

CROSS-TIMBERS OAK WOODLAND REGENERATION AS A FUNCTION OF  
WOODLAND AGE, CANOPY GAP SIZE, AND DEER HERBIVORY

A Thesis by

Beverly J. Cory

Bachelor of Science, The Ohio State University, 1982

Submitted to the Department of Biology  
and the faculty of the Graduate School of  
Wichita State University  
in partial fulfillment of  
the requirements for the degree of  
Master of Science

December 2017

© Copyright 2017 by Beverly J. Cory

All Rights Reserved

CROSS-TIMBERS OAK WOODLAND REGENERATION AS A FUNCTION OF  
WOODLAND AGE, CANOPY GAP SIZE, AND DEER HERBIVORY

The following faculty members have examined the final copy of this thesis for form and content, and recommend that it be accepted in partial fulfillment of the requirement for the degree of Master of Science, with a major in Biological Sciences.

---

Leland Russell, Committee Chair

---

Greg Houseman, Committee Member

---

Brandon T. Buerge, Committee Member

“And into the forest I go,  
to lose my mind and find my soul.”  
- John Muir

## ACKNOWLEDGEMENTS

I would like to thank my adviser, Leland Russell, for his never-ending patience, guidance, and tireless efforts to keep me focused and on track. I would like to extend my gratitude to my committee members, Greg Houseman and Brandon Buerge, for their willingness to be part of my committee and for offering valuable suggestions in the improvement of my study. I could not have accomplished this study without the help of KDWPT professionals, Vickie Cikanek, John Christianson, John Johnson, Amber Johnson and Kim Jones, and BSA Quivira Council members, Warren McCoskey and Paul King. I would also like to thank Bill and Caleb Stotts for allowing me to walk in their beautiful woodlands. A special thank you goes out to my fellow students, family and friends for their continued support, encouragement and field help.

## ABSTRACT

Oak woodlands and forests in much of eastern North America are undergoing a decline as a result of changes in disturbance regimes and herbivore populations. This conservation concern has stimulated research focusing on oak woodland regeneration. To address possible changes in tree species composition in the Cross Timbers region, a post oak (*Quercus stellata*) / blackjack oak (*Q. marilandica*) dominated, xeric vegetation type extending from Texas into Kansas, I compared canopy gap size, frequency, cause, and identities of replacement species in gaps within five young woodlands and three old woodlands in southeastern Kansas. There was no difference in gap characteristics due to woodland age, but a weak difference due to site. There was a significant difference between gap replacement species and current canopy composition. Blackjack oak was over-represented as a replacement species in canopy gaps, but this may be due to its prolific resprouting. Eastern red cedar (*Juniperus virginiana*) was also over-represented in gaps, but this was due to over-representation at one site. Overall, there was no evidence of a trend to large imminent change in woodland composition.

Large deer populations have been hypothesized to retard forest and woodland regeneration through intensive browsing of saplings. To address possible negative effects of white-tail deer (*Odocoileus virginianus*) browsing on oak regeneration in a Cross Timbers woodland, I used fencing to manipulate deer access to post oak saplings that occurred in varying sizes of canopy gaps. Light availability had a positive effect on sapling growth. Though intensity of deer browse was low, and all saplings survived, browse-excluded saplings showed greater growth than exposed saplings. Browse intensity and effect on saplings was independent of light availability. While current deer densities in Kansas Cross Timbers woodlands are not severely affecting juvenile oaks in the short term, further increases in densities should be avoided.

## PREFACE

This study developed out the serendipitous moment of developing a project for my study, Dr. Russell's interest in plant-animal interactions, and the BSA Quivira Council camp staff voicing their concerns to me regarding the health and viability of their oak woodland camp property located in Chautauqua County, Kansas.

The study was developed to address the concerns regarding oak-woodland regeneration across the eastern United States, as well as in the Cross Timbers ecoregion. Though many studies have been conducted in the eastern U.S. woodlands, few studies have addressed the transition zone of eastern woodland to central grasslands, along the xeric boundaries for tree species growth and survival, and where deer densities may also be large enough to impact oak woodland regeneration.

## TABLE OF CONTENTS

Chapter	Page
1. INTRODUCTION.....	1
2. METHODOLOGY.....	9
2.1 Descriptive Analysis: Canopy Gap Survey.....	9
2.1.1 Study System: The Cross Timbers Ecoregion in Kansas.....	9
2.1.2 Study Sites.....	10
2.1.3 Canopy Gap Survey Field Methods.....	11
2.1.4 Woodland Age Determination.....	12
2.1.5 Woodland Composition Determination.....	14
2.1.6 Statistical Analysis.....	14
2.2 Experimental Analysis: White-tailed Deer Herbivory Exclusion.....	15
2.2.1 Study Site.....	15
2.2.2 Study Species.....	16
2.2.3 Deer Herbivory Exclusion Field Methods.....	16
2.2.4 Statistical Analysis.....	19
3 RESULTS.....	22
3.1 Descriptive Analysis: Canopy Gap Survey.....	22
3.2 Experimental Analysis: White-tailed Deer Herbivory Exclusion.....	23
4. DISCUSSION.....	25
4.1 Descriptive Analysis: Canopy Gap Survey.....	25
4.2 Experimental Analysis: White-tailed Deer Herbivory Exclusion.....	28
4.3 Conclusions.....	32
REFERENCES.....	34
APPENDIX.....	43

LIST OF TABLES

Table		Page
2.1	Summary of Study Sites for Descriptive Analysis: Canopy Gap Survey.....	44
3.1	Summary of Descriptive Statistics for Post Oak ( <i>Quercus stellata</i> ) Age Structures at Three of the Study Sites in the Cross Timbers Ecoregion, Kansas.....	45
3.2	Tree Canopy Composition and Possible Replacements Found in Canopy Gaps (n=33) at Eight Cross Timbers Woodlands, Kansas.....	46

## LIST OF FIGURES

Figure	Page
2.1 Map of eastern Kansas.....	47
3.1 Post oak ( <i>Quercus stellata</i> ) age structures at three Cross Timbers woodlands, Kansas.....	48
3.2 Extended canopy gap area (m <sup>2</sup> ) of old (n=3) and young (n=5) Cross Timbers woodlands, Kansas.....	49
3.3 Distribution of canopy gaps by size category (m <sup>2</sup> ) in Cross Timbers woodlands (n=8), Kansas.....	50
3.4 Extended canopy gap area (m <sup>2</sup> ) by site in Cross Timbers woodlands, Kansas.....	51
3.5 Causes of canopy gaps in eight Cross Timbers woodlands (n= 33), Kansas.....	52
3.6 Tree canopy composition by tree species vs. canopy gap replacement species; pooled across sites in Cross Timbers woodlands (n=8), Kansas.....	53
3.7 Proportional change in natural log-transformed aboveground biomass from March 2016 to August 2017 in post oak ( <i>Quercus stellata</i> ) at Quivira Scout Ranch, Kansas, with main effects of average light above each sapling and deer exclusion treatment.....	54
3.8 Mean (SE) proportional change in natural log-transformed aboveground biomass from March 2016 to August 2017 in post oak ( <i>Quercus stellata</i> ) at Quivira Scout Ranch, Kansas.....	55
3.9 Proportional change in perpendicular height from March 2016 to August 2017 in post oak ( <i>Quercus stellata</i> ) at Quivira Scout Ranch, Kansas, with main effects of average light above each sapling and deer exclusion treatment.....	56
3.10 Mean (SE) proportional change in perpendicular height from March 2016 to August 2017 in post oak ( <i>Quercus stellata</i> ) at Quivira Scout Ranch, Kansas.....	57
3.11 Intensity of browse experienced by post oak ( <i>Quercus stellata</i> ) saplings categorized by % of available stems browsed from June 2016 to August 2017 at Quivira Scout Ranch, Kansas.....	58
3.12 Proportional distribution of post oak ( <i>Quercus stellata</i> ) stems browsed by time period.....	59

## LIST OF ABBREVIATIONS / NOMENCLATURE

CTAT	Cross Timbers State Park – Ancient Oaks Trail
CTOT	Cross Timbers State Park – Overlook Trail
ELK	Elk City Lake State Park – Post Oak Trail
FR	Fall River State Park – Post Oak Trail
QSR	Quivira Scout Ranch
STR	Stotts Ranch
WFL	Woodson State Fishing Lake
WWA	Woodson Wildlife Area
cm	Centimeter
d.b.h.	Diameter at Breast Height
km	Kilometer
ln	Natural Log-Transformed
m	Meter
mm	Millimeter
n	Sample Size
r	Radius
g	Grams

## LIST OF SYMBOLS

$^{\circ}$	Degree
$\geq$	Greater Than or Equal to
$>$	Greater Than
$<$	Less Than
$+$	Add
$-$	Subtract
$*$	Multiply
$\%$	Percent
$\pi$	Pi
$^2$	Squared
$^{\wedge}2$	Squared

# CHAPTER 1

## INTRODUCTION

Oak species (*Quercus* spp.) have been a significant component of deciduous forests in the eastern United States for the past 10,000 years (Abrams 1992). The prevalence and dominance of oaks in eastern deciduous forests over this time period may be attributed to multiple factors, including a warmer, drier climate and human land use that promoted fire (Abrams 1992, 2003). Today in the eastern United States oak forest types cover nearly half of all timberland (oak-hickory 36%, oak-pine 8%, and oak-gum-cypress 5%), with the oak-hickory forest type covering 53 million hectares (Johnson et al. 2009).

Oaks are foundation species in many eastern forests, playing an important role in structuring animal and plant communities. Van Dersal (1940) found that 186 different bird and mammal species across North America feed on oaks. Oak woodlands not only provide food and support for a substantial number of wildlife species, but also, with their more open canopies, create an environment for a highly diverse herbaceous understory. In Illinois Ozark oak dominated forests, Fralish (2004) found herbaceous species richness increased  $\geq 200$  percent from an average of 10 species/10 m<sup>2</sup> sample in a closed canopy oak/maple mixed forest to an average of 31.5 species/10 m<sup>2</sup> in open canopy post oak dominated forests.

In spite of the current dominance of oaks in forest and woodland canopies of eastern North America, a decline in recruitment of juvenile oaks to adult size classes has occurred during the middle and later 20<sup>th</sup> century throughout much of the eastern forest biome (Abrams 2003, Lorimer 1984). For example, Karnitz and Asbjornsen (2006) found white oak (*Q. alba*) and red oak (*Q. rubra*) to be the dominant mature species in a remnant woodland site in central Iowa, but the sapling and seedling layers were dominated by shade-tolerant species, with few white oak

and red oak present. Abella et al. (2017) showed that diameter distributions of black oak (*Q. velutina*) and white oak changed over a 14-year period in three vegetation types in northwest Ohio. An unrestored forest shifted toward more large diameter oaks and fewer small diameter oaks, while a restored woodland and restored savanna exhibited an increase in oak saplings in the 1-10 cm range. Russell and Fowler (2002) found either no, or reduced, recruitment to adult size classes of Spanish oak (*Q. buckleyi*) in the previous 35-60 years at four of five sites on the eastern Edwards Plateau, Texas. Healy (1997) noted that oaks may well be reduced to a minor forest component over the next century.

Regeneration failure in oak populations has been attributed to a number of factors, such as fire suppression, competition from later successional tree species, intensive deer and small mammal browsing and acorn predation (Abrams 1992, 2003). Dendrochronological evidence demonstrates that the frequency and/or intensity of fires in eastern North American forests and woodlands decreased in the late 19<sup>th</sup> and early 20<sup>th</sup> centuries (Aldrich et al. 2014, Nyamai et al. 2014). Reductions in fire frequencies and intensities during this time are correlated with greater canopy closure in oak forests and the replacement of oak species by more shade-tolerant, less fire-tolerant species (Abrams 1986, Lorimer 1984, Nowacki et al. 1990).

Nowacki and Abrams (2008) defined “mesophication” as a positive feedback cycle, whereby the micro-environmental conditions (cool, damp, and shaded conditions with less flammable fuel beds) created by shade-tolerant mesophytic species, such as red maple (*A. rubrum*), sugar maple (*A. saccharum*), beech (*Fagus* spp.), blackgum (*Nyssa sylvatica*) and black cherry (*Prunus serotina*), continually improve conditions for these species and deteriorate the micro-environment for shade-intolerant, fire-adapted species. Tall understory trees of *Acer*, *Ostrya*, *Tilia* and other genera are a major obstacle to the development of oak seedlings (Lorimer

et al. 1994). However, Abrams (1992) hypothesized that oak woodlands on dry sites may be stable communities even in the absence of fire. The speed of succession to shade-tolerant mesophytic species is either slowed or halted by the shallow, stony soils and dry, nutrient-poor sites, resulting in reduced understory competition and allowing sufficient light to reach the oak advance reproduction (seedling sprouts that are present before overstory removal) (Frelich and Reich 2002, Johnson 1993, Nowacki and Abrams 2008). Oak woodlands and forests at the western edge of eastern deciduous forest in North America can play a critical role in testing this hypothesis of oak-dominated community stability on xeric sites.

Because oaks are shade-intolerant, light limitation may be preventing their regeneration. As such, forest canopy gaps are likely to be important to allowing seedlings to recruit to adulthood. Minckler et al. (1973) determined that light increases in the center of forest canopy gaps as the ratio of gap diameter to the average height of the adjacent stand increases, and levels off when the ratio reaches 2.0. Even though growth in height and diameter for oak saplings is near maximum at light intensities approaching 50% to 70% of full sunlight (Hodges and Gardiner 1993, Gottschalk 1994), oak saplings still can grow well in gaps if they receive 20% to 50% of full sunlight, which occurs in gaps with a diameter to stand height ratio equal to 1.0 (Marquis 1965).

Successful oak regeneration is dependent upon there being an adequate number of large stems of advanced growth oak saplings present to take advantage of high light conditions when a canopy gap forms (Dey 2002). However, intense herbivory upon juvenile oaks may greatly reduce such advance growth. White-tailed deer (*Odocoileus virginianus*) are preferential foragers and browsers (where browse is the growing soft portion of perennial woody plants) and oaks are often among their preferred browse species. For example, in the Cross Timbers and Prairie

Regions of Texas, the annual food habits of deer consisted of 36% browse with oak being the most important (Dillard et al. 2005).

McCabe and McCabe's (1984) analysis of historical white-tailed deer population trends in North America indicated an initial population of 23 to 34 million deer in 1500. With an influx of European fur-traders beginning in the 1500's, an ever-increasing deer harvest, primarily by Indians, ensued until the early 1800's, reducing the population by 35-50%. In 1850-1900, unrestricted hunting, accelerated land clearing, and the influx of settlers further reduced the population numbers. By the early 1900's the white-tailed deer population across the United States was estimated at 500,000. Seeing the need for deer population management, stringent hunting regulations were put into practice, along with state and federal game refuges being established. Since this time, the deer population has rebounded to over 20 million. Along with the increase in the deer population, the human population has increased from 76 million in 1900 to over 320 million in 2016 (U.S. Census Bureau), with an associated increase in construction of roads and buildings while decreasing forest/rural/wetlands acreage (McCabe and McCabe 1997). Deer densities today may be higher than they were historically because a comparable number of deer are concentrated in a smaller amount of habitat.

At high deer population densities and in the absence of occasional fire, the appearance and ecology of oak forests can be greatly altered (Latham et al. 2005, Rawinski 2008). The understory tree and shrub layer show diminished species diversity, height, density, and vertical structure, frequently reverting to unpalatable or browsing-resilient species (Latham et al. 2005). In several regions, deer browsing also appears to limit oak regeneration (Rooney 2001, Rooney and Waller 2003). Healy (1997), working in 16 mature oak stands in Massachusetts, noted that oak regeneration and a diverse herbaceous understory were maintained at deer densities of 3-6

deer / km<sup>2</sup>, whereas, regeneration was prevented for *Q. rubra*, *Q. alba*, *Q. velutina* and *Q. coccinea* at deer densities above 10 deer / km<sup>2</sup>.

The impact that herbivory has on a plant's performance, including its fitness, depends upon several factors, such as the life stage of the plant, the type of tissue removed, timing of the damage, the genome of the plant, the species-specific responses to the attack, and most notably, the current environmental conditions or resource availability (Orcutt and Nilsen 2000). In particular, the issues of how 1) herbivore damage to plants (Herms and Mattson 1992, Price 1991, and Rhoades 1979) and 2) a plant's ability to compensate for damage (Hilbert et al. 1981, Maschinski and Whitham 1989, and Wise and Abrahamson 2007) vary in relation to resource availability to the plant have been debated by ecologists who study plant-animal interactions for a long time but remain unresolved.

Heterogeneity in light availability in forest and woodland understories provides an opportunity to address the relationship between resource availability to plants and herbivore damage. Tree seedlings and saplings in low-light understory conditions spend extended time within reach of browsers, and must balance the allocation of limited resources between growth, maintenance, and defense (Herms and Mattson 1992). When nutrients and light are readily available, fast-growing species rapidly regrow tissues to compensate for herbivore consumption, but if resources are limited, investment in defensive secondary metabolites may be advantageous (Flaspohler and Froese 2009, Coley et al. 1985). In low resource conditions, replacement of resources lost to herbivores becomes costlier as potential growth rates become more limited by resource availability. One would expect to see higher levels of defense in resource-limited environments (Coley et al. 1985). By contrast, in high resource conditions, the cost of defense is

lost growth potential and being at a competitive disadvantage to faster-growing competitors (Herms and Mattson 1992).

Several studies have addressed the role of resource availability in driving intraspecific variation in plant tissue quality for herbivores. Forkner and Hunter (2000) supplemented *Q. rubra* and *Q. prinus* saplings with fertilizer in Georgia over a two-year period. Fertilization treatments positively influenced the growth and foliage quality of oak trees, while there was an overall trend for lower tannin concentrations. Reed and McCarthy (1996) found that *Q. prinus* inhabiting the more stressful south-facing slopes expressed higher amounts of tannins than those individuals on north-facing slopes in an oak-hickory forest in southeast Ohio. With high resource conditions resulting in higher foliar nitrogen and lower secondary defense compounds, the amount of tissue that herbivores remove is expected to be greater with high resource availability.

In addition to influencing the amount of damage a plant is likely to sustain, resource availability to plants is thought to influence their ability to compensate for tissue loss to herbivores. Maschinski and Whitham (1989) proposed the Compensatory Continuum Hypothesis, where the timing and intensity of herbivory along with resource availability to the damaged plant are factors that determine if herbivory is detrimental, of no consequence, or even beneficial to a plant's fitness. In contrast to the Compensatory Continuum Model, Hilbert et al. (1981) proposed the Growth Rate Model, where a plant's ability to compensate for tissue removal from herbivory is influenced by their current growth rate. Plants in high resource conditions growing at nearly their maximum potential relative growth rate have little prospect to respond positively to herbivory and can compensate for less damage than plants in low resource conditions with growth rates far below maximum. Plants with high relative growth rates at the

time of herbivory require large increases in growth rate to compensate while slow growing plants require only small increases.

In support of the Compensatory Continuum Hypothesis, Baraza et al. (2010) simulated browse in three light conditions (full sunlight, 80% sunlight, 13% sunlight) by clipping saplings of four tree species (*Q. ilex*, *Q. pyrenaica*, *A. opalus*, and *Pinus nigra*) in southeastern Spain. Shade-grown saplings showed more nitrogen concentration and less oxidative capacity of phenolic compounds, and 3 of the 4 species declined in compensatory growth capacity after clipping in the lowest light condition, suggesting that shade-grown saplings are less able to compensate following herbivory. In support of the Growth Rate Model, Nabeshima et al. (2001) planted Mongolian oak (*Q. crispula*) saplings in Tomakomai Experimental Forest, Japan. Though not a simple tradeoff, they found in high light environments a reduction in photosynthetic function and increased induced defenses, resulting in effects of herbivory damage becoming more noticeable.

Light is a limiting resource for slow-growing oak saplings, and they spend decades exposed to deer browse. Therefore, the interaction between juvenile oaks and white-tailed deer in woodland and forest understories provides an opportunity to address, 1) does the intensity of deer browse vary under high and low light conditions; and 2) how well are the saplings able to recover from damage under high and low light conditions?

The Cross Timbers ecoregion, a transition between deciduous forests of southeastern North America and grasslands of the Great Plains, occurs at the xeric extreme of conditions that support eastern deciduous forest. It occupies southeastern Kansas, eastern and central Oklahoma, north-central Texas, and extreme west-central Arkansas (Bragg et al. 2012, Dillard et al. 2005, Hallgren et al. 2012). The Cross Timbers represent a landscape mosaic of oak-dominated

woodlands, oak savannas and grasslands. Hallgren et al. (2012) found that fire suppression in Oklahoma Cross Timbers over the past century has led to reduced dominance of oak and an increase in mesic species that are intolerant of fire. While effects of fire regime have received some study in Cross Timbers ecosystems, there is a lack of studies that have examined effects of deer upon plant populations or communities at the forest-prairie transition zone on the eastern Great Plains. The current deer population in the Cross Timbers region of Kansas is estimated to be high at 6-12 deer / km<sup>2</sup> (Quality Deer Management Association).

The xeric nature of Cross Timbers oak woodlands and high deer population densities makes them an excellent system in which to test the hypotheses that 1) oak populations are stable on dry sites and 2) intense deer browsing reduces oak recruitment even in high light environments. Here I address the roles of light availability in canopy gaps and browsing by white-tailed deer upon a dominant oak species, *Q. stellata* (post oak), in Cross Timbers woodlands of southeastern Kansas. Specifically, my research addressed 1) what is the canopy gap regime in Cross Timbers oak woodlands and how does it vary with woodland age? 2) Would shade-intolerant juvenile post oaks exhibit positive growth and survival in relation to increasing canopy gap size and light availability? 3) Is the current white-tailed deer population in this region sufficiently large to reduce juvenile post oak growth and survival? 4) If juvenile post oak growth rate and survival is positively related to gap size, would deer preferentially browse in large gaps and more strongly reduce juvenile oak growth and survival under high light conditions?

## CHAPTER 2

### METHODOLOGY

#### 2.1 Descriptive Analysis: Canopy Gap Survey

##### 2.1.1 Study System: The Cross Timbers Ecoregion in Kansas

The Cross Timbers ecoregion covers approximately 7,250,000 hectares extending from north central Texas into southeastern Kansas (The Ancient Cross Timbers Consortium). This ecosystem type is characterized as a mosaic of grassland, savanna and woodland. Vegetation physiognomy at a site appears to be determined largely by the underlying soils, where grasslands dominate the finer textured soils and the upland timbers are confined to the coarse textured soils derived from sandstone parent material (Dyksterhuis 1948, Rice and Penfound 1959).

The Cross Timbers woodlands are mostly non-commercial, xeric, oak dominated forests comprised of post oak (*Q. stellata*) and blackjack oak (*Q. marilandica*), with hickory (*Carya* spp.), elm (*Ulmus* spp.), Osage orange (*Maclura pomifera*), hawthorn (*Crataegus* spp.), eastern red cedar (*Juniperus virginiana*), and few other tree species contributing to total stand density. An almost universal trait of Cross Timbers stands is their low stature relative to the potential height of the species present. In Cross Timbers woodlands, the typical maximum canopy height is 12 to 14 m (Hallgren et al. 2012), whereas the potential canopy height for many of the tree species that occur in these woodlands exceeds 21 m (USDA Forest Service).

Since the area is unsuitable for commercial timber harvest and conventional row-crop agriculture, areas of old-growth Cross Timbers can still be found. Remnant old-growth forest is estimated to cover only 360,472 highly fragmented hectares as a result of juniper invasion, aerial application of broadleaf herbicide, and logging for chip mills, suburban development, and historic oil industry and wind energy emplacements (Cross Timbers Urban Forestry Council).

Southeastern Kansas contains the northern terminus of the Cross Timbers ecoregion, which extends into the counties of Chautauqua, Elk, Greenwood, Woodson, Wilson and Montgomery. The average annual precipitation ranges from 99 cm in northeast Woodson County to 114 cm in southeast Montgomery County (USDA Natural Resources Conservation Service 2007).

### **2.1.2 Study Sites**

For quantifying the frequencies, sizes, causes and replacement species of canopy gaps in Cross Timbers woodlands, I used eight study sites that were distributed across five of the six counties that contained Cross Timbers vegetation in Kansas, all except Wilson County. Selected sites include Cross Timbers State Park (Ancient Oaks Trail and Overlook Trail), Elk City Lake State Park (Post Oak Trail), Fall River State Park (Post Oak Trail), Quivira Scout Ranch, Stotts Ranch, Woodson State Fishing Lake and Woodson Wildlife Area (Table 2.1; Fig. 2.1). Each woodland patch was defined by natural (steep ravine) or man-made boundaries (road, parking lot, fence, clear cut, reservoir, or sewage lagoon).

Cross Timbers State Park is located in Woodson County along the Toronto Lake Reservoir, which was constructed on the Verdigris River from 1954 to 1960. The Ancient Oaks Trail (hereafter CTAT) is situated to the northeast of the reservoir, while the Overlook Trail (hereafter CTOT) is situated to the southeast of the reservoir. Elk City Lake State Park is located in Montgomery County along the Elk City Reservoir, which was constructed on Card Creek in the early 1960's. The Post Oak Trail (hereafter ELK) is situated to the northeast of the reservoir. Fall River State Park is located in Greenwood County along the Fall River Lake, which was constructed on Fall River in the late 1940's. Fall River Post Oak Trail (hereafter FR) is situated to the southeast of the lake. Quivira Scout Ranch is a privately-owned Boy Scouts of America

camp located in Chautauqua County along the Murray Gill Lake, which was constructed on North Caney River in the early 1970's. The study site (hereafter QSR) is situated to the northwest of the lake. Stotts Ranch is a privately-owned ranch located approximately 8 km south of New Albany, along the eastern edge of Elk County. The study site (hereafter STR) is along the southeast border of the property. Woodson State Fishing Lake is located in Woodson County and was constructed on Sandy Creek in the 1930's. The study site (hereafter WFL) is situated to the southeast of the lake. Woodson Wildlife Area is located in Woodson County, approximately 5.5 kilometers south of Woodson State Fishing Lake. The study site (hereafter WWA) is situated to the east of Sandy Creek.

### **2.1.3 Canopy Gap Survey Field Methods**

Following the sampling protocols suggested by Runkle (1982a), a line-intersect method was used for sampling extended canopy gaps. A canopy gap is defined as an opening in the forest canopy due to a death of a large branch, a single tree, or up to 10 trees and where active recruitment of new individuals into the canopy is occurring (Runkle 1982a). An extended canopy gap reaches to the base of the trunk of each tree surrounding a gap. The line-intersect sampling method involves sampling any extended canopy gap that touches or crosses the transect path. If a gap extends into another gap (with a constriction point at the connection point), the further gap is not included for analysis.

Using Google Earth mapping tool to establish sampling transects, the starting reference point for the first transect within each woodland site was randomly selected. From this point, a 200-m line was drawn at a compass bearing in order to fit the line within the boundaries of the property, and to be no closer than 40 m to a woodland edge. Four additional parallel 200 m transect lines were drawn 50 m apart. If the boundaries and area of the woodland did not allow

for this ideal layout, transects were either shortened with additional transects being included, or transects were extended, based on the aerial image before starting sampling. While at the site, GPS coordinates and bearings were recorded for the beginning point of each transect. Transects were paced using a Garmin GOSMAO 64st, TOPO U.S. 100K with High-sensitivity GOS and GLONASS Receiver, Model Number: 010-01199-20.

I quantified “gap frequency” as the total number of gaps encountered along the total 1000 m length of sampling transects at the site. For each extended gap that I encountered along the transects, I recorded 1) the cause of the gap, whether as dead limb, broken limb, standing dead stump, broken stump, partly uprooted, or tip over (fully uprooted); 2) the two longest perpendicular axes of each gap, which were used to estimate the area of an ellipse using equation

$$\pi * r_{(\text{axis a})} * r_{(\text{axis b})} \tag{2.1}$$

and, hence, extended gap area; and 3) the possible replacement tree(s). The replacements were categorized in height classes (<1 m , 1-2 m, 2-3 m, 3-4 m, 4-5 m, 5-6 m, and 6-7 m). Only saplings in the tallest height class present in a gap were considered to be possible canopy replacement trees. Several gaps had multiple saplings in the tallest height class and all were considered possible replacements. The GPS coordinates of the axes intercept was also noted for each gap. The species of the canopy tree(s) that was damaged to form the gap was not recorded because, in many cases, the dead tree was sufficiently deteriorated that it could not be identified to species.

#### **2.1.4 Woodland Age Determination**

I separated my sites into “young” and “old” woodlands so that I could compare gap properties between woodlands in these different age categories. According to Frelich and Reich (2002), there have been three proposed definitions to describe old-growth forest. These

definitions are 1) forests that have never been logged or had other severe disturbance by humans, 2) forests that have reached a state where self-replacement can occur without major disturbance, and 3) forests in which the trees are relatively large and old for the species and site. Frelich and Reich (2002) surmise that it is difficult to tell whether old oak forests meet the first definition; and oak forests cannot regenerate without major disturbances (such as fire), so are not able to meet the second definition. Therefore, I employed the third definition. Only a small fraction of trees survives more than 200 years in old-growth oak forests, with 100 years as the average time between successive replacements of trees in the canopy (Johnson et al. 2009). Consequently, several minimum mean threshold ages for consideration (90, 120 and 150 years) as an old oak forest have been suggested for existing oak forests in the United States (Frelich and Reich 2002). In 1982, 18 of 26 post oak increment core samples taken along the Cross Timbers State Park Ancient Oaks Trail were at least 200 years old (The Ancient Cross Timbers Consortium). By using this site as the benchmark, the other 7 study sites were ranked by relative age.

Using published oak population age structures (Rogers and Russell 2014, Stahle 1996, Stahle et al. 1996, Stambaugh and Guyette 2007, The Ancient Cross Timbers Consortium, National Centers for Environmental Information), I categorized FR and WFL as “young woodland” with modal age classes 70 - 79 and 60 - 69 years respectively, whereas, I categorized CTAT, ELK and STR as “old woodland” with modal age classes 200+, 200+, and 120 – 129 years respectively (Table 2.1). I needed to quantify age structures in order to categorize the remaining three sites. Using the same 1000 m canopy-sampling transects, the age structures for CTOT, QSR and WWA were determined by collecting post oak tree core samples at each site (40 samples site<sup>-1</sup>, 1 core tree<sup>-1</sup>). At 50 m intervals along each transect, two of the four quadrants were randomly selected. One tree core was taken from the closest canopy post oak that was  $\geq 10$

cm d.b.h. in each of the two selected quadrants at 120 cm coring height using a 28 cm long by 5 mm diameter Haglöf increment borer. If interior rot was encountered while coring, the tree was abandoned and the next closest canopy post oak in the quadrant was selected.

The methods suggested by Speer (2012) and Grissino-Mayer (n.d.) were used for processing the cores. Core samples were transported to the lab in ARTSTRAW paper straws, dried for at least 48 hours at room temperature, then glued to 9.5 mm by 9.5 mm yellow poplar core mounts using Elmer's washable school glue. Each core was incrementally sanded by first using a belt sander with 80, 120, 240, and 400 grit sandpaper, then finished by hand sanding using 30-, 15-, and 9-micron grit 3M sandpaper. Cores were dot dated using a dissecting microscope.

### **2.1.5 Woodland Composition Determination**

In order to characterize the woodlands at the study sites and to evaluate whether the species composition of replacement tree species in gaps differed from current canopy species composition, I quantified tree species composition at each site by sampling along the same 1000 m transect lengths using the point-quarter method. At each 50-m increment, the species and d.b.h. of the closest living canopy tree in each of four quadrants were recorded (80 trees site<sup>-1</sup>).

### **2.1.6 Statistical Analysis**

All statistical analyses were completed in the R environment version 3.3.1 (R Core Team 2016). R packages used include car (Fox and Weisberg 2011), lme4 (Bates et al. 2015), lmerTest (Kuznetsova et al. 2016), piecewiseSEM (Lefcheck 2015), psych (Revelle 2016), and rcompanion (Mangiafico 2017).

Gap frequencies between the two woodland age types (old, young) met the homogeneity of variance assumption (leveneTest,  $\text{Pr}(>F) = 0.329$ ), but were not normally distributed

(shapiro.test, p-value = 0.006). Therefore, a Wilcoxon rank sum test was used to compare gap frequency (gaps / km) between young vs. old woodlands with site as the unit of observation.

Gap sizes between the two woodland age types met the homogeneity of variance assumption (leveneTest,  $\text{Pr}(>F) = 0.655$ ), and were normally distributed (shapiro.test, p-value = 0.056). A nested ANOVA was used for comparing gap-sizes between young vs. old woodlands. ‘Study site’ is nested within ‘woodland age’ and individual gaps are within ‘study sites’.

For evaluating whether causes of gaps (standing dead, stump break, broken limb, dead limb, or tip over) differ in young vs. old woodlands, Fisher’s Exact Test was used.

To evaluate the similarity in species composition of replacement trees in canopy gaps vs. the woodland canopy, trees were first pooled across sites by species for canopy trees and for replacement trees. Nine species had > 1% representation in the canopy; eight species had < 1% representation and were pooled as “other”. Fisher’s Exact Test was used to determine if possible replacement tree species growing in canopy gaps were of comparable composition to the current woodland canopy. A Nominal Independence for Fisher’s Exact Test adjustment was then applied to determine pairwise significance.

## **2.2 Experimental Analysis: White-tailed Deer Herbivory Exclusion**

### **2.2.1 Study Site**

The site for the deer exclusion experiment covers 0.3 km<sup>2</sup> area at Quivira Scout Ranch (QSR). QSR is located in Chautauqua County, Kansas, at the western edge of the Cross Timbers ecoregion. The mean annual precipitation is 106 cm and mean annual temperature is 14°C (US Climate Data). This site has not been actively managed during the past 10 years. However, with the increase in eastern red cedar encroachment, cedars were aggressively removed and a

prescribed burn was conducted in March 2016. QSR is also leased for hunting during deer season.

### **2.2.2 Study Species**

Post oak was chosen for the study species because 1) it is a dominant species of Cross Timbers oak woodlands (Hallgren et al. 2012); and 2) it is frequently browsed by white-tailed deer (Dillard et al. 2005).

Post oak is widespread in the eastern and central United States from Massachusetts, south to central Florida, and west to southeast Iowa, eastern Kansas, Oklahoma and central Texas. In the Midwest, it grows as far north as southeastern Iowa, central Illinois and southern Indiana (McGregor et al. 1986). Post oak is slow-growing and can live 200 to 400 years (Stahle et al. 1996). In the mesic portions of its range, it generally grows 15 to 18 m in height and 30 to 61 cm in d.b.h. (Carey 1992, Stahle et al. 1996). In the western edge of its range, mature trees grow 9 to 12 m in height and 38 to 46 cm in d.b.h. (Burns and Honkala 1990). Post oak is shade intolerant and because of its slow growth, can be overtopped by other trees (Burns and Honkala 1990). Post oak is moderately resistant to fire and is more drought tolerant than white oak (*Q. alba*), black oak (*Q. velutina*) or northern red oak (*Q. rubra*) (USDA Forest Service). Post oak persists and can become dominant on poor sites because of its drought resistance (Burns and Honkala 1990, Carey 1992, Reich and Hinckley 1989).

### **2.2.3 Deer Herbivory Exclusion Field Methods**

A 'split-plot' experimental design was used with canopy gap size (large vs. small) as the between-plot treatment and deer herbivory (exposed vs. protected) as the within-plot treatment.

Oak saplings grow well in canopy gaps receiving 20% to 50% sunlight (Gottschalk 1994) and gap diameter to canopy height ratios  $\geq 1$  receive  $\geq 50\%$  sunlight (Minckler et al. 1973).

Since the typical Cross Timbers stand canopy height is 12 to 14 m (Hallgren et al. 2012), a gap ratio equal to 1 for a 14-m diameter circle equals an area of 154 m<sup>2</sup>. Therefore, I classified “small” gaps as < 154 m<sup>2</sup> and “large” gaps as ≥ 154 m<sup>2</sup>. A total of thirty-one gaps were identified. Gap area was estimated by measuring the two longest perpendicular axes of the extended gap and calculating the area using equation (2.1). Of the thirty-one gaps, twenty were classified as “small” gaps with size ranging 45 – 141 m<sup>2</sup> and eleven were classified as “large” gaps with size ranging 155 – 377 m<sup>2</sup>.

Latham et al. (2005) and Benner (2007) determined that deer selectively browse stems ranging from 15 cm to 1.5 m tall. Thus, within each gap I selected at least one pair of naturally-occurring post oak saplings where the tallest stems had a perpendicular height from 15 cm to 1.5 m. Saplings within a pair were of similar height. All saplings were at least 1 m apart to ensure they were not from the same root collar. All saplings were marked with a Presco 45-cm orange PVC flag, identified with a numbered metal tag at the base.

I randomly selected sixteen small gaps and nine large gaps for experimental gaps. For every sapling pair within a gap, one sapling was randomly selected to be encircled in March 2016 by a 1 m diameter x 1.2 m high fence (2.5 cm mesh) to protect from deer browsing, leaving the other sapling exposed to deer browsing and, therefore, functioning as a control. Since herbivory by deer was the focus of this study, two 17.5 cm holes were cut along the bottom edge on opposing sides to allow access to small animals. A total of 50 saplings (25 protected vs. 25 exposed) were within small gaps and 50 saplings (25 protected vs. 25 exposed) were within large gaps.

The presence of large cages in a gap may alter deer movement patterns and browsing within that gap. Therefore, no cages were established in the remaining four small gaps and two

large gaps and they served as controls for effects of cage presence on deer use. A total of 10 saplings were monitored in the small control gaps and 10 saplings were monitored in the large control gaps.

In juvenile oaks, if multiple stems emerged from the soil within 30 cm of one another and leaned away from each other, then the stems were considered to be a single genetic individual (genet) (L. Russell, pers obs). The dependent variables measured on each sapling included number of live stems per genetic individual, perpendicular height of tallest live stem, lengths of all live stems, basal diameter of all live stems, number of live stems recently browsed and whether or not the sapling survived. If the stem had one or more branches browsed, it was counted as browsed. The number of browsed branches on a single stem was not recorded. To aid in consistency of identifying stems of the same genet for subsequent measurements, the base of the sapling was encircled with a 30-cm diameter wire loop. Measurements were taken in March, June, and September 2016 and March, June and August 2017.

To identify a non-destructive means of estimating aboveground biomass for saplings used in the experiment from the measurements taken, one post oak sapling per gap that was not being used in the experiment was measured (number of stems, perpendicular height of tallest stem, lengths of all ground stems, and basal diameter of all stems) and then harvested in September 2016. To emulate, as close as possible, the perpendicular height range of the experimental saplings, the height range of the tallest stem for the harvested saplings was 13 to 80 cm. The saplings were dried in a Yamato mechanical convection oven DKN810 at 60° for 3 days and then weighed.

Light availability is a limiting resource for shade-intolerant post oak saplings. To determine if gap size could be a proxy for light availability, light measurements along the 1/4,

1/2, 3/4 lengths of the two longest perpendicular axes of each gap were taken in June 2016 using an AccuPAR LP-80 ceptometer to measure photosynthetic available radiation (PAR). However, after analysis using Pearson Product Moment Correlation, there was no significant correlation between light availability and gap size ( $r = 0.349$ ,  $p\text{-value} = 0.054$ ). Hence, light measurements were taken directly above each sapling in September 2016, March, June, and August 2017. All light measurements were taken within a 4-hour period straddling solar noon.

After the post oak saplings were tagged, measured and fenced in March 2016, a prescribed fire was set by the land owners. To determine if fence enclosures produced a sheltering effect from the fire, sapling stem death was recorded and the degree of melting of the PVC flags was used as an indicator to quantify four categories of burn intensity each sapling encountered.

#### **2.2.4 Statistical Analysis**

All statistical analyses were completed in the R environment version 3.3.1 (R Core Team 2016). R packages used include blmeco (Korner-Nievergelt et al. 2015), car (Fox and Weisberg 2011), lme4 (Bates et al. 2015), lmerTest (Kuznetsova et al. 2016), piecewiseSEM (Lefcheck 2015), psych (Revelle 2016), and rcompanion (Mangiafico 2017).

A Fisher's Exact Test was used to determine if deer exclosures tempered or amplified the intensity of fire exposure during a prescribed burn in March 2016 using four levels of PVC marker flag melt (no melting or singeing, some melting or singeing, extensive melting, absence of flag). Since the presence of caging did not influence the intensity of the burn ( $p\text{-value} = 0.266$ ), burn effects were not considered in subsequent growth analysis.

For harvested saplings, the aboveground biomass met the homogeneity of variance assumption (leveneTest,  $\text{Pr}( > F ) = 0.774$ ), but was not normally distributed (shapiro.test,  $p\text{-value}$

< 0.001). After log transformation of aboveground biomass, the homogeneity of variance strengthened ( $\text{Pr}( > F ) = 0.993$ ), and normality of distribution improved ( $\text{p-value} = 0.023$ ). A multiple linear regression was used with both backward elimination and stepwise addition to identify the combination of size variables that I measured on each sapling that provide the best non-destructive estimate of aboveground biomass.

To analyze effect of large cages on number of stems browsed, a generalized mixed effects linear regression for binomial distribution was used, with one main effect (gap type). The gap was the random effect. The presence of large cages did not affect total stems browsed ( $\text{Pr}(\text{Chi}) = 0.820$ ).

Proportional change in sapling aboveground biomass was calculated by subtracting beginning aboveground biomass from ending aboveground biomass and dividing by beginning aboveground biomass. The proportional change in aboveground biomass met the homogeneity of variance assumption (leveneTest,  $\text{Pr}( > F ) = 0.593$ ) for combinations of the gap size and deer exclusion treatments. It was not normally distributed (shapiro.test,  $\text{p-value} < 0.001$ ). A natural log-transformation slightly decreased the homogeneity of variance ( $\text{Pr}( > F ) = 0.539$ ), but normalized the distribution ( $\text{p-value} = 0.213$ ). Therefore, a mixed effects linear regression was used to analyze natural log-transformed proportional change in aboveground biomass with the three main effects (deer exclusion, gap size and light availability above the sapling) and all interactions. Light availability above each sapling was quantified as the mean of the September 2016, March, June and August 2017 light measurements above the sapling. The gap was the random effect. After initially conducting the analysis using the full model, I successively used likelihood ratio tests (backward elimination) to identify interaction terms and main effects that

did little to improve model fit. I then re-ran models with these uninformative terms dropped to arrive at a final model.

Proportional change in sapling perpendicular height was calculated by subtracting beginning perpendicular height from ending perpendicular height and dividing by beginning perpendicular height. The proportional change in height met the homogeneity of variance assumption (leveneTest,  $\Pr(>F) = 0.402$ ) for combinations of the gap size and deer exclusion treatments. It was not normally distributed, but weakly (shapiro.test,  $p\text{-value} = 0.047$ ). A mixed effects linear regression was used to analyze proportional change in height with the three main effects and all interactions. The gap was the random effect. A similar model selection procedure was used to that used for analysis of proportional change in aboveground biomass.

The initial measurements of the saplings were taken at the same time the deer exclosures were installed, therefore the March 2016 measurements were not included in the analysis for deer browse effects. For each sapling, the number of stems and the number of stems browsed by deer were totaled using the remaining 5 measurement periods. Saplings within deer exclosures did not experience deer browse, so were excluded from the analysis. A generalized mixed effects linear regression for binomial distribution with one main effect (gap size) was used to analyze total stems browsed by deer per sapling as a fraction of total stems available per sapling. The gap was the random effect.

## CHAPTER 3

### RESULTS

#### 3.1 Descriptive Analysis: Canopy Gap Survey

Mean ages at breast height for the three woodlands where I described *Q. stellata* age structures ranged from 64 to 94 years, so all three were classified as “young” woodlands (Table 3.1). The age distributions showed substantial recruitment of post oak at CTOT from 1928 to 1937, at QSR from 1938 to 1947, and at WWA from 1958 to 1967 (Fig. 3.1).

Across 8 woodland sites (old,  $n = 3$ ; young,  $n = 5$ ), I encountered a total of 33 gaps along sampling transects. Woodland age does not affect the mean number of gaps per linear kilometer ( $p$ -value = 0.525). Pooled across both age types, the gap frequency mean was 4.12 gaps / linear km (SE 1.16).

For gap sizes, there was no significant difference between the two age classes ( $\Pr(>F) = 0.570$ ) (Fig. 3.2). Pooling across woodland age categories, the mean extended canopy gap size was 142.53 m<sup>2</sup> (SE 13.85), with a range of 24.88 m<sup>2</sup> to 355.01 m<sup>2</sup>. The modal size class was 75 - 99 m<sup>2</sup> (Fig. 3.3). The effect of site was significant (Fig. 3.4), but rather weak ( $X^2(1, N=8) = 4.09$ ,  $p$ -value = 0.04).

Stand age also does not affect the causes of canopy gaps ( $p$ -value = 0.35). For all canopy gaps, stump break / tip over represented 52% of the causes, while standing dead represented 33% and broken limb 15% (Fig. 3.5).

A significant difference was found in canopy gap replacement species vs. woodland canopy composition ( $p$ -value < 0.001) (Table 3.2). Although post oak dominated these woodland canopies, blackjack oak predominated as the most likely canopy replacement tree in gaps (Fig.

3.6). Eastern red cedars also were over-represented among replacement trees as compared to their representation in the current canopy.

### 3.2 Experimental Analysis: White-tailed Deer Herbivory Exclusion

Natural log-transformed aboveground biomass of post oak saplings was best predicted by a function that included all four of my size measurements; total basal area, number of stems, total length of all stems and perpendicular height of the tallest stem ( $F_{(4,26)} = 51.07$ , p-value < 0.001,  $R^2_{(adj.)} = 0.870$ ). One extreme outlier for the harvested saplings was identified. However, no indication of inaccurate measuring could be detected, therefore, the outlier sapling measurements were included in the analysis. The natural log-transformed aboveground biomass was then calculated for the experimental saplings as

$$1.9777 + (\text{basal area} * .0794) + (\text{stem lengths} * 0.0067) - (\text{stem numbers} * 0.1242) + (\text{perpendicular height} * 0.0080) \quad (3.1)$$

For analysis of treatment effects upon proportional change in (ln)aboveground biomass of the experimental saplings, one extreme outlier was identified. It had a disproportionately large aboveground biomass, so was determined to be an error in sampling. Upon removing the outlier sapling from the samples, the resulting model did not change, it was only strengthened. From the mixed effects linear regression model, likelihood ratio tests removed gap size as a main effect, as well as all interactions between average light over the sapling, gap size, and deer exclusion. The final model retained average light over the sapling and deer exclusion as the main effects, with gap as the random effect. Proportional change in (ln)aboveground biomass increased with average light above the sapling ( $F_{(1,75.492)} = 8.018$ ,  $\text{Pr}(>F) = 0.006$ ) (Fig. 3.7). As a result of the March 2016 prescribed fire, mean proportional change in (ln)aboveground biomass was negative for both saplings protected from deer and saplings exposed to deer, but protected saplings were

closer to their pre-fire (ln)aboveground biomass than were exposed saplings ( $F_{(1,70.657)} = 5.696$ ,  $\text{Pr}(>F) = 0.02$ ) (Fig. 3.8). Exposed saplings showed a 32% greater decrease in mean (ln)aboveground biomass than did protected saplings.

From the mixed effects linear regression model for proportional change in perpendicular height, the likelihood ratio test removed the size of the gap as a main effect, as well as all interactions between average light over the sapling, gap size, and deer exclusion. The final mixed effects linear regression model retained average light over the sapling and deer exclusion as the main effects, with gap as the random effect. Proportional change in perpendicular height increased with average light above the sapling ( $F_{(1,90)} = 8.169$ ,  $\text{Pr}(>F) = 0.005$ ) (Fig. 3.9). Mean proportional changes in perpendicular height were negative for both saplings exposed to and protected from deer herbivory. However, protected saplings were closer to their pre-fire height than were exposed saplings ( $F_{(1,90)} = 4.521$ ,  $\text{Pr}(>F) = 0.036$ ) (Fig. 3.10). Exposed saplings showed an 11% greater decrease in mean height than did protected saplings.

When comparing proportion of available stems browsed per sapling against gap size in a generalized mixed effects linear regression, there was no effect of gap size ( $\text{Pr}(\text{Chi}) = 0.503$ ). The frequency distribution of saplings among browse severity categories was right skewed with 48% of saplings escaping browsing entirely and 18% of saplings have >10% of available stems browsed (Fig 3.11). The proportion of stems browsed was not homogenous across seasons, with March being highest, followed by June, with September being the lowest proportion (Fig. 3.12).

## CHAPTER 4

### DISCUSSION

#### 4.1 Descriptive Analysis: Canopy Gap Survey

Gaps in woodland and forest canopies are crucial to the recruitment of light-demanding tree species to reproductive size classes. Therefore, a woodland's gap regime, including gap frequency and size, can determine which canopy tree species are able to regenerate. According to Runkle (1982b), as a tree ages, it becomes increasingly vulnerable to smaller and more common disturbances, which would lead to the hypothesis that older woodlands would have increased frequency, and possibly larger size, of canopy gaps. These more frequent and larger canopy gaps would allow greater light availability. With greater light penetration to the woodland floor, opportunities for the successful regeneration of shade-intolerant oaks are created. Yet, my results indicate that woodland age does not affect frequency, size or cause of canopy gaps in the Kansas Cross Timbers region. This may be due to post oak dominating the woodland canopy. Post oak is relatively long lived, drought tolerant and fire resistant (Stahle et al. 1996, and USDA Forest Service), therefore persistent in forestalling mortality.

Karki and Hallgren (2015) found gap sizes in three old-growth Cross Timbers forests in Oklahoma that were similar to my findings, but their gap frequency was higher. They found a total of 83 gaps along three 1000-m transects, with average extended gap sizes of 67.8 m<sup>2</sup> (SD 38.4), 95.9 m<sup>2</sup> (SD 47.2) and 56.1 m<sup>2</sup> (SD 21.8). Whereas, I sampled 33 gaps along eight 1000-m transects for a mean extended gap size of 142.53 m<sup>2</sup> (SE 13.85). Nonetheless, the modal gap size I encountered was 75 – 99 m<sup>2</sup>, which more closely followed Karki and Hallgren (2015)'s means. The lower frequency of gaps that I encountered could be attributed to differences in canopy density among sites. I encountered areas of dense canopy where 1) a dead branch was snagged

on surrounding branches and did not create an opening, 2) a standing dead canopy opening was quickly filled in by extended branch growth from the surrounding canopy trees, and 3) a potential tip-over canopy tree was prevented from falling and thus no opening was created.

In comparison to other eastern North American forests and woodlands, gaps in Cross Timbers woodlands appear to be less frequent and smaller. For example, Rebertus and Burns (1997) found the mean extended gap size of 512 m<sup>2</sup> (SD 310) in 15 gaps along seven 100-m transects in a *Quercus*-dominated dry forest in the Ozark Highlands, Missouri. The frequency, as well as the mean gap size is considerably larger when compared to my study. This may be due to canopy gaps in the Ozarks being created primarily by windfall, where trees are uprooted by wind and, in the process, damage surrounding vegetation. In a southern Appalachian mixed *Quercus* forest, Hart and Kupfer (2011) sampled 40 canopy gaps (distance was not reported), with mean extended area of 213.34 m<sup>2</sup> (SE 17.15). Again, the mean gap size is considerably larger when compared to my study. The larger mean size of the gaps can be attributed to the cause of the gaps being uprooted trees (40%). Further, in the xeric environment at the western edge of eastern deciduous forest, Cross Timbers woodlands are smaller in stature than the tree species' growth potential, resulting in smaller canopy openings upon tree mortality.

The effect of site upon gap size in my study is significant, but rather weak, indicating that there is variation among sites in the sizes of extended canopy gaps that is due to something other than stand age. Site differences were beyond the scope of this study, but possible explanatory factors may include topography, site abiotic factors, woodland composition, disease stress, fire effects, and land management regimes. Variability among sites could also be due to small sample sizes at individual sites caused by the constraint of only sampling gaps that intersected the 1 km transect.

My results likewise indicate that woodland age does not affect causes of canopy gaps. In both young and old woodlands, I found stump break and tip over represented the majority of the causes (52%), while standing dead was the next leading cause (33%), with broken limb representing the remaining (15%). The stump breaks were probably originally a standing dead that eventually rotted enough for the main trunk to break off. Tip overs were not common at 6%, so I included them with stump breaks for analysis. Unfortunately, there is a lack of studies reporting the causes of gaps in Cross Timbers woodlands with which to make comparisons. However, in different forest types, Rebertus and Burns (1997) in Missouri Ozark xeric oak forest reported stump break (due to windfall) as the leading cause of gaps (54%), with tip over (25%) and standing dead (21%) as comparable causes. Hart and Kupfer (2011) in Tennessee mixed oak forest reported stump break (40%) and tip over (40%) both being prevalent, whereas, standing dead (20%) caused the remainder of the gaps. The proportion of stump breaks that I encountered was comparable to causes of gaps in other forests and woodlands. The proportion of tip-overs at my Cross Timbers sites was considerably less and may be due to the shorter stature of the canopy, which may make trees less susceptible to windthrow. The proportional representation of standing dead that I encountered was higher than reported for other woodlands and forests, possibly due to the prevalence the relatively short-lived species, blackjack oak (average lifespan 100 years) (Loehle 1988). Karki and Halgren (2015) found that blackjack oak had a higher frequency as a gap maker than its representation in the woodland canopy would suggest.

By comparing current canopy composition with species composition of replacement trees in gaps, I can gain insight into possible future changes in canopy species composition in Kansas Cross Timbers woodlands. Although blackjack oak was not the dominant species in the canopy, it was the dominant replacement species within gaps. Blackjack oak is not only shorter lived than

post oak, Karki and Hallgren (2015) found that blackjack oak was more susceptible than post oak to small scale disturbances. But despite its susceptibility and higher mortality rate, there is evidence that blackjack oak may exhibit abundant sprouting (DeSantis and Hallgren 2011). This may account for blackjack oak's high frequency as a replacement species within canopy gaps. Eastern redcedar was also over-represented as a replacement species when compared to the canopy frequency. However, this result is driven by my ELK site, which has an exceptionally high frequency of eastern redcedar present in both the canopy and as replacements. Still, the three most frequent canopy species (post oak, blackjack oak, and eastern redcedar) were also the three most frequent replacement species. Therefore, my data do not provide evidence for large, imminent changes in canopy composition at most Cross Timbers sites that I surveyed.

#### **4.2 Experimental Analysis: White-tailed Deer Herbivory Exclusion**

Effects of white-tailed deer browsing on tree regeneration in woodlands and forests are a significant conservation concern in eastern North America (Latham et al. 2005, Rawinski 2008, and Rooeny and Waller 2003). However, relatively little is known about effects of deer on juvenile trees at the forest-prairie ecotone of the eastern Great Plains. In my study, exposure to deer browse negatively impacted sapling growth, but did not cause any sapling mortality. To illustrate deer effects on post oak sapling growth, for the initial measurements, sapling mean perpendicular height was 2.23 cm shorter and mean above ground biomass was 98.53 g lighter for saplings that were assigned to be protected from deer vs. saplings that were assigned to be exposed to ambient levels of deer herbivory. After two growing seasons, mean perpendicular height for protected saplings was 4.86 cm taller than exposed saplings, an overall gain of 7.09 cm, while the mean aboveground biomass was 2.11 g heavier for protected saplings than exposed saplings, an overall gain of 100.64 g. Deer may browse on terminal or lateral branches, but the

impact of terminal branch removal is more severe, resulting in short, bushy growth. Saplings with short, bushy growth form may remain under browsing pressure longer, and may eventually succumb to mortality (Nolte and Dykzeul 2000).

Although gap size did not significantly affect the proportion of available stems browsed, browsing damage was not distributed uniformly across post oak saplings and, over-all, intensities of browsing appeared rather low. Nearly half of the exposed saplings (48%) did not suffer any browse, while 34% experienced up to 10% of their available stems browsed. The remaining 18% of the saplings experienced greater than 10% of available stems browsed, with multiple browse episodes. Though browsing did not appear to be intense, the impact on overall sapling growth may be driven by the responses of the few saplings that were browsed heavily. The growth trajectories of browsed vs. unbrowsed saplings are likely to diverge slowly over time, but it would be an overstatement to conclude that deer browsing suppresses post oak regeneration, given the magnitude of the effects.

The total number of stems browsed in March was higher than browse in June, and June was higher than September. Browse in March was before bud break; therefore, no leaf tissue was removed, only the terminal meristem and surrounding stem tissues. The removal of the apical bud could possibly halt the length growth of the stem until a lateral branch would gain the leader position. Though leaf tissue removal was not measured, deer have a large, non-discriminating bite, thus stems browsed in summer would also have experienced leaf tissue loss leading to decreased photosynthetic capability. With this decrease in photosynthesis production, a decrease in the carbon resources available for essential plant functions, such as growth and production of defense chemicals, would ensue (Woolery and Jacobs 2011).

According to the Compensatory Continuum Model (Maschinski and Whitham 1989), the impact of herbivory is related to not only resource availability, but also timing of the herbivory, and intensity of the damage. In a southern Appalachian forest, the consumption of leaves and twig tips of woody deciduous plants by deer were higher in spring and summer, and twig ends were used little by deer during fall and winter, depending upon availability of acorns (Johnson et al. 1995). In the Cross Timbers region in central Oklahoma (Bryant 1996) the percentage of browse peaked in fall diets then declined throughout winter and spring. Woolery and Jacobs (2011) determined that winter browse did not affect growth of northern red oak seedlings, whereas summer browsing was highly detrimental. In my study, browse was highest in winter, then declined through spring and summer, which then suggests that the timing of browse may have reduced its impact. Intensity of browse in my study also has low impact, since 82% of the saplings experienced <10% of their stems browsed.

Connecting the magnitude of deer effects on vegetation that are observed in enclosure experiments with data on local deer densities in the vicinity of the experiment is important for developing land managers' abilities to predict deer effects on plant communities in situations where only deer density data exist. The deer population was slightly higher at QSR than in most Kansas Cross Timbers sites (V. Cikanek KDWPT, pers. comm.). Estimates for deer population densities in this region are 6-12 deer/km<sup>2</sup> (Quality Deer Management Association), which approaches the level of 7.72 deer/km<sup>2</sup> where Tilghman (1989) predicted that oak recruitment would be inhibited in forests of the Allegheny Plateau in Pennsylvania. The eastern Osage Cuestas ecoregion of Kansas has similar deer densities (Quality Deer Management Association). While deer density is certainly one important factor determining deer effects, forage quality and quantity, and proximity to roads and forest cover also contribute to determining use of a site by

deer (Burney and Jacobs 2013). Not all sites are treated equally, and deer selectively browse on plants based on nutrient availability while minimizing ingestion of plant toxins (Burney and Jacobs 2013). The level of damage by deer varies according to population sizes, tree species, seedling size, and presences of alternate forage (Nyberg 1990). In the immediate surroundings of my study site, soybean fields and native pastures can be found, and serve as alternate food sources (V. Cikanek KDWPT, pers. comm.). The landscape context of my site may have lessened the effect of deer by providing an alternate food source.

Consistent with the expectation that light is a limiting resource for shade-intolerant, slow-growing juvenile oaks (Johnson et al. 2009), this study demonstrated that increased light has a positive effect on the growth of the saplings, suggesting increased productivity and fitness in higher resource conditions. The stimulated increase in perpendicular height also indicates a possible successful attainment of canopy height in higher light gaps, as well as escaping from browse pressure quicker. The characteristics of gaps used in the deer herbivory exclusion experiment at QSR (range 45-377 m<sup>2</sup>, mean 146.9 m<sup>2</sup>, modal 50-99 m<sup>2</sup>) were similar to the canopy gaps encountered across the eight Cross Timbers woodlands that I sampled in my gap survey (range 25-355 m<sup>2</sup>, mean 142.5 m<sup>2</sup>, modal 50-99 m<sup>2</sup>). Therefore, the light regimes in my experiment are representative of those experienced by juvenile post oaks in gaps in the Kansas Cross Timbers.

Post oak saplings in low light conditions show decreased proportional change in growth compared to high light conditions, while exposure to deer browse further decreased the proportional change in growth in both light resource conditions. There was, however, a lack of interaction between light availability and deer exclusion, and the effect of browse damage and plant compensatory growth did not vary across resources. In contrast to an abundance of

literature suggesting effects of resource availability on the amount of herbivore damage and on herbivore effects on plant performance, there was 1) no difference in the frequency of browsing in relation to light availability, and 2) no difference in browsing effects upon growth in relation to resource availability. But, for slow growing species, like oak, such differences may take a while to appear.

Fire is thought to have been an important disturbance in oak dominated woodlands and forests of eastern North America historically (Nowacki and Abrams 2008). Immediately after the start of my experiment in March 2016, a prescribed fire affected my study site and caused 80% of my saplings to die back to the soil surface. By August 2017, nearly two growing seasons after the burn, perpendicular height of the tallest stem and aboveground biomass of the saplings had not completely recovered to their values before the burn. The resulting negative proportional change in sapling height over the course of the study suggests that the energy for regrowth appears to have been diverted to growth of additional stems within the genet. Following the prescribed burn in March 2016, 21% of the saplings showed no change in the total number of genet stems, while 62% of the saplings had an increase in the total stem numbers. This suggests that prescribed fire stimulates resprouting from the root collar.

### **4.3 Conclusions**

Though I examined both young and old woodlands in the Cross Timbers region of Kansas, I found no significant effect of woodland age upon frequency, size, or cause of gaps. Despite the fact that the gaps I encountered were, on the average, smaller than those reported elsewhere in eastern North America, possibly indicating limiting light resource availability, I found no evidence for large, imminent changes in canopy composition at most of the Cross

Timbers sites that I surveyed. This suggests the Cross Timbers woodlands may be relatively stable in xeric conditions.

Light availability and intense deer browsing may also affect oak sapling growth and fitness. Consistent with the expectation that light is a limiting resource for shade-intolerant, slow-growing juvenile oaks, this study demonstrated that increased light in canopy gaps has a positive effect on the growth of the saplings. Deer densities in Chautauqua County, Kansas (approx. 7 deer / km<sup>2</sup>) are estimated to be at the lower limit at which deer are predicted to have detrimental impacts on oak woodland regeneration. Although exposure to deer did suppress post oak sapling growth, browsing intensities appeared rather low in this study. The growth trajectories of browsed vs. unbrowsed saplings are therefore likely to diverge slowly overtime. There also was no interaction effect between light availability and deer browse intensity. The frequency and intensity of browsing did not vary with light resources. Further studies are suggested in this region to evaluate deer density impacts extending over a larger geographic area, since deer are not evenly distributed over their range (VerCauteren 2003).

## REFERENCES

## REFERENCES

- Abella SR, Schetter TA, Menard KS, Ziegler ED, Sprow LA, Gallaher T, Jaeger JF, and Walters TL. 2017. Conserving large oaks and recruitment potential while restoring midwestern savanna and woodland. *The American Midland Naturalist* 177(2):309-317.
- Abrams MD. 1986. Historical development of gallery forests in northeast Kansas. *Vegetatio* 65:29-37.
- Abrams MD. 1992. Fire and the development of oak forests. *BioScience* 42:346-353.
- Abrams MD. 2003. Where has all the white oak gone? *BioScience* 53(10):927-939.
- Aldrich SR, Lafon CW, Grissino-Mayer HD, and DeWeese GG. 2014. Fire history and its relations with land use and climate over three centuries in the central Appalachian Mountains, USA. *Journal of Biogeography* 41(11):2093-2104. DOI:10.1111/jbi.12373
- Baraza E, Zamora R, and Hódar J. 2010. Species-specific responses of tree saplings to herbivory in contrasting light environments: An experimental approach. *Ecoscience* 17(2):156-165.
- Bates D, Maechler M, Bolker B, and Walker S. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* 67(1):1-48. DOI:10.18637/jss.v067.i01.
- Becker RA, Wilks AR, and Brownrigg R. 2016. Mapdata: Extra map databases. R package version 2.2-6. Available from: <https://CRAN.R-project.org/package=mapdata>
- Becker RA, Wilks AR, Brownrigg R, Minka TP, and Deckmyn. 2017. Maps: Draw geographical maps. R package version 3.2.0. Available from: <https://CRAN.R-project.org/package=maps>
- Benner JM. 2007. Browsing and regeneration monitoring for Pennsylvania's state forests. DCNR Bureau of Forestry.
- Bivand R, Keitt T, and Rowlingson B. 2017. Rgdal: Bindings for the 'geospatial' data abstraction library. R package version 1.2-2.13. Available from: <http://CRAN.R-project.org/package=rgdal>
- Bragg DC, Stahle DW, and Cerny KC. 2012. Structural attributes of two old-growth Cross Timbers stands in western Arkansas. *The American Midland Naturalist* 167:40-55.
- Bryant FC. 1996. Diets of female white-tailed deer in the cross-timbers region. *Prairie Naturalist* 28(3):125-140.

- Burney OT, and Jacobs DF. 2013. Ungulate herbivory of boreal and temperate forest regeneration in relation to seedling mineral nutrition and secondary metabolites. *New Forests* 44:753-768. DOI: 10.1007/s11056-013-9381-9
- Burns RM, and Honkala BH; [Technical coordinators]. 1990. *Silvics of North America: Volume 2. Hardwoods*. United States Department of Agriculture (USDA), Forest Service, Agriculture Handbook 654.
- Carey JH. 1992. *Quercus stellata*. In: Fire Effects Information System [Internet].
- Coley PD, Bryant JP, and Chapin FS 3<sup>rd</sup>. 1985. Resource availability and plant antiherbivore defense. *Science* 230(4728):895-899.
- Comeleo R. 2012. Level III Ecoregions of Kansas. US EPA Office of Research and Development – National Health and Environmental Effects Research Laboratory, Corvallis OR. [Internet] Available from: <https://catalog.data.gov/dataset/level-iii-ecoregions-of-kansas>
- Cross Timbers Urban Forestry Council [Internet] (Accessed Nov 2015). Available from: <http://www.ctufc.org/ctecosystem.htm>
- DeSantis RD, and Hallgren SW. 2011. Prescribed burning frequency affects post oak and blackjack oak regeneration. *Southern Journal of Applied Forestry* 35(4):193-198.
- Dey D. 2002. The ecological basis for oak silviculture in eastern North America. In: McShea WJ, and Healy WM, editors. *Oak Forest Ecosystems: Ecology and Management for Wildlife*. Baltimore, Maryland: The Johns Hopkins University Press. p. 60-79.
- Dillard J, Jester S, Baccus J, Simpson R, and Poor L. 2005. White-tailed deer food habits and preferences in the Cross Timbers and prairies region of Texas. Texas Parks and Wildlife Department.
- Dyksterhuis EJ. 1948. The vegetation of the western Cross Timbers. *Ecological Monographs* 18(3):325-376.
- Flaspohler DJ, and Froese RE. 2009. Death and *Taxus*: The high cost of palatability for a declining evergreen shrub, *Taxus canadensis*. *Canadian Journal of Forest Research* 39:1366-1374. DOI: 10.1139/X09-064
- Forkner RE, and Hunter MD. 2000. What goes up must come down? Nutrient addition and predation pressure on oak herbivores. *Ecology* 81(6):1588-1600.
- Fox J, and Weisberg S. 2011. *An {R} Companion to Applied Regression, Second Edition*. Thousand Oaks CA: Sage.  
URL: <http://socserv.socsci.mcmaster.ca/jfox/Books/Companion>

- Fralish JS. 2004. The keystone role of oak and hickory in the central hardwood forest. Spetich, MA, ed. 2004. Proceedings: Upland oak ecology symposium: history, current conditions, and sustainability. Gen Tech Rep SRS-73. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station.
- Frelich LD, and Reich PB. 2002. Dynamics of Old-growth oak forests in the eastern United States. In: McShea WJ, and Healy WM editors. Oak Forest Ecosystems: Ecology and Management for Wildlife. Baltimore, Maryland: The Johns Hopkins Press. p. 113-126.
- Gottschalk KW. 1994. Shade, leaf growth and crown development of *Quercus rubra*, *Quercus velutina*, *Prunus serotina* and *Acer rubrum* seedlings. Tree Physiology 14:735-749.
- Grissino-Mayer, HD. (n.d.). The Science of Tree Rings. The University of Tennessee [Internet] (Accessed Jul 2016). Available from: [web.utk.edu/~grissino/](http://web.utk.edu/~grissino/)
- Hallgren SW, DeSantis RD, and Burton JA 2012. Fire and vegetation dynamics in the Cross Timbers forests of south-central North America. Proceedings of the 4<sup>th</sup> Fire in Eastern Oak Forests Conference. GTS-NRS-P-102.
- Hart JL, and Kupfer JA. 2011. Sapling richness and composition in canopy gaps of a southern Appalachian mixed *Quercus* forest. The Journal of the Torrey Botanical Society 138(2):207-219.
- Healy WM. 1997. Influence of deer on the structure and composition of oak forests in Central Massachusetts. In: McShea WJ, Underwood HB, and Rappole JH, editors. The Science of Overabundance: Deer Ecology and Population Management. Washington, DC: Smithsonian Institution Press. p. 249-266.
- Hermes DA, and Mattson WJ. 1992. The dilemma of plants: To grow or defend. The Quarterly Review of Biology 67(3):283-335.
- Hilbert DW, Swift DM, Detling JK, and Dyer MI. 1981. Relative growth rates and the grazing optimization hypothesis. Oecologia 51(1):14-18.
- Hodges JD, and Gardiner ES. 1993. Ecology and physiology of oak regeneration. Loftis D, and McGee CE, editors. Oak Regeneration: Serious Problems, Practical Recommendations. U.S. Forest Service General Technical Report SE-84. P. 54-65.
- Johnson AS, Hale PE, Ford WM, Wentworth JM, French JR, Anderson OF, and Pullen GB. 1995. White-tailed deer foraging in relation to successional stage, overstory type and management of southern Appalachian forests. The American Midland Naturalist 133(1):18-35.
- Johnson PS. 1993. Perspectives on the ecology and silviculture of oak-dominated forests in the central and eastern states. U.S. Dept of Agriculture Forest Service. General Technical Report NC-153.

- Johnson PS, Shifley SR, and Rogers R. 2009. *The Ecology and Silviculture of Oaks*, 2<sup>nd</sup> edition. CAB International, London, UK. p. 221.
- Karki L, and Hallgren SW. 2015. Tree-fall gaps and regeneration in old-growth Cross Timbers forests. *Natural Areas Journal* 35(4):533-541.
- Karnitz H, and Asbjornsen H. 2006. Composition and age structure of a degraded tallgrass oak savanna in central Iowa. *Natural Areas Journal*. 26(2):179-186.
- Korner-Nievergelt F, Roth T, von Felten S, Guelat J, Almasi B, and Korner-Nievergelt P. 2015. *Bayesian Data Analysis in Ecology using Linear Models with R, BUGS and Stan*. Elsevier.
- Kuznetsova A, Brockhoff PB, and Christensen RHB. 2016. lmerTest: Tests in Linear Mixed Effects Models. R package version 2.0-33. <https://CRAN.R-project.org/package=lmerTest>
- Latham RE, Beyea J, Benner M, Dunn CA, Fajvan MA, Freed RR, Grund M, Horsley SB, Rhoads AF, and Shissler BP. 2005. Managing White-tailed deer in forest habitat from an ecosystem perspective: Pennsylvania case study. Report by the Deer Management Forum for Audubon Pennsylvania and Pennsylvania Habitat Alliance, Harrisburg, xix+ 340 pp.
- Lefcheck JS. 2015. piecewiseSEM: Piecewise structural equation modeling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*. 7(5): 573-579. DOI: 10.1111/2041-210X.12512
- Loehle C. 1988. Tree life history strategies: the role of defenses. *Canadian Journal of Forest Research* 18(2):209-222.
- Lorimer CG. 1984. Development of the red maple understory in northeastern oak forests. *Forest Science* 30:3-22.
- Lorimer CG, Chapman JW, and Lambert WD. 1994. Tall understorey (sic) vegetation as a factor in the poor development of oak seedlings beneath mature stands. *Journal of Ecology* 82(2):227-237.
- Mangiafico S. 2017. rcompanion: Functions to Support Extension Education Program Evaluation. R package version 1.10.1. <https://CRAN.R-project.org/package=rcompanion>
- Marquis DA. 1965. Controlling light in small clearcuttings. U.S. Forest Service Research Paper NE-39.
- Maschinski J, and Whitham TG. 1989. The continuum of plant responses to herbivory: The influence of plant association, nutrient availability, and timing. *The American Naturalist* 134(1):1-19.

- McCabe RE, and McCabe TR. 1984. Of slings and arrow: an historical retrospection. In: Halls LK, editor. *White-Tailed Deer: Ecology and Management*. Harrisburg, PA: Stackpole Books. p. 19-72.
- McCabe TR, and McCabe RE. 1997. Recounting whitetails past. In: McShea WJ, Underwood HB, and Rapploe JH, editors. *The Science of Overabundance: Deer Ecology and Population Management*. Smithsonian Institute. p. 11-36.
- McGregor R.L, coordinator, and Barkley TM, Brooks RE, and Schofield EK, eds.: *Great Plains Flora Association*. 1986. *Flora of the Great Plains*. Lawrence, KS: Univ. Press Kansas. 1392 pp.
- Minckler LS, Woerheide JD, and Schlesinger RC. 1973. Light, soil moisture and tree reproduction in hardwood forest openings. U.S. Forest Service Research Paper NC-89.
- Nabeshima E, Murakami M, and Hiura T. 2001. Effects of herbivory and light conditions on induced defense in *Quercus crispula*. *Journal of Plant Research* 114:403-409.
- National Centers for Environmental Information (NOAA) [Internet] (Accessed Aug 2017). Available from: <https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring><https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring>
- Nolte DL, and Dykzeul M. 2000. Wildlife impacts on forest resources. In: Clark L, Hone J, Shivek JA, Watkins RA, VerCauteren KC, and Yoder JK, editors. *Human conflicts with wildlife: economic considerations*. Proceeding of the 3<sup>rd</sup> NWRC Special Symposium. National Wildlife Research Center, Fort Collins, CO. pp. 163-268.
- Nowacki, GJ, and Abrams MD. 2008. The demise of fire and "mesophication" of forests in the eastern United States. *BioScience*. 58(2): 123-138.
- Nowacki GJ, Abrams MD, and Lorimer CG. 1990. Composition, structure, and historical development of northern red oak stands along an edaphic gradient in North-central Wisconsin. *Forest Science* 36(2):276-292.
- Nyamai PA, Goebel PC, Hix DM, Corace III RG, and Drobyshev I. 2014. Fire history, fuels, and overstory effects on the regeneration-layer dynamics of mixed-pine forest ecosystems of eastern Upper Michigan, USA. *Forest Ecology and Management* 322:37-47.
- Nyberg JB. 1990. Interactions of timber management with deer and elk. In: Nyberg JB, and Janz DW (eds) *Deer and Elk habits in coastal forests of southern British Columbia*. BC Ministry of Forests and BC Ministry of Environment, Victoria, BC, pp 99-132.
- Orcutt DM, and Nilsen ET. 2000. *The physiology of plants under stress: Soil and biotic factors*. 2000. John Wiley & Sons.

- Price PW. 1991. The plant vigor hypothesis and herbivore attack. *Oikos* 62(2):244-251.
- Quality Deer Management Association [Internet] (Accessed Nov 2015). Available from: [http://www.i-maps.com/Qdma/frame/default1024\\_ie.asp?C=48449&LinkID=0&NID=0&cmd=map&TL=100000&GL=010100&MF=11000](http://www.i-maps.com/Qdma/frame/default1024_ie.asp?C=48449&LinkID=0&NID=0&cmd=map&TL=100000&GL=010100&MF=11000)
- R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>
- Rawinski TJ. 2008. Impacts of white-tailed deer overabundance in forest ecosystems: an overview. Northeastern Area State and Private Forestry Forest Service, US Department of Agriculture.
- Rebertus AJ, and Burns BR. 1997. The importance of gap processes in the development and maintenance of oak savannas and dry forests. *Journal of Ecology* 85(5):635-645.
- Reed JL, and McCarthy BC. 1996. Patterns of leaf tannin variation in chestnut oak (*Quercus prinus*) and black oak (*Quercus velutina*) with respect to topography in a southeastern Ohio oak-hickory forest. *Bulletin of the Torrey Botanical Club* 123(3):243-248.
- Reich PB, and Hinckley TM. 1989. Influence of pre-dawn water potential and soil-to-leaf hydraulic conductance on maximum daily leaf diffusive conductance in two oak species. *Functional Ecology* 3(6):719-726.
- Revelle W. 2016. psych: Procedures for Personality and Psychological Research, Northwestern University, Evanston, Illinois, USA, <http://CRAN.R-project.org/package=psych> Version = 1.6.6.
- Rhoades DF. 1979. Evolution of plant chemical defense against herbivores. In: Rosenthal GA and Janzen DH, editors. *Herbivores: Their interaction with secondary plant metabolites*. Academic Press, New York. pp. 3-54.
- Rice EL, and Penfound WT. 1959. The upland forests of Oklahoma. *Ecology*. 40:593-608.
- Rogers T, and Russell FL. 2014. Historical patterns of oak population expansion in the Chautauqua Hills, Kansas. *Journal of Biogeography* 41:2105-2114.
- Rooney TP. 2001. Deer impacts on forest ecosystems: A North American perspective. *Forestry* 74(3): 201-208.
- Rooney TP, and Waller DM. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management* 181:165-176.

- Runkle JR. 1982a. Guidelines and sample protocol for sampling forest aps. Gen. Tech. Rep. PNW-GTR-283. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 44p.
- Runkle JR. 1982b. Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology* 63(5):1533-1546.
- Russell FL, and Fowler NL. 2002. Failure of adult recruitment in *Quercus buckleyi* populations on the eastern Edwards Plateau, Texas. *The American Midland Naturalist* 148(2):201-217.
- Speer JH. 2012. *Fundamentals of Tree Ring Research*. University of Arizona Press. 368p.
- Stahle DW. 1996. Stahle - Elk River – QUST - ITRDB KS010. National Centers for Environmental Information. NOAA. [Internet] Available from: <http://www.ncdc.noaa.gov/paleo-search/>
- Stahle DW. 1996. Stahle – Toronto Lake – QUST - ITRDB KS004. National Centers for Environmental Information. NOAA. [Internet] Available from: <http://www.ncdc.noaa.gov/paleo-search/>
- Stahle DW, Therrell MD, Gleavelena MK, and Roe S. 1996. The bioserve potential of the ancient cross timbers on the Frank tract, Osage county, Oklahoma. Available: <http://www.uark.edu/misc/xtimber/rna/Frank%20Tract%20significance.pdf>
- Stambaugh MC, and Guyette RP. 2007. Stambaugh – Lazy S-B Ranch – QUST - ITRDB KS011. National Centers for Environmental Information. NOAA. [Internet] Available from: <http://www.ncdc.noaa.gov/paleo-search/>
- Tilghman N. 1989. Impacts of White-Tailed Deer on Forest Regeneration in Northwestern Pennsylvania. *The Journal of Wildlife Management* 53(3):524-532.
- The Ancient Cross Timbers Consortium. University of Arkansas Tree-Ring Laboratory [Internet] (Accessed Feb 2016). Available from: <http://www.uark.edu/misc/xtimber/rna/xtimberpark.html>
- U.S. Census Bureau [Internet] (Accessed Oct 2017). Available from: [https://www.census.gov/popclock/?eml=gd&intcmp=home\\_pop&utm\\_medium=email&utm\\_source=govdelivery](https://www.census.gov/popclock/?eml=gd&intcmp=home_pop&utm_medium=email&utm_source=govdelivery)
- Van Dersal WR. 1940. Utilization of oaks by birds and mammals. *Journal of Wildlife Management* 4:404-428.
- VerCauteren K. 2003. The deer boom: Discussions on population growth and range expansion of the white-tailed deer. USDA National Wildlife Research Center – Staff Publications. 281.

- Wise MJ, and Abrahamson WG. 2007. Effects of resource availability on tolerance of herbivory: A review and assessment of three opposing models. *The American Naturalist* 169(4):443-454. Stable URL: <http://www.jstor.org/stable/10.1086/512044>
- Woolery PO, and Jacobs DF. 2011. Photosynthetic assimilation and carbohydrate allocation of *Quercus rubra* seedlings in response to simulated herbivory. *Annals of Forest Science* 68(3):617-624.

## APPENDIX

Table 2.1 Summary of Study Sites for Descriptive Analysis: Canopy Gap Survey. Sites were selected if they met the criteria 1) were located within the Cross Timbers vegetation type, 2) had adequate canopy cover to be considered a woodland, 3) was large enough for 1 linear kilometer survey, and 4) had owner's permission.

Site	GPS location	Elevation (m)	Mean / Modal Age	County
<b>Relative Age Classification: Young</b>				
Cross Timbers State Park (Overlook Trail) (CTOT) SE of Toronto Lake	37° 44.423'N 95° 54.905'W	290-310	93 80-89	Woodson
Fall River State Park (Post Oak Trail) (FR) SE of Fall River Lake	37° 39.345'N 96° 3.044'W	317-327	58 70 -79	Greenwood
Quivira Scout Ranch (QSR) SW of Murray Gill Lake	37° 14.309'N 96° 12.811'W	278-294	94 70-79	Chautauqua
Woodson State Fishing Lake (WFL) SE of Woodson Lake	37° 47.431'N 95° 50.286'W	309-326	81 60-69	Woodson
Woodson Wildlife Area (WWA) E of Sandy Creek	37° 44.409'N 95° 50.959'W	295-315	64 50-59	Woodson
<b>Relative Age Classification: Old</b>				
Cross Timbers State Park (Ancient Oaks Trail) (CTAT) NE of Toronto Lake	37° 46.708'N 95° 56.744'W	282-301	222 200+	Woodson
Elk City State Park (Post Oak Trail) (ELK) NE of Elk City Reservoir	37° 16.498'N 95° 46.591'W	297-306	170 200+	Montgomery
Stotts Ranch (STR)	37° 29.342'N 95° 58.057'W	316-321	117 120-129	Elk

Table 3.1 Summary of Descriptive Statistics for Post Oak (*Quercus stellata*) Age Structures at Three of the Study Sites in the Cross Timbers Ecoregion, Kansas. At each site, trees were sampled using the point-quarter method along 1 linear kilometer. The minimum diameter at breast height (d.b.h.) for sampling was 10 cm.

Site	Age range (years)	Mean age ( $\pm$ SE) (years)	Modal age class (years)	% of trees in modal age class
CTOT	39-225	92.92 ( $\pm$ 6.43)	80-89	20.0%
QSR	39-142	94.15 ( $\pm$ 4.55)	70-79	17.1%
WWA	42-134	64.08 ( $\pm$ 3.07)	50-59	46.1%

Table 3.2 Tree Canopy Composition and Possible Replacements Found in Canopy Gaps (n = 33) at Eight Cross Timbers Woodlands, Kansas. At each site, canopy trees were sampled using the point-quarter method along 1 linear kilometer. (8 species had < 5 trees each, so were pooled as “other”). Replacement trees were sampled in canopy gaps that intersected the 1 linear kilometer transect. The tallest possible replacement tree(s) within each gap were counted.

Tree Species		# Trees in Canopy	# Trees in Gap	Fisher’s adjusted pair-wise p-value
<i>Carya ovata</i>	CAOV	21	2	ns
<i>C. tomentosa</i>	CATO	9	0	ns
<i>Juniperus virginiana</i>	JUVI	36	9	JUVI : QUST 0. 002
<i>Quercus marilandica</i>	QUMA	55	21	QUMA: QUST < 0. 001
<i>Q. muehlenbergii</i>	QUMU	14	0	ns
<i>Q. rubra</i>	QURU	11	3	ns
<i>Q. shumardii</i>	QUSH	23	5	QUSH: QUST 0. 066
<i>Q. stellata</i>	QUST	450	16	(see JUVI, QUMA, QUSH)
<i>Q. velutina</i>	QUVE	8	1	ns
Other		13	1	ns

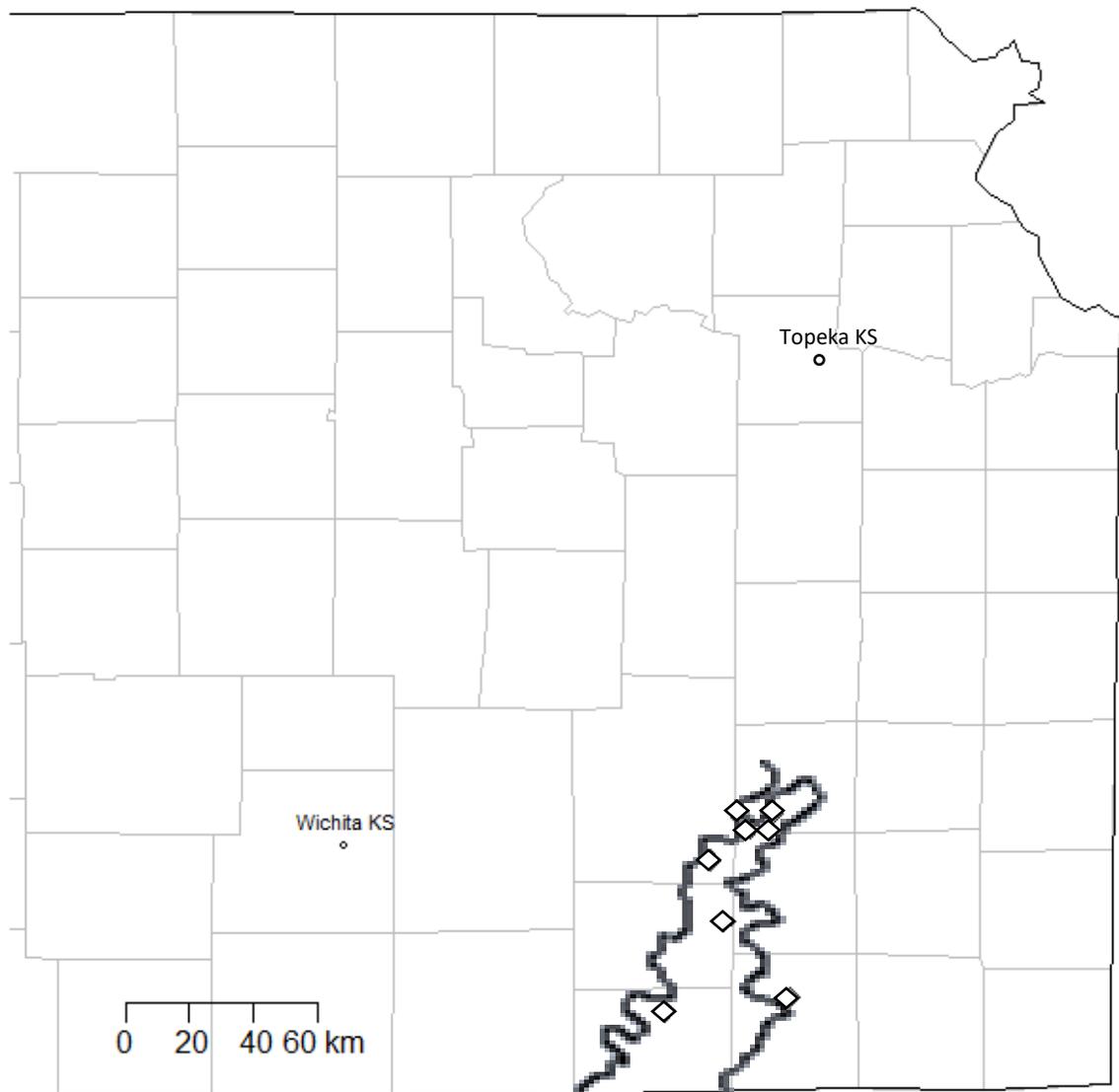


Figure 2.1 Map of eastern Kansas. Canopy gap survey sites (open diamonds) of Cross Timbers ecoregion (polygon outline) (Becker et al. 2016, 2017, Bivand et al. 2017, Comelo 2012).

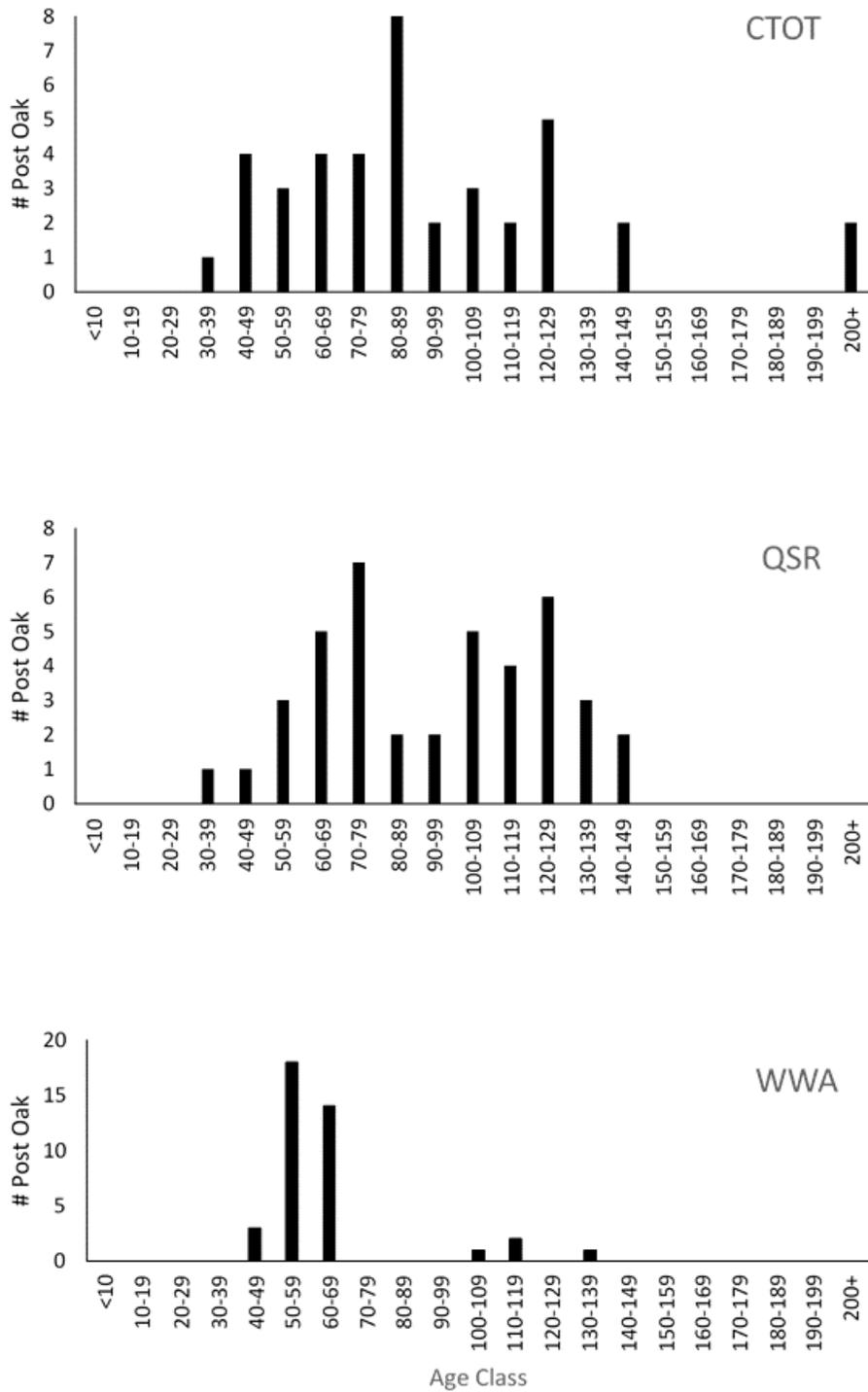


Figure 3.1 Post oak (*Quercus stellata*) age structures at three Cross Timbers woodlands, Kansas. Ten-year age categories were used. At each site, trees were sampled using the point-quarter method along 1 linear kilometer. The minimum diameter at breast height (d.b.h.) for sampling was 10 cm.

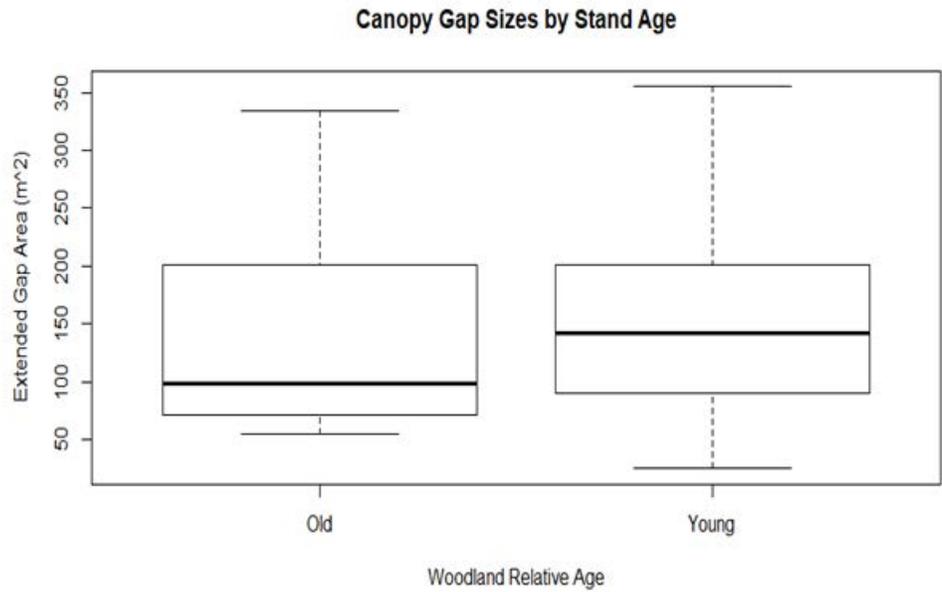


Figure 3.2 Extended canopy gap area (m<sup>2</sup>) of old (n = 3) and young (n = 5) Cross Timbers woodlands, Kansas. The solid bar represents the median area (old = 98.26, young = 142.55), the box spans the interquartile range, while the whiskers indicate the location of the minimum and maximum. The mean areas are old = 141.11 (SE 34.9) and young = 142.98 (SE 14.97).

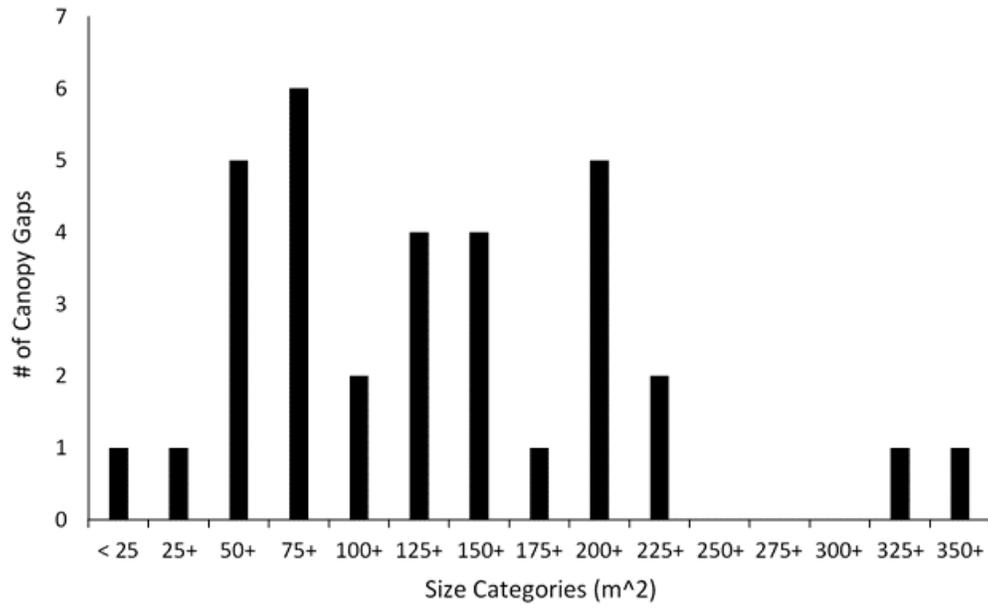


Figure 3.3 Distribution of canopy gaps by size category (m<sup>2</sup>) in Cross Timbers woodlands (n = 8), Kansas.

Canopy Gap Sizes by Site

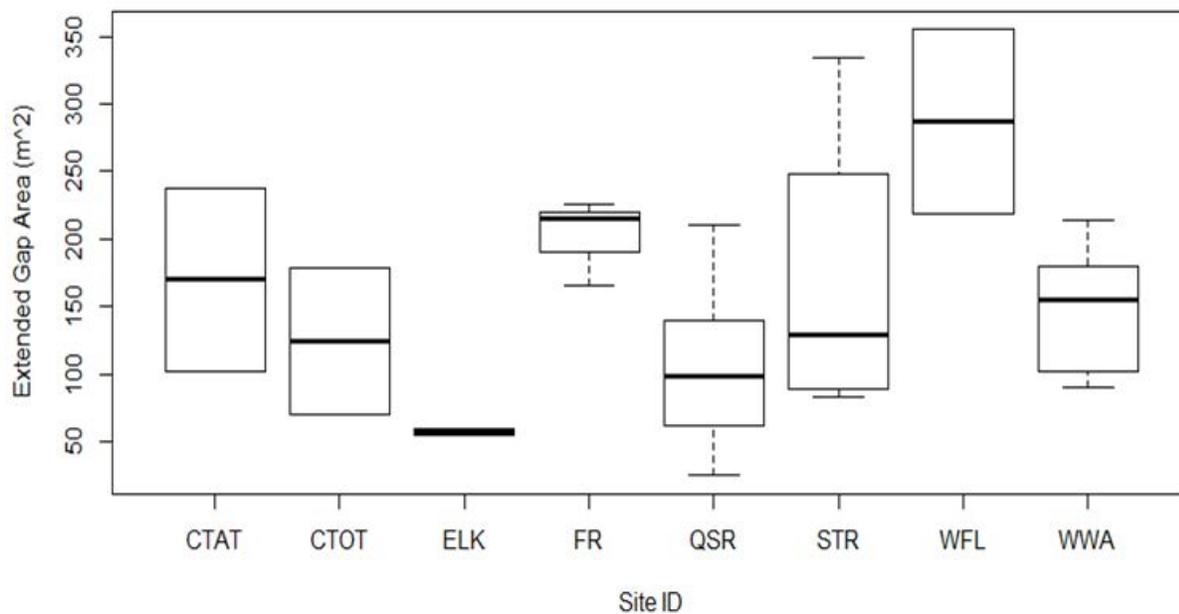


Figure 3.4 Extended canopy gap area (m<sup>2</sup>) by site in Cross Timbers woodlands, Kansas. The solid bar represents the median (CTAT = 169.92, CTOT = 124.26, ELK = 56.88, FR = 214.96, QSR = 98.49, STR = 128.96, WFL = 286.99, WWA = 154.80). The box spans the interquartile range, while the whiskers indicate the locations of the minimum and maximum. The mean areas are CTAT = 169.92 (SE 68.06), CTOT = 124.26 (SE 54.69), ELK = 56.88 (SE 2.23), FR = 201.95 (SE 18.44), QSR = 102.24 (SE 16.88), STR = 168.83 (SE 57.75), WFL = 286.99 (SE 68.02), WWA = 145.94 (SE 18.83).

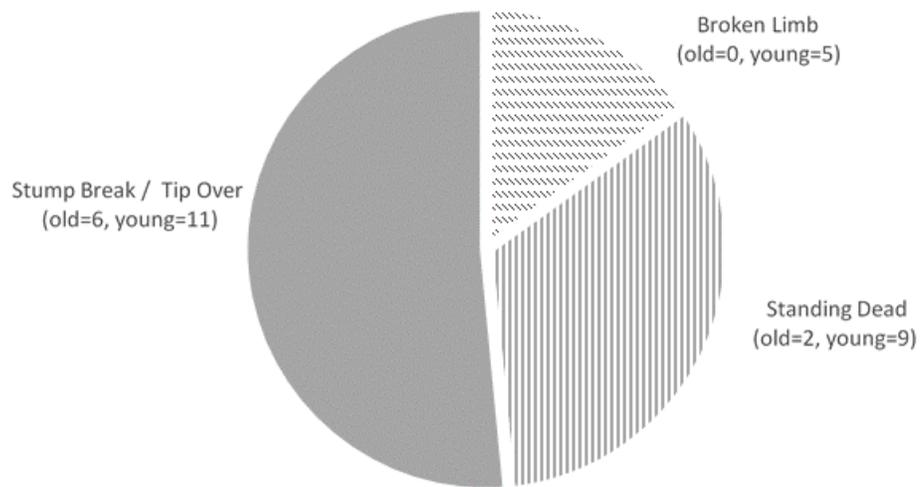


Figure 3.5 Causes of canopy gaps in eight Cross Timbers woodlands (n = 33), Kansas. Stump break / tip over represented 52%, standing dead 33%, and broken limb 15%.

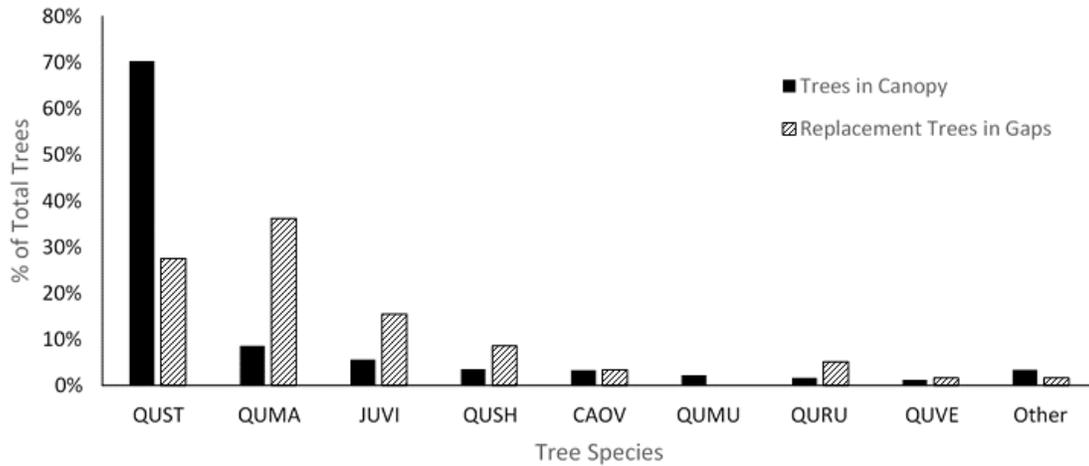


Figure 3.6 Tree canopy composition by tree species vs. canopy gap replacement species; pooled across sites in Cross Timber woodlands (n = 8), Kansas. At each site, canopy trees (n = 640 total, 80 per site) were sampled using the point-quarter method along 1 linear kilometer. The tallest possible replacement trees (n = 58) were recorded in gaps (n = 33) that extended across the 1 linear kilometer sampling transect, with multiple replacement possibilities located in several gaps.

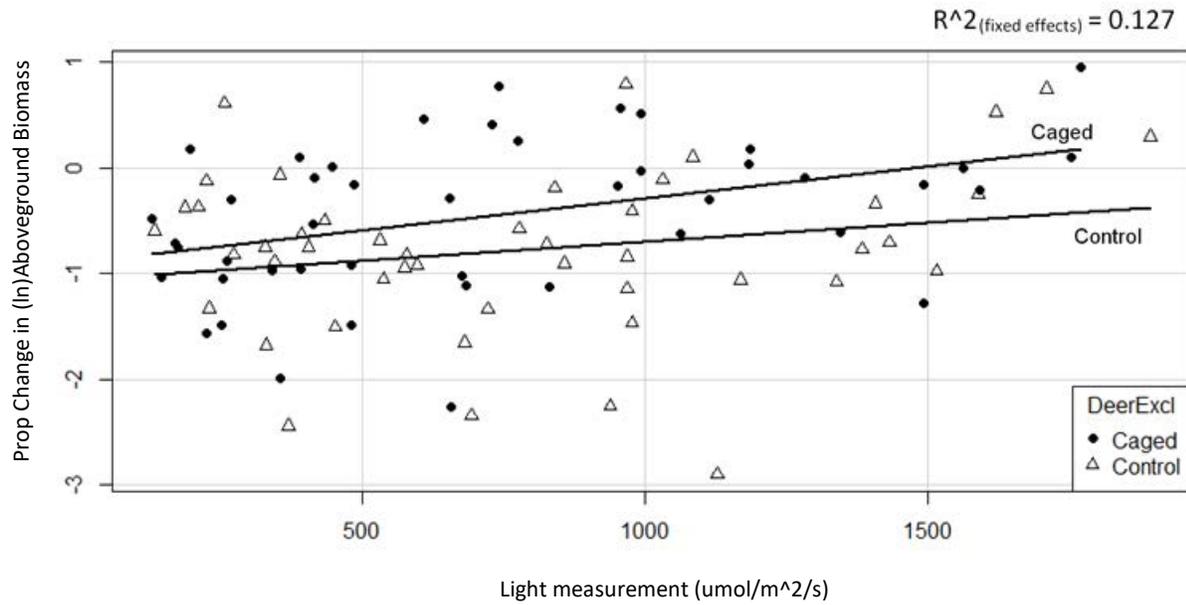


Figure 3.7 Proportional change in natural log-transformed aboveground biomass from March 2016 to August 2017 in post oak (*Quercus stellata*) at Quivira Scout Ranch, Kansas, with main effects of average light above each sapling and deer exclusion treatment. The interaction effect was not significant.

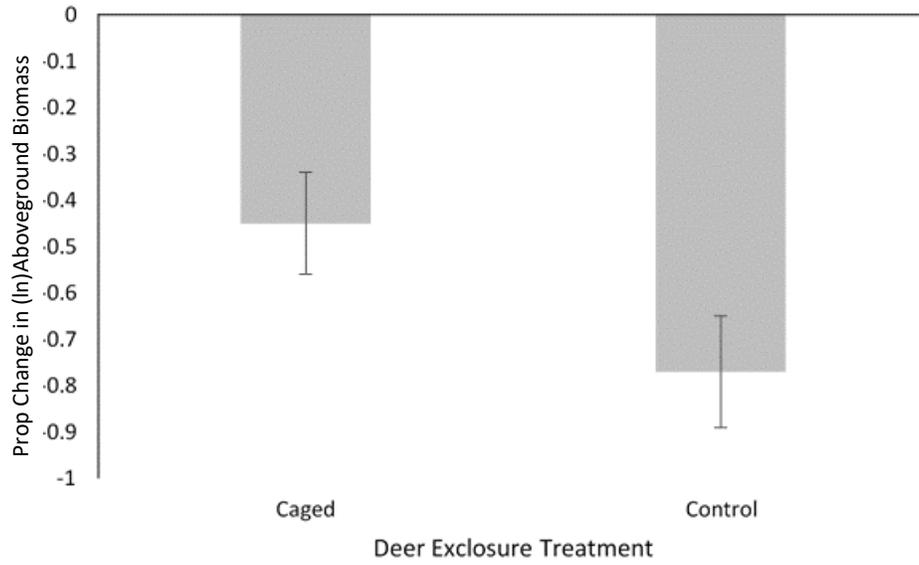


Figure 3.8 Mean (SE) proportional change in natural log-transformed aboveground biomass from March 2016 to August 2017 in post oak (*Quercus stellata*) at Quivira Scout Ranch, Kansas.

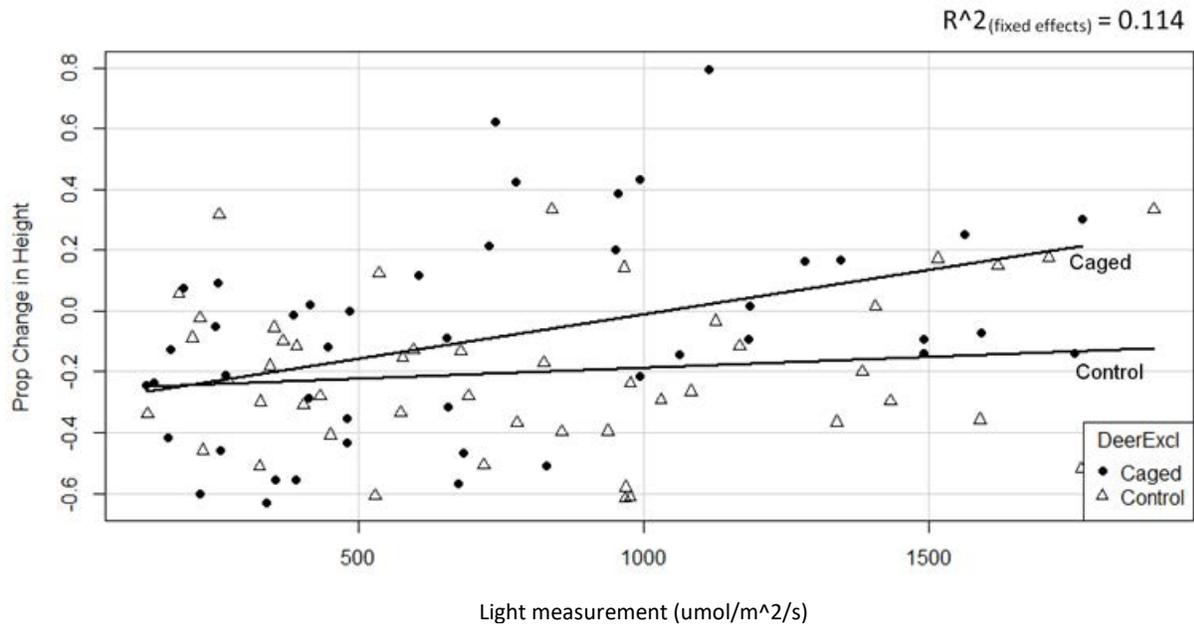


Figure 3.9 Proportional change in perpendicular height from March 2016 to August 2017 in post oak (*Quercus stellata*) at Quivira Scout Ranch, Kansas, with main effects of average light above each sapling and deer exclusion treatment. The interaction effect was not significant.

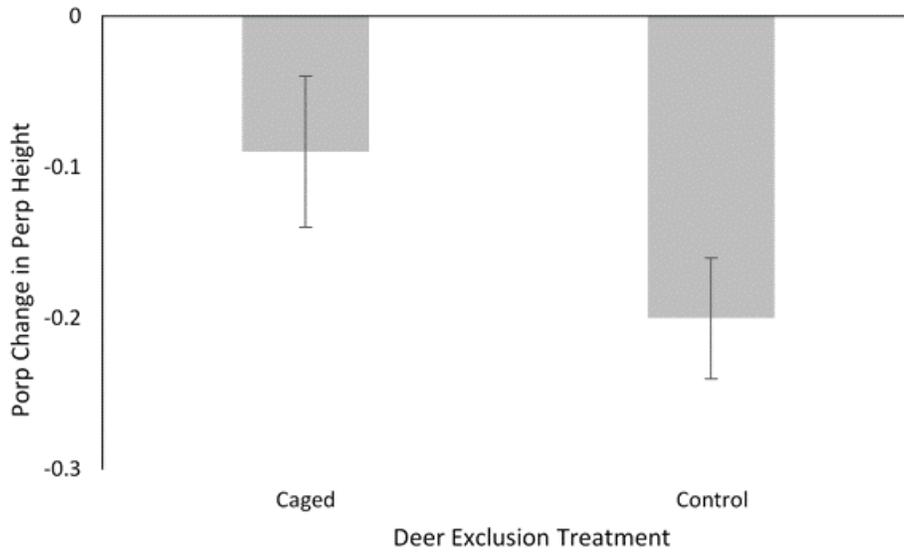


Figure 3.10 Mean (SE) proportional change in perpendicular height from March 2016 to August 2017 in post oak (*Quercus stellata*) at Quivira Scout Ranch, Kansas.

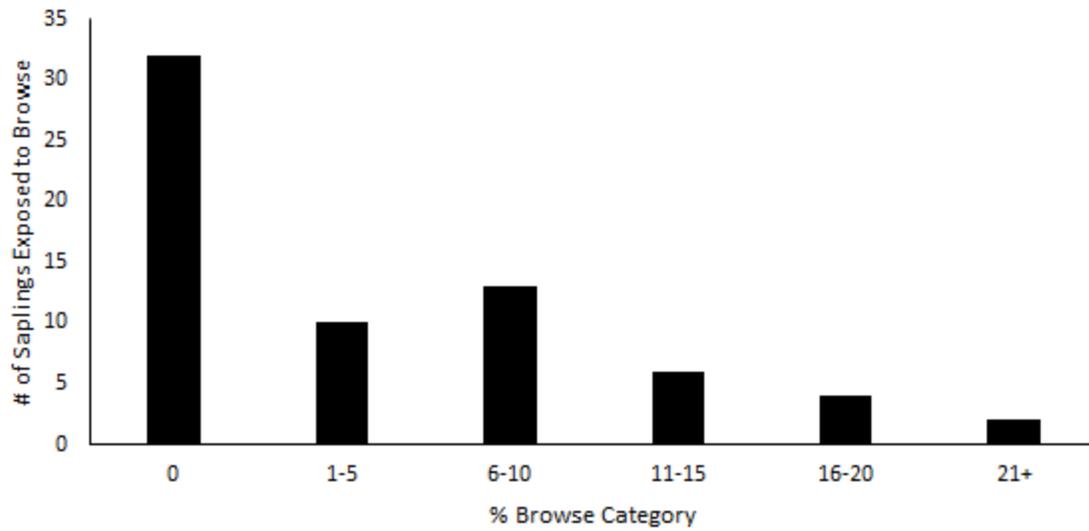


Figure 3.11 Intensity of browse experienced by post oak (*Quercus stellata*) saplings categorized by % of available stems browsed from June 2016 to August 2017 at Quivira Scout Ranch, Kansas.

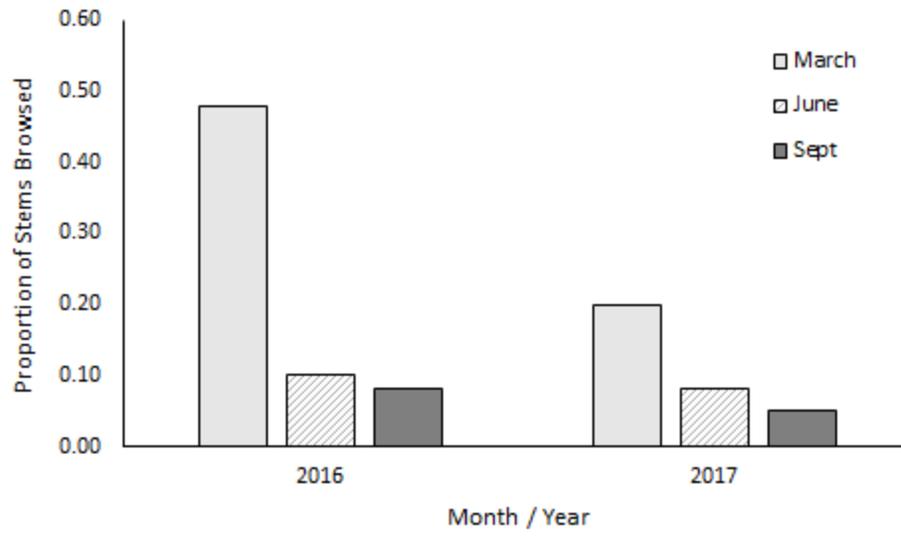


Figure 3.12 Proportional distribution of post oak (*Quercus stellata*) stems browsed by time period.