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Restoration of Central Texas Savanna and Woodland: the Effects of Fire, Deer and Invasive Species on Plant Community Trajectories

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Restoration of Central Texas Savanna and Woodland: the Effects of Fire, Deer and Invasive Species on Plant Community Trajectories

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Dedication

To my grandfather, Felix Andruk, who wanted to come to Texas to see my defense.

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Restoration of Central Texas Savanna and Woodland: the Effects of Fire, Deer, and Invasive Species on Plant Community Trajectories

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The University of Texas at Austin, 2014

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Prescribed fire is a common tool used to restore native diversity, control invasive species, and reduce fuel loads. However, fire alone can be insufficient to restore pre-settlement vegetation; other factors such as differences in native and invasive species pools, deer herbivory, seed availability, and the spatial pattern of the fire can influence vegetation trajectories and restoration outcomes.

Central Texas is a mosaic of savanna and mixed woodlands co-dominated by *Quercus buckleyi* (Texas red oak) and *Juniperus ashei* (Ashe juniper). In a savanna, I studied the joint effects of initial species composition (native-dominated or invasive-dominated) and disturbance (high-intensity fire, clipping, or control) on the ability of native species to establish, survive, and resist invasion by *Bothriochloa ischaemum*, an invasive C_4 grass (ch. 1). Native savanna patches were resistant to invasion following high-intensity fire; fire can be used to selectively control *B. ischaemum*.

In central Texas savanna and woodlands, under fire suppression and overabundant white-tailed deer, *Quercus* spp. are failing to regenerate, while *J. ashei* is increasing in abundance. To better understand vegetation trajectories following *J. ashei* removal in savanna, I studied the soil seedbank along a chronosequence of *J. ashei* invasion (ch. 5). In woodland, I studied the joint effects of prescribed fire and deer (ch. 2), clearing of *J.*

ashei followed by high-intensity slash-pile burns (ch. 3), and wildfires (ch. 4) on the abundance and size of *J. ashei* and of hardwoods. Hardwoods resprouted vigorously after fire; *J. ashei* individuals of all sizes were killed by fire and slow to re-colonize. These management interventions failed to increase *Q. buckleyi* seedling abundance. It is likely that deer control is necessary to allow fire to have positive effects on the regeneration of oaks in this region, and wherever deer are over-abundant. However, deer can indirectly benefit hardwoods by reducing competition with palatable forbs (ch. 3). In general, these results show that fire suppression in central Texas oak-dominated woodlands is causing a shift not to more mesic-adapted species, as observed in the eastern US, but to *J. ashei*, which is at least as xeric-adapted as oak, a process I termed ‘juniperization’.

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Introduction and overview

Ecologists have long thought that climate and soils largely determine terrestrial plant community distribution (Barbour et al., 1998). However, an understanding of the importance of fire as a global disturbance process that structures ecosystem and community composition, structure, distribution, and processes is emerging (Bond and Keeley, 2005). Fires occur in nearly all ecoregions; they have been a key global process since the origin of land plants (Pausas and Keeley, 2009). Fire activity is largely determined by the productivity and aridity of a given region. The intermediate fire productivity hypothesis suggests that fire activity peaks at intermediate productivity levels (Pausas and Ribeiro, 2013). Fire activity is also significantly impacted by human activity. Anthropogenic influence has been particularly important over the past century as there have been significant changes in human population distribution, socioeconomic factors, and land management techniques (Pausas and Keeley, 2009). After a period of increased fire use by humans, effective widespread fire suppression in the United States (US) began in the early to mid 1900's (Agee and Skinner, 2005; Nowacki and Abrams, 2008).

Fire suppression has negatively impacted many different grassland, savanna, shrubland, woodland and forest ecosystems (DeSantis et al., 2010; Nowacki and Abrams, 2008; Romme et al., 2009). Fire suppression impacts differ among ecosystems, but can include loss of native biodiversity (Abrams, 1992; González-Tagle et al., 2008; Sands and Abrams, 2011), degradation of water, air and soil resources (Backer et al., 2004), and the transformation of grasslands and savannas to woodlands (Briggs et al., 2005; Van Auken, 2009). In addition, fuel loads generally increase under fire suppression, increasing the probability of catastrophic wildfires, which create both ecological and social problems (Gill et al., 2013). There is strong interest in mitigating the effects of fire-suppression in forests and woodlands through the use of fuel reduction techniques and prescribed fire (Agee and Skinner, 2005; Brown et al., 2004). Prescribed fires are also widely used to control invasive species and restore native diversity in savannas and grasslands (MacDougall and Turkington, 2007; Peterson and Reich, 2001; Pyke et al., 2010).

In central Texas, fire suppression is changing the distribution and composition of *Quercus fusimormis* (live oak) savanna and mixed species woodlands co-dominated by *Quercus buckleyi* (Texas red oak) and *Juniperus ashei* (Ashe juniper). Under fire suppression, woody plant encroachment is converting diverse savanna into monocultures of *J. ashei* (González, 2010; Van Auken, 2009). To better understand the impacts of *J. ashei* invasion into savannas, and the vegetation trajectories following *J. ashei* removal, I studied the soil seedbank along a chronosequence of *J. ashei* invasion (ch. 5). In woodlands, fire suppression, along with overabundant white-tailed deer (Russell and Fowler, 2004), are contributing to the failure of *Q. buckleyi* to regenerate (Russell and Fowler, 2002). The fire-intolerant, unpalatable *J. ashei* is regenerating. Therefore, these woodlands, along with the savannas, are being converted to *J. ashei* monocultures.

Bothriochloa ischaemum (King Ranch bluestem) is the non-native invasive species of greatest concern in central Texas. This C_4 grass often invades following low-intensity prescribed burns, which are ineffective for its control. There seems to be nothing precluding its potential expansion into and dominance of all non-wooded areas in this region (Gabbard and Fowler, 2007). However, neither *B. ischaemum* nor the common native savanna species persist where woody plant encroachment has created a closed canopy. There are therefore two invasion processes occurring simultaneously in this system: woody plants, primarily *J. ashei*, encroach on savannas, while the grass *B. ischaemum* invades areas that are still open.

To better understand the resistance and resilience of *B. ischaemum*-invaded savanna, I studied the joint effects of initial species composition (native-dominated or invasive-dominated) and disturbance (high-intensity fire, clipping, or control) on the ability of native species to establish, survive, and resist invasion by *B. ischaemum* (ch. 1). I found that native savanna patches are resistant to invasion following high-intensity fire, and that fire can be used to selectively control *B. ischaemum*. This study adds to the growing body of literature that conceptualizes restoration in a resiliency framework (Hobbs et al., 2011; Mori, 2011; Suding, 2011).

The fire regime of central Texas woodlands is much less understood than the fire regime of savanna. There was previous research documenting the effects of prescribed fire in this system, and little research on the effects of wildfires (Doyle, 2012; Reemts and Hansen, 2008). I studied the joint effects of prescribed low-intensity fire and deer (ch. 2), clearing of *J. ashei* followed by high-intensity slash-pile burns (ch. 3), and wildfires (ch. 4) on the abundance, size, and growth rates of *J. ashei* and of hardwoods, particularly *Q. buckleyi*. Hardwoods resprouted vigorously after fire in all studies; the apparent adaptations of native hardwoods to fire are the strongest evidence we have for an important role for fire pre-settlement. Conversely, *J. ashei* individuals of all sizes were killed by fire. They were also slow to re-colonize after fire. The consistently positive response of *Q. buckleyi* and other hardwoods to fire, and the negative response of *J. ashei*, suggest that hardwoods, rather than *J. ashei* dominated pre-settlement woodlands.

My research also shows that fire suppression in central Texas oak-dominated woodlands is causing a shift not to more mesic-adapted species (usually maples, *Acer* spp.) as observed in the eastern US (Nowacki and Abrams, 2008), but to *J. ashei* which is at least as xeric-adapted as oak. Similar transitions from oak-dominated woodlands to juniper-dominated woodlands are occurring throughout the south-central US (Burton et al., 2010; DeSantis et al., 2010; 2011). Therefore, I argue that our thinking of the “oak regeneration problem” needs to be revised and expanded to include the diverse regions that are affected. In general, fire suppression in oak-dominated systems favors the expansion of shade-tolerant, fire-intolerant species. These species, whether mesic-adapted or xeric-adapted, produce shallow dense litter, further decreasing the probability of fire. Eventually, a transition to an alternative less flammable state occurs. As central Texas woodlands are transitioning to a *J. ashei* monoculture, I term this process ‘juniperization’.

The results of my dissertation, and similar studies in other oak-dominated systems (Arthur et al., 2012; Brose et al., 2013; Green et al., 2010), show that re-introducing prescribed fires alone triggers oak resprouting, but often not the production of new oak seedlings. Fires alone are therefore often insufficient to cause the transition from a juniper or maple-dominated woodland back to an oak-dominated one. This may be because other factors such as overabundant deer also limit oak regeneration (Russell and Fowler, 2004). The results of chapter 2 demonstrate that deer control is necessary to allow fire to have positive effects on the regeneration of oaks and other hardwoods in this region. This is likely to be true in much of the US where deer are also over-abundant.

However, protection from deer herbivory may benefit palatable forbs more quickly than hardwood trees (ch. 3). Thus, deer may indirectly benefit less palatable hardwoods by reducing completion with more palatable forbs. Also in chapter 3, I examined the ability of slash-pile burning (cutting, removing, and burning *J. ashei* in 30% of the study site) to restore habitat for the endangered golden-cheeked warbler. These management activities likely increased habitat quality for the golden-cheeked warbler, although they failed to increase *Q. buckleyi* seedling abundance. The habitat fragmentation created by canopy removal in multiple, relatively small areas may have slowed the spread of the invasive grass *Bothriochloa ischaemum*. It also may have reduced deer herbivory in the treated areas. Spatial patterns imposed by slash-pile burns are likely to strongly influence vegetation trajectories in other systems as well.

The results of all of my chapters highlight the importance of considering multiple drivers of plant community response to fire simultaneously. Factors that I studied included differences in native and invasive species pool, deer herbivory, seed availability, and spatial pattern. These factors may have complex interactions that influence vegetation trajectories and the efficacy of management techniques. Therefore, there is no reason to suspect that re-introducing the pre-settlement disturbance alone will be sufficient to restore pre-settlement vegetation dynamics (Collins and Carson, 2002; Kern et al., 2012). Fire ecologists must broaden their definition of a sustainable, desired system to account for ongoing changes in vegetation drivers and societal needs (Brown et al., 2004). This mismatch between historical, present, and future dynamics is a general challenge in restoration ecology (Hobbs et al., 2011), and often, as observed here, the simple reintroduction of the pre-settlement disturbance regime is not enough to shift vegetation trajectories in the desired direction.

Chapter 1: Preventing re-invasion following restoration: the effects of prescribed fire and species choice on native and invaded savanna

ABSTRACT

The use of fire to selectively control invasive species, especially invasive C_4 grasses in C_4-dominated system, is challenging. I examined the joint effects of initial species composition (native-dominated or invasive-dominated) and disturbance (high-intensity fire, clipping, or control) on the ability of native species to establish, survive and resist invasion by the invasive C_4 grass *Bothriochloa ischaemum* in a central Texas savanna. Fire was effective in controlling *B. ischaemum*, evidently because the large amount of standing-dead biomass in *B. ischaemum*-dominated stands supported a high-intensity fire: *B. ischaemum* was not resistant to fire. Invaded plots were also not resilient to fire: added native seeds had high establishment and survival after these plots were burned. Conversely, native-dominated plots were resilient to fire, remaining native-dominated and resistant to invasion after being burned. Fire was much more effective than clipping both at reducing *B. ischaemum* and at increasing survival of native species. Although I found some support both for the restoration use of early successional species and for species that are similar to the invader, a diverse seed mix will likely be the most effective at increasing establishment, survival and persistence of a large number of native species. Diverse seed mixes allow different species to take advantage of the spatial heterogeneity created by differences in pre-fire vegetation and fire intensity. They are often necessary, as we usually do not have enough information to predict which species will be successful.

INTRODUCTION

Fire is used widely as a restoration tool to decrease the abundance of invasive species and increase native abundance (Pyke et al., 2010). However, fire can fail to restore native communities because invaded communities may be resistant to fire. Invasive species, especially fire-tolerant invasive grasses, may not be differentially harmed by fire (DiTomaso et al., 2006; Gabbard and Fowler, 2007), possibly making fire an ineffective restoration tool. Invaded communities may also be resilient to native species colonization post-fire, particularly if the invader grows more quickly than the natives (Flory and Clay, 2009; Gómez-González et al., 2011). Fire can therefore have the unwanted effect of increasing or maintaining invasive abundance (Brooks et al., 2010; McGlone et al., 2006). A related concern is that native communities may not be resistant to invasion after fire (Foxcroft et al., 2010; Pyke et al., 2010).

The resistance and resilience of native and invaded communities depends on the particular disturbance used (Flory and Clay, 2009). Fire has been used successfully to restore native savannas (DiTomaso et al., 2006; Gosper et al., 2011). However, because of the perceived dangers of prescribed fire, clipping and mowing are sometimes used as fire substitutes (Keeley, 2006; MacDougall and Turkington, 2007), but they may be less effective at decreasing invader resistance and resilience (Jutila and Grace, 2002; Pyke et al., 2010).

The resistance and resilience of native and invaded communities can also be altered by species selected for restoration (Falk et al., 2012; Funk et al., 2008). Three major species-selection guidelines are *limiting similarity*, *rapid growth and establishment*, and *sampling-effect* (Abella et al., 2012; Cleland et al., 2012). The *limiting similarity* guideline suggests using species with traits similar to the target invasive to outcompete the invasive because competition tends to limit trait similarity (Emery, 2007; Funk et al., 2008). The *rapid growth and establishment* guideline suggests using early successional and/or fast growing species as they can get to the site earlier and grow faster than the invaders, pre-empting niche space (Cleland et al., 2012; Larson et al., 2013; Simmons et al., 2007). The *sampling-effect* guideline suggests that as more species are included in the restoration, the probability of selecting an effective competitor for the invader and a species adapted to that site increases (Falk et al., 2012; Kennedy et al., 2002; Suding, 2011)

Invasive grasses are a major threat in savannas; they reduce diversity and alter disturbance regimes (Alofs and Fowler, 2010; Foxcroft et al., 2010; Pyke et al., 2010). Exotic C_4 grasses have invaded in North American tall grass prairie (Reed et al., 2005), Australian savannas (Brooks et al., 2010), Brazilian cerrado (Hoffmann et al., 2004) and central Texas (Gabbard and Fowler, 2007). *Bothriochloa ischaemum*, a C_4 Eurasian perennial bunchgrass, was introduced to the United States in the early 1900's. It is one of several Old World bluestems expanding throughout the central and southern Great Plains. In central Texas, *B. ischaemum* var. *songarica* (King Ranch bluestem) is common in non-wooded upland areas, often forming near-monocultures (Gabbard and Fowler, 2007). *B. ischaemum* outcompetes a dominant native grass, *Schizachyrium scoparium* (little bluestem) in the field (Andruk and Fowler, unpublished data), and the greenhouse (Schmidt et al., 2008). It also alters ecosystem processes, increasing soil organic C, total N, and litter decomposition (Ruffner et al., 2012).

Selective control of C_4 grasses in C_4 grasslands and savannas is challenging (Reed et al., 2005; Ruckman et al., 2012b). Herbicides are not effective in long-term control of *B. ischaemum* (Ruffner and T. G. Barnes, 2012). Low-intensity fires have either a neutral or positive effect (Gabbard and Fowler, 2007). High-intensity fires can be more effective (Ruckman et al., 2012b; Simmons et al., 2007; Twidwell et al., 2012). A dominant native grass, *S. scoparium*, responds positively to high-intensity fire (Limb et al., 2011), suggesting that high-intensity fire was a common pre-settlement disturbance and that native communities should be resilient to it.

I examined the joint effects of initial species composition (native-dominated or invasive-dominated) and disturbance (high-intensity fire, clipping, or control) on the ability of native species to establish, survive and resist invasion by *B. ischaemum*. I tested the ability of native communities to resist invasion after high-intensity fire, and the resilience of *B. ischaemum* stands to high-intensity fire. While the literature suggested that high-intensity fire would reduce *B. ischaemum* (Ruckman et al., 2012b; Twidwell et al., 2012), I was concerned that *B. ischaemum* would quickly recover, that fire would harm native species, and that fire might even promote *B. ischaemum* invasion. Finally, I compared the ability of different added species to establish, survive and resist invasion, allowing us to evaluate species-selection guidelines described above.

METHODS

Experimental design

This study was conducted in *Quercus fusiformis* savanna at Balcones Canyonlands National Wildlife Refuge on the eastern Edwards Plateau of central Texas (30.8536° N, -97.9744° W). The dominant native species are short- and mid-height grasses, including *Schizachyrium scoparium*, *Nassella leucotricha*, *Bothriochloa laguroides*, and species of *Bouteloua* and *Aristida* (Fowler and Dunlap, 1986).

In April 2009 I established 80 2x1-m randomly located plots, half were native-dominated (*B. ischaemum* cover $\leq$ 40%), and half were invasive-dominated (*B. ischaemum* cover $\geq$ 60%). I planned to use a full factorial design of three treatments: burned or unburned, clipped or not, and native or invasive initial vegetation. The high-intensity prescribed fire occurred in July 2009. Flame lengths were about 1-m in a predominately backing fire, resulting in prolonged heat duration on each plant. The entire field was burned, except for randomly selected plots left unburned by mowing and wetting around them. The Keetch-Byram Drought Index (KDBI) at the time of the burn was in the 87th percentile (Fig. 1.1). Weather conditions were appropriate for a high-intensity fire (Table 1.1). In the burned plots, most of the plants were killed. There was still a 65% decrease in *B. ischaemum* cover 2 years after the fire, making this a moderate-high severity burn according to the composite burn index (Key and Benson, 2006). Since most of the *B. ischaemum* was killed, I refer to post-fire occupation of burned plots by *B. ischaemum* as invasion (if initially native-dominated) or re-invasion (if initially invasive-dominated. A few plots that were supposed to remain unburned were accidentally burned. Therefore, to maintain adequate sample sizes while preserving the most important treatment combinations, burned-clipped-native, burned-clipped-invasive, and unburned-clipped-native treatment combinations were dropped, for a total of 5 treatment combinations (hereafter, treatment) with 8 to 28 plots each (Table 1.2). Clipping of invasive-dominated plots were also done in July 2009; plants were clipped to the base and litter was evenly spread across the plot.

Seeds of 16 native herbaceous species that represented a range of traits and of *B. ischaemum* were added in November 2009 (Table 1.33). Each 2x1-m plot had 21 parallel lines, 1-m long and 0.1-m apart. Each line was divided in the middle into two 0.5-m-long rows, 42 total rows per plot. Each species was randomly assigned to two 0.5-m rows per plot; one species was added per row. Since there were 17 species, 34 rows (17 x 2) received seeds. The remaining 8 rows were left unseeded as controls.

Seedling establishment was defined as the proportion of added seeds that gave rise to seedlings in April 2010, 5 months after seed addition. (Very few seedlings established after April 2010.) Because almost no seedlings of added species were found in unseeded rows, no corrections were made for background recruitment. Survival was defined as the proportion of individuals (each individually-marked in April 2010) that survived from spring 2010 to fall 2010. In spring 2011 I recorded the percent cover of *B. ischaemum* in each row in each plot, including both previously established and newly-established *B. ischaemum* plants but not plants arising from added seed. The percent cover of all species, not including plants arising from added seeds was recorded in spring 2009, spring 2010, fall 2010 and spring 2011.

Data analysis

The effects of treatment (Table 1.2) on the probability of establishment and survival of plants arising from sown seed were analyzed using six generalized linear mixed models, each with a binomial distribution and logit link function (PROC GLIMMIX, SAS 9.3). Treatment, growth-form (grass or forb) or species and their interactions were fixed effects. Plot nested within treatment was a random effect. I first analyzed the effects of treatment, growth-form, and their interaction on establishment and on survival (two separate analyses). I then analyzed the effect of treatment, species identity, and their interaction on the establishment of grasses and forbs separately. All species whose establishment rates were not significantly different from zero were then dropped, leaving one dataset with five forb species (Fig. 1.2b), and a second with four grass species (Fig. 1.3b). These reduced datasets were used to test the effects of treatment, species identity, and their interaction on grass species and forb species survival separately. In any analysis in which a fixed effect was significant, all possible contrasts were tested with the Tukey-Kramer test.

To test the effects of treatment and added species identity on the ability of *B. ischaemum* to invade or re-invade burned rows and to persist in unburned and clipped rows, I analyzed whether *B. ischaemum* was present in each row in spring 2011 (plants from added seed excluded) using a generalized linear mixed model with a binomial distribution and logit link function. The analyzed dataset included only those rows with the four grass species and five forb species with good establishment (Figs 2b and 3b). Added native seed establishment and survival were included as covariates in two separate models, but neither the covariates themselves, nor their interactions were significant, and were therefore dropped from final models.

After excluding all plants arising from added seed, percent cover of *B. ischaemum*, total native forb cover, total native grass cover, and species richness were calculated for each plot pre-treatment and post-treatment. I used four analyses of covariance to examine the effect of treatment on percent cover or richness post-treatment, with pre-treatment cover or richness, respectively, as the covariate. Because the treatment x covariate interaction was insignificant in the analyses of forb cover, grass cover, and species richness, it was dropped. There was a significant treatment x covariate interaction in the *B. ischaemum* analysis. In native-dominated plots, *B. ischaemum* cover was not related to pre-treatment cover. Therefore native-dominated plots were dropped from the dataset and the ANCOVA was performed again. I also calculated the difference between initial and final cover of *B. ischaemum* for the whole dataset and used ANOVA to test differences among treatments.

RESULTS

Establishment and survival from added seed

Native forbs had significantly higher establishment than native grasses (forb mean 0.047, grass mean 0.001, $P < 0.0001$). Grasses had a significantly higher survival than forbs (grass mean 0.257, forb mean 0.017, $P < 0.0001$). Pooled forb establishment in the clipped-invasive (CI) treatment was significantly higher than in the burned-native (BN) treatment ($P = 0.008$, Fig. 1.2a). However, forb species responded to treatments differently (species x treatment interaction, $P < 0.0001$, Fig. 1.2c). The medium-sized annual forb *Gaillardia pulchella* had the highest establishment in the burned plots (both native and invasive) and the lowest in the clipped plots, while the tall biennial *Ipomopsis rubra* had its highest establishment in the clipped plots and lowest in the burned (Fig.

1.2c). *G. pulchella* had the highest overall establishment, significantly (*P* < 0.0001) higher than *I. rubra* (*P* < 0.0001) (Fig. 1.2b). Pooled forb survival was significantly higher in the burned-invasive (BI) treatment than all other treatments (*P* = 0.008, Fig. 1.2d). Because of very high survival in the burned-invasive plots, overall forb survival was *greater* in invasive-dominated plots than in native-dominated plots (contrast of native vs. invasive-dominated plots, *P* < 0.0001, Fig. 1.2d). Individual forb species did not differ in their survival, nor was there a significant treatment x species interaction.

Grass establishment differed significantly among treatments (*P* < 0.001, Fig. 1.3a), primarily due to low establishment in unmanipulated-invasive plots. Grass species responded to treatments differently (species x treatment interaction, *P* < 0.0001, Fig. 1.3c). The largest differences among species were in the burned-invasive plots, where only *B. laguroides*, the native congener of the invasive, established well (Fig. 1.3c). *B. laguroides* had the highest overall establishment, significantly (*P* < 0.0001) higher than *Aristida purpurea* (*P* < 0.0001), which was in turn significantly (*P* < 0.0001) higher than *B. ischaemum* (Fig. 1.3b). Pooled grass survival did not depend significantly on treatment. *B. ischaemum* had a significantly higher survival than other grass species (*P* < 0.0001). However, there was a significant species x treatment interaction: *B. ischaemum* survived better in all treatments except the unburned-native treatment where *B. laguroides* had the highest survival (Fig. 1.3d).

Bothriochloa ischaemum ***occupation***

Treatments differed in *B. ischaemum* occupation (binary response: occupied, not). Burned-invasive plots were 40% less likely to have *B. ischaemum* than unmanipulated-invasive plots (BI v UI, *P* < 0.0001, Fig. 1.4a). Clipping had no apparent effect on *B. ischaemum* persistence. Burned-native plots were less likely to be invaded than unmanipulated-native plots (BN v UN), but not significantly so (Fig. 1.4a). Overall, species differences were significant (P = 0.035). *Bothriochloa ischaemum* was equally likely to be present in rows planted with grasses or forbs. Rows planted with *A. purpurea* were significantly less likely to be occupied by *B. ischaemum* than rows planted with *B. ischaemum* (Fig. 1.4b), but the differences were slight. Rows planted with the different forb species were equally likely to be invaded**.** There was no interaction between treatment and species.

Background vegetation

Background vegetation included all vegetation that did not arise from added seeds. The relationship between background *B. ischaemum* cover pre- and post-treatment differed significantly among treatments in invaded plots (P = 0.001, Fig. 1.5a). In burned-invasive plots, the more *B. ischaemum* that was present before the fire, the less afterwards (slope = -0.43, P = 0.035, Fig. 1.5a). In the clipped and unmanipulated plots, pre-fire *B. ischaemum* cover had the expected positive relationship with post-fire *B. ischaemum* cover. The net change in *B. ischaemum* cover was negative everywhere, but by far the greatest change (64.79% decrease) was in the burned-invasive plots. Burning native-dominated plots did not significantly change *B. ischaemum* cover (Fig. 1.5b). Burning significantly increased native species richness in invasive-dominated plots (Fig 1.5c), primarily due to an increase in native forbs in burned-invasive-dominated plots (Fig. 1.5d). Native grass cover was not significantly affected by treatment.

DISCUSSION

My results indicate that high-intensity fire is an effective method of invasive species control for *B. ischaemum* in central Texas, as has been found elsewhere (Gosper et al., 2011; Twidwell et al., 2012). High-intensity fire did not promote the invasion of *Bothriochloa ischaemum* into native-dominated patches; native species were resistant to invasion following fire. The native community was also resilient to fire, because native-dominated patches tended to be re-colonized by native species. Therefore, these results indicate that high-intensity fire will not have the undesirable result of promoting invasion in this system, although it has been found to do so elsewhere (Keeley, 2006; McGlone et al., 2006).

Bothriochloa ischaemum was mostly killed by high-intensity fire: this species is not resistant to high-intensity fire. The invaded community is also not resilient to fire because invasive-dominated patches tended to be colonized by native species. Furthermore, *B. ischaemum* re-invasion of these patches was slow, and seeded *B. ischaemum* performed about the same as seeded native grasses over the course of the experiment. These conclusions are compatible with, and extend, the studies of (Ruckman et al., 2012b; Simmons et al., 2007) regarding *B. ischaemum*.

Different effects of fire on native and invaded communities

The control of invasive C_4 grasses in C_4-dominated savannas can be difficult because the native and invasive species share many traits (Reed et al., 2005; Ruckman et al., 2012b). Therefore, the initial concern, which proved to be unfounded, was that restoration using fire would harm native species as well as, or more than, invasive species (e.g. (Kettenring and Reinhardt Adams, 2011; Rinella et al., 2009). A related concern was that post-fire conditions would favor invasive species (Keeley, 2006; McGlone et al., 2006). However, in this system, high-intensity fire successfully suppressed *B. ischaemum* in the short-term, increased native species richness and forb cover, and improved the success rate of re-seeding with native species. Thus, in central Texas, high-intensity fire can selectively control the major invasive species and favor native species. Similar results have been found in other C_4-dominated systems (Twidwell et al., 2012), but see (Brooks et al. 2010).

There are at least two possible explanations for fire having a greater impact on pre-existing *B. ischaemum* than on pre-existing native plants: (a) different physiological status at the time of the fire, and (b) higher fuel loads in invaded plots. Post-burn recovery of *B. ischaemum* is slower when plants are burned in earlier reproductive stages (Ruckman et al., 2012b). I did not directly measure pre-fire physiological status, but estimate that about half of the reproductive tillers of *B. ischaemum* were flowering and almost all of the rest were pre-flowering. However, based on my results, I suspect a different mechanism. It is highly likely that *B. ischaemum* cover was correlated with *B. ischaemum* biomass, both live and standing-dead, (ungrazed *B. ischaemum* stands have very large amounts of standing dead biomass [T. Basham, unpublished data].) The standing-dead biomass in *B. ischaemum* plots likely provided higher fuel loads there, which probably increased fire intensity and therefore the death rate of existing plants. This could also have reduced post-fire competition. This scenario accounts for the significant negative relationship between pre-fire and post-fire *B. ischaemum* cover. Higher intensity fires have been found to increase light availability, nutrient availability, colonization sites, and the amount of bare ground in other systems (Gagnon et al., 2012; Reich et al., 2001). Therefore, I suggest that fire intensity, determined by fuel load and weather, is as important or more important than physiological state of *B. ischaemum* in determining the success of fire.

Disturbance type

Clipping or mowing are sometimes used as fire substitutes (MacDougall and Turkington, 2007). Clipping increased forb establishment, probably because the clipped grass helped retain the added seeds. However, fire was nine times more effective than clipping at increasing forb survival, twice as effective at decreasing *B. ischaemum* cover, and slightly more effective at increasing forb cover and native species richness. Thus, disturbance type exerted a strong effect on both invasive species control and native species response, as also found elsewhere (Flory and Clay, 2009; Kettenring and Reinhardt Adams, 2011). Furthermore, fire did not increase *B. ischaemum* occupation of native plots, so there is no biological reason to substitute clipping for fire.

Species choice

A major goal in restoration ecology is the development of native vegetation communities that are resilient to invasion (Suding, 2011), although the choice of species to best meet this goal is a challenge (Falk et al., 2012; Funk et al., 2008). Some studies have had success using the *limiting similarity* guideline which emphasizes the use of species that are similar to the invader (Emery, 2007), but others have not (Abella et al., 2012; Larson et al., 2013). The native congener of the invader, *Bothriochloa laguroides* has physiological traits very similar to *B. ischaemum* (Ruckman et al., 2012b), suggesting that it might outcompete it. However, *B. laguroides* was only partially successful: it had higher establishment than *B. ischaemum*, and higher survival in the unmanipulated-native plots, but it was not more successful than other species at preventing re-invasion.

Another species selection guideline suggests using *early successional and/or disturbance-adapted species* for restoration because they may grow and reproduce more rapidly than invaders, pre-empting niche space (Cleland et al., 2012; Larson et al., 2013; Simmons et al., 2007). *Gaillardia pulchella*, which was highly successful at establishing in the burned plots in this study, is an example of such a species.

The *sampling effect* guideline (Falk et al., 2012; Kennedy et al., 2002) suggests the use of a diverse locally-adapted seed mix. Diverse mixes can be successful because (a) biodiversity may inhibit invasion, (b) a diverse mix is more able to take advantage of spatial and temporal heterogeneity, which may be particularly important in the highly heterogeneous post-fire environment (e.g. Gagnon et al., 2012), (c) a diverse mixes are more likely to have species adapted to different sites, and (d) we usually do not have enough information to predict which species will be successful. For example, the successful early successional forb, *G. pulchella*, had thirteen times higher establishment than *Monarda citriodora*, although both are common early successional species. There was no way to know *a priori* which of these two common species would perform better in the particular post-fire environment of this study.

Disturbance type (fire, clipping, control) was a more important predictor of *B. ischaemum* invasion and persistence than added species identity in this short-term study. I expect this to continue in the long-term. While some studies have found that the choice of species composition has limited long-term impact (Quinn and Holt, 2009), others have found the opposite (J. D. Bakker and Wilson, 2004). However, species identity was important enough in this system to support the use of a diverse species mix.

IMPLICATIONS FOR PRACTICE

- Native C_4 grasses can be resistant to invasion by invasive C_4 grass after high-intensity fire. Consider high intensity fire to selectively control invasive C_4 grasses in other systems formerly dominated by native C_4 species.

- Increased fuel load, due to high amounts of standing dead biomass, is the most likely reason that fire controlled *Bothriochloa ischaemum.* If possible, managers should wait to burn until the fuel load will allow a high-intensity fire.

- I recommend re-seeding with a diverse seed mix, containing both early successional species and species that are similar to the invader, especially after high-intensity fire.

Table 1.1: Weather conditions on the date of the burn, July 24, 2009. Ignition began at 12:00 and stopped at 17:00.

temperature (°C) range	relative humidity range	wind-speed mph (miles per hour)	1 hour % fuel moisture	100-hour % fuel moisture	1000-hour % fuel moisture
33.3 - 37.2	30 - 42%	4 - 5	5.6 - 8.1	13.1	12.1

Table 1.2: Treatment codes (tr) and descriptions imposed in summer 2009 at Balcones Canyonlands NWR, TX on plots with different initial vegetation. N plots, number of plots per treatment.

tr	**description**	**N plots**
BI	burned-invasive	18
BN	burned-native	28
UI	unmanipulated-invasive	14
UN	unmanipulated-native	12
CI	clipped-invasive	8
total		80

Table 1.3: Species, with their four-letter codes, used in seed addition following treatment at Balcones Canyonlands NWR in November 2009. PLS, pure live seed. PLS rate provided by Native American Seed Source, Junction, TX. Seeds of all native species were purchased from this vendor, except for *Bothriochloa laguroides*, whose seeds were collected from BCNWR in fall 2009. Seed of the invasive *B. ischaemum* was purchased from Callahans General Store (Austin, TX). Effective number of seeds added = number of seeds added x PLS.   * indicates species that had significant establishment (Fig. 1.2b, 3b). The number of seeds added per species was dependent on cost, availability, and recommended seeding rates (Simmons et al., 2007).

species	species code	life history	PLS rate	effective # seeds added
*Schizachryium scoparium**	SCSC	perennial grass	0.6254	500
*Bothriochloa laguroides**	BOLA	perennial grass	0.5000	500
*Bothriochloa ischaemum**	BOIS	perennial grass	0.3800	500
Leptochloa dubia	LEDU	perennial grass	0.936	500
Bouteloua curtipendula	BOCU	perennial grass	0.7727	500
*Aristida purpurea**	ARPU	perennial grass	0.8655	500
Bouteloua gracilis	BOGR	perennial grass	0.6809	500
Hilaria belangeri	HIBE	perennial grass	0.4640	170
*Ipomopsis rubra**	IPRU	biennial forb	0.8564	800
*Ratibida columnifera**	RACO	perennial forb	0.5364	500
*Monarda citriodora**	MOCI	annual forb	0.5364	800
*Gaillardia pulchella**	GAPU	annual forb	0.8482	100
Liatris mucronata	LIMU	perennial forb	0.5075	100
Senna roemeriana	SERO	perennial forb	0.6000	30
*Glandularia bipinnatifida**	GLBI	perennial forb	0.6500	70
Desmanthus illinoensis	DEIL	perennial forb	0.9187	300
Asclepias asperula	ASAS	perennial forb	0.7300	30

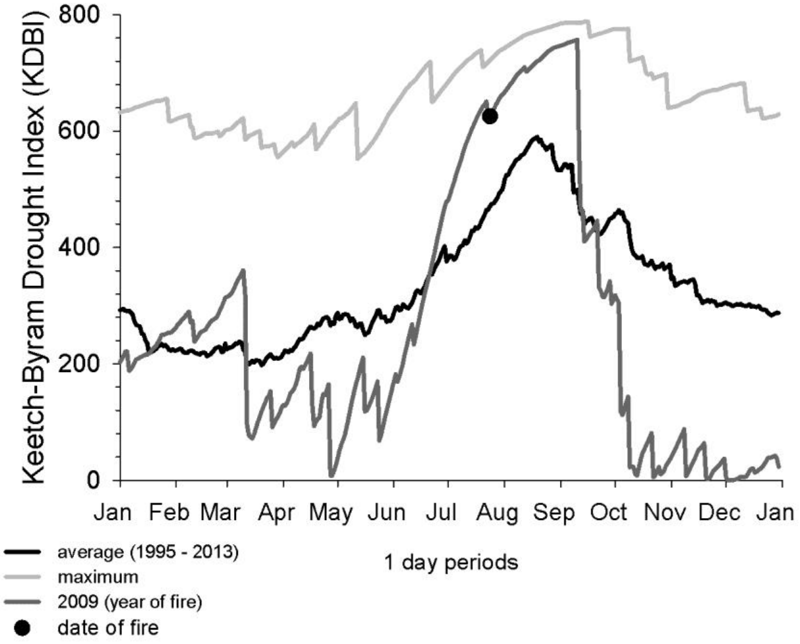

Figure 1.1: The Keetch-Byram Drought Index (KDBI) long-term average from 1995 to 2013 (black line), maximum (light gray), and observed in 2009 (dark gray). From model 8L1PE2, 6528 Wx observations taken at Balcones Canyonlands National Wildlife Refuge.

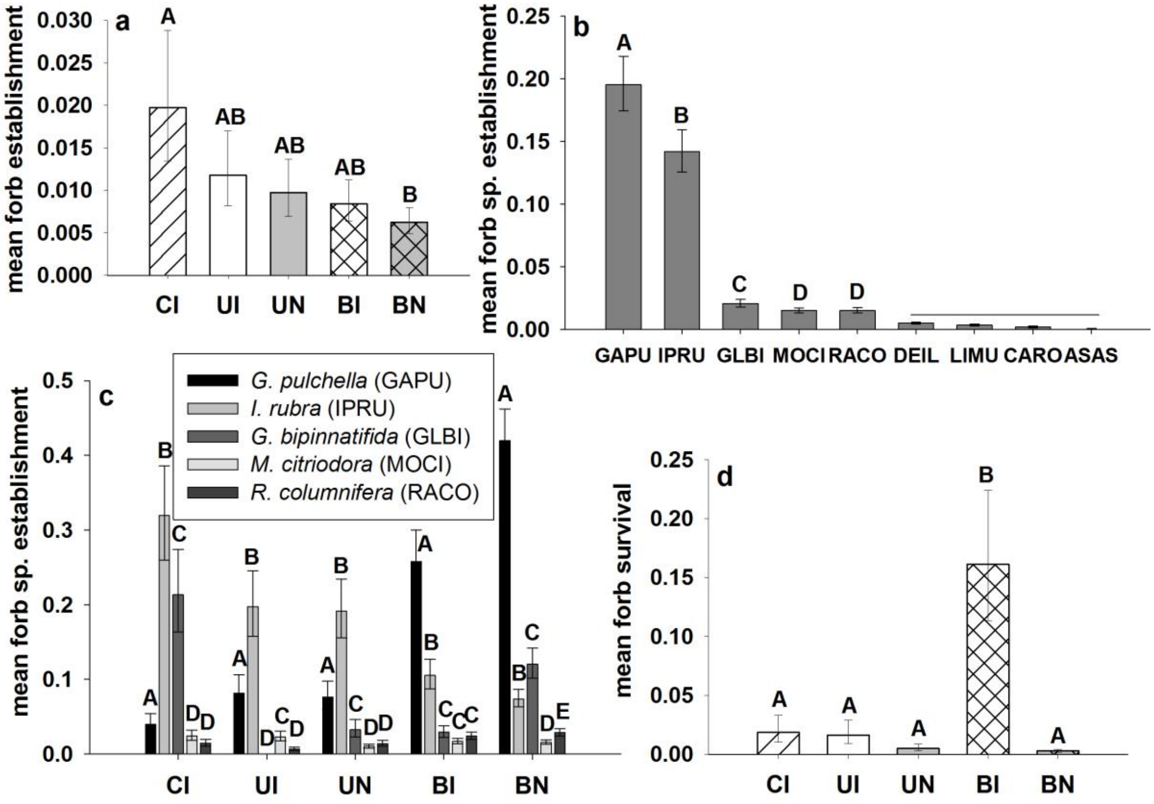

Figure 1.2: The effects of treatment and initial species composition on forbs. Establishment recorded 5 months post-treatment in spring 2010; survival recorded in fall 2010. Treatment acronyms: C=clipped, U=unmanipulated, B=burned, I=invasive, N=native. See Table 3 for species acronyms. (2a) Pooled forb establishment across treatments, (2b) Individual forb species establishment. (2c) Effect of treatment on different forb species (treatment x species interaction). (2d) Pooled forb survival across treatments. Bars with the same letter are not significantly different. Letters indicate significant differences between species within treatments in 2c and 2d. In 2a and 2b, bars with the same letter are not significantly different.

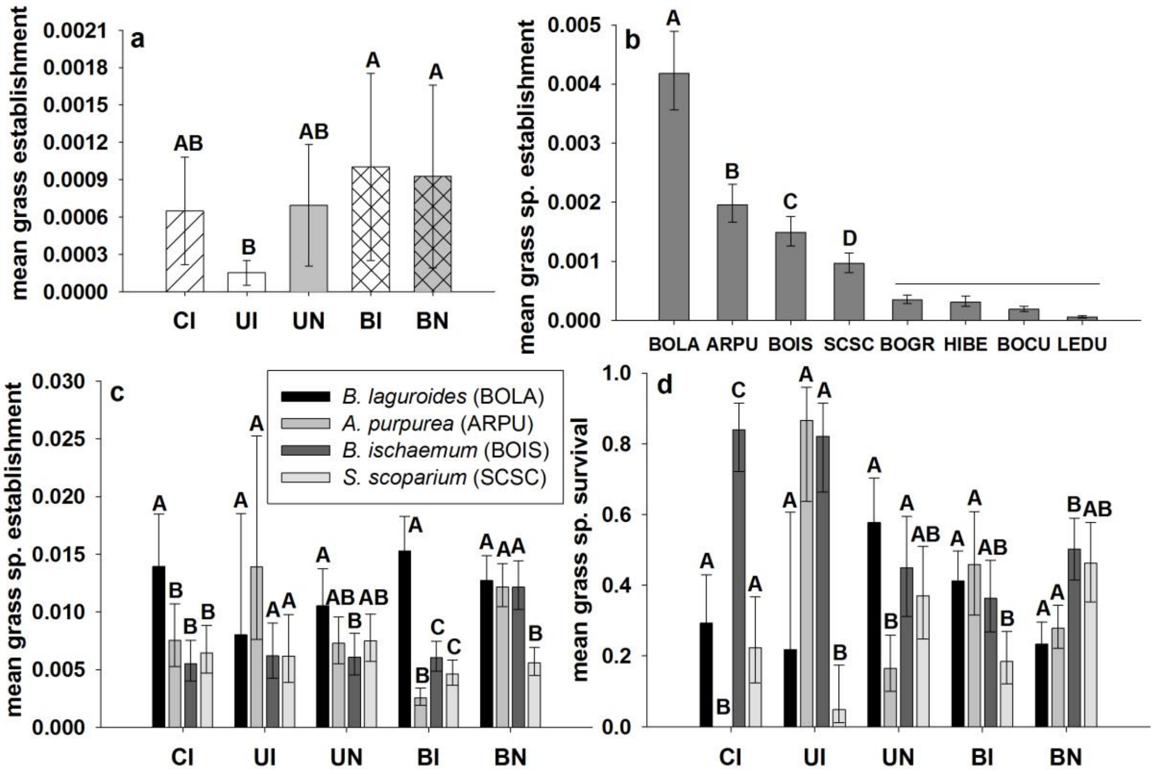

Figure 1.3: The effects of treatment and initial species composition on grasses. Establishment recorded 5 months post-treatment in spring 2010; survival recorded in fall 2010. Treatment acronyms: C=clipped, U=unmanipulated, B=burned, I=invasive, N=native. See Table 3 for species acronyms. (3a) Pooled grass establishment across treatments, (3b) Individual grass species establishment. (3c) Effect of treatment on different grass species establishment (treatment x species interaction. (3d) Effect of treatment on different grass species survival (treatment x species interaction). Letters indicate significant differences between species within treatments in 3c and 3d. In 3a and 3b, bars with the same letter are not significantly different.

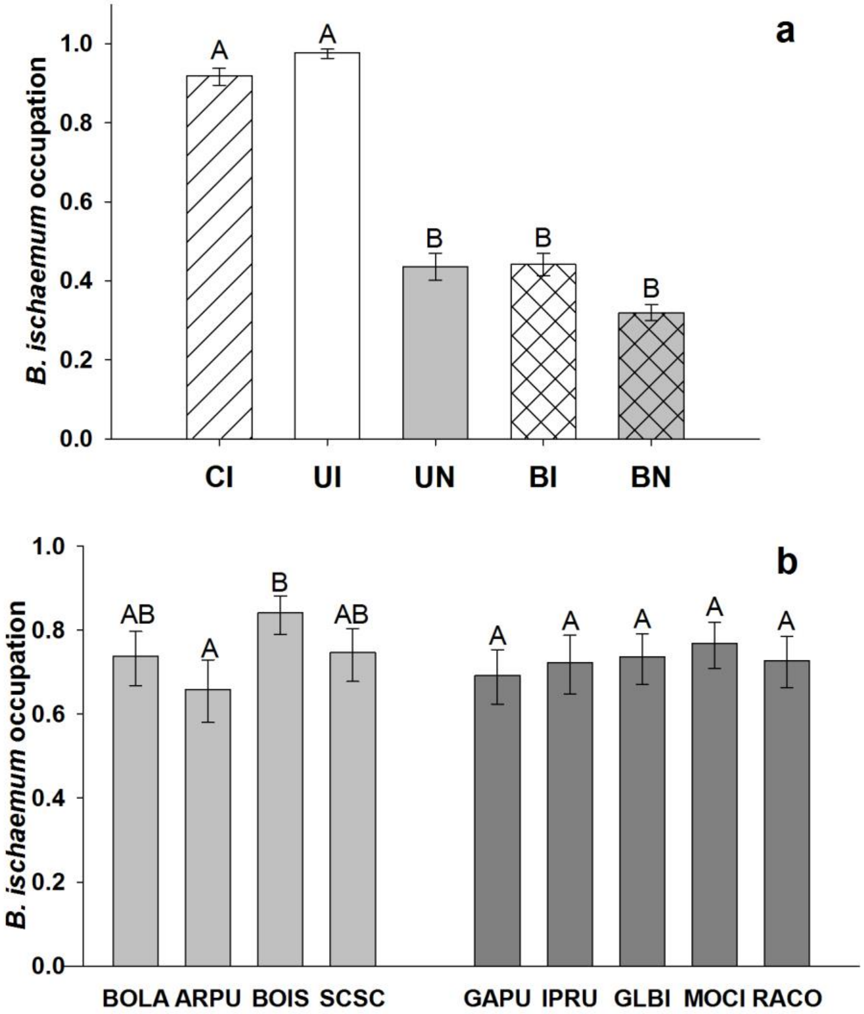

Figure 1.4: Probability that the invasive grass *Bothriochloa ischaemum* occupied a row in spring 2011 (20 months post-treatment). (4a) Treatment effects on *B. ischaemum* occupation: persistence in clipped-invasive-dominated plots and unmanipulated-invasive-dominated plots (CI, UI), re-invasion of burned-invasive-dominated plots (BI), and invasion of native-dominated plots (UN, BN). (4b) Species effects on *B. ischaemum* occupation. Grass species (light gray bars) and forb species (dark gray bars) were compared separately. See Table 1.3 for species acronyms. Bars with the same letter are not significantly different.

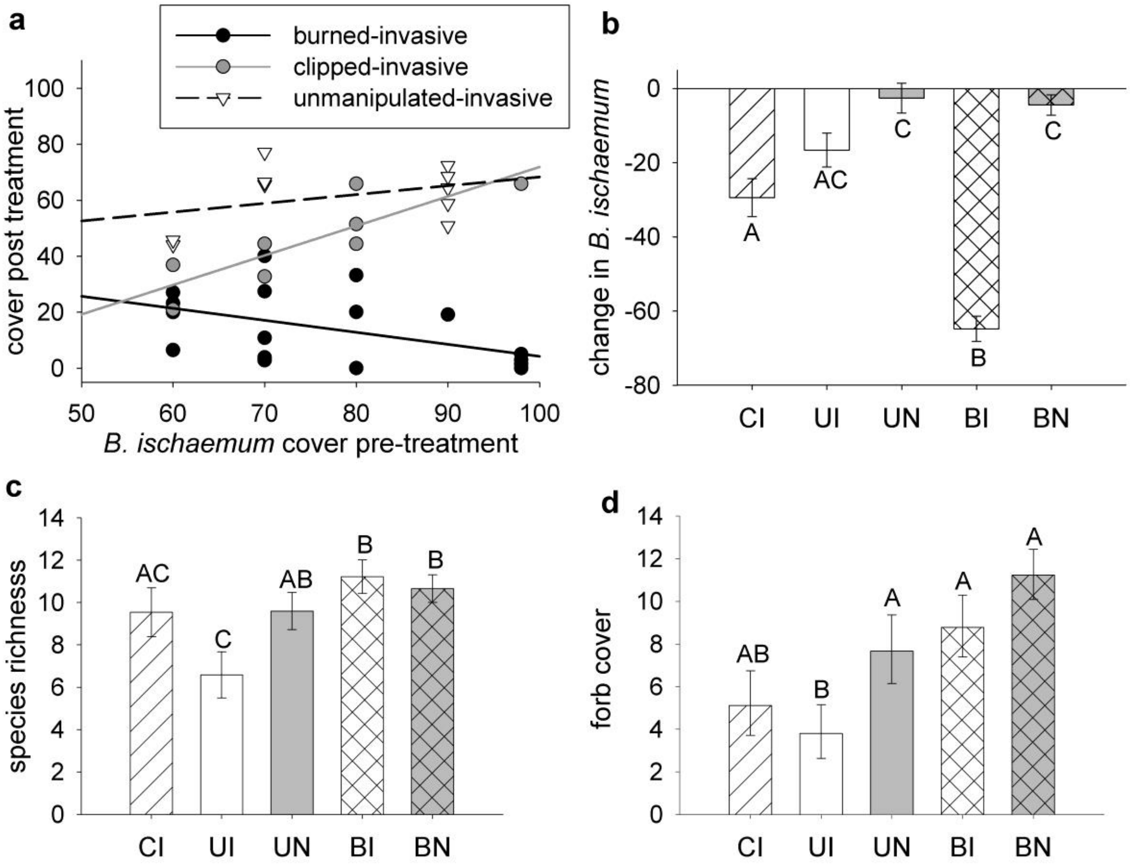

Figure 1.5: Effects of treatment and initial species composition on "background vegetation", i.e, plants not from added seed. (5a) Relationship between pre-treatment *B. ischaemum* cover and post-treatment *B. ischaemum* cover in invaded plots. (5b) Pre-treatment to post-treatment change in *B. ischaemum* across treatments. (5c) Species richness in spring 2011, post-treatment. (5d) Forb cover in spring 2011, post-treatment.

Chapter 2: The joint effects of fire and deer herbivory on hardwood regeneration in central Texas woodlands

ABSTRACT

Oaks (*Quercus* spp.) are not regenerating in forests and woodlands in central Texas and elsewhere. This is usually attributed to fire suppression. However, overabundant white-tailed deer (*Odocoileus virginianus*) also limit oak regeneration. I hypothesized that fire re-introduction and protection from deer would increase the number and growth of hardwood seedlings, saplings, and sprouts in a central Texas woodland co-dominated by Texas red oak (*Quercus buckleyi*) and Ashe juniper (*Juniperus ashei*). I measured the independent and joint effects of prescribed fire and deer herbivory on the number, size, and growth of juniper and hardwoods, tree mortality, canopy cover, and deer browse. I collected data one year before and three years after deer-fence construction and prescribed fire. Fire stimulated re-sprouting in oak and other hardwoods, but had no detectable effect on seedlings or saplings, even three years later. Deer exclusion increased the number of seedlings transitioning to the sapling size class. Both fire and deer exclusion together were required to increase average sprout height above the browseline. The apparent adaptations of native hardwoods to fire are the strongest evidence we have for an important role for fire pre-settlement. The results also suggest that fire suppression in central Texas, and other parts of the south-central US is causing a shift not to more mesic-adapted species as observed in the eastern US, but to juniper (*Juniperus* spp.), which is at least as xeric-adapted as oak. Therefore, our thinking of the 'oak regeneration problem' needs to be revised and expanded to include the diverse regions that are affected. It is likely deer control is necessary to allow fire to have positive effects on the regeneration of oaks and other hardwoods in central Texas, and wherever deer are over-abundant. Moreover, the negative effects of deer herbivory on

oak growth may partially account for reported failures of fires alone to promote hardwood regeneration elsewhere.

INTRODUCTION

Oaks (*Quercus* spp.) are not regenerating in many woodland sites in central Texas, resulting in fewer saplings than mature trees (Doyle, 2012; Russell and Fowler, 2004; 2002). Oak regeneration failure is also occurring in forested sites in the eastern United States (Dey and Fan, 2009; Nowacki and Abrams, 2008), the Ozark Mountains in the central US (Dey and Hartman, 2005), and the western US (Tyler et al., 2006). As oaks decline they are often replaced by shade-tolerant, fire-intolerant species (Hart et al., 2012; Nowacki and Abrams, 2008). This dominance shift has important impacts on ecosystem processes and biodiversity throughout the affected regions (McShea et al., 2007).

Most of the research regarding oak regeneration failure has been done in the Ozarks (central US) and northeastern US, where oaks are frequently replaced by maples (*Acer* spp.) and other shade-tolerant hardwood species, a process known as mesophication (Abrams, 1992). Mesophication occurs under fire suppression because oaks are relatively shade-intolerant and fire-tolerant due to their thick bark and large investment in below-ground resources; maples are relatively shade-tolerant and fire-intolerant (Nowacki and Abrams, 2008; Rentch et al., 2003). Supporting evidence in those regions is provided by the coincidence of fire suppression, oak decrease, and maple increase, and by tree ring studies of fire frequency (Abrams, 1992; Nowacki and Abrams, 2008). However, fire suppression is also shifting species composition in the south-central US. This shift in species composition is not to more mesic species such as maples, but to *Juniperus* spp., which are at least as xeric as oaks (Burton et al., 2010; DeSantis et al., 2011; Murray et al., 2013; Russell and Fowler, 2002; Yao et al., 2012). To further understand the vegetation dynamics in these fire-suppressed *Juniperus*-dominated woodlands, we conducted a prescribed fire experiment in central Texas woodland.

The study of prescribed fire adds to our understanding of the likely pre-settlement role of fire in maintaining oak dominance. However, the use of fire to stimulate oak regeneration in US woodlands and forests is still experimental (T. A. Barnes and Van Lear, 1998; Brose et al., 2007; Burton et al., 2010; Dey and Hartman, 2005; Lanham et al., 2002). A recent review (McEwan et al., 2010) and meta-analysis (Brose et al., 2013) found that single dormant-season fires are often insufficient to increase oak regeneration. Multiple fires combined with overstory thinning are generally more successful than single fires (Hutchinson et al., 2012), but results vary widely. Oaks readily resprout following fire, however, it is unclear if prescribed fire increases oak acorn germination, seedling establishment, or the growth of advanced regeneration (Brose et al., 2013), all key factors in restoring oak dominance. In some systems where community composition and structure have been altered beyond historical conditions, a transition from one stable state to another may have occurred (Briske et al., 2006). If so, the simple reintroduction of fire alone may not be enough to restore oak regeneration.

Central Texas woodlands on limestone-derived soils are co-dominated by *Juniperus ashei* (Ashe juniper, hereafter juniper) and *Quercus buckleyi* (Texas red oak, hereafter oak). Woodlands of this type are common on hillsides on the eastern Edwards Plateau (Diamond and True, 2008). The estimated fire frequency for the past half-century in *Q. buckleyi* woodlands is to be 2.2 to 2.6 years. These fires were likely frequent, heterogeneous surface fires that occurred primarily in dry years (Murray et al., 2013). Historic documents suggest that frequent low and high severity fire maintained much of central Texas as savanna (Bray, 1904). Oak regeneration failure in central Texas appears to be creating juniper-dominated woodlands, rather than mesophication resulting in maples or other mesic-adapted species (Murray et al., 2013; Russell and Fowler, 2002). Similarly, drought and fire suppression are thought to drive the replacement of an oak-dominated community by another juniper, *Juniperus virginiana*, in a xeric site in Oklahoma, US (DeSantis et al., 2011). The estimated fire return interval for post-oak (*Q. stellata*) woodlands in northeast Texas, prior to European influence in 1820, is 6.7 years (Stambaugh et al., 2011); central Texas probably had a similar fire frequency. Based on fire scars, Yao et al. (2012) inferred that most fires in the previous 80 year (i.e., since 1930) in this region have been low intensity. Central Texas woodlands are the driest location east of California in which the oak regeneration failure has been studied: average annual precipitation at the study site was 91.97-cm (NCDC). It has been suggested that xeric oak woodlands should be more resistant to mesophication under fire suppression due to physiological adaptations to drought (Nowacki and Abrams, 2008). This may be true, but it is evidently not protecting oak woodlands in Oklahoma and central Texas from oak regeneration failure and the resulting changes in species dominance that are likely caused by fire suppression.

Fire reintroduction alone may be inadequate to restore oak regeneration because other factors are equally or more important (Arthur et al., 2012; McEwan et al., 2010). The white-tailed deer population is extremely high in central Texas (Mostyn, 2001) and throughout the US. Herbivory by white-tailed deer has been demonstrated to limit oak regeneration in central Texas (Russell and Fowler, 2004; 2002) and elsewhere (Côté et al., 2004; Rooney and Waller, 2003). Deer herbivory and a lack of fire are not mutually exclusive explanations for the failure of oak regeneration. It is likely both are involved, acting either additively or synergistically. However, few previous studies have simultaneously examined the effects of both fire and deer herbivory on oak recruitment despite strong evidence that both are important drivers of plant community trajectories.

This study examined the independent and joint effects of fire and deer herbivory on oak regeneration in central Texas woodlands. Based on the probable role that fire once played, we hypothesized that all hardwood species, but especially oak, would resprout following fire. I also predicted that prescribed fire would decrease canopy cover, increasing light availability. Higher light availability should increase the abundance and height growth rate of hardwood seedlings and saplings. Oaks are a preferred deer browse species while junipers are strongly disliked (Armstrong and Young, 2002). I therefore expected that protection from deer herbivory would increase hardwood sprout, seedling and sapling growth rates. Because it is possible that fire alone may not be enough to allow oak regeneration, we designed the study to measure the independent and joint effects of protection from deer herbivory and fire.

METHODS

Study site

I conducted the study in golden-cheeked warbler habitat at Balcones Canyonlands National Wildlife Refuge (BCNWR), located on the eastern Edwards Plateau of central Texas. A two-way factorial experiment (N=5, 20 total 11-m radius plots) with burning and deer herbivory as treatments was set up in a woodland co-dominated by *Quercus buckleyi* and *Juniperus ashei* (Fig. 2.1). Other hardwood species such as black cherry (*Prunus serotina*) and possumhaw (*Ilex decidua*) were minor components. The site had no recorded history of management or fire since 1970. Deer densities at BCNWR averaged 1 deer/11.33 ha from 2005-2009 (spotlight deer surveys, C. Schwope, pers. comm), lower than the region-wide average of 1 deer/1.62 ha (Mostyn, 2001).

Experimental design

Initial data were collected in summer 2009 from all 20 plots before any treatments were imposed using FIREMON (Fire Effects Monitoring and Inventory Protocol), a standard methodology used in fire-effects research (Lutes et al., 2006). Seedlings (woody plants < 1.5-m tall that were not part of a larger individual) were sampled in a 3.57-meter radius (.01 hectare) circle in the center of each plot, while saplings and mature trees were sampled in the entire 11-m radius plot. I recorded species and height class (0-0.2m, 0.2-0.4m, 0.4-0.8m, 0.8-1.2m, or 1.2-1.5m) of each seedling. I recorded species, number of stems in each DRC (diameter at root crown) class (Table 2.1), and height to the nearest 0.1-m of each sapling (woody individuals > 1.5-m tall, with a DRC < 10.16-cm) and mature tree (woody plants with a DRC ≥ 10.16-cm). In summer 2009 each mature tree was tagged with a unique number. The diameter at breast height (DBH) was measured at the tag in 2009 and subsequent years. A sprout was defined as stem with a DRC < 5.08-cm that arose from the base of a mature tree; sprouts were present pre-fire and post-fire. The number of sprouts in each DRC class (Table 2.1) and the height of the tallest sprout in each DRC class were recorded for each mature tree. I calculated average sprout height per tree as the average of the tallest sprout in each of the two DRC classes of sprouts.

In February 2010 a deer exclosure was constructed in the middle of the site, containing 10 of the 20 plots (Fig. 2.1). Five plots inside and five plots outside the exclosure were randomly assigned to be burned. Additionally, all juniper saplings were cut in the plots that were to be burned. The resulting woody debris was spread out within those plots; an effort was made to avoid piling debris around mature trees. The resulting arrangement of slash would best be represented for fire behavior modeling as SB1, Low Load Activity Fuel, using Standard Fire Behavior Fuel Models (J. H. Scott and Burgan, 2005). A second vegetation survey of all plots was done in summer 2010 after cutting and fence construction, using the methods described above. In December 2010 the prescribed fire was implemented by burning ‘contour strips’ using hand ignition with drip torches to minimize fire intensity. Fire effects varied throughout the study area, but would best be characterized by moderate fire intensity: the sub-canopy was scorched but the upper canopy remained intact. Some of the study area experienced moderate/high fire intensities: the upper canopy was also scorched. Post-fire vegetation was sampled again in summer 2011 and 2012. In 2012 we quantified browsing rate on sprouts by counting the number of deer-browsed and unbrowsed stems. A stem on a given sprout or sapling was considered browsed if at least one branch of current year growth was browsed by deer. In summer 2013 all seedlings and hardwood saplings were re-sampled. Browse was quantified on saplings but not sprouts in 2013.

Hemispherical canopy photographs were taken in each of the 20 plots at 9 locations per plot with a hemispherical lens (Sigma 8mm f/3.5 EX DG circular fish eye lens) in 2011. The photographs were converted into binary images (canopy cover/sky) using Gap Light Analyzer (GLA) imaging software (Frazer et al., 1999). Canopy openness, from 0% (no canopy cover) to 100% (total canopy cover), was calculated from the binary images using GLA, and then averaged for each plot.

Data analysis

Each response variable was analyzed with one or more generalized linear models (Table 2.2). Distributions varied, but in all cases we used the standard link function for that distribution (Table 2.2 legend). If the response variable was a count (e.g. number of seedlings), we initially assumed a Poisson distribution. If we then found that the count data were over-dispersed (Pearson χ^2/df much greater than 1) we used a negative binomial distribution. If the response variable was survival (0 = dead, 1 = alive) or browsing (0 = unbrowsed, 1 = browsed), we used a binomial distribution. If the response variable was height or canopy openness we used a normal distribution with an identity function link. Due to some problems with convergence, all of the models used treatment (3 df) to represent the four treatment combinations: control, burn-only, fence-only, burn-fence. The separate effects of burning, of fencing, and of their interaction were tested with the appropriate contrasts (1 df each). The Kenward Roger degrees of freedom approximation was used in all models. In any analysis with a significant treatment x year interaction effect, comparisons were made among years within treatments and were adjusted with Tukey-Kramer for multiple comparisons.

I examined the effects of fire and deer herbivory on numbers of seedlings, saplings, and sprouts (Table 2.2). There was a marginally significant treatment x year interaction effect ($P = 0.0505$) on oak seedling numbers, apparently due to the drought that occurred in year 3 (year 2010, immediately post-fire, 49% decrease in total rainfall). Therefore, we did two additional analyses of oak seedling number to see if they responded to and recovered from the drought similarly (Table 2.2). The number of oak saplings could not be analyzed separately because there were too many plots with zero oak saplings; we therefore pooled all hardwood saplings and dropped the 3 plots that had no hardwood saplings over the entire 5 years. There were too few non-oak hardwood trees to analyze separately. Instead, two chi-square tests were used to test whether the numbers of non-oak hardwood sprouts were equal in burned or fenced areas pre-treatment and post-treatment (2x2 contingency table, burning or fencing x time).

RESULTS

The number of oak seedlings (individual stems < 1.5-m) was highly dependent on year ($P < 0.0001$, Fig. 2.2a), significantly decreasing in year 3 (2011). That year was exceptionally dry; with a 49% decrease in rainfall. However, treatments did not significantly affect oak seedling numbers during the drought (years 2 (2010) and 3 (2011), Table 2.2, $P = 0.066$) or after the drought (years 4 (2012) and 5 (2013), Table 2.2, $P = 0.747$). There was a significant treatment x year interaction effect on black cherry seedlings ($P < 0.001$, Fig. 2.2b): seedling numbers increased in year 3 (2012) in the burned-only plots and remained high in the following year. There was a significant treatment x year interaction effects on juniper seedlings (Table 2.2, $P < 0.0068$). Fire killed 89.1% of juniper seedlings. There were still significantly fewer juniper seedlings in burned plots in in year 5 (2013) than in year 1 (2009), indicating a slow recovery (Fig 2.2c).

There was a significant treatment x year effect on hardwood saplings (Table 2.2, *P* = 0.0109). There were more hardwood saplings in the fenced-only plots, reaching significance four years after fence construction (year 1 (2009) vs. year 5 (2013) contrast, *P* = 0.044, Fig. 2.3a). The number of hardwood saplings in the burned-fenced treatment decreased by more than half in 2011, probably in response to both fire and drought (year 1 (2009) vs. year 3 (2011) contrast, *P* = 0.043, Fig. 2.3a). However, recovery was dramatic: there were 2.5 times more hardwood saplings in year 5 (2013) than at the start of the experiment (year 1 (2009) vs. year 5 (2013), *P* < 0.0001, Fig. 2.3a). Sapling numbers in the burned-only plots were initially low and never changed significantly, but did show a slight trend of decrease and increase over time. Treatment did not have a significant effect on hardwood sapling height (Fig. 2.3b), but average height tended to decrease in both fenced treatments due to the influx of new individuals into this size class. Browsing rates on burned hardwood saplings were higher (61.25±3.85% browsed) than on unburned saplings (51.04±5.10% browsed), but not significantly so (*P* = 0.1617). No new juniper saplings appeared in the plots after they were cut.

Fire significantly increased the number of oak sprouts (stems with a DRC < 5.08-cm) per tree in year 3 (2011, i.e., 6 months post-fire) in both burned-only and burned-fenced plots (Fig. 2.4a). Some sprouts died in year 4 (2012), significantly so in the burned-only treatment (year 3 (2011) vs. year 4 (2012) contrast, *P* = 0.0006). Sprout numbers increased in all treatments between year 1 (2009) and 2 (2010). Fenced-only trees continued to add new sprouts in year 3 (year 1 (2009) vs. year 3 (2011) contrast, *P* < 0.0001). Diameter at breast height (DBH) was not a significant predictor of oak sprout number (*P* = 0.1211). Fencing significantly increased sprout height in both fenced-only and burned-fenced plots (Fig. 2.4a). Fire and fencing together were required to increase average sprout height above the probable browseline of 1.5m (Fig. 2.4a, dotted line). All hardwood species in the study site sprouted after fire (Table 2.4). Burning nearly tripled the total number of non-oak hardwood sprouts (X^2=0.001, Table 2.3). The proportion of hardwood sprouts in fenced and unfenced plots did not significantly differ (X^2=0.252).

Mature juniper in burned areas had a significantly lower survival in year 4 (2012, 1.5 years after fire) than unburned juniper (P = 0.0035, Fig. 2.4b). Larger juniper trees were more likely to survive to year 3 (2011) (P = 0.0106) and to year 4 (2012) (P = 0.0408). I define top-kill as the death of an oak stem that reaches the tree canopy. The fire top-killed some oaks: 94.15% of oaks survived in unburned areas, while only 72.83% did so in burned areas in year 3 (2011) (P = 0.0183, Fig. 2.4c). Larger oaks were more likely to survive to year 4 (2012) (P = 0.0204); the average DBH of dead trees was 15.77-cm, 17.61-cm of live trees. None of the top-killed oaks died; all of them had sprouts. Sprout number after the fire was not significantly related to oak survival. There was a strong trend (P = 0.0701) for oak sprouts to be browsed more often in burned plots (80.44±2.79% browsed) than in unburned plots (70.84±3.73% browsed). Canopy openness was greater in burned than unburned plots (Fig. 2.5).

DISCUSSION

Effects of fire on regeneration; role of fire in central Texas woodlands

As has been found in other oak-dominated woodlands and forests (Brose et al., 2013; McEwan et al., 2010), low-intensity fire stimulated re-sprouting in oak and other hardwood species. As planned, the fire remained a surface fire and successfully increased light availability while not substantially altering mature tree canopy composition. The fire had no detectable effect on the number of hardwood seedlings (individual plants < 1.5 m tall) or on sapling abundance or height (individual plants taller than seedlings with root crown diameter (DRC) < 10.14 cm) even three years later. In contrast, Brose et al. (2013) reported that fires tend to decrease oak sapling numbers, and increase oak seedling numbers. Yao et al. (2012) reported a non-significant but positive difference in the number of oak seedlings in plots near trees with fire scars < 40 yr old compared with plots near trees without fire scars in central Texas. A combination of deer, drought, and low fire-intensity may have been responsible for the lack of effects on seedlings and saplings in this study, as discussed below.

Resprouting is an important functional trait that allows trees to persist after fire (Clarke et al., 2013) and may be an adaptation to fire (Keeley et al., 2011). All of the hardwood species in the study site re-sprouted after the fire, especially oak, suggesting that these species are fire-adapted. Furthermore, it suggests that periodic low-intensity fires occurred pre-settlement. This hypothesis is also supported by the observation that no mature hardwood trees died and few lost their entire canopies. In the absence of other evidence for pre-settlement fire frequency and intensity, the apparent adaptations of native hardwood species to low-intensity fire are among the strongest evidence we have for an important role for fire pre-settlement. Surface fires from adjacent savannas (Fuhlendorf et al., 1996) were probably an important source of pre-settlement woodland fires. Since settlement, and especially in the past 100 years, fewer savanna fires to burn into woodlands (Twidwell et al., 2013), active fire suppression, and the cessation of deliberate burning have all reduced woodland fire frequency.

Our results support the hypothesis that the decline in fire frequency in central Texas has contributed to the observed decline in oak regeneration (Russell and Fowler, 2002), and the increase in fire-susceptible juniper. They also suggest that our thinking of the ‘oak regeneration problem’ needs to be revised and expanded to include the diverse regions that are affected. For example, junipers have also replaced and encroached upon oaks in Oklahoma woodlands (DeSantis et al., 2011; 2010). Nowacki and Abrams (2008) called the shift from the more xeric-adapted oaks to more mesic-adapted species, predominately maples (*Acer spp.*) ‘mesophication’, and argued it should be slow or non-existent in more xeric sites. All of central Texas, like the south-central US in general, is xeric by comparison with the forests that Nowacki and Abrams (2008) were describing, yet the suppression of fire is apparently also creating a shift in dominance throughout this region (Burton et al., 2011; DeSantis et al., 2011). This shift is not to mesic-adapted species, but to juniper, which is at least as xeric-adapted as oak. However, the shift from a fire-dependent oak-dominated woodland to a surface fire-resistant juniper-dominated woodland shares many characteristics with the transition from an oak-dominated system to a maple-dominated system. In both instances fire-intolerant and shade-tolerant species (maple, juniper) replace oak species; in both instances they alter the fuel load, making surface fire less likely. Maple tree litter is more shallow and dense that oak litter. It therefore retains more moisture and is less likely to burn and to sustain a fire (Knoepp et al., 2005). Similarly, juniper litter is more shallow, dense, and less likely to burn than oak litter (F. Kay, unpublished data). Consequently, wildfires are unlikely to occur as surface fires; if they occur, it will be as crown fires (Reemts and Hansen, 2008). This risk of catastrophic wildfires provides an additional reason for prescribed burning in central Texas woodlands.

The restoration of oak regeneration requires the production of new individuals. Prescribed fire can increase oak seedling abundance by increasing flowering, acorn production, germination, and establishment, also by stimulating advanced regeneration (Arthur et al., 2012). However, oak seedlings did not positively respond to fire in this study. Oak seedling abundance tracked weather conditions, decreasing in the drought, and increasing in subsequent years in all treatments. There are at least three non-mutually exclusive reasons my results differed from some published studies (Brose 2013): (a) insufficient advance regeneration, (b) low fire-intensity, (c) severe drought (a 49% decrease in total rainfall the first year after fire).

Hardwood species are more likely to benefit from a fire if there are well-established plants (advance regeneration) before the fire (Brose et al., 2013). Our study site may not have had enough advance regeneration, likely because of overabundant deer, which can reduce seedling survival (see below). Our prescribed fire may have had too low intensity. Higher intensity fires increase light availability, which increases oak seedling growth (Arthur et al., 2012). Multiple fires, in combination with overstory thinning, are generally more effective at restoring oak regeneration than single fires (Brose et al., 2013; Hutchinson et al., 2012; McEwan et al., 2010). This suggests that oak regeneration in the past might have been episodic and followed high-intensity fires.

The drought probably had multiple negative effects on oaks. It likely reduced post-fire acorn numbers: acorn production is highly dependent on weather, with large variation among individuals and years (Arthur et al., 2012). Because prescribed fires can kill acorns, especially those at the soil surface (Greenberg et al., 2012), oak seedling recruitment is likely dependent upon subsequent acorn crops, which were negatively affected by the drought. Seedling recruitment may be higher in my site in the future after the drought ends. As prescribed fire is used to address dominance shifts in more xeric oak-dominated woodlands (DeSantis et al., 2011), negative drought effects will become increasingly important.

Once oak seedlings are established, they must compete with other species that may better survive the fire and/or grow more quickly (T. A. Barnes and Van Lear, 1998; Brose et al., 2013; Green et al., 2010). In this study, fire killed nearly 90% of juniper seedlings. They did not recover even 2.5 years after the fire, while oak recovered and black cherry increased. I therefore conclude that juniper seedlings recover and grow more slowly than hardwood seedlings after fires in central Texas, at least in the short-term. Reemts and Hansen (2008) found that juniper recovered more slowly than hardwoods after a high-intensity crown-fire in mixed oak-juniper woodland, finding very few juniper saplings even nine years after the fire.

Effects of deer

Deer exclusion increased the number of seedlings entering the sapling size class, an important variable because it reflects growth past the probable browse height. The greatest stem growth was in plots that were both burned and fenced. Growing above the browseline is critical: once a palatable plant passes this threshold, it has a much higher probability of becoming a canopy tree. Many preferred browse species are kept below the browseline due to constant browse pressure (Russell and Fowler, 2004). This constant removal of biomass and subsequent compensatory growth can deplete a plant's carbon reserve and reduce survival (Côté et al., 2004; Russell et al., 2001).

Deer densities at the study site were relatively high, compared to other parts of the US, although lower than is common in this region (Mostyn, 2001). In this region, and the rest of the US, past densities were maintained by human hunting, predators, and reportedly screwworm parasitism (L. Gilbert pers. comm.). The extremely high deer densities in recent decades represent a novel state, which is likely to cause novel vegetation dynamics, especially when fire is re-introduced.

Interaction of fire and herbivory

I found that stems in burned plots were more likely to be browsed than those in unburned plots, although the effect was not significant. This difference was expected, as previous studies have found that fire increases deer browse rate, usually as a result of increasing shrub nutritional value and/or reducing plant physical defenses (Lashley et al., 2011; Schindler et al., 2004).

Both fire and protection from deer herbivory were required to increase average oak sprout height above the probable browseline of 1.5-m. This is a novel finding that demonstrates the importance of including multiple factors in any study of community composition. Although this finding is novel, we expect it to be general because the mechanisms driving it are general. Fire is well known to trigger oak re-sprouting and sprout growth rate (Brose et al., 2013; Lanham et al., 2002). Deer are well known to negatively impact hardwood growth (Rooney and Waller, 2003; Russell et al., 2001). It is therefore likely that deer control will be necessary to allow fire to have positive effects on the regeneration of oaks and other hardwoods in this region and in other regions where deer are overabundant. Moreover, it seems likely that this interaction between fire and deer partially accounts for the failure of fire alone to promote oak regeneration observed in other studies (Brose et al., 2013; McEwan et al., 2010). Overabundant deer coupled with little to no oak advance regeneration are the prevailing conditions across much of the US. These novel conditions make the use of a single fire alone an untenable strategy. This mismatch between historical, present, and future dynamics is a general challenge in restoration ecology (Hobbs et al., 2011). Often, as observed here, the simple reintroduction of the historical disturbance regime is not enough to shift vegetation trajectories in the desired direction (Collins and Carson, 2002; Kern et al., 2012). Future research will need to integrate the multiple drivers of oak regeneration.

Table 2.1: Diameter at root crown classes used to distinguish saplings and mature trees for vegetation sampling 2009-2013.

DRC class midpoint	**Range**	**Size class**
0.76 cm 0.3 in	0 – 1.52 cm 0 – 0.3 in	sapling
3.05 cm 1.2 in	1.52 - 5.08 cm 0.6 – 2.0 in	sapling
7.62 cm 3.0 in	5.08 – 10.16 cm 2.0 – 4.0 in	sapling
12.70 cm 5.0 in	10.16 – 15.24 cm 4.0 – 6.0 in	mature tree
17.78 cm 7.0 in	15.24 – 20.32 cm 6.0 – 8.0 in	mature tree
26.04 cm 10.25 in	20.32 – 31.75 cm 8.0 – 12.5 in	mature tree
> 31.75 cm >12.5 in	> 31.75 cm > 12.5 in	mature tree

Table 2.2: All of the generalized linear models constructed in SAS 9.2 (PROC GLIMMIX). The log was used as the link function for the negative binomial and Poisson distributions, the identity was used for the normal distribution, and the logit was used for the binomial distribution. tr = abbreviation for treatment combination (control, burn-only, fence-only, burn-fence). Random effects were included to account for nesting: a(b) means that factor is nested within factor b. Year was a repeated effect with the subject plot(tr). Cov. Struc, residual covariance matrix structure, CS=compound symmetry, VC=variance components, AR(1)=autoregressive, the covariance structure that minimized the Pearson χ^2/df was chosen individually for each model.

dependent variable	species	distribution	independent	random effects	repeated effect	cov struc
seedling #	oak	negative binomial	tr, year, tr X year	plot(tr)	year	CS
seedling # (years 2 & 3)	oak	negative binomial	tr, year, tr X year, year 1 covariate	plot(tr)	year	CS
seedling # (years 4 & 5)	oak	negative binomial	tr, year, tr X year, year 3 covariate	plot(tr)	year	CS
seedling #	black cherry	negative binomial	tr, year, tr X year	plot(tr)	year	CS
seedling #	juniper	Poisson	tr, year, tr X year	plot(tr)	year	VC
sapling #	hardwoods	negative binomial	tr, year, tr X year	plot(tr)	year	VC
sapling height	hardwoods	normal	tr, year, tr X year, year 1 covariate	plot(tr)	year	VC
sapling browse	hardwoods	binomial	tr	plot(tr)	-	-
tree survival (separately for years 2, 3 and 4)	oak	binomial	tr, DBH, tr X DBH # sprouts, tr X # sprouts	plot(tr)	-	-
tree survival (separately for years 2, 3 and 4)	juniper	binomial	tr, DBH, tr X DBH	plot(tr)	-	-
sprout #	oak	negative binomial	tr, year, tr X year	plot(tr) tree(plot)	year	AR(1)
sprout height	oak	normal	tr, year, tr X year, year 1 covariate	plot(tr) tree(plot)	year	AR(1)
sprout browse	oak	binomial	tr	plot(tr) tree(plot)	-	-
canopy openness	-	normal	tr	-	-	-

Table 2.3: The proportion of non-oak hardwood sprouts in burned and unburned plots pre-treatment and post-treatment at BCNWR 2009-2012. Numbers at the top of the cell are the numbers of sprouts, below are the percent of sprouts in a given category.

	unburned	burned	**TOTAL**
pre-treatment (2009 & 2010)	92 (7.93%)	247 (21.29%)	339 **29.22%**
post treatment (2011 & 2012)	152 (13.1%)	669 (57.67%)	821 **70.78%**
TOTAL	244 **21.03%**	916 **78.97%**	1160

Table 2.4: Hardwood species in the study plots. All of these sprouted after the fire

species	common name
Celtis laevigata	sugarberry
Diospyros texana	Texas persimmon
Fraxinus texensis	Texas ash
Ilex decidua	possumhaw
Quercus buckleyi	Texas red oak
Rhamnus caroliniana	Carolina buckthorn
Prunus serotina	black cherry
Sideroxylon lanuginosum	gum bumelia
Viburnum rufidulum	rusty blackhaw

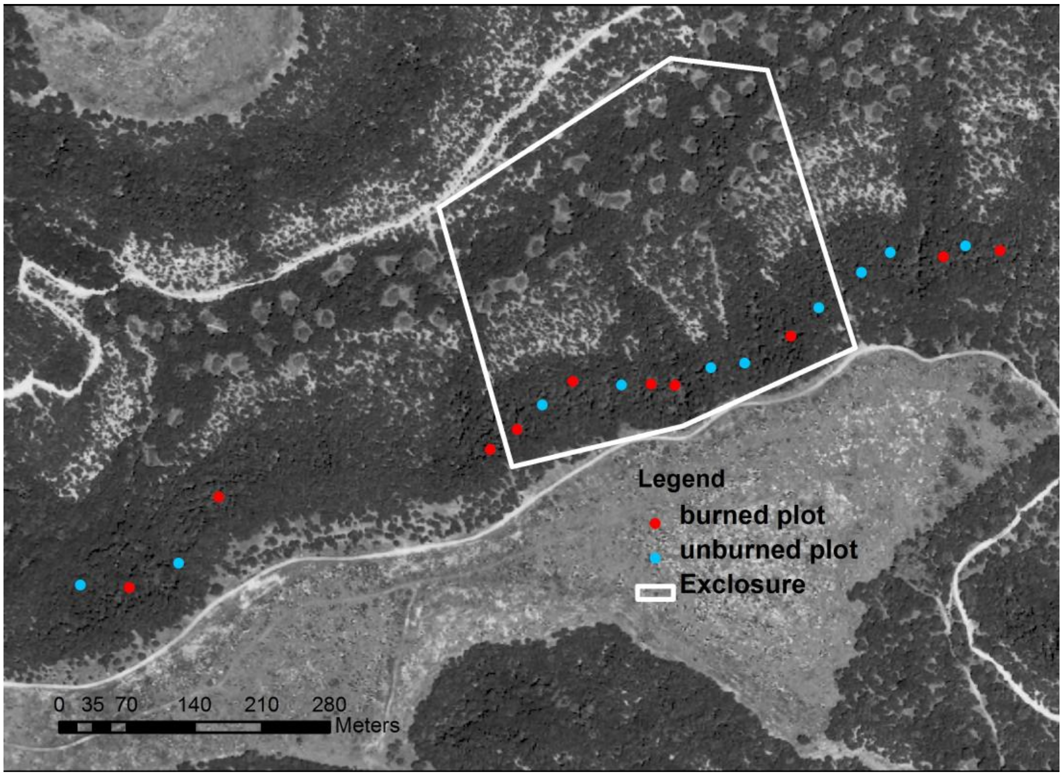

Figure 2.1: Map of the study site. Deer exclosure shown in white. Red points represent burned plots (ten total plots, five inside the exclosure and five outside the exclosure). Blue points represent unburned plots (ten total plots, five inside the exclosure and five outside the exclosure).

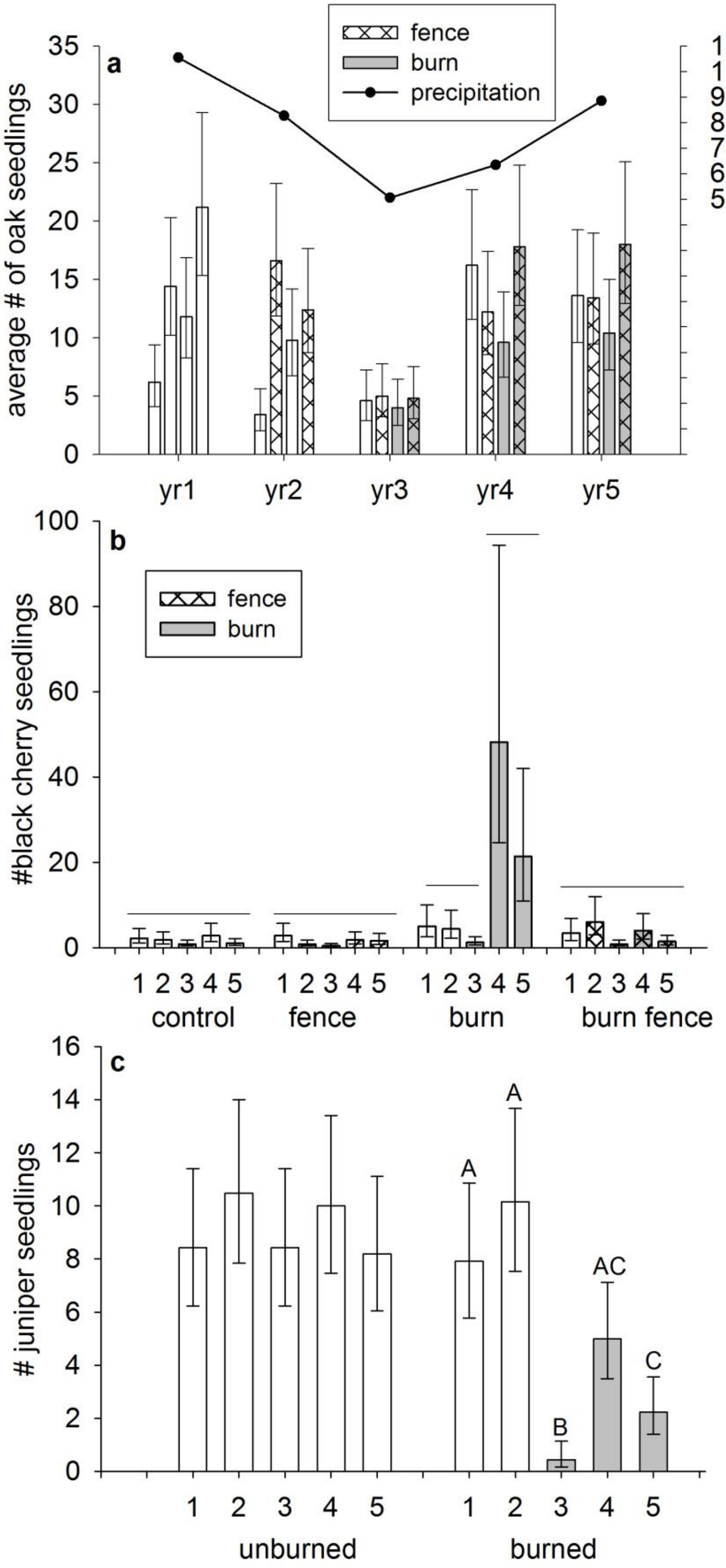

Figure 2.2: The effects of year and treatment on average seedling numbers at Balcones Canyonlands National Wildlife Refuge, 2009-2013. Seedlings are individual stems (not connected to a larger adult) < 1.5m. There was a significant decrease in oak seedling numbers in year 3 (1a). Black cherry seedlings significantly increased in burned plots, lines indicate bars that are not significantly different from each other (2b). The fire killed juniper seedlings, letters indicate significant differences between years within treatments (2c). Error bars are back-transformed ± 1 SE.

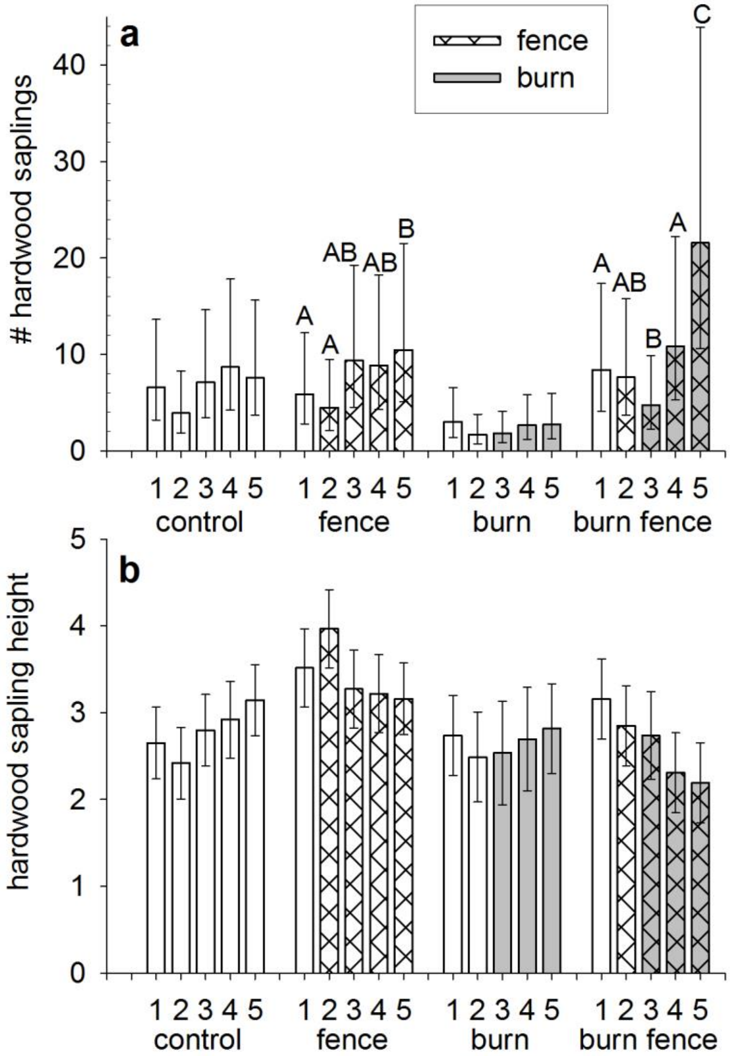

Figure 2.3: The effects of years (2009-2013, labeled 1-5 on the x-axis) and treatment on average pooled hardwood sapling number (2a) and height (2b) at BCNWR. Saplings are stems >1.5-m tall with a diameter at root crown (DRC) < 10.16-cm. Letters indicate significant differences between years within treatments. Error bars are back-transformed ± 1 SE.

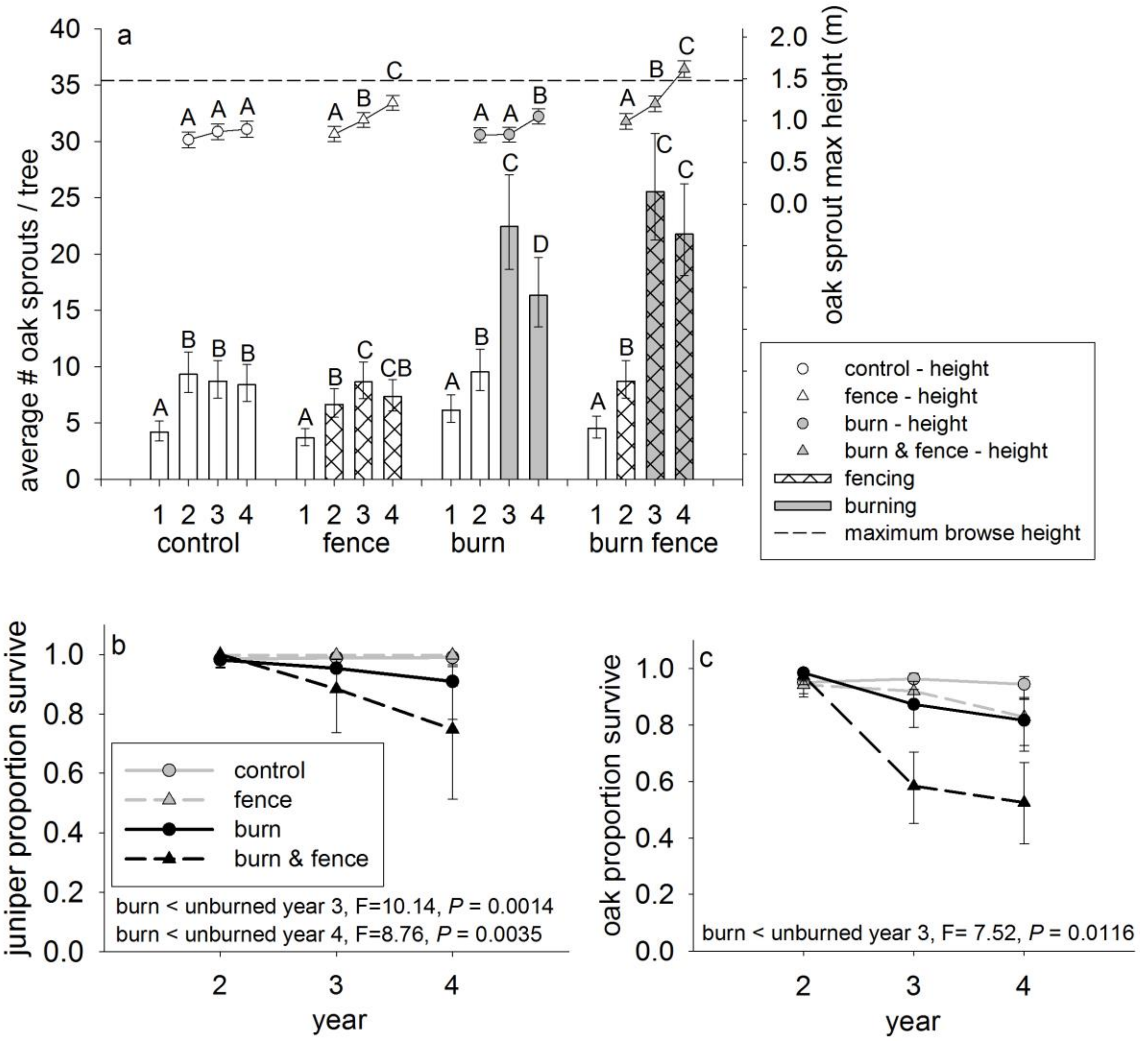

Figure 2.4: The effects of years (2009-2012, labeled 1-4 on the x-axis) and treatment on average number of oak sprouts per tree (bars) and their average height (lines & points) (3a) at BCNWR. Sprouts are stems connected to a mature tree with a DRC < 5.08-cm. There was a significant treatment x year interaction in the analysis of oak sprout number ($P < 0.001$). Letters indicate significant differences between years within treatments. 3b: proportion of mature juniper trees surviving in years 2-4 (2010-2012), 3c: proportion of mature oak trees surviving in years 2-4 (2010-2012), Error bars are back-transformed ± 1 SE.

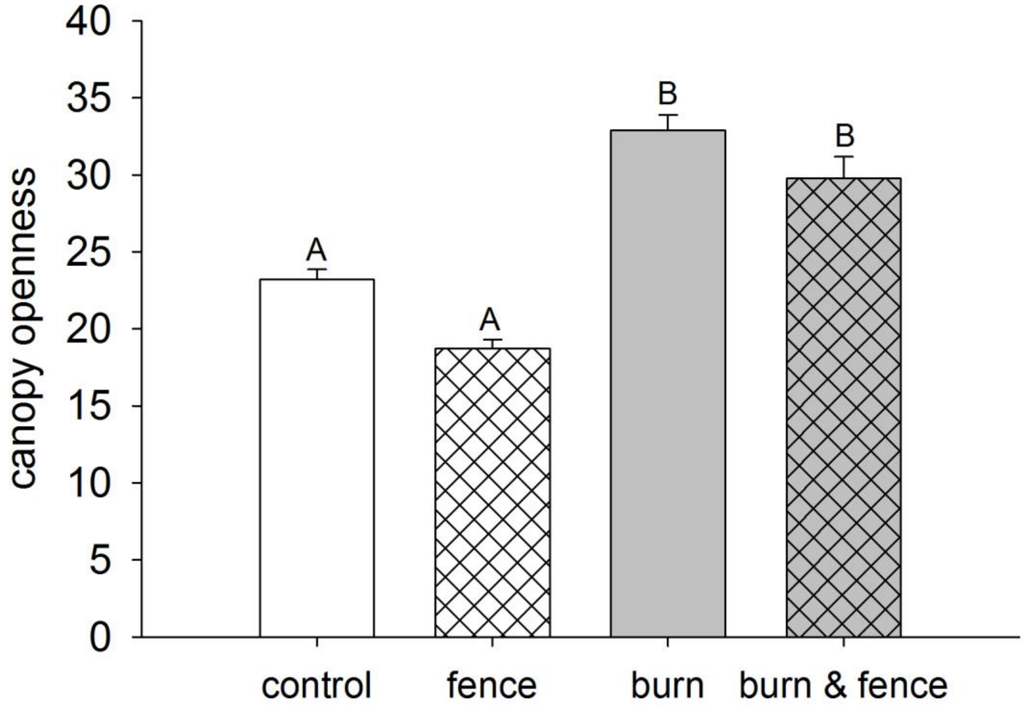

Figure 2.5: The effect of burning and fencing on canopy openness in the year after the fire (year 3, 2011). Canopy openness is one minus the amount of sky covered by tree canopy and was calculated using Gap Light Analyzer (Frazer et al., 1999). Error bars are ± 1 SE. Lines indicate groups that are not significantly different from each other.

Chapter 3: Spatial patterns imposed by slash-pile burns influence plant community trajectories inside and outside a deer exclosure in a central Texas woodland

ABSTRACT

There is strong interest in re-introducing fire in fire-suppressed systems of the United States. Doing so effectively and safely often requires fuel reduction techniques such as thinning and slash-pile burning. Slash-pile burning creates a distinct spatial pattern that is a mosaic of areas where the piles were burned ('cut-burn'), areas that were thinned and the slash removed ('cut-clear'), and untreated areas. The effectiveness of slash-pile burning and other management techniques can be affected by overabundant herbivores. I therefore conducted a factorial experiment in which each management technique (cut-clear, cut-burn, control) was replicated inside and outside a deer exclosure. In central Texas, *Juniperus ashei* (Ashe juniper) encroaches on savanna and woodland, converting them both to *J. ashei*-dominated woodland with low diversity. This negatively impacts the endangered golden-cheeked warbler, which requires mixed *Quercus buckleyi* (Texas red oak) and *J. ashei* woodland with ≥70% canopy cover. To restore golden-cheeked warbler habitat from a *J. ashei*-near monoculture, I reduced canopy cover in the study site by 30% by cutting, removing, and slash-pile burning *J. ashei* in multiple 11 m radius macroplots. I examined the effects of this common management technique on (a) grass, forb, and hardwood cover, (b) individual native and exotic species, and (c) overall plant community composition.

Cutting and removal promoted growth of remnant species, while cutting and slash-pile burning increased disturbance-adapted forbs and woody species. By removing *J. ashei* and promoting native hardwoods these management activities likely increased habitat quality for the endangered golden-cheeked warbler. However, they failed to increase *Q. buckleyi* seedling abundance. The habitat fragmentation created by canopy removal in multiple, relatively small, areas may have slowed the spread of the invasive

grass *Bothriochloa ischaemum*. It also may have reduced deer herbivory in the treated areas. Spatial patterns imposed by slash-pile burns are likely to strongly influence vegetation trajectories in other systems as well. Protection from deer herbivory by a fence significantly increased the abundance of the invasive *Lactuca serriola*. Hardwood cover in fenced cut-clear plots was lower than in unfenced cut-clear plots, indicating that deer may indirectly benefit some less palatable hardwood species by reducing competition with *L. serriola* and other palatable forbs. These results highlight the importance of considering multiple drivers of plant community composition such as spatial patterns and deer herbivory that may influence the efficacy of management techniques, and the possibility of complex interactions among the various drivers.

INTRODUCTION

Effective widespread fire suppression in the United States (US) began in the early to mid 1900's (Agee and Skinner, 2005; Nowacki and Abrams, 2008), with negative impacts on many different grassland, savanna, shrubland, woodland and forest ecosystems (DeSantis et al., 2010; Nowacki and Abrams, 2008; Romme et al., 2009; Van Auken, 2009). Fire suppression impacts differ among ecosystems, but can include loss of native biodiversity (Abrams, 1992; González-Tagle et al., 2008; Sands and Abrams, 2011), degradation of water, air and soil resources (Backer et al., 2004), and the transformation of grasslands and savannas to woodlands (Briggs et al., 2005; Van Auken, 2009). In addition, fuel loads generally increase under fire suppression, increasing the probability of catastrophic wildfires, which create both ecological and social problems (Gill et al., 2013).

Because of the negative impacts of fire-suppression, there is now strong interest in re-introducing fire in fire-suppressed forests and woodlands of the US (Pyke et al., 2010; Ryan et al., 2013). However, doing so safely and effectively often requires fuel reduction techniques, usually involving trimming or cutting down some of the woody plants following by removal or burning of the resulting material (Agee and Skinner, 2005; Brown et al., 2004). The ecological effects of fuel reduction techniques are not well understood. They are likely to be complex, due to the spatial patterns imposed by the management actions, site history, differences in the native and invasive species pool, and interactions with herbivores, among others. I conducted an experiment in a central Texas woodland to determine the effects of a common fuel reduction technique: selectively cutting, piling, and burning woody plants.

In central Texas, fire frequencies in savannas and woodlands probably began to decline when confined grazing in the late 1800's reduced fine fuels. Road construction, more effective water sources for fire-fighting, and continued grazing have further reduced fire frequencies, both in savannas and in woodlands (Fuhlendorf et al., 1996; Murray et al., 2013). The increasing dominance of the fire-sensitive woody species *Juniperus ashei* (Ashe juniper) in both woodlands and (former) savannas is probably in part due to this decreased fire frequency. *J. ashei* invasion reduces fine fuel loads and creates a shallow dense litter (F. Kay, unpublished data). These changes to the fuel load make surface wildfires unlikely and safe prescribed fires extremely difficult (but see Twidwell et al., 2013). They also increase the probability of catastrophic crown fire (Reemts and Hansen, 2008).

Land managers confronted with *J. ashei* monocultures in central Texas and with similar situations elsewhere have generally turned to thinning, that is, cutting down excess fuel (Agee and Skinner, 2005). The material that results from thinning (slash) is usually not marketable and for cost reasons must be disposed of on-site (Agee and Skinner, 2005; Korb et al., 2004). It is commonly gathered into ‘slash piles’ and allowed to dry, after which each pile is burned when conditions are suitable. Although this technique is common and widespread, there has been no research on the effects of this management technique in central Texas and only limited research elsewhere. In a ponderosa pine restoration in Arizona, US, it was found that slash-pile burning killed nearly all of the viable seed in the seedbank and the arbuscular mycorrhizal fungi in the soil. It also significantly decreased soil N and C (Korb et al., 2004). These impacts can be long lasting: slash pile burning significantly impacted the vegetation, soil nutrient levels, and soil seedbank at least 6 years after initial treatment in a longleaf pine system (Creech et al., 2012). The practice of slash-pile burning creates a distinct spatial pattern that is a mosaic of areas where the piles were burned ('cut-burn'), areas that were thinned and the slash removed ('cut-clear'), and untreated areas. I predicted that each of these three types of areas would have a distinct response to its treatment, creating a predictable spatial mosaic of plant assemblages and community trajectories. I also predicted that both the cut-burn and cut-clear treatments would increase native plant diversity, which is extremely low in sites dominated by *J. ashei* (Yager and Smeins, 1999).

Of special interest was whether thinning and slash-pile burning by itself would promote the establishment and growth of *Quercus buckleyi* (Texas red oak) and other desirable hardwood species in a nearly pure stand of *J. ashei*, without further reduction in canopy cover by fire or additional thinning. *Q. buckleyi* is desirable because it is used by the endangered golden-cheeked warbler (*Setophaga chrysoparia*). This migratory songbird nests in central Texas woodlands co-dominated by *J. ashei* and *Q. buckleyi* with an average canopy cover of ≥70% (Groce et al., 2010). *Q. buckleyi* is not regenerating in these woodlands (Russell and Fowler, 2002); this is probably true of other hardwood species as well. It is likely that fire suppression (ch. 2) and overabundant herbivores (Russell and Fowler, 2004) are contributing to the failure of *Q. buckleyi* to regenerate. I was therefore interested in whether a 30% reduction in canopy cover by thinning and slash-pile burning can increase the establishment and growth of *Q. buckleyi* and other hardwoods, thereby increasing golden-cheeked warbler habitat quality.

A common concern for land managers is whether a given management practice will have the unwanted side effect of favoring invasive species (Brooks et al., 2010;

McGlone et al., 2006). Both thinning and fire can release nutrients, increase light availability, and open colonization sites (Scharenbroch et al., 2012). Invasive species are often disturbance-tolerant, have high dispersal rates, and can grow faster than native species (DiTomaso et al., 2006). Therefore, there was concern that the cut-clear or cut-burn treatments would increase invasive species abundance. Slash-pile burns may create areas that are particularly favorable to invasive species as they cause severe soil heating, which can negatively impact the soil seedbank, the microbial community, and soil chemistry (Creech et al., 2012; Korb et al., 2004). However, severe soil heating does not necessarily promote invasive species: non-native species grew less quickly in severely burned soils than moderately burned soils after a wildfire in the Cascade Range of Oregon (Hebel et al., 2009). Fuel reduction techniques such as mastication have also been found to increase invasive species, sometimes more so than prescribed fire alone (Potts and Stephens, 2009).

Another complexity of using any management intervention is the potential for the expected effects on plants to be altered by herbivory. White-tailed deer (*Odocoileus virginianus*) are overabundant in central Texas (Mostyn 2001) and elsewhere in the US (Côté et al., 2004). High deer densities can increase the abundance of unpalatable (Rooney, 2009) and generalist species (Holmes and Webster, 2010), including invasive species (Batzli and Dejaco, 2013). They can also limit the regeneration of palatable species (Côté et al., 2004; Russell and Fowler, 2004). The joint effects of fire or other management activities and deer herbivory are not well known. Overabundant white-tailed deer were found to prefer burned areas to unburned areas in a pinyon-juniper system (Leopold and Krausman, 2002). Deer have also been shown to limit post-fire resprouting on Saint Catalina Island, CA (Ramirez et al., 2012). To better understand the interactions between management activities and herbivory, I conducted a factorial experiment in which each management treatment (cut-clear, cut-burn, control) was imposed both inside and outside of a deer-exclusion fence. I predicted that protection from deer would increase the abundances of palatable hardwood and forb species; statistical interactions between fencing and the vegetation treatments were also tested.

METHODS

Study site

The study site was located in Balcones Canyonlands National Wildlife Refuge (BCNWR), on the eastern Edwards Plateau of central Texas. This site had no recorded history of management or fire since 1970. When this study began, 96% of the mature trees (individuals with a diameter at root crown > 10.16 cm) in the study site were *J. ashei*. Deer densities at BCNWR averaged 1 deer/11.33 ha from 2005 through 2009 (spotlight deer surveys, C. Schwope, unpublished); compare this with a region-wide average of 1 deer/1.62 ha (Mostyn, 2001).

Experimental design

The central part of the site was fenced to exclude deer in February 2010 (Fig. 3.2). Also in February 2010, 30% of the canopy cover in the study site was removed. A 30% reduction in canopy cover was selected because the endangered golden-cheeked warbler prefers habitat with ≥ 70% canopy cover (Groce et al., 2010). This reduction was accomplished by cutting all of the *J. ashei* individuals in randomly located 11 m radius circles (Figs. 3.1, 3.2). As 96% of the mature trees were *J. ashei*, this cutting effectively removed 30% of the canopy cover. I refer to each cut circle as a macroplot (Figs. 3.1, 3.2). The cut *J. ashei* plants in each macroplot were piled into a ~5.5 m radius circle in the center of that same macroplot in February 2010. These piles were burned in small, high-intensity fires in December 2010. The fire consumed all piled plant material in the cut-burn treatment. No vegetation was burned outside the designated pile area. This resulted in a circular cut-burn plot surrounded by a doughnut-shaped cut-clear plot within each treated macroplot (Fig. 3.1). For this study, I randomly selected five treated macroplots inside the exclosure and another five treated macroplots outside the exclosure to survey. Ten 11 m radius control macroplots were also randomly located, five outside the exclosure and five inside the exclosure (Fig. 3.2).

Data collection

Initial data were collected in summer 2009 using FIREMON (Fire Effects Monitoring and Inventory Protocol), a standard methodology used in fire-effects research (Lutes et al. 2006) before any treatments were imposed. Seedlings (woody plants < 1.5 m tall that were not part of a larger individual) were sampled in a 3.57 m radius (.01 hectare) circle in the center of each macroplot. I recorded species and height class (0-0.2 m, 0.2-0.4 m, 0.4-0.8 m, 0.8-1.2 m, or 1.2-1.5 m) of each seedling.

The cut-burn plot in each treated macroplot was defined by the area of the burned slash pile and was about 5.5 m in radius. The remainder of each treated macroplot was the cut-clear plot. I sampled woody and herbaceous response in the treated macroplots in 2011 and 2012 with four 11 m transects per macroplot originating from the macroplot center in each cardinal direction (N, S, E, W). The goal was to survey 22 m of the cut-clear treatment and 22 m of the cut-burn treatment in each treated macroplot; in an ideal macroplot (Fig. 3.1) each 22 m transect would have had 5.5 m of cut-burn and 5.5 m of cut-clear. However, the piles of cut *J. ashei* were not always perfectly circular in outline and exactly 5.5 m in radius. To obtain the desired 22 m in each type of plot, I randomly added or subtracted transect length as needed. In the untreated control macroplots I surveyed 5.5 m of transect in each cardinal direction. I recorded where every vascular plant first intersected the transect and where it no longer intersected the transect in order to calculate cover (meters intersected tape / total tape length).

Data analysis

I used Nonmetric-MultiDimensional Scaling (NMDS, in R, vegan package, metaMDS function) to examine the effects of treatments and fencing on overall plant community response (measured as cover of each species along transects), and on woody seedlings alone (measured as abundances with FIREMON protocol). Data collected 18-months post-fire was used in an ordination of cover. The ordination of woody seedling abundances used data from two dates, 6 months and 18 months after the fire, because the numbers of seedlings of a few species increased 6 months post-fire and then subsequently decreased. Specifically, I used the 6-month data for the four species that decreased by more than 10 individuals between 6 and 18 months post-fire: *Rhus lanceolata*, *Garrya ovata*, *Prunus serotina*, and *Ageratina havanensis*. I used the 18-month data for the remaining species. I constructed and analyzed a Bray-Curtis dissimilarity matrix that was Wisconsin double-standardized with 1000 iterations. Two and three dimensions were tested.

To test whether the overall plant community (cover data) differed significantly between treatments combinations, I used perMANOVA on Bray-Curtis dissimilarities using 999 permutations per test (R, Adonis function). This test partitioned the dissimilarities between plots on the basis of treatments, analogous to a classic MANOVA (multivariate analysis of variance). Each cut-burn plot was in the center of a macroplot, with a cut-clear plot around it (Fig. 3.2); therefore the two treatments (cut-clear and cut-burn) were not independent of each other, although both were independent of fencing. To overcome this, I constructed three separate models, each including fencing and only 2 of the 3 management treatments (Table 3.1). In the third of these separate models, which included cut-burn plots and cut-clear plots only, I included macroplot as a stratification factor because one cut-burn and one cut-clear plot was nested within each treated macroplot (Fig. 3.1). Although fencing was not fully replicated (a single fenced area, with an unfenced area on either side; Fig. 3.2), it was not possible to include this spatial factor in the analyses; fencing is treated as factorial to the cutting treatments in all the analyses. PerMANOVA assumes that variance associated with each treatment is equal. To test this assumption, I used a permutation-based test of multivariate homogeneity (R, Betadisperser function), analogous to Levine's test for univariate data with 999 permutations.

To test whether seedling abundance differed between cut-burn plots and control plots I also used perMANOVA and the permutation-based test of multivariate homogeneity. Cut-clear plots were not compared because there was no seedling data collected from cut-clear plots: seedling data was collected only in a 3.57 m radius plot in the center of each 11 m radius macroplot, which fell entirely in the cut-burn area (Fig. 3.1).

I calculated total cover per plot of native forbs, grasses, and hardwoods by adding up the total transect overlap for each group (m) and dividing by total transect length per plot (22 m). The cover of the exotic species *Lactuca serriola* and *Bothriochloa ischaemum* were calculated separately. I analyzed the effects of treatment, fencing, and year on cover using generalized linear models assuming a normal distribution and identity link function (SAS 9.2, PROC GLIMMIX). The cut-burn plots were in the center of the macroplots, with cut-clear plots around them (Fig. 3.1); the two treatments (cut-burn and cut-clear) were not independent from each other. Therefore I constructed three separate models, each including fencing, year, and only 2 of the 3 management treatments as fixed effects (Table 3.2). I started the model selection process with a full model (year, treatment, treatment x year, fencing, fencing x year, treatment x fencing, treatment x fencing x year), and subsequently dropped terms, dropping interactions before main effects. Year was included as a fixed effect. In addition, year was initially included as a repeated measure (the subject of year was plot) only if the null model likelihood ratio test indicated that including a repeated measure covariance structure was preferred to using diagonal covariance structure of the ordinary least-squares model. I tested two repeated measure covariance structures, simple variance components and autoregressive. AICc was used to compare models with different terms and covariance structures. Once a final model was selected using AICc, I examined the significance of the included terms and did Tukey-Kramer adjusted comparisons between treatments and years. In all analyses the Kenward Roger degrees of freedom approximation was used. Cover was square root transformed when necessary to meet normality requirements.

I used generalized linear models to analyze the effect of treatments (cut-burn and cut-clear, control) and fencing (fenced, unfenced) on seedling species richness and the abundance of *J. ashei*, *Quercus* spp. (*Q. buckleyi* and *Q. fusiformis*), and *Rhus lanceolata* seedlings (SAS 9.2, PROC GLIMMIX). There was no seedling data collected from the cut-clear plots (see above). In the analysis of seedling species richness, I included all 3 data collections (pre-fire, 6 months post-fire, 18 months post-fire) and assumed a normal distribution. Year was included as a repeated measure with an autoregressive covariance structure. In the analysis of *J. ashei*, *Quercus* spp., and *R. lanceolata* seedling abundance I used a negative binomial distribution with a log link function. In the *J. ashei* model I analyzed 6-month and 18-month post-fire responses separately. For *R. lanceolata* I analyzed 6-month response since it was most abundant then (Fig. 3.9). For *Quercus* spp., I used the pre-fire data as a covariate and analyzed the 18-month post-fire response since these species were most abundant then.

RESULTS

Ordinations

The cut-burn and cut-clear treatments each affected the relative cover of different species. The cover ordination with 2 dimensions had a stress of 0.215 and a non-metric R^2 of 0.954. The ordination with 3 dimensions had a stress of 0.151 and a non-metric R^2 of 0.977. The most striking differences were between cut-burn plots and control plots;

cut-clear plots were intermediate. The species most strongly associated with the cut-burn treatment were *Latuca serriola* (LASE) and *Baccharis neglecta* (BANE) (Fig. 3.3). *J. ashei* (JUAS) and *Quercus fusiformi*s (QUFU) were associated with the control treatment. Plant community composition differed significantly between the three treatments (perMANOVA, Table 3.1, Fig. 3.4). There was no significant effect of fencing or the treatment x fencing interaction. The multivariate analysis of homogeneity showed there was no significant difference in community variability between any of the treatments.

Burning affected the relative abundances of seedlings of different woody species. The seedling ordination with 2 dimensions had a stress of 0.132 and a non-metric R^2 of 0.982. The ordination with 3 dimensions had a stress of 0.083 and a non-metric R^2 of 0.993. *R. lanceolata* (RHLA) and *B. neglecta* (BANE) were associated with the cut-burn treatment (Fig. 3.5). *J. ashei* (JUAS), *Quercus* spp. (QUBU, QUFU), *Ilex vomitoria* (ILVO), and *P. serotina* (PRSE) were associated with the control (Table 3.3). Seedling composition significantly differed between cut-burn and control plots (perMANOVA, F = 3.26, $P = 0.004$, Table 3.1); there was no significant effect of fencing or the treatment x fencing interaction. However, these results should be interpreted with caution as the test of multivariate homogeneity showed that woody seedling community variability was higher in the cut-burn plots than in the control plots (betadisper, F=2.476, $P = 0.027$). The average distance to treatment centroid was 0.5958 in the cut-burn treatment, more than the 0.4519 in the control treatment. This is reflected in the length of the lines connecting plots to treatment centroids (Fig. 3.5).

Cover analyses

Cut-clear plots had significantly more native forb cover than control plots ($P = 0.036$, Fig. 3.6a). Cut-burn plots also had significantly more native forb cover than control plots (*P* = 0.003, Fig. 3.6a). Forb cover increased more quickly in cut-clear than in cut-burn plots (Fig. 3.6a). Cut-clear plots had significantly more native grass cover than control plots (*P* = 0.036, Fig. 3.6b) and than cut-burn plots (*P* < 0.001, Fig. 3.6b). Cut-burn plots had significantly less native grass cover than control plots (*P* = 0.003, Fig. 3.6b). Cut-clear plots had significantly more hardwood cover than control plots (*P* = 0.036, Fig. 3.6c) and than cut-burn plots (*P* = 0.010, Fig. 3.6c). There was a significantly treatment x fencing interaction in the analysis of hardwood cover in cut-burn and cut-clear plots (*P* = 0.0205). Unexpectedly, there was significantly less hardwood cover in fenced-cut-clear plots than unfenced-cut-clear plots (*P* = 0.038, Fig. 3.6d). Fencing increased hardwood cover in cut-burn and control plots as expected, although not significantly.

The non-native invasive grass *Bothriochloa ischaemum* did not substantially invade treated areas (Fig. 3.7a). There was however significantly more *B. ischaemum* in cut-clear plots than in cut-burn or control plots 18 months after the fire (Fig. 3.7a). The non-native forb *L. serriola* was not present in any of the control plots. It only invaded treated plots inside the deer exclosure. There was more *L. serriola* in cut-burn than cut-clear plots, but not significantly so (Fig. 3.7b). Within the treated plots, there was significantly more *L. serriola* cover inside the deer exclosure than outside the exclosure (Fig. 3.7b, *P* = 0.03).

Seedling abundance

Different seedling species responded to treatments differently (Fig. 3.8). However, there were some generalities. Seedling species richness was not significantly different among plots pre-treatment. It significantly *increased* in control plots and unfenced plots 6-months post-fire, while neither cutting followed by burning nor fencing increased it. By 18-months post-fire, seedling richness had increased in both the cut-burn and the fenced plots (Fig. 3.9ab). There were significantly fewer *J. ashei* and *Q. fusiformis* seedlings in cut-burn plots. *Rhus lanceolata*, a fire-tolerant reseeder and resprouter, was common in cut-burn plots (Fig. 3.9c).

DISCUSSION

Our results demonstrate that cutting overstory *Juniperus ashei* followed by removal of the cut material, and cutting followed by high-intensity slash-pile burning, have significant and distinctive effects on plant community trajectories. The vegetation response observed in the burn-cut treatment was somewhat similar to responses observed in other studies of high-intensity 'slash pile burns' (Creech et al., 2012; Korb et al., 2004; O'Connor et al., 2013). The slash-pile fires in this study were of very high intensity and severity: they killed all plant individuals and partially mineralized the soil. Colonization into burn-cut plots was predominately by weedy forbs and early successional shrubs. In contrast, cutting and removing *J. ashei* caused remnant hardwoods and grasses to increase in cover, probably by increasing light and water availability. These commonly used management activities likely increased habitat quality for the endangered golden-cheeked warbler, although they interacted with invasive species and deer herbivory to produce some unexpected results.

Golden-cheeked warbler habitat

The endangered golden-cheeked warbler requires mixed *Q. buckleyi* and *J. ashei* woodland with at least 70% canopy cover. Our results indicate that simply removing 30% of the canopy cover in a *J. ashei* near-monoculture does increase habitat quality for the warbler, but this management action alone is not likely to be enough. Both the cut-clear and the cut-burn treatments increased hardwood cover and seedling species richness. Additionally, *J. ashei* did not recolonize after either treatment. Other studies have also found that *J. ashei* is slow to re-colonize after high-intensity fires (Reemts and Hansen, 2013; 2008). However, neither treatment nor protection from deer herbivory increased the establishment or growth of the woodland co-dominant *Q. buckleyi*. Similarly, low-intensity fires (ch. 2) and wildfires (ch. 4) were also unsuccessful in increasing *Q. buckleyi* seedling abundance. *Q buckleyi* is of particular importance to the golden-cheeked warblers as they forage on it much more often than predicated by its abundance, especially in April, i.e., early in the breeding season (Marshall et al., 2013). Therefore, this restoration technique of selectively removing 30% of the canopy cover to increase light availability, and hence native forbs, grasses and hardwoods, while maintaining large *J. ashei* individuals is an novel and viable strategy to begin the restoration of habitat for this endangered bird species. However, either a larger proportion of canopy cover needs to be removed or active planting of *Q. buckleyi* and other hardwoods is needed to have a substantial effect on *Q. buckleyi*.

Do slash-pile burns promote invasive species?

I was concerned that the cut-burn treatment would favor invasive species because slash pile burning has been found to increase invasive and ruderal species elsewhere (Korb et al. 2004). *Bothriochloa ischaemum* (King Ranch Bluestem) is the invasive plant species of greatest concern in central Texas. It often invades after prescribed fire (C. Schwope, pers. comm). Unexpectedly, *B. ischaemum* did not substantially invade the cut-clear or the cut-burn plots. The 4.5% cover of *B. ischaemum* in the cut-clear plots was probably not from remnant *B. ischaemum* plants that were present pre-treatment because *B. ischaemum* does not persist under tree canopies (Gabbard and Fowler, 2007). The 2% cover of *B. ischaemum* in the cut-burn plots was also due to recent colonists as the slash-pile burn killed all of plants there. *B. ischaemum* is less successful at establishing than native grasses after fire in intensely burned savannas (ch. 1, Andruk & Fowler, in review), possibly explaining why it was found in such low abundance in the cut-burn plots. An alternative, but not mutually exclusive, explanation is that habitat fragmentation, that is, the intact *J. ashei* stand around each of the treated macroplots (Fig. 3.2), may have limited the spread of *B. ischaemum* into the study plots. Habitat fragmentation by woody plant encroachment has been shown to impede the spread of this invasive grass (Alofs and Fowler, 2013; 2010). These results indicate that the spatial pattern imposed by leaving *J. ashei* as a barrier to seed dispersal has the potential to limit the spread of invasive species. Managers attempting to restore grassland or savanna by removing woody plants may wish to consider initially leaving bands of woody plants as barriers to seed addition as a technique to reduce the rate of colonization by invasive species. I would then recommend either seeding with native species, or waiting until there has been sufficient colonization and establishment of native species, before clearing the remainder of the area.

Although *B. ischaemum* invasion was minor following the treatments, there was a substantial invasion by the European exotic forb *Lactuca serriola* var. *serriola,* but only in treated plots that were protected from deer herbivory. *L. serriola* is the most common exotic *Lactuca* in North America. It is usually restricted to disturbed habitats such as roadsides, parking lots, and gas stations (Lebeda et al., 2012). Its abundance was not anticipated and its association with protection from deer herbivory was completely unexpected. Our results suggest that *L. serriola* propagules are extremely widespread in central Texas, even in relatively undisturbed and isolated sites such as my rural study site. Lack of disturbance and overabundant deer may therefore be currently limiting the spread of *L. serriola* in this region. It is also possible that *L. serriola* is in the lag phase of an invasion and will eventually colonize many undisturbed, isolated sites in this region. *L. serriola* recently expanded its ecological amplitude in the Netherlands; it is now found in undisturbed habitats there (Hooftman et al., 2006).

Positive indirect effects of deer on hardwoods

The substantial *L. serriola* invasion in fenced cut-clear plots may have negatively impacted hardwood cover. There was significantly less hardwood cover in cut-clear fenced plots than cut-clear unfenced plots. The woody species present in all the cut-clear plots were predominately remnant woodland species such as *Diospyros texana*, *Q. buckleyi* and *Ilex vomitoria*. These remnant woodland species are probably not adapted to competition with ruderal weeds such as *L. serriola*, and may have been negatively impacted by competition from *L. serriola*. In disturbed areas, deer herbivory, if not too intense, may therefore be indirectly benefitting some of the less favored hardwood species by controlling *L. serriola* and perhaps other palatable species. However the direct negative effects of browsing on most of the woody species are substantial in this region and may often outweigh the indirect positive effects I evidently found. Another study found indirect positive effects of deer on palatable woody species; mature red oaks (*Quercus rubra*) that were protected from deer grew less than those individuals that were exposed to deer (Lucas et al., 2013). The authors suggested that trees that were exposed to deer received higher nutrient inputs from deer fecal and urine deposits, as well as a reduction in belowground competition by deer browsing on understory vegetation. In general, when deer are excluded from a forest community understory biomass increases (Rooney, 2009). This increased biomass increases resource competition, potentially slowing shrub or tree recovery after deer exclusion or reduction (Tanentzap et al., 2012). More long-term studies are needed to understand the indirect effects of deer on trees following management interventions.

Direct effects of herbivory

There was no direct effect of the deer exclosure on forb cover, grass cover, woody seedling abundance or richness. I also found no evidence of increased deer browsing in cut-burn or cut-clear as compared to control areas after the fire. Other studies have generally found that deer prefer to browse in recently burned areas (Leopold and Krausman, 2002; Ramirez et al., 2012). There are several reasons why deer may have not preferred cut-clear or cut-burn areas to control areas in this study. First, the slash-pile burns killed previously established individuals. Recovery of native forbs, grasses and hardwoods was relatively slow in these severely burned areas (Fig. 3.6); a longer-term study might detect more effects of deer herbivory in these severely burned plots. Additionally, the high degree of habitat fragmentation (Fig. 3.2, see above) may have slowed deer movement and offered some protection to the palatable species growing in the unfenced-treated areas. The treated macroplots were surrounded by large *J. ashei* trees, which is strongly disliked by white-tailed deer (Dillard et al., 2005). It has been demonstrated that deer browse less on preferred species growing nearby unpalatable species than on preferred species growing nearby other preferred species (Tanentzap et al., 2011). The general term for this phenomenon is associational resistance (Smit et al., 2009). Future studies should compare browsing rates after larger more accessible fires and smaller localized slash-pile burns to understand how the spatial impacts of these management interventions may affect deer behavior and herbivory.

The spatial pattern of the two management treatments (cutting followed by removing the cut material, or cutting followed by burning the cut material) imposed a corresponding spatial pattern on the treated area. Cutting and removal promoted the growth of remnant species, while cutting and slash-pile burning increased disturbance-adapted forbs and woody species. In addition, the habitat fragmentation created by canopy removal in multiple, relatively small areas may have slowed the spread of the invasive *B. ischaemum*. It also may have reduced deer herbivory in the treated areas. Spatial patterns imposed by slash-pile burns are likely to strongly influence vegetation trajectories in other systems as well. Protection from deer herbivory by a fence significantly increased the abundance of the invasive *L. serriola*, which may have negatively impacted remnant hardwoods in the cut-clear areas. These results highlight the importance of considering multiple drivers of plant community composition such as spatial patterns and deer herbivory that may influence the efficacy of management techniques, and the possibility of complex interactions among the various drivers.

Table 3.1: Results from the perMANOVA analysis of cover (overall species response), and seedlings (woody seedlings). Seedlings were only compared between cut-burn plots and control plots because there were no seedling data collected from cut-clear plots.

Comparison	**Factor**	**Cover perMANOVA**	**Seedling perMANOVA**
cut-burn vs. control	*treatment*	F = 2.29, *P* = 0.0009	F = 3.26, *P* = 0.004
	fence	F = 1.27, *P* = 0.144	F = 0.930, *P* = 0.461
	treatment x fence	F = 1.12, *P* = 0.264	F = 0.818, *P* = 0.578
cut-clear vs. control	*treatment*	F = 1.83, *P* = 0.008	---
	fence	F = 1.21, *P* = 0.188	---
	treatment x fence	F = 0.93, *P* = 0.534	---
cut-clear vs. cut-burn	*treatment*	F = 1.56, *P* = 0.043	---
	fence	F = 1.38, *P* = 0.088	---
	treatment x fence	F = 0.71, *P* = 0.903	---

Table 3.2: Results from the analyses of the effects of year (6-months post-fire, 18-months post fire), treatment (cut-burn, cut-clear, control) and their interaction on native grass cover, native forb cover and hardwood cover; ns = non-significant.

Comparison	**Factor**	**Native grass cover**	**Native forb cover**	**Hardwood cover**
cut-burn vs. control	*year*	F = 27.93, $P < 0.001$	F = 10.07, $P = 0.003$	F = 8.64, $P = 0.009$
	treatment	F = 12.63, $P = 0.002$	F = 10.23, $P = 0.003$	ns
	treatment x year	ns	F = 6.73, $P = 0.014$	ns
cut-clear vs. control	*year*	F = 23.33, $P = 0.002$	ns	ns
	treatment	F = 15.05, $P = 0.001$	F = 36.97, $P = 0.001$	F = 5.12, $P = 0.036$
	treatment x year	F = 5.11, $P = 0.038$	ns	ns
cut-burn vs. cut-clear	*year*	F = 21.63, $P = 0.003$	F=8.64, $P = 0.009$	ns
	treatment	F = 29.58, $P < 0.001$	ns	F = 8.24, $P = 0.010$
	treatment x year	F = 5.02, $P = 0.039$	ns	ns

Table 3.3: Woody seedling species, their 4 letter code, their common name, and correlations with NMDS 1 (axis 1) and NMDS 2 (axis 2). See Fig. 3.5 for ordination graph

species	**code**	**common name**	**axis 1**	**axis 2**
Ageratina havanensis	AGHA	Havana snakeroot	0.700	-0.143
Baccharis neglecta	BANE	Roosevelt weed	-0.117	-1.207
Celtis laevigata v. *reticulata*	CELA	netleafhackberry	0.782	-0.757
Diospyros texana	DITE	Texas persimmon	0.910	-0.148
Garrya ovata spp. *lindheimeri*	GAOV	Lindheimers silktassel	0.602	-0.142
Ilex decidua	ILDE	possumhaw	0.715	-0.497
Ilex vomitoria	ILVO	yaupon	0.744	0.135
Juniperus ashei	JUAS	Ashe juniper	0.514	0.619
Juglans microcarpa	JUMI	little walnut	0.730	-0.941
Mahonia trifoliolata	MATR	agerita	0.644	-0.241
Prunus serotina	PRSE	black cherry	1.081	-0.114
Ptelea trifoliata	PTTR	wafer ash	0.640	-0.550
Quercus buckleyi	QUBU	Texas red oak	-0.020	0.977
Quercus fusiformis	QUFU	live oak	0.148	0.693
Rhus copallinum	RHCO	winged sumac	0.669	-0.459
Rhus lanceolata	RHLA	flame-leaf sumac	-1.510	-0.128
Rhus virens	RHVI	evergreen sumac	0.081	0.852
Sideroxylon lanuginosum	SILA	gum bully	0.744	-0.706
Ulmus americana	ULAM	American elm	0.669	-0.459
Ulmus crassifolia	ULCR	cedar elm	0.760	-0.920
Wedelia texana	WETE	hairy wedelia	-1.075	-1.396
Yucca rupicola	YURU	Texas yucca	-0.900	0.361

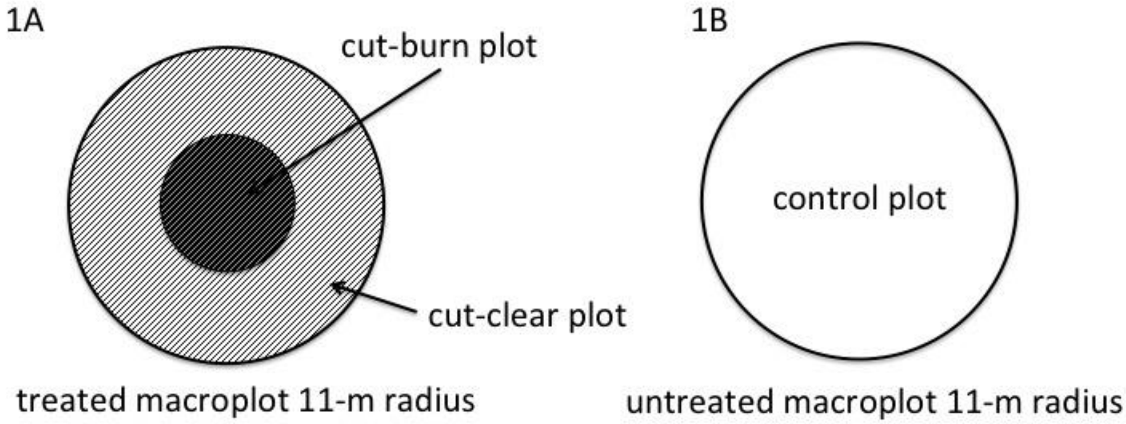

Fig. 3.1: Experimental design. (1a) All *J. ashei* individuals were cut in 11-m treated macroplots. They were piled into a slash pile (~5.5 m) in the center of that treated macroplot and burned, creating a cut-burn plot. The cut-clear plot is the torus ('doughnut') surrounding the cut-burn plot. (1b) Untreated macroplots 11-m radius, contains the control plot.

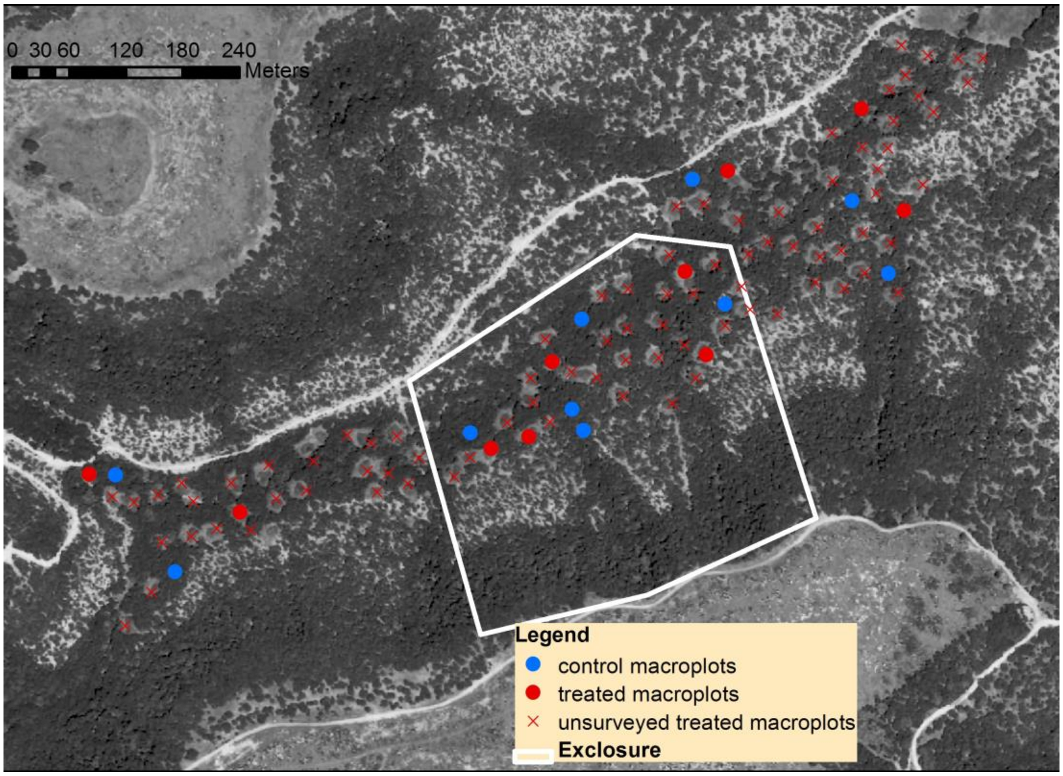

Fig. 3.2: Map of the study area. The white line indicates the deer-exclosure fence. Unsurveyed treated macroplots are shown as a red X (this treated area represents 30% of the study site). We randomly selected ten of these treated macroplots to survey, five inside the deer exclosure and five outside the deer exclosure, shown as red points. Ten control macroplots were randomly located, five inside the deer exclosure and five outside the deer exclosure, shown as blue points.

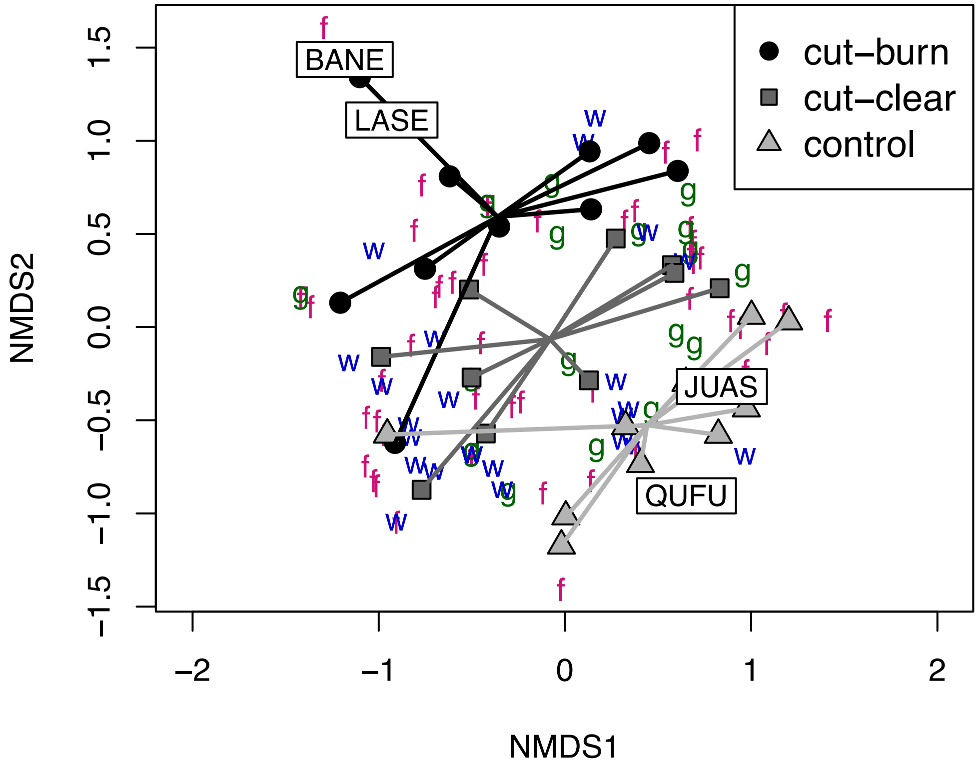

Fig. 3.3: Results from NonMetricMultiDimensional scaling analysis of vegetation cover data. Black points and lines are burn-cut plots, dark gray squares and lines are cut plots, light gray triangles and lines are control plots. Lines connecting points meet in the centroid of each treatment. Forbs are denoted by a pink letter “f”, grasses by a green letter “g”, and woody species by a blue letter “w”. Species of interest: *Baccharis neglecta* (BANE), *Lactuca serriola* (LASE), *Juniperus ashei* (JUAS), and *Quercus fusiformis* (QUFU) are denoted by their 4 letter code.

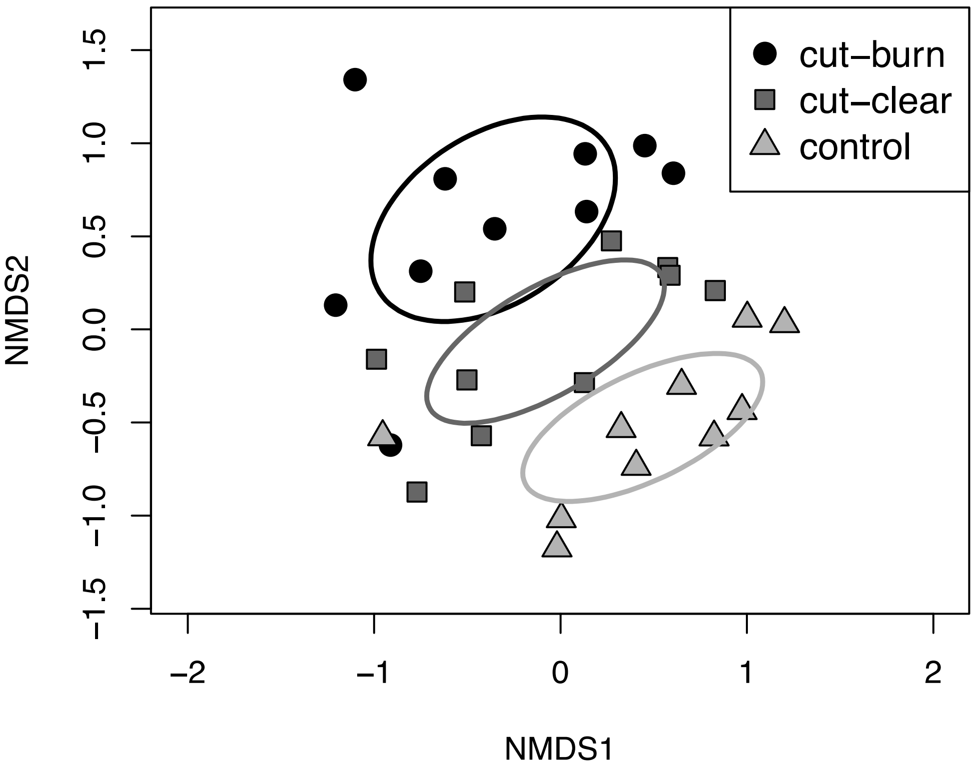

Fig. 3.4: Results from NonMetricMultiDimensional scaling analysis of vegetation cover data. Black points and lines are burn-cut plots, dark gray squares and lines are cut plots, light gray triangles and lines are control plots. Ellipses represent one SD around the centroid of each treatment. See Table 3.1 for significant differences between the treatment groups.

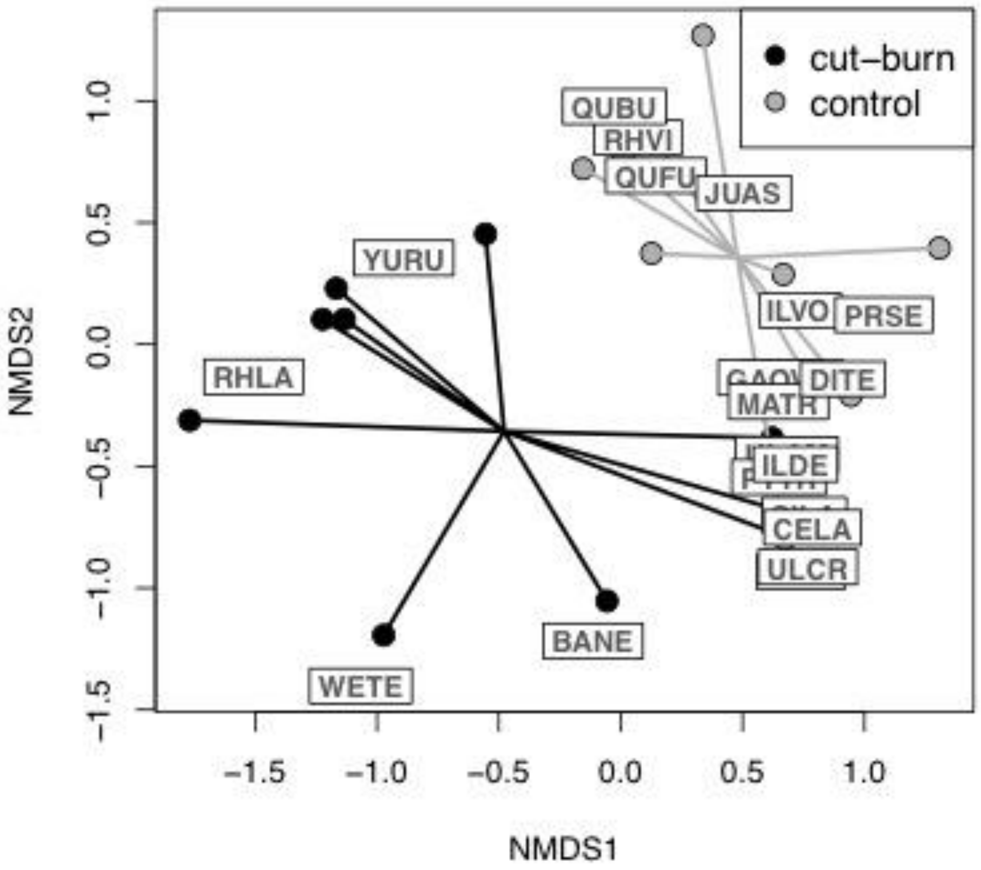

Fig. 3.5: Results from NonMetricMultiDimensional scaling analysis of woody seedling abundance. Points represent plots. Lines connecting points meet in the centroid of each treatment (black points and lines are burn-cut plots, gray points and lines are control plots). Species are denoted by their 4 letter code (first two letters of genus, first two letters of species). See Table 3.3 for a list of seedling species with their 4 letter codes.

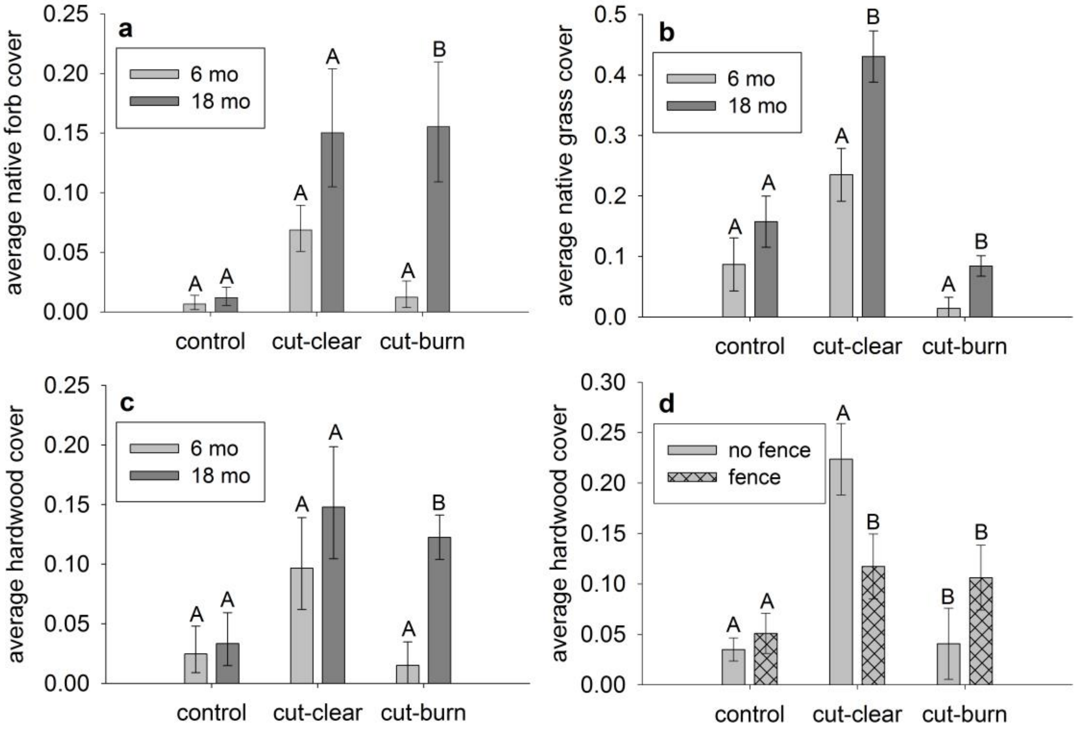

Fig. 3.6: The effects of treatment on (a) native forb cover; (b) native grass cover; (c) hardwood cover. Letters indicate significant differences between the 6-month and 18-month time surveys. (d) The effects of fencing on average hardwood cover 18-months post-fire. Overall differences (across survey dates) for each treatment pairwise-comparison are listed in the text (also see Table 3.2).

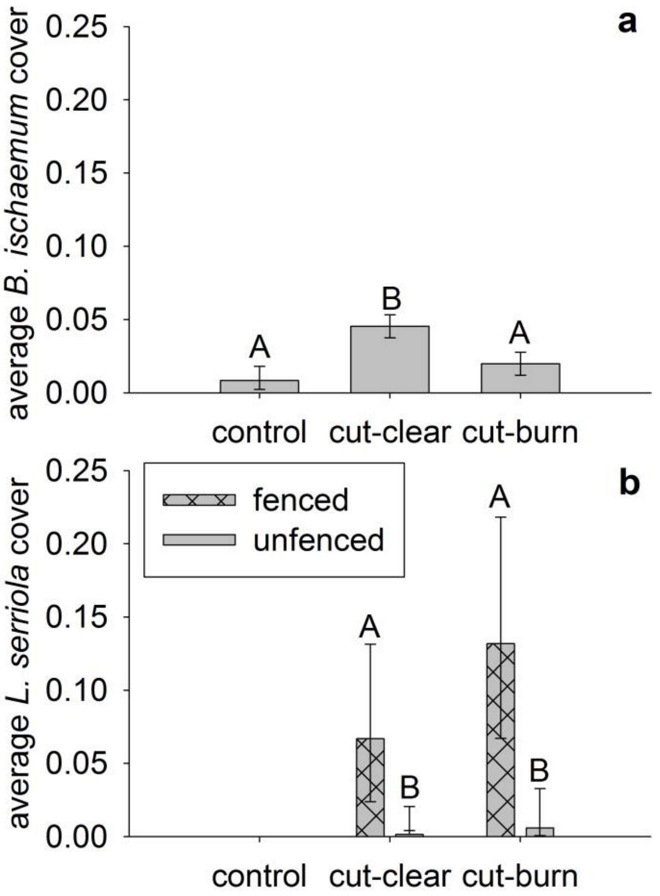

Fig. 3.7: The effects of treatment on (5a) the invasive grass *B. ischaemum* cover 18-months post-fire, letters indicate significant differences between treatments; (5b) the exotic forb *L. serriola* cover 18-months post fire, letters indicate significant differences between fenced and unfenced plots within each of the cut and burned treatments.

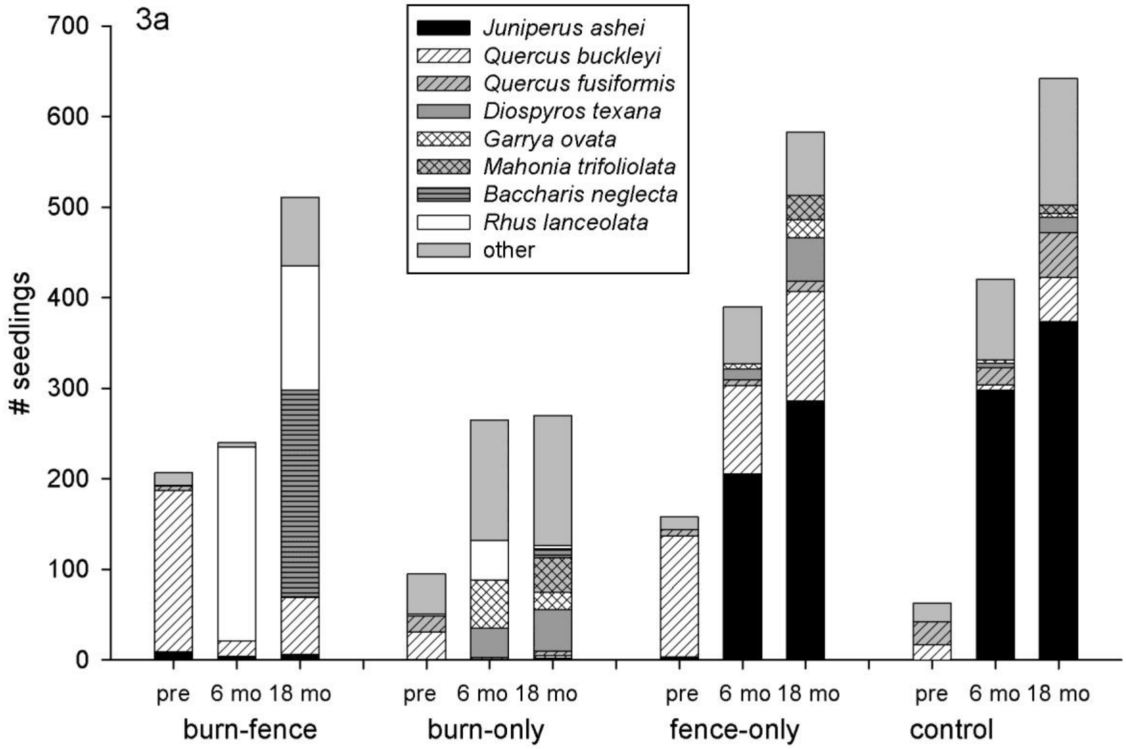

Fig. 3.8: Common seedling species abundance pre-treatment, 6-months post-fire, and 18-months post-fire.

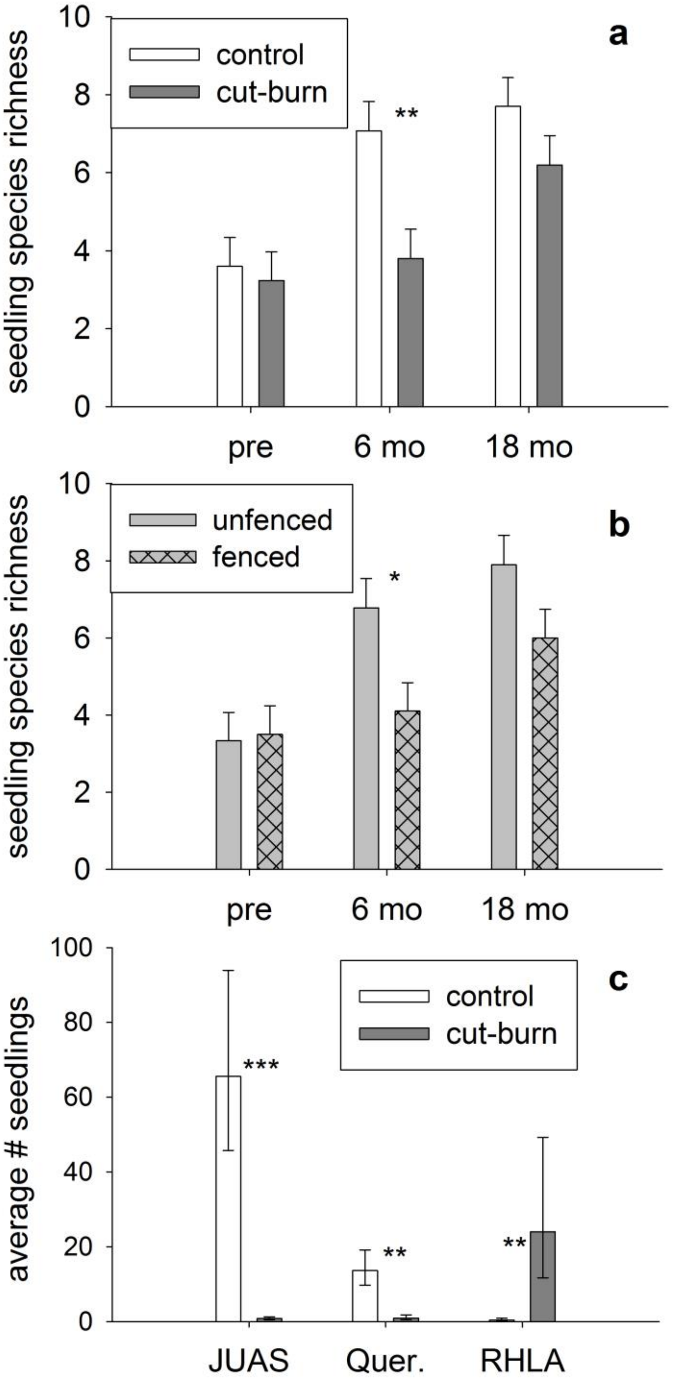

Fig. 3.9: Results from seedling abundance analyses comparing cut-burn to control plots (no seedling data collected from cut-clear plots) (a) the effect of fire on seedling species richness; (b) the effect of deer fencing on seedling species richness; * indicate significant differences between treatments in each time period; (c) Common seedling species responses to fire. JUAS, *J. ashei*; Quer., *Q. buckleyi* and *Q. fusiformis*; RHLA, *R. lanceolata*, * indicate significant differences between unburned and burn-cut plots.

Chapter 4: The effects of wildfires in endangered golden-cheeked warbler (*Setophaga chrysoparia*) habitat

ABSTRACT

The endangered golden-cheeked warbler breeds in central Texas woodland co-dominated by *Quercus buckleyi* (Texas red oak) and *Juniperus ashei* (Ashe juniper). Oaks (*Quercus* spp.) are not regenerating in forests and woodlands in central Texas and elsewhere. *J. ashei* is increasing in abundance. This transition is usually attributed to fire suppression. To better understand the ability of fire to impact or restore golden-cheeked warbler habitat, I examined the effects of four different wildfires on the abundance and size of hardwoods and of *J. ashei* in 2 burned and 2 unburned plots per wildfire site. Canopy cover was also measured to determine if wildfires reduce canopy cover below 70%, which is thought to be ideal for the endangered warbler. Wildfire sites differed in fire frequency, fire seasonality, and time since fire.

Fire killed some *J. ashei* seedlings, saplings and mature trees while causing a net increase in the total number of hardwood saplings and sprouts. Wildfire effects on *Q. buckleyi* seedling abundance were mixed. Similar results have been found in other studies in central Texas and nearby regions. These results suggest *Q. buckleyi* and other hardwoods, as opposed to *J. ashei,* dominated pre-settlement woodlands. Hardwoods resprouted most vigorously in sites that were burned twice and after dormant season fires. Average canopy cover was not reduced below 70%, indicating that wildfires generally do not reduce canopy cover below the minimum requirement for the golden-cheeked warbler. Fire can be used to restore and maintain golden-cheeked warbler habitat, multiple dormant season fires are likely to be most effective at increasing hardwood regeneration.

INTRODUCTION

Oaks (*Quercus* spp.) are not regenerating in many woodland sites in central Texas, resulting in fewer saplings than mature trees (Doyle, 2012; Russell and Fowler, 2004; 2002). Oak regeneration failure is also occurring in forested sites in the eastern United States (Brose et al., 2013; Nowacki and Abrams, 2008), the Ozark Mountains in the central US (Dey and Hartman, 2005), and the western US (Tyler et al. 2006). As oaks decline they are usually replaced by shade-tolerant, fire-intolerant species (Doyle, 2012; Hart et al., 2012; Nowacki and Abrams, 2008; Russell and Fowler, 2002). This shift in dominance has significant impacts on ecosystem processes and biodiversity throughout the affected regions (Dey and Fan, 2009; McShea et al., 2007; Nowacki and Abrams, 2008). Oak regeneration failure has been ascribed to fire suppression (Brose et al., 2013; DeSantis et al., 2011; Dey and Hartman, 2005; Nowacki and Abrams, 2008), overabundant white-tailed deer (Russell and Fowler, 2004), and complex interactions including climate and land use changes (Arthur et al., 2012; McEwan et al., 2010).

Central Texas woodlands occur on limestone-derived soils and are often co-dominated by *Juniperus ashei* (Ashe juniper) and *Quercus buckleyi* (Texas red oak). Other common native hardwoods include *Prunus serotina* and *Ulmus crassifolia*. Woodland canopy height rarely exceeds 10 m. Woodlands of this type are common on hillsides on the eastern Edwards Plateau (Diamond and True, 2008). *J. ashei* is a non-resprouting multi-stemmed tree. It is killed by high-intensity wildfires and has low re-establishment after such fires (Reemts and Hansen, 2013; 2008). In contrast, *Q. buckleyi* resprouts after both low-intensity prescribed fires (ch. 2) and high-intensity wildfires (Reemts and Hansen, 2013). The estimated fire return interval in central Texas woodland for the past half-century may have been as high as 2.2 to 2.6 years. These fires were likely of low to moderate intensity and occurred in the early growing season of dry years (Murray et al., 2013). Currently, fire is suppressed in these woodlands. This fire suppression is likely contributing to a shift in species composition from diverse mixed woodlands to nearly pure stands of *J. ashei* (ch. 2).

This shift in species composition impacts the endangered golden-cheeked warbler (*Setophaga chrysoparia*). This bird breeds in central Texas in mixed species woodland with an average canopy cover of 70% (Groce et al., 2010). It requires the bark of mature *J. ashei* to build nests and forage (DeBoer and Diamond, 2006). It also need a mixture of other hardwood species that are good sources of prey items (Groce et al., 2010; Marshall et al., 2013). Golden-cheeked warbler preferred tree species for foraging changes as arthropod prey availability shifts during the year; they rely heavily on *Q. buckleyi* early in the breeding season (Marshall et al., 2013). Therefore, a lack of *Q. buckleyi* regeneration has been identified as a serious threat to the golden-cheeked warbler (Groce et al., 2010). Because fire suppression is likely contributing to *Q. buckleyi* regeneration failure, the use of prescribed fire has the potential to maintain high-quality golden-cheeked warbler habitat and also to restore habitat in which there are insufficient *Q. buckleyi* and other hardwood trees.

Since current policy restricts the use of prescribed fire in golden-cheeked warbler habitat (but see ch. 2), I studied the effects of unplanned wildfires. I measured the effects of fire on the number, size, and growth of *J. ashei* and hardwood individuals, especially *Q. buckleyi*. I expected that burned areas would have fewer *J. ashei* seedlings, saplings and mature trees than unburned areas. Wildfires were also expected to increase the number and growth rate of hardwoods, particularly *Q. buckleyi*. Finally, I was interested in whether wildfires reduced the canopy cover in these woodlands below 70%, making them unsuitable for golden-cheeked warblers.

METHODS

Study site and experimental design

I surveyed vegetation response to wildfire at four sites in Balcones Canyonlands National Wildlife Refuge (Table 4.1). This refuge is located on the eastern Edwards Plateau of central Texas. Each site had an area that was burned when a nearby-prescribed fire in a savanna escaped its intended boundary. Sites differed in fire frequency, fire seasonality, and time since fire. Additionally, the one-fire-thin site showed past evidence of thinning of large *J. ashei*, as evidenced by numerous large stumps; the date of this cutting is unknown. Within each of these four sites, I randomly located two 11 m radius plots in the burned area, and two additional 11 m radius plots (control plots) in an adjacent unburned woodland. Control areas had similar slopes and aspects similar to their paired to burned areas.

Vegetation surveys were completed using FIREMON (Fire Effects Monitoring and Inventory Protocol), a standard methodology used in fire-effects research (Lutes et al., 2006). All of the sites were surveyed in June 2009, except for the one-fire-recent site, which was sampled in June 2010. Seedlings (woody plants < 1.5-m tall that were not part of a larger individual) were surveyed in a 3.57-meter radius (.01 hectare) circle in the center of each plot, while saplings and mature trees were surveyed in the entire 11-m radius plot. I recorded species and height class (0-0.2 m, 0.2-0.4 m, 0.4-0.8 m, 0.8-1.2 m, or 1.2-1.5 m) of each seedling. Species, number of stems in each DRC (diameter at root crown) class, and height to the nearest 0.1-m were recorded for each sapling (woody individuals > 1.5 m tall, with a DRC < 10.16 cm) and mature tree (woody plants with a DRC ≥ 10.16 cm). In summer 2009 or 2010 each mature tree was tagged with a unique number. The diameter at breast height (DBH) was measured at the tag. A sprout was defined as stem with a DRC < 5.08 cm that arose from the base of a mature tree. The number of sprouts in each DRC class and the height of the tallest sprout in each DRC class were recorded for each mature tree.

In addition to vegetation surveying at these plots, canopy cover was compared in burned and unburned areas to estimate the effects of fire on light availability. Canopy photographs were taken at 9 locations per plot in 2 sites (two-fires, one-fire-recent) with a fisheye lens (Sigma 8mm f/3.5 EX DG circular fisheye lens). The photographs were converted into binary images (canopy vs sky) using the program Gap Light Analyzer. Canopy openness was calculated from binary images and compared between sites and burned and unburned areas.

Data analysis

I used a generalized linear model with a Poisson distribution and log link to analyze the effects of fire, site, and their interaction on the number of *J. ashei* seedlings and saplings, *Q. buckleyi* seedlings, pooled non-oak hardwood seedlings, and pooled hardwood saplings. Non-oak hardwoods included all hardwood species except for *Q. buckleyi*. The generalized chi-square / DF was used to assess fit to the Poisson distribution. I calculated average sapling height by averaging sapling height weighted by the number of sapling stems with that height in each plot. An analysis of variance (ANOVA) was used to analyze hardwood sapling height. *J. ashei* sapling height could not be analyzed because there were too few sapling individuals in the burned plots.

Sprouts are defined as stems originating from the base of a mature tree with a DRC < 5.08 cm. I calculated the average number of sprouts per tree per plot. I calculated average sprout height by averaging sprout height weighted by the number of sprout stems with that height. The average number of sprouts per tree per plot was analyzed with a generalized linear model with a Poisson distribution, as described above. Average sprout height per tree per plot was analyzed with an ANOVA. Fire, site and their interaction were included as fixed effects.

Some hardwood individuals had their main stem (DRC ≥ 10.16-cm) killed by fire; many of these individuals were producing basal sprouts after the fire. A generalized linear model with a binomial distribution and logit link (logistic regression) was used to analyze the effect of fire, site, species (*J. ashei*, *Q. buckleyi*, pooled non-oak hardwoods), and fire x species on the proportion of mature hardwood trees whose main stem was alive. A separate analysis was done to examine the effect of fire, the number of living sprouts per tree, and their interaction on the proportion of living hardwood trees whose main stem was alive. This was done to determine whether hardwood trees whose main stem was killed by the fire were more likely to have a greater number of sprouts. In both of these analyses, a random factor was included to account for the nesting of plot within site x fire. The between-within method was used to compute the denominator degrees of freedom for fixed effects.

I used an ANOVA to analyze the effect of fire, site and their interaction on canopy openness. Percent canopy openness, i.e. 100 minus percent canopy cover, was log transformed to meet normality requirements.

In any of the above analyses, if site was significant, pairwise comparisons between sites were made. If fire x site was significant, I compared burned and unburned plots within each site. These comparisons were adjusted with Tukey-Kramer.

RESULTS

There was a significant fire x site interaction effect in the analysis of *Q. buckleyi* seedling abundance (*P* = 0.027, Fig. 4.1). There were significantly fewer *Q. buckleyi* seedlings in the burned than the unburned area of the one-fire-recent site (*P* = 0.0342) and the one-fire-thin site (*P* = 0.0043). There were significantly more *Q. buckleyi* seedlings in the burned than the unburned area of the one-fire-old site (*P* = 0.0056). There was no significant difference in *Q. buckleyi* seedling abundance between the burned and unburned areas in the two-fires site. There was no significant effect of fire, site or their interaction in the analysis of *J. ashei* seedling abundance. Averaging across burned and unburned areas, sites differed in non-oak seedling abundance (*P* = 0.0218). The one-fire-recent site had an average of 51.15 non-oak seedlings, significantly more than the one-fire-thin site, which had an average of 9.88 non-oak seedlings (*P* = 0.0148). There was no significant effect of fire or fire x site.

Fires increased the number of pooled hardwood saplings: there were significantly more in burned plots than in unburned plots (*P* = 0.0005, Fig. 4.2). Sites differed in pooled hardwood sapling number (averaging across burned and unburned plots, *P* = 0.0034): the two-fires site had significantly more hardwood saplings than the one-fire-thin site (*P* = 0.029), as did the one-fire-recent site (*P* = 0.042), and the one-fire-old site (*P* = 0.027, Fig. 4.2). There was no significant fire x site interaction. Fires killed *J. ashei* saplings: there were significantly fewer in burned plots than in unburned plots (*P* = 0.0005, Fig. 4.2). There was no significant difference in *J. ashei* sapling number among sites (averaging across burned and unburned plots), although they were much less abundant in the one-fire-thin site. There was no significant fire x site interaction. Burned hardwood saplings were significantly shorter than unburned hardwood saplings (*P* = 0.001, Fig. 4.3). This indicates recent growth of smaller individuals into this sapling size class; hence a decrease in average height. Averaging across burned and unburned plots, the one-fire-recent hardwood saplings were significantly shorter than those in other sites (Fig. 4.3). There was no significant fire x site interaction.

I observed a large number of hardwood saplings and mature trees producing sprouts after wildfire. Woody species that had sprouts after a fire included: *Ageratina havanensis* (Havana snakeroot), *Baccharis neglecta* (Rooseveltweed), *Cercis canadensis* var. *texensis* (Texas redbud), *Diospyros texana* (Texas persimmon), *Forestiera pubescens* (stretchberry), *Fraxinus texensis* (Texas ash), *Garrya ovata* ssp. *lindheimeri* (Lindheimer’s silktassel), *Ilex decidua* (possumhaw), *Ilex vomitoria* (yaupon), *Juglans* *microcarpa* (black walnut), *Melia azedarach* (chinaberry, invasive), *Mimosa texana* (Texas mimosa), *Ptelea trifoliata* (common hoptree), *Prunus serotina* (black cherry), *Q. buckleyi*, *Quercus sinuata* (Bastard oak), *Rhus aromatica* (fragrant sumac), *Rhus lanceolata* (flame-leaf sumac), *Sideroxylon lanuginosum* (gum bully), and *Ulmus crassifolia* (cedar elm).

There was a significant fire x site interaction in the analysis of average sprout number per tree per plot (*P* = 0.0002). Mature trees in the burned portions of the two-fires and one-fire-old sites had significantly more sprouts than mature trees in the unburned portions of those sites (*P* = 0.0044 and *P* = 0.0035, respectively, Fig. 4.4). Fire did not significantly affect average sprout number per tree in the one-fire recent site. There was no overall effect of fire on the average number of sprouts per tree per plot. There was no significant effect of fire, site or their interaction in the analysis of average sprout height. However, the average height of unburned sprouts was 2.44 ± 0.43, taller than that of burned sprouts, 1.81 ± 0.25, suggesting recent sprout growth in the burned areas. There was no significant fire x site interaction effect.

Significantly more mature trees (DRC $\geq$ 10.16-cm) had living main stems in unburned areas than in burned areas (94.06% as compared to 39.99%, *P* = 0.0035). On average 78.13% of the mature hardwood trees with dead main stems had basal sprouts, so these individuals had not completely died. There was no significant relationship between the number of sprouts a mature hardwood tree had and the probability that its main stem was alive. There was a significant fire x species interaction in the analysis of proportion of mature trees with living main stems (*P* = 0.0203, Fig. 4.5). The proportion of living *J. ashei* trees was significantly lower in burned than in unburned areas (Fig. 4.5, *P* = 0.0051); since *J. ashei* does not resprout, dead *J. ashei* trees with dead main stems were completely dead. There were nearly 50% fewer mature *Q. buckleyi* and non-oak mature trees with living main stems in burned areas than in unburned areas, but this difference was not statistically significant for either species group (Fig. 4.5).

Burned areas had significantly higher canopy openness than unburned areas (Fig. 4.6, $P < 0.001$). There was no significant effect of site or fire x site, although plots in the burned two-fires site were more open those in the one-fire-recent site.

DISCUSSION

Fire killed some *J. ashei* seedlings, saplings and mature trees while causing a net increase in the total number of hardwood saplings and sprouts. Similar results have been found in central Texas (Doyle, 2012; Reemts and Hansen, 2013; 2008; Yao et al., 2012), the nearby cross timbers region (Burton et al., 2010; Clark and Hallgren, 2003), and the eastern US (Brose et al., 2013). The high sprouting rate of the diverse hardwood community suggests that these species are adapted to periodic fire. The strong negative responses of *J. ashei* seedlings, saplings, and mature trees to wildfires suggest that this species may have been relatively rare in the past when wildfires were more common.

Resprouting is an important functional trait that allows trees to persist after fire (Clarke et al., 2013) and may be an adaptation to fire (Keeley et al., 2011). In this study, a large number of common central Texas shrubs and trees were observed producing sprouts in the burned areas; *Q. buckleyi* was most common. Another study found that *Quercus marilandica* and *Q. stellata* reproduced primarily by resprouting in a cross timbers woodland (Clark and Hallgren, 2003), indicating that resprouting is an important mechanism of oak persistence in nearby woodlands. In general, resprouting is the dominant method of oak reproduction and persistence (Brose et al., 2013; Lawes and Clarke, 2011; McEwan et al., 2010).

Fire frequency

Mature trees growing in the burned portions of the two-fires and one-fire-old sites had significantly more sprouts than mature trees grown in the unburned portions of these sites. This may be because multiple fires increase hardwood sprouting more so than single fires in central Texas. Similarly, a large increase in sprouts was observed after two high-intensity wildfires in another central Texas woodland (Reemts and Hansen, 2013). These results demonstrate that the central Texas tree species can survive and thrive after multiple fires. This seems to be true of regional oak-dominated communities as well. Repeated prescribed fires increased the cover of *Quercus havardii* (sand shinnery oak) in Oklahoma more than single prescribed fires (Harrel et al., 2001). Oaks in the Ozark mountains also vigorously resprouted after repeated fires (Fan et al., 2012). These authors argue that repeated fires favor oak in the long-term due to its conservative reproductive strategy. Repeated fires are likely successful because oaks tend to allocate more carbon to root development than shoot development, making them superior resprouters than their competitors (Arthur et al., 2012; Brose et al., 2013).

Fire seasonality

In addition to fire frequency and time since fire, sites differed in fire seasonality (Table 4.1). The two-fires and one-fire-recent sites burned in the winter dormant-season, while the one-fire-old and one-fire-thin sites burned early in the growing-season. Mature trees growing in areas that had received dormant season fires had significantly more sprouts than trees growing in their respective controls. Mature trees growing in the area that received one growing season fire without any thinning (one-fire-recent site) did not have significantly more sprouts than trees growing in their respective controls. The greater oak sprouting following dormant season fire than growing season fire may have been due to differences in plant carbohydrate reserves at the time of the burn. Plant carbohydrate reserves are generally lowest early in the growing-season after leaf-out (Harrington, 1989). Plants that were burned during this period of low carbohydrate reserves (early growing season fire) may have been less able to sprout than those plants that were burned in the dormant season.

Most prescribed fires intended to increase oak regeneration occur in the dormant-season when it is typically safer to burn. Growing-season fires are generally of higher intensity than dormant-season fires. For example, three dormant-season fires were needed to match the effects of one growing-season fire in the upper Piedmont of South Carolina (T. A. Barnes and Van Lear, 1998). A meta-analysis found that oaks sprouted at a higher rate than mesophytic species after growing-season fires, but there was no difference in sprouting production between these two groups after dormant-season fires (Brose et al., 2013). Therefore, contrary to my results, it seems that in most cases growing-season fires are more effective than dormant-season fires, especially if the goal is mesophytic species control. *J. ashei,* a more xeric species than *Q. buckleyi,* is most flammable during the winter and early spring (Owens et al., 1998), suggesting that it will be equally susceptible to winter dormant-season fire and early growing-season fires. Therefore, due to the superior hardwood sprouting rates observed after dormant-season fires in this study, I recommend their use in central Texas woodland restoration projects.

Pre-settlement fire regimes

Pre-settlement fires in central Teas may have occurred more frequently early in the growing season than in the dormant season. The estimated fire return interval in central Texas woodland for the past half-century is 2.2 to 2.6 years. These fires were likely low to moderate intensity fires that occurred in early in the growing season of dry years (Murray et al., 2013). Growing season wildfires are also thought to be common in other oak-dominated forests (Petersen and Drewa, 2006). However, a tree ring study from northeast Texas woodland found that prior to 1820, fires occurred every 6.7 years and only in the dormant season (Stambaugh et al., 2011). Tree ring data from a western

Maryland oak forest indicates that pre-settlement fires occurred every 7.6 years and predominately in the dormant season (Shumway and Abrams, 2001). The mean fire return interval of the western Ozark Mountains is estimated to be 7.5 years from 1633 to 1731, and 2.8 years from 1732-1840. These fires also occurred predominately during the dormant season (Stambaugh et al., 2013).

These regional studies put the estimated central Texas fire return interval on the very high end. They also suggest that dormant season fires were generally more common than growing season fires in similar regions. If central Texas fires did actually occur in the early growing season with such a high frequency, vegetation would have been very different than it is currently. There is mounting evidence that woodland *J. ashei* individuals of all sizes are killed by fire and are slow to recover post-fire. *J. ashei* was negatively affected by wildfire (this study), low-intensity prescribed fire (ch. 2), cutting and clearing or cutting and slash pile burning (ch. 3), and high-intensity wildfire (Reemts and Hansen, 2013; 2008). It was also slow to recover after all of these fire types. Additionally, *J. ashei* is most flammable in the winter dormant season and in the early spring growing season (Owens et al., 1998). This suggests that the pre-settlement fires that predominately occurred during this period would have severely restricted its abundance. In contrast to *J. ashei*, *Q. buckleyi* and other hardwood species resprout vigorously after wildfire (this study), low-intensity prescribed fire (ch. 2), and high-intensity wildfire (Reemts and Hansen, 2013). These studies suggest that *Q. buckleyi* and other hardwoods, as opposed to *J. ashei*, dominated pre-settlement woodlands.

Resprouting hardwood species likely severely reduce light availability and perhaps water availability for re-colonizing *J. ashei* seedlings. *J. ashei* growth rates are highest in areas with more light availability such as canopy edges, although establishment and survival rates are generally highest in shaded woodlands (Van Auken et al., 2005). *J. ashei* re-colonization will likely be low in areas with extremely abundant resprouting hardwoods due to light and soil resource competition.

Competition from resprouting hardwoods likely also limits *Q. buckleyi* and other hardwood seedling establishment and survival. *Q. buckleyi* seedlings have high light requirements. There were significantly fewer *Q. buckleyi* seedlings in the burned areas than in the unburned areas in the one-fire-thin and one-fire-recent sites, presumably because the fire killed them. However, there were significantly more *Q. buckleyi* seedlings in the burned area than in the unburned area of the one-fire-old site. This site was surveyed 4 years after the wildfire. It is possible that *Q. buckleyi* seedling recovery takes a few years. It is also possible that *Q. buckleyi* exhibits mast seed production. In oaks, mast seeding is characterized by large variations in seed production between years and between individuals within a population (Kelly, 1994). Masting is common in North American oak forests; for example, large individual and year-to-year variation in acorn production was observed in an oak communities in Massachusetts (Healy et al., 1999) and southern Appalachia (Greenberg, 2000). If *Q. buckleyi* exhibits a similar masting pattern to other red oaks, this may explain why I did not observe new oak seedlings. It is possible that I did not survey the plots following a mast year, or that the plots did not contain the "superior producers" that often produce the majority of a population's acorn crop.

In sum, there is little evidence that oak seedling abundance increases in response to wildfires (this study), low-intensity prescribed fire (ch. 2), cutting and clearing or cutting and slash pile burning (ch. 3), or high-intensity wildfire (Reemts and Hansen, 2013). This is problematic, as restoration of oak regeneration requires the production of new individuals. Prescribed fire can increase oak seedling abundance by increasing flowering, acorn production, germination, and establishment, and by stimulating advanced regeneration (Arthur et al., 2012). However, fire can limit oak seedling abundance by killing acorns, especially those at the soil surface (Greenberg et al., 2012). There is mixed evidence as to the ability of fire to increase oak seedling regeneration in other regions as well (Arthur et al., 2012; Brose et al., 2013). Fire in combination with thinning seems to be the most effective as it substantially increases light availability (Hutchinson et al., 2012).

Endangered golden-cheeked warbler habitat

The wildfires in this study increased light availability by reducing canopy cover to 68.27%. Unburned areas had 84.28% canopy cover. Endangered golden-cheeked warblers are predominately found in areas where the canopy cover exceeds 70%. However, they have also been documented in areas with 35-40% canopy cover (Groce et al., 2010; Reemts and Hansen, 2008). Therefore these wildfires probably did not reduce canopy cover below the minimum requirement for the golden-cheeked warbler.

Golden-cheeked warblers exhibit a wide range of preferences for different tree species. They have been observed in habitats that range from 10 to 90% *J. ashei* and 10 to 85% hardwood trees. Habitats with higher hardwood abundance (75-90%) have been found to be positively related to warbler occurrence (Groce et al., 2010). However, warblers have also been found to prefer areas with higher *J. ashei* abundance (DeBoer and Diamond, 2006). Golden-cheeked warblers forage heavily on *Q. buckleyi* early in the breeding season as it has higher arthropod biomass then. *J. ashei* is a preferred foraging species later in the season (Marshall et al., 2013). In this study, 45% of mature *J. ashei* trees were alive in burned areas, as compared to 99% in unburned areas. The overall living mature tree composition in burned areas was 44% *J. ashei*, 40% *Q. buckleyi*, and 15% non-oak hardwoods. This composition is very similar to that of the unburned areas: 55% *J. ashei*, 30% *Q. buckleyi*, and 15% non-oak hardwoods. Both the unburned and burned areas qualify as suitable habitat.

However, only 22.48% of mature trees were alive in the burned portion of the one-fire-thin site. This site also had much higher herbaceous biomass and diversity (not recorded) than the others. These observations suggested that vegetation trajectories at this site are leading to a shrubland or savanna instead of a hardwood-dominated woodland. This was confirmed in summer 2011-2013 when visual inspection indicated the burned portion of the site was dominated by *Rhus lanceolata* (flame-leaf sumac) with a diverse herbaceous understory. *R. lanceolata* is common in shrubland habitats. Shrubland is important habitat for the endangered black-capped vireo (*Vireo atricapilla*) (Pope et al., 2013); it is also being converted to *J. ashei*-dominated woodland under fire suppression (Fuhlendorf and Smeins, 1997; Pope et al., 2013). The vegetation trajectories in the burned area one-fire-thin site demonstrate that wildfires can initiate earlier successional shrubland as opposed to restoring or maintaining hardwood-dominated woodland. Thinning of *J. ashei* probably increases the probability that the transition from woodland to shrubland will occur. In the past, it is possible that early successional shrublands matured into later successional mixed *Q. buckleyi* – *J. ashei* woodlands, which matured into *J. ashei*-dominated woodlands. If so, land managers could integrate habitat management for the endangered golden-cheeked warbler and the black-capped vireo.

Flexible land management is needed; it is likely that pre-settlement vegetation was a complex mosaic of savanna, earlier successional shrubland, and later successional woodland. Despite the ability of fire to produce to shrubland vegetation, the results of this study suggest that fires can be used successfully to restore and maintain golden-cheeked warbler habitat. Multiple dormant season fires are likely to be most effective at increasing hardwood regeneration.

Table 4.1: The four sites that accidentally burned when prescribed fires escaped their designated areas at Balcones Canyonlands National Wildlife Refuge. Site name was based on whether they received one or two fires and on how recently the site was surveyed after fire. The one-fire-thin was thinned of *J. ashei* at an unknown date, as evidenced by numerous large *J. ashei* stumps.

Site	Date of fire(s)	Fire seasonality
two-fires	Feb. 1998, Jan. 2009	dormant-season
one-fire-old	Mar. 2006	growing-season
one-fire-recent	Jan. 2009	dormant-season
one-fire-thin	Mar. 2009	growing-season

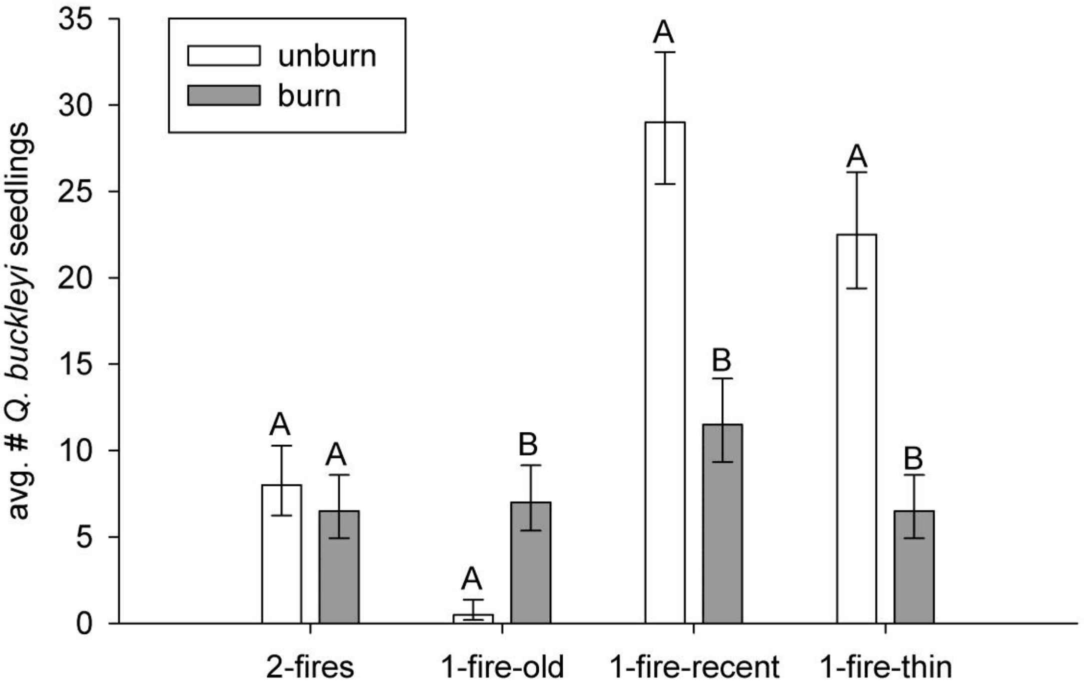

Figure 4.1: There was a significant fire x site interaction effect in the analysis of *Q. buckleyi* seedling abundance (*P* = 0.027). Seedlings are individual woody plants < 1.5 m tall. Letters indicate significant differences between unburned and burned areas within each site.

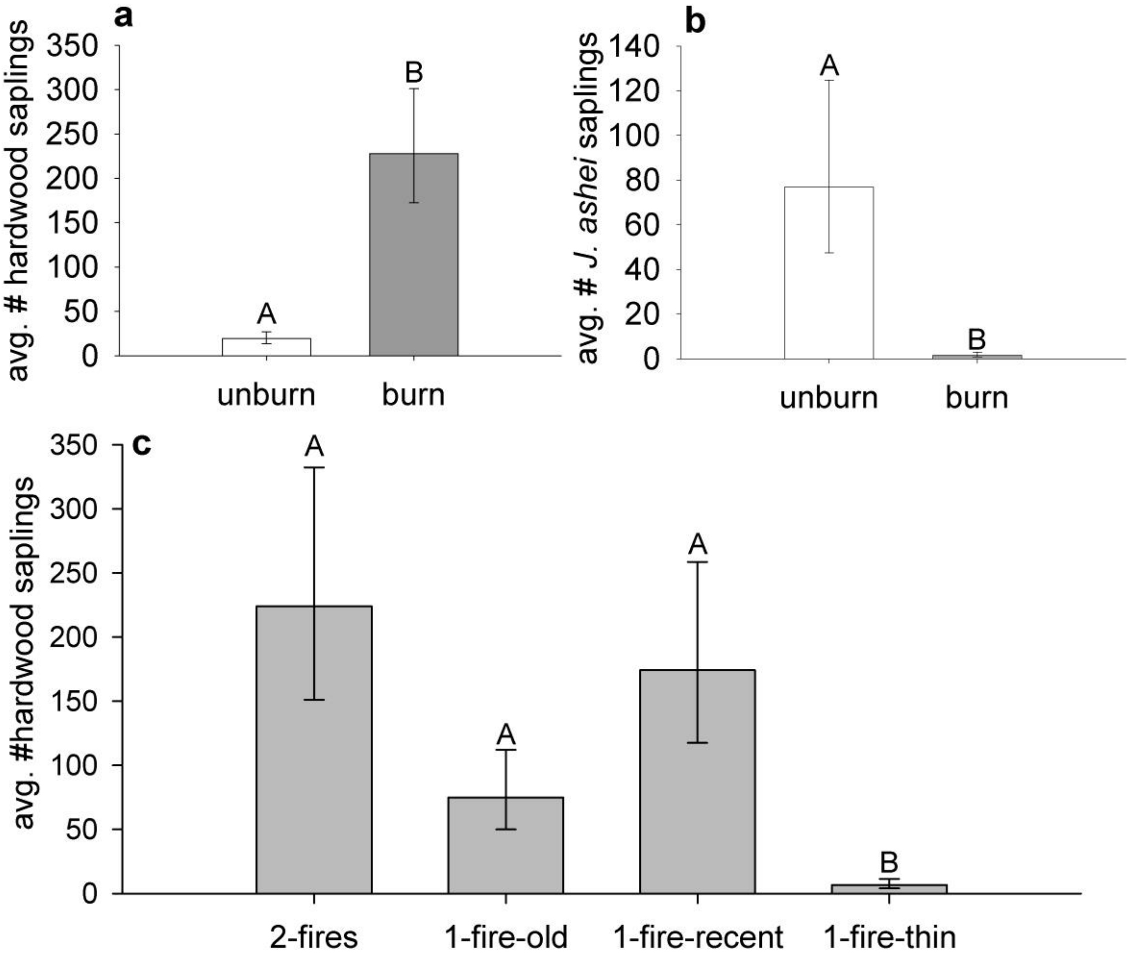

Figure 4.2: Effects of fire and site on saplings (individuals > 1.5 m tall with a DRC < 10.16 cm). (a) There were significantly more pooled hardwood saplings in burned than unburned areas; (b) there were significantly less *J. ashei* saplings in burned than unburned areas; (c) pooling across burned and unburned areas, sites differed in the number of hardwood saplings. Letters indicate significant differences between groups.

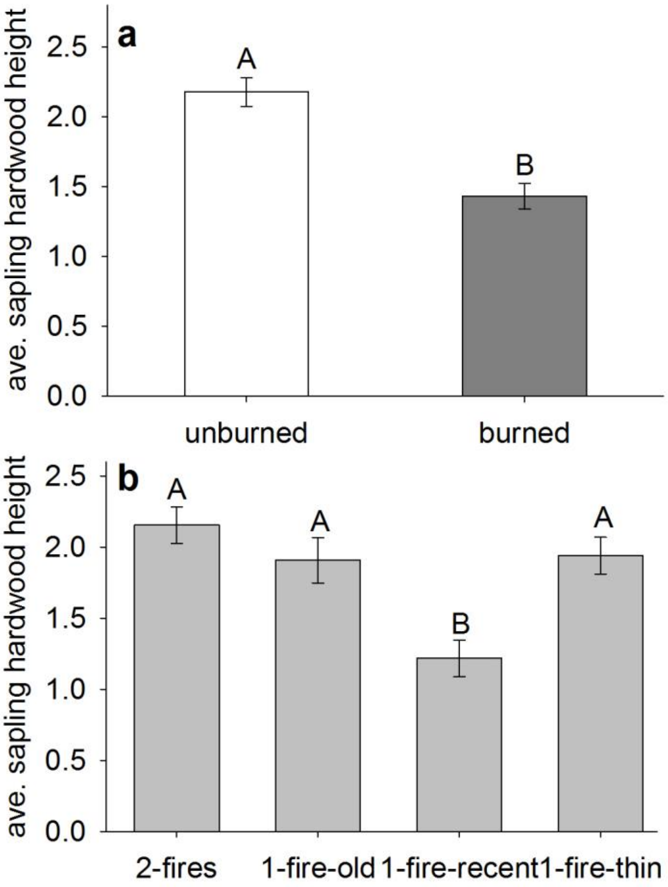

Figure 4.3: The effects of fire and site on average pooled hardwood sapling height. (a) Hardwood saplings in burned areas were significantly shorter than those in unburned areas; (b) hardwood saplings at the one-fire-recent site were significantly shorter than those at the other sites. Letters indicate significant differences between groups.

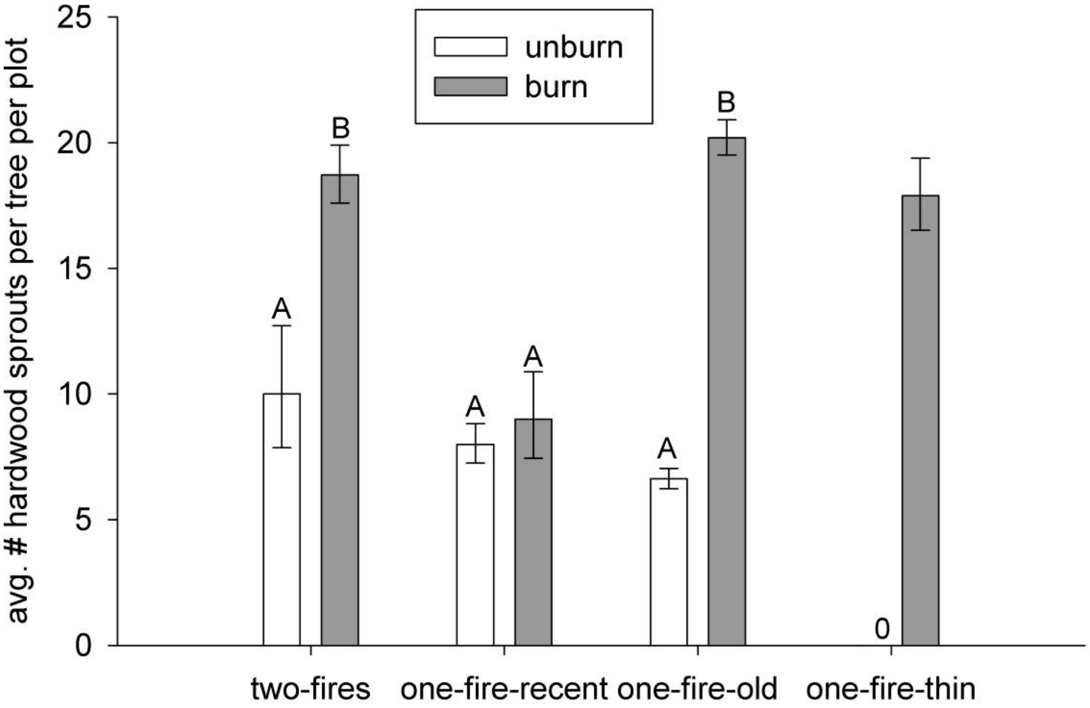

Figure 4.4: There was a significant fire x site interaction in the analysis of average sprout number per tree per plot (*P* = 0.0002). Letters indicate significant differences between burned and unburned areas within each site. None of the unburned hardwood trees in the one-fire-thin site had sprouts, as indicated by the 0.

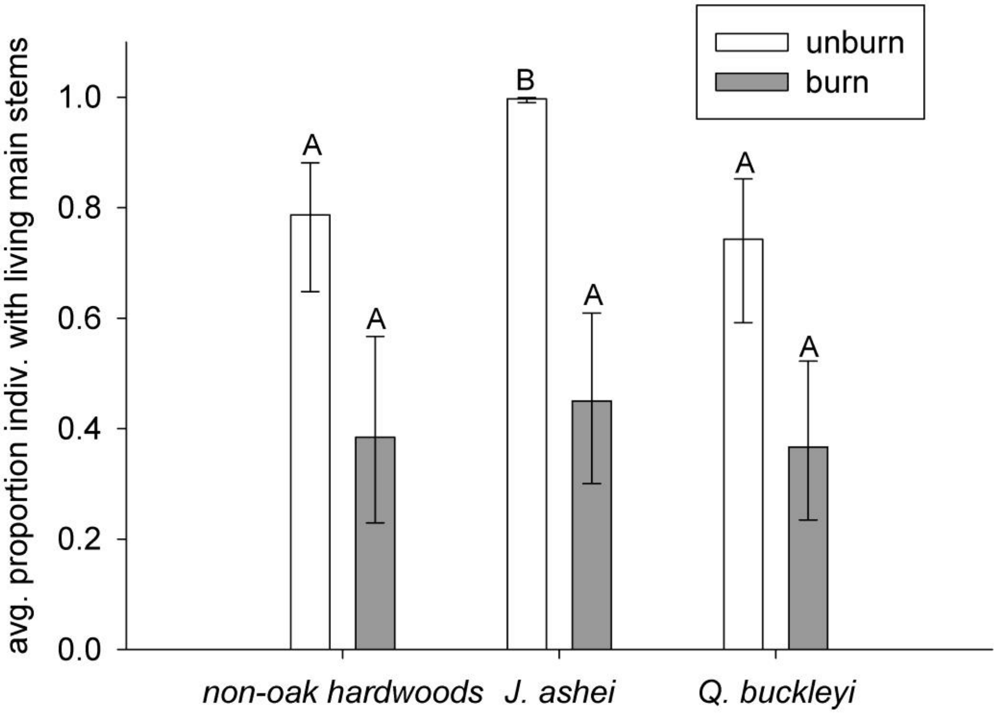

Figure 4.5: There was a significant fire x site interaction in the analysis of the proportion of mature hardwood trees with living main stems (P = 0.0203). Letters indicate significant differences between burned and unburned areas within each species group.

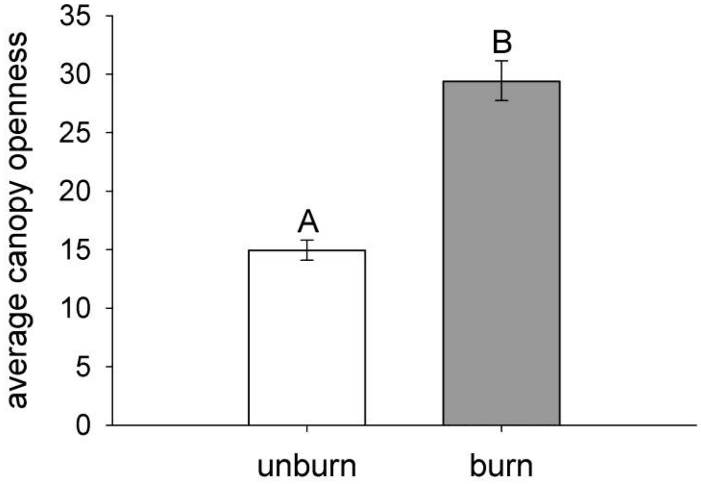

Figure 4.6: Burned areas had significantly higher canopy openness than unburned areas (*P* < 0.001). Canopy openness is 100 minus canopy cover.

Chapter 5: The effects of woody plant encroachment on central Texas soil seedbank

INTRODUCTION

Savannas, defined as communities with a mosaic of woody and herbaceous plants, constitute 15-25% of the world's terrestrial vegetation (Asner et al., 2004). Fire, herbivory, and differences in water uptake are current explanations for the mechanism of grass-tree coexistence in savannas (Sankaran et al., 2004). However, herbaceous and woody species do not always coexist in savannas. Savannas and grasslands worldwide, and on the Edwards Plateau of central Texas, are being converted to woodlands, a process termed woody plant encroachment (Briggs et al., 2005; Van Auken, 2009). This is thought to be directly due to fire suppression, and indirectly due to fuel reduction via cattle grazing (Van Auken 2009). Woody plant encroachment in central Texas is predominantly by *Juniperus ashei* (Ashe Juniper, (González, 2010). *J. ashei* is fire-sensitive and unpalatable to white-tailed deer (*Odocoileus virginianus*, (Armstrong and Young, 2002). It is thought to be the dominant woody encroacher in this system because high white-tail deer densities in this region (Mostyn, 2001) prevent palatable woody species from also encroaching.

The native dominants of the herbaceous component of eastern Edwards Plateau savannas are a group of short- and mid-height native grasses, including *Schizachyrium scoparium*, *Nassella leucotricha*, *Bothriochloa laguroides,* and species of *Bouteloua* and *Aristida* (Fowler & Dunlap 1986). Many native forb species also occur in these savannas. *Bothriochloa ischaemum,* a Eurasian perennial bunchgrass, was introduced in the early 1900's for erosion control and forage (Coyne and Bradford, 1985). *B. ischaemum* is now found in most non-wooded upland areas on the eastern Edwards Plateau, and often forms near-monoculture stands. There seems to be nothing precluding its potential expansion into and dominance of all non-wooded areas in this region (Gabbard and Fowler, 2007). However, neither *B. ischaemum* nor the common native savanna species persist where woody plant encroachment has created a closed canopy. There are, therefore, two invasion processes occurring simultaneously in this system: woody plants, primarily *J. ashei*, encroach on savannas, while the grass *B. ischaemum* invades areas that are still open (Fig 5.1).

Management to remove woody plant encroachment starts with mechanical clearing (cutting down trees), often followed by prescribed fire (Bates et al., 2011; Brudvig and Asbjornsen, 2007). Although, some studies have found that it is possible to only use prescribed fire (Twidwell et al., 2013), or only clearing (Halpern et al., 2012). After clearing the undesired woody plants, the resulting cut material is often evenly spread across the study site to dry. It is then burned under safe conditions; this results in a high fuel load and a relatively high fire-intensity, which can kill many of the existing plants. In central Texas, there are often very few plants left after *J. ashei* invasion; it significantly reduces understory diversity (Yager and Smeins, 1999). Therefore, vegetation trajectories following *J. ashei* removal depend largely on dispersal and the soil seedbank.

Woody plant encroachment has the potential to degrade seedbanks, especially of short-lived species. For example, a site that was invaded by *J. ashei* 40 years ago had lower seedbank diversity than an intact grassland (D'Souza and P. W. Barnes, 2008). Similarly, *Juniperus* encroachment into dry grassland in Sweden following 80 years of ungrazing reduced seedbank diversity by 80% (J. P. Bakker et al., 1996). All invasions have the potential to impact soil seedbanks. For example, invasion by the invasive exotic *Parthenium hysterophorus* L. significantly reduced soil seedbank diversity in an Australian rangeland (Navie et al., 2004). Areas that have been invaded for longer have been shown to be more degraded than more recently invaded areas. For example, native flora recovery was greater in areas that were more recently invaded by *Acacia longifolia* than those that were invaded further in the past (Marchante et al., 2011).

Knowledge of the relationship between time since invasion and seedbank quality can help prioritize sites for restoration (Richter and Stromberg, 2005). It can also direct restoration techniques. For example, re-seedling after restoration may be needed in sites where early successional species are missing from the soil seedbank. A lack of early successional seeds may also make a site more vulnerable to invasive species following restoration. Conversely, a lack of invasive seeds may make a site a good candidate for restoration. This is because the native species remaining in the seedbank and in the surrounding area may have a greater chance of establishment without immediate invasive competitive. For these reasons, I am particularly interested in the depletion rate of invasive *B. ischaemum* seed. Finally, understanding the relationship between time since invasion and seedbank quality also adds to our understanding of the long-term impacts of species invasions, which are understudied (Strayer et al., 2006). For these reasons, I studied the effects of woody plant encroachment on the soil seedbank in sites that have been invaded by woody plants, primarily *J. ashei*, for increasing amounts of time.

METHODS

Historical aerial photographs of Travis County, Texas were obtained from 1939, 1951, 1962, 1980, 1995, 2004, and 2010 (Table 5.1). They were converted into binary images of woody and herbaceous cover in ArcGIS using a supervised maximum likelihood classification for 3-band infrared images (1995, 2004, 2010), and an unsupervised classification for black and white images (1939, 1951, 1964, and 1980). These images have been scanned, rectified, and classified mostly by A. Gonzalez, but also by K. Alofs and C. Andruk. Seven invasion histories were studied, corresponding to the available photographs (Table 5.1). The study area was a plateau top at Balcones Canyonlands National Wildlife Refuge, Marble Falls, TX. I used a stratified random sample to select 10 random plots per invasion history in ArcGIS (Fig. 5.2). Sample locations all had a slope between 0 and 15 degrees to ensure environmental homogeneity.

Field data collection took place from January 21 to 31, 2011. A 5-cm diameter by 5-cm deep soil core was taken from the center of each plot, and at 0.5-m north, south, east and west around each plot. Litter was included in the sample. All of the soil cores from a single plot were pooled. Other variables measured at the plot included: slope, canopy cover of *J. ashei* and of hardwoods, litter depth, and duff depth. Collected soil samples were dried at room temperature in a paper bag for 1 week prior to germinating. They were then sieved through a mesh to remove rocks and break up clumped soil. Previous studies have found no impact of cold stratification on germination success (D'Souza 2008), so I did not cold stratify. The soil was spread out on a 23.8 cm W x 25.4 cm L x 6 cm D plastic tray on top of sterile vermiculite.

These trays were randomly arranged on an outside table at the University of Texas Brakenridge Field Laboratory in February 2011. The outside setting and timing was chosen to provide for the weather conditions when many central Texas species germinate. Although an inside controlled setting would have likely resulted in more germinants, the outside setting provides realism. Plastic piping was used to build a structure over the table, on which fine mesh was attached. This mesh prevented windborn seeds from entering the experiment. To monitor contamination, four empty trays with sterile soil were included in the experimental design. The samples were monitored and watered every other day. The seedling emergence method was used to classify the soil seedbank (Heerdt et al., 1996). This method only identifies species that germinate, all seeds that were inviable or otherwise failed to germinate were not counted. Seedlings were removed after they were identified. Some seedlings were removed from the tray and grown in a larger pot to allow for identification. The trays were monitored from February 2011 to late April 2011.

Poisson regression with a log link was used to analyze the number of germinants in each invasion history category. I included years since invasion by woody plants (Table 5.1), life form (grass or forb), and their interaction as predictor variables. The Kenward-Roger adjusted covariance matrix was used to estimate degrees of freedom.

RESULTS

There was no evidence of contamination; no germinants emerged from the control plots with sterile soil. There were serious problems with the experimental set-up. There was no added soil in the trays, because there was so little soil it dried extremely quickly. This small amount of dry soil prevented seeds from germinating and reduced seedling survival. As a consequence, only a few individuals could be identified to species. Most individuals were only classified as a grass or forb. In total, we counted 461 germinants. Average overall density was 6.59 seedlings per sample, or 623.89 seedlings / m^2. Average density in plots that were herbaceous from 1939 to 2011 was 40.2 seedlings per sample, or 4094.74 seedlings / m^2.

There was a significant difference in the total number of germinants from each invasion history ($P < 0.001$). 87.20% of the germinants were from plots that were herbaceous from 1939 to the 2011; the remaining invasion histories had very few germinants (Fig. 5.3). There was also a significant invasion history x life form interaction ($P < 0.001$, Fig. 5.3). Grasses were abundant in plots that were herbaceous from 1939 to 2011. They had an average of 38.9 germinants per plot (3962.32 seedlings / m^2) there; average numbers significantly decreased in subsequent invasion histories. Forbs were never abundant, having an average of only 1.3 germinants per plot (132.42 seedlings / m^2) in plots that were open from 1939 to 2011 (Fig. 5.3).

Bothriochloa laguroides (silver bluestem) dominated the seedbank; it had 279 germinants, 60.52% of the total. It was only found in plots that were herbaceous from

1939 to 2011. The invasive *B. ischaemum* was the second most common identified species; it had 86 germinants, representing 18.66 % of the total. *B. ischaemum* had a longer persistence in the seedbank that *B. laguroides*: it was found in three plots that had were herbaceous from 1939 to 2011, two plots that were invaded seven years ago, and one plot that was invaded 16 years ago. There were six germinants that were identified as *Croton monanthogynous* (prairie tea), a common ruderal species that is often seen growing in recently cleared or burned sites. It potentially has very long-lived seeds, it was found in one plot that was never invaded and in another plot that was invaded 72 years ago. Other ruderal species that were identified include annual grasses: four individuals of *Dichanthelium oligosanthes* (Scribner's rosette grass) and five individuals of *Limnodea arkansana* (Ozark grass), and annual forbs: five individuals of *Oxalis* spp. The perennial forb *Melampodium leucanthum* (blackfoot daisy) was also observed. There were 11 unidentified germinants from the Lamiaceae (mint) family.

DISCUSSION

The data seem to suggest that woody plant encroachment negatively impacts the seedbank in as little as 7 years. However, this should be interpreted with caution, as this study did not identify enough germinants to make an accurate assessment of seedbank diversity. D'Souza and Barnes (2008) found 2,644 seedlings/m^2 from 116 different species in a similar study site. This study found 623.89 seedlings/m^2 from 11 different species. However, 87.20% of the germinants were found in plots that had never been invaded, indicating that seedbank density quickly declines. There are several possible reasons why I failed to find higher representation of the seedbank.

First, it is possible that the seedbank at the study site is truly depauperate, although this seems unlikely given the higher diversity found in previous studies. A second possible reason is that cold stratification or fire disturbance is needed to induce germination of central Texas savanna species. A seedbank study from central Texas stated that preliminary analysis found no effect of cold stratification on germination (Souza et al., 2011). Cold stratification was also not used in other studies that examined the seedbank in savanna systems with the seedling emergence method (Cohen et al., 2004; Williams et al., 2005). Therefore, the lack of cold stratification probably does not account for the low seedbank diversity found in this study. However, heat induced germination may be important. Some dominant central Texas grass species seeds have exhibited high germination under lab conditions that stimulated a rapid fire with high temperatures (Ruckman et al., 2012a). Heat-induced germination is common in other savannas as well. In Australia, the germinable soil seedbank was significantly enhanced by smoke and heat (K. Scott et al., 2010). The relationship between heat and germination of common central Texas species warrants further investigation.

Finally, it is likely that I would have observed higher germination, at least in the plots that were herbaceous from 1939 to 2011, if the experimental set-up was modified. I would recommend multiple soil seedbank sampling events spaced throughout the season. Many species germinate and grow in the normally wet fall (October through November). Sampling before this time period would potentially capture more species. I would also recommend adding sterile soil to the soil seedbank sample. This would allow the soil to hold water for longer, which would probably increase the germination rate. It would also increase the number of seedlings that survived long enough to be identified or successfully transplanted and then identified. Although the outdoor experimental set-up provided realism, it caused me to miss many species that were actually present in the seedbank. If the goal is to simply document the soil seedbank composition, I recommend conducting the experiment in a greenhouse or other controlled setting.

These data indicate that the longer ago woody plants, primarily *J. ashei*, occupied a site, the more depaurparate the soil seedbank community. This suggests that restoration projects to remove *J. ashei* should target more recently invaded sites. However, more recently invaded sites are more likely to have *B. ischaemum* seeds in the soil seedbank. *B. ischaemum* was present in sites that had been invaded by *J. ashei* up to 16 years ago. It is my opinion that the added benefit of increased soil seedbank diversity in more recently invaded sites likely outweighs the negative impact of *B. ischaemum* presence in such sites. *B. ischaemum* is extremely common in central Texas and will likely be present nearby *J. ashei* removal sites anyway, and can therefore establish through dispersal. In conclusion, I recommend that this experiment be repeated with the modifications suggested above.

Table 5.1: Invasion histories studied in the seedbank analysis. Available historical aerial photographs (1939, 1951, 1962, 1980, 1995, 2004, and 2010) determined the dates that were chosen.

invasion history	years since invasion
woody from 1939 to 2011	72
woody from 1951 to 2011; herbaceous previously	60
woody from 1962 to 2011; herbaceous previously	49
woody from 1980 to 2011; herbaceous previously	31
woody from 1995 to 2011; herbaceous previously	16
woody from 2004 to 2011; herbaceous previously	7
herbaceous from 1939 to 2011	0

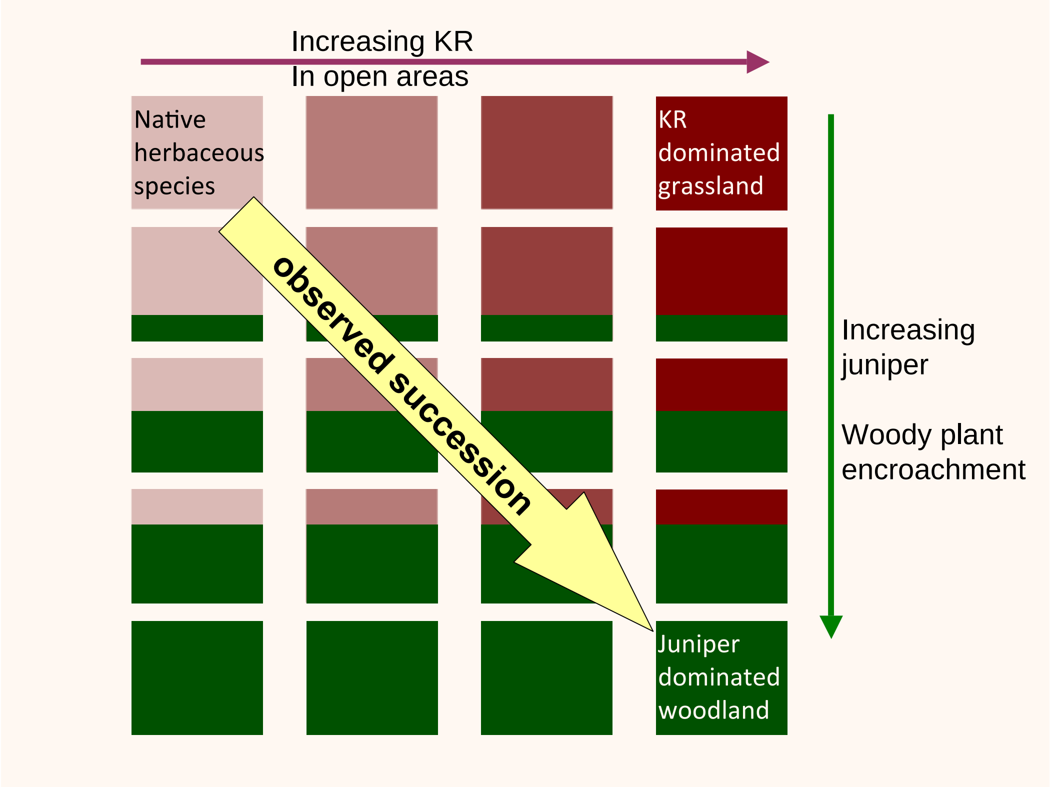

Figure 5.1: There are two invasions that occur simultaneously in central Texas savanna. *Bothriochloa ischaemum* (King Ranch bluestem, abbreviated KR here) replaces native herbaceous species in open areas. Woody plant encroachment by juniper (*J. ashei*) converts open areas to closed areas. The typical observed successional pathway involves increasing *B. ischaemum* (King Ranch bluestem, KR) and increasing juniper (*J. ashei*) simultaneously.

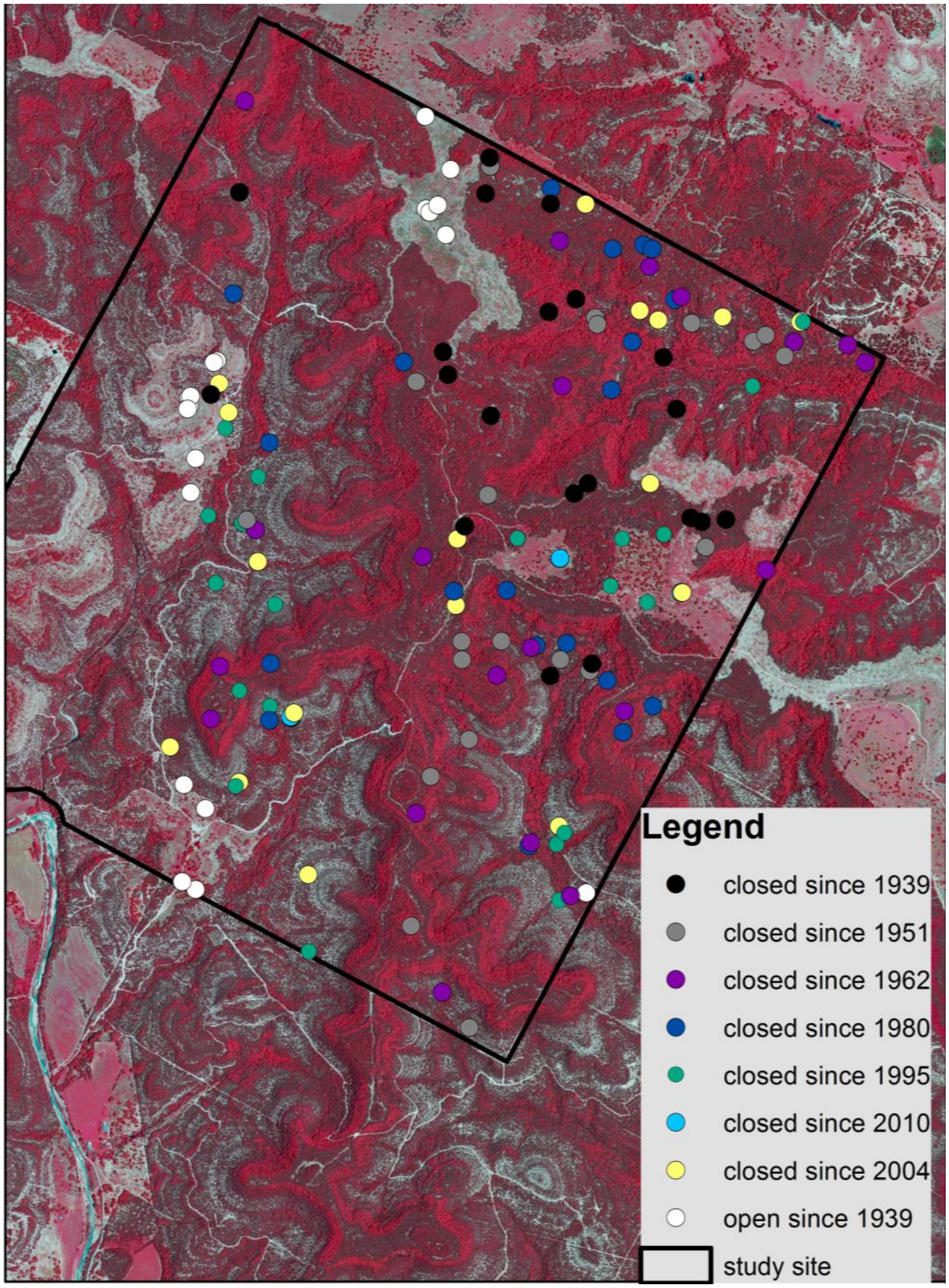

Figure 5.2: Plot locations used to survey the soil seedbank. Closed means the plot was covered by woody plants; open means the plot was covered by herbaceous plants.

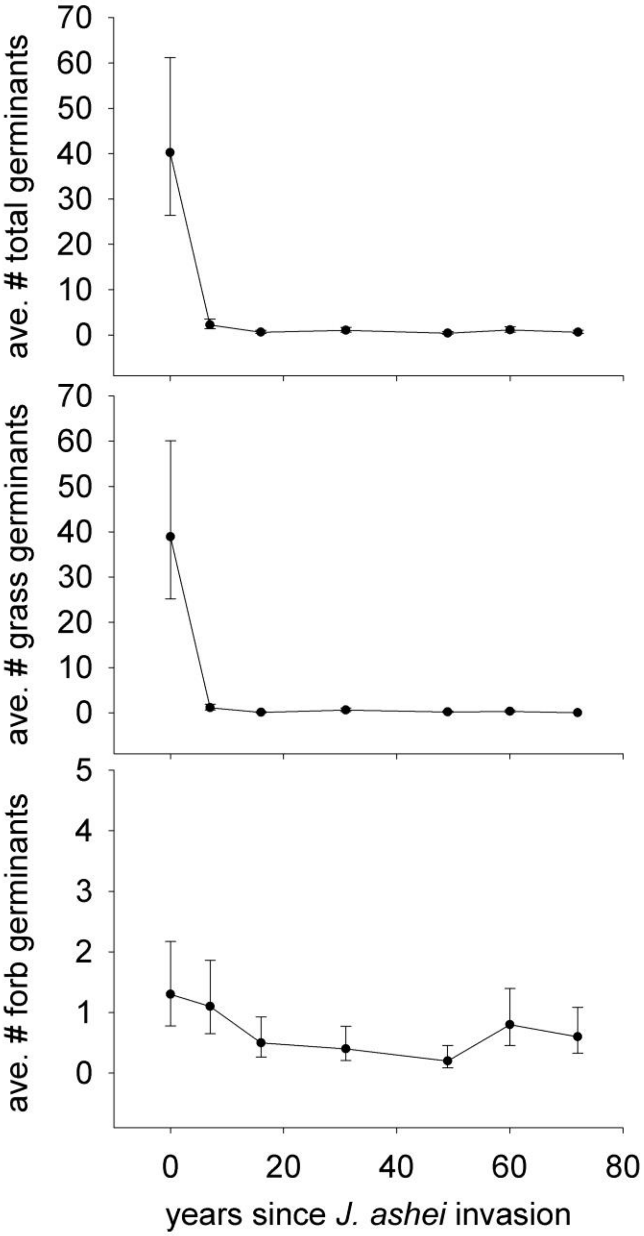

Figure 5.3: The average number of total germinants, grass germinants and forb germinants in the soil seedbank collected from plots with 7 different invasion histories (Table 5.1). Error bars represent 1 SE. Note the different y-axis scales.

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