STAND DYNAMICS OF AN OLD-GROWTH OAK FOREST IN THE CROSS TIMBERS OF OKLAHOMA

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PREFACE

My dissertation is composed of a general introduction and 5 manuscripts intended for publication in separate scientific journals. Chapter Two, "Characterization of an old-growth forest in the cross timbers of Oklahoma", will be submitted to *American Midland Naturalist*. Chapter Three, "Dynamics of oak (*Quercus marilandica* and *Q. stellata*) reproduction in an old-growth cross timbers forest", was recently accepted for publication in the *Southeastern Naturalist*. We submitted Chapter Four, "Age estimation of *Quercus marilandica* and *Q. stellata*: applications for interpreting stand dynamics", to the *Canadian Journal of Forest Research* in May, 2003. Chapter Five, "Release response of *Quercus stellata* in a xeric oak forest of the cross timbers of Oklahoma", will be submitted to *Ecological Applications*. Chapter Six, "Dynamics of the historic fire regime in an old-growth forest in the cross timbers of Oklahoma", is intended for submission to the *Canadian Journal of Forest Research*. Each manuscript is formatted according to guidelines for the appropriate journal and requires no additional material. Each manuscript is arranged in the following order: text, literature cited, appendices, tables, and figures.

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DEDICATION

I dedicate this Dissertation to my husband, Jay Clark. Jay, thanks for everything, even the "motivational" speeches. You're the reason I came to Oklahoma and you're the reason I was able to finish so quickly. I thank God for your sense of humor, intelligence, passion, and your love for me. I am so glad we did this together and we can now look forward to many wonderful years together without the pressures of school. Hopefully we will have the comforts of some mountainous environment with both bears and trees.

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CHAPTER ONE

INTRODUCTION

Oak (*Quercus* spp.) species are extensively distributed throughout eastern North American forests, often dominating certain forest types or existing as a minor component in other forests (Abrams 1992, Braun 1950). Oaks are an important component of many ecological processes, in addition to fulfilling a variety of society's aesthetic and recreational values. Despite the pervasiveness and importance of oaks, stand dynamics of oak forests are not well understood, particularly in xeric oak systems.

The Cross Timbers of Oklahoma are considered an ecotone between the prairies of the Great Plains and the hardwood forests of the Ozarks. The vegetation of the Cross Timbers is a mosaic of xeric oak woodlands scattered throughout patches of savanna and prairie openings. The Cross Timbers region consists of 4.8 million hectares, with nearly half in Oklahoma (Hoagland *et al.* 1999, Küchler 1964). Oak is self-replacing on upland forest sites in the Cross Timbers and has few competitors that can survive under stressful site conditions created by frequent fire and drought. However, the current dominant vegetation could be converted with long term changes in climate (Bruner 1931, Clements 1936, Braun 1950, Wyckoff 1984).

Much of the Cross Timbers forests were not extensively logged nor farmed like much of the eastern deciduous forests and subsequently, the Cross Timbers may contain some of the largest tracts of presettlement forests in the eastern United States (Stahle and Chaney 1994, Therrell and Stahle 1998). However, few of these old-growth stands have been studied to gain an understanding of their ecology and management for utilization, including preservation.

Although expanses of old-growth forests exist in the Cross Timbers, these forests have been affected by changes in fire frequency and the advent of grazing since the beginning of the 20th century (Rice and Penfound 1959, Wyckoff 1984). Many oak savannas that once dominated the cross timber's landscape are now closed-canopy forests due to fire suppression and grazing by domesticated animals (Bruner 1931, Dyksterhuis 1948, Johnson and Risser 1975, Abrams 1992). The cessation of fire has also increased the abundance of eastern red cedar (*Juniperus virginiana*), a species that has invaded native grasslands and forested areas throughout this area since European settlement (Engle et al. 1996a). Understanding the effects of disturbances, such as fire, on the oak component in this area is critical to preserving the remaining relics of ancient Cross Timbers forest and restoring the original ecosystem, if desired.

A private landowner, Mr. Irvin Frank, forged an agreement to transfer ownership of a tract of forested land, known as the Keystone Ancient Forest Preserve (KAFP), to the State of Oklahoma and to allow The Nature Conservancy (TNC) the rights to manage the property. The unique ecological and educational values of the KAFP were first recognized by Dr. David Stahle and Dr. Matthew Therrell, of the Tree-Ring Laboratory in the Department of Geosciences at the University of Arkansas. The management of this property by TNC will provide aesthetic and recreational opportunities to the public and a scientific laboratory for researchers. In order to preserve the integrity of old-growth forests like the KAFP, managers need to first understand the ecological processes that govern these areas.

Old-growth forests have provided information on historical disturbance patterns, successional processes, and natural stand characteristics of various forest ecosystems throughout North America (Hett and Loucks 1976, Lorimer 1980, Lorimer and Frelich 1989, Veblen et al 1991, Mikan et al. 1994, Tyrell and Crow 1994, Abrams and Orwig 1995, Orwig et al. 2001). Through the examination of tree-ring growth, age structure, and stand composition and structure, old forests can provide historical information on forest succession, disturbance history, and climatic variation (Lorimer 1985, Fritts and Swetnam 1989). Guided by these studies, managers will be better able to restore disturbed ecosystems to their "presettlement" status (Lorimer and Frelich 1994).

Research is needed that will examine the critical mechanisms by which the original Cross Timbers vegetation was maintained. Some efforts to restore Cross Timbers ecosystems have relied partially on descriptive evidence from early explorers (Irving 1835, Gregg 1844) and ecologists (Bruner 1931, Dykesterhuis 1948, Rice and Penfound 1959), but have not been based on empirical investigations of the natural processes of the Cross Timbers ecosystem (Bidwell and Masters 1994, Engle et al 1996b). The research presented herein examined the stand dynamics of an old-growth forest in the Cross Timbers by analyzing stand characteristics, age structure, tree-ring and climate chronologies, and disturbance history. Understanding the ecological processes of the pre-settlement Cross Timbers forests is significant, as society simultaneously threatens and demands forest conservation.

The objectives of this project were: 1) to determine important attributes of the old-growth oak forests in the Cross Timbers and how these attributes changed across a topo-edaphic gradient (Chapter Two), 2) to examine regeneration dynamics of the primary oak species (Chapters Three and Six), and 3) to examine the historical disturbance regime and the primary factors affecting forest succession, including disturbance and climate (Chapters Five and Six). To achieve the first objective, I examined physical and structural characteristics of the forest, including soil composition, course woody debris, diameter distributions, canopy structure and species composition. To achieve the second objective, I examined the mechanisms of recruitment, including seeding vs. sprouting and the age structure of the seedling and sapling populations. The third objective required examination of the population structure and tree-rings to determine response to known disturbance and climatic events. Existing methodology was examined and tested in order to achieve this last objective (Chapter Four and Five). I reconstructed the fire history of the KAFP through fire scar analysis using tree-rings and examined the effects of climate in promoting fire and fire effects on tree recruitment and species composition (Chapter Six). This project represents the first comprehensive study utilizing vegetation and site sampling, dendrochronology, and disturbance history information to understand stand dynamics of an old-growth forest in the Cross Timbers. I hope this study will provide a basis for future research in this unique and largely unrecognized ecosystem.

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CHAPTER TWO

CHARACTERIZATION OF AN OLD-GROWTH FOREST IN THE CROSS TIMBERS OF OKLAHOMA

Abstract

We examined three stands in a 50 ha old-growth forest in Osage county, Oklahoma to determine the changes in species composition and structure across a topo-edaphic gradient and to examine conformity to stand structure models commonly used to characterize old-growth forests. Stand characteristics differed from traditional concepts of old-growth that have been based on highly productive forests; this forest contained relatively small, stunted trees, and had a relatively low number of tree species. Species composition was typical of most cross timber forests; *Quercus stellata* dominated the overstory in each stand, and *Q. marilandica* was an important subordinate species. The abundance of oak throughout each canopy layer indicated that replacement of oak by other species was not occurring, unlike many oak dominated forests in the eastern United States. *Juniperus virginiana* was a relatively rare overstory species throughout the forest, but occupied specific microhabitats on steep rocky bluffs where fire protection appears to favor longevity. One stand had relatively high sapling density of *J. virginiana*, which we attribute to an increase in the seed rain from surrounding fields and prairies. Principle components and redundancy analyses revealed a moisture gradient that was largely a function of soil texture. Total coarse woody debris was relatively low compared to other dry oak forests in eastern North America (1.8 to 8.7 m^3 per ha), and decreased with increasing dryness of the site. These stands did not conform to traditional models of balanced stand structure that have been developed primarily in mesic forests dominated by shade-tolerant species. Sapling populations (3-9 cm diameter classes) were representative of the episodic recruitment processes of oak, manifest through reduced aggregate crown area and stem densities.

Keywords: Cross Timbers; old-growth forests; *Quercus*; gradient analysis; crown area distributions; negative exponential function; Weibull function

Introduction

Studies of eastern North American old-growth forests have provided information on natural stand processes and characteristics of various forest ecosystems (Hett and Loucks, 1976; Lorimer, 1980; Tyrell and Crow, 1994; Abrams and Orwig, 1995). Most studies have been conducted in old-growth forests that contain high aesthetic qualities that lends to their protection and study. The concept of old-growth is generally related to cathedral-like trees growing in mesic environments with complex stand structure, large tree size, and high production of dead biomass (Franklin et al., 1981). Dry hardwood forests, like those in the Cross Timbers, have not been as well protected, studied nor appreciated because of their nonconformity to traditional images of old-growth (Therrell and Stahle, 1998; Orwig et al., 2001). The vegetation of the Cross Timbers consists of a mosaic of xeric oak woodlands, savannas and prairie openings scattered throughout approximately 4.8 million hectares, with nearly half in Oklahoma (Fig. 1) (Hoagland et al., 1999; Küchler, 1964). Old-growth Cross Timbers forests are dominated by stunted *Quercus stellata* and *Q. marilandica* trees and are currently found predominately on rocky escarpments or ridges unsuitable for logging and agricultural practices (Therrell and Stahle, 1998). The Cross Timbers may hold many thousands of hectares of old-growth forest, and contain some of the largest contiguous tracts of undisturbed forests left in the eastern United States (Therrell and Stahle, 1998). The study of these unique forests could potentially help managers not only in the Cross Timbers, but those who wish to protect and restore the oak component in forests that are shifting in dominance to non-oak species.

The loss of the oak component in many eastern North American forests has been attributed to changes in disturbance regimes since European settlement (Abrams, 1992, 1996). Perhaps the most notable change in species composition of oak savannas and grassland prairies throughout the Midwest has been the increased abundance of *Juniperus virginiana* (Bragg and Hulbert, 1976; Engle et al., 1996), but dynamics of this species in Cross Timbers forests are not well understood. We can speculate, however, that reductions in oak dominance will likely result in negative effects to many wildlife populations (McShea and Healy, 2002). To better conserve and restore old-growth oak forests, managers should first understand the important external and abiotic factors that influence species composition, such as soil moisture and fire, and they should be able to identify characteristics specific to old-growth habitat. Coarse woody debris (CWD) is a key component in nutrient cycling, is used as habitat for plant and animal species, and is, thus, an indicator of ecosystem health; CWD (Franklin et al. 1981; Harmon et al., 1986). However, the dead biomass component of old-growth structure has not been well studied in Midwestern forest communities (Spetich et al., 1999), including the Cross Timbers.

Stand structural characteristics such as crown area and diameter distributions have been studied to characterize population structures and to aid managers in maintaining a sustainable flow of timber resources (Leak, 1975; Goff and West, 1975; Hett and Loucks, 1976; Goodburn and Lorimer, 1999). Models of old-growth stand structure include examination of crown area and diameter distributions (De Liocourt, 1898; Leak, 1996; Goodburn and Lorimer, 1999). According to traditional theories of balanced all-aged stands, such as the equal area hypothesis, each size class should occupy an approximately equal amount of growing space (Nyland, 1996, p. 204). Additionally, diameter distributions should approximate the negative exponential model (Meyer and Stevenson, 1943). However, alternative models may exist to describe population structures (Goff and West, 1975, Hett and Loucks, 1976) and shade intolerant species, such as oak, have gone largely understudied.

The goal of our study was to characterize an old-growth forest in the Cross Timbers across a topo-edaphic gradient. Our specific objectives were to examine species composition, volume of coarse woody debris, and stand structure related to growing space allocation and diameter distributions. We discuss stand characteristics in relation to other Cross Timber sites and to more mesic eastern North American old-growth forests.

Methods

Study area

The 50 ha study area is part of the Keystone Ancient Forest Preserve (KAFP) and is managed by The Nature Conservancy (TNC). The KAFP lies in the northern range of the Cross Timbers region (Küchler, 1964), approximately 32 km west of Tulsa, Oklahoma in southern Osage County (Fig. 1). The KAFP borders Keystone Reservoir on the Arkansas River. Average annual precipitation is 101 cm and average winter and summer temperature are 3° and 26° C, respectively (Oklahoma Climatological Survey, 2002). Previous researchers have characterized the KAFP as old-growth due to the presence of *Q. stellata* and *J. virginiana* trees greater than 300 and 500 years-old, respectively (Therrel and Stahle, 1998). Elevation ranges from 251 to 304 m; topography is moderately to steeply sloping with underlying bedrock of shale and sandstone. Soils are in the Niotaze-Darnell complex, with a sandy loam surface layer (Bourlier et al., 1979).

We found limited evidence of past anthropogenic disturbances, particularly on the steep forested side-slopes. Wildfire burned throughout the majority of the forest in 1994 and 1996 (Roe, 1998). Although intensity of the fires was not measured, they apparently were relatively low-intensity ground fires and did not kill any overstory trees. We found evidence for earlier fires from a fire scar analysis with moderate-scale fires occurring approximately every 9 years (Clark 2003).

Field sampling

We delineated three stands based primarily on aspect and elevation (Fig. 1). The 11-ha Southwestern Slope stand was located on the steep upper slopes with a southwestern aspect. The 14-ha Northeastern Slope stand was located on steep lower slopes with a northeastern aspect and had the lowest elevation. The Bench stand was 5 ha in size and was located on relatively level terrain northwest of the main ridge top. We randomly placed 3 to 5 3000-m^2 square plots within each stand. Trees were delineated into different canopy strata: seedling ($\leq$ 1m height), sapling, (> 1 m height, but < 10 cm diameter at breast height (DBH)), and overstory tree ($\geq$ 10 cm DBH). We recorded all overstory trees on each plot and sampled saplings and seedlings in four 8-m^2 and 4-m^2 randomly placed nested plots, respectively, within each large plot. Diameter at breast height was measured to the nearest cm for each overstory tree and for each sapling $\geq$ 3 cm DBH. Crown measurements were made on 141 randomly selected *Q. stelleta* trees $\geq$ 3 cm DBH. We measured radii of total and exposed crown along the four cardinal directions, using a clinometer to locate the edge of each crown. Exposed crown was the portion not overtopped by another tree's crown. Crown area was calculated as the sum of four quarter ellipses, using the length of the radii in each cardinal direction.

At each 8-m^2 plot center, we measured slope (percent) with a clinometer, aspect (azimuths in degrees), and elevation with a GPS unit; canopy cover, measured with a densiometer, was recorded at plot center and each corner. We collected composite soil samples to a depth of 10 cm within each 8-m^2 plot in the last week of April 2002.

Each 3000-m^2 plot was divided into 16 equal area grids and we randomly selected four grids to estimate rock cover and to measure CWD. Height and DBH were measured for snags $\geq$ 8 cm DBH. Downed material that was $\geq$ 8 cm at either end was measured for length of main stem, down to 3 cm diameter, and diameters of logs were recorded at both ends. Species was recorded when possible, and genus was noted in all measurements. A decay class was assigned to snag or downed log (Table 1).

Data analyses

We calculated plot and stand means for species tree density, DBH and basal area (BA; overstory trees only). We calculated importance of overstory trees by averaging species relative density and relative basal area (Cottam and Curtis, 1956). Aspect was converted to two continuous variables of northness (Nness) and eastness (Eness) using the following formulas:

$$\text{Nness}=\cos(\text{aspect}) \tag{1}$$

$$\text{Eness}=\sin(\text{aspect}) \tag{2}$$

The Soil, Water, and Forage Analytical Laboratory at Oklahoma State University analyzed soil samples for texture, pH, percent organic matter and abundance of P, K, NO_3-N, SO_4-S, Ca, Mg, Fe, Zn, and B.

Volume of downed wood was calculated using Smalian's formula,

$$\text{volume} = \left(\frac{A_1 + A_2}{2}\right)L \tag{3}$$

where A_1 and A_2 are areas of each log end and L is the log length. Volume of snags was estimated from BA and stem height (ht; measured with a clinometer) using formulas adapted from Tyrell and Crow (1994). Equations for snags of decay class 1, 2 and 3, respectively, were:

$$\text{volume} = (\text{BA} \times \text{ht})0.50 \tag{4}$$

$$\text{volume} = (\text{BA} \times \text{ht})0.75 \tag{5}$$

$$\text{volume} = \text{BA} \times \text{ht} \tag{6}$$

where BA = basal area (m^2) and ht=total stem height (cm).

We used principle components analysis (PCA) to identify environmental gradients that explain the greatest variability in species composition. Before analysis, seedling and sapling relative densities were combined to create an understory data set. We used CANOCO to perform all gradient analysis (ter Braak and Šmilauer, 1998) using importance values for overstory species and relative density for understory species.

Analyses were performed on the overstory and understory data sets separately. We square-root transformed and centered the species prior to all correspondence analyses.

We used redundancy analysis (RDA), a constrained form of PCA, to determine if the environmental variables we recorded could help explain the variation in species composition. RDA was performed on the overstory and understory data sets separately. We used 19 environmental variables in the RDA consisting of slope, rock cover, aspect, and soil characteristics; soil element concentrations were log transformed for the RDA, as suggested by Palmer (1993). We used the Stepwise procedure to eliminate redundant variables and to reduce the ordination's dimensions by selecting only those environmental variables that best explain the variation in species composition. Because the significance tests of variables in the Stepwise RDA are virtually meaningless when used as an exploratory technique (Palmer, 1993), we did not choose variables based on *p* values alone. Percent sand, Eastness (Eness), Elevation, and concentrations of SO_4-S were selected as the important environmental variables for the overstory RDA; percent clay, and concentrations of B and Mg were included in the understory RDA. Continuous environmental variables were represented by vectors, whereby the length represents how well the measured variable explains variation associated with species composition. Plots were represented by points and species are shown by arrows. The proximity of a species or plot to a vector is a measure of its association with that variable.

Regression equations using DBH as the explanatory variable were derived from crown area measurements made on the 141 randomly selected *Q. stellata* trees, as described above. Total crown area (TCA) was estimated from DBH for every tree $\geq$ 3 cm DBH on our plots using PROC REG in SAS (SAS Institute 1990):

$$\log(\log(\mathrm{TCA}+1)=\log(a)+b(\mathrm{DBH}) \qquad (7)$$

where the constants *a* and *b* were estimated to be 0.21 and 0.84, respectively. We used PROC NLIN to estimate the ratio of exposed crown area (ECA) to TCA from DBH using a form of the logistic growth equation:

$$\frac{\mathrm{ECA}}{\mathrm{TCA}}=\frac{1}{1+e^{(a+b(\mathrm{DBH}))}} \qquad (8)$$

where the constants *a* and *b* were estimated to be 4.25 and -0.52, respectively. ECA was calculated by multiplying the estimated ratio by TCA; use of the logistic growth equation insured that ECA was never greater than TCA. Estimated shaded crown area was calculated by subtracting ECA from TCA. Distributions of aggregate exposed and shaded crown area by 2 cm diameter classes for each stand were created using estimates derived from the above regression equations.

We tested the fit of the negative exponential and the 3-parameter Weibull probability density functions (PDF) to diameter distributions of *Q. stellata* in each stand. The negative exponential model implies a constant reduction of stem number with each successively larger size class (Meyer and Stevenson, 1943). The PDF of the negative exponential function for random variable DBH is:

$$f(x)=\left(\frac{1}{\beta}\right)e^{-(\mathrm{DBH}-\alpha)/\beta},\ \beta>0,\ \alpha=2.5 \qquad (9)$$

where β and α are the scale and location parameters, respectively. The Weibull function is more flexible than the negative exponential and can assume a variety of shapes depending on the shape parameter, γ (Bailey and Dell, 1973). The PDF for the Weibull function is

$$f(x)=\left(\frac{\gamma}{\beta}\right)\left(\frac{\mathrm{DBH}-\alpha}{\beta}\right)^{\gamma-1} e^{-[(\mathrm{DBH}-\alpha)/\beta]^{\gamma}},\ \beta>0,\ \alpha=2.5,\ \gamma>0 \qquad (10)$$

When $\gamma > 1$, the curve is unimodal and approaches the normal distribution as $\gamma \simeq 3.6$. At $\gamma = 1$, the curve becomes the negative exponential distribution; if $\gamma < 1$, the model resembles a reverse-J shape of a steeply descending monotonic curve. In both models, the α parameter was set to the lower bound of the smallest DBH class. Parameter estimates were obtained with maximum likelihood methods using PROC NLIN in SAS (SAS Institute, 1990). The dependent variable was set to zero and the corresponding model was the square root of -2 multiplied by the log of the Weibull or negative exponential function of the random variable, DBH. This procedure causes PROC NLIN to find the parameter estimates that maximize the log-likelihood function, which is equivalent to minimizing the sum of squares error for the model. Strub (1999) used this method to find maximum likelihood estimates for mortality functions. We weighted terms in the log-likelihood corresponding to observations by the inverse of plot size using the *weight* option in PROC NLIN. Similar to methods of Zhang et al. (2001), we calculated bias of each model by the taking the difference between the observed (N_j) and predicted ($\hat{N}_j$) number of trees in each *j*th diameter class. We compared the relative fit of the negative exponential and Weibull models by examining the root mean square error (RMSE) and by performed a χ^2 goodness-of-fit test. The RMSE was calculated from the equation:

$$\mathrm{RMSE}=\sqrt{\frac{\sum_{j=1}^{m}(N_j-\hat{N}_j)^2}{m}} \qquad (11)$$

where m is the number of diameter classes. The likelihood ratio test was used to determine the goodness-of-fit for each model using $(m\text{-}q\text{-}1)$ degrees of freedom, where q represents the number of model parameters:

$$\chi^2 = -2\sum_{j=1}^{m} N_j \times \log\left(\frac{\hat{N}_j}{N_j}\right) \tag{12}$$

Results

Species composition and site characteristics

Quercus stellata and *Q. marilandica* together comprised greater than 80 percent of the overstory in each stand (Fig. 2). The Southwestern and Northeastern Slope stands were relatively steep-sloped stands with high rock content and loam soil, whereas the Bench stand was relatively level with low rock content and clay loam soil (Table 3). *Quercus stellata* had similar overstory densities in the Southwestern Slope and Bench stands (~630 trees per ha), but was only half as dense in the Northeastern Slope stand. *Quercus marilandica* had the highest density in all canopy layers in the Northeastern Slope stand, where this species occupied approximately 40 percent of the total seedling density. *Juniperus virginiana* was most dense in the Bench stand, particularly as saplings. This species existed primarily as large trees on rocky steep bluffs or terraces in the Southwestern Slope and Northeastern Slope stand. The Southwestern Slope stand had the highest tree density throughout all the canopy layers and the highest overstory BA (19.3 m^2 per ha), while the Bench stand had the lowest seedling and sapling densities. The Northeastern Slope stand contained the largest overstory trees (18.1 cm DBH), but the lowest amount of BA (17.8 m^2 per ha), likely because of the stand's relatively low overstory density (581 trees per ha). This stand also had the most number of species in each canopy layer and the highest canopy cover (67.3 percent). The Bench stand tended to have higher concentrations of soil nutrients, especially SO_4-S, Ca, Mg, and K, but had lower concentrations of P. All stands had similar concentrations of NO_3-N.

Coarse woody debris

Total coarse woody debris (CWD) volume ranged from 8.7 m^3 per ha for the Southwestern Slope stand to 1.8 m^3 per ha for the Bench stand (Table 4). Coarse woody debris was highly variable across stands, as indicated by the large standard error values. Downed wood volume constituted over 70 percent of the CWD in the Southwestern Slope and Northeastern Slope stands, but snags made up the majority of the CWD volume (61 percent) in the Bench stand. *Juniperus virginiana* occupied a relatively large portion of downed wood volume in the Southwestern Slope and Bench stands, where the species was most abundant. *Quercus stellata* and *Q. marilandica* represented the majority of the downed wood volume in the Northeastern Slope and Bench stands. Greater than 80 percent of snags in the Southwestern Slope and Bench stands were *Quercus stellata*, but the Northeastern Slope stand had a greater diversity of snag species. However, 32 percent of the oak snags in this stand could not be identified to species, and the actual proportion of post oak snags in this stand may be considerably higher. Snag density was highest in the Southwestern Slope stand and lowest in the Bench stand.

Volume of CWD was primarily distributed in decay classes 2 and 3 in each stand (Fig. 3). Stands differed in relative composition of species within decay class. *Juniperus virginiana* was most common in decay class 2 of the Southwestern Slope stand, but was more common in the first decay class in the Bench stand. *Quercus stellata* increased in abundance from decay class 1 to 3 in all stands, and *Q. marilandica* was most prevalent in decay classes 1 or 2, particularly in the Northeastern Slope stand.

Ordination analysis

The ordinations for the overstory and understory PCA were similar and only the overstory results were presented. Species found in mesic forests, such as *Q. velutina* and *Q. shumardii,* had the lowest scores along the first axis, and species that can tolerate more xeric conditions, such as *Q. stellata* and *J. virginiana*, had the highest axis one scores (Fig. 4). One exception was the location of *Q. marilandica.* Normally a xeric site species, *Q. marilandica* was positioned near the Northeastern Slope stand plots along the left side of axis one. The location of *Fraxinus americana* should be interpreted cautiously because the species was rare in all stands. The Northeastern Slope, Southwestern Slope, and Bench stand plots were clustered to the left, middle and right portions of axis 1, respectively. Species along axis two appeared to be positioned according to successional status or nutrient demands. Species known to colonize following disturbances and that can tolerate low soil nutrient conditions, such as *J. virginiana*, tended to have lower axis two scores whereas species that can persist in later successional stages and have higher nutrient demands, such as *Q. velutina*, had higher axis two scores. Axis 1 explained 49 percent of the variation in species composition and axis 2 explained an additional 30 percent (Table 5). Interpretation of a third axis was not conducted.

The RDA triplots (Figs. 5 and 6) had similar arrangements of plots and species along axis 1 as the PCA ordinations, although in reverse order for the understory RDA. Axis one appeared to be strongly associated with soil texture in both the overstory and understory ordinations. The most mesic species grew on plots with sandy soil, and species that can tolerate dryer site conditions grew on plots with clayey soils. The abundance of *Q. marilandica* in the understory did not appear to be correlated with any environmental variable in the model, but was positively correlated with an easterly aspect in the overstory RDA. Higher elevation indicated dryer site conditions in the overstory ordination.

In addition to soil texture, the first RDA axes in both ordinations were also associated with nutrient variables. The vector for SO_4-S was positioned along the right side of axis one in the overstory ordination, and the vectors for Mg and B were positioned along the left side of axis one in the understory ordination. Higher concentrations of clay tended to be associated with higher concentrations of soil nutrients. We could not clearly interpret axis 2 in either the overstory or understory ordinations. The first two axes accounted for the majority of the variation in the species-environment relationship for both ordinations (Table 5).

Crown area distribution

None of the stands exhibited uniform aggregate crown area distributions by diameter class for *Q. stellata* (Fig. 7), but distributions were generally bimodal in shape. All stands had increasing total crown area from size class 3 to 9 cm, and appeared to have relatively low crown area in the mid-size classes (19-23 cm DBH). In the Southwestern Slope and Bench stands, total crown area was highest for large saplings and small overstory trees (7-15 DBH), respectively. However, total crown area was highest for large overstory trees (>29 cm DBH) in the Northeastern Slope stand. Shaded crown area generally decreased from the smallest to the largest size classes in all stands. The majority of crown area occupied by small saplings were shaded, but trees greater than 17 cm DBH generally had fully exposed crowns.

Diameter distribution models

The Weibull distribution provided a better fit than the negative exponential model to the diameter distribution of *Q. stellata* for all stands, according to the χ^2 tests (Table 6). The Northeastern Slope stand had the best fit to both models, and the Weibull distribution provided only a slight improvement over the negative exponential in this stand. Neither the Weibull nor the negative exponential models, however, adequately fit the diameter distributions of the Southwestern Slope and Bench stands, as indicated by the relatively low *p* values. The estimated shape parameters of the Weibull models were greater than 1 for all stands (Fig. 8), indicative of a unimodal shaped curve; the Bench stand had the most unimodal shaped diameter distributions (γ=1.4). All stands had increasing densities in the smallest size classes, and the greatest decrease in density in the small and mid-size overstory tree size classes (9-20 cm DBH); there were plateaus in the mid-size classes (19-25 cm), particularly in the Southwestern Slope and Bench stands. The negative exponential model tended to overestimate small saplings (< 7 cm DBH) and underestimate large saplings and small overstory trees (7-15 cm), particularly for the Southwestern Slope and Bench stands. Both models tended to overestimate the density of mid-size trees.

Discussion

Differences in species composition across a topo-edaphic gradient

A moisture gradient was the primary factor controlling changes in species composition, stand density and basal area among stands. Due to the xeric site conditions of upland forests in the Cross Timbers, the moisture gradient was relatively weak and was primarily a function of soil texture and aspect. The ordinations revealed that available soil moisture was probably highest in the Northeastern Slope stand and lowest in the Bench stand. Soil nutrient characteristics also appeared to be an important factor in controlling species composition. Our results are supported by a previous study at the KAFP that found species composition was largely controlled by moisture and nutrient gradients (Roe 1998). Nutrient concentrations appeared to be particularly important in controlling the abundance of *Q. marilandica*. The low concentration of nutrients in the Northeastern Slope stand, particularly SO_4-S and B may have favored *Q. marilandica*'s dominance, as this species has been shown to perform better than *Q. stellata* under low soil fertility (Johnson and Risser, 1972; Klahr, 1989). Roe (1998) also found that the abundance of Q. marilandica was higher in nutrient poor stands. However, the relatively high presence of *Q. marilandica* in this stand may also be related to unknown disturbance factors; this species colonizes after disturbance, but is usually replaced by the longer-lived *Q. stellata* (Kroh and Nisbet, 1983).

Similar to other studies in the Cross Timbers, all stands were dominated by two species adapted to dry site conditions, with *Q. stellata* decreasing in importance with slight increases of available soil moisture (Rice and Penfound, 1959; Risser and Rice, 1971a, 1971b; Johnson and Risser, 1972; Dooley and Collins, 1984; Roe 1998). Our stands, however, had a higher occurrence of *J. virginiana* than would be expected, given previous reports of none or very few overstory individuals in other cross timber forests (Rice and Penfound, 1959; Kroh and Nisbet, 1983; Rossen, 1994). The unique topography of the study site probably lends to the persistence of relatively large, old *J.*

virginiana, particularly in the Southwestern Slope stand. Microhabitats of steep, rocky bluffs allow for longevity and possible escape from fire (Therrell and Stahle, 1998; Larson et al., 2000).

Although the portion of overstory growing space occupied by *J. virginiana* is relatively small, this species may be increasing in abundance, particularly in the Bench stand. This putative change in species composition cannot be attributed to lack of disturbance, as the occurrence of fire at the KAFP has increased slightly over the past century (Clark, 2003). These findings are contrary to previous studies that found cedar invasion was directly related to recent fire suppression practices (Ormsbee et al., 1976; Rollins, 1985; McPherson et al., 1988; Fralish et al. 1991; Engle et al., 1996). We speculate that the increasing abundance of this species throughout the sapling layer of the Bench stand may be due to the increasing seed available from surrounding fields and prairies currently being invaded by this species (Bragg and Hulbert, 1976; Engle et al., 1996). Additionally, the relatively open site conditions and the decreased available soil moisture in this stand would favor establishment and competitive ability of this species in this stand, compared to oak species (Ormsbee et al., 1976; Wittwer, 1985; Oswald et al., 1996).

Soil water availability was also a factor in changes in tree density across stands. Other studies have shown that xeric sites tend to have more oak regeneration than mesic sites, due to increased light availability (Carvell and Tryon, 1961; Johnson, 1993). This explains the higher abundance of oak seedlings and saplings in the Southwestern Slope stand, when compared to the Northeastern Slope stand, but does not explain the relatively low amount of oak regeneration in the Bench stand. We speculate that the Bench stand's low available soil moisture limits regeneration of even xeric oak species.

Due to the relatively high oak densities in the understory, successional replacement of overstory oak species does not appear to be occurring, even in the most mesic Northeastern Slope stand. Oak species replacement by more shade tolerant species has occurred in many eastern hardwood forests, (Adams and Anderson, 1980; Beck and Hooper, 1986; Lorimer et al., 1994) and is primarily attributed to changes in the disturbance regime (Crow, 1988; Abrams and Nowacki, 1992; Abrams, 1998). The KAFP forest and possibly many other forests in the Cross Timbers may thus represent unique ecosystems in which oaks dominate and are not successional to other species. Cross timber's forests are likely so limited by water that non-oak hardwood species can not become dominant competitors. However, *Juniperus virginiana* may become a more important component of the forests at the KAFP partially due to the apparent seed rain from surrounding sites (Engle et al. 1996).

Coarse woody debris

The amount of CWD found in these stands was low compared to more mesic forests of eastern North America (Tyrell and Crow, 1994; Spetich et al., 1999). Our highest estimates of CWD were only 11 percent of estimates found in midwestern old-growth stands (Spetich et al., 1999), and approximately half of the total volume found on xeric hardwood sites in Massachusetts (Orwig et al., 2001). Recent fires in the area would have dramatically reduced the total volume of CWD, including both snags and ground material (Mike Palmer, pers, comm.). Unfortunately, comparison of CWD volumes in this study to other Cross Timbers sites is difficult due to the limited information available. We can speculate, however, that the small stature of the forests would likely result in an initially low dead biomass component compared to other eastern hardwood forests. Additionally, the frequent occurrence of fire in these forests (Hoagland et al., 1999; Clark, 2003) would maintain relatively low volumes of CWD.

Like previous studies, the majority of the CWD volume was in the intermediate decay classes and in downed wood, as opposed to snags (Harmon et al., 1986; Spetich et al., 1999). Decay class distributions indicate that the relatively high *J. virginiana* component in Bench stand is a relatively new phenomenon. The species occupied a relatively large proportion of the stand's CWD volume, particularly of the least decayed class. Due to *Juniperus virginiana*'s resistant to rot and decay, this species was overrepresented in CWD volume relative to its canopy density of the Southwestern Slope stand. Additionally, the relatively high CWD volume total in this stand was due to the abundance of *J. virginiana* CWD. Coarse woody debris increasesd from the most xeric to mesic sites, partially due to increased site productivity (Huston, 1996; Spetich et al., 1999), and due to the decreased occurrence of fire in the Northeastern Slope stand (Clark, 2003).

Stand structure and stability

These stands did not conform to traditional models of balanced all-aged structure according to the aggregate crown area and diameter distribution for *Q. stellata*. The primary deviation was in the reduced crown area or density occupied by small saplings and overstory trees. The equal area hypothesis did not apply to these stands even when examining the less stringent criteria of equal growing space allocation using total crown area. One would expect exposed crown area to be reduced in smaller trees because crown expansion of larger trees already present in or bordering canopy gaps at the time of gap formation, but total crown area has been shown to be approximately equal among cohorts in old-growth northern hardwood stands (Goodburn and Lorimer, 1999). The equal area hypothesis has been largely tested on shade tolerant species (Smith, 1986; Goodburn and Lorimer, 1999), and may not apply to shade intolerant species like oak. Our results do offer some support, however, to a study conducted in shade-intolerant ponderosa pine stands that found less growing space was occupied by younger cohorts (O'Hara, 1996).

The diameter distributions of the Southwestern Slope and Bench stands had significant deviations from the negative exponential model. The Weibull distribution offered a better fit to the diameter distributions, compared to the negative exponential, largely because the Weibull could account for the peak in density at the large sapling size classes. However, the Weibull distribution was still inadequate in characterizing the population structure, particularly for the Southwestern Slope stand. Neither the negative exponential nor the Weibull models could account for the rotated sigmoid form of the diameter distributions; except for the relatively low density of small saplings, all stands show terraces in the mid-diameter classes (20-32 cm) and increased slopes in the upper diameter classes ($\geq$ 32 cm). The theory of the rotated sigmoid model implies that mid-diameter trees have lower mortality rates because they have obtained canopy status, whereas larger diameter trees have higher mortality rates because they have reached senescence (Goff and West, 1975; Leak, 1996). The statistical modeling capabilities are somewhat limiting, but the distributions would likely be best fit by a mixture of two component Weibull distributions (Zhang et al., 2001; Liu et al., 2002).

Despite the relatively low abundance of saplings, we speculate that these stands are sustaining current populations of oak species. Regeneration is clearly not lacking in these stands, as evidenced by the high seedling densities (~2,400 to 8,000 stems per ha), and recruitment into the sapling size class is episodic and dependent on periodic disturbances, such as fire (Johnson, 1993). Previous researchers have described this as a bottleneck effect, whereby oak seedlings have difficulty recruiting to the sapling layer unless the overstory is disturbed (Harcombe and Marks, 1978; Johnson, 1993; Goebel and Hix, 1996; Russell and Fowler, 1999). However, our hypothesis of stand stability in this forest cannot truly be tested without long-term mortality and ingrowth data.

Stand structure at the KAFP clearly differed from traditional models of equilibrium that have been developed in mesic forests on shade tolerant species that typically require relatively low levels of disturbance for their maintenance (Meyer and Stevenson, 1943). Additionally, model inference has generally been used to infer sustainable harvest of all-aged forests for timber production (Leak, 1996; Goodburn and Lorimer, 1999). Our results suggest that traditional models may be inadequate in characterizing oak species, and extrapolation of traditional models, like the negative exponential, in determining sustainability of non-commodity objectives, such as preservation or restoration, may not be warranted. We feel that these results will provide land managers with important information on restoration or preservation of natural stand structure of old-growth oak forests, particularly those of the Cross Timbers.

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Table 1. Criteria for determining decay class of course woody debris (CWD); adapted from Spetich et al. (1999)

Type of CWD	Decay Class		
Snags	1	2	3
Branches/Crown	Twigs present	Large branches present	Absent
Bark	Tight	Loose or absent	Absent
Bole	Recently dead	Standing decayed	Heavy decay
Ground	1	2	3
Bark	Intact	Trace to absent	Absent
Twigs ≥ 3cm	Present	Absent	Absent
Texture	Intact	Hard	Soft/powdery
Portion on ground	Log elevated at support points	Log near or on ground	All on ground

Table 2. Species abbreviations used in subsequent figures.

Species	Abbreviation
All *Quercus*	QU
Q. stellata	QUST
Q. marilandica	QUMA
Q. shumardii	QUSH
Q. velutina	QUVE
Q. muehlenbergii	QUMU
Carya texana	CATE
Juniperus virginiana	JUVI
Fraxinus americana	FRAM
Rhus copallinum	RHCO
Vaccinium arboreum	VAAR
Bumelia lanuginosa	BULA
Prunus mexicana	PRME

Table 3. Mean values for various stand characteristics with associated standard error.

	Southwestern Slope	Northeastern Slope	Bench
Overstory density (trees per ha)	817.8 (59.7)	581.4 (21.9)	792.2 (82.4)
Sapling density	2205.4 (295.7)	1933.6 (306.8)	1575.3 (217.0)
Seedling density	12726 (1811.4)	12380.15 (1240.3)	5786.47 (2725.8)
Overstory BA (m^2 per ha)	19.32 (0.4)	17.76 (0.5)	18.05 (0.7)
Overstory mean DBH (cm)	15.9 (0.4)	18.1 (0.4)	16.0 (0.7)
Percent rock cover	35.5 (11.6)	42.0 (4.5)	7.3 (2.6)
Percent slope (degrees)	17.0 (1.6)	19.7 (2.1)	5.5 (1.3)
Aspect (azimuths)	240.6 (5.3)	70.7 (4.5)	231.2 (38.4)
Percent Canopy cover	62.2 (3.7)	67.3 (1.3)	60.4 (5.6)
Elevation (m)	289.0 (8.2)	260.8 (3.3)	282.5 (3.5)
pH	5.1 (0.1)	4.8 (0.1)	5.3 (0.2)
NO_3 (kg per ha)	2.7 (0.1)	2.6 (0.1)	2.7 (0.2)
SO_4 (kg per ha)	26.2 (1.1)	24.2 (0.5)	29.3 (1.1)
Ca (kg per ha)	1706.0 (229.2)	852.9 (131.7)	2863.6 (820.1)
Mg (kg per ha)	484.7 (78.0)	271.0 (49.6)	892.4 (210.0)
P (ppm)	4.4 (0.7)	6.4 (0.4)	3.3 (1.0)
K (ppm)	91.6 (7.6)	62.1 (4.9)	123.0 (23.0)
Fe (ppm)	49.3 (2.9)	59.1 (3.9)	35.8 (3.6)
Zn (ppm)	3.3 (0.4)	3.3 (0.2)	1.7 (0.1)
B (ppm)	0.2 (0.02)	0.1 (0.01)	0.2 (0.03)
Organic matter (percent)	3.5 (0.3)	3.1 (0.1)	2.9 (0.2)
Percent Sand	43.4 (2.4)	50.3 (2.5)	29.6 (3.3)
Percent Silt	39.3 (1.2)	38.8 (1.8)	43.1 (3.5)
Percent Clay	17.3 (2.1)	10.9 (1.8)	27.3 (5.8)

Table 4. Total volume of standing and downed coarse woody debris (CWD) and distributions by species for each stand (standard error)

		Stand	
	Southwestern Slope	Northeastern Slope	Bench
Standing CWD			
Number (trees ha^{-1})	51 (13.6)	27 (9.4)	17 (4.4)
Total (m^3 ha^{-1})	2.5 (0.9)	1.1 (0.4)	1.1 (0.9)
Species (%)			
Quercus stellata	84	36	95
Q. marilandica	13	22	0
Q. velutina	0	0	0
Q. shumardii	0	0	0
Quercus-unknown species	3	32	0
Carya texana	0	0	0
Juniperus virginiana	0	10	5
Downed CWD			
Total (m^3 ha^{-1})	6.2 (4.2)	3.5 (1.1)	0.7 (0.2)

Table 4. Continued.

Species %				
	Q. stellata	11	33	54
	Q. marilandica	5	34	9
	Q. velutina	0	1	0
	Q. shumardii	0	14	0
	Quercus-unknown species	2	6	8
	Carya texana	1	7	0
	Juniperus virginiana	81	5	29
Volume of all course woody debris		8.7 (3.9)	4.6 (1.5)	1.8 (0.8)

Table 5. Eigenvalues and variance explained by the first two axis for principle components analysis (PCA) and redundancy analysis (RDA) for overstory and understory data

		Overstory		Understory	
PCA		Axis 1	Axis 2	Axis 1	Axis 2
	Eigenvalue	0.492	0.304	0.411	0.205
	Cumulative % variance explained	49.2	79.6	41.1	61.6
RDA					
	Eigenvalue	0.447	0.205	0.355	0.125
	Cumulative % variance explained by species-environment relation	60.6	88.4	64.3	86.8

Table 6. Parameter estimates, root mean square error (RMSE) and associated $\chi 2$ test of the fit of *Quercus stellata* diameter distributions to the negative exponential and Weibull probability density functions for each stand

	Negative Exponential					Weibull					
Stand	α	β	RMSE	χ^2	p	A	β	γ	RMSE	χ^2	p
Southwestern Slope	2.50	7.95	23.81	119.83	<0.0001	2.50	8.57	1.25	14.46	73.66	0.0006
Northeastern Slope	2.50	11.03	5.75	37.78	0.61	2.50	11.54	1.13	5.16	33.67	0.75
Bench	2.50	9.34	17.56	111.60	<0.0001	2.50	10.27	1.40	9.75	42.14	0.22

Figure 1. Distribution of Cross Timbers region (adapted from Küchler, 1964) with approximate location of Keystone Ancient Forest Preserve and location of plots in each stand (●= Southwestern Slope stand; ■=Northeastern Slope stand; ▲=Bench stand).

Figure 2. Species density for each canopy layer in each stand. Species abbreviations are listed in Table 2.

Figure 3. Volume of coarse woody debris by decay class and species in each stand.

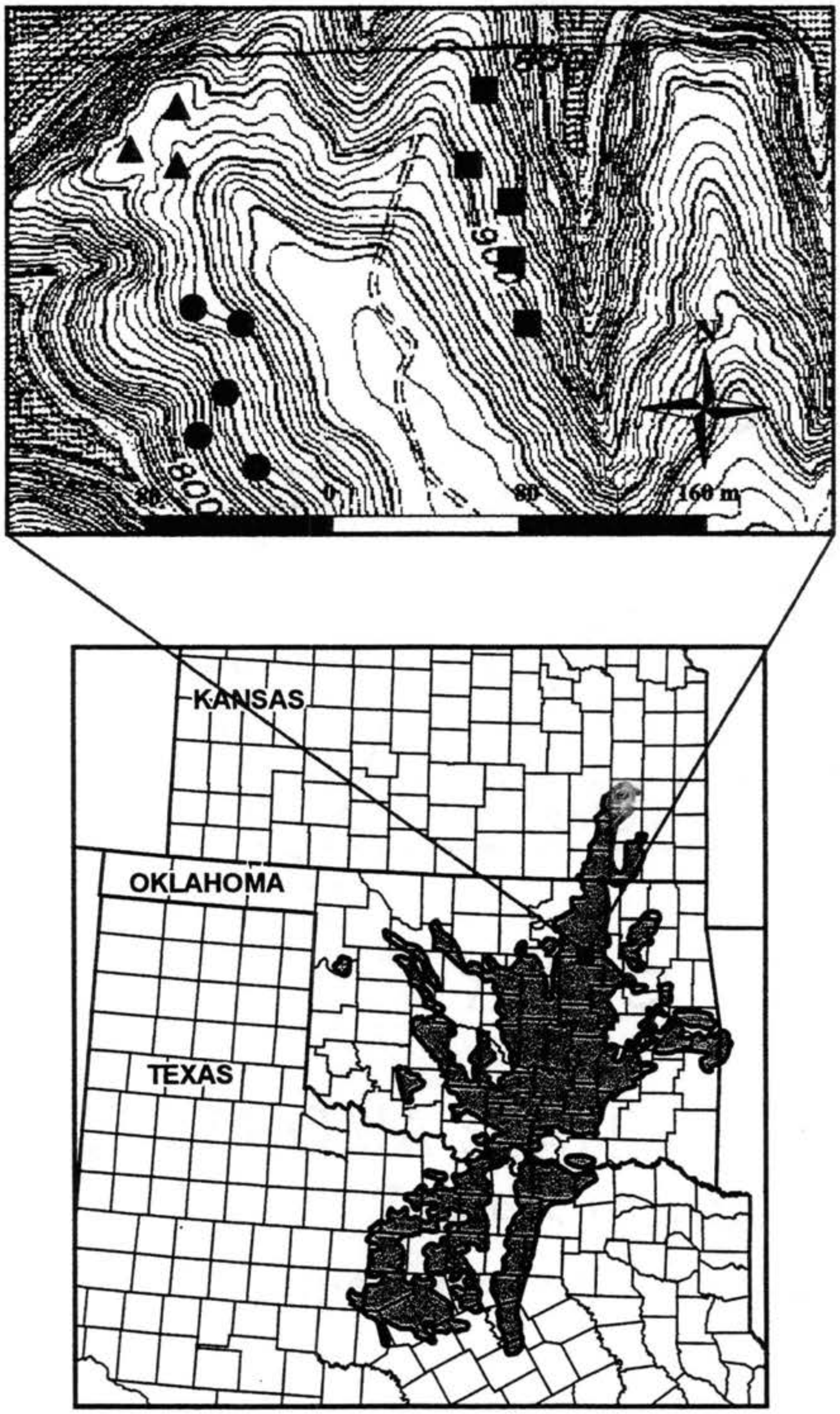
Figure 4. Principle components analysis of overstory tree species importance values in each stand. Squares, circles and triangles represent plots in the Northeastern Slope, Southwestern Slope, and Bench stands, respectively.

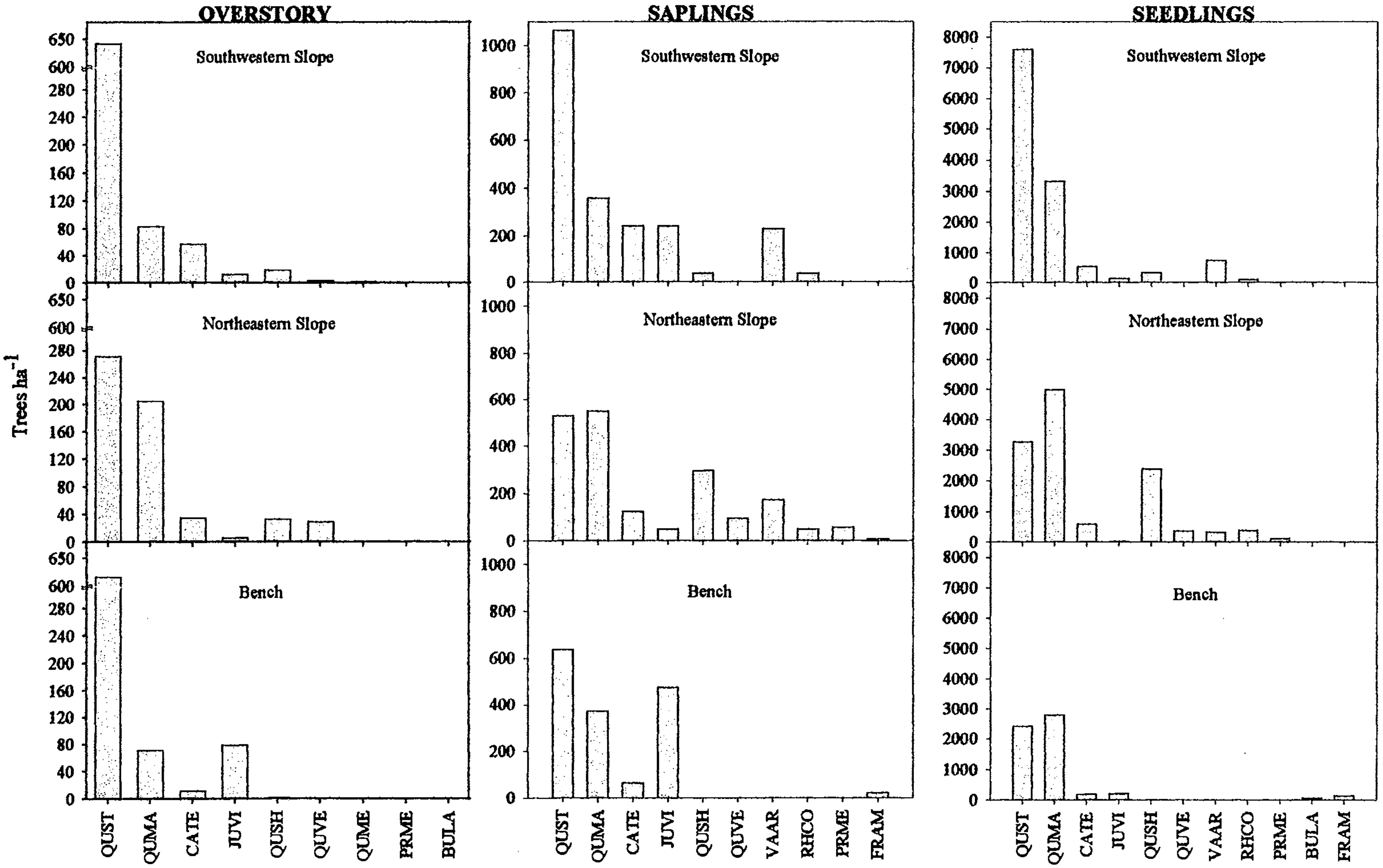
Figure 5. Redundancy analysis ordination triplot using overstory tree relative density of plots in each stand. Symbols follow those in Fig. 4.

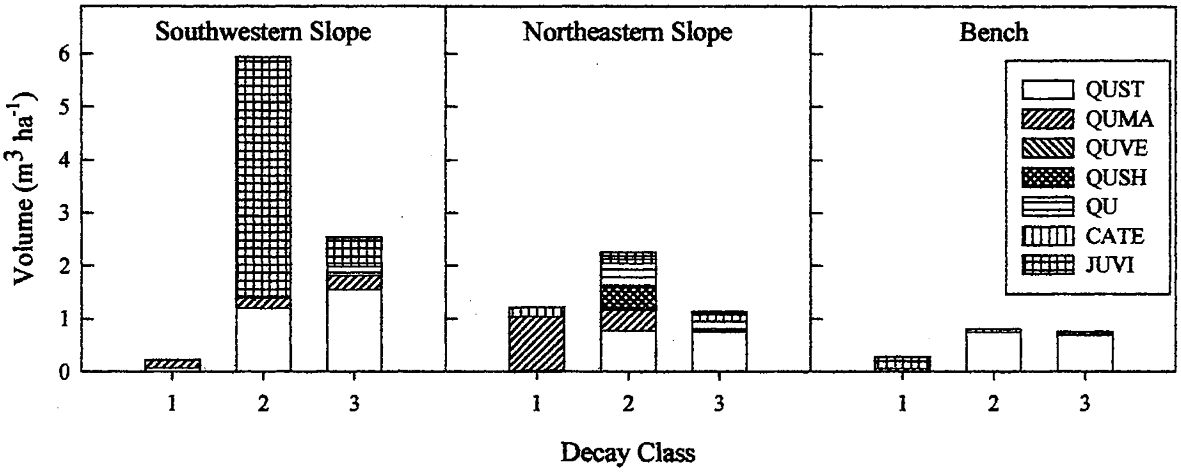
Figure 6. Redundancy analysis ordination triplot using understory tree relative density of plots in each stand. Symbols follow those in Fig. 4.

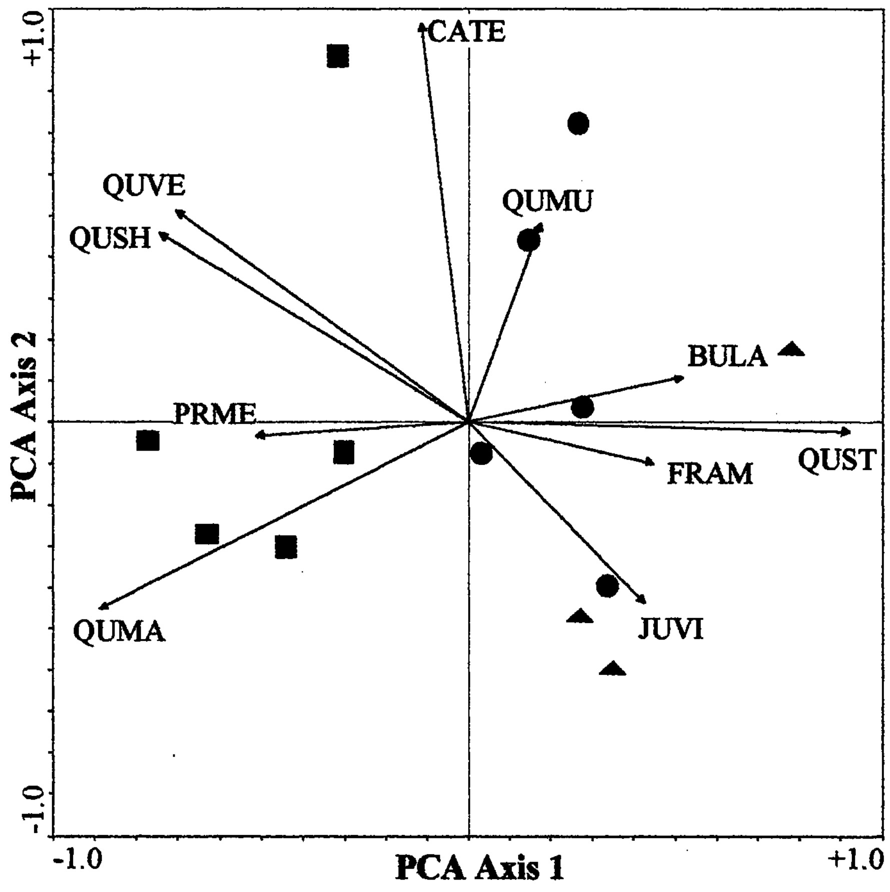
Figure 7. Aggregate exposed and shaded crown area by diameter class for each stand.

Figure 8. Diameter distributions of *Quercus stellata* and estimated densities from the negative exponential and Weibull models for each stand.

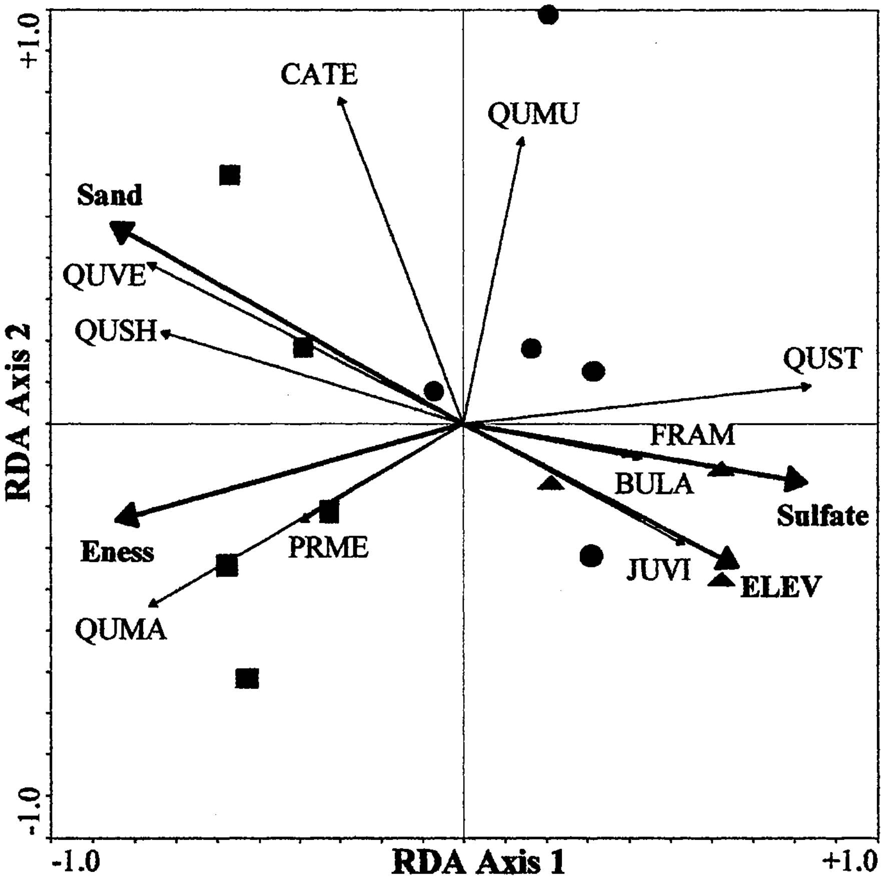

800
N
80
0
80
160 m
KANSAS
OKLAHOMA
TEXAS


OVERSTORY
SAPLINGS
SEEDLINGS
Southwestern Slope
Northeastern Slope
Bench
Trees ha-1
650
600
280
240
200
160
120
80
40
0
1000
800
600
400
200
0
8000
7000
6000
5000
4000
3000
2000
1000
0
QUST
QUMA
CATE
JUVI
QUSH
QUVE
QUME
PRME
BULA
VAAR
RHCO
FRAM

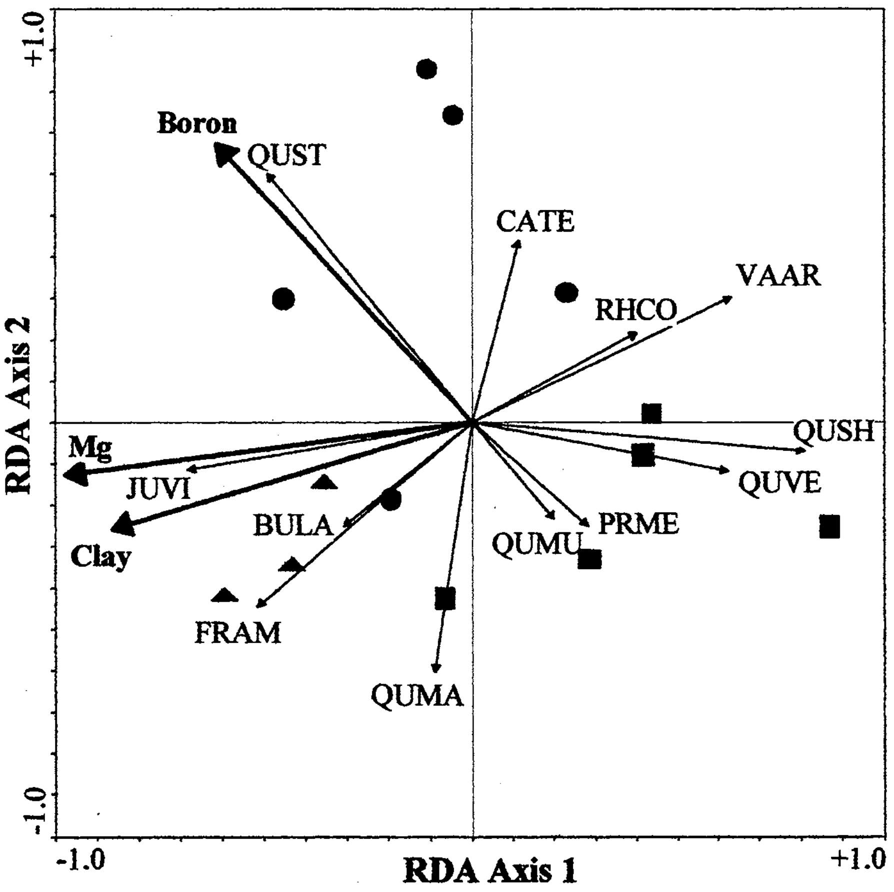

Southwestern Slope
Northeastern Slope
Bench
Volume (m3 ha-1)
0
1
2
3
4
5
6
QUST
QUMA
QUVE
QUSH
QU
CATE
JUVI
1
2
3
Decay Class



CATE
QUVE
QUSH
QUMU
BULA
PRME
QUST
FRAM
QUMA
JUVI
+1.0
-1.0
PCA Axis 2
-1.0
PCA Axis 1
+1.0



+1.0
-1.0
RDA Axis 2
-1.0
RDA Axis 1
+1.0
CATE
QUMU
Sand
QUVE
QUSH
QUST
FRAM
BULA
Sulfate
Eness
PRME
JUVI
ELEV
QUMA


RDA Axis 2
+1.0
-1.0
RDA Axis 1
-1.0
+1.0
Boron
QUST
CATE
VAAR
RHCO
QUSH
Mg
JUVI
QUVE
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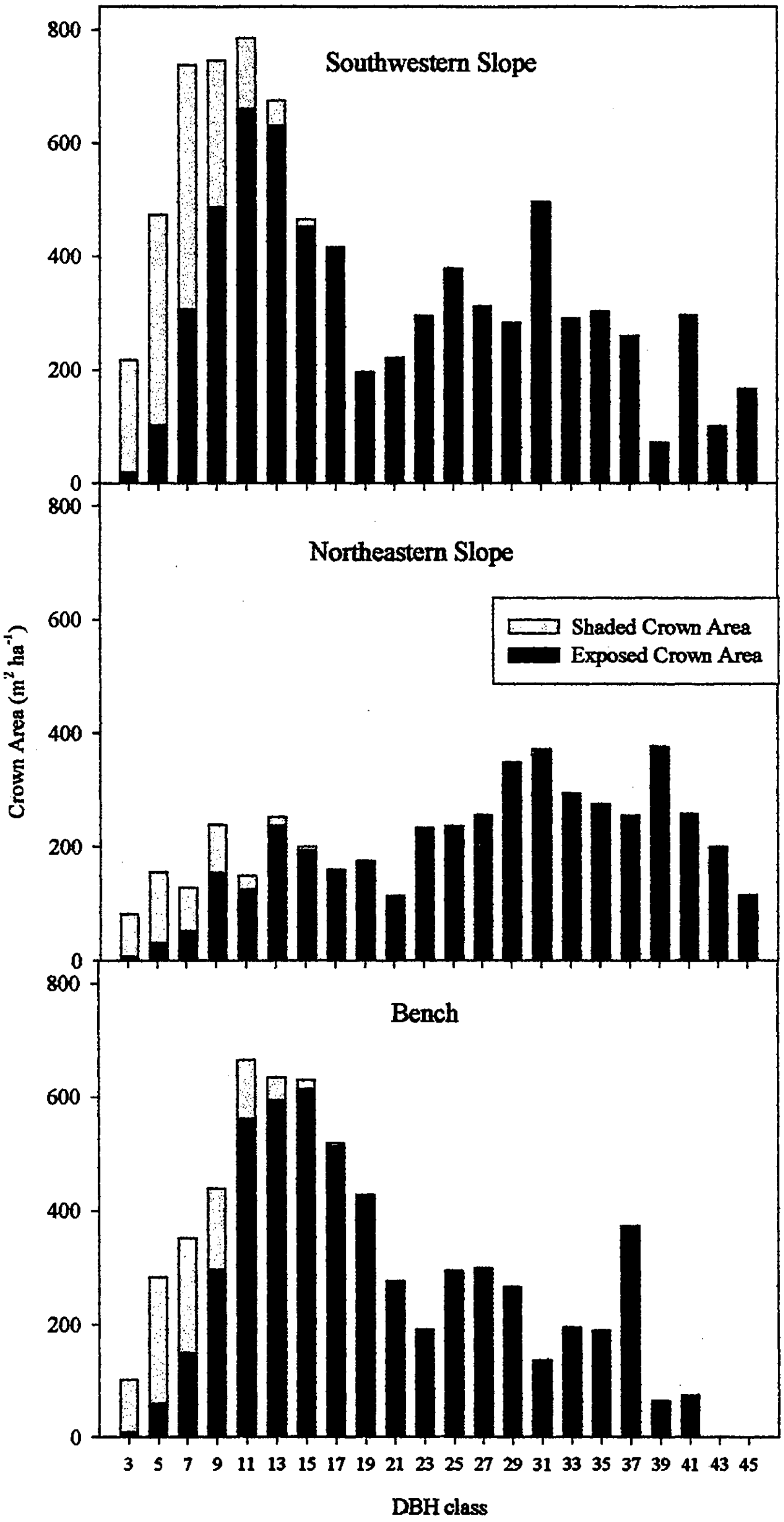
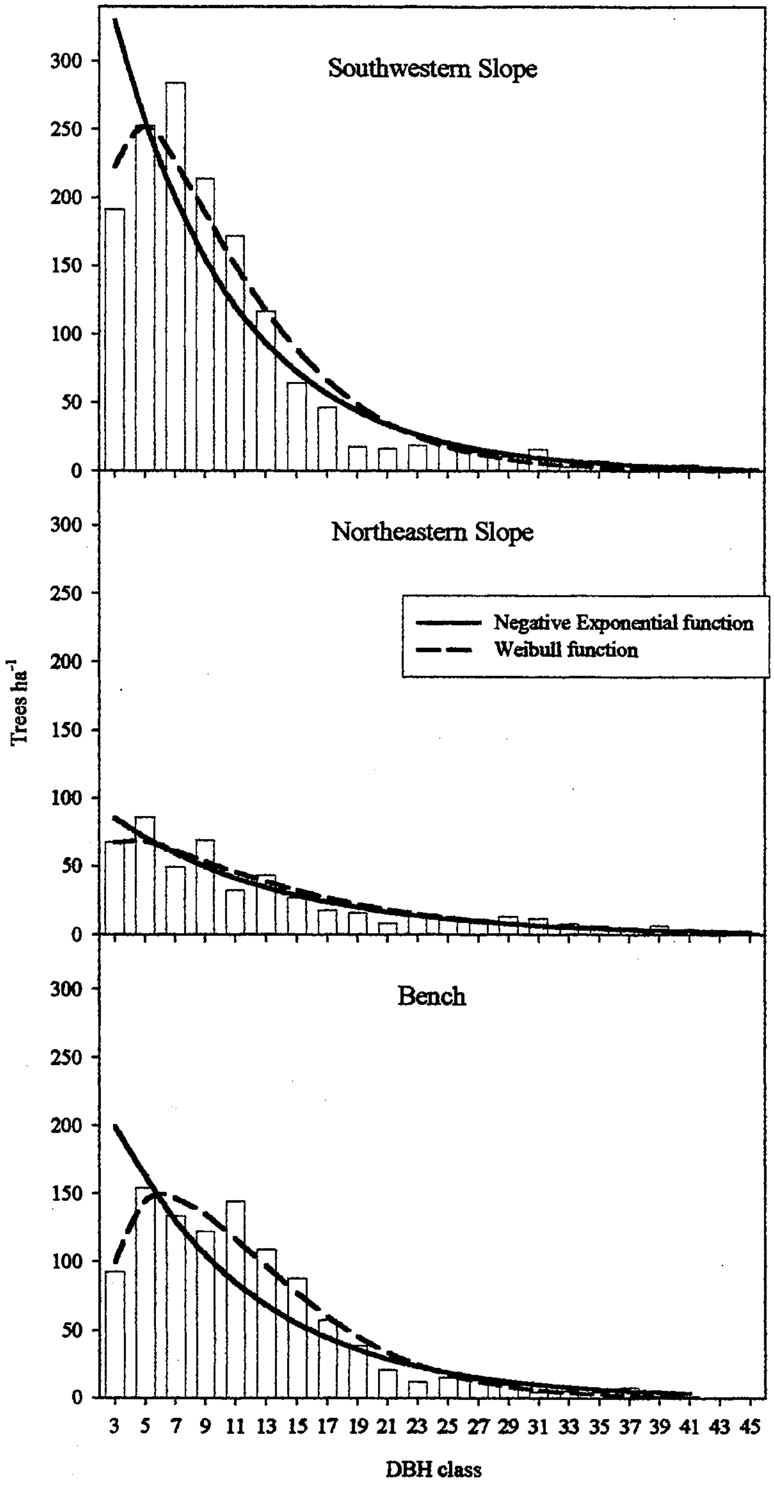
PRME
QUMU
Clay
FRAM
QUMA


Southwestern Slope
Northeastern Slope
Bench
Shaded Crown Area
Exposed Crown Area
Crown Area ($m^2\ ha^{-1}$)
0
200
400
600
800
3 5 7 9 11 13 15 17 19 21 23 25 27 29 31 33 35 37 39 41 43 45
DBH class


Southwestern Slope
Northeastern Slope
Bench
Negative Exponential function
Weibull function
Trees ha^{-1}
DBH class
0
50
100
150
200
250
300
3 5 7 9 11 13 15 17 19 21 23 25 27 29 31 33 35 37 39 41 43 45

CHAPTER THREE

DYNAMICS OF OAK (*QUERCUS MARILANDICA* AND *Q. STELLATA*) REPRODUCTION IN AN OLD-GROWTH CROSS TIMBERS FOREST

ABSTRACT

We present a case study from three topographically distinct stands in an old-growth Cross Timbers forest in north central Oklahoma. We determined the primary mode of reproduction, i.e., sprouting versus seedling, and population dynamics of small *Quercus marilandica* and *Q. stellata* reproduction ($\leq$ 1 m height) in relation to previous disturbance events and changes in site conditions. Approximately 99 percent of the reproduction were of sprout origin and most were stump sprouts (root crown diameter > 5 cm). Surprisingly, root sprouts were an important component of reproduction across stands, comprising 24 and 30 percent of stems for *Q. marilandica* and *Q. stellata*, respectively. Mode of reproduction varied by stand, with seedling sprouts (root crown diameter $\leq$ 5 cm) occurring more frequently on the most xeric site. Stem growth rates increased from xeric to mesic stands and were highest for stump sprouts. Stem longevity was similar across stands and mode of reproduction and was probably limited by low available light. Despite the relatively short life span of aboveground stems (x~6 years), tap-roots of seedling sprouts were capable of prolonged persistence

(x~20 years) through recurrent dieback and sprouting. Stem age structure indicated disturbance encouraged sprouting, as evidenced by increasing populations following fire and declining densities in the absence of perturbation. Seedling establishment for both species appeared to be episodic, as determined by age of tap-roots. Establishment by acorns probably provides a minimal input to oak populations on a yearly basis, but is an important component in the auto-accumulation of oak reproduction over time.

INTRODUCTION

The Cross Timbers is a mosaic of xeric oak woodlands with patches of savanna and prairie openings (Hoagland et al. 1999), covering approximately 4.8 million ha primarily in central Oklahoma and northern Texas (Küchler 1964). The two dominant trees, *Quercus stellata* (Wangenh.) and *Q. marilandica* (Münchh.), are generally of short-stature and low commercial value for timber production. Portions of the Cross Timbers occupy areas of relatively steep rocky terrain deemed unsuitable for most agricultural practices. Consequently, the Cross Timbers may contain some of the largest tracts of old-growth oak dominated forests in North America, (Stahle and Chaney 1994, Therrell and Stahle 1998). Unfortunately, the regeneration dynamics of oak in the Cross Timbers have not been extensively studied.

Research on oak regeneration has been largely conducted in mesic forests and has focused primarily on problems associated with oak replacement by shade tolerant species (Beck and Hooper 1986, Lorimer 1984, Tryon and Carvell 1958). In contrast, oak species in dry habitats tend to be self-replacing under their own canopy (Rebertus and Burns 1997, Ruffner and Abrams 1998), but are both encouraged and limited by factors such as drought, herbivory, and fire (Rice and Penfound 1959, Abrams 1992, Russell and Fowler 2002). Oak species in xeric habitats exhibit adaptations to these factors, such as prolific sprouting and deep rooting (Abrams 1996). Additionally, oak seedlings in dry oak forests may be able to survive longer in the understory as compared to those in mesic habitats due to higher light intensities (Carvell and Tyron 1961, Johnson 1993). However, we are not aware of studies that have specifically examined the types of reproduction and age structure of oak seedlings in the Cross Timbers. A better understanding of oak reproductive dynamics in an old-growth stand in the Cross Timbers may help managers and landowners achieve conservation and restoration goals.

Our primary objective was to examine the modes of recruitment and population structure of *Q. marilandica* and *Q. stellata* reproduction for three topographically distinct stands in an old-growth Cross Timbers forest. We also examined the ability of oak reproduction to persist in closed canopy stands and the reproduction response to past disturbances.

STUDY SITE DESCRIPTION

The study site was part of the Keystone Ancient Forest Preserve (KAFP), a nature preserve managed by The Nature Conservancy. The KAFP is located in the northern range of the Cross Timbers (Küchler 1964) approximately 32 km west of Tulsa, Oklahoma in southern Osage County at the confluence of the Cimarron and Arkansas Rivers (Fig. 1). Elevation ranges from 251 to 304 m;

topography is moderately to steeply sloping with underlying bedrock of shale and sandstone; soils are predominately sandy loam (Bourlier et al. 1979). Average annual precipitation is 101 cm and average winter and summer temperature is 3° and 26° C, respectively (Oklahoma Climatological Survey 2002).

The woody vegetation is typical of forests in the Cross Timbers region with *Quercus stellata* and *Q. marilandica* dominating the canopy; *Carya texana, Q. velutina*, *Juniperus virginiana* and *Q. shumardii* are important subordinate species (Roe 1998). The site has been characterized as old-growth due to limited evidence of past disturbances and the occurrence of *Q. stellata* trees > 300 years-old and *J. virginiana* trees > 500 years-old (Therrell and Stahle 1998).

Three separate stands were selected, based primarily on aspect and slope position. The first stand, Southwestern Slope, was approximately 11 ha and is located on the steep upper slopes with a southwestern aspect. The second stand, Northeastern Slope, was approximately 14 ha and is located on steep lower slopes with a northeastern aspect. The third stand, Bench, was approximately 5 ha in size, located on relatively level terrain just north of the main ridge top. Other studies in the Cross Timbers have indicated that soil moisture availability is the primary factor controlling species composition and site quality (Rice and Penfound 1959, Johnson and Risser 1972, Clark 2003). Previous analysis of species composition, soil composition, average tree height and DBH indicated that the Bench and Northeastern Slope stands were the most xeric and the most mesic sites, respectively, in this study (Clark 2003). The Southwestern Slope and Bench stands had the highest overstory densities and the Northeastern Slope stand had the lowest (Table 1). Canopy cover was lowest in the Bench stand and highest in the Northeastern Slope stand. Oak reproduction less than 1 m tall in the Bench stand was approximately half as dense as reproduction in the other two stands. Additionally, the Bench stand had the lowest sapling density compared to the Southwestern Slope and Northeastern Slope stand. Reproduction (trees $\leq$ 1 m in height) density across stands was nearly equally divided between *Q. stellata* and *Q. marilandica*.

Recent fire history of the KAFP

To aid in our understanding of the effects of disturbance on population structure and regeneration dynamics of oaks, we examined the results of a fire scar analysis at the KAFP (Clark 2003). A relatively widespread fire burned in each stand of the KAFP in 1994, scarring nearly 100 percent of the sample trees in the fire scar analysis. The Northeastern Slope stand experienced a relatively localized fire event in 1996, scarring a small number of sample trees in the fire scar analysis. Similarly, the Bench stand had relatively localized fire events in 1992 and 1993.

METHODS

Field sampling methods

Approximately 14 percent of reproduction (*Q. marilandica* and *Q. stellata*) less than or equal to 1 m in height were randomly selected for sampling within 12 to 20, randomly placed square 0.004 ha plots in each stand. We destructively sampled reproduction in August 2001 following budset. A total of 126 *Q. marilandica* and 122 *Q. stellata* trees were excavated or clipped at the root collar:

92, 93, and 63 from the Southwestern Slope, Northeastern Slope, and the Bench stands, respectively.

Terminology and definitions of reproduction categories

We classified mode of reproduction into four categories based on origin of the stem and laboratory analysis of age of the tap root, as described below (Fig. 2):

1. Stump sprout: the stem originated from the root collar of a live tree or from the crown of an underground root system (similar to the definition of 'grub' described by Johnson et al. (2002, p. 98). The cross sectional diameter of the parent tree's root collar or the diameter of the underground root crown was greater than 5 cm.
2. Seedling sprout: the stem originated from the root collar of a live tree or from the crown of an underground root system. The cross sectional diameter of the parent tree's root collar or the diameter of the underground root crown was less than 5 cm. The tap root was determined to be older than the corresponding stem.
3. Root sprout: the stem originated from a lateral root. The origin of the stem was more than 25 cm from the proximal end of the root.
4. Seedling: the stem originated from seed (the stem and tap root were the same age). The cross sectional diameter of the root collar was less than or equal to 5 cm.

The terminology used to describe reproduction in oak forests is often ambiguous and conflicting. We adapted the above terms and definitions from several sources and some clarification is warranted. Previous definitions of stump sprout reference a sprout originating from a parent tree that was cut

(Johnson et al. 2002, p. 98). In our definition, the status of the parent tree is unimportant. Only the diameter of the parent tree's root collar or the diameter of the underground root crown is used to differentiate between a stump or seedling sprout. The arbitrary size limit of 5 cm was chosen, in part, because the entire root system could be easily excavated. Additionally, Leffelman and Hawley (1925) explain that a sprout from a tree with root collar diameter of less than approximately 5 cm appears to be utilizing the entire root system. Contrastingly, the root system of a stump sprout may contain portions of dead and decaying material. Our definition of root sprout was consistent with previous ones (Leffelman and Hawley 1925) and should not be confused with sprouts from rhizomes, which have morphological characteristics that distinguish them from roots and stems. The terms seedling sprout and seedling were adapted from Leffelman and Hawley (1925) and the former is consistent with descriptions by Johnson et al. (2002, p.98).

Measurements and aging of stems and roots

Excavated trees were transported to a laboratory for measurement and age determination. Stem height was measured from the root collar of the stem to the top of the terminal bud. Stem age was determined for all reproduction. For seedlings with stems less than approximately 1 cm in diameter at the root collar, we counted rings on a thin cross section taken just above the stem's root collar using a dissecting microscope. The annual rings could also be counted on thicker cross sections stained with phloroglucinol using a stereo microscope.

For each seedling sprout and seedling, we determined the approximate age of the tap-root. Annual rings of trees become less distinguished as the tap-root extends deeper into the soil (Fayle 1968, Fritts 1976), therefore, root cross sections were taken within 2 cm of the root/shoot interface. If the root was relatively small in diameter, i.e., less than 1 cm, a thin cross section was cut and stained with phloroglucinol and the annual rings counted under a stereo or dissecting microscope. The majority of the roots, however, were larger than 1 cm in diameter, and their cross sections were air dried and sanded with progressively finer grades of sandpaper (100 to 400 grit). The sanded sections were examined under a stereo microscope and the annual rings were counted, similar to methods of Stout (1956). Pholorglucinol was sometimes added after sanding to more clearly distinguish the annual rings. We were unable to age roots of 2 trees in the Southwestern Slope stand due to very inconspicuous ring growth.

Descriptive statistics

Descriptive statistics were prepared separately for each species within a stand. Mean height, stem age, and growth rate (height/stem age) were calculated for all reproduction and mean root age was calculated for seedling sprouts and seedlings. Correlations were calculated between stem height and stem age for all reproduction and among root age, root diameter, stem height, and stem age for seedling sprouts and seedlings using PROC CORR in SAS (SAS Institute 1990). Frequency distributions were prepared for stem height (10 cm classes), stem age (one-year classes) and root age (five-year classes, seedling sprouts and seedlings only).

Differences in growth and age between species, stands, and sprout type should be interpreted cautiously due to small sample size and lack of statistical tests. We felt it was not appropriate to conduct statistical tests of stand effects due to the exploratory nature of the research and the lack of replication (Heffner et al. 1996, Hulbert 1984).

RESULTS AND DISCUSSION

Sprouting capabilities

Recurrent sprouting was important to the persistence of *Q. stellata* and *Q. marilandica* on these relatively dry sites. Sprouting accounted for 99 percent of the reproduction overall and seedlings did not constitute more than 3 percent of the reproduction in any stand (Table 2). Our findings were consistent with an earlier report that over 90 percent of *Q. stellata* and *Q. marilandica* reproduction in an undisturbed stand in the Missouri Ozarks was of sprout origin (Liming and Johnston 1944). The overwhelming dominance of sprouting in our study compared to lower values (<74 percent) in more mesic hardwood forests (Crow et al. 1994, Merz and Boyce 1956, Powell 1976, Ward 1966) gives some support to the hypothesis that xerophytic oak species depend more on sprouting than mesophytic oak species (Johnson et al. 2002, pp.118-121).

The most common source of reproduction was stump sprouts in the Southwestern Slope and Northeastern Slope stands and seedling sprouts in the Bench stand. Stumps may be a larger source of reproduction than roots due to a greater number of dormant buds at the root collar (Ward 1964, Wilson and Kelty 1994). Stump sprouts generally had the tallest reproduction and fastest growth rates (Table 3), likely due to their larger root area, which allows greater access to water and nutrient resources (Sander 1971). Seedling sprouts were generally less abundant, smaller and slower growing than stump and root sprouts. This finding was consistent with earlier studies that showed a positive relation between stump diameter and stem height (Lowell et al. 1987, Sander 1971).

The proportion of seedling sprouts tended to increase from the more mesic slope stands to the drier Bench stand, which may be due to reduced understory competition in the latter (Table 1). In the more mesic Northeastern Slope stand, it is possible that relatively dense understory competition favored the faster growing stump sprouts.

Sprouting from roots surprisingly constituted a relatively high proportion of reproduction across stands and species (23 to 33 percent), which may be related to the relatively high occurrence of fire and drought associated with the Cross Timbers. Roots may be more protected against heat from fire or water loss associated with drought compared to the root collar or root crown of stumps or seedlings. Root sprouting has not been regarded as an important mode of regeneration for oak species in general (Johnson 1992, Johnson et al. 2002, p. 100, Leffelman and Hawley 1925, Merz and Boyce 1956), even in dry oak forests (Liming and Johnston 1944). However, studies that have excavated seedlings to determine origin of the stem are relatively rare or often used ambiguous terminology and field methods. For example, studies in the Cross Timbers have used the terms root sprouts or root suckers to refer to the type of reproduction on their study sites (Arévalo 2002, Powell and Lowry 1980), but it remains unclear whether the origin of sprouts in these studies was actually confirmed or if the term was used to simply refer to reproduction in general. Despite the difficulties in conflicting use of terms and definitions among various studies, our findings do suggest that root sprouting may be a previously unrecognized source of reproduction in some areas of the Cross Timbers.

Reproduction persistence under closed canopy stands

Aerial portions of oak reproduction were relatively slow growing (growth rate~6.4 cm/year) and short-lived (stem age~6 years) (Table 3), supporting previous studies that found the absence of large oak stems under closed canopies (Russell and Fowler 1999, 2002, Steiner et al. 1993), especially in more mesic forests (Johnson 1992, Tryon and Carvell 1958, Ward 1966). Low light, drought, and herbivory could have contributed to the slow growth and young stem ages of reproduction (Russell and Fowler 2002). The similarity in mean and maximum ages and sizes indicated that the two species had similar responses to factors affecting stem longevity and growth across stands.

Root age of seedling sprouts and seedlings was more variable (2 to 67 years) than stem age, but was relatively similar across stands and species (Table 4). Roots could attain 30 years old in all stands, and overall mean root age was approximately 20 years. The oldest tree sampled was a 67 year-old *Q. stellata* in the Southwestern Slope stand, which had a corresponding stem age of 8 years. Our results support theories that oak stems in the shade will remain small and recurrently die back due to carbon allocation to the roots at the expense of stem growth (Abrams 1996, Johnson 1993). This strategy for persistence was manifested in the 14-year average age difference between the tap-root and corresponding stem of seedling sprouts. Root age was weakly correlated with both stem height and stem age for Q. *marilandica*, but Q. *stellata* had stronger correlations (Table 5), providing some evidence that older and putatively larger roots can provide more energy for growth and persistence to the aerial portion of the tree.

Our results give some support to theories of increased persistence of oak reproduction as site quality decreases (Carvell and Tryon 1961, Matney 1974, Johnson 1993). Root systems of oak reproduction in this study appeared to have greater longevity compared to more mesic forests (Crow et al. 1994, Johnson 1992, Merz and Boyce 1956, Ross et al. 1982, Ward 1966), which may be due to the reduced crown cover and competition from non-oak species found in these stands. However, differences in root age characteristics between this study and others (Crow et al. 1994, Johnson 1992, Merz and Boyce 1956, Ross et al 1982) may be partially related to methodology (Powell 1976). Unfortunately, previous researchers often did not explain how they aged roots beyond using magnification, but we found it difficult at best, even with sanding and staining. Therefore, age estimates of roots in this study and in others might be underestimates, as the rings in roots of woody species are less distinguished compared to the corresponding stem (Fayle 1968, Schweingruber 1996, pp. 50-51).

Population dynamics

Species had similarly shaped distributions for both size (Fig. 3) and age (Fig. 4) within a stand. The majority of oak reproduction was in the smaller size classes, as evidenced by the right-skewed or monotonically decreasing distributions. The shape of the age distributions differed from the corresponding size distributions within a species, with the majority of trees in the older age classes. Distinguishable cohorts were created following the relatively intense and widespread 1994 fire event, particularly in the Northeastern Slope and Bench stands. Additionally, the Northwestern Slope stand had a relatively small peak in reproduction immediately following the fire in 1996. Our results support earlier studies that found fire favors oak reproduction (Crow et al. 1994, Powell and Lowry 1980). The Southwestern Slope stand had bell-shaped age distributions, particularly *Q. marilandica*, with the largest peak in reproduction of both species occurring in 1997. We can not easily explain this increase in reproduction, but it may be due to unknown disturbance events, such as wind or ice damage. Reproduction did not show a response to the 1992 and 1993 fires in the Bench stand, but these fires were relatively localized and may not have affected the seedlings we sampled in this study.

The similarity in population structure between *Q. marilandica* and *Q. stellata* was not surprising, as these species commonly exist together in cross timber stands (Rice and Penfound 1959). Our results do not support previous studies that found differences in population structure and response to disturbance between red and white oak species (Powell and Lowry 1980, Tryon and Carvell 1958).

Establishment by seed varied by stand and species and appeared to be episodic (Fig. 5). None of the stands had a constant seedling input or mortality of reproduction by seed, which would have been evidenced by monotonically decreasing densities from the youngest to the oldest root age classes. The Bench stand had a peak of reproduction by seed for both species in the 1980s. The Northeastern Slope stand had maximum densities in the early 1970s, and establishment by seed has since been declining. The Southwestern Slope had similar densities across age classes, particularly for *Q. marilandica*. Except for the Southwestern Slope stand, reproduction by seed in the past decade for both species appears to be low. Both species appear to have similar longevity in the understory through recurrent sprouting, but the oldest root system was a *Q.stellata.*

Peaks of seedling establishment by seed appeared to differ by stand and species, suggesting that episodic processes varied by site and species differences in seed production. Previous studies have shown that seedling establishment and mortality is affected by fluctuations in seed production, occurrence of fire, acorn herbivory, and drought (Crow et al. 1994; Gammon et al. 1960; Russell and Fowler 1999, 2002). The high occurrence of sprouting we found suggests that yearly fluctuations in acorn production might not be important to the short-term establishment of reproduction. However, acorn production would play an important role in the auto-accumulation of these species in the understory over time (Johnson et al. 2002, pp. 121-130).

CONCLUSIONS

The KAFP represents an auto-accumulating ecosystem of oak reproduction according to this definition: "four or more cohorts of oak reproduction representing at least two decades of accumulation" (Johnson 1993). Reproduction shoot growth and population dynamics appeared to be very similar for the two major oak species and to vary only slightly among stands. Sprouting capabilities in these stands differed from regeneration processes described by Johnson et al. (2002, p. 98), due to the relatively large proportion of root sprouts. However, studies in dry oak forests of the Cross Timbers are relatively rare, and our findings may represent species adaptations to the region's frequent drought and occurrence of wildfire (Abrams 1996, Hoagland et al. 1999, Johnson 1993).

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Table 1. Density (trees/ha) of overstory (≥ 10 cm DBH), sapling (<10 cm DBH and > 1m height) and seedling (≤ 1 m height) trees and percent canopy cover of each stand (standard error) (from Clark 2003).

	Southwestern Slope Stand	Northeastern Slope Stand	Bench Stand
Overstory density	817 (59.7)	581 (21.9)	792 (82.4)
Sapling density	2205 (295.7)	1933 (306.8)	1575 (217.0)
Seedling density	12726 (1811.4)	12380 (1240.3)	5786 (2725.8)
Canopy cover	62.2 (3.7)	67.3 (1.3)	60.4 (5.6)

Table 2. Relative importance of reproduction types for *Quercus marilandica* (QUMA) and *Q. stellata* (QUST) within and across stands. Raw number of trees is in parenthesis.

	Southwestern Slope		Northeastern Slope		Bench		Across stands	
	QUMA	QUST	QUMA	QUST	QUMA	QUST	QUMA	QUST
Stump sprout	53 (16)	40 (24)	65 (41)	63 (19)	24 (8)	30 (9)	52 (66)	43 (52)
Root sprout	23 (7)	33 (20)	22 (14)	23 (7)	27 (9)	30 (9)	24 (30)	30 (36)
Seedling sprout	23 (7)	25 (15)	11 (7)	13 (4)	45 (15)	40 (12)	23 (29)	26 (31)
Seedling	0	2 (1)	2 (1)	0	3 (1)	0	1 (1)	1 (1)

Table 3. Stem height (cm), stem age (years), and growth rate (cm/year) across and within reproduction types and stands for *Quercus marilandica* (QUMA) and *Q. stellata* (QUST). Number in parenthesis corresponds to standard error.

		Southwestern Slope		Northeastern Slope		Bench		Across stands	
		QUMA (n=30)	QUST (n=60)	QUMA (n=63)	QUST (n=30)	QUMA (n=33)	QUST (n=30)	QUMA (n=126)	QUST (n=120)
Stump sprout	Height	38.8 (3.9)	37.9 (3.3)	49.4 (4.0)	49.7 (5.4)	36.1 (7.7)	35.3 (6.9)	45.2 (2.9)	41.7 (2.8)
	Age	5.7 (0.4)	5.6 (0.4)	6.0 (0.4)	6.5 (0.4)	5.5 (0.8)	6.1 (0.7)	5.9 (0.3)	6.0 (0.3)
	Growth rate	6.8 (0.5)	7.5 (0.9)	8.2 (0.6)	8.0 (0.8)	6.7 (1.1)	5.7 (0.7)	7.7 (0.4)	7.4 (0.6)
Root sprout	Height	27.9 (4.8)	31.4 (3.5)	41.9 (4.7)	37.4 (7.3)	37.3 (7.8)	36.9 (6.2)	37.2 (3.4)	33.9 (2.8)
	Age	5.6 (0.5)	6.3 (0.3)	5.4 (0.6)	5.6 (0.7)	6.2 (0.6)	6.7 (0.4)	5.7 (0.4)	6.2 (0.2)
	Growth rate	4.9 (0.6)	5.1 (0.5)	8.8 (1.3)	6.4 (0.9)	5.5 (0.8)	5.5 (0.8)	6.9 (0.7)	5.5 (0.4)
Seedling sprout	Height	33.0 (11.5)	28.4 (4.0)	34.0 (3.2)	38.1 (8.)	17.3 (3.1)	23.5 (3.8)	25.1 (3.5)	27.7 (2.7)
	Age	5.7 (0.8)	6.3 (0.3)	6.1 (0.6)	7.8 (0.3)	4.9 (0.6)	5.8 (0.7)	5.4 (0.4)	6.3 (0.3)
	Growth rate	5.3 (1.2)	4.4 (0.5)	5.9 (0.9)	4.9 (0.9)	3.5 (0.4)	4.3 (0.4)	4.5 (0.4)	4.4 (0.3)
Seedling	Height	--	41.9 (--)	13.0 (--)	--	16.5 (--)	--	14.8 (1.8)	41.9 (--)
	Age	--	9.0 (--)	2.0 (--)	--	4.0 (--)	--	3.0 (1.0)	9 (--)
	Growth rate	--	4.7 (--)	6.5 (--)	--	4.1 (--)	--	5.3 (1.2)	4.7 (--)
Across reproduction types	Height	34.9 (3.5)	33.4 (2.1)	45.5 (2.9)	45.3 (4.0)	27.3 (3.5)	31.0 (3.3)	38.2 (2.0)	35.8 (1.7)
	Age	5.7 (0.3)	6.0 (0.2)	5.8 (0.3)	6.4 (0.3)	5.4 (0.4)	6.1 (0.3)	5.7 (0.2)	6.2 (0.2)
	Growth rate	6.0 (0.4)	5.9 (0.5)	8.1 (0.5)	7.2 (0.6)	4.8 (0.4)	5.1 (0.4)	6.7 (0.3)	6.0 (0.3)

Table 4. Mean root age in years (standard error) and range of age for *Quercus marilandica* (QUMA) and *Q. stellata* (QUST) seedling sprouts and seedlings within and across stands.

	Southwestern		Northeastern					
	Slope		Slope		Bench		Across stands	
	QUMA	QUST	QUMA	QUST	QUMA	QUST	QUMA	QUST
	n=6	n=15	n=8	n=4	n=16	n=12	n=30	n=31
Mean	23.5	19.7	23.1	23.3	18.8	18.2	20.9	19.6
root age	(3.92)	(4.07)	(4.03)	(2.93)	(2.15)	(2.60)	(1.74)	(2.10)
Range	11-36	6-67	2-36	16-28	4-41	2-32	2-41	2-67

Table 5. Correlation coefficients among *Quercus marilandica* (QUMA) and *Q. stellata* (QUST) reproduction growth characteristics

	Southwestern Slope		Northeastern Slope		Bench		Across stands	
	QUMA	QUST	QUMA	QUST	QUMA	QUST	QUMA	QUST
Stem age-height	0.64[†]	0.50†	0.63[†]	0.24	0.72[†]	0.61[†]	0.64[†]	0.45[†]
Root age-stem age[a]	0.42	0.42	-0.26	0.26	-0.12	0.64[†]	0.07	0.45[†]
Root age-height[b]	0.33	0.67[†]	0.32	0.72	-0.03	0.68[†]	0.21	0.65[†]

[a] Correlations of root age with stem age were conducted on seedling sprouts only.

[b] Correlations of root age with height were conducted on seedling sprouts and seedlings only.

[†] Correlation coefficient was significantly different from zero ($p<0.05$).

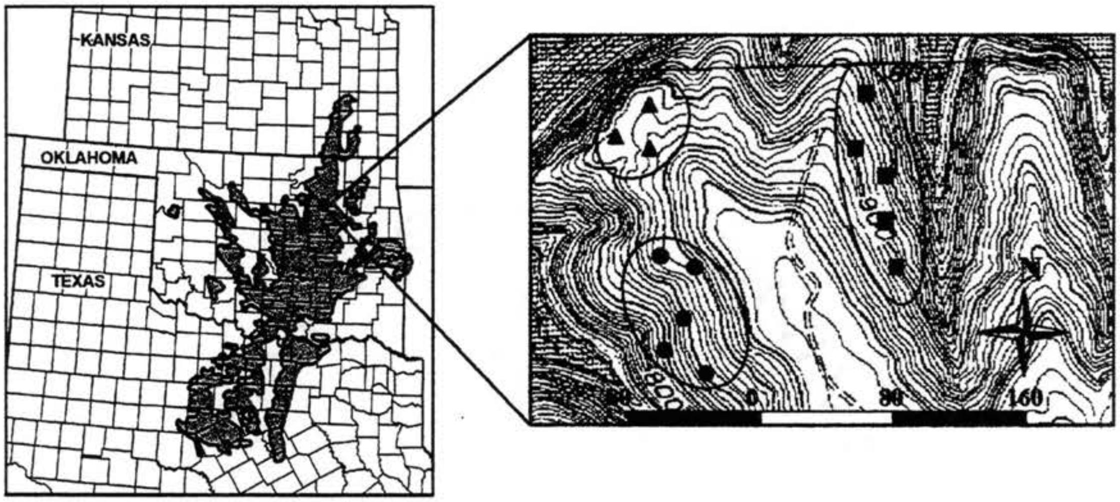
Figure 1. Cross Timbers region and location of study site and stand delineations, where circles, squares, and triangles represent plots in the Southwestern Slope, Northeastern Slope, and Bench stands, respectively.

Figure 2. Examples of root sprout (a), seedling sprout (b), and stump sprout (c).

Figure 3. Height class distributions for *Quercus marilandica* (solid line) and *Q. stellata* (dotted line) in each stand.

Figure 4. Stem age distributions for *Quercus marilandica* (solid line) and *Q. stellata* (dotted line) in each stand.

Figure 5. Establishment by seed of *Quercus marilandica* and *Q. stellata* reproduction by five-year age classes in each stand as determined by age of tap roots of seedling sprouts and seedlings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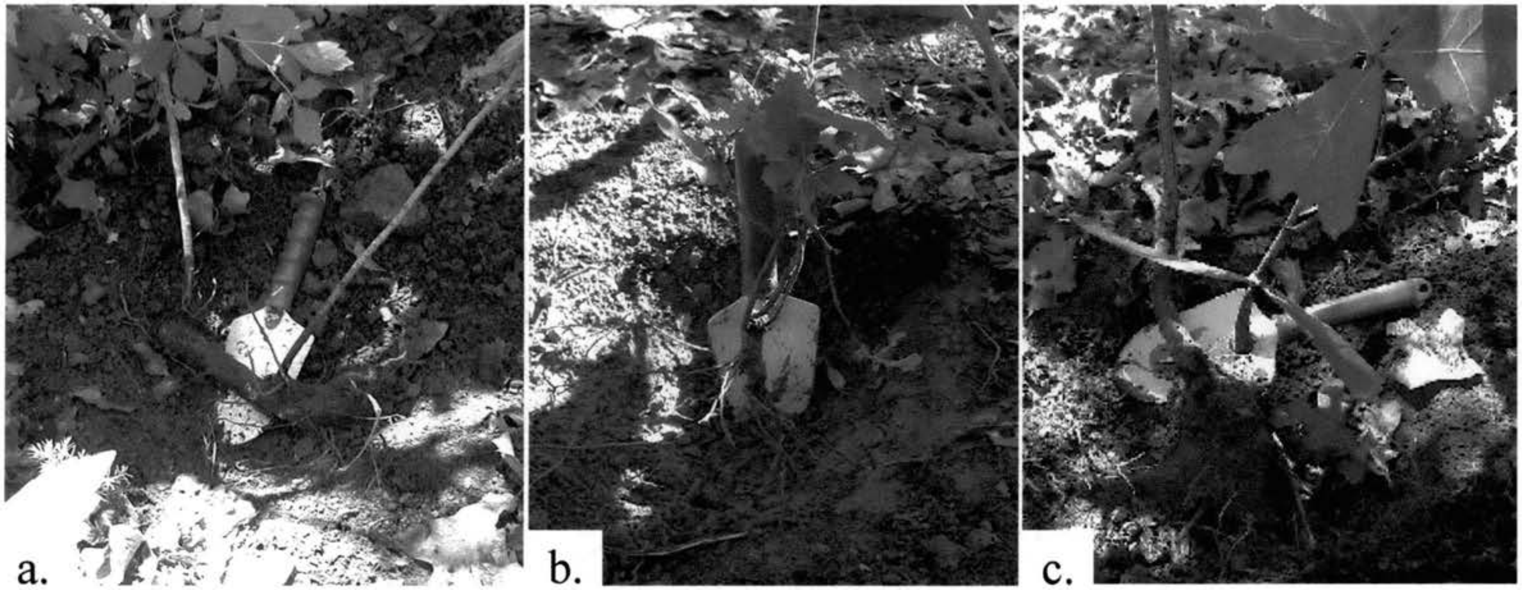

Figure 2. Clark and Hallgren

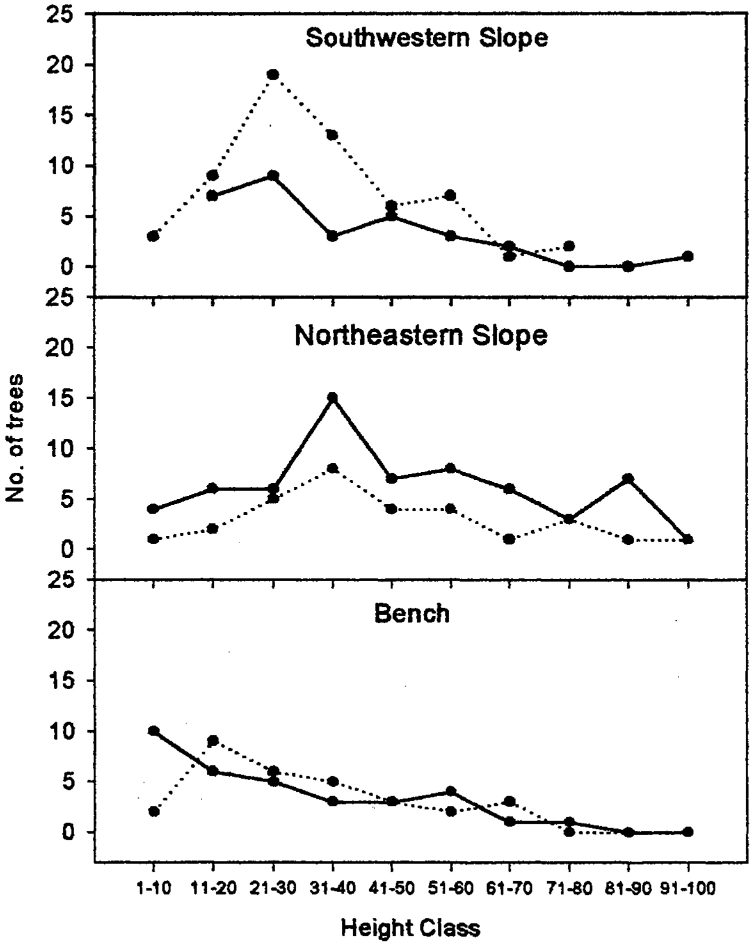

Figure 3. Clark and Hallgren.

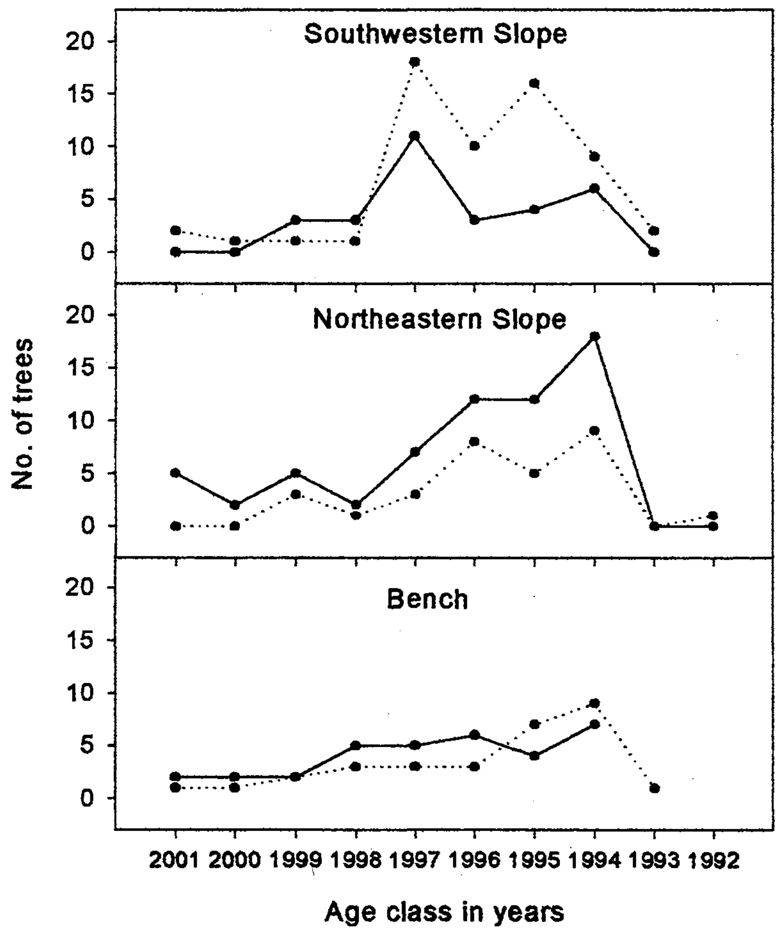

Figure 4. Clark and Hallgren

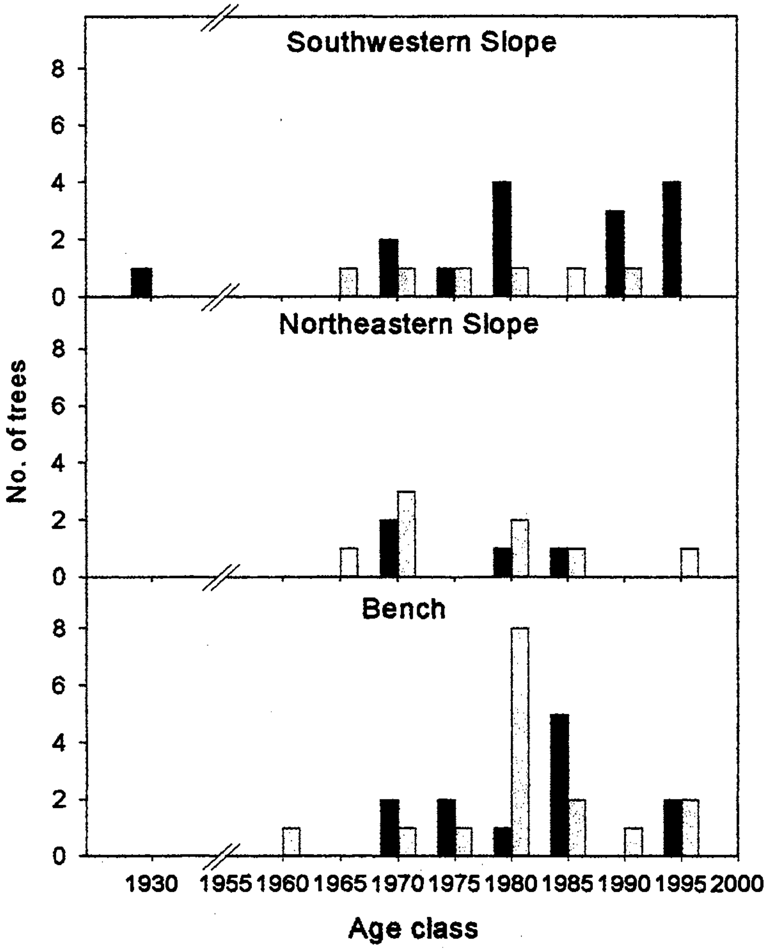

Figure 5. Clark and Hallgren

CHAPTER FOUR

AGE ESTIMATION OF *QUERCUS MARILANDICA* AND *Q. STELLATA*: APPLICATIONS FOR INTERPRETING STAND DYNAMICS

Abstract: Age determination of trees from increment cores is often difficult due to eccentric tree growth, misalignment of the increment borer, tree rot, and coring heigher than the root collar. We compared methods to correct age of cores that fail to intercept the tree's pith for two oak species, blackjack oak (*Quercus marilandica*) and post oak (*Q. stellata*), and we determined the difference in age of cores obtained at tree base versus breast height (1.4 m). Methods to correct age of off-center cores were relatively similar for both species; visual estimation of number of rings to pith was the quickest method, with an average error of less than 5 years. To correct age of rotten cores, regression using diameter at breast height (DBH) provided the lowest error (9-13 years), compared to a method that used mean ring widths to estimate age. Difference in coring height between tree base and breast height averaged 9 years for both species. Age correction for coring height may not be necessary when using 10 to 15 year recruitment classes. Researchers can accurately reconstruct age structure of oak-dominated forests using recommended methods, with the exclusion of large, rotten and putatively old trees.

Introduction

Age structure of a stand can provide important information on stand dynamics, such as disturbance events or the decline of a species (Lorimer 1980; Abrams and Orwig 1995; Russell and Fowler 2002). Tree age is usually inferred from annual rings obtained from increment cores. The primary difficulty in using increment cores to reconstruct age structure is the ability to accurately determine tree pith date. There are three primary problems encountered when determining age from increment cores: 1) the failure to reach tree pith because of misalignment of increment borer or eccentric tree growth 2) the failure to reach tree pith because the tree is rotten, and 3) coring at heights higher than the root collar.

The accuracy needed to age trees will depend on the study's objectives. Grouping recruitment dates into 5 or 10 years may be sufficient for most studies of stand dynamics, but would not be adequate for studies that require annual resolution of tree age (Villalba and Veblen 1997*a*, 1987*b*). Various geometric or graphical techniques have been developed to correct age of cores that bypass the pith because of eccentric tree growth or failure to align the borer properly (Applequist 1958; Liu 1986; Duncan 1989). These techniques are based on various assumptions, such as constant growth rates or concentric ring patterns, which may be biologically unrealistic. Villalba and Veblen (1997*a*) tested a more objective approach that involved a tracing technique to estimate the length of the missing radius to pith coupled with growth curves to estimate the number of rings in the missing radius. This method would likely provide an improvement over geometric methods or the "pith locator" of Applequist (1958) because of the increased flexibility in determining changes in ring width and patterns.

A technique used to estimate age of rotten trees involves extrapolating the mean ring widths of the rotten core to estimate the number of rings to the pith (Norton et al. 1987). Some researchers have used regression to create predictive equations of age on diameter at breast height (DBH) (Lorimer 1980; Glitzenstein et al. 1986). Both techniques have various assumptions that may contribute to errors in age estimation. Unlike the mean ring width method, regression does not consider the effect of changing growth patterns among trees. However, the method of extrapolating mean ring widths to estimate age of rotten trees assumes that the tree's pith is in the geometric center of the tree, i.e., one-half of diameter at breast height (DBH).

To determine the exact date of tree recruitment, cores should be obtained at the tree's base. Some shade tolerant species can survive for decades in the understory and cores obtained at heights higher than tree base can largely underestimate age (Niklasson 2002; Gutsell and Johnson 2002). In contrast, shade intolerant species, such as oak, are generally not able to persist as seedlings for a long time without release (Tryon and Carvell 1958; Steiner et al. 1993; Russell and Fowler 1999; Johnson et al. 2002). However, the age difference due to coring height has not been tested for oak species and may be a significant source of error depending on the objectives of the study.

We are not aware of any study that has specifically addressed problems with age correction of increment cores collected from oak species. In this study, we determine the efficiency, ease, and validity of various age correction methods and discuss applications to dendroecology research for two oak species, blackjack oak (*Quercus marilandica*) and post oak (*Q. stellata*). Applications of these results are intended to aid researchers using age structure to study stand dynamic processes of oak ecosystems. Our objectives were threefold: 1.) to test methods of age estimation for increment cores that did not intercept the pith due to eccentric tree growth or misalignment of the borer, i.e., off-center increment cores, 2.) to test methods of age estimation for cores obtained from trees that are partially rotten, and 3.) to determine age differences in cores obtained at ground level versus breast height (1.4 m).

Methods

Study area and sample collection

We sampled a 90 ha portion of the Keystone Ancient Forest Preserve (KAFP), which is located approximately 32 km west of Tulsa, Oklahoma in southern Osage County at the confluence of the Cimarron and Arkansas Rivers. The preserve lies in the northern range of the Cross Timbers (Küchler 1964) and is managed by The Nature Conservancy. The two most common species at the KAFP are blackjack and post oak. The site was previously characterized as old-growth due to limited evidence of past disturbances and the occurrence of post oak trees > 300 years-old and eastern red cedar (*Juniperus virginiana*) trees > 500 years-old (Therrel and Stahle 1998). Elevation ranged from 251 to 304 m; topography was moderately to steeply sloping with underlying bedrock of shale and sandstone.

We collected one to two increment cores or cross sectional samples from blackjack (n=72) and post oak (n=115) trees. Increment cores were collected from overstory trees (≥ 10 cm DBH) and both increment cores and cross sections were collected from saplings (≤ 9 cm DBH). We selected trees that had at least one associated core which contained pith. We measured each sample tree for diameter at breast height (DBH; mm).

Each core and cross section was sanded with progressively finer grades of sandpaper for better distinction of tree-rings. The samples were aged using standard cross-dating techniques, which provide confidence that each tree was dated to the exact calendar year (Douglass 1941; Stokes and Smiley 1996). Tree-ring widths were measured to the nearest 0.001 mm using an incrementing measuring device. We used program COFECHA, version 6.06P, to check the accuracy of cross-dating (Holmes 1983), and we determined that all trees were correctly aged.

Estimating age of off-center increment cores

We tested three methods to estimate the number of rings to pith for off-center cores: 1.) ocular estimation, 2.) a tracing technique adapted from Villalba and Veblen (1997*a*), and 3.) Duncan's technique (Duncan 1989). We selected cores from 11 blackjack oak and 17 post oak overstory trees, respectively to test these methods. Two cores were associated with each tree, one core that intercepted the pith and one (or more) that bypassed the pith. None of the cores had breaks or rot that would obscure ring boundaries.

The ocular method comprised two-stages. First, off-center cores were placed in one of the following three categories by ocular estimation: 1.) near pith, 1 to 2 rings from pith; 2.) close to pith, 3 to 5 rings from pith; and 3.) far from pith, greater than 5 rings from pith. Second, the exact number of rings to pith was estimated by eye for cores in each category. Bias was avoided by having the same individual judge all cores before the corresponding core with pith was examined.

The second and third methods differed in estimation of the missing radius to pith (MSR), defined as the distance to the chronological radius from the innermost ring boundary (Figure 1). The tracing technique was conducted by placing transparent tape on each core that bypassed the pith and tracing the innnermost 20 rings onto the tape. We transferred the tape to paper and drew curved lines to connect the arcs of the innermost rings to produce an elliptical or circular ring pattern (Figure 1). MSR was determined by averaging the shortest and longest diameters of the innermost drawn ring boundaries; measurements were made to the nearest 0.05 mm using vernier calipers.

For Duncan's technique, we estimated MSR as follows:

$$[1] \qquad \mathrm{MSR} = \frac{L^2}{8H} + \frac{H}{2},$$

where H and L were the height and length, respectively, of the innermost ring (Figure 1); measurements were made to the nearest 0.05 mm using a calibrated eyepiece micrometer on a stereo microscope.

For both the tracing technique and Duncan's technique, we estimated the number of years in MSR using 2 approaches. For the first approach, we used cumulative radial growth curves (CGC) to determine the number of rings in MSR for off-center cores. We created the CGC by averaging cumulative ring width of the innermost 30 rings using cores collected from 21 and 62 blackjack and post oak overstory trees, respectively, that contained pith. The CGC showed that growth was essentially linear from pith to the first 30 rings (Figure 2). The cores used to create CGC were not part of the sample cores used in testing methods of estimating age of off-center cores. For the second approach, we calculated mean ring widths (MRW) using the innermost 10, 20 and 40 rings for each off-center core. Three values for number of rings in MSR were thus calculated by dividing MSR by each of the three MRW.

For each method, estimated total age was calculated as the sum of the estimated number of rings in MSR and the number of visible rings on the off-center core. The methods described above yielded 9 estimates of total age for each off-center core. We examined mean absolute errors in age estimation for each method.

Estimating age of rotten cores

We tested two methods to determine the number of missing rings to pith of rotten cores. 1.) technique adapted from Norton et al. (1987) and 2.) least-squares linear regression. We selected cores from 19 blackjack and 44 post oak overstory trees that contained pith, attached bark and were unbroken to test these two methods.

For the first method, we used total core length and the geometric radius (GR) to determine the number of missing rings to pith for a rotten core. We measured total core length from the middle of pith to the outside of the bark. We located and measured four partial core lengths from the outside bark to 90, 80, 70 and 60 percent of the total core length. These four partial core lengths represent cores with 10, 20, 30 and 40 percent of the core missing due to rot. We counted the number of rings corresponding to each partial core. We calculated geometric radius by dividing DBH by 2. When a tree's growth is eccentric, GR will be different than chronological radius, as determined by location of the tree's pith (Figure 1). For each partial core length (PC), the number of missing rings to pith (NMR) was estimated using the following equation:

$$[2] \qquad \mathrm{NMR} = \frac{\mathrm{GR} - \mathrm{PC}}{\mathrm{MRW}},$$

where MRW was calculated for the innermost 10 (MRW10), 20 (MRW20) and all rings (MRWT) on the partial core. Total age was estimated by summing NMR and the number of rings on the partial core.

For the second method, we used least-squares linear regression to predict total age from tree DBH for each sample core. We developed predictive equations using data from 52 blackjack and 70 post oak increment cores and cross sections collected from overstory and sapling trees. The cores used to create predictive equations were not part of the sample cores used in testing methods of estimating age of rotten cores.

For each method, we examined mean absolute errors in age estimation, as well as mean absolute percent deviation from true age. The methods described above yielded 13 estimates of total age for each rotten core.

Age corrections for increment cores sampled at breast height

To determine age differences in cores collected at ground level versus breast height (1.4 m), we obtained 2 cores or cross sections from 39 and 34 blackjack oak and post oak saplings, respectively. One sample was obtained within 10 cm of the root collar and the other sample was obtained at breast height. Age corrections due to coring height were determined by subtracting age of cores obtained at ground level from age of cores obtained at DBH. Differences among species in estimating the number of years to add to obtain age at tree base were examined.

Results

Off-center increment cores

The various methods were relatively similar in estimating age of off-center increment cores, particularly for blackjack oak, which had less than 2 years difference in error among all methods (Figure 3). The ocular method was slightly less effective at estimating age for off-center cores for blackjack oak, but had one of the lowest error rates for post oak. The tracing methods provided slight reductions in error (4.0-4.8 years) for post oak compared to Duncan's methods (6.5-8.0 years). Although the difference in error was small among methods, the tracing method with CGC did provide one of the lowest error rates for both species. Error generally increased as the number of rings used in calculating MRW increased for both the tracing and Duncan's methods, but the difference was relatively small, i.e., $\leq$1 year. The majority of errors for post oak were overestimates of true age, while methods used on blackjack oak tended to underestimate age (Figure 4). For post oak, the percentage of overestimates tended to increase as the number of rings using in calculating MRW increased, but the opposite was true for blackjack oak.

Our *a priori* categorization of pith types, e.g., near pith, close to pith, far from pith, accurately reflected the actual number of missing rings to the pith (Table 1); the actual number of rings to pith was lowest for cores in the near pith category and highest for samples in the far from pith category. In Table 1, we show error across pith categories for two methods, ocular and the tracing method with the CGC. Error in age estimation of off-center cores generally increased as rings to pith increased. The difference in error between the two methods were least pronounced for cores in the near pith and far from pith categories. Ocular estimation was generally not as effective as the tracing method for cores in the close to pith category.

Rotten cores

Age estimation of rotten cores using regression provided the lowest error compared to the use of mean ring widths (MRW) for both species (Figure 5). All MRW methods had mean errors of at least 24 percent of the total age for both species, and had errors as high as 38 percent for post oak. Error in age estimation using MRW increased as partial core length decreased and were relatively similar among the MRW10, MRW20 or MRWT, particularly for post oak. Regression provided an approximate 16 to 43 percent decrease in error compared to the MRW methods when calculated independent of tree age and a 17 to 46 percent decrease in error calculated as mean number of years. Error rates across all methods of age estimation were higher for post oak than blackjack oak.

The chronological radius, determined from the total core length, was smaller than the geometric tree radius, calculated from DBH, in 18 out of 19 samples for blackjack oak and in 40 out of 44 samples for post oak. The discrepancy between chronological radius and geometric radius resulted in a large number of overestimates of tree age for the MRW methods; approximately 80 to 90 percent of age estimates were overestimates for both species, depending on percent of partial core used. The mean difference in chronological and geometric radius was +10.5 mm for both species, which translates into an overestimate of age from 12 to 14 years, on average, due to eccentric growth alone when using MRW10. One post oak core was 45 mm shorter than the geometric radius, resulting into an 85 to 145 year overestimate of age due solely to eccentric tree growth.

Post oak trees were older, larger, had higher standard errors in age (Table 2), but both species had similar predictability of age using regression (R^2=0.70) (Figure 6). For post oak, regression underestimated age of the largest trees (dbh>20 cm). Age estimation error had a significantly positive relationship with tree size for both species (0.60≥ R ≤0.70) (Figure 7), indicating that age of larger and putatively older trees will be more difficult to predict using DBH.

Age corrections due to coring height

Both species had approximately 9 years age difference in cores obtained at DBH vs. tree base (Table 3). Age difference in coring height could be close to 3 decades for both species. Post oak had slightly slower growth rates from seedling to breast height compared to blackjack oak.

Discussion

The ability to predict age of off-center increment cores

Our results showed that number of missing rings to pith could, on average, be accurately estimated by eye to within 5 rings of true pith, an error that is probably acceptable for most studies of stand dynamics. The use of ocular methods provides advantages over the other techniques, such as the amount of time needed to create CGC, and tracing and/or measuring missing pith. Additionally, ocular estimation may be the only choice for age estimation when cores are damaged and the use of tracing or measuring techniques is not possible. However, because ocular estimation was less accurate as distance to pith increased, we would recommend using the two-stage approach of placing cores in pith categories prior to exact age estimation. For cores in the near pith category, ocular estimation will suffice, but one of the other methods should be used for cores in categories further away from the pith. The error associated with age estimation using ocular methods will depend on the researcher's familiarity with species growth patterns and tree rings in general, and only a person that has experience in dendrochronology of the species of interest should attempt to estimate number of rings in the missing pith by ocular methods.

Duncan's technique was probably the least reliable method because it assumes concentric growth of rings in the missing radius, while the tracing technique allows more flexibility in determining ring patterns. We propose that error associated with this method will increase as the missing radius, and the possibility of tree-ring eccentricity, increases. The relatively large difference in error between the two species for this method supports this hypothesis. Post oak was larger, older, and number of years in missing pith was higher, compared to blackjack oak.

The use of CGC coupled with tracing methods has been shown to be a reliable technique for slower growing species (Villalba and Veblen 1997*a*). Growth rates remained relatively constant for the first 30 years of growth at breast height, however and CGC did not provide much of an improvement over the use of MRW in this study. The use of MRW may provide an advantage for studies that do not have a relatively large sample of trees with pith for development of the CGC.

The ability to predict age from rotten cores

Regression provided an improvement in overall error rates of age estimation of rotten cores, and it also required less data manipulation than the MRW methods. The regression method does require a relatively large number of samples that hit pith for development of the predictive equations, and this may be a problem in studies with low numbers of samples. Additionally, we would recommend using the entire range of the diameter distribution to compute the predictive equations of age vs. dbh, which may require additional sampling of the smaller diameter trees if the study is restricted to the overstory portion of the population.

The higher errors associated with the MRW methods were due to eccentric tree growth. It was surprising that the vast majority of our samples were taken on the "short" side of the tree. We speculate that because we often obtained samples on the uphill side of the tree, ring growth was suppressed due to formation of tension wood (Schweingruber 1993, p. 5). Unfortunately, in field situations, one can not detect eccentric tree growth of rotten cores, but this growth form is common in forests with high winds and unstable soil (Schweingruber 1993, p. 3-8). Our results indicate that eccentric growth may be a very large source of error in age estimation of post oak and blackjack oak trees, if one uses the MRW methods. We, therefore, recommend using regression techniques to estimate age of rotten trees for species that may be predisposed to eccentric growth because of harsh growing conditions.

Our results support other findings that show the relationship between age and DBH was more variable with larger and older trees (Harcombe and Marks 1978; Abrams and Orwig 1996; Abrams and Copenheaver 1999). Unfortunately, our sample of old, large trees that were not hollow and in which we hit pith was relatively limited. We know, however, that oak trees in excess of 300 years exist at the KAFP, and they are often relatively small, i.e., DBH<30 cm (Therrell and Stahle 1998). Errors associated with age estimation using regression will increase for the largest and oldest portion of the post oak population and age estimation will be increasingly unreliable.

Effects of coring height on interpretation of stand dynamics

By not correcting for age differences in coring height, recruitment dates of individual post and blackjack oak trees in this stand would be underestimated by close to a decade, on average. Some researchers speculate that coring at the ground level may provide a more correct interpretation of stand dynamics and disturbance processes than coring at taller heights, particularly for shade tolerant species that can persist for decades as small seedlings (Niklasson 2002; Gutsell and Johnson 2002). Coring at ground level, however, is more physically difficult in hardwoods like oak, without the use of mechanical drill bits. Additionally, it is more difficult to hit pith when coring at ground level because trees are often wider at the base than at breast height.

Researchers working in oak dominated forests often group recruitment dates by 10 or 15 year increments (Glitzenstein et al. 1986; Abrams et al. 1997, 1998), in part to avoid the error associated with aging trees at height above the root collar. Our results show that post oaks and blackjack oaks in this stand exhibited relatively short longevity at heights less than 1.4 m. Ten to 15 year grouping of recruitment dates would on average include the base age of trees and we feel would provide an adequate interpretation of population structure in relation to major disturbance events. One should be aware that stem age, even at the root collar, will not be indicative of the tree's germination date because oak regeneration is capable of multiple sprouting from the same root system (Merz and Boyce 1956; Johnson 1993; Clark 2003). However, root age is difficult to determine through dendrochronological methods (Fayle 1968; Schweingruber 1996; Clark 2003). Furthermore, stand dynamic processes inferred from population structure is probably best conducted using stem age, as stem sprouting is generally triggered by disturbance events such as fire or overstory tree death.

Conclusions

The ability to correctly determine tree age is important to researchers who use age structure to interpret stand dynamic processes, such as disturbance and climatic effects on population structure and tree-growth (*sensu* Villalba and Veblen 1997*a*). Our results will be most applicable to oaks growing on dry sites at the western extent of the eastern hardwood forests, but because many oak species share similar growth characteristics, our findings could be applied to other oak species growing in a variety of habitats. The trees at the KAFP were relatively small in diameter in comparison to oak trees growing in more mesic forest ecosystems, however, and overall error rates would likely be greater for a population of larger sized trees.

We recommend using the tracing technique with the CGC in determining number of missing rings to pith for off-center cores, but only if the trees have relatively constant growth for the first few decades from pith. Slower-growing species would likely have more variable growth patterns and the added effort required to compute MRW for each tree would probably be warranted. The regression technique provided the most reliable estimates of age for rotten trees, and involved the least amount of data manipulation and effort to apply. However, age estimates of the largest portion of the population will be unreliable with regression. This presents an interesting problem when interpreting age structure, as approximately 41 percent of post oaks greater than 20 cm DBH and 63 percent of blackjacks oak greater than 15 cm DBH were hollow at the KAFP. Additionally, for many of these larger trees, more than half of the tree's estimated geometric radius is rotten and the most recent rings are usually suppressed. Thus, age estimates using MRW would also be unreliable. For forests with a high proportion of rotten trees, researchers may have to rely more on size structure and tree-ring analysis, e.g., development of growth change chronologies (Nowacki and Abrams 1997), than on tree age structure when trying to interpret stand dynamics.

We found that age correction for coring height is probably not necessary for blackjack and post oak trees at the KAFP if grouping trees into age classes of a decade or more. Age corrections for coring height may not be necessary for many oak species, which usually exhibit shade intolerance and are incapable of prolonged persistence as small seedlings (Merz and Boyce 1956; Crow et al. 1994; Clark 2003). Furthermore, age at breast height may provide a more realistic predictor of future population growth as opposed to age at base because the shorter oak seedlings are often affected by factors such as browsing and shading (Russell and Fowler 2002).

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Table 1. Number of missing rings to pith and error in estimating total age using ocular method and tracing method with cumulative growth curves (TCGC) for each pith type (standard error).

			True	Error (years)	
Pith Type	Species	n	Rings to pith	Ocular	TCGC
Near pith	QUMA	2	0.5 (0.5)	1.5 (0.5)	1.0 (1.0)
	QUST	5	2.2 (1.6)	1.8 (1.1)	2.9 (0.7)
Close to pith	QUMA	4	9.3 (2.5)	6.3 (1.5)	3.5 (0.6)
	QUST	7	6.3 (2.6)	4.1 (1.7)	1.7 (1.3)
Far from pith	QUMA	5	11.2 (2.3)	4.4 (2.6)	3.8 (1.5)
	QUST	5	13.0 (2.1)	5.0 (1.6)	4.4 (1.2)

Table 2. Mean total tree age and diameter at breast height (DBH) of trees used in age estimation of rotten cores (standard error).

		Total tree age		DBH (cm)	
Species	n	Mean	Range	Mean	Range
QUMA	19	47.5 (2.2)	29-70	12.1 (7.3)	10-24
QUST	44	64.0 (4.7)	28-185	13.7 (6.0)	10-26

Table 3. Mean age difference due to coring at DBH vs. tree base (standard error).

Species	n	Mean	Range
QUMA	39	8.5 (1.2)	1-27
QUST	34	9.4 (1.3)	1-30

Figure 1. Cross-sectional diagram of tree with eccentric growth where the geometric (A) and chronological (B) centers differ. Diagram of off-center increment core is shown with height (H) and length (L) of innermost growth ring and sketch (dotted lines) of its ring boundary with length of missing radius (MSR).

Figure 2. Cumulative growth curve for *Quercus marilandica* (n=21) and *Q. stellata* (n=62).

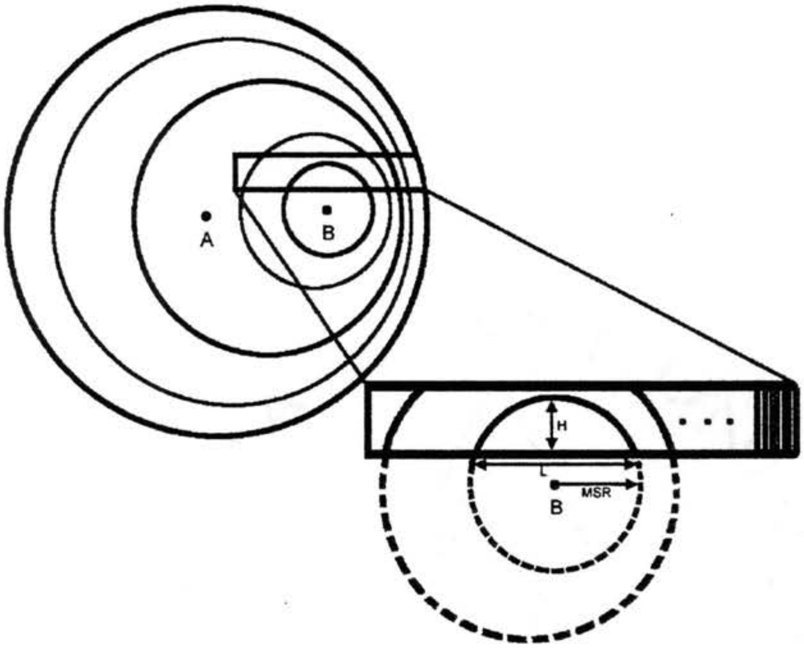
Figure 3. Mean error in estimating age with associated standard errors of various age estimation methods. Number above bar indicates number of samples used for each method. The tracing technique of Villalba and Veblen (1997*a*) with cumulative growth curves and with mean ring widths of 10, 20 and 40 innermost rings is abbreviated as TCGC, T10, T20 and T40, respectively. Duncan's (1989) method is similarly abbreviated.

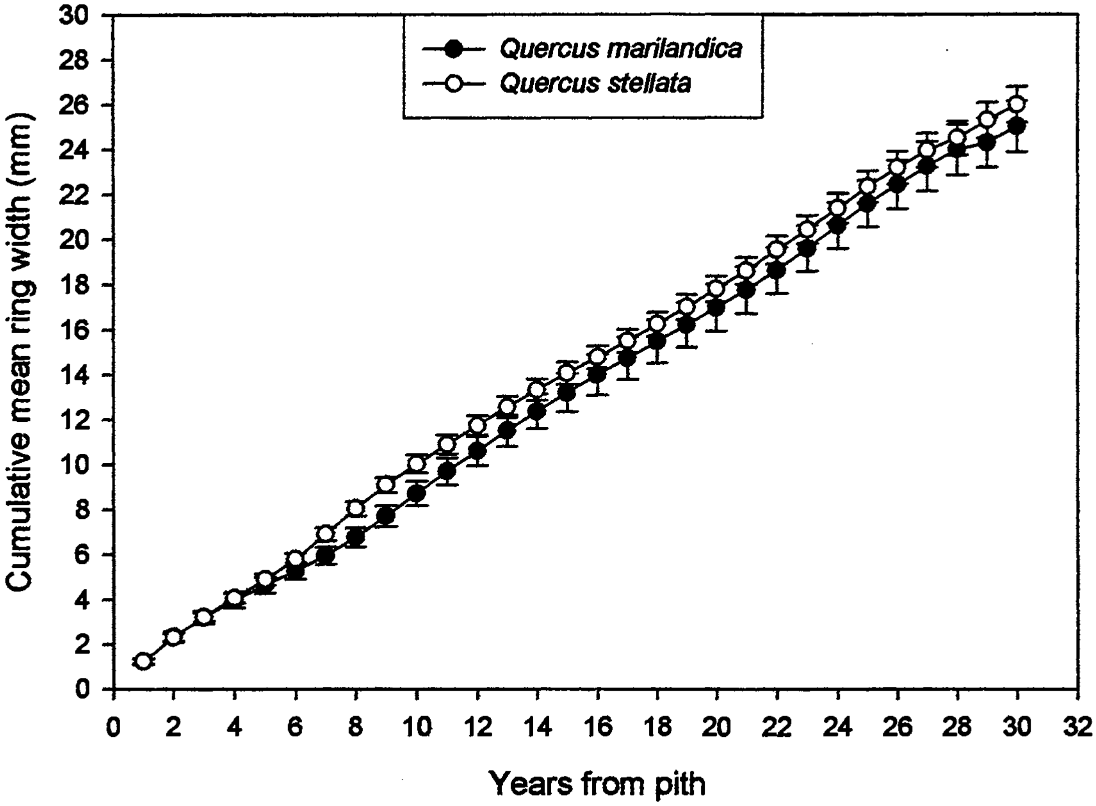
Figure 4. Percent overestimates and underestimates of true age using various age estimation methods. Abbreviations follow those in Figure 3.

Figure 5. Mean absolute percent deviation from true age for methods using regression (Reg) and mean ring widths of the innermost 10 (MRW10), 20 (MRW20) and all rings (MRWT) for each partial core length. Number above bar represents mean number of rings in age estimation error.

Figure 6. Relationship between age and diameter at breast height (DBH) and associated predictive regression line and equation for each species.

Figure 7. The relationship between mean age estimation error of rotten cores with diameter at breast height (DBH) using age predictions from regression analysis.


A
B
H
L
MSR
B


Quercus marilandica
Quercus stellata
Cumulative mean ring width (mm)
Years from pith
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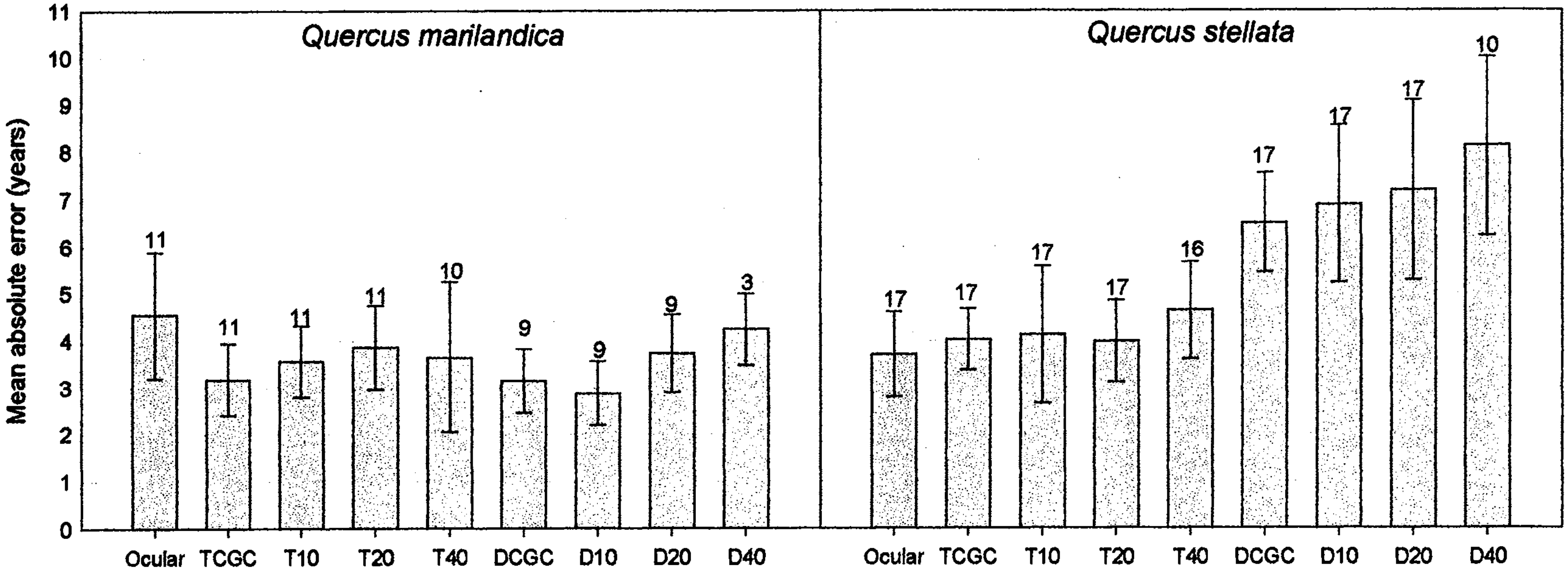
Quercus marilandica
Quercus stellata
Mean absolute error (years)
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11
11
11
10
9
9
9
3
17
17
17
17
16
17
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17
10
Ocular
TCGC
T10
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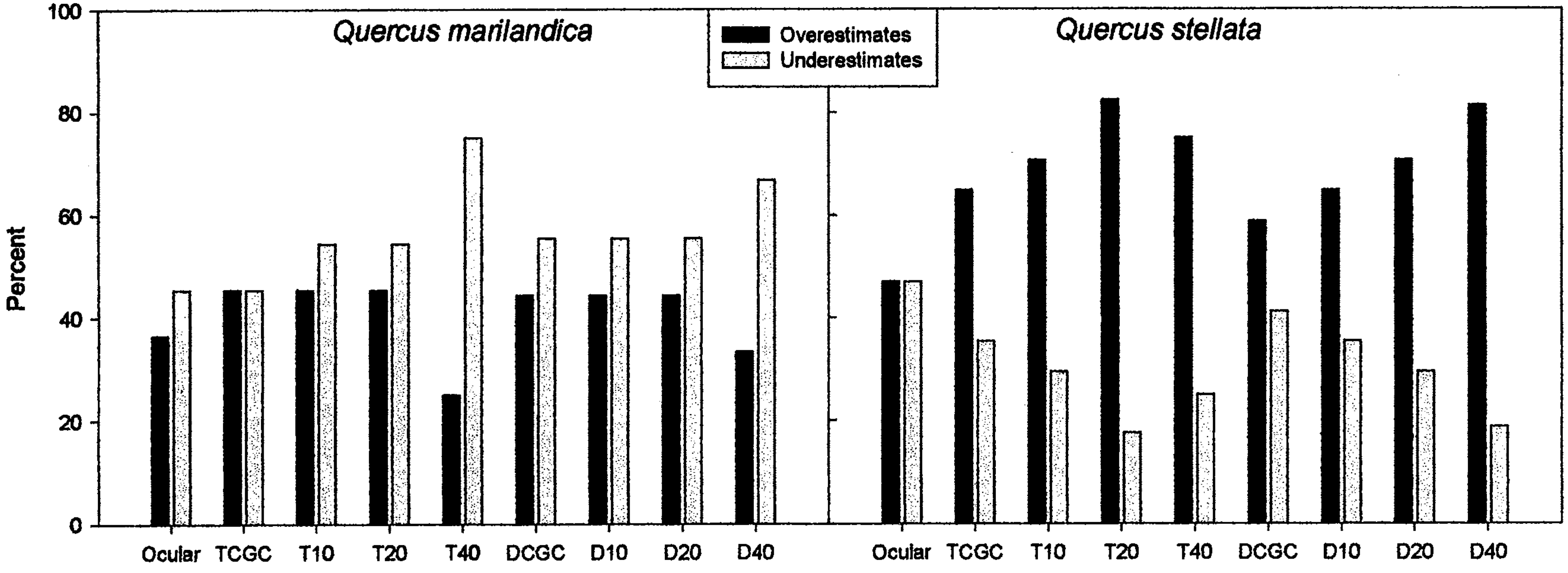
Quercus marilandica
Quercus stellata
Overestimates
Underestimates
Percent
0
20
40
60
80
100
Ocular
TCGC
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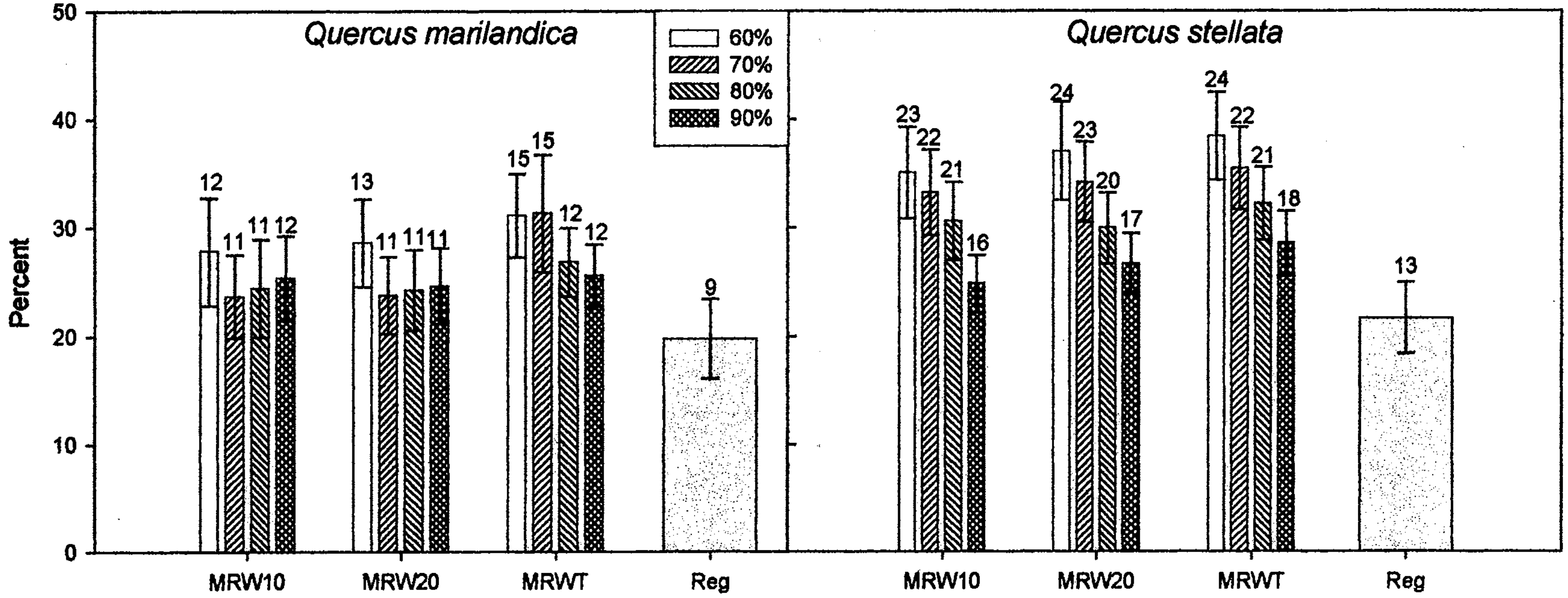
DCGC
D10
D20
D40


Quercus marilandica
Quercus stellata
□ 60%
▨ 70%
▧ 80%
▩ 90%
Percent
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10
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12
11
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16
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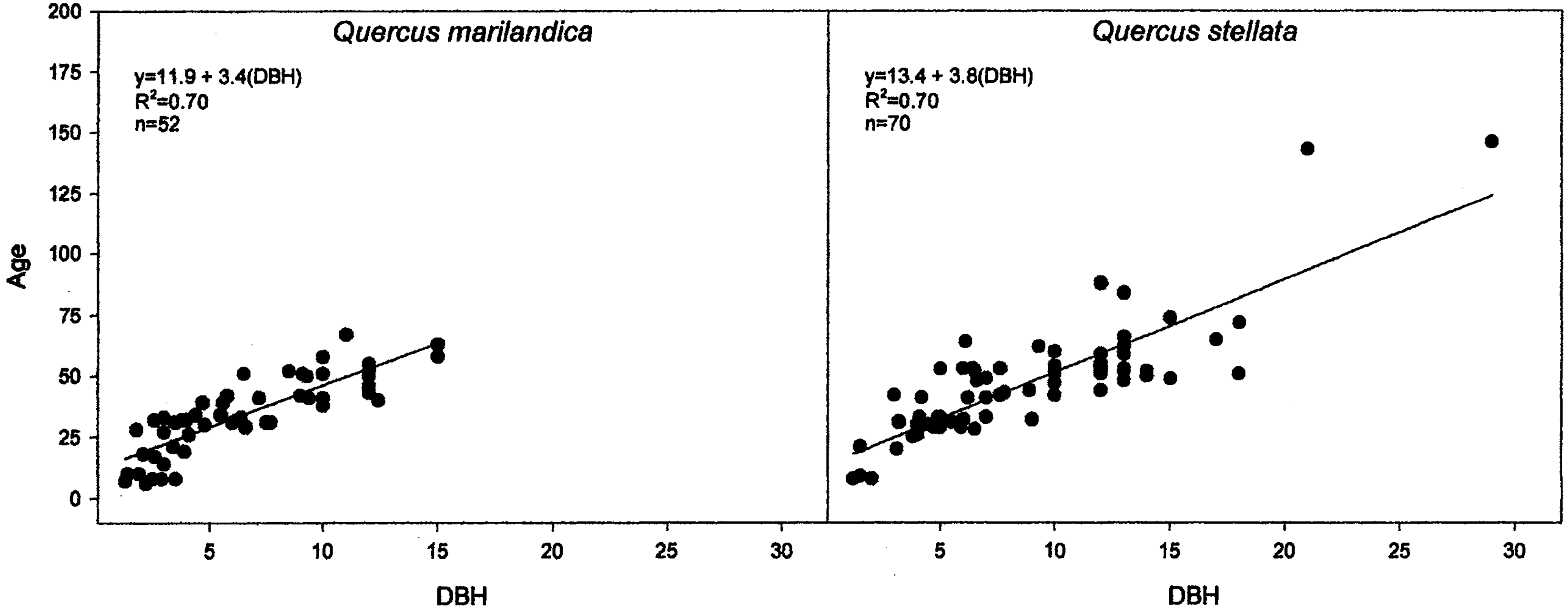
Quercus marilandica
y=11.9 + 3.4(DBH)
R^2=0.70
n=52
Quercus stellata
y=13.4 + 3.8(DBH)
R^2=0.70
n=70
Age
200
175
150
125
100
75
50
25
0
5
10
15
20
25
30
DBH
5
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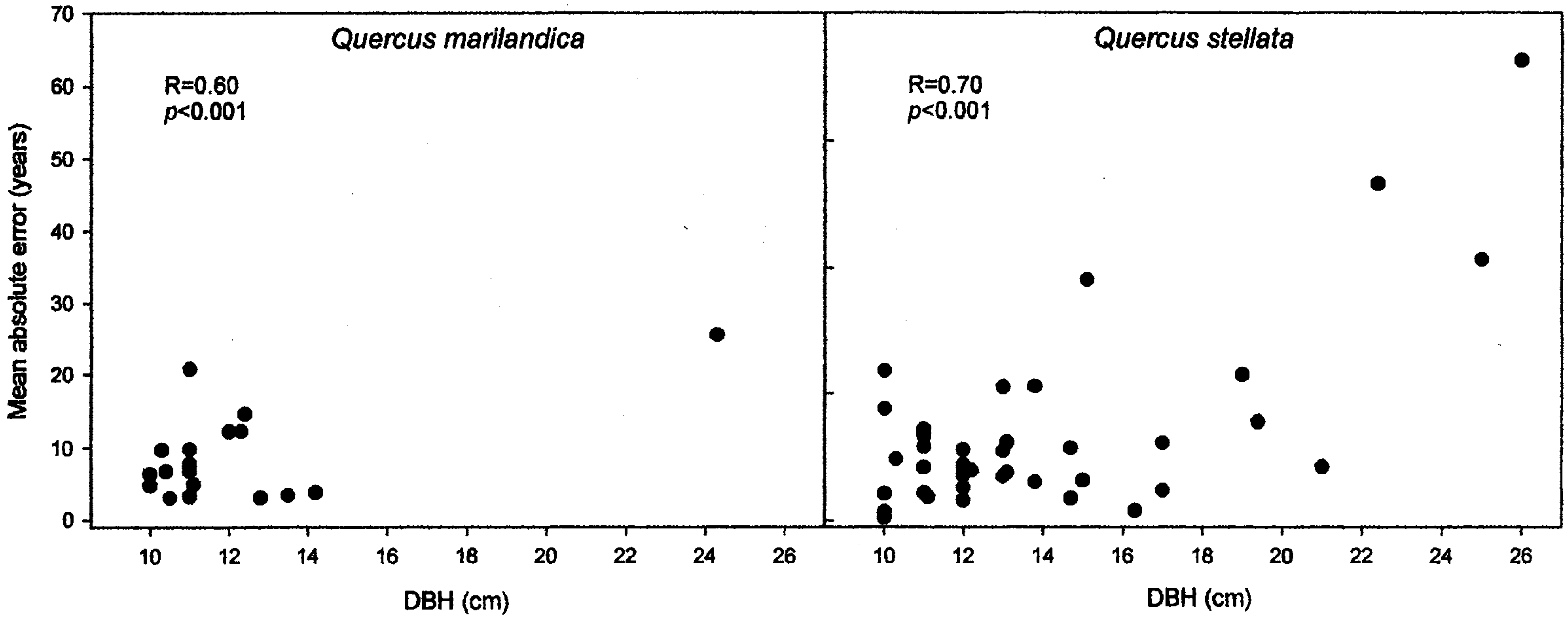
15
20
25
30
DBH


Quercus marilandica
R=0.60
p<0.001
Quercus stellata
R=0.70
p<0.001
Mean absolute error (years)
0
10
20
30
40
50
60
70
10
12
14
16
18
20
22
24
26
DBH (cm)
DBH (cm)

CHAPTER FIVE

RELEASE RESPONSE OF *QUERCUS STELLATA* IN A XERIC OAK FOREST

Abstract

Dendroecological studies have generally been conducted in mesic forest ecosystems where climatic influence on tree growth would be relatively low and effects of canopy disturbances would be relatively high. Techniques used to identify canopy disturbances have gone largely untested in xeric forest communities, where decadal climatic trends may be difficult to filter. Using three dendroecological methods, we examined growth releases in *Quercus stellata* growing at the edge of its range in an old-growth stand in the Cross Timbers region of Oklahoma. Growth releases are defined as sustained increases in tree-ring width and are positively related to disturbance intensity. The most commonly used technique of simple radial growth averaging revealed the highest number of releases, but most were explainable by climatic events. A newly developed technique that incorporates the effects of prior growth rate into release criteria had similar patterns of release detection as simple radial growth averaging, but with fewer releases. We examined a third technique designed to filter climate by removing a common climate signal from the tree-ring chronologies. Differences between regional and local climatic conditions lead to false release detections with this method. We propose that climate was the primary factor mediating tree growth and is probably an important influence on the occurrence of disturbance in these stands. Our results indicate that the methodology for release detection will have to be refined for xeric woodlands. A major theoretical challenge will be the frequent interaction between prolonged drought and classic canopy disturbances such as fire.

Key Words: *Quercus stellata,* Cross Timbers, drought, release detection, dendroecology, disturbance

Introduction

Tree-ring research has focused historically on deciphering the relationship between tree-ring growth and climate (Douglass 1920, Douglass 1941, Fritts 1966, Fritts 1976), and methods have been developed to remove effects of age, increasing tree size, and exogenous and endogenous disturbances (Fritts 1976, Blasing et al. 1983, Cook and Kairiukstis 1990). In contrast, many forest ecology studies have attempted to remove or filter the effects of climate (i.e., drought) from tree-rings to reveal canopy disturbances that result in immediate removal of portions of the canopy (i.e., fire, wind, ice damage) (Lorimer 1980, Lorimer and Frelich 1989, Nowacki and Abrams 1997, Black and Abrams in press). Most of these dendroecological studies have been conducted in relatively mesic forests using shade tolerant species (Lorimer 1980, Lorimer and Frelich 1989, Abrams et al. 1998, Abrams et al. 2001), where a tree's response to climate is relatively low and response to disturbance is relatively high. In more xeric forests, however, interactions between climate and disturbance are probably largely controlling stand dynamics

(Abrams and Orwig 1995, Abrams et al. 2000), and filtering effects of climate may be extremely difficult.

The most effective studies of stand dynamics use a combination of techniques such as tree-ring analysis and examination of stand structure (Foster et al. 1996). Canopy disturbances have been identified through tree-ring analysis as long-term sustained increases in tree growth of residual trees (Lorimer 1980, Lorimer and Frelich 1989, Nowacki and Abrams 1997), whereby disturbance intensity is positively related to growth response (Frelich 2002, pp. 53-54). These growth increases will hereafter be called releases. Disturbances usually coincide with an increase in tree recruitment (Lorimer 1985, Mikan et al. 1994, Abrams and Orwig 1995, Abrams et al. 2000, Orwig et al. 2001, Pollmann 2003). Climatic events such as drought may also affect recruitment (Olano and Palmer 2003), though often not as dramatic as a major canopy disturbance event (Villalba and Veblen 1997).

Release events are generally determined using radial growth averaging of tree-ring widths, hereafter referred to as the "average growth" technique (Nowacki and Abrams 1997). Releases are detected as a change in percent growth above a specified threshold, whereby percent growth change is calculated using a 10 to 15 year moving average of radial growth (Lorimer and Frelich 1989, Nowacki and Abrams 1997). The method is intended to filter short-term climatic trends and reveal the long-term growth response to canopy disturbance events. Another recently developed technique for release detection incorporates effects of prior growth rate into a tree's release response and is hereafter referred to as the "prior growth" technique (Black and Abrams in press). The technique utilizes radial growth averaging, but conditions release detection on the current growth rate of the tree. At high prior growth values, release response is low and vice versa. This method will theoretically filter the effects of age, size and crown position from release response of a tree, because these variables are all correlated to prior growth rate. The method has also been shown to filter effects of long-term drought in mesic stands of *Tsuga canadensis*, but has not been used for dry site species such as *Quercus stellata*.

Radial growth averaging techniques have not been recommended for identifying disturbances in extremely dry oak forests, like those of the Cross Timbers, because as dryness increases, canopy cover decreases, and response to disturbance will become less important than climatic influence on tree growth (Lorimer and Frelich 1989; Nowacki and Abrams 1997). However, radial growth averaging techniques can be useful for understanding tree growth response to prolonged climatic events (Abrams and Orwig 1995, Abrams et al. 2000). Alternative methods for release detection have not been suggested.

In addition to techniques that use radial growth averaging, we examine a previously untested method, hereafter referred to as the "climate removal" technique (Nash et al. 1995). The technique involves removing the common growth signal from each measured radius, presumably due to climate. This technique was used by Nash et al. (1975) to determine effects of insect infestations and air pollution on tree growth (Swetman et al. 1985), but, to our knowledge, has not been used for reconstruction previously unknown release events. We hypothesize that this method would be more appropriate than radial growth averaging techniques, due to the extremely xeric conditions of our study area in the Cross Timbers.

Dendroecological studies in the dry oak forests, like those of the Cross Timbers, represent a unique challenge because of the potentially high frequency of canopy disturbances such as fire, wind and ice storms (Bruner 1931, Dyksterhuis 1948, Hoagland et al. 1999) and stressful site conditions related to prolonged drought (Stahle et al. 1985a). Decoupling climatic events and canopy disturbances may be difficult in Cross Timbers forests because tree-growth is strongly related to climate (Stahle and Hehr 1984, Stahle et al. 1985a) and prolonged drought can cause overstory tree mortality (Rice and Penfound 1959, Olano and Palmer 2003).

To our knowledge, release detection methods described above have not been used in extremely xeric forests. There are perhaps millions of hectares of xeric oak forests throughout the world and relatively little information on stand dynamic processes. Our objective was to document radial growth releases in a xeric old-growth Cross Timbers forest, and to determine the relative importance of climate (e.g., drought) to standwide growth releases. We discuss the applicability of widely used and previously untested dendroecological methods in detecting growth releases in a relatively xeric forest community.

Study Area

The study area was part of the Keystone Ancient Forest Preserve (KAFP), managed by The Nature Conservancy. The KAFP lies in the northern range of the Cross Timbers region (Küchler 1964), approximately 32 km west of Tulsa, Oklahoma in southern Osage County at the confluence of the Cimarron and Arkansas Rivers. The region is characterized as a mosaic of xeric oak woodlands, savannas and prairie openings scattered throughout approximately 4.8 million hectares, with nearly half in Oklahoma (Hoagland et al. 1999, Küchler 1964). Average annual precipitation is 101 cm and average winter and summer temperature are 3° and 26° C, respectively (Oklahoma Climatological Survey 2002). Previous researchers have characterized the KAFP as old-growth due to the absence of anthropogenic disturbances such as logging and the presence of *Q. stellata* and *J. virginiana* trees greater than 300 and 500 years-old (Therrell and Stahle 1998). Elevation ranges from 251 to 304 m; topography is moderately to steeply sloping with underlying bedrock of shale and sandstone. Soils are a Niotaze-Darnell complex, with a sandy loam surface layer (Bourlier et al. 1979).

The sampling area was restricted to an 11 ha stand located on a steep side slope (18 ± 1.6 percent) with a southwestern aspect. The stand is a closed-canopy forest with 62 percent canopy cover and an overstory tree ($\geq$ 10 cm DBH) density of 818 trees ha^{-1} (Clark 2003). *Quercus stellata* constitutes approximately 80 percent of the tree density, and we, therefore, assume that this species would capture any standwide disturbances. *Quercus marilandica, Carya texana, Juniperus virginiana* and *Q. shumardii* are important subordinate species (Chapter One).

Methods

We randomly placed 5-0.3 ha square plots within the stand and randomly selected 14 to 30 *Q. stellata* trees $\geq$ 10 cm diameter at breast height (DBH) within each plot for coring; we numbered each tree in the plots and selected *Q. stellata* trees to core using randomly generated numbers. A total of 110 trees were cored at 1.0 to 1.4 m height. We measured DBH of each cored tree. Cores were dried, mounted and sanded with progressively finer grades of sandpaper (100-400 grit). We cross-dated each core with a regional post oak chronology that was available on the International Tree-ring Data Bank (ITRDB) (Appendix 1; NOAA 2002). Cross-dating provided confidence that each core was dated to the exact calendar year (Douglass 1941; Stokes and Smiley 1996). Tree-ring widths were measured to the nearest 0.001 mm using a Velmex stage micrometer. If multiple cores were collected from a tree, we measured the core that came closest to pith. For cores in which we missed the pith by an estimated 5 years or more, we used a graphical technique to estimate the pith date; otherwise, we made a visual estimation of number of years to pith (Villalba and Veblen 1997, Clark 2003). Regression was used to predict pith date using DBH for rotten cores (Clark 2003). We used program COFECHA, version 6.06P, to check the accuracy of cross-dating (Holmes 1983; Cook et al. 1997), and we determined that all cores were correctly dated.

Regional climate data

Instrumental Palmer drought severity indices (PDSI) from 1896 to 2001 and reconstructed PDSI from 1800 to 1895 were obtained by averaging data from grid points 81, 82, 93 and 94 in central Oklahoma (Cook et al. 1999). The PDSI ranges from -4 (extreme drought) to 4 (extreme wet) and represents several environmental variables that affect tree growth, including drought duration, soil water holding capacity, temperature and precipitation (Palmer 1965). We adjusted the reconstructed values by multiplying by the ratio of the two variances:

$$\mathrm{rPDSI} \times \left(\frac{\sigma_{\mathrm{iPDSI}}}{\sigma_{\mathrm{rPDSI}}} \right) = \mathrm{adjPDSI},$$

where rPDSI, iPDSI, adjPDSI are the reconstructed, instrumental values and adjusted reconstructed values, respectively. The PDSI chronology was smoothed using a local smoothing technique involving tricube-weighting and polynomial regression available in SigmaPlot v. 7 (SPSS 2001).

Radial growth analysis

We used program ARSTAN, version 3.02V (Cook et al. 1997) to produce the standardized, residual and ARSTAN chronologies of the overstory trees. Raw tree-ring widths of each individual tree chronology were detrended by fitting one of several growth curves (e.g., negative exponential, negative straight line function). Detrending removes effects of age, increasing tree size, and absolute growth rate (Fritts 1976, Cook and Kairiukstis 1990). A ring width index was created by dividing the tree-ring widths by the predicted curve values. The standardized chronology is produced using a biweight robust mean of the ring width indexes, which will minimize the effects of extreme index values in the computation of the mean index chronology. The residual chronology is produced using an autoregressive modeling technique and has a strong common signal among sample trees with little low-order persistence. Persistence arises from the physiological partitioning of growth potential and reserves, due in part to impact of climate and disturbance events that carryover from one year to the next. The residual chronology has been found to be a strong indicator of yearly fluctuations in climatic events (Cook et al., Stahle et al. 1985b). The ARSTAN chronology attempts to provide the most robust estimation of both exogenous climate and endogenous growth dynamics in the resulting time series (Cook 1985). The ARSTAN chronology was smoothed using a local smoothing technique involving tricube-weighting and polynomial regression available in SigmaPlot v. 7 (SPSS 2001).

Average growth method

The average growth method identifies sustained releases in growth through a radial growth averaging technique (Nowacki and Abrams 1997; Frelich 2002, pp. 53-54). Percent growth change was calculated for all years and for each individual tree using the formula,

$$[(M_2-M_1)/M_1]*100,$$

where M_1 is equal to the sum of tree-ring widths of the previous ten years and M_2 is equal to the sum of tree-ring widths of the current and subsequent nine years (Nowacki and Abrams 1997). Percent growth change was not calculated for the first and last ten years of the tree chronology because of the required number of years for the calculation. Releases are often determined to be "significant" when a change in growth exceeds a specified threshold (Lorimer and Frelich 1989; Nowacki and Abrams 1997). Moderate intensity release events were determined to be significant when percent growth change exceeded 30 percent. This threshold level was determined from the mean positive percent growth change value obtained with our data (data not shown) and is similar to the 25 percent threshold used for oak species by Nowacki and Abrams (1997). Because release potential changed across age classes (Appendix 2), we lowered the threshold value for detection of moderate intensity release events to 15 percent for trees greater than 100 years old. Sixty and 30 percent threshold values were used to identify higher intensity releases (i.e., major releases) for trees less than 101 and greater than 100 years old, respectively.

Standwide releases were determined when at least 25 percent of the trees in a year exhibited a significant release response. We restricted our standwide release detection to years in which we had at least 2 trees in the sample, yielding a percent growth change chronology for this method from 1816 to 1991.

Prior growth method

The prior growth method redefines the release potential of trees by examining the relationship between prior growth rate and percent growth change (Black and Abrams in press). A boundary line is established at the uppermost threshold of this relationship and a release is identified when a growth pulse falls within a specified percentage of the boundary line. Boundary line construction should be species specific and should incorporate as many data as possible in order to accurately describe the upper threshold of release response (Black and Abrams in press). Although Black and Abrams (in press) found that one boundary line was adequate for all *Tsuga canadensis* stands in their study, they did not examine trees growing on xeric sites, which may exhibit different relationships between prior growth and release response (Bryan Black, personal communication). We, therefore, constructed our boundary line using tree-ring data from the KAFP in addition to data from 8 stands located within the Cross Timbers region, representing a total of 48,992 years of growth (Appendix 1) (NOAA 2002).

We calculated prior growth for each year by summing tree-ring width of the previous ten years. We plotted prior growth and percent growth change (as defined above) and constructed a boundary line at the upper threshold of percent growth change (Fig. 1). The boundary line was constructed by dividing the prior growth values into 8 equal segments and averaging the top 5 percent growth change values within each segment, which yielded an equal sample size and ensured that only the maximum releases in each segment were included (Black and Abrams in press). We fit all positive segment averages to straight line, exponential, power and logarithmic curves using PROC REG in SAS (SAS 1990). The data were linearly transformed when necessary. The boundary line was best fit using a logarithmic model with the equation $y=425.6 - 382.7(\log_e(\text{prior}+1))$ ($R^2=0.95$).

The threshold value for detection of significant release events for this method was determined by examining release response for the few years following a prolonged drought event (Black and Abrams in press). Theoretically, releases following prolonged drought events are considered "drought rebounds" (i.e., below-average growth due to inadequate moisture, followed by above-average growth due to increased precipitation), and are not considered related to canopy disturbance events (Black and Abrams in press). We recognize, however, that droughts can cause overstory tree mortality (Rice and Penfound 1959, Olano and Palmer 2003), and surviving trees may respond to the increased available resources once precipitation levels return to normal. We, therefore, chose to examine release response following a relatively low-intensity drought at the KAFP, the 1930's drought (1936 to 1940), (i.e., the "dust bowl"). We assume that the 1930's drought would not have been severe enough to cause significant overstory tree mortality in this forest. Although we have no empirical evidence for this assumption, this drought was of lower intensity at the KAFP compared to other droughts of this century.

First, we plotted percent growth change against prior growth for 1941 to 1945 post-drought years (Fig. 2). Next, we determined the threshold (expressed as a percentage of the boundary line) that filtered the majority of growth pulses during these years. We examined how distance to the boundary line varied with age class, and set the threshold values accordingly (Figure 3). The threshold value for moderate intensity release events was set to 30 percent for younger trees (< 101 years) and to 15 percent for older trees (>100 years). The threshold value for major releases were set to 60 and 100 percent for younger trees and between 30 and 100 percent for older trees. Points falling above the threshold were considered to be significant release events. Because this method is more conservative than the average growth method (Black and Abrams in press), we lowered the standwide release detection threshold from 25 to 10 percent of trees exhibiting a significant release response in a given year. We restricted standwide releases to years in which at least 2 trees were in the sample, yielding a percent growth change chronology for this method from 1816 to 1991.

Climate removal method

This method was designed to remove the effects of climate from individual tree chronologies. First, a regional climate chronology was created by averaging the residual indices from chronologies developed by Stahle et al. (1985a) (Appendix 1). The regional chronology is assumed to represent the common climate signal among trees at the KAFP and trees sites across the region. Support for this assumption is given by the relatively strong correlations among the residual chronologies of the regional sites and the KAFP (R=0.40-0.57) (Appendix 6).

A predicted residual index (PRI) was computed for each year for each individual tree at the KAFP (Nash et al. 1975, Swetnam et al. 1985):

$\mathrm{PRI} = \mathrm{sdTRI}/\mathrm{sdRC}\ (\mathrm{RC}_{i=1..n} - \mathrm{MEAN}(\mathrm{RC}))$,

where sdTRI corresponds to the standard deviation of the individual tree-ring index, sdRC corresponds to the standard deviation of the regional chronology, RC_i corresponds to the residual index for the regional chronology in year i, and MEAN(RC) is the mean of the regional chronology corresponding to *n* years. The PRI's were subtracted from the tree-ring indexes (TRI) to produce the corrected tree-ring indices (CI), which should represent tree growth with effects of climate removed:

$$CI = TRI - PRI$$

The CI's were calculated for each individual tree. A measure of growth increase for each tree in a given year was calculated by examining the difference between the yearly CI value and the mean CI of the chronology, which will be equal to one (Swetnam et al. 1985):

$$\%GC = (CI - 1) * 100,$$

where %GC is the percent growth change related to canopy disturbance events. The standard deviation of percent growth change for each individual tree was calculated for ages > 100 and for ages < 101. A percent growth change of greater than the mean plus the standard deviation, corresponding with the appropriate age, was used as the significant threshold value for release detection for each tree. A release of moderate intensity was detected at percent growth change values greater than the mean plus one standard deviation; a release of major intensity was detected at percent growth change value greater than the mean plus two standard deviations. Standwide releases were determined when at least 25 percent of the trees in a year exhibited a significant release response. We restricted standwide release detection to years in which at least 2 trees were included in the sample, yielding a percent growth change chronology for this method from 1807 to 1995.

Assessment of disturbances and climatic influences

We determined if releases were related to climatic patterns by examining the overstory age structure and conducting a superposed epoch analysis using program EVENT (Cook et al. 1997). Releases occurring concurrently with a pulse in tree recruitment generally indicate a reduction in the overstory canopy cover caused by tree death (Lorimer 1985, Abrams and Orwig 1995, Pollmann 2003). We used program EVENT to determine if tree growth differed in years preceding, during or following a putative standwide release event and to identify potential biases in release detection for each method. The EVENT analysis was performed separately for each release detection method using the standardized tree-ring index chronology as an indicator of tree growth. Additionally, the EVENT analysis was conducted to determine if the residual regional indices differed in years surrounding releases detected using the climate removal method. The program computed average tree-ring index values for a window of time surrounding an "event" year (i.e., a year in which standwide release events were detected), and we compared the actual values to randomly generated predicted values. The predicted values represent random simulations of tree-ring index values. Each simulation contained the number of standwide release events detected. A departure value was calculated for each year in the event window by subtracting the actual tree-ring index value minus the predicted value. A statistically significant departure value was detected when the actual value was greater than or less than the 95 percent confidence limits (based on a normal distribution) of the predicted value.

Results

Climatic events at the KAFP

Drought was common at the KAFP, with years of below-normal PDSI values (PDSI<-1) occurring more frequently than years with normal (1>PDSI>-1) or above-normal PDSI values (PDSI>1) (Table 1). The most extended and perhaps severe drought occurred from the late 1850's to the mid 1860's, according to the PDSI chronology (Fig. 4A). This drought lasted approximately 11 years with average PDSI of –1.7. The ARSTAN chronology indicated that trees responded to this severe drought through reduced tree growth, with the year 1855 having the lowest ARSTAN index value of the chronology (0.47) (Fig. 5).

During the 20th century, prolonged droughts (i.e., years of below normal PDSI for 3 consecutive years) occurred at approximately 25-year intervals. The climate data and the ARSTAN chronology indicated that the most severe and prolonged droughts of the 20th century occurred during the early 1910's, the mid 1930's, the late 1950's, the late 1960's and the early 1980's. The 1950's drought was perhaps the most severe of these 20th century droughts according to the PDSI chronology, with PSDI values remaining below –2 for 5 consecutive years. The ARSTAN chronology did not always agree with the climate data, however. This was most notable during the 1980's drought when PDSI values were generally normal (Fig. 4A), but tree-growth was below normal for approximately 9 years (Fig. 5).

Release detection

The average growth method yielded the highest total number of standwide releases compared to the other methods (n=65) (Table 2). The prior growth method had similar release detection patterns as the average growth method (Fig. 4B, C), but with fewer number of standwide release events (n=12). The release detection pattern of the climate removal method did not resemble the other two methods, with the majority of releases detected as single event years. In contrast, releases detected with the average growth and prior growth methods generally lasted for several concurrent years (Fig. 4D, E).

Release detection was more likely to occur during dry years (i.e., PDSI < -1) compared to wet years (i.e., PDSI > 1), particularly for the climate removal method (Table 2). Additionally, the average growth and prior growth methods tended to detect releases during or following prolonged drought events (Fig 4A, C, and D). This pattern was most pronounced for the droughts of the 1840's, 1850's, and the 1930's. The climate removal method generally did not follow this pattern, with the exception of the 1950's drought, which was followed by release detection using this method.

Patterning of release detection during or following drought was supported by the superposed epoch analysis (Fig. 6). Releases detected using the average growth method tended to occur after years of significantly reduced tree growth, indicating drought, and were followed by years of significantly increased tree growth, indicating increased precipitation (Fig 6A). Similar patterns were also evident for the prior growth method, but were not significant (Fig 6B). In contrast, the climate removal method detected releases in years of above-average growth, which is indicative of years of high precipitation. However, when the superposed epoch analysis was conducted using the residual regional indices, release detections were significantly more likely in years in which trees at the regional sites had below-average tree growth . In fact, 78 percent of the release events were years in which the residual regional chronology indices were below normal (Table 2). Thus, this method tended to detect releases in years when the residual index values from the regional chronology were smaller than the tree-ring indices from the KAFP. Of the ten smallest residual regional index values, 7 were years in which significant standwide release events were detected. Comparatively, only 14 (33 percent) standwide release events were in years that the tree-ring indices from the KAFP were below normal.

Release detection patterns using any method generally did not coincide with pulses of tree recruitment, except during the late 1940's and early 1950's (Fig 4B, C, D and E). All methods detected releases during this time, which coincided with a relatively long period of above-average precipitation (Fig 4A).

Discussion

Releases could not be separated from climatic events, particularly drought, in this study. Each release identified by the three methods can be at least partially related to the patterning of dry and wet episodes or as a byproduct of the methodology we used. We propose two feasible explanations for our results: 1) the predominance of climate in controlling tree growth obscures effects of canopy disturbances in the dry woodlands of the KAFP, and 2) climate may mediate canopy disturbances either by the death of trees during prolonged drought or by the higher occurrence of disturbances such as fire during or following dry periods.

The superposed epoch analysis and the general patterning of releases with drought events support the first explanation. The stressful site conditions at the KAFP results in reduced competition, relatively low canopy cover (62 percent) and a higher percentage of exposed crown (Clark 2003). Thus, canopy disturbances may have a relatively small effect on overstory trees compared to climate (Nowacki and Abrams 1997). *Quercus stellata* growing in the Cross Timbers has a high sensitivity to climate variables, particularly available moisture (Stahle and Hehr 1984; Stahle 1986). These results help confirm theories of previous researchers that trees growing on marginal sites may have reduced response to canopy disturbances because of the overriding effect of climate on tree growth (Lorimer and Frelich 1989; Nowacki and Abrams 1997).

There was only limited evidence for the latter explanation (i.e., releases during or following drought concurrent with a pulse of tree recruitment). However, inferences from recruitment data are difficult because of age discrepancies due to coring height (Villalba and Veblen 1997), differential mortality of overstory trees (Lorimer 1985) and the possibility of other unknown disturbances during that time. Previous dendroecological studies have generally not considered drought as a disturbance (or a factor influencing disturbance) probably because most of these studies have been conducted in mesic forest ecosystems where effects of drought are assumed to be minimal (Abrams et al. 1998, 2000, 2001; Orwig et al. 2001; Black and Abrams in press). However, drought has caused tree mortality in forest ecosystems that are more mesic than the Cross Timbers (Jenkins and Pallardy 1995, Olano and Palmer 2003). Additionally, drought appears to partially control the occurrence of fire in the Cross Timbers (Clark 2003). In fact, the release event in the late 1940's that coincided with a pulse of tree recruitment could be related to a known fire event that occurred in 1945 (Clark 2003). The recruitment pulse may also be attributed to mortality associated with the drought of the 1930's. However, this would contradict our assumption that the dust bowl drought at the KAFP was not so severe as to cause overstory tree mortality.

The lack of refinement in the application of the methodology, particularly for xeric forests, increases the difficulty in detection of possible releases related to canopy disturbances. The subjectivity in applying dendroecological methods was problematic in identification of significant growth releases. For example, the threshold values of significant growth change for release detection was based on limited evidence of release potential of post oak trees in this stand. Changes to the threshold values would have yielded different results and perhaps different interpretation of release events in this stand. Additional information on *Quercus stellata* response to drought would have benefited our application of the prior growth method, considering the boundary line threshold values were set somewhat arbitrarily. However, only limited empirical information is available on effects of prolonged drought on stand dynamics in xeric oak stands (Rice and Penfound 1959, Jenkins and Pallardy 1995). In future studies, researchers should perhaps consider a more statistical approach in identifying growth releases such as incorporation of standard error estimates into the 10-year running mean average of percent growth change. Although techniques to apply these types of statistics are being developed (Ed Cook, personal communication), it is not yet widely available in tree-ring analysis programs such as ARSTAN. We would consider an approach that examines the residuals from a regression analysis of PDSI values with the ARSTAN indices.

We hypothesized that the climate removal method might provide a less arbitrary approach in identifying growth releases than methods of simple radial growth averaging.

We had hoped the climate removal method would reduce some uncertainty in applying threshold values to identify growth releases. However, a potentially serious problem with the climate removal method was that it tended to detect releases in years when the residual index values from the regional chronology were smaller than the individual tree-ring indices. In other words, the method falsely detected releases in dry years, which was likely due to differences between regional climate and local weather conditions at the KAFP. The majority of releases tended to occur during the drought year and did not continue. Drought or canopy disturbances would generally have an effect on tree growth for more than one year (Nowacki and Abrams 1997). We suspect that the majority of release detections with this method were not related to canopy disturbance nor climatic effects on tree growth, but were products of the methodology. Thus, we would not recommend using this method until possibilities for correcting these problems can be addressed.

In addition to our two primary explanations for our results proposed above, one must consider the possibility that canopy disturbances at the KAFP are not of sufficient intensity to cause release response of trees. However, this seems unlikely given the important role that disturbances have had in the Cross Timbers region. Fire was historically common in the Cross Timbers and has been shown to help maintain stand structure and species composition (Bruner 1931, Johnson and Risser 1975, Rice and Penfound 1959, Clark 2003). Additionally, we suspect that wind, hail, ice and frost damage are also common disturbances (Stahle 1986), although rarely mentioned in the literature.

In conclusion, we found that climate was important in controlling tree growth and may be an important component of disturbance in the region. The commonly used methodology of radial growth averaging was useful for examining tree growth response to known climatic events, but did not alleviate the difficulty in disentangling climate from canopy disturbance effects. We suspect that this would only be possible with additional empirical evidence including effects of standwide canopy disturbance and drought events on tree-growth and mortality.

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Appendix 1. Tree-ring chronologies used for cross-dating, development of boundary line construction (BLC) and for development of regional chronology (RC) used in climate removal method for detecting disturbance events. Data were obtained from the International Tree-ring Data Bank (NOAA 2002).

Site	Contributor	Latitude/ Longitude	Chronology length	Use in study
Keystone Lake	Stahle, D.W.	36N,96W	1613-1995	CD, BLC
Lake Eufaula	Stahle, D.W.	35N,95W	1745-1982	BLC, RC
Lake Arbuckle	Stahle, D.W.	32N,96W	1698-1995	BLC, RC
Neosho River	Stahle, D.W.	36N,94W	1675-1982	BLC, RC
Bluestem Lake	Stahle, D.W.	36N,96W	1737-1982	BLC, RC
Oakwood	Stahle, D.W.	35N,98W	1772-1982	BLC, RC
Mud Creek	Stahle, D.W.	34N,97W	1691-1995	BLC, RC
Quanah Mountain	Stahle, D.W.	34N,98W	1686-1982	BLC, RC
Canadian River	Stahle, D.W.	35N,98W;	1680-1982	BLC, RC

Appendix 2. Average tree-ring width and positive percent growth change (standard deviation) across age classes for 92 trees at the Keystone Ancient Forest Preserve.

Age class	Tree-ring width (mm)	Percent growth change
0-24	0.78 (0.01)	30.2 (1.3)
25-49	0.71 (0.01)	32.6 (1.0)
50-74	0.62 (0.01)	29.8 (1.6)
75-99	0.60 (0.01)	29.2 (1.0)
100-124	0.60 (0.02)	15.9 (1.1)
125+	0.52 (0.01)	15.0 (0.92)

Appendix 3. Correlations among residual tree-ring chronologies of Keystone Ancient Forest Preserve (KAFP) and sites used to develop regional chronologies of climate in the climate removal method.

	KAFP	Neosha River	Lake Arbuckle	Lake Bluestem	Lake Eufaula
KAFP	1.00	-	-	-	-
Neosho River	0.46	-	-	-	-
Lake Arbuckle	0.47	0.40	-	-	-
Bluestem Lake	0.57	0.50	0.49	-	-
Lake Eufaula	0.56	0.57	0.49	0.51	-

Table 1. Number and percent of years with wet (Palmer drought severity index (PDSI) >1), dry (PDSI<1) and normal (1≥PDSI≥-1) climatic conditions from 1807 to 1995 for the north-central Cross Timbers region.

	Number	Percent
Wet	57	30.2
Dry	69	36.5
Normal	63	33.3

Table 2. Characteristics of release detection for each method. Wet, dry and normal years corresponds to years with Palmer drought severity index (PDSI >1, PDSI <-1 and 1≥ PDSI ≥-1, respectively).

	Average growth	Prior growth	Climate removal
Total years with significant release detected	65	12	41
Percent of releases detected during dry years	41.5	41.7	43.9
Percent of releases detected during wet years	30.8	33.3	24.4
Percent of releases detected during normal years	27.7	25.0	31.7
Percent of releases detected when residual regional chronology indices were below normal	NA	NA	78.0

Figure Legends

Fig. 1. Percent growth change versus $\log_e$(prior growth+1) for *Quercus stellata* at the Keystone Ancient Forest Preserve and an additional 8 sites in the Cross Timbers region.

Fig. 2. Drought rebound pulses following the 1930's drought (1941-1945) with the predicted region-wide boundary line and 30 and 15 percent of the boundary line value. Data is subdivided into young (<101 years-old) and old (>100 years-old) trees.

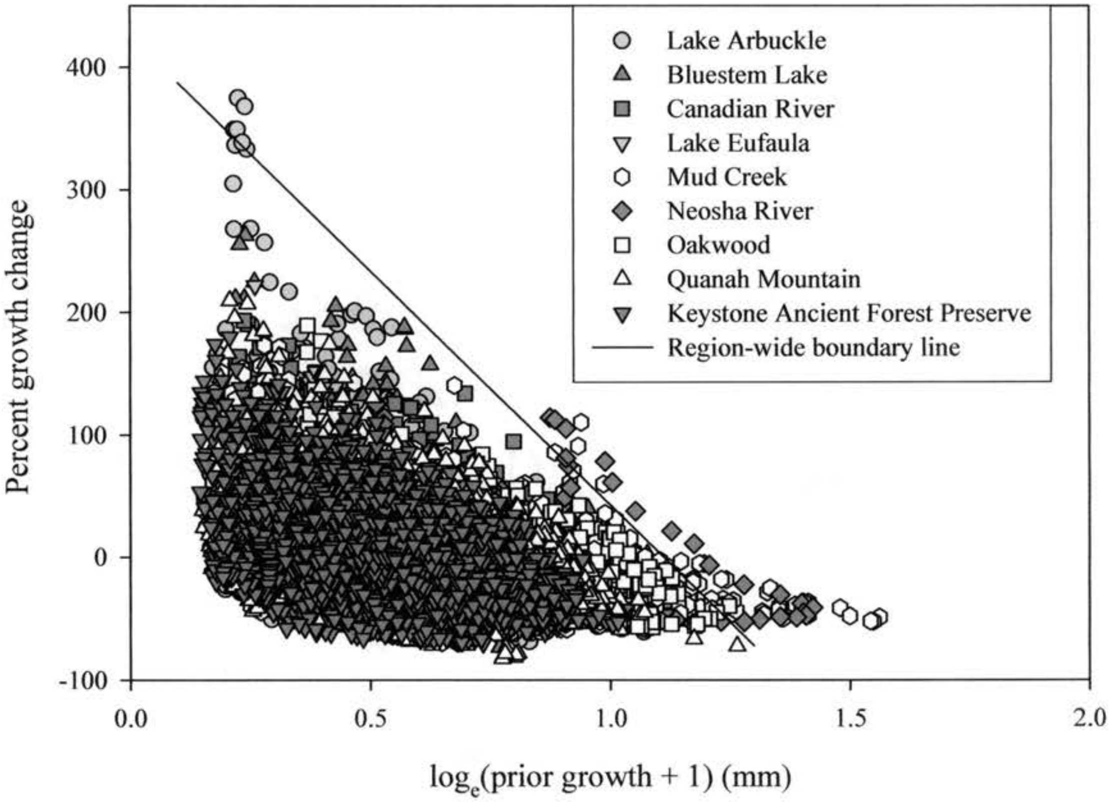
Fig. 3. Percent growth change versus $\log_e$(prior growth+1) of each age class for Q*uercus stellata* at the Keystone Ancient Forest Preserve. The predicted region-wide boundary line is shown.

Fig. 4. Average annual Palmer drought severity indices for the north-central Cross Timbers region with smoothed curve (A). Recruitment dates (1.37 m height) for *Quercus stellata* (B). Percent of trees with significant release response for each year using the average growth method (C), prior growth method (D) and climate removal method (E). Dotted lines in graphs C-E represent threshold for standwide release events; white bars represent minor releases and black bars represent major releases.

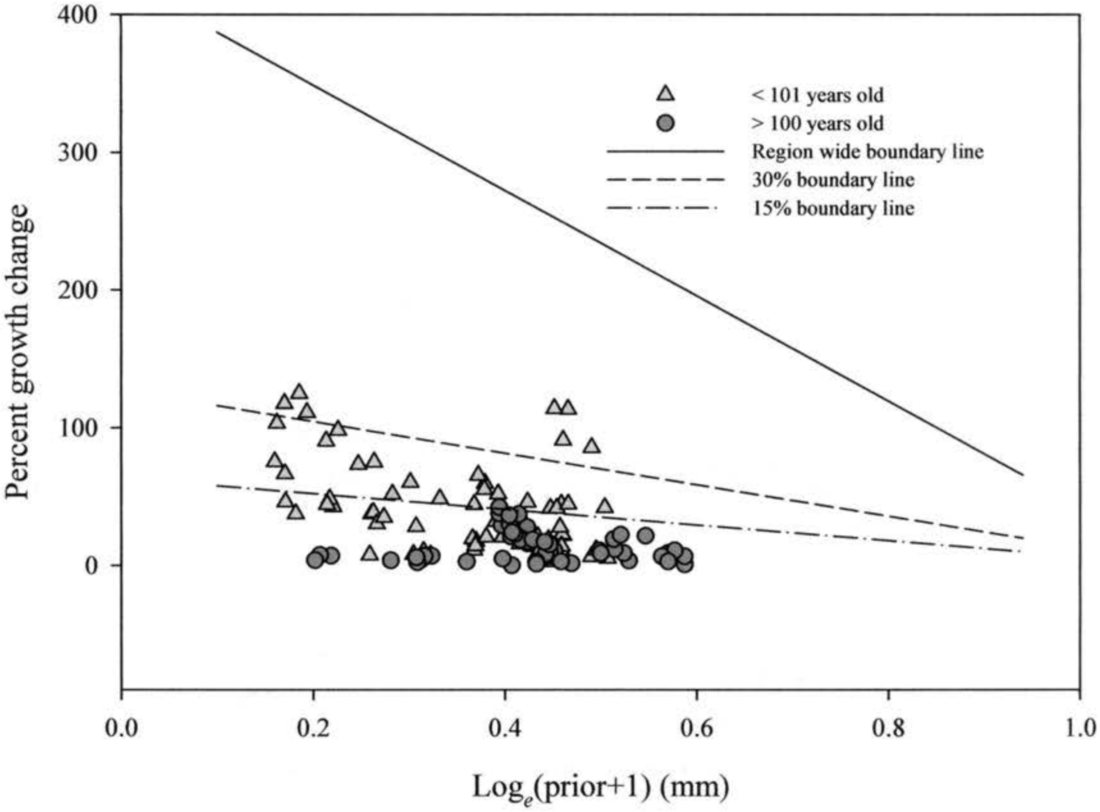
Fig. 5. ARSTAN chronology for *Quercus stellata* at the Keystone Ancient Forest Preserve with smoothed curve.

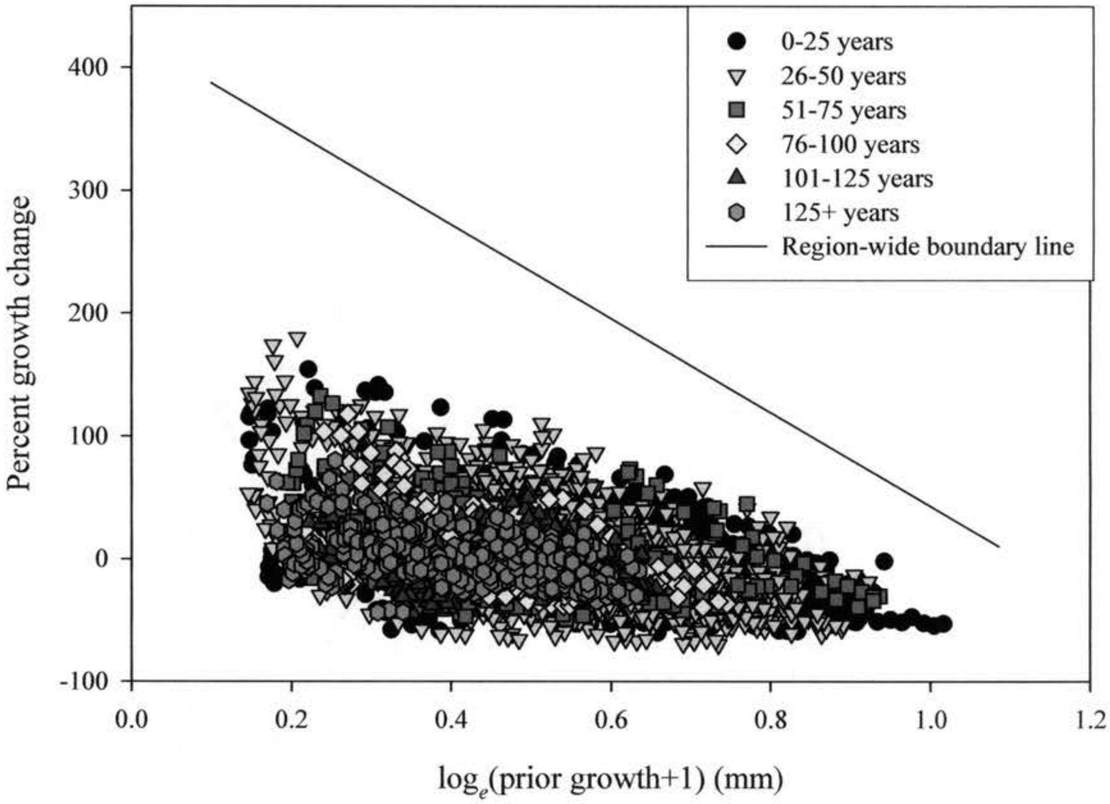
Fig. 6. Departure from predicted standardized tree-ring index for 5 years preceding, during and 5 years following a standwide release event detected using the average growth method (n=65) (A), the prior growth method (n=12) (B) and the climate removal method (n=41) (C); departure from predicted residual regional chronology index for the climate removal method (D). Error bars represent 1 standard deviation from the mean. Asterisk

represents years in which actual index was significantly different than predicted index ($p<0.05$).

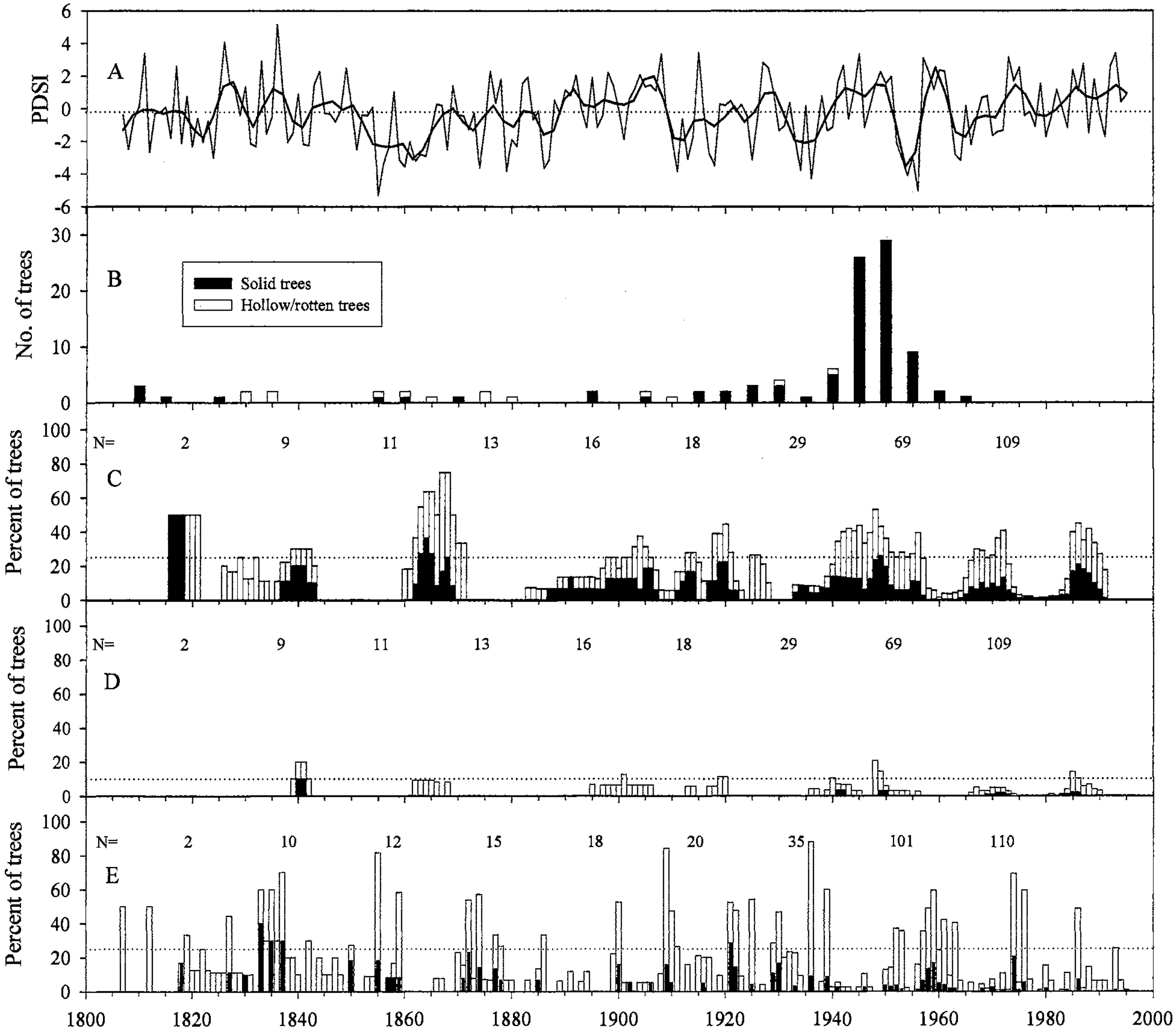


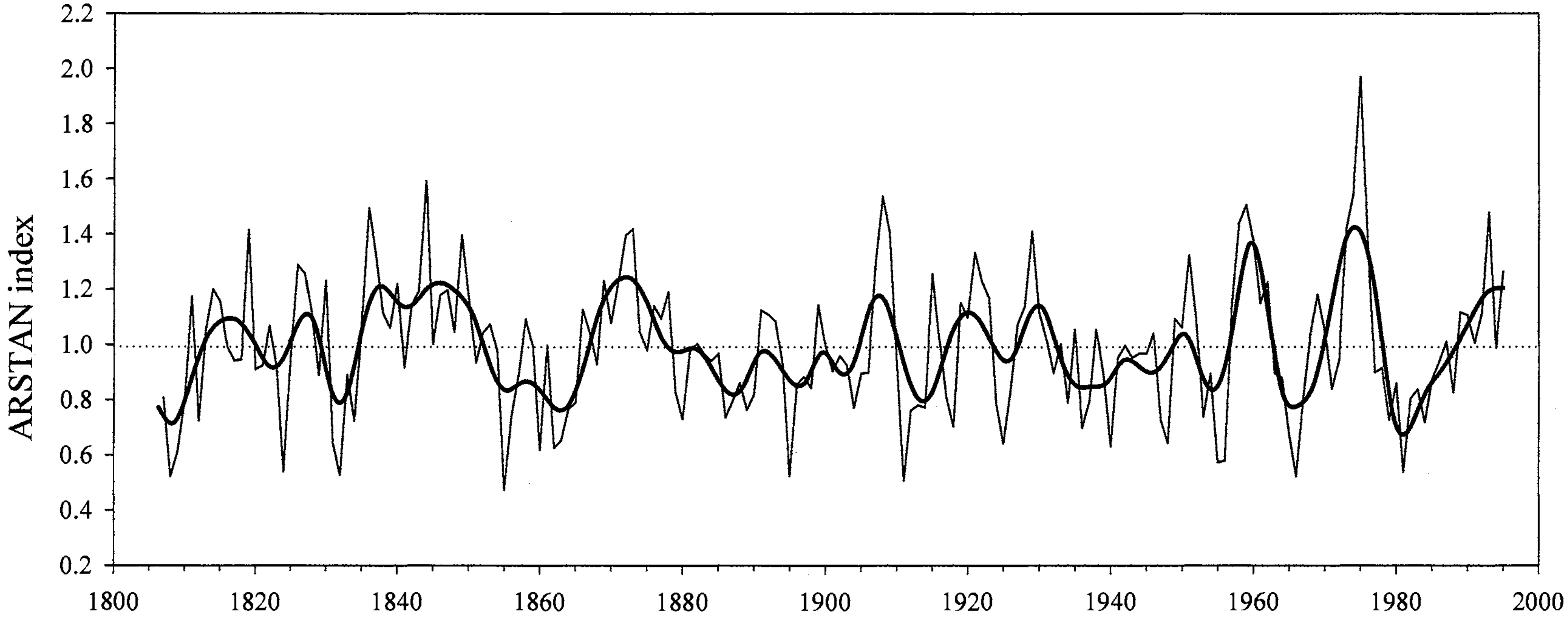
400
300
200
100
0
-100
Percent growth change
0.0
0.5
1.0
1.5
2.0
log$_e$(prior growth + 1) (mm)
Lake Arbuckle
Bluestem Lake
Canadian River
Lake Eufaula
Mud Creek
Neosha River
Oakwood
Quanah Mountain
Keystone Ancient Forest Preserve
Region-wide boundary line

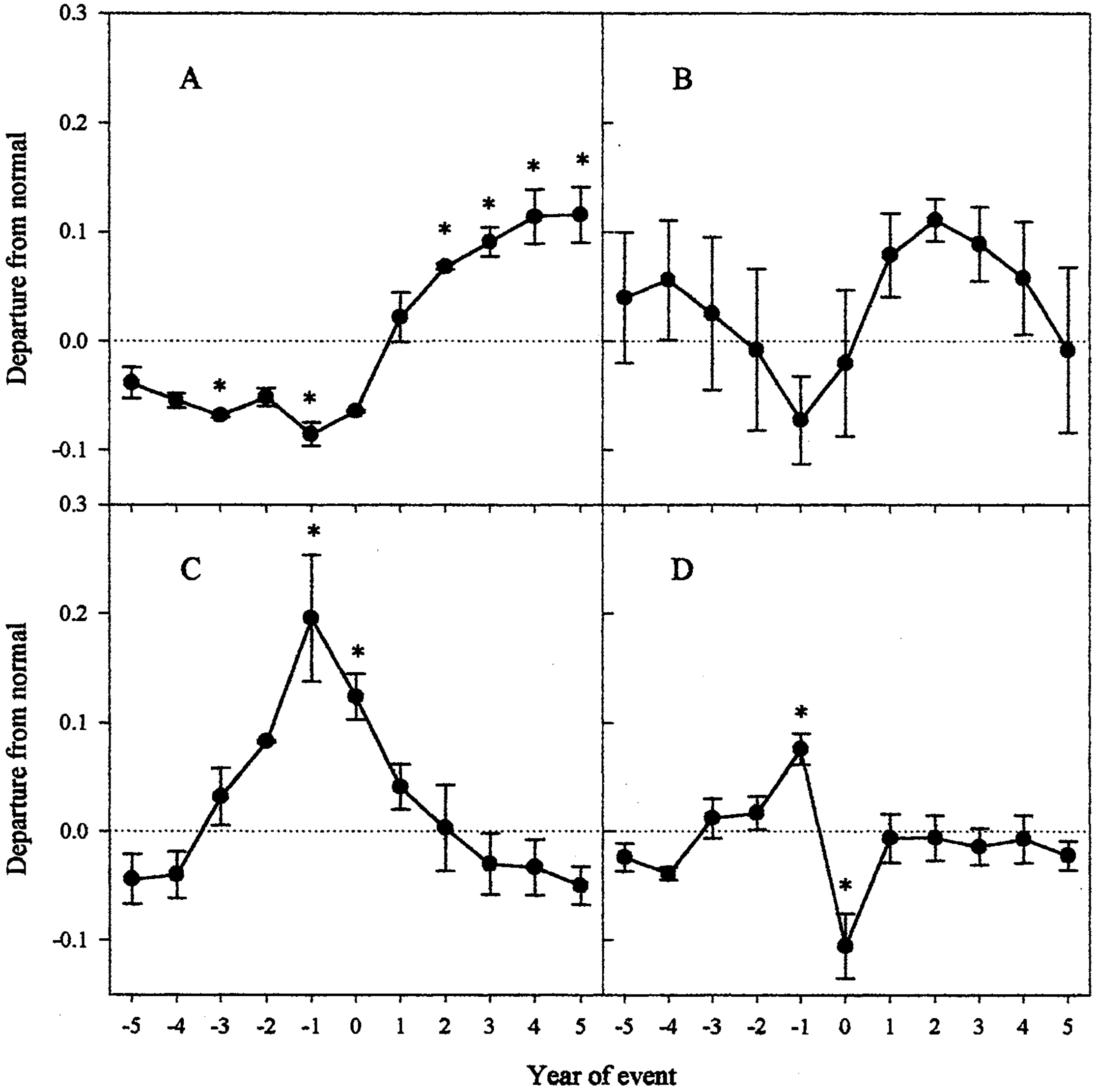

400
300
200
100
0
Percent growth change
0.0
0.2
0.4
0.6
0.8
1.0
Log$_e$(prior+1) (mm)
< 101 years old
> 100 years old
Region wide boundary line
30% boundary line
15% boundary line



400
300
200
100
0
-100
0.0
0.2
0.4
0.6
0.8
1.0
1.2
Percent growth change
log$_e$(prior growth+1) (mm)
● 0-25 years
▽ 26-50 years
■ 51-75 years
◇ 76-100 years
▲ 101-125 years
⬢ 125+ years
Region-wide boundary line


A
PDSI
6
4
2
0
-2
-4
-6
B
No. of trees
30
20
10
0
Solid trees
Hollow/rotten trees
C
Percent of trees
100
80
60
40
20
0
N=
2
9
11
13
16
18
29
69
109
D
Percent of trees
100
80
60
40
20
0
N=
2
9
11
13
16
18
29
69
109
E
Percent of trees
100
80
60
40
20
0
N=
2
10
12
15
18
20
35
101
110
1800
1820
1840
1860
1880
1900
1920
1940
1960
1980
2000


ARSTAN index
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
1800
1820
1840
1860
1880
1900
1920
1940
1960
1980
2000


A
B
C
D
Departure from normal
Departure from normal
0.3
0.2
0.1
0.0
-0.1
0.3
0.2
0.1
0.0
-0.1
-5 -4 -3 -2 -1 0 1 2 3 4 5
-5 -4 -3 -2 -1 0 1 2 3 4 5
Year of event
*

CHAPTER SIX

DYNAMICS OF THE HISTORIC FIRE REGIME IN AN OLD-GROWTH FOREST IN THE CROSS TIMBERS OF OKLAHOMA

Abstract: We investigated fire and recruitment dynamics of an old-growth Cross Timbers forest in Oklahoma. Fire frequency over the last 200 years was relatively high compared to similar studies conducted in Ozark forests, with fires occurring approximately every 2 years, and larger scale fires occurring every 8.5 years. Topo-edaphic conditions were important in controlling the fire regime of this forest, with fires occurring less frequently on the most mesic site. Contrary to our research hypothesis, fires became more frequent following Oklahoma statehood and the onset of European settlement in the area. We attribute the increase in fire frequency to increasing anthropogenic ignitions in the area in the last century. Our hypotheses that fire would be significantly more likely to occur following periods of drought and that fire would favor recruitment of hardwood species were both confirmed. In contrast, *Juniperus virginiana* recruitment occurred during fire-free periods, and may be increasing in abundance, due to the seed rain from cedar-invaded surrounding prairies and fields. The sequence of drought followed by fire appears to be an important process in the long-term maintenance of hardwood species this forest.

Introduction

Fire has influenced the vegetation patterns of many forest areas for millennia (Delcourt and Delcourt 1998; Clark et al. 1996; Bonnikson 2000). Plant species composition, diversity and structure have been affected by fire in forest communities of eastern North America (Crow et al. 1994; Arthur et al. 1998; Plocher 1999; Leahy and Pregitzer 2003) and in the forest-prairie ecotones of the Midwest (White 1983; Anderson and Brown 1986; Tester 1989; McClenahen and Houston 1998; Briggs et al. 2002). Oak forests appear to be particularly dependent on periodic disturbances such as fire for their development and long-term maintenance (Crow 1988; Abrams 1992, 1996; Johnson et al. 2002). As a result of decreased fire frequency since removal of Native Americans and onset of European settlement (Guyette and Cutter 1991; Cutter and Guyette 1994; Delcourt and Delcourt 1998; Guyette and Dey 2000; Ruffner and Abrams 2002), the oak component has been reduced in many oak forests (Abrams 1986; Glitzenstein et al. 1986; Nowacki et al. 1990; Abrams and Nowacki 1992; Abrams et al. 1998; Mclenahen and Houston 1998; Abrams and Copenheaver 1999; Harrod and White 1999; Shumway et al. 2001; Orwig et al. 2001). In contrast, disturbance has not been regarded as a requirement for self-replacement of oak species in dry oak forests (Johnson 1993; Abrams et al. 1997), but reductions in fire frequency may threaten species diversity and existing stand structure. Increased densities of invasive species, like *Juniperus virginiana*, may be a significant threat to dry forest ecosystems of the Cross Timbers and Ozark regions (Dyksterhuis 1948; Beilmann and Brenner 1951; Engle et al. 1996; Heikens 2000).

Historically, fires in the Cross Timbers forests of Oklahoma probably occurred frequently and helped to maintain a mosaic of vegetation types (Rice and Penfound 1959;

Penfound 1962; Engle 1997; Hoagland et al. 1999), but little empirical evidence exists on the historic fire regime and factors influencing fire in this region. Climate has been a contributing factor to fire ignition and/or spread throughout forest regions of eastern North America (Bergeron 1991; Guyette and Cutter 1991), and we suspect that climate is important in conditioning the fire regime of the Cross Timbers. Drought is frequent in the region, occurring at approximately 20-year intervals (Hoagland et al. 1999; Clark 2003). In addition to climate, topo-edaphic conditions are also related to fire frequency and spread (Pyne et al. 1996; Guyette and Dey 2000). Generally, fires are less frequent on sites with increased fuel moisture and are less likely to spread over topographically "rough" areas (Pyne et al. 1996; Guyette and Dey 2000).

In this study, we examine how temporal, climatic, and topo-edaphic factors influenced the fire regime of an old-growth Cross Timbers forest. We also examine the relationship between fire and recruitment of the most abundant tree species. Our specific objectives were to 1) establish the fire history of this site through dendrochronological dating of fire scars, 2) examine the effects of climate and site conditions on fire occurrence and spread, and 3) determine the relationship between tree recruitment patterns with known fire events. We had three hypotheses: 1) fire frequency has decreased since European settlement, 2) fire events were more likely to occur during periods of prolonged drought, and 3) fire promoted oak recruitment into the sapling layer.

Study Area

The study area was part of The Nature Conservancy's Keystone Ancient Forest Preserve (KAFP). The KAFP lies in the northern range of the Cross Timbers region (Küchler 1964), approximately 32 km west of Tulsa, Oklahoma in southern Osage

County at the confluence of the Cimarron and Arkansas Rivers (Fig. 1). The region is characterized as a mosaic of xeric oak woodlands, savannas and prairie openings scattered throughout approximately 4.8 million hectares, with nearly half in Oklahoma (Hoagland et al. 1999; Küchler 1964). Average annual precipitation is 101 cm and average winter and summer temperature are 3° and 26° C, respectively (Oklahoma Climatological Survey 2002). Previous researchers have characterized the KAFP as old-growth due to the presence of *Q. stellata* and *J. virginiana* trees greater than 300 and 500 years-old, respectively, and the absence of anthropogenic disturbances (Therrell and Stahle 1998). Elevation ranges from 251 to 304 m; topography is moderately to steeply sloping with underlying bedrock of shale and sandstone. Soils are a Niotaze-Darnell complex, with a sandy loam surface layer (Bourlier et al. 1979).

We delineated three stands based primarily on aspect and elevation. The 11 ha Southwestern Slope stand was located on the steep upper slopes (slope=17 percent) with a southwestern aspect. The 14 ha Northeastern Slope stand was located on steep lower slopes (slope=20 percent) with a northeastern aspect and had the lowest elevation. The Bench stand was 5 ha in size and was located on relatively level terrain (slope=6 percent) just north of the main ridge top.

Methods

Field sampling

We randomly placed 3 to 5 0.3 ha plots within each stand, and placed 12 to 20 0.008 ha square sub-plots within each larger plot (Fig. 1). Within the subplots, we randomly sampled 98 saplings (> 1 m height, < 10 cm diameter at breast height (DBH)) from the most abundant species for age structure analysis by obtaining cores or cross sections within 10 cm of the root collar; we numbered each tree in the sub-plots and selected trees from each species using randomly generated numbers. The number of saplings selected within a species was consistent with species relative densities (Clark 2003; Table 1). By sampling smaller size trees at the base, we could examine recruitment response to recent fire events at a near annual resolution (Villalba and Veblen 1997); all cores and cross sections either hit pith or were determined to be within 1 or 2 years of pith.

Fire scars from four of the most abundant tree species at the KAFP, *Q. stellata*, *Q. marilandica*, *Carya texana*, and *Q. shumardii*, were used to reconstruct the fire history of the KAFP. We obtained 11, 8 and 8 cross sections from dead tree logs or snags within the Southwestern Slope, Northeastern Slope and Bench stands, respectively. We also obtained 2 cross sections along the main ridgeline, just outside of the designated stands' boundaries. For downed logs, cross sections were taken as close to the log's base as possible (< 30 cm from base) to improve chances of detecting injury from fire (Guyette and Cutter 1991; Smith and Sutherland 1999). We similarly obtained wedges from the base of standing snags. To provide a fire history of most recent fire events, we also documented fire scars on sapling cross sections. We analyzed 13, 3, and 2 saplings that contained fire scars from the Southwestern Slope, Northeastern Slope and Bench stands, respectively. Including dead trees and saplings, we collected a total of 46 samples for the fire scar analysis from post oak (n=23), blackjack oak (n=10), hickory (n=9) and shumard oak (n=4).

Dendrochronological techniques

Sapling and dead tree samples were dried and sanded with progressively finer grades of sandpaper (100-400 grit) and cross-dated using a regional post oak chronology that was available in the International Tree-ring Data Bank (ITRDB) (NOAA 2002). Cross-dating provides confidence that samples were dated to the exact calendar year (Douglass 1941; Stokes and Smiley 1996). Sapling tree-ring widths were measured to the nearest 0.001 mm using a Velmex stage micrometer. Portions of cores containing rot were not measured. Many of the cross sections exhibited eccentric ring growth and were measured along the radius that was intermediate in average ring width. We were not able to cross-date nor measure the *Juniperus virginiana* samples because of the high occurrence of missing rings and false rings, and ages of these trees should be considered ring counts and not exact ages.

We identified fire scars on the dead tree samples and dated them to an exact calendar year. Fire scars are defined as wounds resulting from cambial death due to excessive heating or scorching (Smith and Sutherland 2001). All fire scars were associated with abnormal vessel formation and production of callus tissue, i.e., undifferentiated cells that contain little lignin (Smith and Sutherland 2001), which resulted in wide growth rings in the year of and sometimes just following the fire. Fire scars from two known and documented fire events at the KAFP in 1994 and 1996 were also used as reference for identifying fire scars in previous years. Fire scars sometimes produced woundwood ribs at the margins of the fire scar (Smith and Sutherland 2001), particularly if the fire injured a large portion of the tree's circumference. However, some fires caused relatively localized injury and did not cause formation of woundwood ribs.

We determined the recruitment conditions of *Q. stellata*, *Q. marilandica*, *Carya texana* and *Q. shumardii* saplings by examining initial and subsequent tree-ring growth patterns. Trees were considered "gap" trees (i.e., recruitment under high light conditions) if exhibiting high growth rates for the first 10 years from pith followed by flat or declining trends (Figure 2A) or if the tree exhibited average initial growth rates followed by flat or slightly increasing trends (Figure 2B) (Lorimer and Frelich 1989; Nowacki and Abrams 1997). Trees with low growth rates during the first 10 years from pith were considered to have originated under shaded conditions and were not considered gap trees (Figure 2C).

Fire scar analysis

Fire scar analysis was conducted using FHX2 software (Grissino-Mayer 2001). Samples were included in the analysis from the year of the first fire scar to the year of the tree's outer ring. However, samples were not included in the analysis for the time period between 2 consecutive fire events that lasted > 100 years. We performed fire scar analyses for each stand and across stands; separate analyses were also conducted for all fire events, and for moderate scale fires, defined as fires that scarred > 33 percent of sample trees. We determined the fire return interval data was not normally distributed according to the Kolmogorov-Smirnov (K-S) test for goodness of fit ($p<0.05$). We, therefore, used the median fire return interval as an indicator of fire frequency, which is a better descriptor of the central tendency of a dataset than the mean when the data is not normally distributed.

We calculated a fire index to determine how fire effects have changed through time (Guyette and Cutter 1991). The index intends to compensate for the effects of sampling size bias; generally, sample size will increase with more recent fire history, and number of fire scars detected will increase with increasing sample size. We calculated the index by dividing the number of fire scars in each 10-year time interval by the number of trees in the record for the same interval.

We performed temporal change analysis to determine if fire frequency has significantly changed since the onset of European settlement in the area. A t-test was used to determine differences in the mean fire return interval and the percent of trees scarred for two time periods, 1772 to 1907 and 1908 to 2001. The first time period represents the beginning of the fire scar record to Oklahoma statehood, which coincided with the beginning of European settlement in Osage County; prior to 1907, the county was occupied by Osage and Cherokee Native Americans. The data were first transformed to the standard normal distribution to apply the t-test. We also performed a non-parametric K-S test, which uses a d-statistic. The test determines differences in any fire interval year between the distributions of the two time periods. A relatively large difference is indicative of a change in the fire regime.

Analysis of climatic effects

Instrumental PDSI from 1896 to 2001 and reconstructed PDSI for 1800 to 1895 were obtained by averaging data from grid points 81, 82, 93 and 94 in central Oklahoma (Cook et al. 1999). The PDSI ranges from -4 (extreme drought) to 4 (extreme wet) and represents several environmental variables that affect tree growth, including drought duration, soil water holding capacity, temperature and precipitation (Palmer 1965). We adjusted the reconstructed values by multiplying by the ratio of the two variances:

$$\mathrm{rPDSI} \times \left(\frac{\sigma_{\mathrm{iPDSI}}}{\sigma_{\mathrm{rPDSI}}} \right) = \mathrm{adjPDSI},$$

where rPDSI, iPDSI, adjPDSI are the reconstructed, instrumental values and adjusted reconstructed values, respectively. The PDSI chronology was smoothed using a local smoothing technique involving tricube-weighting and polynomial regression available in SigmaPlot v. 7 (SPSS 2001).

We conducted a superposed epoch analysis using program EVENT (Cook et al. 1997) to determine if climate differed in years preceding, during or following a fire event. We conducted the analysis for two types of fire events, a moderate scale fire as described above, and a large scale fire, defined as a fire that burned in all three stands. The latter type of fire event would represent only the most widespread fires at the study site. We used the PDSI chronology as an indicator of climate. The EVENT program computes average PDSI values for a window of time surrounding a fire year and compares them to randomly generated predicted values. The predicted values represent 1000 random simulations generated for each fire event. A departure value is then calculated for each year in the event window that represents the actual value minus the predicted value. A statistically significant departure value is detected when the actual value is greater than or less than the 95 percent confidence limits (based on a normal distribution) of the predicted value.

Results

Topoedaphic and temporal patterns of fire frequency

Seventy-seven fires occurred on the KAFP from 1773 to 2001 at approximately 2 year intervals (Fig. 3 and Table 2). Moderate scale fires occurred every 8.5 years. Approximately 40 percent of fires scarred only one tree in our sample. Fires occurred most frequently in the Southwestern Slope stand and least frequently in the Northeastern Slope stand. The Bench stand had the longest single fire free interval (62 years).

Number of fires and number of scars per tree increased over the last 150 years (Fig. 3 and Fig. 4), and the fire return interval was significantly shorter after 1907 (Table 3). The K-S test provided further support for difference in the fire regime between the two time periods (Table 3). Although, the percent of trees scarred was significantly lower after European settlement (Table 3), the number of samples in the fire chronology was also higher (Fig. 2) and potential for sample size bias in this analysis may exist.

Effects of climate

The superposed epoch analysis indicated that climate was a contributing factor in the occurrence and spread of fire. PDSI was significantly lower for one year preceding moderate scale fires (n=9) and for three years preceding large scale fire events (n=3) (Fig. 5). Furthermore, the most prolonged wet and cool period of the chronology (1800-1849) had the lowest fire index values (< 0.5), indicating minimum effects of fire during this time (Figs. 4 and 6). The concurrence of moderate and large-scale fire events with periods of below normal PDSI values can also be seen in Figure 5; the majority of moderate scale fires occurred subsequent to or during periods when PDSI was below normal. This pattern was especially noticeable for the two large scale fires in 1955 and 1957, which occurred during and one year following the most severe and prolonged drought of the 20th century.

Recruitment dynamics

Recruitment pulses of hardwood species tended to occur following fire events in each stand (Figs. 7). Sapling recruitment for the four hardwood species occurred within 2 years following a fire 57 to 100 percent of the time, depending on species. A large recruitment pulse occurred following the 1945 fire in the Southwestern Slope and Northeastern Slope stands. Fire in 1964 in the Southwestern Slope stand and fire in 1966 in the Northeastern Slope and Bench stands were also followed by relatively large pulses in recruitment. Recruitment response to fire was similar among species, except for *Juniperus virginiana*. This species tended to recruit during fire free periods, particularly in the Bench stand, where it had the highest abundance and appeared to be increasing in density.

The majority of saplings from all species and in all stands were classified as gap trees (Table 4), indicating that recruitment was more likely to occur under high light conditions. *Quercus stellata* and *Carya texana* generally had high initial growth rates followed by decreasing or flat growth trends. *Quercus marilandica* and *Q. shumardii* generally had average initial growth rates followed by flat growth trends. The Northeastern Slope stand had the highest percentage of gap trees (100 percent) and trees with high initial growth rates for all species, compared to the other stands. The Bench stand had the lowest percentage of gap trees for *Q. stellata* (73 percent).

Discussion

Support for predictions

We did not find support for our first hypothesis that fire frequency has decreased since European settlement. In fact, number of fires and scars per tree increased over time. These results differed from numerous studies conducted in oak forests throughout the mid-western and eastern United States, which have shown evidence for decreased fire frequency over the last one to two centuries (Guyette and Cutter 1991; Cutter and

Guyette 1994; Abrams et al. 1997; Orwig et al. 2001; Shumway et al. 2001). We did find support for our second and third hypothesis that climatic conditions affect fire frequency and that fire tends to promote recruitment of hardwood species. The concurrence of drought, fire and oak recruitment was not surprising given the strong influence that drought has on other aspects of stand dynamics in the region, including tree mortality (Rice and Penfound 1959), stand density (Johnson and Risser 1975) and annual tree growth (Stahle and Hehr 1984; Stahle et al. 1985).

Temporal changes in the fire regime

The historic fire return interval at the KAFP was shorter than those reported in Missouri Ozark forests (Guyette and Cutter 1991; 1994; Batek et al. 1999) and in oak gallery forests of Northeastern Kansas (Abrams 1985) of similar or larger size. The relatively short fire return interval may be at least partially related to the frequent occurrence of drought in the Cross Timbers (Stahle et al. 1985; Clark 2003), which may increase possibility for fire ignition and spread (Pyne et al. 1996). Frequent lighting strikes may also contribute to fire ignitions at the KAFP. Although lightning is not considered an important component of the historic fire regime in the Cross Timbers or Ozark forests (Guyette and Dey 2000), the unique topography and landscape features may be contributing factors in lightning caused ignitions. The KAFP has relatively high elevation on the northwest-facing bluffs along the Keystone Lake Reservoir of the Arkansas River, which may increase probability of lightning strikes (Bergeron 1991). The influence of lightning on fire ignition was further substantiated by the fact that 40 percent of all fire events were only found in one sample tree, indicating a high occurrence of relatively localized fires. However, more data is needed to examine lightning effects on the fire regime of this forest.

The increase in fire frequency after European settlement cannot be easily explained, but is probably related to cultural influences on the fire regime. Following statehood, human population in the region has increased, which will increase the potential for ignitions (Guyette and Cutter 1991; Guyette et al. 2002). While fire frequency has increased since European settlement, the percent of trees scarred after 1907 was significantly lower, indicating a possible decrease in the ability of fire to spread across the landscape. We must consider that sample size bias may be a contributing factor in this finding, but construction of manmade barriers (e.g., roads) and construction of Keystone Dam in 1960, would have reduced the ability of fire to spread across the landscape. This process has been referred to as a "fuel-fragmentation" stage (Guyette et al. 2002).

Drought influences on fire

The fire regime of this forest was partially controlled by climatic fluctuations, with the highest probability of fire following periods of drought. The most widespread fires followed extended drought conditions, but even short duration droughts appeared to encourage fire. The relationship between fire and climate has been conflicting among past studies, even within the same climatic region. Cutter and Guyette (1994) showed a lack of a relationship between fire and drought, which they attributed to the frequent burning by Native Americans in the area. In contrast, large-scale fire events were associated with drought in a *Quercus stellata* savannah in the Ozarks (Guyette and Cutter 1991). Drought is probably an important contributing factor to the historic and current fire dynamics of closed canopy forests throughout the region. Cross Timbers species are particularly sensitive to climate, producing narrow rings (Stahle and Hehr 1984), and exhibiting high mortality during severe droughts like that of the 1950's (Rice and Penfound 1959). We suspect that fires tended to occur in the year following drought because of increased large fuel loads related to drought-induced mortality of trees (Rice and Penfound 1959; Jenkins and Pallardy 1995; Olano and Palmer 2003) coupled with a return to normal fine-fuel loads of herbaceous cover, which would facilitate fire spread.

Differences across the topoedaphic gradient

We attribute the differences in fire return intervals among stands to differences in slope position and aspect. The Southwestern Slope and Bench stands would putatively have the highest solar radiation levels, because of their reduced canopy cover and aspect (Pyne et al. 1996; Clark 2003). These stands would, thus, have the highest probability of fire ignition and spread, as our results support. In contrast, the Northeastern Slope stand would have the highest fuel moisture levels and less probability of fire. This stand also has some protection from fire to the east, due to the presence of a drainage (Fig. 1), which may serve as a natural fire break. Additionally, this stand would be protected from fires carried by westerly winds, due to its northeasterly exposure.

Sapling recruitment response to fire

Oak recruitment into the sapling layer constituted one or more distinct cohorts that were formed following fire events. Our results support theories that oaks exhibit a "bottleneck" effect, whereby recruitment from seedlings to saplings is encouraged by periodic disturbances (Johnson 1992; 1993; Johnson et al. 2002). Evidence of the bottleneck effect in this forest is also supported by previous studies at the KAFP that showed seedling populations were high (~6000 to 12000 trees ha^{-1}), while sapling populations were relatively low (~1500 to 2000 trees ha^{-1}) (Clark 2003, *in press*).

According to the tree-ring analysis, oaks appeared to recruit under high-light conditions, indicative of disturbances that would remove portions of the midstory or overstory (Lorimer and Frelich 1989; Nowacki and Abrams 1997). Oaks were most likely to recruit under canopy gaps in the more mesic Northeastern Slope stand, as evidenced by the higher percentage of gap trees in this stand. We suspect that the higher canopy density in this stand would not allow oaks to recruit without removal of some portion of the canopy.

Oaks have adaptations, such as thick bark and deep rooting, that allow them resistance to fire (Hengst and Dawson 1994; Abrams 1996). Additionally, fire promotes prolific sprouting of oaks, particularly for the more xerophytic species (Penfound 1968; Crow et al. 1994; Johnson et al. 2002; Clark *In press*). *Carya texana* was also encouraged by fire in this forest, indicating that this species may have similar adaptations and recruitment dynamics as the oak species. In contrast to hardwood species, fire appeared to restrict the establishment of *Juniperus virginiana*, a species that has been invasive in prairie and glade communities throughout the Midwest (Bragg and Hubert 1976; Engle et al. 1996). *Juniperus virginiana* appeared to recruit under fire-free conditions and would likely increase in these stands in the absence of fire (Beilmann and Brenner 1951). The sapling population structure suggests that this species is increasing in the Bench stand, with no recruitment prior to 1964. This finding is further substantiated by the fact that large overstory species were relatively rare in this stand (Clark 2003). The apparent increase in cedar sapling populations in the Bench stand could not be explained by a reduction in fire frequency. Instead, we attribute the changes in cedar populations to the seed rain from surrounding prairie and glade areas being invaded by this species (Snook 1985; Engle et al. 1996). Additionally, establishment and competitive ability of *Juniperus virginania* was likely favored by the stand's more droughty conditions (Ormsbee et al. 1976; Wittwer 1985; Oswald et al. 1996; Clark 2003).

Conclusions

The sequence of drought, fire and hardwood recruitment were important to the long-term maintenance of forest composition and structure. We speculate that increased large-fuel loads accumulated during the first years following drought and return to normal fine-fuel loads the year following drought would favor fires during this time. Fire promoted sprouting of hardwood species and probably helped to create or maintain canopy gaps, in addition to gaps formed during periods of drought. In contrast, fire appeared to restrict recruitment of the invasive species, *Juniperus virginana*. Despite relatively high fire return intervals, this species was increasing in areas with favorable micro-site conditions. The apparent seed rain from cedar-invaded fields and prairies throughout the Cross Timbers region is likely a contributing factor. Unlike many other dendroecological studies in eastern North America, fire frequency has not decreased since European settlement. Maintenance of a relatively high fire return interval was probably related to region's frequent occurrence of drought, increase in human ignitions, and ignition by lightning strikes.

This study represented a unique opportunity to examine the disturbance history and recruitment dynamics of an old-growth forest in the Cross Timbers. Large tracts of remnant oak stands exist throughout the Cross Timbers (Therrell and Stahle 1998), and understanding the factors affecting their long-sterm sustainability will become more important as society simultaneously demands and threatens forest conservation. Climate change could affect fire frequency (Bergeron et al. 2002) and thereby alter the sequence of drought and fire needed to maintain species composition of this forest (Wyckoff 1984). Conservation or restoration of old-growth forests in the Cross Timbers will require understanding the complex interactions between climate, topoedaphic conditions, and anthropogenic influences (Guyette and Dey 2000).

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Table 1. Number of saplings sampled for age structure analysis in each stand.

Species	Southwestern Slope	Northeastern Slope	Bench
Quercus stellata	21	11	11
Q. marilandica	10	12	7
Carya texana	6	2	0
Q. shumardii	0	5	0
Juniperus virginiana	3	1	9
Total	40	31	27

Table 2. Median fire return interval (FRI) with associated coefficient of variation (CV) by stand for all fire events and for moderate intensity fires (>33 percent scarred).

	Southwestern Slope	Northeastern Slope	Bench	Across stands
All fires:				
FRI	2.5	5.5	3.5	2.0
CV	0.86	1.17	1.65	0.9
min interval	1	1	1	1
max interval	18	45	62	15
Moderate intensity fires:				
FRI	5	7	7	8.5
CV	0.81	0.98	1.2	1.28
min interval	1	1	1	1
max interval	20	45	62	96

Table 3. Differences in fire return interval and percent trees scarred for pre and post European settlement time periods. .

	Time period		
	1772-1907	1908-2001	
Fire intervals:	Mean		K-S d-stat
All fires	4.1[†] (3.5)	2.0 (1.17)	0.322[‡]
Moderate intensity fires	13.4 (18.3)	16.3 (18.3)	0.417
Percent trees scarred:			
All fires	27.8[†] (17.9)	16.6 (10.6)	0.413[‡]
Moderate intensity fires	48.9 (20.7)	41.9 (10.3)	0.306

[†] Differences between means of two time periods were significant ($p<0.05$).

[‡] D-statistic was significant ($p<0.05$)

Table 4.Percent gap trees and percent of trees exhibiting initial and subsequent growth patterns for saplings sampled at root collar.

	Southwestern Slope			Northeastern Slope				Bench	
	QUST	*QUMA*	*CATE*	*QUST*	*QUMA*	*CATE*	*QUSO*	*QUST*	*QUMA*
n	21	10	6	11	12	2	5	11	7
Gap trees	86	80	100	100	100	100	80	73	86
Initial growth:									
High	57	20	67	82	90	100	20	55	29
Average	29	60	33	18	10	0	60	18	57
Low	14	20	0	0	0	0	20	27	14
Subsequent growth:									
Decreasing	38	0	50	81	75	100	0	28	29
Increasing	14	10	0	0	0	0	20	18	14
Flat	48	90	50	18	17	0	60	36	57
Irregular	0	0	0	0	8	0	20	18	0

Figure 1. Distribution of Cross Timbers region (adapted from Küchler, 1964) with approximate location of Keystone Ancient Forest Preserve and location of plots in each stand (●= Southwestern Slope stand; ■=Northeastern Slope stand; ▲=Bench stand).

Figure 2. Examples of gap trees exhibiting high initial growth rates (A) and average initial growth rates (B) followed by flat growth trends; example of a tree initiated under shaded conditions with low initial growth and increasing growth trends (C).

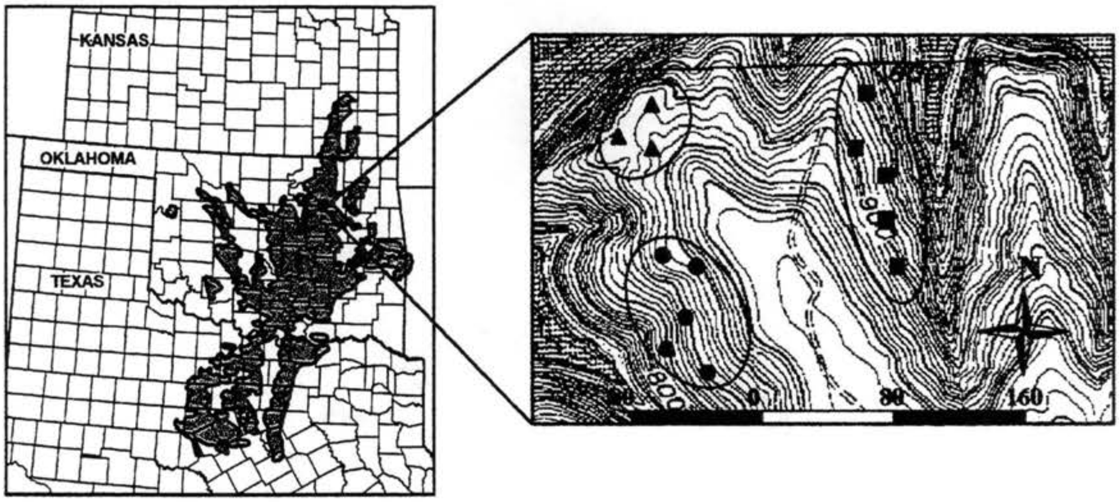
Figure 3. Fire chronology where horizontal lines represent individual sample trees and vertical dashes represent fire events; dashed horizontal line (-----) represents period not included in analysis and solid horizontal line represents (——) period included in fire analysis. Bottom bar is the master fire chronology for the entire forest;

Figure 4. Fire index values (scars per tree) per ten-year intervals. Top graph represents sample size used in analysis.

Figure 5. Departure from normal PDSI values surrounding moderate scale fire events (> 33 percent sample trees scarred; year 0 represents fire event; n=9) (A), and large scale fire events (fires burned in all three stands; n=3) (B); asterisks indicate years in which departure values were significant (p<0.05).

Figure 6. Palmer drought severity index (PDSI) chronology with smoothed curve and moderate (>33 percent trees scarred) and large scale (fires burned in all three stands) fire events.

Figure 7. Recruitment of saplings (aged at root collar) in the Southwestern Slope (A), Northeastern Slope (B) and the Bench (C) stands. Arrows represent moderate intensity fire events (> 33 percent sample trees scarred).


KANSAS
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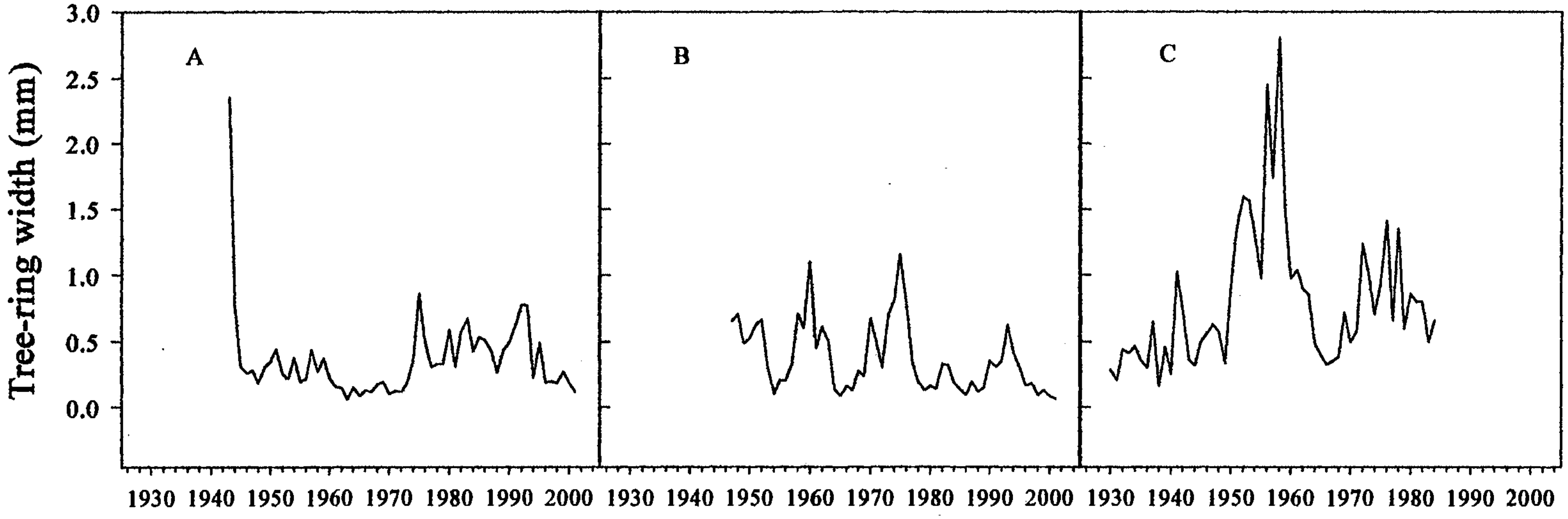
A
B
C
Tree-ring width (mm)
3.0
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2.0
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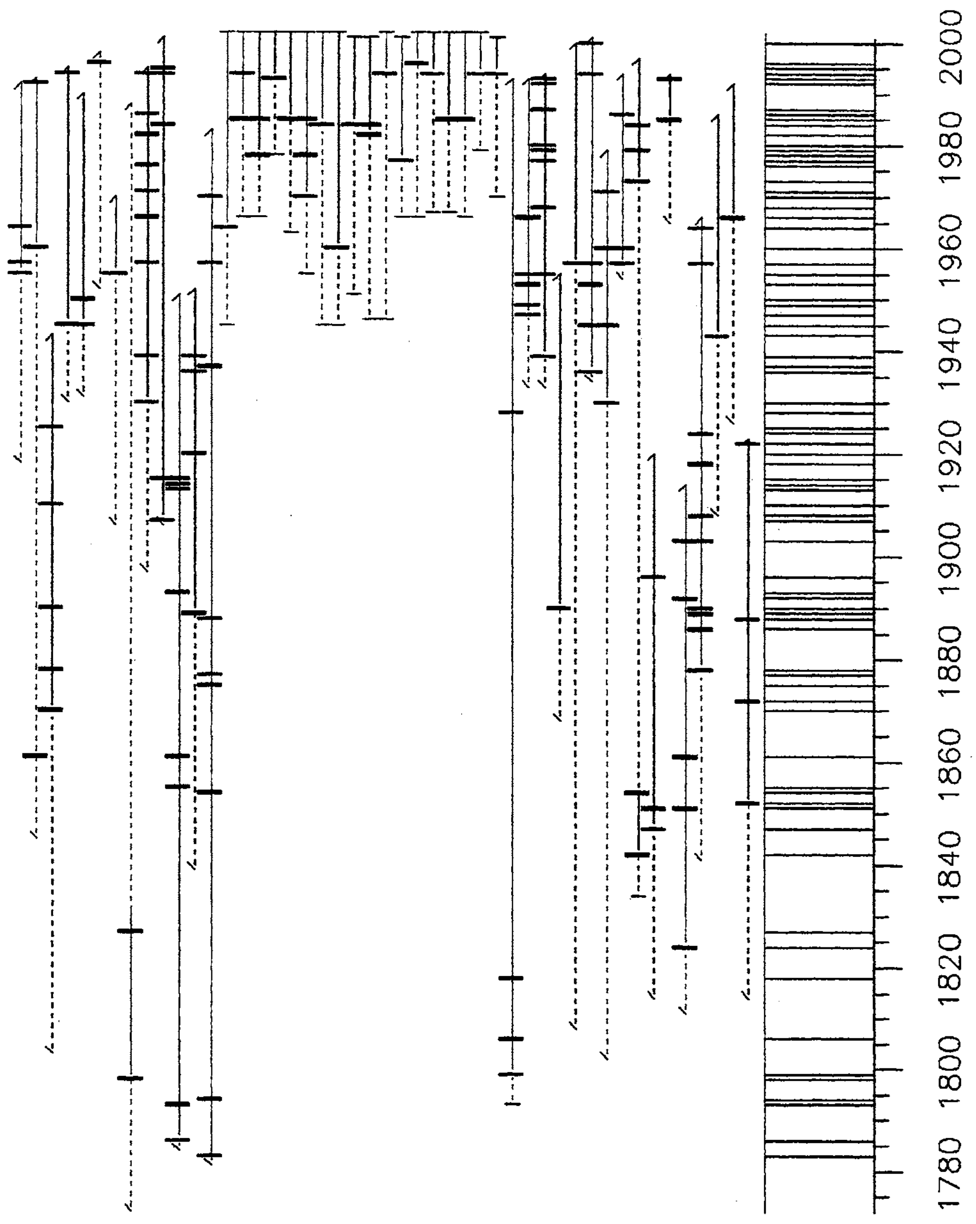
1930 1940 1950 1960 1970 1980 1990 2000
1930 1940 1950 1960 1970 1980 1990 2000
1930 1940 1950 1960 1970 1980 1990 2000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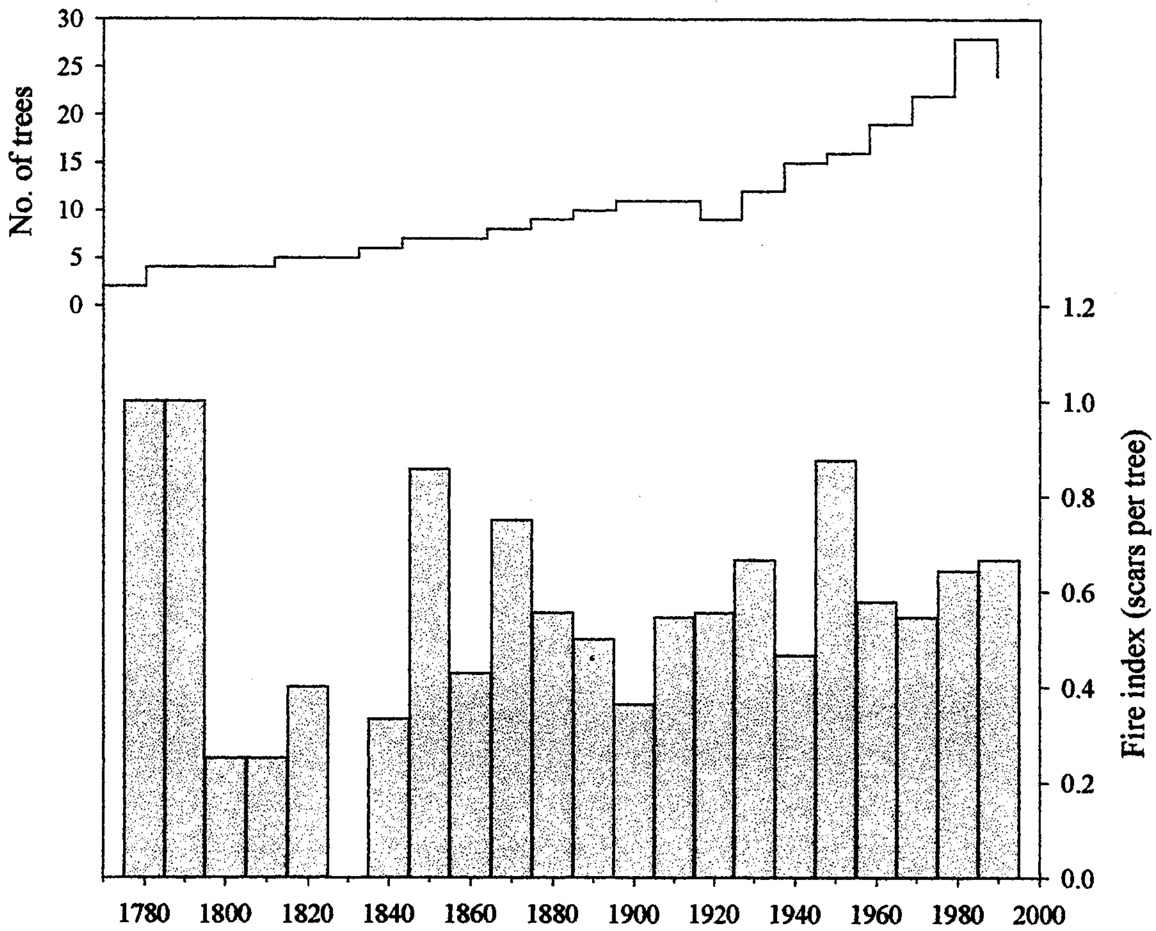
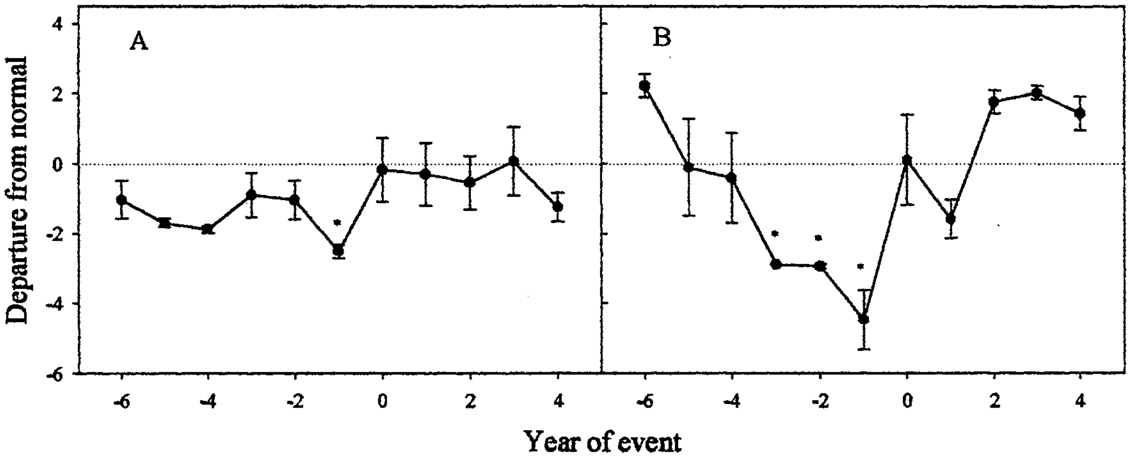
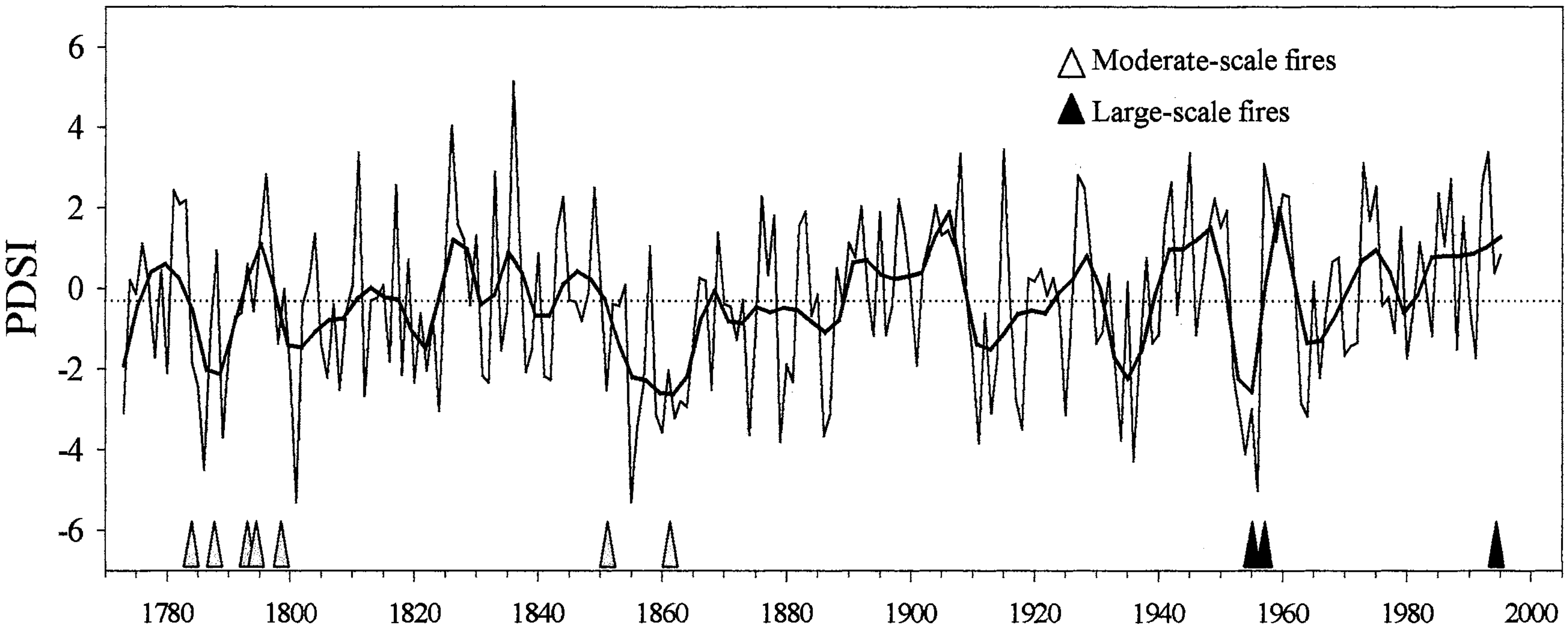
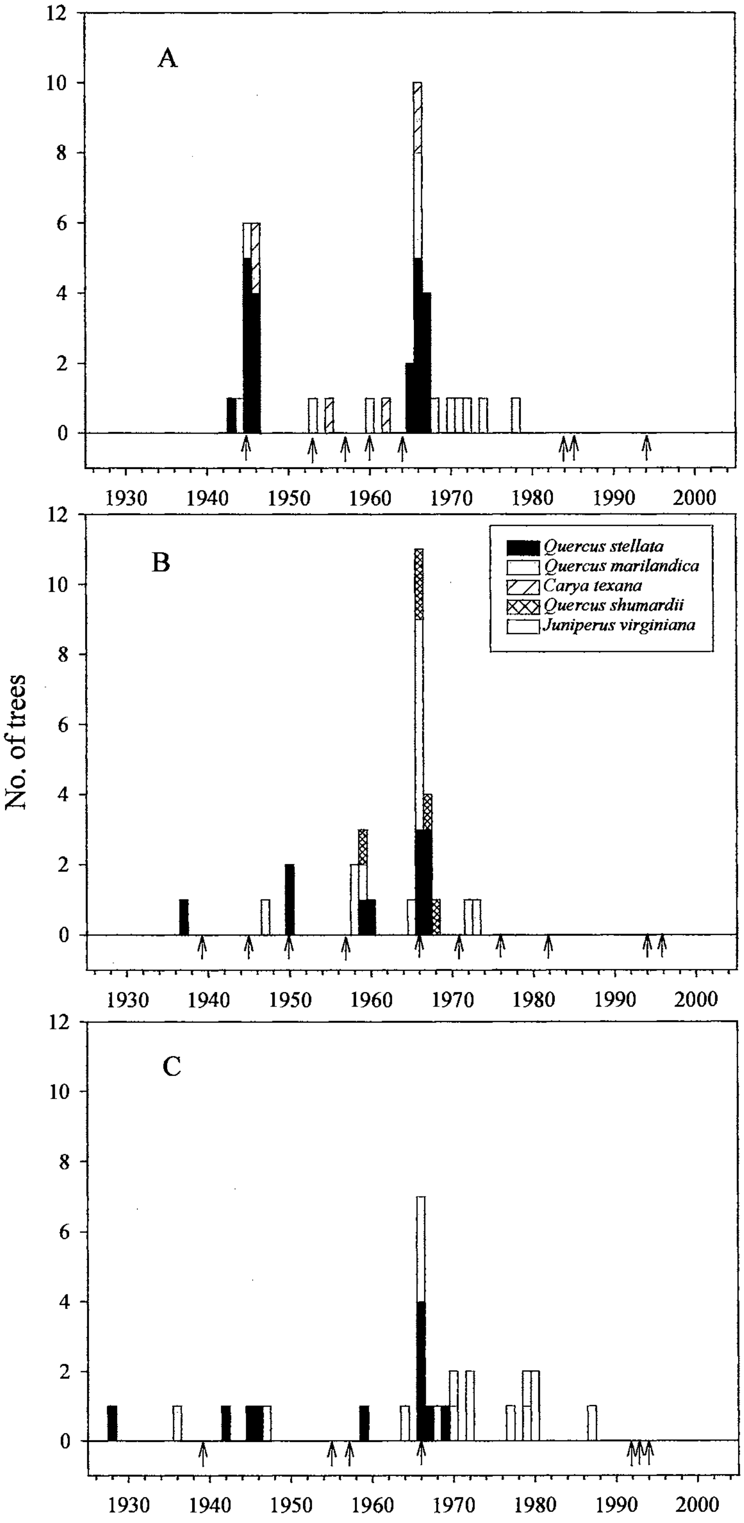
1960
1980
2000


No. of trees
30
25
20
15
10
5
0
Fire index (scars per tree)
1.2
1.0
0.8
0.6
0.4
0.2
0.0
1780
1800
1820
1840
1860
1880
1900
1920
1940
1960
1980
2000


A
B
Departure from normal
4
2
0
-2
-4
-6
-6
-4
-2
0
2
4
-6
-4
-2
0
2
4
Year of event
*
*
*
*


△ Moderate-scale fires
▲ Large-scale fires
PDSI
6
4
2
0
-2
-4
-6
1780
1800
1820
1840
1860
1880
1900
1920
1940
1960
1980
2000



A
B
C
No. of trees
0
2
4
6
8
10
12
1930
1940
1950
1960
1970
1980
1990
2000
■ Quercus stellata
☐ Quercus marilandica
▨ Carya texana
▩ Quercus shumardii
☐ Juniperus virginiana

VITA ②

Stacy Clark

Candidate for the Degree of

Doctor of Philosophy

Thesis: STAND DYNAMICS OF AN OLD-GROWTH OAK FOREST IN THE CROSS TIMBERS OF OKLAHOMA

Major Field: Plant Science

Biographical:

Personal Data: Born in Atlanta, Georgia, on March 26th, 1974, raised in Chattanooga, Tennessee until the age of 18. Parents are Mr. James Lay, Jr. and Ms. Paula Lay

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Professional Membership: Society of American Foresters, Forest History Society, Oklahoma Academy of Sciences, Tree-ring Society, Xi Sigma Phi