SAVANNA RESTORATION THROUGH PRESCRIBED FIRE: DEMOGRAPHIC

AND PHYSIOLOGICAL RESPONSES OF OAK AND HICKORY SEEDLINGS

AND SAPLINGS TO A CHANGING LIGHT ENVIRONMENT

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In Partial Fulfillment

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Master of Science, Biology

By

Douglas P. Aubrey

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SAVANNA RESTORATION THROUGH PRESCRIBED FIRE: DEMOGRAPHIC AND PHYSIOLOGICAL RESPONSES OF OAK AND HICKORY SEEDLINGS AND SAPLINGS TO A CHANGING LIGHT ENVIRONMENT

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Douglas P. Aubrey

ABSTRACT

Prescribed fire is a common tool for restoring and maintaining degraded oak savannas in the Midwest. Long-term success of restoration and maintenance ultimately depends upon new individuals entering the canopy. However, little is known about seedling and sapling response to this periodic disturbance. This study identifies how fire affects community structure and composition of dominant savanna seedlings and saplings, and takes the novel approach of linking conceptually and empirically demographic responses of seedlings and saplings to growth and gas exchange. This study was conducted within the Drury Conservation Area, located in Taney County, Missouri where there is both historical presence of oak savannas, and varying fire histories. Study sites representing unburned closed forest (n=2) and recently burned closed forest (n=2) were established in 2001. Twelve belt transects with an average area of $102m^2$ were established and sampled to determine indirect links between fire history effects on canopy leaf production and the demography and physiology of seedlings and saplings (*Quercus spp.*, *Carya spp.*, *Juniperus spp.*). Following prescribed burns, canopy light penetration was significantly greater in burned forest sites than in unburned forest sites. Density, basal area, mortality, and recruitment appear to be increasing in burned forest sites relative to unburned forest sites. Maximum and ambient net photosynthetic rates increased between habitats as light availability increased. Data suggest that current prescribed fire regimes are positively affecting white oak regeneration in previously closed forests, while effectively removing cedar seedlings.

KEYWORDS: Prescribed fire, Canopy coverage, Savanna restoration, Demography, Gas-exchange, *Quercus spp.*, Light availability

This abstract is approved as to form and content

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CHAPTER I

CURRENT UNDERSTANDING OF MIDWEST OAK SAVANNA ECOLOGY

Introduction

Oak dominated savannas were once common ecosystems throughout the Midwest landscape (Cottam, 1949; Curtis, 1959; Nuzzo, 1986; Ladd, 1991). However, these diverse communities have degraded and vanished due to fire suppression and various land-use changes resulting from European settlement. Over the past two decades, there has been a growing interest in preserving intact savanna remnants as well as restoring degraded remnants. Because periodic fire is believed to have played a critical role in the evolution and maintenance of Midwest savannas, restoration and management attempts have focused heavily on reintroducing fire into these systems.

Prescribed burning has been shown to shift the structure and composition of closed forest towards that of savanna (White, 1986; Apfelbaum and Haney, 1991; Peterson and Reich, 2001), but little is known regarding seedling and sapling dynamics in response to this disturbance. Therefore, it is important to focus on the growth rates and size structure of seedlings and saplings to make long-term predictions about habitat recovery and stability following burns. In addition, understanding seedling and sapling leaf-level net photosynthetic rates in burned areas may allow for mechanistic predictions of canopy recruitment as canopy light penetration increases.

Research Overview

This research examined the effects of recently implemented prescribed burns on the structure, composition, and physiology of seedlings and saplings of the dominant overstory tree species within the Drury Conservation Area (DCA) located in southwest

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Missouri. Specifically, the effects of three biennial prescribed burns on canopy light penetration and the resulting response of seedlings and saplings to the changing light environment and disturbance were examined. Intact remnant savannas were qualitatively compared with the burned forest to assess the effectiveness of prescribed burning as a tool for restoration of degraded Midwest savannas.

For these purposes, areas that were burned for the first time in over fifty years during the spring of 1999 were compared with adjacent areas that have not been burned in over fifty years. Oak (*Quercus spp.*), hickory (*Carya spp.*), and eastern redcedar (*Juniperus virginiana*) were the focus for the purpose of examining changes in community structure and composition as well as physiological changes in response to a changing light environment. Oak species were further categorized into the traditional red oak species and white oak species groups. An overview of the current knowledge of savanna ecosystems is presented here. Information contained within this review should be of interest to ecologists and land managers attempting to preserve or restore these diverse ecosystems.

Savanna Ecosystems

The term savanna refers to a community consisting of widely spaced open-grown trees (Cottam, 1949; Curtis, 1959; Apfelbaum and Haney, 1987; Ladd, 1991) that allow an appreciable amount of light penetration to the ground layer, and thus, support a diverse assemblage of herbaceous and grass species (Curtis, 1959; Ladd, 1991; Anderson, 1998; McCarty, 1998; Leach and Givnish, 1999). Savannas have been described as grasslands with trees (Cottam, 1949). These communities are often defined by the structure and composition of the overstory tree species, but are also dominated by a rich ground layer

of forbs and grasses (Curtis, 1959). In the Midwest, the overstory tree species of savannas are predominantly composed of *Quercus* (oak) species (Gleason, 1913; Curtis, 1959; Pallardy et al., 1988; Ladd, 1991; Anderson, 1998). However, it has been argued that based on historical species assemblages, forb species richness outweighs grass species richness in Midwest savannas; and therefore, these communities may be more correctly referred to as forblands (Leach and Givnish, 1999). In addition, many descriptions of savannas indicate a minimal presence, if at all, of shrubs and saplings (Apfelbaum and Haney, 1987; Ladd, 1991).

The definition used above is vague in that it does not provide specific, measurable parameters, but it does generally describe what is considered as savanna in the Midwest. The term savanna has been used by many ecologists and described differently in reference to canopy cover. Canopy cover of Midwest savannas is highly variable (King, 2000a) and the value of percent canopy used by ecologists to classify savannas in the Midwest varies greatly among researchers and states (Nuzzo, 1986; Leach and Ross, 1995). For example, Curtis (1959) defined Midwest savannas as having more than one mature tree per acre but less than 50% canopy cover; the Nature Conservancy defined savanna as having 10-30% canopy cover (Taft, 1997); Nelson (1985) defined Missouri savannas as having 10-50% canopy cover; and Nuzzo (1986) defined Ohio savannas as areas with complete canopy cover. The discrepancy in agreeing on a single definition for Midwest savannas results from the highly variable physiognomy of these systems, their transitional nature, and difficulty in interpreting their historical information (Nuzzo 1986). Consequently, many other names have been used to describe savanna

communities, including: oak openings, barrens, and scrub or brush prairies (Cottam, 1949; Nuzzo, 1986).

Midwest savannas may more clearly be defined as ecotones (Mendelson et al., 1992) or transitional areas (Anderson, 1998), between two distinct habitats: prairie and forest. Therefore, they support species of both prairie and forest communities. Ecotones in general have been described as highly diverse communities because they support species from distinctly different habitats. Oak savannas have specifically been described as highly diverse communities (Curtis, 1959; Leach and Givnish, 1999; Bader, 2001) supporting many plant and animal species that reach their peak abundance in these communities (Curtis, 1959; Anderson, 1998; Leach and Givnish, 1999). For example, the savanna understory has often been compared to that of a prairie (Curtis, 1959; Anderson, 1998). Prairies support a highly diverse assemblage of herbaceous and grass species, and in turn, a diverse faunal assemblage. Differential pollen profiles from savannas, forests, and prairies lend further support to savannas as ecotone communities. For example, savanna pollen profiles contain larger proportions of herbaceous pollen than forests and smaller proportions of hardwood pollen, but lower herbaceous pollen and higher oak pollen than prairies (Griffin, 1994).

Landscape heterogeneity is an important factor correlated to species diversity (Abrams, 1988; Huston, 1994). The high species diversity found in Midwest savannas results from the variable canopy structure which creates a mosaic of microhabitats (Anderson and Brown, 1986; Ko and Reich, 1993; Barton and Gleeson, 1996; Leach and Givnish, 1999). As a consequence, there is great variability (i.e., high heterogeneity) in

light quantity and quality, nutrient availability, soil moisture, and air and soil temperature within savannas (Ko and Reich, 1993).

The Role of Fire in Savanna Ecosystems

Since early in the twentieth century, ecologists have recognized that disturbance can significantly affect plant community structure and composition (Clements, 1916; Gleason, 1926), and it is widely agreed upon that fire played an integral role in the development and maintenance of Midwest savanna systems (Gleason, 1913; Curtis, 1959; Anderson and Fralish, 1975; Vogl, 1977; Pallardy et al., 1988; Apfelbaum and Haney, 1991; Ladd, 1991; Abrams and Nowacki, 1992; Abrams, 1996; McPherson, 1997; Taft, 1997; Anderson, 1998). Debate still exists, but it is generally agreed upon that Native Americans were responsible for igniting fires which shaped the composition and structure of vegetation across the landscape which maintained savannas (Cottam, 1949; Guyette and McGinnes, 1982; Pyne, 1982; Ladd, 1991; Abrams, 1996). Native Americans inhabited present day Missouri for over 10,000 years prior to European settlement (Chapman, 1975). In the White River watershed area of Missouri, The Osage Indians are thought to have been the most important source of fire ignition prior to European settlement (Guyette and McGinnes, 1982). Native fire ignitions appear to have been most common in the fall after most perennial grasses and forbs had died back for the season (White, 1983; Ladd, 1991; McCarty, 1998). Fire scars analyses suggest that before European settlement average fire intervals were between 2.8 and 3.2 years in areas of southern Missouri (Guyette and McGinnes, 1982; Cutter and Guyette, 1994).

Fire maintains savanna systems by eliminating fire-sensitive competitors of oak (Curtis, 1959; Bazzaz, 1979; Crow, 1988; Apfelbaum and Haney, 1991; Lorimer, 1994;

Moser et al, 1996) as well as by limiting the number of oaks that reach the canopy, resulting in widely-spaced canopy trees (Cottam, 1949; Curtis, 1959; Apfelbaum and Haney, 1987; Ladd, 1991; Ko and Reich, 1993). Fire resistance is a function of bark thickness (Hengst, 1994) and, when mature, even fire-sensitive species may achieve fire-tolerance (Peterson and Reich, 2001). However, most seedlings and saplings (fire-tolerant or fire-sensitive) are top-killed when burning occurs, and sprout from rootstocks shortly afterward (Lorimer, 1985; Apfelbaum and Haney, 1991; Stearns, 1991; Abrams, 1992; Abrams and Nowacki, 1992; Hruska and Ebinger, 1995; Abrams, 1996; Bowles and McBride, 1998). Species that favor root development over height growth have a competitive advantage when subjected to recurring fire as the greater amount of stored carbohydrates allow for more vigorous growth after sprouting (Crow, 1988). Thus, fire may have minimal effects on mature trees, but drastic effects on seedlings and saplings. Burning facilitates germination of many savanna tree, grass, and herbaceous species by removing leaf litter (Leach and Ross, 1995) and increasing short-term nutrient availability (especially nitrogen) immediately following a burn (Raison, 1979; Boerner, 1988; Reich et al., 1990). The combination of these fire effects has shaped and maintained these communities for thousands of years by selecting for fire-adapted species assemblages (Anderson, 1998).

Guyette and McGinnes (1982) have speculated that the removal of the Osage Indians from Missouri resulted in increased average fire intervals as Indian removal coincides with European settlement and decreased fire frequencies. Following European settlement, average fire intervals in areas of Missouri increased to 24 years (Cutter and Guyette, 1994) as a result of fire suppression, land fragmentation, road construction,

agriculture, and grazing (Curtis, 1959; McCune and Cottam, 1985; Abrams, 1986; Abrams, 1996; Bowles and McBride, 1998).

In the absence of fire, savannas are invaded by later successional, fire-sensitive, shade-tolerant species (Carvell and Tyron, 1961; Lorimer, 1984; Nigh et al., 1985; Pallardy et al., 1988; Lorimer, 1989; Abrams and Downs, 1990; Reich et al., 1990; Abrams and Nowacki, 1992; Abrams et al., 1998; Arthur et al., 1998; Cook, 2000; Abrams, 2003). When mature these species obstruct canopy light penetration from reaching the ground layer and alter community characteristics (Gleason, 1913; Cottam, 1949; Curtis, 1959; McCune and Cottam, 1985; Anderson and Brown, 1986; Nuzzo, 1986; Crow, 1988; Pallardy et al., 1988; Crow et al., 1994; Cole and Taylor, 1995; Abrams, 1996). The closing canopy further facilitates increased shade-tolerant understory species establishment and continues to depress the quantity and quality of light available to the ground layer. Consequently, there is a decrease in biotic diversity (Parker and Weaver, 1989; Taft, 1997; Bowles and McBride, 1998).

Oaks as Dominant Species in Savannas

Most fire susceptible trees are removed after fire as a result of cambium heat stress and subsequent increased vulnerability to insect damage and disease rather than direct burning (Huddle and Pallardy, 1996). Oaks however are extremely well adapted for persistence through recurring fire. Mature oaks possess thick bark that insulates the cambium from the heat stress imposed by fire (Lorimer, 1985). Furthermore, most species of oak, when mature, are highly resistant to rot after fire scarring (Abrams, 1985; Lorimer, 1985). Therefore, mature oaks are generally minimally affected by fire. Oaks also possess large root systems (Crow, 1988) and the ability to vigorously resprout after

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being top-killed by fire (Lorimer, 1985; Stearns, 1991; Abrams, 1992; Abrams and Nowacki, 1992; Abrams, 1996). However, this ability decreases with physiological aging of large trees (Houston, 1987), as large oaks do not appear to resprout, possibly due to decaying root systems (Peterson and Reich, 2001). Acorn germination also benefits from the removal of litter and increased nutrient availability caused by fire (Raison, 1979; Lorimer, 1985; Reich et al., 1990; Abrams, 1992; Kruger and Reich, 1997). As a consequence of these attributes, oaks have a competitive advantage over invading species when fire is periodic (Crow, 1988); and therefore, the presence and dominance of oak is often associated with periodic fire (Abrams, 1992; Abrams and Nowacki, 1992).

Competitive ability is an important factor governing the invasion of native communities (Owens, 1996) and under closed canopy conditions, oak seedlings and saplings are at a competitive disadvantage with later successional species (Abrams, 1996). Under a closed canopy forest, light is often the limiting resource and its availability can greatly influence tree establishment and growth (Canham, 1988). Oaks are not well adapted to low-light conditions caused by a closed canopy and seedlings do not exhibit long-term growth or survival under these conditions (Crow 1988; Lorimer, 1989; Burns and Honkala, 1990). For example, *Quercus rubra* (red oak) seedlings were shown to fix less CO_2 than required for respiration when grown in low-light conditions (Crow, 1988). However, Kaelke et al. (2001) demonstrated a positive carbon balance in oak seedlings grown under low-light conditions, suggesting factors other than those directly related to carbon gain might explain the lack of oak persistence under a closed canopy. Lorimer (1993) suggested that increased browsing pressure from deer might explain why oak regeneration fails to reach the forest canopy. Shade-tolerant tree species

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that compete with oak typically have higher rates of carbon gain, higher survival rates, faster growth rates, and consequently, higher abundance than oaks (Lorimer, 1984; Crow, 1988; Lorimer et al., 1994). Furthermore, shade tolerance decreases with age for oaks (Carvell and Tyron, 1961), which severely limits the number of seedlings that enter the sapling stages and represents a bottleneck in oak canopy recruitment under closed canopy conditions (Abrams and Downs, 1990).

Decline and Current Status of Midwest Savannas

Oak savanna habitat historically covered an estimated 12 million ha in the Midwest (Nuzzo, 1986). The occurrence of Midwest savannas peaked about 3,500 – 8,000 years ago during a period of warming following the last glacial period (Anderson, 1998). Currently, less than 2607 ha (0.02% of the original distribution) of this once widespread community type remains (Nuzzo, 1986).

Nigh and Pallardy (1983) suggest that Missouri oak woodlands have been experiencing structural and compositional changes that could not have persisted since before European settlement. For example, many oak forest understories are primarily composed of later successional species (Abrams, 1986; Pallardy et al., 1988; Abrams and Downs, 1990). In the Midwest, *Acer rubrum*, *A. saccharum*, and *Juniperus virginiana* represent common invaders of degraded oak savannas (Abrams, 1992; Abrams and Nowacki, 1992; Haney and Apfelbaum, 1993; Barton and Gleeson, 1996). When these competitors mature and fill the canopy, the result is a closed canopy forest with lower plant species richness and different faunal assemblages as compared to savannas (Apfelbaum and Haney, 1987).

The Use of Prescribed Burning in Restoring Midwest Savannas

There has been a recent interest among conservation-oriented groups to preserve and restore remnant savanna habitats in the Midwest. In fact, every Midwestern state has implemented savanna restoration projects at some point during the past two decades (Leach and Ross, 1995). In Missouri, restoration of degraded savanna habitats have been attempted since the early 1980's (McCarty, 1998). Due to its historical importance in the maintenance and evolution of oak savannas, fire has been a common and essential tool used in the restoration process (Apfelbaum and Haney, 1987; Peterson and Reich, 2001). The primary objectives of savanna restoration involve reducing canopy tree density and basal area and eliminating understory shrubs and trees; both of which facilitate the establishment of a ground layer rich in herbaceous and grass species through increasing the availability of light to the understory (White, 1986; Bowles and McBride, 1998; Peterson and Reich, 2001). Previous restoration attempts have demonstrated that even severely degraded savanna remnants may be successfully restored even when degradation has resulted in losses of biological diversity (Leach and Ross, 1995; McCarty, 1998). Prime areas for restoration efforts can be identified by the presence of multiple stemmed mature oaks, which are indicative of an area formerly being a savanna (Cottam, 1949; Curtis, 1959). The restoration and maintenance of savanna systems is highly dependent on fire frequency and intensity (Apfelbaum and Haney, 1987). Most restoration projects begin with prescribed fire treatments between late winter and early spring with a one to three year burning interval, with sites containing little herbaceous cover receiving annual burns (McCarty, 1998). Generally, short burn intervals result in low fuel loading, which allows for low intensity burns to spread quickly and non-uniformly and allows the

survival of many trees (Ladd, 1991). Conversely, long burn intervals result in high fuel

loading, which allows for high intensity fires which can convert closed canopy forests to

open forests or savannas by killing mature trees (Paulsell, 1957; Scowcroft, 1966;

Anderson and Brown, 1986). Thus, initial burning of remnant savannas should result in a

reduction of canopy coverage and basal area, and subsequent burns should be sufficient

for controlling oak sprouts and prevent litter buildup while the ground layer becomes

reestablished. Typically, single burn events do not have a lasting affect on reducing

understory competition (Crow, 1988; Moser et al., 1996; Kruger and Reich, 1997).

However, annual or biennial burns have resulted in rapid reductions of canopy and

subcanopy density and have minimized understory competition (Peterson and Reich,

2001). However, prescribed burning alone may prove insufficient in reducing canopy tree

density and basal area in sites that have been protected from fire for extended time

periods and have numerous large mature trees (White, 1983; Peterson and Reich, 2001).

Mechanical thinning or girdling has been used under these circumstances yielding

positive results of decreased canopy density (Bowles and McBride, 1998; McCarty,

1998; Peterson and Reich, 2001); but the cost is much higher than that of prescribed fire.

Herbaceous and grass species generally increase in richness and abundance

following prescribed burns (White, 1983; White, 1986; Leach and Givnish, 1999), and

have been shown to further increase as burn frequency increases (Tester, 1989).

Prescribed burning has been shown to result in 40% and 37% increases in herbaceous

layer cover in degraded savannas under high and low intensity burns, respectively

(Apfelbaum and Haney, 1987). Herbaceous and grass diversity has been shown to

increase by 36% under high intensity fires and 28% under low intensity fires (Apfelbaum

and Haney, 1987). Furthermore, species that were inhabitants of historical savanna, but were not present before burning was implemented have reappeared following burning (Apfelbaum and Haney, 1987). Legumes, which are important components of the nitrogen cycle, have also been shown to increase after burning (Hruska and Ebinger, 1995). Tester (1989) found that alternating two years of annual burning followed by two years without burning can maximize species richness. Also of importance, prescribed burning has been effective at eliminating the shrub layer (White, 1983). Apfelbaum and Haney (1987) demonstrated that high intensity burns decreased the shrub layer 65%, while low intensity burns only removed a small proportion.

When first implemented, prescribed burning generally decreases canopy tree density and basal area (White, 1986; Peterson and Reich, 2001). High frequency burning (1-3 years) has been shown to remove the sapling layer and suppress sprouts, whereas low frequency burning (>3 year interval) allows for dense sapling growth (Peterson and Reich, 2001). Peterson and Reich (2001) demonstrated a negative correlation between increasing fire frequency and seedling density. Low intensity burns have resulted in minimal amounts of small oak mortality (Reich, 1990), and do not appear to affect oaks that have reached a dbh (diameter at breast height) >25 cm (White, 1983; Peterson and Reich, 2001). However, low intensity burns may be ineffective at maintaining savannas that contain high densities of established woody plants (Peterson and Reich, 2001). Crow et al. (1994) further demonstrated that fire resulted in high ramet mortality, but low genet mortality, supporting the notion that large root systems are critical for resprouting.

Generally, oaks less than 3m tall are top-killed by fire only to re-sprout (Hruska and Ebinger, 1995). These sprouts rapidly develop when burning is absent (Bowles and

McBride, 1998) and can grow 6m within nine years (Cain, 1995). Savanna canopy recruitment appears to occur in distinct cohort groups that are related to periods of decreased burn frequency and intensity (Apfelbaum and Haney, 1987; Apfelbaum and Haney, 1991; Crow et al., 1994). Thus, burning-free intervals are necessary for oaks to reach sufficient size that will prevent them from becoming top-killed when burning is re-introduced (Apfelbaum and Haney, 1991; Rebertus and Burns, 1997; Peterson and Reich, 2001).

Summary

Midwest savannas may best be thought of as ecotone communities containing species typical of both prairie and forest habitats. These communities are distinguished by the widely spaced open-grown oak trees in the canopy, but dominated by a diverse assemblage of herbaceous species which thrive due to the large amount of light reaching the ground layer. Consequently, savannas are highly diverse in terms of flora and fauna. Midwest savannas likely owe their development and maintenance to periodic fire. It is believed that Native Americans were responsible for igniting many of these fires which shaped the landscape of the Midwest before European settlement. This idea is supported by the decrease in fire frequency following Native American departure from the region. As a result of decreasing fire frequencies, many savannas were transformed into closed canopy forests as shade-tolerant fire-sensitive species invaded these areas in the absence of disturbance. As a result of invasive encroachment, shade-intolerant oak seedlings are at a competitive disadvantage and become successively replaced; leading to further degradation and elimination of a once widespread habitat.

For over twenty years, savanna restoration has been implemented throughout the Midwestern region, relying heavily on the efficacy of prescribed fire as a tool for both restoration and management. Prescribed burning has been shown to reduce canopy coverage, remove shrub and sapling layers, and re-establish the ground layer components of degraded savannas. However, there remain many questions about the most effective fire frequencies, fire intensities, and seasonal implementation to obtain desired results.

A primary objective of savanna restoration efforts is to restore the open-canopy characteristics and restore the oak sprout layer. There is also a critical need to determine burn frequencies and intensities that will facilitate the maintenance of oak sprouts. An understanding of these processes is imperative for successful restoration and management attempts.

These concerns were addressed by examining the effects of three biennial prescribed burns on canopy light penetration and the consequent changes in seedling and sapling structure, composition, and physiology as a function of fire and light environment. Demographic analysis is necessary to predict the trend of a population (i.e., increase, decrease, or stasis) and is essential to the decision making process involved with restoration of degraded systems or maintenance of restored systems. However, demographic analysis only demonstrates what has happened to the population previously as a result of disturbance and does not offer a mechanism that can be used to predict future community dynamics. To better understand the mechanism that drives changes in a population, species physiological responses to the disturbance (direct and indirect) must be evaluated. Species responses to disturbance can be examined through their physiological response to the disturbance (i.e. changes in light availability) and these

responses can then be related to their demography. If demographic changes that have occurred since burning was first implemented follow species physiological responses to light availability, then physiological responses would appear to be the mechanism that governs demographic change and thus would be a valid predictor of future community structure and composition. Therefore, a physiological understanding of the focal species is necessary to make long-term predictions concerning population dynamics and is critical when attempting to implement restoration or management plans. By assessing both the demography and physiology of seedlings and saplings, data was generated that will allow for more accurate predictions of how community structure and composition will be affected (i.e., change) by attempts involving prescribed burning for savanna restoration in southwest Missouri.

OAK SAVANNA RESTORATION THROUGH PRESCRIBED FIRE:

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HICKORY SEEDLINGS AND SAPLINGS TO A CHANGING LIGHT

ENVIRONMENT

CHAPTER II

Introduction

Midwest savannas are communities consisting of widely spaced canopy trees (Cottam, 1949; Curtis, 1959; Apfelbaum and Haney, 1989; Ladd, 1991) that allow an appreciable amount of light penetration to the ground layer (Curtis, 1959; Ladd, 1991; McCarty, 1993; Anderson, 1998; Leach and Givnish, 1999). Historically, oak savannas covered an estimated 12 million ha in the Midwest (Nuzzo, 1986), and it is widely agreed that fire played an integral role in their development and maintenance (Gleason, 1913; Curtis, 1959; Anderson and Fralish, 1975; Vogl, 1977; Apfelbaum and Haney, 1987; Pallardy et al., 1988; Ladd, 1991; Ladd, 1991; Abrams and Nowacki, 1992; Abrams, 1996; McPherson, 1997; Taft, 1997; Anderson, 1998). For example, fire scar analyses suggest that before European settlement average fire intervals were between 2.8 and 3.2 years in areas of southern Missouri (Guyette and McGinnes, 1982; Cutter and Guyette, 1994). Following European settlement and subsequent Native American displacement, average fire intervals in areas of southern Missouri increased to 24 years (Cutter and Guyette, 1994) as a result of fire suppression, land fragmentation, road construction, agriculture, and grazing (Curtis, 1959; McCune and Cottam, 1985; Abrams, 1986; Abrams, 1996; Bowles and McBride, 1998;).

Currently, less than 2607 ha (0.02% of the original distribution) of this diverse and once widespread community remain (Nuzzo, 1986) and a recent effort to preserve and restore remnant savanna habitats is occurring in the Midwest. In fact, every Midwestern state has implemented savanna restoration projects at some point during the past two decades (Leach and Ross, 1995). In Missouri, restoration of degraded savanna habitats has been attempted since the early 1980's (McCarty, 1998).

Because periodic fire is believed to have played a critical role in the evolution and maintenance of Midwest savannas, restoration and management attempts have focused heavily on reintroducing fire into these systems. In the absence of fire, savannas are invaded by later successional, fire-sensitive, shade-tolerant species. In the Midwest, *Acer rubrum*, *A. saccharum*, and *Juniperus virginiana* represent common invaders of degraded oak savannas (Abrams, 1992; Abrams and Nowacki, 1992; Haney and Apfelbaum, 1993; Barton and Gleeson, 1996). When mature, these species obstruct canopy light penetration from reaching the ground layer and alter community characteristics, particularly herbaceous species diversity (Gleason, 1913; Cottam, 1949; Curtis, 1959; McCune and Cottam, 1985; Anderson and Brown, 1986; Nuzzo, 1986; Crow, 1988; Pallardy et al., 1988; Crow et al., 1994; Cole and Taylor, 1995; Abrams, 1996). Although prescribed fire has been shown to shift the structure and composition of closed forest towards that of savanna (White, 1986; Apfelbaum and Haney, 1989; Peterson and Reich, 1990), relatively little is known about seedling and sapling dynamics in response to this disturbance. Ultimately, savanna habitats depend upon new individuals or oak sprouts entering the canopy (Ladd, 1991; Haney and Apfelbaum, 1993; Crow, et al., 1994; Leach and Ross, 1995; McCarty, 1998). Without sapling recruitment into the canopy, the

savanna will revert to grassland (Curtis, 1959; Ladd, 1991). Alternatively, if recruitment is excessive, the savanna will succeed into a closed forest (Curtis, 1959; Ladd, 1991; Leach and Givnish, 1999).

Examining seedling and sapling demographic response to prescribed fire will add to our understanding of how dominant savanna seedlings and saplings persist and are recruited to the canopy (Jenkins and Rebertus, 1994). Demographic analysis is necessary to predict trends of a population (i.e., increase, decrease, or stasis) (Davy and Jefferies, 1981; Schemske et al., 1994) and is essential to the decision making process involved with restoration of degraded systems or maintenance of restored systems (Plocher, 1994; Leach and , 1995). To better understand the mechanism that drives changes within a population, species physiological responses must be evaluated (Caldwell and Pearcy, 1994; Forseth, et. al., 2001). For example, species net-photosynthetic responses to light availability may be a valid predictor of future community structure and composition. Therefore, a combination of demographic and physiological data should be used to predict future community structure and composition in populations undergoing periodic disturbance (Forseth et al., 2001).

To understand how initial prescribed burning of a closed canopy remnant savanna affects oak and hickory seedling and sapling dynamics, the effects of three biennial prescribed burns on seedling and sapling composition, canopy light penetration, and gas exchange in southwest Missouri were studied. Prescribed burns were implemented in 1999 on degraded (i.e., closed canopy) savanna remnants in the Drury Conservation Area (DCA) in Taney County Missouri and continued in 2001 and 2003. All prescribed burns occurred in the spring during March or April. King (2000b) suggests that canopies at

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these sites have been closed for a significant period due to the complete absence of high light obligate herbaceous species. Furthermore, if these areas had historically been closed forest, then some shade-tolerant herbaceous species might be expected, for which there is no evidence (King, 2000b). Conversely, intact (i.e., open canopy) savanna remnants at DCA were never completely covered by trees due to the rich herbaceous diversity that remains intact (King, 2000b).

The overall objectives of this research were to: (1) examine the effectiveness of prescribed burning as a tool for eliminating cedar seedlings and saplings; (2) determine how burning directly and indirectly changes the number and size of oak and hickory seedlings and saplings; (3) examine changes in canopy light penetration that occur after prescribed burning; (4) understand the physiological response of oak and hickory seedlings and saplings to increased light availability. To address these objectives, direct (mortality) and indirect (recruitment, density, basal area, canopy light penetration, and gas exchange) effects of prescribed burning on seedlings and saplings of the dominant canopy trees (*Quercus spp., Carya spp., Juniperus spp.*) were examined. Oaks were chosen because they are the dominant species within intact savannas at DCA and the desired dominant species of restoration efforts. Hickories were chosen because they are also common to intact savannas at DCA and may possibly compete with oak as understory light availability increases. Cedars were chosen because they invade savannas when fire is absent and decrease canopy light penetration when mature. DCA is ideal for investigating fire effects, as there is both historical presence of oak savannas within the area, and varying fire histories. To quantify the effects of prescribed burns on canopy light penetration and seedling and sapling structure, composition, and gas exchange, sites

that received three biennial prescribed burns were compared with adjacent sites that have not experienced recent burning, but shared a similar fire history prior to the initial burn. The demography and physiology of seedlings and saplings of intact savanna remnants at DCA which have been routinely burned were also examined. These savanna habitats act as a historical comparison for burned forests from which restoration success was qualitatively assessed.

This study tests the following predictions: (1) Prescribed burning kills most cedar seedlings and saplings; (2) Prescribed burning removes the aboveground portions of oak and hickory seedlings and saplings but does not cause mortality; (3) Prescribed burning results in multiple sprouting of white and red oak but not hickory seedlings; (4) Prescribed burning increases the recruitment of all oak species; (5) Prescribed burning increases canopy light penetration; (6) White oak and hickory are light limited and respond positively to increases in light associated with prescribed burning and therefore experience greater carbon gain than red oak.

Methods

Site Description. This study was conducted at the Bull Shoals Field Station (BSFS), located within the 1200 ha Drury Conservation Area (DCA) (36°N latitude, 93°W longitude) in Taney County, Missouri (Appendix A). Elevations at DCA range from 183-335 m. The soil type throughout DCA consists mainly of Gasconade-Opequon-Clarksville association (MDC, 1991). Thirty year mean daily maximum temperature during the growing season (April through September) is 28°C, and thirty year mean annual precipitation is 1097.02 mm. Currently, an estimated 60% of the vegetation at

DCA is oak-hickory forest, and of this, approximately 50% is degraded (i.e., the canopy has closed) remnant upland savanna (MDC, 1991).

Total cover of the degraded remnant upland savanna ("closed forest") in DCA has been estimated as 76% trees predominantly composed of *Quercus velutina* Lam. (44%), *Q. falcata* Michaux (15%), and *Q. stellata* Wangenh. (11%), 5% shrubs/vines, and 5% herbs (King, 2000b). The subcanopy is primarily composed of *Cornus florida* L., *Ulmus alata* Michaux, and *Ulmus rubra* Muhlenb. The shrub layer is composed of *Rubus, Toxicodendron*, and *Vitis* species. The canopy is dense, and consequently, the ground layer is rather depauperate of herbaceous species and consists mainly of leaf litter.

The Missouri Department of Conservation (MDC) implemented prescribed burning on approximately 70% of the area of closed forest in 1999, 2001, and 2003 with the goal of re-establishing savanna habitat. Prior to this, the closed forest areas had not burned in over fifty years. All prescribed burns have been conducted in March and April on the same forest areas. The 1999 burn was probably of higher intensity due to accumulated fuels, while the subsequent burns were of lower intensity.

Total cover of savanna at DCA has been estimated as 41% trees, predominantly composed of *Quercus stellata* Wangenh. (51%), *Carya texana* Buckley (23%), and *Q. velutina* Lam. (11%), 15% shrubs/vines, and 39% herbs (King, 2000b). The savanna portions lack a subcanopy with the exception of a few emergent canopy species. The shrub layer is dominated by *Rhus aromatica* Aiton, but it is less dominant than the ground layer component. Savannas at DCA have been maintained with periodic prescribed burns over the past fifty years; however burn frequency is variable between the sites.

Experimental Design. Four permanent study plots (100 m x 100 m) representing unburned closed forest habitat (n=2) and burned closed forest habitat (n=2) were established in 2000 (Appendix B). Burned and unburned forest plots were adjacent to one another with a gravel road acting as a fire buffer between them, with unburned forest acting as a control. To account for environmental variation, the adjacent plots were statistically treated as blocks. In addition, two study plots representing savanna habitat were also established. The savanna habitat was not included in statistical analyses because those areas have sporadic burn histories and are not adjacent to both burned and unburned closed forest. Therefore, savanna plots were used to examine if characteristics of burned forests were approaching those of savannas.

Within each habitat type and 100 m x 100 m plot (unburned forest, burned forest, savanna), a random point was selected to place a leaf litter collection basket. This process was repeated four times at each site. In 2001, three permanent belt transects were established by connecting the four baskets within each site. Belt transects had an average area of 102 m^2 (4 m wide with various lengths). Transect lengths were variable due to the random placement of collection baskets.

Within each transect, all red oak (*Quercus falcate* Michaux, *Q. marilandica* Muenchh., *Q. rubra* L., *Q. shumardii* Buckley, and *Q. velutina* LAM.), white oak (*Quercus alba* L., *Q. macrocarpa* Michaux, *Q. muhlenbergii* Englem., and *Q. stellata* Wangenh.) hickory (*Carya texana* Buckley and *C. tomentosa* (Poiret) Nutt.), and cedar (*Juniperus ashei* Buchholz and *Juniperus virginiana* L.) individuals <2.0m in height were identified, tagged, and mapped from 2001-2003. The initial number of seedlings and

saplings tagged totaled 114 in the unburned forest sites, 197 in the burned forest sites, and 219 in the savanna sites.

Demographic Sampling. Seedling and sapling community characteristics (structure and composition) were assessed by measuring stem diameter, stem number, and stem height of all tagged individuals annually between June and July. Stem diameter measurements of all stems were obtained at ground level using Spi dialMax 2000 calipers (KWB, Switzerland) with 0.1mm precision. Stem height was measured using a meter stick with 1.0 mm precision; only the tallest stem of an individual was measured. Individual seedling and sapling density and dominance, as well as total density and dominance were calculated for each habitat annually from 2001-2003. Individual densities were calculated as the number of individuals per area sampled. Individual dominances were calculated as the sum of species basal area (cm^2/m^2). Yearly transect mortality and recruitment were measured between 2001-2002 and 2002-2003. Mortality was defined as the absence of an individual that was present in the previous sampling period. Recruitment was defined as the presence of an individual not present the previous year.

Stem diameter and height also allowed for annual plant volume estimates. At the time of sampling, only the tallest stem of each individual was measured. In order to estimate plant volumes, linear regression was used to generate equations yielding stem height as a function of stem diameter. Analysis of covariance (MiniTab version 14, Minitab, Inc., 2003) was performed to determine if height and diameter relationships varied between species and habitats. ANCOVA revealed significantly different height-

diameter regression for each species in each habitat; therefore, different linear equations were used for each species for each habitat type (Appendix C).

Stem volume was calculated as the volume of a cylinder ($2\pi rh$) using stem diameter as cylinder diameter and stem height as cylinder height. Plant volume was then estimated as the sum of stem volumes. Volumes were then log transformed and relative changes were calculated for individual plants between 2001-2002, and 2002-2003. Relative changes in stem number were calculated as the difference in stems present on an individual between years.

Canopy Light Penetration Sampling. Leaf area index (LAI) was used as a measurement of canopy light penetration to determine if burning was resulting in a more open overstory canopy. LAI is an indirect estimate of the ratio of overstory leaf area relative to ground area; therefore, a high LAI indicates low light levels penetrating the canopy, and a low LAI indicates high light penetration. Results are approximate since a particular percent absorbance per leaf layer is assumed. LAI values range from 0-12, with 0 indicating complete light penetration and 12 indicating no light penetration. LAI estimates require the measurement of above canopy photosynthetically active radiation (PAR) values (obtained from large canopy openings), below canopy PAR values, measurements of the sun's zenith angle (the angle the sun makes with respect to the point in the sky directly overhead), and the fraction of beam radiation (comparison measurements of total available PAR with measurements of diffuse radiation). Low understory PAR values translate into high LAI values; high understory PAR values translate into low LAI values.

LAI was obtained using an AccuPAR-80 light interception device (Decagon Devices, Inc. Pullman, WA, USA) to measure PAR. Understory PAR was measured 1.2 m above ground-level at five randomly spaced points along each of the three transects per site, which were used to calculate one LAI value for each transect per site per sample time (n=6 per habitat type). Measurements were collected three times during the growing season (mid-May, mid-July, and Mid-August) in 2002 and 2003. In addition, measurements were collected monthly from April through September in 2003 to examine leaf phenology.

Gas Exchange Sampling.

<u>Instantaneous Net Photosynthetic Rates.</u> The response of net photosynthesis and stomatal conductance to maximum and ambient light levels were measured on single leaves of five randomly selected plants from each deciduous species in each transect in 2001, 2002, and 2003. A single attached leaf from each plant was placed into the chamber of a portable gas exchange system (LI-6400, Li-Cor, Lincoln, NE, USA). Temperature (25° C), CO_2 concentration ($360\mu mol\ s^{-1}$), and flow rate ($500\mu mol\ s^{-1}$) were maintained at constant levels within the leaf chamber during measurements. Photosynthetically Active Radiation (PAR) was maintained at $1200\mu mol\ m^{-2}\ s^{-1}$ for maximum net photosynthetic rates (A_{MAX}) measurements, and at current ambient light levels for ambient net photosynthetic rates (A_{AMB}). The same individuals were measured in June, July, and August. Whenever possible, the same leaf was measured during each sampling effort.

<u>Light Curves.</u> The response of net photosynthesis to increasing PAR was measured on single leaves of randomly selected plants from each deciduous species in each habitat. A minimum of three individuals from each species were measured within both sites for each

habitat for a minimum of six individuals per habitat. Net photosynthesis was measured on each plant at each of eight decreasing PAR values (1500, 1200, 800, 500, 300, 150, 50, and $0 \mu mol\ m^{-2}\ s^{-1}$) per plant. Plants were allowed sufficient time to equilibrate at each PAR value. All measurements were collected in mid-July. Light response curves allowed for the estimation of light compensation points, quantum yields, and light saturation points.

The light compensation point is the amount of light a plant requires so that dark respiration rates and photosynthetic rates are equivalent. Quantum yield is the ratio of absorbed photons to photons used for chemical reactions; the steeper the slope, the more efficient the plant is at utilizing lower intensities of light for chemical reactions. Light saturation is the light intensity that is required to induce the highest rate of net photosynthesis; beyond this intensity of light, photosynthesis will not increase unless other limiting resources (i.e., CO_2) are made available. Therefore, light saturation values were obtained by determining the corresponding light intensity at each curve's asymptote. These values were determined using net photosynthetic rates derived from the nonlinear mixed models analysis (Peek et al. 2002). Saturation was assumed to occur when the first decimal of the net photosynthetic rate ceased to increase.

Statistical Analysis. The effect of prescribed fire on canopy light penetration was assessed using a multi-factorial ANOVA. The experiment was a nested block design with repeated measures. Year (2002 and 2003), month (May, July, and August), and habitat (unburned forest and burned forest) were treated as fixed factors. Block (n = 2) and transect (n = 18) were treated as random factors, with transect nested under both block and habitat.

The effects of fire on understory structure and composition (density, dominance, mortality, recruitment, relative volume change, and stem number change) were assessed using multi-factorial ANOVAs as above, except that there were three years of data (2001, 2002, and 2003), and species (cedar, hickory, red oak, and white oak) were included in the model and treated as fixed factors. For recruitment, an additional random factor of quadrat (n=299) was included.

The effect of saturating and ambient PAR levels on species and habitat specific maximum and ambient net photosynthetic rates were assessed using a multi-factorial ANOVA as above, except that month (June, July, and August) was used instead of year, cedar was not included in the model, and individual plant (n=270) was treated as a random factor and nested under block, habitat, transect, and species.

All ANOVA conclusions were based on an alpha of 0.10. The analyses were performed using the GLM procedure of Minitab 14 (Minitab, Inc., 2003).

The effects of increasing PAR levels on species and habitat specific maximum net photosynthetic rate, quantum yield, and light compensation point were assessed using the nonlinear mixed models procedure described by Peek et al. (2002). Habitat (unburned forest, burned forest, and savanna), species (hickory, red oak, and white oak), and PAR (0, 50, 150, 300, 500, 800, 1200, and 1500) were treated as fixed factors. All conclusions were based on an alpha of 0.05. P values are not exact due to estimated F statistics. The analysis was performed using the nonlinear mixed models procedure in SAS Version 8 (SAS Institute, Inc., 2000).

Results

    Demography

Density. There was a significant year-by-species interaction ($P = 0.007$) (Appendix D),

which was due to cedar seedling mortality during years when burning occurred (2001,

2003) followed by recruitment in the year when burning did not occur (2002) (Table 1).

Averaged over the three-year period, burned forest sites contained 30% more individuals

per unit area than unburned forest sites (Table 1), although the difference was only

marginally significant ($P = 0.067$). There was also a marginally significant difference in

density between years ($P = 0.058$). Total density of burned forest sites increased 36% in

2002 when there was no burn and decreased 11% in 2003 following a burn. Unburned

forest density increased 22% between 2001 and 2002 and was similar between 2002 and

2003.

    Species proportional contributions towards total density were not significantly

different between unburned and burned forest sites. In both habitats, red oak species

account for the majority of total density, followed by hickory, white oak, and cedar

species. However, red oak species accounted for less of the total density in burned forest

sites (48%) as compared to unburned forest sites (68%) (Table 1). In contrast, both white

oak and hickory species accounted for more of the total density in burned forest sites

(15% and 31%, respectively) as compared to unburned forest sites (6% and 20%,

respectively) (Table 1).

Dominance. There was no statistically significant effect of habitat type on dominance

between burned forest sites and unburned forest sites (Appendix E); however, total basal

area per area sampled averaged over the three year period was 46% higher in burned

forest sites as compared to unburned forest sites. Even though cedar density was similar between unburned and burned forest sites; cedar accounted for 6% of the total basal area in unburned forest sites and <1% of the total basal area in burned forest sites when averaged over the three-year period (Table 1). This was due to cedar being removed from the burned forest sites when burning occurred; consequently, only newly germinated seedlings were present and contributed minimally towards dominance. Mortality. There was a significant main effect of species on mortality ($P = 0.021$) (Appendix F), which was due to higher cedar mortality. There was also a species-by-year interaction ($P = 0.020$), a species-by-habitat interaction ($P = 0.046$), and a habitat-by-species-by-year interaction ($P = 0.002$). There was a marginally significant habitat-by-year interaction ($P = 0.078$). Cedar was most susceptible to mortality in the burned forest sites, exhibiting 88% mortality following the prescribed burn. All other species exhibited less than 10% mortality following the prescribed burn, with hickory species exhibiting the lowest mortality of all (3%), followed by white oak (8%), and red oak species (9%). When burning was absent (2002), there was no cedar mortality in the burned forest sites. However, white oak species exhibited 5% mortality; whereas red oak and hickory species both exhibited 1% mortality when burning was absent (2002).

Plant mortality averaged between 2002 and 2003 was greater in burned forest sites than unburned forest sites (Table 1); however, there was no statistically significant main effect of habitat type on mortality. Mortality was only 2% in both the unburned forest sites and burned forest sites between 2001 and 2002 (when burning was absent). Between 2002 and 2003, when burning occurred; mortality was 27% for burned forest sites, and 7% for unburned forest sites (Table 1).

Recruitment. There was a significant year-by-species interaction on recruitment (P = 0.034) and a marginally significant habitat-by-year interaction (P = 0.091) (Appendix G). Red oak and hickory recruitment were greater for both habitats in 2002 (Table 1). Plant recruitment in the burned forest sites was 43% greater than in the unburned forest sites in 2002, but only 26% greater in 2003 (Table 1).

Relative Volume and Relative Stem Number Changes. There were no significant main effects or interactions on relative volume or relative stem number changes within individuals (Appendices H and I). Burned forest sites exhibited negligible relative volume changes over the three-year period, whereas unburned forest sites experienced positive relative volume changes (Table 2). However, relative volume changes were not consistent with absolute stem number changes. Volume did not increase as stem numbers increased in the burned forests sites, but increased when stem numbers remained static in the unburned forest (Table 2).

Canopy Light Penetration. Canopy light penetration as measured by leaf area index (LAI) was significantly greater in burned forest sites than unburned forest sites (P = 0.037) (Appendix J) for both years sampled (Figure 1). The mean understory PAR values over the two year period were 97.9μmol m^{-2} s^{-1}for the unburned forest and 363.6μmol m^{-2} s^{-1} for the burned forest. Therefore, understory PAR is reduced 93% in unburned forest sites and 73% in burned forest sites relative to the above canopy PAR and plants in the burned forest understory receive, on average, 27% more light than plants in the unburned forest. There was also a significant decrease in LAI (P = 0.025) in both burned (31%) and unburned (17%) forests between 2002 and 2003 (Figure 1). A high

LAI indicates low light levels penetrating the forest canopy (low understory PAR), and a low LAI indicates high light penetration (high understory PAR).

There was a marginal main effect of month on LAI ($P = 0.073$), which was driven by lower LAI values in the unburned forest sites in April and May as compared to June through September (Figure 2). There is a clear trend present in 2003 suggesting that maximum leaf expansion occurs earlier in the season for burned forest sites than for unburned forest sites (Figure 2).

Gas Exchange.

<u>Instantaneous Net Photosynthetic Rates.</u> There was a significant habitat effect on A_{MAX} and A_{AMB} ($P = 0.026$ and 0.018, respectively) (Appendices K and L). Maximum and ambient net photosynthetic rates (A_{MAX} and A_{AMB}) were higher in burned forest sites than unburned forest sites (Table 3). Averaged over all sampling periods in 2003, burned forest sites exhibited 30% higher A_{MAX} and 50% higher A_{AMB} than unburned forest sites. There were no statistically significant effects of habitat on stomatal conductance (Table 3) (Appendices M and N); however, stomatal conductance was greater in burned forest sites than in unburned forest sites when measured at ambient and maximum light levels.

Month of sampling had a significant main effect on A_{MAX} and a marginally significant main effect on A_{AMB} ($P = 0.026$, 0.075, respectively). A_{MAX} decreased 33% between June and July, and 20% between July and August; whereas A_{AMB} increased 10% between June and July, and decreased 25% between July and August (Table 3). Stomatal conductance decreased significantly within both habitats from June to August under both saturated and ambient light intensities ($P = 0.016$, and $P = 0.024$, respectively) (Table 3).

Species had a significant main effect on A_{AMB} ($P = 0.030$) and a marginal effect on A_{MAX} ($P = 0.094$). White oak species generally exhibited the highest A_{MAX} and A_{AMB} followed by hickory and red oak species (Table 3). A_{MAX} and A_{AMB} were 23% and 22 % higher among white oak species as compared to red oak species, and 19% and 12% higher than hickory species, respectively. There was no statistically significant effect of species on stomatal conductance (Table 3), but stomatal conductance was highest in white oak species, followed by hickory species, and lowest in red oak species.

Light Curves. Light curves were obtained to estimate light compensation points (x-intercept), quantum yield (slope), and light saturation points (determined by the maximum net photosynthetic rate, i.e., the asymptote) of the focal species in each of the three habitat types.

Habitat had a significant main effect on asymptote ($P < 0.05$), light compensation point ($P < 0.05$), and quantum yield ($P < 0.05$) (Table 4). Light saturation points were higher in burned forest sites (mean = 300 µmol m^{-2} s^{-1}) than unburned forest sites (mean = 500 µmol m^{-2} s^{-1}) (Figure 4). Light compensation points followed the same trend, indicating that rates of dark respiration increase with increasing light intensity. Quantum yields were lower in burned forest sites than in unburned forest sites (Figure 4), indicating that plants experiencing lower light intensities photosynthesize more efficiently at lower light levels.

Species had a significant main effect on asymptote ($P < 0.05$) and quantum yield ($P < 0.05$) (Table 5). Light saturation points and light compensation points were highest for white oak, followed by red oak, and hickory species (Figure 3). Quantum yield was highest in red oak, followed by hickory and white oak species (Figure 3). However, as

light intensity increased, white oak had the greatest photosynthetic capacity, and red oak had the lowest photosynthetic capacity. The lack of a species effect on light compensation points suggests that dark respiration rates do not vary greatly between species groups.

Comparison of Burned Forest and Savanna. In 2003, LAI levels of the savanna sites were 56% lower than the burned forest sites indicating that, although burning had increased light availability in the burned forest, canopy light penetration had not yet reached that of savanna (Table 6). However, seasonal trends in light availability of the burned forest sites appeared more similar to the savanna sites than the unburned forest sites. Maximum leaf expansion occurred earlier for both burned forest sites and savanna sites (Table 6).

Savanna sites contain more seedling and sapling individuals per unit area than burned forest sites (Table 7). Averaged over the three-year period, total density within savanna sites was 18% higher than burned forest sites and 42% higher than unburned forest sites in 2003. Species' proportional contributions towards total density were also different between the savanna and burned forest sites. Averaged over the three-year period, white oak accounted for 41% of the total density in savanna sites, while cedar accounted for 29%, red oak accounted for 17%, and hickory accounted for 13%. In 2003, red oak accounted for 49% of the total density in burned forest sites, while hickory accounted for 32%, white oak accounted for 17%, and cedar accounted for 2%. Also, absolute densities of red oak and hickory species were lower in savanna sites than in burned forest sites, suggesting that these species may be of lesser importance than white oak species in savanna habitats (Table 7).

Direct comparisons of mortality for burned forest sites and savanna sites are difficult because the two savanna sites are burned with different frequencies and often on separate years. However, fire appears to have similar effects on mortality in both the burned forest sites and the savanna sites (Tables 2 & 6). Averaged over the three-year period, mortality was 10% lower in savanna sites than in burned forest sites during 2003.

Averaged over the three-year period, recruitment was 82% higher in savanna sites than burned forest sites in 2003. Most of this difference was due to cedar recruitment; otherwise, hickory, red oak, and white oak recruitment were relatively similar between the savanna and burned forest sites (Tables 2 & 7).

Averaged over all sampling periods, savanna sites showed higher A_{AMB} and lower A_{MAX} than burned forest sites (Table 8). A_{MAX} was 15% higher in burned forest sites than savanna sites; however, A_{AMB} was 11% higher in savanna sites, suggesting that plants in the savanna generally receive more light. A_{MAX} and A_{AMB} were higher in savanna sites than burned forest sites through both June and July, but decreased more than burned forest sites in August. Light saturation points were higher in savanna sites (mean = 500 μmol m^{-2} s^{-1}) than in burned forest sites (mean = 1200 μmol m^{-2} s^{-1}) (Figure 3). Quantum yields were lower in savanna sites than burned forest sites (Figure 3). Species trends were similar to those of the burned forest (Tables 2 & 8).

Discussion

Seedling and Sapling Community Structure and Composition. Individual cedars persisted in the unburned forest, but were only transient components of the burned forest. When burning occurred, most cedars were removed from the burned forest; however, burning also appeared to facilitate cedar establishment the year of and the year

following prescribed fire. The lack of cedar saplings in burned forests sites suggests that the initial high intensity burn was sufficient for their eradication. However, numerous large cedars (>2.0 m in height) remain present in the burned forest areas, indicating that not even the initial high intensity burn was adequate for their removal. It has been suggested that even fire-sensitive species may persist through fire when mature because their bark has reached sufficient thickness to protect the cambium from heat (Peterson and Reich, 2001). In order to remove these individuals, mechanical thinning should be implemented. Once mature trees are removed, low intensity biennial burns appear sufficient for preventing excessive cedar growth, but seedlings readily germinate in the mineral seedbeds. Therefore, it is important to determine the maximum size and average age of cedar that low intensity burning will effectively remove as periods of fire suppression (possibly up to ten years) will be required to allow the oak sprouts to emerge into canopy recruits.

There were no statistically significant differences of density or dominance between burned forest sites and unburned forest sites, but density was 30% greater and basal area was 46% greater among seedlings and saplings in burned forest sites compared to unburned forest sites over the three-year period. The increase in density was most likely attributed to fire enhancing the suitability of seedbeds which allows for increased germination rates (Kruger and Reich, 1997; Leach and Ross, 1995; Lorimer, 1985). The increase in basal area in burned forest sites was most likely attributed to fire increasing understory light availability, which allowed for increased rates of photosynthesis and increased carbon gain relative to unburned forests sites. The increase of white oak species

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density and basal area might be expected as canopy light penetration increases given that *Quercus stellata* is the dominant canopy species in the savanna sites at DCA.

Red oak, white oak, and hickory species all experienced top-killing by fire, but resprouted very quickly (the growing season after a fire) with more stems of smaller diameter. The resprouting capabilities of oak in response to fire have been well documented (Apfelbaum and Haney, 1987; Stearns, 1991; Abrams, 1992) and are likely the primary reason why little mortality was observed among these species. Hickory species appear to persist through burning via the same mechanism of resprouting. Previous studies have shown prescribed burning to result in minimal mortality for oak seedlings and saplings with similar dynamics of top-killing and reprouting (Reich et al., 1990; Crow et al., 1994)

The sprouting of oak is important because these sprouts will become the future canopy structure of savannas and a primary goal of restoration and management is to keep the sprouting oaks present but also controlled in terms of height (McCarty 1998). The results of this study suggest that current burning frequency and intensity are allowing for the persistence and successful control of oak sprouts. However, when fire is suppressed, oak sprouts develop rapidly (Anderson, 1998; Bowles and McBride, 1998; Crow, 1988) and may grow 6.0m within nine years (Cain, 1995). This rapid growth is most likely attributed to the large root systems of oak sprouts (Lorimer, 1985), which in frequently burned areas may be centuries old (Anderson, 1998). Therefore, if burning were excluded from this system for a decade, these sprouts would have ample time to grow past the point of being top-killed and would likely enter the canopy. The result would be the perpetuation of an oak forest, not an oak savanna. Under the current

biennial fire regime, these plants will probably continue to be top-killed and undergo fluctuations of stem numbers and diameters.

Light is often a primary limiting resource under a forest canopy and its availability can greatly influence tree establishment and growth (Canham, 1988). Oaks are generally not well adapted to shade conditions caused by a closed canopy and seedlings do not exhibit long-term growth or survival under these conditions (Crow, 1988; Lorimer, 1989; Burns and Honkala, 1990). Many studies have noted that oak regeneration is poor under closed canopy forest conditions (Lorimer, 1985; McCune and Cottam, 1985). The regeneration of white oak species appears to be negatively affected by the closed canopy conditions at DCA; however, red oak species appear to do well as they contribute the largest proportion of density and basal area in unburned forest sites.

Mean basal area was higher in burned forest sites than unburned forest sites and can be attributed to relatively equitable mortality (with the exception of cedar) between the sites, and higher densities within burned forest sites. Cedar seedlings contributed a negligible amount of basal area towards dominance measures; therefore, total basal area was primarily a function of oak and hickory basal areas. Basal area increased considerably in the burned forest from 2001 to 2002 when burning was absent and was relatively static between 2002 and 2003. The increase in basal area between the first two years was driven by recruitment and subsequent density increases. However, the relative stability of basal area between the second and third year occurred as density decreased, indicating that basal area was increasing. These data suggest that burning has resulted in increased carbon gain and growth.

Canopy Light Penetration. Canopy light penetration was 43% greater in burned forest sites than unburned forest sites at DCA following three biennial prescribed burns. This is an important result as the long-term goal of burning is to restore degraded savanna communities back to their pre-settlement characteristics, of which canopy light penetration is a key driving force and a defining characteristic (Curtis, 1959; Nelson, 1985; Nuzzo, 1986; Leach and Ross, 1995; Taft, 1997). These data should be interpreted cautiously because very little baseline data were collected prior to the initial burn, although initial canopy coverage was assumed to be analogous between the unburned forest and burned forest sites because the sample sites were adjacent to one another. However, canopy light penetration was 17% greater in burned forest sites than unburned forest sites in May of 2000, and 36% greater in June of 2001 (data not presented). Other studies have demonstrated that prescribed fire is an effective tool in opening closed forest canopies in the Midwest (Paulsell, 1957; Scowcroft, 1966; Anderson and Brown, 1986; McCarty, 1998;). However, it has also been noted that prescribed burning alone is often an insufficient force to alter the canopy characteristics of a forest over a short period of time in sites that have been long protected from fire and have accumulated large mature trees (White, 1983; Peterson and Reich, 2001). Under these circumstances, mechanical thinning has been used to reduce canopy density (Bowles and McBride, 1998; McCarty, 1998; Peterson and Reich, 2001), but the economic cost is much higher than that of prescribed fire.

It is possible that burning altered leaf production in such a way as to increase canopy light penetration. For example, burned forest sites reached maximum leaf expansion between May and June whereas the unburned forest continues leaf expansion

until sometime between June and July. The effects of fire on overstory leaf phenology have not been studied, but it is possible that altered phenology is an important component of understanding fire effects on light penetration. For example, fire may alter leaf phenology by temporarily increasing plant-water status (Borchert, 1994; Eamus, 1999) which may result in earlier bud-break and leaf-expansion in seedlings and saplings in burned areas relative to unburned areas (Saha, 1991).

Plant Gas Exchange.

<u>Response to Maximum and Ambient Light Levels.</u> There was an apparent positive correspondence between increased canopy light penetration and increased maximum (A_{MAX}) and ambient (A_{AMB}) net photosynthetic rates. These results suggest that red oak, white oak, and hickory seedlings and saplings are capable of responding to increased light availability (as indicated by higher A_{MAX} values in burned forest and savanna) and potentially experience greater carbon gain throughout the season (as indicated by higher A_{AMB} values in burned forest and savanna). However, it would be naive to assume that these physiological results are due exclusively to increased light availability as both light and nitrogen are common limiting resources for plant photosynthesis and growth (Sipe and Bazzaz, 1995; Reich et al., 1997; Walters and Reich, 1997; Fahey et al. 1998) and burning has been shown to increase nitrogen availability in forest ecosystems (Raison, 1979; Boerner, 1988; Reich, 1990). However, estimates of foliar nitrogen concentrations at these sites in DCA suggest that this is not the case (P. Brown, unpublished data). Burning appears to have stimulated foliar nitrogen in May immediately after the burn in the burned forests, but not in the burned savanna. Between June and September, foliar nitrogen concentrations were highest in the unburned forest, followed by the burned

forest and savanna, and decreased throughout the season. Reich (1990) found similar trends of peak availability immediately after burning and continual decreases throughout the season. Thus, foliar nitrogen concentration and light availability are not apparently correlated, whereas the relationship between increasing net photosynthetic response and light availability are positively related. This suggests that light availability is the major limiting resource within the closed canopy forest at DCA. This agrees with the findings of Finzi and Canham (2000).

Species-specific response to maximum and ambient light availability was greatest for white oak, followed by hickory and red oak. This suggests that white oak will gain more carbon than the other species as light availability increases. However, it has been suggested that leaf-level gas exchange may not be a good predictor of whole-plant carbon gain (Barton 1996) which can be correlated to basal area. I suggest that leaf-level gas exchange is a valid predictor of whole-plant carbon gain at DCA as white oak basal areas increase more than would be expected based on densities in burned forest and savanna sites. This suggests that leaf-level gas exchange may be a useful tool in predicting future community composition and structure in restoration attempts.

Response to Increasing Light Intensity. Light response curves indicate that all species in the unburned forest have acclimated to the low-light environment and do not respond to increased light availability. White oaks are the only species that respond to increased light levels in the burned forest, whereas all species have acclimated to the high-light environment of the savannas. This suggests that white oak is more capable of utilizing recent increases in light availability than the other species. Red oak species should perform better than the other species in the closed canopy conditions because of their

lower dark respiration rates and higher light-use efficiency. The prediction that red oak species are more shade-tolerant than white oak species is supported by density and basal area measurements which demonstrate that red oak species are more abundant and represent the majority of basal area in the unburned forest. At the other extreme, light response curves indicate that white oak species should perform better than the other species in environments with greater light availability because of their higher light-saturation points and higher A_{MAX}. This is supported by increased density and basal area of white oak relative to other species in burned forest and savanna sites.

Assessment of Restoration Progress. After only three biennial prescribed burns, characteristics of the burned forest sites at DCA appear to be transitioning between the unburned forest sites and the savanna sites. Most notably, and arguably most importantly, canopy light penetration has increased in the burned forest sites. This has allowed for greater light availability to the seedlings and saplings and consequently, greater density and basal area in the understory of burned forest sites. Typically, the initial stage of savanna restoration is dominated by oak and hickory sprouts (McCarty, 1998), which is the case at DCA. The second and third stages of savanna restoration involve dramatic increases of herbaceous species and cover (McCarty, 1998). The burned forest sites at DCA have not yet experienced a drastic increase in herbaceous species, but appear to be at an intermediate stage between the abundance levels in the burned forest and savanna sites (*Pers. Observation*). The biennial fire frequency appears to be effective at maintaining the oak and hickory sprouts as well as removing, although not eliminating, cedars from the areas. Increases in both the density and basal area of oak sprouts should be expected through the future burn cycles.

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Although no quantitative data were collected, qualitative observations suggest that burning has removed much of the shrub layer in burned forests and has increased the abundance of herbaceous species in the understory. Other studies have demonstrated similar trends in shrub reduction, and herbaceous species abundance with low intensity burns at intervals of one to three years (White, 1983; White, 1986; Apfelbaum and Haney, 1991). These observations lend support to the argument that burning is shifting characteristics of the closed forest towards those of a savanna.

Summary.

Cedar is the only species that experienced considerable mortality when burning occurred. Red oak, white oak, and hickory experienced minimal mortality and although individuals of these species were top-killed from burning, the majority resprouted vigorously. Recruitment increased for all species following burning, and white oak recruitment in the burned forest sites was nearly three times that of unburned forest sites. Prescribed burning has resulted in an increase in canopy light penetration at DCA. The increased canopy light penetration resulted in greater basal areas, especially for white oak and hickory. All species can respond to the high-light environment of the savanna sites, indicating that all of these species are capable of utilizing increased light if they become established in a high-light environment. However, white oak is the only species that responds to the increased light availability in burned forest sites (i.e., when grown in low to moderate light levels and below light saturation). This suggests that white oak is more capable of utilizing increased light in the short term and should continue to increase in basal area in the burned forest sites.

Table 1. Comparison of demographic characteristics of unburned and burned forest sites (means ± standard error). Density was calculated as individuals m⁻². Dominance was calculated as the sum of basal areas (cm²) for each species per area sampled (m²). Percent mortality was calculated as the absence of an individual that was previously present. Recruitment was calculated as the presence of a new individual m⁻².

Unburned Forest

	Year	Cedar	Hickory	Red Oak	White Oak	Total
Density/m²	2001	0.013±0.0091	0.046±0.014	0.16±0.037	0.012±0.0047	0.231
	2002	0.016±0.0092	0.064±0.017	0.21±0.037	0.018±0.0058	0.308
	2003	0.018±0.0071	0.061±0.016	0.20±0.038	0.022±0.0055	0.301
Dominance cm²/m²	2001	0.040±0.031	0.107±0.058	0.643±0.273	0.012±0.0047	0.802
	2002	0.054±0.046	0.093±0.042	0.701±0.332	0.018±0.0073	0.866
	2003	0.067±0.056	0.103±0.045	0.811±0.413	0.030±0.0090	1.011
Mortality (%)	2002	0.00±0.00	0.00±0.00	5.40±3.60	1.00±1.00	1.60±1.10
	2003	10.00±10.00	3.15±3.15	7.10±4.00	8.35±8.35	7.15±2.81
Recruitment/m²	2002	0.012±0.0012	0.061±0.0061	0.16±0.0084	0.024±0.0024	0.063±0.021
	2003	0.023±0.010	0.012±0.0012	0.051±0.029	0.013±0.013	0.025±0.0087

Burned Forest

	Year	Cedar	Hickory	Red Oak	White Oak	Total
Density/m²	2001	0.012±0.010	0.100±0.032	0.145±0.086	0.046±0.0080	0.303
	2002	0.062±0.030	0.134±0.052	0.219±0.096	0.060±0.010	0.476
	2003	0.0090±0.004	0.136±0.045	0.207±0.088	0.070±0.0080	0.422
Dominance cm²/m²	2001	0.00013±0.00011	0.182±0.072	0.738±0.70	0.344±0.21	1.264
	2002	0.0012±0.00078	0.193±0.071	1.13±1.08	0.491±0.23	1.815
	2003	0.00071±0.00040	0.222±0.12	1.18±0.11	0.461±0.25	1.864
Mortality (%)	2002	0.00±0.00	1.35±1.35	1.25±1.25	5.25±5.25	1.96±1.29
	2003	88.1±0.10	2.70±2.70	8.90±3.20	7.65±2.85	26.8±13.4
Recruitment/m²	2002	0.198±0.060	0.110±0.078	0.245±0.047	0.040±0.001	0.148±0.036
	2003	0.033±0.033	0.019±0.011	0.034±0.015	0.050±0.009	0.034±0.008

Table 2. Relative volume changes and relative stem number changes (means ± standard error). Stem volume was calculated as the volume of a cylinder ($2\pi rh$) using stem diameter and stem height as cylinder diameter and stem height. Plant volume was then estimated as the sum of stem volumes. Volumes were then log transformed and relative changes were calculated for individual plants between 2001-2002, and 2002-2003. Relative changes in stem number were calculated as the difference in stems present on an individual between years.

	Year	Cedar	Hickory	Red Oak	White Oak	Total
				Unburned Forest		
Relative Volume Changes	2002	-0.039±0.17	-0.25±0.11	0.0037±0.066	-0.023±0.14	-0.055±0.052
	2003	0.44±0.21	0.48±0.094	0.41±0.074	0.46±0.088	0.43±0.05
Relative Stem Number Changes	2002	0±0	0±0	-0.01±0.073	0.33±0.33	0.0092±0.053
	2003	0±0	-0.032±0.032	-0.043±0.048	0±0	-0.036±0.033
				Burned Forest		
Relative Volume Changes	2002	NA	0.50±0.10	0.57±0.068	0.14±0.19	0.47±0.058
	2003	0.59±0.54	-0.38±0.11	-0.35±0.073	-0.28±0.16	-0.33±0.058
Relative Stem Number Changes	2002	NA	-0.082±0.075	0.012±0.071	-0.45±0.16	-0.10±0.052
	2003	0±0	0.099±0.11	0.21±0.083	0.24±0.27	0.18±0.067

Table 3. Comparison of maximum (A_{MAX}) and ambient (A_{AMB}) net photosynthetic rates and stomatal conductance (means ± standard error) for unburned and burned forest sites. All measurements were collected in 2003.

	Month	Hickory	Red Oak	White Oak	All Species
			Unburned Forest		
A_{MAX} (μmol CO_2 m^{-2} s^{-1})	June	5.46±0.24	5.05±0.21	5.65±0.19	5.39±0.13
	July	3.54±0.23	3.02±0.21	3.92±0.24	3.49±0.14
	August	2.64±0.15	2.45±0.17	3.04±0.21	2.71±0.11
Conductance (μmol m^{-2} s^{-1})	June	0.13±0.0079	0.092±0.0073	0.11±0.0066	0.11±0.0045
	July	0.049±0.0042	0.038±0.0031	0.056±0.0056	0.048±0.0027
	August	0.033±0.0026	0.031±0.0019	0.033±0.0028	0.033±0.0014
A_{AMB} (μmol CO_2 m^{-2} s^{-1})	June	2.29±0.38	1.48±0.26	1.65±0.27	1.80±0.18
	July	2.12±0.22	1.74±0.24	1.90±0.25	1.92±0.14
	August	1.35±0.20	1.19±0.19	1.40±0.31	1.32±0.14
Conductance (μmol m^{-2} s^{-1})	June	0.12±0.0071	0.085±0.0065	0.096±0.0052	0.10±0.0039
	July	0.045±0.0040	0.035±0.0030	0.056±0.0052	0.046±0.0025
	August	0.029±0.0023	0.029±0.0020	0.034±0.0025	0.064±0.0065
			Burned Forest		
A_{MAX} (μmol CO_2 m^{-2} s^{-1})	June	6.78±0.30	7.07±0.22	8.14±0.28	7.32±0.17
	July	4.59±0.25	4.40±0.27	6.17±0.41	5.05±0.20
	August	3.50±0.30	3.11±0.29	5.64±0.51	4.10±0.25
Conductance (μmol m^{-2} s^{-1})	June	0.14±0.0098	0.15±0.0097	0.17±0.011	0.15±0.0060
	July	0.069±0.0092	0.059±0.0091	0.11±0.016	0.079±0.0072
	August	0.052±0.0055	0.041±0.0053	0.11±0.016	0.067±0.0047
A_{AMB} (μmol CO_2 m^{-2} s^{-1})	June	3.90±0.39	3.82±0.42	4.44±0.43	4.05±0.24
	July	2.98±0.20	2.97±0.30	4.13±0.38	3.36±0.18
	August	2.29±0.27	2.10±0.29	3.53±0.47	2.65±0.21
Conductance (μmol m^{-2} s^{-1})	June	0.13±0.009	0.14±0.0090	0.15±0.0096	0.14±0.0054
	July	0.063±0.0084	0.054±0.0083	0.10±0.014	0.072±0.0063
	August	0.049±0.0054	0.035±0.0047	0.11±0.015	0.064±0.0046

Table 4. Habitat effects on photosaturated photosynthesis (A_{MAX}), apparent quantum yield (A_{qe}), and light compensation point (LCP) averaged across all species groups. Values presented are means ± standard error. Similar letters denote non-significant difference between groups at $P=0.05$.

	(A_{MAX})	(A_{qe})	(LCP)
Unburned Forest	3.87 ± 0.84^a	0.15 ± 0.025^a	1.59 ± 4.23^a
Burned Forest	5.15 ± 0.92^a	0.11 ± 0.024^b	5.07 ± 4.74^a
Savanna	7.08 ± 0.91^b	0.06 ± 0.021^c	14.31 ± 4.61^b

Table 5. Species effects on light-saturated photosynthesis (A_{MAX}), apparent quantum yield (A_{qe}), and light compensation point (LCP). Values presented are means ± standard error. Similar letters denote non-significant difference between groups at P=0.05.

	(A_{MAX})	(A_{qe})	(LCP)
Hickory	5.10±0.84[a]	0.12±0.022[a]	7.01±4.21[a]
White Oak	6.52±0.93[a]	0.084±0.024[b]	8.78±4.76[a]
Red Oak	4.48±0.90[b]	0.12±0.025[c]	5.18±4.61[a]

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Table 6. Mean ± standard error leaf area index (LAI) and photosynthetically active radiation (PAR) values for burned forest and savanna sites. All measurements were collected in the middle of each month in 2003.

		April	May	June	July	August	September
Burned Forest	LAI	0.48±0.062	1.91±0.257	2.01±0.496	1.83±0.245	1.69±0.256	2.17±0.256
	PAR	928.0±67.5	304.0±56.8	443.0±124.0	447.3±73.1	310.0±56.1	330.0±59.2
Savanna	LAI	0.17±0.056	1.03±0.166	0.81±0.156	0.90±0.242	0.80±0.199	0.74±0.189
	PAR	1399.3±83.3	637.7±63.0	924.0±116.0	847.0±102.0	708.0±97.1	876.0±112.0

Table 7. Demographic characteristics of savanna sites (means ± standard error). Density was calculated as individuals m^{-2}. Basal area was calculated as the sum of basal areas (cm^2) for each species per area sampled (m^2). Percent mortality was calculated as the absence of an individual who was previously present. Recruitment was calculated as the presence of a new individual m^{-2}. Values were averaged from data collected in 2001, 2002, and 2003.

			Savanna		
	Cedar	Hickory	Red Oak	White Oak	Total
Density/m^2	0.15±0.041	0.067±0.0086	0.090±0.010	0.21±0.033	0.517
Dominance cm^2/m^2	0.0044±0.0017	0.36±0.13	0.21±0.046	1.65±0.44	2.22
Mortlaity (%)	53.4±21.9	6.92±3.53	2.68±1.96	2.90±1.96	16.48±7.45
Recruitment/m^2	0.50±0.20	0.042±0.010	0.073±0.029	0.16±0.083	0.19±0.068

Table 8. Maximum (A_{MAX}) and ambient (A_{AMB}) net photosynthetic rates and stomatal conductance (means ± standard error) for savanna sites. All measurements were collected in 2003.

		Savanna		
	Month	Hickory	Red Oak	White Oak	All Species
A_{MAX} (μmol CO_2 m^{-2} s^{-1})	June	7.78±0.44	8.54±0.63	9.47±0.37	8.60±0.29
	July	5.00±0.32	4.52±0.28	7.11±0.38	5.55±0.22
	August	1.46±0.23	1.25±0.19	2.66±0.34	1.79±0.17
Conductance (μmol m^{-2} s^{-1})	June	0.22±0.019	0.16±0.019	0.22±0.015	0.20±0.01
	July	0.055±0.0044	0.048±0.0036	0.097±0.011	0.067±0.0047
	August	0.017±0.0017	0.016±0.0018	0.027±0.0033	0.20±0.0015
A_{AMB} (μmol CO_2 m^{-2} s^{-1})	June	5.36±0.79	5.80±0.74	6.77±0.69	5.98±0.43
	July	4.36±0.34	3.94±0.27	6.20±0.41	4.84±0.222
	August	1.21±0.23	1.02±0.18	2.48±0.35	1.58±0.17
Conductance (μmol m^{-2} s^{-1})	June	0.20±0.017	0.15±0.020	0.20±0.013	0.18±0.010
	July	0.052±0.0043	0.046±0.0033	0.093±0.011	0.064±0.0046
	August	0.016±0.0015	0.014±0.0015	0.026±0.0032	0.019±0.0014
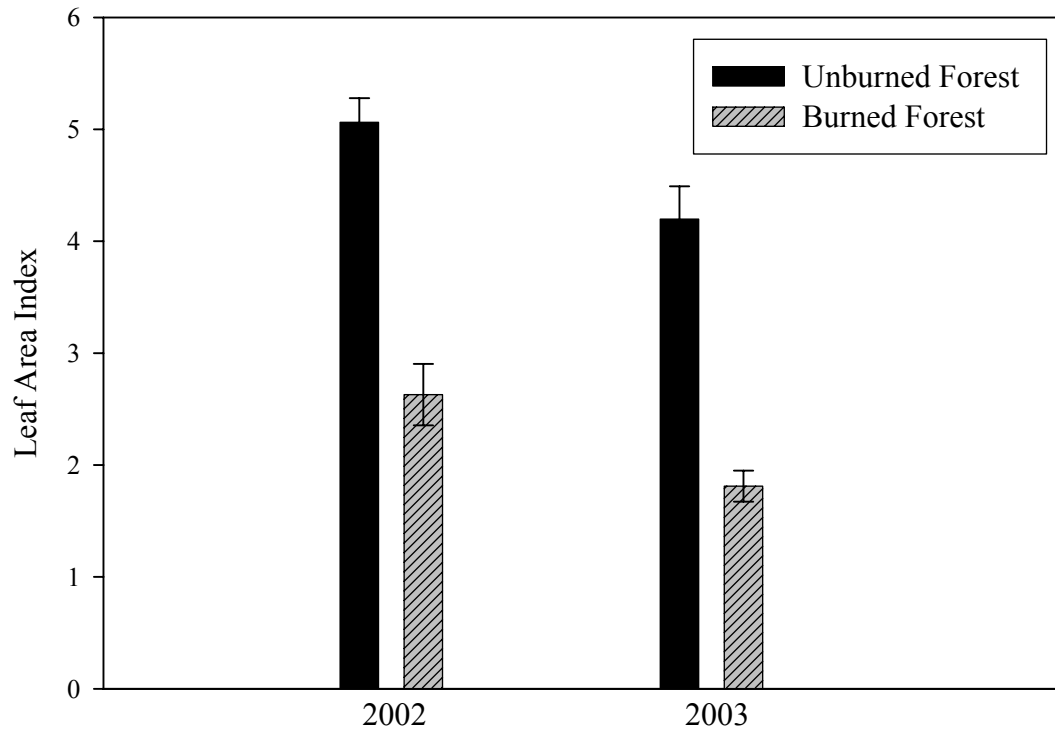
Figure 1. Mean (± standard error) leaf area index values for unburned and burned forest habitats averaged from mid-month measurements of May, July, and August.
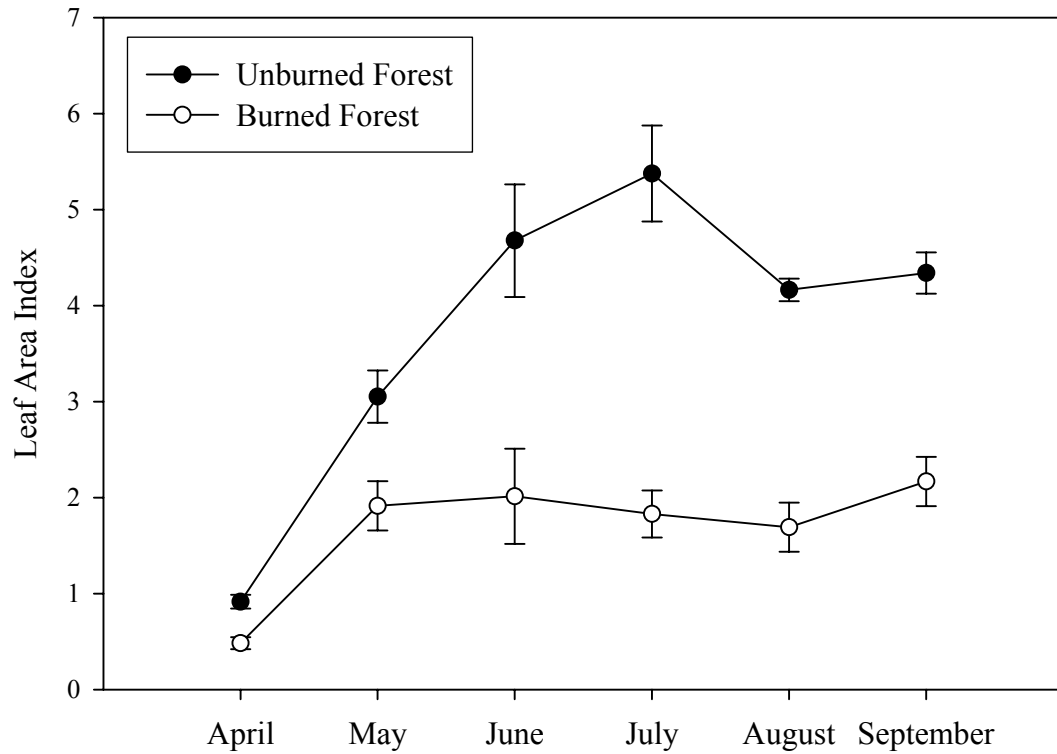
Figure 2. Seasonal trends of mean ± standard error leaf area index measured in 2003. Measurements were collected mid-month.
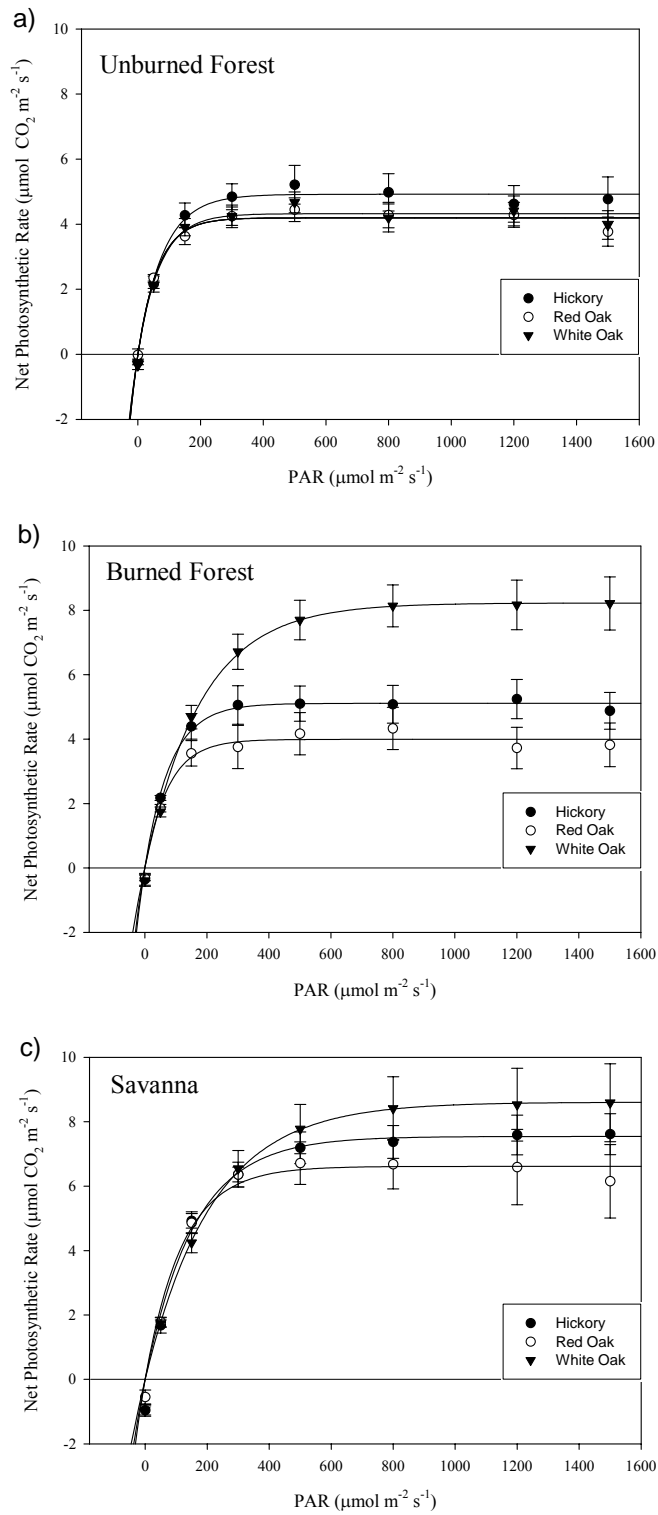
Figure 3. Plot of mean ± standard error net photosynthetic
rate against increasing light availability.

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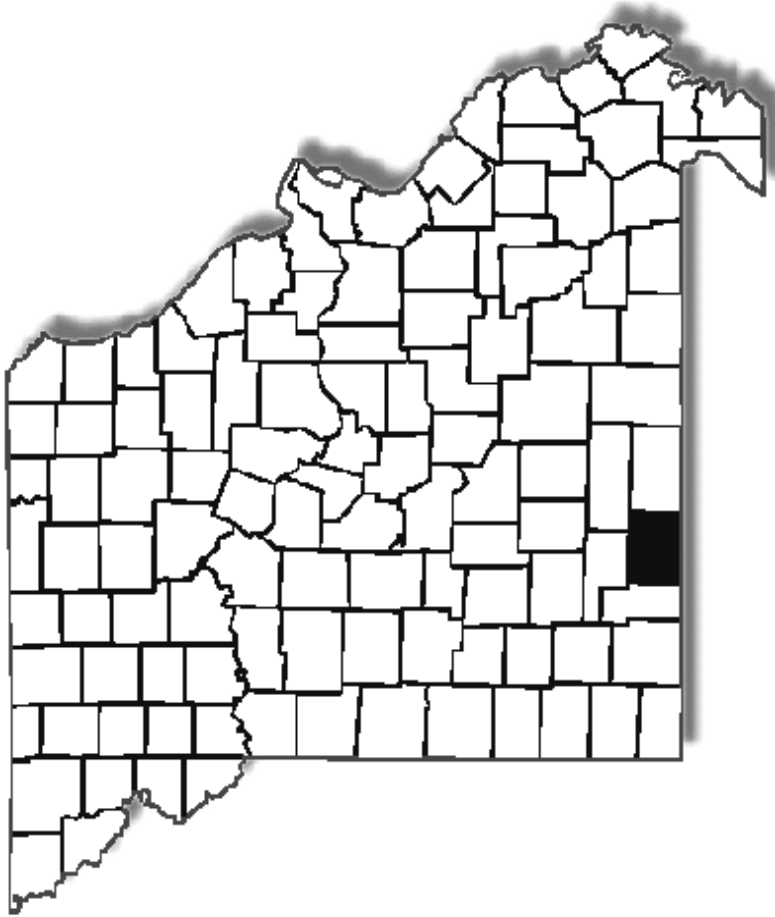
Appendix. A. Map of Missouri highlighting Taney County.
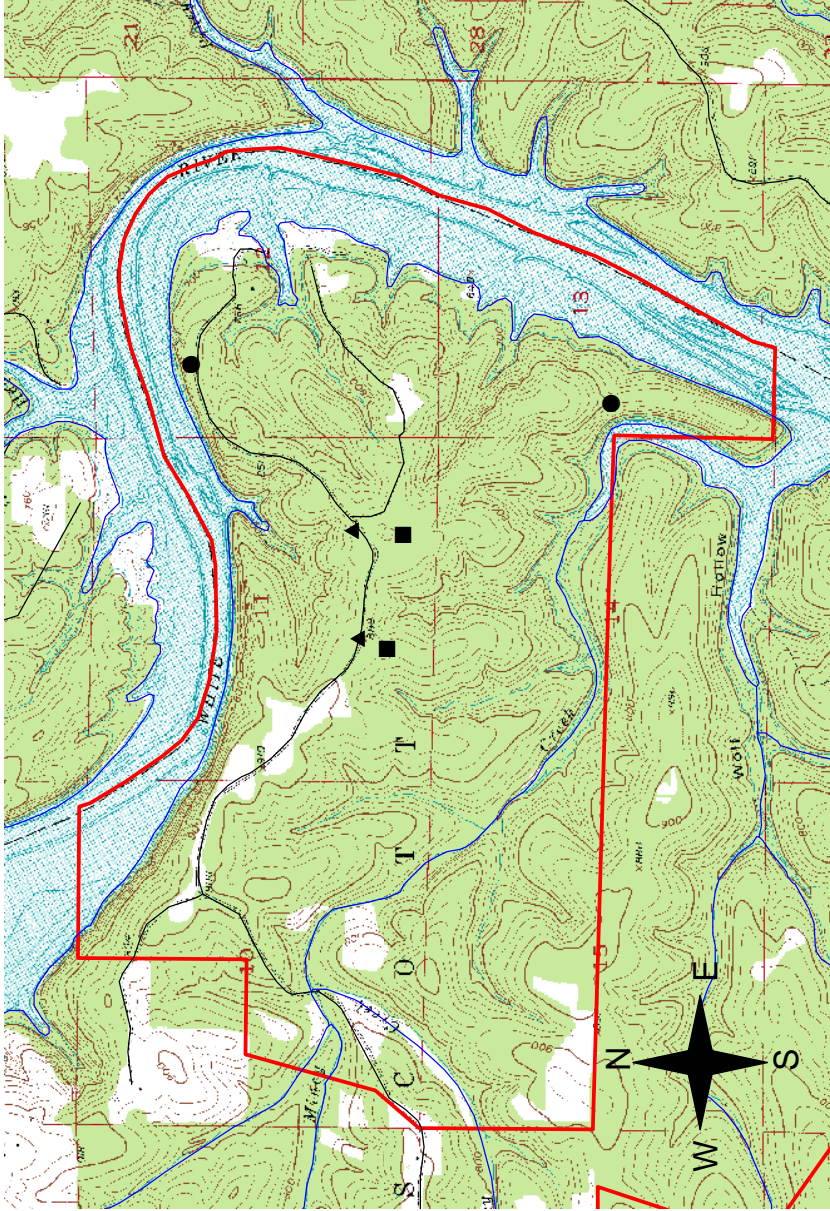
Appendix B. Map of Drury Conservation Area showing sampling sites. Triangles represent unburned forest sites, squares represent burned forest sites, and circles represent savanna sites.

Appendix C. Linear equations for calculating stem height as a function of stem diameter. Separate equations were necessary for each species in both habitats as the relationship between stem diameter and stem height varied between habitat types as determined by ANCOVA. Equations were obtained using linear regression. R-squares ranged between 57.3% to 81.0%.

	Regression Equation	R-Squared
Hickory – Unburned Forest	Height = 12.3 + 3.49Diameter	57.3%
Hickory – Burned Forest	Height = 6.8 +5.17Diameter	68.6%
Red Oak – Unburned Forest	Height = 5.41 + 5.91Diameter	81.0%
Red Oak – Burned Forest	Height = 2.60 +7.29Diameter	77.2%
White Oak – Unburned Forest	Height = 5.77 + 6.75Diameter	65.7%
White Oak – Burned Forest	Height = 2.56 + 8.63Diameter	72.3%

Appendix D. ANOVA table for density as a function of species, habitat and year. A nested block design with repeated measures was used to assess the effect of prescribed fire on individual density. Year (2001, 2002, and 2003), habitat (unburned forest and burned forest), and species were treated as fixed factors. Block (n=2) and transect (n=18) were treated as random factors, with transect nested under both block and habitat. F and P values are only presented when P<0.10. F and P values are not presented for main effects and interaction terms containing blocking variables.

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Year	2	0.024125	0.024125	0.012063	16.36	0.058
Block	1	0.038746	0.038746	0.038746		
Habitat	1	0.032654	0.032654	0.032654	88.62	0.067
Species	3	0.621895	0.621895	0.207298		
Year*Block	2	0.001474	0.001474	0.000737		
Year*Habitat	2	0.003946	0.003946	0.001973		
Year*Species	6	0.011737	0.011737	0.001956	9.72	0.007
Block*Habitat	1	0.000368	0.000368	0.000368		
Block*Species	3	0.301638	0.301638	0.100546		
Habitat*Species	3	0.024019	0.024019	0.008006		
Year*Block*Habitat	2	0.001556	0.001556	0.000778		
Year*Block*Species	6	0.001208	0.001208	0.000201		
Year*Habitat*Species	6	0.004009	0.004009	0.000668		
Block*Habitat*Species	3	0.031538	0.031538	0.010513		
Year*Block*Habitat*Species	6	0.00273	0.00273	0.000455		
Transect(Block Habitat)	8	0.132022	0.132022	0.016503		
Year*Transect(Block Habitat)	16	0.006911	0.006911	0.000432		
Species*Transect(Block Habitat)	24	0.555072	0.555072	0.023128		
Year*Species*Transect(Block Habitat)	48	0.025891	0.025891	0.000539		
Error	0	*	*	*		
Total	143	1.821542				

Appendix E. ANOVA table for total basal area, a measure of dominance as a function of species, habitat and year. A nested block design with repeated measures was used to assess the effect of prescribed fire on basal area, a measure of dominance. Year (2001, 2002, and 2003), habitat (unburned forest and burned forest), and species were treated as fixed factors. Block (n=2) and transect (n=18) were treated as random factors, with transect nested under both block and habitat. F and P values are only presented when $P<0.10$. F and P values are not presented for main effects and interaction terms containing blocking variables.

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Year	2	0.002672	0.002672	0.001336		
Block	1	0.050904	0.050904	0.050904		
Habitat	1	0.012862	0.012862	0.012862		
Species	3	0.152552	0.152552	0.050851		
Year*Block	2	0.002086	0.002086	0.001043		
Year*Habitat	2	0.001005	0.001005	0.000502		
Year* Species	6	0.00381	0.00381	0.000635		
Block*Habitat	1	0.000531	0.000531	0.000531		
Block* Species	3	0.19538	0.19538	0.065127		
Habitat* Species	3	0.011606	0.011606	0.003869		
Year*Block*Habitat	2	0.000615	0.000615	0.000308		
Year*Block* Species	6	0.004037	0.004037	0.000673		
Year*Habitat* Species	6	0.001278	0.001278	0.000213		
Block*Habitat* Species	3	0.012549	0.012549	0.004183		
Year*Block*Habitat* Species	6	0.001716	0.001716	0.000286		
Transect(Block Habitat)	8	0.231147	0.231147	0.028893		
Year*Transect(Block Habitat)	16	0.012133	0.012133	0.000758		
Species *Transect(Block Habitat)	24	0.51459	0.51459	0.021441		
Year* Species *Transect(Block Habitat)	48	0.022535	0.022535	0.000469		
Error	0	*	*	*		
Total	143	1.234009				

Appendix F. ANOVA table for mortality as a function of species, habitat and year. A nested block design with repeated measures was used to assess the effect of prescribed fire on plant mortality. Year (2001, 2002, and 2003), habitat (unburned forest and burned forest), and Species were treated as fixed factors. Block (n=2) and transect (n=18) were treated as random factors, with transect nested under both block and habitat. F and P values are only presented when $P<0.10$. F and P values are not presented for main effects and interaction terms containing blocking variables.

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Year	1	2.87443	1.85862	1.85862		
Block	1	0.46299	0.22399	0.22399		
Habitat	1	0.53529	0.89149	0.89149		
Species	3	8.20532	2.4423	0.8141	17.56	0.021
Year*Block	1	0.43755	0.11482	0.11482		
Year*Habitat	1	0.73954	1.2036	1.2036	65.52	0.078
Year*Species	3	9.29713	2.82127	0.94042	18.25	0.020
Block*Habitat	1	0.00078	0.03816	0.03816		
Block*Species	3	0.06256	0.13909	0.04636		
Habitat*Species	3	2.59623	2.37232	0.79077	9.89	0.046
Year*Block*Habitat	1	0.12213	0.01837	0.01837		
Year*Block*Species	3	0.09359	0.15456	0.05152		
Year*Habitat*Species	3	2.35828	2.17696	0.72565	104.54	0.002
Block*Habitat*Species	3	0.21696	0.2399	0.07997		
Year*Block*Habitat*Species	3	0.01116	0.02082	0.00694		
Transect(Block Habitat)	8	0.24833	0.24702	0.03088		
Year*Transect(Block Habitat)	8	0.30437	0.30437	0.03805		
Error	953	37.39739	37.39739	0.03924		
Total	1000	65.96404				

Appendix G. ANOVA table for recruitment as a function of species, habitat and year. A nested block design with repeated measures was used to assess the effect of prescribed fire on plant recruitment. Year (2001, 2002, and 2003), habitat (unburned forest and burned forest), and Species were treated as fixed factors. Block (n=2), transect (n=18), and quadrat (n=299) were treated as random factors, with transect nested under both block and habitat, and quadrat nested under block, habitat, and transect. F and P values are only presented when P<0.10. F and P values are not presented for main effects and interaction terms containing blocking variables.

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Year	1	7.0323	6.1103	6.1103		
Block	1	0.0001	0.0151	0.0151		
Habitat	1	2.3708	2.6803	2.6803		
Species	3	4.9331	4.6183	1.5394		
Year*Block	1	0.1932	0.178	0.178		
Year*Habitat	1	1.6528	1.77	1.77	48.73	0.091
Year*Species	3	3.828	3.2097	1.0699	12.23	0.034
Block*Habitat	1	0.1139	0.0787	0.0787		
Block*Species	3	1.1527	0.9879	0.3293		
Habitat*Species	3	0.8578	0.7655	0.2552		
Year*Block*Habitat	1	0.0662	0.0363	0.0363		
Year*Block*Species	3	0.4661	0.2625	0.0875		
Year*Habitat*Species	3	1.4151	1.574	0.5247		
Block*Habitat*Species	3	0.6351	1.0081	0.336		
Year*Block*Habitat*Species	3	1.2681	1.1833	0.3944		
Transect(Block Habitat)	8	2.085	2.0794	0.2599		
Year*Transect(Block Habitat)	8	0.7371	0.7382	0.0923		
Species*Transect(Block Habitat)	24	9.0289	9.2076	0.3836		
Year*Species*Transect(Block Habitat)	24	7.5337	7.7698	0.3237		
Quadrat(Block Habitat Transect)	287	38.7569	38.7569	0.135		
Species*Quadrat(Block Habitat Transect)	861	106.2688	106.2688	0.1234		
Error	1148	147.3703	147.3703	0.1284		
Total	2391	337.7659				

Appendix H. ANOVA table for relative volume change as a function of species, habitat and year. A nested block design with repeated measures was used to assess the effect of prescribed fire on plant relative volume change. Year (2001, 2002, and 2003), habitat (unburned forest and burned forest), and Species were treated as fixed factors. Block (n=2) and transect (n=18) were treated as random factors, with transect nested under both block and habitat. F and P values are only presented when P<0.10. F and P values are not presented for main effects and interaction terms containing blocking variables.

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Year	1	16.7182	0.528	0.528		
Block	1	6.393	0.4758	0.4758		
Habitat	1	6.8166	0.4225	0.4225		
Year*Block	1	4.4809	1.3804	1.3804		
Year*Habitat	1	63.1919	48.4722	48.4722	43.54	0.094
Block*Habitat	1	0.1961	0.5156	0.5156		
Year*Block*Habitat	1	1.7862	1.1193	1.1193		
Species	3	1.5391	2.8842	0.9614		
Transect(Block Habitat)	8	6.5155	5.4444	0.6806		
Year*Species	3	2.3805	3.3116	1.1039		
Block*Species	3	0.9648	1.1552	0.3851		
Habitat*Species	3	3.3188	3.9193	1.3064	2.35	0.071
Year*Block*Species	3	0.7514	1.0883	0.3628		
Year*Transect(Block Habitat)	8	8.7395	8.7395	1.0924		
Error	625	347.0044	347.0044	0.5552		
Total	663	470.7969				

Appendix I. ANOVA table for stem number change as a function of species, habitat and year. A nested block design with repeated measures was used to assess the effect of prescribed fire on stem number change. Year (2001, 2002, and 2003), habitat (unburned forest and burned forest), and Species were treated as fixed factors. Block (n=2) and transect (n=18) were treated as random factors, with transect nested under both block and habitat. F and P values are only presented when P<0.10. F and P values are not presented for main effects and interaction terms containing blocking variables.

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Year	1	3.9458	0.4698	0.4698		
Block	1	0.2695	0.0466	0.0466		
Habitat	1	0.8862	0.1658	0.1658		
Year*Block	1	1.872	1.5123	1.5123		
Year*Habitat	1	3.9348	4.6197	4.6197		
Block*Habitat	1	0.0036	0.01	0.01		
Year*Block*Habitat	1	1.6576	0.7728	0.7728		
Species	3	0.5877	0.1923	0.0641		
Transect(Block Habitat)	8	4.3934	4.3408	0.5426		
Year*Species	3	2.2924	1.734	0.578		
Block*Species	3	1.3764	0.4612	0.1537		
Habitat*Species	3	1.5262	1.9737	0.6579		
Year*Block*Species	3	2.0551	1.6477	0.5492		
Year*Transect(Block Habitat)	8	9.7542	9.7542	1.2193		
Error	625	374.7162	374.7162	0.5995		
Total	663	409.2711				

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Appendix J. ANOVA table for leaf area index as a function of habitat, month and year. A nested block design with repeated measures was used to assess the effect of prescribed fire on canopy light penetration. Year (2002 and 2003), month (May, July, and August), and habitat (unburned forest and burned forest) were treated as fixed factors. Block (n=2) and transect (n=18) were treated as random factors, with transect nested under both block and habitat. F and P values are only presented when $P<0.10$. F and P values are not presented for main effects and interaction terms containing blocking variables.

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Year	1	12.7597	12.7597	12.7597	627.48	0.025
Month	2	6.036	6.036	3.018	12.76	0.073
Block	1	0.0012	0.0012	0.0012		
Habitat	1	104.5217	104.5217	104.5217	297.44	0.037
Year*Month	2	2.4834	2.4834	1.2417		
Year*Block	1	0.0203	0.0203	0.0203		
Year*Habitat	1	0.0105	0.0105	0.0105		
Month*Block	2	0.4731	0.4731	0.2365		
Month*Habitat	2	9.707	9.707	4.8535		
Block*Habitat	1	0.3514	0.3514	0.3514		
Year*Month*Block	2	13.4462	13.4462	6.7231		
Year*Month*Habitat	2	1.4612	1.4612	0.7306	32.53	0.030
Year*Block*Habitat	1	0.8472	0.8472	0.8472		
Month*Block*Habitat	2	3.4767	3.4767	1.7383		
Year*Month*Block*Habitat	2	0.0449	0.0449	0.0225		
Transect(Block Habitat)	8	3.3408	3.3408	0.4176		
Year*Transect(Block Habitat)	8	7.0371	7.0371	0.8796		
Month*Transect(Block Habitat)	16	12.2947	12.2947	0.7684		
Year*Month*Transect(Block Habitat)	16	8.3744	8.3744	0.5234		
Error	0	*	*	*	*	

Appendix K. ANOVA table for maximum net photosynthetic rates (A_{MAX}) as a function of species, habitat and month. A nested block design with repeated measures was used to assess the effect of saturating PAR levels on species and habitat specific maximum net photosynthetic rates. Month (June, July, and August), habitat (unburned forest and burned forest), and species (red oak, white oak, and hickory) were treated as fixed factors. Block (n=2), transect (n=18), and individual plant (n=270), were treated as random factors, with transect nested under block and habitat, and individual plant nested under block, habitat, and transect. F and P values are only presented when P<0.10. F and P values are not presented for main effects and interaction terms containing blocking variables.

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Month	2	817.282	814.602	407.301	36.77	0.026
Block	1	6.713	7.466	7.466		
Habitat	1	353.643	345.962	345.962	587.32	0.026
Species	2	151.654	161.891	80.946	9.63	0.094
Month*Block	2	24.778	22.155	11.077		
Month*Habitat	2	6.805	7.551	3.776		
Month*Species	4	8.288	9.585	2.396		
Block*Habitat	1	0.844	0.589	0.589		
Block*Species	2	14.086	16.815	8.407		
Habitat*Species	2	47.523	50.046	25.023	25.88	0.037
Month*Block*Habitat	2	11.784	10.103	5.052		
Month*Block*Species	4	2.897	4.05	1.013		
Month*Habitat*Species	4	8.237	9.574	2.393		
Block*Habitat*Species	2	2.603	1.934	0.967		
Month*Block*Habitat*Species	4	3.973	4.35	1.087		
Transect(Block Habitat)	8	177.995	178.057	22.257		
Month*Transect(Block Habitat)	16	44.836	42.747	2.672		
Species*Transect(Block Habitat)	16	34.096	34.539	2.159		
Month*Species*Transect(Block Habitat)	32	48.191	49.114	1.535		
Plant(Block Habitat Species Transect)	142	427.188	427.188	3.008		
Error	282	318.789	318.789	1.13		
Total	531	2512.207				

Appendix L. ANOVA table for ambient net photosynthetic rates (A_{AMB}) as a function of species, habitat and month. A nested block design with repeated measures was used to assess the effect of ambient PAR levels on species and habitat specific net photosynthetic rates. Month (June, July, and August), habitat (unburned forest and burned forest), and species (red oak, white oak, and hickory) were treated as fixed factors. Block (n=2), transect (n=18), and individual plant (n=270), were treated as random factors, with transect nested under block and habitat, and individual plant nested under block, habitat, and transect. F and P values are only presented when P<0.10. F and P values are not presented for main effects and interaction terms containing blocking variables.

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Block	1	0.698	0.552	0.552		
Habitat	1	374.387	363.733	363.733	1188.55	0.018
Species	2	32.692	38.61	19.305	32.88	0.030
Month	2	82.522	82.908	41.454	12.39	0.075
Block*Habitat	1	0.492	0.306	0.306		
Block*Species	2	2.224	1.174	0.587		
Block*Month	2	7.529	6.69	3.345		
Habitat*Species	2	36.587	39.208	19.604		
Habitat*Month	2	22.367	22.017	11.009		
Species*Month	4	7.856	9.047	2.262		
Block*Habitat*Species	2	15.209	11.378	5.689		
Block*Habitat*Month	2	9.428	8.292	4.146		
Block*Species*Month	4	10.121	11.567	2.892		
Habitat*Species*Month	4	2.885	3.801	0.95		
Block*Habitat*Species*Month	4	3.431	3.763	0.941		
Transect(Block Habitat)	8	211.028	208.473	26.059		
Species*Transect(Block Habitat)	16	64.494	65.36	4.085		
Plant(Block Habitat Species Transect)	142	501.131	501.584	3.532		
Species*Month*Transect(Block Habitat)	32	65.67	65.03	2.032		
Month*Transect(Block Habitat)	16	53.586	53.586	3.349		
Error	282	550.232	550.232	1.951		

Appendix. M. ANOVA table for stomatal conductance under saturated light levels as a function of species, habitat and month. A nested block design with repeated measures was used to assess the effect of saturating light levels on stomatal conductance. Month (June, July, and August), habitat (unburned forest and burned forest), and Species (hickory, red oak, and white oak) were treated as fixed factors. Block (n=2) and transect (n=18) were treated as random factors, with transect nested under both block and habitat. F and P values are only presented when $P<0.10$. F and P values are not presented for main effects and interaction terms containing blocking variables.

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Month	2	0.670083	0.591735	0.295868	60.87	0.016
Block	1	0.042622	0.035289	0.035289		
Habitat	1	0.177318	0.184487	0.184487		
Species	2	0.074431	0.077602	0.038801		
Month*Block	2	0.008922	0.009721	0.00486		
Month*Habitat	2	0.003306	0.004336	0.002168		
Month*Species	4	0.00965	0.010452	0.002613		
Block*Habitat	1	0.031171	0.031096	0.031096		
Block*Species	2	0.044449	0.043769	0.021885		
Habitat*Species	2	0.050779	0.052955	0.026477		
Month*Block*Habitat	2	0.001275	0.000892	0.000446		
Month*Block*Species	4	0.006549	0.006523	0.001631		
Month*Habitat*Species	4	0.019688	0.018651	0.004663		
Block*Habitat*Species	2	0.014322	0.014545	0.007272		
Month*Block*Habitat*Species	4	0.005984	0.005958	0.00149		
Transect(Block Habitat)	8	0.11131	0.11131	0.013914		
Error	473	0.766611	0.766611	0.001621		
Total	516	2.03847				

Appendix N. ANOVA table for stomatal conductance under ambient light levels as a function of species, habitat and month. A nested block design with repeated measures was used to assess the effect of ambient light levels on stomatal conductance. Month (June, July, and August), habitat (unburned forest and burned forest), and Species (hickory, red oak, and white oak) were treated as fixed factors. Block (n=2) and transect (n=18) were treated as random factors, with transect nested under both block and habitat. F and P values are only presented when $P<0.10$. F and P values are not presented for main effects and interaction terms containing blocking variables.

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Month	2	0.531954	0.468098	0.234049	39.94	0.024
Block	1	0.031359	0.02566	0.02566		
Habitat	1	0.140779	0.146949	0.146949		
Species	2	0.072513	0.073619	0.03681		
Month*Block	2	0.010868	0.011721	0.00586		
Month*Habitat	2	0.003637	0.004469	0.002235		
Month*Species	4	0.013852	0.015245	0.003811		
Block*Habitat	1	0.026263	0.026108	0.026108		
Block*Species	2	0.032629	0.031555	0.015778		
Habitat*Species	2	0.04064	0.042946	0.021473		
Month*Block*Habitat	2	0.001968	0.001546	0.0000773		
Month*Block*Species	4	0.006718	0.006734	0.001683		
Month*Habitat*Species	4	0.017423	0.016775	0.004194		
Block*Habitat*Species	2	0.012865	0.012961	0.00648		
Month*Block*Habitat*Species	4	0.004703	0.00467	0.001168		
Transect(Block Habitat)	8	0.088596	0.088596	0.011074		
Error	473	0.630654	0.630654	0.001333		
Total	516	1.667421				