Comparative Seed Heat Tolerances Among Native and Non-indigenous Invasive Grassland Species

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ABSTRACT

Prescribed burning is a popular method for the control of invasive species; however, research is lacking on the application of fire in a species-specific manner. We assess whether heat sensitivity differences among seeds of Texas grassland species can be used to target invasive species in prescribed burns. We conducted heat treatments on the invasive yellow bluestem (*Bothriochloa ischaemum*), and 5 native species, little bluestem (*Schizachyrium scoparium*), silver beardgrass (*Bothriochloa laguroides*), sideoats grama (*Bouteloua curtipendula*), Indiangrass (*Sorghastrum nutans*), and Texas bluebonnets (*Lupinus texensis*) at 125, 175, 225, and 250°C and at durations of 30, 60, 120 and 240 s. Temperature affected percent germination of yellow bluestem, while duration affected all species except Texas bluebonnet. A temperature*duration interaction affected sideoats grama. We also calculated a native species:yellow bluestem index of germination response which provided a measure of the responses of the native species relative to yellow bluestem. Little bluestem was the only species that germinated at higher percentages than yellow bluestem across all treatments, although, at the highest temperature Indiangrass outperformed yellow bluestem. Among native species, intermediate temperatures and exposure times had the least damaging effects on germination. Burning during the non-growing season will result in little damage to grass tissue and greater damage to the seeds of native species, while active-season burns applied at an optimal time are likely to have greater consequences for the target invasive. The use of invasive-species-targeted prescribed fire will require careful planning to maximize damage to the invasive while minimizing damage to the native seed bank.

Keywords: *Bothriochloa ischaemum*, Central Texas perennial grassland, prescribed burning, seed bank, selective control, yellow bluestem

In the Western U.S., prescribed fire is increasingly employed to accomplish a variety of objectives. Some managers aim to restore native species through reinstatement of the historical fire regime (e.g., Tveten and Fonda 1999), while others aim to generate habitat for early-successional native fauna or to control woody species encroachment (e.g., Gillen et al. 1987, Van Auken 2000, Heisler et al. 2003). Increasingly, prescribed fire is used to selectively control focal invasive species (e.g., McGlone and Huenneke 2004, Sweet et al. 2008). While methods of invasive species control are effective where the invasive species has a unique disadvantage relative to native species (Copeland et al. 2002), in many circumstances native and invasive species are ecologically and biologically similar. For example, in North America we frequently encounter situations where an invasive, C4, perennial grass is targeted in a C4, perennial-dominated grassland or an invasive annual forb is targeted in an annual-dominated herbaceous community.

Selective control through a disturbance mechanism is also complicated by the fact that non-indigenous, invasive species are often better equipped to respond to increases in available space and/or resources following removal and are notorious for their ability to respond positively to disturbance (Hobbs and Huenneke 1992, Lake and Leishman 2004).

Several studies have shown that invasive species can be selectively controlled using prescribed burns (Willson 1991, DiTomaso et al. 1999, Simmons et al. 2007). Simmons and colleagues (2007) demonstrated that in central Texas grasslands active-season burns (late summer/fall) are more effective in controlling the non-indigenous invasive, C4 grass, yellow bluestem (*Bothriochloa ischaemum*) than dormant-season burns (winter/early spring), at least in the short-term. In a study conducted on yellow bluestem in the same region, we found that pre-fire native and exotic species phenologies were a reliable determinant of fire control efficacy, which suggests that, where native and invasive

species differ sufficiently in their phenologies, land managers may be able to capitalize on these differences to target an invasive species (Ruckman et al. in press). Likewise, Kyser and colleagues (2008) found control of the invasive annual grass, medusahead (*Taeniatherum caput-medusa*), was more effective in northern California at lower elevations with warmer winters than at higher elevations. Their findings were attributed to higher fuel loads and hotter, more damaging fires at the lower elevations.

On the other hand, due to their responsiveness to disturbance in general, herbaceous invasive species may likely be facilitated by fire (Keeley 2006). Indeed, several studies demonstrate that invasive species abundance can increase following fire (Hamilton and Scifres 1982, Grilz and Romo 1994, Reed et al. 2005, Gabbard and Fowler 2007, Butler and Fairfax 2008, Setterfield et al. 2010).

These mixed results among a variety of habitat types and species suggest that invasive species response to fire will be species, community, and ecosystem dependent, and that land managers should test the efficacy of fire for selective control of invasive species on a small scale prior to broadscale application.

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 2000, 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). The concern is that herbaceous invaders are functionally similar to their native competitors. For example, many invaders 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). Several possible mechanisms to explain this variability among and within species are under investigation, including differences in how species tolerate heat through up-regulation of heat-shock proteins, isoprenes, and antioxidants, and how species break dormancy through regulation of seed moisture content and seed coat strength (Kozlowski and Pallardy 2002).

In perennial C4 grasslands of central Texas, the exotic perennial C4 grass, yellow bluestem, was introduced to improve degraded rangeland and is now considered invasive. As an alternative to herbicides, fire is being used as a tool to control the species; however, the optimal timing of fire application and its ultimate efficacy remain unknown. The goal of this study was to determine whether seed germinability exhibits differential sensitivity to variation in temperature and duration of heat exposure among 5 highly desirable (high forage value) native grassland species and yellow bluestem. We aimed to acquire information on how the precise timing of a prescribed fire can be used to maximize damage to the seeds of an undesirable species.

Methods

Yellow bluestem is a warm-season, perennial bunchgrass introduced to North America from Eurasia in the 1920s to control erosion and improve degraded rangelands. The species now occurs in 17 states and dominates a diverse array of habitat types. Once established, yellow bluestem homogenizes grassland ecosystems (Gabbard and Fowler 2007) and reduces habitat quality for bird (Flanders et al. 2006, Hickman et al. 2006) and rodent (Sammon and Wilkins 2005) communities. While many land owners and managers do not recognize yellow bluestem as a problem species, it is increasingly perceived as an invasive weed of low forage value (Gabbard and Fowler 2007). We selected 5 native species for this study, including little bluestem (*Schizachyrium*

scoparium), silver beardgrass (*Bothriochloa laguroides*), sideoats grama (*Bouteloua curtipendula*), Indiangrass (*Sorghastrum nutans*), and Texas bluebonnets (*Lupinus texensis*). These species are widely used throughout Texas for restoration of mid- to tall grass prairies. We purchased the native seeds from Native American Seed Company (Junction, TX) and yellow bluestem seeds from Douglass W. King Company (San Antonio, TX). Both suppliers reported that the seeds were collected in the fall season preceding our study. Prior to any treatments, the seeds were dry stratified for 30 d in a -9.4 °C freezer. No attempt was made to clean or determine the initial moisture content of the seeds.

We employed a three-way (4 × 4 × 6) factorial treatment structure with temperature, duration, and species as factors. We exposed seeds to heat in a convective oven (Fisher Scientific Forced Air Isotemp 650G, Sparta, NJ), using 4 temperature settings (125, 175, 225 and 250°C) and 4 durations (30, 60, 120 and 240 s), representative of the common range of grassland fires (Morgan 1999, Sweet et al. 2008). We also included controls for each species, where seeds were not exposed to heat and left at ambient laboratory temperatures (approximately 21 °C) following stratification.

We conducted 3 consecutive trials, with each trial occurring in a single day. Each trial included 2 replicates of each treatment combination (time × duration × species) and 4 replicates of the control. For each replicate, we spread 100 seeds on an 8.5-cm diameter glass Pyrex Petri dish, lined with 90-mm dry filter paper, and heated them at the designated temperature for the designated duration. We estimated seed numbers per tray by weight, based on previously determined seed number to weight ratios. We took care to place seeds as quickly as possible in a pre-heated oven. Because the oven temperature dropped temporarily when its door was opened, we calculated exposure time from the moment the oven

reached the designated temperature level (5 s, on average).

Immediately following the heat treatment, we placed seeds of each replicate treatment combination on a soil surface in plastic seedling trays (48 × 25.5 × 6 cm, T.O. Plastic Seedling Trays, Hummert International, Earth City, MO) filled with approximately 175 g seedling soil (Sunshine Redi-Earth Plug and Seedling Soil, Sun Gro Horticulture, Bellevue, WA). We placed the seedling trays in larger, plastic drain trays and added 3 L of deionized water to each drain tray to allow wicking from below into the seedling trays. We misted the soil surface with deionized water to saturation and placed a clear plastic vinyl propagation dome over each tray to minimize evaporation and maintain a high humidity environment for the duration of the germination process.

While germinating, we maintained seeds in a controlled environment at 22°C, under 34-watt fluorescent bulbs placed 33 cm above the propagation domes. The light intensity at the soil surface was approximately 200 µmol/m²/s. At 1 and 2 wks following sowing, we recorded the number of germinated individuals for each seedling tray. After 1–2 wks, depending on the species, the number of germinated seeds began to decline. We used the measures made for the highest recorded levels of germination for each treatment replicate in our analysis.

We analyzed the data using a multifactorial ANOVA with the main effects trial, species, temperature, and duration, and all possible interactions. Because trial number did not significantly determine the percent germination, we removed it from the model shown here. Differences among species in their intrinsic germination rates made direct comparisons among species in their responses to our treatments difficult. To compare the effects of a given heat exposure treatment on the germinability of a native species with that of the invader yellow bluestem, we calculated the following index of germination advantage:

$$GA_{S,T,D} = \log\left[\frac{N_{S,T,D}/N_{S,C}}{N_{I,T,D}/N_{I,C}}\right]$$

where N is the number of germinated seeds, and the subscripts S, T, D, and C stand for the target species, temperature, duration, and control, respectively. The subscript, I, refers to the invasive species. Division by the number of germinated seeds in the control treatment standardizes species responses with respect to intrinsic differences species may have in germination rates. Dividing the standardized germination response of a native species by that of yellow bluestem expresses the treatment effect on the native species relative to the treatment effect on the invader. A value greater than 0 for log GA 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 sideoats grama where the square of the index was used (mode of transformation was determined using the Ladders of Power Determinant). We calculated the index GA for each replicate treatment combination, using for the control the average of 2 randomly chosen germination numbers within a trial. We then calculated the effect of species, temperature, and duration on log GA (or GA^2, in the case of sideoats grama) using multifactorial ANOVA. All analyses were performed using SPSS Inc. (Release 11.0.1, 2001).

Results

A complete ANOVA conducted on the number of germinated seeds (per 100) showed highly significant effects of species, temperature, duration, and all two- and three-way interactions. These data were analyzed by ANOVA on each species individually (Table 1). Only Texas bluebonnet was not significantly affected by either temperature or duration (Table 1). At the other extreme, germination of sideoats grama was significantly affected by the interaction between these variables (Table 1). The higher the temperature combined with greater exposure, the greater the loss of germinating seeds due to longer exposure times (Figure 1E). In 3 species (sideoats grama, little bluestem, and silver beardgrass), only duration had a significant effect on germination (Table 1), with longer exposure resulting in fewer germinated seeds (Figures 1B, C, F). Germination of silver beardgrass was by far the most negatively affected by the heat treatments and was intolerant to heat exposure even at low temperatures and short exposure times (Figure 1F). This result is in marked contrast to little bluestem, where heat exposure had a strong stimulatory effect under almost all treatment combinations (Figure 1B). For yellow bluestem, both temperature and duration significantly reduced germination (Table 1, Figure 1A).

For the relative germination index log GA, little bluestem stood out as the species with the greatest relative percent germination as compared to yellow bluestem when seeds were exposed to heat (Figure 2A). The relative germination of Indiangrass seeds also exceeded that of yellow bluestem, while all other species germinated less readily than yellow bluestem following the heat treatment. 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 yellow bluestem. Across the selection of native species, no temperature or duration favored germination of the native species overall; however, in general, intermediate temperature (175°C) and exposure times (60 s) had the least negative effects (Figure 2B,C).

Most species, under most conditions, had neither very strong advantages or disadvantages with respect to yellow bluestem, as many averages of GA clustered around the log GA = 0 (Figure 3), but a few exceptions are noteworthy. For Texas bluebonnet and

sideoats grama, long exposure to high temperature had especially negative effects on seed germination compared to yellow bluestem (Figure 3C, E). Although yellow bluestem also suffered from high temperature and long exposure (Figure 1A), sideoats grama and Texas bluebonnet were substantially more negatively affected. Finally, any combination of temperature and duration resulted in relatively higher germination for little bluestem (Figure 3A) and lower germination for silver beardgrass (Figure 3D).

Discussion

Grassland fires are highly variable in their surface temperatures, and the duration of exposure (Gibson et al. 1990, Morgan 1999) and fire character is dependent on well-known relationships between fuel load, fuel moisture status, relative humidity, and topographic considerations, among other factors (Brown and Smith 2000). We therefore have the knowledge to manipulate, to some degree, the character of prescribed burns. This study demonstrates that attributes of a prescribed burn could be used to selectively manage invasive species where resident native species are sufficiently different in their responses to heat exposure.

In this study, the 6 focal species (5 native, 1 exotic) demonstrated varied responses to heat treatment. Where species germinations are not relativized for intrinsic germination rates (Table 1, Figure 1), we found that seeds of Indiangrass, little bluestem, and silver beardgrass are affected only by duration while yellow bluestem and sideoats grama are affected by both temperature and duration of heat exposure. This simple analysis suggests that application of a rapid, high temperature fire may select for 3 of the native grasses and negatively affect germination of 1 native, sideoats grama, and the focal invasive, yellow bluestem.

Where species' intrinsic rates of germination are taken into account

Table 1. Treatment effects on species germination. *P* values for main effects of temperature and duration of exposure to heat (and their interaction) on individual species germination for yellow bluestem (*Bothriochloa ischaemum*) and 5 native grasses in central Texas.

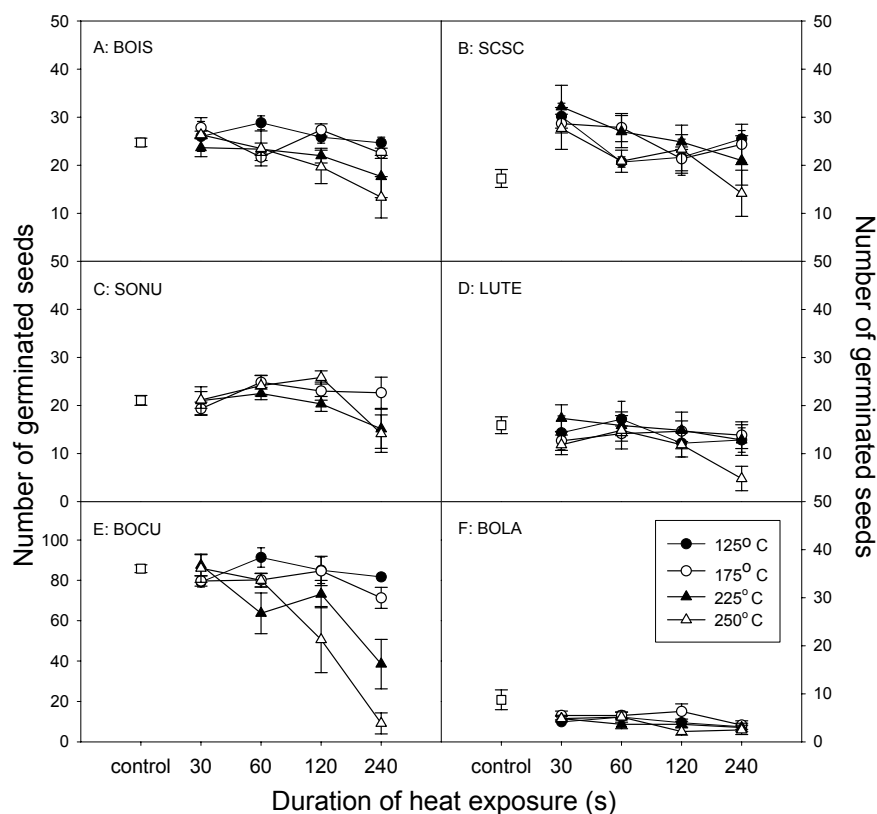| Species	Parameter Estimates (*p* values)		
	Temperature	Duration	Temperature*Duration
yellow bluestem	0.004	0.003	0.252
little bluestem	0.236	0.006	0.6
Indiangrass	0.337	0.009	0.427
Texas bluebonnet	0.163	0.176	0.818
sideoats grama	>0.001	>0.001	>0.001
silver beardgrass	0.072	0.016	0.545

Figure 1. Germination of yellow bluestem (*Bothriochloa ischaemum*) seeds and seeds of 5 native grasses as a function of temperature and duration of exposure to heat. A. BOIS = yellow bluestem; B SCSC = little bluestem; SONU = Indiangrass; LUTE = Texas bluebonnets; BOCU = sideoats grama; BOLA = silver beardgrass.

(Figures 2 and 3), little bluestem and Indiangrass still exhibit high germination rates relative to yellow bluestem. Little bluestem had high germination compared to yellow bluestem under all treatment combinations (Figure 3A), while Indiangrass had a germination advantage only under treatments of intermediate duration (Figure 3B). All other species in this analysis were disadvantaged relative to yellow bluestem following heat treatment (Figure 2A).

Overall, the relative disadvantage to the native species was minimized under intermediate temperature (175–220 °C) and exposure times (60s) (Figure 2B, C). Assuming that re-establishment of native species post-fire will create a more competitive environment for an invasive, these findings suggest that, under conditions promoting germination from the seed bank, prescribed burns designed to target the seed bank of yellow
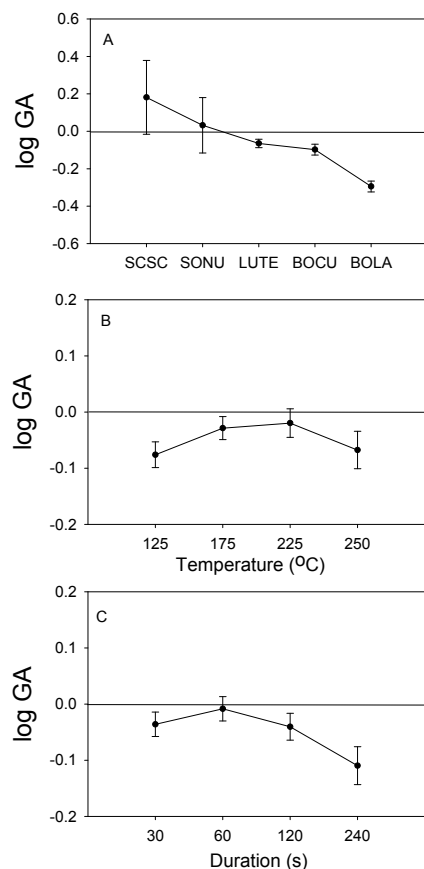
Figure 2. Log *GA* [measure of germination relative to yellow bluestem (*Bothriochloa ischaemum*)] for individual species (A), temperature (B), and duration (C). Values above zero indicate that the native species had higher relative germination rates than yellow bluestem. Note that for B and C all species are combined. SCSC = little bluestem; SONU = Indiangrass; LUTE = Texas bluebonnets; BOCU = sideoats grama; BOLA = silver beardgrass.

Figure 3. Log *GA* [germinability of the native species relative to yellow bluestem (*Bouteloua ischaemum*)] for each of 5 native species as a function of heat treatments of varying intensities and duration. SCSC = little bluestem; SONU = Indiangrass; LUTE = Texas bluebonnets; BOCU = sideoats grama; BOLA = silver beardgrass

bluestem will have greater success if little bluestem and/or Indiangrass are relatively well represented. This statement assumes that seeds on the soil surface experience conditions similar to those in our study and that the intrinsic germination rates of our seeds can be generalized across commercial operations and in the field.

Based on our findings, damage to native species can be minimized by avoiding fires that burn either too cold and slow or too hot and long. We recognize that this may be a tall order for grassland managers. Prescribed burns are generally planned far in advance and are designed to minimize the risk of uncontrolled spread. They are scheduled when humidity is high and
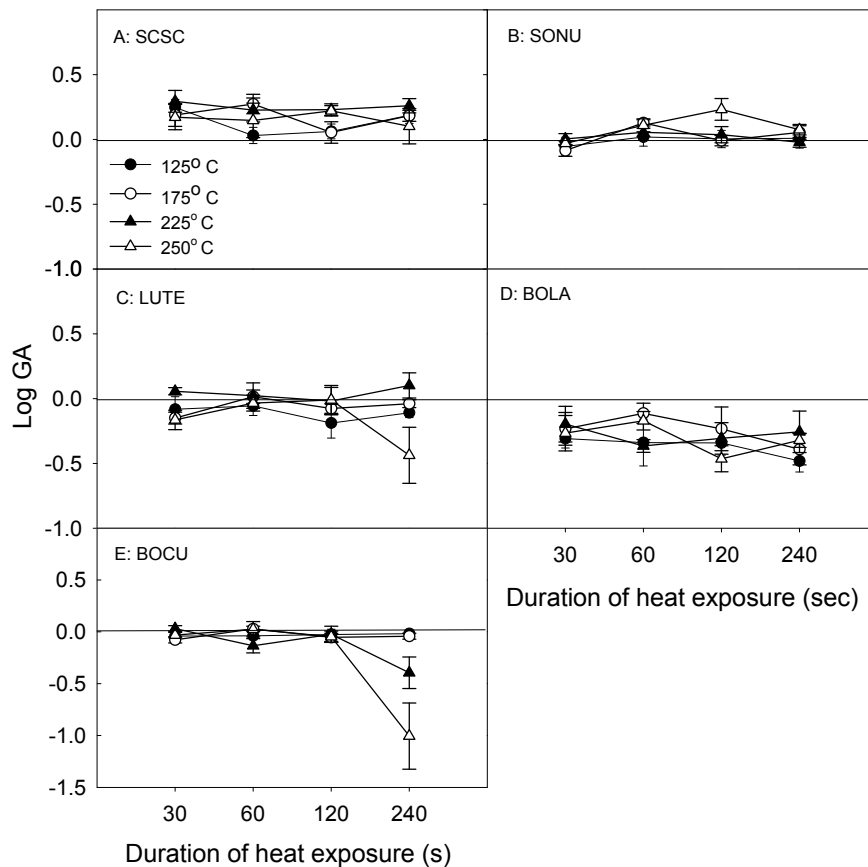
wind speeds are low, since these are considered to be the primary factors that determine fire intensity and rate of spread (Bessie and Johnson 1995). Additional factors affecting burn intensity and duration are flame aspect (head, back, or flank), fuel load and moisture status, and site topography; however, Bessie and Johnson (1995) demonstrated that fire behavior is more closely linked to meteorological variables than fuel load characteristics, suggesting that control over meteorological variables could compensate for a lack of control over fuel load.

Land managers should also consider whether post-burn recovery in their systems is driven more by vegetative growth or establishment from seed. Benson and Hartnett (2006) examined succession of perennial tall grass prairies following spring fire and found that seedlings accounted for <1% of recruitment, while vegetative

reproduction via rhizomes contributed to 99% of new growth by the end of the growing season. In a later study, Benson and colleagues (2004) concluded that frequent burning in tallgrass prairies stimulated rhizome bud development, which increased the belowground bud bank and further promoted the vegetative reproductive response. At the same time, frequent burns decreased the quantity of viable seed in the seed bank (Benson et al. 2004). In our study system, perennial grass species recovery following fire will depend on the nature of the fire as well as rainfall patterns. The climate of the Edwards Plateau of central Texas, where we study yellow bluestem invasion, is subtropical-subhumid and is characterized by dry winters and hot summers with an average rainfall of around 600 mm/yr; however, rainfall is highly variable and highly localized. In a year with substantial

rain, recovery following a devastating fire would likely occur as a result of re-establishment from the seed bank, while vegetative growth would be favored in a lower rainfall or drought year.

The nature of post-fire recovery, whether species re-establish from seed or vegetative parts, may also depend on the season during which a fire is applied. In a yellow bluestem dominated ecosystem in central Texas, Simmons and others (2007) found higher native species abundances in sites that were burned during the active growing season (late summer/fall) than in sites burned during the dormant season (winter). As in many arid grassland ecosystems, burning is usually during the cooler months when burns are easier to control. The work by Simmons and others (2007) suggests that these conventional approaches to prescribed burning may be further promoting invasion. The mechanism for this effect remains unclear; however, the current working hypothesis is that perennial grasses burned during the growing season are hampered in their ability to store resources belowground, compromising their ability to grow in spring.

Our findings suggest a dual mechanism selecting for higher yellow bluestem abundances after a dormant season burn. If fire applied during the dormant season has little effect on mature individuals of yellow bluestem but causes relatively higher damage to the native than the yellow bluestem seed bank, then we would expect consistent selection for dominance of yellow bluestem seedlings over time.

Our findings are broadly applicable in so far that they suggest that sensitivity of grass seeds to temperature and heat duration can be expected to vary widely among species in a community. They may in fact constitute a common component of niche differentiation in fire-adapted grassland systems. In these systems, fire is one of many stochastic drivers, along with precipitation and grazing pressure, which control species abundance and

diversity. A corollary is that changes in fire regimes can reduce diversity and promote the spread of invasive species. Managers aim to control drivers such as fire to increase the proportions of desirable species and decrease those of undesirable species; however, complex interactions between drivers and their communities, and among drivers, can make the outcomes of management interventions complex and uncertain. Without careful study and analysis, the effects of prescribed burns on grassland community species composition and abundance are unlikely to be tractable and predictable year after year. Our study implies that there is no standard recipe for controlling invasive grasses by prescribed burn, but that intricate knowledge of species differences, and a high degree of control over fire regimes, or selectiveness regarding the timing of a controlled burn, may be required to achieve management objectives. More studies of this type are warranted to refine prescribed burning as a tool to control invasive species and manipulate grassland seed bank species composition.

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