



Fire effects on invasive and native warm-season grass species in a North American grassland at a time of extreme drought

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Keywords

Bothriochloa ischaemum; fire temperature; grassland fire; invasive species control; KR bluestem; little bluestem; *Schizachyrium scoparium*; yellow bluestem

Nomenclature

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Abstract

Question: Can the timing of cutting or burning be used to selectively damage an invasive C₄ grass species while limiting collateral damage to dominant native C₄ grass species in a grassland community?

Location: A medium to short grass prairie in central Texas, US.

Methods: We conducted six cut and burn trials between June 2011 and January 2012 during an exceptional drought year. Target species were the native, perennial, C₄ grass *Schizachyrium scoparium* (little bluestem) and the introduced, perennial, C₄ grass *Bothriochloa ischaemum* (yellow bluestem). Burn trials were conducted inside a steel barrel using standardized fuel loads. To assess recovery, we counted the first cohort of new tillers that emerged after treatment and tillers that grew in the subsequent spring. We also recorded phenological status, meteorological variables and burn temperatures to determine if tiller recovery was predictable.

Results: *Bothriochloa ischaemum* responded more negatively to burning than to cutting, but these treatments were no different for *S. scoparium*. Both species produced the smallest number of tillers after the summer burns, and the burn date × species interaction was insignificant. On average, peak fire temperature inside tussocks was 100 °C higher in *B. ischaemum* than in *S. scoparium*. Judging from the reduction in tiller densities in undisturbed plots from spring 2011 to spring 2012, *B. ischaemum* was also more sensitive to drought. Multivariate models were significant and related burn recovery to peak fire temperature, among other factors, and recovery from cutting to ambient temperature on the day of cutting. In *B. ischaemum*, plants with higher investment in early reproductive growth suffered more burn damage.

Conclusions: We identified no optimal burn time that maximized discrimination between the two species. Nonetheless, the invasive species was more sensitive to both drought and fire, possibly due to higher heat exposure of growing points. Thus, burning during the summer of a drought year may constitute the sought-after treatment that selectively favours native species. Ultimately, successful management will involve fuel and temperature management combined with assessment of the relative phenologies of the target species prior to burning. This study suggests that a hot fire at a time when the invasive species has a larger investment in early reproductive growth will provide the best control.

Introduction

The invasion and subsequent spread of exotic C₄ grasses into tropical, subtropical and semi-arid grasslands have markedly reduced grassland diversity and proven extremely difficult to control (Reed et al. 2005; Ripley et al.

2010). The exotic grasses are often functionally similar to a large cross-section of species in the recipient community (i.e. they are also fire-adapted, warm-season, perennial grasses). This poses a special challenge to grassland restoration since it is unclear how to target invasive species without causing equal or more collateral damage to native

species (Reed et al. 2005; Simmons et al. 2007; Wilsey et al. 2011). Specifically, the risk associated with almost any disturbance treatment is the unintentional facilitation of the invasive species, which often recover more vigorously from disturbance.

Only a few studies thus far have examined whether the timing of disturbance vis á vis differences in the physiological or phenological status of invasive and native species can be used to produce favourable outcomes in invasive species control (Simmons et al. 2007; Ruckman et al. 2012b). Fire timing allows for discrimination among grassland species based on major trait axes (e.g. in flowering time between C_3 herbs vs C_4 grasses; Howe 2011; Boughton et al. 2013). Even within communities of functionally equivalent species there is sufficient difference in phenological timing to suggest that members of the same functional type could also be differentially sensitive to a burn or cut if it was scheduled during periods of phenological offset (Wilsey et al. 2011; Catorci et al. 2012).

Arguably, the most important driver of grassland phenology in semi-arid climates is precipitation (Fuhlendorf & Smeins 1997; Limb et al. 2011). Precipitation triggers tiller initiation and flowering, but not simultaneously for all species (Silletti & Knapp 2002; Craine et al. 2012). Species with a rapid or early growth response will be the first to remobilize below-ground carbohydrate reserves and seek a rapid return on investment through a swift completion of the life cycle (Wolkovich & Cleland 2014). Other species use a strategy of slow but steady resource accumulation. These two general strategies place grassland species in different states of development and 'resource debt' at burn time and this should affect their recovery (Svejcar 1990). Species burned or cut with a recently mobilized and therefore depleted storage of below-ground resources would be limited in producing new tillers during recovery.

Precipitation also affects fuel quality and quantity, which in turn affects plant exposure to heat (Keeley 2009). Species can be more or less tolerant to these physical conditions based on the location, insolation and flammability of live tissues, especially meristems (Pyke et al. 2010). The complexity of fire ecology makes it difficult in practice to determine whether species-specific effects of fire are due to phenological differences, which should be reproducible, or merely accidental consequences of meteorological and fuel condition at the time of burning. In this study, we addressed this challenge by using an experimental design that constrained fire conditions and included the measurement of fire temperatures.

From June 2011 to January 2012, we conducted six burn trials under the controlled conditions of a fixed fuel load inside a steel barrel used to contain fire. Our purpose was to test (1) whether variation in fire timing at the scale

of 1 m can affect re-growth dynamics of grasses, and (2) whether exotic and native species of same functional type (i.e. perennial, C_4 grasses) respond differently to such variation. An additional goal was to identify environmental and phenological drivers of post-fire recovery. Thus, we quantified environmental conditions before, during and after each burn trial, as well as plant size and phenological status at burn time. To quantify recovery, we counted new tillers and we also counted the tillers in plots that were cut and not burned to distinguish between the effects of heat and biomass loss.

Unbeknownst to us at the beginning of the experiment, the experimental year developed into a record-breaking drought year in Texas, and the results from this study have to be interpreted in the light of this special circumstance. While we cannot say what would have happened in an ordinary year, at least we have a record of variables that accompanied this unusual year and therefore *some* opportunity to speculate how the drought might have influenced the outcomes of controlled burns.

Our experimental system was the understorey of a typical savanna site on the Edwards Plateau in central Texas, an ecosystem dominated by C_4 , perennial bunch grasses. Typical for the region, the site had been invaded by *Bothriochloa ischaemum* (yellow or King Ranch (KR) bluestem), which has widely replaced the historically dominant C_4 , perennial grasses, such as *Schizachyrium scoparium* (little bluestem). At the experimental site, remnant populations of *S. scoparium* were still interspersed within a matrix of *B. ischaemum*.

Methods

Species and site information

Bothriochloa ischaemum var. *songarica* [L.] Keng belongs to one of several genera containing non-indigenous, invasive, perennial grass species collectively referred to as 'Old World Bluestems' (Correll & Johnston 1979). Native to mesic grasslands of Europe, Asia and Africa, *B. ischaemum* was introduced to the US in the early 1900s in an effort to 'improve' rangelands. It rapidly spread in the southern regions and is now naturalized in 17 states, including Texas. Once established, it is almost impossible to eradicate, in part because it is less palatable to cattle, which prefer native grasses. The Missouri Department of Conservation classifies *B. ischaemum* and its close relative *B. bathii* as aggressive, weedy degraders of pasturelands.

Schizachyrium scoparium [Michx.] Nash is a perennial grass native to 48 states in the US (Loflin & Loflin 2006). Both species are warm-season, perennial grasses with C_4 photosynthesis. *S. scoparium* flowers predominantly from September to October in central Texas, while *B. ischaemum* can flower continuously, provided environmental

conditions are favourable. The two species have similar habitat requirements and often grow side by side.

The study was conducted in the Balcones Canyonlands sub-region of the eastern Edwards Plateau. The study site had upland soils from the Rumble-Comfort association. Site-specific climate information for the experimental period was obtained from Ameriflux tower US-FR2, ~2 km from the research site. Mean monthly temperatures were close to average over the study period, but precipitation from February to October was 45% below average, and there was almost no rain from June to September (Fig. 1). Average precipitation and temperature conditions were obtained from a 30-yr record measured at San Marcos Municipal Airport.

Experimental design

The experiment followed a blocked factorial design, with species blocked independently since there was little spatial overlap between patches of the two target species. The factors were species (two: *B. ischaemum*/*S. scoparium*), treatment (two: cut/burn) and treatment timing (four dates in the growing season: Jun, Jul, Sept and Oct 2011 and two dates in the dormant season: Nov 2011 and Jan 2012). Cut and burn treatments were applied on the same treatment days. There were five blocks for each species. All plots were selected at the start of the experiment based on the criteria that they contained at least one bunch of the target species ≥ 2 -cm wide at the base and that they were at least 3 m away from the nearest neighbouring plot. They were then randomly assigned to cut, burned or left untreated as a

control, and randomly selected without replacement for each treatment date. Plot size was dictated by the size of the burn barrel, which measured 45 cm in diameter, larger than the size of most single tussocks. Treatments were replicated three times per block for a total of 15 replicates per species \times treatment combination.

The dates of treatment and data acquisition are summarized in Table 1. The tillers in each experimental plot were counted four times. They were first counted just before the treatment was applied (=initial count). The tillers that emerged immediately after the treatment were counted twice a few weeks apart (=post-treatment counts). The last count was conducted during the next growing season and included all plots (=final count). We omitted the consideration of untreated control plots in the post-treatment assessment, judging that this contrast would only show the obvious effects of disturbance, while our focus was on species and treatment differences in recovery from disturbance. However, the final tiller count included untreated controls to compare the longer-term impact of treatment vs no treatment. For this purpose, we added an additional three plots per block as controls.

Pre-treatment measurements

On the morning of the treatment, all biomass above 3–4 cm in plots slated for cutting and burning was removed and stored in paper bags for later analysis. We removed biomass in both treatments to determine pre-burn plant size and phenological status by plot and to have greater control over fuel condition. Thus, strictly speaking, our

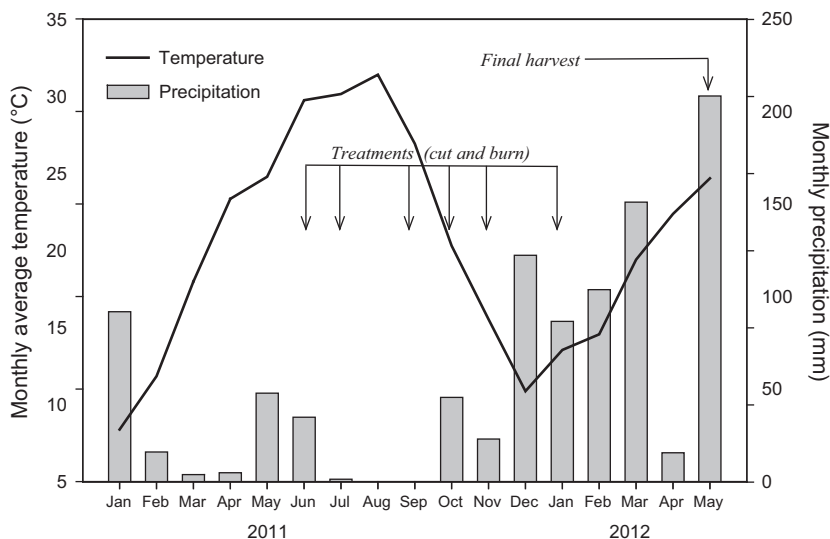


Fig. 1. Average daily temperature and monthly precipitation from 2011 to the end of the experiment in May 2012. Arrows indicate treatment months and the month of the final tiller count. Throughout the experiment, cut and burn treatments were applied on the same day.

Table 1. Dates of treatments and tiller counts.

Date of treatment and initial count	Post-burn tiller count 1	Post-burn tiller count 2	Final tiller count
8 Jun 2011	20 Jul 2011	19 Aug 2011	23 May 2012
8 Jul 2011	19 Aug 2011	16 Oct 2011	23 May 2012
24 Sept 2011	16 Oct 2011	6 Nov 2011	23 May 2012
17 Oct 2011	6 Nov 2011	22 Nov 2011	23 May 2012
6 Nov 2011	22 Nov 2011	6 Dec 2011	23 May 2012
10 Jan 2012	10 Feb 2012	27 Feb 2012	23 May 2012

'burn' treatment was really a 'cut and burn' treatment. The implications of this experimental strategy are addressed in the Discussion section.

For the biomass analysis, we separated dead from live biomass and divided live tillers into four numerical categories: (1) for the vegetative/pre-elongation stage, (2) for the elongation stage, (3) for the flowering stage, and (4) for post-reproductive stage with seed maturation completed. Plots without live tillers were assigned the index value 0. Tillers were then dried at 70 °C for 4 d and weighed. Average phenological indices per plot were calculated as the sum of tiller categories divided by the total number of tillers (Moore et al. 1991).

Burn procedures

Burns were conducted inside a steel barrel to contain fire. This made it safe and legal to conduct burn trials at any time of year, even during the burn ban imposed in the summer of 2011. The barrel was 1.22-m tall, 45-cm wide and open at the bottom (covering an area of 0.16 m²). The top was closed to retain flying ambers, but a pipe was attached to the top for ventilation. A standard amount of fuel (120 g of mixed dried grass stems and leaves previously collected from the study site) was added to the burn barrel and lightly padded down. This amount of fuel was above the average amount of biomass cut from plots across all treatment dates, which was 87 ± 37 g [range: 17–215 g] and 82 ± 48 g [range: 10–279 g] for *B. ischaemum* and *S. scoparium*, respectively. There was no statistically significant difference between the average plot biomass for *B. ischaemum* and *S. scoparium* (*t*-test on log-transformed biomass: $P = 0.224$). Thus, while the average added fuel was above the average amount produced by plots during the study period, it was well within the range of biomass values found between individual plots. Because of this and the small difference in the natural fuel load produced by the two species, we judged the burn condition to be a reasonable approximation of natural conditions.

The burn barrel design, ventilation procedure and the amount of fuel added was tried and tested in the month leading up to the first burn. Our goal was to achieve (1) at least charring, if not outright combustion of the grass

stubble that remained on the ground after cutting and (2) temperature regimes that followed published values for grassland fires (e.g. Fidelis et al. 2010). To supply the fire with sufficient oxygen, air was blown through a small hole in the barrel using an electric leaf blower.

Each plot was instrumented with four high-temperature thermocouples (HH309A; Omega Corporation, Stamford, CT, US). The thermocouples were placed on the open soil surface, on the surface surrounded by the stubble of tillers that remained after cutting, and at 1 cm and 2 cm soil depth. Temperatures were recorded in 2-s intervals for several minutes.

Post-treatment measurements

After each treatment, we monitored plots for new tiller emergence. After the first growth cohort seemed well established, we conducted the first post-treatment count (Table 1). Plots were counted again after 2–3 wk to ensure that we did not miss any delayed tiller growth. Since the first and second tiller counts were always very close, we used only the second tiller count in the analysis. The final tiller count was conducted during the next growing season on 23 May 2012 and also included untreated control plots.

Statistical analysis

The effects of species, treatment and treatment date on tiller numbers were examined using a GLM with negative binomial distribution. This analysis was conducted on both post-treatment and final tiller numbers. Here, we summed tiller numbers across the three replicate plots per block to avoid pseudo-replication, since species were spatially separated and could not be replicated within blocks. Thus, the replication number was five (equal to the block number).

We conducted multivariate analysis to determine the most parsimonious explanatory model for the prediction of final tiller numbers. By 'explanatory model', we mean a model that included not just the treatment factors block and date, but also measured variables such as fire temperature and tiller number. Models were compared based on the small sample size correction value of the Akaike information criterion (AIC_c; Johnson & Omland 2004) and the

AIC_c weights. A model variable was assumed to have predictive power only if the confidence interval of its coefficient did not overlap with zero.

This analysis was conducted using individual plots as samples, but separately for the four species × treatment combinations. The two species were analysed separately to determine whether different variables controlled recovery from disturbance. Cut and burn plots were analysed separately because some predictor variables (specifically temperatures under fire) were unique to the treatment. Across the six treatment dates and with 15 plots per treatment, the total sample size for these analyses was 90.

A total of 33 variables were considered and initially tested as single predictor variables. These included plant variables describing the state of the plot just before treatment (total live and dead above-ground biomass, total live tiller number, average live tiller biomass, average phenological index of live tillers), climate variables describing average temperature and cumulative precipitation before and after treatment over 1, 2 or 4 wk, ambient conditions on the day of treatment (average air temperature, dew point temperature and average temperature on the soil surface obtained from the initial readings of the high temperature thermocouples used in burn plots) and burn conditions expressed in four maximal temperature readings (at the surface, inside the bunch, 1 cm below the surface and 2 cm below the surface). Because of the extreme variability of fire temperature measured at a point, we entered this variable into the analysis in three different ways: using the raw data from the individual plots, data averages within blocks or averages within dates. Similarly, the ambient temperature at the soil surface was averaged by block or date.

Variables with appreciable predictive power over the null (intercept only) model were then tested in combination and with interaction terms not exceeding three terms. However, we did not combine variables with a high degree of collinearity in the same model. For example, we only used one of the four peak fire temperatures and either block or date averages in the models. Air temperature, dew point temperature and soil temperatures were also among the variables with a high degree of collinearity and were not used in the same model. We did allow models that included date and block effects in combination with measured variables. Overall, we identified ten covariates with appreciable predictive power. They were date- or block-averaged peak fire temperatures in all four within-plot locations, average biomass per tiller, initial tiller count, phenological index and average soil surface, air and dew point temperature on the day of treatment. The number of models tested was between 40 and 60. We also show results for the block-only, date-only and intercept-only

models to examine if models that included explanatory covariates performed better than factorial models using only block and date.

Results

Burn conditions and treatment response

Peak temperatures at the surface were typically reached within the first 30 s after ignition and flames died down after 2 min. Examples for the July and January burns are shown in Fig. 2. In general, three temperature patterns were observed: (1) peak temperatures during cold-season burns (Oct, Nov, Jan) were cooler by 80 °C on average than for warm-season burns (Jun, Jul, Sept), despite standardized fuel loads ($P = 0.004$, $n = 179$ in a comparison of peak temperatures at the surface). (2) Peak temperatures measured inside the remaining grass stubble were much lower by 145 °C on average than at the open surface ($P < 0.001$, $n = 179$ in a paired comparison). (3) Temperatures inside grass bunches were higher by 100 °C on average for *B. ischaemum* than for *S. scoparium* ($P < 0.001$, $n = 179$).

The number of tillers that emerged right after treatment differed significantly between dates, species, treatments and the interaction of species and treatments (Table 2, Fig. 3a). On average, *S. scoparium* produced more tillers after burning than *B. ischaemum* and responded similarly to cutting and burning. In contrast, *B. ischaemum* produced significantly less tillers after burning than after cutting. While the date of treatment affected tiller numbers, there were no significant interactions between date and species or treatment.

Final tiller numbers differed significantly between species, treatments and the interaction of species × treatments (Table 2; Fig. 3b). The significant interaction indicated that *B. ischaemum* remained more suppressed by burning even into the following growing season. Date of treatment effects was only marginally significant and there were no significant interactions with date (Table 2).

All burn trials reduced final tiller numbers in *B. ischaemum* to 32–64% of untreated control plots (Table 3). In contrast, plots that were cut had tiller numbers between 82% and 170% of the control. Cutting treatments in October, November and January tended to increase final tiller numbers in both species. The effects of burning were more variable, but in both species, burning in June caused the largest reduction in tiller numbers, and burning in January the largest increase in tiller numbers relative to the control.

The average tiller numbers counted in plots before treatment or in untreated control plots declined between June 2011 and May 2012 (Table 3). For *B. ischaemum*, tiller numbers declined by 55% on average, which was significant ($P = 0.012$). For *S. scoparium* the decline was

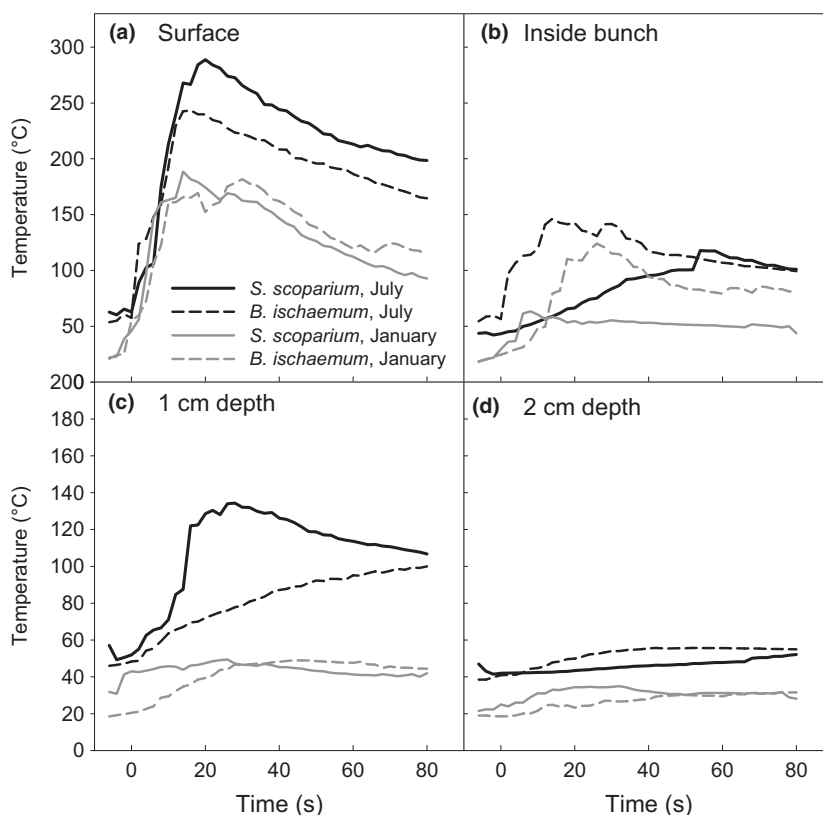


Fig. 2. Examples of fire temperatures during a summer (July) and a winter (January) burn. Shown are average temperatures across 15 burn plots in four positions within plots (a–d). Across burn trials, time zero was synchronized at the point that temperatures began to rise at the surface. Differences in initial temperature reflect the difference in ambient conditions between July and January.

Table 2. General linear model (negative binomial distribution) analysis conducted on counts of the first new tillers that grew after each treatment (post-treatment) and on the final tiller count conducted in May 2012. *P*-values above 0.1 are highlighted in bold.

Source	df	Post-treatment tiller counts		Final (spring) tiller counts	
		Wald's χ^2	<i>P</i>	Wald's χ^2	<i>P</i>
Date	5	52.023	0.003	31.544	0.055
Species	1	89.718	<0.001	32.742	<0.001
Treatment	1	40.914	<0.001	14.246	0.030
Date × Species	5	12.468	0.510	2.551	0.972
Date × Treatment	5	3.882	0.930	2.249	0.973
Species × Treatment	1	39.679	<0.001	17.489	0.016
Date × Species × Treatment	5	7.564	0.761	4.282	0.926

22% on average and was not statistically significant (*P* = 0.449).

Predictors of treatment response

For *B. ischaemum*, block effects were strong predictors of final tiller numbers (Table 4). In both cut and burn treatments, blocks 1–3 had more tillers on average than blocks 4 and 5, as the comparison of β -values in Table 5 shows. In

burned plots, final tiller numbers were also dependent on some measure of peak fire temperature, as well as average tiller biomass at burn time. The model that used peak temperature 1 cm below the ground (DPT3) had the strongest support overall, based on AIC_c weights, and substantially more support than the model that instead used peak temperature at 2-cm depth instead (DPT4). Both temperature and tiller biomass affected final tiller numbers negatively (Table 4). In cut plots, the inclusion of air temperature on

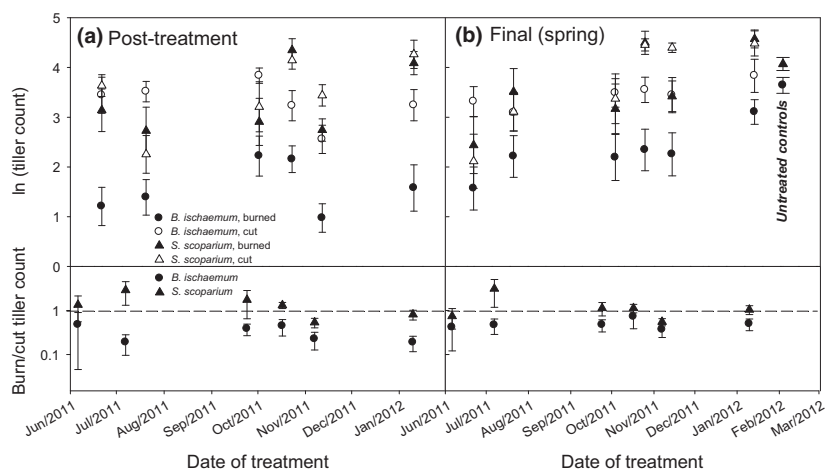


Fig. 3. Post-treatment (a) and final (May 2012) (b) tiller numbers for plots treated on different dates. Shown are block averages and their standard errors. The average tiller number per plot in untreated control plots is shown in the top right corner of figure (b). Top: Average log tiller numbers; Bottom: The tiller number ratio in burned and cut plots in the same block.

Table 3. Average live tiller numbers and SD in brackets per plot ($n = 30$ on 6 June 2011, $n = 15$ on 23 May 2012). Plot size was 0.16 m².

	<i>B. ischaemum</i>		<i>S. scoparium</i>	
Counted on 6 June 2011				
Before treatment	111 (44)		92 (37)	
Counted on 23 May 2012				
Control	50 (43)		72 (42)	
Treatment Dates	Burn	Cut	Burn	Cut
06/06/2011	13 (19)	41 (33)	45 (53)	33 (44)
07/07/2011	18 (17)	41 (42)	76 (72)	46 (43)
09/24/2011	23 (28)	44 (25)	57 (52)	65 (53)
10/17/2011	24 (27)	51 (49)	102 (56)	94 (45)
11/7/2011	25 (34)	52 (49)	48 (41)	84 (28)
01/10/2012	32 (27)	85 (92)	116 (65)	113 (56)

the day of treatment slightly improved the prediction over the block-only model (Table 4).

In contrast, block effects were not significant for *S. scoparium*. In burned plots, peak temperature at 2-cm soil depth, tiller numbers on the day of treatment and the interaction between these two terms appeared in all three top models (Table 4). Models that included peak fire temperatures at any other depth were not among the top nine models. The three top models also used one of three co-linear predictor variables (average air temperature on the day of treatment, dew point temperature or date-averaged temperature at the soil surface), but the model that used air temperature had substantially more support than all others. Peak fire temperature, by itself, was not a significant factor in the model (Table 5), but the interaction term was, indicating that the positive effect of high initial tiller density was counterbalanced by a negative effect of fire temperature.

In cut plots of *S. scoparium*, the most successful models all included either the phenology index or the initial tiller count (with positive effects) and some measure of ambient temperature on the day of the treatment (with negative effects). The best model contained the phenology index and temperature at soil level. To interpret the effect of phenology, it is important to note that the index numbers for this species varied between 0 (no green tillers) and 1 (vegetative stage). Therefore, the positive effect of the phenological index means that plots that had vegetative tillers when cut produced more tillers in the following spring than plots that had no vegetative tillers.

Figure 4 illustrates the varied effects of temperature on final tiller counts. In the burn treatments, the effect of fire temperature was clearly to reduce final tiller numbers, although it did not explain a large fraction of total variation. The June burn produced some of the hottest fires; the October and January burns produced the coolest fires. In the cutting treatment, measures of ambient temperature on the day of treatment were stronger predictors of final tiller numbers and temperature conditions were clearly dependent on season. June, July and September temperatures were generally higher than October, November and January temperatures, and the January temperatures were by far the coldest.

Discussion

We originally designed this experiment to identify environmental conditions and seasonal effects that would maximize the difference in burn damage between the invasive and native species. However, we found that species and treatment differences were remarkably consistent between

Table 4. AICc comparisons of multivariate GLM models for the prediction of final tiller numbers. The best three models are shown, plus block-only, date-only and intercept-only models. The model with the most support is shown in bold.

Model	AIC _c	Δ_i	Relative likelihood	w_i
<i>B. ischaemum</i> , Burned				
Block + B + DPT3	694.4	0	1	0.540
Block + B + DPT4	695.8	1.4	0.497	0.268
Block + B + DPT2	696.5	2.1	0.350	0.189
Block	704.8	10.4	0.006	0.003
Intercept	747.2	52.8	3.42 E-12	1.85 E-12
Date	751.8	57.4	3.43 E-13	1.85 E-13
<i>B. ischaemum</i> , Cut				
Block + TA	849.0	0	1	0.470
Block + TD	850.0	1.0	0.607	0.285
Block	850.3	1.3	0.522	0.245
Intercept	876.2	27.2	1.2 E-06	5.8 E-07
Date	880.9	31.9	1.2 E-07	5.6 E-08
<i>S. scoparium</i> , Burned				
BPT4 + IT + BTP4* IT + TA	925.8	0	1	0.833
BPT4 + IT + BTP4* IT + TD	927.9	4.5	0.105	0.088
BPT4 + IT + BTP4* IT + DTS	930.3	4.7	0.095	0.079
Block	947.3	21.5	2.1 E-05	1.8 E-05
Date	947.6	21.8	1.9 E-05	1.5 E-05
Intercept	948.1	22.3	1.4 E-05	1.2 E-05
<i>S. scoparium</i> , Cut				
P + BTS	942.4	0	1	0.547
IT + IT*TA	943.3	0.9	0.651	0.356
TA + P*TA	946.1	3.7	0.160	0.088
Date	950.8	8.4	0.015	0.008
Intercept	954.5	12.1	0.002	0.001
Block	959.6	17.2	1.9 E-04	1.0 E-04

B, average dry mass per live tiller on treatment date; BPT4, block-averaged peak temperature at 2-cm soil depth; BTS, block-averaged temperature at the soil surface on the day of treatment; DTS, date-averaged temperature at the soil surface on the day of treatment; DPT2–4, date-averaged peak temperatures inside tussocks and at 1- and 2-cm soil depth, respectively; IT, initial tiller number on treatment date; P, phenological index on the day of treatment; TA, average air temperature on the day of treatment; TD, dew point temperature on the day of treatment.

burn trials. Thus, the main experimental result was that *S. scoparium* was similarly affected by the cutting treatment and the cut/burn treatment, while *B. ischaemum* clearly responded more negatively to burning. This was evident immediately after treatment in the emergence of new tillers, indicating that fire killed substantially more meristems in *B. ischaemum* than in *S. scoparium*.

Although we did not find the date \times species interaction we had hoped for, the timing of treatment clearly mattered in plant recovery. In general, cutting or burning in June, July and August had predominantly negative effects on subsequent tiller growth in both species, and predominantly neutral or positive effects when done in October, November and January (Table 3). The neutral effects can be explained by the minimal resource loss that the removal of dead biomass would impose on dormant plants, as well as cooler fire temperatures being less damaging to buried growing points (Daubenmire 1968; Copeland et al. 2002). Positive effects are commonly explained by litter reduction causing an improvement to light interception at the start of

the spring growing season (MacDougall & Turkington 2007).

But why did *B. ischaemum* respond consistently more negatively to burning? Average temperatures rose to greater extremes inside *B. ischaemum* tussocks, which may have caused higher axillary meristem mortality. *B. ischaemum* had less basal stem density than *S. scoparium*, which would have provided less heat insulation for axillary meristems (Hofstede et al. 1995). In addition, *B. ischaemum* had the strongest response to fire temperature measured 1 cm below the ground, while *S. scoparium* was most sensitive to temperatures 2 cm below the ground, indicating probable locations of the rhizome bud banks (Benson et al. 2004). In a previous experiment, we also found a lower heat tolerance of *B. ischaemum* seeds compared with *S. scoparium* seeds (Ruckman et al. 2012a), and several other studies documented a negative response of *B. ischaemum* to growing season burning (Berg 1993; Simmons et al. 2007). Thus overall, *B. ischaemum* appears to be less well adapted to coping with fire, at least in comparison

Table 5. Parameter estimates for the top ranked explanatory models from Table 3. The effect of Block 5 was arbitrarily set to zero.

Model	β	SE	Lower CI	Upper CI	P^*
<i>B. ischaemum</i> , Burned					
Block 1	0.771	0.3565	0.073	1.470	0.030
Block 2	1.231	0.3552	0.534	1.927	0.001
Block 3	1.370	0.3644	0.656	2.085	<0.001
Block 4	-1.146	0.3681	-1.867	-0.424	0.002
Block 5	0	–	–	–	–
B	-3.431	1.5897	-6.546	-0.315	0.031
DPT3	-0.006	0.0028	-0.012	0.000	0.027
<i>B. ischaemum</i> , Cut					
Block 1	0.544	0.3437	-0.130	1.217	0.114
Block 2	0.526	0.3418	-0.144	1.196	0.124
Block 3	1.414	0.3436	0.734	2.090	<0.001
Block 4	-0.360	0.3410	-1.028	0.309	0.291
Block 5	0	–	–	–	–
TA	-0.032	0.0174	-0.066	0.002	0.065
<i>S. scoparium</i> , Burned					
BPT4	0.015	0.0100	-0.005	0.034	0.141
IT	0.038	0.0093	0.020	0.057	<0.001
BTP4* IT	-4.75 E-04	0.0001	-7.7 E-04	-1.84 E-04	0.001
TA	-0.066	0.0188	-0.103	-0.030	<0.001
<i>S. scoparium</i> , Cut					
P	1.823	0.529	0.785	2.860	0.001
BTS	-0.032	0.010	-0.051	-0.012	0.002

*Based on the Wald Chi-square test.

B, average dry mass per live tiller on treatment date; BPT3, block-averaged peak temperature at 1-cm soil depth; TA, average air temperature on the day of treatment; BPT4, block-averaged peak temperature at 2-cm soil depth; IT, initial tiller number on treatment date; P, phenological index on the day of treatment; BTS, block-averaged temperature at the soil surface on the day of treatment.

with *S. scoparium* and especially under conditions favouring hot fires.

Our burn treatment differed in one important way from the typical procedure of prescribed burning, in that plants were first cut to within 3–4 cm of ground level and then burned using a standard amount of added fuel. Because of this, we can be more confident that treatment differences between cut and burn plots were caused only by the presence or absence of fire, and not by indirect and potentially complex effects of the plant's own biomass on local fire characteristics. The method may have exaggerated fire effects on *B. ischaemum* relative to a conventional burn regime. The present experiment cannot resolve if standardizing fuel quantity and quality or cutting biomass before burning enhances the negative effect of fire on *B. ischaemum*, but if so, it would be easy to adapt burn procedures to take advantage of this effect.

Another important consideration is that the year of the experiment was not an ordinary year. The 2011 Texas drought was the driest year in recorded history (Hoerling et al. 2013). The severity of the drought was clearly

reflected in the reduction of tiller numbers in untreated plots between June 2011 and May 2012 (Table 3). While the tiller density of *B. ischaemum* in untreated plots declined by 55% in the course of the drought year, the June burn further reduced tiller densities by 74% relative to control plots, so that the total tiller reduction compared to the previous year was 88%. In *S. scoparium*, tiller numbers in untreated plots declined by 22% in 1 yr (not a statistically significant difference), and the June burn caused a 37% reduction in tiller densities relative to control plots, for a total reduction in 1 yr of 51%. Thus, the combination of June burning and drought represented double jeopardy to *B. ischaemum* and was far less detrimental for *S. scoparium*.

It is generally believed that C_4 grasses cut or burned during the elongation phase suffer the largest loss of storage products (Bond & van Wilgen 1996), and previously we showed that *B. ischaemum* suffered more damage when burned in a more advanced reproductive state (Ruckman et al. 2012b). In this study, we found that average tiller biomass had a significantly negative effect on final tiller numbers in burn plots. From June 2011 to January 2012, green tillers were either in the vegetative or the elongation stage, and the higher the percentage of elongating tillers, the higher the average tiller biomass. Thus, the effect of tiller biomass was tantamount to a phenological effect, indicating, as did the earlier studies, that plants with higher investment in early reproductive growth suffered more burn damage. In contrast, the vast majority of *S. scoparium* tillers were either completely dormant or had tillers in the pre-elongation stage throughout the experiment, which explains why we did not find a phenological effect on the recovery of this species.

However, we did not see a phenological effect on *B. ischaemum* recovery in plots that were cut and not burned. Perhaps the loss of storage product, without additional meristem death through heat exposure, did not impose significant hardship. On the other hand, we did pick up significant effects of ambient temperature in both species. One explanation is that cutting biomass on a hot and dry day resulted in higher plant water loss before the wound response sealed exposed tissues.

For *B. ischaemum*, block effects were the largest single source of variation, indicating that critical site-related drivers of meristem survivorship and/or tiller growth in *B. ischaemum* were not captured in variables such as tiller number, size or stage at the time of treatment or fire temperature. They may instead be found in variables such as tissue nitrogen concentration or water status, which we did not measure. Strong block effects suggest that *B. ischaemum* grows across a wide range of site conditions, in accordance with its invasiveness. The lack of a block effect in *S. scoparium* may indicate either that this species selects

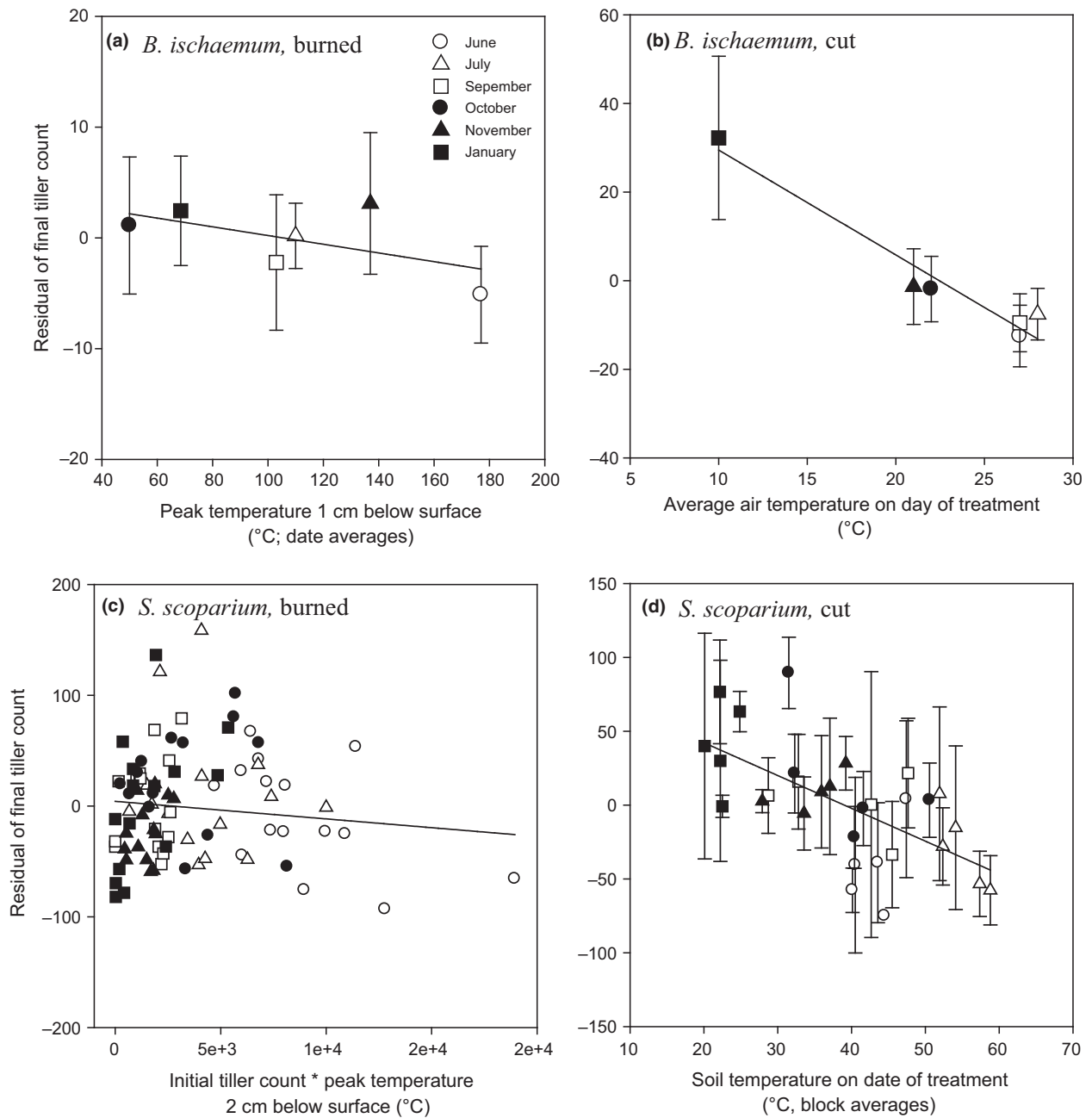


Fig. 4. The effects of day-of-treatment temperature on subsequent tiller growth in each treatment group's top model. The y-axes show the regression residuals when all effects except the effect of temperature (on the x-axis) are accounted for. Error bars represent standard deviations. All temperatures effects on final tiller counts were significantly negative: (a) Peak fire temperature 1 cm below the surface; (b) Average air temperature on the day of cutting; (c) The product of tiller number on the day of treatment and peak fire temperature at 2 cm depth; (d) Soil temperature on the day of cutting.

microsites more narrowly or that the species is better able to compensate for differences in microsite quality.

Mesic grasslands worldwide owe their existence to the forces of grazing, fire and drought, and it has long been assumed that adaptations that protect grasses from grazing also protect them from fire and drought (Anderson 1990;

Koerner & Collins 2014). However, recent comparisons between North American and South African grasslands have revealed that responses to fire can differ among grass species with different biogeographic origins due to differences in the types of adaptations to grassland conditions (Kirkman et al. 2014). The mesic grasslands of Eurasia

where *B. ischaemum* originates had been used for millennia by pastoralists who used fire to deter woody plant establishment (Pyne 1997). However, the abundance of weedy grasses and forbs in these grasslands also suggests selection for tolerance to cropping and trampling by hoofed grazers (Woodward 2008). It is likely that grazing by domestic animals in Eurasia was more intense than grazing by wild ungulates in North America (Mack & Thompson 1982; D'Antonio & Vitousek 1992) and that this might have reduced the fuel quantity and the intensity of grassland fires (Simmons et al. 2007). From this perspective, one might expect a scarcity of adaptations to increase tolerance to hot-burning fires in the old world grasses, including more deeply buried growing points.

The experiment also documented a higher sensitivity to drought conditions in *B. ischaemum*. While we cannot say whether the invasive species' response to fire was magnified by the subsequent drought conditions, since we lacked a no-drought control, the data certainly indicate a compounded effect of fire and drought, which was almost entirely lacking in *S. scoparium*.

Fire followed by an extended drought period may have more negative effects on species with opportunistic growth dynamics and a habit of trying to recover losses quickly (Wolkovich & Cleland 2014). Thus, while we can expect that invasive Old World grasses are generally well adapted to grazing, fire and drought, we should not expect them to have exactly the same tolerances as native species to all levels or combinations of stress factors a native ecosystem normally produces.

Conclusion

In the arid southwest of North America and in Australia, invasive grasses are primarily known for fanning wildfires to the detriment of native ecosystems (Knapp 1996; Rossiter et al. 2003; Olsson et al. 2012; Schlesinger et al. 2013). Perennial grasses generally recover well after fire and, where they invade ecosystems of historically low fire frequency, they can cause irreversible ecosystem degradation (Brooks et al. 2004). In contrast, fire is a natural component of mesic grasslands (Stocker & Hupp 2008), as is occasional severe drought (Hoerling et al. 2013), and the two may well have coincided historically (Higgins 1984; Anderson 1990). With the advent of livestock grazing, a switch to fire exclusion or controlled burning in winter may have created unprecedented opportunities for exotic grasses with higher grazing tolerance and lower fire tolerance. It is unknown whether there exists a trade-off between grazing and fire tolerance, but this experiment highlighted that one should not assume *a priori* that the same plant functional types from similar biomes with different biogeographic origins have the same tolerance to all

combinations of drought, fire and grazing (Polley et al. 2013). Focusing future research on identifying selective responses to multiple rather than single stressors, and extreme rather than ordinary conditions, may be a promising way forward for the control of exotic, invasive C_4 species in native C_4 grasslands. We also need better mechanistic understanding of the way in which trait variation within plant functional types and across biogeographic regions affects responses to drought, fire and grazing. Management strategies should be sensitive to opportunities arising from a combination of stress factors, even though it may seem that 'worst-case scenarios', such as fire at a time of severe drought, should be a thing to be avoided. While a practice of drought burning would be difficult if not impossible to implement in urbanized areas because of the perceived or real threat to property, it has been possible to obtain exemptions to burn bans for well-considered prescribed fire management in rural grasslands. The primary concern of fire marshals is generally not the burning of grasslands, which poses little threat if well managed, but the burning of slash piles, which can become unmanageable and cause dangerous crown fires.

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