CAUSES AND EFFECTS OF OAK DECLINE IN AN UPLAND OAK-HICKORY FOREST OF EASTERN OKLAHOMA

By

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Abstract:

Oak decline has greatly altered the structure and composition of temperate hardwood forests and is caused by a complex interaction of environmental stresses and pests. These stresses can be biotic or abiotic and can be diverse, ranging from insect infestation to drought. Oak decline affected Okmulgee Game Management Area (OGMA) in eastern Oklahoma between 2007 and 2008. The purpose of this study was to determine the causes and ecological effects of oak decline in a xeric oak-hickory forest of eastern Oklahoma.

This study found that the oak decline occurrence in OGMA was associated with a complex of stress factors including, distance to water, slope, elevation, aspect, drought, false spring and three plant pathogens. Total canopy mortality due to oak decline affected understory species composition, species richness and biomass. Graminoid cover increased 2–4 fold, species richness increased 60–80%, and biomass increased 4–10 fold. Forb species richness increased 1.7–2.0 fold. Oak decline had an impact on forest composition and structure. Live basal area was greatly reduced in affected areas and mortality affected all size categories except stems less than 5 cm dbh. Oak decline was associated with a shift in the relative basal area and caused an increase in the sprouts of subordinate species. Oak decline did not, however, affect the species composition of stem density. Sprout density was not affected, but sprout height doubled in decline areas. Oak decline also was associated with an increase in true seedlings of oak species in the understory.

Although the catastrophic disturbance over large areas caused by oak decline is rare in the Cross Timbers, it may be a mechanism for maintaining species diversity in this vegetation ecotone between eastern forests and western grasslands. Therefore, this study concluded that, given the evidence found and the current fire regime of the study area it is difficult to accurately predict the future of these stands. Due to the frequent fires the areas affected by oak decline possibly might persist as an oak savanna. However, due to high amounts of regeneration, the areas might possibly return to a closed canopy oak-hickory forest.

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INTRODUCTION TO OAK DECLINE STUDY

Oak and mixed oak forests are the most important hardwood forest type in North America and the entire Northern Hemisphere. Approximately 51% of forests in the eastern United States are dominated by oak species (Spetich et al. 2002). Oak dominated forests are valuable economically and ecologically. Oak trees play an important role in forests because mast production of oak species plays a vital role in the food webs of the forest (Feldhamer 2002). A loss of oak trees can have a negative effect on wildlife due to habitat and food loss (McShea et al. 2007). Regions dominated by oak are being threatened by the recent increase in occurrences of oak decline.

Studies have suggested that oak decline is the most widespread problem causing mortality of oaks (Starkey and Oak 1989). Oak decline can be common and damaging to a forest. Researchers conducted a 15 year study in the Bent Creek Experimental Forest in western North Carolina that indicated up to 48% of all oak tree deaths were attributed to oak decline (Greenberg et al. 2011). A study conducted in the southern Appalachian mixed-oak forest of the Coweta basin showed that 2% of the region was affected by oak decline in 1988 (Clinton et al. 1993). Due to the frequency and destruction of these mortality events, oak decline is one of the most serious forest disease problems in the southern and eastern United States (Oak 2002).

Oak decline is not new; it has affected Europe for over three centuries. The earliest record of oak decline is in 1739-1748 in north-eastern Germany (Thomas et al. 2002). Several European countries have been affected by oak decline in the last several decades. Southern and eastern Europe were affected in the 1950s and 1960s respectively. Western Europe experienced oak decline in the 1970s. In the 1980s several more European countries exhibited oak decline (Tomiczek 1993). According to Thomas et al. (2002), oak decline has been recorded in Europe as far east as the former USSR and as far west as the United Kingdom and Portugal in the last three decades.

Oak decline has also developed into a very serious problem in the United States. Decline in oak stands has been recorded as far back as the 1920s in the U.S. (Houston 1987). Since then, there has been an increase of reports of oak decline, which have occurred in nearly every region where oak is found. It is difficult to determine if this increase is due to an increase in prevalence or simply an increase of understanding in diagnosing decline symptoms.

Oak decline is caused by a complex interaction of environmental stresses and pests (Wargo et al. 1983). Ciesla and Donaubauer (1994) defined decline as "an episodic event characterized by premature, progressive loss of tree and stand vigor and health over a given period without obvious evidence of a single clearly identifiable causal factor such as physical disturbance or attack by an aggressive disease or insect." General forest decline has been characterized as increased crown transparency of a forest stand caused by a reduction in leaf area, but overall low mortality. Oak decline is different because it not only reduces biomass production, but also leads to tree death. Oak decline can affect single trees, large groups of trees within stands, or entire stands (Thomas et al. 2002).

This mechanism of tree death can occur in as short as a few months, but generally takes 2-4 years (Tomiczek 1993).

Oak decline symptoms are very diverse and are often overlooked or misdiagnosed. They can be categorized as major or minor symptoms. The major symptoms include, but are not limited to: increased crown transparency, discoloration or yellowing of leaves, dieback of buds, branches or the whole crown, extensive twig abscission and epicormic sprouts on either the branches or trunk. Some of the minor and often overlooked symptoms are: reduction in leaf sizes, slime flux on the trunks, reduced shoot length, necrotic or dead foliage, progressive necroses of bark and cambium, anomalous ramification, sapwood discoloration, damaged mycorrhiza, fungal infections, insect infestations, reduction in diameter growth, nutrient imbalances and biochemical stress indications (Fuhrer 1998, Thomas et al. 2002). Due to the variety and complexity of the symptoms exhibited, oak decline is often overlooked and misdiagnosed.

Several concepts or theories have been derived to explain this sudden loss of tree health (Ciesla and Donaubauer 1994, Houston 1992, Manion 1991, Mueller-Dombois 1992, Sinclair 1965). Although none of these theories have been entirely proven or universally accepted, they are all loosely based on similar principles. The general consensus is that stress factors can be divided into three general categories: predisposing, inciting and contributing. Predisposing factors are generally long term and slow changing factors. Some examples are soil type, site conditions and the climate. These factors inhibit the tree’s natural ability to withstand injury-inducing agents and inhibit the tree’s response capabilities to injury. Inciting factors are usually of short duration and can be either physiological or biological in nature. Some examples include defoliating insects, drought and frost. These factors generally produce dieback of small trees. Without further stress factors, the dieback will often cease and the tree will recover. This commonly occurs in forests. However, if sufficiently severe, prolonged or repeated in successive seasons, inciting factors can ultimately cause dieback and death. Contributing factors further weaken and ultimately kill the tree. Examples of these factors are boring insects, bark beetles and pathogenic fungi.

Removal of canopy trees in a closed canopy forest due to oak decline can greatly affect the understory. This is because of the increase in availability of light for photosynthesis. This increase likewise increases the temperature and reduces the relative humidity in the understory. Canopy loss can also increase the availability of water and mineral nutrients by the formation of "root gaps" (Parsons et al. 1994). Several studies have shown that the overall cover and biomass of understory vegetation increases with canopy loss (Ford and Newbould 1977, Klinka et al. 1996, Stone and Wolfe 1996). In theory, eliminating the canopy trees and increasing available resources could increase understory biodiversity (Thomas et al. 1999) or could result in increased dominance by one or a few understory species and thereby reduce biodiversity (Alaback and Herman 1988).

This research project was conducted to provide new knowledge about the causes and effects of oak decline in an oak-hickory forest. By identifying the probable causes of oak decline, foresters can identify areas that are susceptible to oak decline and recognize early signs of decline. By determining the effects of oak decline on the understory, mid-story and canopy of an oak-hickory forest, land managers can better understand the ecological implications of an oak decline occurrence. The information gained from this study will be useful to prevent oak decline occurrences and to improve management practices following occurrences in oak-hickory forests.

This study was conducted at the Okmulgee Game Management Area (OGMA) in eastern Oklahoma. OGMA was affected by oak decline between 2007 and 2008. Of the 3,700 hectares in OGMA, approximately 3.5% were strongly affected by oak decline. OGMA is approximately 95% wooded with post oak (*Quercus stellata*, 77%), blackjack oak (*Q. marilandica*, 9%) and black hickory (*Carya texana*, 8%) dominating the canopy (Karki et al. 2007). OGMA is located in a region known as the Cross Timbers. The Cross Timbers are a mosaic of upland oak-hickory forest, savanna and prairie communities. This area is an ecotone between eastern forests and grasslands. In this mosaic of vegetation types, disturbance plays a vital role. Disturbances, such as fire, wind, drought, ice storms and herbivory are relatively common in the Cross Timbers (Karki 2007). These disturbances generally create small gaps resulting from the death of one or two canopy trees. Oak decline can remove large stands of trees. This represents a rare, but large disturbance, which can have strong ecological implications.

This thesis has been written in three chapters. The first chapter “The Role of Stress Factors in Oak Decline in the Cross Timbers of Oklahoma” investigated the probable causes of oak decline in the study area. The second chapter “Understory Response to Oak Decline in an Upland Oak-Hickory Forest of Oklahoma” investigated the effects of oak decline on the understory of an oak-hickory forest in the five years following an occurrence. The third chapter “Influence of Oak Decline on Forest Composition and Structure in a Xeric Oak-Hickory Forest of Oklahoma” investigated the effects of oak decline on canopy and mid-story composition and sprout regeneration in the five years following an occurrence. All three chapters will be submitted for publication in an appropriate scientific journal.

CHAPTER I

THE ROLE OF STRESS FACTORS IN OAK DECLINE IN THE CROSS TIMBERS OF OKLAHOMA

Abstract

Oak decline affected Okmulgee Game Management Area in eastern Oklahoma between 2007 and 2008. Oak decline is caused by a complex interaction of biotic and abiotic stresses. These stresses are categorized as predisposing, inciting and contributing factors. Predisposing factors are generally long term and slow changing factors. For this study we selected soil type, slope, aspect, distance to water and elevation for analysis. Inciting factors are usually of short duration and can be either physiological or biological in nature. Examples of these factors are drought, insect defoliation and frost. Contributing factors further weaken and ultimately kill the tree. Examples of these factors are boring insects, bark beetles and pathogenic fungi. These stress factors were examined post-occurrence using GIS analysis, binary logistic regression, weather data and by direct observation of trees affected.

Distance to water appeared to be an influential predisposing stress factor. The proximity to water possibly led to underdeveloped root systems, and therefore made these trees more susceptible to drought. Slope, elevation and aspect were also correlated with decline. Areas affected by oak decline tended to be close to water, on lower elevation and on steeper slopes facing northeast, east or southeast. There is strong spatial dependence in these predisposing factors. Drought may have played a role in the decline and likely made the trees more susceptible to other stresses. A false spring in 2007 was suspected to be a major contributor to the decline. No insect infestations were identified as contributing factors. However, three plant pathogens were isolated and identified: *Biscogniauxia mediterranea, Botryosphaeria obtusa* and *Discula quercina*. These plant pathogens are suspected to have contributed to the oak decline. In summary, this study found that the oak decline occurrence at Okmulgee Game Management Area occurring between 2007 and 2008 was associated with a complex of stress factors including, but not limited to, distance to water, slope, elevation, aspect, drought, false spring and three plant pathogens.

Keywords: oak decline, stress factors, cross timbers, spring freeze, drought

1. Introduction

Oak tree species (*Quercus* spp.) are dominant in most of the hardwood forests of the Northern Hemisphere. In the Central Hardwood Region of the United States, mixed oak forests occupy over 50% of the forested land base (Johnson et al. 2002). Oak forests are valuable economically and ecologically. Oak trees are a “keystone” to biological diversity because their mast production plays a vital role in the food webs of the forest (Feldhamer 2002). These regions dominated by oak are being threatened by the recent increase in occurrences of oak decline. Oak decline is the most widespread problem plaguing oaks (Starkey and Oak 1989).

Oak decline is caused by a complex interaction of biotic and abiotic stresses. In this context, a decline is defined as “an episodic event characterized by premature, progressive loss of tree and stand vigor and health over a given period without obvious evidence of a single clearly identifiable causal factor, such as physical disturbance or attack by an aggressive disease or insect.” (Ciesla and Donaubauer, 1994, pg. 3) General forest decline has been characterized as increased crown transparency of forest stand, but overall low mortality. Oak decline differs because it not only reduces biomass, but also leads to tree death. Oak decline can affect single trees, large groups of trees within stands or entire stands (Thomas et al. 2002). This complex of factors leading to tree death can occur in as short as a few months, but generally takes 2-4 years (Tomiczek 1993).

Oak decline can be very detrimental to a forest. Researchers conducted a 15 year study in the Bent Creek Experimental Forest in western North Carolina, which indicated that up to 48% of all oak tree deaths were attributed to oak decline (Greenberg et al.

2011). A study conducted in the southern Appalachian mixed-oak forest of the Coweta basin showed that 2% of the region was affected by oak decline in 1988 (Clinton et al. 1993).

Several concepts or theories have been developed to explain this sudden loss of tree and stand vigor (Ciesla and Donaubauer 1994, Houston 1992, Manion 1991, Mueller-Dombois 1992, Sinclair 1965). Although none of these theories has been entirely proven, or universally accepted, they are all loosely based on similar principles. For the purpose of this paper, we have adopted the predisposing, inciting and contributing factors concept originally suggested by Sinclair (1965) and expanded upon by several researchers (Manion 1991, Ciesla and Donaubauer 1994). This concept states that there are three separate types of stress factors that play a role in forest decline. The first are the predisposing factors which are generally long term and slow changing factors. Some examples are soil type, site conditions and the climate. These factors inhibit the tree's natural ability to withstand injury-inducing agents. These factors can also inhibit the tree's response to injury. The second are the inciting factors. Inciting factors are usually of short duration and can be either physiological or biological in nature. Some examples are defoliating insects, drought and frost. These factors generally produce dieback of small trees. Without further stress factors, the dieback will often cease when the stress ceases and the tree will recover. This is commonly seen in forests. However, stress alone, if sufficiently severe, prolonged or repeated in successive seasons, can ultimately cause forest dieback and death. The third are the contributing factors. Contributing factors further weaken and ultimately kill the trees. Examples of these factors are boring insects, bark beetles and pathogenic fungi.

Several studies have examined the causes of oak decline and the role that biotic and abiotic factors play in causing tree death (Fuhrer 1998, Haavik et al. 2012, Houston 1992, Jung et al. 2000, Lawrence et al. 2002, Manion 1991, Mueller-Dombois 1992, Tainter 1983, Thomas et al. 2002, Wargo et al. 1983). Several of these studies were conducted in Europe and the majority of the studies carried out in the US occurred in the Ozark, Ouachita and Appalachian mountain ranges. No studies have been conducted to determine the role of predisposing, inciting and contributing factors in oak decline in the Cross Timbers of Oklahoma. The findings of such a study can gain useful knowledge that might help foresters and land managers to better understand, anticipate and respond to oak decline occurrences. The purpose of this study was to determine the role or importance that stress factors played in an occurrence of oak decline in Okmulgee Game Management Area of eastern Oklahoma.

2. Methods

2.1. Study Area

Okmulgee Game Management Area (OGMA), located in Okmulgee County in eastern Oklahoma, was affected by oak decline between 2007 and 2008. Of the 3,700 hectares in OGMA, approximately 3.5% were affected by oak decline (Fig. 1). OGMA is a portion of the Okmulgee Wildlife Management Area and is managed by the Oklahoma Department of Wildlife Conservation. OGMA is located in a region known as the Cross Timbers. The Cross Timbers are a mosaic of upland oak-hickory forest, savanna and prairie communities. This area is an ecotone between eastern forests and grasslands. OGMA is approximately 95% wooded with post oak (*Quercus stellata*, 77%), blackjack oak (*Q. marilandica*, 9%) and black hickory (*Carya texana*, 8%) dominating the canopy (Karki et al. 2007).

OGMA has a subtropical climate with a mean annual temperature of 16º C, and daily mean highs of 34º C in August and daily mean lows of -2º C in January. The area receives an average annual precipitation of 104 cm, although there is substantial interannual variation (OCS 2010). OGMA contains 13 different soil types, but is dominated by Hector-Endsaw soil complex (HtE), which covers approximately 75% of the OGMA. HtE is characterized as well drained, non-arable, shallow, stony fine sandy loam with bedrock at a depth of about 30 cm. It has a hill or mountain topography of 5-30 percent slopes (Sparwasser et al. 1968).

2.2. Predisposing Factors

Five possible predisposing site factors were selected for analysis: slope, aspect, soil type, elevation and distance to water. Other predisposing factors such as tree density, basal area, tree age, tree species, canopy position and tree size (dbh) were not included in this analysis because it is difficult to obtain accurate measurements for these factors post-occurrence. Aerial photographs obtained from Google Earth showed OGMA in 2004, before the occurrence of oak decline, and 2008, shortly after the occurrence (Google 2010). Areas affected by oak decline between 2004 and 2008 were digitized. A digital elevation model (DEM) was obtained from the National Elevation Dataset with a 3-meter resolution and 1/3 arcsecond (Gesch 2007). Slope, aspect and hydrology were calculated from this DEM using ArcGIS 10.1 (ESRI 2011). Slope was measured as percent rise. Aspect was converted to cardinal (north, east, south, west) and intercardinal (northeast, southeast, southwest, northwest) directions for analysis. Using the DEM-derived hydrology raster, euclidean distance was measured to obtain a continuous raster showing distance from a water source for all points in the study area. Elevation was centered by subtracting the minimum elevation found in the OGMA. A soil map obtained from the web soil survey was provided by the USDA (Soil Survey). The coordinate system used was GCS_North_Amercian_1983 and the projection system used was NAD_1983_UTM_Zone_15N.

These predisposing factors were analyzed by creating 53,435 randomly located points throughout OGMA. Of these randomly generated points, 3.5% (1,888) were located in areas affected by oak decline. Random point generation was constrained to be at least 10 m apart. All five predisposing factors were extracted from the datasets to these randomly located points. These datasets were entered into SPSS 21.1 and analyzed using forward selection of predictors (IBM Corp. 2012). Significance was determined using p=0.05 as a cutoff. This binary logistic regression enabled us to analyze the ability to predict oak decline using predisposing factors. Using raster calculator we generated a predictive map of areas that might be susceptible to oak decline. Using data from the extracted points, we also analyzed the percent land coverage. This analysis allowed us to compare the relative proportions of the predisposing factors in total OGMA to decline areas.

2.3. Inciting Factors

In order to determine the effects of inciting factors, such as drought and frost, weather data were obtained from the Oklahoma Mesonet (OCS 2014) and the National Climatic Data Center (NOAA NCDC 2013). The monthly summaries from 1998 to 2012 were accessed from the Mesonet site located in Okmulgee, OK. OGMA is located on the edge of the east central climate division, bordering the central and northeast climate divisions. Palmer Drought Severity Index (PDSI) data were used to determine the effects of drought and were accessed for the east central climate division of Oklahoma. PDSI ranges from +6 (extremely wet) to -6 (extremely dry) (Palmer 1965). PDSI data for the east central climate division was not available for 2006; therefore, it was obtained from the central climate division for that year. Average monthly temperature and minimum daily temperature were examined for trends that might contribute to oak decline.

2.4. Contributing Factors

Researchers investigated the possible causes of this specific incident of oak decline shortly after the occurrence in 2008 (Damon Smith, personal communication, 10/6/2008). A general field inspection was conducted. Affected trees were examined and conditions were observed to determine the effect of any contributing factors such as pathogenic fungi and insect infestations.

3. Results

3.1. Predisposing Factors

Distance to water, slope, elevation and aspect were suspected of being predictors for oak decline and therefore were possibly predisposing factors. Distance to water appears to be an important predisposing factor ($p<0.001$, Fig. 2, Fig. 3a). As distance to water decreased, the likelihood of being affected by the decline increased. The average distance to water for a point affected by oak decline was 165 m, with a maximum of 617 m (Table 1). This is significantly lower than points in non-decline areas, with an average of 385 m, and a maximum of 1051 m. Slope was a significant predisposing factor (*p*<0.001, Fig. 3b). Average slope for points in decline areas was 14.7%, compared with 8.9% for non-decline points (Table 1). Elevation was significantly different in decline areas (*p*<0.001, Fig. 3c). Average elevation was higher for non-decline points (236 m), than decline points (221 m, Table 1). Aspect was a significant predictor (Fig. 3d). Slopes that faced northeast, east, southeast and south appear to have been predisposed to oak decline. In contrast, slopes that faced north and northwest had reduced amounts of decline. Aspect in the OGMA was approximately evenly distributed between all cardinal and intercardinal directions: 12.5±0.37%. However, areas affected by oak decline were dominated by northeast (18.69%), east (27.93%) and southeast (14.46%) facing slopes (Table 2). None of the soil types were significant predictors of oak decline. The logistic regression equation was able to relatively accurately predict areas that were at risk or predisposed to oak decline (Fig. 4). However, the regression did not predict any areas to be affected by oak decline with a probability higher than 65%. The regression equation for this binary logistic regression was:

$$LN\left[\frac{P}{1-P}\right] = 0.060(Slope) - 0.003(Elevation) + 0.840(East) - 0.876(North) + 0.649(Northeast) - 0.971(Northwest) + 0.285(South) + 0.424(Southeast) - 0.006(Distance\ to\ Water) - 2.008$$

3.2. Inciting Factors

Four out of five years from 2002 to 2006 had less than average PDSI (Fig. 5). 2003 and 2005 had relatively low PDSI (-1.27, -1.46), but 2006 was exceptionally low (-3.61). Low PDSI indicates a relatively dry year. Ten out of the 15 years from 1998 to 2012 had lower than average PDSI. There were no significant trends that might contribute to oak decline in the records of average monthly temperature. In examining the minimum daily temperatures from 2004 to 2008, there was a consistent mid to late spring frost that usually lasted only one night. March 2007 started with average minimum daily temperatures that ranged from just below freezing to 14º C (Fig. 6). This was the 2nd warmest March on record, approximately 8 degrees above normal (OCS 2007). Starting March 19th (Day 78), the minimum daily temperature greatly increased and ranged from 13º C to 18º C for the remainder of the month. From March 26th (Day 85) to April 4th (Day 94) the mean daily minimum was 12.6º C. Minimum daily temperature plunged, starting April 4th (Day 94). April 7-8th (Day 97-98) had minimum daily temperatures below freezing, with April 8th registering at –5.0º C. This qualifies as a false spring event that could damage cambium of mature post oak trees according to Stahle (1990).

3.3. Contributing Factors

There were no widespread and identifiable insect infestations detected in areas affected by oak decline. There were, however, three different "dieback" plant pathogens isolated from affected trees: *Biscogniauxia mediterranea, Botryosphaeria obtusa* and *Discula quercina*. All of these pathogens are considered "weak" in their ability to cause disease and are commonly found in forests. These organisms are typically associated with other "events" such as environmental or abiotic stress factors.

4. Discussion

This study found that the oak decline occurrence in Okmulgee Game Management Area between 2007 and 2008 was likely associated with a complex of stress factors (Fig. 7). Although it may be impossible to conclusively determine the causes of oak decline, we were able to identify several stress factors which were correlated with the decline. Distance to water, slope, elevation, and aspect possibly predisposed areas to oak decline. We suspected that these stress factors made trees growing there susceptible to further stresses. We suspected that these trees were probably further weakened by inciting factors such as drought and a false spring in 2007. We suspected that plant pathogens, *Biscogniauxia mediterranea, Botryosphaeria obtusa* and *Discula quercina*, also played a role in the oak decline. Several of these stress factors were directly related to and facilitated each other.

Distance to water was a statistically significant predisposing factor. As distance to water decreased, the likelihood of a tree being affected by oak decline increased. This may appear counter-intuitive because the closer to a water source, the more access a tree might have to water, especially during a drought. However, the optimal partitioning theory suggests that plants allocate biomass to the organ (root, stem, or leaves) that acquires the most limiting resource (Thornley 1972, McCarthy and Enquist 2007). Therefore, in an area close to a water source, where water would generally not be a limiting resource, carbon would be allocated away from the roots to either the stem or the leaves. Subsequently when a drought occurs and water levels decrease, trees in areas close to water sources would have "underdeveloped" root systems and consequently are more susceptible.

Another proposed, but less likely, explanation for the strong correlation between distance to water and tree death was there might have been a water-borne pathogen that affected these trees, such as *Phytophthora* or *Pythium*, that was not identified. These plant pathogens are well adapted to wet soils and are often called "water molds". *Phytophthora* has been identified as a major stress factor contributing to oak decline in other areas (Jonsson 2004, Jung et al. 2000). Kabrick et al. (2004) found there was greater red oak mortality on upper slope positions than on lower slopes and upland waterways. However, our results suggested that upland waterways played a vital role in this oak decline occurrence.

Other predisposing factors that were found to be useful predictors were elevation, slope and aspect. The effects of elevation and aspect might be directly linked to the false spring experienced in 2007. Gu et al. (2008) found that higher elevations were less severely impacted by the spring freeze because plants at higher altitudes had not experienced warm enough temperatures before the freeze to cause leaf-out. This is most likely caused by a difference in landscape position and cold air drainage. Our study found that decline, on average, affected areas with steeper slopes pointed northeast, east and southeast. This contradicts the findings of Kabrick et al. (2008), who found no significant mortality differences related to slope or aspect. Starkey and Oak (1989) found no statistically significant differences in aspect and rate of mortality, however they did find that overall damage was minimal on northeast and east facing slopes. This directly opposes the findings of this study, which found the eastern slopes to be the most heavily affected. This variation in results might be explained by differences in region or territory. Most likely this variation in results can be attributed to the relation of oak mortality to streams in this study. Soil type might have contributed to the oak decline, although it is difficult to determine this because approximately 75% of OGMA is Hector-Endsaw complex (HtE). Approximately 88% of the areas affected by oak decline were classified as HtE. Areas affected by oak decline tended to be within 200 m of water, between 210-230 m in elevation, on slopes with 5-20 percent rise and facing northeast, east or southeast. There were other predisposing factors that could have contributed to the decline, such as tree density, basal area, tree age, tree species, canopy position and tree size (dbh). However, post-occurrence we were unable to accurately estimate these factors.

It is important to note that the effects of the predisposing factors found to be useful predictors in this study (distance to water, slope, aspect and elevation) are highly confounded and difficult to tease apart. Streams are naturally at lower elevations and often have steeper slopes leading into them due to erosion. Due to the correlation of all of these factors it is difficult to imply direct causation. The map that was generated from the binary logistic regression was able to accurately predict areas that were at risk or predisposed to oak decline. However, according to the regression no areas were predicted to be affected by oak decline at a probability higher than 65%. This suggests that there were possibly other factors that contributed to the decline death spiral.

The two inciting factors that we found that might have contributed to the decline by further weakening the trees were drought and a false spring. Drought is often considered to be the most influential inciting factor in oak decline (Law and Gott 1987, Starkey et al. 1989, Stringer et al. 1989, Tainter et al. 1983). However, in this region, drought is a common stress and the oak species that dominate the canopy have developed both morphological and physiological adaptations (Thomas et al. 2002). Oaks have developed deep-reaching root systems, hairs on the undersurface of leaves, and can regulate stomatal conductance (Thomas et al. 2002). These adaptations to drought allow oak species to persist in xeric site conditions. However, proximity to water could have prevented trees from developing a deep-reaching root system, as well as producing hairs to enhance surface area. The absence of these drought stress adaptations ultimately may have left the trees more susceptible. Due to the fact that drought stress can reduce shoot growth, it could have also made the tree more susceptible to other stresses. In this matter, drought often acts as a gateway stress that leads to other stress factors.

The warm temperatures followed by extreme cold temperatures in 2007 qualified as a false spring according to the criteria established by Stahle (1990). A false spring was defined as a 10-day warm spell, starting 13 days before a frost event. During this warm spell, the mean daily minimum temperature must be ≥4.4º C and no daily temperature ≤ -2.8º C. The mean daily minimum temperature for this time period in OGMA was 12.6º C and no temperature fell below freezing. A frost event was defined as any daily low temperature ≤ -5.0º C on or after March 21st in Oklahoma (Stahle 1990). The frost event in OGMA occurred on April 8th and reached -5.0º C.

This false spring may have played a large role in the decline. A spring freeze can affect newly formed leaves, shoots, developing flowers and fruits, (Gu et al. 2008) and the tree stem itself (Thomas et al. 2002). This particular freezing event affected a very broad region across southeastern United States and is often called the "2007 Easter freeze." This freeze had disastrous effects on natural vegetation and crops alike due to the timing in a crucial transition period for plants from dormancy to growth (Gu et al. 2008). The above average temperatures leading into the spring freeze caused plants to break dormancy early. Gu et al. (2008) showed that in the southeastern United States, these unusually warm temperatures caused the Normalized Difference Vegetation Index (NDVI) to develop much faster in 2007 prior to the freeze than in 2006. They also showed that after the freeze, the opposite pattern was seen. The "rushing green wave of vegetation development" that occurred before the freeze was quickly turned into a "green retreat."

Gu et al. (2008) showed that in temperate deciduous forests in the southeast region of the US, leaf-out started approximately 15 days earlier due to warmer temperatures in 2007. Early leaf-out followed by drastically low temperatures can cause defoliation of tree species. This causes a smaller canopy made up of fewer and smaller leaves, which reduces light acquisition and could possibly reduce fine root production due to reduced photosynthate production (Augspurger 2011).

A spring freeze can act as a defoliating agent, but it can also greatly affect the stem of the tree. As previously mentioned decline areas tended to be at lower elevations near water which would leave them susceptible to cold air drainage. Spring frost can greatly damage the xylem of a plant. Water in the xylem generally freezes between 0 and -2 degrees Celsius. When the water is thawed, the leaves are already active with transpiration. This transpiration reduces the pressure in the xylem and dissolved gases will form gas bubbles. These gas bubbles can lead to embolism of the vessel and can eventually lead to total blockage of the water transport (Thomas et al. 2002). Oak, hickory, ash and elm species have ring porous wood. Early in the growing season large vessels are produced (earlywood), which transition to smaller, thinner vessels later in the season (latewood). Large earlywood vessels form before leaf expansion and are the major conduit for water transport to the new leaves, very little water is conducted in the vessels of earlier annual rings because they are gas filled (Zimmerman et al. 1971). These vessels have been shown to be sensitive to climatic variations (Woodcock 1989). A false spring could severely damage the developing large earlywood vessels. This damage could thoroughly impair the tree's ability to withstand further stress or damage. Frost can negatively affect "energy acquisition, storage, growth, reproduction, and next year's buds in the current year and canopy development, architecture, and even survival in subsequent years" (Augspurger 2011). These negative responses to the false spring most likely contributed considerably to the oak decline spiral.

The negative effects of a false spring discussed thus far, addressed the physical impacts that such an event can have on an individual tree. But, generally, these effects are felt by entire stands of trees and can have short-term and long-term ecological impacts. These impacts could consist of, but are not limited to, major effects on carbon sequestration, disturbance regimes, forest composition, ecosystem functions, and biosphere-atmosphere interactions (Hufkens et al. 2012). Studies suggest that the occurrence of frost, after leaf-out, is projected to become more common due to climate change (Cannell and Smith 1986, Meehl et al. 2000, Gu et al. 2008). This increase in the occurrences of false springs could greatly affect the composition and vigor of forests across the US.

There is likely a strong link between the predisposing factors (distance to water, slope, aspect and elevation) and the effects of the false spring in our study area. The areas affected were at lower elevations, on steep slopes and near water. There is a strong possibility that these areas were more strongly affected by the low temperatures due to cold air drainage and the formation of "frost pockets". Therefore, the predisposing factors found to be significant might simply describe the areas that are most susceptible to extreme low temperatures due to topography of the study area.

After the predisposing and inciting stress factors have weakened the trees, contributing factors can successfully infest the trees and cause tree death. The three plant pathogens isolated were *Biscogniauxia mediterranea, Botryosphaeria obtusa* and *Discula quercina*. All three pathogens are, for the most part, considered to be opportunistic. The common name of the disease that *Biscogniauxia mediterranea* causes is Hypoxylon dieback of oak. This pathogen is in the same genus as *Biscogniauxia atropunctata,* the causal agent of Hypoxylon canker in Oklahoma. Hypoxylon has been associated with oak decline in other regions (Haack and Blank 1991). The pathogen can be an aggressive secondary pathogen, and is most commonly associated with trees that are drought stressed. The common name of the disease caused by *Botryosphaeria obtusa* is black rot. While not commonly associated with oak*,* this fungus can be a common inhabitant of many woody plants. It colonizes the bark and lives as a saprobe unless the tree is predisposed by environmental stress or wounds, at which point it can be a pathogen. Severe leaf spotting can result in defoliation, which weakens the tree, and limb cankers can girdle and eventually kill entire branches (Travis et al. n.d.). Other *Botryosphaeria* spp. have been implicated in other more severe diseases of many woody plants, especially grapes and apples. *Discula quercina* causes oak anthracnose, which is typically a foliar disease. The fruiting bodies, however, are found on young wood and bark. Twig dieback has been associated with this fungus on oaks in California and Oregon. This fungus frequently occurs on the leaves and twigs of declining oaks. Some fungal endophytes spend all, or nearly all, of their lifetime in the host plant with only limited or no pathogenic effect (Schardl et al. 2004). However the fungus can switch to active growth when the plant is subjected to stress (Carroll 1986). Possibly due to the stress of predisposing factors and inciting factors, these fungi appeared to play at least a contributing role in the decline complex. However, the presence/ absence of fungus could not be directly linked to tree mortality because these fungi are commonly found in healthy forests as well.

5. Conclusion

Determining the cause of an oak decline occurrence is very difficult. However, we were able to identify several stress factors that might have played a role in the oak mortality. Distance to water appeared to be an influential predisposing stress factor. The proximity to water possibly led to reduced root systems, and therefore made these trees more susceptible to drought. Slope, elevation, and aspect also appeared to be influential. Areas affected by oak decline tended to be close to water, on lower elevation, and on steeper slopes facing northeast, east or southeast. The effects of these predisposing factors (distance to water, slope, elevation and aspect) are all highly correlated and are strongly spatially dependent. Drought may have played a role in the decline and possibly made the trees more susceptible to other stresses. A false spring in 2007 was suspected of being a major contributor to the decline. No insect infestations were identified as contributing factors. However, three plant pathogens were isolated and identified: *Biscogniauxia mediterranea, Botryosphaeria obtusa* and *Discula quercina*. These plant pathogens might have contributed to the oak decline. In summary, this study found that the oak decline occurrence at Okmulgee Game Management Area, occurring between 2007 and 2008, was correlated with a complex of stress factors including, but not limited to: distance to water, slope, elevation, aspect, drought, false spring and three plant pathogens. The extent to which this complex of factors affected other forests across south central United States is not known. It is possible other areas suffered similar decline. Occurrences of forest decline have important consequences for forest succession and the pattern of vegetation in the region.

Tables and Figures

Table 1. Range of predisposing factors. OGMA indicates the entire Okmulgee Game Management Area. Non-decline indicates areas that were not affected by oak decline. Decline indicates areas affected by oak decline.

Predisposing Factor	OGMA	Non-Decline	Decline
Slope		Percent	
Maximum	74.1	74.1	64.5
Mean	9.4	8.9	14.7
Minimum	0.0	0.0	0.1
Elevation		Meters	
Maximum	290.87	290.87	253.39
Mean	236.19	235.51	221.27
Minimum	190.21	190.21	196.83
Distance to Water		Meters	
Maximum	1050.76	1050.76	616.85
Mean	380.98	384.76	165.12
Minimum	0	0	0

Table 2. Relative proportion land coverage of each variable within a predisposing factor. OGMA indicates the entire Okmulgee Game Management Area. Decline indicates the areas affected by oak decline. Slope is measured as percent rise. Elevation and distance to water is measured in meters. Data are displayed as percent of total area.

Predisposing Factors		OGMA	Decline
	Area	36,123,562.73 m²	1,289,126.84 m²
Soil Type			
	Collinsville-Talihina complex (CtE)	6.5	6.2
	Dennis silt loam, eroded (DeC2)	0.7	1.2
	Hector-Endsaw complex (HtE)	82.0	87.7
	Karma loamy fine sand (KsD)	1.7	1.6
	Verdigris silt loam (Vg)	1.0	1.2
	Verdigris-Madill complex (Vp)	8.1	2.2
Aspect			
	North	13.3	7.2
	Northeast	11.9	18.4
	East	11.6	27.5
	Southeast	11.8	14.8
	South	11.8	8.9
	Southwest	11.6	8.2
	West	13.7	10.2
	Northwest	14.4	4.9
Slope			
	0-5	34.7	6.4
	5-10	33.5	22.5
	10-15	13.9	30.4
	15-20	7.4	20.8
	20-25	4.1	10.8
	>25	6.3	9.2
Elevation			
	190-210	18.7	15.2
	210-230	21.5	65.3
	230-250	29.8	18.5
	250-270	19.1	1.0
	270-290	10.9	0.0
	>290	0.1	0.0
Distance to Water			
	0-100	12.8	42.3
	100-200	14.1	22.8
	200-300	14.6	14.2
	300-400	13.9	8.2
	400-500	12.6	4.8
	500-600	11.2	4.0
	>600	20.7	3.6

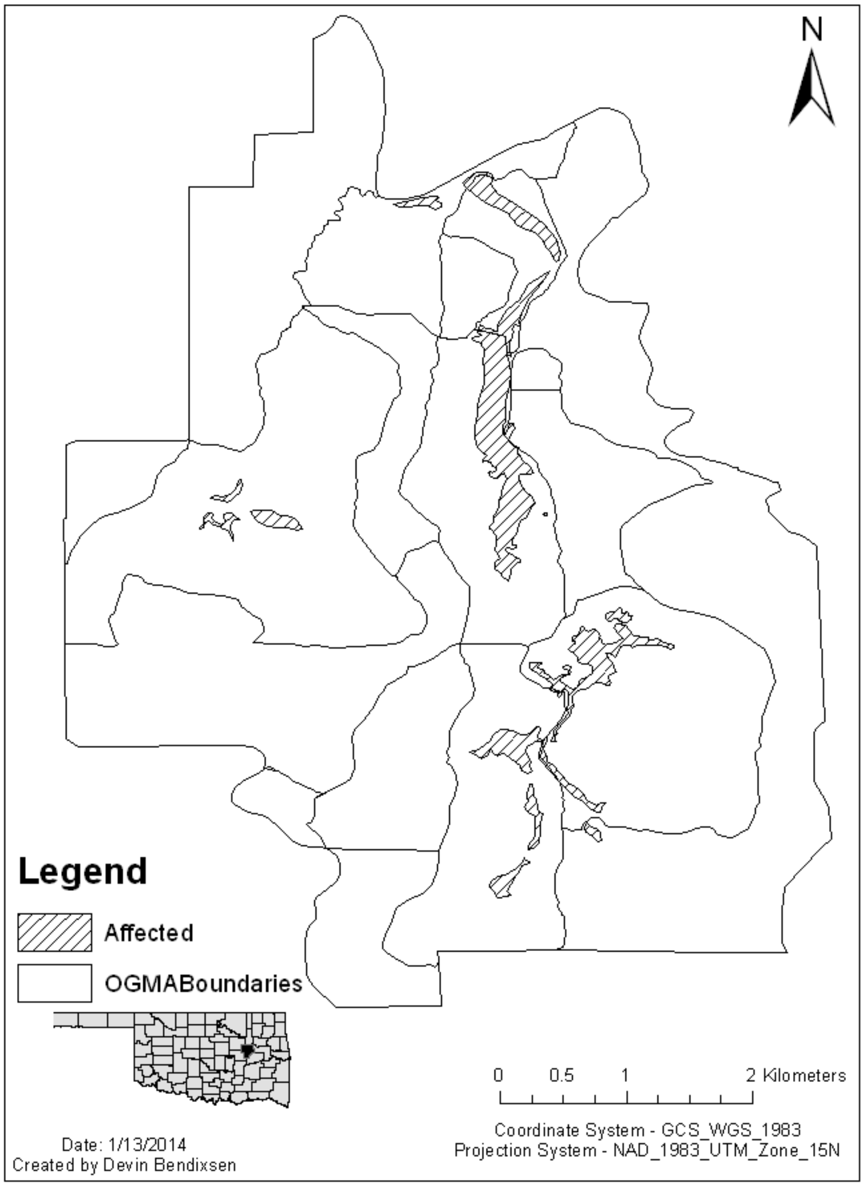

Fig. 1. Map of Okmulgee Game Management Area indicating the unit boundaries and the areas affected by oak decline between 2007 and 2008.

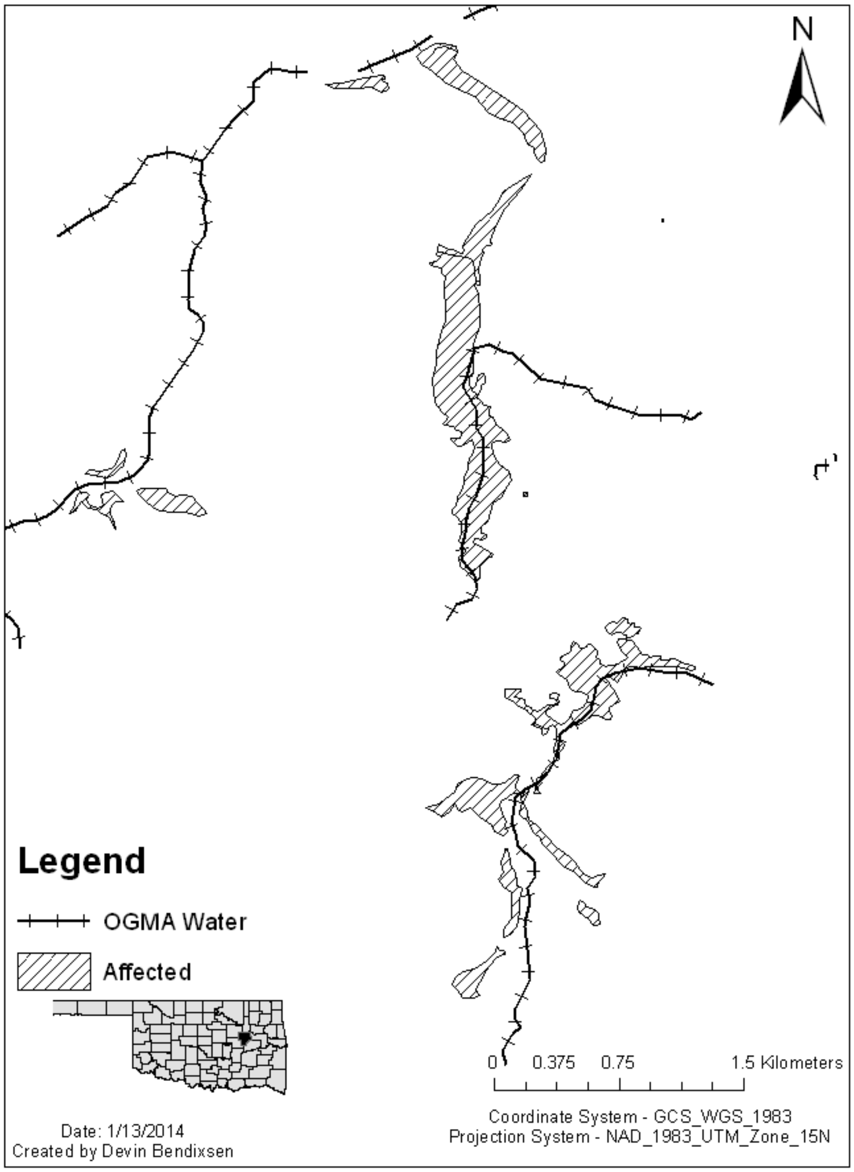

Fig. 2. Map of Hydrology at Okmulgee Game Management Area indicating areas affected by oak decline.

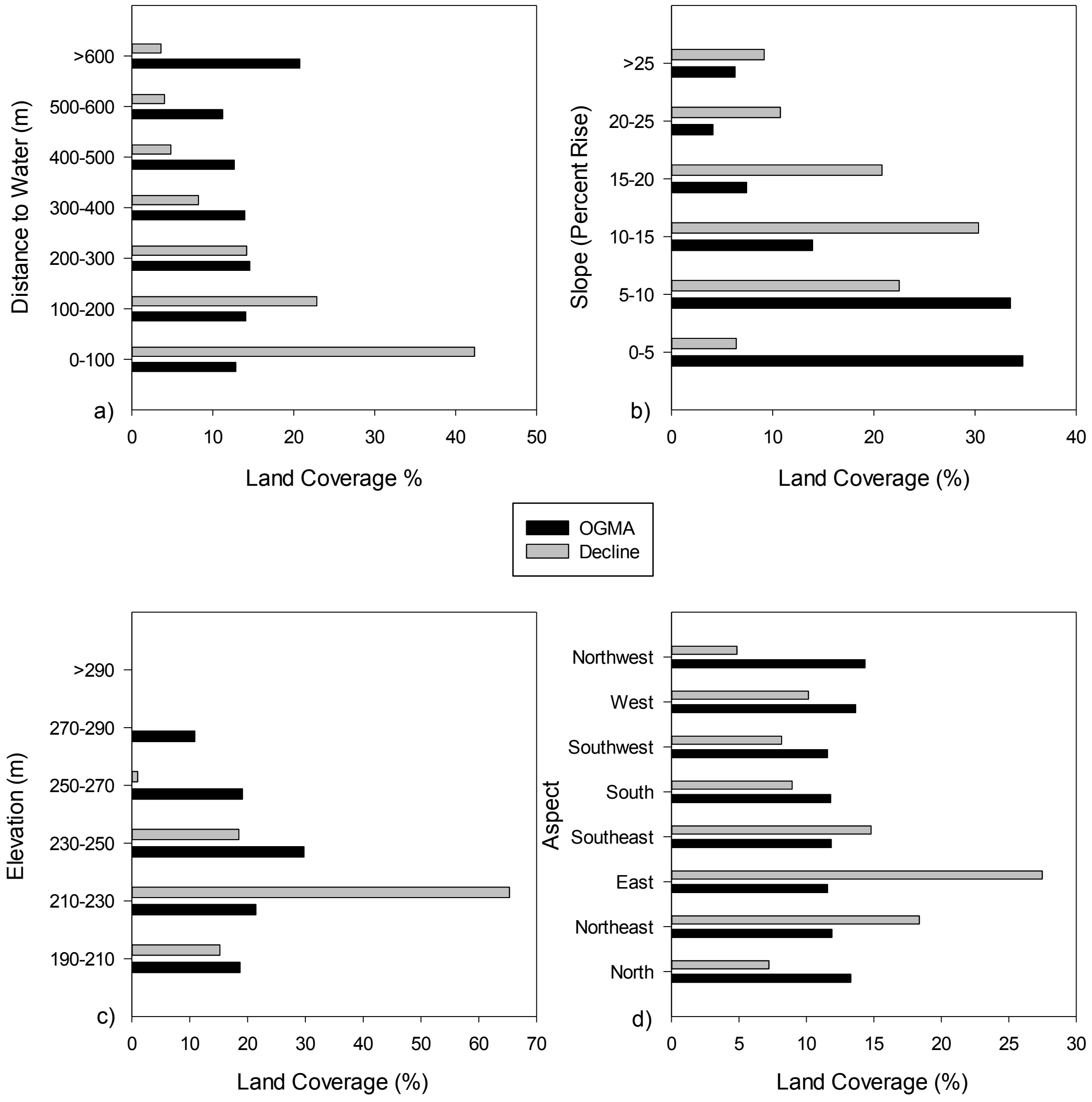

Fig 3. Predisposing Factors: a) Distance to water, b) Slope, c) Elevation, d) Aspect. OGMA indicates all areas within Okmulgee Game Management Area. Decline indicates areas affected by oak decline. Units are percent land coverage. Slope is measured as percent rise.

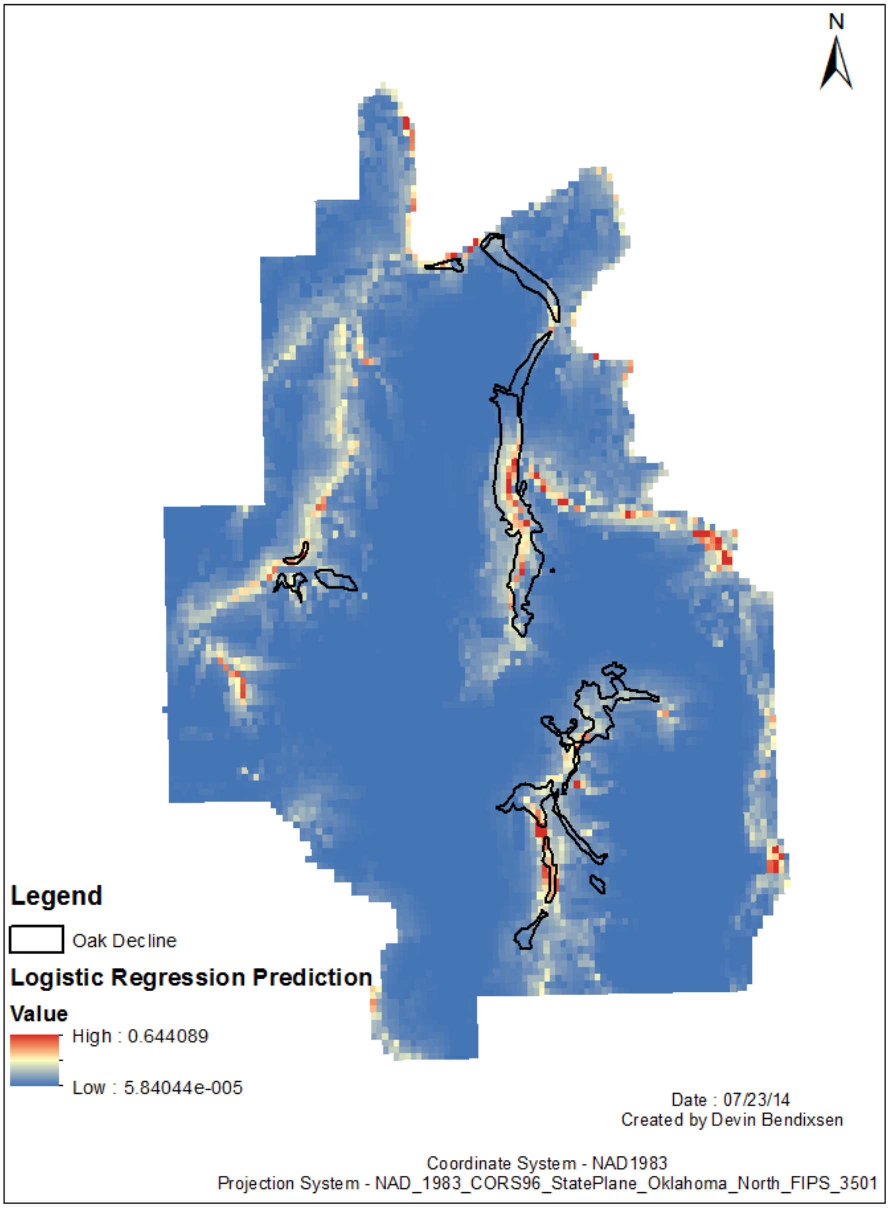

Fig. 4. Map of Binary Logistic Regression Prediction. Black outline indicates areas affected by oak decline between 2007 and 2008

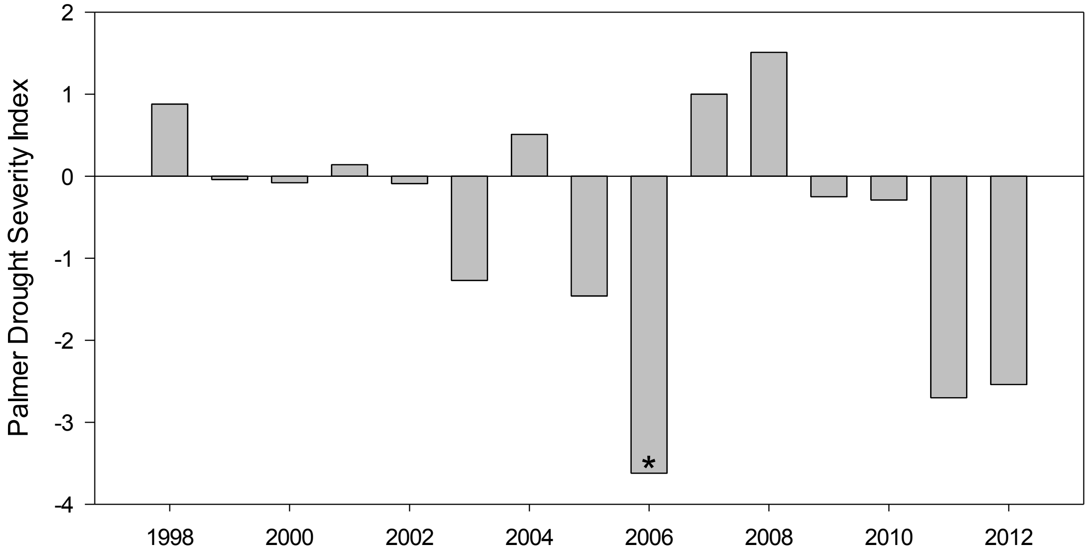

Fig. 5. Palmer Drought Severity Index (PDSI) for East Central Climate Division of Oklahoma (NOAA NCDC 2013). Asterisk indicates value taken from central climate division.

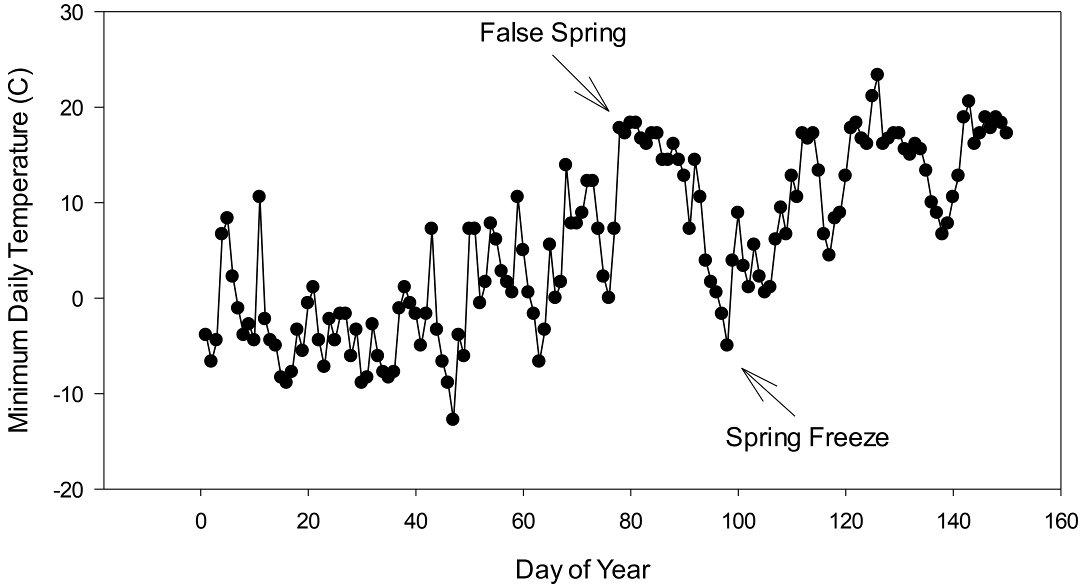

Fig. 6. Minimum daily temperature in Okmulgee Game Management Area for 2007.

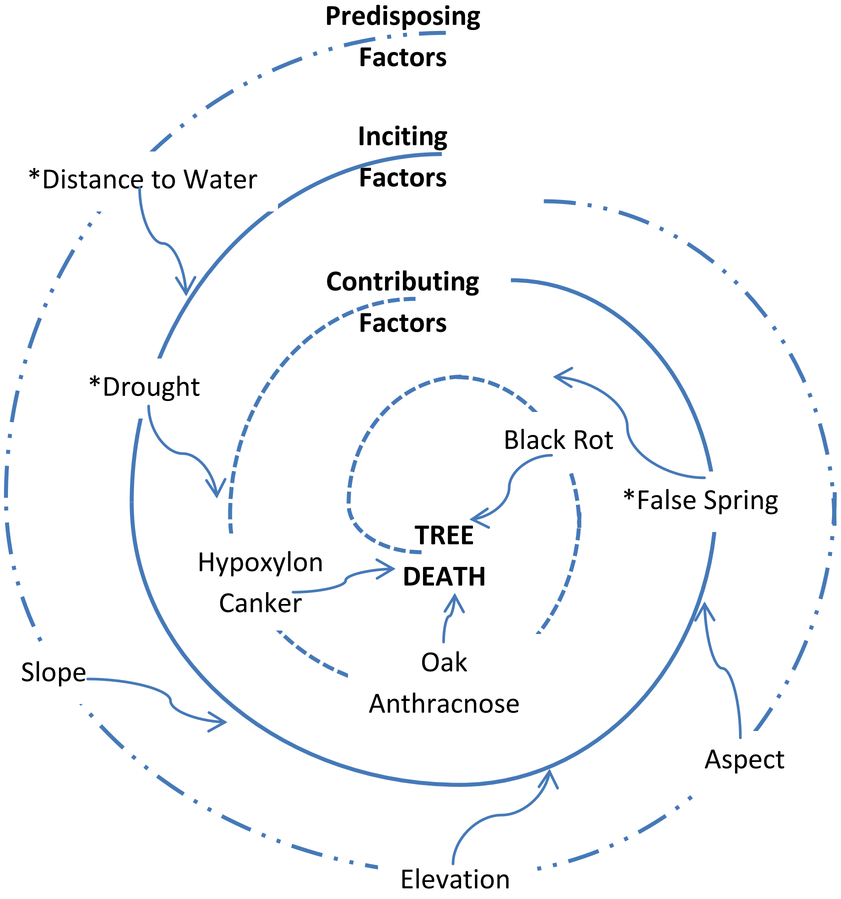

Fig. 7. Decline Spiral for Okmulgee Game Management Area Oak Decline Occurrence 2007-2008. Modified from Manion 1981. Asterisks indicate factors that are suspected of playing a major role in the decline.

CHAPTER II

UNDERSTORY RESPONSE TO OAK DECLINE IN AN UPLAND OAK-HICKORY FOREST OF OKLAHOMA

Abstract

Considered to be the most widespread problem affecting oak forests, oak decline has greatly altered the structure and composition of affected temperate hardwood forests. The purpose of this study was to determine the changes in understory species composition, species richness and biomass in upland oak forests during five years following canopy mortality over large areas due to oak decline. The study area was in the Cross Timbers; a vegetation type characterized as a mosaic of upland oak forest, savanna and prairie communities. Natural disturbances, such as fire, drought, wind and ice storms are relatively common in the Cross Timbers. Large catastrophic disturbances are rare, but may play an important role in maintaining the mosaic of vegetation types. This study used vegetation and biomass survey to measure species composition, species ground cover, species richness and biomass of the understory in non-decline and decline areas immediately following canopy mortality in Okmulgee Game Management Area.

Canopy mortality due to oak decline had very large effects on understory species composition, species richness and biomass. The response to oak decline was similar across five years post-disturbance and varied by plant functional group. Graminoid cover increased 2–4 fold, species richness increased 60–80%, and biomass increased 4–10 fold. Forb species richness increased 1.7–2.0 fold. Biological diversity, composition, and biomass of legumes and woody understory plants remained unchanged following oak decline. The dramatic increase in diversity and composition of graminoid species, and diversity of forb species may benefit wildlife including white-tailed deer. Although the catastrophic disturbance over large areas caused by oak decline is rare in the Cross Timbers, it may be a mechanism for maintaining species diversity in this vegetation ecotone between eastern forests and western grasslands. Most of the woody species in these forests resprout following disturbance, therefore their continued presence was more certain than many species in other functional groups. This may explain the lack of a strong response to opening the canopy. Although graminoid species increased dramatically in the opening, the woody plants probably will eventually recover and grow into a forest canopy similar to the one seen prior to oak decline.

keywords : oak decline, understory, biomass, species richness

1. Introduction

Periodic occurrences of decline and death of oaks over widespread areas are becoming increasingly more of a concern for wildlife ecologists and foresters. Oak decline is considered to be the most widespread problem affecting oak forests (Starkey and Oak 1989) and is caused by a complex interaction of environmental stresses and pests (Wargo et al. 1983). Tree death may occur in as short as only a few months, but generally occurs in a span of 2-4 years (Tomiczek 1993). Mortality can range from a few scattered trees to hundreds of acres (Oak 2002). Decline of oaks can have a negative effect on wildlife species who depend on oak due to habitat loss and food loss (McShea et al. 2007). Several concepts or theories have been put forth to explain this sudden loss of tree and stand vigor (Ciesla and Donaubauer 1994, Houston 1992, Manion 1991, Mueller-Dombois 1992, Sinclair 1965). The general consensus is that oak decline is caused by a complex interaction of biotic and abiotic stress factors.

In closed canopy forests, removal of canopy trees affects the understory by increasing the availability of light for photosynthesis, increasing the temperature, and reducing relative humidity. Canopy loss also increases the availability of water and mineral nutrients by the formation of "root gaps" (Parsons et al. 1994). Overall vegetation cover and biomass of understory vegetation increases with canopy loss (Ford and Newbould 1977, Klinka et al. 1996, Stone and Wolfe 1996). In theory, eliminating the canopy trees and increasing available resources, could allow for a greater number of understory species to flourish (Thomas et al. 1999). In contrast, canopy reduction could result in increased dominance by one or a few understory species, and thereby reduce understory diversity (Alaback and Herman 1988).

Several studies have been conducted on the causes of oak decline (Fuhrer 1998, Haavik et al. 2012, Thomas et al. 2002, Wargo et al. 1983). However, there have been fewer studies that have investigated the non-immediate effects oak decline has on stand density, basal area and species composition of the canopy (Greenberg et al. 2011, Heitzman 2003, Kabrick et al. 2004). Several studies have investigated the effect of canopy loss on the understory (Ford and Newbould 1977, Klinka et al. 1996, Stone and Wolfe 1996, Thomas et al. 1999); however, there have been very few studies that have investigated the effects of canopy loss due to oak decline.

The effects of canopy loss due to oak decline might differ significantly from the effects of canopy loss by silvicultural manipulations that remove or reduce canopy for several reasons. The physical disturbance during a decline is substantially less than during silvicultural manipulations. This might allow for a substantial difference in immediate understory response. Silvicultural manipulations generally remove the trees, but during oak decline the trees died in place for an unknown reason. This study investigated the "natural" process of succession following a natural occurrence, rather than following silvicultural practices.

Natural disturbances, such as fire, drought, wind and ice storms, are relatively common in the Cross Timbers (Karki 2007) and are suspected of playing a major role in maintaining the mosaic of oak forest, savanna and prairie. Fire, inside a closed canopy, increases plot richness of forbs and graminoids and increases biomass of graminoids (Burton et al. 2011). This is due, in part, to removal of woody midstory which releases site resources such as light, water and nutrients. This study investigated the effects of total canopy removal caused by oak decline. By measuring immediately and five years post-occurrence we were able to determine if the changes in the understory were transitory or possibly long-term. Therefore, the purpose of this study was to determine the magnitude of changes in understory species composition, species richness, and biomass in upland oak forests through the course of five years following total canopy mortality across large areas due to oak decline. We also investigated the ecological implications of these effects. We suspected that, due to the release of site resources by canopy mortality, species composition would transition to greater graminoid and forb dominance and species richness and biomass would greatly increase.

2. Methods

2.1. Study Area

Okmulgee Game Management Area (OGMA, 35°37'29.05" N, 96°03'32.52" W) in eastern Oklahoma is a portion of the Okmulgee Wildlife Management Area, which is managed by the Oklahoma Department of Wildlife Conservation. OGMA covers approximately 3,700 hectares and is approximately 95% wooded (Burton n.d.). The forest is dominated by post oak (*Quercus stellata*, 77%), blackjack oak (*Quercus marilandica*, 9%), and black hickory (*Carya texana*, 8%) (Karki 2007). Averages for tree and stand characteristics were ($\bar{x}$±SE): diameter 16 ± 3 cm, height 13 ± 1 m, basal area 26 ± 6 m^2 ha^{-1}, and stem density 1400 ± 400 stems ha^{-1} (Karki 2007). Approximately 3.5% of OGMA was affected by oak decline characterized by nearly complete canopy mortality during 2007 and 2008. The study was conducted in the three management units where most of the oak decline occurred. The units ranged in size from 150 to 220 ha and had been burned three times in the 12 years prior to measurement. Two of the study units were treated with a dormant season prescribed burn following oak decline, one in 2011 and the other in 2010. The third unit was burned by wildfire in August 2011. The prescribed burns were conducted in March and were low intensity and the summer burn was higher intensity. Prescribed burn conditions were considered ideal for achieving the goals of fuel and vegetation management (Weir 2009).

OGMA has a humid subtropical climate with a mean annual temperature of 16º C. The area has daily mean highs of 34º C in August and daily mean lows of -2º C in January. The area receives an average precipitation of 104 cm annually (Oklahoma Climatological Survey 2010). Hector-Endsaw soil complex covers approximately 75% of the OGMA and is characterized as well drained, non-arable, shallow stony fine sandy loam with bedrock at a depth of about 30 cm. It has a hilly topography of 5-30 percent slopes (Sparwasser et al. 1968).

OGMA is located in a region known as the Cross Timbers. The Cross Timbers is a mosaic of upland oak forest, savanna and prairie communities. This area is considered to be an ecotone between eastern forests and grasslands, which originally covered nearly 10 million ha in Kansas, Oklahoma and Texas. The Cross Timbers contain some of the largest tracts of old growth post oak/blackjack oak forests. This is due to the low value of its timber, and shallow soils, which precluded extensive exploitation (Stahle 2007).

2.2. Understory Vegetation Survey

For the purpose of this study, OGMA was divided into decline and non-decline areas. Decline areas were defined as areas that suffered nearly complete canopy mortality between 2007 and 2008. In the summer of 2008, shortly after the area was affected by oak decline, measurements were taken in the two most heavily affected units.

In the decline and non-decline areas of each of the units, square 100 m^2 (0.01 hectare) study plots were randomly located using the random point tool in ArcCatalog (ESRI 2011). In 2008, there were 10 plots in each unit, 5 in decline areas and 5 in non-decline areas, for a total of 20 plots. In the summer of 2013, the study was expanded to include the three most heavily affected units. There were 30 newly-established plots in each unit, 15 in decline areas and 15 in non-decline areas, for a total of 90 plots (Fig. 8). No plots were allowed within 10 m of manmade clearings, such as food plots or roads. Once a point was located, one of the four directions, southwest, southeast, northwest or northeast, was randomly selected for orientation of the square plot. Slope and aspect were measured from the highest point of the plot. The four sides of the plot were then laid out in the cardinal directions using a compass. In 2013, pieces of rebar were placed in the north-east corner as permanent plot markers.

A 1 m^2 sub-plot was situated in each corner of the 100 m^2 plots. In each sub-plot, overstory canopy cover was estimated using a forest canopy Model-A Spherical Densiometer (Nuttle 1997, Paletto and Tosi 2009). A Braun-Blanquet cover scale was then used to visually estimate the ground and plant cover within each sub-plot (Wikum and Shanholtzer 1978). An assigned cover class value of 1 is ≤ 1 %, 2 is > 1 % and ≤ 6 %, 3 is > 6 % and ≤ 25 %, 4 is > 25 % and ≤ 50 %, 5 is > 50 % and ≤ 75 %, and 6 is > 75 %. Litter depth was also measured four times in each sub-plot and averaged for each plot. Using a field guide (Tyrl et al. 2008) and the Oklahoma State University herbarium (OKLA), all plants were identified to species level with the exception of a few taxonomic groups, which were classified to genus level (Table 1). USDA Plants was used as the nomenclature source (USDA, NRCS. 2013).

2.3. Biomass Survey

Biomass measurements were taken in 2008 and then repeated in 2013. In 2008, five 150 meter transects were placed in the decline and non-decline areas of the two most heavily affected units. In each 150 meter transect, four 0.25 m^2 plots were spaced 50 meters apart. In 2013, five 200 meter transects were placed in the decline and non-decline areas of each of the three most heavily affected units. Each transect contained five 0.25 m^2 plots spaced 50 meters apart. In each plot, all plant material <1.4 m in height was clipped and separated according to functional group: graminoids, legumes, woody plants, and forbs (Burton et al. 2011, Tyrl et al. 2008). All dead plant matter was classified as litter. All plant samples were rooted in the plot. All woody and litter samples were collected that were <2.5 cm diameter. These samples were dried using the agronomy drying ovens at Oklahoma State University. After being dried for two weeks, the samples were each weighed to the nearest 0.01g.

2.4. Data Analysis

Stand characteristics such as canopy cover, slope and aspect were compared in decline and non-decline areas and across years. Aspect was converted to a north-south component (cos(aspect)) and east-west component (sin(aspect)) for analysis. Species data were used to determine species richness. Means and standard errors of richness were calculated for all year-decline combinations (2008 decline / 2008 non-decline / 2013 decline / 2013 non-decline). Richness was analyzed by plot richness and treatment richness. Treatment richness was the total amount of species found in each management unit of a specific year-decline combination. Plot richness and treatment richness were also analyzed by individual functional group richness. Biomass was analyzed by averaging biomass samples for each live functional group (woody, forb, graminoid and legume) and litter in each year-decline combination. Changes in functional group proportions were analyzed by averaging the species ground cover for each live functional group, litter, bare ground, and rock in each year-decline combination. Graminoids were further analyzed by C3 and C4 pathways of photosynthesis. Statistical analyses were done using two-way ANOVA using SPSS 21.1 statistical software (IBM Corp. 2012). Proportional data were transformed before analysis using an arcsine transformation. For this study the OGMA management units combined with their year (2008 or 2013) and their stand condition (decline or non-decline) were used as the experimental units, such that all samples taken in Unit 1 in 2008 decline stands were averaged and counted as one sample. In 2008, there were 5 sub-plots in each stand condition in each of two management units. In 2013, there were 15 sub-plots within each stand condition in each of three management units. Therefore in 2008, n=2 and in 2013, n=3. We considered the statistical tests to be exploratory; thus I did not adjust for multiple comparisons and interpret 'significance' cautiously. Effects were considered significant only when the statistical test produced a p-value ≤ 0.05.

Species ground cover data were back transformed from the cover abundance scale to the midpoint of the cover class. Multivariate analysis was used to determine the relationship between species composition and oak decline. A canonical correspondence analysis (CCA) was created with year-decline as sole explanatory variable (Palmer 1993). For this analysis, species cover was square root transformed and rare species were downweighted. Multivariate analysis was done using Canoco 5.03 (ter Braak and Šmilauer 2002).

3. Results

3.1. Stand Characteristics

Canopy cover was lower in decline stands compared to non-decline stands by nearly 50% in 2008 and 70% in 2013 (decline effect: $p<0.001$, Fig. 9b). Canopy cover did not change in non-decline stands from 2008 to 2013 and decreased by nearly 50% in the decline stands for the same period (year effect: $p=0.002$, Fig. 9b). Slope ($p=0.073$) and aspect (north-south component ($p=0.591$), east-west component ($p=0.620$)) of the vegetation plots were not significantly different across all year-decline combinations.

3.2. Understory Vegetation

3.2.1. Plant Species Composition

There were 78 plant species measured in 2008 and 116 plant species measured in 2013. The total between both years was 123 species: 54 forb, 29 woody, 24 graminoid, 15 legume and one succulent species. Due to not identifying certain graminoid groups to species, namely *Carex* spp., there were undoubtedly more total graminoid species than reported. The CCA ordination of species scores (Fig. 10) demonstrated the relationship between functional groups, year, and oak mortality. CCA Axis 1 represented time and CCA Axis 2 represented oak mortality. Species scores showed a tendency for graminoid and forb species to be more prominent in decline stands. In contrast, woody species showed a tendency to be found in non-decline stands. Legume species showed no strong tendencies.

We found no changes caused by oak decline or year on amount of bare ground ($p=0.604$), rock ($p=0.479$), legume ($p=0.444$), forbs ($p=0.109$) or woody ($p=0.638$) plant cover for 2008 and 2013 (Fig. 11a, 10b). Graminoid (decline effect: $p<0.001$) and total vegetation (decline effect: *p*=0.010) cover greatly increased in decline stands in both 2008 and 2013 (Table 3). Graminoid cover in decline stands was lower in 2013 than in 2008 (year effect: *p*=0.018). This change was also caused by a year-decline interaction (p=0.003). C3 and C4 graminoids showed no difference in response. Litter cover was not affected by decline in 2008 and decreased by nearly 80% in 2013 (*p*<0.001, Fig. 11b). This change was caused by decline, year and a year-decline interaction.

3.2.2. Plant Species Richness

We found no changes caused by oak decline on total plot species richness in 2008 and 2013 (Fig. 12). Forb plot species richness was approximately double in decline areas for both 2008 and 2013 (decline effect: *p*=0.001), and remained nearly unchanged from 2008 to 2013 (year effect: *p*=0.746). Graminoid plot species richness was increased in decline areas by 80% in 2008 and 55% in 2013 (decline effect: *p*=0.002). We found no change in graminoid plot species richness between 2008 and 2013 in both decline and non-decline areas (year effect: *p*=0.100). Legume (*p*=0.597) and woody (*p*=0.080) plot species richness showed no significant differences in decline and non-decline areas and were consistent for 2008 and 2013.

With increased sample size, treatment species richness in 2013 was higher than 2008 in decline and non-decline areas (Fig. 13). However, within each year, treatment species richness was higher in decline areas than in non-decline areas. Treatment forb species richness was twice as high in decline areas in 2008 and approximately 65% higher in 2013. Treatment graminoid species richness was increased in decline areas by 60% in 2008 and 30% in 2013. Treatment legume and woody richness were not affected by oak decline.

3.3. Biomass

Total vegetation biomass increased by 450% in decline areas in 2008 and 370% in 2013 (decline effect: $p<0.001$, Fig. 14). Total vegetation remained constant between 2008 and 2013 in decline and non-decline areas (year effect: $p=0.195$). Graminoid biomass increased tenfold in decline areas immediately following oak decline (2008) and remained about 4 times higher five years later (decline effect: $p=0.002$). Graminoid biomass remained constant in decline and non-decline areas from 2008 to 2013 (year effect: $p=0.100$). Forb ($p=0.452$), legume ($p=0.597$) and woody ($p=0.080$) biomass were not significantly affected across the year-decline combinations. Oak decline had no significant effect on litter biomass ($p=0.402$): 2008: non-decline 8427±628 kg ha^{-1}, decline 5723±1077 kg ha^{-1}, and 2013: non-decline 7772±548 kg ha^{-1}, decline 6158±1548 kg ha^{-1}. Litter depth was not affected by decline in 2008, but was reduced by 75% in 2013 (decline effect: $p=0.030$, year effect: p=0.001, Fig. 9a).

4. Discussion

This study suggested that oak decline altered understory species composition, and increased understory species richness and biomass. Our findings supported the idea that, due to the release of site resources by canopy removal due to oak decline, understory species composition would transition to greater graminoid and forb dominance and species richness and biomass would increase. The majority of these changes was realized within a year of forest decline and was still apparent five years later. The loss of canopy caused by oak decline resulted in more graminoid and forb species in the understory. Graminoids were the functional group making the greatest gains in cover, diversity, and biomass from canopy mortality. Forbs also increased in diversity. The increased availability of resources to the forest floor generated a large increase in graminoid and total vegetation biomass in the understory.

The multivariate analysis and functional group percent cover analysis showed a significant change in the species composition of the understory. The shift in species composition to greater graminoid and forb presence agreed with other studies that investigated understory response to canopy removal (Gilliam et al. 1995). Thomas et al. (1999) determined that total vegetation cover was consistently higher in forests that were highly thinned and Fredericksen et al. (1999) demonstrated there existed a significant negative relationship between summer ground cover and basal area. Our study corroborated both of these findings. An intriguing part of our findings was that the graminoid ground cover spiked shortly after the oak decline occurrence and was still elevated, but significantly lower five years later. This indicated that in the sudden increase in availability of light and nutrients, graminoids quickly dominated the understory. In the five years following, the graminoids were possibly outcompeted by other functional groups, such as woody seedlings or forbs. Weather patterns from year to year may have also greatly affected graminoid growth. Associated with the elevated graminoid and total vegetation cover was a large increase in biomass.

Litter cover was not significantly different between decline and non-decline areas in 2008. This was expected because litter has been found to build up over time and does not suddenly decrease. However, after five years, the amount of litter cover and litter depth significantly decreased in decline areas. This may be due, at least in part, to increased rainfall and sunlight exposure, as well as a decrease in leaf accumulation. However, the overall biomass of litter showed no significant differences. This suggested that an increase in wind and water movement in decline areas might have played a role in litter arrangement, causing litter to be clumped rather than evenly distributed across the landscape. This could explain why litter depth and cover detected differences, but biomass did not because the mass of litter was not changed, just readjusted. Fires occurring after the decline occurrence might have also played a role in litter accumulation. It is of course difficult to interpret the findings for litter cover because the findings were complicated by a year-decline interaction.

Multivariate analysis suggested species composition was slightly different in 2013, five years after occurrence of oak decline, than it was in 2008, shortly after the occurrence. The differences, however, were not specific to just the decline areas and were roughly evenly distributed in decline and non-decline areas. This implied that the change in species composition was not strictly a successional response to the disturbance. The much larger sample size in 2013, also contributed to the differences seen. We suspected at least a portion of this difference was caused by yearly deviations in species composition due to variations in climate, such as precipitation and temperature. The summer rainfalls in 2007 and 2008 were 46 and 37 cm, respectively (McPherson et al. 2007). This was significantly higher than 9 and 24 cm in 2012 and 2013 and most likely partially contributed to the difference in species composition. With only two different sampling times it was difficult to assess the nature of the temporal variation.

Treatment species richness was higher in decline areas. Bormann and Likens (1979) hypothesized that species diversity should be highest during early succession and again during late succession. Our findings endorsed this hypothesis, and suggested that treatment species richness increased following a large scale disturbance, such as oak decline. This difference in treatment species richness was due in large part to the increase in graminoid and forb species. These differences suggested that in the increased light and resource availability of affected areas, more species of graminoids and forbs became prevalent, whereas they might have been extremely rare or absent in unaffected areas. This increase in species richness was consistent with findings of Thomas et al. (1999). However, Fredericksen et al. (1999) found no significant relationship between remaining basal area and species richness or species diversity.

This study also found that an oak decline occurrence did not significantly affect, positively or negatively, the richness of woody and legume species soon after the disturbance. This finding agreed with the finding of Thomas et al. (1999); which found that species with woody stems showed significantly smaller responses to thinning than did herbaceous plant species. Burton et al. (2010) found that low intensity surface fires, acting as a disturbance in a closed canopy greatly decreased woody species richness. Smith and Miller (1987), however, found that richness of woody species was highest in stands with the most intensive overstory removal. This increase in woody species richness might be realized after more time has passed since the disturbance. Five years was a relatively short time for an oak-hickory forest to recover from such a severe disturbance. The difference might be explained by the simple point that our study is unique, in that it had intensive canopy loss and the added complication of prescribed fire. The decrease in canopy cover in decline areas by 2013 might be explained by dead or dying trees finally falling down in the five years following the first measurements.

This study determined that oak decline caused a significant overall effect on understory species composition, species richness, and biomass. These results might have been expected according to previous studies that have shown that with canopy removal, large changes are common. The important question remaining was "How do these changes affect the ecology and structure of this ecoregion?" As previously mentioned, the Cross Timbers represent a mosaic of oak forest, savanna, and prairie. In this mosaic of vegetation types, disturbance plays a vital role. Disturbances, such as fire, wind, drought, ice storms and herbivory have been found to be relatively common in the Cross Timbers (Karki 2007). These disturbances have generally created small gaps resulting from the death of one to two canopy trees. Burton et al. (2011) found that low-intensity dormant season fire was beneficial for understory herbaceous vegetation. During fire suppression following Euro-American settlement, woody vegetation expanded at the expense of savanna and prairies in the Cross Timbers (Rice and Penfound 1959, DeSantis et al. 2010, 2011). Researchers further found that the rate of canopy closure increased in oak savannas with a decrease in fire frequency (Johnson and Risser 1975, Henderson and Epstein 1995). DeSantis et al. (2010) determined that in the Cross Timbers, oak dominated forests appeared to be in transition to closed-canopy mesophytic forests due, in part, to drought and fire suppression. These studies demonstrated that, in the absence of fire, species composition and canopy closure could change so drastically as to change the vegetation type.

Earlier research in the Cross Timbers found that frequent, low intensity prescribed burns at least every three to four years increased herbaceous cover, species diversity, and biomass production mainly by increasing forbs and C3 grasses (Burton et al. 2011). This response occurred under a uniform overstory canopy with 89-96% cover and was attributed, at least in part, to burning, reducing the woody midstory (Burton et al. 2010, 2011). The current study in forest stands burned every three to four years, found an even larger herbaceous response for cover, species diversity, and biomass production when forest decline reduced the overstory canopy to 52% after one year and 25% after five years. The reduction in cover from 52 to 25% did not cause an incremental increase in understory because most of the cover was already dead and had fallen down over the period from 2008 to 2013. The herbaceous response to forest decline was mainly due to increased graminoids and forbs. There was no significant difference between C3 and C4 graminoid response.

Burton et al. (2010, 2011) found that regular prescribed fire reduced the woody midstory in a closed canopy oak-hickory forest. Oak decline removed most of the canopy. By combining the effects of oak decline and regular prescribed fire, the canopy was removed and the ability of the forest to re-establish a woody midstory was greatly hindered and delayed. This study found that due to the fire regime of the stands studied (burned 3 or 4 years earlier), a woody midstory was not able to be established in the five years post-disturbance. A suggested possibility is that the dominant canopy tree species of the area (post oak, blackjack oak) were relatively slow growing species (growth rate $\approx$ 6.4 cm/year, Clark et al. 2003). Therefore, the majority of sprouts were not able to grow to a great enough height to survive the ground fires. We suspected that this complex of disturbances might explain the mosaic of vegetation types in the Cross Timbers.

The mosaic of oak-hickory forests, savannas and prairies represented by the Cross Timbers, might be viewed as different stages of succession. Gaskill (1906) suggested that variations in vegetation types might be traced to two factors: first, physical conditions such as climate, soil and topography and second, anthropogenic and natural disturbances such as fire and wind. Prairies might be considered as areas still in early succession, dominated by grasses, herbs, and a few shrubs. Savannas might be viewed as further developed in terms of succession and have been invaded by woody pioneers. These woody pioneers, however, do not form a closed canopy and allow for an unbroken herbaceous layer consisting primarily of grasses and forbs. One of the most important factors that control the presence of savannas is fire. Fire keeps successional stages, especially savanna from progressing. Oak-hickory forest might be viewed as the climax forest, with a mostly closed canopy, woody midstory, and herbaceous layer. This study suggested that oak decline caused a transition from a mostly closed canopy climax forest with a broken herbaceous layer to a savanna with an open canopy dominated by grasses and forbs. It is important to note that prairies are generally found on different soil types. The savanna and forest vegetation is mostly restricted to the coarse textured soils derived from sandstones or granites (Dwyer and Santelmann 1964, Rice and Penfound 1959). Grasslands are found predominantly on fine textured soil derived from shale and limestone. Therefore, it is likely, that no amount of natural disturbance would be able to cause a transition from an oak-hickory forest to an open prairie.

The majority of disturbances in the Cross Timbers are relatively small. These small disturbances create small gaps that are, generally, quickly filled by subordinate mid-story trees. Tornados are a large disturbance which can occur; however, the return interval for a F2+ tornado is 2090 years (NOAA 2007). The infrequency of this large-scale disturbance removed it from playing a key role in maintaining the mosaic of vegetation types. Although small disturbances, such as fire or drought, have played an important role in the Cross Timbers, their effects might not be sufficient to explain the wide array of vegetation types. Although the catastrophic disturbance over large areas caused by oak decline is rare in the Cross Timbers, it may maintain species diversity in this vegetation ecotone between eastern forests and western grasslands. This study demonstrated that oak decline might contribute significantly to the amount of disturbance needed in order to maintain the mosaic of oak-hickory forest, savanna and prairies of the Cross Timbers.

5. Conclusion

This study found that oak decline had a dramatic effect on understory species composition, species richness, and biomass. Our findings indicated that oak decline created a favorable understory environment for species richness and biomass, and, in particular, benefited graminoid and forb species. The increase of sunlight to the forest floor, caused by oak decline, significantly increased species richness, ground cover, and biomass of graminoid species. Forb species richness also significantly increased. These increases in turn increased the treatment species richness, total vegetation ground cover, and total understory biomass in decline areas. In conclusion, this study proposed that oak decline through its removal of the oak-hickory canopy, might play an important role in maintaining the mosaic of oak-hickory forests, savannas, and prairies that supports a large diversity of plants and wildlife in the Cross Timbers of Oklahoma.

Tables and Figures

Table 3 – List of plants identified at Okmulgee Game Management Area. Numbers indicate average percent ground cover. Bold type indicates a species that on average covered ≥1% ground cover. Nomenclature source is from U.S. Department of Agriculture (USDA 2013). “spp.” or “sp.” indicates plants that were not identified to species level.

Scientific Name	2008		2013	
	Non-Decline	Decline	Non-Decline	Decline
Forb				
Allium sp. L.		0.13	0.14	0.44
Amaranthus blitoides S.Wats.		0.75	0.28	0.61
Ambrosia artemisiifolia L.			0.86	0.16
Ambrosia trifida L.			0.15	
Anemone caroliniana Walter				0.19
Antennaria parlinii Fernald	0.89	**2.89**	**3.53**	0.69
Artemisia campestris L.		0.13		0.28
Artemisia ludoviciana Nutt.		0.13		0.36
Cirsium altissimum (L.) Hill	0.10	**1.13**	0.12	0.89
Conyza canadensis (L.) Cronquist		0.13	0.56	**4.86**
Commelina spp. L.		0.13		0.19
Coreopsis spp. L.		0.28		0.42
Croton michauxii G.L. Webster				0.22
Diodia spp. L.	0.13			0.28
Echinacea pallida (Nutt.) Nutt.				0.28
Elephantopus carolinianus Willd.				0.28
Erechtites hieraciifolia (L.) Raf. Ex DC.		0.39		0.23
Erigeron tenuis Torr. & A. Gray			0.12	0.32
Eupatorium spp. L.		0.43		0.28
Galium circaezans Michx.	0.38	0.13	0.19	0.19
Gamochaeta purpurea (L.) Cabrera				0.25
Helianthus hirsutus Raf.	0.25	0.38	0.84	**2.49**
Hieracium gronovii L.				0.63
Hypericum hypericoides (L.) Crantz	0.15	0.13	0.13	0.23
Hypericum punctatum Lam.				0.89
Lactuca canadensis L.			0.19	0.24
Lepidium sp. L.			0.14	0.28
Lechea tenuifolia			0.21	0.28
Monarda russeliana Nutt. ex Sims	0.50	0.13	0.94	0.34
Oxalis spp. L.		0.13	0.25	0.44
Paronychia fastigiata (Raf.) Fernald			0.22	0.56
Passiflora lutea L.				0.19
Packera obovata (Muhl. ex Willd.) W.A.			0.56	0.47

Penstemon spp. Schmidel		0.25		
Forb continued				
Phytolacca americana L.				0.78
Polygonum spp. L.			0.13	0.13
Pseudognaphalium obtusifolium (L.)				0.28
Ptilimnium nuttallii (DC.) Britton				0.39
Ruellia spp. L.		0.11	0.22	0.15
Rudbeckia hirta L.			0.42	0.47
Sabatia angularis (L.) Pursh			0.28	
Solanum carolinense L.		0.38	0.58	0.39
Solanum ptycanthum Dunal				0.15
Solidago ulmifolia Muhl. ex Willd.	0.41	0.28	**1.36**	0.99
Symphyotrichum oolentangiense (Riddell)	0.63	0.29	0.64	0.31
Symphyotrichum patens (Aiton) G.L.	0.14	0.50	0.57	0.53
Teucrium canadense L.			0.28	0.92
Triodanis perfoliata (L.) Nieuwl.				0.28
Vernonia spp. Schrb.		0.18	0.22	
Viola spp. L.	0.13	0.25		0.15
Woodsia obtusa (Spreng.) Torr.				0.19
Graminoid				
Agrostis sp. L.				0.53
Andropogon gerardii Vitman	0.39	**1.21**	0.42	0.13
Andropogon virginicus L.		**1.13**	0.42	0.56
Bouteloua curtipendula (Michx.) Torr.				0.28
Carex spp. L.	**1.43**	**7.00**	**1.24**	**1.73**
Chasmanthium latifolium (Michx.) Nash		0.88	**1.54**	0.96
Coelorachis cylindrica (Michx.) Nash				0.17
Cyperus echinatus (L.) Alph. Wood		0.39	0.13	0.12
Danthonia spicata (L.) Pers.	0.44	**1.23**	**2.34**	**1.33**
Dichanthelium acuminatum (Sw.) Gould &	0.15	0.23	**1.51**	**1.46**
Dichanthelium clandestinum (L.) Gould			0.14	0.27
Dichanthelium linearifolium (Scribn. Ex	0.19	0.20	**2.75**	**3.89**
Dichanthelium oligosanthes (Schult.)	0.63	**1.75**	0.15	0.54
Dichanthelium sphaerocarpon (Elliot)	0.13	0.49		0.15
Elymus spp. L.	0.11	0.10	0.22	0.61
Eragrostis spp. von Wolf		0.74		
Gymnopogon ambiguus (Michx.) Britton, Sterns & Poggenb		0.88	0.41	0.72
Juncus spp. L.		0.54	**1.93**	**6.89**
Muhlenbergia spp. Schreb.	0.18			0.19
Panicum anceps Michx.		0.18	**1.43**	0.75
Poa pratensis L.	0.63	0.25	0.85	0.50
Schizachyrium scoparium (Michx.) Nash	**1.10**	**3.78**	0.31	**2.66**
Sporobolus spp. R. Br.		0.88	0.42	0.25

Tridens flavus (L.) Hitchc.	0.11	**1.30**	0.65	**2.74**
Legume				
Amphicarpaea bracteata (L.) Fernald			0.10	0.23
Baptisia bracteata Muhl. ex Elliot				0.19
Chamaecrista fasciculata (Michx.) Greene	0.25	0.25		0.28
Clitoria mariana L.	0.53	0.11	0.14	
Desmodium laevigatum (Nutt.) DC.	0.26	0.75		
Galactia volubilis (L.) Britton	0.14	0.11	0.30	0.12
Lespedeza cuneata (Dum.Cours.) G.Don	**1.51**	0.88	0.19	
Lespedeza procumbens Michx.	0.18	0.38	0.47	0.86
Lespedeza repens (L.) W.P.C. Barton	0.29	0.45	0.34	0.15
Lespedeza violacea (L.) Pers.	0.11	0.50	0.16	0.29
Lespedeza virginica (L.) Britton	0.25	0.26	0.25	0.32
Mimosa nuttallii L.	0.50	0.14	0.22	0.69
Tephrosia virginiana (L.) Pers.				0.18
Succulent				
Opuntia macrorhiza Engelm.			0.56	
Woody				
Carya texana Buckl.	0.46	0.10	**1.38**	0.97
Cercis canadensis L.	0.38			0.28
Celtis laevigata Willd.			0.19	0.30
Celtis occidentalis L.			0.53	
Cocculus carolinus (L.) DC.	0.13		0.28	
Crataegus viridis L.				0.19
Diospyros virginiana L.			0.67	
Ilex decidua Walter				0.19
Juniperus virginiana L.			0.28	
Parthenocissus quinquefolia (L.) Planch.	0.33	0.76	0.43	0.55
Platanus occidentalis L.				0.28
Prunus mexicana S. Watson	0.88	0.88	0.89	0.67
Quercus marilandica Muenchh.	**4.64**	**5.13**	**2.18**	**1.73**
Quercus shumardii Buckley				0.28
Quercus stellata Wangenh.	**1.90**	**1.36**	**2.73**	**1.93**
Quercus velutina Lam.	**1.38**		0.39	
Rhus aromatica Aiton	**4.35**	0.88	**2.74**	**1.19**
Rhus copallinum L.	0.10	0.20		**1.69**
Rhus glabra L.			0.24	0.23
Rosa spp. L.		0.95		0.39
Rubus spp. L.		0.88	0.19	0.63
Salix nigra Marshall		0.10		
Sideroxylon lanuginosum Michx.			0.19	
Smilax spp. L.	0.88	0.25	0.39	0.86
Symphoricarpos orbiculatus Moench	0.59		0.18	0.42
Toxicodendron radicans L.	0.48	0.49	0.28	

Ulmus alata Michx.	**1.54**	**5.74**	**3.86**	**4.40**
Vaccinium arboreum Marshall	0.88	0.56	0.64	0.15
Vitis spp. L.	0.10	0.13	0.64	

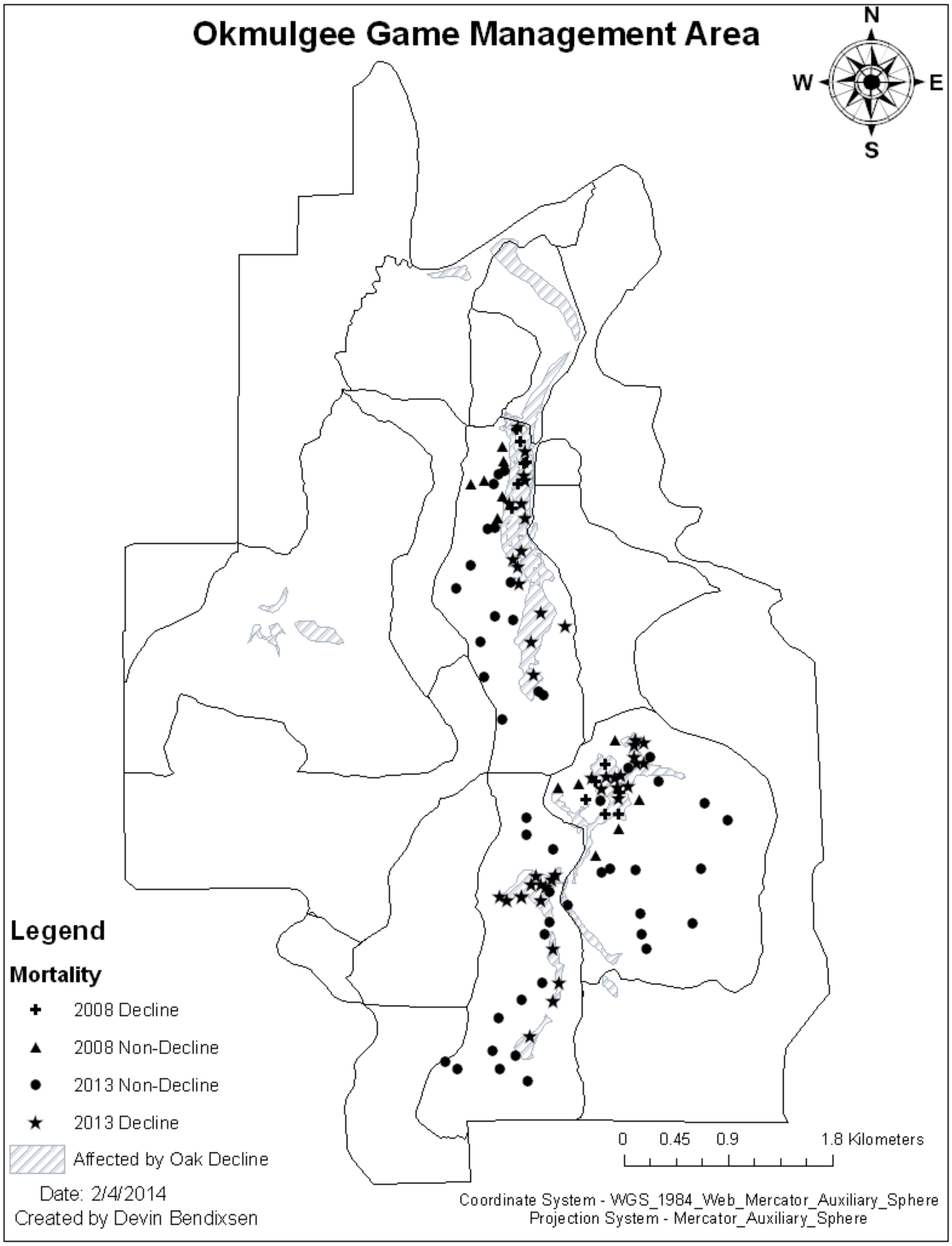

Fig. 8. Map of Okmulgee Game Management Area showing unit boundaries and indicating areas affected by oak decline between 2007 and 2008. Vegetation survey plots conducted in 2008 and 2013 are marked accordingly.

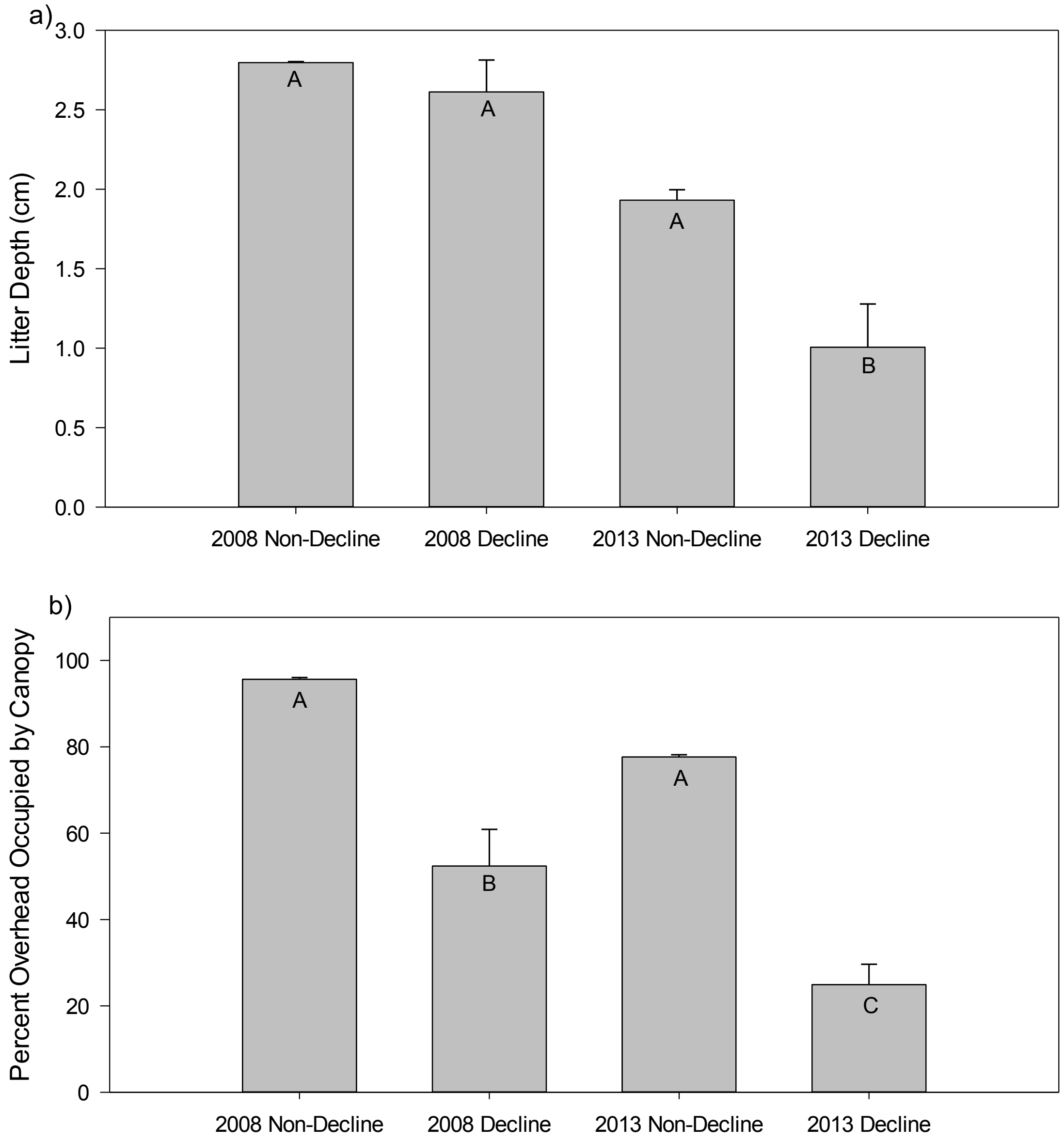

Fig. 9. Stand characteristics of vegetation survey plots: a) Litter depth, b) Canopy cover. Statistical significance was determined using two-way ANOVA. Matching letters indicate no statistical differences. Bars represent the standard error of mean.

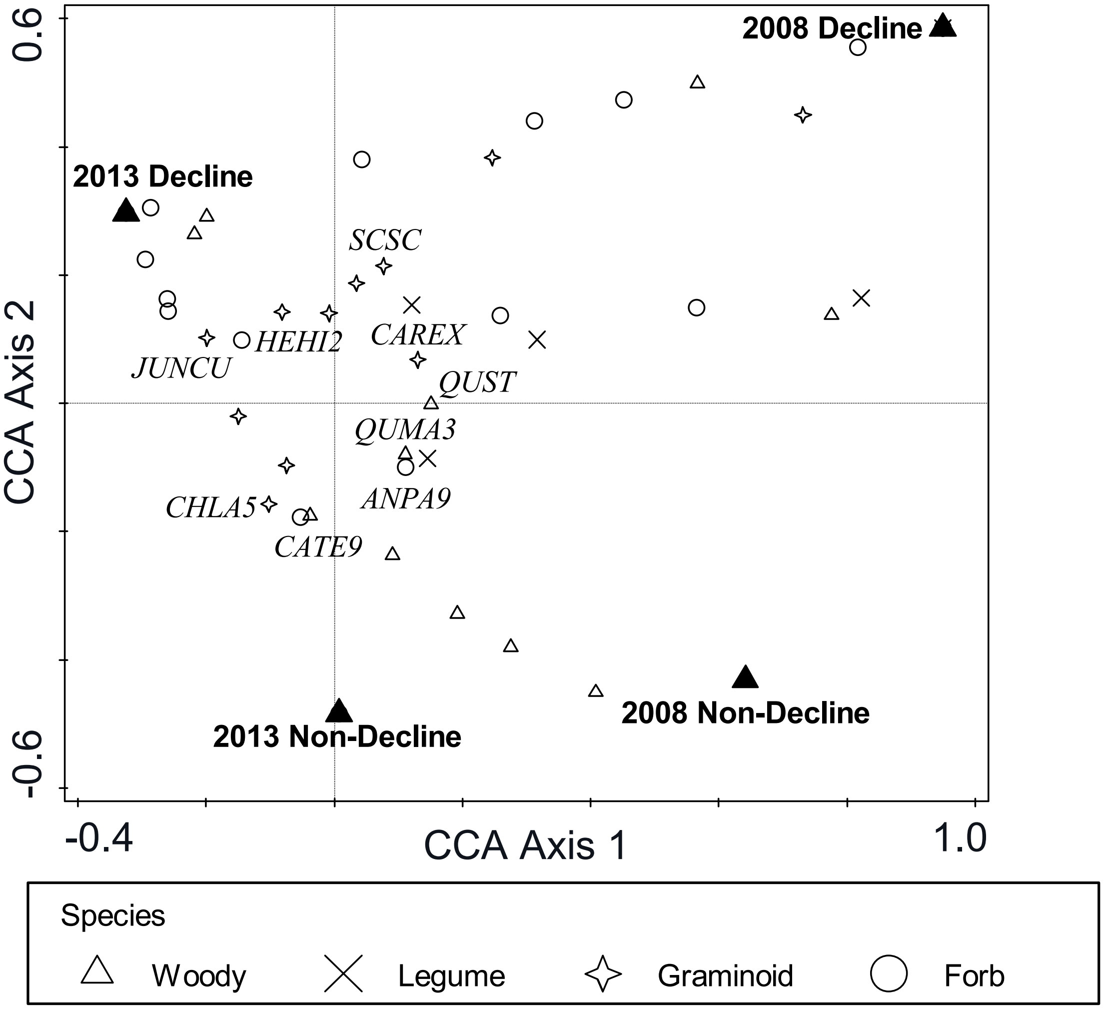

Fig. 10. Ordination of species along the first two axes produced by canonical correspondence analysis (CCA). Direct gradient analysis of all combinations of Year and Mortality. Axis 1 is interpreted as time and Axis 2 as oak mortality. Display limited to species that occurred in >10% of all plots. Several of most common species are labeled. ANPA9 – *Antennaria parlinii*, CAREX – *Carex spp*., CATE9 – *Carya texana*, CHLA5 – *Chasmanthium latifolium*, HEHI2 – *Helianthus hirsutus*, JUNCU – *Juncus spp*., QUMA3 – *Quercus marilandica*, QUST – *Quercus stellata*, SCSC – *Schizachyrium scoparium* (Axis 1 – eigenvalue – 0.1375, explained variation (cumulative) – 3.65) (Axis 2 – eigenvalue – 0.1166, explained variation (cumulative) – 6.75), pseudo-F=4.0, p=0.001.

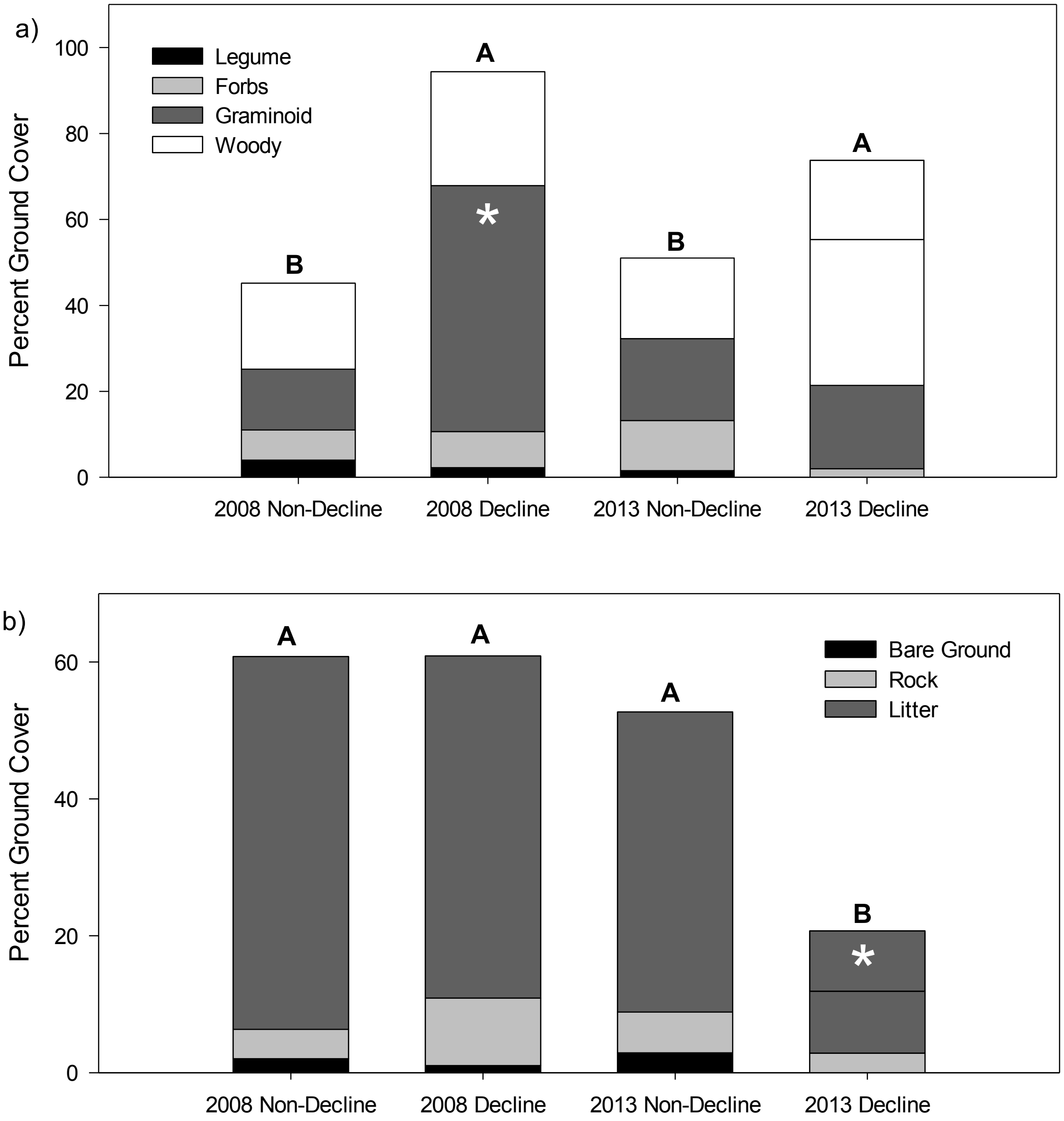

Fig. 11. Functional group species ground cover: a) Live plant cover. b) Non-plant cover. Proportions are averaged percent ground cover for each functional group in each year-decline category. Total represents total vegetation. Litter is defined as all dead plant material. Statistical significance was determined using two-way ANOVA. Matching letters indicate no statistical differences. Asterisk indicates values associated with forest decline ($p \leq 0.05$).

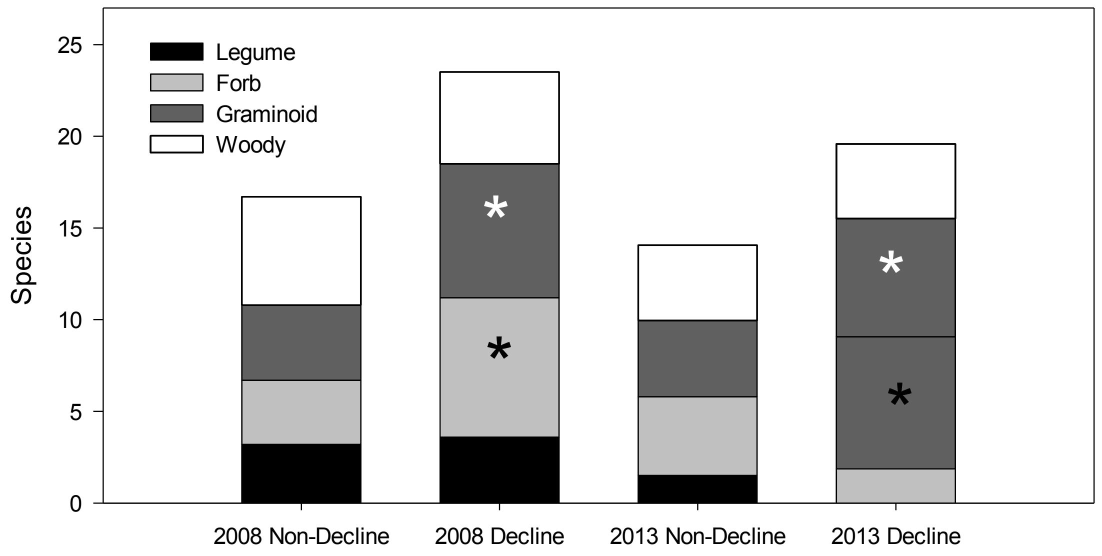

Fig. 12. Plot species richness of understory plants by functional group. Statistical significance was determined using two-way ANOVA. Asterisk indicates values associated with forest decline ($p \leq 0.05$).

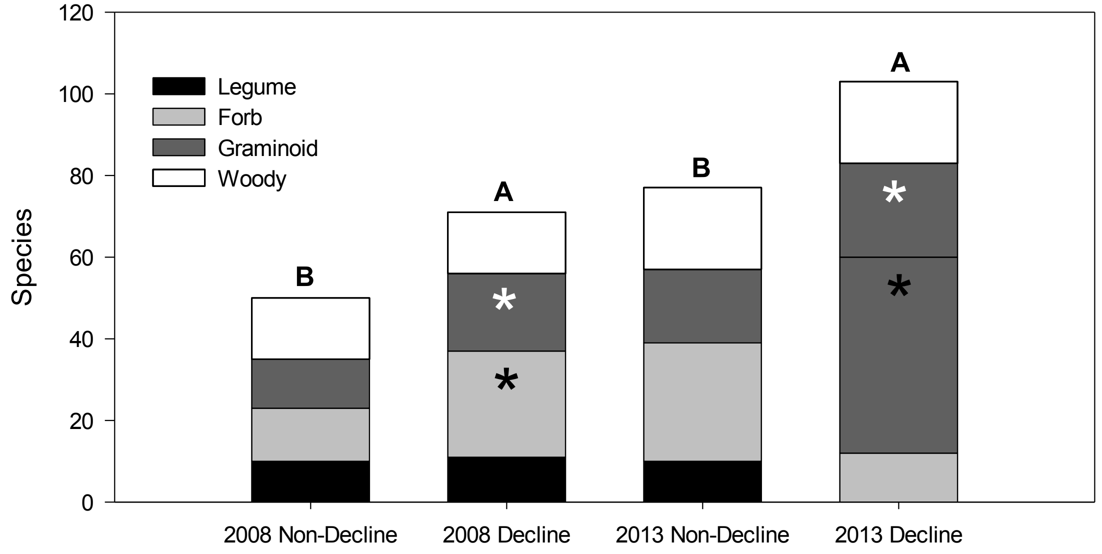

Fig. 13. Treatment species richness. Treatment species richness within each functional group for each year-decline category is shown. Within a year, letters indicate which treatment species richness are different and asterisks indicates species richness of functional groups that were associated with oak decline.

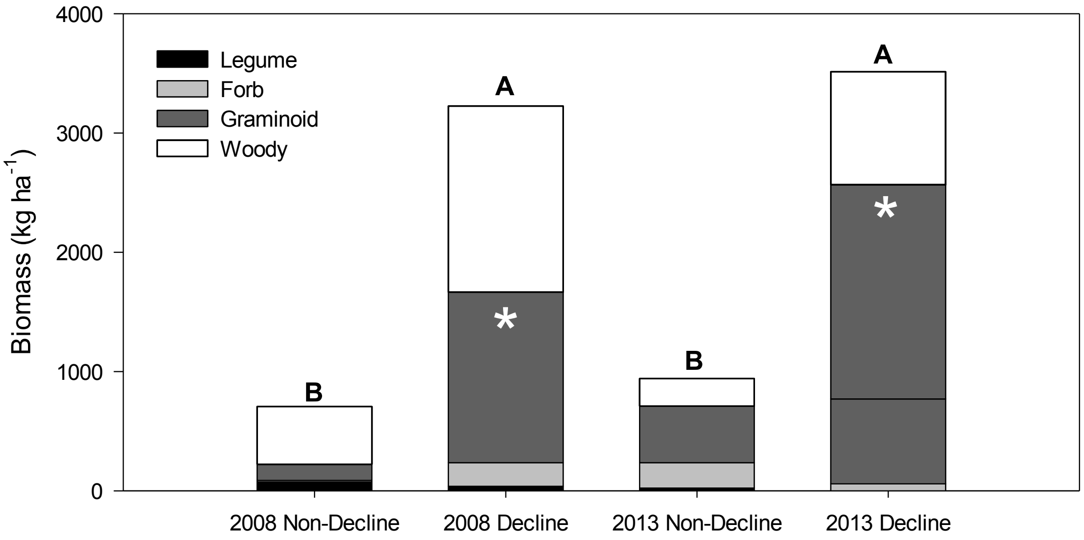

Fig. 14. Understory biomass in 2008 and 2013. Statistical significance was determined using two-way ANOVA. Within a year, letters indicate which total biomass values are different and asterisks indicate biomass of functional groups that were associated with oak decline ($p \leq 0.05$).

CHAPTER III

INFLUENCE OF OAK DECLINE ON FOREST COMPOSITION AND STRUCTURE IN A XERIC OAK-HICKORY FOREST OF OKLAHOMA

Abstract

The loss of trees associated with oak decline can greatly influence the species composition and structure of a forest. Changes in forest composition and structure can have a major impact on the ecosystem services of a community. This study followed an occurrence of oak decline in Okmulgee Game Management Area in 2007. Vegetation surveys (100 m^2) were taken in decline and non-decline areas in 2008 and 2013 to determine the effects of oak decline on the composition of the current overstory, potential effects on future stand composition, and structure in a xeric oak-hickory forest of eastern Oklahoma.

Live basal area was greatly reduced in affected areas and the mortality was not limited to oak species. Post oak (*Quercus stellata*) and blackjack oak (*Q. marilandica*) were the most heavily affected, but black hickory (*Carya texana*) was also affected. Mortality occurred in all size categories except stems less than 5 cm dbh. Oak decline caused a relative increase in winged elm in the overstory basal area and other formerly subordinate species such as fragrant sumac, winged sumac, and blackberry in the understory as sprouts. Oak decline did not, however, affect the species composition of stem density for large trees, small trees and saplings. Sprout density was not affected by oak decline, but sprout height doubled in decline areas. Oak decline also caused an increase in true seedlings of oak species in the understory. The findings from the overstory basal area and sprouts following the decline suggested that a transition to a more mesic forest type might be occurring. However, changes in species composition that might have suggested mesophication were not found in large tree, small tree or sapling density. Therefore, this study concluded that, given the evidence found and the current fire regime (burned every 3 or 4 years) of the study area, it is difficult to predict the future of the areas affected by oak decline. Due to the fire regime it is possible the areas might persist as an oak savanna; however due to the high amounts of regeneration it is possible that the areas will return to a closed canopy oak-hickory forest.

keywords : oak decline, overstory, species composition, mesophication

1. Introduction

Oak decline is a disease complex that affects oak or mixed oak forests. Oak dominated forests represent 51% of eastern United States forests (Spetich et al. 2002). Oak decline is not a relatively new occurrence. It has affected Europe for over three centuries, with the earliest record occurring in the 1740s (Thomas et al. 2002). Oak decline has been documented in the United States for over 100 years (Houston 1987, Law and Gott 1987). Due to the frequency and damage of these mortality events, oak decline has been determined to be one of the most serious forest disease problems in the southern and eastern United States (Oak 2002).

Wargo et al. 1983 determined that oak decline is caused by a complex interaction of environmental stresses and pests. Stresses weaken the tree and make it more susceptible to other stresses. This complex has often been represented as a death spiral with different stages of stresses (Manion 1991). These stresses may be biotic or abiotic and are very diverse, ranging from insect infestation to drought (Wargo et al. 1983, Thomas et al. 2002, Haavik et al. 2012).

Oak decline causes a loss of tree and stand vigor and health without obvious evidence of a single clearly identifiable causal factor (Ciesla and Donaubauer, 1994, pg. 3). This loss of tree and stand vigor and health has lead to tree death, which reduces live tree basal area of a forest. Tree death can occur in as short as a few months, but usually develops in the span of 2-4 years (Tomiczek 1993) and can range from a few trees to hundreds of acres (Oak 2002). Red oak group species (*Quercus* section *Lobatae*) are particularly susceptible (Starkey and Oak 1989, Greenberg et al. 2011). Generally tree diseases focus on a certain age-class, usually affecting either the younger or older trees. Oak decline is different, in that, it affects all age classes (Fuhrer 1998). This discovery has contradicted the age-related trend that occurs in most tree diseases.

The loss of trees associated with oak decline can greatly influence the species composition and structure of a forest. Changes in forest composition and structure can have a major impact on the ecosystem. Oak trees play an important role in forests, mostly because their mast production plays a vital role in the food webs of oak forests (Feldhamer 2002). A reduction of oak trees in a forest can have a negative effect on wildlife dependent on oak due to habitat and food loss (McShea et al. 2007). The purpose of this study was to determine the influence that oak decline had on species composition of the overstory trees and sprout regeneration in a xeric oak-hickory forest of eastern Oklahoma and thus determine the likely successional pathway for the forest.

2. Methods

2.1. Study Area

This study was conducted at the Okmulgee Game Management Area (OGMA) located in eastern Oklahoma. OGMA covers approximately 3,700 hectares and was affected by oak decline between 2007 and 2008. OGMA is located in the Cross Timbers, which represents a mosaic of oak-hickory forest, oak savanna and prairie communities. However, OGMA is mostly oak-hickory forest and is approximately 95% wooded with post oak (*Quercus stellata*, 77%), blackjack oak (*Quercus marilandica*, 9%), and black hickory (*Carya texana*, 8%) dominating the canopy (Karki et al. 2007). This study was conducted in the three management units where the majority of the oak decline occurred. The units ranged in size from 150 to 220 ha and had been burned three times in the 12 years prior to measurement. Two of the study units were treated with a prescribed burn following the oak decline, one in 2011 and the other in 2010. The third unit was burned by wildfire in August 2011.

2.2. Vegetation and Regeneration Survey

OGMA was divided into decline and non-decline areas. Decline areas were defined as areas that were reduced to a live basal area <8 m^2 ha^{-1} between 2007 and 2008. Measurements were taken in 2008 in the two most heavily affected units. Measurements were repeated in 2013 and expanded to the three most heavily affected units. In the decline and non-decline areas of each of the units, study plots were randomly located using the random point tool in ArcCatalog (ESRI 2011). In 2008, there were 10 plots in each unit, 5 in decline areas and 5 in non-decline areas, for a total of 20 plots. In 2013, there were 30 newly established plots in each unit, 15 in decline areas and 15 in non-decline areas, for a total of 90 plots. No plots were allowed within 10 m of manmade clearings, such as food plots or roads. In 2013 pieces of rebar were placed in the north-east corner of each plot as permanent markers. For all surveys, trees were identified to species level using a field guide (Tyrl et al. 2008) and the Oklahoma State University herbarium (OKLA). USDA Plants was used as the nomenclature source (USDA, NRCS. 2013).

Vegetation surveys were conducted within square 100 m^2 (0.01 hectare) plots at each randomly located plot point. Once a plot point was located, one of the four directions, southwest, southeast, northwest or northeast, was randomly selected for orientation of the square plot. The four sides of the plot were then laid out in the cardinal directions using a compass. Within each 100 m^2 plot, the diameter of all woody plant species ≥ 1.4 m at breast height (dbh, ≈1.4 m) was measured. Measurements taken in 2008 were used to determine live and dead basal area by species and size class. From the measurements taken in 2008 and 2013 species composition and species richness of remaining live trees were determined.

At each randomly located plot, a round regeneration survey plot with a diameter of 3 meters (area=7.065 m^2) was conducted. All tree sprouts ≤2 meters tall were identified by species and measured for height in each regeneration plot. In 2013 surveys, origin of sprout or true seedling was also determined. Sprout origin was categorized as stump sprout, seedling sprout or root sprout. Definitions of sprout origin were adopted and modified from Clark and Hallgren (2003) and DeSantis and Hallgren (2011).

(1) Root sprout (RO): the stem originated from a lateral root. The origin of the stem was more than 25 cm from the proximal end of the root.

(2) Stump sprout (ST): the stem originated from the root collar of a live tree or from the crown of an underground root system with a diameter >5 cm.

(3) Seedling sprout (SS): the stem originated from the root collar of a live tree or from the crown of an underground root system with a diameter <5 cm.

(4) Seedling (SE): the stem is suspected to have originated from seed due to isolation from other live trees. The origin of this stem was more than 25 cm from any live tree and not originating from a lateral root. The stem was the same diameter above and below the root collar and there was no evidence of dieback and resprouting.

2.3 Data Analysis

Means and standard errors of basal area, mortality, species composition and species richness were calculated for all year-decline combinations (2008 decline / 2008 non-decline / 2013 decline / 2013 non-decline). Overstory trees were analyzed by basal area and stem density. Stem density was broken into four categories; large trees, small trees, saplings, and sprouts. Large trees were defined as greater than breast height and a dbh greater than 10 cm. Small trees were defined as greater than breast height and a dbh between 5 and 10 cm. Saplings were defined as greater than breast height and a dbh less than 5 cm. Sprouts were defined as less than 2 m. Richness was analyzed by plot richness and treatment richness. Treatment richness was all species found in a specific year-decline combination. Statistical analyses were done using two-way ANOVA using SPSS 21.1 statistical software (IBM Corp. 2012). Proportional data were transformed before analysis using an arcsine transformation. For this study the OGMA management units combined with their year (2008 or 2013) and their stand condition (decline or non-decline) were used as the experimental units, such that all samples taken in Unit 1 in 2008 decline stands were averaged and counted as one sample. In 2008, there were 5 sub-plots in each stand condition in each of two management units. In 2013, there were 15 sub-plots within each stand condition in each of three management units. Therefore in 2008, n=2 and in 2013, n=3. We considered the statistical tests to be exploratory; thus we did not adjust for multiple comparisons and interpret ‘significance’ cautiously. Effects were considered significant only when the statistical test produced a p-value ≤ 0.05.

3. Results

3.1. Vegetation

3.1.1. Overstory Mortality

Oak decline affected approximately 3.5% of OGMA between 2007 and 2008. Live basal area was reduced from 20.36 to 1.67 $m^2 ha^{-1}$ in the affected areas (Fig. 15, decline effect: $p<0.001$). Mortality in decline areas was highest for post oak (Fig. 16, 91.7%), followed by blackjack oak (85.1%). These percentages were greatly increased from areas not affected by oak decline (22.0% for blackjack oak, 2.9% for post oak). The decline appeared to have affected black hickory; however the mortality consisted of one rather large black hickory tree that greatly skewed the data. The oak decline appeared to not affect winged elm. Although the decline strongly affected both post and blackjack oak, the majority of tree deaths were post oak because it was the most dominant tree species. The oak decline affected all size classes (Fig. 17), except the smallest, <5 cm dbh.

3.1.2. Overstory Species Composition

Proportion of winged elm (*Ulmus alata*) in the overstory was increased in decline areas in 2008 and 2013 (decline effect: $p=0.002$, Fig. 18). Proportion of black hickory sharply increased in decline areas in 2008 (decline effect: $p<0.001$), but returned to non-decline levels by 2013 (year effect: $p=0.740$). This change was caused by the decline, as well as a year-decline interaction. Post oak ($p=0.267$) and blackjack oak ($p=0.161$) showed no significant changes in proportional basal area across year-decline treatments. Winged sumac (*Rhus copallina*), smooth sumac (*Rhus glabra*), fragrant sumac (*Rhus* *aromatica*), Mexican plum (*Prunus mexicana*), farkleberry (*Vaccinium arboreum*), honeylocust (*Gleditsia triacanthos*), black oak (*Quercus velutina*), red mulberry (*Morus rubra*), chittamwood (*Sideroxylon lanuginosum*), sugarberry (*Celtis laevigata*), blackberry (*Rubus spp.*) and eastern redcedar (*Juniperus virginiana*) were all identified as subordinate tree and shrub species and comprised the "other" species category. These "other" species experienced no significant increases in proportion of basal area across year-decline treatments (*p*=0.566). In both 2008 and 2013, the basal area in non-decline and decline areas, was dominated by post oak. In non-decline areas in both years, blackjack oak was the second most important species. In decline areas in 2008 winged elm was approximately equal with blackjack oak (17%) and continued to increase by 2013. In 2013, winged elm accounted for approximately 25% of total live basal area in decline areas.

The density of large trees was reduced 70-80% in decline areas in 2008 and 2013 (Fig. 19). Likewise, small tree density was reduced 40% in decline areas. Post oak dominated the large trees in decline and non-decline areas for 2008 and 2013. Post oak and blackjack oak dominated the small trees for all year-treatment combinations. Saplings increased five-fold in decline areas in 2008 and two-fold in 2013. Saplings were dominated by winged elm. No significant changes in proportional species composition of stem density were found in large trees, small trees or saplings.

Plot species richness of canopy trees and midstory trees (>1.4m height) was approximately equal in decline and non-decline areas and between 2008 and 2013 (*p*=0.898). The treatment species richness was approximately equal in decline (6.5) and non-decline (5.8) areas in 2008 (*p*=0.546). The treatment richness in non-decline areas did not change significantly between 2008 and 2013; however, treatment richness in decline areas increased by an average of 4.5 species in the canopy and mid-story (year-decline effect: *p*=0.017).

3.2. Regeneration

3.2.1. Sprout Species Composition

The proportion of blackjack oak sprouts significantly decreased in decline areas in 2008 (year-decline effect: *p*=0.015, Fig. 20). However, by 2013, the proportion of blackjack oak sprouts in decline areas was not different from non-decline areas. The proportion of sprouts of "other" species significantly increased in decline areas in 2013 (decline effect: *p*=0.017). The "other" species category was dominated by fragrant sumac (6%), winged sumac (5%) and blackberry (4%). Post oak, black hickory, and winged elm demonstrated no significant changes across year-decline combinations (*p*=0.097, *p*=0.176, *p*=0.657). In general, the regeneration was highly dominated by winged elm across all year-decline combinations (Fig. 20). Post oak was the second most important, in terms of proportion of sprouts.

Plot species richness of sprouts was approximately equal in decline and non-decline areas and between 2008 and 2013 (*p*=0.141). The treatment species richness was approximately equal in decline and non-decline areas in 2008 (*p*=0.891). With increased sample size in 2013, more species were identified; however, they were approximately equal in decline and non-decline areas (*p*=0.674).

3.2.2. Sprout Density, Height and Type

The sprouts per hectare did not vary significantly in decline and non-decline areas and between 2008 and 2013 (*p*=0.116, Fig. 19). Sprout height was approximately double in decline areas compared to non-decline areas for 2008 and 2013 (decline effect: *p*=0.006, Fig. 21). Sprout height did not significantly change in decline and non-decline areas between 2008 and 2013 (Year effect: *p*=0.802). In non-decline areas in 2013, the majority of sprouts for all major species were identified as stump sprouts (Fig. 22). In areas affected by decline, stump sprouts were proportionally reduced for all major species (7-40%). For black hickory and post oak, there was an increase in proportion of root sprouts in decline areas. For winged elm and "other" species, there was an increase in proportion of seedling sprouts. Blackjack oak, post oak, winged elm and "other" species increased in the proportion of seedlings.

4. Discussion

This study demonstrated that oak decline had a large impact on the forest composition and structure of a xeric oak-hickory forest. Oak decline strongly affected canopy blackjack oak and post oak. Canopy mortality affected all size classes except the smallest trees <5 cm dbh. Oak decline changed relative basal area of species in the overstory. However, species composition of proportional stem density was not affected by oak decline for large trees, small trees and saplings. Sprouts of subordinate tree and shrub species, especially sumac species, increased proportionally in the five years following oak decline. We found no evidence to suggest that sprout density was significantly affected by oak decline, but sprout height was doubled in decline areas. Oak decline also caused an increase of true oak seedlings in regeneration.

The vegetation survey determined there was a great reduction in live basal area immediately following the occurrence of oak decline and remained in this state five years later. The survey also showed that the dead basal area was largely unchanged over five years. This suggested that the snags will remain standing for years following death. This can present a significant difference in nutrient cycling as well as benefit wildlife habitat.

By investigating the effects of oak decline shortly after the occurrence in 2008, we were able to identify whether any tree species were particularly susceptible to oak decline. We found that post oak was among the most susceptible to oak decline. Post oak belongs to the white oak group (*Quercus* section *Quercus*). Blackjack oak was also heavily affected by oak decline and belongs to the red oak group (*Quercus* section *Lobatae*). Studies have suggested that red oak species are more susceptible to oak decline (Starkey and Oak 1989, Stringer et al. 1989, Heitzman 2003, Kabrick et al. 2004) Greenberg et al. (2011) found that the decline-related mortality rate for the red oak group was more than double the white oak group. The findings of this study agreed that red oak species were heavily affected by oak decline, killing approximately 85% of live trees. However, this study suggested that oak decline had an equal, if not greater, effect on white oak species, killing approximately 92% of live trees. This difference in findings was most likely explained by the fact that many of the studies on oak decline in the United States have come from the Missouri Ozarks where a leading causal factor is outbreaks of red oak borer (Heitzman 2003, Kabrick et al. 2004, Heitzman et al. 2007, Fan et al. 2008). Another possible explanation is that the study area for this study was dominated by post oak (77%), with blackjack oak playing a subordinate role (9%). The effects of oak decline, much like the causes, can vary significantly from one event to another. It is possible that the oak decline in this study area was simply a different "type" of oak decline than seen elsewhere.

The number of dead trees found in non-decline areas was also significantly higher for blackjack oak (22%) than post oak (3%). Blackjack oak may suffer a higher rate of mortality than post oak or perhaps just persists longer as snags. Oak decline did not appear to have affected winged elm; however, the small relative basal area of winged elm in the study area may have precluded it from noticeable effects. Therefore, this study found that this occurrence of oak decline was most likely genus specific and negatively affected the two oak species in the study area: blackjack oak and post oak.

Oak decline affected blackjack oak and post oak across a wide array of size classes. However, trees less than 5 cm dbh showed almost no mortality. Although it is difficult to infer tree age from tree size (dbh), it may be hypothesized that oak decline affects all age classes but is less likely to affect younger, smaller trees. Fuhrer (1998) stated that oak decline has been recorded from all age classes. This finding contradicted the usual age-related trend associated with most tree diseases. Previous studies on oak decline have suggested that oak decline usually causes higher mortality in older trees (Biocca et al. 1993, Jenkins and Pallardy 1995, Starkey and Oak 1989). Studies have also shown that oak mortality was highest in large diameter classes (Mistretta et al. 1981, Law and Gott 1987). However, the findings of Heitzman (2003) suggested that mortality occurred in all diameter classes with smaller trees equally at risk as larger stems. The findings of our study agreed with this finding except that stems smaller than 5 cm were found to be less at risk. One theory proposed to explain the cause of declines suggested that decline is a complex condition involving a number of interacting factors where the major factor is the synchronous senescence of a cohort of trees in one place (Mueller-Dombois 1992). This cohort senescence theory suggested that the decline was caused by a cohort of trees reaching maturity and senescing at approximately the same time. The findings of this study suggested that this was not the case in eastern Oklahoma. The decline affected all size classes; however, trees less than 5 cm were less affected.

Oak decline not only reduced the overall basal area of the forest, but also affected the species composition of the basal area in the mid-story and canopy trees. Although post oak had the highest mortality rate, it remained dominant due to its overwhelming dominance in the stands initially. Winged elm did not show mortality due to oak decline, and therefore was able to take advantage of the increased resource availability and quickly increased its relative position in overstory basal area. By 2013 winged elm represented 25% of the total basal area in decline areas. However, this increase in the proportion of basal area contributed to winged elm in decline areas was not seen in the proportion of winged elm stems present in large trees, small trees or saplings. Therefore, this suggested that although winged elm appeared to have increased in relative basal area, it did not increase its relative dominance of the total tree stems. This suggested that possibly due to high survival in all size classes (sapling, small trees, and large trees) the proportional basal area was elevated, however the proportional amount of winged elm trees remained unchanged across year-decline treatments. Likewise, this study found no evidence that oak decline had an effect on the relative species composition of stem density.

Accompanying the new availability of resources found in the decline areas, was a large increase in the treatment richness. This could be expected due to the increased resource availability in the open canopy system. Heitzman et al. (2007) found that oak decline caused a shift from formerly red oak-dominated stands toward a more mixed assemblage of white oak, hickory, red oak, blackgum, and red maple in northwest Arkansas. This shift was most likely related to the high populations of red oak borer in that area preferentially killing red oaks. Our study area remained dominated by white oak species, but demonstrated an increase in basal area of formerly subordinate species, such as winged elm.

The decline also had a noticeable impact on species composition of regeneration less than 2 meters tall. The decline caused a decrease in blackjack oak sprouts and a large proportional increase in other species sprouts by 2013. The decline did not measurably kill the subordinate other tree species, therefore they were able to sprout and spread. However, this increase was not seen in trees greater than breast height, which suggested that these subordinate trees increased in abundance, but remained shrub-like and failed to reach the overstory. This increase in subordinate species was dominated by sumac species. Sumac species are often clonal and have been shown to sprout readily following disturbance (Miller et al. 1995). Sumac seeds have also been shown to germinate at higher rates following fire (Cain and Shelton 2003). Therefore, following a large disturbance such as oak decline, and in an area with a consistent fire regime, it can be suspected that sumac would prosper. However, sumac are not likely to form a canopy that would negatively affect the shade-intolerant oak species.

This introduces a very important and yet difficult topic that is integral to this study; the compounded effects of fire. After the canopy was removed by oak decline in our study area, each of the management units was burned. Burton et al. (2010, 2011) found that regular prescribed fires could have a large impact on an oak-hickory forest, including reducing the woody midstory. Fires can also greatly reduce a forests ability to regenerate and replace itself (Clark and Hallgren 2003). Therefore the compounded effects of oak decline and regular prescribed fire might create a unique situation in which it would be very difficult to definitively predict the future of these affected stands.

The increase in winged elm in the overstory basal area, and the increase of “other” subordinate trees as sprouts might represent a significant change in forest structure. One aspect of fire suppression that has become a concern for ecologists is mesophication. Mesophication is the conversion of oak forests to more shade tolerant or mesic forest species (Nowacki and Abrams 2008). In the absence of disturbance, such as fire, a variety of other highly competitive mesophytic hardwoods can regenerate. These can include elm, sumac, red maple, sugar maple, birch, cherry and blackgum. DeSantis et al. (2010) found that in the Cross Timbers, oak dominated forests appeared to be in transition to closed-canopy mesophytic forests, due, in part, to drought and fire suppression. Burton et al. (2010) found that in the absence of fire, mesophytic species intolerant of fire appeared to replace oak. Our study suggested that oak decline, acting as a large, unique disturbance, might have created a favorable environment for more mesic species, such as elm and sumac to persist. Fire can greatly reduce the number of surviving sprouts and this has been found to particularly impact less fire adapted mesophytic species (Clark and Hallgren 2003). Therefore, if fire were to be suppressed in this study area, the forest might transition from a xeric upland oak-hickory forest to a more mesic forest type.

Although canopy removal by oak decline is a major disturbance, the amount of total sprouts was not affected. In contrast, sprout density has been shown to increase following fire, especially of oak species (DeSantis and Hallgren 2011). Although there were no significant differences in sprout density between decline and non-decline areas, there were significant differences in sprout height. In areas affected by oak decline in 2008 and 2013, sprouts were significantly taller. Due to the increased amount of sunlight and nutrients available to new sprouts, the sprouts were able to increase productivity. DeSantis and Hallgren (2011) found that the average sprout height was approximately 23 cm tall under a closed canopy. Their finding agreed with findings of the current study, which suggested that in non-decline areas, the average sprout was approximately 26 cm tall. However, sprouts in areas affected by oak decline were more than double this height (58 cm). The sprouts in the newly opened areas appeared to grow much faster than the average growth rate for oak species in the Cross Timbers (≈6.4 cm/year, Clark and Hallgren 2003).

Another important finding of this study was the change in the origin of sprouts in areas affected by oak decline. For areas not affected by oak decline, the amount of stump sprouts, root sprouts, seedling sprouts, and seedlings were comparable with the findings of other studies conducted in the Cross Timbers of Oklahoma (Clark and Hallgren 2003, DeSantis and Hallgren 2011) and in the Missouri Ozarks (Liming and Johnston 1944). However, in areas affected by oak decline, we saw a consistent decrease in stump sprouts for all species. For black hickory and post oak, there was an increase in proportion of root sprouts in decline areas. For winged elm and “other” species, there was an increase in proportion of seedling sprouts. The most intriguing finding was an increase in the proportion of true seedlings for blackjack oak, post oak, and “other” species. This finding was especially important for the oak species because they are considered to be nearly exclusive sprouters and true seedlings are rarely found (Clark and Hallgren 2003). In more mesic hardwood forests, the amount of sprouting has been found to be lower and the amount of true seedlings has often been higher than in xeric forests (Merz and Boyce 1956, Ward 1966, Powell 1976, Crow et al. 1994). Therefore a consequence of oak decline may be maintenance of genetic diversity in oak species.

5. Conclusion

This study demonstrated that oak decline had a noticeable impact on the forest composition and structure of a xeric oak-hickory forest in eastern Oklahoma. Live basal area was greatly reduced in affected areas and the mortality was not limited to oak species. Post oak and blackjack oak were the most heavily affected, but black hickory was also affected. This mortality affected all size categories, but stems less than 5 cm were less at risk. Oak decline caused an increase in winged elm in the overstory basal area and other formerly subordinate species such as fragrant sumac, winged sumac, and blackberry in the understory as sprouts. Oak decline did not, however, affect the proportional species composition of stem density for large trees, small trees and saplings. Sprout density was not affected by oak decline, but sprout height was significantly increased in decline areas. Oak decline also caused a significant increase in true seedlings of oak species in the understory.

Given the complex species composition in the overstory and sprouts, and the relatively short period of time since the stands were affected by oak decline, it remains difficult to predict whether the stands will transition to one or any of the following: (1) an oak savanna with an open canopy, (2) a closed canopy forest dominated by post oak, or (3) a more mesic dominated forest type. The findings from the overstory basal area and sprouts following the decline suggested that a transition to a more mesic forest type might be occurring. However, these shifts in species composition that might have suggested mesophication were not found in large tree, small tree or sapling density. Therefore, this study concluded that, given the evidence found and the current fire regime of the study area it is difficult to accurately predict the future of these stands. Due to the frequent fires the areas affected by oak decline possibly might persist as an oak savanna. However, due to high amounts of regeneration, the areas might possibly return to a closed canopy oak-hickory forest. This transition can be greatly affected by a change in the current fire regime. Fire suppression might lead to a quicker return to a closed canopy forest, possibly with a greater amount of winged elm. The stands appeared to be in the establishment phase of natural succession (Peet and Christensen 1987) and long-term monitoring would be needed to determine if and how this decline will affect the future of this portion of the Cross Timbers.

Figures

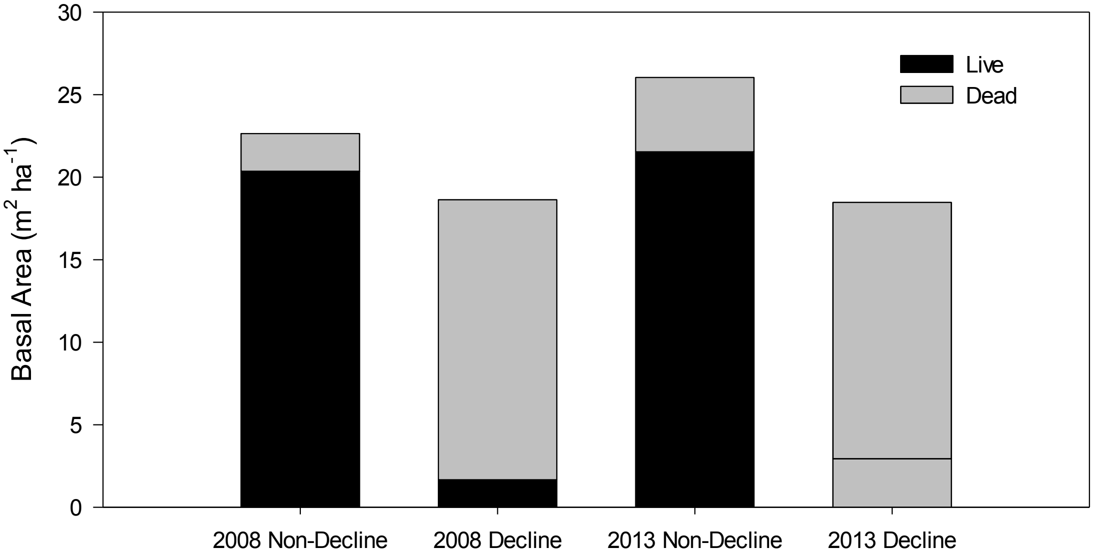

Fig. 15. Basal area (live and dead) for trees greater than breast height (1.4m) in 2008 and 2013 for declined and non-decline stands.

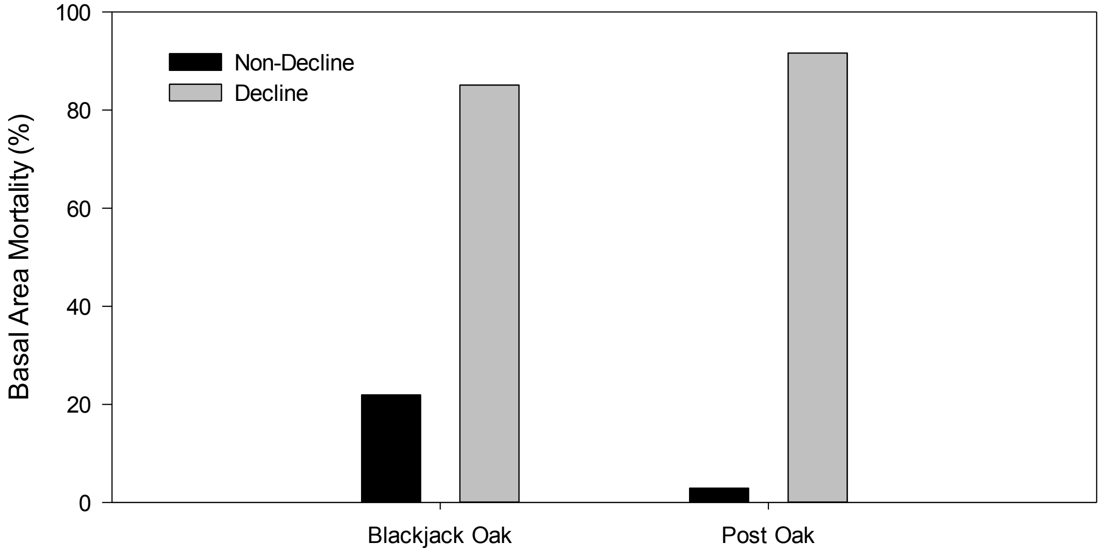

Fig. 16. Percent basal area mortality for trees greater than breast height (1.4 m) for dominant overstory species in 2008 for decline and non-decline stands.

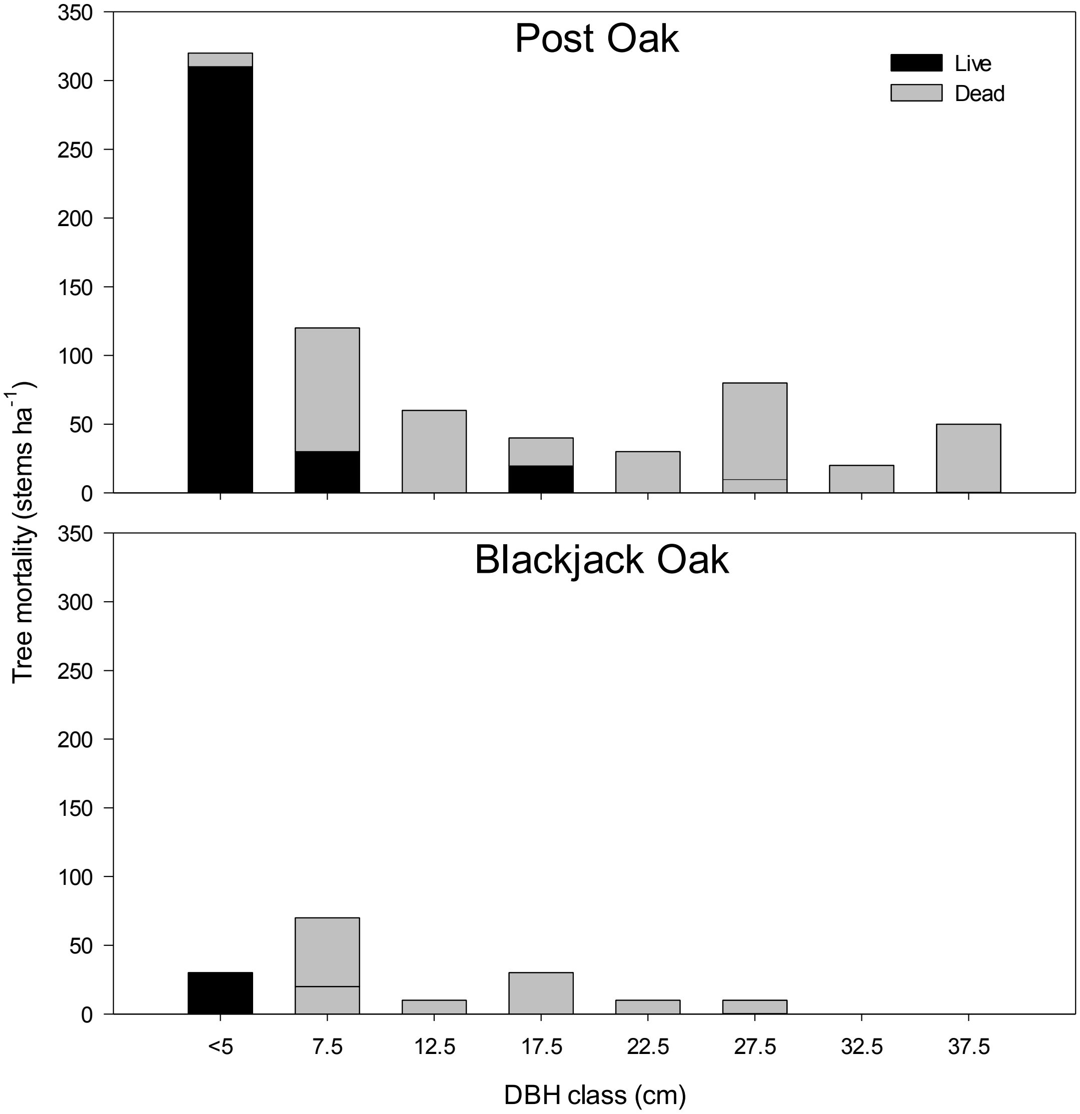

Fig. 17. Tree mortality and survival of oak species according to size class. Measurements are from decline areas in 2008. Size classes represent the midpoint of the size category. Statistical significance was determined using two-way ANOVA. Asterisk indicates values associated with forest decline ($p \leq 0.05$).

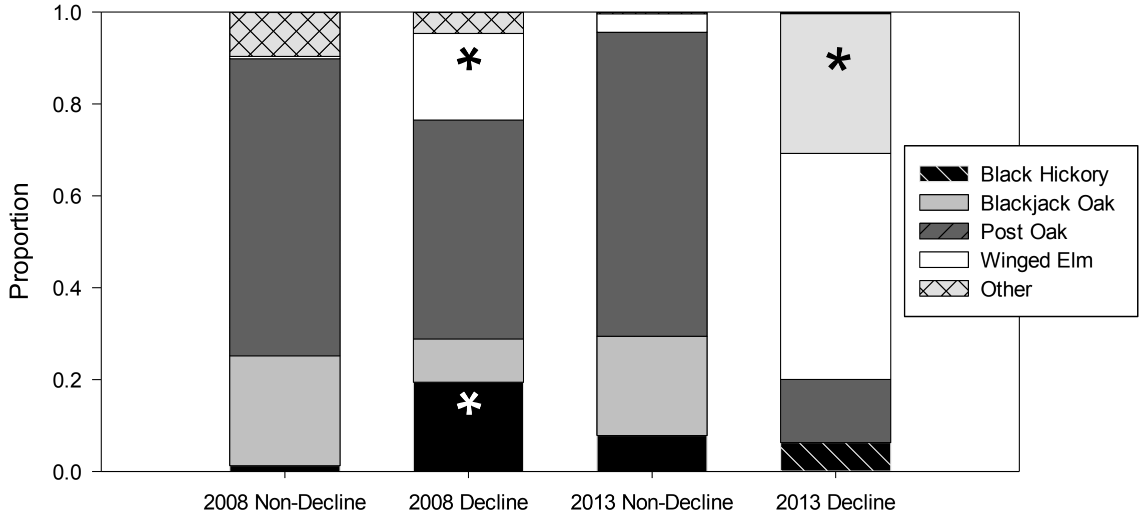

Fig. 18. Species composition of trees taller than breast height (≈1.4m). Proportional basal area according to dominant tree species and "other" species. Statistical significance was determined using two-way ANOVA. Asterisk indicates values associated with forest decline (*p*≤0.05).

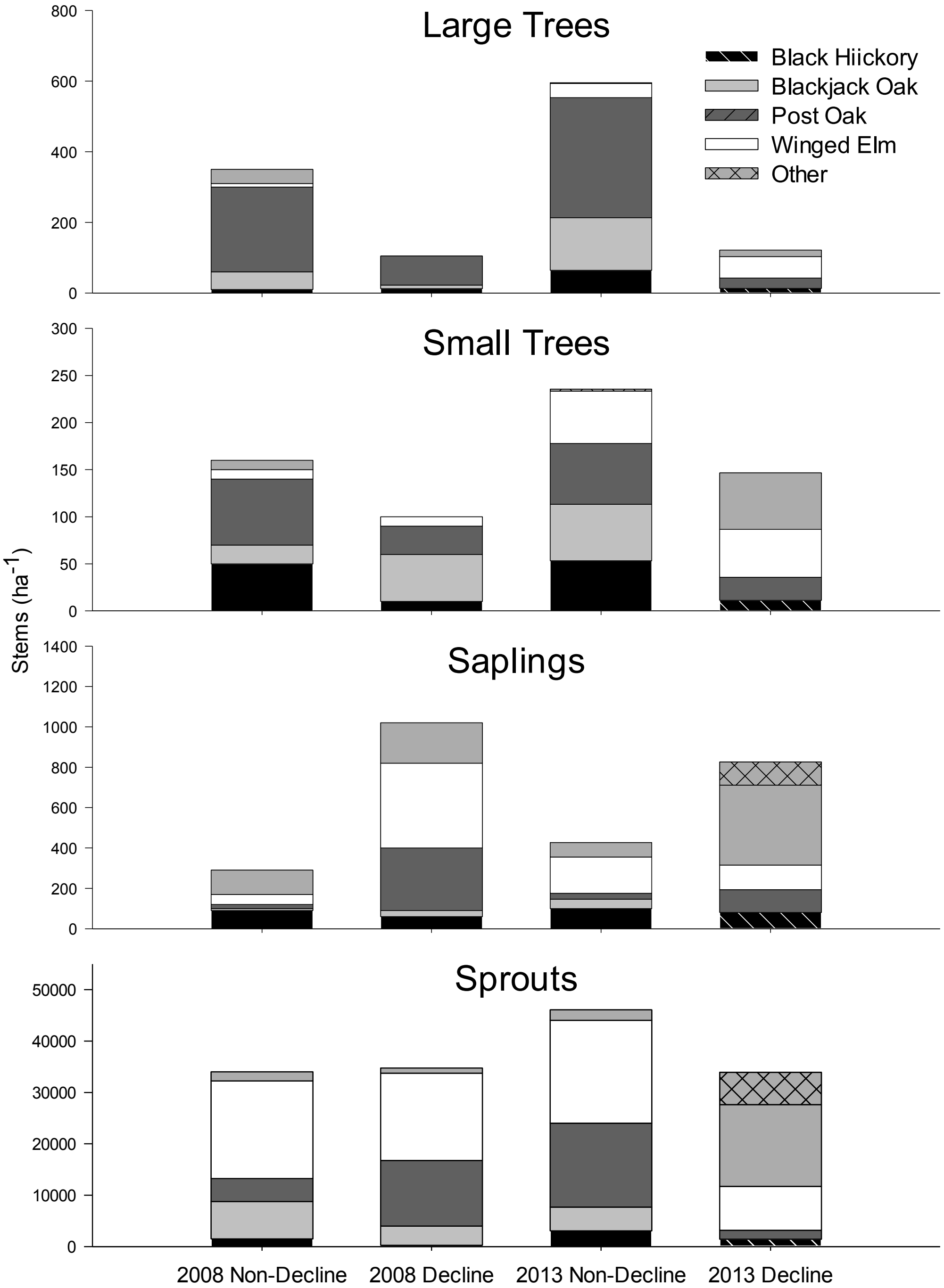

Fig. 19. Species composition of sprouts, saplings, small trees, and large trees. Sprouts are defined as a stem less than 2 m. Saplings are defined as stems with a dbh less than 5 cm. Small trees are defined as stems with a dbh greater than 5 cm, but less than 10 cm. Large trees are defined as stems with a dbh greater than 10 cm.

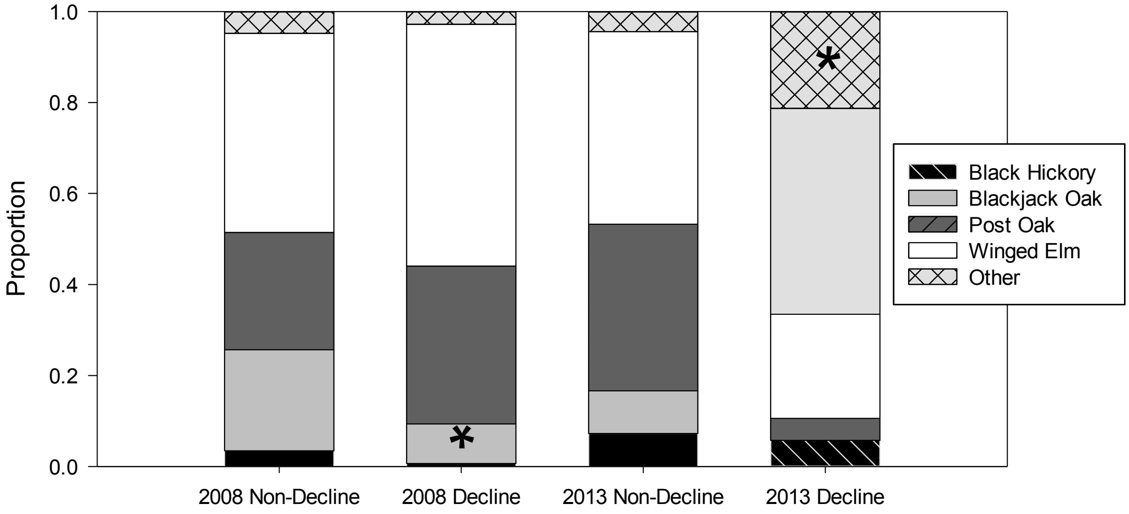

Fig. 20. Species composition of sprouts (<2m). Proportion of sprouts according to dominant tree species and "other" species. Statistical significance was determined using two-way ANOVA. Asterisk indicates values associated with forest decline ($p \leq 0.05$).

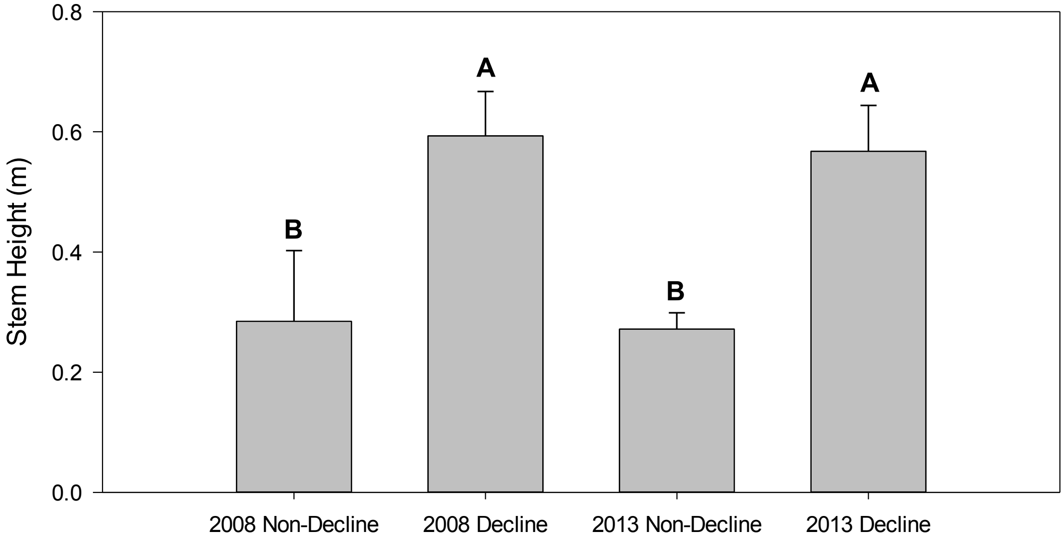

Fig. 21. Stem height of sprouts in decline and non-decline areas. Matching letters indicate no statistical differences. Statistical significance was determined using two-way ANOVA.

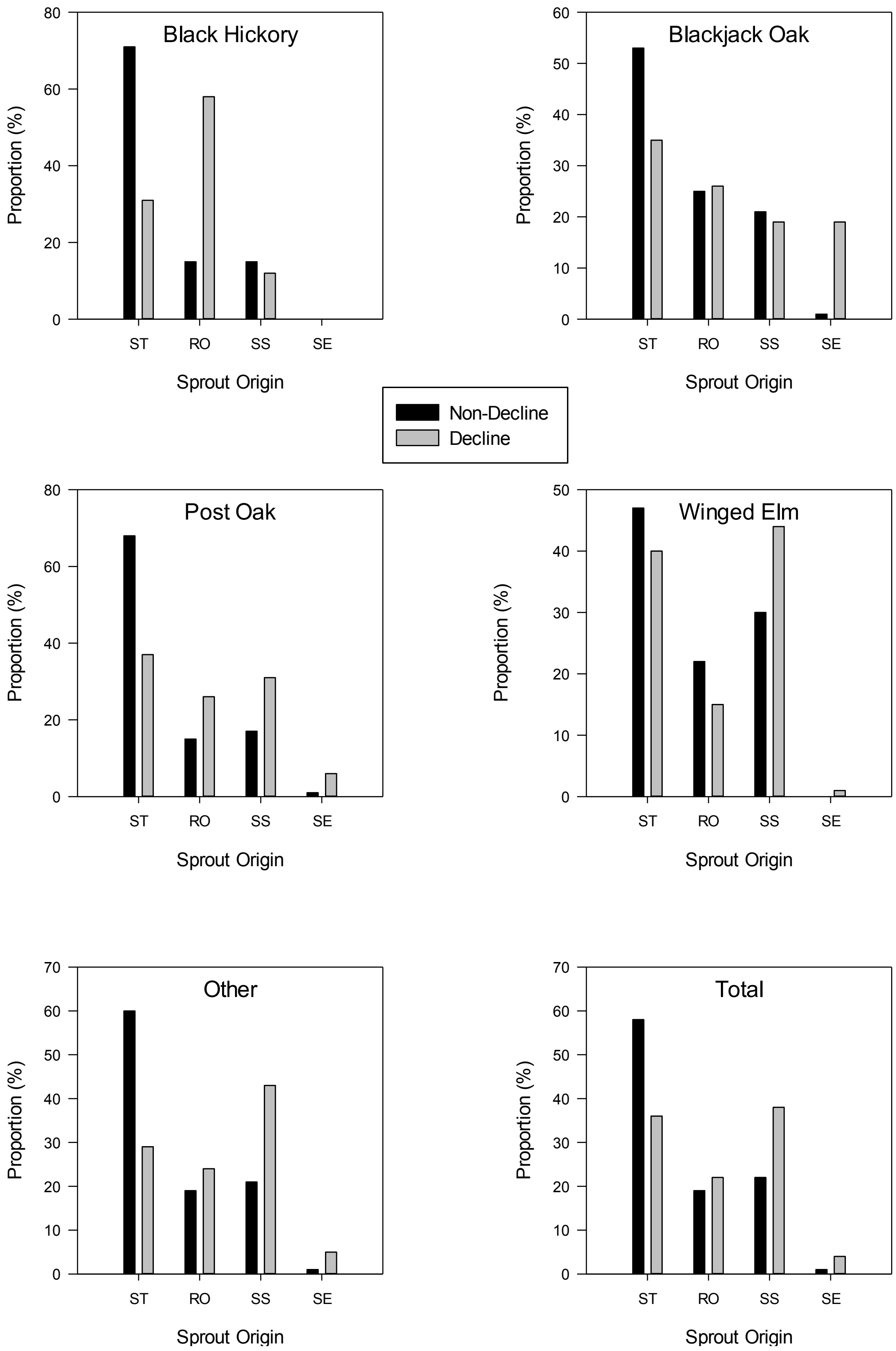

Fig. 22. Stem origin according to species. ST indicates stump sprout. RO indicates root sprout. SS indicates seedling spout. SE indicates true seedling.

CONCLUSION TO OAK DECLINE STUDY

The findings of this research offered important understanding on both the causes and the effects of oak decline in the first five years of recovery. Although the oak decline in eastern Oklahoma between 2007 and 2008 did not have a definite single cause, it was associated with a complex of predisposing, inciting and contributing factors. Decline stands were more likely to be found on steep slopes facing east meaning this could have been a predisposing factor. Other factors associated with decline were low elevation and proximity to water. There is a strong likelihood of spatial dependence of these four predisposing factors (distance to water, slope, elevation and aspect). Drought in the years leading up to the decline was suspected of weakening the trees. A false spring event in 2007 caused obvious damage to new foliage in the region and may have been a major contributor to the decline. Three plant pathogens (*Biscogniauxia mediterranea, Botryosphaeria obtusa* and *Discula quercina*) were also identified in decline stands and may have contributed to the ultimate death of these trees.

The near complete mortality of the overstory resulted in a large increase in understory species diversity and biomass productivity especially for graminoid and forb species. Live basal area decreased by over 90% in the decline stand. Blackjack and post oak suffered the highest mortality. Winged elm increased in the overstory. Decline stands saw a large increase in the number of sprouts of subordinate species such as fragrant sumac, winged sumac, and blackberry. However, no significant changes were found in the proportional species composition of stem density for large trees, small trees or saplings. Oak decline had no effect on sprout density and more than doubled sprout height. Oak decline also caused a substantial increase in true seedlings of oak species in the understory.

Oak decline created an open low density stand of trees similar to a savanna and it was not clear how the stand will evolve over time. Prolific sprouting of mesic species suggested without fire the stand might possibly return to a closed canopy forest and winged elm may become a major component of the overstory in contrast to the previous forest where it was a minor component. However, the lack of proportional increase in stem density of winged elm in saplings, small trees and large trees suggested that winged elm will most likely continue to play a minor role in the overstory of the future closed canopy forest. This scenario will likely see gradual reduction of the understory species diversity and biomass production as the canopy closes. An important question is whether frequent fire could cause the current open condition to persist, thereby contributing to the mosaic of forest and savanna. If fire is continued to be applied every three to five years, it would likely slow woody plant return in these stands. Some species would continue to sprout for many years (Clark and Hallgren 2003) but most would not grow into the canopy due to slow growth and frequent burning. The short duration of succession in the decline stands limits the predictive value of the study results. Future measurements with and without burning would provide valuable information about succession in forest stands affected by oak decline.

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APPENDICES

APPENDIX I – Summarized list of plants identified at Okmulgee Game Management Area. All species were identified and collected within the sample plots across decline and non-decline areas. Bold type indicates species that occurred in more than 10 percent of all sample plots. U.S. Department of Agriculture ("§") is used as nomenclature source (USDA 2013). Tyrl et al. was used as source for functional group classification. "sp. or spp." indicates that species were taxonomically impractical to identify due to developmental stage and are lumped to genus level.

PLANTS§	Scientific Name	Common Name
	Forb	
ALLIU	***Allium spp.***	**Wild Onion**
AMBL	***Amaranthus blitoides***	**Mat Amaranth**
AMAR2	***Ambrosia artemisiifolia***	**Annual Ragweed**
AMTR	*Ambrosia trifida*	Ragweed, Giant
ANCA9	*Anemone caroliniana*	Carolina anemone
ANPA9	***Antennaria parlinii***	**Parlin's Pussytoes**
ARCA12	*Artemisia campestris*	Field Sagewort
ARLU	***Artemisia ludoviciana***	**White Sagebrush**
CIAL2	***Cirsium altissimum***	**Tall Thistle**
COMME	*Commelina spp.*	Dayflower
COCA5	***Conyza canadensis***	**Horseweed**
COREO2	*Coreopsis spp.*	Golden Tickseed
CRMIE	*Croton michauxii*	Michaux's Croton
DIODI	*Diodia spp.*	Buttonweed
ECPA	*Echinacea pallida*	Coneflower, Pale-purple
ELCA3	*Elephantopus carolinianus*	Elephantsfoot
ERHI2	***Erechtites hieraciifolia***	**Burnweed**
ERTE7	***Erigeron tenuis***	**Slinderleaf Fleabane**
EUPAT	*Eupatorium spp.*	Thoroughwort
GACI2	*Galium circaezans*	Wood's Bedstaw
GAPU3	*Gamochaeta purpurea*	Purple Everlasting
HEHI2	***Helianthus hirsutus***	**Rough Sunflower**
HIGR3	*Hieracium gronovii*	Hawkweed
HYHY	***Hypericum hypericoides***	**St. Andrew's Cross**
HYPU	*Hypericum punctatum*	Spotted St. Johnswort

LACA	***Lactuca canadensis***	**Canada Lettuce**
LETE	*Lechea tenuifolia*	Narrowleaf Pinweed
LEPID	***Lepidium sp.***	**Clasping Pepperweed**
MORU	***Monarda russeliana***	**Redpurple Beebalm**
OXALI	*Oxalis spp.*	Woodsorrel
PAOB6	*Packera obovata*	Roundleaf Ragwort
PAFA3	*Paronychia fastigiata*	Hairy Forked Nailwort
PALU2	*Passiflora lutea*	Yellow Passion Flower
PENST	*Penstemon spp.*	Beardtongue
PHAM4	*Phytolacca americana*	Pokeweed
POLYG4	***Polygonum spp.***	**Knotweed Forb**
PSOB3	*Pseudognaphalium obtusifolium*	Rabbit-tobacco
PTNU	*Ptilimnium nuttallii*	Laceflower
RUHI2	*Rudbeckia hirta*	Black-eyed Susan
RUELL	*Ruellia spp.*	Wild Petunia
SAAN	*Sabatia angularis*	Rosepink
SOCA3	*Solanum carolinense*	Horsenettle
SOPT7	*Solanum ptycanthum*	West Indian Nightshade
SOUL2	*Solidago ulmifolia*	Elmleaf Goldenrod
SYOO	*Symphyotrichum oolentangiense*	Skyblue Aster
SYPAP2	*Symphyotrichum patens*	Late Purple Aster
TECA3	*Teucrium canadense*	Canada Germander
TRPE4	*Triodanis perfoliata*	Venus' Looking-glass
VERNO	*Vernonia spp.*	Iron Weed
VIOLA	*Viola spp.*	Violet
WOOB2	*Woodsia obtusa*	Cliff Fern
	Graminoid	
AGROS2	*Agrostis sp.*	Bentgrass
ANGE	*Andropogon gerardii*	Big Bluestem
ANVI2	*Andropogon virginicus*	Broomsedge Bluestem
BOCU	*Bouteloua curtipendula*	Sideoats Gramma
CAREX	*Carex spp.*	Sedge
CHLA5	*Chasmanthium latifolium*	Fishing Pole Grass
COCY	*Coelorachis cylindrica*	Cylinder Jointtail Grass
CYEC2	*Cyperus echinatus*	Globe Flatsedge
DASP2	*Danthonia spicata*	Poverty Oatgrass
DIAC2	*Dichanthelium acuminatum*	Tapered Rosette Grass
DICL	*Dichanthelium clandestinum*	Deertongue
DILI2	*Dichanthelium linearifolium*	Slimleaf Panicgrass
DIOL	*Dichanthelium oligosanthes*	Heller's Rosette Grass
DISP2	*Dichanthelium sphaerocarpon*	Roundseed Panicgrass
ELYMU	*Elymus spp.*	Wildrye
ERAGR	*Eragrostis spp.*	Lovegrass

GYAM	*Gymnopogon ambiguus*	Bearded Skeletongrass
JUNCU	*Juncus spp.*	Rush
MUHLE	*Muhlenbergia spp.*	Muhly Grass
PAAN	*Panicum anceps*	Beaked Panicgrass
POPR	*Poa pratensis*	Kentucky Bluegrass
SCSC	*Schizachyrium scoparium*	Little Bluestem
SPORO	*Sporobolus spp.*	Dropseed
TRFL2	*Tridens flavus*	Purpletop Tridens
	Legume	
AMBR2	*Amphicarpaea bracteata*	Hogpeanut, American
BABR2	*Baptisia bracteata*	Longbract Wild Indigo
CHFA2	*Chamaecrista fasciculata*	Partridge Pea
CLMA4	*Clitoria mariana*	Butterfly Pea
DELA2	*Desmodium laevigatum*	Tick Trefoil
GAVO	*Galactia volubilis*	Milkpea
LECU	*Lespedeza cuneata*	Sericea Lespedeza
LEPR	*Lespedeza procumbens*	Trailing Lespedeza
LERE2	*Lespedeza repens*	Creeping Lespedeza
LEVI6	*Lespedeza violacea*	Violet Lespedeza
LEVI7	*Lespedeza virginica*	Slender Lespedeza
MIMOS	*Mimosa nuttallii*	Sensitivebriar
TEVI	*Tephrosia virginiana*	Goat's Rue
	Succulent	
OPMA2	*Opuntia macrorhiza*	Twistspine Pricklypear
	Woody	
CATE9	*Carya texana*	Black Hickory
CELA	*Celtis laevigata*	Sugarberry
CEOC	*Celtis occidentalis*	Common Hackberry
CECA4	*Cercis canadensis*	Eastern Redbud
COCA	*Cocculus carolinus*	Carolina Moonseed
CRVI2	*Crataegus viridis*	Green Hawthorn
DIVI5	*Diospyros virginiana*	Persimmon
ILDE	*Ilex decidua*	Deciduous Holly
JUVI	*Juniperus virginiana*	Eastern Redcedar
PAQU2	*Parthenocissus quinquefolia*	Virginia Creeper
PLOC	*Platanus occidentalis*	Sycamore
PRME	*Prunus mexicana*	Mexican Plum
QUMA3	*Quercus marilandica*	Blackjack Oak
QUSH	*Quercus shumardii*	Shumard Oak
QUST	*Quercus stellata*	Post Oak
QUVE	*Quercus velutina*	Black Oak
RHAR4	*Rhus aromatica*	Fragrant Sumac
RHCO	*Rhus copallina*	Winged Sumac

RHGL	*Rhus glabra*	Smooth Sumac
ROSA5	*Rosa spp.*	Wild Rose
RUBUS	*Rubus spp.*	Blackberry
SANI	*Salix nigra*	Black Willow
SILA20	*Sideroxylon lanuginosum*	Chittamwood
SMILA2	*Smilax spp.*	Greenbrier
SYOR	*Symphoricarpos orbiculatus*	Buckbrush
TORA2	*Toxicodendron radicans*	Poison Ivy
ULAL	*Ulmus alata*	Winged Elm
VAAR	*Vaccinium arboreum*	Farkleberry
VITIS	*Vitis spp.*	Grape

APPENDIX II – List of randomly located plots within the Okmulgee Game Management Area. The UTM coordinates utilize the following coordinate system: NAD (1983) Zone 15 North.

Year	Unit	Mortality	Litter Depth	Canopy Cover	Slope	Aspect	Understory Richness	Overstory Richness	Basal Area
2008	1	Decline	2.63	30.6%	5	40	21	2	1.58
	1	Decline	2.25	49.7%	10	59	20	1	2.49
	1	Decline	2.41	38.5%	14	95	18	2	0.33
	1	Decline	1.84	43.6%	21	74	23	1	0.20
	1	Decline	2.93	56.8%	14	81	20	3	1.61
	1	Non-Decline	2.94	96.9%	5	39	16	4	29.94
	1	Non-Decline	2.81	94.5%	4	47	28	4	15.59
	1	Non-Decline	2.71	96.7%	8	239	16	2	10.30
	1	Non-Decline	2.75	95.0%	21	119	16	2	27.53
	1	Non-Decline	2.75	92.8%	16	100	19	3	13.23
	2	Decline	2.41	45.9%	11	316	25	4	0.05
	2	Decline	1.72	63.6%	6	41	43	4	0.13
	2	Decline	3.25	52.1%	6	280	20	4	0.04
	2	Decline	3.19	58.7%	16	218	23	5	0.21
	2	Decline	3.51	84.0%	23	142	22	4	10.10
	2	Non-Decline	3.06	96.7%	16	123	14	3	30.00
	2	Non-Decline	2.41	96.6%	3	150	13	1	24.47
	2	Non-Decline	3.03	97.0%	4	204	15	2	17.92
	2	Non-Decline	2.70	94.7%	7	269	16	3	16.75
	2	Non-Decline	2.81	95.2%	12	318	14	4	17.88
2013	1	Decline	1.31	15.8%	16	92	20	4	3.163
	1	Decline	0.66	64.6%	20	112	18	2	1.086
	1	Decline	1.19	48.2%	10	39	22	4	1.229
	1	Decline	1.06	26.8%	25	40	23	4	1.872
	1	Decline	1.25	40.8%	10	72	12	6	4.335
	1	Decline	1.69	47.5%	15	76	16	3	9.389
	1	Decline	0.34	8.7%	17	91	18	4	2.727
	1	Decline	0.44	10.9%	3	57	21	4	1.127
	1	Decline	0.50	16.1%	6	321	21	3	1.801
	1	Decline	0.56	19.4%	7	256	18	2	3.25
	1	Decline	0.50	22.7%	10	43	16	4	3.548
	1	Decline	1.38	36.7%	4	27	15	4	1.944

Year	Unit	Mortality	Litter Depth	Canopy Cover	Slope	Aspect	Understory Richness	Overstory Richness	Basal Area
2013	1	Decline	1.31	54.0%	30	322	18	5	6.164
	1	Decline	0.72	25.6%	2	321	21	2	1.1
	1	Decline	1.59	19.5%	11	29	23	2	8.067
	1	Non-Decline	2.91	82.9%	8	157	14	2	10.6
	1	Non-Decline	2.56	85.2%	30	115	12	2	16.19
	1	Non-Decline	2.13	87.3%	5	110	16	3	23.82
	1	Non-Decline	2.13	88.0%	4	267	15	4	20.01
	1	Non-Decline	2.13	85.7%	31	39	8	2	18.48
	1	Non-Decline	0.69	85.6%	5	44	16	2	23.71
	1	Non-Decline	1.88	80.8%	9	334	10	3	32.9
	1	Non-Decline	1.38	65.6%	2	161	17	3	24.98
	1	Non-Decline	0.84	56.7%	2	149	15	4	18.58
	1	Non-Decline	1.13	69.9%	3	330	18	3	14.78
	1	Non-Decline	2.44	81.1%	2	318	13	3	33.06
	1	Non-Decline	1.56	61.0%	2	64	16	3	16.4
	1	Non-Decline	1.28	81.4%	3	59	14	3	26.41
	1	Non-Decline	2.81	78.3%	9	319	13	2	15.56
	1	Non-Decline	1.88	76.8%	3	45	16	4	30.9
	2	Decline	1.25	62.8%	15	139	17	3	6.01
	2	Decline	1.06	20.2%	9	213	22	4	0.989
	2	Decline	1.06	15.4%	5	195	16	3	2.489
	2	Decline	1.06	11.0%	6	213	20	5	1.897
	2	Decline	1.19	16.2%	6	326	24	5	2.424
	2	Decline	1.25	24.7%	9	220	21	4	9.1
	2	Decline	0.88	20.6%	4	83	19	4	7.706
	2	Decline	1.13	29.9%	4	208	19	3	2.115
	2	Decline	1.25	51.6%	6	322	27	2	1.67
	2	Decline	2.44	34.6%	2	198	25	4	3.162
	2	Decline	2.06	41.9%	8	194	21	2	1.503
	2	Decline	2.50	41.2%	18	325	27	5	1.236
	2	Decline	1.69	30.5%	8	296	19	5	2.523
	2	Decline	1.13	16.6%	15	63	18	4	2.259
	2	Decline	2.50	14.8%	9	62	18	6	6.322
	2	Non-Decline	1.63	82.4%	5	32	11	3	14.2
	2	Non-Decline	2.31	83.8%	7	218	21	5	21.97

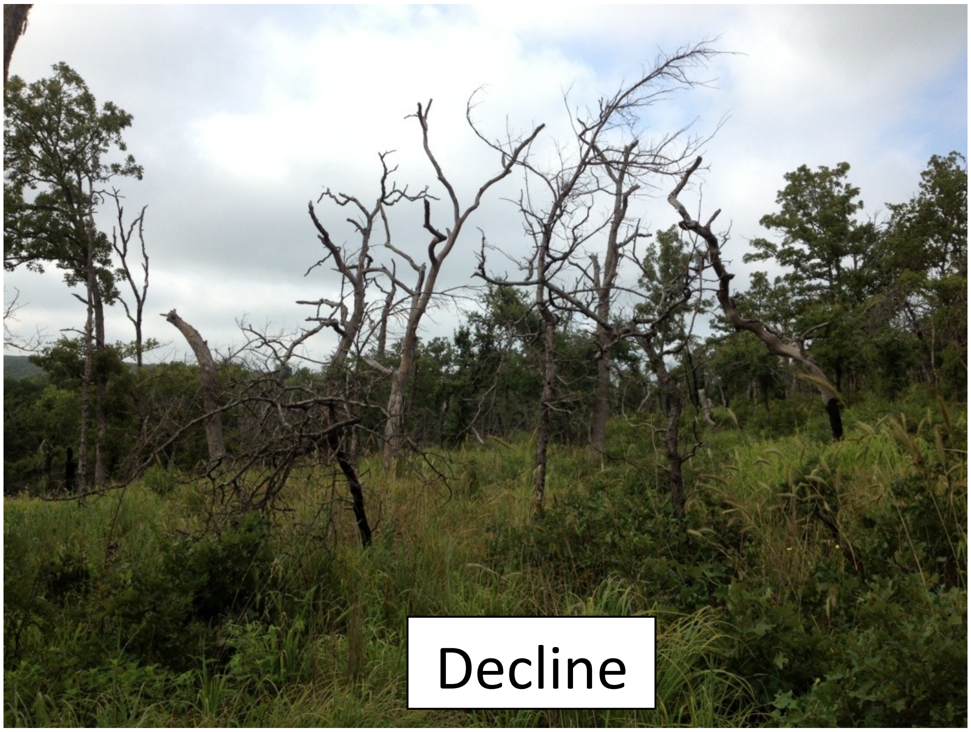
Year	Unit	Mortality	Litter Depth	Canopy Cover	Slope	Aspect	Understory Richness	Overstory Richness	Basal Area
2013	2	Non-Decline	2.09	79.2%	1	224	8	5	20.11
	2	Non-Decline	1.81	66.7%	4	314	17	6	31.77
	2	Non-Decline	1.81	79.7%	3	314	16	5	22.68
	2	Non-Decline	2.19	81.1%	3	314	13	4	17.26
	2	Non-Decline	1.25	66.4%	9	177	13	4	20.23
	2	Non-Decline	1.19	64.8%	2	356	16	4	16.24
	2	Non-Decline	2.06	83.7%	5	165	15	4	20.08
	2	Non-Decline	1.28	83.1%	2	327	13	4	24.35
	2	Non-Decline	1.69	83.5%	9	208	13	4	28.5
	2	Non-Decline	1.06	67.5%	2	215	19	3	15.55
	2	Non-Decline	3.19	80.5%	3	316	9	3	21.79
	2	Non-Decline	2.50	80.0%	2	204	17	1	21.38
	2	Non-Decline	2.25	68.4%	1	197	15	3	19.1
	6	Decline	0.44	13.7%	15	150	23	4	2.202
	6	Decline	0.00	4.8%	14	198	20	1	0.004
	6	Decline	0.50	25.4%	18	130	17	4	1.355
	6	Decline	1.25	11.8%	21	111	20	1	1.327
	6	Decline	0.38	20.3%	3	207	15	3	3.77
	6	Decline	0.31	16.7%	21	52	19	3	1.744
	6	Decline	0.69	30.2%	5	41	15	4	5.168
	6	Decline	0.44	15.8%	4	212	19	3	3.605
	6	Decline	0.50	8.3%	18	172	18	3	1.924
	6	Decline	0.25	9.8%	15	146	17	4	2.631
	6	Decline	0.66	6.9%	12	153	18	1	2.516
	6	Decline	0.44	10.2%	15	142	19	0	0
	6	Decline	0.63	23.4%	7	38	23	2	2.29
	6	Decline	1.06	8.1%	18	37	24	0	0
	6	Decline	0.81	27.3%	15	139	23	4	2.459
	6	Non-Decline	0.94	58.8%	5	150	16	2	15.68
	6	Non-Decline	0.94	79.1%	5	292	15	4	12.39
	6	Non-Decline	2.06	91.2%	5	319	18	5	32.25
	6	Non-Decline	3.00	88.7%	7	111	8	4	25.13
	6	Non-Decline	2.03	78.8%	15	47	17	3	20.98
	6	Non-Decline	2.19	78.3%	17	64	10	3	27.36
	6	Non-Decline	1.94	71.9%	1	119	12	3	20.08

Year	Unit	Mortality	Litter Depth	Canopy Cover	Slope	Aspect	Understory Richness	Overstory Richness	Basal Area
2013	6	Non-Decline	2.50	88.3%	2	146	6	3	26.25
	6	Non-Decline	1.53	73.3%	16	78	14	2	21.1
	6	Non-Decline	1.16	75.7%	2	74	17	3	24.4
	6	Non-Decline	2.31	79.2%	25	86	14	3	14.01
	6	Non-Decline	2.44	86.5%	11	116	13	4	21.77
	6	Non-Decline	2.06	76.4%	1	140	16	3	14.46
	6	Non-Decline	2.94	76.6%	3	74	16	4	21.25
	6	Non-Decline	2.88	74.2%	2	104	16	2	24.31

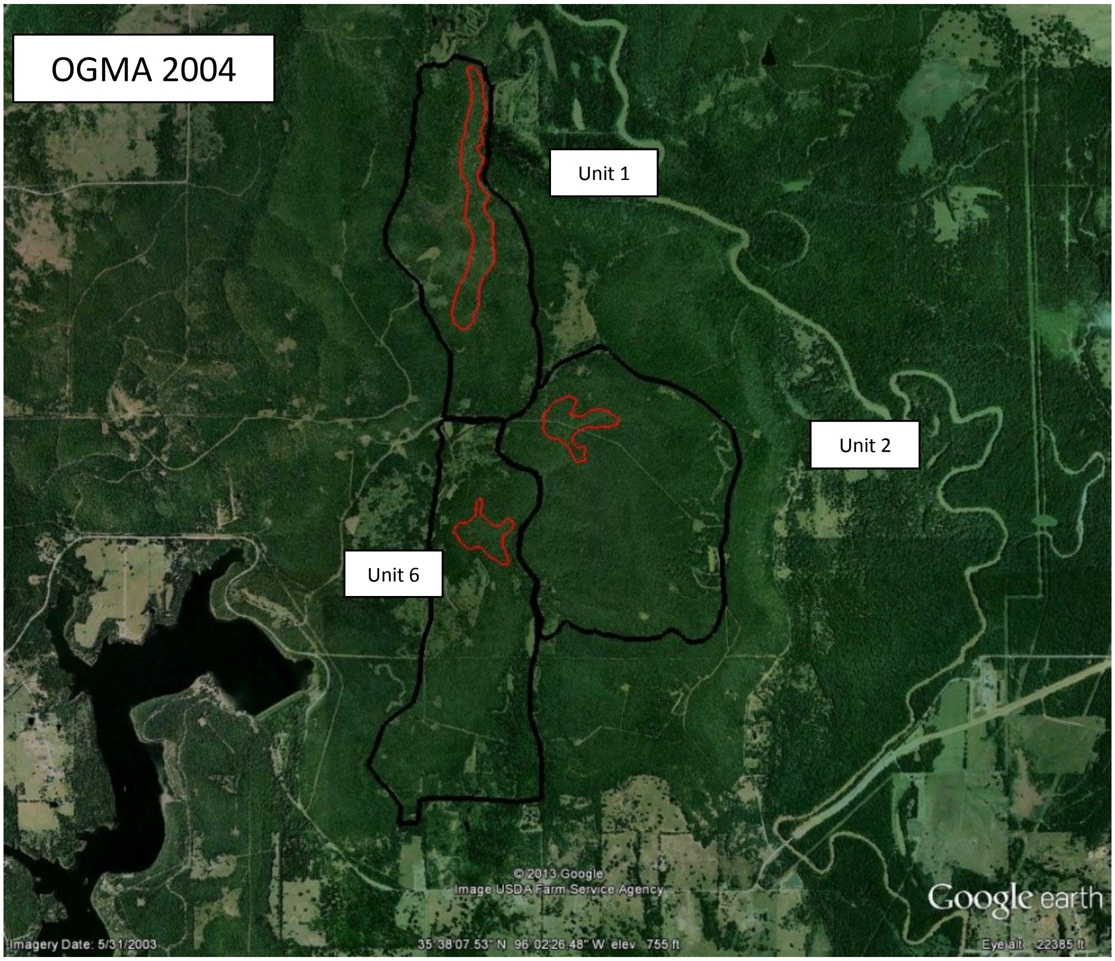
APPENDIX III – Fire history of Okmulgee Game Management Area. "x" indicates a year in which that management unit had a prescribed burn. "x*" indicates a summer wildfire.

Year	OGMA Management Unit		
	1	2	6
2012			
2011	x		x*
2010		x	
2009			
2008			x
2007	x	x	
2006			
2005			
2004		x	
2003	x		
2002			x
2001	x		
2000	x	x	
1999	x		
1998	x		
1997	x		x
1996			
1995	x		
1994		x	
1993	x		x
1992		x	
1991			
1990			
1989	x		
1988			
Fires in Last Decade	3	3	3
Total Fires per Decade	4.4	2.4	2
Time since Last Fire	2	3	2

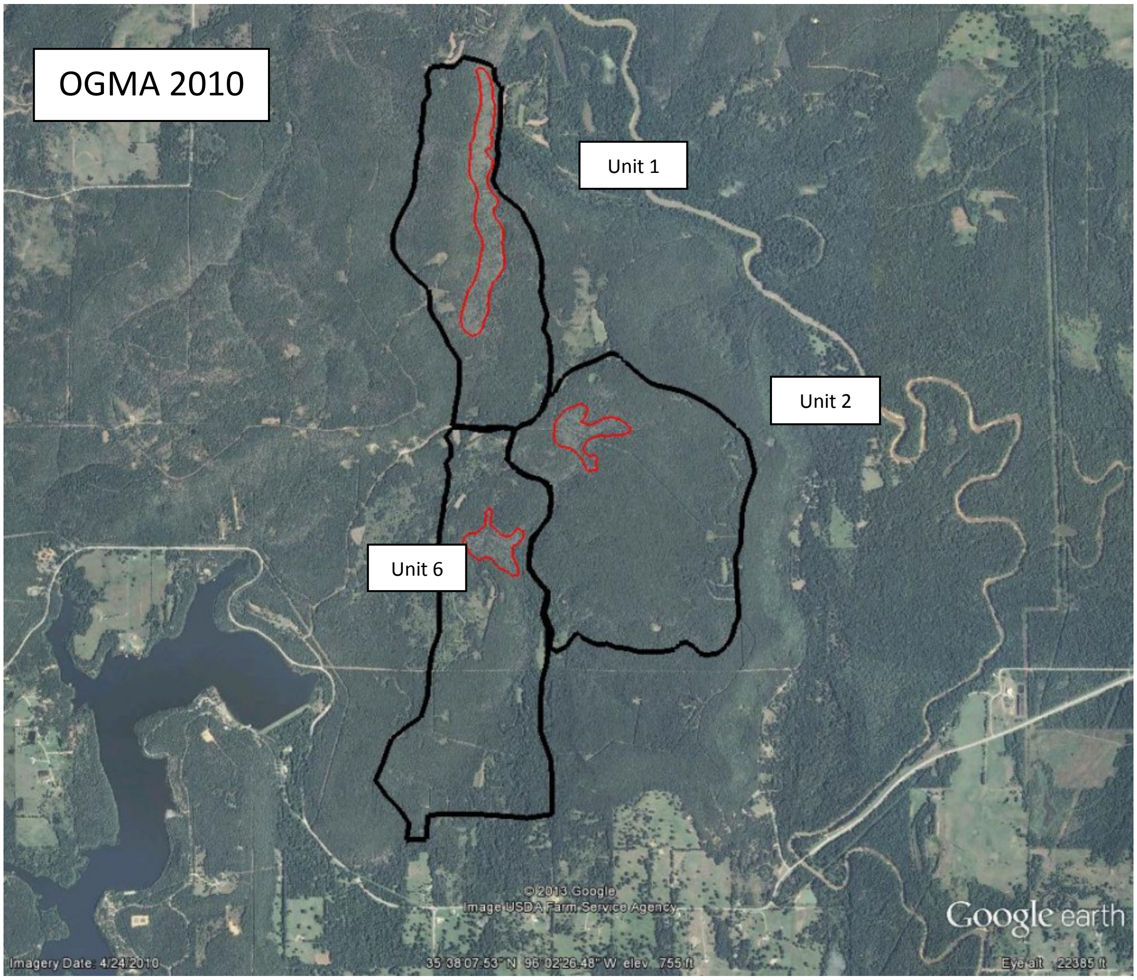
APPENDIX IV – Photographs taken of decline and non-decline areas. The images were taken in order to illustrate the change in forest structure and species composition due to oak decline. Photograph of decline stand was taken 07/31/13 in Unit 1. Photograph of non-decline stand was taken 08/02/13 in Unit 1.



APPENDIX V – Select aerial photographs (Google 2010) of Okmulgee Game Management Area (OGMA).



a) Okmulgee Game Management Area 2004 before the oak decline occurrence. Black indicates OGMA unit boundaries. Red indicates decline areas.



b) Okmulgee Game Management Area 2010 after the oak decline occurrence. Black indicates OGMA unit boundaries. Red indicates decline areas.

c) Okmulgee Game Management Area Unit 1 2004 before the oak decline occurrence.

d) Okmulgee Game Management Area Unit 1 2008 after the oak decline occurrence.

VITA

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