DISTURBANCE HISTORY AND DYNAMICS IN FOREST AND PRAIRIE COMMUNITIES

By

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DISTURBANCE HISTORY AND DYNAMICS IN FOREST AND PRAIRIE COMMUNITIES

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CHAPTER I

INTRODUCTION

Disturbances, of some type, affect every vegetation type on the globe. Disturbances alter the composition of biotic communities, affect nutrient cycling, and shift the functioning of ecosystems (Sousa 1984), shaping the biological world in myriad ways. Disturbances may occur with relatively regular periodicity or infrequently, occurring with frequency equal to or longer than the lifespan of the dominant vegetation of the ecosystem (Turner et al. 1998). Understanding the history and legacy of disturbance in an area is an important component for understanding its present dynamics and composition (Foster et al. 2003).

In this dissertation, I present three studies examining the history and effects of disturbances in different ecosystems. In two studies I use tree-ring records to examine long-term dynamics of fire events and the cause of growth releases. In the final study, I examine long term patterns of compositional and architectural change in two stands following a windstorm. In the next paragraphs, I give a brief description of each study and its primary findings, and reflect on the work contained herein.

In chapter II, I present the reconstructed fire history of The Nature Conservancy's Tallgrass Prairie Preserve (TGPP), located in Osage County, Oklahoma. To reconstruct fire history, I examined cross-sections of post oak (*Quercus stellata*) stems for fire scars recorded in the tree-ring record. Assigning each scar to its year of occurrence, I was able to reconstruct the fire occurrence frequencies for several sites within the preserve spanning the last two and a half centuries. Shifts in the TGPP's historical fire regime were coincident with shifts in historical land uses, primarily the shift from traditional uses under Native Americans to the establishment of the cattle industry. Ranchers in the region increased fire application, resulting in more frequent fires than that which occurred during Native American time periods. Despite the intensification of the fire regime in the region, the Flint Hills, in which the TGPP is located, is unique among North American landscapes for having a relatively uninterrupted history of fire occurrence. Chapter II is presently under review by the *Journal of Vegetation Science* and is co-authored by Michael W. Palmer.

In chapter III, I evaluate two different methods for their efficacy in identifying tree growth-releases in tree-ring series in the xeric Cross Timbers forest. Trees constrained by competition or resources may experience a sustained increase in growth rate if a disturbance frees a tree from competition or makes additional resources available (e.g., light). Numerous studies have implemented different criteria for the detection of releases, primarily in more mesic forest systems (Rubino & McCarthy 2004). Here I tested two methods, the percent growth change method and time series analysis with ARIMA models and intervention detection. Both methods were successfully implemented but were unsuccessful in identifying disturbance-induced growth-release events. The sorts of disturbances that would be expected to produce a tree-release event (i.e., windstorm, ice storm, tree fall, etc.) all occur within the

Cross Timbers region, but tree growth appears to be so limited by climatic conditions that they appear to be relatively insensitive to the effects of disturbances.

In chapter IV, I describe the recovery and dynamics of two forests twenty-five years after a windstorm at the Cedar Creek Ecosystem Reserve in Minnesota. Both sites (one oak dominated, the other pine dominated) sustained major damage, which reduced a substantial portion of the basal area in both sites. In the years after recovery, the two stands are converging in species composition as late successional species are becoming more abundant in each site. In this case, it appears that disturbance has allowed for accelerated succession, where late successional species have benefited by having early successional dominants removed from the forest overstory. Additionally both forests have had similar structural patterns through time, though in the most recent samplings, it appears that the pine forest is approaching the pre-disturbance architectural state of the forest. Chapter IV has been contributed to by Vaskar Thapa and Michael W. Palmer.

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As evident in the preceding summaries, various types of disturbances affect forests. In the studies presented in this dissertation, I have taken different approaches in examining the effects of disturbance. These different approaches highlight important, but different generalizations about the nature of disturbance:

In evaluating the fire history of the TGPP, we see not only the temporal dynamics of fire, but in this case, how its occurrence is strongly affected by human activities. Anthropogenic burning is an ancient practice, variously conducted to promote desirable vegetation, fireproof human developments, reduce invertebrate pests, and facilitate wildlife hunting (Pyne 2001). In the forests of Eastern North America, anthropogenic fire served to promote oak dominance and maintenance (Abrams 1992). Oak forests are presently jeopardized by decades of fire exclusion and suppression which has facilitated the increase of more mesophytic tree species (Nowacki & Abrams 2008). Additionally, the tallgrass prairies of the North American Great Plains are thought to owe their origin and maintenance to anthropogenic fires that reduced or eliminated woody cover (Axelrod 1985, Anderson 2006). Even though not all disturbances are necessarily anthropogenic in origin, few biological communities exist that have not been altered to some extent by human presence/activities, either by modification of the physical environment or the introduction of new species. Understanding the nature of historical land-uses/human activities is important not only for understanding present community composition, diversity, and structure, soil characteristics, nutrient cycling, etc. (Foster et al. 2003), but also for improving the effectiveness of conservation and management for natural areas (Swetnam et al. 1999).

The study of growth releases in post oak tree-ring series was unable to ascribe growth release events to disturbance events, illustrating that though disturbances may be frequent, or devastating, they may not necessarily produce expected effects given the action of other environmental or biological factors. For another example, an experiment that replicated windstorm damage in a forest, showed that biogeochemical cycling remained unexpectedly stable at the site despite massive physical disruption to the soil (Cooper-Ellis et al. 1999). This stability was attributed to the tree sprouting response which served to mediate the soil environment by rapidly producing a new forest canopy post-disturbance (Cooper-Ellis et al. 1999). Understanding the various interacting factors, natural history, and basic biology of a species or community is critical in understanding and interpreting responses to disturbance.

In examining compositional change in Minnesota oak and pine forests following a windstorm, we see that disturbance affects the process of community change, or succession, due to differential mortality and/or the response of species in the period post-disturbance. In this case succession accelerated as later successional tree species have become more prevalent at both sites. Community change following disturbance is not a novel finding, but it again highlights the importance of disturbance in altering the temporal continuum of community development.

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Globally, human activities, both direct and indirect, are altering disturbance regimes and, consequently, also altering the dynamics and composition of communities around the globe (Turner 2010). These changes will inevitably result in challenges for maintaining biological diversity and ensuring the stability of ecosystem processes for conservationists and land managers. Using different approaches in studies of disturbance will increase our understanding and ability to accurately predict the consequences of disturbance regime change. In the future, research on the effects and outcomes of disturbance should continue to pursue a more integrated approach, evaluating the whole suite of disturbances and/or environmental variables that affect community change. Understanding interactions between different types of disturbances, invasive species, changing climate, and altered land-uses will better facilitate land management and the processes that affect the dynamics of species, communities, and ecosystems.

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CHAPTER II

A CONTINUOUS HISTORY OF FIRE AT THE TALLGRASS PRAIRIE PRESERVE, OSAGE COUNTY, OKLAHOMA

Abstract

Questions: Given that most modern fire-prone landscapes have experienced disruptions of their historic fire regimes, are the well-maintained tallgrass prairies of the Flint Hills reflective of a history of continuous fire occurrence? Did fire frequency, severity/size, and seasonality change under different periods of land use? Is fire occurrence related to drought conditions?

Location: Forest edge of Cross Timbers stands at the Tallgrass Prairie Preserve located in the Flint Hills of Osage County, Oklahoma, USA.

Methods: 76 *Quercus stellata* cross-sections were collected from Cross Timbers stands at or near the grassland edge. Dendrochronological methods were used to identify years of formation for tree-rings and fire scars at sites in the TGPP. Superposed Epoch Analysis was used to evaluate the effect of drought conditions on fire occurrence.

Results: For the preserve, 46.6% of the years between 1729 and 2005 recorded fire. At the 1.3km^2 East Side site (N=41), the mean fire interval between 1759 and 2003 was 2.59 years. Fire interval length changed over the period of record, decreasing from a mean fire interval of 3.76 years in the early part of the record to 2.13 years in modern times. No extended periods occurred where fire was absent from the study area. Drought conditions had no significant effect on fire occurrence.

Conclusions:

In contrast with many fire-prone landscapes worldwide, the prairies of the Flint Hills have experienced no recent fire suppression or exclusion. Changes in fire frequency mark transitions in land-use, primarily from being traditionally used by Native Americans to being managed for cattle production.

Keywords

Cross Timbers; Dendrochronology; Fire history; Fire suppression; Osage Nation; *Quercus stellata*; Tallgrass prairie; Tree-ring

Abbreviations

EAS = Euro-American settlement; MFI = mean fire interval; TGPP = Tallgrass Prairie Preserve

Introduction

Fire is a common disturbance, shaping the vegetation of nearly every biome of the world (Bond et al. 2005). Though common, fire is also a unique disturbance, not simply because of the effects it produces, but also because of the degree to which it can be manipulated and controlled by humans (Pyne 2001). Though humans have used fire for tens of thousands of years, the technological achievements of the twentieth century have made it possible to control fire on large scales (Pyne 2001). This ability, coupled with negative perceptions about the value of fire, resulted in its outright suppression or exclusion in many places (Pyne 2001; Mouillot & Field 2005).

The condition of recent fire suppression or exclusion is relatively common around the globe. Areas of the Campos vegetation of Brasil (Behling et al. 2007), Scandinavian forests (Arno 1998), eucalyptus forests in Australia (Ward et al. 2001), and coniferous forests in China (Chang et al. 2007) are among the many ecosystems worldwide that have experienced recent fire suppression due to changes in human management or land use. The consequences of fire suppression can be severe for biological systems, and may result in a loss of biodiversity, loss of ecosystem function, and structural and compositional ecosystem change (Swetnam et al. 1999; Bond & Keeley 2005; Nowacki & Abrams 2008). Lack of burning also results in the accumulation of high fuel levels that can burn with unprecedented intensity, increasing risk for both natural environments and human developments—which can confound efforts for ecosystem restoration (Varner et al. 2005). Not all areas have, however, experienced recent fire exclusion. Those places are, in general, characterized by a relatively undisrupted history of traditional management by indigenous peoples. Examples of such places include portions of the cerrados of Brazil (Mistry et al. 2005), African savannas (Sheuyange et al. 2005), and portions of tropical savanna in Arnhem Land, northern Australia (Yibarbuk et al. 2001).

In North America, Euro-American settlement (EAS) marked a dramatic shift in fire occurrence. In many eastern areas, initial settlement brought a brief increase in fire occurrence as early settlers intensively applied fire to clear land for agricultural development (Guyette et al. 2002; Guyette et al. 2003; Guyette & Spetich 2003). This initial pulse of fire was supplanted by an era of fire suppression where cultural attitudes shifted and during which settlers sought to protect their developments from the potentially damaging effects of fire (Guyette et al. 2002; Guyette & Spetich 2003). The pattern of post-settlement fire suppression seems to hold for much of North America's Great Plains, with the exception of the tallgrass prairies of the Flint Hills region, located in Eastern Kansas and Northern Oklahoma.

Like many other grassland systems, the tallgrass prairie is, in part, a product of fire (Axelrod 1985). Since the last glacial maximum, the unique climate, geology, and topology of the North American continental interior provided the context for fire and grazing to promote the formation of vast grasslands (Axelrod 1985). These grasslands supported perhaps tens of millions of bison (Shaw 1995) which in turn supported the native peoples of the plains. Early historical accounts from settlers and explorers indicate that Native Americans were responsible for igniting many grass fires on the prairies (Irving 1835; Higgins 1986). Native Americans used fire for a number of purposes (Russell 1983), but fire's greatest utility likely came in bison hunting. Fresh growth available in recently burned patches serves to attract and concentrate animals (Coppedge & Shaw 1998) thereby facilitating hunting.

As alluded to above, the fire history of the Flint Hills region does not appear to include any extended periods of fire suppression. The Flint Hills contain the most expansive (26 280 km^2) and intact tallgrass prairies remaining in North America (Samson et al. 2004). The prairies are primarily used as rangeland for livestock production (Kollmorgen & Simonett 1965; Kindscher & Scott 1997). In order to promote grass growth and control woody plant encroachment, ranchers in the region burn their pastures on a near annual basis, a practice that has been ongoing since cattle were first brought to graze the Flint Hills (Hensel 1923; Smith & Owensby 1978; Fuhlendorf & Engle 2001). Fire clearly is, and appears to have been, an important and regular feature of the Flint Hills region, but to date no study has clearly characterized the fire history of the region.

Though a few sites (mostly in northern prairies) have yielded fire chronologies from charcoal sequences (e.g., Brown et al. 2005; Nelson et al. 2006), long-term fire patterns are generally not well-recorded in grasslands. Several sites throughout the Great Plains have, however, yielded long-term fire history information from fire scars recorded in the rings of trees in or near grasslands (e.g., Abrams 1985; Clark et al. 2007; Stambaugh et al. 2009). Scars form when fire kills a portion of the cambial tissue around the tree bole (Smith & Sutherland 2001) leaving a record of the event. Dendrochronological (tree-ring) analysis of fire scars is an often used method for reconstructing the historical fire regime of an area. In the southern Flint Hills, grasslands form a mosaic with the Cross Timbers forest, a long band of post oak (*Quercus stellata*) and blackjack oak (*Quercus marilandica*) dominated forest spanning portions of Kansas, Oklahoma, and Texas. The Cross Timbers forest is unique among eastern forests in that it contains substantial amounts of old-growth forest (Therrell & Stahle 1998). In the Cross Timbers, fire typically produces tree-mortalities only under unusually extreme fire behavior conditions (Engle et al. 1996), therefore trees at or near the forest edge have the potential to serve as a long-term proxy record of the prairie's fire history.

For this study, I seek to address the following questions: 1) Is the occurrence of fire within the Flint Hills region continuous or have periods of fire suppression or exclusion occurred? 2) Are temporal changes in fire occurrence correlated with changes in human culture and land-use? 3) Have climatic conditions (drought) played a significant role in fire occurrence? To address these questions I collected cross-sections from post oaks for fire scar analysis at The Nature Conservancy's Tallgrass Prairie Preserve (TGPP), located in the Flint Hills of northern Oklahoma. This study expands on previous tree-ring based Flint Hills fire history reconstructions by Abrams (1985) at the Konza Preserve in the northern Flint Hills and Shirakura (2006) at the TGPP by developing a multi-century chronology with greater sample depth through time.

Methods

Site Description

The Nature Conservancy's TGPP was established in 1989 and is located north of Pawhuska in Osage County, Oklahoma (36° 56'N, 96° 25' W) (Fig. 1). The TGPP's 15 800 hectares make it the largest protected area of tallgrass prairie in North America.

Situated in the southern Flint Hills, the topography of the preserve is characterized by rolling hills. The limestone and sandstone soils of the preserve are thin and rocky, which precluded widespread cultivation in the region (Kollmorgen & Simonett 1965). The climate is continental with annual precipitation averaging 94 cm and temperatures ranging between -4° C and 33° C over the course of the year. The preserve's grasslands are dominated by C_4 grasses, including *Andropogon gerardii*, *Schizachyrium scoparium*, *Sorghastrum nutans* and *Panicum virgatum*. Approximately 10% of the preserve is Cross Timbers forest, dominated by post oak (*Quercus stellata*) and blackjack oak (*Quercus marilandica*).

Within the Flint Hills region, the most widespread land and cattle management system consists of annual burning followed by double-stocked livestock (Smith & Owensby 1978). Uniformly applied, this practice homogenizes much of the Flint Hills landscape (Fuhlendorf & Engle 2001). In contrast, the TGPP is managed with a randomized prescribed fire program (Hamilton 2007). On average, fire occurs on a three year rotation where 40% of the burns occur during the dormant spring season, 20% during the summer, and 40% during the dormant fall (Hamilton 2007). The preserve's bison unit is grazed by approximately 2700 animals (Allen et al. 2009). Cattle grazing is also conducted on the preserve as part of on-going cattle management research (Hamilton 2007; Allen et al. 2009). The overall management goal at the TGPP is to maintain a heterogeneous landscape capable of supporting a full complement of tallgrass prairie biodiversity (Hamilton 2007).

Site History

The land the TGPP encompasses was historically and is presently within the domain of the Osage Nation. In pre-EAS times, the tribe was primarily centralized in the Ozark Plateau of Missouri and Arkansas, but the Osage annually travelled to the western prairies to hunt bison and other game (Wilson 1985; Burns 2004). In 1832, American author Washington Irving vividly documented the Osage hunts, including observations of nine separate instances where Osage hunters set fire to the prairies (Irving 1835).

Beginning in the early 1800s, increasing pressure from and conflict with European and American settlers forced the Osage into a series of land concessions. In 1826, the American government assigned the Osage a reservation encompassing a 240 by 80 kilometer strip of land along the southern border of Kansas (Burns 2004). Displacement from native lands was certainly not unique to the Osage. Passage of the Indian Removal Act in 1830 forced many of the eastern tribes to head west to Indian Territory, resulting in the tragic Trail of Tears. The Cherokee were originally given the land that the TGPP now resides on (Burns 2004), but after the American Civil War (1861-1865), a new reservation was needed for the Osage as white settlers were increasingly and occasionally violently encroaching on their Kansas lands (Wilson 1985). Consequently, the Osage's Kansas lands were bought back by the federal government and the proceeds of that sale applied to the purchase of a reservation from the Cherokee (Wilson 1985). The 5665 km^2 purchased in 1873 exists today as Osage County, Oklahoma and are still to some extent under the jurisdiction of the Osage Nation.

The mid to late 1800s saw many changes to the area, notably the extirpation of bison, the introduction of cattle, the discovery of oil on the reservation, and increased settlement. The reservation's first cattle leases were authorized in 1883 (Burrill 1972), formally marking the beginning of cattle ranching on the reservation. In 1915, James A. Chapman and Horace G. Barnard established the Chapman-Barnard Ranch. At one point their ranch encompassed approximately 400 km^2 of the Osage Reservation (Warehime 2000). The Chapman-Barnard Ranch primarily ran a cow-calf operation which incorporated prescribed fire to improve pasture forage (Hamilton 2007). In 1989, a portion of their ranch was purchased by The Nature Conservancy, marking the establishment of the TGPP.

Data collection and analysis

I collected 76 full or partial post oak (*Quercus stellata*) cross-sections from the TGPP between 2006 and 2009 to use for our assessment of the TGPP's fire history. I cut cross-sections from dead trees that were knocked down during the installation of the preserve's bison fences. I also opportunistically collected samples from stumps or snags throughout the preserve. All samples I collected were within 500 m of the prairie/forest edge. Cross-sections were cut within 30 cm of ground level in order to capture the most fire scars. Since post oak's probability of scarring decreases with increasing diameter (Guyette & Stambaugh 2004), I sampled as wide a range of diameters as possible to minimize potential biases. I recorded the Universal Transverse Mercator (UTM) coordinates for each sample. Our sampling effort encompassed all the forested portions of the preserve (N = 76), but most of the samples came from four areas (Fig. 1): East Side (N = 41; 1.3 km^2), Bar-X Pasture (N = 14; 0.3 km^2), Sand Creek Ridge (N = 4; 0.02 km^2), and South Fence (N = 5; 0.01 km^2).

Cross-sections were surfaced using an electric planer and belt sander to reveal the cellular structure of the tree-rings and fire scars. I determined calendar years by cross-dating tree-rings using the skeleton plot technique (Stokes & Smiley 1968) and then measured the tree-ring widths with a Velmex measuring stage. I used the measurements to validate the accuracy of our dating using the program COFECHA (Holmes 1983). Fire scars were identified based on the presence of callus tissue and cambial injury (Smith & Sutherland 2001) and then assigned to the first year of growth response present in the wound. Seasonality of fire scars was determined based on the position of the scar within the ring and were classified as dormant (between rings), earlywood, latewood, and undetermined.

I used the FHX2 program (Grissino-Mayer 2001) to summarize fire scar statistics and graph and analyze fire events and fire return intervals for the preserve. I computed the mean fire return interval (MFI) for each site and the preserve as a whole. Additionally, since fire interval distributions are usually skewed, I used Kolmogorov-Smirnov Goodness-of-Fit tests to determine if the Weibull distribution modeled fire intervals better than normal distributions. I also used the Weibull model to calculate the upper and lower exceedance intervals that delimit significantly short or long fire intervals. Size of sampling area is important in fire history reconstructions since more fire events are typically encountered with increasing area. At approximately 1.3 km^2, the East Side site is comparable in area and sample size to other sites in the Cross Timbers region that researchers have assessed for fire history (e.g., Clark et al. 2007; Stambaugh et al. 2009)); therefore the East Side site will be the focus of several of our analyses.

Following Guyette et al. (2003) and Clark et al. (2007) I calculated a fire index for the East Side site in order to assess changes in fire frequency through time. This fire index compensates for changing sample size through time. In this study, as with most fire history studies, more recent periods tend to be better represented than older periods. In order to compensate for this temporal bias, I calculated the fire index by dividing the number of fire scars in each decade by the total number of trees in that same interval.

Sample size and time period covered was limiting for several sites, therefore I restricted our analysis of temporal change in fire intervals and severity to the preserve as a whole and samples collected at the East Side site. In order to statistically evaluate changes in fire intervals through time, I calculated fire intervals for four time periods: 1) traditional use period (pre-1826) — Osage were likely using the land in a more or less traditional manner, 2) population flux period (1826-1870) — corresponds with Osage removal to Kansas and replacement by the Cherokee, 3) transitional period (1871-1914) — corresponds with the return of the Osage, the extirpation of bison, the introduction of cattle, the discovery of oil and increasing EAS, and 4) ranching period (1915-1989) — era of the Chapman-Barnard Ranch. I also more broadly assessed pre-EAS and post-EAS fire intervals. I transformed our fire interval data to a standard normal distribution and performed *t*-tests ($\alpha = 0.05$) to determine if MFI differed between pre and post-EAS. Similarly, I tested for a significant difference between the traditional use period, and all subsequent periods defined above. I also tested changes in fire severity, defined as change in percent trees scarred for the different time periods.

Climate can also have an important effect on a region's fire regime. I used Superposed Epoch Analysis (Grissino-Mayer 2001) to determine the influence of regional droughts on fire event occurrence. Drought data was derived from long-term reconstructions of Palmer Drought Severity Indices (PDSI; Cook & Krusic 2004). I bootstrapped data for 1000 simulated fire events in order to derive confidence limits. I assessed a ten year window around each fire event (6 years preceding and 4 years succeeding) in order to determine if drought was significantly different from average during the time span. I performed Superposed Epoch Analysis on data from the East Side site on all fire events recorded by at least two trees.

Results

The tree-ring record I recovered from post oaks in this study spanned 277 years (1729-2005). Individual tree time spans covered between 60 and 244 years, averaging 116 years. Intercorrelation between tree-ring widths was 0.622 with a mean sensitivity (year to year variability) of 0.346. For the whole preserve, I identified a total of 292 fire scars occurring in 129 (46.6%) of the years (Fig. 2). Of the 255 fire scars that I was able to identify to season, 76.9% occurred during the dormant season, a time-frame spanning approximately mid August to early March . The preponderance of growing season fire scars (14.5%) occurred in the earlywood, indicating early-mid spring fires. The remaining 8.7% of fire scars occurred later in the growing season.

Fire intervals

During the period of record there were few extended time periods where fire did not occur (Fig. 2). Intervals of one year were most common in the composite record for the East Side site (Fig. 3A), though point samples (individual trees) tended to experience longer intervals (Fig. 3B). This pattern is consistent with that observed by Shirakura (2006) where they observed that only about 5% of their tree samples were scarred by a given fire. For the East Side site, the upper exceedance interval was 5.12 years and the lower exceedance interval was 0.52 years. Intervals outside of that range would be significantly long or short.

As seen in Fig. 4, fire index values fluctuated throughout the entire period of record; these fluctuations generally correspond with changes in human culture and/or land-use. During the end of the traditional use period in the 1820s there is an abrupt cessation of fire followed by a gradual increase in fire followed by another cessation in the 1890s, the middle of the transitional period. The first cessation is coincident with the Osage’s removal to their Kansas reservation. The second cessation is coincident with the establishment and expansion of ranching on the reservation. Fire persisted into the 20th century, apparently intensifying during the last two decades of the century.

For the whole preserve and the four sites, MFI for periods of record ranged from 2.04 to 6.74 years (Table 1). The Kolmogorov-Smirnov tests determined that the Weibull distribution adequately explained fire intervals for the preserve and individual sites. The Weibull median interval ranged from 1.72 to 3.87 years (Table 1). Again due to limited sample size at some sites, I only assessed temporal changes in fire intervals for the entire preserve and for the East Side site. As shown in Table 2, fire intervals were significantly different in the pre-EAS and post-EAS periods. Most of the change in MFI at the preserve occurred during the transitional and ranching periods (Table 2). Changes in severity of fire as determined by percentage of trees scarred were also significantly different between early periods and late periods, likely indicative of a shift towards patchier or less intense fires (Table 2).

Fire and drought

Superposed Epoch Analysis revealed no significant relationship between fire events and drought. Though no general pattern was evident, several years stood out that had apparently widespread fires (more than 4 trees recording fire scars) in years of moderate to severe drought. Notable years where fire events and drought conditions coincided were 1812, 1874, 1939, 1953, and 1957. Since the late 1970s, well-recorded fires tended to occur more in years of wetter than average conditions, notably 1979, 1985, 1986, 1993, and 1995.

Discussion

Anthropogenic burning is an ancient practice (Pyne 2001) that has shaped the flora and fauna of grass-dominated ecosystems around the globe. Some of the most well preserved grass-dominated systems are those that are managed in a traditional mode (i.e., by indigenous persons) or in a way that emulates aspects of traditional management. For example, in northern Australia, unmanaged fires burn unchecked across vast portions of the tropical savanna during the dry season each year, negatively impacting fire-sensitive species and habitats (Yibarbuk et al. 2001). In contrast, Dukaladjarranj, an intensively fire-managed Aboriginal estate within the region, contains tropical savannas with high biological diversity, including rare species and threatened communities that are protected from high-intensity fires (Yibarbuk et al. 2001). Until recently, Maasai pastoralists in

East Africa propagated numerous small fires, creating a mosaic of burned areas with enhanced vegetation diversity that provided improved forage for cattle and protection from potentially catastrophic dry season fires (Butz 2009). Recent changes in governmental fire policy, increased human population pressure, and extended drought have limited the Maasai's ability and inclination to continue their traditional burning practices, potentially jeopardizing savanna health (Butz 2009). The restriction or exclusion of human-caused fires often results in the degradation of grassland communities, resulting in near global concern over the stability and persistence of grass-dominated ecosystems.

At the TGPP, fire occurrence and frequency also appears to be strongly tied to cultural history and land use. Marked changes in the TGPP's fire regime occurred during the transition from traditional land-uses by native peoples, to the establishment of the cattle industry. As illustrated above, the global trend in recent fire history has been towards fewer fires, if not outright suppression or exclusion. The Flint Hills are unusual in that fire has persisted as a regular component of landscape management. Fire's persistence in the TGPP can primarily be attributed to the early recognition by cattle-producers in the region that the native practice of burning prairies for game management also served the interests of livestock management by maintaining an open landscape and increasing the palatability and availability of forage.

The fire history patterns observed at the TGPP are generally coincident with that observed at other sites in the tallgrass prairie / Cross Timbers region. In southern Osage County, Clark et al. (2007) observed a similar decrease in fire return interval frequency from 4.9 years to 2.1 years. Shirakura's (2006) study was limited to the latter half of the twentieth century, but also found a near annual recurrence of fire at another site in the TGPP. In central Oklahoma, DeSantis et al. (2010) observed a decrease in fire interval from 4 to 2 years in an old-growth Cross Timbers forest. In contrast, at a prairie edge in the western Cross Timbers, Stambaugh et al. (2009) observed a slight increase in fire interval length, from 4.4 to 5.1 years. Consistent with Clark et al. (2007) and Stambaugh et al. (2009) I observed lower percentages of trees scarred in the post-EAS period than in earlier periods (Table 2). Though biases due to sample size and preservation in older time periods cannot be discounted, this regionally repeated pattern indicates an overall increase in fire frequency and decrease in fire intensity and/or size of fires in modern periods. Also, consistent with the aforementioned studies I did not find a strong relationship between fire and climate (drought) during the years around the fire event. This is not surprising given the high number of fire events observed at the TGPP.

Though fire has persisted in the Flint Hills region, it has persisted in a form that has some negative ecological consequences. As described in the methods section, the fire management program practiced at the TGPP is different from that employed on most lands within the Flint Hills region. Most land-holders in the region practice the intensive-early stocking system (Smith & Owensby 1978) which consists of early spring fires followed by double-stocked cattle for two and a half months. The annual burning coupled with heavy grazing results in a relatively homogenous landscape (Fuhlendorf & Engle 2001). The homogenized landscape has deleterious effects on grassland diversity, most notably for grassland birds (Fuhlendorf et al. 2006). In contrast, the TGPP’s management plan emphasizes landscape heterogeneity, and applies fire on average every three years to randomly selected units. Given the random nature of the selection, some units may be burned more or less frequently, but most fires are likely to occur within the upper and lower exceedance intervals reported here (Table 1). Based on our results, it appears the TGPP's fire management practices more closely match the fire regime of the traditional use period prior to settlement than that currently practiced under the intensive-early stocking system.

Conclusions

Understanding a site's history is an important component to understanding its present ecology as the legacies of past events and land-uses can leave residual effects that may affect species assemblages, disturbance regimes, and ecosystem dynamics both presently and on into the future (Foster et al. 2003). The fire history of the Flint Hills region is largely a result of anthropogenic factors, with fire varying in frequency with different cultural periods and associated land-uses. Though fire has persisted, the modern practice of near-annual burning appears to lack the variability that characterized the historic fire regime, presenting some deleterious ecological consequences, particularly for grassland diversity. Despite this, the continuous application of fire in the Flint Hills has undoubtedly maintained much of the historic nature of its prairies.

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Tables

Table 1. Descriptive statistics and fire intervals for sites at the TGPP.

	All Sites	East Side	Bar-X Pasture	South Fence	Sand Creek Ridge
Years of Coverage	1729-2005	1759-2005	1859-2004	1916-2005	1850-2003
Number of Sample Trees	76	41	14	5	4
Total Intervals	128	87	27	26	19
Mean Fire Interval	2.04	2.59	4.89	2.88	6.74
Weibull Median Interval	1.47	2.05	3.31	2.18	3.87
Minimum Fire Interval	1	1	1	1	1
Maximum Fire Interval	36	16	25	17	47
Lower Exceedance Interval	0.3	0.52	0.61	0.5	0.54
Upper Exceedance Interval	4.21	5.12	10.22	5.85	14.33

Table 2. Temporal change analysis for MFI and % samples scarred (as a proxy for widespread and/or intense fires). Values in parentheses indicate standard error.

	Time Span	Description	All Sites (N=76)		East Side (N=41)	
mean fire return interval	1770-1871	Pre-EAS	3.36	(0.55)	3.76	(0.74)
	1871-2005	Post-EAS	1.33*	(0.08)	2.13*	(0.25)
	1770-1825	Traditional use	3.69	(0.79)	3.91	(0.95)
	1826-1870	Population flux	2.5	(0.60)	2.69	(0.62)
	1871-1914	Transitional	1.72*	(0.22)	2.39	(0.55)
	1915-1989	Ranching	1.21*	(0.08)	2.24*	(0.34)
% scarred	1770-1871	Pre-EAS	8	(0.94)	8.79	(1.26)
	1871-2005	Post-EAS	4.45*	(0.37)	5.65*	(0.55)
	1770-1825	Traditional use	10.44	(1.53)	13.17	(2.00)
	1826-1870	Population flux	5.71*	(0.80)	5.03*	(0.66)
	1871-1914	Transitional	3.17*	(0.45)	4.19*	(0.61)
	1915-1989	Ranching	4.77*	(0.54)	5.8*	(0.82)

* indicates significance with either Pre-EAS or Traditional use period from *t*-tests at $p < 0.05$

Figures

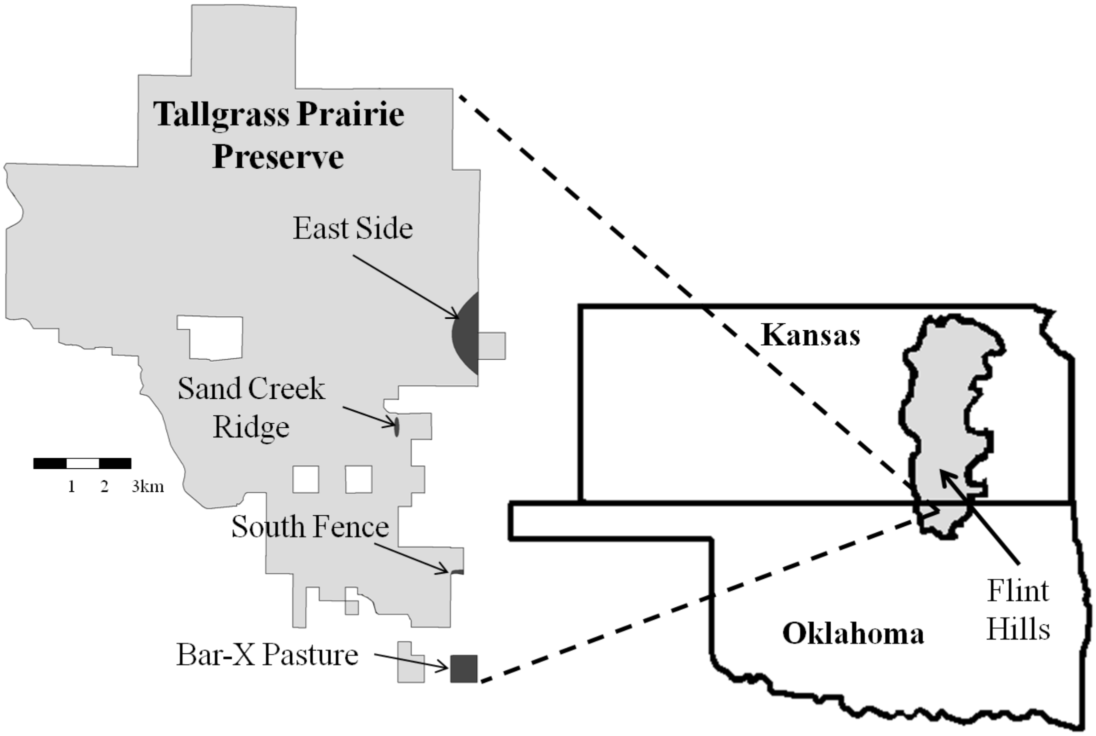

Fig. 1. Map of the Flint Hills region, TGPP, and sample locations. Note: sample areas indicated on the map are approximate outlines.

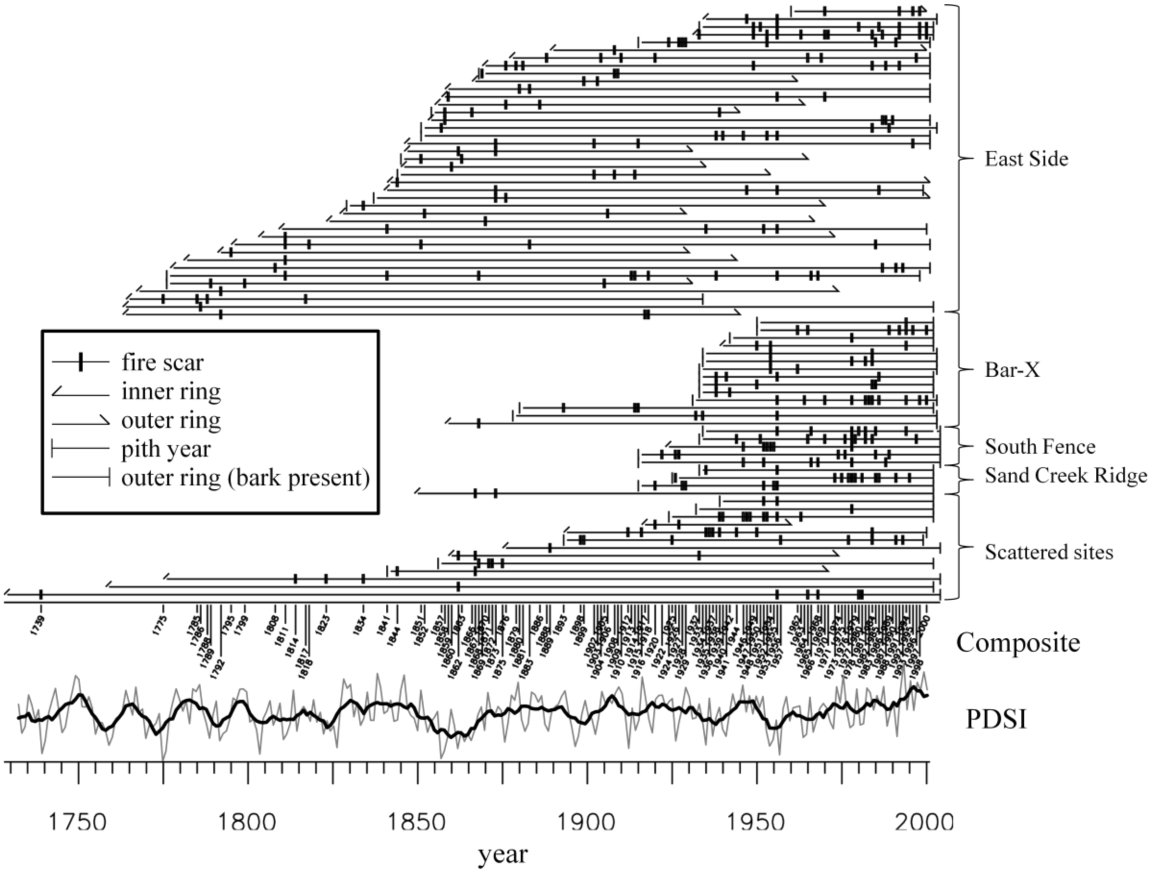

Fig. 2. Fire history chart for the TGPP. Each horizontal line represents an individual tree's record at a given site. Samples for each site are indicated in brackets along the right side of the graph. The composite record indicates every fire occurrence at the TGPP. PDSI for the region is illustrated below the composite line, and is highlighted by a 7-year running average.

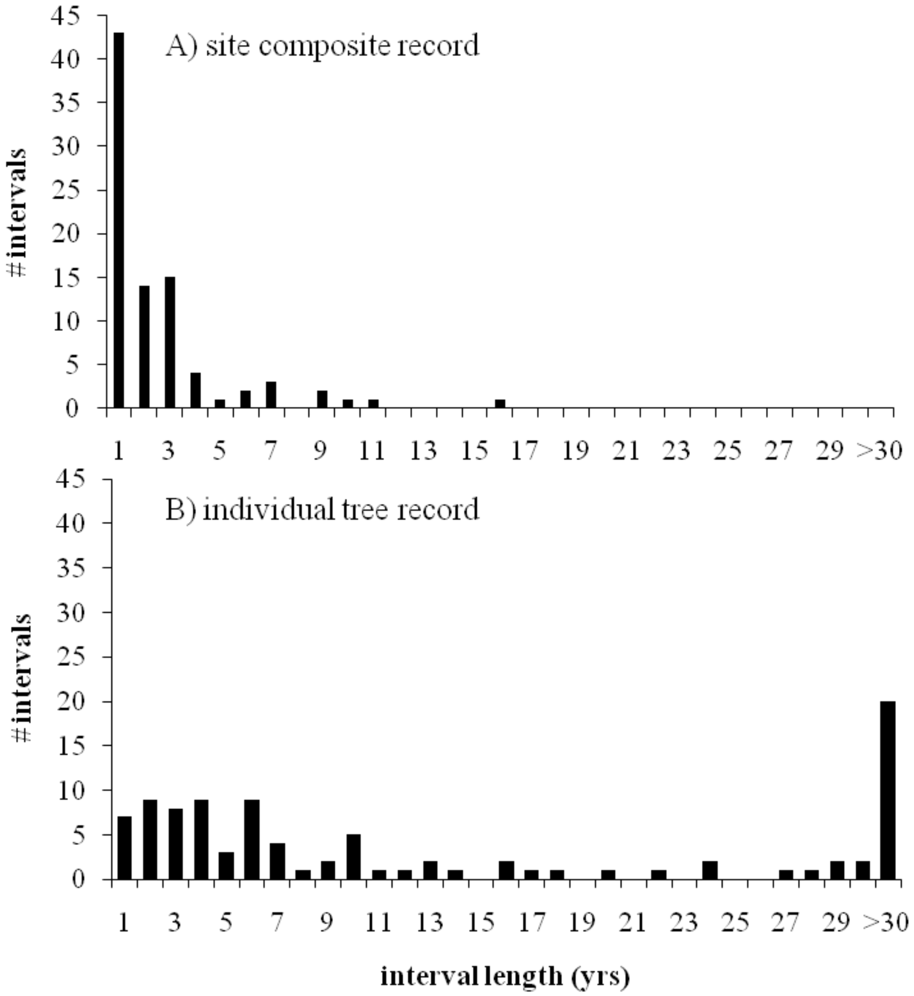

Fig. 3. Distribution of fire intervals from all samples collected at the East side site (N = 41) for both the **A)** site composite record and **B)** individual tree record.

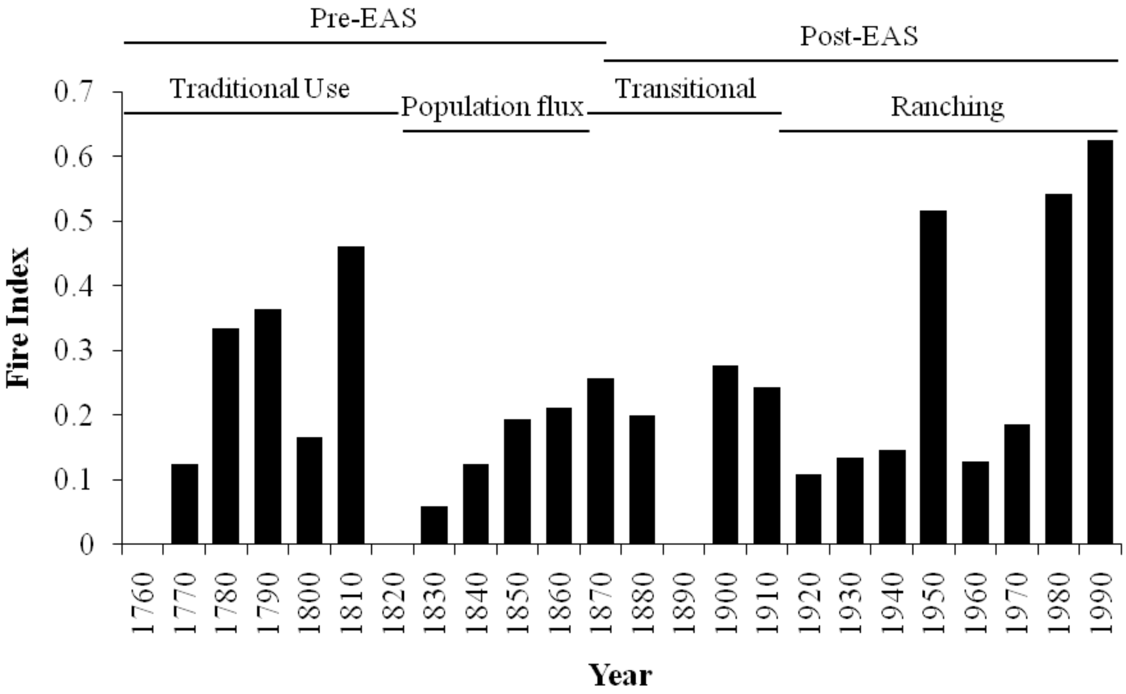

Fig. 4. Fire index for the East Side site at the TGPP. Higher index values indicate more fire events. Lines above the chart indicate the time-spans of the different historical and cultural periods assessed in this study.

CHAPTER III

IDENTIFYING GROWTH RELEASE EVENTS IN XERIC OAK FORESTS

Abstract

Tree-ring growth releases occur when limiting resources suddenly become available, inducing a high growth rate. In xeric forest systems, trees are typically highly limited by available precipitation and so their release potential in response to environmental disturbances may be limited. In this study I evaluate the efficacy of two methods, originally developed for the more mesic, denser forests of Eastern North America, for detecting tree growth releases in an arid forest environment. I used post oak (*Quercus stellata*) tree-ring data from seven locations in northern Oklahoma and southern Kansas. I used two methods, the percent growth change method and time-series analysis with ARIMA modeling and intervention detection to identify growth releases. Both methods identified periods of tree growth-release, but in both cases releases were correlated with climatic reversals from dry to wet conditions. Climatic conditions appear to supersede the growth response, obscuring potential growth responses due to environmental disturbances.

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Introduction

In mesic temperate forests, environmental disturbances, both local and stand-wide, may be inferred from patterns of growth suppression or release in tree-ring series (Nowacki & Abrams 1997). Local disturbances, such as treefall gaps, may prompt higher rates of growth in adjacent or understory trees as they respond to newly available light (Rentch et al. 2010). A severe disturbance that causes widespread mortality to overstory trees may produce a synchronous stand-wide release in understory trees that quickly grow to occupy the vacated canopy (Eisenhart & Veblen 2000). In the deciduous forests of Eastern North America, these growth dynamics play an important role in shaping forest composition and structure. Since patterns of release in tree-ring series can elucidate the occurrence of historical disturbances, factors limiting for tree growth, and the dynamics of growth for recruitment to the forest overstory, a number of methods have been developed to detect abrupt increases in growth due to a formerly limiting variable becoming suddenly available (Rubino & McCarthy 2004).

In more xeric forests, the importance of the dynamics described above is less certain. Due to their arid nature, xeric forest tree growth is generally strongly constrained by available water (e.g., Stahle & Hehr 1984), hypothetically limiting their potential to exhibit a growth release even if a disturbance did occur. Disturbances of many types (tree-fall, fire, wind, insect outbreak, etc.) occur in xeric forests, but the extent to which they produce a reliably detectable growth release is questionable.

An abrupt, large-magnitude, and sustained increase in radial growth is defined as a release (Frelich 2002), a condition which usually arises from some sort of disturbance. Numerous studies have employed a variety of techniques to identify patterns of tree growth release (Rubino & McCarthy 2004). The most widely applied technique (according to Rubino & McCarthy (2004)), is that developed by Nowacki and Abrams (1997) which utilizes radial growth averaging to calculate percent growth change between adjacent time segments. Years where growth change values surpass release thresholds (e.g., 25, 50, or 100% depending on the tree, species, or site) are then characterized as releases. An extension of this method was refined by Black and Abrams (2003) to incorporate release criteria dependent on the prior growth rate's magnitude to develop species-specific boundary lines that can be used to assess a species' potential to respond to a disturbance. The extent to which these methods are useful identifying releases in more xeric forest systems has yet to be evaluated.

In this paper I test the efficacy of two methods for identifying growth releases in tree-ring records from a xeric forest system. Additionally, I seek to determine the cause of any release identified, that is whether or not releases arise from climatic conditions or some sort of disturbance. I will identify releases in post oak, a dominate species of the Cross Timbers forest of the south-central United States. The two methods I evaluate here are the radial growth-averaging method developed by Nowacki and Abrams (1997) and time series analysis with intervention detection described as a method for tree-ring studies by Downing and McLaughlin (1990).

Methods

In order to evaluate the two release detection methods, I used tree-ring data collected from a number of sites (Fig. 1) located in the Northern Cross Timbers region. The Cross Timbers constitute a long band of post oak (*Quercus stellata*) and blackjack oak (*Quercus marilandica*) dominated forest spanning portions of Kansas, Oklahoma, and Texas. The Cross Timbers occupy the ecotone between North America's eastern deciduous forests and the Great Plains of the continental interior. The Cross Timbers are xeric, with annual average precipitation ranging between 102 cm in the eastern Cross Timbers, and 71 cm in the western Cross Timbers (Sutherland 1977). A number of natural disturbances affect the Cross Timbers including fire (Clark et al. 2007, Stambaugh et al. 2009), tornados (Shirakura et al. 2006), and ice storms (Cortinas Jr. et al. 2004). I obtained tree-ring data from Cross Timbers sites from the International Tree-Ring Databank (ITRDB 2010) and from our own study site at the Tallgrass Prairie Preserve. All tree-ring series used in this analysis come from post oak, which is generally the most abundant and longest lived tree species in the Cross Timbers. All data comes from sites located in the northern Cross Timbers (Table 1). For all the datasets, multiple cores had been extracted per tree. When multiple series were present from the same tree, I averaged the measurements in order to evaluate growth responses on a tree-level basis.

The first method I applied was the percent growth-change method (*%GC*) described by Nowacki and Abrams (1997) and modified by Rubino and McCarthy (2004). This method was originally applied to the detection of releases in closed canopy oak forests in Eastern North America. This method calculates yearly intervals of percent growth change between preceding and succeeding ten year medians:

$$\%GC = \frac{(M_2 - M_1)}{M_1} \times 100$$

Here *%GC* = percent growth change, M_2 = subsequent ten year median, and M_1 = preceding ten year median. The ten year time span used for calculating medians is intended to filter out short-term climatic responses while retaining intermediate responses likely to be associated with canopy disturbance (Nowacki & Abrams 1997). In their original study, Nowacki and Abrams (1997) established a minimum threshold of 25% growth change to identify growth releases. Given that tree growth within the Cross Timbers is highly correlated with available precipitation (Stahle & Hehr 1984), I examined tree maximal growth responses due to climate in order to establish an appropriate threshold for identifying growth-release in this region. To identify an appropriate threshold, I performed correlations on the *%GC* data with Palmer Drought Severity Index (PDSI; (Cook & Krusic 2004)) data converted into a similar format. This procedure follows Nowacki and Abrams (1997). Here I estimated each tree's maximal growth change response due to climate by inserting the largest PDSI difference occurring during that tree's lifespan into regression equations. *%GC* responses due to climate varied substantially, but most trees exhibited a maximal response less than 50% growth change (Table 2). Trees that exhibited a higher maximal response were excluded from further analysis. Upon identification of the 50% threshold, I then examined the resultant release chronology to see if any climatic response persisted in the release chronology.

For the second method, I fit an ARIMA (autoregressive integrated moving average) model and performed intervention detection in R (Team 2010). I generated ARIMA models (ARIMA; (Box et al. 1994)) for each tree-ring series following:

$$\emptyset(\boldsymbol{B})\boldsymbol{\nabla}^{\boldsymbol{d}}\boldsymbol{z_t} = \boldsymbol{\theta}(\boldsymbol{B})\boldsymbol{a_t}$$

Here, $\emptyset(B)$ is the autoregressive operator where B, the backward-shift operator, is defined as $Bz_t = z_{t-1}$, ∇^d is a difference operator of order d, z_t is the modeled time series, $\theta(B)$ is a moving average operator, and a_t is a white-noise process of random and independent shocks with a mean of zero and variance of σ_a^2. ARIMA models were automatically generated using the forecast package (Hyndman 2010) within R. For a complete description of ARIMA models, consult Box et al. (1994). Intervention detection, as described by Chang and Tiao (1983) identifies interventions, or outliers, in ARIMA modeled time-series. I used the TSA package (Chan 2010) within R to perform intervention detection and detect outlying years in each tree-ring series at the 95% confidence level. In this case, I assumed that outliers occur due to some novel event that induces a growth response that would exceed the tree's normal climatic response. To evaluate climatic relationships I used Superposed Epoch Analysis (SEA; (Grissino-Mayer 2001)) to determine if any relationships existed between the outlier years and reconstructed values of PDSI. Tree-growth is often correlated with PDSI, an index incorporating both temperature and precipitation to assess the relative wetness or dryness of the environment. SEA tests for associations between events (in this case, releases) and climatic conditions in a user-specified window of time around the event. In this case, I bootstrapped data for 1000 simulated release events in order to derive confidence limits and assessed a ten year window around each release event (6 years preceding and 4 years succeeding) in order to determine if drought was significantly different from normal during the time span.

Results

The percent growth change method identified a number of release events in tree-ring series from all sites assessed (Figure 2). Several releases were apparent at the stand level, with many trees showing a release response, while others were present in only one to a few trees. Additionally, some releases were apparent across sites, with two to several sites showing strong simultaneous release responses. This generally strong pattern of release synchrony within and between sites suggests that gap-phase type patterns of tree growth are not particularly common or important in the Cross Timbers. Visual inspection of the timing of major release events (many trees recording) suggests that releases occurred either during wetter than average conditions or as trees were recovering from drought conditions.

I was able to successfully model each tree-ring series with an ARIMA model and test the residuals of that model for outliers using intervention detection. The percentage of trees with at least one outlier ranged from 36% to 80% between sites. In general the percentage of trees having a positive outlier in a given year was low (Table 3) with the majority of outliers occurring only in one tree-ring series per site. Though not widely recorded, the occurrence of outliers does not appear to be randomly distributed with respect to climate. Outliers assessed with SEA were generally all preceded by drier than average conditions followed by a reversal towards wetter than average conditions (Figure 3). In all cases, outliers were strongly associated with climatic shifts, either as a recovery from drier conditions (Fig. 3A, C) or during wetter than average years (Fig. 3D, E, F, G) This suggests that substantial increases in growth are primarily driven by climatic reversals, from dry to wet conditions.

Discussion

The two methods I tested here failed to provide conclusive evidence of the occurrence of disturbance-induced releases within the xeric Cross Timbers. Though the *%GC* method has been widely implemented in more mesic forest ecosystems of Eastern North America for detecting disturbance-induced released events, here I found (consistent with Nowacki and Abrams (1997) warning) that the *%GC* method does not appear capable of filtering out climatic impacts on tree growth rates in more xeric systems. In a similar study, Clark (2003) found similar results for a Cross Timbers site and also had difficulty disentangling the climatic effects on tree-growth in the evaluation of *%GC*. Though disturbance-induced releases were not detected, the pattern of synchronous growth release suggests that gap-phase dynamics are either not prevalent or not important in the Cross Timbers.

Time series analysis with ARIMA modeling and outlier detection revealed two important points about high growth years: 1) that they when they occur, they are generally represented in a small percentage of trees at a site, and 2) that their occurrence significantly coincides with climatic reversals from dry to wet conditions. That outliers infrequently occurred and were not well shared among trees at a site suggests that the variation in tree growth is so constrained by climate that the occurrence of an environmental disturbance may not induce a significant change in tree growth. This point is further evidenced by the strong relationship between climatic reversals and the outliers that did occur.

Stahle and Hehr (1984) determined that post oak chronologies became increasingly sensitive to climate along the precipitation gradient in the Cross Timbers region, producing climate-explained variance comparable to that found in the arid conifer-dominated systems of western North America. Given post oak's strong climate sensitivity, disturbances may have a low impact on tree growth. In a study evaluating numerous tree species' release potential, Black et al. (2009) found that several shade-intolerant species, including post oak, failed to achieve their maximal release potential as they increased in age and size, hypothesizing that their failure to release could be due to wide spacing of trees and full tree crowns that would receive little benefit or additional sunlight if neighboring trees were removed. Even in mostly closed canopy conditions, Cross Timbers stands still have relatively high light levels, suggesting that light conditions are generally not limiting for growth. In Cross Timbers' understory, species richness and abundance is more highly associated with litter characteristics, though light still plays a significant, if weaker, role (Van Els et al. 2010) Though conditions may vary between sites, it appears that light is insufficiently limiting to induce a growth-release in Cross Timbers' post oak when it suddenly becomes more available.

Some limitations to this present study may be improved upon by further research. In particular, experimental thinning of Cross Timbers stands could be conducted in order to more accurately gauge growth responses to canopy gaps and disturbance. Additionally, though ITRDB datasets were invaluable to this study, they were not originally collected with the intent of assessing tree growth responses. Several of the datasets are primarily composed of older trees. Older trees may not record the same growth dynamics as trees that have established more recently.

The Cross Timbers, like many forest systems have experienced marked changes in recent history. Since the 1950s, the Cross Timbers' species composition has shifted, with marked increases occurring in mesophytic and invasive woody species (DeSantis et al. 2010). The long-term effect of this compositional shift of on tree-growth is as yet, unknown, but as additional stressors/environmental dynamics are added to the system, it seems possible that in the future trees in the Cross Timbers may compete more strongly for light and resources with neighboring trees. In this scenario, trees may become more sensitive to disturbance, making disturbance-induced releases more detectable in tree-ring series.

Conclusions

The two methods tested here were originally developed for identifying releases in the denser, more mesic forests of Eastern North America and as such were unable to conclusively distinguish disturbance-induced tree-releases from prevailing climatic conditions. These methods did highlight the limiting effects of climate on tree-growth in xeric forest systems and showing that releases were primarily climatically derived rather than resulting from an environmental disturbance. Climatic limitations on tree-growth in xeric forest systems are likely to complicate the process of identifying environmental disturbances via tree-ring growth releases.

Acknowledgements

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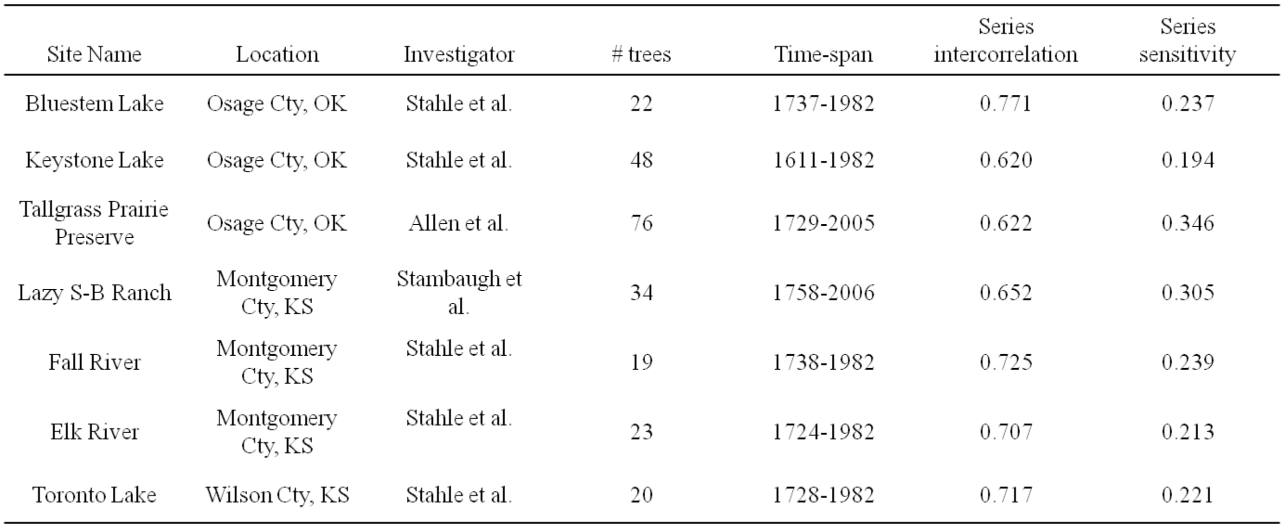
Tables

Table 1: Descriptions of datasets used in this study.

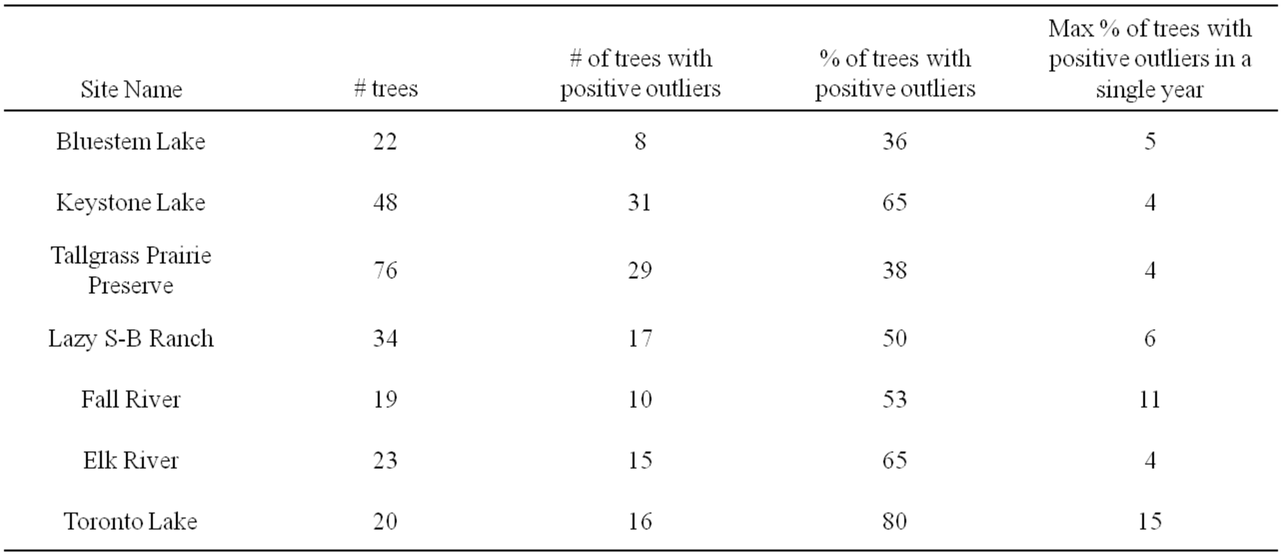


Site Name	Location	Investigator	# trees	Time-span	Series intercorrelation	Series sensitivity
Bluestem Lake	Osage Cty, OK	Stahle et al.	22	1737-1982	0.771	0.237
Keystone Lake	Osage Cty, OK	Stahle et al.	48	1611-1982	0.620	0.194
Tallgrass Prairie Preserve	Osage Cty, OK	Allen et al.	76	1729-2005	0.622	0.346
Lazy S-B Ranch	Montgomery Cty, KS	Stambaugh et al.	34	1758-2006	0.652	0.305
Fall River	Montgomery Cty, KS	Stahle et al.	19	1738-1982	0.725	0.239
Elk River	Montgomery Cty, KS	Stahle et al.	23	1724-1982	0.707	0.213
Toronto Lake	Wilson Cty, KS	Stahle et al.	20	1728-1982	0.717	0.221

Table 2: Tree growth responses to climate at each site.

Site Name	# trees	Range for growth-change due to climate (%)	Average growth-change due to climate (%)	% of trees with responses above 50% release threshold
Bluestem Lake	22	8.8 – 43.4	22.8	0.0
Keystone Lake	48	Neg – 55.3	12.9	4.2
Tallgrass Prairie Preserve	76	Neg – 178.9	14.1	5.2
Lazy S-B Ranch	34	Neg – 114.4	29.6	11.8
Fall River	19	1.3 – 100.0	20.6	5.3
Elk River	23	8.0 – 49.9	23.9	0.0
Toronto Lake	20	8.4 – 42.9	23.7	0.0

Table 3: Results of intervention detection after ARIMA modeling.



Site Name	# trees	# of trees with positive outliers	% of trees with positive outliers	Max % of trees with positive outliers in a single year
Bluestem Lake	22	8	36	5
Keystone Lake	48	31	65	4
Tallgrass Prairie Preserve	76	29	38	4
Lazy S-B Ranch	34	17	50	6
Fall River	19	10	53	11
Elk River	23	15	65	4
Toronto Lake	20	16	80	15

Figures

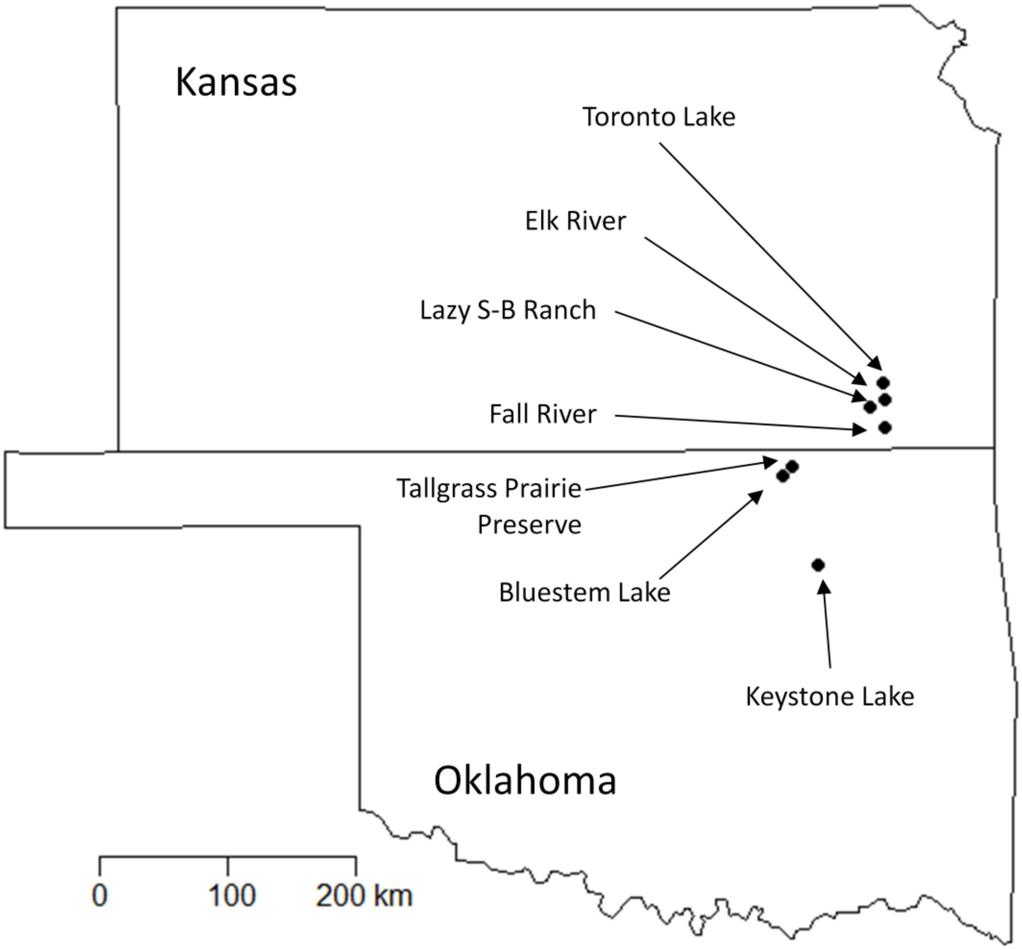


Figure 1: Map of study sites in Oklahoma and Kansas.

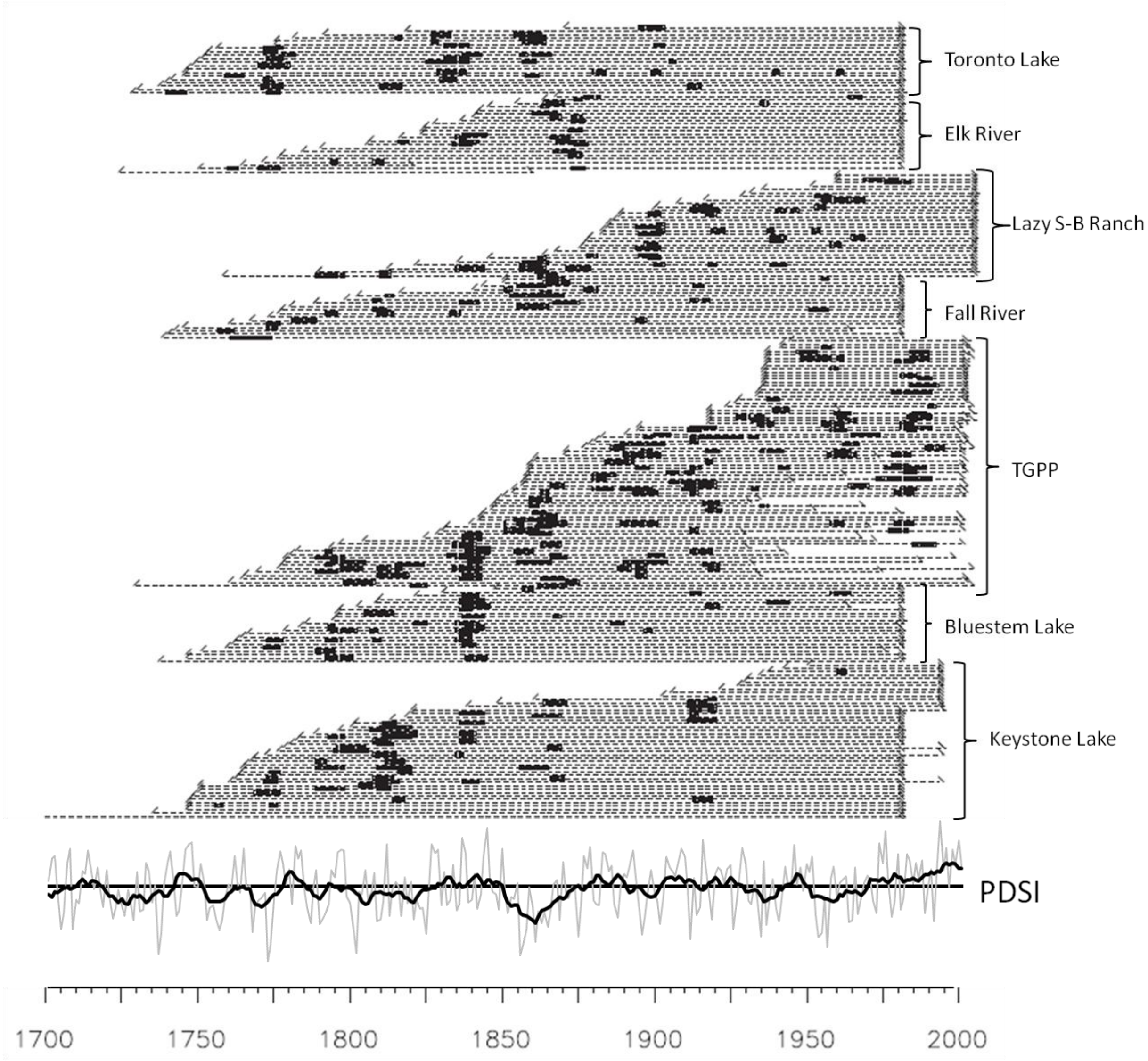


Figure 2: Growth releases detected by the percent growth-change method for each tree-ring series in each site. Each dashed horizontal line indicates a tree-ring series, the thickened parts of each line indicate the occurrence and length of a >50% growth release. The lower frequency variation of the PDSI line (gray line) is highlighted by a ten-year running average (black line).

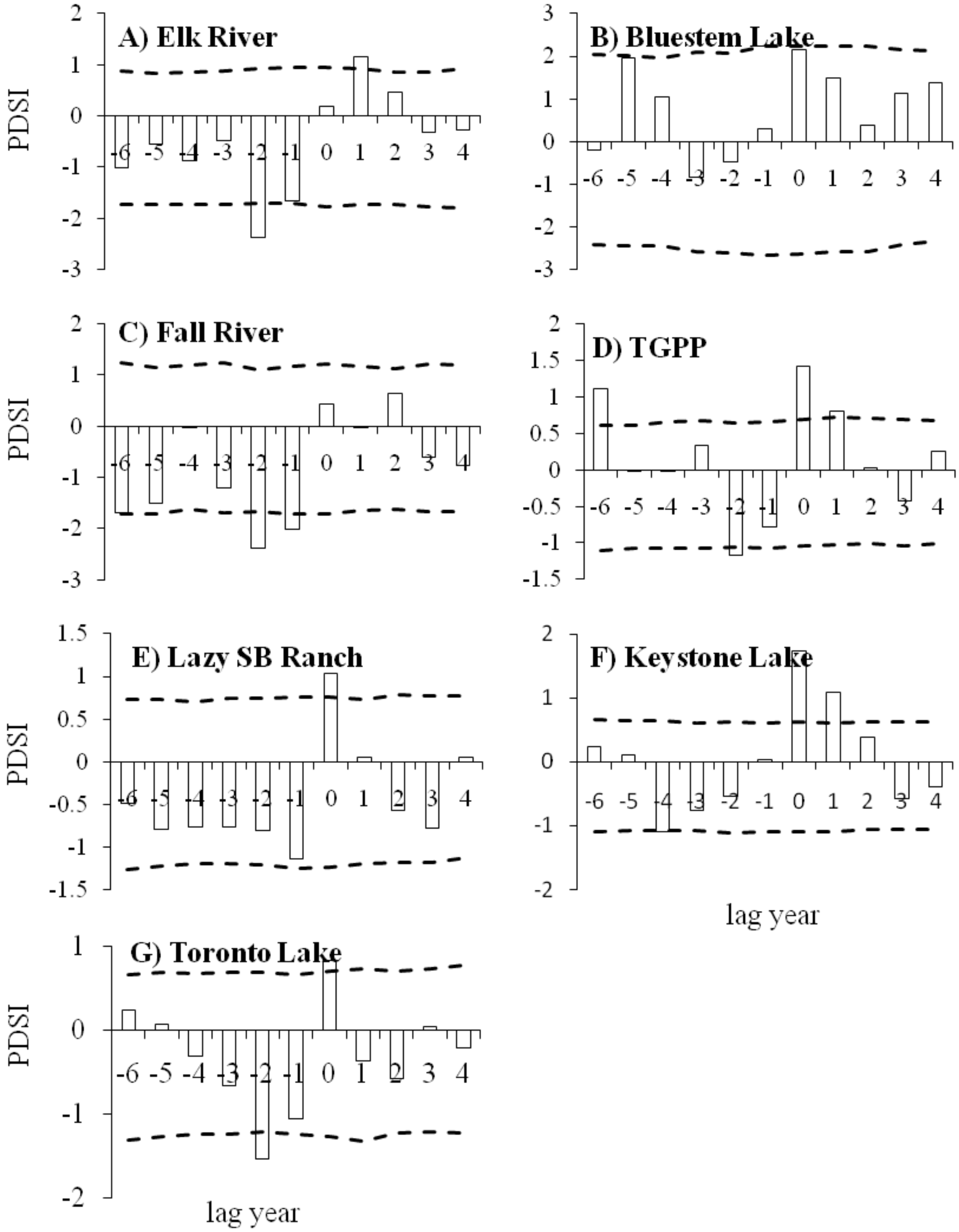


Figure 3: SEA on first-year of growth release from ARIMA modeling with intervention detection. The "0" year indicates the outlying year. Dashed lines indicate 95% confidence intervals.

CHAPTER IV

COMPOSITIONAL CONVERGENCE AND FOREST ARCHITECTURE FOLLOWING A WINDSTORM IN TWO MINNESOTA FORESTS

Abstract

Questions: Are two originally distinct forest communities converging in composition 25 years after a catastrophic windstorm? Is the architecture of these communities similar following the windstorm?

Location: Oak and pine forests in the Cedar Creek Natural History Area LTER Site, Anoka and Isanti Counties, Minnesota, USA

Methods: All tree species were recorded and stems measured in two permanent plots in two forest communities, one dominated by oak, the other by pine. Plots were resampled 4 times in the 25 years following the windstorm to monitor forest recovery. Ordination and diameter distributions were used to describe the compositional and structural characteristics of the two forest communities.

Results: Forests are compositionally converging 25 years after the windstorm towards a late-successional forest type. Structurally, both forests have had similar architectures through time and have transitioned from weakly bimodal diameter distributions to reverse-J distributions. However, structural characteristics and species composition are different between sites.

Conclusion: The compositionally converging forests demonstrate a case of accelerated succession resulting in more mesophytic communities. Structural characteristics and abundances of individual species within that pattern of convergence, though, are different, and may maintain a measure of ecological dissimilarity into the future.

Keywords:

convergence, diameter distribution, LTER, Minnesota, succession, wind disturbance

Nomenclature: Kartesz (1994)

Introduction

The effects of disturbance in forests are variable and may change both the physiognomy and composition of communities. Windstorm disturbance often results in size-dependent mortality as larger trees are more susceptible to wind effects (Arévalo et al. 2000, Rich et al. 2007). This size-dependent mortality may influence the recruitment process and have an effect on the overall demographics and composition of the forest community (Coomes & Allen 2007). Between stands the results of recruitment and mortality following a windstorm may cause communities to converge or diverge compositionally (Frelich & Reich 1995).

The structural features of forest communities can also affect community biodiversity (Rouvinen & Kuuluvainen 2005). Given that severe windstorms are expected to increase throughout the upper Midwest with climate change (Overpeck et al. 1990), understanding the recovery processes and structural dynamics will be increasingly important for both conservation and forest management (Rich et al. 2007).

I revisited two forest stands that were catastrophically impacted by a severe windstorm in 1983 (Arévalo et al. 2000), in order to evaluate forest responses since disturbance. One stand was originally oak-dominated and the other pine-dominated. In this study I seek to evaluate the long term response and recovery of the two stands following the windstorm. Specifically I seek to address the following questions: 1) Arévalo et al. (2000) speculated that the two forest stands are converging in species composition due to accelerated succession, is this trend true following continued sampling? 2) Have the two stands followed the same physiognomy through time and how have the structural characteristics of the stands affected their current composition?

Methods

Study area

The study was conducted using data from two permanently marked plots in the Cedar Creek Ecosystem Science Reserve, one of the U.S. National Science Foundation's Long Term Ecological Research (LTER) sites, located in Anoka and Isanti Counties, Minnesota. The plots were established after a windstorm damaged the area in July 1983. The plots were placed in two different forest sites: an oak site initially dominated by *Quercus borealis* and a pine site initially dominated by *Pinus strobus*. The pine site is believed to have been at an earlier stage of succession than the oak site due to its even-age structure (Arévalo et. al 2000). The two plots were less than 1 km apart and had similar sandy soils and level topography.

Field sampling

I collected data from a 50m ×50m plot in the oak forest and a 60m×50m plot in the pine forest. In both plots diameter at breast height (DBH), species, mortality and damage categories were recorded for all living and dead stems greater than 1cm in diameter. When measuring the DBH of trees with multiple stems, each stem was regarded as a separate stem if it branched below 1.4m on the main stem. The first sampling was conducted in July 1983, two weeks after the windstorm. The plots were then resampled in 1990, 1993, 1997, 2004, and 2008 for all variables mentioned above.

Trees killed by the storm were marked during the 1983 sampling and used to reconstruct the pre-storm forest structure.

Data analysis

I applied Detrended Correspondence Analysis (DCA; Hill & Gauch 1980) using CANOCO 4.5 (ter Braak & Šmilauer 1998) to explain species compositional change in the two forest sites over time following the windstorm. I used tree species basal area from each sampling period from 1983 to 2008 for our ordination. I also used Principal Components Analysis (PCA; ter Braak 1983) to explain the architectures of the two forest communities through time. I used frequency of 10cm DBH classes for all trees in each community for our PCA.

To analyze tree size distributions over time, I used all stems that were greater than or equal to 2.5 cm in DBH. I examined the shape of the DBH distributions over time to interpret the structural characteristic of the two forest types. To assess inequality in the DBH distributions for both forest types I calculated the Gini (*G*) coefficient (see Weiner & Solbrig 1984) for each sampling period. The Gini coefficient measures the degree of deviation from an evenly dispersed distribution, and provides a good measure of density effects on growth and the effects of size-selective mortality (Knox & Peet 1989). I calculated Gini coefficients using the reldist package (Handcock & Morris 1999) for the software program R (R Development Core Team 2010).

Additionally, I assessed the recovery responses of the originally dominant trees at both sites: *Q. borealis* and *P. strobus*. I also evaluated the response of the primary recruiting tree species in both sites. For the pine site, this was *Q. borealis* and for the oak site, it was *Acer rubrum*.

Results

Ordination of tree basal area continued to reveal a pattern of compositional convergence between the two sites (Fig. 1). The first axis of the DCA clearly separates the two sites, with the pine forest following a path through ordination space towards the oak forest (Fig. 1). It appears that disturbance has accelerated succession with both forests moving towards later successional species at the top of the panel and away from early successional species at the bottom (Fig. 1). The initial effect of the disturbance on species composition is the same direction as that followed by both forest sites through time.

Similarly, both forests appear to be following the same trajectory structurally (Fig. 2). In Fig. 2, PCA axis 1 represents a gradient of tree size, with years with smaller sized trees predominating orientated towards the right side of the panel and years predominated by larger trees towards the left side of the panel. PCA axis 2 represents a gradient of forest development, with the highly disturbed forest appearing at the bottom of the panel and the recovering/undisturbed forest appearing at the top of the panel, illustrating structural change since the storm. Both forests following the storm went through a period of high regeneration, where the smaller size classes were more important (Fig. 2). Until the most recent samplings, the pine forest appears to be lagging behind the oak forest in terms of recovery (Fig. 2). This is likely because the pine forest was more severely damaged by the windstorm and the oak forest had more prolific stump-sprouting (Arévalo et al. 2000). The most recent samples (in 2004 and 2008) appear to show a trend out of the recovery phase as more trees are moving into the larger size classes and both forests are becoming more similar in physiognomy. In particular, the pine site appears to be approaching a configuration that more closely resembles the pre-disturbance forest state (Fig. 2).

In both forests, pre-storm diameter distributions appeared weakly bimodal (Fig. 3A-B), but after the storm and through time they have become reverse-J distributions (Fig. 3A-B) since larger size classes experienced higher mortality from the storm and numerous trees recruited post-disturbance (Arévalo et al. 2000). Calculations for the Gini coefficient revealed that the high levels of mortality sustained in both forests lead to higher structural inequality in the diameter distributions following the windstorm (Fig. 4). The pine forest likely had higher structural inequality than the oak forest after the storm (Fig. 4) because though it sustained higher levels of mortality (Arévalo et al. 2000) several larger trees survived the original storm. Regardless, recruitment after the storm has allowed the smaller size classes to dominate the distribution (Fig. 3A-B). Though distribution shapes are similar, the density of the oak forest was consistently higher than the pine forest throughout the study period (Fig. 3A-B).

The windstorm reduced overall tree density in both forests (Fig. 5A-B) which allowed for increased recruitment of trees through time; this recruitment is likely responsible for the compositional convergence of the two forests. While the oak site stills appears to be thinning after peaking in tree density during the early 1990s (Fig. 5A), the pine forest appears to be relatively stable in tree density (Fig. 5B). Both sites are still increasing in overall basal area (Fib 6A-B), though the oak forest basal area is now comparable to pre-storm levels (Fig. 6A). *Q. borealis* is continuing to contribute the most basal area following the storm in the oak forest (Fig. 6A). The same can be said of *P. strobus* in the pine forest (Fig. 6B). However, these two species no longer represent the most common tree in their respective forests in terms of density, as sapling recruitment for both species has been low. Later successional species such as *A. rubrum* (Fig. 5A) in the oak site and *Q. borealis* in the pine site have increased the most following the storm (Fig. 5B). It should be noted however that while *Q. borealis* is increasing in the pine site, its overall basal area is still relatively low Fig. 6B)

Discussion

This study and Arévalo et al.'s (2000) previous study found a convergence trend in species composition over 25 years following windstorm damage in the oak and pine forests. This convergence trend is primarily driven by the establishment of later successional species in both sites, representing an instance of "accelerated" succession (Arévalo et al. 2000). In both sites, the instantaneous directional change in composition resulting from the storm is the same direction as subsequent change in forest composition through time.

Succession in northern forests primarily follows an order of successional replacement from shade intolerant to shade tolerant species (Curtis 1959). However, the direction and change of communities following disturbance is dependent on the type and severity of disturbance and also the natural history and demographics of constituent tree species. Peet and Christensen's (1980) study of change in mixed stands of *Pinus taeda* over fifty years demonstrated that forest succession was largely a result of the underlying dynamics of tree establishment and mortality in the population. In the oak site in particular, the windstorm appears to have accelerated the autogenic succession process, (Arévalo et al. 2000) by removing the overstory oaks and allowing *A. rubrum,* a late-successional hardwood, to increase substantially in the site in both density and basal area. Pickett (1982) further supported the importance of population dynamics by identifying phases of dominance in accordance with the life history traits of species during old-field succession. Christensen and Peet (1984) also showed that early in succession, community composition was less predictable due to the diversity of habitats available, determining that the ability of a given tree species to colonize early on played a great role in determining the stand composition at an early stage. In the pine site, damage levels were higher and the recruiting species more varied as both shade tolerant and intolerant species simultaneously increased in the site (Arévalo et al. 2000).

As shown by the PCA, the overall architectural characteristics of the two forests have followed similar trajectories through time, though in contrast with the compositional trend, the direction of the trajectories has changed through time as the recovering forests are now approaching an architectural state similar to the pre-disturbance forests. The initial weak bimodal distribution of DBH classes of these forests changed into reverse-J shaped distributions. Shifts towards reverse-J shaped distributions following disturbance is common and has been reported in a number of forest types (Leak 1996, McLaren et al. 2005, Zenner 2005). Meyer (1952) and Leak (1996) suggested that the reverse J-shaped curve indicates a balanced forest structure. Forests with the reverse-J distribution exhibit increased capacity to recover following wind disturbance as smaller trees can quickly recruit into larger classes. This concept is well recognized in forestry to sustain constant yield during periodic cutting (Meyer 1952, Chapman & Blatner, 1991). In this case though, the replacing species are not the original overstory dominants, resulting in a new forest composition.

Though *A. rubrum* is increasing in the oak forest, *Q. borealis* has maintained a well-stratified diameter distribution in the years following the storm. The persistent structural diversity of *Q. borealis* may give it a competitive advantage in resource extraction (Yokozawa 1999), which may facilitate its persistence through time. The same may be true in the pine forest where *P. strobus* may maintain a competitive advantage due to its well-stratified diameter distribution in the site.

Conclusions

Here I have shown that these two forest communities are compositionally converging as late-successional species are generally becoming more important in both stands. Disturbance has facilitated an increase of shade-intolerant trees in these forests. Additionally, these two sites have experienced similar changes in forest architecture through time. However, the structural dynamics and relative abundances of individual species within those two sites is likely to keep them ecologically distinct for some time into the future.

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Figures

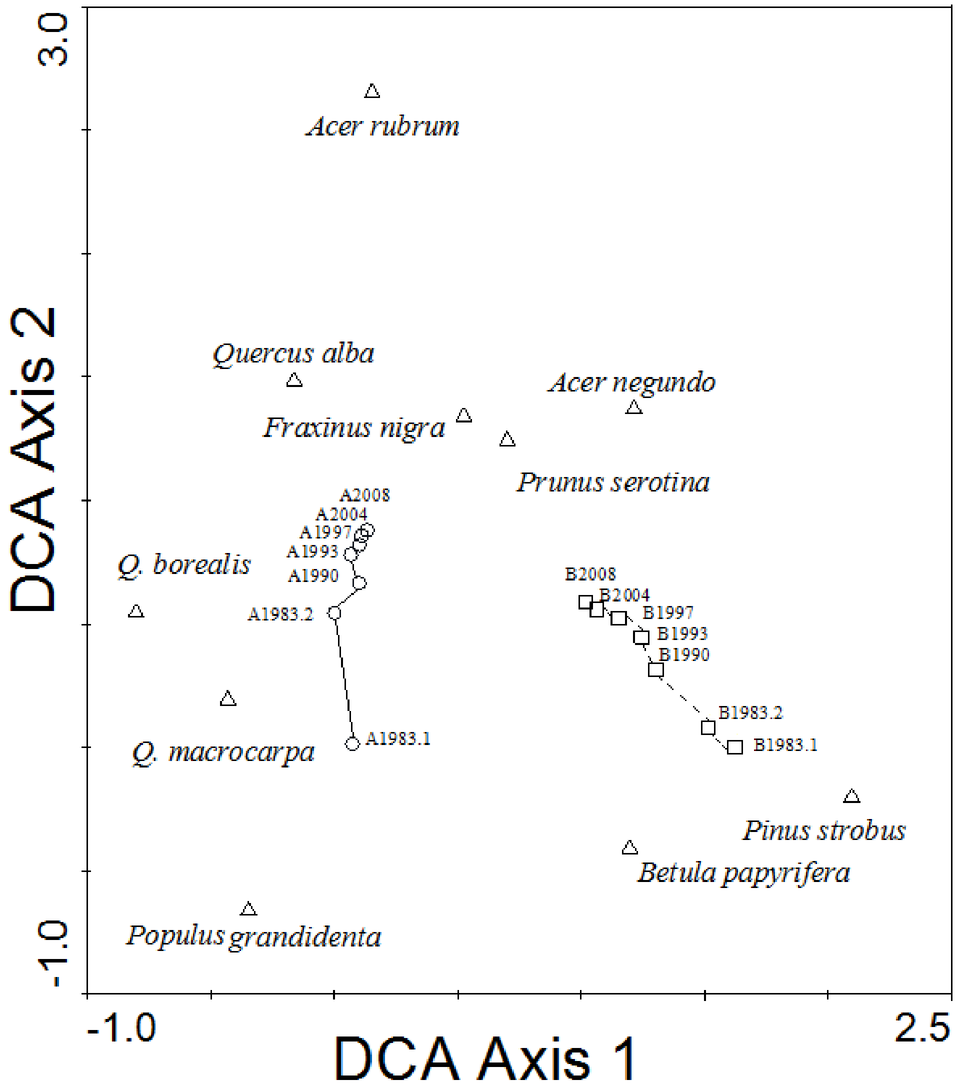


Fig. 1. DCA biplot of species scores and site scores for the first and second axis based on basal area of trees (eigenvalues were 0.700 and 0.125). The site scores are represented by circles or squares depending on site. The "A" prefix for each site scores indicates the oak dominated site; the "B" prefix indicates the pine-dominated sites. 1983.1 indicates before the storm; 1983.2 indicates after the storm. The solid line indicates the path of Site A through ordination space, the dashed line indicates the path of Site B through ordination space. Species scores (triangle symbols) for the most abundant species are shown above.

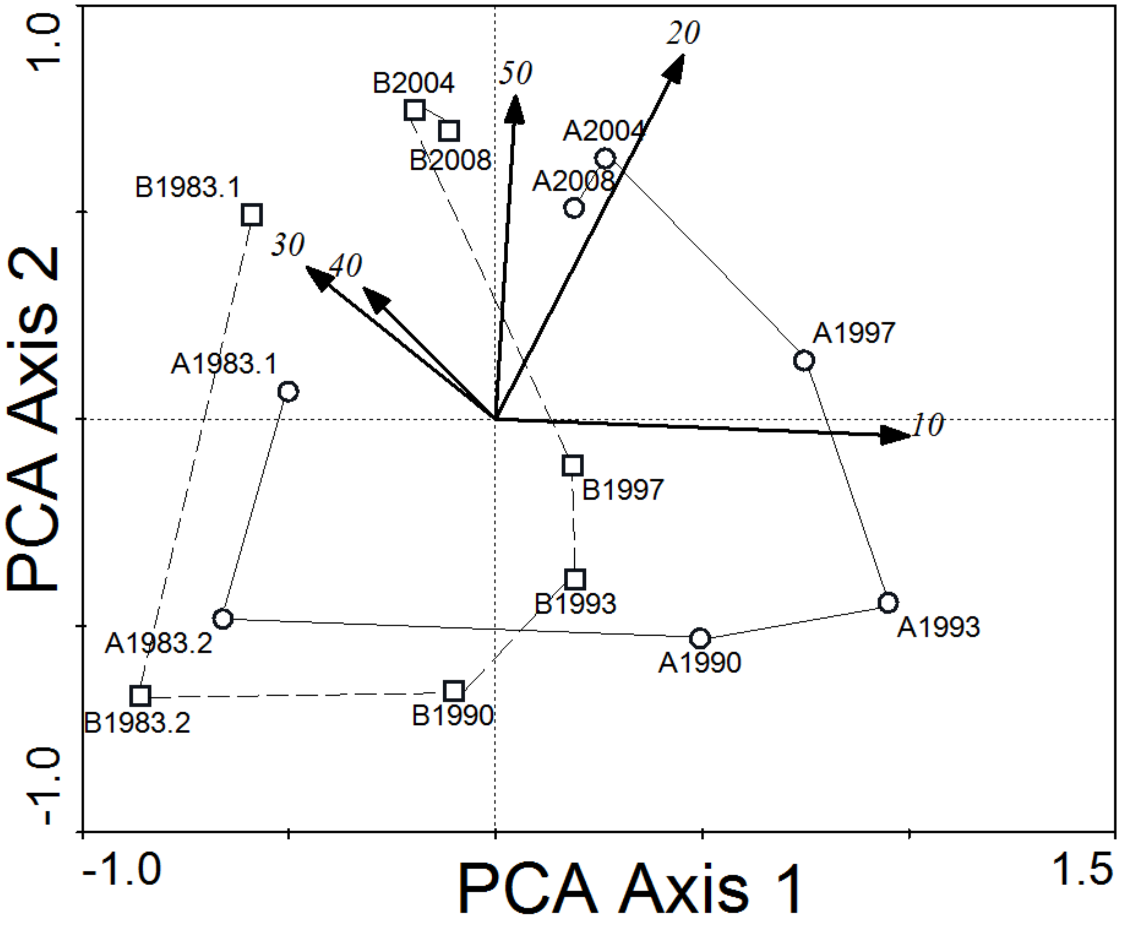


Fig. 2. PCA biplot of DBH classes based on their frequencies in the oak and pine forest over 1983 to 2008. The eigenvalues for the first and second axes were 0.868 and 0.092. 10, 20, 30, 40 and 50 represent DBH classes of 2.5-10cm, 10-20cm, 20-30cm, 30-40cm and 40-50cm respectively. Symbols and site descriptors are the same as Fig. 1.

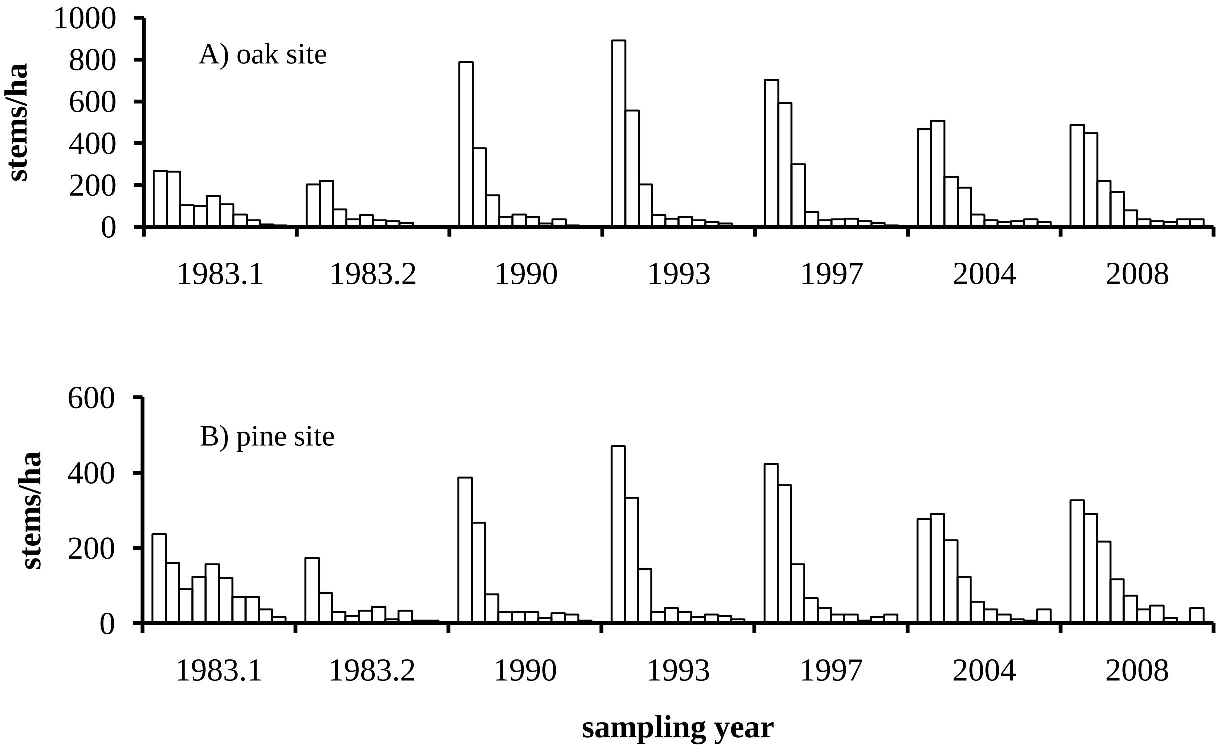


Fig. 3A-B. Diameter distributions for A) oak forest and B) pine forest during each sampling year. Each bar represents a 5cm DBH class interval, the leftmost bar represents <5cm, and the rightmost bar represents >45cm. 1983.1 indicates before the windstorm, 1983.2 indicates after the storm.

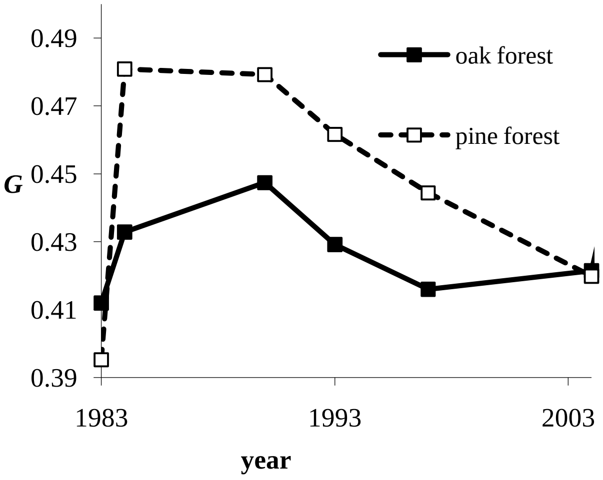
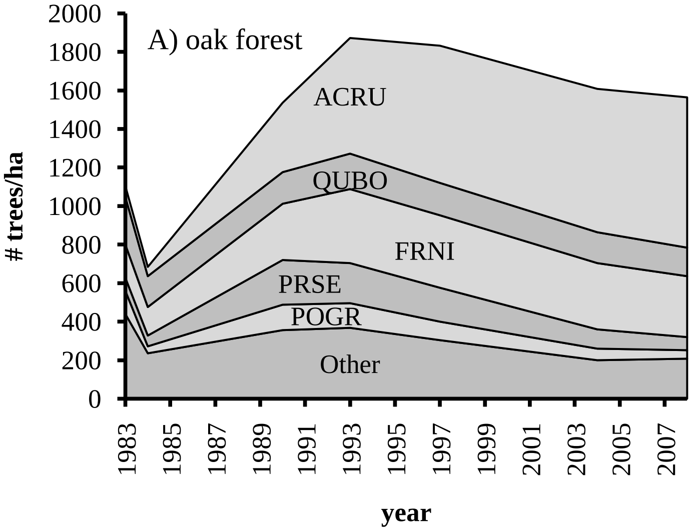


Fig. 4. Gini coefficient (*G*) of site diameter distributions through time.



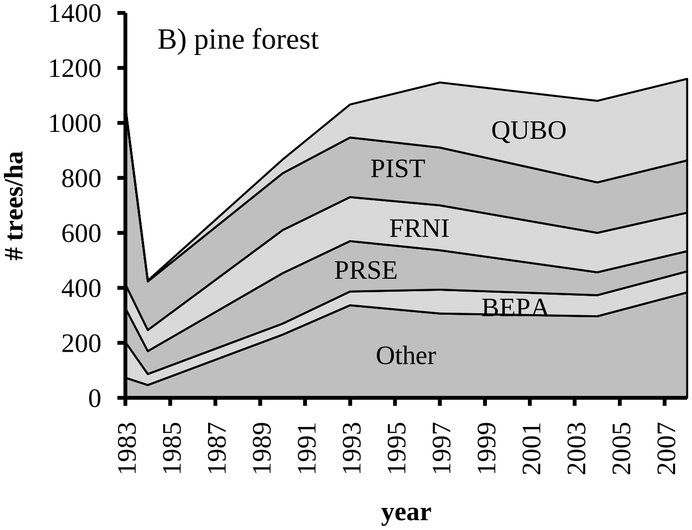


Fig. 5A-B. Density of tree species through time. ACRU = *Acer rubrum*; BEPA = *Betula papyrifera*; FRNI = *Fraxinus nigra*; PIST = *Pinus strobus*; POGR = *Populus grandidentata*; PRSE = *Prunus serotina*; QUBO = *Quercus borealis*. The “Other” category encompasses all other tree species present at the site. Excluding the “Other” category, species are arranged top to bottom in order of increasing shade-intolerance (following Burns & Honkala 1990).

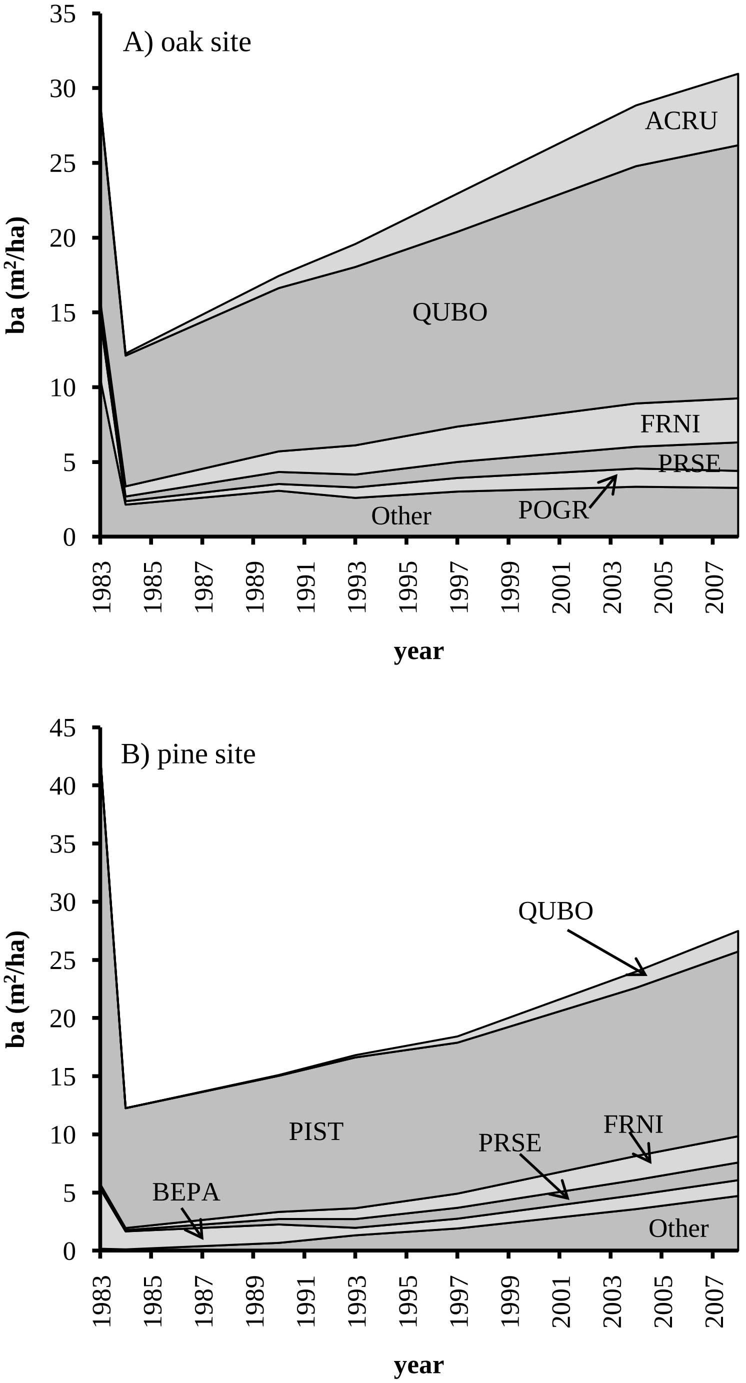


Fig. 6A-B. Basal area of selected tree species through time. Abbreviations and ordering of species is the same as for Fig. 5.

VITA

Matthew Stewart Allen

Candidate for the Degree of

Doctor of Philosophy

Thesis: DISTURBANCE HISTORY AND DYNAMICS IN FOREST AND PRAIRIE COMMUNITIES

Major Field: Plant Science

Biographical:

Education:

Completed the requirements for the Doctor of Philosophy in Plant Science at Oklahoma State University, Stillwater, Oklahoma in December, 2010.

Completed the requirements for the Bachelor of Arts in Biology at Hastings College, Hastings, Nebraska in May, 2004.

Experience:

Teaching Assistant at Oklahoma State University from 2005-2010 for Introductory Biology and General Ecology.
Research Assistant at Oklahoma State University 2006-2007.
Burn Crew Technician/Land Manger for the Nature Conservancy, Wood River, Nebraska, 2005.

Name: Matthew S. Allen Date of Degree: December, 2010

Institution: Oklahoma State University Location: Stillwater, Oklahoma

Title of Study: DISTURBANCE HISTORY AND DYNAMICS IN FOREST AND PRAIRIE COMMUNITIES

Pages in Study: 78 Candidate for the Degree of Doctor of Philosophy

Major Field: Plant Science

Scope and Method of Study:

The objective of this research was to evaluate the effects and dynamics of disturbance in grassland and forest communities. To accomplish this I performed three studies. The first study reconstructed the long-term history of fire at the Tallgrass Prairie Preserve in Osage County, Oklahoma using fire-scarred post oak trees. The second study evaluated two methods utilized to detect growth releases in tree-ring series for their efficacy in identifying disturbance-induced release events in Cross Timbers forest. The third study examined community response and change 25 years following a catastrophic windstorm at pine and oak forest sites in south-central Minnesota.

Findings and Conclusions:

At the Tallgrass Prairie Preserve, fire was present throughout the whole period of record (1729-2005). Changes in fire frequency were generally coincident with changes in land-use, most markedly the transition from Native American land-use to the establishment of cattle ranching in the region. The two methods used to detect growth-releases in tree-ring series were unable to identify releases resulting from disturbance. The difficulty in identifying releases is primarily attributed to the climatic limitations imposed on post oak growth in the Cross Timbers region. Consequently, observed releases were generally coincident with climatic reversals from drier to wetter conditions. The pine and oak forests in Minnesota exhibited compositional convergence 25 years post disturbance as later successional species become more important in each site. Forest architecture also exhibited marked changes through time, with forest recovery proceeding at slightly different rates. The most recent samplings indicate both sites are approaching an architectural state similar to that of the pre-disturbed forest.

ADVISER'S APPROVAL: Dr. Michael W. Palmer