

OPTIMIZING THE USE OF BURNING IN THE CONTROL OF *BOTHRIOCHLOA*  
*ISCHAEMUM* IN THE TEXAS HILL COUNTRY

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## **CHAPTER I: RAINFALL - BURN TIME INTERACTIONS AFFECT THE SUCCESS OF *BOTHRIOCLOA ISCHAEMUM* CONTROL IN THE TEXAS HILL COUNTRY**

### **Summary**

The invasion of *Bothriochloa ischaemum* (common name: King Ranch bluestem) into North American grasslands has caused a marked reduction in the biodiversity of native flora and fauna. To control the invasive species land managers need an effective, low cost treatment. Mowing, herbicide and fire are the most common means to control unwanted range grasses, but these methods are not consistently effective. For example, winter prescribed burns have proven ineffective and may even encourage *B. ischaemum* growth in grasslands, while new evidence suggests that summer burns may be more effective in *B. ischaemum* control. This work examines whether the effectiveness of control by fire, measured by the number of tillers that re-emerged after the fire, depends on the timing of the burn treatment and the rainfall history leading up to the burn. In the field, two separate factorial experiments were conducted to assess the effect of burn time (September versus October) and precipitation (ambient or less than ambient). Rainfall was controlled using “rain-out” shelters to reduce available soil water before burning. Site A contained a near monoculture of *B. ischaemum* while site B contained *B. ischaemum* and native grass species, chiefly *Bothriochloa laguroides* (Silver bluestem), *Schizachyrium scoparium* (Little bluestem), *Sorghastrum nutans* (Yellow Indian grass),

and *Sporobolus compositus* (Tall dropseed). At site A, 235.5 mm of rain were withheld between May 11 and August 1, 2008 and at site B, 27.7 mm between August 21 and September 28, 2008. At both sites, the effects of withholding rainfall, time of burn and the interaction of the two on *B. ischaemum* tiller re-growth were highly significant. At both sites and across precipitation treatments the earlier burn was more detrimental to *B. ischaemum* than the later burn. For site A, the drought imposed in May-August had little effect on recovery after the September burn, but reduced re-growth by 35% after the later burn. By contrast, at site B, the much shorter imposed drought had little effect on recovery after the October burn, but caused greater re-growth after the earlier burn. For the native grasses at site B, all factors and their interactions were also highly significant and withholding rain had a positive effect in the aftermath of the earlier burn and a negative effect in the aftermath of the later burn. Both experiments confirmed that a growing season burn is more detrimental to post-burn recovery than a late-season burn, but also demonstrated that precipitation leading up to the fire can affect outcomes. The second experiment demonstrated that *B. ischaemum* and native grasses responded differentially to rainfall/burn time treatments, although we were unable to identify treatment combinations that targeted the invasive more than the native species. Further investigation of differential species responses to precipitation and burn time may identify prescribed burn scenarios that are significantly more detrimental to the invader than to native grasses. Such information would allow land managers to more effectively control unwanted range grasses, considering not only the timing of the burn but also the precipitation patterns and the physiological status of species prior to the burn date.

## Introduction

The study of invasive species has become an increasingly important ecological field of study as the biodiversity reducing effects and economic strain of invasive species are better documented. Invasive species are among the top five causes of loss of native biodiversity in every ecosystem that has been monitored (Vitousek *et al.*, 1996, Wilcove *et al.*, 1998, Sala *et al.*, 2000). The main threat to roughly 42% of all endangered species is the presence of invasive species (Pimentel *et al.*, 2005). Invasive species in the United States cause environmental damages and losses adding up to \$120 billion per year, of which \$35 billion of damage is attributed to invasive plants (Pimentel *et al.*, 2005).

In grassland communities, invaders can cause a decline in native grass species diversity (Dukes, 2001; Gabbard and Fowler, 2007), typically reduce forage quality (Pimentel *et al.*, 2000) and consumer diversity (e.g. rodents (Sammon and Wilkins, 2005) and birds (Hickman *et al.*, 2006)). The invasive grass, *Bothriochloa ischaemum* (common name King Ranch (KR) bluestem, Old World bluestem, or yellow bluestem) is a typical example: established originally to control erosion and provide livestock fodder, it now occurs in 17 states and dominates a diverse array of habitat types (Sammon and Wilkins, 2005). While many land owners and managers do not recognize *B. ischaemum* as a problem species, as it can be nutritious for cattle if fertilized (Can *et al.*, 2006), there are an increasing number of ranchers and land managers who aim to manage for biodiversity and seek to reduce *B. ischaemum* abundance.

Common methods for controlling invasive or undesirable grasses include fire, mowing, and herbicide treatments (Ogg, 1991; Bowles *et al.*, 1996; DiTomaso, 2000;

Maron and Jeffries, 2001; Cione et al., 2002; Torra et al., 2008). While these methods can be effective where the invasive species has a unique disadvantage tolerating the treatment (Copeland et al., 2002), more commonly, native and invasive species are ecologically and biologically very similar. Where species are similar, removal methods can be ineffective or even counter-productive, because of collateral damage to native species. In addition, non-indigenous invasive species may be better equipped to respond to increases in available space and resource following removal and are notorious for their ability to respond positively to disturbance associated with removal treatments (Young et al., 2002).

The ability to control *B. ischaemum* in central Texas has been met with limited success. For example, mowing and herbicide application were shown to be ineffective at selectively controlling *B. ischaemum* (Simmons et al., 2007). While these treatments temporarily reduced *B. ischaemum* abundance, the percent cover of the species actually increased over pre-treatment cover in the year following mowing and single herbicide treatments (Simmons et al. 2007). In a survey study, Gabbard and Fowler (2007) found no significant relationship between *B. ischaemum* abundance and the grazing or cool-season fire history of sites. In general, fire used to control invasive flora has been effective in only 20% of experimental studies (D'Antonio, 2000). In D'Antonio's review (2000) of the effect of fire on invasive species, treatments were only successful if the invasive species was in some way less tolerant of the particular burn treatment than the native species.

To better understand how fire will affect *B. ischaemum* and the native grass species, it is important to consider the historical fire regime under which the species evolved. In Europe and Asia, where *B. ischaemum* originated, fire-for the most part- has been important in the evolution of grassland species (Naveh, 1974; Jiang et al., 2008). Native grasses of the U.S. central prairies also evolved under high fire frequency (Stewart 2002; Jurney et al., 2004; Anderson, 2006) and fire is considered a necessary component to maintain grassland diversity in North America (Vogl, 1974; Axelrod, 1985). Since fire is common to both *B. ischaemum*'s community of origin and its new community, it is unlikely that *B. ischaemum* control by fire is a simple matter of eradicating a fire sensitive species in a matrix of fire adapted species. Thus, fire – *per se* – should not, and according to most studies, does not selectively damage *B. ischaemum*. However, the timing and circumstances of fire may have differential effects on grassland species.

Most prescribed burns are conducted in winter due to safety concerns. Unfortunately, in winter, most spring/fall-active grasses including *B. ischaemum* are dormant and store all of their internal resources safely below ground where they are protected from fire damage (DeLuca and Zouhar, 2000). It is thus no surprise that winter burns are neither particularly damaging to spring/fall-active grasses, nor selective in their capacity to inflict damage on invasive species. However, one recent study suggests that burning during the active growing season is more damaging in general and possibly more damaging to *B. ischaemum* than to its native competitors, and furthermore that the precise timing of the burn within the active growing season affects outcomes (Simmons et al., 2007). The mechanisms involved are not known, but a plausible explanation is that species in different physiological and phenological states differ in the distribution of

internal resources at the time of fire. For example, a species in the seed filling stage might be harder hit by fire than a species in the post seed-scatter stage, when internal resources have been mobilized to below-ground structures, protected from the effects of fire.

In water-limited grasslands, the timing of growth and senescence for the ecosystem as a whole, is determined primarily by moisture conditions interacting with temperature (Lynch, 1971; Cable, 1975; Duncan and Woodmansee, 1975; Hufstader, 1976; Hufstader, 1978; Risser et al., 1981; Gibbens, 1991; Briggs and Knapp, 1995). Nonetheless, at smaller scales, species generally do not all grow, flower and set seed at exactly the same time (Gulmon et al., 1982; Stanton, 1988). In other words, their phenologies are often offset. Thus, grass species grown under similar conditions tend to develop at unique times (Fowler and Antonovics, 1981). It has been suggested that developmental timing is one way in which plant species partition the available niche space and ultimately maintain the species diversity of grassland communities (Harper, 1977; Hutchinson, 1978; Burrows, 1990; Davis et al., 2000).

Thus, two key observations provide a basis for developing a more effective method of invasive species control by fire: 1) competing species in a community differentiate in terms of phenology, and 2) different phenological states are differentially sensitive to fire, related to the distribution of internal resources above- and below-ground. Thus, it should be possible to selectively damage unwanted species by precisely timing the application of fire so that unwanted species are in a more vulnerable phenological and/or physiological state than one or more native species.

Building upon the study by Simmons et al. (2007), wherein growing season burn was identified as a more effective method to control *B. ischaemum*, we aimed to study two aspects of the use of fire to control the invasive species. First, we designed an experiment to test whether the timing of a prescribed burn and precipitation patterns preceding the burn interact to affect the amount of fire-related damage on *B. ischaemum*, as determined by the species' ability to recover after fire. Second, we sought to determine whether the amount of fire damage correlates with the physiological and developmental stage of *B. ischaemum* at the time of the fire. Finally, while our ability to compare the degree of fire damage between species was limited, to the extent possible we also investigated whether the timing of fire and preceding rainfall patterns damaged differentially, *B. ischaemum* and the sympatric native, *Bothriochloa laguroides* (Silver bluestem).

## **Methods**

### *Study Species*

*B. ischaemum* is native to Europe and Asia (Correll and Johnston, 1979). The environmental factors that determine the biogeography of *B. ischaemum* in Asia include longitude, mean annual temperature, elevation and precipitation (Zhang and Zhang, 2006). In Texas and Oklahoma, *B. ischaemum* and related Old World bluestem grasses dominate more than 1 million hectares of rangeland (White and Dewald, 1996). In the U.S., *B. ischaemum* grows alongside native grasses including *Bothriochloa laguroides* (Silver bluestem), *Andropogon gerardii* (Big bluestem), *Andropogon glomeratus* (Bushy bluestem), *Bouteloua curtipendula* (Sideoats grama), *Schizachyrium scoparium* (Little

bluestem), *Sorghastrum nutans* (Yellow Indian grass), *Sporobolus compositus* (Tall dropseed) and *Panicum virgatum* (Switch grass).

Both *B. ischaemum* and *B. laguroides* are C<sub>4</sub> grasses. This type of photosynthetic system reduces the amount of water loss per carbon molecule gain (Sage, 1999). The timing of C<sub>4</sub> grass development strongly depends on the timing of late spring and summer rainfall events, though even amongst C<sub>4</sub> grasses there is still an observable difference in their phenology (Kemp, 1983; Reynolds et al., 2000).

### *Study Area*

The experiment was conducted on a private ranch, 60 miles southwest of Austin, Texas (latitude 29° 58' 48" N, longitude 98° 32' 36" W). Temperatures vary from a mean January daily minimum of 1.11°C to a mean August daily maximum of 34.4°C, annual precipitation is 87.63 cm. The property consists of grassland with some wooded areas on shallow, alkaline, undulating, loamy and clayey soils (Davidson and Davidson, 2008). Two experiments were conducted on sites within 200 meters of one another. At site A, the soil was approximately 45 cm deep, on average and almost exclusively covered by *B. ischaemum*. At site B, the soil was 30 cm deep, on average and supported a greater diversity of grasses, including *B. ischaemum*, *B. laguroides*, *S. compositus* and *S. scoparium*. Neither site had been grazed, mowed, cultivated or burned in the past 16 years and vegetation was characteristic of central Texas' eastern Edwards Plateau (Davidson and Davidson, 2008).



### *Experimental Design*

We conducted two experiments using in both a 2 x 2 factorial design with each treatment combination replicated five times. The factors were burn time (28 September 2008, 20 October 2008) and precipitation (ambient, water withheld for some period prior to the first burn). Twenty experimental plots were established in a randomized complete block design. All plots were 3 x 3 m<sup>2</sup> and separated by at least 1 m.

Rainout shelters consisted of a 3 x 3 m<sup>2</sup> sheet of greenhouse polyfilm (SunSaver – IR/AC 6 mil Clear) atop a 3 x 3 m, ½” galvanized steel pipe frame. The polyfilm was taped on all four edges for reinforcement and grommetted. Cable ties and wire were used to attach the polyfilm to the frame. The frame rested upon four, 2 m t-posts at the four corners. The roof was positioned with approximately a 15% slant to facilitate runoff, with the top edge approximately 1.5 m and the low edge about 1 m above the ground. A rain gutter was attached along the full length of the lower edge to capture runoff water and the gutters drained into plastic tubing which routed the water downhill several meters away from the plot area.

Rain-out shelters are known to increase temperature under the shelter. To quantify this effect, the air temperature was measured 5 cm above ground in the center of five unsheltered and five sheltered plots for several days from 17 July – 1 August, 2008. Daytime temperature was increased by about 1°C, consistent with other studies using rainout shelters at 1 – 2 m above ground (e.g. Schwinning et al., 2005).

At site A (*B. ischaemum* dominated), rainout shelters were erected on the plots and left in place from May 11, 2008 through August 1, 2008. During this interval a rain gauge positioned between the two experimental sites recorded 235.5 mm of rainfall (Fig. 1.1). The rain-out shelters were disassembled, moved, and erected on site B on August 21, 2008 and left in place until September 28, 2008. During this interval the rain gauge recorded 27.7 mm of rainfall (Fig. 1.1).

#### *Burn treatment*

Burn treatments were administered to individual plots, and plots were burned either in September or October. Fire was contained by bordering each plot with 1 m tall aluminum panels and was fueled by a fair amount of litter produced in the 2007 growing season. Plots were usually fully burnt within 3 minutes. During the September burn the average temperature was 32°C and the average relative humidity was 23.2%. The average temperature during the October burn was 28°C and the average relative humidity was 37.5%. The average fuel load at site A was 148 g/m<sup>2</sup>, and at site B was 236 g/m<sup>2</sup>.

#### *Pre-burn and post-burn data collection*

After the rainout shelters had been set up, we took biweekly to monthly measurements of predawn water potentials using a PMS 1000 pressure chamber (PMS, OR, USA), as a measure of soil water availability in the root zone. Two blades were randomly selected per plot and their values were averaged. All samples were taken from the center square meter of each plot, where the rainout shelters were most effective at

keeping rain out. This method of sampling from the center square meter was used for types of data collected.

The developmental stage of *B. ischaemum* was recorded prior to burning in each plot following the protocol outlined by Moore et al. (1991). To quantify the average life stage of tillers in each plot, every culm in the center square meter was categorized into one of three distinct phenological stages, and consequently assigned the values 1, 2 or 3. A score of 1 was assigned to those culms in a pre-reproductive/elongation stage. A 2 was assigned to those culms in the reproductive stage and a score of 3 was given to those in a post-reproductive phase. During the elongation phase, seed fill is occurring. During the reproductive phase, seeds are fully mature and the post-reproductive phase is identified by shattered seed heads.

Additionally, three tillers from each plot were randomly selected in the center square meter and brought back to the lab to be scanned for total leaf and stem area. The samples were then dried in an oven set to 40°C for three days before weighing to quantify the average per tiller above ground biomass. At site A, only *B. ischaemum* was assessed in this way. At site B, this data was collected for both *B. ischaemum* and *B. laguroides*.

On April 24th of the following year, we counted the number of tillers growing inside the center square meter of every plot, separated by species at site B.

### *Statistical Analysis*

Plant water potentials, tiller dry mass and average developmental stage were analyzed by analysis of variance with burn date and the shelter treatment as fixed factors.

Post-burn tiller counts were analyzed by Poisson regression (Kaitala, 1996; Jacob and Evans, 1998; Van Der Wal et al., 2000; Von Holle and Daniel Simberloff, 2005), with the shelter treatment and the burn date as the independent variables. A standard ANOVA was not appropriate for this analysis because the response variable was a count and no transformation could be found to render it with normal distribution. Analyses were performed in Program R (Generalized Linear Model for R version 2.8.1, The R Foundation for Statistical Computing).

## Results

Block turned out to have insignificant effects, thus we omit block effects in the analysis presented here. At site A, burn date, the shelter treatment and their interaction all had highly significant effects on the post-burn tiller counts (Table 1.1). In sheltered and unsheltered plots, the September burn was far more detrimental to *B. ischaemum* than the October burn, although the sensitivity to burn date was much higher in unsheltered plots (Figure 1.2A). In unsheltered plots, there were on average 13 x more tillers growing in plots burned in October compared to September. This ratio was only 3.6 for sheltered plots. While drought stress slightly aided recovery after the more damaging earlier burn, it substantially reduced recovery after the less damaging October burn.

At site B, burn date, the shelter treatment and their interaction also had highly significant effects on the post-burn tiller count on *B. ischaemum* (Table 1.2, Figure 1.2B). The earlier burn was again more damaging than the later burn, and shelter treatment again weakened the effect of burn date. However, the shelter treatment greatly aided recovery after the September burn, rather than slightly weakening it.

The earlier burn was also more damaging for *B. languioides*, the most common native grass at site B, but there were no significant burn date – shelter treatment interactions. (Table 1.3, Figure 1.2C). For this species, the brief shelter treatment uniformly aided tiller growth in the following spring, increasing tiller density by a factor of about 1.5.

To help explain the mechanism through which burn date and the shelter treatment may have influenced post-fire recovery, we examined several indicators of phenology and physiology prior to the burn date. Figure 3 shows the average life stages of *B. ischaemum* and *B. languioides* before burning. At both sites, the phenology of *B. ischaemum* tillers was significantly affected by burn date (Tables 1.4, 1.6). A greater proportion of *B. ischaemum* tillers at both sites were in a phenologically more advanced state before the later of the two burns, as might be expected (Tables 1.5, 1.8). For example, between 12 to 16 % (site A) and 13 to 30% (site B) of randomly selected tillers were in the post-reproductive phase prior to the October burn, versus none (both sites) prior to the September burn (Tables 1.5, 1.8). However, the shelter treatment had a significant effect on life stage only at site B where shelters were up for a shorter time, withheld much less rain, and had not yet caused significant effects on predawn water potentials (Figure 1.1). At site B, the effect of shelter was to accelerate development, for example, before the September burn, 64% of all tillers randomly selected in unsheltered plots were in the immature elongation stage, versus 47% in sheltered plots (Table 1.8). By contrast, at site A, shelters did not significantly affect life stage prior to burning (Table 1.4). Instead, plants in sheltered plots had experienced significant amounts of

water stress in July (Figure 1.1). The water stress resulted in reduction of tiller biomass during the month of July when tillers in unsheltered plots were rapidly gaining biomass (Fig. 1.4). After the shelters were taken off in early August, tillers in previously sheltered plots commenced growing but tiller biomass in sheltered and unsheltered plots remained significantly different until two weeks before the September burn.

For *B. laguroides* at site B, neither burn date nor the shelter treatment had significant effects on tiller growth the following spring (Figure 1.3C, Table 1.3). At the time of the September burn, *B. laguroides* was phenologically more advanced compared to *B. ischaemum*, for example, 57 to 70% of all *B. laguroides* tillers were either in the reproductive or post-reproductive stage in September, compared to 36 to 53 % in *B. ischaemum* (Table 1.8). These differences in maturity were still evident prior to the October burn. Predawn water potentials of *B. laguroides* in September were not significantly different between sheltered and unsheltered plots (data not shown) as was the case for *B. ischaemum* (Figure 1.1).

## **Discussion**

The primary purpose of this study was to examine whether burn date and precipitation history leading up to a prescribed burn interacted in their effects on *B. ischaemum*, as measured by the growth of tillers in the first spring after fire. A secondary goal was to link outcomes to differences in the phenological and/or physiological status of plants at the time of the burn. Although the two burn dates were only three weeks apart, burn time had significantly different effects on spring tiller growth (Figure 1.2,

Tables 1.1, 1.2), confirming an earlier observation that fire earlier in the growing season is more detrimental than fire later in the growing season (Simmons et al. 2008). In this study, across experiments and shelter treatments, there were 3.8 times more *B. ischaemum* tillers growing in plots burned in October than in September. This substantial effect is surprising, especially because the maturity of *B. ischaemum* culms at the time of the burn was different only by degrees (Figure 1.3). The most tangible difference was that at the time of the September burn, 11 – 17% (site A) and 17 – 21% (site B) more culms were classified pre-reproductive compared to October and no culms were post-reproductive (Tables 1.5, 1.8). At site A, the fraction of reproductive culms changed little (Table 1.5). This suggests a substantially higher vulnerability to fire when the population has more culms in an elongation seed fill stage and a reduced vulnerability when the population has more culms in a post-reproductive stage of the perennial grass life cycle.

Differences in fire damage due to the timing of a burn could be related to the amount of carbon and nutrient reserves stored below ground at the time of the burn, since these constitute the reserves that remain available to fuel spring growth. Stores of carbon, nitrogen and phosphorus are constantly in flux, generally declining when growth is most rapid (or demand exceeds supply) and increasing when growth stops or plants senesce (or supply exceeds demand) (Chapin et al., 1990). An event that removes all above-ground biomass should therefore compromise recovery growth the most when coinciding with the end of the exponential growth phase. Populations of *B. ischaemum* are continuously developing new tillers during the warm season, soil moisture allowing, thus populations typically contain tillers in all life stages. This suggests that a population as a whole is

more vulnerable when a greater fraction of culms are in a pre-reproductive stage and just setting seed, consistent with our observation.

Episodes of resource shortage, such as the drought that was imposed in the experiment at site A also interfere with storage metabolism by draining reserves or failing to create resource surplus. Thus, even though the shelter treatment did not modify the life stage distribution of the population (Table 1.5), plants had very likely lower levels of carbohydrate reserves in roots at the time of the burn. This could explain the negative effect of the shelter treatment on tiller growth at site A for populations burned in October (Figure 1.2). An alternative explanation is that drought mortality simply adds to fire mortality of meristems. However, there was no significant shelter effect on populations burned in September, suggesting that the effects of drought and fire are not simply additive but mediated by storage dynamics. Possibly, drought effects were not significant for populations burned in September, because carbohydrate storage levels were low either way, dominated by the large fraction of culms in the pre-reproductive phase (Table 1.5).

The shelter effect at site B was different. First, the shelters did not exclude a large amount of precipitation (only 23 mm; Figure 1.1) and caused no statistically significant effects on predawn water potentials. However, shelters did accelerate culm maturation rates (Figure 1.3B). This may have been due to a temperature effects rather than an effect on soil moisture, as the life cycle of some grasses is known to accelerate at higher temperature (Yuan et al., 2007; Azarnivand and Dastmalchi, 2008). Whatever the mechanism, this experiment tested the relationship between phenology and fire vulnerability more directly, as life stage was manipulated independent of season. For *B*.



*ischaemum*, the relationship between average life stage and tiller growth in spring was quite consistent, in that the lowest average life stage score (September burn, no shelter) at the time of the burn was associated with the lowest average tiller count in spring and the highest average life stage score was associated with the highest average tiller count (October burn, shelter). Remarkably, the two intermediate life stage scores, which were very similar (1.6 for September burn, shelter and 1.5 for October burn, no shelter) resulted in very similar intermediate tiller counts also (131 and 132, respectively).

The observed interaction between burn date and shelter treatment may have been caused by a nonlinear effect of life stage at the time of the burn on tiller growth the following spring. For example, an increase in the average life stage score from 1.3 to 1.6, associated with a 20% decrease in the proportion of pre-reproductive culms, may have had a larger effect on tiller growth than an increase from 1.6 to 1.9, associated with a 13% decrease in the proportion of pre-reproductive culms (Table 1.8).

For *B. laguroides* at site B, the later burn was also less detrimental than the earlier burn, and the rainout shelters had a consistently positive effect on tiller growth (Figure 1.2C, Table 1.3), although the average life stage was significantly affected by neither burn date nor the shelter treatment (Figure 1.3C, Table 1.7). However, the treatment effects on the phenological status of *B. laguroides* were somewhat more complex than the shelter effect on *B. ischaemum*, and not adequately represented in the average life stage score. Both the later burn date and the shelter cover increased the frequency of pre-reproductive culms, and increased the frequency of post-reproductive culms, at the cost of reproductive culms, whose frequency decreased (Table 1.8). Thus, while the average

life stage score remained approximately constant, the population of culms in October and under shelter were skewed towards both immature and post-mature stages compared to populations in September and in the open. This may explain why the later burn date and the shelter cover had equivalent effects on tiller growth, since their effects on phenology were also similar. Furthermore, it suggests that the late season growth of new tillers in this native species cause less of a drain on below-ground storage status than in the invasive species *B. ischaemum*. This could be a reflection of the less opportunistic life history strategy of a non-invasive native species that presumably places more emphasis on risk reduction, especially towards the end of the growing season (Chapin et al. 1990). If this difference can be corroborated as a general pattern, invasive species could be targeted especially well by timing a prescribed burn to coincide with a relatively wet late season.

Two relatively consistent patterns emerged from this study. The first was that when a perennial grass population is burned in a less mature state of development, spring regrowth is generally reduced. This effect seemed to be largely independent of whether maturity was influenced by season or climate conditions (e.g. as manipulated by rainout shelters). A likely explanation is that pre-reproductive culms tend to drain internal resources from root storage, the only form of storage that survives a burn treatment, thereby leaving less resource to fuel recovery growth. Other explanations are of course possible, for example, fire parameters (temperature, fire duration) could affect meristem and seed mortality. However, this would not explain the - across-studies - increasingly consistent effect of burn date on re-growth, as earlier fires are not necessarily hotter or

longer lasting than later fires. That said, demonstrating explicitly the linkages between resource storage dynamics and recovery after fire in perennial C<sub>4</sub> grasses would certainly strengthen the evidence.

The second pattern that emerged was that growing season water stress also had the potential to reduce tiller re-growth in the following spring, even if not accompanied by an effect on the phenological state of a population. This also can be explained based on effects on below-ground storage and would suggest that the date of burn alone cannot predict the degree of fire damage caused in a given year. In this experiment, we did not evaluate if different species had different burn time – drought interactions, but this seems likely, since it is well known that grassland species differ in their responses to precipitation patterns (e.g. Knapp et al., 2002).

While this study did not identify conditions for which a prescribed fire had more damaging effect on the invader than on a native species, the study did show that fire effects can vary by species and in relation to burn date and the precipitation history leading up to the fire. A more comprehensive experimental exploration of this topic, especially if coupled with measurements of the storage status of populations, would be most informative and likely lead to useful generalizations that would help set better guidelines for the precision-timing of prescribed burns for invasive species control.

The “optimal timing” of a growing season burn, i.e., the timing that would result in the most damage to the invasive species and least damage to the native flora, is likely to shift from year to year, and may exclude some years completely, depending on rainfall patterns and possible other factors such as temperature. Given such uncertainty,

scheduling a prescribed based on the straight-forward measurement of the phenological status of invasive and the native species would provide a simple, practical solution to a complex ecological problem. At least in principle, invasive species can be selectively suppressed by fire, if prescribed burns are conducted when invasive flora and native flora have sizeable developmental offsets. Thus, not all years may be equally suitable for prescribed burns, as not all years may be equally effective establishing such phenological offsets.

**Table 1.1.** ANOVA results from the Poisson Regression Analysis of *B. ischaemum* post-burn tiller count at site A.

Coefficients:	Estimate	Standard Error	z Value	P value
Intercept	4.07073	.05842	69.680	2.0e-16
Shelter	-.68974	.10107	-6.824	8.8e-12
Date	1.02669	.06808	15.080	2.0e-16
Shelter-Date Interaction	1.11538	.11062	10.083	2.0e-16

**Table 1.2.** ANOVA results from the Poisson Regression Analysis of *B. ischaemum* post-burn tiller count at site B.

Coefficients:	Estimate	Standard Error	z Value	P value
Intercept	4.73795	.04185	113.22	2.0e-16
Shelter	-1.31695	.09103	-14.47	2.0e-16
Date	.35580	.05457	6.52	7.1e-11
Shelter-Date Interaction	1.29085	.10380	12.44	2.0e-16

**Table 1.3.** ANOVA results from the Poisson Regression Analysis of post-burn tiller count of *B. laguroides* at site B.

Coefficients:	Estimate	Standard Error	z Value	P value
Intercept	3.22684	0.08909	36.221	< 2.0e-16
Shelter	-0.74194	0.15685	-4.730	2.2e-6
Date	0.51083	0.11269	4.533	5.8e-6
Shelter-Date Interaction	0.32208	0.19134	1.683	9.2e-2

**Table 1.4.** ANOVA results for the average life stage of *B. ischaemum* just before burning at site A.

	Df	Sum Sq	Mean Sq	F value	P value
Shelter	1	0.015	0.012	0.689	0.419
Date	1	0.384	0.384	17.474	0.001
Shelter-Date Interaction	1	0.014	0.014	0.640	0.436
Residuals	16	0.351	0.022		

**Table 1.5.** Distribution of phenological states of *B. ischaemum* across treatments at site A.

	% pre-reproductive		% reproductive		% post-reproductive	
	Control	Shelter	Control	Shelter	Control	Shelter
September	77	77	23	23	0	0
October	66	60	22	24	12	16



**Table 1.6.** ANOVA results for the average life stage of *B. ischaemum* just before burning at site B.

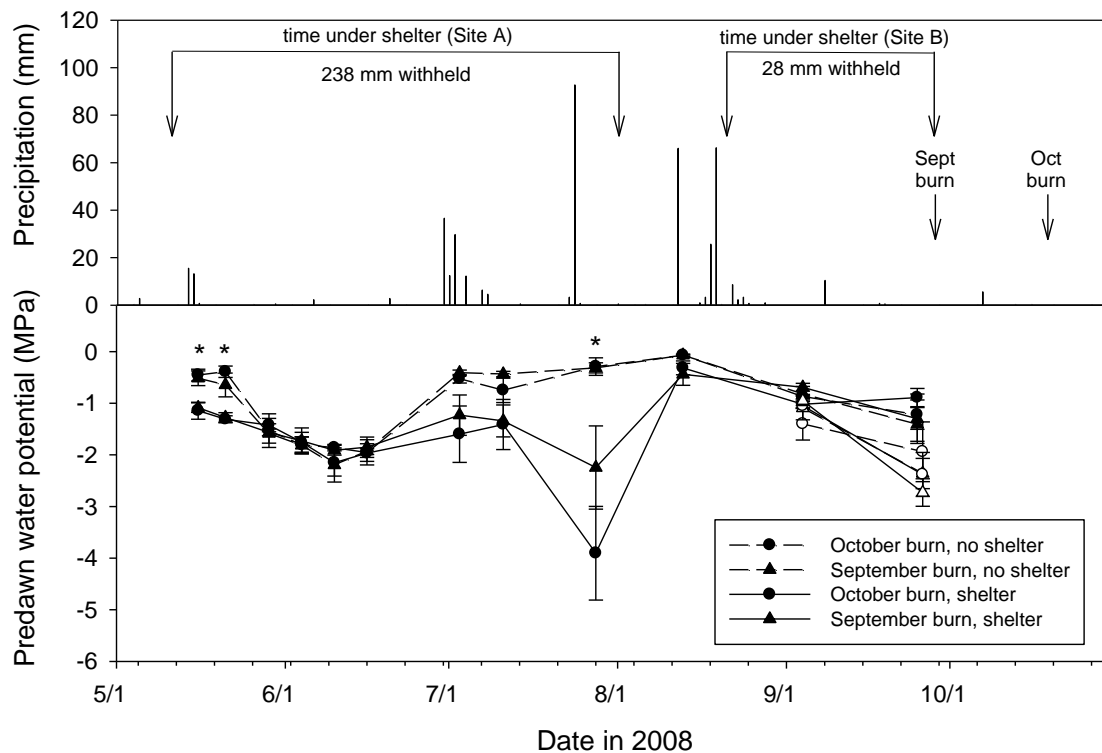
	Df	Sum Sq	Mean Sq	F Value	P Value
Shelter	1	.01512	.01512	.6889	.419
Burn Date	1	0.38364	0.38364	17.4742	.001
Shelter: Burn Date	1	0.01404	0.01404	.6397	.436
Residuals	16	.35128	.02195		

**Table 1.7.** ANOVA results for the average life stage of *B. laguroides* just before burning at site B.

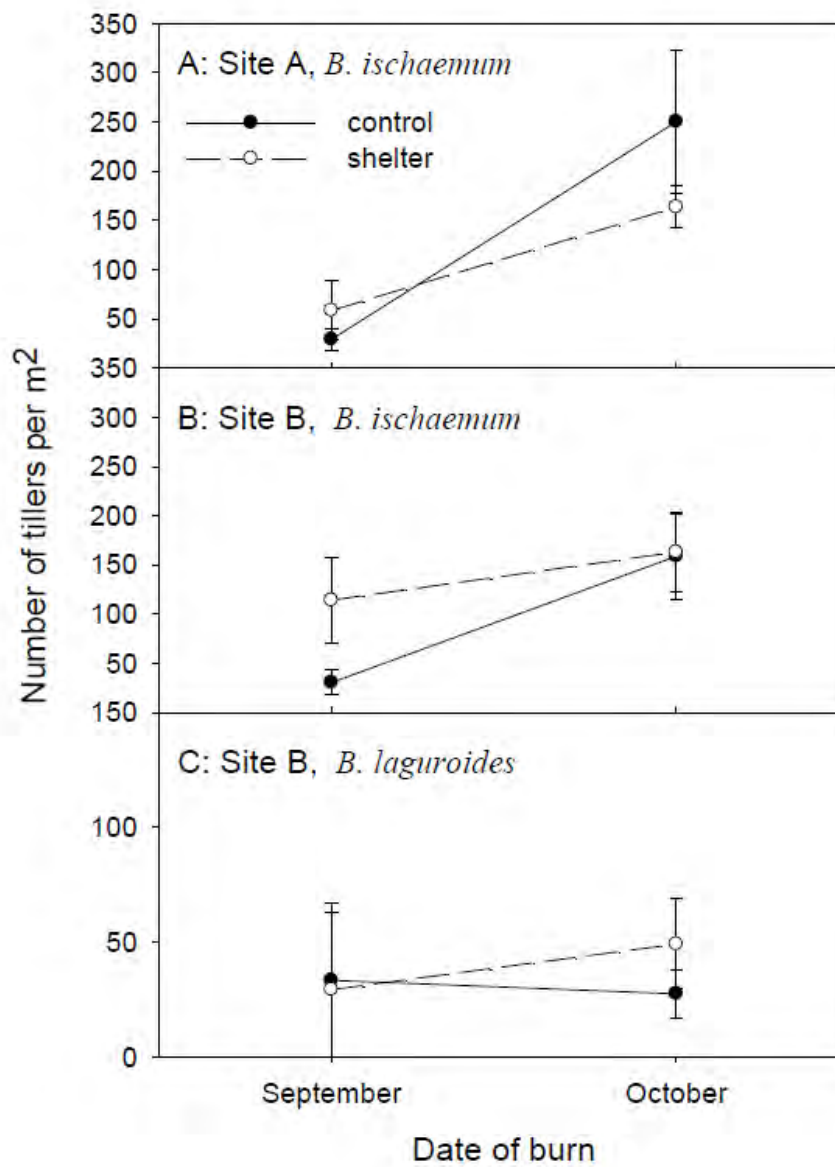
	Df	Sum Sq	Mean Sq	F Value	P Value
Shelter	1	2.88e-07	2.88e-07	.1.393e-06	.9991
Burn Date	1	0.2424	0.2424	1.1721	.2950
Shelter: Burn Date	1	0.0245	0.0245	.1184	.7353
Residuals	16	3.3083	.2068		

**Table 1.8.** Distribution of phenological states of *B. ischaemum* and *B. laguroides* across treatments at site B.

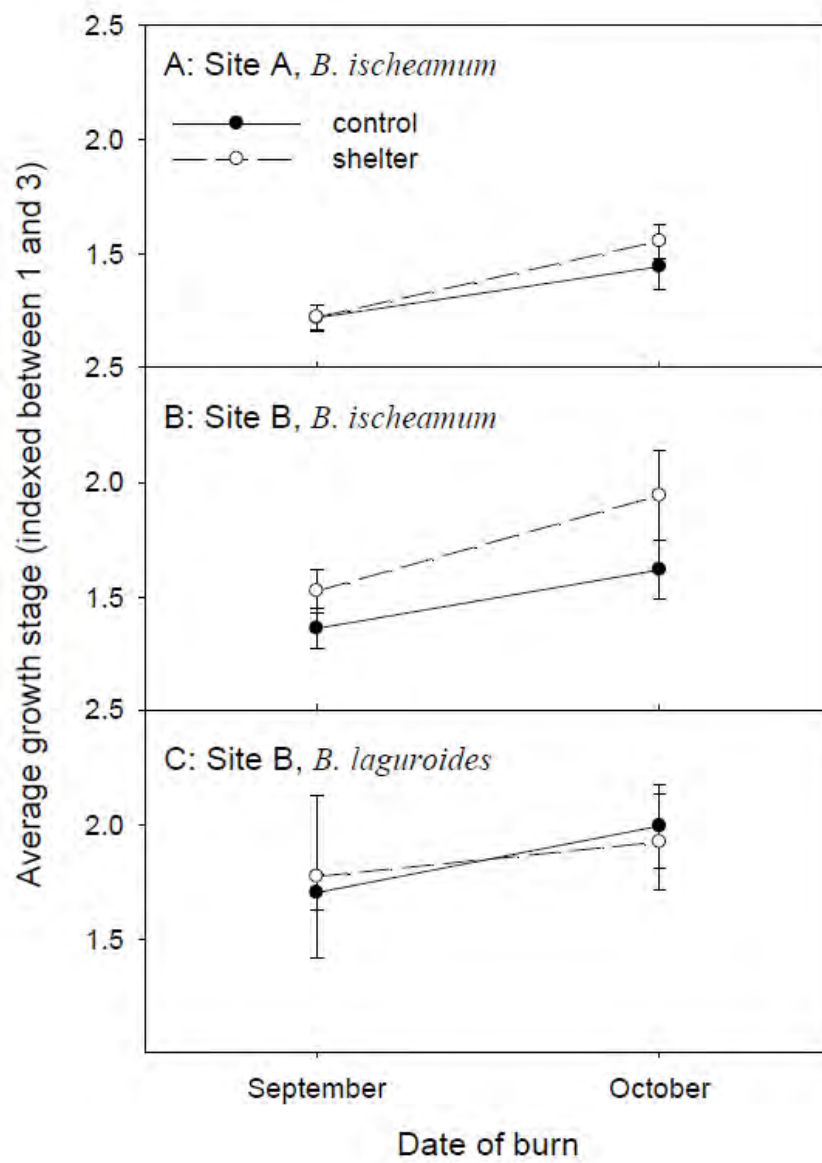
		% pre-reproductive		% reproductive		% post-reproductive	
		Control	Shelter	Control	Shelter	Control	Shelter
<i>B. ischaemum</i>	September	64	47	36	53	0	0
	October	43	30	41	46	13	30
<i>B. laguroides</i>	September	30	43	70	37	0	20
	October	38	46	24	14	38	49



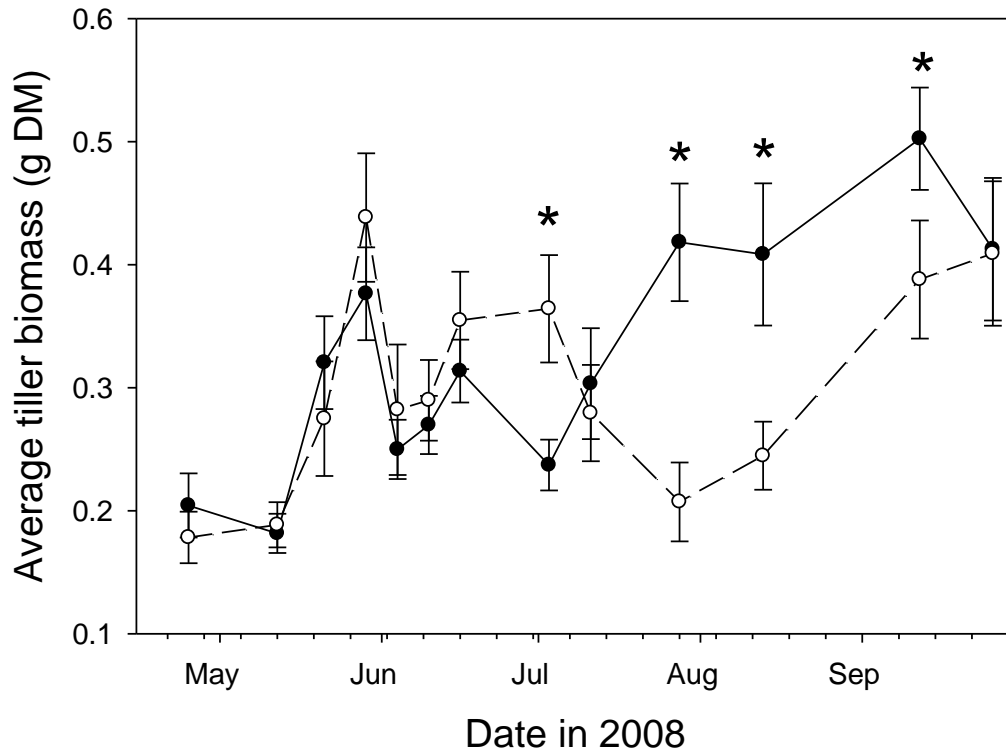
**Figure 1.1.** Precipitation record for the five months leading up to the burn treatments (top panel) and average water potentials for *B. ischaemum* by treatment (bottom panel). Closed circles are for site A, open circles (only two measurements) for site B. Significant water potential differences between sheltered and unsheltered plots (based on ANOVA,  $p < 0.05$ ) are indicated by “\*”.



**Figure 1.2.** Post-burn tiller counts for the dominant species at sites A and B as a function of burn date and the rainout shelter treatment.



**Figure 1.3.** Average life stage prior to burning for the dominant species at sites A and B as a function of burn date and the rainout shelter treatment.



**Figure 1.4.** Average biomass of *B. ischaemum* tillers at site A in sheltered (closed symbols) and unsheltered (open symbols) plots. Significant water potential differences between sheltered and unsheltered plots (based on ANOVA,  $p < 0.05$ ) are indicated by “\*”.

## CHAPTER II: SENSITIVITY OF SEEDS TO HEAT EXPOSURE IN FIVE NATIVE HERBACEOUS SPECIES OF CENTRAL TEXAS GRASSLANDS AND THE INVASIVE GRASS *BOTHRIOCLOA ISCHAEMUM*

### Summary

The invasive, non-indigenous, C4 grass *Bothriochloa ischaemum* (KR bluestem), poses a significant threat to the biodiversity of North American grasslands. To date, control mechanisms for *B. ischaemum* have included prescribed burns, grazing, herbicide, and mowing. Burns are an increasingly popular control method, often with the goal of selectively damaging the invasive species more than the native species. This study tested for species differences in the fire sensitivity of seeds, which can affect the outcomes of burn treatments if communities, at least in part, reestablish from surviving seeds. Heat treatments were conducted on *B. ischaemum* and five other native species, *Schizachyrium scoparium* (Little bluestem), *Bothriochloa laguroides* (Silver bluestem), *Bouteloua curtipendula* (Sideoats grama), *Sorghastrum nutans* (Indian grass), *Lupinus texensis* (Bluebonnets), in temperature-controlled ovens. Seed viability was tested by determining the germination fraction of heat-stressed seeds and comparing them to those of non-stressed seeds. Heat treatments varied in intensity from 125°C to 250°C and in duration from 30 seconds to 4 minutes, a range of conditions typical for grassland fires. Temperature affected the germination rates of *B. ischaemum* and only one native species: *B. curtipendula*, while heat duration affected all species except *L. texensis*. One species, *B. curtipendula*, exhibited temperature x duration interactions. We also calculated an

index of germination response to treatment relative to the germination response of *B. ischaemum* in the same treatment to determine conditions that selectively favor the native species. In this analysis, *S. scoparium* was the only species that had germination advantage of *B. ischaemum* under all treatments. At the highest temperature, *S. nutans* also outperformed *B. ischaemum*. Thus, most fire conditions will selectively favor *B. ischaemum* germination over four out of the 5 species tested here. Across species, intermediate temperature (175 – 220 °C) and intermediate exposure times (60 s) had the least selectively damaging effects on the germination rates of native species. The results suggest that careful planning of fire regimes should be part of an overall strategy to shift the competitive advantage from invasive to native species, by maximizing damage to the seeds of invasive species, while minimizing collateral damage to native species.

## **Introduction**

The detrimental effect of invasive species on ecosystems is well documented (Mack et al., 2000; Sala et al., 2000). Invasive species are among the top five causes of loss of native biodiversity in every ecosystem that has been monitored (Sala et al., 2000). As a reflection of the economic strain caused by invasive species, they are now the focus of many studies and monitoring efforts (Rejanek and Richardson, 1996; Mack et al., 2000; Sakai et al., 2001).

Invasion biology has become an increasingly popular field of study as the economic strain due to invasive species is more thoroughly documented. Indeed,

invasive species in the United States alone cause environmental damages and losses adding up to nearly \$120 billion per year and they are the main threat to roughly 42% of all endangered species (Pimentel et al., 2005).

In grassland communities, invaders can cause a decline in native grass species diversity (Schooler et al., 2006), typically reduce forage quality (Pimentel et al., 2000), alter the soil salinity balance (Pimentel et al. 2000), the soil mineral content (Evans et al., 2001) and the natural fire cycle (Brooks et al. 2004). In addition they are known to reduce consumer diversity (DiTomaso, 2001; Flanders et al., 2006).

The invasive grass, *Bothriochloa ischaemum* (King Ranch (KR) bluestem or Yellow bluestem) is a case in point: this warm-season, perennial bunchgrass was introduced to North America from Eurasia in the 1920's, originally to control erosion and provide livestock fodder. Today the species occurs in 17 states (<http://plants.usda.gov/java/profile?symbol=BOISS>), dominates a diverse array of habitat types and has caused widespread collateral damage to native grass (Gabbard and Fowler, 2007), bird (Hickman et al., 2006) and rodent (Sammon and Wilkins, 2005) communities.

With such overwhelming necessity to find the means to prevent and reduce the impacts of invasive species, it has become the goal of many scientists and land managers to develop management practices to combat invasive species. Common methods of control for invasive flora include biological, chemical and mechanical means. In the Western U.S., prescribed fire is increasingly used to control invasive plant species with a



variety of objectives in mind. Some aim to restore the historical fire regime that the natives evolved to thrive in (Tveten and Fonda, 1999). Some burn to generate habitat for succession of native fauna (Gillen et al., 1987) and still others expect that prescribed fire will selectively control the invasive species more than the native species (McGlone and Huenneke, 2003).

The use of fire to selectively control herbaceous invasive species has had varied success (Keeley, 2006; Gabbard and Fowler, 2007; Simmons et al., 2007). In several studies invasive species were selectively controlled following burning (Willson, 1991; DiTomaso et al., 1999; Simmons et al., 2007) while in other studies burn treatments increased the presence of invasive species (Grilz and Romo, 1994; Gabbard and Fowler, 2007; Pauchard et al. 2007). Keeley (2006) suggested that herbaceous invaders often capitalize on disturbance, thus fire is more likely to facilitate than suppress invaders. On the other hand, precisely timed prescription burning, designed to alter competitive balances in favor of the native community could have a better chance of success.

In this vein, Simmons et al. (2007) recently suggested, and was able to demonstrate, that active-season burns (late summer/fall) are more effective in controlling *B. ischaemum* than dormant-season burns (winter/early spring), at least in the short-term. The mechanism for this effect remains unclear, however, the current working hypothesis is that perennial grasses burned during the growing season are deprived of opportunities to store internal resources below-ground, thereby compromising their ability to re-sprout in spring. It is unlikely, however, that this approach is sufficiently selective, since several

native species are also still active in late summer and may be equally harmed by fire. Additional considerations in scheduling prescribed fires may therefore be required to help skew the competitive balance in favor of the native flora.

It is well documented that different species show markedly different responses in germinability following seed heating (Paula and Pausas, 2008; Sweet et al., 2008) and prescribed burns (Odion and Davis, 2006; Overbeck et al., 2006; Allen et al., 2008; Behenna et al., 2008). Generally, species from fire-prone communities are relatively heat-tolerant and often require heat exposure to achieve maximal germination rates (Tieu et al. 2001, Allen 2008). Furthermore, seeds of non-sprouters have a higher probability of being heat tolerant and heat stimulated (Paula and Pausas, 2008). The problem is that herbaceous invaders like *B. ischaemum* are functionally very similar to their native competitors. For example, many of them also evolved in fire-prone ecosystems and have relatively heat tolerant seeds. However, recent studies suggest that even within functional types from the same community, seed heat tolerance can vary considerably between species (Sweet et al., 2008).

Grassland fires are naturally variable in terms of the surface temperatures they produce and the duration of the heat stress (Gibson et al., 1990; Morgan, 1999). Fire characteristics are dependent on well known relationships of fuel load, fuel moisture status, relative humidity, topographic considerations and other factors (Brown and Smith, 2000). Our goal for this study was to ascertain whether seed germinability exhibits differential sensitivity to variation in temperature and the duration of heat exposure

among five native members of a grassland community and its invader, *B. ischaemum*. The native species included one forb and four grasses commonly used in grassland restoration. We hoped to acquire additional information on how the precise timing of a prescribed fire can be used to maximize damage to undesirable species, thus adding to the toolbox of techniques available to strengthen the competitive edge of a native community over its invader.

## Methods

We employed a three-way complete factorial design with temperature, duration and species as factors. Seeds were exposed to heat in a convective Fisher Scientific Isotemp oven. We used four temperature settings (125, 175, 225 and 250°C) and four durations (30, 60, 120 and 240 s), representative of the common range of grassland fires (Morgan 1999, Sweet et al. 2008). The six species, purchased from the Native American Seed Company (Junction, TX), and frozen for a week to break dormancy, included *Bothriochloa ischaemum* (King Ranch bluestem), *Bothriochloa laguroides* (Silver bluestem), *Bouteloua curtipendula* (Sideoats grama), *Schizachyrium scoparium* (Little bluestem), *Sorghastrum nutans* (Indian grass) and the native wildflower, *Lupinus texensis* (Texas bluebonnet). Also included in this study were controls for each species, where seeds were not exposed to heat.

The experiment was conducted in three consecutive trials, with each trial conducted in one day. A trial contained two replicates of each treatment combination and

four replicates of the control. Thus the complete experiment replicated each treatment combination six times and the control twelve times. For each replicate, approximately 100 seeds were spread on 8.5 cm diameter glass Pyrex Petri dish, lined with 90 mm dry filter paper and placed in the oven set at the designated temperature and for the designated duration. Seed numbers per tray were estimated by weight, based on previously determined seed number to weight ratios.

Immediately following the heat treatment, all seeds in a batch (100) were scattered on the surface of a plastic seedling tray (25.5 cm x 12 cm x 6 cm) filled with approximately 175g Sun Gro Redi-Earth Plug and Seedling Soil. Four seedling trays were randomly combined and placed in larger, plastic drain tray measuring 48 cm x 25.5 cm x 6 cm. Three liters of deionized water was added to each drain tray to allow moisture to be wicked up into the seedling trays. A clear plastic lid was placed over each tray to minimize evaporation and to maintain a high humidity environment for the seeds.

While germinating, seeds were maintained in a controlled environment at 22° C, under 34 watt fluorescent bulbs. At one week and two weeks following sowing, the number of germinated individuals was recorded for each seedling tray. After two weeks, and for some species after one week, the number of seedlings began to drop off. Only the highest recorded seedling count entered the analysis.

The data were analyzed initially using a multifactorial ANOVA with the main effects: trial number, species, temperature and duration and all possible interactions. Trial

number did not significantly determine the rates of germination and was therefore omitted from the analysis reported here.

To compare the effects of a given heat exposure treatment on the germinability of a native species with that of the invader *B. ischaemum*, we calculated the following index:

$$I_{S,T,D} = \log \left[ \frac{N_{S,T,D} / N_{S,C}}{N_{I,T,D} / N_{I,C}} \right] \text{ (eq. 1)}$$

where N is the number of germinated seeds, the subscripts S, T, D stand for the species, temperature and duration, respectively, the subscript I refers to the invasive species and the subscript C to the control treatment. The division by the number of germinated seedlings in the control treatment standardizes species responses with respect to intrinsic differences species may have in germination ratios. Dividing the standardized germination response of a native species by that of *B. ischaemum* expresses the treatment effect relative to the treatment effect on the invader, so that a value greater than one (or greater than 0 for log *I*) indicates that a treatment provides a relative advantage to the native species and may contribute to shifting competitive balances in the desired direction. Finally, taking the logarithm normalizes the distribution of the index to permit parametric analysis, except in the case of *B. curtipendula* where the square of the index was used (mode of transformation was determined using the Ladders of Power Determinant). The index *I* was calculated for each seed batch, using for the control the average of two germination numbers in the same replication set. The effect of species, temperature and duration on log *I* (or *I*<sup>2</sup>, in the case of *B. curtipendula*) was calculated

using multifactorial ANOVA. All analyses were performed using SPSS Inc. (Release 11.0.1, 2001).

## Results

A complete analysis of variance conducted on the number of germinated seedlings (per 100) showed highly significant effects of species, temperature, duration and all two- and three-way interactions (results not shown). To better understand this complex data structure, we next performed ANOVA on each species individually (Table 2.1). Only one species, *L. texensis*, was not significantly affected by either temperature or duration. Only a 4 min exposure to 250°C showed a markedly different germination number compared to the control (Figure 2.1A). At the other extreme, for *B. curtispindula*, temperature, duration and their interaction were all highly significant. The higher the temperature the greater the loss of germinating seedlings due to longer exposure times (Figure 2.1F). In three species, *S. nutans*, *S. scoparium* and *B. laguroides*, only duration had a significant effect on germination, with longer exposure resulting less germinating seedlings (Figures 2.1B, D, E). For *B. ischaemum*, both temperature and duration significantly reduced germination (Figure 2.1C).

A complete factorial ANOVA of the relative germination index  $\log I$  (for all species except *B. curtispindula*, whose index was transformed by squaring) (eq. 1) and also showed significant effects of all main factors and their two- and three-way interactions (data not shown). Focusing first on main effects, *S. scoparium* stood out as

the species with the greatest relative germination rate in comparison with *B. ischaemum* when seeds were exposed to heat (Figure 2.2A). The relative germination rate of *S. nutans* seeds exceeded that of *B. ischaemum* overall, and all other species germinated less readily following the heat treatment relative to *B. ischaemum*. This means that the seeds of the majority of the native species tested were relatively more suppressed by the heat treatment than the seeds of *B. ischaemum*.

The germination of *B. laguroides* was by far the most negatively affected by the heat treatments. The relatively high proportion of germinating seeds of *S. scoparium* relative to the germination of *B. ischaemum* was due to the fact that heat exposure had a strong stimulatory effect on *S. scoparium* under almost all treatment combinations (Figure 2.1D), while *B. laguroides* was intolerant to heat exposure even at low temperature and short exposure times (Figure 2.1E).

Across the selection of native species, no temperature or duration favored germination of the native species overall, but in general, intermediate temperature (175°C) and exposure times (60 s) had the least negative effects (Figure 2.2B, C).

Most species under most conditions had neither very strong advantages or disadvantages with respect to *B. ischaemum*, as many averages clustered around the  $\log I = 0$  line (Figure 2.3), but a few exceptions are noteworthy: In two species, *L. texensis* and *B. curtispindula*, long exposure to high temperature had especially negative effects on seed germination compared to *B. ischaemum* (Figure 2.3A, E). Although *B. ischaemum*

also suffered from high temperature-long exposure (Figure 2.1C), these two species were much more negatively affected. Furthermore, any combination of temperature and duration provided a relative germination advantage to *S. scoparium* (Figure 2.3C) and a relative disadvantage to *B. laguroides* (Figure 2.3D).

## **Discussion**

Many perennial C<sub>4</sub> grasses have evolved in the presence of disturbance by fire. Following a burn, these species regenerate by a combination of mechanisms: re-sprouting from surviving meristems and/or recruitment of new individuals from the seed bank (Enright & Goldblum, 1999; Pausas et al., 2006). The abundance of species following a burn treatment is, at least in part, due to the response of seeds to heat exposure. In some species, heat exposure can enhance the germinability of seeds by increasing the permeability of the seed coat, thereby releasing the seed from dormancy (Keeley, 1991; Keeley & Fotheringham, 2000). Alternatively, burning can have a neutral or negative effect on seed viability (Clarke et al., 2000). We found all of these responses across the six study species examined here, and the response of the invasive species was not fundamentally different from those of the native species. However, we did find subtle variation among species in the response to temperature and the duration of heat exposure (Figure 2.1). Thus, we could identify species and heat regimes that were relatively harmless to native species and relatively more damaging to the invasive species.



One species, *S. scoparium*, had a relative germination advantage over *B. ischaemum* under all treatment combinations (Figure 2.3C). *S. nutans* had a germination advantage only under some conditions, especially in those treatments of intermediate duration (Figure 2.3B). For all other species and conditions, *B. ischaemum* responded more favorably to the heat treatment (Figure 2.2). Overall, the relative disadvantage to the community of native species was minimized under intermediate temperature (175 – 220 °C) and intermediate exposure times (60 s) (Figure 2.2).

These findings suggest that prescribed burns to target the seedbank of *B. ischaemum* will have greater success if *S. scoparium* and/or *S. nutans* are relatively well represented in the seedbank. This effect on the seedbank will affect grassland composition if native seedlings will establish and survive. Additionally, damage to native species can be minimized by avoiding fires that burn either too cold and slow or too hot and long.

That said, there are two factors that may limit the effectiveness of using prescribed burns as a tool to combat invasive species via effects on the seedbank. First, it is difficult to precisely control the intensity and duration of a fire. Second, by some accounts, only a small fraction of the vegetation recovery after a burn is driven by germinating seeds.

Regarding the first limitation, prescribed burns are generally scheduled in advance and are planned so as to minimize the risk of uncontrolled spread. Thus, there is

often little flexibility in controlling meteorological variables. Fires are usually scheduled when humidity is high and wind speeds are low, since these are among the factors that reduce fire intensity and rate of spread (Bessie and Johnson, 1995). Additional factors affecting burn intensity and duration are wind speed, aspect of fire (head, back or flank), fuel load, moisture status of fuel and the topographic situation of the site. Bessie and Johnson (1995) surveyed the effect of fires over time and the accompanying meteorological variables and fuel load characteristics and determined that fire behavior was more closely linked to weather variation than fuel variation. Thus, some residual control over meteorological variables could compensate for a lack of control over fuel load. For example, the time of day affects temperature and relative humidity, thus there is some opportunity to control fire conditions by restricting the hours in which the burn is conducted: if a high fuel load could render a fire too hot, scheduling a burn early in the day could moderate peak temperatures and vice versa.

The second potential limitation, that fire effects on the seedbank has negligible consequences for community recovery, is perhaps a more serious issue. Benson and Hartnett (2006) looked at the succession of perennial tall grass prairies following spring fire and found that seedlings accounted for less than 1% of recruitment, while vegetative reproduction via rhizomes contributed to 99% of new growth by the end of the growing season.

Another study by Benson et al. (2004) concluded that frequent burning in tall grass prairies stimulated rhizome bud development and thus increased the below-ground

bud bank, further promoting the vegetative reproductive response. At the same time, frequent burns decreased the quantity of viable seed in the seed bank (Benson et al., 2004).

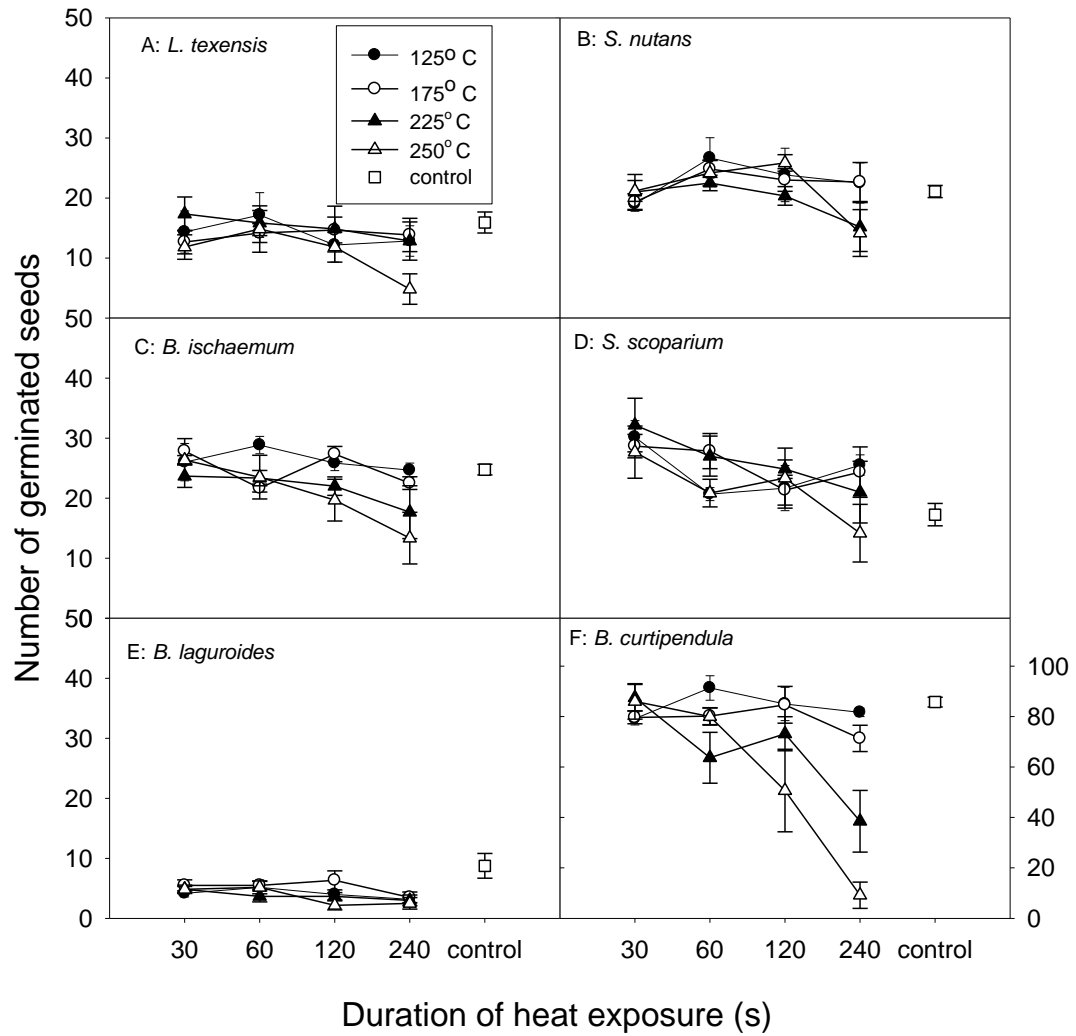
It remains to be seen how generalizable this conclusion is. In our field experiment, initial growth in the first spring after fire was dominated by tillers sprouting out of burnt tussocks, but many new seedlings appeared in fall. The post burn year (2009) was exceptionally dry in central Texas, with few opportunities for grass growth until early fall. It stands to reason that where vegetation cover is relatively slow to recover to pre-burn levels, either due to drought conditions or other disturbances, the seedbank will make a correspondingly greater contribution to the species composition of the post-burn community. Furthermore, reproduction from seed is likely more common in disturbed grasslands, such as those which contain invasive species (M. Simmons, personal observation).

From a management perspective, it is important to mention that burn treatments may enhance germination, not from the heat of the flames but rather from the effect of smoke on the seeds. Smoke initiates growth in many species, including grass species (Baxter et al., 1994; Dixon et al., 1995; Keeley and Fotheringham, 1998; Gómez-González et al., 2008;). The effect of smoke on germination was not considered in this study.

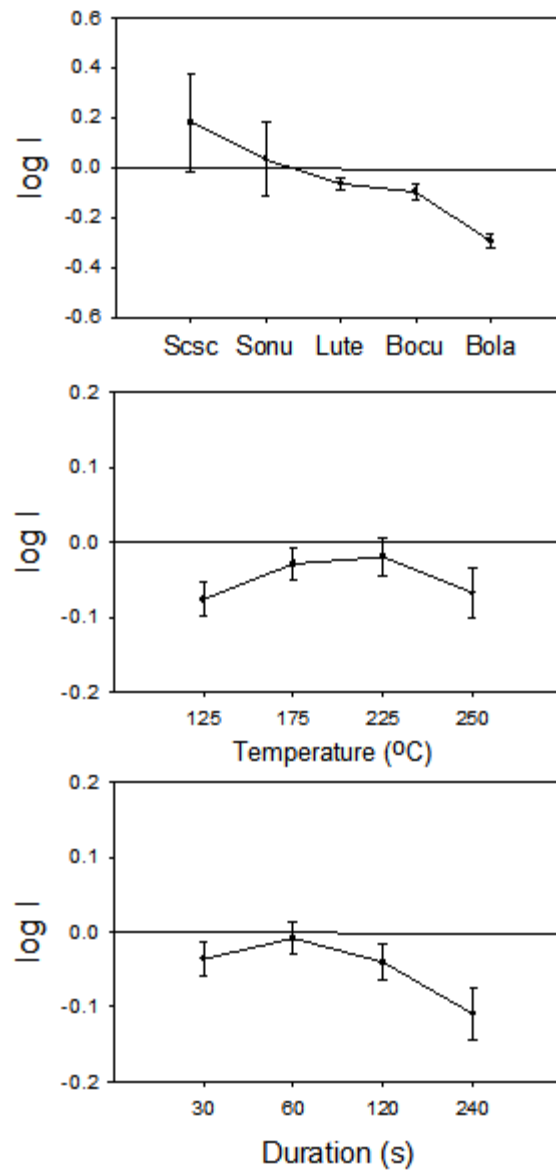
Grasslands are inherently variable and highly dynamic systems, and the drivers of such variability (precipitation, grazing pressure, fire) play a large role in controlling species abundances. The goal of managers is to control some drivers, such as fire, to increase the proportions of desirable and decrease those of undesirable species. However, complex interactions between drivers and their communities, and between drivers, can make the outcomes of management interventions complex and uncertain. Prescribed burns, for example, are unlikely to have highly predictable effects on communities year after year, even if much about the burn, e.g. its timing with respect to the growing season, atmospheric conditions, etc., is controlled. The present study showed that even relatively small variation in fire temperature and duration can have surprisingly large effects on the seedbank. While the seedbank may not commonly govern post-burn recovery, it can in some years and some locations. A better understanding of the conditional effects of management practices may provide a basis for developing grassland management as a far more adaptive endeavor. In this vein, controlling fire to manipulate seedbank effects is one additional tool in the land manager's toolbox.

**Table 2.1.** ANOVA for factors temperature and duration performed individually for species.

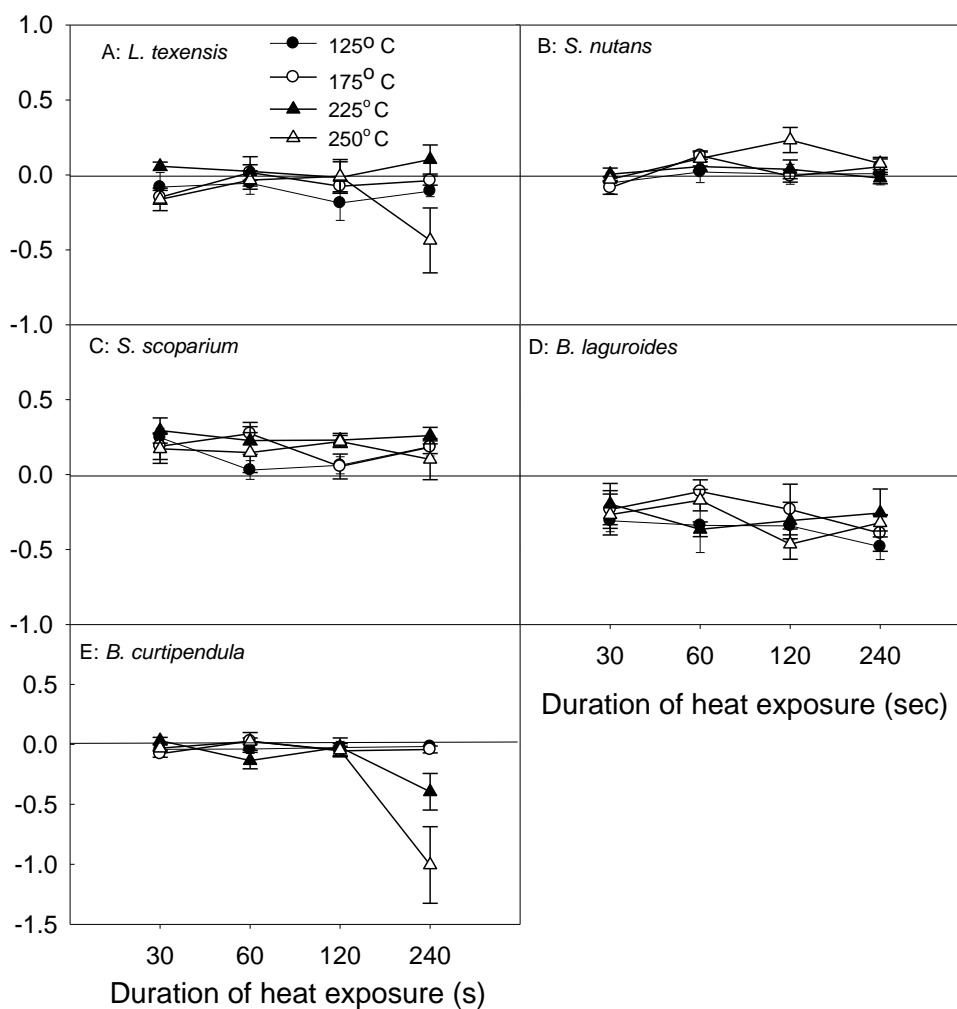
Parameter Estimates	Species					
	<i>B. ischaemum</i>	<i>B. curtipendula</i>	<i>S. nutans</i>	<i>S. scoparium</i>	<i>B. laguroides</i>	<i>L. texensis</i>
	p	p	p	p	p	p
Temperature	0.004	>0.001	0.337	0.236	0.072	0.163
Duration	0.003	>0.001	0.009	0.006	0.016	0.176
Temperature x Duration	0.252	>0.001	0.427	0.600	0.545	0.818



**Figure 2.1.** Effect of varying duration and intensity of heat stress on germination of all six species.



**Figure 2.2.**  $\log I$  (germinability of the native species with respect to the germinability of *B. ischaemum*) with respect to each species (top panel), temperature treatment (middle panel) and duration treatment (bottom panel).



**Figure 2.3.** Log *I* (germinability of the native species with respect to the germinability of *B. ischaemum*) for each of five native species with heat treatments of varying intensities and duration.



## LITERATURE CITED

- Allen E.A., J.C. Chambers, and Nowak, R.S. "Effects of a Spring Prescribed Burn on the Soil Seed Bank in a sagebrush Steppe Exhibiting Pinyon-Juniper Expansion." *Western North American Naturalist* 68 (2008): 265-77.
- Anderson, R.C. "Evolution and origin of the Central Grassland of North America: Climate, Fire, and Mammalian Grazers." *The Journal of the Torrey Botanical Society* 133 (2006): 626-647.
- Axelrod, D.I. "Rise of the Grassland Biome, Central North America." *Botanical Review* 51 (1985): 163-202.
- Azarnivand, H. and H. Dastmalchi. "Effect of Temperature on Phenology in Triple-Awned Grass (*Stipagrostis plumosa*)." Unpublished manuscript, Natural Resources College of Tehran University, 2008.
- Bessie, W. and E.A. Johnson. "The Relative Importance of Fuels and Weather on Fire Behavior I Subalpine Forests." *Ecology* 76 (1995): 747-762.
- Baxter, B., J. Van Staden, J. Granger, and N. Brown. "Plant-Derived Smoke and Smoke Extracts Stimulate Seed Germination of the Fire-Climax Grass *Themeda trianda*." *Environmental and Experimental Botany* 34 (1994): 217-223.
- Behenna, M., S. Vetter, and S. Fourie. "Viability of Alien and Native Seed Banks After Slash and Burn: Effects of Soil Moisture, Depth of Burial and Fuel Load." *South African Journal of Botany* 74 (2008): 454-462.
- Bowles, M., J. McBride, N. Stoyhoff, et al. "Temporal Changes in Vegetation Composition and Structure in a Fire-Managed Prairie Fen." *Natural Areas Journal* 16 (1996): 275-288.
- Briggs, J.M. and A.K. Knapp. "Interannual Variability in Primary Production in Tallgrass Prairie: Climate, Soil Moisture, Topographic Position, and Fire as Determinants of aboveground biomass." *American Journal of Botany* 82 (1995): 1024-1030.
- Brown, J.K. and J.K. Smith. *Wildland Fire in Ecosystems: Effects of Fire on Flora*. Gen. Tech. Rep. RMRS-GTR-42-vol. 2. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, 2000.

- Burrows, C.J. *Processes of Vegetative Change*. First edition. Routledge, London, England, 1990.
- Cable, D.R. "Influence of Precipitation on Perennial Grass Production in the Semi-Desert Southwest." *Ecology* 56 (1975): 981-986.
- Can, E., N. Celiktas, R. Hatipoglu, S. Yilmaz, and S. Avci. "The Effects of Nitrogen and Phosphorus Fertilization on the Plant Characteristics of Turkish Yellow Bluestem (*Bothriochloa ischaemum* L.)." *International Journal of Agriculture and Biology* 8 (2006): 154-156.
- Chapin, F.S., E.D. Schulze, and H. Mooney. "The Ecology and Economics of Storage in Plants." *Annual Review of Ecology and Systematics* 21 (1990): 423-447.
- Cione, N.K., P.E. Padgett, and E.B. Allen. "Restoration of a Native Shrubland Impacted by Exotic Grasses, Frequent Fire, and Nitrogen Deposition in Southern California." *Restoration Ecology* 10 (2002): 376-384.
- Copeland, T.E., W. Sluis, and H.F. Howe. "Fire Season and Dominance in an Illinois Tallgrass Prairie Restoration." *Restoration Ecology* 10 (2002): 315-323.
- Correll, D.S. and M.C. Johnston. *Manual of the Vascular Plants of Texas*. University of Texas at Dallas, Richardson, Texas, 1979.
- D'Antonio, C.M. "Fire, Plant Invasions, and Global Changes." Pages 65-93 in H.A. Mooney and R.J. Hobbs, editors. *Invasive species in a changing world*. Island Press, Washington, DC, 2000.
- Davidson, D. and P. Davidson. "Ten Years of Ecological Restoration on a Texas Hill Country Site." *Ecological Restoration* 26 (2008): 331-339.
- Davis, M., J.P. Grime, and K. Thompson. "Fluctuating Resources in Plant Communities: a General Theory of Invisibility." *Journal of Ecology* 88 (2000): 528-534.
- DeLuca, T. and K. Zouhar. "Effects of selection harvest and prescribed fire on the Soil Nitrogen Status of Ponderosa Pine Forests." *Forest Ecology and Management* 138 (2000): 263-271.
- DiTomaso, J., G. Kyser, and M. Hastings. "Prescribed Burning for Control of Yellow Starthistle (*Centaurea solstitialis*) and Enhanced Native Plant Diversity." *Weed Science* 47 (1999): 233-242.
- DiTomaso, J.M. "Invasive Weeds in Rangelands: Species, Impacts, and Management." *Weed Science* 48 (2000): 255-265.

- Dixon, K., S. Roche and S. Pate. "The Promotive Effect of Smoke Derived from Burnt Native Vegetation on Seed Germination of Western Australian Plants." *Oecologia* 101 (1995): 185-192.
- Donald, W.W. and A.G. Ogg. "Biology and Control of Jointed Goatgrass – a Review." *Weed Technology* 5 (1991): 3-17.
- Dukes, J.S. "Biodiversity and Invasibility in Grassland Microcosms." *Oecologia* 126 (2001): 563–568.
- Duncan, D.A. and R.G. Woodmansee. "Forecasting Forage Yield from Precipitation in California's Annual Rangeland." *Journal of Range Management* 28 (1975): 327-329.
- Evans R.D., R. Rimer, L. Sperry, et al. "Exotic Plant invasion Alters Nitrogen Dynamics in an Arid Grassland." *Ecological Applications*. 11 (2001): 1301-1310.
- Flanders, A.A., W.P. Kuvlesky, D.C. Ruthven, et al. "Effects of Invasive Exotic Grasses on South Texas Rangeland Breeding Birds." *AUK* 123 (2006): 171-182.
- Fowler, N. and J. Antonovics. "Small-Scale Variability in the Demography of Transplants of Two Herbaceous Species." *Ecology* 62 (1981): 1450-1457.
- Gabbard, B. and N. Fowler. "Wide Ecological Amplitude of a Diversity-Reducing Invasive Grass." *Biological Invasions* 9 (2007): 149-160.
- Gibbens, R.P. "Some Effects of Precipitation Patterns on Mesa Dropseed Phenology." *Journal of Range Management* 44 (1991): 86-90.
- Gillen, R.L., D. Rollins, and J. Stritzke. "Atrazie, Sprig Buring, and Nitrogen for Improvement of Tallgrass Prairie." *Journal of Range Management* 40 (1987): 444-447.
- Gómez-González, S., A. Sierra-Almeida, and L.A. Cavieres. "Does Plant-Derived Smoke Affect Seed Germination in Dominant Woody Species of the Mediterranean Matorral of Central Chile?" *Forest Ecology and Management* 255 (2008): 1510-1515.
- Grilz, P.L. and J.T. Romo. "Water Relations and Growth of *Bromus inermis* (smooth brome) Following Spring or Autumn Burning in a Fescue Prairie." *American Midland Naturalist* 132 (1994): 340–348.
- Gulmon, S.L., N.R. Chiariello, H.A. Mooney, and C.C. Chu. "Phenology and Resource Use in Three Co-Occurring Grassland Annuals." *Oecologia* 58 (1982): 33-42.

- Harper, J.L. *Population Biology of Plants*. Academic Press, New York, New York, USA, 1977.
- Hickman K., G. Farley, R. Channell, and J. Steier. "Effects of Old World Bluestem (*Bothriochloa ischaemum*) on Food Availability and Avian Community Composition within the Mixed-Grass Prairie." *The Southwestern Naturalist* 51 (2006): 524–530.
- Hufstader, R.W. "Precipitation, Temperature, and the Standing Crop of Some Southern California Grassland Species." *Journal of Range Management* 29 (1976): 433-435.
- Hufstader, R.W. "Growth Rates and Phenology of Some Southern California Grassland Species." *Journal of Range Management* 31 (1978): 465-467.
- Hutchinson, G.E. *An Introduction to Population Ecology*. Hew Haven, Connecticut, Yale University Press, 1978.
- Jacob, H. and E. Evans. "Effects of Sugar Spray and Aphid Honeydew on Field Populations of the Parasitoid *Bathyplectes curculionis*." *Environmental Entomology* 27 (1998): 1563-1568.
- Jiang, W., S.A.G. Leroy, N. Ogle, G. Chu, L. Wang, and J. Liu. "Natural and Anthropogenic Forest Fires Recorded in the Holocene Pollen Record from a Jinchuan Peat Bog, Northeastern China." *Palaeogeography, Palaeoclimatology, Palaeoecology* 261 (2008): 47-57.
- Jurney, D., R. Evans, J. Ippolito, and V. Bergstrom. *The Role of Wildland Fire in portions of Southeastern North America*. Paper presented at the 22nd Tall Timbers Fire Ecology Conference. Kanaskas, Alberta, 2004.
- Kaitala, Arja. "Oviposition on the Back of Conspecifics: An Unusual Reproductive Tactic in a Coreid Bug." *Oikos* 77 (1996): 381-389.
- Kartesz, John T. on "Biota of North America," USDA.gov.  
<http://plants.usda.gov/java/profile?symbol=BOISS> (accessed July 22, 2009).
- Keeley, J. and C.J. Fotheringham. "Smoke-Induced Seed Germination in California Chaparral." *Ecology* 79 (1998): 2320–2336.
- Kemp, P. "Phenological Patterns of Chihuahuan Desert Plants in Relation to the Timing of Water Availability." *Journal of Ecology* 71 (1983): 427-436.

- Knapp, A.K., P.A. Fay, J.M. Blair, S.L. Collins, M.D. Smith, J.D. Carlisle, C.W. Haper, B.T. Danner, M.S. Lett, and J.K. McCarron. "Rainfall Variability, Carbon cycling, and Plant Species Diversity in a Mesic Grassland." *Science* 298 (2002): 2202-2205.
- Lynch, D. "Phenology, Community Composition and Soil Moisture in a Relict at Austin, Texas." *Ecology* 52 (1971): 890-897.
- Mack, R.N., D. Simberloff, and W.M. Lonsdale. "Biotic invasions: Causes, Epidemiology, Global Consequences, and Control." *Ecological Applications* 10 (2000): 689-710.
- Maron, J.L and R.L. Jeffries. "Restoring Enriched Grasslands: Effects of Mowing on Species Richness, Productivity, and Nitrogen Retention." *Ecological Applications* 11 (2001): 1088-1100.
- Moore, K.J., L.E. Moser, K.P. Vogel, S.S. Waller, B.E. Johnson, and J.F. Pedersen. "Describing and Quantifying Growth-Stages of Perennial Forage Grasses." *Agronomy Journal* 83 (1991): 1073-1077.
- Naveh, Z. "The Evolutionary Significance of Fire in the Mediterranean Region." *Plant Ecology* 29 (1974): 199-208.
- Odion, D.C. and F.W. Davis. "Fire, Soil Heating, and the Formation of Vegetation Patterns in Chaparral." *Ecological Monographs* 70 (2000): 149-169.
- Payton, I. and D. Brasch. "Growth and Nonstructural Carbohydrate Reserves in *Chionocholea rigida* and *C. macra*, and Their Short-Term Response to Fire." *New Zealand Journal of Botany* 16 (1978): 435-460.
- Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. "The Environmental and Economic Costs of Non-Indigenous Species in the United States." *BioScience* 50 (2000): 53-65.
- Pimentel, D., R. Zuniga, and D. Morrison. "Update on the Environmental and Economic Costs Associated with Alien-Invasive Species in the United States." *Ecological Economics* 52 (2005): 273- 288.
- R Development Core Team. "R: A Language and Environment for Statistical Computing". *R Foundation for Statistical Computing*. Vienna, Austria, 2008.
- Rejmanek, M. and D.M. Richardson. "What Attributes Make Some Plant Species More Invasive?" *Ecology*. 77 (1996): 1655-1661.

- Reynolds, J.F., P. Kemp, and J.D. Tenhunen. "Effects of Long-Term Rainfall Variability on Evapotranspiration and Soil Water Distribution in the Chihuahuan Desert: A Modeling Analysis." *Plant Ecology* 150 (2000): 145-159.
- Risser, P.G., E.C. Birney, H.D. Blocker, W.S. May, W.J. Parton, and J.A. Wiens. *The True Prairie Ecosystem*. Hutchinson and Ross, Stroudsburg, Pennsylvania, USA, 1981.
- Sage, R.F. "Why C<sub>4</sub> Photosynthesis." In: *C<sub>4</sub> Plant Biology*, Academic Press, San Diego, CA, 1999.
- Sakai, A.K., F.W. Allendorf, J.S. Holt, D.M. Lodge, J. Molofsky, K.A. With, S. Baughman, R.J. Cabin, J.E. Cohen, N.C. Ellstrand, D.E. McCauley, P. O'Neil, I.M. Parker, J.N. Thompson, and S.G. Weller. "The Population Biology of Invasive Species." *Annual Review of Ecology and Systematics* 32 (2001): 305-332.
- Sala, O.E., F.S. Chapin, J.J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L.F. Huenneke, R.B. Jackson, A. Kinzig, R. Leemans, D.M. Lodge, H.A. Mooney, M. Oesterheld, N.L. Poff, M.T. Sykes, B.H. Walker, M. Walker, and D.H. Wall. "Biodiversity — Global Biodiversity Scenarios for the Year 2100." *Science* 287 (2000): 1770–1774.
- Sammon, J.G. and K.T. Wilkins. "Effects of an Invasive Grass (*Bothriochloa ischaemum*) on a Grassland Rodent Community." *Texas Journal of Science* 57 (2005): 371-382.
- Schooler S.S., P.B. McEvoy, and E.M. Coombs. "Negative Per Capita Effects of Purple Loosestrife and Reed Canary Grass on Plant Diversity of Wetland Communities." *Diversity and Distributions* 12 (2006): 351-363.
- Schwinning, S., B.I. Starr, and J.R. Ehleringer. "Summer and Winter Drought in a Cold Desert Ecosystem (Colorado Plateau) I: Effects on Soil Water and Plant Water Uptake." *Journal of Arid Environments* 60 (2005): 547-566.
- Simmons, M., S. Windhager, P. Power, J. Lott, R. Lyons, and C. Schwope. "Selective and Non-selective Control of Invasive plants: The Short-Term Effects of Growing-Season Prescribed Fire, Herbicide, and Mowing in Two Texas Prairies." *Restoration Ecology* 15 (2007): 662-669.
- SPSS for Windows, Rel. 11.0.1. Chicago, IL, 2001.
- Stanton, N.L. "The Underground in Grasslands." *Annual Review of Ecology and Systematics* 19 (1988): 573-589.

- Stewart, O. C. *Forgotten Fires, Native Americans and the Transient Wilderness*. Edited by H. T. Lewis and M. K. Anderson. University of Oklahoma Press, Norman, OK, 2002.
- Torra, J., J.L. Gonzalez-Andujar., and J. Recasens. "Modeling the Population Dynamics of *Papaver rhoeas* Under Various Weed Management Systems in a Mediterranean Climate." *Weed Research* 48 (2008): 136-146.
- Tveten, R.K. and R.W. Fonda. "Fire Effects on Prairies and Oak Woodlands on Fort Lewis, Washington." *Northwest Science* 73 (1999): 145-158.
- Van Der Wal, R., M. Egas, A. Van Der Veen, and J. Bakker. "Effects of Resource Competition and Herbivory on Plant Performance Along a Natural Productivity Gradient." *Journal of Ecology* 88 (2000): 317-330.
- Vitousek, P.M., C.M. D'Antonio, L.L. Loope, and R. Westbrooks. "Biological Invasions as Global Environmental Change." *American Scientist* 84 (1996): 468-478.
- Vogl, R. J. "Effects of Fire on Grasslands" in T.T. Kozlowski and C.E. Ahlgren, editors. *Fire and ecosystems*. Academic Press, New York, NY, 1974.
- Von Holle, B and D. Simberloff. "Ecological Resistance to Biological Invasion Overwhelmed by Propagule Pressure." *Ecology* 86 2005: 3212-3218.
- White, L. and C. Dewald. "Yield and Quality of WW-Iron Master and Caucasian Bluestem Regrowth." *Journal of Range Management* 49 (1996): 42-45.
- Wilcove, D. and D. Rothstein. "Quantifying Threats to Imperiled Species in the United States." *BioScience* 48 (1998): 607-615.
- Willson, G.D. "Morphological Characteristics of Smooth Brome Used to Determine a Prescribed Burn Date." From the Proceedings of the Twelfth North American Prairie conference, University of Northern Iowa, Cedar Falls, IA, 1991.
- Young J.A, C.D. Clements, and R.R. Blank. "Herbicide Residues and Perennial Grass on Establishment Perennial Pepperweed Sites." *Journal of Range Management* 55 (2002): 194-196.
- Yuan, W., G. Zhou, Y. Wang, X. Han, and Y. Wang. "Simulating Phenological Characteristics of Two Dominant Grass Species in a Semi-Arid Steppe Ecosystem." *Ecological Research* 22 (2007): 784-791.
- Zhang, J. and G. Zhang. "A study on Niches of Dominant Species in *Bothriochloa ischaemum* Grasslands." *Japanese Society of Grassland Science* 52 (2006): 85-93.

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