RESEARCH ARTICLE

Effects of Phenology at Burn Time on Post-Fire Recovery in an Invasive C$_4$ Grass

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Abstract

The spread of non-indigenous, C$_4$ grasses threatens global conservation of savannas and subtropical grasslands. Identifying control methods to selectively target these invasives has proven difficult. Here, we tested the hypothesis that the effectiveness of prescribed burns for control is determined, in part, by the phenology of the target species at burn time. We conducted two experiments in a sub-humid, C$_4$ grassland in central Texas. The focal invasive was the C$_4$, perennial bunchgrass *Bothriochloa ischaemum* (L.) Keng (KR bluestem). Burns were conducted in early and late fall when plants were in different phenological states. In addition, we attempted to manipulate phenological state through temporary rainout shelters to expedite maturation. The two experiments differed in the timing of the rainout shelter application (experiment 1: May to July, experiment 2: August and September), but otherwise had the same complete factorial design (burn time x shelter). Across experiments, when at least 50% of all tillers were pre-reproductive at burn time, either due to shelter treatment or time of year, spring tiller densities were significantly lower than when plants were burned in a more advanced reproductive state. Trends in fall biomass generally followed trends in spring tiller densities, with one exception where plants in no-shelter plots burned in October had lower biomass than expected based on tiller densities. Treatment responses for the native C$_4$ grass *B. laguroides* were consistent with those of *B. ischaemum*. These findings suggest that strategic burns can be used to reduce the subsequent recovery of invasive C$_4$ grasses while not disadvantaging native grasses.

Key words: *Bothriochloa ischaemum*, Edwards plateau, invasive species control, King Ranch bluestem.

Introduction

Conservation and restoration of plant communities, in which native and non-indigenous invasive species operate in functionally similar capacities, poses a particularly challenging problem, as the invasives are difficult to selectively target for control (Grace et al. 2001; Corbin & D'Antonio 2010). The invasion of non-indigenous, C$_4$ grasses into native, C$_4$ grasslands and savannas exemplifies this challenge (Reed et al. 2005), and this is of consequence on all continents where C$_4$ grasslands exist (Foxcroft et al. 2010), to include North America (Brockway et al. 2002), South America (Hoffmann et al. 2004), Australia (Laffan 2006; Rossiter-Rachor et al. 2009), and Africa (Milton 2004). In C$_4$ grasslands, fire is often required to control woody encroachment and maintain grass species diversity (Bond & Parr 2010); however, in systems where the intensity or return interval of the current fire regime differs from historical conditions, the spread of non-indigenous, fire-adapted invasive species may be facilitated by opening up competitor-free space (Foxcroft et al. 2010).

Prescribed burns that selectively control invasive grasses may present a solution (Simmons et al. 2007), but success depends on the degree of selectivity. A simple model may illustrate this. Consider a Lotka–Volterra competition model where two species have identical niches (Cobin & D'Antonio 2010) and differ only in intrinsic growth and density-independent mortality rates:

$$\frac{dN}{dt} = r_N N(1 - N - I) - m_N N \qquad (1)$$

$$\frac{dI}{dt} = r_I I(1 - N - I) - m_I I \qquad (2)$$

Here, N and I are scaled densities of a native and invasive grass, respectively, r is the intrinsic growth rate, and m is the rate of mortality due to factors independent of resource competition (e.g. fire). We assume that the invasive grass is the better competitor by setting $r_I > r_N$. Without fire ($m_I = m_N = 0$), the equilibria of this model are neutrally stable and final frequencies of I and N depend on initial frequencies and r-values (Fig. 1). Fire makes it possible for one species to outcompete the other. Specifically, the native species becomes dominant if

$$\frac{m_N}{r_N} < \frac{m_I}{r_I} \qquad (3)$$

Otherwise, the invasive species becomes dominant. Despite being simple, the model illustrates very clearly that it is not enough to merely impose selective mortality to control an

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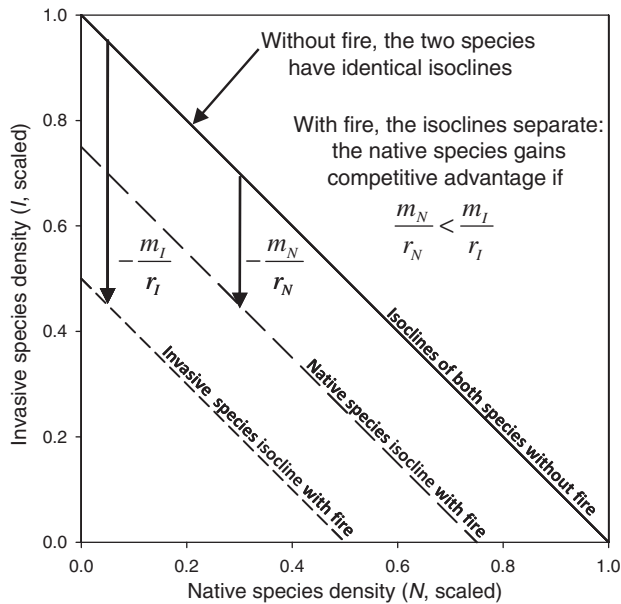[3] Department of Biology, Trinity University, San Antonio, TX 78212, U.S.A.

Figure 1. The zero-growth isoclines ($dN/dt = 0$, $dI/dt = 0$) of two species N (native) and I (invasive) with identical resource requirements but different intrinsic growth rates (r_N, r_I) and fire mortalities (m_N, m_I). Without fire, the two isoclines are identical and equilibrium densities could be anywhere on the joint isoclines, depending on the initial densities of N and I. With fire, isoclines shift down by the quantities $-m_N/r_N$ and $-m_I/r_I$. The species with the lower m/r value will have a competitive advantage over the other, in this case, the native species.

invasive species; rather, the ratio of invasive to native mortality must exceed the ratio of their growth rates. Furthermore, if selective mortality falls short of this goal, the application of fire will facilitate the competitive exclusion of the native species (Fig. 1).

On the basis of this consideration, predicting the effects of a prescribed burn is paramount to successful control of invasive species. Naturally, this is easier in theory than application, as fire effects vary widely with weather conditions, fuel density, and the physiological status of the grasses at the time of the fire, as well as post-fire conditions (Simmons et al. 2007). This variability can be a liability for grassland restoration. On the other hand, if fire effects can be anticipated, variability can be turned into an asset, as prescribed burns could be limited to occasions when invasive species have proportionally greater fire mortality.

Despite their overall ecological similarities, C_4 grasses have distinct developmental schedules and respond differentially to temperature cues and moisture triggers, a difference that is considered essential for maintaining grassland species diversity (Chesson et al. 2004; Craine et al. 2010). As a result, species may be, at any given time, in distinct phenological and physiological states. This provides a promising avenue for imposition of differential mortality by fire, as different phenological stages are associated with different levels of vulnerability (e.g. Menke & Trlica 1981; Nofal et al. 2004). Grasses have variable levels of storage products sequestered in their stem, roots, and rhizomes, depending on the relative

strengths of supply and demand for carbohydrate and nitrogen (Chapin et al. 1990). For example, fructosans stored in the stems of perennial grasses decline in some species during stem elongation and seed filling, both stages of rapid growth and high carbon demand (Waite & Boyd 1953). Likewise, nitrogen products are translocated from rhizomes and roots to the growing shoot during times of rapid vegetative growth, and back again during leaf senescence (Hayes 1985). Thus, periodically, both carbohydrate and nitrogen reserves become minimized in rhizomes and roots, typically just following the stem elongation phase. The lack of reserves in storage organs and the loss of carbohydrates in above ground parts through combustion may make it difficult for individuals to recover after a burn.

We tested the hypothesis that pre-burn phenological state affects recovery after fire in an invasive, C_4 grass. We anticipated that it could be difficult to isolate the effect of phenology from other time-sensitive factors, such as burn and post-burn weather conditions. Therefore, we manipulated pre-burn phenological state through the use of shelters to exclude rainfall.

We selected for study *Bothriochloa ischaemum* (common name King Ranch [KR] bluestem, Old World bluestem, or yellow bluestem) as our focal invasive and grasslands in the Texas Hill Country as our model system. To date, the use of prescribed burns to control this species has had limited to no success (Gabbard & Fowler 2007). Nonetheless, most prescribed burns in Texas are conducted in late fall and winter, when fire is easier to control, and the work by Simmons et al. (2007) showed that warm-season burns are more damaging in general and possibly more damaging to *B. ischaemum* than to its native competitors. In addition, the specific timing of the burn within the active growing season also affected recovery (Simmons et al. 2007).

Our specific objective was to address three questions: (1) Do environmental conditions prior to burning change the effect of burn time on tiller regrowth of a focal invasive, (2) Is the capacity for post-fire regrowth correlated with its pre-burn phenological state, and (3) Do effects of environmental condition and burn time on post-burn recovery differ for a more desirable species with similar ecological function?

Methods

Study Species and Area

Bothriochloa ischaemum is a C_4 grass native to Europe and Asia (Correll & Johnston 1979). Established originally to control erosion and provide livestock fodder, *B. ischaemum* now occurs in 17 U.S. states and dominates a diverse array of habitat types (Sammon & Wilkins 2005). In Texas and Oklahoma, *B. ischaemum* and related Old World bluestem grasses dominate more than 1 million ha of rangeland (White & Dewald 1996). Given sufficient soil moisture, *B. ischaemum* flowers throughout the warm season, which in Texas typically occurs from April to October. The species is very responsive to rainfall. Indeed, during a long summer drought, we observed individuals develop from the senescent to flowering stage only 4 weeks after a single 25-mm rainfall event. In

contrast, some of the most dominant native species have less plastic phenologies. For example, during this same time little bluestem (*Schizachyrium scoparium*) and silver bluestem (*B. laguroides*) began flowering only in midsummer and were not rainfall responsive.

The study was conducted in the Edwards Plateau savanna ecoregion in an oak-juniper savanna underlain by mid- to short grasslands (Küchler 1964). The experiments were conducted on a private ranch, 60 miles southwest of Austin, Texas (latitude 29°58′48″N, longitude 98°32′36″W), in two adjacent pastures that had not been grazed, mowed, cultivated, or burned in the past 16 years (Davidson & Davidson 2008). Temperatures in the region range from 2.3/16.2°C (min/max) on average in January to 20.7/34.1°C in August. Annual precipitation is 792 mm based on the 60 record from nearby Fredericksburg (NOAA station id 413329). The sites were characterized by shallow, alkaline, undulating, loamy, and clayey soils (Davidson & Davidson 2008).

Experimental Design

We conducted two plot-scale experiments, in each case using a 3×2 complete factorial design with $n = 5$ and factors burn treatment (no-burn, 28 September 2008 burn, 20 October 2008 burn) and precipitation (no shelter [ambient], shelter [drier than ambient]). Burn times were selected to coincide with the middle and end of the fall growing season. The main difference between the experiments was the time interval during which the shelter treatment was applied, from 11 May to 31 July in experiment 1 and from 21 August to 28 September in experiment 2.

Site conditions were slightly different for the two experiments. At the site of experiment 1 (site A), the soil was 45 cm deep and the grass cover was almost exclusively composed of *B. ischaemum*. At the site of experiment 2 (site B), the soil was 30 cm deep and supported a greater diversity of grasses, including *B. ischaemum*, *B. laguroides*, *Sporobolus compositus*, and *S. scoparium*. The greater grass diversity at site B allowed us to quantify the fire recovery of a second grass species, the native C_4 bunch grass *B. laguroides*.

In both experiments, five blocks were distinguished based on heterogeneities in grass cover at the time of plot establishment. Each block was assigned six plots to accommodate all treatment combinations. Plots were 3×3–m wide and separated from one another by at least 1 m.

Shelter Treatment

In 2008, precipitation from May through December was well below average, with the exception of July and August, which received more than twice the average amount of rainfall expected for this time of year (Fig. 2a). Consequently, at site A, rainout shelters had the effect of intensifying and extending the ambient drought condition. At site B, all plots received precipitation from the major rainfall events of the summer and the rainout shelter treatment withheld only several minor rainfall events (Fig. 2b).

Rainout shelters consisted of a 3×3–m sheet of greenhouse polyfilm (SunSaver − IR/AC 6 mil Clear, EnviroCept Greenhouses & Supply, Benton City, WA, U.S.A.) atop a 3×3–m, ½″ galvanized steel pipe frame, supported by four t-posts. The polyfilm had a 15% slant to facilitate runoff, with the top edge approximately 1.5 m above the ground. A rain gutter was attached along the lower edge to capture runoff and drain it through plastic tubes to at least 1 m outside the perimeter of the experimental plots.

Burn Treatment

Burn treatments were applied to plots encircled by 1-m tall galvanized steel (roofing) panels to contain the fire. Plots were burned either on 28 September 2008 ($T_{avg} = 32$°C, RH = 23%) or 20 October 2008 ($T_{avg} = 28$°C, RH = 38%). Fire was fueled by litter that had accumulated in the 2007 growing season. Plots burned fairly homogeneously in 3 minutes on average. Due to equipment failure, we were unable to record peak fire temperatures.

Pre- and Post-Burn Data Collection

Measures of plant fitness were collected from the interior 1 m² of each plot. At site A, pre-burn data were collected biweekly starting with the establishment of the rainout shelters in May and ending on the date of the first burn in September. Similarly on site B, but since rainout shelters were on site for only 4 weeks, data were collected only twice before the first burn. In each plot, for each data collection date, predawn water potentials were measured on two randomly chosen leaves using a PMS 1000 pressure chamber (PMS, OR, U.S.A.) as an indicator of soil water availability in the grass root zone. Three more tillers were randomly collected for further lab analysis. The green leaf area of the tillers was imaged using a flatbed scanner and the leaf area estimated using the image analysis program Winfolia (Regent Instruments, Inc., Quebec, Canada). Tillers were then dried to a constant weight at 70°C for 3 days and weighed. At site A, *B. ischaemum* was sampled and at site B, both *B. ischaemum* and *B. laguroides* were sampled.

Prior to each burn event, we determined the developmental stage of *B. ischaemum* at site A and of *B. ischaemum* and *B. laguroides* at site B, following a simplified version of the protocol outlined by Moore et al. (1991). All culms in the center square meter were categorized into one of three distinct phenological stages. A score of 1 was assigned to culms in a pre-reproductive/elongation stage, a score of 2 to culms in the reproductive stage, and a score of 3 to culms in a post-reproductive phase, identified by the presence of shattered seed heads. A phenological index was calculated by determining the average score per plot.

In the following spring, on 24 April 2009, we counted the number of *B. ischaemum* tillers sprouting in the center square meter of every burn plot at site A, and similarly for *B. ischaemum* and *B. laguroides* tillers at site B. After another 6 months, on 18 October 2009, we harvested all aboveground biomass from the center square of all burn and no-burn plots.
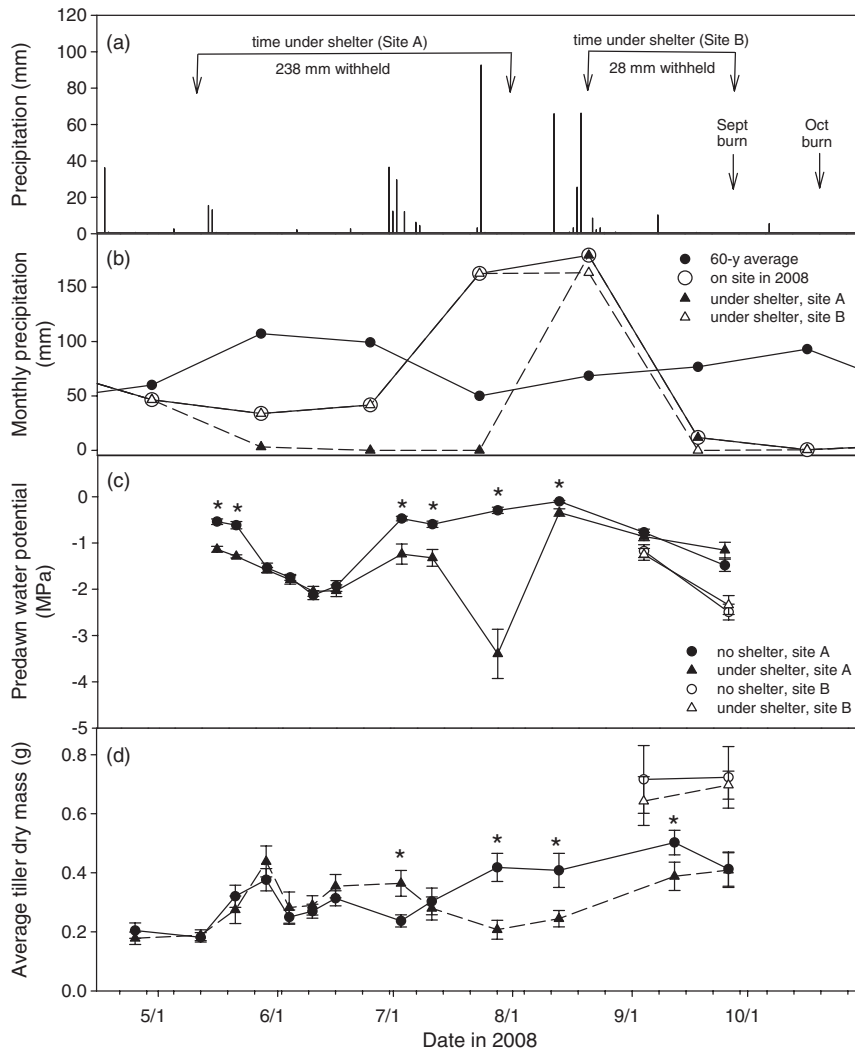
Figure 2. Precipitation, plant water status, and tiller growth for experimental populations in the year of the prescribed burn. (a) Precipitation. Arrows indicate the periods in which the rainout shelters were employed on the respective sites and the two burn days. (b) Average monthly precipitation, actual precipitation, and estimated precipitation in shelter plots at sites A and B. (c) Average predawn water potentials ($\pm$SE; $n = 5$) for *Bothriochloa ischaemum* by shelter treatment. (d) Average tiller biomass ($\pm$SE; $n = 5$) of *B. ischaemum* by shelter treatment. Significant differences between sheltered and unsheltered plots (based on ANOVA, $p < 0.05$) are indicated by "*."

The biomass of grass species was separated by species and lumped for all herbaceous dicots and then dried and weighed.

Statistical Analysis

Block effects were found to be nonsignificant and we do not report them here. Plant water potentials, tiller dry mass, and phenological index were assessed by analysis of variance with burn treatment and the shelter treatment as fixed factors. Post-burn tiller densities were square-root transformed ($\sqrt{Y + 0.5}$) to equalize error variances. A single plot with rainout shelter and September burn was removed from the analysis in experiment 2 (site B) to achieve equality of variances. This plot was the only plot across the two experiments that had no tillers in spring and no biomass in fall for either species. We assumed therefore that no meristems had survived in this plot,

possibly due to an initially low plant density, and could not produce treatment representative post-burn recovery responses.

To test for correlation between phenological index and post-burn tiller count, we performed analysis of covariance, omitting the shelter treatment as a main factor. Analyses of variance, covariance and repeated analysis of variance were conducted using the GLM procedure in SPSS, version 15 (SPSS, Inc., Chicago, IL, U.S.A.).

Results

Shelter Effects on Water Status and Tiller Biomass

At site A, the predawn water potentials of *Bothriochloa ischaemum* in sheltered and open plots diverged during the

12 weeks that the rainout shelters were on site (Fig. 2c), indicating that the shelter treatment effectively altered available soil water. Average tiller biomass was initially (in July) higher under shelter (Fig. 2d), possibly the result of accelerated growth and development due to the shelter's temperature effect (e.g. Schwinning et al. 2005), but then dropped off steeply as water became limiting. Meanwhile, tiller biomass in open plots increased from July to September. Tiller biomass also increased in the shelter treatment once the rainout shelters were removed in early August. By the end of September, just before the first burn, the biomass of tillers in both shelter treatments was indistinguishable.

At site B, the effect of the rainout shelter treatment on the predawn water potentials (Fig. 2c) and tiller biomass (Fig. 2d) of the two species was insignificant. We attribute this to the fact that there was little precipitation during the 5 weeks that the shelters were on site.

Tiller Regrowth After Fire

At site A for *B. ischaemum*, tiller numbers were significantly affected only by burn time ($p < 0.001$; Fig. 3a). There were nearly five times more tillers sprouting in plots burned in October compared to September. At site B for *B. ischaemum*, the effect of burn time ($p = 0.014$), shelter ($p = 0.024$), and their interaction ($p = 0.045$) was significant (Fig. 3b). Overall, there were also more tillers counted in plots burned in October, but there were almost as many tillers counted in sheltered plots that were burned in September. Treatment effects on *B. laguroides* at site B were not significant (Fig. 3c).

Damage by Fire as a Function of Phenological Stage

At site A, *B. ischaemum* tillers were significantly more advanced phenologically before the October burn than before the September burn ($p = 0.001$), but shelter had no effect on phenology (Fig. 3d). At site B, *B. ischaemum* tillers under the shelter were marginally more mature than their counterparts in open plots ($p = 0.056$; Fig. 3e) and plants before the October burn were more mature than before the September burn ($p = 0.012$). Treatment effects on the phenological status of *B. laguroides* were not significant (Fig. 3f).

Analysis of covariance revealed no significant effect of phenological stage on post-fire tiller count at site A, but at site B, there was a marginally significant effect of phenological index overall ($p = 0.061$) and a significant interaction between phenological index and burn time ($p = 0.018$), indicating that the effect of phenology on tiller count was different for the September and October burns. Regression analysis highlights these differences (Fig. 4). The only significant regression between phenological index and tiller count occurred for the September burn at site B (adjusted $r^2 = 0.5251$). This regression slope was significantly different from zero at $p = 0.027$. Thus, although shelter accelerated development in both burn groups (Fig. 3e), *B. ischaemum* benefited from accelerated development, in terms of spring tiller growth, only when burned in September. There was no significant correlation between tiller count and phenological index for *B. laguroides* (data not shown).

Treatment Effects on Post-Burn Recovery After 1 Year

In burn plots at site A, 89% of all aboveground biomass was composed of *B. ischaemum*, with the rest composed mostly
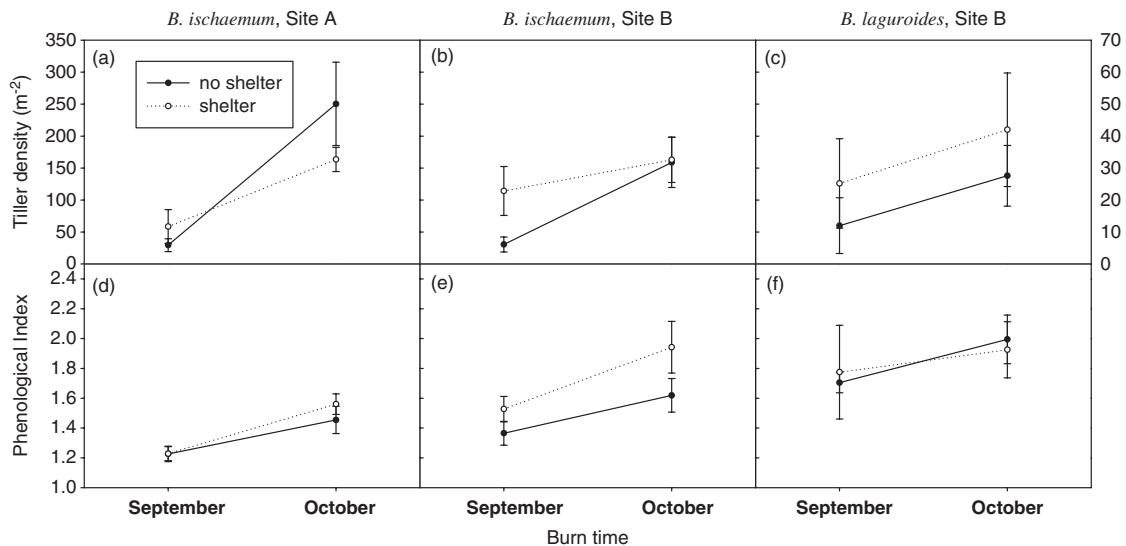

Figure 3. Average post-burn tiller densities measured in the spring of the year following the burn year (top row, a–c) and average phenological index at burn time (bottom row, d–f) for the focal species in the two experiments at sites A and B (±SE; $n = 5$). At site A, the phenological state of *Bothriochloa ischaemum* was significantly more advanced in October, and tiller densities were significantly higher in plots burned in October. Rainout shelter effects were not significant. At site B, both time and shelter cover had significant effects on the phenological state of *B. ischaemum* and spring tiller densities were significantly affected by burn time, shelter, and burn time–shelter interactions. No significant treatment effects were detected for *B. laguroides* at site B.
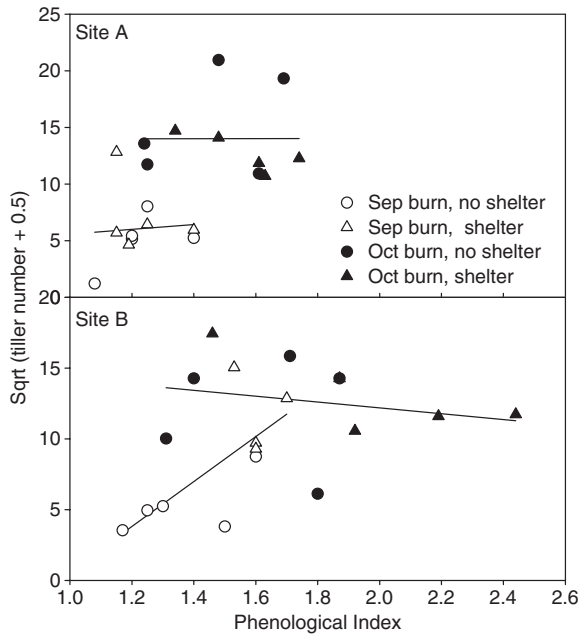
Figure 4. Spring tiller densities (square-root transformed) for *Bothriochloa ischaemum* as a function of phenological state at burn time. Only the regression for the September burn at site B was significant.

of herbaceous dicots. Biomass had not fully returned to control levels (Fig. 5a). No-burn plots showed no significant differences in response to the shelter treatment. Excluding

no-burn control plots, only burn time effects on *B. ischaemum* aboveground biomass were significant ($p < 0.001$), consistent with the tiller density patterns seen in spring (Fig. 3a).

At site B, total biomass was more variable (Fig. 5b), and generally not significantly different between treatments, except that open plots burned in October had significantly less total aboveground biomass than open, no-burn plots. Similarly for *B. ischaemum* biomass only, which on average accounted for 55% of total biomass at this site, open plots in both burn treatments had significantly less biomass than open, no-burn plots (Fig. 5c). For *B. laguroides*, biomass variability was too great to exhibit any significant differences between groups (Fig. 5d). Excluding no-burn control plots, only shelter effects were significant, and for both species ($p = 0.008$ and 0.009, respectively). These results mirror only in part patterns found in spring. While both shelter and burn time effects were significant in spring, only the shelter effects persisted into fall (Fig. 3b).

Species Differences in Response to Treatment

We used repeated analysis of variance to assess whether species responded differently to treatments at site B. For the spring tiller densities, burn time ($p = 0.004$) and species ($p = 0.05$) effects were significant. Shelter effects were only marginally significant ($p = 0.075$), consistent with previous results; however, there were no significant species × treatment interactions. For fall biomass, only shelter ($p = 0.002$) and species ($p = 0.001$) effects were significant, again without
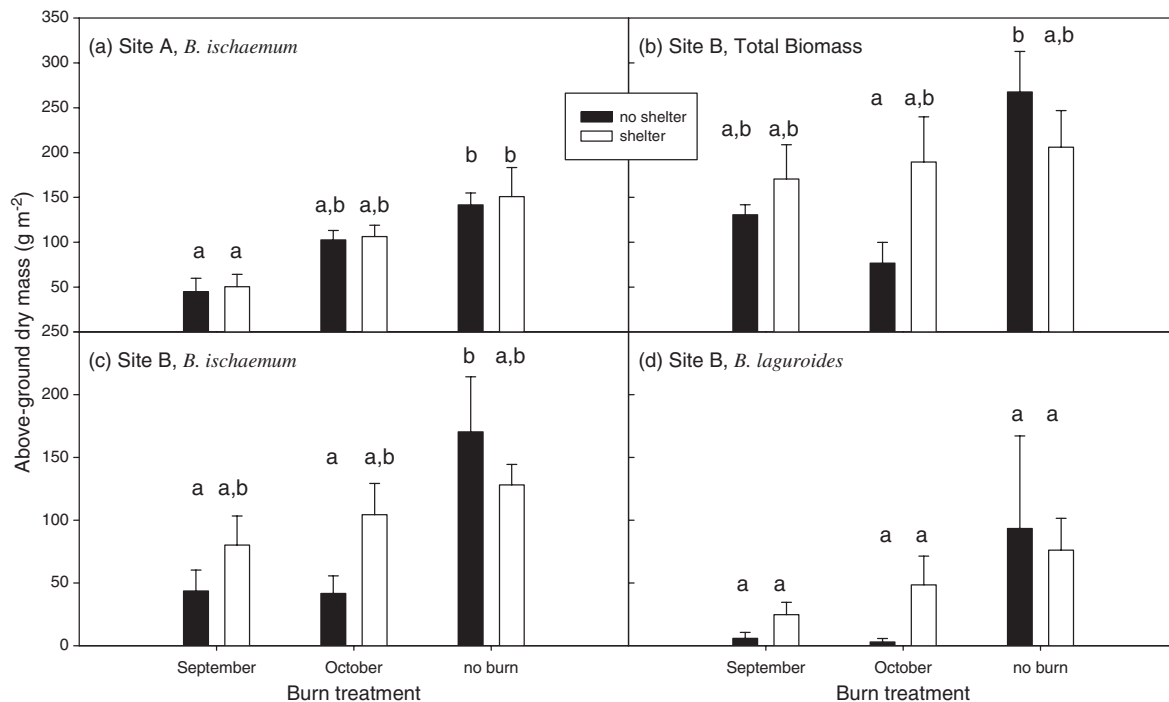

Figure 5. Aboveground dry matter harvested from the center square meter of experimental plots at sites A and B in the fall of the year following the burn year ($\pm$SE; $n = 5$) (a–d). Within each panel, bars marked by different letters are significantly different at the $p = 0.05$ level, as determined by post hoc analysis of variance between group means.

significant species × treatment interactions. Thus, the two species responded to treatment in the same way, both in the short and in the long term.

Discussion

Invasive C_4 grasses in the Neotropics and Australia, especially those intentionally introduced to improve forage production or prevent soil loss, are often characterized by high grazing and fire tolerance compared to native species, due in part to the more intense occurrence of these disturbance factors in the species regions of origin (Foxcroft et al. 2010). It is therefore unlikely that burning per se can reduce the occurrence of invasive C_4 grasses. Our goal was to test whether the judicious use of fire, timed with respect to the phenological stage of an invasive target species, can be used to lessen the invasive species' competitive advantage.

We burned in the mid- and late-growing season of *Bothriochloa ischaemum* and also aimed to manipulate phenological state by employing rainout shelters. At site A (experiment 1), rainout shelters intensified ambient drought conditions, but following their removal, a wetter than average month of August synchronized tiller growth and development across plots. By contrast, at site B (experiment 2), the short-term exclusion of just minor rainfall events immediately before burning accelerated tiller development, most likely due to higher temperature under the shelters (Yuan et al. 2007). Irrespective of the mixed success of rainout shelters, results from both experiments were consistent with the hypothesis that the target species was more vulnerable to fire when burned in a less advanced phenological stage. Specifically, post-burn recovery was sensitive to phenological stage between phenological indices 1.0 and 1.5, where 1.0 indicates 100% pre-reproductive tillers and 1.5 indicates 50% pre-reproductive and 50% reproductive with 0% post-reproductive tillers.

These results are consistent with those of Simmons et al. (2007), who also found mid-growing season burns more detrimental to *B. ischaemum* than late- growing season burns. While this group also found no treatment effects on native C_4 grasses, both studies were hampered by small sample sizes for native species that made the quantification of treatment effects difficult.

The strategic timing of fire has been used successfully in grassland restoration, but chiefly where invasive species flowered in a different season than the native community, so that fire can be timed to coincide with the vegetative and early reproductive growth of the invasive species, while most native species are still dormant (DiTomaso et al. 2006). Growing-season fire is not reported to be an effective method for controlling invasive, C_4, warm-season grasses. On the contrary, fire is shown to facilitate such invasions at the expense of native C_4 grasses, as seen in North American prairies (Hamilton & Scifres 1982; Reed et al. 2005) and Australian savannas (Butler & Fairfax 2003; Setterfield et al. 2010).

The most relevant result from this study is that subtle variation in phenological status at burn time, separated by just weeks, can have sizeable effects on post-burn plant growth. This insight offers managers a tool that can be applied systematically to weaken the competitive strength of an invasive grass among functionally equivalent native species.

Overall, treatment effects on spring tiller densities were similar to effects on fall biomass, which suggests that plants with greater meristem damage remained disadvantaged throughout the following growing season, but there was one exception. At site B, while tiller densities were equally high in shelter and no-shelter plots after the October burn, fall biomass was higher in shelter plots and independent of burn time. This implies that a second mechanism, in addition to meristem survivorship, affects post-burn recovery, possibly involving a shelter effect on the nutrient loss rate due to fire (Ojima et al. 1994; Picone et al. 2003; Brye 2006). Whatever the mechanism, the consistent long-term effect of just 5 weeks of shelter cover in September underscores how highly sensitive the outcomes of prescribed burns can be to slight variation in environmental conditions just prior to a prescribed burn.

The "optimal" timing of a growing season burn (i.e. the timing that would result in the most damage to the invasive species and the 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 temperature trends. Given such uncertainty, scheduling a prescribed burn based on the straight-forward measurement of the phenological status of invasive and native species would provide a simple, practical solution to a potentially complex ecological problem. However, whether or not management involving the strategic timing of prescribed burns will succeed also depends on the frequency of year types that sufficiently discriminate between native and invasive species, as well as the magnitude of the differential effect relative to any systematic recruitment, growth, or competitive advantages the invasive species may have (per equation 3).

Implications for Practice

- Prescribed burns can control invasive grasses in C_4 grasslands only if selective fire mortality exceeds the average competitive advantage of the invasives.
- The outcomes of prescribed burns in grasslands are highly sensitive to pre-burn weather conditions and should be conducted only if the probability of selective mortality is high.
- Screening the phenological status of invasive and native species prior to burning can help predict the selectivity of fire damage.

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