtis laevigata* Willd., CEOC2 – *Cephalanthus occidentalis* L., and RHGL – *Rhus glabra*. Other saplings for 0 fires per decade include; CREN – *Crataegus engelmannii* Sarg., CRVI – *Crataegus viridis* L., RHGL, SILA, VIRU – *Viburnum rufidulum* Raf., and JUVI - *Juniperus virginiana*.**



**Figure 5 | Principal components analysis of stem densities of saplings, small trees, and large trees within the OGMA treatments. Treatment samples are represented by circles and number corresponds to the fire frequency (fires per decade) of the treatment. Species not defined in figure 4 but present in figure 5 include; CECA – *Cercis canadensis* L., CATE – *Carya tomentosa* (Poiret) Nuttall , CRCR – *Crataegus crus-galli* L., DIVI – *Diospyros virginiana* L., ILDE – *Ilex deciduas* Walter, PRSE – *Prunus serotina* Ehrh., MORU – *Morus rubra* L.. Species that that were only sampled once, throughout the study, were removed from the PCA figure.**

## Trees

Small and large tree densities, basal area, and species composition showed no relation to fire frequency (Table 2, Figure 4). There was not a significant relationship between fire frequency and entire treatment richness or plot richness (Figure 3). Fire frequency had a greater impact on the species composition of saplings than trees (Figures 4 & 5). *Prunus mexicana* appeared to be increasing into the tree size distribution with reduced fire (Figure 4). Neither axis in PCA appeared to show a particular pattern in the placement of species or samples by fire frequency (Figure 5).

## **DISCUSSION**

One of the major findings of our study was that periodic low intensity fires were necessary to maintain dominance of oak species even in xeric forests at the ecotone between the southern Great Plains and the Central Hardwood Forest. In the absence of fire, mesophytic species intolerant of fire appeared to replace oak. Although oak sapling density was not affected by fire frequency from zero to five fires per decade, when fire frequency was less than two per decade the abundance of fire intolerant species common to mesic eastern forests increased sharply. Several of these species were capable of growing to tree size in the canopy and it may take longer than twenty years to see this happen. These results were evidence that mesophication as proposed for 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, because of the droughty conditions and lack of replacement species (Abrams 1992, 2003).

The reintroduction of fire into this forest did not affect cover of tree and shrub regeneration of any species. The lack of oak sapling response to fire frequency was surprising. Oaks are considered fire-adapted; they produce a large root system early and are capable of persistent resprouting after top-kill (Abrams 1996, Clark and Hallgren 2003). As early successional, shade-intolerant, and fire-tolerant species they are believed to benefit from fire (Clark 1993, Abrams 2003, McDonald et al. 2003). 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 increase sprouts after fire (Penfound 1963, Powell and Lowry 1980). 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 combined with frequent fire prevented their growth into the sapling size > 1.4 m at high fire frequencies (Rice and Penfound 1959, Abrams 1992, Russell and Fowler 2002). In contrast, low fire frequencies may have resulted in restricted oak sapling production due to competition from the additional 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).

There were over 15 relatively minor tree species in sapling and tree size classes, in addition to the abundant *Ulmus alata* and *Carya texana*, that appeared to be intolerant of fire and capable of increasing at low fire frequencies. These species could be expected to increase in density on the lower fire frequency units in the future, as understory saplings replace the dominant trees. Species from these genera have been found to increase in other oak forest locations in the absence of fire or anthropogenic disturbance (Dorney and Dorney 1989, McClain et al. 1993, Abrams 1996, Rentch and Hicks 2005). The sapling species at this site most likely to grow into the forest canopy based on expected maximum height included: *Carya texana*, *C. tomentosa*, *Celtis laevigata*, *Diospyros virginiana*, *Fraxinus americana*, *Gleditsia triacanthos* L., *Juniperus virginiana*, *Sideroxylon lanuginosum*, and *Ulmus alata* (Little 2002). The lack of abundance in the current canopy may be the result of a fire free or infrequent fire period not being long enough for the species to grow into the canopy. This process of species replacement may be slower in the xeric forests of the Cross Timbers.

Our results suggest biennial winter burning can control the density of fire intolerant woody shrubs and saplings but not oak saplings. These findings were consistent with those of other studies conducted in oak forests under more mesic conditions. Hickory (*Carya* spp.), southern red oak (*Quercus falcata* Michx.), post oak (*Q. stellata*), water oak (*Q. nigra* L.), and willow oak (*Q. phellos* L.) saplings were not suppressed after 30 years of no burning, periodic winter and summer burning, and annual winter burning in a mesic pine-grass forest (Waldrop et al. 1992). In contrast, these same hardwoods declined sharply under annual summer burning over the same

period. These results support the findings that winter burns may control how large hardwood sprouts will grow but only summer burns will control the number of sprouts (Waldrop et al. 1992, Komarek 1974).

While the primary factor limiting species other than oak at this site may be climatic, fire regimes appear to play an important role in oak dominance. Non-oak species in the sapling size classes have been greatly reduced in density by two decades of frequent fire. However, this length of time has been insufficient to reveal the impact of fire regimes on the composition of larger size classes. More complete understanding of the effects of fire frequency in these forests would benefit from study of annual burning, growing season burning, and periods of treatment longer than 20 years.



## CHAPTER 2: FIRE FREQUENCY EFFECTS ON THE DIVERSITY OF UNDERSTORY PLANT FUNCTIONAL GROUPS

### ABSTRACT

This study examined the effects of long-term prescribed fire at varying frequencies on understory vascular plant cover and species diversity in an upland oak forest of eastern Oklahoma. Twenty 0.01 ha plots were randomly located in each of eight management units with fire frequencies ranging from zero to five per decade. All woody plants  $\geq 1.4$  m in height were sampled on the 0.01 ha plots and cover of understory woody regeneration and herbaceous plants  $< 1.4$  m tall was estimated on four  $1 \text{ m}^2$  sub-plots nested in each corner of the 0.01 ha plots. Frequent fire increased the abundance of herbaceous species while having no significant effect on understory woody plants. Diversity of understory vascular plant species had a strong positive relation with fire frequency. The lack of herbaceous species with negative responses to frequent fire suggests that this ecosystem was adapted to fire or other forms of disturbance. This information should help forest managers utilize fire at different frequencies to increase landscape heterogeneity, manage wildlife habitat, and promote biodiversity in these upland forests.

## INTRODUCTION

Since the latter part of the Pleistocene ten to fifteen thousand years ago, human beings through their use of fire have shaped ecosystems of the North American continent (Delcourt 2004). In the absence of the once high diversity of Pleistocene megafauna many of North America's tallgrass prairies and savannas require fire or another form of anthropogenic disturbance to maintain herbaceous dominance, as precipitation is adequate for the development and dominance of woody plant species (Gleason 1913, Cowles 1928, Abrams 1986, Bond and Keeley 2005, Bond et al. 2005, Martin and Greene 2005). These ecosystems are highly dependent on the unique human tool of fire. Many species of oak (*Quercus* spp.) rely on physiological adaptations to frequent fire or other disturbance to maintain dominance over fire intolerant species (Abrams 1992, Van Lear et al. 2000, McShea and Healy 2002, Nowacki and Abrams 2008). In forested regions frequent fire will greatly increase the herbaceous component of forest understories with varying impacts on overstory oak trees (Waldrop et al. 1992, Van Lear et al. 2000, Peterson et al. 2007).

Throughout the southern tallgrass prairie and western portions of the Central Hardwood Forest frequent fires have been almost exclusively the result of human land use (Pyne 1996, 1997, Guyette et al. 2002). Because of the many uses of fire by aboriginal people, it is certain that fire regimes in both time and place varied tremendously. The regime of fires set by local people would have varied according to

topography, vegetation, and local population density creating a diverse mosaic of fire regimes on the landscape (Guyette and Cutter 1991, Pyne 1997, Guyette et al. 2002).

After decades of omission, prescribed fire is returning today as a human tool for the management of vegetation throughout North America's public lands, particularly in the southern Great Plains and the Southeast (Pyne 1996). Because of the recent redevelopment of fire practices in southeastern forests, much of the research concerning prescribed fire effects on forest vegetation has been relatively short-term, and long-term data may be necessary to detect important effects of understory fire (Hutchinson et al. 2005, Laughlin et al. 2008). In addition, many of these studies were done in conjunction with mechanical treatments such as harvesting or thinning of overstory trees (Masters 1991, Laughlin et al. 2008). Forest managers utilize mechanical treatments to rapidly increase production of fine fuels such as grasses and forbs prior to burning. This rapidly accelerates and alters the effects of applied fire to establish an earlier successional stage (Masters et al. 1993, Peterson et al. 2007). The effect of mechanical treatments on grasses and forbs may also be short-term, lasting no more than a few years without the application of fire (Baskett et al. 1957, Murphy and Ehrenreich 1965, Masters et al. 2006). However, mechanical treatment may be too costly for management budgets or may conflict with societal values, such as the preservation of old growth timber. Land managers are in need of quantitative data to support development of prescribed fire as a management tool.

The Intermediate Disturbance Hypothesis described by Connell (1978) to explain unimodal responses of plant diversity to a gradient of disturbance intensity has now been tested in a variety of conditions in order to predict the levels of disturbance such as fire that result in the highest species richness (Roxburgh et al. 2004). The Most Frequent Fire Hypothesis predicts that the highest understory plant species diversity will occur at the highest fire frequency in which primary productivity and resulting fuels will allow (Glitzenstein et al. 2003). The Most Frequent Fire Hypothesis provides a basis for a great deal of the management strategies in southern longleaf pine (*Pinus palustris*) forest management in the southeastern United States (Glitzenstein et al. 2003).

The overall goal of this research reported here was to determine the effects of fire frequency on herbaceous vegetation and provide a basis for improved management prescriptions for xeric oak forests. A major objective was to quantify the effects of fire frequency and time since fire on abundance and diversity of herbaceous species. Another objective was to determine the effects of fire frequency on environmental variables such as overstory canopy cover, litter cover and depth and exposed soil. The response of environmental variables may help explain the response of herbaceous vegetation. Results were evaluated in the context of the Intermediate Disturbance Hypothesis and the Most Frequent Fire Hypothesis.

The research was conducted on the Okmulgee Wildlife Management Area (OWMA) where prescribed burns have been conducted for over 20 years at frequencies ranging from zero to five per decade. Although the range of burn frequencies did not

include the highest level of disturbance caused by annual burning, the range of fire frequencies at the OMWA should be suitable for determining whether increasing disturbance frequency affects species diversity.

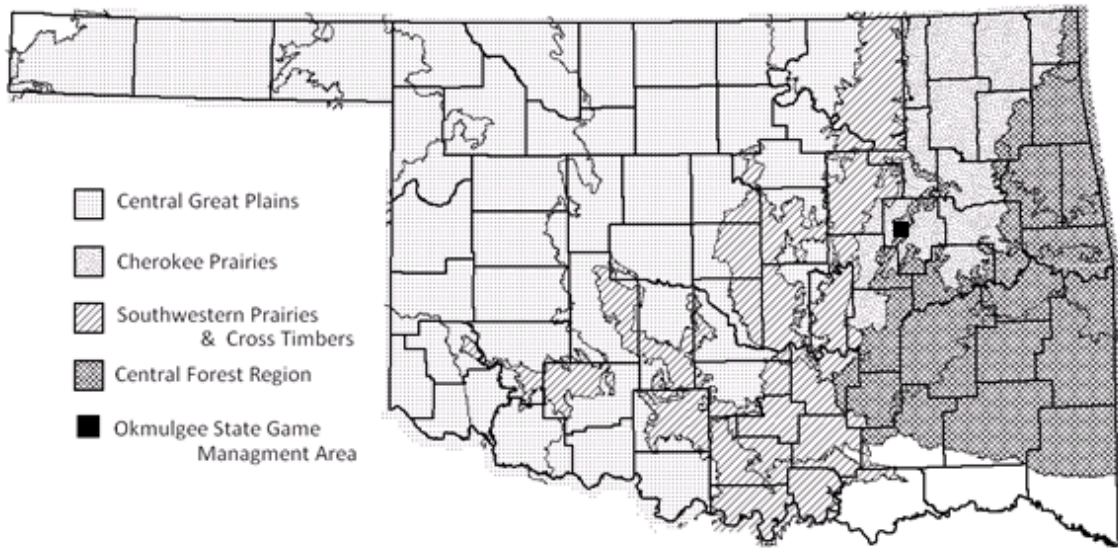
## **METHODS**

### Study Area

This study was located at the Okmulgee State Game Management Area (OGMA) in Okmulgee County, Oklahoma (Figure 6). The primary objective for the OGMA is providing habitat for game species and increasing hunting and fishing opportunities for license holders. Like other areas managed by the Oklahoma Department of Wildlife Conservation, additional objectives include providing habitat for non-game species and maintaining biodiversity.

The OGMA is primarily forestland; approximately 85 percent of 2,400 hectares is upland forest on non-arable soils and rugged topography of 5-30 percent slopes. Due to poor timber value and shallow rocky soils these sites have remained comparatively undisturbed (Stahle and Chaney 1994). The upland forests at OGMA are dominated by post oak, *Quercus stellata*, with subdominants of blackjack oak, *Q. marilandica*, and black hickory, *Carya texana* (Chapter 1). Duck and Fletcher (1945) classified this area as part of the Post Oak – Blackjack Oak forest type, locally referred to as the Cross Timbers Forest. More recent land type classifications have placed this area into the East and Central Farming and Forest Region - Arkansas Valley and Ridges (N-118B) land use type (USDA NRCS 2006).

## OKLAHOMA



**Figure 6 | Location of the Okmulgee State Game Management Area (OGMA) and surrounding land resource areas. Modified illustration from USDA NRCS (2006). OGMA is in a forest peninsula at the western edge of the central forest region, surrounded by the lower lying mesic Cherokee Prairies.**

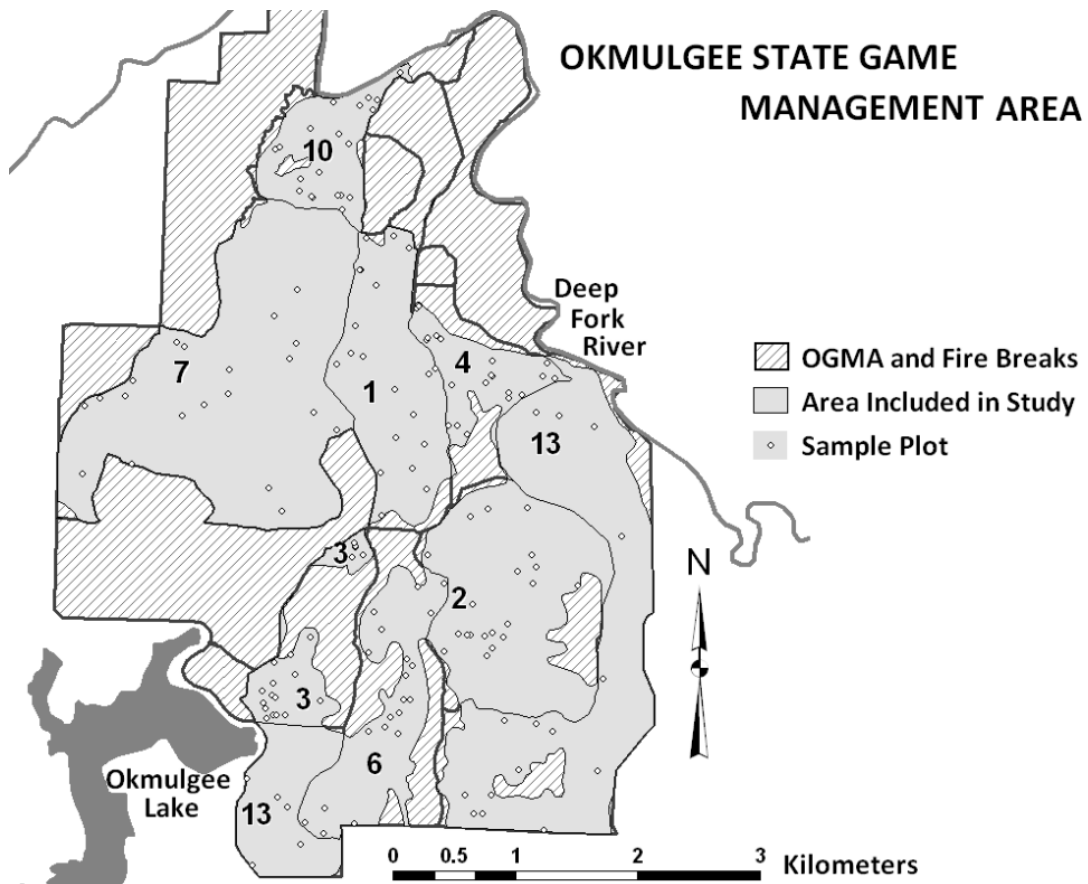
Mean annual temperature for Okmulgee County is 16.1° C; however, temperatures have a range of mean highs of 33.9° C in July to mean lows of -3.9° C in January. The area has a humid subtropical climate receiving approximately 111 cm of precipitation annually; however, precipitation can be highly variable with a range of 54.5 cm to 156.2 cm annually (Oklahoma Climatological Survey 2005).

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

In 1988, a prescribed burn plan was established for the OGMA with the goal of increasing forage production and landscape heterogeneity. The burn treatment units ranged in size from 100 to 600 ha and fire frequencies ranged from zero to five per decade (Figure 7). It was assumed the vegetation was largely the same in all units prior to the beginning of treatment. Within five years the units that were burned showed a significant increase in graminoid cover compared to the non-burned treatment (Burton 1993). There were no significant differences among the various burn frequencies.

All fires were carefully documented and set in the months of February and March (Table 3). Prescribed fires were set when relative humidity was between 30 to 50 percent, temperature < 27° C, and winds < 25 kph; conditions considered ideal by

managers for prescribed fire containment. In March 2005 unit 10 experienced the only wildfire



**Figure 7 | Okmulgee State Game Management Area prescribed burn treatment units and plot locations. Area included in study contains undisturbed upland forests on the Hector-Endsaw complex soil type. Numbers correspond to burn unit identification number.**



**Table 3 | Year and month of prescribed fires by units. \*Indicates arson set fire occurring outside of management prescriptions.**

Year	Burn Unit							
	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								
Total Fires	10	5	4	7	4	2	6	0
Fires per Decade	5.0	2.5	2.0	3.5	2.0	1.0	3.0	0.0
Years Since Last Fire	1	1	3	0	0	3	3	20+

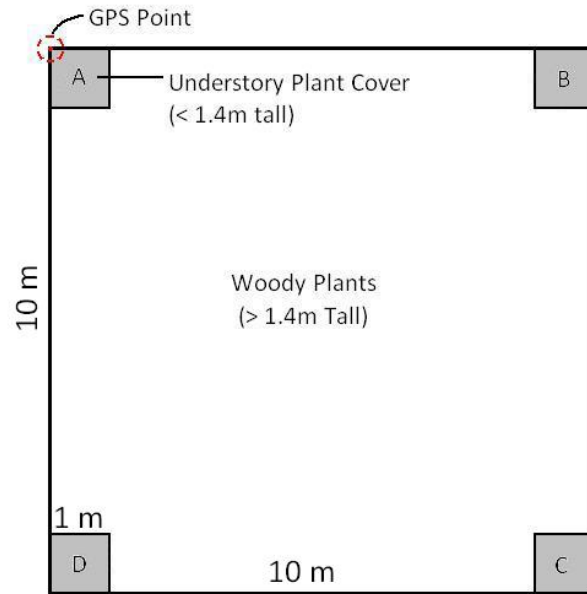
during the past 20 years that was outside the prescriptions described above; relative humidity was less than 20 percent and wind speeds were in excess of 35 kph.

### Sample Design

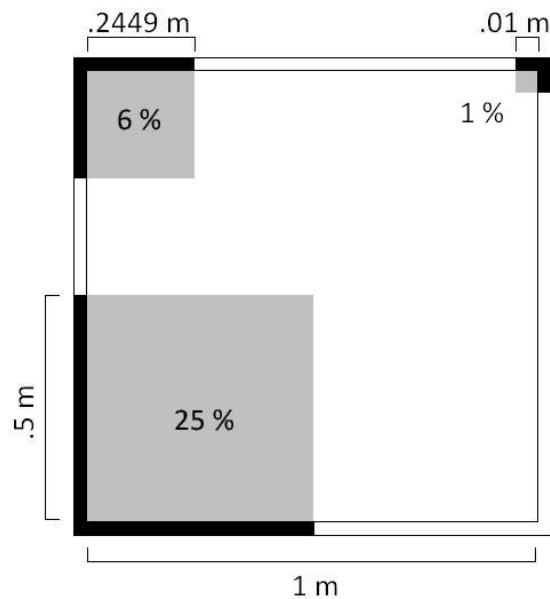
ArcMap was used to map treatment units and randomly locate 20 sample plots within each (ESRI 2007; Appendix II, III). No sample plots were located within 10 m of a firebreak, road or other human caused opening. I located each plot in the field with a Trimble Geo XT® GPS unit utilizing Wide Area Augmentation System (WAAS) for sub-meter accuracy from June 19 to August 8, 2008.

After the plot corner was located in the field, a plot stake was spun to randomly determine the direction of the corner as southeast, southwest, northeast, or northwest. The sides of the plot were measured in each of the cardinal directions using an engineering compass to form a 10 x 10 meters (0.01 ha) square (Figure 8). Measurements made within each plot included diameter at breast height (1.4 m) of all shrubs, saplings, and trees greater than 1.4 meters tall, slope, and aspect.

Four square 1 m<sup>2</sup> sub-plots were nested within each of the four corners of the sample plots (Figures 8). At each sub-plot, I visually estimated the following percentages: exposure of soil, leaf litter, rock, vascular plant functional group, vascular plant species, and overstory canopy cover. I visually estimated ground and plant cover within the one meter sub-plots utilizing a customized Braun-Blanquet cover scale (Kent and Coker 1992; Figure 9). A 1m<sup>2</sup> PVC plastic frame was marked on each corner with a



**Figure 8 | Sample plot layout. Woody plants greater than breast height were measured in 10 x 10 m plot and all other vascular plants were sampled within four 1 x 1 m nested sub-plots.**



**Figure 9 | Sub-plot frame design and cover classes. An assigned cover class value of 1 is  $\leq 1\%$ , 2 is  $> 1\% \ \& \ \leq 6\%$ , 3 is  $> 6\% \ \& \ \leq 25\%$ , 4 is  $> 25\% \ \leq 50\%$ , 5 is  $> 50\% \ \leq 75\%$ , and 6 is  $> 75\%$ .**

cover scale increment. A key was used to identify all plants to species level with the exception of a few taxonomic groups which were classified to genus level (Diggs et al. 1999, Yatskievych 1999; Appendix I); therefore, measurements of richness are estimations. Nomenclature for all plant species follows the PLANTS database (USDA NRCS 2008). I measured litter depth at 4 points in the sub-plots using a 150 mm metric dial caliper's depth gauge to the nearest 0.5 cm. Overstory canopy cover directly over the center of each sub-plot was measured using a forest canopy Model-A Spherical Densiometer (Lemmon 1956, Nuttle 1997).

In September of the same year, biomass samples were collected from three treatments with zero (unit 13), two and one-half (unit 2) and five (unit 1) burns per decade. One year had elapsed since the last fire for both units that had been burned. I collected biomass from five 200 meter transects in each treatment. Transects were randomly located and consisted of 5 quarter meter square frames spaced 50 meters apart. All plant matter was collected to mineral soil surface from plants < 1.4 meters tall. Living plant matter was classified by functional group, and dead plant matter was classified as litter. Samples were dried at 70° C and weighed.

### Data Analysis

Species cover data was used to calculate richness, diversity, and evenness indices. Species diversity was calculated using Simpson's diversity index ( $1/D$ ) and Shannon's diversity index ( $H'$ ) (Begon et al. 2006). The means and standard errors of response variables including ground cover, foliar cover, species richness and diversity

indices were calculated for each of the eight treatments based on 20 samples per treatment. Basal area ( $\text{m}^2 \text{ha}^{-1}$ ) was calculated from the dbh measurements. Foliar cover was analyzed by species and functional group. All plant functional group and species cover data values were square-root transformed by plot prior to statistical analysis. The treatment with no fire was excluded from time since last fire analysis.

Regression analysis was conducted to determine the significance of the relation between response variables and both fire frequency and time since last fire by species and plant functional group. When the P value for the regression was  $\leq 0.05$  the relation was considered significant and when it was  $> 0.05$  and  $\leq 0.10$  it was considered weakly significant. Analysis of variance was conducted to test for effects of fire frequency on biomass and foliar cover at  $P \leq 0.05$  for zero, two and one-half, and five fires per decade. Rare species that only occurred in two or less treatments were not included in species response analysis.

## **RESULTS**

### Forest Structure

Total basal area ranged from 22.6 to 26.7  $\text{m}^2 \text{ha}^{-1}$  and was not significantly altered by fire frequency ( $P = 0.8617$ ). Overstory canopy cover ranged from 88.5 to 95.7 percent and likewise showed no significant response to fire frequency ( $P = 0.1702$ ). The lowest percent canopy cover was measured in treatment unit 10 (three fires per decade). This treatment was the only sampled unit to have experienced a wildfire

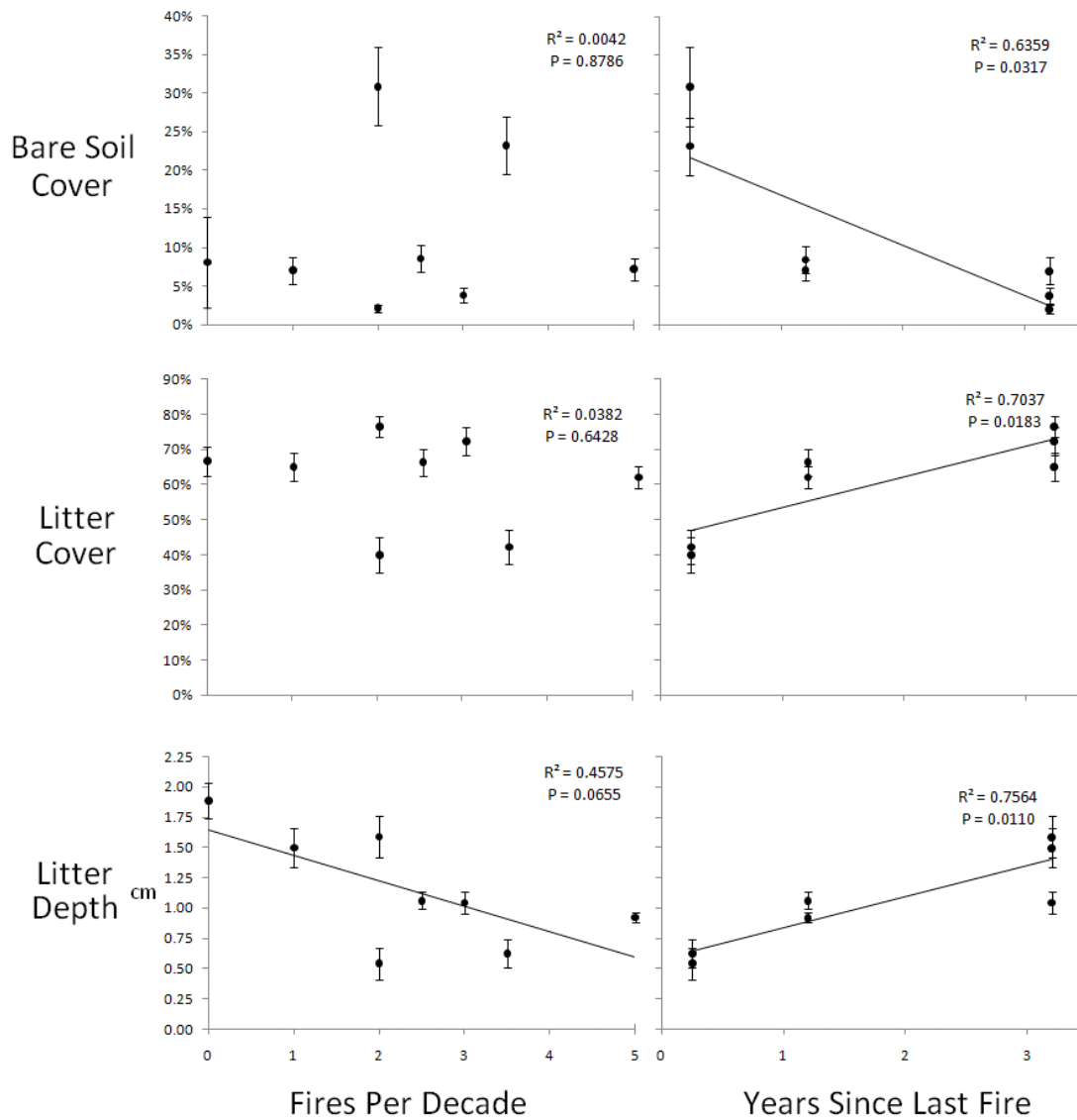
outside of normal prescription conditions and mortality of some fire intolerant species, such as *Ulmus alata*, was apparent.

### Ground Cover

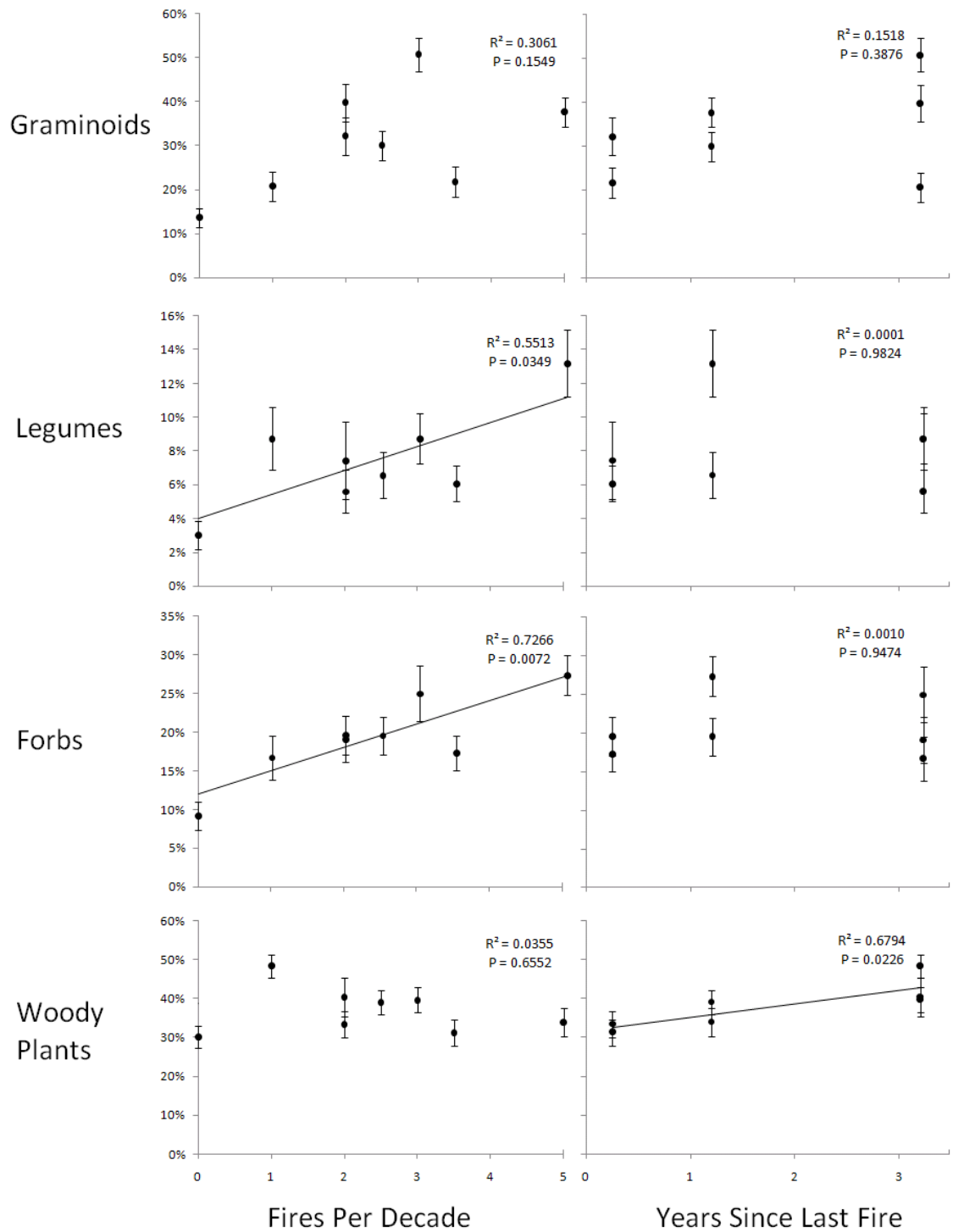
Ground surface covers responded more strongly to time since last fire than to fire frequency (Figure 10). The effect of time since last fire was significant for exposed soil, litter cover, and litter depth ( $P < 0.05$ ). Exposed soil, rock, and litter cover were strongly affected by time since last fire but not by fire frequency. Mean litter depth ranged from 1.89 cm in the treatment with no fire to 0.54 cm in treatment unit 6 (two fires per decade / three months since last fire) and was weakly affected by fire frequency ( $P = 0.0655$ ). Surface rock cover ranged from 26.4 to 10.1 percent and a change in cover was not detected based on fire frequency or time since last fire ( $P = 0.890, 0.188$  respectively).

### Understory Functional Groups

Effect of fire frequency on understory vegetation cover varied for each plant functional group (Figure 11). Cover of forbs, both legume and non-legume, significantly increased with fire frequency ( $P = 0.0349, 0.0072$  respectively). Woody plant cover ranged from 30.2 to 48.3 percent and showed no significant of fire frequency. Graminoid cover ranged from 13.5 to 50.7 percent and showed no significant effect of fire frequency. Woody plant cover did not show an effect of fire frequency; however, it is the only plant functional group that increased with time since last fire ( $P = 0.655$ ,



**Figure 10 | Fire frequency and time since last fire effects on ground surface cover. Points represent observed mean cover for each cover type or mean depth of litter at each treatment unit. Error bars indicate standard error of treatment unit means. Solid lines indicate significant linear relationships.**



**Figure 11 | Fire frequency and time since last fire effects on plant understory cover by functional group. Points represent mean cover for each functional group at each treatment unit. Error bars indicate standard error of treatment unit means. Solid lines indicate significant linear relationships.**



0.023 respectively). The proportion of total understory cover that was woody was negatively affected by increasing fire frequency ( $P = 0.009$ ) but not time since last fire ( $P = 0.655$ , data not shown).

### Understory Biomass

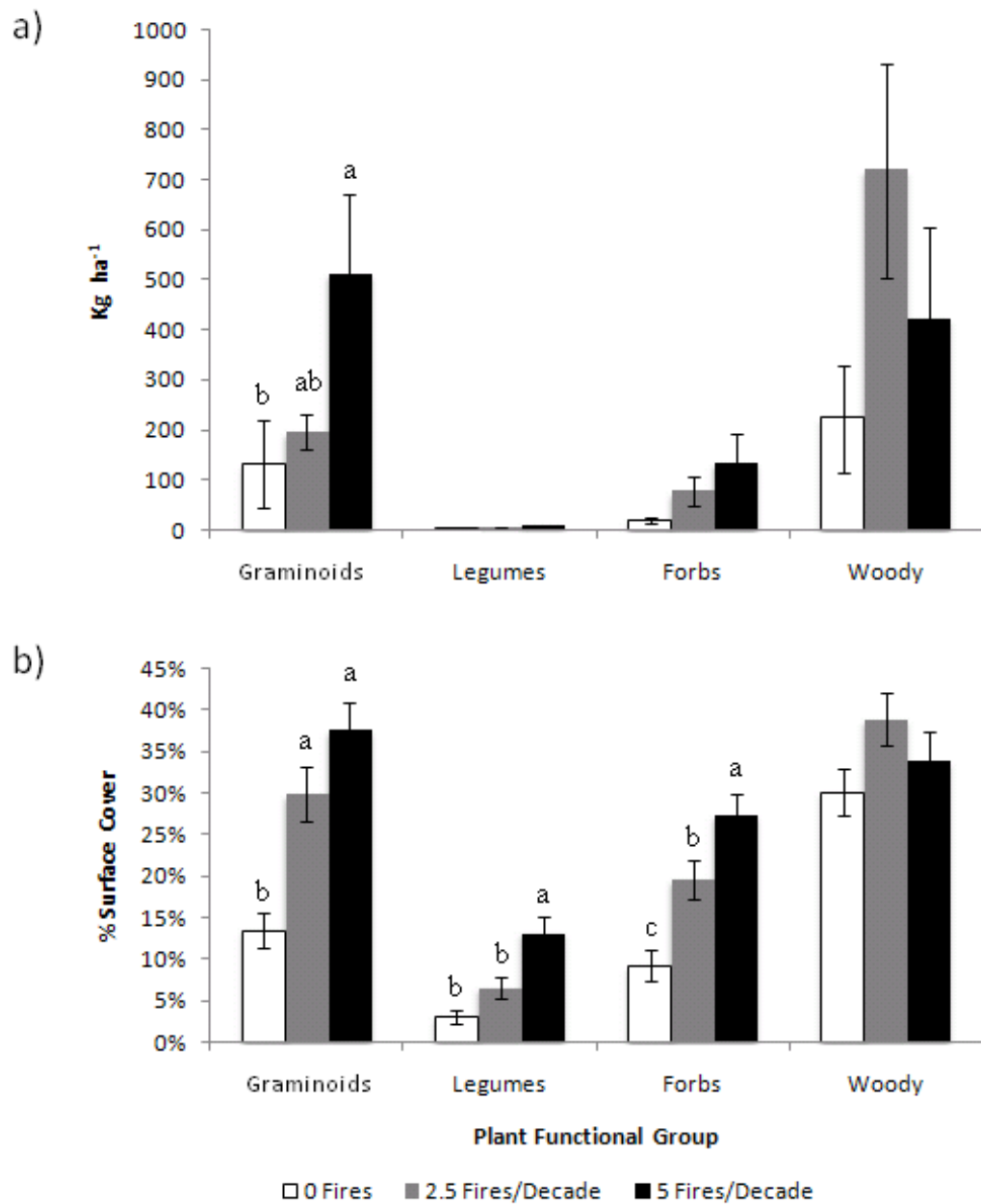
Total understory live vegetation biomass ranged from 371 to 1070  $\text{Kg ha}^{-1}$  and showed no significant relation to fire frequency. Graminoid biomass increased with increasing fire frequency (Figure 12). Cover by functional group of zero, two and one-half, and five fires per decade responded to fire frequency in a similar way to biomass. Graminoid, legumes, and forbs showed significant increases in cover with increasing fire frequency.

### Understory Plant Richness

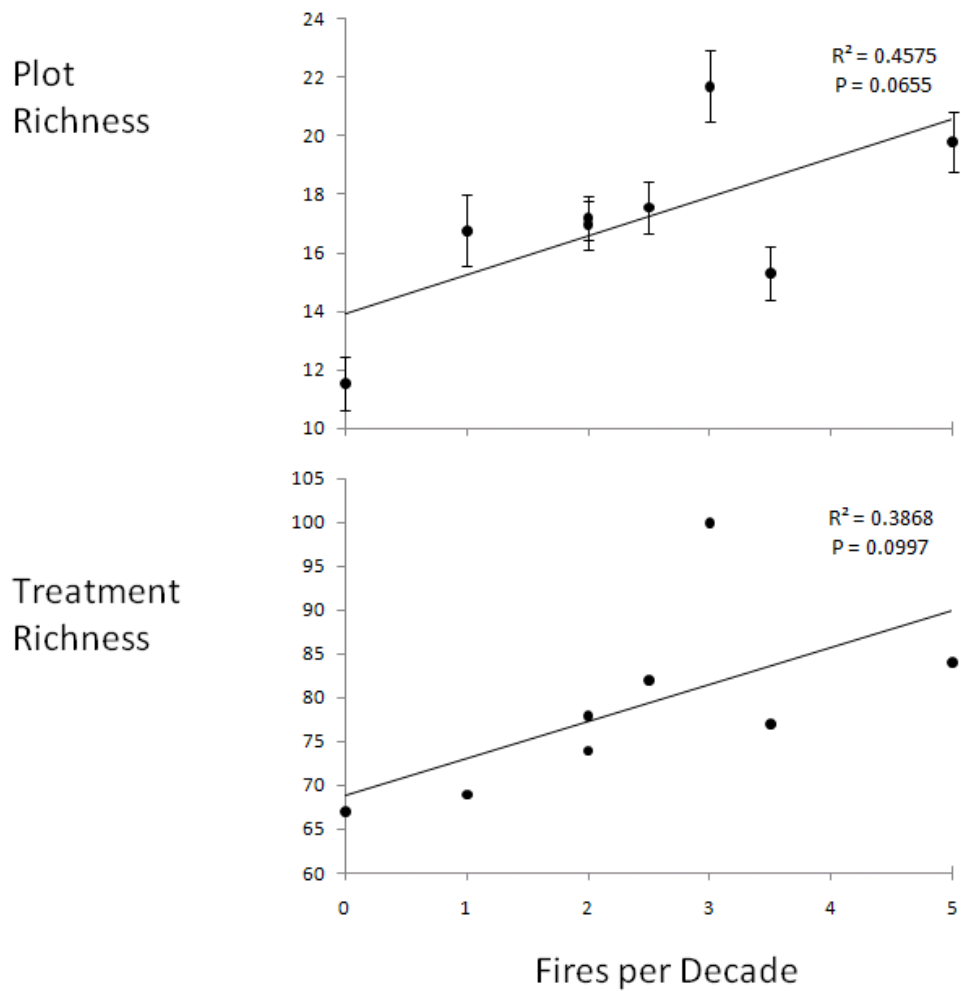
Over 170 species or genera were found within plots or sub-plots during the sampling period. Mean plot species richness and total treatment richness showed increases with fire frequency (Figure 13). The lowest mean plot richness was 11.35 in unit 13, which has had no fires in at least twenty years. No clear trends were apparent for effect of time since last fire on species richness. Fire frequency appeared to have a greater impact than time since last fire on richness.

### Plant Functional Group Species Richness

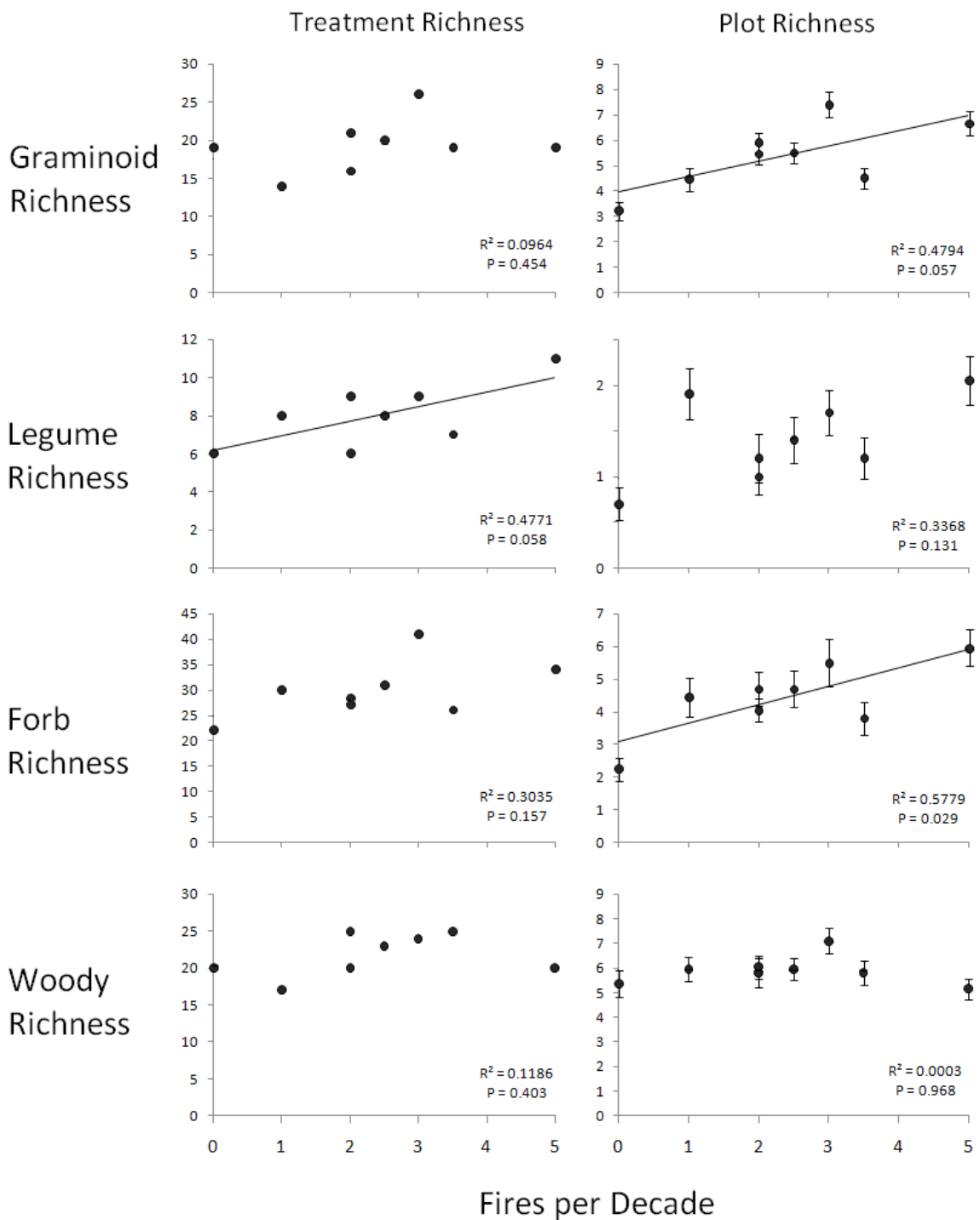
Species richness responses to fire frequency depended on plant functional group (Figure 14). Forb richness showed a significant linear increase in mean plot richness



**Figure 12 | Effect of fire frequency on understory plants by functional group. a) Biomass of treatment units. b) Cover values of same treatment units. Error bars represent standard error of sample treatment means. Letters indicate significant differences.**



**Figure 13 | Effect of fire frequency on mean plot and total treatment vascular plant richness. Error bars indicate standard error of treatment unit means. Solid lines indicate linear relations that were weakly significant.**



**Figure 14 | Effect of fire frequency on functional group species richness. Error bars indicate standard error of treatment unit means. Solid lines indicate significant linear relationships.**

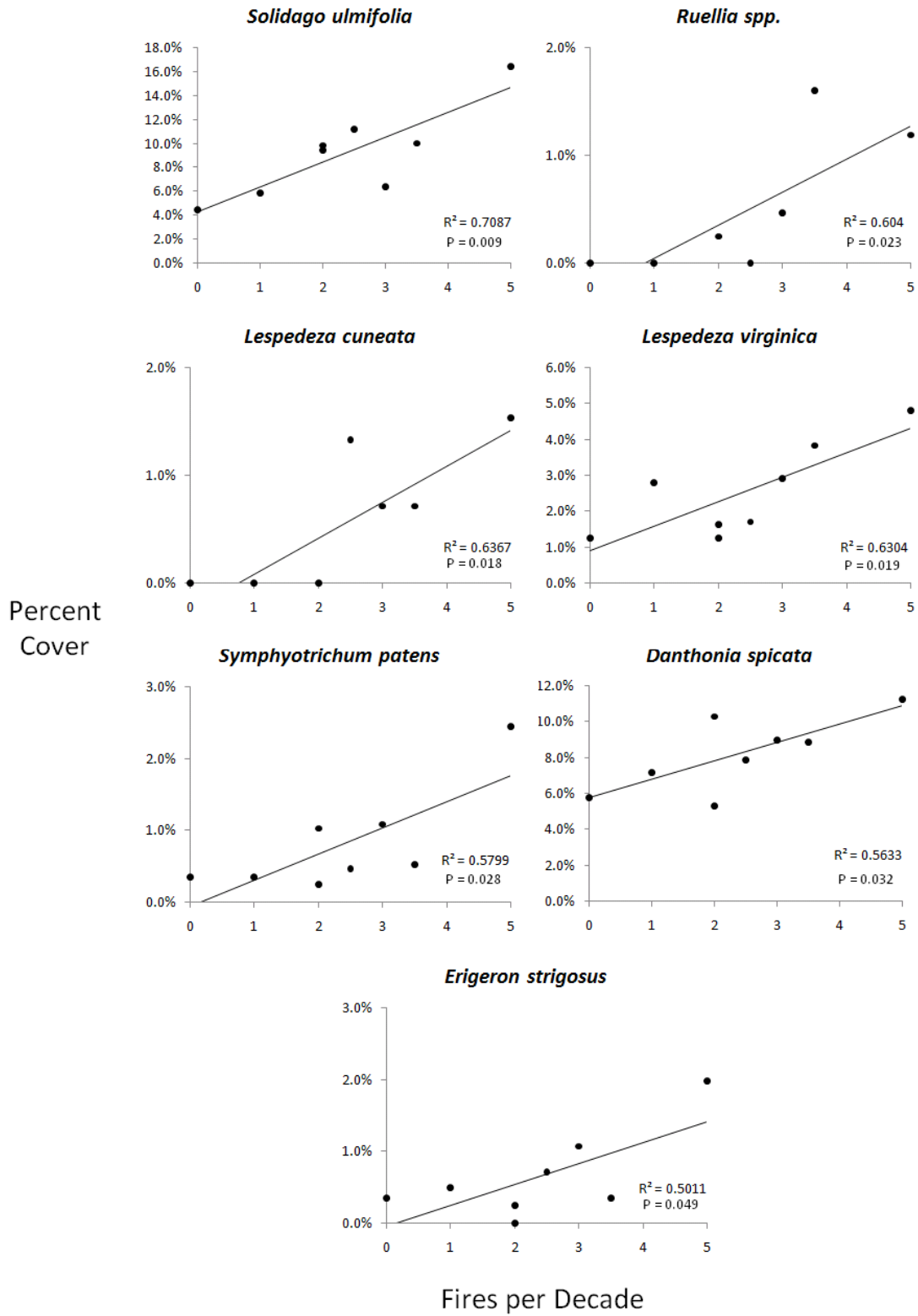
with fire frequency. All herbaceous plant functional groups showed increases in richness with increasing fire frequency at either the mean plot level or treatment level. Understory woody plant richness was not affected by fire frequency. None of the plant functional groups showed a significant species richness response to time since last fire ( $P > 0.10$ ).

#### Understory Plant Species Responses

The four woody species which occurred in at least 50 percent of the sample plots were: *Ulmus alata*, *Rhus aromatica*, *Parthenocissus quinquefolia*, and *Quercus stellata*. None of these species had a measurable response to fire frequency or times since last fire ( $P < 0.05$ ). The five herbaceous species occurring in 50 percent of the plots included the C<sub>3</sub> graminoids *Danthonia spicata*, *Dichanthelium linearifolium*, and *Carex* spp. and the forbs *Solidago ulmifolia* and *Monarda russeliana*. Both *D. spicata* and *S. ulmifolia* showed increases in cover with increasing fire frequency.

When utilizing presence-absence of species within plots, six herbaceous species showed increases in abundance with increasing fire frequency. These species include the perennial forbs *Solidago ulmifolia*, *Ruellia* spp., *Rudbeckia hirta*, *Penstemon* spp., and *Conyza canadensis* and the legume *Lespedeza virginica* (data not shown).

When considering species cover values, seven understory plant species had positive linear responses to increased fire frequency (Figure 15). The species were all herbaceous species and included: *S. ulmifolia*, *Lespedeza cuneata*, *L. virginica*, *Ruellia* spp., *Symphotrichum patens*, *Danthonia spicata*, and *Erigeron strigosus*. The number



**Figure 15 | Effect of fire frequency on cover of herbaceous species. Solid lines indicate significant linear relationships.**

of species with positive responses to fire frequency in cover would have increased to 20 if  $P < 0.10$ .

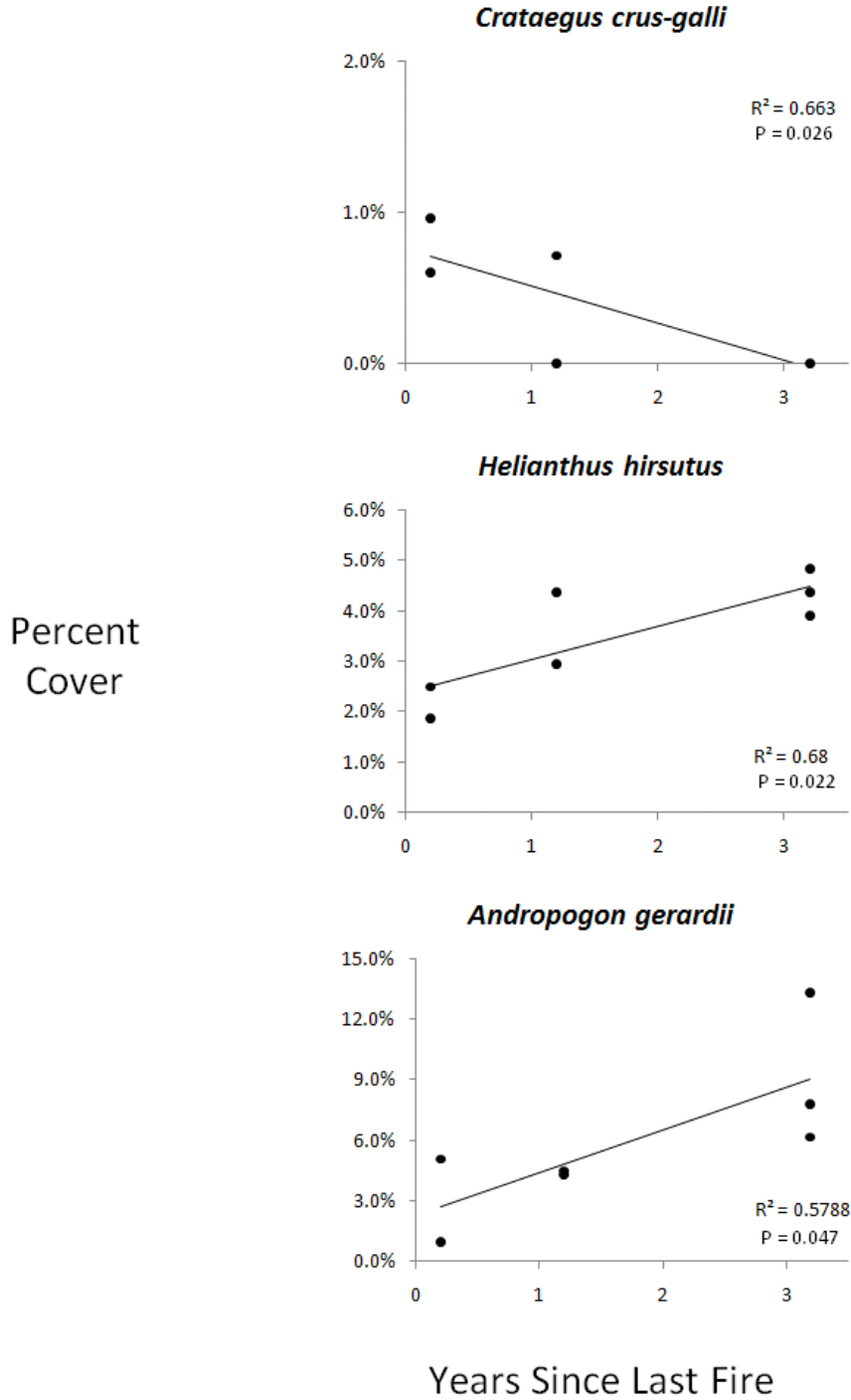
The five species that declined in presence-absence as time passed since last fire included the woody species *Crataegus crus-galli*, *Prunus serotina*, and *Quercus rubra*, the graminoid *Carex* spp., and the legume *Amphicarpaea bracteata*. Only one species, *Rhus glabra*, significantly increased in presence after time since last fire.

The woody species *Crataegus crus-galli* decreased in cover with time since last fire, while the commonly encountered perennial forb *Helianthus hirsutus* and  $C_4$  graminoid *Andropogon gerardii* had increasing abundances after time progressed since last fire (Figure 16). Nine species responded to time since last fire, at  $P < 0.10$ .

Only five species occurred exclusively in the treatment with no fire and all these species occurred in a single plot within the treatment; therefore, they should be considered rare not fire intolerant. In fact, all are commonly encountered in prairie locations that would be considered fire dependent. The number of rare species was not affected by either fire frequency or time since last fire (data not shown).

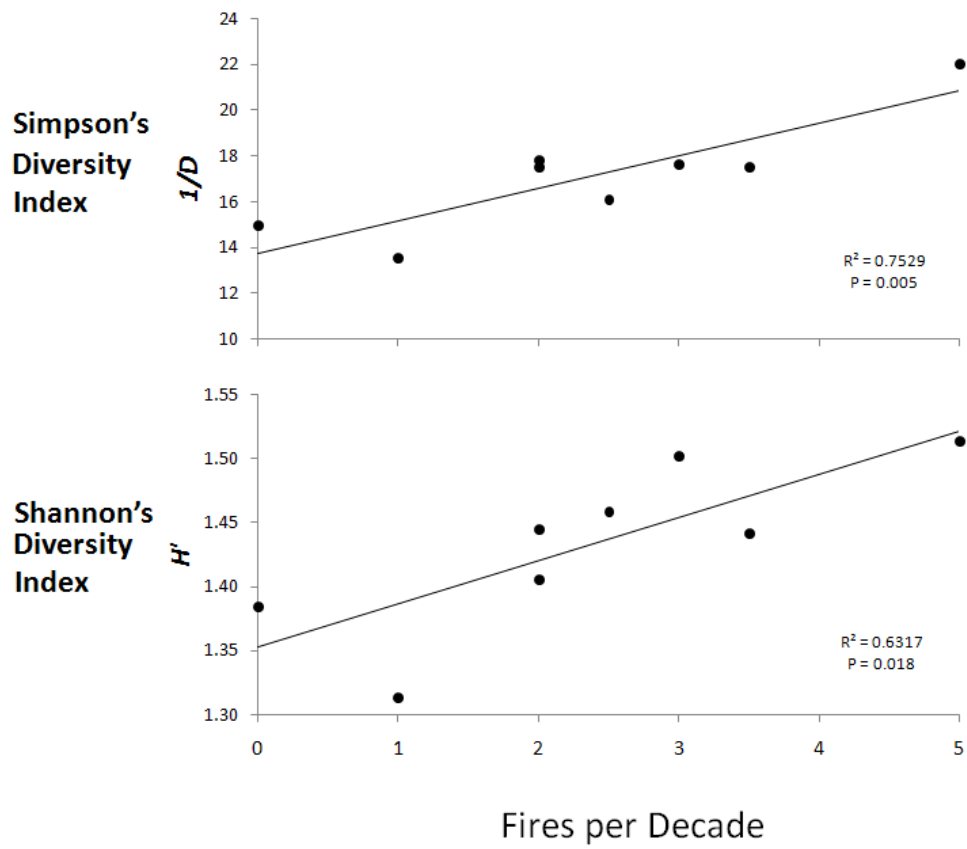
### Species Diversity

Understory plant species diversity was greater for more frequently burned treatments. Both the Shannon's diversity index ( $H'$ ) and Simpson's diversity index ( $1/D$ ) responded positively to fire frequency ( $P = 0.018, 0.005$  respectively; Figure 17). Responses of diversity to fire frequency were not unimodal but linear.



**Figure 16 | Effect of time since last fire on species cover. Solid lines indicate significant linear relationships.**





**Figure 17 | Effect of fire frequency on species diversity indices. Solid lines indicate significant linear relationships.**

Simpson's Index of Diversity and Shannon's Diversity Index were not linearly correlated with time since last fire. Although richness was highest for the unit which had experienced a wildfire in 2005 (Unit 10), species evenness was lowest by Simpson's equitability index ( $E = 0.17$ ) for this unit. Equitability was highest for the highest burn frequency for both indices ( $E = 0.27, J = 0.79$ ). No significant relationship of fire frequency or time since last fire for either index of evenness was found ( $P < 0.10$ ).

## **DISCUSSION**

The results of this study demonstrated that twenty years of prescribed fire in this oak dominated forest had very little impact on the overstory component while significantly increasing herbaceous vegetation cover, biomass, and diversity. This suggests low light under dense canopy cover is likely not the only factor limiting understory herbaceous plants. Other studies have found understory plant diversity may be maximized at intermediate levels of canopy cover which provides high plant resource heterogeneity (Leach and Givnish 1999). In contrast, the current study found plant diversity to respond directly to an increase in fire frequency alone where there were no observable differences in canopy cover or basal area. Light resource heterogeneity does not appear to be involved in the significant increase in plant diversity at this study site. This is the first study to show a significant response to fire frequency of understory plant composition in xeric oak forests.

Litter consumption by repeated burning could explain in part the increases in herbaceous vegetation by creating a more favorable environment for germination and establishment of plants. Reduced litter may increase germination success by increasing mineral soil surface temperatures during spring months and reducing potential physical barriers to seed deposition, hypocotyl development, and seedling emergence (Sydes and Grimes 1981, Facelli and Pickett 1991b). The obstacles created by woody plant litter may give woody plants a competitive advantage over herbaceous plants during establishment in forest understories (Facelli and Pickett 1991a). In xeric longleaf pine (*Pinus palustris*) woodlands herbaceous vegetation was more severely impacted by litter deposition and subsequent forest floor development than by overstory canopy cover and midstory tree density (Hiers et al. 2007).

Burning may indirectly affect herbaceous plants through its large immediate and beneficial effects on availability of plant nutrients. The availability of macronutrients such as potassium and phosphorus can increase in the mineral soil due to their release from organic material and deposition into the soil (Grove et al. 1986, Lynham et al. 1998). However, the fate of phosphorus due to volatilization is not well studied (Neary et al. 2005). Although total nitrogen in the litter layer is reduced by volatilization during heating by surface fires, after low intensity fires it has been found that a portion of nitrogen stored in the litter is converted to plant available nitrogen ( $\text{NH}_4\text{-N}$ ) and deposited into the mineral soil (Covington and Sackett 1986, Kutiel and Naveh 1987, Neary et al. 2005). The release of mineral bases in ash may generate a more favorable environment for free living nitrogen-fixing bacteria with higher nutrient availability and

pH (Barbour et al. 1987). By-products of incomplete combustion, such as charcoal, may also increase nutrient retention capacity by improving exchange capacity (Glaser et al. 2002).

Secondary impacts of frequent litter removal by fire may include the destruction of secondary plant chemicals such as tannins and the concomitant reduction in their impacts on nutrient cycling. Tannins deposited into the mineral soil by decomposing woody plant litter may limit N mineralization by binding proteins of decomposing plant matter thus decreasing microbial efficiency and reducing decomposition rates (Basaraba and Starkey 1966, Kalburtji et al. 1999, Kraus et al. 2003, Talbot and Finzi 2008). Tannins have been found to reduce N-fixation in certain plants (Schimel et al. 1998). The reduction in the capacity for legumes to fix nitrogen in these nitrogen limiting soils would greatly affect their abundance in an environment with few fires. In nutrient poor soils herbaceous species may have more difficulty becoming established relative to persistent long lived woody sprouts. The impacts of tannins in soil ecosystems may be capable of modifying forest successional pathways and general ecosystem function (Kraus et al. 2003).

An increase in herbaceous vegetation may have resulted from the reduction of saplings and shrubs at the higher fire frequencies (Chapter 1). In the absence of fire shrubs and saplings may have a more amensalitive interaction with herbaceous species for light resources, with herbaceous species being negatively impacted. Conversely, saplings may not be excluding herbaceous vegetation directly by light interception but

indirectly by increasing litter deposition (Hiers et al. 2007). When fires are frequent understory saplings and shrubs may be more competitive with herbaceous species for light resources because they have the same stature. However, the competitive effects of herbaceous vegetation on woody plants may be slight or insignificant (Knoop and Walker 1985). The density of many woody plants, such as *Crataegus crus-galli*, may not be altered by frequent fire, as most readily re-sprout and may simply be moved from the sapling or shrub class to the smaller sprout and seedling vegetation class following fires.

The interaction of fire and herbivory has not been well studied in forested ecosystems and its impacts on forest vegetation have not been appreciated (Laughlin et al. 2008). Browse may become more palatable and nutrient rich immediately after a fire (Reich et al. 1990, Van de Vijver et al. 1999, Ferwerda et al. 2006). This may cause grazing and browsing populations to move and congregate in recently burned areas (Fuhlendorf and Engle 2001, 2004, Fuhlendorf et al. 2009). The perennial sunflower (*Helianthus hirsutus*), a highly palatable species for white-tailed deer (*Odocoileus virginianus*), was not found to significantly increase with fire frequency, while strongly increasing with time since last fire. If this species were heavily browsed in the units with recent and frequent burns, this may explain why we could not detect an increase with fire frequency. I observed many instances where plants, particularly newly emergent forbs such as *H. hirsutus*, were browsed. Preference for more palatable species such as forbs which greatly increased with more frequent fire may have important impacts on regeneration of less desirable woody species such as oaks (Bryant et al. 1981). When

production of herbaceous plants is low on landscapes where fire is absent oak regeneration may be suppressed by deer because they cannot find enough preferred forage. The fire-floral-faunal interactions in forest ecological studies are deserving of further study.

I found that vascular plant richness significantly increased up to the highest fire frequency of five fires per decade. This could be viewed as support for the Most Frequent Fire Hypothesis because the highest burn frequency produced the highest diversity of understory plants, but higher burn frequencies were not tested at the OGMA. Plant species richness and diversity in a Minnesota oak forest and savanna increased with fire frequency up to 5 fires per decade and then decreased at higher frequencies. That maximum diversity occurred at an intermediate fire frequency was taken as support for the Intermediate Disturbance Hypothesis (Tester 1989, Peterson and Reich 2008). The results of the current study are inconclusive in supporting either of the two hypotheses, as the study did not include fire frequency higher than five fires per decade. Herbaceous fuel production was likely to be adequate for increased burning frequencies in units that had a history of frequent fire (Table 3, *personal communication* B. Burton). Additional fires per decade could either continue to increase understory vegetation diversity at this site (Glitzenstein et al. 2003) or reduce diversity as more frequent fire may begin to remove species, particularly woody species (Grime 1973, Peterson and Reich 2008).

The results of this study show that herbaceous diversity can be managed over time with long-term fire management prescriptions. While the results of timber thinning to remove canopy cover can produce more immediate responses (Engle et al. 2006, Masters et al. 2006), long-term management of forests with prescribed fire can meet many management objectives without the high costs of mechanical or chemical treatments of overstory vegetation.

## OVERALL CONCLUSIONS & IMPLICATIONS FOR MANAGEMENT

The findings of this research lead to the conclusions that frequent low-intensity fire is necessary to maintain both the dominance of fire tolerant oak species and the high biodiversity of herbaceous plants. Fire-intolerant shrub and sapling density and richness increase as fire frequency is reduced from zero to five fires per decade. More specifically, the following conclusions are supported:

- Twenty years of low intensity fire at a frequency of five per decade is not sufficient for the reduction in tree density and canopy cover of existing stands.
- Frequent low intensity fires in the range of two to five per decade are sufficient to maintain oak overstory dominance, as this frequency will control fire-sensitive woody shrubs and saplings while not reducing the density of oak saplings that eventually grow into the canopy.
- Herbaceous species in the xeric oak forests appear to be well adapted to periodic low intensity fire, as many species showed a positive response and none showed a negative response to fire frequency.
- Landscapes with a diverse mosaic of forest understories can be produced by prescribe burning at varying frequencies and times since last fire.



## LITERATURE CITED

- Abrams, M. D. 1986. Historical development of gallery forests in northeast Kansas. *Vegetatio* 65:29-37.
- Abrams, M. D. 1992. Fire and the development of oak forests - in eastern North-America, oak distribution reflects a variety of ecological paths and disturbance conditions. *Bioscience* 42:346-353.
- Abrams, M. D. 1996. Distribution, historical development and ecophysiological attributes of oak species in the eastern United States. *Annals of Forest Science* 53:487-512.
- Abrams, M. D. 2003. Where has all the white oak gone? *Bioscience* 53:927-939.
- Alexander, H. D., M. A. Arthur, D. L. Loftis, and S. R. Green. 2008. Survival and growth of upland oak and co-occurring competitor seedlings following single and repeated prescribed fires. *Forest Ecology and Management* 256:1021-1030.
- Axelrod, D. I. 1985. Rise of the grassland biome, central North-America. *Botanical Review* 51:163-201.
- Barbour, M. G., J. H. Burk, and W. D. Pitts. 1987. *Terrestrial Plant Ecology* (2<sup>nd</sup> ed.). The Benjamin/Cummings Publishing Company Inc., Menlo Park, CA.
- Basaraba, J. and R. L. Starkey. 1966. Effect of plant tannins on decomposition of organic substances. *Soil Science* 101:17-23.
- Baskett, T. S., R. L. Dunkeson, and S. C. Martin. 1957. Responses of forage to timber stand improvement in the Missouri Ozarks. *The Journal of Wildlife Management* 21:121-126.

- Begon, M., R. T. Colin, and J. L. Harper. 2006. *Ecology: From Individuals to Ecosystems* (4th ed.). Blackwell Publishing, Malden, MA.
- Blake, J. G. and B. Schuette. 2000. Restoration of an oak forest in east-central Missouri - early effects of prescribed burning on woody vegetation. *Forest Ecology and Management* 139:109-126.
- Bond, W. J. and J. E. Keeley. 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution* 20:387-394.
- Bond, W. J., F. I. Woodward, and G. F. Midgley. 2005. The global distribution of ecosystems in a world without Fire. *New Phytologist* 165:525-537.
- Bowman, D., J. K. Balch, P. Artaxo, W. J. Bond, J. M. Carlson, M. A. Cochrane, C. M. D'Antonio, R. S. DeFries, J. C. Doyle, S. P. Harrison, F. H. Johnston, J. E. Keeley, M. A. Krawchuk, C. A. Kull, J. B. Marston, M. A. Moritz, I. C. Prentice, C. I. Roos, A. C. Scott, T. W. Swetnam, G. R. van der Werf, and S. J. Pyne. 2009. Fire in the earth system. *Science* 324:481-484.
- Brockway, D. G. and C. E. Lewis. 1997. Long-term effects of dormant-season prescribed fire on plant community diversity, structure and productivity in a longleaf pine wiregrass ecosystem. *Forest Ecology and Management* 96:167-183.
- Brown, J. K. and J. K. Smith. 2000. *Wildland fire in ecosystems: effects of fire on flora*. Gen. Tech. Rep. RMRS-GTR-42 2. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT
- Bruner, W. E. 1931. The vegetation of Oklahoma. *Ecological Monographs* 1:100-188.
- Bryant, F. C., C. A. Taylor, and L. B. Merrill. 1981. White-tailed deer diets from pastures in excellent and poor range condition. *Journal of Range Management* 34:193-200.
- Burton, L. D. 1993. *A Vegetational Comparison of Burned Areas in Northeastern Oklahoma*. Master's Thesis. Northeastern State University, Tahlequah, OK.

- Clark, F.B. 1993. An historical perspective of oak regeneration. *in* Loftis, D. & McGee, C.E. (eds.) *Oak regeneration: Serious problems, practical recommendations*. USDA Forest Service, Southeastern Forest Experimentation Station, Asheville, NC.
- Clark, S. L. and S. W. Hallgren. 2003. Dynamics of oak (*Quercus marilandica* and *Q. stellata*) reproduction in an old-growth cross timbers forest. *Southeastern Naturalist* 2:559-574.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs - high diversity of trees and corals is maintained only in a non-equilibrium state. *Science* 199:1302-1310.
- Covington, W. W. and S. S. Sackett. 1986. Effect of periodic burning on soil-nitrogen concentrations in ponderosa pine. *Soil Science Society of America Journal* 50:452-457.
- Cowles, H. C. 1928. Persistence of prairies. *Ecology* 9:380-382.
- 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. 2004. *Prehistoric Native Americans and Ecological Change: Human Ecosystems in Eastern North America Since the Pleistocene*. Cambridge University Press, Cambridge, UK.
- DeSantis, R. D., S. W. Hallgren, M. W. Palmer, T. B. Lynch, and J. A. Burton. Submitted 2009. Long-term directional changes in upland oak forests throughout Oklahoma, USA. *Journal of Vegetation Science*.
- Diggs, G. M., B. L. Lipscomb, and R. J. O'Kennon. 1999. *Shinner's and Mahler's Illustrated Flora of North Central Texas*. Botanical Research Institute of Texas (BRIT). Fresno, CA.
- Dorney, C. H. and J. R. Dorney. 1989. An unusual oak savanna in northeastern Wisconsin - the effect of Indian-caused fire. *American Midland Naturalist* 122:103-113.
- Duck, L. G. and J. B. Fletcher. 1945. *A survey of the game and fur bearing animals of Oklahoma*. Oklahoma Game and Fish Commission, Division of Wildlife Restoration and Research, Oklahoma City, OK.

- Engle, D. M., T. G. Bidwell, and R. E. Masters. 1996. Restoring cross timbers ecosystems with fire. *American Wildlife and Natural Resources Conference* 61:190-199.
- Engle, D. M., T. N. Bodine, and J. E. Stritzke. 2006. Woody plant community in the cross timbers over two decades of brush treatments. *Rangeland Ecology & Management* 59:153-162.
- ESRI. 2007. ArcView 9.2. Environmental Systems Research Institute, Redlands, CA.
- Facelli, J. M. and S. T. A. Pickett. 1991a. Indirect effects of litter on woody seedlings subject to herb competition. *Oikos* 62:129-138.
- Facelli, J. M. and S. T. A. Pickett. 1991b. Plant litter - its dynamics and effects on plant community structure. *Botanical Review* 57:1-32.
- Ferwerda, J. G., W. Siderius, S. E. Van Wieren, C. C. Grant, A. Peel, A. K. Skidmore, and H. H. T. Prins. 2006. Parent material and fire as principle drivers of foliage quality in woody plants. *Forest Ecology and Management* 231:178-183.
- Fralish, J. S. 2002. The Central Hardwood Forest: its boundaries and physiographic provinces. *in* 13th central hardwood forest conference. North Central Research Station, USDA Forest Service, Urbana-Champaign, IL.
- Fuhlendorf, S. D. and D. M. Engle. 2001. Restoring heterogeneity on rangelands: Ecosystem management based on evolutionary grazing patterns. *Bioscience* 51:625-632.
- 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.
- Fuhlendorf, S. D., D. M. Engle, J. Kerby, and R. Hamilton. 2009. Pyric herbivory: rewilding landscapes through the recoupling of fire and grazing. *Conservation Biology* 23:588-598.
- Glaser, B., J. Lehmann, and W. Zech. 2002. Ameliorating physical and chemical properties of highly weathered soils in the tropics with charcoal - a review. *Biology and Fertility of Soils* 35:219-230.

- Gleason, H. A. 1913. The relationship of forest distribution and prairie fires in the middle west. *Torreyia* 13:173-181.
- Glitzenstein, J. S., D. R. Strenig, and D. D. Wade. 2003. Fire frequency effects on longleaf pine (*Pinus palustris* P. Miller) vegetation in South Carolina and northeast Florida, USA. *Natural Areas Journal* 23:22-37.
- Grime, J. P. 1973. Competitive Exclusion in Herbaceous Vegetation. *Nature* 242:344-347.
- Grove, T. S., A. M. Oconnell, and G. M. Dimmock. 1986. Nutrient changes in surface soils after an intense fire in Jarrah (*Eucalyptus marginata* Donn ex Sm) forest. *Australian Journal of Ecology* 11:303-317.
- 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.
- Hart, J. L., S. L. van de Gevel, and H. D. Grissino-Mayer. 2008. Forest dynamics in a natural area of the southern Ridge and Valley, Tennessee. *Natural Areas Journal* 28:275-289.
- Hiers, J. K., J. J. O'Brien, R. E. Will, and R. J. Mitchell. 2007. Forest floor depth mediates understory vigor in xeric *Pinus palustris* ecosystems. *Ecological Applications* 17:806-814.
- Hodges, J. D. and E. S. Gardiner. 1992. Ecology and Physiology of Oak Regeneration. *in* Oak regeneration: serious problems practical recommendations. USDA Forest Service, Southeastern Forest Experiment Station General Technical Report SE-84, Knoxville, TN.
- Huddle, J. A. and S. G. Pallardy. 1996. Effects of long-term annual and periodic burning on tree survival and growth in a Missouri Ozark oak-hickory forest. *Forest Ecology and Management* 82:1-9.
- Huston, M. 1979. General hypothesis of species-diversity. *American Naturalist* 113:81-101.

- Hutchinson, T. F., R. E. J. Boerner, S. Sutherland, E. K. Sutherland, M. Ortt, and L. R. Iverson. 2005. Prescribed fire effects on the herbaceous layer of mixed-oak forests. *Canadian Journal of Forest Research* 35:877-890.
- Johnson, F. L. and P. G. Risser. 1975. A quantitative comparison between an oak forest and an oak savannah in central Oklahoma. *The Southwestern Naturalist* 20:75-84.
- Kabrick, J. M., D. C. Dey, R. G. Jensen, and M. Wallendorf. 2008. The role of environmental factors in oak decline and mortality in the Ozark Highlands. *Forest Ecology and Management* 255:1409-1417.
- Kalbertji, K. L., J. A. Mosjidis, and A. P. Mamolos. 1999. Litter dynamics of low and high tannin sericea lespedeza plants under field conditions. *Plant and Soil* 208:271-281.
- Kent, M. and P. Coker. 1992. *Vegetation Description and Analysis: A Practical Approach*. Belhaven Press, London, UK.
- Knoop, W. T. and B. H. Walker. 1985. Interactions of woody and herbaceous vegetation in a southern African savanna. *Journal of Ecology* 73:235-253.
- Komarek, E. V. 1974. Effects of fire on temperate forests and related ecosystems: southeastern United States. *in Fire and Ecosystems*: Edited by T.T. Kozlowsky, C.E. Ahlgren. Academic Press, New York, NY.
- Kraus, T. E. C., R. A. Dahlgren, and R. J. Zasoski. 2003. Tannins in nutrient dynamics of forest ecosystems - a review. *Plant and Soil* 256:41-66.
- Kutiel, P. and Z. Naveh. 1987. Soil properties beneath *Pinus halepensis* and *Quercus calliprinos* trees on burned and unburned mixed forest on Mt Carmel, Israel. *Forest Ecology and Management* 20:11-24.
- Laughlin, D. C., J. D. Bakker, M. L. Daniels, M. M. Moore, C. A. Casey, and J. D. Springer. 2008. Restoring plant species diversity and community composition in a ponderosa pine-bunchgrass ecosystem. *Plant Ecology* 197:139-151.

- Leach, M. K. and T. J. Givnish. 1999. Gradients in the composition, structure, and diversity of remnant oak savannas in southern Wisconsin. *Ecological Monographs* 69:353-374.
- Lemmon, P. E. 1956. A spherical densiometer for estimating forest overstory density. *Forest Science* 2:314-320.
- Little Jr, E. L. 2002. *Forest Trees of Oklahoma: How to Know Them* (17th ed.). Oklahoma Forestry Services, State Department of Agriculture, Oklahoma City, OK.
- Loftis, D. L. 1990. Predicting post-harvest performance of advance red oak reproduction in the southern Appalachians. *Forest Science* 36:908-916.
- Lorimer, C. G. 1992. Causes of the oak regeneration problem. *in* *Oak Regeneration: Serious Problems Practical Recommendations*. USDA Forest Service, Southeastern Forest Experiment Station General Technical Report SE-84, Knoxville, TN.
- Lorimer, C. G., J. W. Chapman, and W. D. Lambert. 1994. Tall understory vegetation as a factor in the poor development of oak seedlings beneath mature stands. *Journal of Ecology* 82:227-237.
- Lynham, T. J., G. M. Wickware, and J. A. Mason. 1998. Soil chemical changes and plant succession following experimental burning in immature jack pine. *Canadian Journal of Soil Science* 78:93-104.
- Magurran, A. E. 2003. *Measuring biological diversity*. Blackwell Publishing, Malden, MA.
- Martin, P. S. and H. W. Greene. 2005. *Twilight of the Mammoths: Ice age Extinctions and the Rewilding of America*. University of California Press, Berkeley, CA.
- Masters, R. E. 1991. *Effects of Timber Harvest and Prescribed Fire on Wildlife Habitat and Use in the Ouachita Mountains of Eastern Oklahoma*. Ph.D. Dissertation. Oklahoma State University, Stillwater, OK.
- Masters, R. E., R. L. Lochmiller, and D. M. Engle. 1993. Effects of timber harvest and prescribed fire on white-tailed deer forage production. *Wildlife Society Bulletin* 21:401-411.

- Masters, R. E., J. Waymire, T. G. Bidwell, R. Houchin, and K. Hitch. 2006. E-990 Influence of timber harvest and fire frequency on plant community development and wildlife: integrated land management options. Oklahoma State University, Coop. Ext. Serv., Stillwater, OK.
- McClain, W. E., M. A. Jenkins, S. E. Jenkins, and J. E. Ebinger. 1993. Changes in the woody vegetation of a bur oak savanna remnant in central Illinois. *Natural Areas Journal* 13:108-114.
- McDonald, R.I., R.K. Peet and D.L. Urban. 2003. Spatial pattern of *Quercus* regeneration limitation and *Acer rubrum* invasion in a Piedmont forest. *Journal of Vegetation Science* 14: 441-450.
- McEwan, R. W. and B. C. McCarthy. 2008. Anthropogenic disturbance and the formation of oak savanna in central Kentucky, USA. *Journal of Biogeography* 35:965-975.
- McShea, W. J. and W. M. Healy. 2002. *Oak Forest Ecosystems: Ecology and Management for Wildlife*. The Johns Hopkins University Press, Baltimore, MA.
- Murphy, A. and J. H. Ehrenreich. 1965. Effects of timber harvest and stand improvement on forage production. *The Journal of Wildlife Management* 29:734-739.
- Neary, D. G., K. C. Ryan, L. F. DeBano. 2005. (revised 2008). *Wildland Fire in Ecosystems: Effects of Fire on Soils and Water*. Gen. Tech. Rep. RMRS-GTR-42-vol.4. U. S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, UT.
- Nelson, D. M., F. S. Hu, E. C. Grimm, B. B. Curry, and J. E. Slate. 2006. The influence of aridity and fire on Holocene Prairie communities in the eastern Prairie Peninsula. *Ecology* 87:2523-2536.
- Nowacki, G. J. and M. D. Abrams. 2008. The demise of fire and "Mesophication" of forests in the eastern United States. *Bioscience* 58:123-138.
- Nuttle, T. 1997. Densiometer bias: Are we measuring the forest or the trees? *Wildlife Society Bulletin* 25:610-611.



- Oklahoma Climatological Survey. 2005. Okmulgee County Climate Summary. Available online <<http://agweather.mesonet.org/index.php/data/section/climate>>. College of Atmospheric & Geographic Sciences, University of Oklahoma, Norman, OK
- Penfound, W.T. 1963. The composition of post oak forest in south-central Oklahoma. *The Southwestern Naturalist* 8:114-115.
- Peterson, D. W. and P. B. Reich. 2001. Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. *Ecological Applications* 11:914-927.
- Peterson, D. W. and P. B. Reich. 2008. Fire frequency and tree canopy structure influence plant species diversity in a forest-grassland ecotone. *Plant Ecology* 194:5-16.
- Peterson, D. W., P. B. Reich, and K. J. Wrage. 2007. Plant functional group responses to fire frequency and tree canopy cover gradients in oak savannas and woodlands. *Journal of Vegetation Science* 18:3-12.
- Powell, J. and D.P. Lowry. 1980. Oak (*Quercus* spp) sprouts growth rates on a central Oklahoma shallow savannah range site. *Journal of Range Management* 33:312-313.
- Pyne, S. J. 1996. *Introduction to Wildland Fire* (2<sup>nd</sup> ed.). John Wiley & Sons, New York, NY.
- Pyne, S. J. 1997. *Fire in America: Cultural History of Wildland and Rural Fire*. University of Washington Press, Seattle, WA.
- Reich, P. B., M. D. Abrams, D. S. Ellsworth, E. L. Kruger, and T. J. Tabone. 1990. Fire affects ecophysiology and community dynamics of central Wisconsin oak forest regeneration. *Ecology* 71:2179-2190.
- Rentch, J. S. and R. R. Hicks. 2005. Changes in presettlement forest composition for five areas in the central hardwood forest, 1784-1990. *Natural Areas Journal* 25:228-238.
- Rice, E. L. and W. T. Penfound. 1959. The upland forests of Oklahoma. *Ecology* 40:593-608.

- Roxburgh, S. H., K. Shea, and J. B. Wilson. 2004. The Intermediate Disturbance Hypothesis: patch dynamics and mechanisms of species coexistence. *Ecology* 85:359-371.
- Schimel, J. P., R. G. Cates, and R. Ruess. 1998. The role of balsam poplar secondary chemicals in controlling soil nutrient dynamics through succession in the Alaskan taiga. *Biogeochemistry* 42:221-234.
- Sparwasser, W. A., V. A. Bogard, and O. G. Henson. 1968. Soil Survey: Okmulgee County Oklahoma. U.S. Government Printing Office, Washington, D.C.
- Stahle, D. W. 2007. The Ancient Cross Timbers Consortium. Available online <<http://www.uark.edu/misc/xtimber/>>. University of Arkansas Tree-Ring Laboratory, Fayetteville, AR.
- Stahle, D. W. and P. L. Chaney. 1994. A predictive model for the location of ancient forests. *Natural Areas Journal* 14:151-158.
- Stambaugh, M. C. and R. P. Guyette. 2006. Fire regime of an Ozark wilderness area, Arkansas. *American Midland Naturalist* 156:237-251.
- Sydes, C. and J. P. Grime. 1981. Effects of tree leaf litter on herbaceous vegetation in deciduous woodland: II. an experimental investigation. *Journal of Ecology* 69:249-262.
- Talbot, J. M. and A. C. Finzi. 2008. Differential effects of sugar maple, red oak, and hemlock tannins on carbon and nitrogen cycling in temperate forest soils. *Oecologia* 155:583-592.
- ter Braak, C. J. F. and P. Šmilauer. 2002. Canoco for Windows 4.5. Biometris - Plant Research International, Wageningen, NL.
- Tester, J. R. 1989. Effects of fire frequency on oak savanna in east-central Minnesota. *Bulletin of the Torrey Botanical Club* 116:134-144.
- United States Department of Agriculture, Natural Resource Conservation Service. 2006. Land Resource Regions and Major Land Resource Areas of the United States, the Caribbean,

and the Pacific Basin. United States Department of Agriculture Handbook 296. NRCS LANDCARE Office, Des Moines, IA.

United States Department of Agriculture, Natural Resource Conservation Service. 2008. The PLANTS Database. Available online <<http://plants.usda.gov>>. National Plant Data Center, Baton Rouge, LA.

Van de Vijver, C., P. Poot, and H. H. T. Prins. 1999. Causes of increased nutrient concentrations in post-fire regrowth in an East African savanna. *Plant and Soil* 214:173-185.

Van Lear, D. H., P. H. Brose, and P. D. Keyser. 2000. Using prescribed fire to regenerate oaks. *in* Proceedings: Workshop on Fire, People, and the Central Hardwoods Landscape. United States Forest Service, Northeastern Research Station, General Technical Report NE-274, Richmond, KY.

Waldrop, T. A., D. L. White, and S. M. Jones. 1992. Fire regimes for pine grassland communities in the southeastern United States. *Forest Ecology and Management* 47:195-210.

Wrangham, R. W., J. H. Jones, G. Laden, D. Pilbeam, and N. Conklin-Brittain. 1999. The raw and the stolen - cooking and the ecology of human origins. *Current Anthropology* 40:567-594.

Yatskievych, G. 1999. Steyermark's Flora of Missouri. Missouri Dept. of Conservation in cooperation with Missouri Botanical Garden Press, St. Louis, MO.

## APPENDICES

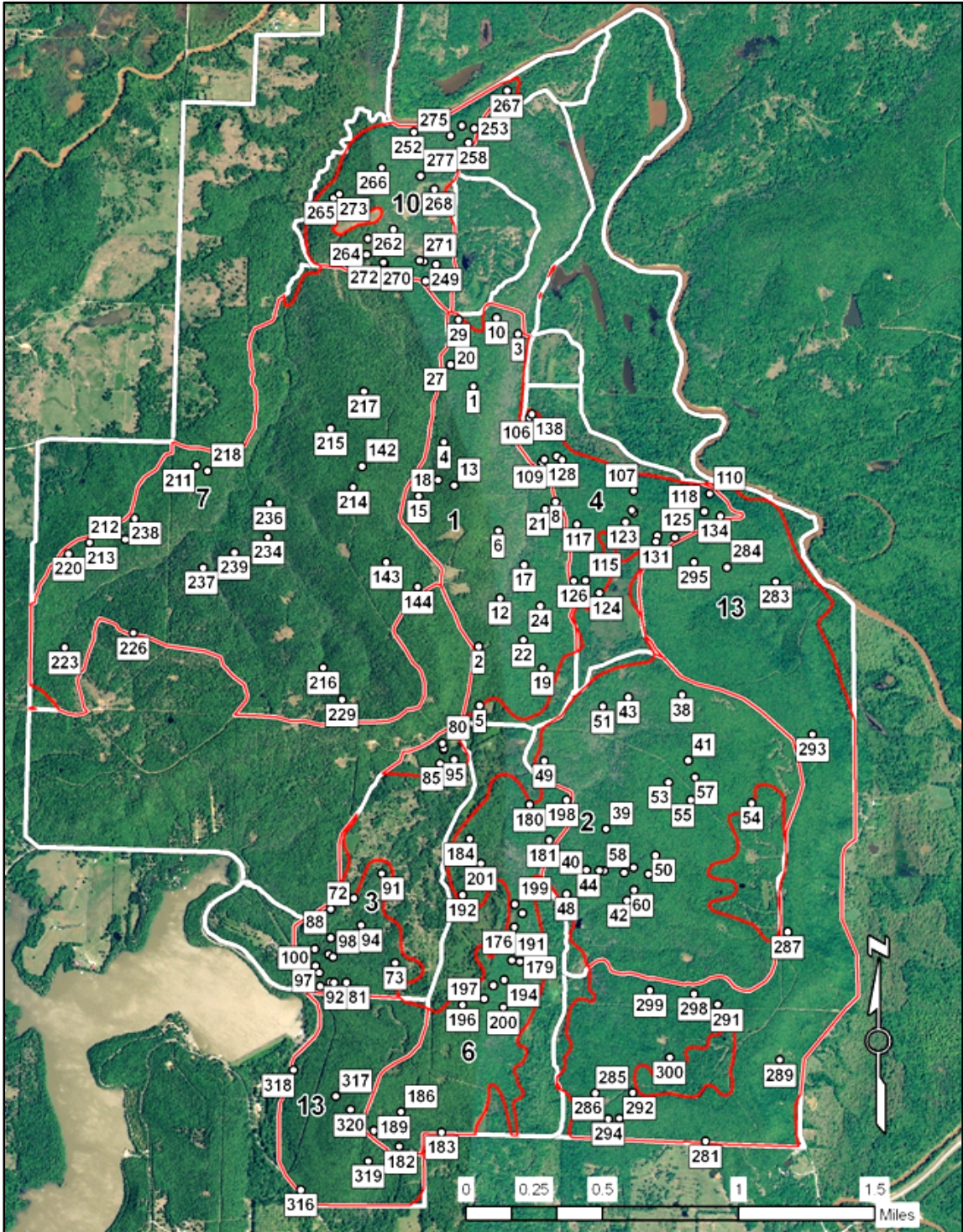
**APPENDIX I | Summarized list of upland vascular plants identified at Okmulgee Game Management Area. All species, unless otherwise indicated, were collected within the sample plots placed in the upland forest. Bold type scientific names indicate species that occurred in more than 10 percent of the sample plots. “§” U.S. Department of Agriculture PLANTS Symbol (NRCS 2008). “sp. or spp.” indicates that species that were taxonomically impractical to identify due to developmental stage and are lumped to genus level. “†” indicates species that are lumped to genus level; however, do not likely contain other species listed below in the same genus. “‡” *Crataegus engelmannii* was documented as occurring in the 100 m<sup>2</sup> plots; however, *C. engelmannii* and *C. crus-galli* are not distinguished from each other for the understory 1 m<sup>2</sup> sub-plots due to difficulties with differentiation and were recorded as the latter. “\*” indicates a species that may deserve noting; however, it was not recorded within a plot due to growth habit, rarity, etc.**

PLANTS <sup>§</sup>	Scientific Name	Common Name	Group
ACALY	<i>Acalypha sp.</i>	Copperleaf	Forb
ACSA2	<i>Acer saccharinum</i>	Maple, Silver	Woody
AGROS2	<i>Agrostis sp.</i>	Bentgrass	Graminoid
ALLIU	<i>Allium spp.</i>	Wild Onion	Forb
AMPS	<b><i>Ambrosia psilostachya</i></b>	Ragweed, Common	Forb
AMTR	<i>Ambrosia trifida</i>	Ragweed, Giant	Forb
AMAR5	<i>Ampelopsis arborea</i>	Peppervine	Woody
AMBR2	<b><i>Amphicarpaea bracteata</i></b>	Hogpeanut, American	Legume
ANGE	<b><i>Andropogon gerardii</i></b>	Big Bluestem	Graminoid
ANDRO2	<i>Andropogon spp. †</i>	Bluestem	Graminoid
ANVI2	<b><i>Andropogon virginicus</i></b>	Broomsedge Bluestem	Graminoid
ANPA9	<b><i>Antennaria parlinii</i></b>	Parlin's Pussytoes	Forb
ARCA	<i>Arabis canadensis</i>	Sicklepod	Forb
ASVE	<i>Asclepias verticillata</i>	Whorled Milkweed	Forb
ASPLE	<i>Asplenium sp.</i>	Spleenwort Fern	Forb
BABR2	<i>Baptisia bracteata</i>	Longbract Wild Indigo	Legume
BOCU	<i>Bouteloua curtipendula</i>	Sideoats Gramma	Graminoid
BROMU	<i>Bromus spp.</i>	Brome	Graminoid
CARA2	<i>Campsis radicans</i>	Trumpet Vine	Woody
CAREX	<b><i>Carex spp.</i></b>	Sedge	Graminoid
CAAL27	<i>Carya alba (tomentosa)</i>	Mockernut Hickory	Woody
CATE9	<b><i>Carya texana</i></b>	Black Hickory	Woody
CELA	<i>Celtis laevigata</i>	Sugarberry	Woody
CEOC	<i>Celtis occidentalis</i>	Common Hackberry	Woody
CEOC2	<i>Cephalanthus occidentalis</i>	Buttonbush	Woody
CECA4	<i>Cercis canadensis</i>	Eastern Redbud	Woody
CHAS	<i>Chaetopappa asteroides</i>	Arkansas Leastdaisy	Forb
CHFA2	<i>Chamaecrista fasciculata</i>	Partridge Pea	Legume
CHLA5	<b><i>Chasmanthium latifolium</i></b>	Fishing Pole Grass	Graminoid
CIAL2	<i>Cirsium altissimum</i>	Tall Thistle	Forb
CLMA4	<i>Clitoria mariana</i>	Butterfly Pea	Legume
COCA	<i>Cocculus carolinus</i>	Carolina Moonseed	Forb
COCY	<i>Coelorachis cylindrica</i>	Cylinder Jointtail Grass	Graminoid
COCA5	<b><i>Conyza canadensis</i></b>	Horseweed	Forb
COREO2	<i>Coreopsis spp.</i>	Golden Tickseed	Forb
CRCR2	<i>Crataegus crus-galli ‡</i>	Cockspur Hawthorn	Woody
CREN	<i>Crataegus engelmannii</i>	Cockspur Hawthorn	Woody

CRVI2	<i>Crataegus viridis</i>	Green Hawthorn	Woody
CYEC2	<i>Cyperus echinatus</i>	Globe Flatsedge	Graminoid
DASP2	<b><i>Danthonia spicata</i></b>	Poverty Oatgrass	Graminoid
DELA2	<i>Desmodium laevigatum</i>	Tick Trefoil	Legume
DIAC2	<b><i>Dichanthelium acuminatum</i></b>	Tapered Rosette Grass	Graminoid
DICL	<i>Dichanthelium clandestinum</i>	Deertongue	Graminoid
DILI2	<b><i>Dichanthelium linearifolium</i></b>	Slimleaf Panicgrass	Graminoid
DISP2	<i>Dichanthelium sphaerocarpon</i>	Roundseed Panicgrass	Graminoid
DICHA2	<b><i>Dichanthelium spp.</i></b>	Rosette Grass	Graminoid
DIVI5	<i>Diospyros virginiana</i>	Persimmon	Woody
ECPA	<i>Echinacea pallida</i>	Coneflower, Pale-purple	Forb
ELMO2	<i>Eleocharis montevidensis</i>	Sand Spikerush	Graminoid
ELCA3	<i>Elephantopus carolinianus</i>	Elephantsfoot	Forb
ELCA4	<b><i>Elymus candensis</i></b>	Canada Wildrye	Graminoid
ELVI3	<i>Elymus virginicus</i>	Virginia Wildrye	Graminoid
ERAGR	<i>Eragrostis spp.</i>	Lovegrass	Graminoid
ERHI2	<b><i>Erechtites hieraciifolia</i></b>	Burnweed	Forb
ERST3	<i>Erigeron strigosus</i>	Prairie Fleabane	Forb
ERTE7	<i>Erigeron tenuis</i>	Slenderleaf Fleabane	Forb
FRAM2	<i>Fraxinus americana</i>	White Ash	Woody
FRPE	<i>Fraxinus pennsylvanica*</i>	Green Ash	Woody
GAVO	<b><i>Galactia volubilis</i></b>	Milkpea	Legume
GACI2	<b><i>Galium circaezans</i></b>	Wood's Bedstew	Forb
GAPI2	<i>Galium pilosum</i>	Hairy Bedstew	Forb
GAPU3	<i>Gamochaeta purpurea</i>	Purple Everlasting	Forb
GLTR	<i>Gleditsia triacanthos</i>	Honeylocust	Woody
GYDI	<i>Gymnocladus dioicus</i>	Kentucky Coffeetree	Woody
GYAM	<i>Gymnopogon ambiguus</i>	Bearded Skeletongrass	Graminoid
HEHI2	<b><i>Helianthus hirsutus</i></b>	Rough Sunflower	Forb
HIGR3	<i>Hieracium gronovii</i>	Hawkweed	Forb
HYHY	<b><i>Hypericum hypericoides</i></b>	St. Andrew's Cross	Forb
HYPV	<i>Hypericum punctatum</i>	Spotted St. Johnswort	Forb
ILDE	<i>Ilex decidua</i>	Deciduous Holly	Woody
JUVI	<i>Juniperus virginiana</i>	Eastern Redcedar	Woody
LACA	<b><i>Lactuca canadensis</i></b>	Canada Lettuce	Forb
LETE	<i>Lechea tenuifolia</i>	Narrowleaf Pinweed	Forb
LECU	<i>Lespedeza cuneata</i>	Sericea Lespedeza	Legume
LEPR	<i>Lespedeza procumbens</i>	Trailing Lespedeza	Legume
LERE2	<b><i>Lespedeza repens</i></b>	Creeping Lespedeza	Legume
LEVI6	<b><i>Lespedeza violacea</i></b>	Violet Lespedeza	Legume
LEVI7	<b><i>Lespedeza virginica</i></b>	Slender Lespedeza	Legume
LIATR	<i>Liatris sp.</i>	Blazing Star	Forb
LIME2	<i>Linum medium</i>	Stiff Yellow Flax	Forb
MATEL	<i>Matelea sp.</i>	Milkvine	Forb
MIMOS	<i>Mimosa nuttallii</i>	Sensitivebriar	Legume
MORU	<b><i>Monarda russeliana</i></b>	Redpurple Beebalm	Forb
MORU2	<i>Morus rubra</i>	Red Mulberry	Woody
MUHLE	<b><i>Muhlenbergia sp.</i></b>	Muhly Grass	Graminoid
OXST	<i>Oxalis stricta</i>	Yellow Woodsorrel	Forb
OXVI	<i>Oxalis violacea</i>	Violet Woodsorrel	Forb
PAOB6	<i>Packera obovata</i>	Roundleaf Ragwort	Forb
PAFA3	<i>Paronychia fastigiata</i>	Hairy Forked Nailwort	Forb
PAQU2	<b><i>Parthenocissus quinquefolia</i></b>	Virginia Creeper	Woody
PALU2	<i>Passiflora lutea</i>	Yellow Passion Flower	Forb
PENST	<i>Penstemon spp.</i>	Beardtongue	Forb
PHEME	<i>Phemeranthus sp.</i>	Fameflower	Forb

PHAM4	<i>Phytolacca americana</i>	Pokeweed	Forb
PLOC	<i>Platanus occidentalis</i>	Sycamore	Woody
POLYG4	<i>Polygonum spp.</i>	Knotweed	Forb
PRME	<b><i>Prunus mexicana</i></b>	Mexican Plum	Woody
PRSE2	<i>Prunus serotina</i>	Black Cherry	Woody
PSOB3	<i>Pseudognaphalium obtusifolium</i>	Rabbit-tobacco	Forb
PTNU	<i>Ptilimnium nuttallii</i>	Laceflower	Forb
QUMA3	<b><i>Quercus marilandica</i></b>	Blackjack Oak	Woody
QUMU	<i>Quercus muehlenbergii</i>	Chinkapin Oak	Woody
QURU	<b><i>Quercus rubra</i></b>	Northern Red Oak	Woody
QUSH	<i>Quercus shumardii*</i>	Shumard Oak	Woody
QUST	<b><i>Quercus stellata</i></b>	Post Oak	Woody
QUVE	<b><i>Quercus velutina</i></b>	Black Oak	Woody
RHAR4	<b><i>Rhus aromatica</i></b>	Fragrant Sumac	Woody
RHCO	<i>Rhus copallina</i>	Winged Sumac	Woody
RHGL	<i>Rhus glabra</i>	Smooth Sumac	Woody
ROSA5	<i>Rosa spp.</i>	Wild Rose	Woody
RUBUS	<b><i>Rubus spp.</i></b>	Blackberry	Woody
RUHI2	<i>Rudbeckia hirta</i>	Black-eyed Susan	Forb
RUELL	<i>Ruellia spp.</i>	Wild Petunia	Forb
SAAN	<i>Sabatia angularis</i>	Rosepink	Forb
SACA15	<b><i>Sanicula canadensis</i></b>	Black Snakeroot	Forb
SCSC	<b><i>Schizachyrium scoparium</i></b>	Little Bluestem	Graminoid
SCPA7	<i>Scutellaria parvula</i>	Skullcap	Forb
SEVA4	<i>Securigera varia</i>	Crownvetch	Legume
SEMA11	<i>Senna marilandica*</i>	Maryland Senna	Legume
SILA20	<i>Sideroxylon lanuginosum</i>	Chittamwood	Woody
SMILA2	<b><i>Smilax spp.</i></b>	Greenbriar	Woody
SOCA3	<i>Solanum carolinense</i>	Horsenettle	Forb
SOPT7	<i>Solanum ptycanthum</i>	West Indian Nightshade	Forb
SOLID	<i>Solidago spp.†</i>	Goldenrod	Forb
SOUL2	<b><i>Solidago ulmifolia</i></b>	Elmleaf Goldenrod	Forb
SPOB	<i>Sphenopholis obtusata</i>	Prairie Wedgescale	Graminoid
SPORO	<i>Sporobolus spp.</i>	Dropseed	Graminoid
SYOR	<b><i>Symphoricarpos orbiculatus</i></b>	Buckbrush	Woody
SYLA3	<i>Symphyotrichum laeve</i>	Smooth Blue Aster	Forb
SYOO	<b><i>Symphyotrichum oolentangiense</i></b>	Skyblue Aster	Forb
SY PAP2	<i>Symphyotrichum patens</i>	Late Purple Aster	Forb
TEVI	<i>Tephrosia virginiana</i>	Goat's Rue	Legume
TECA3	<i>Teucrium canadense</i>	Canada Germander	Forb
TORA2	<i>Toxicodendron radicans</i>	Poison Ivy	Woody
TRADE	<i>Tradescantia spp.</i>	Spiderwort	Forb
TRFL2	<b><i>Tridens flavus</i></b>	Purpletop Tridens	Graminoid
TRPE4	<i>Triodanis perfoliata</i>	Venus' Looking-glass	Forb
ULAL	<b><i>Ulmus alata</i></b>	Winged Elm	Woody
VAAR	<b><i>Vaccinium arboreum</i></b>	Farkleberry	Woody
VERBE	<i>Verbena sp.</i>	Vervain	Forb
VEVI3	<i>Verbesina virginica</i>	White Crownbeard	Forb
VERNO	<i>Vernonia spp.</i>	Iron Weed	Forb
VIRU	<i>Viburnum rufidulum</i>	Rusty Blackhaw	Woody
VIOLA	<i>Viola spp.</i>	Violet	Forb
VITIS	<b><i>Vitis spp.</i></b>	Grape	Woody
WOOB2	<i>Woodsia obtusa</i>	Cliff Fern	Forb
ZAAM	<i>Zanthoxylum americanum*</i>	Pricklyash	Woody

**APPENDIX II | Sample plots and numbers, prescribe burn treatment units, and sampled areas on 2008 aerial photo. Red lines outline sampled area on Hector-Endsaw soil complex. Aerial photo courtesy of Oklahoma Geographic Information Council.**



**APPENDIX III | List of randomly located plots within the Okmulgee Game Management Area. I randomly assigned plot numbers and sampled in order to minimize effects of date of sample. The UTM coordinates below utilize the following coordinate system: NAD (1983) Zone 15 North. Start corner refers to the corner of the plot in which the UTM coordinate refers.**

Unit #	Plot #	Sample Date	Start Corner	Slope (%)	Aspect (°)	Easting	Northing	Unit #	Plot #	Sample Date	Start Corner	Slope (%)	Aspect (°)	Easting	Northing
1	001	6/21	NE	5	200	223940	3950208	3	072	7/01	SE	6	150	223235	3947188
	002	6/26	NE	1	40	223970	3948672		073	7/08	SW	8	260	223477	3946804
	003	7/01	SE	8	60	224203	3950517		074	6/19	NE	7	220	223034	3946667
	004	7/05	SE	6	290	223766	3949879		075	7/12	NE	4	10	223086	3946855
	005	7/06	SE	5	310	223977	3948324		076	7/16	SE	2	140	223764	3948066
	006	7/16	NW	12	100	224086	3949356		077	6/19	NW	7	225	223030	3946746
	008	7/16	NE	12	260	224425	3949528		079	7/25	SE	5	150	223765	3948072
	010	7/18	SW	11	70	224077	3950614		080	7/16	SE	4	130	223759	3948102
	012	7/25	NE	9	90	224097	3948960		081	7/22	NW	11	230	223189	3946689
	013	7/24	NW	10	310	223825	3949624		085	7/18	SW	10	170	223742	3947982
	015	7/24	NE	24	350	223617	3949561		086	7/28	NE	7	220	223093	3946692
	017	7/25	NE	13	320	224241	3949156		088	8/02	SE	6	200	223097	3947122
	018	7/24	SW	14	280	223732	3949655		091	8/02	NW	6	80	223399	3947332
	019	8/01	SE	6	240	224349	3948545		092	7/28	SW	7	210	223117	3946689
	020	8/01	SW	4	210	223809	3950338		094	8/02	SW	2	300	223275	3947028
	021	8/04	NW	5	360	224366	3949485		095	8/02	SW	6	240	223825	3948006
	022	8/08	NW	8	290	224233	3948711		097	8/02	NW	5	220	223008	3946788
	024	8/08	NE	4	330	224335	3948913		098	8/02	NW	5	20	223109	3946838
	027	8/08	SE	3	210	223803	3950339		100	8/07	SW	4	30	223003	3946887
	029	8/08	SE	6	140	223854	3950601		103	8/07	SE	4	310	223096	3946952
2	036	6/22	NE	2	100	224829	3947336	4	106	6/22	NE	24	250	224271	3950025
	037	7/08	SW	9	360	224712	3947348		107	6/26	NE	28	20	224888	3949590
	038	7/02	SE	5	220	225172	3948387		109	7/11	NW	5	290	224345	3949762
	039	7/06	NE	11	10	224725	3947595		110	6/26	NW	32	20	225337	3949574
	040	7/08	NW	4	340	224607	3947352		111	7/11	SE	10	30	224886	3949465
	041	7/21	NE	9	20	225209	3948000		115	7/02	NE	8	30	224601	3949062
	042	7/08	SE	8	230	224846	3947174		117	7/06	NE	7	280	224553	3949393
	043	7/21	SW	5	180	224855	3948375		118	7/15	NW	9	20	225304	3949469
	044	7/26	NE	5	30	224682	3947351		119	7/25	SW	3	320	225129	3949314
	046	7/26	NW	4	10	224974	3947330		121	7/31	NE	3	80	224432	3949797
	048	7/26	NW	28	230	224489	3947213		122	7/25	NE	10	10	224877	3949478
	049	7/26	NE	3	30	224360	3947998		123	7/25	SE	6	320	224837	3949409
	050	7/26	NE	8	250	225014	3947441		124	7/31	NW	6	290	224684	3948988
	051	8/01	SW	7	160	224706	3948318		125	7/25	SW	5	310	225027	3949327
	053	8/01	SW	4	260	225091	3947871		126	7/31	SW	7	30	224533	3949060
	054	8/06	NE	5	270	225585	3947749		128	7/31	SE	19	50	224466	3949775
	055	8/06	NE	4	280	225224	3947766		129	8/04	SW	4	330	224359	3949777
	057	8/06	NE	9	50	225250	3947900		131	8/08	SW	5	320	225019	3949290
	058	8/08	SW	4	300	224886	3947367		134	8/08	SW	11	40	225398	3949444
	060	8/08	SW	5	260	224891	3947235		138	8/08	NW	8	340	224286	3950045



Unit #	Plot #	Sample Date	Start Corner	Slope (%)	Aspect (°)	Easting	Northing
6	176	7/01	NW	5	120	224183	3947016
	178	7/01	SW	6	110	224057	3946674
	179	7/01	SE	7	60	224214	3946813
	180	7/11	SE	2	240	224273	3947739
	181	7/06	NW	9	130	224389	3947529
	182	7/12	SW	6	30	223501	3945720
	183	7/22	SW	6	90	223753	3945805
	184	7/18	SW	2	80	223918	3947537
	186	7/22	SE	24	120	223513	3945924
	189	7/22	NE	8	90	223352	3945815
	190	7/28	NE	35	90	224230	3947098
	191	7/28	SW	5	80	224165	3946821
	192	8/02	SW	6	60	223875	3947205
	194	7/28	SW	3	80	224122	3946705
	196	7/28	NE	3	170	223876	3946557
	197	8/02	SW	6	150	224004	3946595
	198	8/02	NW	20	110	224491	3947768
	199	8/02	NE	10	90	224184	3947151
	200	8/07	NE	5	140	224117	3946542
	201	8/07	NE	10	30	223984	3947391
7	142	7/11	SE	8	10	223283	3949738
	143	8/01	NE	6	40	223426	3949171
	144	8/01	SE	12	20	223611	3949023
	211	6/24	NW	5	130	222305	3949742
	212	6/24	NE	2	320	221883	3949303
	213	6/24	NW	15	120	221674	3949284
	214	7/11	SE	11	330	223231	3949612
	215	7/17	NE	8	270	223098	3949960
	216	7/17	NW	28	30	223053	3948547
	217	7/17	SE	5	320	223294	3950179
	218	7/23	NE	8	90	222369	3949710
	220	7/23	NW	9	160	221549	3949220
	223	7/23	NE	8	10	221526	3948667
	226	7/23	SE	8	290	221931	3948751
	229	7/23	SE	6	320	223164	3948359
	234	8/04	NW	26	210	222728	3949318
	236	8/04	SE	9	30	222736	3949519
	237	8/04	NW	25	60	222344	3949139
	238	8/04	SE	6	20	221939	3949430
	239	8/04	NE	11	20	222527	3949228

Unit #	Plot #	Sample Date	Start Corner	Slope (%)	Aspect (°)	Easting	Northing
10	246	6/21	SE	2	180	223656	3950832
	247	6/21	SW	5	200	223646	3950944
	248	7/05	SW	8	40	223873	3951748
	249	7/12	SE	4	210	223719	3950928
	252	7/05	NE	25	360	223588	3951709
	253	7/05	NE	5	360	223945	3951731
	257	7/18	SE	4	180	223468	3951137
	258	7/24	SW	8	310	223911	3951647
	262	8/05	SW	4	180	223318	3951082
	264	8/05	SE	15	350	223309	3950985
	265	8/05	SW	7	310	223113	3951321
	266	7/24	SW	12	270	223398	3951498
	267	7/24	NE	12	60	224138	3951954
	268	7/24	NE	2	190	223708	3951373
	270	8/05	NW	4	350	223415	3950932
	271	8/05	NE	3	20	223623	3950950
	272	8/05	SE	5	360	223410	3950940
	273	8/05	NW	5	290	223148	3951343
	275	8/05	SE	7	70	223804	3951687
	277	8/05	NE	5	140	223627	3951451
13	281	7/02	SW	15	170	225312	3945752
	283	7/15	NW	8	130	225726	3949055
	284	7/15	NE	20	160	225438	3949142
	285	7/02	SW	3	280	224881	3946038
	286	7/08	SW	8	270	224659	3946036
	287	7/02	NW	10	90	225796	3946988
	289	7/21	SE	5	320	225751	3946231
	291	7/26	NW	6	220	225383	3946558
	292	8/06	SE	3	260	224803	3945886
	293	8/06	SW	10	60	225944	3948153
	294	8/06	NE	21	240	224737	3945884
	295	7/15	SE	13	140	225245	3949170
	298	8/06	NE	8	200	225245	3946622
	299	8/06	NW	6	200	224983	3946644
	300	8/06	NE	9	310	225099	3946246
	316	6/21	SW	17	230	222921	3945465
	317	7/12	NE	14	290	223126	3946016
	318	7/17	NW	24	300	222877	3946171
	319	8/07	NW	8	130	223319	3945634
	320	8/07	NW	9	70	223213	3945937

**APPENDIX IV | Select photographs of various treatment units. The images were taken in order to illustrate structure and composition changes due to fire frequency. All figures were taken on relatively level ground near a sample plot.**



**Treatment Unit 13 – No fires in over twenty years. Photograph taken 6/26/2008 near plot # 295.**



**Treatment Unit 7 – One fire per decade, three years since last burn. Photograph taken 6/24/2008 near plot # 212.**



**Treatment Unit 3 – Two fires per decade, three years since last burn. Photograph taken on 8/02/2008 near plot # 088.**



**Treatment Unit 2 – Two and one half fires per decade, one year since last burn. Photo taken 7/08/2008 near plot # 040.**



**Treatment Unit 10 – Three fires per decade, three years since last burn. Photo taken 7/12/2008 near plot # 249.**



**Treatment Unit 1 – Five fires per decade, one year since last burn. Photo taken 8/01/2008 near plot # 020.**

## VITA

Jesse Aaron Burton

Candidate for the Degree of

Master of Science

Thesis: FIRE FREQUENCY EFFECTS ON VEGETATION OF AN UPLAND OLD GROWTH FOREST IN EASTERN OKLAHOMA

Major Field: Natural Resource Ecology & Management

### Biographical:

Personal Data: Born in Moscow, Idaho, on May 9, 1984, raised in rural Okmulgee Co., Oklahoma until the age of 18. Parents are Bruce H. and Louise D. Burton.

Education: Received Bachelor of Science Degree in Environmental Science with an emphasis in Natural Resources from Oklahoma State University in May, 2006; completed the requirements for the Master of Science Degree in Natural Resource Ecology & Management with a specialization in Forest Resources from Oklahoma State University in July, 2009.

Experience: Employed as a graduate teaching assistant at Oklahoma State University, Department of Zoology from August 2007 to May 2008; employed as a research technician at Oklahoma State University, Department of Natural Resource Ecology & Management the month of June, 2008; employed as a graduate research assistant at Oklahoma State University, Department of Natural Resource Ecology & Management / Oklahoma Cooperative Fish and Wildlife Research Unit from July 2008 to July 2009.

Professional Memberships: The American Association for the Advancement of Science, The Ecological Society of America, Oklahoma State University Natural Resource Ecology & Management Graduate Student Organization, Oklahoma State University Laboratory for Innovative Biodiversity Research & Analysis, The Nature Conservancy, The Wildlife Society.



Name: Jesse Aaron Burton

Date of Degree: July, 2009

Institution: Oklahoma State University

Location: Stillwater, Oklahoma

Title of Study: FIRE FREQUENCY EFFECTS ON VEGETATION OF AN UPLAND OLD  
GROWTH FOREST IN EASTERN OKLAHOMA

Pages in Study: 78

Candidate for the Degree of Master of Science

Major Field: Natural Resource Ecology & Management

Scope and Method of Study: The purpose of this study was to determine the effects of prescribed fire frequency on the forest understory plant community and forest composition in an old-growth forest of eastern Oklahoma. The study was conducted at the Okmulgee Game Management Area in the summer of 2008. Prescribed fires over the past 20 years had a frequency of zero to five per decade. Tree density and basal area was measured on 20 plots of 0.01 ha in each of eight treatment units. Overstory canopy cover, ground cover, and understory plant cover were sampled from four – 1 m<sup>2</sup> sub-plots nested in each of the sample plots.

Findings and Conclusions: Frequent low-intensity fire is necessary to maintain the dominance of fire tolerant oak species and the high biodiversity of herbaceous plants in the forest understory. Fire-intolerant shrub and sapling density and richness increase as fire frequency is reduced from five to zero fires per decade. Twenty years of low intensity fire at a frequency of five per decade is not sufficient for the reduction in tree density and canopy cover. Frequent low intensity fires in the range of two to five per decade are sufficient to maintain oak overstory dominance, as this frequency will control fire-sensitive woody shrubs and saplings while not reducing the density of oak saplings that eventually grow into the canopy. Fire frequencies from two to five per decade can significantly improve the habitat for wildlife that benefit from increased diversity and production of palatable herbaceous plants. Fire frequencies as low as two per decade can reduce the habitat quality for wildlife species that benefit from a high density and diversity of shrubs and saplings in forest understories. While no herbaceous species were reduced in presence or cover by higher fire frequencies, many herbaceous species responded positively to increased fire frequencies. Landscapes with a diverse mosaic of forest understories can be produced by prescribe burning at varying frequencies and times since last fire.

ADVISER'S APPROVAL: Stephen W. Hallgren

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