

CAN PRESCRIBED FIRE BE USED TO MANAGE A C₄ INVASIVE GRASS IN A C₄
GRASSLAND?

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Can prescribed fire be used to manage a C₄ invasive grass in a C₄ grassland?

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CHAPTER I.

Introduction

Worldwide, invasive grasses have greatly decreased grassland species diversity (Gabbard and Fowler 2007; Grace et al. 2001; Harmony et al. 2004; Milton 2004) and proved extremely difficult to control (D'Antonio et al. 2011; Ditomaso et al. 2006; Manea et al. 2011; Milton 2004; Schmidt et al. 2008). This is particularly true for introduced non-indigenous C₄ grasses in C₄ grasslands and rangelands. Not only are these grasses functionally similar to the resident species, they are also tolerant to heavy grazing and drought (Gabbard and Fowler 2007; Gould 1975). Functional similarity implies that species share major morphological, physiological, and phenotypic traits (Smith et al. 1997; Woodward and Cramer 1996), allowing the invasive species to exert intense competition on native species (Corbin and D'Antonio 2010).

Reversing this trend is a particularly challenging restoration dilemma because it is unclear how invasive grasses can be targeted for eradication without causing equal or greater damage to the functionally similar native species (Corbin and D'Antonio 2010; Lesica and Martin 2003; Reed et al. 2005; Simmons et al. 2007). The aim of this research was to explore if, despite their overall similarities, more subtle differences between invasive and native C₄ species, based on differences in temporal niches, can be used to selectively target invasive C₄ grasses in C₄ grasslands. Such differences might include variation in developmental timing (Sugihara et al. 2006), including the initiation of

vegetative growth, flowering and senescence, which could make species differentially vulnerable to the timing of disturbances such as fire (Ansley and Castellano 2007a).

Both native and non-native perennial C_4 grasses can be expected to be fire tolerant, since the sub-tropical grasslands where many C_4 species evolved often burn in summer due to lightning strike (Ansley et al. 2008; Higgins 1984; Howe 1994a; Pyke et al. 2010; Ripley et al. 2010). Many perennial bunch grasses resprout readily from meristems that survive inside protected bunches or underground (Ditomaso et al. 2006; Olson and Richards 1988; Pyke et al. 2010; Raunkiaer 1934). However, the timing of fire with respect to the physiological status of a species, or the severity of fire, may produce variability in species response to recovery following fire. This may explain species persistence and diversity in grasslands (Howe 1994a). For the same reason, carefully scheduled prescribed burns may provide opportunities for selectively suppressing invasive species.

Grass species are most vulnerable to the removal of above-ground biomass when nitrogen and carbohydrate content of roots are at a minimum (Menke and Trlica 1981; Nofal et al. 2004). Storage substrates are at a minimum during the early stage of vegetative growth and, to a lesser extent, during the early reproductive phase (Bond and Midgley 2001; Gagnon et al. 2010; McConell and Garrison 1966; Pate et al. 1990; Waite and Boyd 1953). Thus, fire should be most devastating to those species that are in an early vegetative or flowering state.

The interaction between fire and drought stress also plays a role in determining the capacity to recover from a fire (Rew and Johnson 2010). Both pre- and post-burn precipitation are considered important factors to plant growth in C_4 grasslands (Fuhlendor

and Smeins 1997; Limb et al. 2011; Teague et al. 2008; Wright 1974). To the extent that species differ in access to soil water or drought tolerance, they could experience drought stress at different times or to different degrees and respond differentially to the combination of drought stress and fire, for example, in terms of meristem survivorship and carbon available for meristem growth.

While differences in phenological and physiological states are likely sources for species-specific fire effects, they are by no means the only plausible causes. Fire characteristics, too, have been found to play a role in how plants respond to fire (Ansley et al. 2008; Ewing and Engle 1998; Keeley 2009; Twidwell et al. 2009). The combination of fuel quantity, fuel moisture, soil moisture, and microclimate generate different fire characteristics, for example, different peak temperatures and residence times (Keeley 2009; Sugihara et al. 2006; Wright and Bailey 1982). Species differing in their tolerance to these physical conditions, and interactions with the location and flammability of live tissues may also contribute to the specificity of fire effects on individual plants (Pyke et al. 2010; Wright 1971).

Considering the three mechanisms through which species-specific fire effects are hypothesized to be generated (i.e., differences in phenological status, water stress or fire characteristics) we would expect that the discriminating potential of fire should be strongest at a time when species express their physiological differences most strongly, in other words, during the growing season. By the same token, we would expect much weaker capacity for discrimination during dormant periods, either in winter or summer for C₄ grasses, when all species are in identical and least vulnerable states. Indeed, the common practice of prescribed burning in winter, during the peak of dormant season for

C₄ grasses, could be responsible for the lack of success controlling invasive C₄ grasses by fire (Gabbard and Fowler 2007).

There has been a substantial amount of research conducted on the effects of fire set at different times of the year in C₄ grasslands (Ansley et al. 2006; Engle and Bidwell 2001; Howe 1994b). Most of these studies have been framed as a comparison between dormant-season and growing-season fire effects on C₄ perennial grasses. However, while the state of dormancy can be considered a well-defined physiological state, the state of growth cannot, as it can include any plant condition between the most vulnerable state of early vegetative growth and the least vulnerable state of late senescence. In addition, while some species may follow a mostly fixed and synchronous developmental schedule, others may continually initiate and mature new tillers, depending on environmental favorability. If physiological and phenological status is indeed one of the main drivers of species response to fire, the exact status of species' at burn time requires more careful consideration when developing techniques for C₄ grassland management. Scheduling burns with respect to calendar month are expected to be ineffective as growth and developmental dynamics depend strongly on water availability, which typically varies greatly from year to year in semi-arid regions.

Many C₄ perennial grasslands in Texas have been invaded by KR bluestem (*Bothriochloa ischaemum*). As a perennial bunch grass with C₄ photosynthesis, KR bluestem is functionally similar to the native grassland species in this ecosystem. In many areas, it has all but replaced the species that was previously among the most dominant in the community, little bluestem (*Schizachyrium scoparium*). In my experiment, I selected

these two species, because of their similarity in habitat preference and potential for dominance, to test if the exact timing of fire can be used to select against KR bluestem.

Specifically, I tested the hypothesis that plant condition at burn time, represented by a suite of variables, dictates post-fire recovery. Post-fire recovery was assessed at two time periods, shortly after each burn, when tillers had just begun to resprout, and in the first spring after the last burn, when all burn trials were collectively evaluated at the same time to assess longer-term effects of burning on different dates. This last data set also included a control to evaluate treatment effects relative to “doing nothing.”

Post-fire recovery not only depends on the extent of damage, but also on post-fire environmental conditions, for example, a mild burn followed by dry weather may still result in poor regrowth. In order to separate the damaging effects of fire from those of post-fire growth conditions, a clipping treatment was also included in the design. Clip and burn treatments were conducted on the same days.

I conducted six burn trials over the course of one year, each time recording multiple environmental and biotic factors, in an effort to identify key drivers and covariates associated with the magnitude of the burn effect on the two species, including precipitation, soil temperature (at three depths) during the burn, phenological status, water potential, biomass, and tiller count before a burn.

My specific objective was to address three questions: 1) Do fire and clipping effects on regrowth differ between fire application times and species, and if so, by how much? 2) Do treatment effects persist into the first spring after the last treatment? 3) Can physical and physiological factors be identified (to replace date) that are repeatedly

associated with the greatest degree of burn or clip damage, and do these factors differ between species?

Methods

Species, Study Site, and Climate

The genus *Bothriochloa* belongs to a group commonly described as old world bluestems (OWB), which contains multiple species classified as invasive in the U.S. KR bluestem is an invasive C₄ perennial grass naturalized in over 17 states in the U.S.A., including Texas. Little bluestem is a C₄ perennial grass native to 48 states in the U.S.A. It is present in all eco-regions of Texas (Loflin and Loflin 2006). The two species are functionally similar C₄ perennial grasses and are commonly found growing side by side.

The study was conducted at Freeman Ranch near San Marcos, Texas. Freeman Ranch is a 1700 hectare tract of land that lies within the Balcones Canyonlands subregion of the eastern Edwards Plateau of central Texas. The property is located in southeastern Hays County, Texas (29 56' N; 98 W), midway between the cities of San Marcos and Wimberley. The average yearly precipitation for San Marcos is 864 mm (30 years, San Marcos Municipal Airport). The specific study site lies within the upland-Rumple-Comfort soil type which is comprised of relatively shallow rocky soils that have developed over limestone (Carson 2000). Mean monthly temperature and monthly precipitation during the study period (on-site weather station) are compared to the 30 year average in Figures 1 and 2 respectively.

Vegetation consists of Plateau live Oak (*Quercus virginiana* var. *fusiformis*) and Ashe juniper (*Juniperus ashei*), with honey mesquite (*Prosopis glandulosa*) and huisache

(*Acacia farnesiana*). The understory is composed chiefly of three native C₄ grasses, little bluestem, sideoats grama (*Bouteloua curtipendula*) and indiagrass (*Sorghastrum nutans*), in addition to KR bluestem, which is dominant.

Experimental design

The design was factorial and blocked within species, as species tended to be distributed in monospecific patches. In April 2011, I located 10 patches of about 30 m² area that contained a sufficiently high density of either KR bluestem or little bluestem and designated them as blocks, five per species. Within blocks, I located 39 suitable plots, circular areas of 0.16 m² that contained at least one bunch of the target species ≥ 2 cm wide at the base and at least 3 m away from any neighboring plot. These plots were flagged and numbered.

Treatments (clipped or burned), treatment date (6 dates between June 2011 and January 2012; Table 1) and one unclipped and unburned control were randomly assigned in triplicates to flagged plots in each block at the start of the experiment.

Pre-burn sampling

On the morning of each treatment date, leaf blade pre-dawn water potentials were taken on one plant per block, using a Scholander pressure chamber (PMS Instruments, Albany, OR, USA). After cutting, leaf blades were immediately sealed in plastic bags to prevent water loss and measured not longer than one hour after collection.

Beginning at sunrise, all biomass above 3.5 cm in plots slated for clipping or burning on that day was cut and stored individually in paper bags for later analysis.

Burned plots were also clipped to determine plant state at burn time, and to control the amount of fuel between plots and burn times. Biomass analysis was conducted on the day(s) immediately following the burn and included 1) separating and discarding the biomass of other than the target species, 2) separating litter from live, green biomass, and 3) separating live tillers into four phenological stages. A phenological score of 1 was assigned to tillers in a vegetative /pre-elongation phase, composed of tillers with a central culm ≤ 0.5 cm length. A score of 2 was given to tillers in the elongation stage with central culm > 0.5 cm length, but without near-mature flowers encased in a leaf sheath or exposed. A score of 3 was assigned to tillers in the flowering stage, including flowers still encased in a leaf sheath or exposed or in the seed filling stage. A score of 4 was assigned to tillers in the post-reproductive phase with seed maturation completed. Tillers in each category were counted and dried at 70° C for four days to obtain stable dry weights. Average phenological indices per plot were calculated by summing over the product of tiller stage (1-4) and tiller numbers in the respective stage class, and then dividing by total live tiller number (Moore et al. 1991).

Burn procedures and measurements

Burns were conducted in a steel barrel to contain fire. This made it safe and legal to conduct burn trials at any time of year, even during burn bans. The barrel was 1.22 m tall with an open base area of 0.16 m² and a removable cap on top (Figure 3). To further improve fire safety, grass surrounding the burn plots was mowed and raked to create a 0.5 – 1 m fire break. Five persons always attended a burn trial equipped with three backpack water sprayers.

Before burning, four high-temperature thermocouples (HH309A, Omega Corporation, Stamford, CT, USA) were arranged in the burn plot and held in place by barbed steel staples; one on the open soil surface, one inside the bunch near the soil surface, one at 1 cm soil depth and one at 2 cm soil depth. Pilot experiments had shown that temperatures attenuated very rapidly with depth, making it less important to observe soil temperatures any lower than at 2 cm depth. Temperatures were recorded in 2 sec intervals over the 2-4 minute burn time.

Since most above-ground biomass was removed before the burn, a standard amount of fuel (120 g of dried grass stems and leaves) was added to the burn barrel. After ignition, the barrel was ventilated with an electric leaf blower through a whole cut out about 10 cm above ground area. While this procedure introduced some artificiality, it did limit variability in fire intensity between plots and burn dates.

Burns lasted for two minutes on average. After the flames had died down, the leaf blower was turned off and the burn barrel was lifted off. Temperatures continued to be recorded until the surface temperature had dropped below 100° C. Plots were then sprinkled with water to extinguish ambers.

Post-treatment sampling

Post-fire and post-clipping growth were measured three times following each burn trial; immediately after the first green tillers reappeared after each treatment and again several weeks later to determine if more tillers had emerged after the first count. First and second tiller counts were very close, but for the analysis of the post-treatment effects, the second

tiller count was used. Tillers were counted one last time on May 2012 for all burn and clip plots simultaneously (Table 1).

Statistical analysis

Effects of date, treatment, and species on tiller numbers were tested using a general linear model with a negative binomial distribution (Negative Binomial Distribution). For the analysis of the final count data, tiller counts in the non-manipulated control were also included.

To hone in on the immediate effect of fire on plant recovery, I calculated a variable that I called “meristem survivorship” (β) by dividing the post-treatment tiller count T_1^b of burn plots by the tiller count of clipped plots T_1^c , each summed across blocks:

$$\beta = T_1^b/T_1^c \quad (\text{eq. 1})$$

This ratio reflects meristem survivorship if one assumes that a) the number of viable meristems were equal on average before treatment in burned and clipped plots, b) clipping did not change the number of viable meristems, and c) all, or at least a similar proportion of surviving viable meristems sprouted after both the burn and clip treatments.

The variable β , while likely an inaccurate measure of true meristem survivorship, nevertheless has the advantage of representing fire effects on plant vigor independently of the confounding effects of pre- and post-treatment environment and bunch size differences between species. For statistical analysis, it was log transformed and examined by ANOVA. I also used ANOVA to examine treatment and date effects on the log ratios of tiller counts in burned or clipped plots over control plot counts for the spring data.

I performed a model selection analysis to determine which factors, if any, best predicted variability in the spring tiller count. The four species and treatment combinations were analyzed independently and the best model was selected using the Akaike Information Criterion (AIC). Numerous models were constructed with different numbers and combinations of predictor variables representing plant morphological and physiological state at the time of treatment, environmental conditions before and after treatment, and fire intensity. Models that had more than 90 predictors (main effects and their interactions) were excluded because the number of predictors would have exceeded sample size. Some of the predictors varied at the plot level (tiller count, average green tiller weight, phenological index and peak fire temperatures) while others varied at the block level (water potential) or date (precipitation and mean air temperature). The intercept-only and the date-and-intercept-only models were also analyzed to determine if state-based predictive models performed any better. All predictor variables used in this analysis are listed in Table 2, along with their ranges, means and coefficients of variation (Table 3).

For procedures of model selection and comparison, I followed the recommendations of Johnson and Omland (2004). Model evaluation was based on the small sample size correction value (AIC_c). The top model was determined as the one that minimized this value ($AIC_{c,min}$). To determine a degree of support for each model, a $\Delta AIC_{c,i}$ value was determined by subtracting from each model $AIC_{c,i}$ the $AIC_{c,min}$. Models for which the $\Delta AIC_{c,i} \leq 2$ were considered to have substantial support. The relative likelihood of a competing model compared to the top model was estimated by dividing the Akaike weight (w) of the top model by the weight of the competing model. The

predictive power of individual coefficients was judged on the basis of their confidence intervals lying outside zero.

Results

Initial treatment response

Post-burn tiller numbers depended significantly on Date, Species and Treatment (Table 4, Figure 4). Overall, little bluestem had significantly more tillers than KR bluestem. Tiller numbers for different burn dates also varied significantly, but without a readily apparent pattern through time. The lowest tiller numbers were counted after the June and November burn dates.

There were also significant interactions, the strongest of which was between Species and Treatment, indicating comparatively greater sensitivity to burning compared to cutting in KR bluestem, which was lacking in little bluestem. The significant Date*Species interaction indicated that species responded differentially to the date of treatment, but Date*Treatment interactions were not significant. Thus, burn and clip treatments had largely consistent effects across burn dates.

Estimated meristem survivorship after fire was significantly different for the two species, but did not differ between burn dates, nor was there a Date*Species interaction (Table 5, Figure 5). Survivorship was not different from unity for little bluestem, indicating that for this species, burning and clipping had equivalent effects on estimated meristem survivorship values. Meristem survivorship was significantly less than 1 for KR bluestem. Across all dates, meristem survivorship for KR bluestem was 32%, i.e. burn plots had only about 1/3 of the post-treatment tiller numbers than clipped plots.

Treatment response in the following spring

Final tiller counts also depended on Treatment, Treatment Date and Species and main effects were qualitatively consistent with the analysis on post-treatment counts (Table 6). As for the interactions, the Species*Treatment interaction was still significant, indicating that the KR bluestem's more negative response to burning lasted into the following spring. However, the Date*Species interaction was no longer significant, suggesting that short term environmental effects had produced them in the post-treatment counts that did not carry over into spring.

When treatment effects were analyzed independently for each species and treatment, tiller numbers for KR bluestem were significantly different between treatment dates in the burn treatment ($p = 0.011$), but not in the clip treatment ($p = 0.575$). For little bluestem, tiller numbers were significantly affected by treatment date, for both burned ($p = 0.024$) and clipped plots ($p = 0.02$).

All burn dates for KR bluestem except for the most recent January burn resulted in a statistically significant reduction in tiller numbers compared to the control (Figure 6; Table 7). The fewest tillers relative to the control, 16%, were observed in response to the earliest burn date in June. By contrast, the number of KR bluestem tillers in all clip treatments, regardless of the date of clipping, were statistically indistinguishable from the control, indicating that clipping had no lasting negative effect on tiller numbers. For little bluestem, only the June clip and burn treatments resulted in a statistically significant reduction in tiller numbers compared to the control.

To elucidate the effect of the burn and clip treatments independently of additional environmental effects on final tiller numbers, I also analyzed the log ratio of final tiller counts in treatment plots over those in control plots separately for burn and clip treatments (Figure 7). There was a significant species effect in burned plots ($p < .013$), but not in clipped plots ($p = 0.311$), showing once again that KR bluestem responded more negatively than little bluestem to burning. Date*Species effects were however not significant in either treatment (for burning: $p = 0.997$; clipping: $p = 0.44$), reinforcing what I found in the previous analysis, that date effects were consistent between species.

Lastly, comparing tiller numbers in non-manipulated control plots between 6 June 2011 and 26 May 2012, I found that KR bluestem tiller numbers significantly declined from 130 to 56 tillers per plot ($p = 0.024$). Tiller numbers for little bluestem declined from 94 to 72 tillers per plot, but was not statistically significant ($p = 0.461$).

Predicting responses

For KR bluestem in plots that were burned, the top model contained the predictors initial tiller count, biomass per tiller, and the interaction between initial tiller count and biomass per tiller (Table 8). A significantly positive effect was produced by the initial tiller count and significantly negative effects by biomass per tiller and by the interaction between initial tiller count and biomass per tiller (Table 9; Figures 8 and 9). Thus, plots with a higher initial tiller count had more tillers the following spring, indicating that larger or more vigorous bunches recovered more tillers than smaller bunches. However, plots that had larger tillers, especially when there were more of them, tended to have fewer tillers in spring, thus reversing the effect of tiller number. The top ranked model was 2.8 times

more likely to explain final count tillers than the closest competing model and over 26,000,000 times more likely to explain final count tillers than the date model.

The best model for predicting the spring tiller count for KR bluestem in clipped plots contained the predictors initial tiller count, phenological index, and the interaction between initial tiller count and phenological index (Table 8). As before, a significantly positive effect was produced by the initial tiller count. Even though the best model contained the phenological index term, as a predictor, I considered its effect non-significant, since its confidence interval overlapped with zero. A significantly negative effect was produced by the product of initial tiller count and phenological index (Table 9; Figure 10), suggesting that the loss of more tillers with more advanced phenology negatively affected growth. The top model was 2.9 times better at predicting tiller numbers than the strongest competing model and 46,000 times better than the date model.

The best model for little bluestem burn plots contained the predictors initial tiller count and mean temperature in the month after each burn (Table 8). As for KR bluestem, a significantly positive effect was produced by initial tiller count. A significantly negative effect was produced by mean environmental temperature one month after burn date (Table 9; Figure 11). The top model was 7.1 times more likely to predict spring tiller numbers than the strongest competing model and 23,190 times more likely than the date model.

The top model for little bluestem clipped plots was identical to that for burned plots (Table 8, Figure 12), consistent with the lack of treatment differentiation between clipping and burning for this species. The top model was 109 times more likely to predict

tiller numbers than the strongest competing model and 4,909 more likely than the date model.

Discussion

To control an invasive grass in a community of functionally similar species by fire, it is paramount that fire has a more damaging effect on the invasive than on the native species. I designed an experiment to test if the physiological and ecological state of a community, as affected by season and environment, affected the selectivity of fire damage in significant ways. In the experiment, fire had a consistently more damaging effect, both in the short- and longer-term, on the invasive species KR bluestem than on its main competitor, little bluestem, and a more damaging effect than clipping. The most likely explanation is that fire killed a substantial number of meristems in KR bluestem, but not in little bluestem.

While the timing of treatment did affect the severity of the damage, the response of the two species to the date of treatment varied largely in concert (Figures 5 & 8). In addition, date effects on clipped and burned plots were largely the same. Taken together this suggests that a) the effect of treatment date on recovery growth was chiefly mediated by the loss of biomass, rather than by fire itself, and b) environmental effects made the two species similarly vulnerable to biomass loss. Both species were most negatively affected by the June burn, and since KR bluestem was more negatively affected by burning overall, the June burn date can be identified as the one with the most favorable outcome in terms of KR bluestem control. Both species were least negatively affected by the January burn. These results corroborate earlier findings that C₄ grasses are most damaged by fire during their growing season (Engle and Bidwell 2001; Simmons et al.

2007; Trollope 1980). However, I did not find support for the hypothesis that species vary to some extent independently in the amount of damage taken when burned at different times during the growing season.

These results must be interpreted in the context of the very unusual environmental conditions that prevailed in the experimental year. According to NOAA, central Texas was in a state of increasingly severe drought between June and September 2011. This exceptionally strong environmental driver may have given species little opportunity to express differences in their physiological or phenological dynamics, which in other experiments was more evident (Knapp 1985). In my experiment, due to the drought, both species remained in an early vegetative state until November, indicating a level a physiological stress that prohibited tiller maturation.

KR bluestem proved not only more sensitive to fire but also to drought, compared to little bluestem, as indicated by the changes in tiller numbers in control plots between 2011 and 2012. The drought alone reduced tiller numbers to 43% from the previous year, and the June burn treatment reduced tiller numbers to an additional 16% relative to the control in 2012. Thus, the combined reduction for KR bluestem was to 7% from the tiller numbers found at the site in the previous year, compared to a reduction to only 48% for little bluestem. Clearly, the combination of the early burn treatment, followed by persistent drought conditions had quite a devastating effect on KR bluestem, but only a moderately negative effect on the native species.

Why was KR bluestem more vulnerable to fire than little bluestem?

Bunch grasses typically vary in the amount of fire damage they take (Ansley and Castellano 2007a). In other studies this has been related to the position of the meristems relative to the temperature gradients that fire creates (Choczynska and Johnson 2009). Underground meristem banks provide particularly good insulation from heat damage, since even a thin soil layer acts as a strong heat insulator (Pyke et al. 2010).

Casual observation suggested the existence of underground rhizomes in little bluestem at our field site, but I found no equivalent structures in KR bluestem. New tillers appeared from the base of the bunch, above the soil surface. If this is where the meristems are located, they would be directly exposed to peak temperatures.

Despite the standardized fuel load, peak fire temperatures inside little bluestem bunches were on average 100°C cooler than inside KR bunches (Table 3). This is likely related to a difference in bunch structure. Little bluestem forms densely packed bunches that could provide heat insulation for axillary meristems located close to ground level inside them. By contrast, KR bluestem's bunches are much less packed, giving little protection to meristems at its core.

My study cannot answer if other fire regimes, including both hotter and colder fires would have the same discriminating effects on the two species, since I held fuel load and fuel water content constant between plots and burn times. In fact, the absence of stronger date effects, as observed in similar studies working with natural fuel (Simmons et al. 2007) may in part be explained by this experimental design choice. Mean surface fire temperatures (200-450 °C) were within the range reported for natural grassland fires

(Fidelis et al. 2010), but residence times were likely higher, because flames were confined by the burn barrel.

More work needs to be done to understand the potential of controlling physical fire characteristics for invasive grass control, but my results suggest a new avenue for invasive species control, particularly in cases when the invasive species has a morphological disadvantage in coping with fire intensity.

The prediction of fire damage on the basis of physiological and phenological state

The use of fire in invasive grass control would benefit greatly from the ability to predict the degree of fire damage to native and invasive species before a burn is conducted. In this way, burns that would be ineffective for control could simply be avoided.

In my experiment, predictability was mixed; it was higher for KR bluestem and quite low for little bluestem, but this was to a large extent due to the lack of variability in the phenological state of little bluestem, which remained in an early vegetative state.

In both species, as well as for burn and clip plots, the initial tiller count was positively correlated with the final tiller count, which shows that larger or more vigorous bunches have the capacity to produce more tillers after a burn, as might be expected. Beyond this factor, the two species, as well as the clip and burn treatment separated in terms of predictor variables.

For KR bluestem in the burn treatment, plots that contained larger tillers, and more, larger tillers (factor IT*B in Table 8) had decreased capacity to recover from fire. This indicates that a recent investment in vegetative tiller growth compromises a plant's capacity to recover from fire, in agreement with the hypothesis that below-ground

resource storage is minimized in early vegetative growth and that such storage is needed to fuel recovery growth (Bond and Midgley 2001; Gagnon et al. 2010; McConell and Garrison 1966; Pate et al. 1990; Waite and Boyd 1953). For reasons unknown, in the clip treatment, phenological index, rather than biomass, conveyed the negative effect. However, this difference could be spurious because, in general, there was less variation to explain and the best model was weaker.

By contrast, the factor that affected little bluestem's capacity to recover from fire was related to post-fire environmental conditions, specifically temperature. Higher average temperature one month after the burn or clip treatment had a significantly negative effect on recovery growth, which led to burns conducted in June and July having the highest fire damage.

It is however conspicuous that, despite the different predictors for the two species, the June and July burns had the most negative effects on both species. This points to the simpler explanation that burning in the early phase of a long summer drought were most detrimental to both species. This points to limitations of the correlation analysis for identifying factors that control burn damage. With only six burns, all conducted during the same, unusual year, it is quite likely that one factor of the many that were measured, varied in conjunction with the response variable, but this does not guarantee that the true or the only driver of growth response was correctly identified. Ideally, this experiment should be repeated over several years and involve tens of burn times to cover a representative range of environmental conditions and phenological states.

Interactions between treatment and drought

It is paradoxical that plants with the most time to recover (i.e., those that were clipped or burned in June 2011) had in fact fewer tillers in the following spring than plants with several fewer months to recover. This suggests that biomass loss followed by severe drought is far more devastating to C₄ plants than, for example, drought followed by biomass loss. I observed that many of the tillers produced after the June and July burns did not survive the summer drought. Thus, plants were not able to capitalize on their investment in post-treatment tiller production and instead suffered a second round of biomass loss. Adding to the poor performance of the post-treatment tiller cohort, the lack of a protective litter layer would have increased their stress level. By contrast, tillers in the control plots may have had a better chance to capture resources in the early stages of the drought and time to remobilize resources below ground as the drought intensified, thereby minimizing resources losses.

Management implications

- Fire conditions producing intense heat at the soil surface with sufficiently high residence times can kill a high fraction of KR bluestem meristems, while being far less destructive to meristems of little bluestem.
- Prescribed burns taking place in the winter dormant-season are least effective for controlling KR bluestem.
- Burns scheduled in the early stages of a summer drought will produce the most dramatic reduction in KR bluestem tiller density in the following year, by

compounding low drought tolerance with low fire tolerance, and this combination will have a far less negative effect on little bluestem.

- KR bluestem is most vulnerable to biomass loss when bunches are in a vegetative phase with large tillers.

Table 1. Dates of treatments and tiller counts.

Burn	Date of treatment (and initial count)	Post-burn tiller count 1	Post-burn tiller count 2	Final count
1	June 8 2011	July 20 2011	Aug 19 2011	May 23 2012
2	July 8 2011	Aug 19 2011	Oct 16 2011	May 23 2012
3	Sep 24 2011	Oct 16 2011	Nov 6 2011	May 23 2012
4	Oct 17 2011	Nov 6 2011	Nov 22 2011	May 23 2012
5	Nov 6 2011	Nov 22 2011	Dec 6 2011	May 23 2012
6	Jan 10 2012	Feb 10 2012	Feb 27 2012	May 23 2012

Table 2. Covariates used in model selection analysis.

Plant condition at treatment date	- Biomass per tiller, phenological index, initial tiller count, water potential
Environmental factors	- Precipitation two months before treatment, average temperature two months before treatment, precipitation one month after treatment, average temperature one month after treatment, precipitation three months after treatment, average temperature three months after treatment
Fire effects	- Peak average fire temperature at the surface outside the bunch, inside the bunch, 1 cm below soil surface, and 2cm below soil surface

Table 3. Range, mean, and coefficient of determination for each covariate analyzed in the model selection analysis.

		KR bluestem	Little bluestem
Initial Tiller Count (#)	Range	0 - 203	0 - 217
	Mean	64.6	57.1
	CV (%)	81.5	71.8
Biomass Per Tiller (grams)	Range	0 - 1.91	0 - 1.06
	Mean	0.1005	0.1621
	CV (%)	165.6	95
Green Biomass Weight (grams)	Range	0 - 26.9	0 - 42.4
	Mean	6.83	8.02
	CV (%)	102.8	83
Phenological Index (Index score)	Range	0 - 2.1	0 - 1.06
	Mean	1.26	0.96
	CV (%)	38.5	20.2
Fire Temp. Surface Outside Bunch (°C)	Range	45 - 1149	27 - 970
	Mean	340.2	280.8
	CV (%)	60	62.5
Fire Temp. inside Bunch (°C)	Range	19 - 669	18 - 660
	Mean	215.8	112.5
	CV (%)	86.8	112.6
Fire Temp. 1cm Below Soil Surface (°C)	Range	26 - 821	20 - 708
	Mean	107.5	104.8
	CV (%)	115.1	110.4
Fire Temp. 2cm Below Soil Surface (°C)	Range	18 - 554	18 - 401
	Mean	60.1	58.4
	CV (%)	104.6	91.9
Precipitation 2 Months Before Treatment (mm)	Range	5.6 - 177.1	5.6 - 177.1
	Mean	84.7	84.7
	CV (%)	65.4	65.4

Table 3. continued

Mean Temp. 2 Months Before Treatment (°C)	Range	8.9 - 28.8	8.9 - 28.8
	Mean	22.06	22.06
	CV (%)	30.5	30.5
Precipitation 1 Month After Treatment (mm)	Range	0 - 104.2	0 - 104.2
	Mean	53.16	53.16
	CV (%)	90.2	90.2
Mean Temp. 1 Month After Treatment (°C)	Range	10.5 - 30.1	10.5 - 30.1
	Mean	20.2	20.2
	CV (%)	37.1	37.1

Table 4. General linear model (Negative Binomial Distribution) analysis of initial post-treatment tiller number.

Source	Wald's Chi Square	Df	P
Date	52.023	5	<0.001
Species	89.718	1	<0.001
Treatment	40.914	1	<0.001
Date*Species	12.468	5	0.029
Date*Treatment	3.882	5	0.567
Species*Treatment	39.679	1	<0.001
Date*Species*Treatment	7.564	5	0.182

Table 5. ANOVA of meristem survivorship (eq.1).

Source	Mean Square	Df	F	P
Intercept	3.608	1	29.360	<0.001
Species	4.098	1	33.344	<0.001
Date	0.152	5	1.233	0.308
Date*Species	0.120	5	0.979	0.441

Table 6. General Linear Model (NBD) of the final tiller count without no-burn, no-clip control.

Source	Wald's Chi Square	Df	P
Date	31.544	5	<0.001
Species	32.742	1	<0.001
Treatment	14.246	1	<0.001
Date*Species	2.551	5	0.769
Date*Treatment	2.249	5	0.814
Species*Treatment	17.489	1	<0.001
Date*Species*Treatment	4.282	5	0.510

Table 7. Final tiller counts for KR bluestem and little bluestem as % of control plots. The asterisk indicates a significant difference from 100%.

KR bluestem

Date	Burn	Clip
June	16 *	72
July	33*	67
September	41*	77
October	43*	91
November	45*	97
January	56	151

Little bluestem

Date	Burn	Clip
June	63*	46*
July	86	60
September	79	90
October	141	130
November	67	117
January	160	156

Table 8. Top five covariance models, intercept-only model and intercept-date-only model, if not already included in the top five models for the prediction of final tiller count on the basis of Akaike's Information Criterion. All models were General Linear Models (Negative Binomial Distribution) with any combination (main effect and interaction terms) of covariates from Table 2. All models include the intercept coefficient. The AIC_c for small sample sizes was used. The best model in each set is shown in bold. IT = initial tiller count on treatment date; P = phenological index on treatment date; B = average biomass per tiller on treatment date; F = peak average fire temperatures 2 cm below soil surface; TA = mean environmental temperature one month after treatment; PB = total precipitation one month before treatment; PA = total precipitation one month after treatment date.

Model	AIC_c	ΔAIC	AIC_c weight	w_i/w_{top}
<i>KR bluestem burn</i>				
IT + B + IT*B	716.945	0	0.736478	1
IT + B + TA +IT*B	719.026	2.081	0.260181	2.8
IT + P + IT*P	729.451	12.506	0.001417	519.6
B	733.921	16.976	0.000152	4856.2
Intercept	734.504	17.559	0.000113	6499.6
Date	751.097	34.152	2.83E-08	26062290
<i>KR bluestem clip</i>				
IT + P + IT*P	870.821	0	0.46588911	1
GB	872.974	2.153	0.15876858	2.9
P	873.917	3.096	0.09908199	4.7
IT + B + IT*B	874.007	3.186	0.09472213	4.9
B + P	875.875	5.054	0.03722377	12.5
Intercept	887.677	16.677	0.00010187	4573.3
Date	892.3	21.479	1.0097E-05	46143
<i>Little bluestem burn</i>				
IT + TA	921.423	0	0.83109997	1
IT + F + IT*F	925.337	3.914	0.11741916	7.1
GB	928.159	6.736	0.02863845	29.0
IT + B	929.127	7.704	0.01765025	47.1
IT	931.593	10.17	0.00514358	161.6
Date	941.526	20.103	3.5838E-05	23190.6
Intercept	957.8	36.377	1.0483E-08	79280281
<i>Little bluestem clip</i>				
IT+TA	932.453	0	0.978642	1
TA	941.847	9.394	0.00892776	109.6
PA	942.816	10.363	0.00549955	177.95
PB	948.095	15.642	0.00039265	2492.4
Date	949.451	16.998	0.00019932	4909.9
Intercept	953.695	21.242	2.3877E-05	40986

Table 9. Parameter estimates for the top ranked models from Table 8. Except for the intercept, parameters with confidence intervals not overlapping zero are considered significant and are shown in bold.

Model	β	Std. Error	lower CI	Upper CI	
<i>KR bluestem burn</i>					
Intercept		3.151	0.1863	2.786	3.516
Initial tiller	0.01	0.0036	0.002	0.017	
Biomass per tiller	-4.044	1.5137	-7.011	-1.078	
Initial tiller*Biomass per tiller	-0.084	0.0312	-0.145	-0.022	
<i>KR bluestem clip</i>					
Intercept		4.113	0.3695	3.389	4.837
Initial tiller	0.029	0.0109	0.007	0.050	
Phenological index		-0.114	0.3104	-0.722	0.494
Initial tiller*Phenological index	-0.21	0.0076	-0.035	-0.006	
<i>Little bluestem burn</i>					
Intercept		4.680	0.3022	4.088	5.272
Initial tiller	0.010	0.0032	0.004	0.016	
Mean Temp. One Month After Treatment	-0.057	0.0160	-0.088	-0.026	
<i>Little bluestem clip</i>					
Intercept		5.294	0.3163	4.674	5.914
Initial Tiller	0.010	0.0031	0.004	0.016	
Mean Temp. One Month After Treatment	-0.85	0.0168	-0.118	-0.052	

Table 10. Range, mean, and coefficient of variation by month for initial tiller count and biomass per tiller for KR bluestem burn plots.

		Initial Tiller Count	Biomass Per Tiller
June	Range	51 - 190	0.07 - 0.3
	Mean	129.3	0.133
	CV (%)	37.3	24.8
July	Range	51 - 172	0.05 - 0.18
	Mean	122.5	0.123
	CV (%)	28.4	25.6
September	Range	0 - 11	0.0 - 0.48
	Mean	2.7	0.087
	CV (%)	130.9	154.6
October	Range	23 - 113	0.03 - 0.16
	Mean	69.9	0.0656
	CV (%)	45.7	25.2
November	Range	38 - 156	0.04 - 0.17
	Mean	90.2	0.081
	CV (%)	41.1	51.8
January	Range	1 - 30	0.0 - 0.02
	Mean	9.6	0.009
	CV (%)	77.8	42.5

Table 11. Range, mean, and coefficient of variation by month for initial tiller count (#) and phenological index (score) for KR bluestem clip plots.

		Initial Tiller Count	Phenological Index
June	Range	42-175	1.26-1.95
	Mean	93.1	1.63
	CV (%)	34.1	14.5
July	Range	48-203	1.35-1.76
	Mean	105.5	1.59
	CV (%)	36.8	9.7
September	Range	0-17	0-2.1
	Mean	4.2	0.98
	CV (%)	117.3	84.6
October	Range	22-130	1.04-1.91
	Mean	66.4	1.32
	CV (%)	55.1	13.4
November	Range	30-118	1-1.93
	Mean	66.9	1.4
	CV (%)	39.2	19.6
January	Range	0-39	0-1.17
	Mean	13.4	0.88
	CV (%)	94.5	41.8

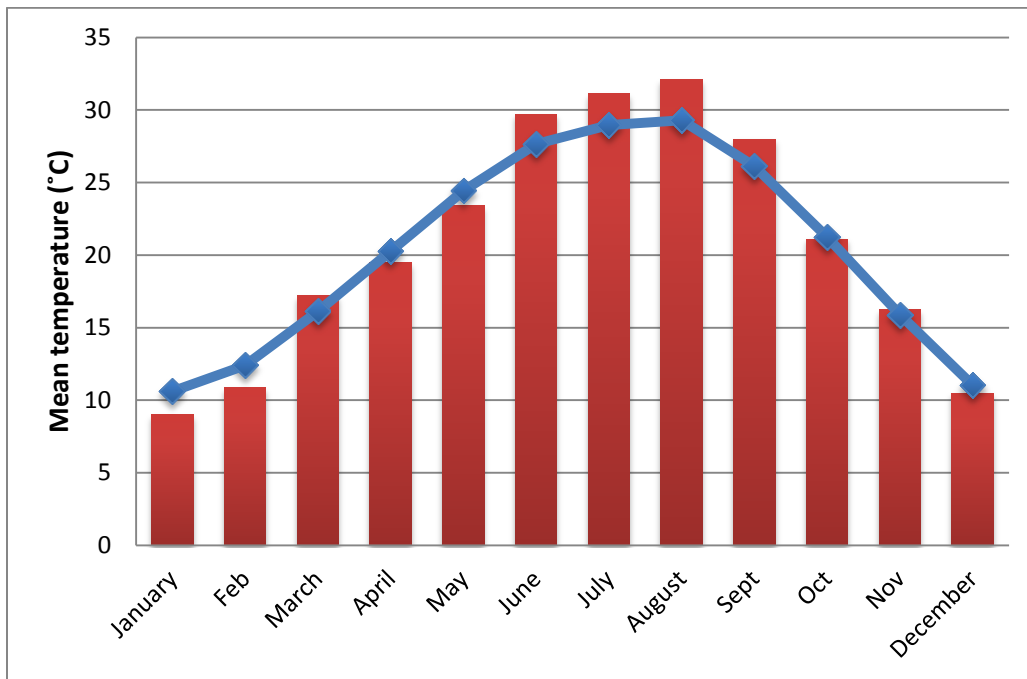


Figure 1. Mean monthly temperatures in 2011 (bars) compared with the 30 year average monthly mean (line) (NOAA 2012).

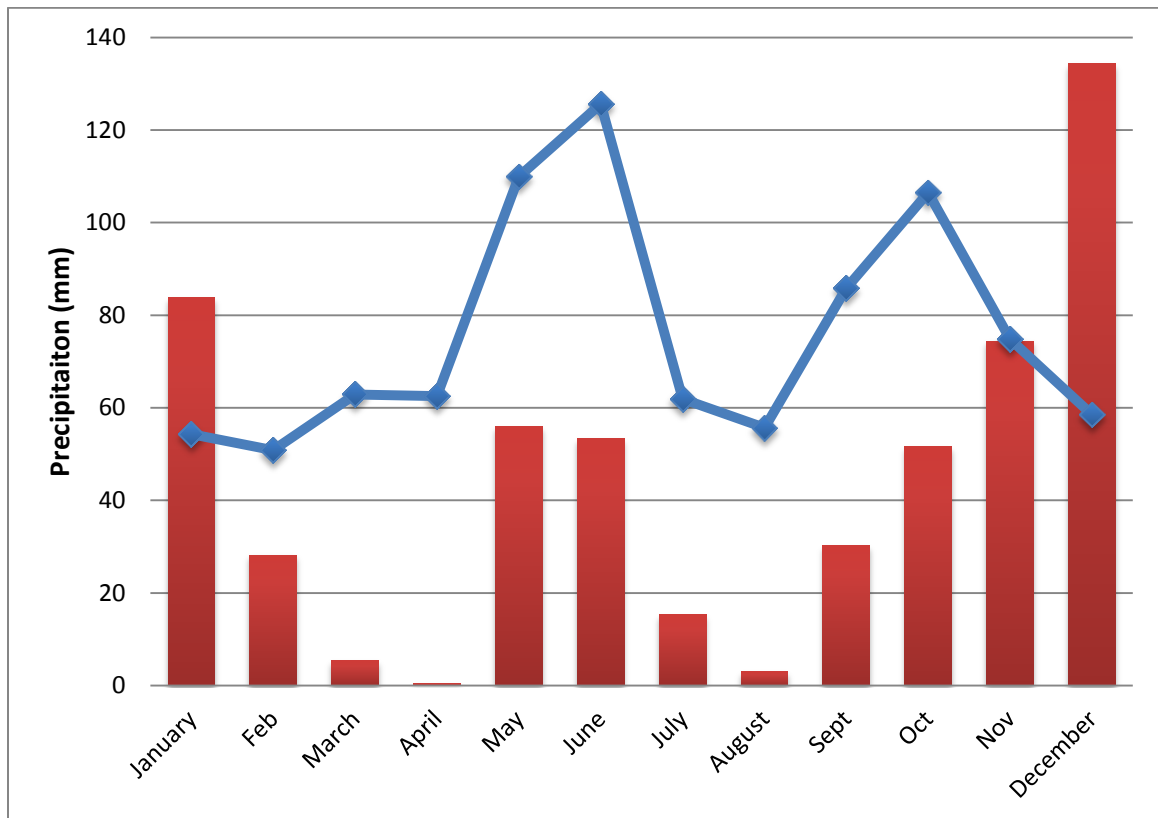


Figure 2. Monthly precipitation for 2011 (bars) compared with the 30 year average monthly precipitation (line) (NOAA 2012).



Figure 3. Burn barrel in action.

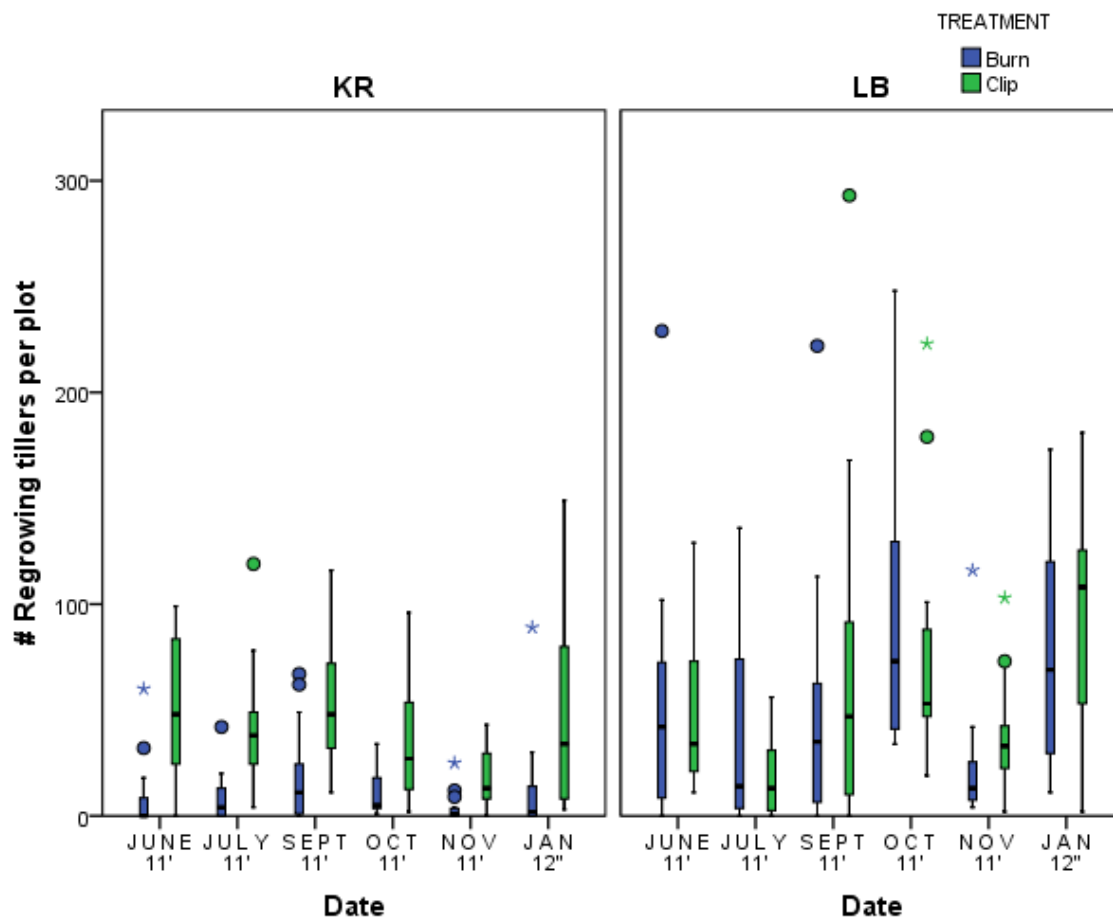


Figure 4. Boxplots for initial tiller numbers for burn (blue) and clip (green) treatments, recorded 4-8 weeks after treatments.

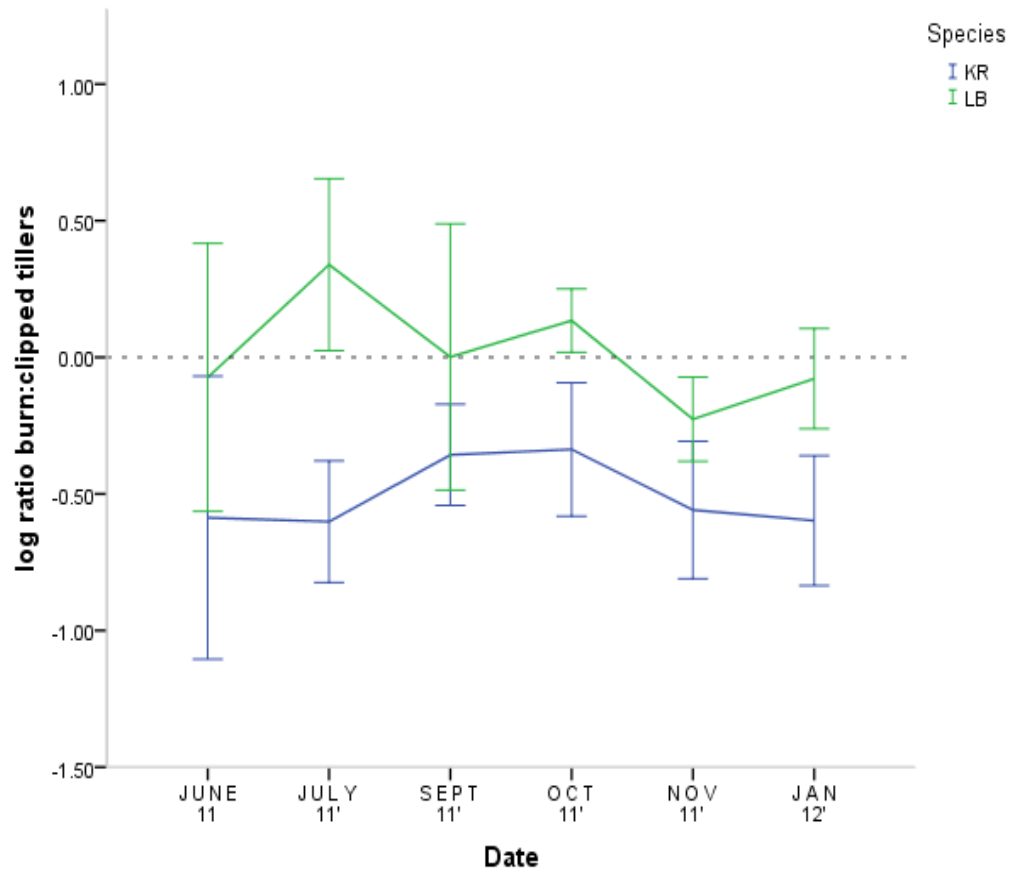


Figure 5. The log of meristem survivorship (based on eq. 1) in the fire treatment. Bars represent ± 2 SE.

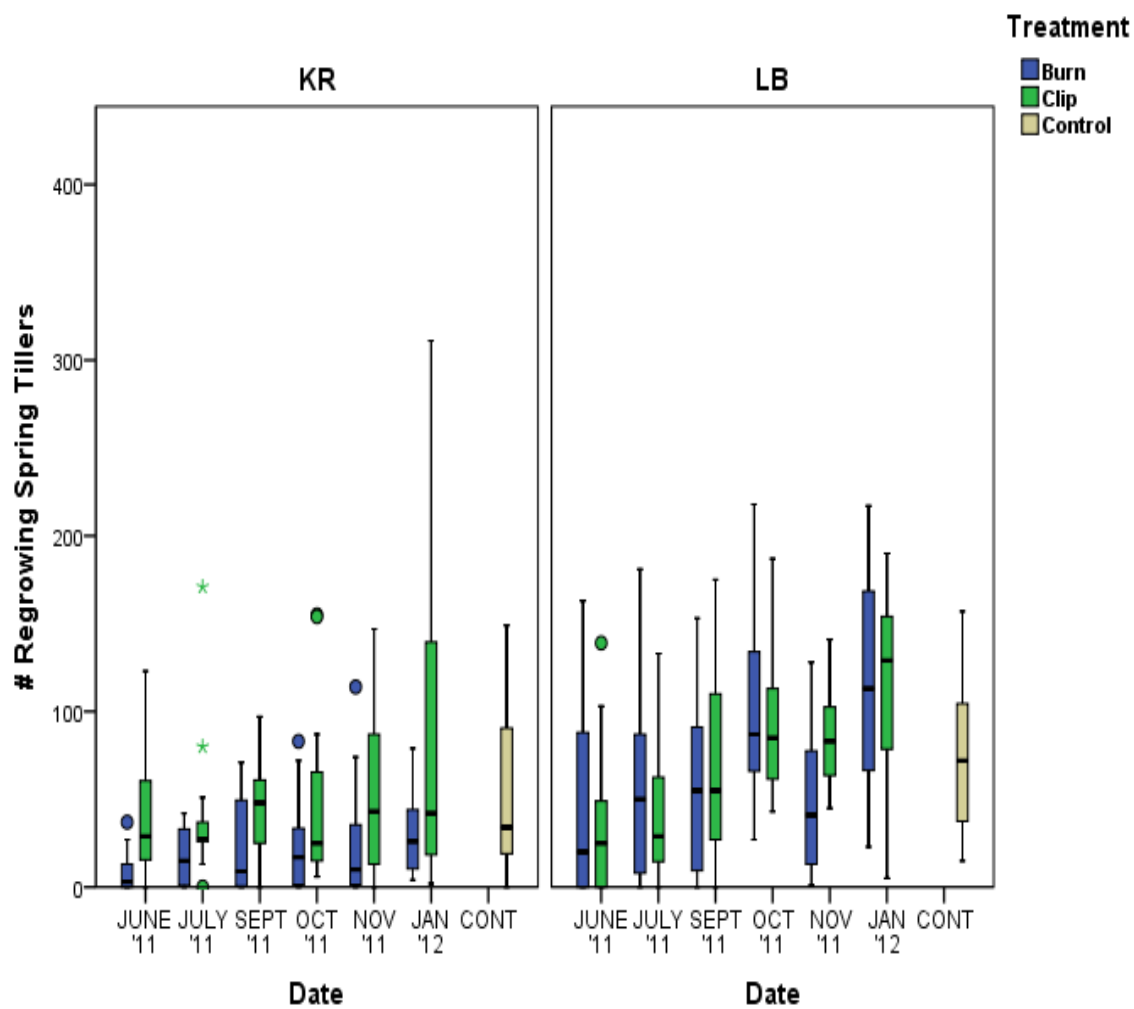


Figure 6. Boxplot of final tiller counts for burn (blue) and clip (green) treatments. Symbols as in Figure 4.

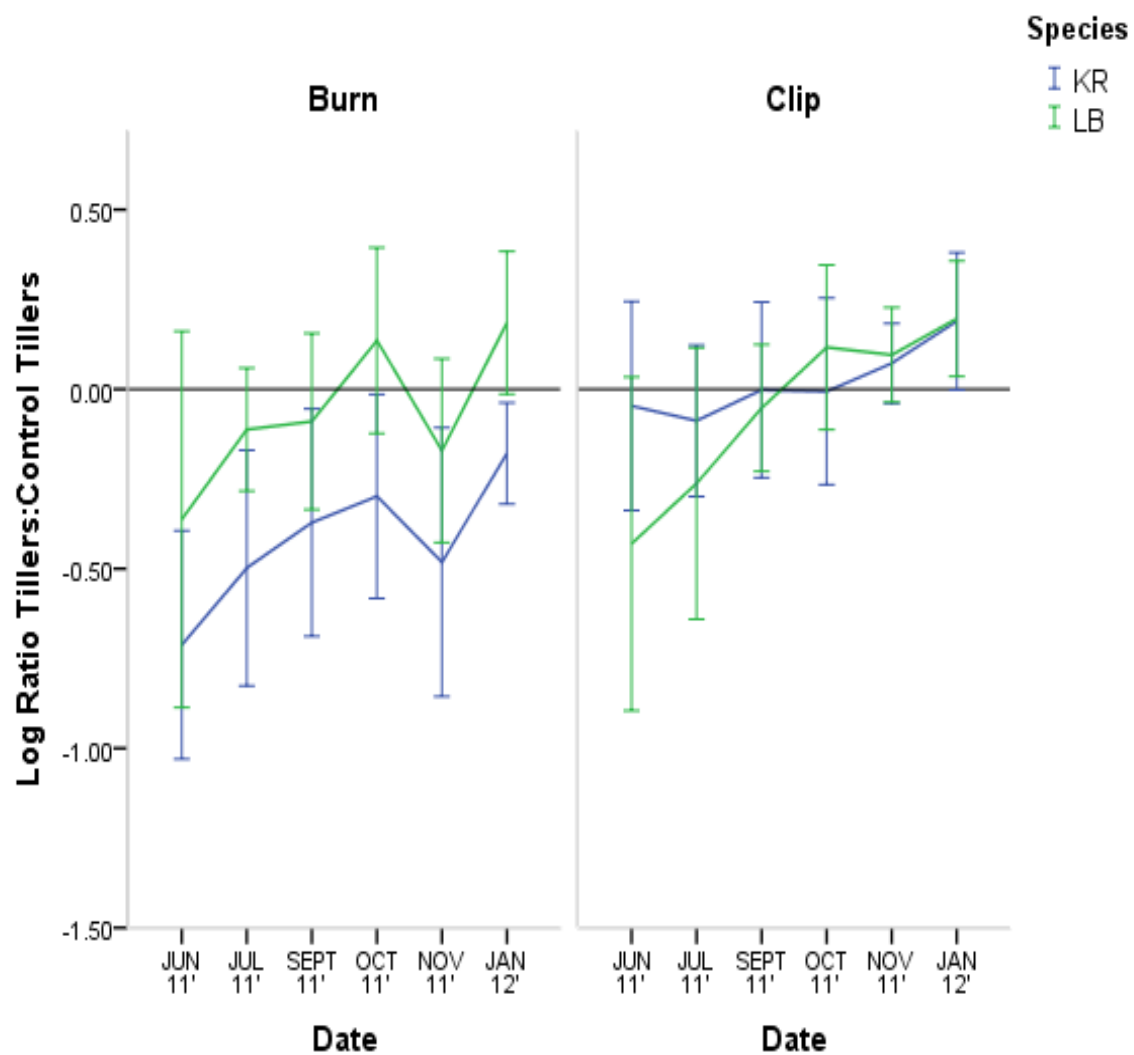


Figure 7. The log ratios of final tiller numbers in burn or clipped plots over control plots. Bars represent ± 2 SE.

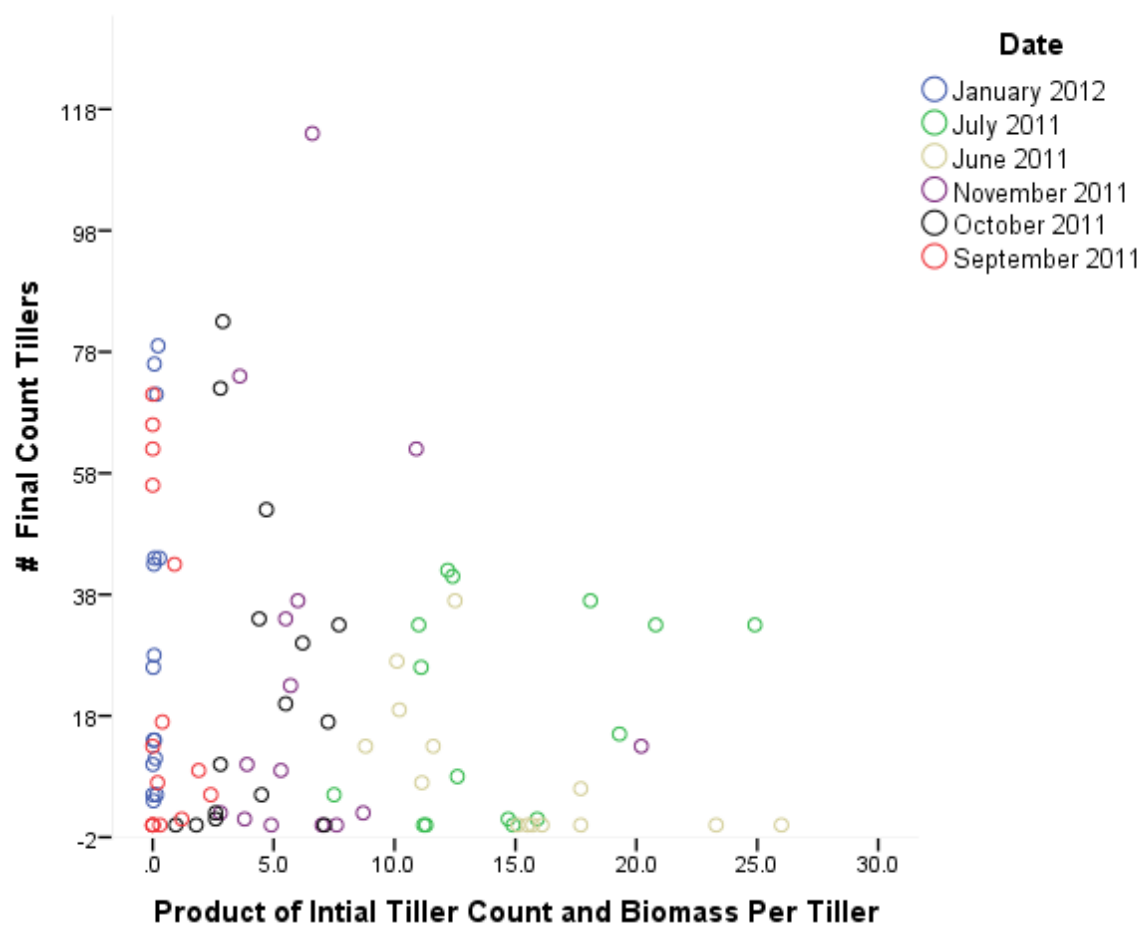


Figure 8. Final tiller counts of KR bluestem in burn plots plotted against the product of initial tiller count and average biomass per tiller at burn time (a significant predictor of tiller count).

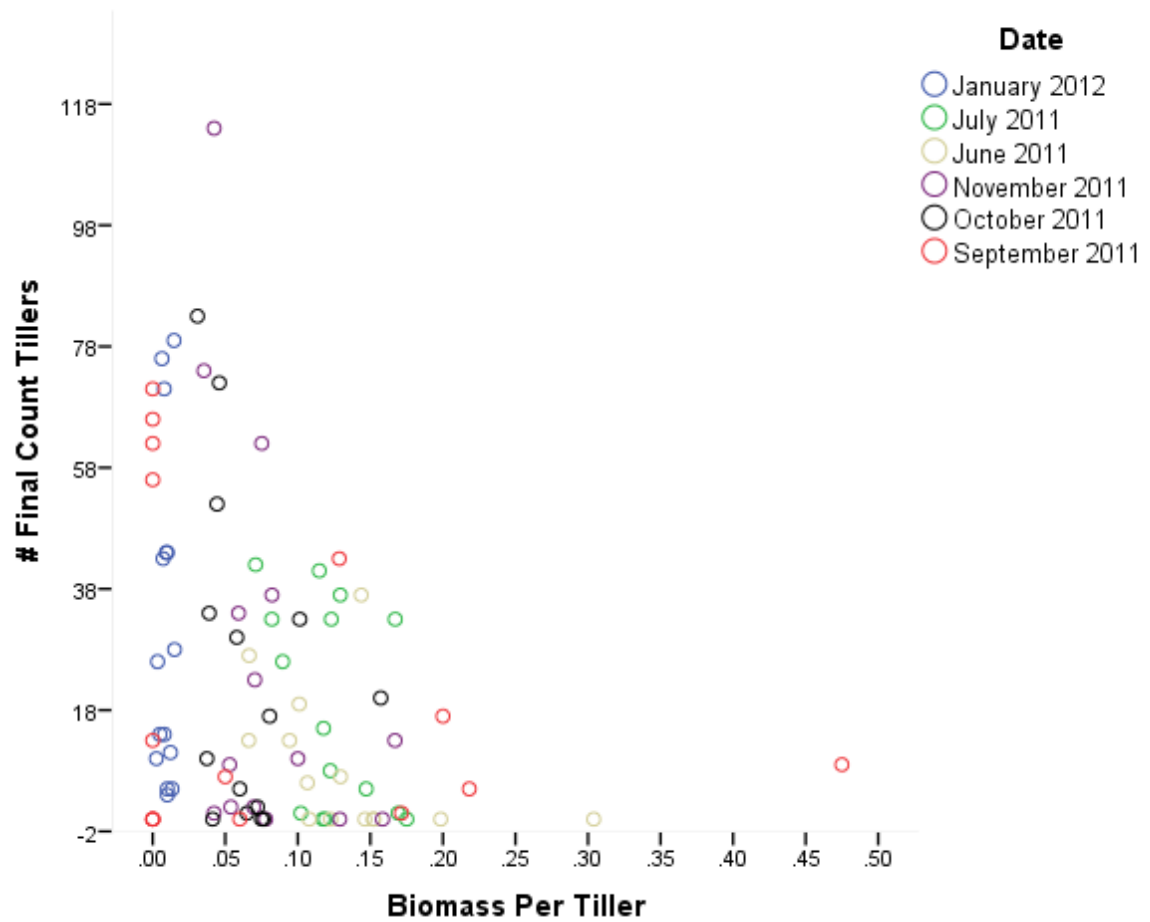


Figure 9. Final tiller counts of KR bluestem in burn plots plotted against average biomass per tiller at burn time (a significant predictor of tiller count).

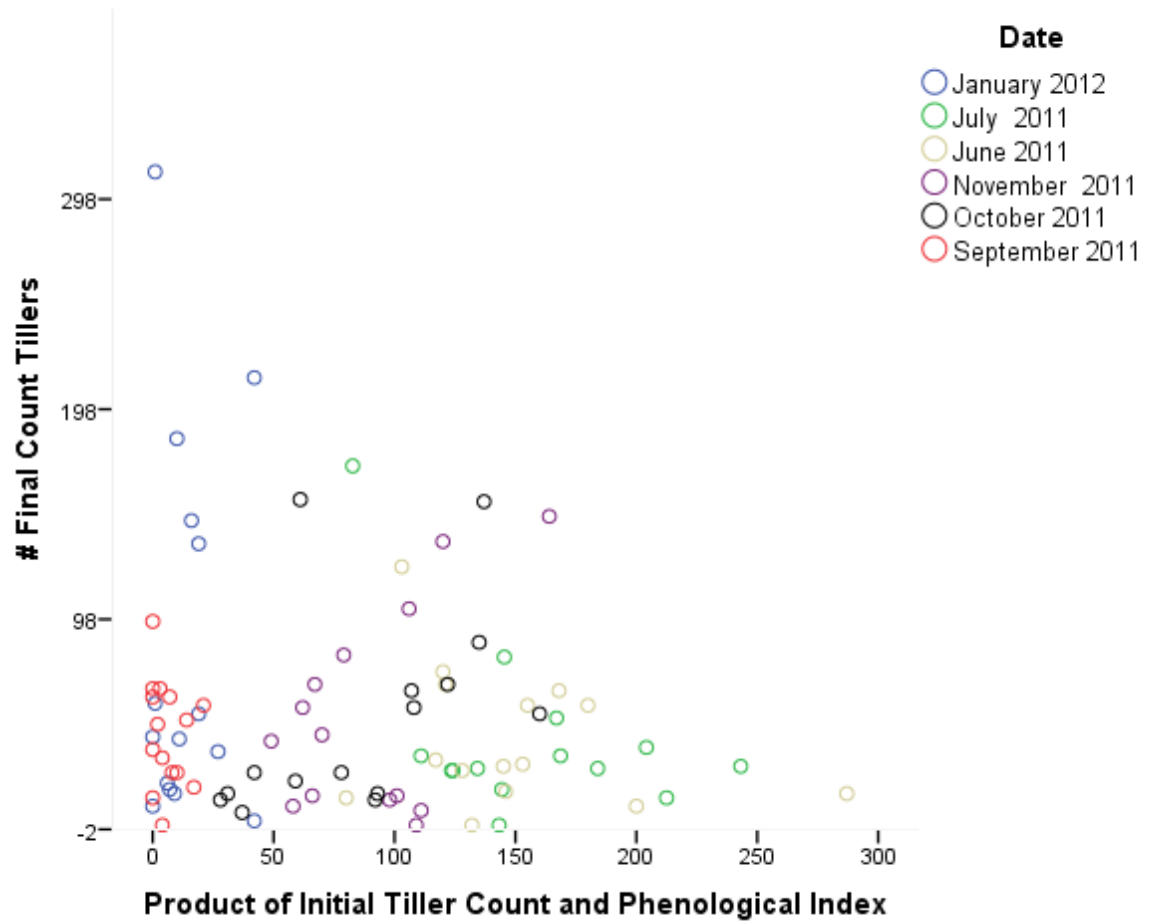


Figure 10. Final tiller count for KR bluestem in clip plots plotted against the product of initial tiller count and phenological index at burn time.

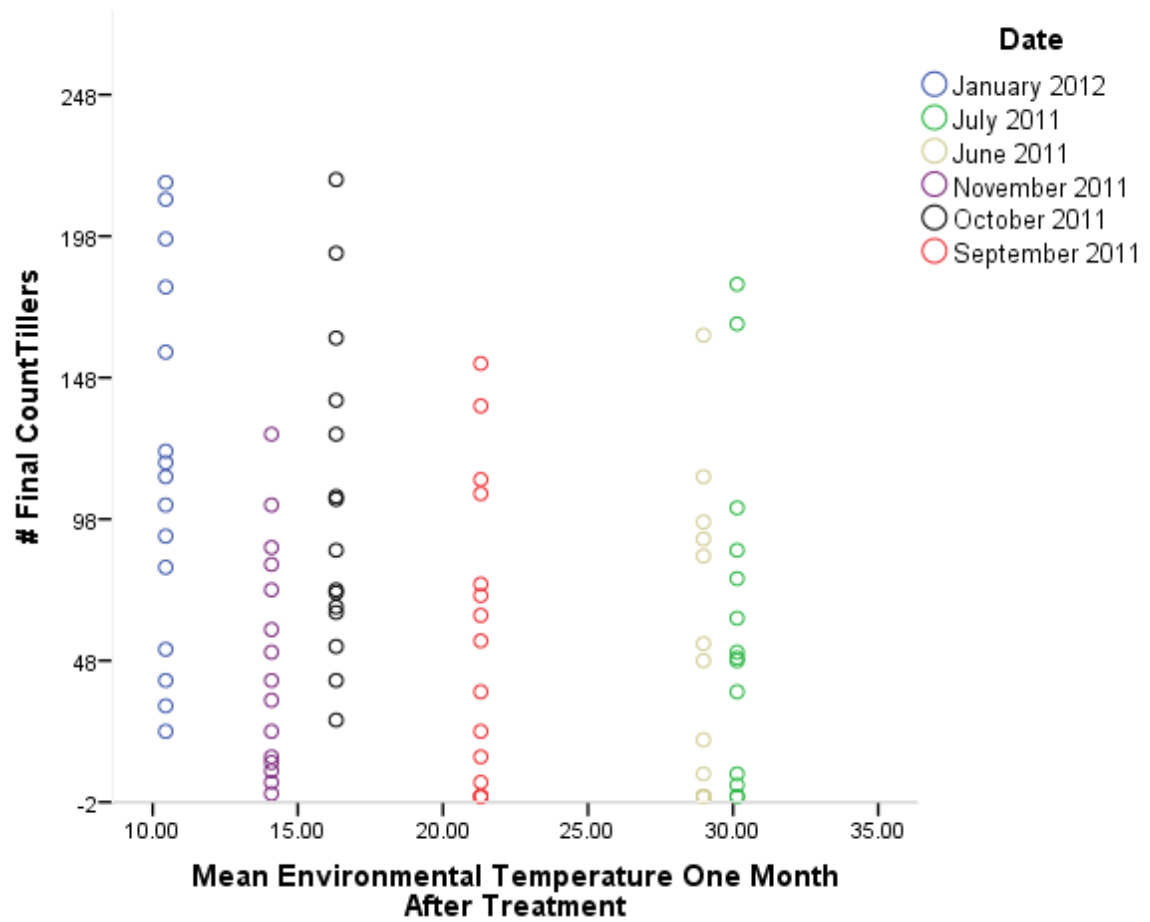


Figure 11. Final tiller count of little bluestem in burn plots plotted against mean temperature one month after burn treatment date (a significant predictor of tiller numbers).

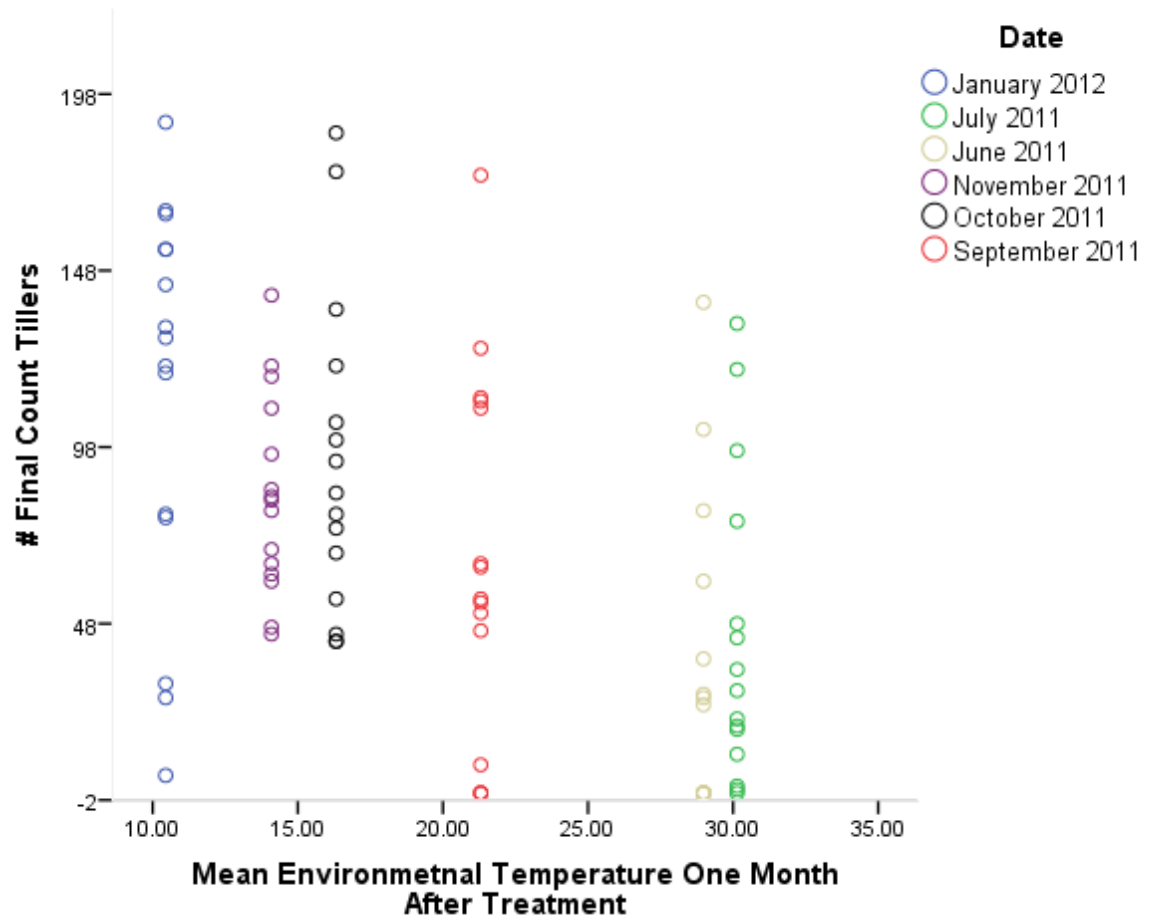


Figure 12. Final tiller count of little bluestem in clipped plots plotted against mean temperature one month after clip treatment date.

LITERATURE CITED

- Ansley RJ and Rasmussen GA. 2005. Managing native invasive juniper species using fire. *Weed Technology* 19(3):517-22.
- Ansley RJ, Pinchak WE, Jones DL. 2008. Mesquite, tobosagrass, and common broomweed responses to fire season and intensity. *Rangeland Ecology & Management* 61(6):588-97.
- Ansley RJ, Pinchak WE, Teague WR, Kramp BA, Jones DL, Barnett K. 2010. Integrated grazing and prescribed fire restoration strategies in a mesquite savanna: II. fire behavior and mesquite landscape cover responses. *Rangeland Ecology & Management* 63(3):286-97.
- Ansley RJ and Castellano MJ. 2007a. Texas wintergrass and buffalograss response to seasonal fires and clipping. *Rangeland Ecology & Management* 60(2):154-64.
- Ansley RJ and Castellano MJ. 2007b. Effects of summer fires on woody, succulent, and graminoid vegetation in southern mixed-prairie ecosystems: A review. 23rd Tall Timbers Fire Ecology Conference: Fire in Grassland and Shrubland Ecosystems (23):63-70.
- Ansley RJ, Castellano MJ, Pinchak WE. 2006. Sideoats grama growth responses to seasonal fires and clipping. *Rangeland Ecology & Management* 59(3):258-66.
- Ansley RJ, Boutton TW, Mirik M, Castellano MJ, Kramp BA. 2010. Restoration of C(4) grasses with seasonal fires in a C(3)/C(4) grassland invaded by *Prosopis glandulosa*, a fire-resistant shrub. *Applied Vegetation Science* 13(4):520-30.
- Anderson RC. 1990 The historic role of fire in the North American grassland. In: S.L. Collins and L.L. Wallace. Eds. Fire in North American tallgrass prairie. University of Oklahoma Press, Norman, OK.
- Axelrod DI. 1985. Rise of the grassland biome, Central-North American. *Botanical Review* 51(2):163-201.
- Bidwell TG and Engle DM. 1992. Relationship of fire behavior to tallgrass prairie herbage production. *Journal of Range Management* 45(6):579-84.
- Bond WJ and Midgley JJ. 2001. Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology & Evolution* 16(1):45-51.

- Bond WJ and Parr CL. 2010. Beyond the forest edge: Ecology, diversity and conservation of the grassy biomes. *Biological Conservation* 143(10):2395-404.
- Bragg TB and Hulbert LC. 1976 Woody plant invasion of unburned Kansas bluestem prairie. *Journal of Range Management* 29(1):19-23.
- Briggs JM and Knapp AK. 1995. Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position, and fire as determinants of aboveground biomass. *American Journal of Botany* 82(8):1024-1250.
- Brown JR and Archer S. 1989. Woody plant invasion of grasslands: establishment of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) on sites differing in herbaceous biomass and grazing history. *Oecologia* 80(1):19-26.
- Carroll I, Cardinale JB, Nisbet RM. 2011. Niche and fitness differences relate the maintenance of diversity to ecosystem function. *Ecology* 92(5):1157-1165.
- Carson D. 2000. Soils of the Freeman Ranch, Hays County, Texas. *Freeman Ranch Publication Series* 4.
- Chesson P, Gebauer RLE, Schwinning S, Huntly N, Wiegand K, Ernest MSK, Sher A, Novoplansky A, Weltzin JF. 2004. Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia* 141(2):236-53.
- Choczynska J and Johnson EA. 2009. A soil heat and water transfer model to predict belowground grass rhizome bud death in a grass fire. *Journal of Vegetation Science* 20:277-287.
- Copeland T, Sluis W, Howe H. 2002. Fire season and dominance in an Illinois tallgrass prairie restoration. *Restoration Ecology* 10(2):315-23.
- Corbin JD and D'Antonio CM. 2010. Not novel, just better: Competition between native and non-native plants in California grasslands that share species traits. *Plant Ecology* 209(1):71-81.
- D'Antonio CM, Hughes RF, Tunison JT. 2011. Long-term impacts of invasive grasses and subsequent fire in seasonally dry Hawaiian woodlands. *Ecological Applications* 21(5):1617-1628.
- DiTomaso JM, Brooks ML, Allen EB, Minnich R, Rice PM, Kyser GB. 2006. Control of invasive weeds with prescribed burning. *Weed Technology* 20(2):535-48.
- Engle DM and Bidwell TG. 2001. The response of central North American prairies to fire season. *Journal of Range Management* 54(1):2-10.

- Engle DM, Mitchell RL, Stevens RL. 1998. Late growing-season fire effects in mid-successional tallgrass prairies. *Journal of Range Management* 51(1):115-21.
- Ewing AL and Engle DM. 1988. Effects of late summer fire on tallgrass prairie microclimate and community composition. *American Midland Naturalist* 120(1):212-23.
- Fidelis A, Delgado-Cartay MD, Blaco CC, Muller SC, Pillar VD, Pfadenhauer J. 2010. Fire intensity and severity in Brazilian campos grasslands. *Interciencia* 35(10):739-745.
- Fuhlendorf SD and Smeins FE. 1997. Long-term vegetation dynamics mediated by herbivores, weather, and fire in a *Juniper-Quercus* savanna. *Journal of Vegetation Science* 8(6):819-828.
- Gabbard BL and Fowler NL. 2007. Wide ecological amplitude of a diversity-reducing invasive grass. *Biological Invasions* 9(2):149-60.
- Gagnon PR, Passmore HA, Platt WJ, Myers JA, Paine CET, Harms KE. 2010. Does pyrogenicity protect burning plants? *Ecology* 91(12):3481-6.
- Gould FW. 1975. *The Grasses of Texas*. Texas A&M University Press, College Station, Texas.
- Grace, JB, Smith MD, Grace SL, Collins SL, Stohlgren TJ. 2001. Interactions between fire and invasive plants in temperate grasslands of North America. Pages 40-65 in K.E.M. Galley and T.P. Wilson (eds.). *Proceedings of the Invasive Species Workshop: the Role of Fire in the Control and Spread of Invasive Species*. Fire Conference 2000: the First National Congress on Fire Ecology, Prevention, and Management. Miscellaneous Publication No. 11, Tall Timbers Research Station, Tallahassee, FL.
- Harmoney KR, Stahlman PW, Hickman KR. 2004. Herbicide effects on established yellow Old World bluestem (*Bothriochloa ischaemum*). *Weed Technology* 18(3):545-550.
- Higgins KF. 1984. Lightning fires in North Dakota grasslands and in pine-savanna lands of South Dakota and Montana. *Journal of Range Management* 37(2):100-3.
- Howe HF. 1994a. Managing species-diversity in tallgrass prairie - assumptions and implications. *Conservation Biology* 8(3):691-704.
- Howe HF. 1994b. Response of early-flowering and late-flowering plants to fire season in experimental prairies. *Ecological Applications* 4(1):121-33.

- Johnson BJ and Omland KS. 2004. Model selection in ecology and evolution. *Trends in Ecology and Evolution* 19(2):101-108.
- Keeley JE. 2009. Fire intensity, fire severity and burn severity: a brief review and suggested useage. *International Journal of Wildland Fire* 18(1):116-126.
- Knapp AK. 1985. Effect of fire and drought on the ecophysiology of *Andropogon gerardii* and *Panicum virgatum* in a tallgrass prairie. *Ecology* 66(4) 1309-1320.
- Lesica P and Martin B. 2003. Effects of prescribed fire and season of burn on recruitment of the invasive exotic pant, *Potentilla recta*, in a semiarid grassland. *Restoration Ecology* 11(4):516-523.
- Limb RF, Fuhlendorf SD, Engle DM, Kerby JD. 2011. Growing-season disturbance in tallgrass prairie: Evaluating fire and grazing on *Schizachyrium scoparium*. *Rangeland Ecology & Management* 64(1):28-36.
- Loflin B and Loflin S. 2006. *Grasses of the Texas Hill Country*. Texas A&M University Press, College Station, Texas.
- Menke JW and Trlica MJ. 1981. Carbohydrate reserve, phenology, and growth cycles of 9 Colorado range species. *Journal of Range Management* 34(4):269-77.
- Milton S. 2004. Grasses as invasive alien plants in South Africa. *South African Journal of Science* 100:69-75
- Moore KJ, Moser LE, Vogel KP, Waller SS, Johnson BE, Pedersen JF. 1991. Describing and quantifying growth-stages of perennial forage grasses. *Agronomy Journal* 83(6):1073-7.
- Nofal HR, Sosebee RE, Wan CG, Borrelli J, Zartman R, McKenney C. 2004. Mowing rights-of-way affects carbohydrate reserves and tiller development. *Journal of Range Management* 57(5):497-502.
- Olson BE and Richards JH. 1988. Annual replacement of the tillers of *Agropyron desertorum* following grazing. *Oecologia* 76(1):1-6.
- Pate JS, Froend RH, Bowen BJ, Hansen A, Kuo J. 1990. *Annals of Botany* 65(6):5 585-601.
- Pyke DA, Brooks ML, D'Antonio C. 2010. Fire as a restoration tool: A decision framework for predicting the control or enhancement of plants using fire. *Restoration Ecology* 18(3):274-84.

- Raunkiaer C. 1934. *The life forms of plants and statistical plant geography*; being the collected papers of C. Raunkiaer. Translated by Gilbert-Carter, H., A.I. Fausboll and A. G. Tansley. The Clarendon Press, Oxford, United Kingdom.
- Reed HE, Seastedt TR, Blair JM. 2005. Ecological consequences of C-4 grass invasion of a C-4 grassland: A dilemma for management. *Ecological Applications* 15(5):1560-1569.
- Rew LJ and Johnson MP. 2010. Reviewing the role of wildfire on the occurrence and spread of invasive plant species in wild land areas of the intermountain western United States. *Invasive Plant Science and Management* 3(4):347-64.
- Ripley B, Gillian D, Osborne CP. 2010. Experimental investigation of fire ecology in the C(3) and C(4) subspecies of *Alloteropsis semialata*. *Journal of Ecology* 98(5):1196-1203.
- Sax DF, Stachowicz JJ, Gaines SD. Eds. 2005. *Species Invasions: Insights into Ecology, Evolution, and Biogeography*. Sinauer Associates, Sunderland, Massachusetts.
- Schmidt CD, Hickman KR, Channell R, Harmoney K, Stark W. 2008. Competitive abilities of native grasses and non-native (*Bothriochloa* spp.) grasses. *Plant Ecology* 197(1):69-80.
- Simmons MT, Windhager S, Power P, Lott J, Lyons RK, Schwoppe C. 2007. Selective and non-selective control of invasive plants: The short-term effects of growing-season prescribed fire, herbicide, and mowing in two Texas prairies. *Restoration Ecology* 15(4):662-9.
- Smith TM, Shugart HH, Woodward FI. Eds. 1997. *Plant functional types, their relevance to ecosystem properties and global change*. Cambridge University Press, Cambridge MA.
- Sugihara NG, Van Wagtenonk JW, Schaffer KE, Fites-Kaufman J, Thode AE. Eds. 2006. *Fire: In California Ecosystems*. University of California Press, Berkeley, California.
- Teague WR, Duke SE, Waggoner JA, Dowhower SL, Gerrard SA. 2008. Rangeland vegetation and soil response to summer patch fires under continuous grazing. *Arid Land Research and Management* 22(3):228-241.
- Trollope WSW. 1980. Controlling brush encroachment with fire in the savanna areas of South Africa. *Proceedings of the Grassland Society of South Africa* 19:173-177.
- Twidwell D, Fuhlendorf SD, Engle DM, Taylor CA. 2009. Surface fuels sampling strategies: linking fuel measurements and fire effects. *Rangeland Ecology and Management* 62 (3):223-229.

- Vogl RJ. 1974 Effects of fire on grasslands. *In*: T.T. Kozlowski and C.E. Ahlgren. Eds Fire and ecosystems: a series of monographs, texts and treatises. Academic Press, New York, NY.
- Waite R and Boyd J. 1953. The water-soluble carbohydrates of grasses .1.- changes occurring during the normal life-cycle. *Journal of Science Food Agriculture* 4(4):197-204.
- Woodward FL and Cramer W. 1996. Plant functional types and climatic changes: introduction. *Journal of Vegetation Science* 7(3):306-308.
- Wright HA. 1971. Why squirreltail is more tolerant to burning than needle-and-thread. *Journal of Range Management* 24(4):277-284.
- Wright HA. 1974. Effect of fire on southern mixed prairie grasses. *Journal of Range Management* 27(6):417-419.
- Wright HA and Bailey AW. 1982. *Fire ecology*. John Wiley and Sons. New York, NY.

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