TREE FALL GAP DYNAMICS IN THE CROSS TIMBERS OF OKLAHOMA

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Submitted to the Faculty of the
Graduate College of the
Oklahoma State University
in partial fulfillment of
the requirements for
the Degree of
MASTER OF SCIENCE
December, 2007

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TIMBERS OF OKLAHOMA

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ACKNOWLEGEMENTS

I am grateful to my adviser Dr. Stephen W. Hallgren for his advices, support and encouragement during my study and research. I would like to thank my committee members Dr. Michael W. Palmer and Dr. Rodney Will for their suggestions.

I am grateful to Ryan DeSantis, Mauricio Moreno, Ed Lorenzi and Bruce Burton for their help in field data collection.

I am grateful to my parents and my wife for their support and encouragement in every step of my life.

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CHAPTER I

INTRODUCTION

Background

Disturbance regime plays a key role for the dynamics of most terrestrial ecosystems (White, 1979; Pickett and White, 1985). The size, intensity and frequency of disturbance are the key factors for the creation of patch mosaics (Runkle, 1981; 1985). There is no uniform model that fits for all situations because vegetation dynamics depend on many factors such as the vegetation before disturbance, types of disturbance, etc. (Peterson and Pickett, 1995). Veblen (1992) differentiated three modes of regeneration: gap-phase, catastrophic, and continuous. The gap phase regeneration mode refers to regeneration in gaps less than 1 acre is size and resulting from the death of one or few trees (Watt, 1947). The catastrophic mode refers to regeneration after the sudden release of resources after stand-devastating disturbances like wildfire, volcanic ash deposition, landslide or blowdown, and continuous mode refers to an attainment of canopy position by some shade tolerant species in the absence of canopy opening disturbances (Veblen, 1992).

Replacement of canopy tress by tree-by-tree replacement methods is the common method in natural forests where large scale stand replacing disturbance are not frequent relative to the longevity of tree species (Kimmins, 1997; Fajardo and de Graaf, 2004). In forest where large-scale disturbances are rare, gaps formed due to mortality of single or multiple overstory trees control stand dynamics (Kneeshaw and Bergeron, 1998). After the formation of canopy gaps, they are filled by the previously suppressed or newly colonized trees. Forest composition and population dynamics are greatly affected by this process (Brokaw, 1985). An understanding of recruitment pattern following the formation of gaps can be used to predict long-term forest dynamics (Coates, 2000; 2002). The replacement pattern in gaps can be used to assess whether the current disturbance regime to the canopy is sufficient to maintain the forest community or whether periodic large scale disturbances are necessary (Runkle, 1981; Lertzman, 1992). Canopy gap regeneration processes help to maintain high species diversity (Grubb, 1977; Denslow, 1980; Orians, 1982). The formation of gaps promotes the early- and mid-successional tree species in old growth communities (Pickett, 1980; Runkle, 1981).

Most of the Cross Timbers has not been used for logging and farming unlike much of other eastern deciduous forest which was heavily exploited, and it may have some of the largest tracts of relatively undisturbed pre-settlement forest in the eastern United States (Stahle and Chany, 1994; Therrell and Stahle, 1998). The vegetation of the Cross Timbers is characterized by a mosaic of xeric post oak (*Quercus stellata*) and blackjack oak (Q*. marilandica*) woodlands, savannas, and prairie openings (Kuchler, 1964; Hoagland et al., 1999). The range of the

Cross Timbers is limited to southeastern Kansas, central Oklahoma and north central Texas (Figure 1). It includes approximately 4.8 million ha, nearly half in Oklahoma (Figure 2) (Kuchler, 1964; Hoagland et al., 1999; Clark et al., 2005). Although the Cross Timbers occupies a large area of the south central region of the United States, studies of stand dynamics after the creation of gaps due to small scale disturbance are very limited. This indicated the need of further research of gap dynamics in the Cross Timbers.

Purpose of the study

The overall goal of the research was to learn whether gap-phase succession in the Cross Timbers was leading to a change in the vegetation composition and structure. The Cross Timbers are threatened by changes in fire regime, urbanization, pollution, over grazing and global change. It is possible that these threats could cause changes in succession that lead to changes in the vegetation. A study was conducted in the Cross Timbers forests to characterize gap formation and filling. The three hypotheses of major importance in this study were as follows: (1) the proportion of gap makers from a species is the same as the proportion of that species in the canopy of the closed forest, (2) gap size has no effect on regeneration of each species and (3) the gap maker replacement probabilities by gap fillers are such as to maintain the presence of dominant species in the stand at the current levels.

CHAPTER II

REVIEW OF LITERATURE

The number of publications related to small scale disturbances in the Cross Timbers is very small compared to the other types of forest in North America. This section presents a review of the studies conducted in the Cross Timbers. The literature review comprises three different sections. Section one examines the physical environment that shapes the vegetation types in the Cross Timbers. Section two consists of overview of the vegetation. Section three gives overview of disturbance in the Cross Timbers.

Physical Environment

Geology and Soil

The Cross Timbers are located on the Osage plains of the Central Lowland Physiographic Province. The major characteristics of the landforms in the region are low, east facing cuestas, river bluffs, tablelands, gentle slopes, and deep ravines (Hunt, 1974). The surface geology of the region is mainly characterized by Pennsylvanian, Permian, and Cretaceous sedimentary formations that dip gently westward and strike north to south (Hunt, 1974). According to Curtis and Ham (1972), the main composition of the rolling hills and broad plains in central Oklahoma are Permian shales and sandstones. There is close association between the vegetation and soil texture (Bruner, 1931; Dyksterhuis, 1948). The forests are usually found on sandy shallow soils and the prairie on the finer deeper soils (Dwyer and Santlemann, 1964). The parent materials of the soils in the Oklahoma and Kansas are Pennsylvanian sandstones (Dyksterhuis, 1948). Alfisols with a minor component of Inseptisols are the predominant soil order in the Cross Timbers (Hoagland et al., 1999). The Northern Cross Timbers mainly consist of Stephenville (yellow red to light brown) and Darnell (grayish brown to light brown) soils whereas Windthorst (reddish brown to yellowish brown) soils are predominant in the southern Cross Timbers (Aandahl, 1982). The soils in the Cross Timbers are moderately leached (Dwyer and Santelman, 1964).

Climate

The subtropical humid climatic zone with hot summers and mild winters characterize the Cross Timbers (Trewartha, 1968). Precipitation varies longitudinally and temperature varies latitudinally (Court 1974). The annual precipitation averages are 102 cm and 71 cm in the eastern and western end of the Cross Timbers, respectively (Sutherland, 1977). Most of the annual precipitation occurs in during the spring months (Harrision, 1974). The length of the growing season varies from 180 days in the north to 240 days in the southern part of the Cross Timbers (Harrison, 1974). The mean annual potential evapotraspiration was 99.7 cm and mean annual water deficit was 10.2 cm in this region (Nelson and Zillgitt, 1969).

Vegetation and species composition

Axelrod (1985) stated that the increase of the aridity in the central North America due to the Miocene uplift of the Rocky Mountains, growth of the Antarctic ice sheet, and the cooling of oceanic water promoted the development of grasslands. The migration of oak and hickory into the eastern Oklahoma flora some 12000 years ago displaced pine, spruce and fir (Delcourt and Delcourt, 1981). Some previous paleobotanical studies suggested that hickory species were more abundant in northeastern Oklahoma approximately 1000 years ago and they declined with the increase of the abundance oak species (Hall, 1982).

The Cross Timbers region is a mosaic of prairie, woodland, and savanna vegetation, but post oak and blackjack oak characterize the vegetation of this region (Dyksterhuis, 1948; Rice and Penfound, 1959). These two species make up about 70% of the basal area in the Cross Timbers (Rice and Penfound, 1959; Kennedy, 1973). The physiological traits and life history are different for these two species. The forest stands of Cross Timbers in Oklahoma are species poor, short in stature, and associated with grasslands (Bruner, 1931). Post oak is abundant on soils with high organic content (Klahr, 1989; Collins and Klahr, 1991). Post oak prefers the shallow rocky soil whereas blackjack oak is better competitor on deeper more productive soil (Dwyer and Santelman, 1964). Other woody species of secondary importance in the Cross Timbers includes black hickory (*Carya texana*), black oak (*Q. velutina*), and red-cedar (*Juniperus virginiana*) (Rice and Penfound, 1955, 1959; Penfound, 1963; Johnson and

Risser, 1972). The composition of woody understory species mainly comprises chittamwood (*Bumelia lanuginosa*), red bud (*Cercis canadensis*), roughleaf dogwood (*Cornus drummondii*), Mexican plum (*Prunus mexicana*), buckbrush (*Symphoriocarpos orbiculatus*), winged sumac (*Rhus copallina*), smooth sumac (*Rhus glabra*), winged elm (*Ulmus alata*), and fox grape (*Vitis vulpina*) (Gould, 1902; Lathorp, 1958; Harrision, 1974; Johnson and Risser, 1974, 1975). There are regional and site by site variation in the actual composition and density of understory species in the Cross Timbers (McCluskey, 1972). Depending on slope, aspect, and geographic location, the ratio of post oak and blackjack oak ranges from 2:1 to 3:1 in Cross Timbers stands (Kennedy, 1973; Sims, 1988).

Disturbances in Cross Timbers

The Cross Timbers are prone to many types of small as well as large scale disturbances. The effects of disturbance with different spatial and temporal scale have different effect on the Cross Timber vegetation. Some of the common disturbances are as follows:

Fire

Fire, natural or anthropogenic, is an important factor in the maintenance of the Cross Timber vegetation mosaic (Hoagland et al., 1999; Clark, 2003; Shirakura, 2006). Native Americans used fire as a tool for the Cross Timbers and prairie management (Anderson, 1990; Hoagland et al., 1999). Woody vegetation was expanded at the expense of savanna and prairies due to fire suppression following European settlement of the region (Rice and Penfound, 1959; Sims, 1988). The rate of canopy closure increases in oak savannas with a decrease of fire frequency (Johnson and Risser, 1975; Henderson and Epstein, 1995). Fire has profound effects on species composition and abundance in the Cross Timbers (Hoagland et al., 1999; Clark, 2003). Fire seasonality and its return interval also have effects on species composition and oak forest dynamics (Engle et al., 1996; Clark, 2003; Shirakura, 2006).

Wind

Tree uprooting by winds is common in every forested region of the world. Winds can cause uprooting of whole trees or snapping of the stem or branches. Winds which are more severe than tree resistance cause damage to the trees in the forest. Texas and Oklahoma receive winds from the south most of the year (Oliver and Larson, 1996). The study of tornado damage in the Cross Timbers by Shirakura et al. (2006) showed that blackjack oak is more susceptible than post oak to the tornado damage and the abundance of post oak is increased after the tornado damage.

Ice storm

Ice storms generally occur from January to March in the contiguous United States. The damage of trees is due to weight of ice deposited on it. Severe damage of ice storm causes breakage of limbs or whole trees (Oliver and

Larson, 1996). There was huge damage to trees over wide areas in Oklahoma due to a large ice storm in January, 2002 (Anonymous, 2002).

Drought

The region is prone to major droughts at approximately 20-year intervals (Rice and Penfound, 1959; Johnson and Risser, 1975). Major droughts occur in this region due to eastward shift of the Rocky Mountain midtroposhpheric ridge (Corcoran, 1982). The extended droughts in the early 1930s and 1950s destroyed thousands of upland trees in Oklahoma (Rice and Penfound, 1959). Drought has profound effects on vegetation composition of the Cross Timbers. The effect of drought on the two dominant species is not the same. Blackjack oak is more susceptible to drought than post oak (Rice and Penfound, 1959; Johnson and Risser, 1975).

Herbivory

Although the number of studies on the influence of herbivory is small, vertebrate and invertebrate herbivory has influence on the vigor and structure of the Cross Timbers vegetation. Post oak is susceptible to predation by insects, including defoliators, leaf miners, tent caterpillars, sawflies, leaf miners, aphids, lace bugs, scales, gall wasps as well as parasitized by fungal pathogens, such as oak wilt (*Ceratocystis fagacerum*) and chestnut blight (*Cryphonectria parasitica*) (Stransky, 1990). Cotton-tailed rabbit herbivory is common in ecotone habitats in the Cross Timbers (Lochmiller et al., 1991).

Brief overview of study of the gaps

There are a large number of publications on gap dynamics in different types of forest ecosystems in the USA. Tree fall gaps have been well studied in North America particularly in the eastern deciduous forests with a focus on the rate of canopy gap creation by tree fall (Henry and Swan, 1974; Oliver and Stephens, 1977; Runkle 1982, 1985; Matlack et al., 1993), and environmental conditions within tree fall gaps (Tyron and Trimble, 1969; Collins and Pickett, 1987; Canham et al., 1990; Bazzaz and Wayne, 1994).

The study of gaps have focused on different aspects of gaps and their effects like rate of gap creation (Henry and Swan, 1974; Oliver and Stephens, 1977, Runkle, 1782, 1985), tree fall gap closure rate (Hibbs, 1982; Runkle, 1982; Runkle and Yatter, 1987), gap environment (Tyron and Trimble, 1969; Canham 1988a; Canham et al., 1990; Bazzaz and Wayne, 1994), impact of gaps on herbaceous plants (Anderson et al., 1969; Collins and Pickett, 1987, 1988a; Ehernfeld, 1980), response of different tree species to the gap creation (Runkle, 1981, 1982, 1984; Hibbs, 1982, Canham, 1985, 1988b, 1989, Runkle and Yatter, 1987; Peterson and Campbell, 1993; Bazzaz and Wayne, 1994), the effect of gaps of varying size on species composition, density and growth rate (Clebsch and Bushing, 1989; Mou and Warrillow, 2000), and effect of gap dynamics formation on abundance of tree species (Runkle 1982, 1985; Denslow 1987; Whitemore 1989).

The creation of gaps plays crucial role in species coexistence in a variety of forests (Denslow 1980, 1987; Orians, 1982; Lertzman, 1992). The alteration of physical environment within as well as among gaps can provide opportunities for species that could not established under a closed canopy. The differential ability of species to exploit gaps of different sizes and different portions of larger gaps is the main emphasis of the hypothesis of coexistence (Lertzman, 1992). The process of gap creation has important effects on forest composition, forest architecture, and population dynamics (Runkle, 1981; Brokaw, 1985).

The intermediate disturbance hypothesis (IDH, Connell, 1978) is often implied to explain how gap phase regeneration may maintain coexistence between many species having similar resource use strategies, and dispersal and competitive abilities (Attiwill 1994). The study of gap dynamics suggested the difference in shade tolerance is the main factor affecting spatial and temporal pattern of species recruitment in canopy gaps (Connell, 1978; Brokaw, 1985). Typically, large gaps favor the recruitment of light demanding (pioneer) species, although the threshold of gap size varies greatly for pioneer species (Brokaw, 1985), while establishment of shade tolerant trees are greatly favored in smaller gaps or under the forest canopy (Denslow, 1980; Whitemore, 1989). The gaps of varying size may creates niche partitioning through a gradient of differential resource availability, to which species tree species respond differently (Grubb 1977; Denslow 1980).

In general, small gaps or small increases in light levels from diffuse radiation increases the survival and growth of shade tolerant species, usually existing as advance regeneration. The physiological and morphological plasticity of shade tolerant species allows rapid response to environments due to increased light levels. Less tolerant species may still be present in canopies of shade tolerant forests due to their capacity of opportunistic exploitation of larger gap (McCarthy 2001). Therefore, the diversity in gap size may be significant for the maintenance of canopy diversity in old-growth forests (Barden 1979, 1981; Runkle, 1982).

Research in gap dynamics in many forest ecosystems has increased our understanding of forest dynamics after small scale gap creating disturbances. The impact of tree fall gaps due to the result of small scale disturbance can be used for the management of different forest ecosystems (McCarthy, 2001).

CHAPTER III

METHODOLOGY

Study Locations

All data were collected in summer 2006 at three different locations in the Cross Timbers of Oklahoma, Keystone Ancient Forest Preserve, Okmulgee Wildlife Management Area and the Tall Grass Prairie Preserve (Figure 2). These study locations were chosen in different parts of Oklahoma to be representative of the Cross Timbers. They were relatively lightly disturbed by human influences such as timber harvesting and agricultural clearing. They were under the control of government agencies or other organizations that allowed controlled access for research. The fire regime was almost certainly altered in some way from pre-European settlement. The three locations are described below.

The Keystone Ancient Forest Preserve (KAFP) is located in southern Osage county of Oklahoma in the northern range of the Cross Timbers region at 36^0 12' N and 96^0 13' W. Elevation varies from 251 to 304 meters. The KAFP borders the Arkansas River and Keystone reservoir (Clark et al. 2005). It lies approximately 32 km west of Tulsa. There are post oak (*Quercus stellata*) and redcedar (*Juniperus virginiana*) trees greater than 300 and 500 years old, respectively, in the KAFP. Due to it relatively undisturbed condition, previous researchers characterized this forest as old growth (Therrell and Stahle, 1998). It is managed by The Nature Conservancy.

The Okmulgee Wildlife Management Area (OWMA) is located in Okmulgee county of Oklahoma in the east-central part of Oklahoma. It is located at $35^{0}38'$ N and $96^{0}03'$ W and encompasses an area of 10,900 acres. The elevation ranges varied from 183 to 290 meters. Prescribed fires have been conducted almost every year in this area for more than 20 years (Bruce Burton, Personal communication, 2006). The frequency of prescribed light under burns varied from 10 times to 2 times in the last 20 years depending on the management unit. The forest of the region comprises blackjack oak, post oak and black hickory (*Carya texana*) on the rocky ridges, oaks on the sandy terraces along the Deep Fork of the Canadian River (also called the Deep Fork River). The geologic formations of the region are of sedimentary origin. It has temperate, continental climate of the moist, sub humid type (Anonymous, 1968). The OWMA is managed by the Oklahoma Division of Wildlife Conservation.

The Tall Grass Prairie Preserve (TGPP) lies in Osage County in north-central Oklahoma at 36^{0} 40' N and 96^{0} 21' W. The elevation ranges form 253 to 366 meters. More than 90 percent of land in the Tall Grass Prairie Preserve is covered by grassland and the rest with forest. The forested region of the area is the Cross Timbers dominated by post oak and blackjack oak (Palmer et al, 2003). It encompasses an area of 15,783 hectares. The TGPP is owned and managed by the Nature Conservancy which purchased the former Barnard Ranch in 1989 to restore the tall grass prairie ecosystem (Anonymous, 1993).

Data collection

A canopy gap was defined as the canopy opening due to the death of one or a few canopy trees in a closed canopy stand. The expanded gap was defined as the sum of canopy gap area and the area around the canopy up to base of canopy trees surrounding the canopy gap (Runkle, 1982). The effect of the canopy opening on regeneration was considered to reach to the edge of the expanded gap. Each potential gap was evaluated for inclusion in the study. Only gaps that appeared to be the result of the death of one or more canopy trees were included. Every gap selected had evidence of at least one dead canopy tree, a standing dead tree or a dead tree on the ground. The smallest gap maker had a DBH of 7 cm. In some cases the evidence of a dead canopy tree was a rotten stump. Only gaps with both an opening in the canopy and evidence of at least one gap maker were included in the study.

At each site, 6 or 7 line-intersect transects ranging from 50-200 meters in length were placed randomly to measure different gap parameters. The total length of transects at each location was 1000 meters. As transects were intended to sample natural tree-fall gaps, they were placed away from the influence of roads, wide stream beds and rock outcrops. Distance along each transect was measured with a tape or a LASER range finder (Contour XLR, LaserCraft, Inc., 1450 Oakbrook Drive, Suite 900, Norcross, GA 30093). A gap was sampled if the transect was intersected by its associated expanded gap. The lengths of transect intersected by the expanded and canopy gap were measured. The area of the expanded gap was measured with a LASER range finder using each boundary tree of the expanded gap as a target. The lengths of the long and short axes of the canopy gaps were measured with a plot tape or with the LASER range finder depending on size of the gap and presence of trees blocking the view across the gap. The edges of the canopy gap along the axes were determined by standing under the edge of the gap and sighting its exact location with a clinometer tilted to 90°. The area of the canopy gap was calculated as the sum of the four quarters of an ellipse (Runkle, 1982). Regeneration (height < 1 m) was counted by species and larger gap fillers in the expanded gap were counted by height classes (1-3, 3-5, and 5-10 meters) and species. Counts were done in the expanded gap because the effect of the increased light below the canopy gap extended farther than the edge of the canopy gap (Runkle, 1982).

The undisturbed forest canopy was sampled by placing 2 to 5 plots adjacent to each transect in closed forest away from the influence of gaps caused by tree falling, rock outcrops, roads, and any other cleaning. All trees under 1 m height were counted by species in 10 m^2 circular plots and trees above 1 m height were counted by species in 100 m^2 circular plots. Height and DBH of canopy trees were measured in each 100 m^2 control plot by species.

Data analysis

The transect and its associated control plots in the adjacent closed forest were considered an experimental unit for statistical analysis. There were 6 or 7 transects at each location. Canopy gap percent area and expanded gap percent area of the forest were calculated as the percent length of transect covered by the canopy gap and expanded gap, respectively. The simple t-test was used to test the significance of differences among sites in mean canopy and expanded gap cover and of differences between expanded gap and control plot seedling densities at each location. All the statistical tests were done at the significance level of 0.05.

The relative frequency of canopy trees with a DBH greater than or equal to 7 cm were compared by species for control plots and gap makers to learn whether certain species were equally represented as canopy trees and gap makers. The minimum DBH of 7 cm was used because this size represented a small canopy trees and was the smallest DBH of a gap maker. The distribution of trees by DBH class in terms of trees per hectare was plotted by species for each location. The effects of the gap size on regeneration of different species were tested with simple linear regression of density of seedling against expanded gap size.

The replacement probabilities for each gap filler tree species for each gap maker species were determined for each gap where gap fillers were found. There were a few gaps with no gap fillers. Only tree species which reached for forest canopy were considered potential gap filler species. For each gap, probabilities for gap fillers were calculated only for tress in the tallest height class. For all gaps with gap fillers in the 5 to 10 m height class, only trees in this height class were considered. Likewise, for all gaps with regeneration in the 3 to 5 m height class but none in the taller height class, only trees in this height class were considered. Finally, for all gaps with regeneration only in the 1 to 3 m height class, trees in this height class were considered. When there was more than one gap maker the replacement probabilities were calculated separately for each gap maker. The mean replacement probabilities were calculated for the combined data across height classes.

CHAPTER IV

RESULTS

Stand composition in the study sites

There were 11 different canopy tree species in the study sites of the Cross Timbers: *Betula nigra, Bumelia lanuginosa, Carya texana* , *Fraxinus americana*, *Juniperus virginiana*, *Morus rubra, Quercus marilandica*, *Quercus rubra*, *Quercus stellata, Quercus velutina,* and *Ulmus alata*. The total basal area varied from 22 to 27 m^2 ha^{-1} and was not different among the three sites (Table 1). The most important species for basal area were post oak (70 to 83 %), black hickory (7 to 15 %) and blackjack oak (6 to 7 %). Diameter distribution in terms of trees ha^{-1} was similar for the three sites (Figures 3 to 5). In the case of post oak the highest number of trees was in the DBH classes from 7 and 9 cm at the KAFP, 11 to 17 cm at OWMA, and 9 and 11 cm at the TGPP; the numbers of trees in smaller and larger DBH classes declined from these high levels. Most of the blackjack oak trees were in the 7 to 21 cm classes. None of the diameter distributions resembled the reverse j-shaped curve.

General gap parameters

The total number of gaps was 26 each in the Tall Grass Prairie Preserve and Okmulgee Wildlife Management Area, and 31 in Keystone Ancient Forest Preserve. The average canopy gap cover varied from 5.3 % to 8.9 %, and expanded gap cover varied from 19.7 % to 26.0 % (Table 2). There was no difference among sites for the amount of canopy gaps and expanded gaps. The average size of the canopy gap varied from 12.7 to 25.9 m^2 and the average size of the expanded gaps varied from 54.1 to 85.4 m^2 (Table 2). More than 70 % of the canopy gaps were less than 20 m^2, and more than one third of the expanded gaps were less than 40 m^2 in size (Figures 6 and 7).

Gap makers

There were 7 gap maker species in the study area: *Carya texana*, *Juniperus virginiana*, *Morus rubra, Quercus marilandica*, Quercus *stellata*, *Quercus velutina*, *Ulmus alata* (Table 3). More than 80 % of gap makers were blackjack and post oak. The percent composition of post oak in the control plots varied from 63 to 77 % and blackjack oak composition varied from 9 to 10 %. The percent contribution of post oak for gap making varied from 7 to 55 % and the contribution of blackjack oak varied from 25 to 85 % (Table 3). The DBH of gap makers varied from 7 - 49 cm (Figure 8-10). At the KAFP the gap makers were fairly well distributed across the DBH range from 7 to 39 cm for all species. The gap makers at the OWMA covered a wide range of sizes for post oak (11 to 49 cm) and much less for blackjack oak (11 to 31 cm) and other species (15 to 23 cm). At the TGPP the preponderance of gap makers were blackjack oak which were fairly well distributed across the range of DBH classes 7 cm and larger with a peak at 17 cm.

Gap size and regeneration

I tested the relationship between the size of the expanded gap and seedling density by tree species with linear regression (Table 4). The value of R^2 varied from 0.003 to 0.55. Only two species at KAFP (CATE and FRAM) and one each at OWMA (QUMA) and TGPP (FRAM) showed a significant regression. All the significant regressions had positive slopes. The results of the t-test showed that there was no significant difference in mean seedling density for any species between control plots and expanded gaps except for one species at the TGPP (Table 5).

Replacement probabilities for gap makers

Post oak tended to have the highest probability for replacing almost all gap maker species. The probability for post oak being replaced by itself varied from 0.37 to 1.00 and replacement probability of blackjack oak being replaced by post oak varied from 0.32 to 0.59. The probability of blackjack oak being replaced by itself varied from 0.05 to 0.30 (Table 6).

CHAPTER V

DISCUSSION

This study showed a higher percentage cover of canopy gaps in the Cross Timbers than found by some researchers in the eastern deciduous forest of North America (2.5 to 2.8 %, Cho and Boerner, 1991; and 4.4 %, Barden, 1989). In contrast, other researchers have found higher gap coverage in the eastern deciduous forests (9.6%, Runkle, 1982) and in dry forests of the Missouri Ozarks (17 %, Rebertus and Burns, 1997). Gaps were small in size in the forests of the Cross Timbers. The majority of gaps were less than 100 m^2 in size which is consistent with the findings of the gaps studied of Cho and Boerner (1991) in two old growth Ohio forests and a study by Runkle (1982) in temperate deciduous forests in the eastern United States. Pham et al. (2004) showed that the size of gaps depended on the number of gap makers. The size of the gaps was small in the Cross Timbers because the creation of gaps was due to the death of a small number of gap makers (1-4).

The results of this study showed that blackjack oak was more susceptible than post oak to the small scale disturbances in the Cross Timbers. The cause of death could not be determined. It appeared some trees may have suffered breakage from ice storms, but it was impossible to determine whether the damage occurred before or after death. Many of the dead trees had evidence of fungal attack, but it was not certain whether this occurred before or after tree death. Shirakura et al. (2006) in a study on the effect of tornado damage in the Tall Grass Prairie Preserve also found blackjack oak to be more susceptible to damage from the tornado than post oak. Other studies have shown species of the red oak group to be more susceptible to wind damage in North Carolina (hurricane winds, Greenberg and Mcnab 1998) and Minnesota (Dyer and Baird 1997). Also, forest decline in Arkansas had a more severe effect on species of the red oak group (Heitzman et al., 2007).

The Cross Timbers region is susceptible to many kinds of disturbances. The study by Rice and Penfound (1959) showed that the region is prone to drought approximately every 20 years which may be one of the most important reasons for death of gap making canopy trees. These authors believed blackjack oak was more susceptible to drought caused mortality than post oak. There were other disturbances like tornados, and fungal disease which may cause the death of canopy trees in the Cross Timbers.

The DBH distribution of canopy trees (Figures 3 to 5) was not similar to the reverse j-shaped curve typical to old growth forest. The DBH distributions were measured in closed canopy forests and did not sample gaps or forest edge where the small trees would be expected. There was an abundance of trees smaller than breast height (Table 5) and a range of small DBH classes with fewer trees than the larger classes. The recruitment of oaks from the understory to the midstory depends on disturbance (Johnson, 1993; Clark, 2003). This result corroborates the findings of the study of (Clark, 2003) at KAFP which showed that the stand had low densities in the smallest DBH size classes.

Pioneer tree species are more susceptible to disturbance than non-pioneer tree species (Webb, 1989; Zimmerman et al., 1994; and Arevalo et al., 2000). This may be due to the low strength of their stem wood (Zimmerman et al., 1994). Blackjack oak has characteristics of a pioneer species that may make it more susceptible to disturbance than other species in the Cross Timbers (Shirakura et al., 2006).

The results of this study showed gap size had no or inconsistent effects on density of regeneration. It is possible that the gaps were too small to have a strong effect on regeneration. Another explanation for the lack of an effect is that some other environmental factor besides light had a stronger effect that was independent of gap size such as severe drought. The sizes of the gaps in the Cross Timbers were small compared to other areas. The Denslow and Hartshorn (1994) review of tropical gap study showed that the variation of light availability was the most important factor for the tree seeding establishment and early growth. Gap size, shape, canopy height and latitude were most important for light conditions at ground layer (Canham et al., 1990). Light availability was clearly an important factor, but other factors were important in regeneration as revealed by studies of effects of mineral soils and other substrate types within gaps (Putz, 1983; Lawton and Putz, 1988; Stewart et al., 1991; Lertzmen, 1992).

The replacement probabilities for the two dominant tree species, post oak and blackjack oak, were quite different. Post oak was clearly favored to replace itself and blackjack oak. Post oak was more shade tolerant than blackjack oak (Iverson et al., 1999; Arevalo, 2002). This finding was consistent with the findings of others study that shade tolerant species were favored by gaps over non-shade tolerant species (Runkle 1981, 1982; Canham, 1985; Pham et al., 2004).

The findings of this study suggest the forest composition of the Cross Timbers may change after the creation of gaps. The stands may become more and more dominated with post oak and blackjack oak will decrease. The significant decrease in the composition of blackjack oak means there may be less amount of gap cover in the future as it was the dominant gap maker. This will affect many plant and animal species which depends on blackjack oak and the regular production of gaps for their survival.

The result of this study showed that creation of gaps was a common phenomenon in the forest in the Cross Timbers. The study of gap dynamics helps the policy makers and conservationist develop policies for conservation and restoration. The findings of this study may helpful to explain the effects of gaps on structure and composition of other xeric forest ecosystems.

The study of gap dynamics in the Cross Timbers is very limited. Like other forest ecosystems in the world, the Cross Timbers are also prone to small scale gap creating disturbances. The understanding of gap dynamics after small scale disturbances is important for land management and conservation of this unique vegetation type.

CHAPTER VI

CONCLUSIONS

From the findings of this study of gap dynamics in the Cross Timbers of Oklahoma, I drew the following conclusions:

- The Cross Timbers forests were characterized by numerous small gaps created by the death of one or two trees.
- There was abundant regeneration of canopy tree species under the canopy of the closed forest.
- Gap size did not appear to have a differential affect on success of gap fillers perhaps due to their small size and influence of other factors such as drought or disease.
- Blackjack oak may decrease in the Cross Timbers forest because its frequency as a gap maker was greater than its frequency in the canopy, it was more likely to be replaced in a gap by post oak and black hickory than by itself and it was not significant gap filler for other gap makers.

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Table 1. Stand basal area by species at three locations in the Cross Timbers. See Table 7 for list of abbreviations used for locations and species. (Mean and standard deviation).

Species	KAFP	OWMA	TGPP
	Basal Area (m^2 ha^{-1})		
Total	22.01 (8.77)	26.36 (5.15)	27.13 (5.48)
	Percent of total		
BENI	0.18	0.00	0.00
BULA	0.00	0.11	0.00
CATE	14.90	8.92	6.56
FRAM	0.23	0.00	4.20
JUVI	3.27	0.00	0.00
MORU	0.00	0.08	0.00
QUMA	6.82	7.44	6.01
QURU	1.77	0.00	0.00
QUST	69.51	76.78	83.12
QUVE	3.32	2.50	0.00
ULAL	0.00	4.17	0.11

Table 2. Gap characteristics at three locations in the Cross Timbers of Oklahoma. See Table 7 for list of abbreviations for locations. (Mean and standard deviation).

Gap Characteristics	Locations		
	KAFP	OWMA	TGPP
Number	31	26	26
Canopy gap			
Percent of forest area	8.9 (3.6)	8.1 (5.5)	5.3 (3.3)
Area (m^2)	22.0 (29.3)	25.9 (28.3)	12.7 (10.2)
Expanded gap			
Percent of forest area	24.0 (7.0)	26.0 (10.6)	19.7 (11.4)
Area (m^2)	61.7 (55.9)	85.4 (53.1)	54.1 (27.1)
Number of gap makers	1.73	1.44	1.27

Table 3. Species composition of forest canopy and gap makers at three locations in the Cross Timbers. See Table 7 for list of abbreviations used for locations and tree species.

Location	Species	Number of trees (Control Plot)	Percent	Number of trees (Gap Makers)	Percent
KAFP	BULA	0	0.00	0	0.00
	CATE	33	12.79	5	11.36
	FRAM	1	0.38	0	0.00
	JUVI	9	3.48	2	4.55
	MORU	0	0.00	0	0.00
	QUMA	27	10.46	11	25.00
	QURU	4	1.56	0	0.00
	QUST	182	70.55	24	54.55
	QUVE	2	0.77	2	4.55
	ULAL	0	0.00	0	0.00
	Total	258	99.99	44	100.01
OWMA	BULA	1	0.4	0	0.00
	CATE	34	13.38	0	0.00
	FRAM	0	0.00	0	0.00
	JUVI	0	0.00	0	0.00
	MORU	0	0.00	0	0.00
	QUMA	24	9.44	15	42.86
	QURU	0	0.00	0	0.00
	QUST	159	62.6	15	42.86
	QUVE	10	3.93	3	8.57
	ULAL	26	10.25	1	2.86
	Unknown	0	0.00	1	2.86
	Total	254	100.00	35	100.01
TGPP	BULA	0	0.00		0.00
	CATE	41	10.94	0	0.00
	FRAM	8	2.14	0	0.00
	JUVI	0	0.00	0	0.00
	MORU	1	0.26	1	2.44
	QUMA	34	9.06	35	85.37
	QURU	0	0.00	0	0.00
	QUST	290	77.34	3	7.32
	QUVE	0	0.00	0	0.00
	ULAL	1	0.26	1	2.44
	Unknown	0	0.00	1	2.44
	Total	375	100.00	41	100.01

Table 4. Results of regression analysis for the relation of seedling density versus gap size. See Table 7 for list of abbreviations used for locations and tree species.

Location	Species	Slope	Intercept	R^2	P
KAFP	CATE	0.01	40.61	0.25	0.003
	FRAM	0.33	50.85	0.41	<0.001
	JUVI	0.10	43.84	0.02	0.39
	QUMA	0.001	56.26	0.01	0.54
	QUST	0.001	52.50	0.03	0.30
	QUVE	0.007	55.34	0.09	0.08
OWMA	BENI	-0.01	86.32	0.008	0.65
	CATE	0.003	81.46	0.003	0.76
	QUMA	0.005	57.67	0.55	0.0001
	QUST	0.0007	75.32	0.03	0.30
	QUVE	-0.01	90.90	0.04	0.32
	ULAL	-0.0008	92.00	0.009	0.63
	VAAR	0.002	80.33	0.003	0.78
TGPP	BULA	0.06	51.67	0.08	0.15
	CATE	0.004	52.00	0.01	0.59
	FRAM	0.003	48.03	0.20	0.02
	JUVI	0.02	51.85	0.003	0.77
	QUMA	0.0002	53.08	0.003	0.77
	QUST	-0.001	64.08	0.09	0.13
	QUVE	0.02	53.24	0.008	0.15
	ULAL	0.001	52.80	0.01	0.60

Table 5. Regeneration <1 meter height class by species in forest stand and expanded gap at three locations in the Cross Timbers. See Table 7 for list of abbreviations used for locations and tree species.

Location	Species	Control plot	Expanded gap	p > t
		Stems ha^{-1}		
KAFP	BENI	0	0	
	BULA	0	0	
	CATE	1098	1903	0.27
	FRAM	36	152	0.34
	JUVI	393	164	0.39
	QUMA	7679	4584	0.54
	QUST	11383	7273	0.40
	QUVE	571	902	0.75
	ULAL	0	0	
	VAAR	0	0	
	total	21160	14978	
OWMA	BENI	600	34	0.13
	BULA	0	0	
	CATE	2044	1169	0.16
	FRAM	0	0	
	JUVI	0	0	
	QUMA	2100	6451	0.19
	QUST	15939	16943	0.90
	QUVE	417	222	0.43
	ULAL	2571	3605	0.19
	VAAR	1250	627	0.61
	total	24921	29051	
TGPP	BENI	0	0	
	BULA	29	127	0.65
	CATE	229	359	0.59
	FRAM	5629	1685	0.23
	JUVI	29	12	0.59
	QUMA	519	2627	0.03
	QUST	8297	5427	0.31
	QUVE	114	23	0.45
	ULAL	1762	772	0.31
	VAAR	0	0	
	total	16608	11032	

Table 6. Replacement probabilities by species for gap at three locations in the Cross Timbers. See Table 7 for list of abbreviations used for tree species.

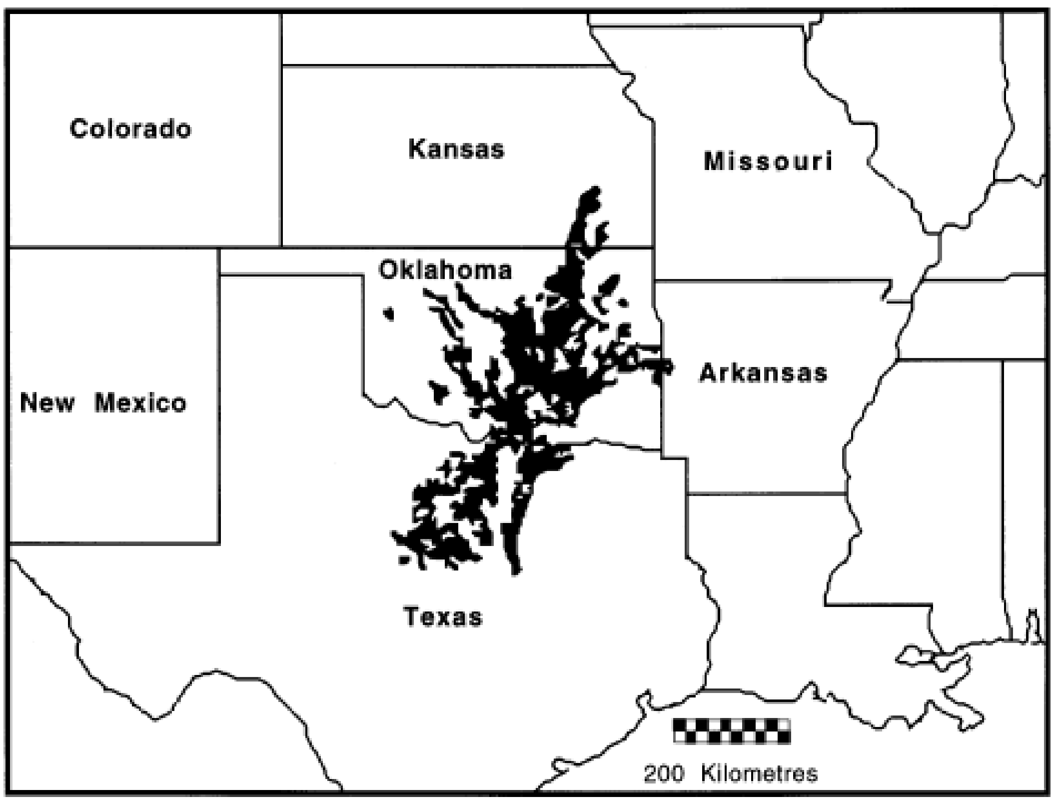
Keystone Ancient Forest Preserve					
	Gap fillers				
Gap makers	QUST	QUMA	CATE	JUVI	QUVE
QUST	0.69	0.06	0	0.22	0.03
QUMA	0.59	0.18	0.17	0	0.06
CATE	0.56	0.03	0.17	0.02	0.13
JUVI	0.66	0	0	0.34	0

Okmulgee Wildlife Management Area						
	Gap fillers					
Gap makers	QUST	QUMA	CATE	ULAL	QUVE	BULA
QUST	0.37	0.03	0.34	0.19	0.06	0.01
QUMA	0.32	0.05	0.31	0.22	0.10	0
QUVE	0.17	0.17	0.49	0.17	0	0

Tall Grass Prairie Preserve			
	Gap fillers		
Gap makers	QUST	QUMA	CATE
QUST	1.00	0	0
QUMA	0.49	0.30	0.21
ULAL	0.75	0.25	0

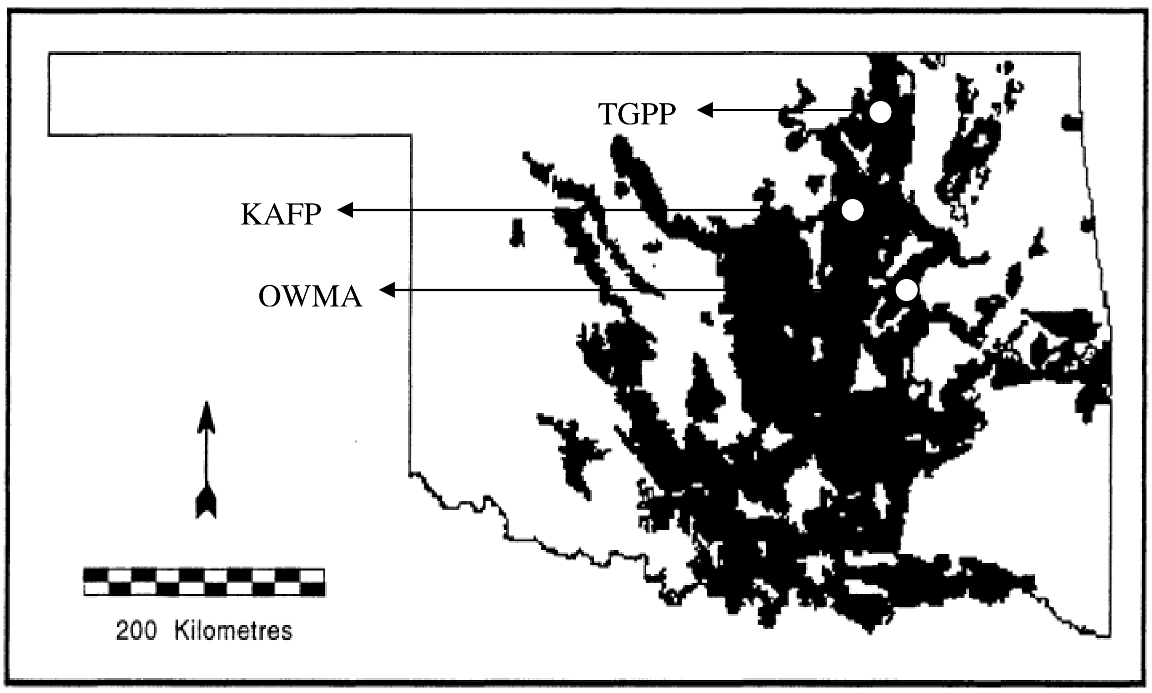
Table 7. List of abbreviations.

Location or genus and species	Abbreviation
Keystone Ancient Forest Preserve	KAFP
Okmulgee Wildlife Management Area	OWMA
Tall Grass Prairie Preserve	TGPP
Betula nigra	BENI
Bumelia lanuginose	BULA
Carya texana	CATE
Fraxinus Americana	FRAM
Juniperus virginiana	JUVI
Morus rubra	MORU
Quercus marilandica	QUMA
Quercus rubra	QURU
Quercus stellata	QUST
Quercus velutina	QUVE
Ulmus alata	ULAL
Vaccinium arboretum	VAAR



(Source Therrell and Stahle, 1998)

Figure 1. Distribution map of the Cross Timbers.



(Source Therrell and Stahle, 1998)

Figure 2. Location of the three research sites in the Cross Timbers of Oklahoma, Tall Grass Prairie Preserve (TGPP), Keystone Ancient Forest Preserve (KAFP) and Okmulgee Wildlife Management Area (OWMA).

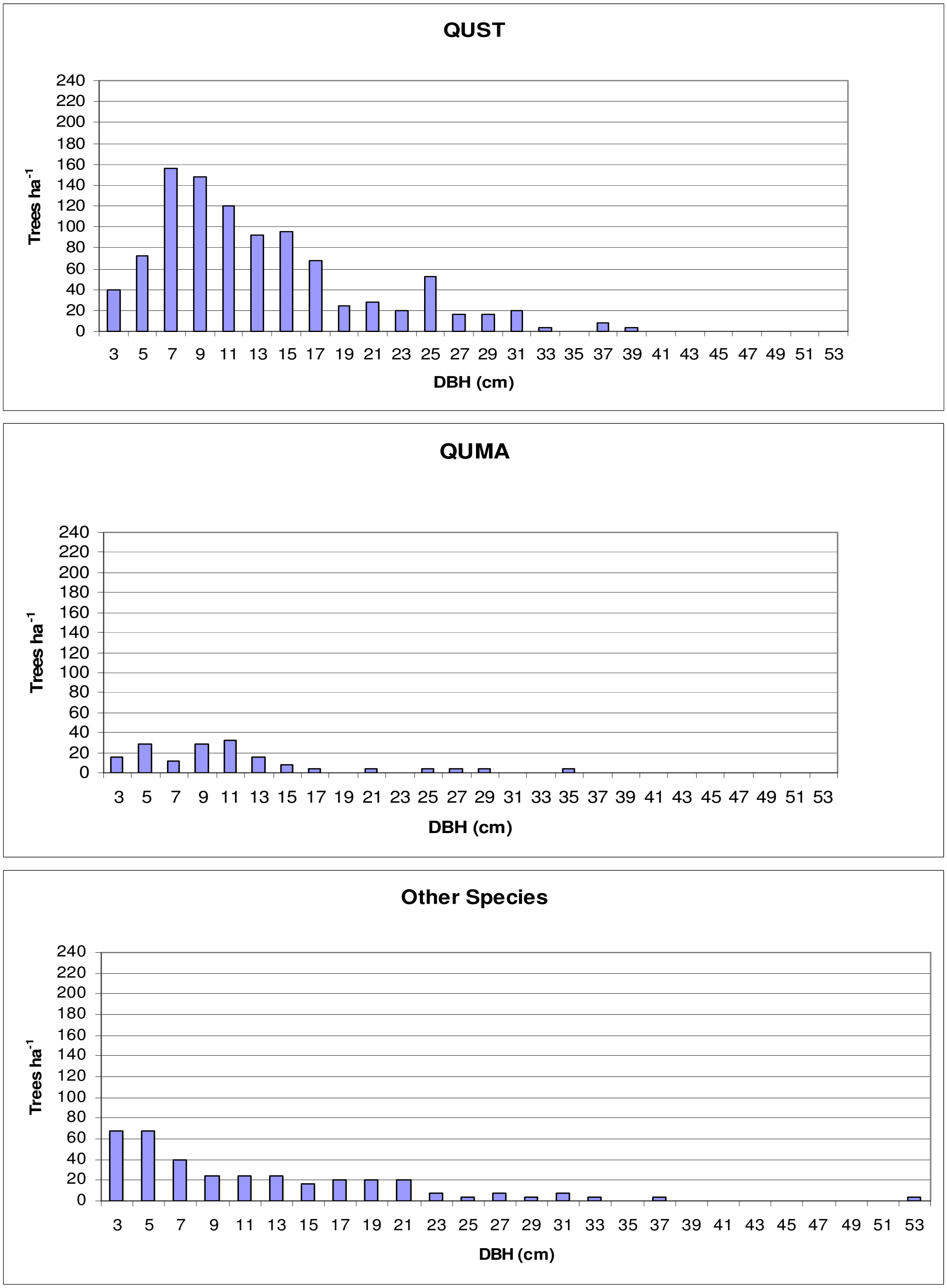


Figure 3. DBH class distribution of trees in Keystone Ancient Forest Preserve. See Table 7 for list of abbreviations.

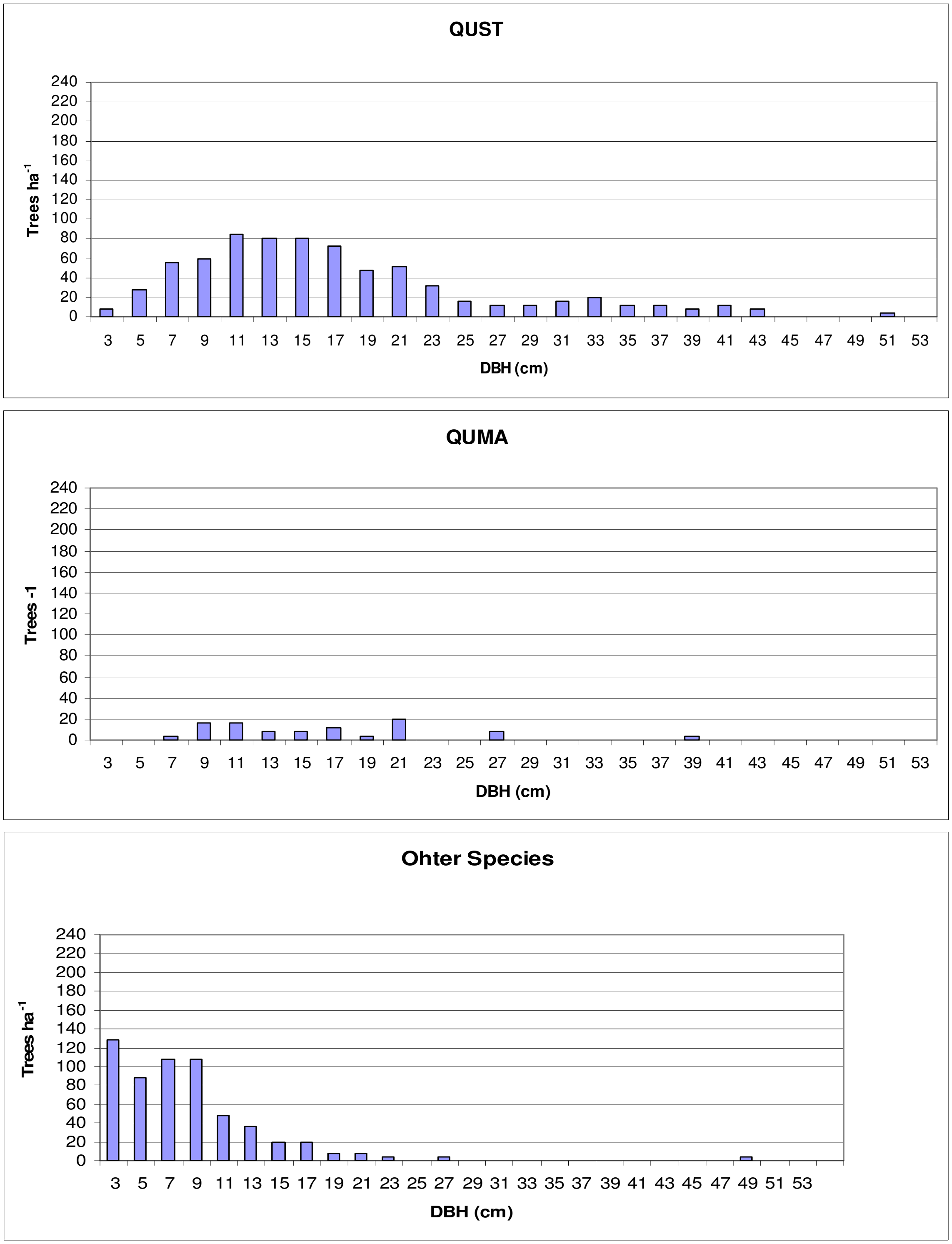


Figure 4. DBH class distribution of trees in Okmulgee Wildlife Management Area. See Table 7 for list of abbreviations.

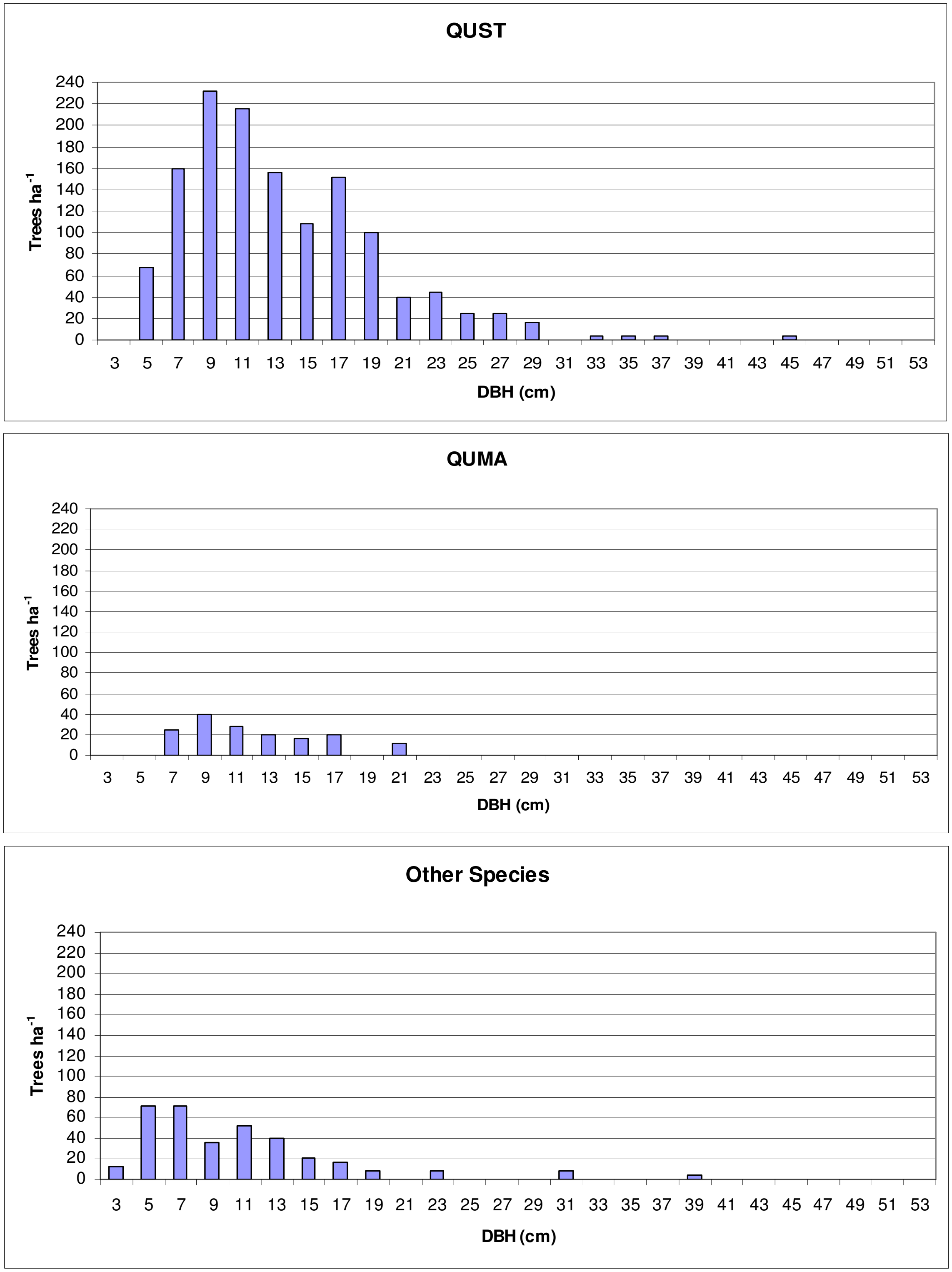
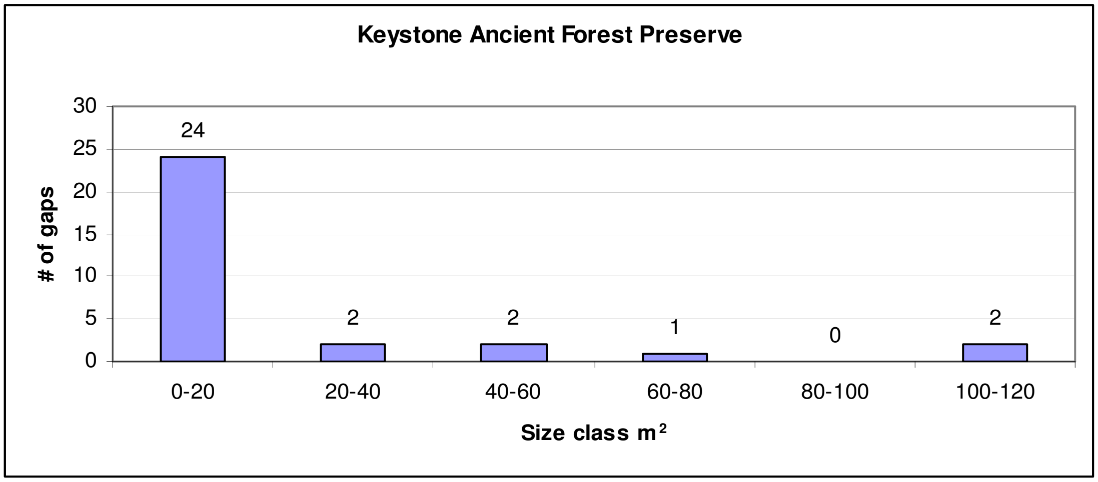
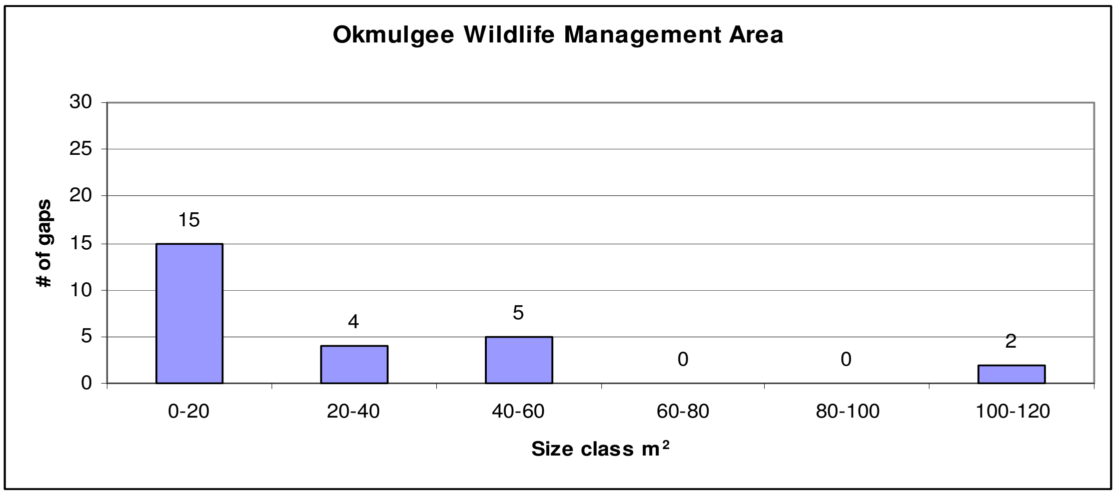


Figure 5. DBH class distribution of trees in Tall Grass Prairie Preserve. See Table 7 for list of abbreviations.





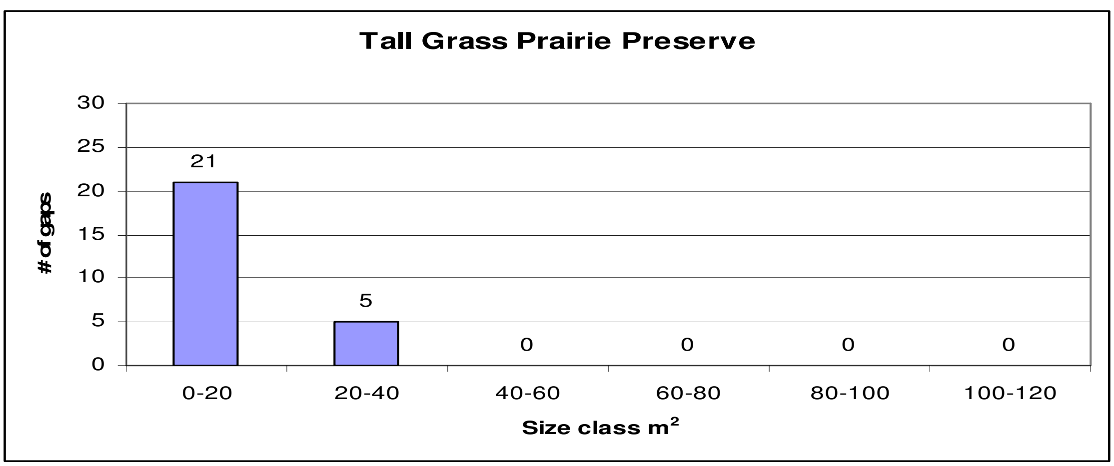
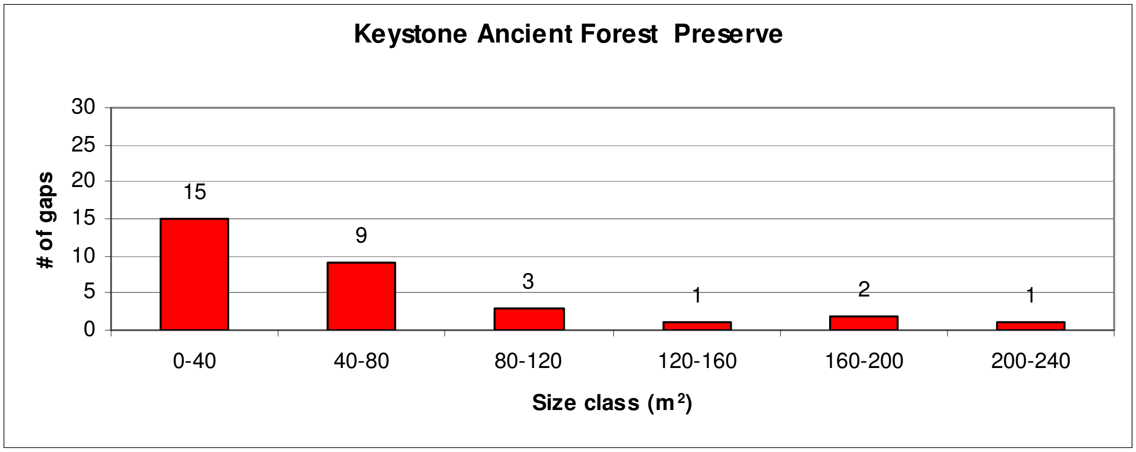
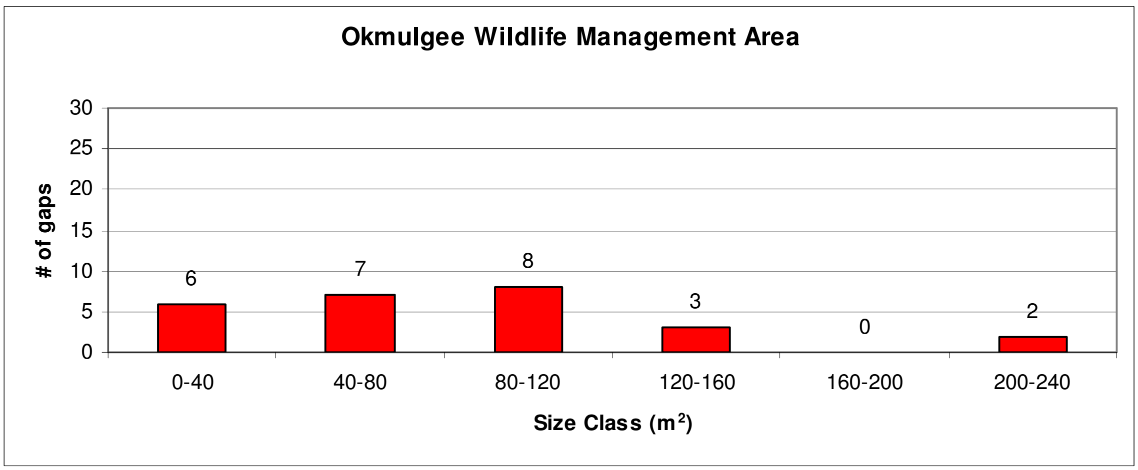


Figure 6. Size class distribution of canopy gaps in the Cross Timbers of Oklahoma.





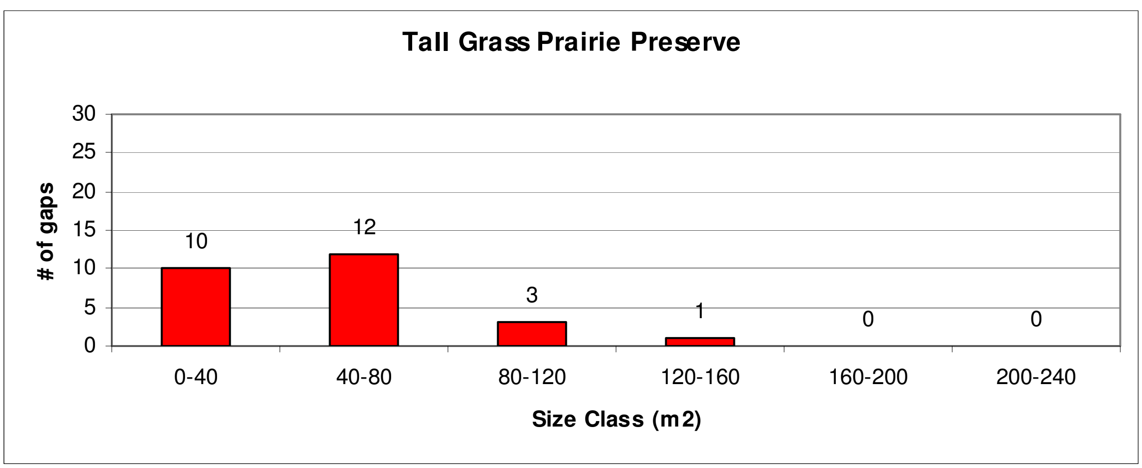
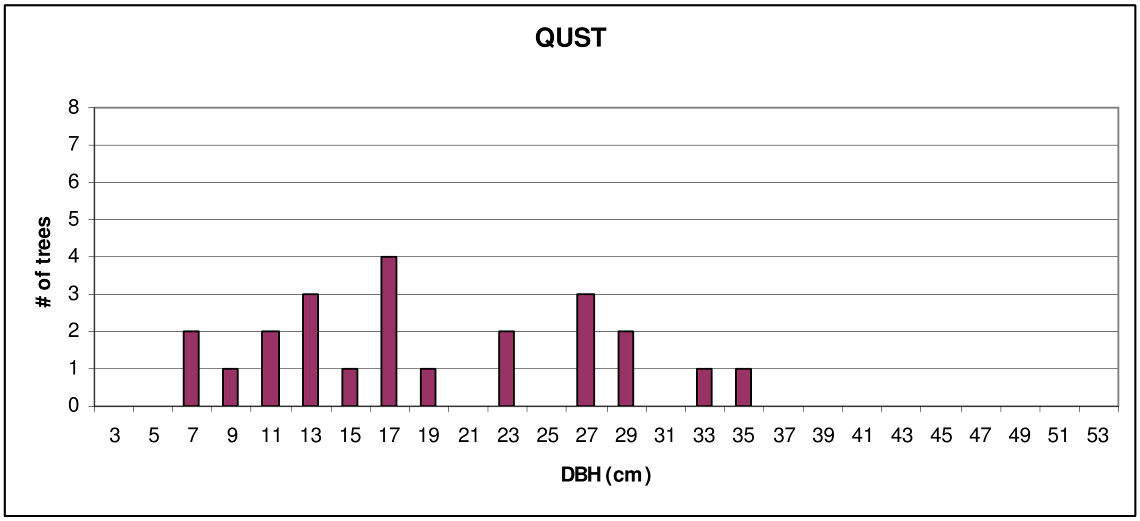
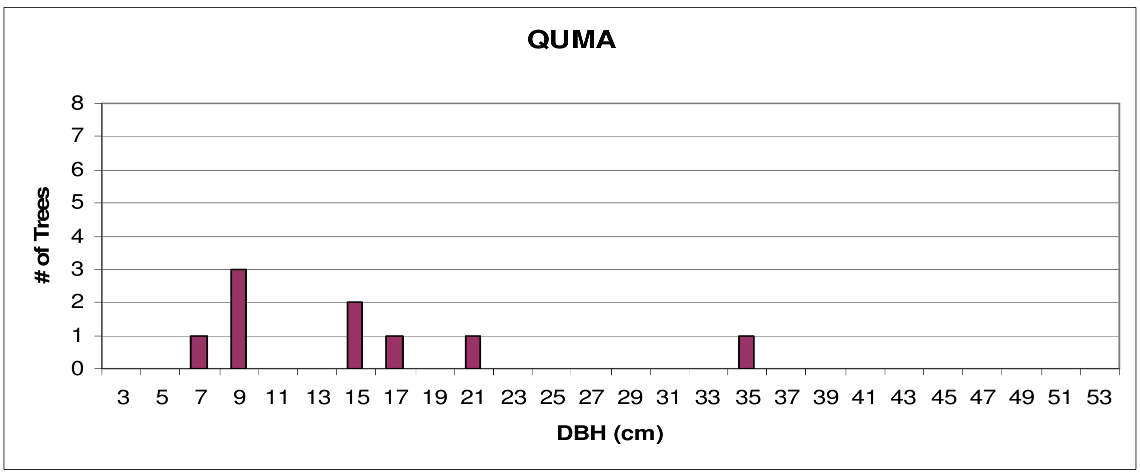


Figure 7. Size Class distribution of the expanded gaps in the Cross Timbers of Oklahoma.





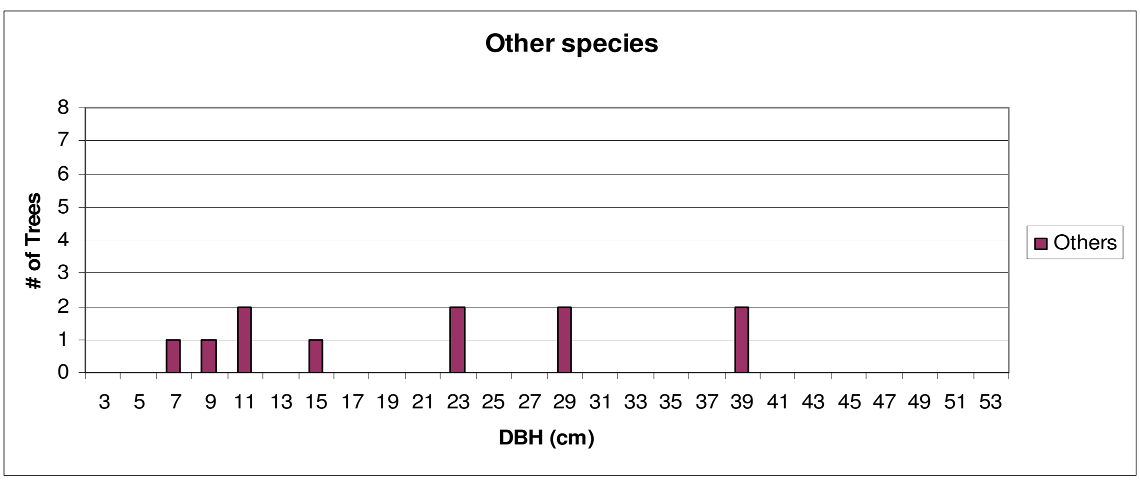
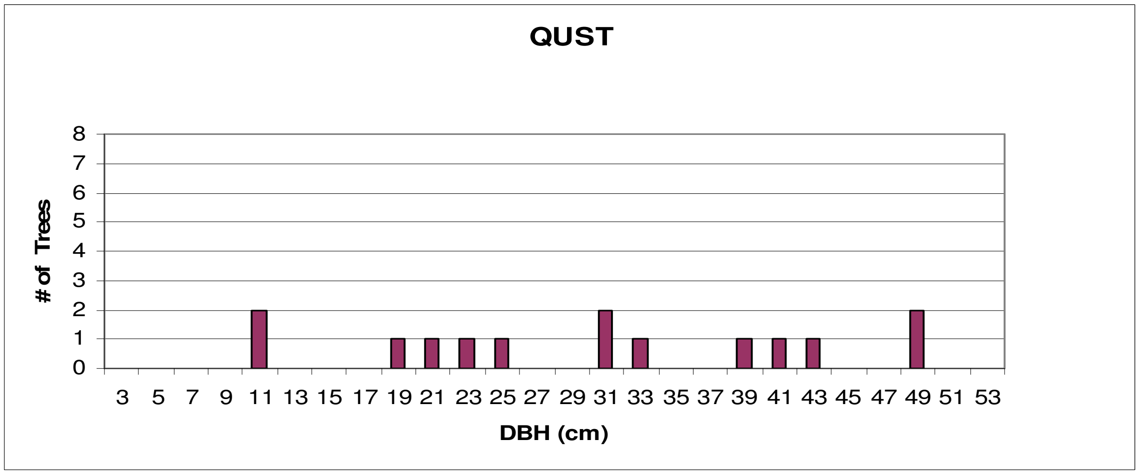
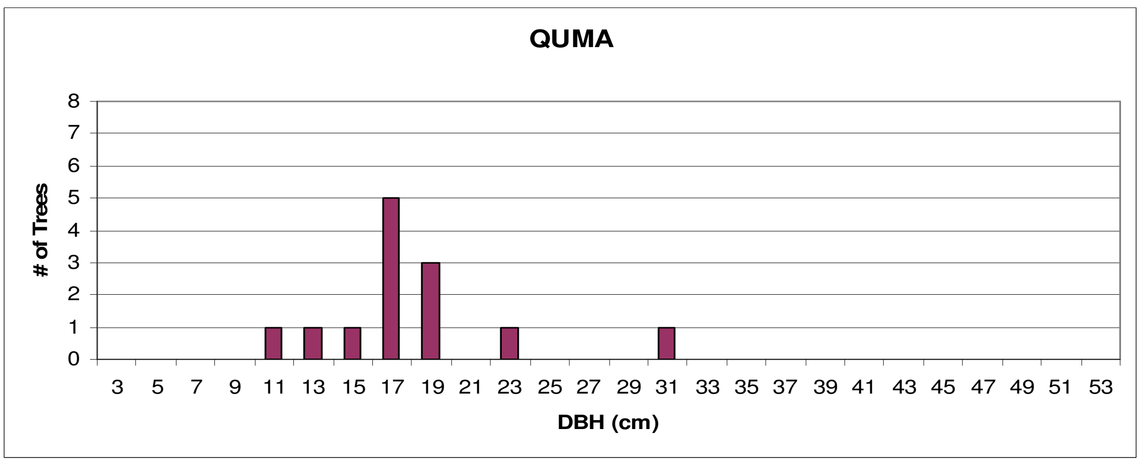


Figure 8. DBH class distribution of gap maker trees in Keystone Ancient Forest Preserve. See Table 7 for list of abbreviations.





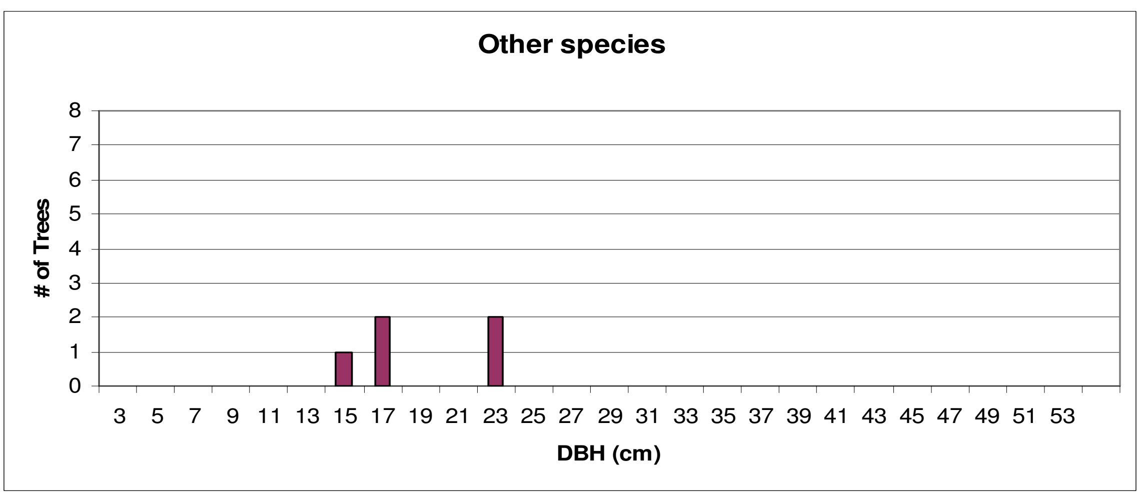
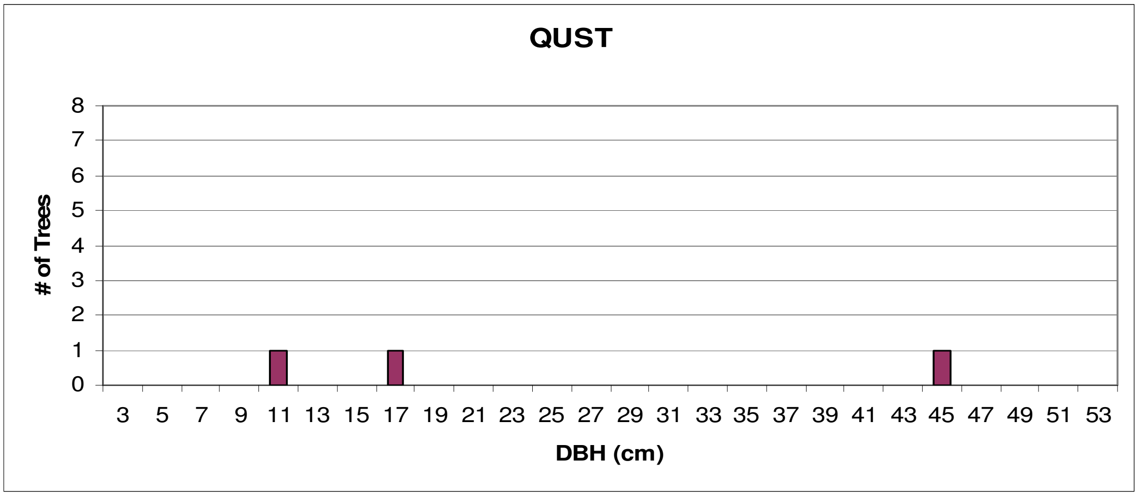
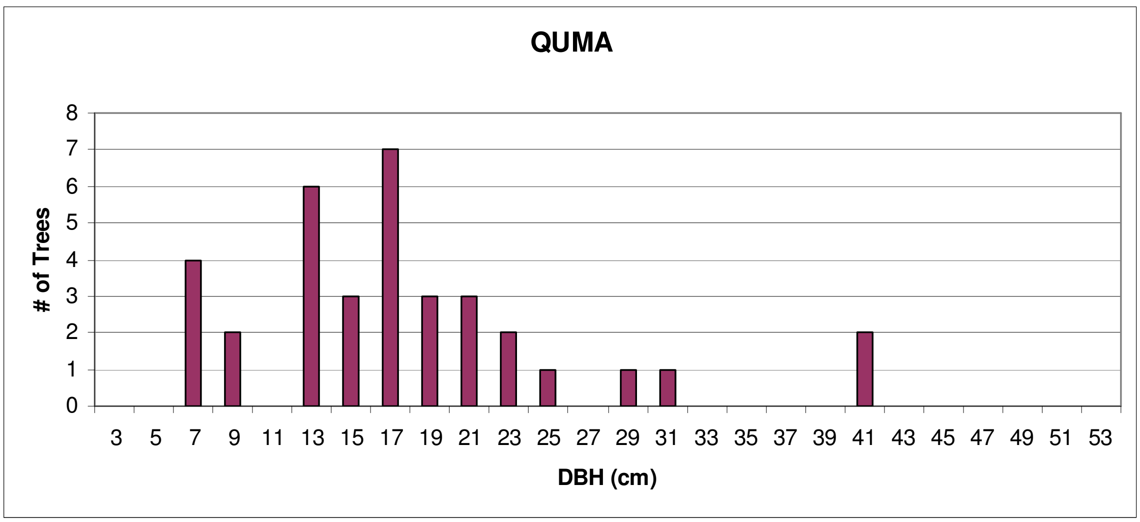


Figure 9. DBH class distribution of gap maker trees in Okmulgee Wildlife Management Area. See Table 7 for list of abbreviations.





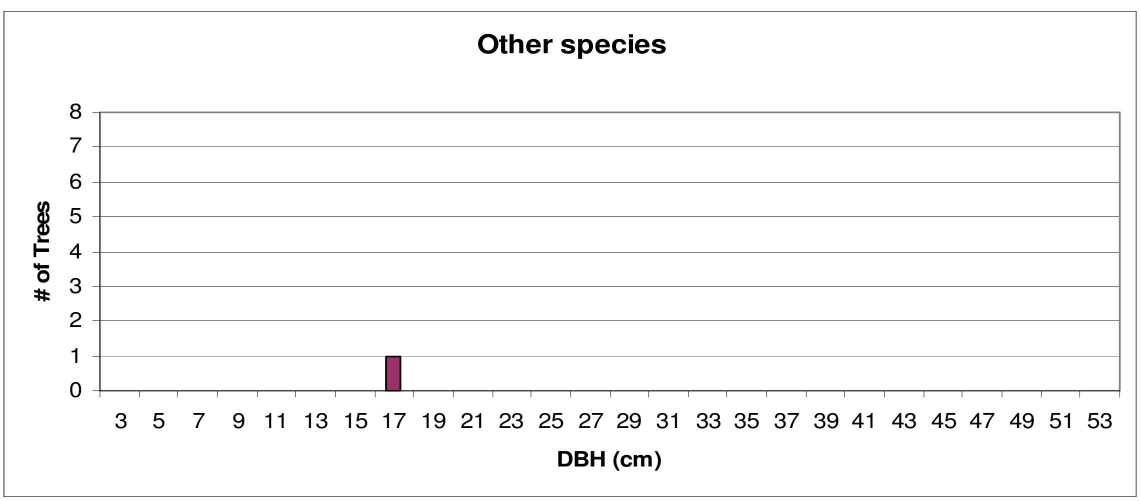


Figure 10. DBH class distribution of gap maker trees in Tall Grass Prairie Preserve. See Table 7 for list of abbreviations.

VITA

Laxman Karki

Candidate for the Degree of

Master of Science

Thesis: TREE FALL GAP DYNAMICS IN THE CROSS TIMBERS OF OKLAHOMA

Major Field: Forest Resources

Biographical:

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Experience: Graduate Research Assistant from August, 2005 to July, 2007 at Oklahoma State University, Department of Forestry.

Professional Memberships: Nature Nepal

Name: Laxman Karki Date of Degree: December, 2007

Institution: Oklahoma State University Location: Stillwater, Oklahoma

Title of Study: TREE FALL GAP DYNAMICS IN THE CROSS TIMBERS OF OKLAHOMA

Pages in Study: 58 Candidate for the Degree of Master of Science

Major Field: Forest Resources

Scope and Method of Study: The purpose of this study was to determine the effects of tree fall gaps on forest composition in the Cross Timbers of Oklahoma. The three hypotheses of major importance in this study were as follows: (1) the proportion of gap makers from a species is the same as the proportion of that species in the canopy of the closed forest, (2) gap size has no effect on regeneration of canopy tree species and (3) the gap maker replacement probabilities by gap fillers are such as to maintain the presence of dominant species in the stand at the current levels. This study was carried out in Cross Timbers forests at the Tall Grass Prairie Preserve, Keystone Ancient Forest Preserve and Okmulgee Wildlife Management Area. The line-intersect method was used to determine the amount of gaps and to sample gaps for detailed measurement. At each site, 6 to 7 transects totaling 1000 m were installed. The nearby closed canopy forest was sampled for comparison.

Findings and Conclusions: The canopy gaps covered 5 to 9 percent of the forest area and the expanded gap up to the bases of the surrounding trees covered 20 to 24 percent of the area. There were no differences among sites. Post oak (*Quercus stellata*) contributed 63 to 77 percent of the canopy trees and 7 to 55 percent of the gap makers while blackjack oak (*Q. marilandica*) contributed 9 to 10 percent of the canopy trees and 25 to 85 percent of the gap makers. There was no difference in regeneration of seedling less than 1 m tall between the closed forest and the canopy gap and gap size did not affect regeneration density. Post oak replaced itself in 37 to 100 percent of the gaps and blackjack oak in 32 to 59 percent of the gaps. In contrast, blackjack oak replaced itself in 5 to 30 percent of the gaps and post oak in 0 to 6 percent of the gaps. The results suggested blackjack may be declining in the Cross Timbers forest because it was relatively more frequent as a gap maker than as a component in the canopy and it was not replacing itself as often as it was replaced by other species. Post oak may be increasing in the forest because it was less frequent as a gap maker than it was as a canopy tree and it had the highest replacement probabilities of any species.

ADVISER'S APPROVAL: Dr. Stephen W. Hallgren