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Season of prescribed fire determines grassland restoration outcomes after fire exclusion and overgrazing

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Abstract. Fire exclusion and mismanaged grazing are globally important drivers of environmental change in mesic C_4 grasslands and savannas. Although interest is growing in prescribed fire for grassland restoration, we have little long-term experimental evidence of the influence of burn season on the recovery of herbaceous plant communities, encroachment by trees and shrubs, and invasion by exotic grasses. We conducted a prescribed fire experiment (seven burns between 2001 and 2019) in historically fire-excluded and overgrazed grasslands of central Texas. Sites were assigned to one of four experimental treatments: summer burns (warm season, lightning season), fall burns (early cool season), winter burns (late cool season), or unburned (fire exclusion). To assess restoration outcomes of the experiment, in 2019, we identified old-growth grasslands to serve as reference sites. Herbaceous-layer plant communities in all experimental sites were compositionally and functionally distinct from old-growth grasslands, with little recovery of perennial C_4 grasses and long-lived forbs. Unburned sites were characterized by several species of tree, shrub, and vine; summer sites were characterized by certain C_3 grasses and forbs; and, fall and winter sites were intermediate in composition to the unburned and summer sites. Despite compositional differences, all treatments had comparable plot-level plant species richness (range 89-95 species 1000/m^2). At the local-scale, summer sites (23 species/m^2) and old-growth grasslands (20 species/m^2) supported greater richness than unburned sites (15 species/m^2), but did not differ significantly from fall or winter sites. Among fire treatments, summer and winter burns most consistently produced the vegetation structure of old-growth grasslands (e.g., mean woody canopy cover of 9%). But whereas winter burns promoted the invasive grass *Bothriochloa ischaemum* by maintaining areas with low canopy cover, summer burns simultaneously limited woody encroachment and controlled *B. ischaemum* invasion. Our results support a growing body of literature that shows that prescribed fire alone, without the introduction of plant propagules, cannot necessarily restore old-growth grassland community composition. Nonetheless, this long-term experiment demonstrates that prescribed burns implemented in the summer can benefit restoration by preventing woody encroachment while also controlling an invasive grass. We suggest that fire season deserves greater attention in grassland restoration planning and ecological research.

Key words: Blackland Prairie, bud bank, Edwards Plateau, grassy biomes, King Ranch Bluestem, novel ecosystems, regeneration, succession.

INTRODUCTION

Prescribed fire—i.e., burning by land managers under specific conditions to induce desired ecosystem responses—is an essential element of efforts to conserve and restore the biodiversity of Earth's mesic C_4 grasslands (including savannas and open-canopy grassy woodlands; Menges and Gordon 2010, Veldman et. al 2015, Buisson et al. 2019). Management objectives for prescribed fire in grasslands commonly include: maintenance of communities of plants that evolved with fire (Bond and Keeley 2005, Simpson et al. 2016), control of woody plants to prevent forest or shrubland encroachment (Miller et al. 2017), prevention of exotic plant invasions (DiTomaso et al. 2006), improvement of habitat and forage for wildlife or livestock (Main and Richardson 2002, Scasta et al. 2016), and consumption of fuels to reduce hazardous wildfire risk (Reidy et al. 2016, Starns et al. 2019). To achieve these objectives, prescribed fire managers establish fire regimes (e.g., frequency, intensity, and seasonality of fire) that may closely resemble, or deviate substantially from, the historical fire regimes under which old-growth grassland communities developed and species evolved (Ryan et al. 2013, Veldman et al. 2015). Among the aspects of fire regimes that we should expect to be critically important for grassland restoration, but is often overlooked, is the season of fire (Pyke et al. 2010).

Several lines of evidence suggest that fire season should influence grassland restoration. Fire season is integral to fire behavior via interactions with weather and plant phenology; burning during seasons with high temperatures, low humidity, and high proportions of dead fuel offers the greatest control of woody plants (Taylor et al. 2012). Fire season can influence community composition by altering the productivity and relative abundances of C_4 grasses, C_3 grasses, and forbs (Howe 1994, Ansley et al. 2010, Dickson et al. 2019). At the organismal level, many grass and forb species are stimulated to flower, and produce higher proportions of viable seed, in response to fires in a particular season (Outcalt 1994, Fidelis and Blanco 2014). In humid tropical and subtropical climates, such a correspondence between reproductive effort and fire season suggests a long evolutionary history between grassland species and lightning-ignited fires (Simon et al. 2009, Maurin et al. 2014), which historically occurred during seasons commonly referred to as the growing season, rainy season, or warm season (e.g., Ramos-Neto and Pivello 2000, Noss et al. 2015). While this evidence suggests a need to consider prescribed fire season in restoration efforts, we lack long-term experimental evidence of whether burning in particular seasons can restore grasslands toward an old-growth ecosystem state after chronic overgrazing and fire exclusion. To date, long-term experiments on the effects of different fire seasons have been limited to old-growth grasslands that were not in need of restoration (e.g., Towne and Craine 2014), reconstructed grasslands planted on former agricultural land (Howe 2011, Dickson et al. 2019), or study designs that did not assess restoration in reference to old-growth grassland communities (Taylor et al. 2012, Boughton et al. 2013).

Many grasslands exist as hybrid ecosystems (*sensu* Hobbs et al. 2009), characterized by biotic and abiotic attributes that deviate from historical (i.e., old-growth) conditions, but that have not been completely destroyed by intensive land uses such as tillage agriculture, afforestation, or mining (Buisson et al. 2019). Therefore, in addition to studies on how prescribed fire can conserve old-growth grasslands (Towne and Craine 2014) and manage reconstructed grasslands after wholesale destruction (Howe 2011, Dickson et al. 2019), we also need to determine how fire influences the many hybrid grasslands that fall between the extremes of old-growth and novel ecosystem states (Hobbs et al. 2009, Buisson et al. 2019). Two ubiquitous drivers of environmental change that create hybrid grasslands are mismanagement of domestic livestock and fire exclusion (Buisson et al. 2019). Consequences of overgrazing include declines in perennial herbaceous plant species (Van De Koppel et al. 1997), increased abundance of shortgrass species relative to tallgrass species (Fuhlendorf and Smeins 1997), invasion by exotic species (McIntyre et al. 2003), and reduced ecosystem flammability (Hempson et al. 2019). Fire exclusion causes grasslands to become encroached by trees and shrubs (Ladwig et al. 2018), which leads to the loss of fire- and light-dependent savanna plants and animals (Briggs et al. 2002, Abreu et al. 2017, Diaz-Toribio et al. 2019), and further reduces ecosystem flammability (Nowacki and Abrams 2008).

If historical fire-vegetation relationships are disrupted, recovery of old-growth grassland structure and plant community composition can be challenging. During the early stages of woody encroachment, prescribed fire successfully reduces tree and shrub abundance (Ruth et al. 2007, Policelli et al. 2019), but severe woody encroachment inhibits fire spread through altered microclimates and loss of herbaceous fuel (Nowacki and Abrams 2008, Scott et al. 2012). Even if prescribed fire can be applied without mechanical thinning and herbicide application, the rate of recovery of herbaceous plant communities is often very slow (Nerlekar and Veldman 2020) and communities may never return to the composition of old-growth grasslands (Geiger and McPherson 2005, Scott et al. 2012). An apparent hurdle to community recovery, characteristic plant species of old-growth grasslands tend to be poor at colonizing from seed, and instead depend on clonal growth, bud banks, and underground storage organs for persistence (Benson and Hartnett 2006). Thus, restoration of community composition, without sowing seeds or transplants, requires the spread of remnant plant populations on-site, or in some cases may rely on dispersal from nearby populations (Limb et al. 2014, Fensham et al. 2016).

A key function of prescribed fire in grassland restoration is to stimulate reproduction of herbaceous plants—native grasses in particular—and open space for establishment via seed or clonal spread (Benson and Hartnett 2006, Myers and Harms 2009). Unfortunately, through similar mechanisms, prescribed fire can also create a window for exotic grass invasions (Setterfield et al. 2005, Keeley 2015). As such, fire-adapted invasive grasses pose a critical challenge to the use of prescribed fire in grassland conservation and restoration (Reed et al. 2005). Well-documented examples of fire-adapted invasive grasses that exclude native species, alter fire regimes, and perpetuate invasive grass-fire cycles (Fusco et al. 2019), include *Andropogon gayanus* in Australia (Rossiter et al. 2003), *Imperata cylindrica* in the southeastern United States (Holzmueller and Jose 2010), and *Bromus tectorum* in the western United States (Balch et al. 2013). *Bothriochloa ischaemum* (King Ranch Bluestem) is another problematic fire-adapted, invasive grass, which is now widespread in central Texas. Because of its high tolerance to grazing and resistance to drought, this perennial C_4 bunchgrass, native to temperate and subtropical Eurasia, was introduced in the early 1900s to serve as livestock forage (Wied et al. 2020). Whereas prescribed fires in the winter promote *B. ischaemum* invasion (Gabbard and Fowler 2007, Havill et al. 2015), short-term studies suggest that summer fires can reduce *B. ischaemum* abundance (Simmons et al. 2007, Reemts et al. 2018). In light of the phenological and evolutionary importance of season of fire (Miller et al. 2019), we anticipate that long-term application of prescribed fire in the warm season, when *B. ischaemum* is in a fire-sensitive phenological stage (Ruckman et al. 2012), will control this invasive grass during restoration.

In this study, we used a long-term prescribed fire experiment (2001-2019) to assess the influence of burn season on the restoration of historically overgrazed and fire-excluded grasslands in central Texas. We considered three primary suites of response variables that are commonly targeted in grassland and savanna restoration: native herbaceous-layer plant community composition and diversity, vegetation structure (e.g., herbaceous and woody canopy cover), and susceptibility to invasion by exotic grasses. Because assessment of management outcomes through comparison to reference ecosystem states is the standard in restoration ecology (McDonald et al. 2016; Gann et al. 2019), we identified some of the few remaining old-growth grasslands in our study region to serve as reference sites (Veldman et al. 2015, Buisson et al. 2019). We hypothesized that: (1) experimental sites burned in the summer (within the lightning fire season) would support the greatest compositional similarity to old-growth grassland plant communities, followed by sites burned in winter and fall, while communities on unburned sites would be least similar; (2) herbaceous-layer species richness and diversity, independent of season of burn, would be greater in burned grasslands compared to unburned (fire-excluded) sites; (3) fire in any season would maintain the open vegetation structure of old-growth grasslands, whereas unburned sites would be dominated by trees and shrubs; (4) prescribed fire in the summer would limit invasion of *B. ischaemum* relative to prescribed fire in the fall and winter. We expect our results to raise awareness of the value of prescribed fire season to grassland restoration, to highlight the challenge of restoring the plant community composition of old-growth grasslands after fire exclusion and overgrazing, and demonstrate that long-term manipulation of prescribed fire season can control an invasive C_4 grass during grassland restoration.

METHODS

Study System

We conducted this study in savanna-grasslands of central Texas, on the eastern edge of the Edwards Plateau, abutting the Blackland Prairie ecoregion (Gould et al. 1960). Old-growth grasslands of the region are composed of flammable C_4 grasses, including *Andropogon gerardii, Bothriochloa laguroides*, *Bouteloua curtipendula*, *Bouteloua dactyloides*, *Schizachyrium scoparium,* and *Sorghastrum nutans* (Landers 1987). Common tree species, listed in decreasing order of fire tolerance (i.e., bark thickness and resprouting capacity), include *Quercus stellata, Quercus fusiformis, Prosopis glandulosa*, *Ulmus crassifolia,* and *Juniperus ashei* (Landers 1987). The climate is humid subtropical (mean annual temperature of 19.6 °C, mean annual precipitation of 880 mm) with warm summers (June-September), mild to cool falls (October-December), cool winters (January-early March), and mild springs (late March-May); intra-annual precipitation is bimodal, with peak rainfall in May-June and October (NWS 1981-2010; Appendix S1: Fig. S1). Lightning is frequent (>1.0 flash/km^2/month) from April through September, suggestive of spring and summer as the fire seasons (Appendix S1: Fig. S1; Balch et al. 2017) under which the region's grassland plants evolved (Noss et al. 2015).

Prior to colonization in the mid-1800s, by immigrants from central Europe and the southern United States, the region's grasslands were maintained by frequent fires (ignited by lightning and Native Americans) and large herbivores, including *Bison bison* and extinct Holocene megafauna (Smeins et al. 1997). Native American influence on fire regimes was minimal prior to the mid-Holocene and apparently grew in importance into the late Holocene (Cordova and Johnson

2019). Presumably, Native Americans used fire outside the spring-summer lightning season, but the degree of modification of fire regimes, and the extent to which a wider range of fire seasons influenced herbaceous and woody plant dynamics is unclear. While Native Americans certainly influenced vegetation dynamics through fire, many fire-adapted taxa of contemporary grasslands were present, even if not dominant, in the region by 18 to 10 kya (Larson et al. 1972, Cordova and Johnson 2019) and thus predate extensive human influence (Noss et al. 2015).

During the past 150 years, fire exclusion, overgrazing, woody encroachment, and urbanization has dramatically changed most grasslands of central Texas. This period of change began with European land-use practices that fragmented landscapes with fences and heavy grazing by livestock (primarily sheep, goats, and cattle), and ultimately reduced perennial C_4 bunch grasses and limited fire frequency and spread (Smeins 1980). Chronic fire exclusion and overgrazing promoted encroachment by woody species, especially *Juniperus ashei* (Jessup et al. 2003) and increased the abundance of short-grass, often C_3, species (Fuhlendorf and Smeins 1997).

Study Locations

Locations for this study were the Lady Bird Johnson Wildflower Center, in southwest Austin (30°11'N, 97°52'W), and the City of Austin Water Quality Protection Lands, immediately south of Austin in the counties of Travis and Hays (30°5'N, 97°56'W). Beginning in 1995 and culminating in 2002, the Wildflower Center acquired 115 ha of former ranchland that was managed for many decades with fire exclusion and cattle grazing but lacked any known history of intensive soil disturbance (e.g., tillage agriculture). At the time of acquisition, grasslands at the Wildflower Center were undergoing encroachment by woody species (*Juniperus ashei, Quercus fusiformis,* and *Prosopis glandulosa*) and invasion by exotic grasses (*Bothriochloa ischaemum*, in particular, but also *Sorghum halepense* and later *Dichanthium sericeum*).

Populations of native perennial C_4 bunchgrasses and long-lived forbs were reduced to a few scattered individuals. Soils at the Wildflower Center are 35-50 cm deep, well-drained mollisols (Speck Clay Loam) and vertisols (Crawford Clay; Soil Survey 2020). Old-growth grassland sites, which we identified as reference communities, were located on the Water Quality Protection Lands, 4 to 17 km southwest of the Wildflower Center. Between 1998 and 2019, the city of Austin acquired 11,500 ha over a portion of the Edwards Aquifer to protect the quality and quantity of groundwater recharge. Like the Wildflower Center, the portions of the Water Quality Protection Lands included in this study were former ranchland (heavily grazed until 2000; McCaw et al. 2018), with old-growth grasslands reduced to several small sites. The City of Austin currently manages the Water Quality Protection Lands with prescribed fire to restore grasslands and limit woody encroachment. The soils of the old-growth grassland study sites on Water Quality Protection Lands are 25-100 cm deep, well-drained mollisols (Rumple-Comfort, rubbly association gravelly clay loam, with minor components of Tarpley; Soil Survey 2020).

Experimental Design

In 2001, the Wildflower Center established a prescribed fire experiment by randomly assigning 24 degraded grassland sites (hereafter, “experimental sites”; mean 0.6 ha per site with sites stratified by soil type across a 28 ha area) to one of four treatments: summer burns (June-September), fall burns (October-December), winter burns (January-March), or unburned (fire exclusion, unmanaged control). For each set of six experimental sites assigned to the summer, fall, and winter treatments, all sites were burned in 2001, 2002, 2004, 2008, 2013, 2015, and 2017, during their respective prescribed fire seasons. At the time of sampling (2019), this equated to a mean fire frequency of 0.39/yr and mean fire return interval of 2.7 yr for the burned sites. Based on observed fire weather for the three most recent years (2013, 2015, and 2017), summer burns occurred within ranges of 33-38°C, 35-57% relative humidity (RH), and surface wind speeds of 3-14 km/h; fall burns occurred at 17-26°C, 34-62% RH, and surface wind speeds of 3-11 km/h; winter burns occurred at 12-21°C, 23-44% RH, and surface wind speeds of 5-13 km/h. Although the experimental sites are of restoration interest to the Wildflower Center, there have been no restoration interventions (such as seed additions or herbicide control of exotics) other than prescribed fire.

Selection of Old-growth Grasslands

In central Texas, plant communities are rare that fit the descriptions of the historical grasslands of the Edwards Plateau and Blackland Prairie ecoregions (Landers 1987) and conform to the concept of old-growth grasslands (Veldman et al. 2015). Because the Wildflower Center does not support any old-growth grasslands, in April 2019, prior to sampling the experimental sites, we surveyed the Water Quality Protection Lands to identify sites that could serve as reference communities for assessment of restoration outcomes in the experiment. To target our surveys, we first mapped areas where land managers knew of populations of the long-lived perennial C_4 grasses *Andropogon gerardii*, *Bouteloua curtipendula, Schizachyrium scoparium*, or *Sorghastrum nutans* (Landers, 1987). With those areas as starting points, we found six sites that met the following criteria. All sites: 1) burned at least once since 2007, 2) were dominated by one or more of the aforementioned native perennial C_4 grasses, 3) had low cover of exotic invasive grasses (visually estimated to be <10%), 4) lacked dense trees and shrubs indicative of chronic fire exclusion, 5) occurred on well-drained clay soils that were comparable to those of the Wildflower Center, and 6) were large enough to accommodate a 20 × 50-m sampling plot.

The City of Austin began conducting prescribed burns on these old-growth grassland sites between 2007 and 2010, with a mix of winter and summer burns. Then from 2010 to 2017, all burns were conducted in the summer. From 2007 to the time of sampling in 2019, mean fire frequency for the old-growth sites was 0.18/yr with mean fire return interval of 6.8 yr. Four out of the six old-growth grassland sites last burned in the summer 2017, two years prior to sampling; of the other two sites, one was last burned in the summer of 2015 and the other in 2010. Typical ranges for fire weather during summer burns was 32-37°C, 30-41% RH, and surface wind speeds of 11-16 km/h.

According to the ecological site descriptions (i.e., soil-vegetation associations) of the United States Department of Agriculture, Natural Resource Conservation Service (USDA-NRCS), the experimental sites at the Wildflower Center are classified as mix of Redland (USDA 2013a) and Deep Redland (USDA 2013b), while the old-growth sites on the Water Quality Protection Lands are classified as a mix of Gravelly Redland (USDA 2013c), Low Stony Hill (USDA 2013d), and Redland (USDA 2013a). A *post hoc* reading of these ecological site descriptions (after sampling and analysis of herbaceous plant communities) suggests that the old-growth grassland sites that we selected are indeed among the best remaining, and geographically closest, examples of the reference ecosystem for the experimental sites at the Wildflower Center. The four ecological site descriptions (USDA 2013a-d) are extremely similar in herbaceous plant community composition, topography, soil characteristics, and ecological dynamics, including responses to fire and grazing. Our old-growth grassland sites span a range of conditions that overlap with the composition and vegetation structure of all four descriptions, and are not clearly better matches to any one description compared to the others (USDA 2013a-d). We view this as consistent with the standards of the Society for Ecological Restoration (Gann et al. 2019), which suggests identification of multiple reference sites that cover the range of variation that occurs in the reference ecosystem. As further evidence that our old-growth grasslands are appropriate reference sites, we note that the Wildflower Center supports small remnant populations of the grass species that dominate the old-growth grassland sites (Appendix S1: Table S1), and that these same species are listed as the dominant tall- and midgrasses in the Redland, Deep Redland, Gravelly Redland, and Low Stony Hill ecological site descriptions (USDA 2013a-d).

Field Sampling

At both the Wildflower Center and Water Quality Protection Lands, we sampled the herbaceous-layer community and woody canopy cover in both spring (30 April – 23 May) and fall (7 October – 1 November) of 2019; during the fall sampling only, we also quantified invasive grass cover and measured the woody plant community (i.e., density of trees, shrubs, and vines). In each site, we established a 20 × 50-m plot (hereafter 1000 m^2), which contained ten evenly spaced 1 × 1-m subplots (hereafter 1 m^2) and two 50-m transects spaced 10 m apart (Appendix S1: Fig. S2; modified from Peet et al. 1998). At the Wildflower Center, we used ArcGIS version 10.6.1 to center the plots in each experimental site, and thereby maximize the distance between the edges of the plot and boundary of the treatment area. For old-growth grasslands at the Water Quality Protection Lands, we randomly positioned plots in larger sites and oriented the plots to fit within smaller sites.

To characterize grassland plant community composition, richness, and diversity, we identified all herbaceous-layer plants (i.e., graminoids, forbs, shrubs, vines, and small trees <1.3 m tall) that were rooted in each of the ten 1-m^2 subplots. After sampling subplots, we recorded the presence of additional herbaceous-layer species within the full 1000 m^2 plot. To measure invasion by exotic grasses, during fall sampling, we used a gridded quadrat to visually estimate the percent cover of *B. ischaemum* rooted within each 1-m^2 subplot. We identified all grass species following Gould (1975) and all other species following Diggs et al. (1999). To verify species identities, we collected specimens to compare with the collection at the S.M. Tracy Herbarium at Texas A&M University.

To assess vegetation structure, we estimated the percent cover of live herbaceous material (i.e., green material, not species-specific, excluding woody species) rooted in or overhanging each 1-m^2 subplot. We measured canopy cover of trees and shrubs with a spherical canopy densiometer held at 1.3 m above each 1-m^2 subplot (Lemmon 1956). To determine the stem density of shrubs and small trees (≥1.3 m tall and <5 cm diameter at breast height of 1.3 m, DBH), as well as small woody vines (≥1.3 m long and <2.5 cm diameter, Gerwing et al. 2006), we counted stems that occurred in two 50 × 2-m belt transects. To determine basal area, we first measured the DBH of all trees 5 to 10 cm DBH, and woody vines ≥2.5 cm in diameter in two 50 × 4-m transects. For trees ≥10 cm DBH, we sampled the entire 1000 m^2. Because *Juniperus ashei* and *Prosopis glandulosa* branch extensively below 1.3 m, we recorded the diameter at root collar for these species, instead of DBH (adapted from USDA 2015).

Statistical Analyses

For all analyses, we treated the $n = 6$ plots per treatment as statistical replicates. For compositional analyses, we combined the fall and spring data to determine the presence of each species in the ten 1-m^2 subplots and the 1000-m^2 plot. We then scored the within-plot frequency of each species on a scale of 0 to 11: a score of 0 indicated the species was absent; a rank of 1 indicated the species was present in the 1000-m^2 plot, but not in any 1-m^2 subplots; and ranks of 2 to 11 correspond to the frequency of a species in the 1-m^2 subplots (i.e., species present in all ten subplots scored an 11). We chose to use within-plot frequency instead of cover-based abundances because we wanted our community measures to emphasize the presence of locally rare species, which are important in restoration and tend to be down-weighted in cover-based abundance estimates. Also, we used frequency, instead of cover, because cover by species varies throughout the year with phenology, and because cover underrepresents species that invest in belowground biomass (Pausas et al. 2018). For data collected on multiple subplots or transects within each plot (e.g., small stem density), or measured in both spring and fall (e.g., woody canopy cover), we calculated the arithmetic mean of the multiple measurements to represent each plot in the analyses. The one exception to this approach was our logistic modeling of the local-scale relationship between canopy cover and invasive grass cover, in which we retained the data from 1-m^2 subplots and treated plots as statistical blocks (see description of *B. ischaemum* analyses below).

To visualize compositional differences among experimental sites in relation to old-growth grasslands, we ordinated sites based on their herbaceous-layer species with non-metric multidimensional scaling (NMDS). We performed the NMDS in R v. 3.6.2 (R Core Team 2019) using the *Vegan* package (Oksanen et al. 2019), based on Bray-Curtis dissimilarity and using k = 3 dimensions. To identify the species driving the separation of sites in the ordination, we used the envfit() function in *Vegan* to select significant species with $p < 0.001$, based on randomizations with 999 permutations. To interpret how plant functional types were distributed among treatments, we classified the significant species by duration (annual/biennial or perennial) and placed them in one of the following groups: forbs, C_3 graminoids (i.e., grasses and sedges), C_4 graminoids, trees, shrubs, or vines (Gould, 1975, Diggs et al. 1999).

To determine the potential for fire treatments to restore historical plant communities, we calculated the mean compositional similarity between each experimental plot at the Wildflower Center and each of the six old-growth grassland plots at the Water Quality Protection Lands, as 1 – (Bray-Curtis Dissimilarity Index). To determine reference values for this similarity metric (i.e., expected beta-diversity of fully restored grasslands), we calculated the mean similarity of each old-growth plot to the other five old-growth grasslands. To compare plant diversity among treatments, we analyzed herbaceous-layer species richness at the 1-m^2 and 1000-m^2 scales and calculated Shannon-Wiener and Simpson's (1-D) diversity indices, based on within-plot frequency scores (0-11) for each species. We assessed the effects of fire treatments on vegetation structure in analyses of herbaceous cover, canopy cover of trees and shrub, tree basal area ($\geq$5 cm DBH), and small stem density ($\geq$1.3 m tall and <5 cm DBH). We tested for main effects of treatments using ANOVA and Tukey's Honestly Significant Difference (HSD) post-hoc comparison in R v. 3.6.2 (R Core Team 2019). Prior to analysis, we applied square root transformations to woody canopy cover, tree basal area, and small stem density data, which were not normally distributed.

To assess the effects of seasonal burn treatments on exotic grass invasion, we used a series of analyses. To start with, just as for the diversity and structural variables, we compared cover of *B. ischaemum* among treatments with ANOVA and Tukey's HSD. To determine if summer fires reduce grass invasion by altering the relationship between canopy cover and *B. ischaemum*, we performed linear regressions for all experimental sites (n = 24), summer burn plots individually (n = 6), and other experimental treatments combined (i.e., fall, winter, and unburned, n = 18). To understand the apparently different canopy-grass relationship in summer sites versus the other treatments, we used logistic regression to model the probability of invasion by *B. ischaemum* in 1-m^2 subplots as a function of canopy cover. This approach let us assess the canopy-invasion relationship at the local scale at which tree-grass interactions occur (Hoffmann et al. 2012), and thus detect relationships that might be obscured at the plot scale (1000 m^2). To set a threshold for invasion, we produced a frequency histogram of *B. ischaemum* cover in 1-m^2 subplots for all treatments combined (*N* = 240). We visually inspected the distribution, which was zero inflated and roughly bimodal, to establish a cutoff between subplots with high cover (≥25%) versus those with low cover or absence (<25% cover) of *B. ischaemum* (Appendix S1: Fig. S3). We created logistic regression models to predict high invasive grass cover in subplots of each experimental fire treatment, with canopy cover as a fixed effect and plot (*n* = 6 per treatment) as a random effect. We fit these mixed effects models in R v. 3.6.2 (R Core Team 2019) using the glmer() function from the *Lme4* package (Bates et al. 2015).

RESULTS

Herbaceous-Layer Community Composition and Diversity

The historically fire-excluded and overgrazed grasslands at the Wildflower Center, regardless of experimental fire treatments during 2001-2019, were compositionally distinct from old-growth grasslands on the Water Quality Protection Lands. Across these locations, we recorded a total of 253 herbaceous-layer species, of which 34 were present only in old-growth grasslands and 71 were present only in the experimental sites (Appendix S1: Table S1). In our ordinations of plant communities, old-growth grasslands were separated from the experimental sites along NMDS axis 1 (Fig. 1a). Significant species associated with old-growth grasslands in the ordination were: perennial C_4 grasses, *Andropogon gerardii, Bouteloua curtipendula, Bouteloua rigidiseta, Schizachyrium scoparium,* and *Sorghastrum nutans*; perennial forbs, *Brickellia cylindracea, Convolvulus equitans, Glandularia bipinnatifida, Hedyotis nigricans, Lespedeza texana, Liatris mucronata, Rhynchosia senna, Stillingia texana,* and *Wedelia texana*; and annual forbs, *Chamaesyce serpens, Evax verna, Galium virgatum, Hedeoma acinoides, Hymenopappus tenuifolius, Tetraneuris linearifolia,* and *Warnockia scutellarioides,* (Figs 1b-c).

Among the seasonal fire treatments, NMDS axis 2 separated the unburned sites from the summer sites (Fig. 1a), with the fall and winter sites appearing intermediate in composition. The position of significant species and functional types along NMDS axis 2 (with many forb species associated with summer sites and species of tree, shrub, and vine associated with unburned sites) suggests that NMDS axis 2 reflects a fire-intensity and light-availability gradient (Fig. 1b-c). The species at the summer burn end of NMDS axis 2 were: a perennial C_3 grass, *Nassella leucotricha;* an annual C_3 grass *Sphenopholis interrupta;* annual forbs, *Agalinis heterophylla, Gaura brachycarpa, Geranium carolinianum*, *Lepidium virginicum, Rudbeckia hirta,* and *Triodanis perfoliata;* perennial forbs, *Ambrosia psilostachya, Bouchetia erecta, Evolvulus sericeus*, and *Sida abutifolia*. At the unburned end of axis 2, characteristic species of the herbaceous layer were: small shrubs and trees (<1.3 m tall individuals), *Berberis trifoliolata, Celtis laevigata, Diospyros texana, Forestiera pubescens, Juniperus ashei, Quercus fusiformis*, and *Sideroxylon lanuginosum*; perennial climbing vines, *Cissus incisa, Matelea reticulata,* and *Smilax bona-nox;* an annual C_3 sedge, *Carex planostachys*; and an annual forb, *Parietaria pensylvanica*. Consistent with the equidistant separation of old-growth grasslands and experimental sites along NMDS axis 1 (Fig. 1a), none of the experimental treatments were superior at improving compositional similarity to the reference old-growth grasslands (mean similarities to old growth of 0.43 to 0.46; Fig. 2).

At the 1000-m^2 scale, plant diversity of all experimental sites was similar to old-growth grasslands: we found no significant differences in herbaceous-layer species richness (Fig. 3a), Shannon-Wiener diversity (Appendix S1: Fig. S4a), or Simpson's diversity (Appendix S1: Fig. S4b). Likewise, mean local-scale species richness (mean richness in 1-m^2 subplots) in fall and winter sites did not differ significantly from either unburned sites or old-growth grasslands (Fig.

3b). By contrast, local-scale species richness was higher in both old-growth grasslands (mean 20 species/m^2; p=0.015) and summer sites (mean 23 species/m^2; p<0.001) compared to unburned sites (mean 15 species/m^2; Fig. 3b).

Vegetation Structure

In two key aspects of vegetation structure—herbaceous ground cover and woody canopy cover—sites that were burned, regardless of season, were similar to old-growth grasslands (Fig. 4a,b). Unburned sites had far lower herbaceous cover (mean 27%) and higher woody canopy cover (mean 67%) compared to old-growth grasslands (means of 70% and 9%, for herbaceous and canopy cover, respectively, Fig. 4a,b). Among fire treatments, only summer sites consistently approximated old-growth grassland structure for all variables (i.e., herbaceous cover, woody canopy cover, tree basal area, and small stem density) while also differing consistently from the woody-dominated unburned sites (Fig. 4a-d). For winter sites, tree basal area (mean 2.5 m^2/ha) was similar to old-growth grasslands (mean 2.7 m^2/ha) and lower than unburned sites (mean 22.6 m^2/ha), but small stem density was intermediate to (i.e., not significantly different from) unburned and old-growth sites. Of note, among the burned sites, the fall treatment had the greatest variation in all structural variables, and did not differ significantly from unburned sites or old-growth sites in basal area or small stem density (Fig. 4c,d).

Invasive Grass Cover

Cover of the invasive grass, *Bothriochloa ischaemum*, was low in summer and unburned sites (mean 6% and 10%, respectively), and highest in winter sites (mean 51%; Fig. 5); cover in fall burned sites (mean 23%) was not significantly different from any other treatment. Linear regression of *B. ischaemum* cover in relation to woody canopy cover indicated that summer burns produced a very different canopy-grass relationship than we observed across other treatments. Whereas *B. ischaemum* cover declined as a function of canopy cover across winter, fall, and unburned sites combined, summer burns constrained both woody canopy cover and invasive grass cover (Fig. 6).

To further examine the relationship between fire season, woody canopy cover, and *B. ischaemum* invasion, we constructed a logistic regression model to relate the odds of high invasive grass cover (≥25%) in subplots of 1 m^2 (Appendix S1: Fig. S3) to canopy cover. Independent logistic models (Table 1) for fall, winter, and unburned sites, all showed significant negative relationships between woody canopy cover and odds of high *B. ischaemum* cover. By contrast, no such relationship with canopy existed for summer burned sites; the significant negative intercept in the summer burn model indicates consistently low odds of invasion, even where there is no canopy cover (Table 1).

DISCUSSION

After 18 years and seven prescribed fires in historically fire-excluded and overgrazed grasslands, burning in any of three seasons (i.e., summer, fall, or winter) produced the vegetation structure of old-growth grasslands, but did not restore plant community composition. Grasslands destroyed by afforestation or tillage agriculture are typically slow to recover in the absence of introduced propagules (Nerlekar and Veldman 2020). But, because our experimental sites had no known history of intensive soil disturbance and began the experiment in 2001 with generally open vegetation structure, we hypothesized that burning would move plant community composition closer to that of old-growth grasslands. Contrary to our hypothesis, our compositional results gave no indication of old-growth grassland community recovery in response to summer burns, nor any other treatment (Figs. 1, 2). These results are consistent with a growing body of literature on the limitations of grassland restoration without the addition of propagules, whether with prescribed fire (Laughlin et al. 2008) or without (Cava et al. 2018). This lack of community recovery is often attributed to propagule limitation: previous studies have concluded that long-lived perennial bunch grasses and forbs, which characterize old-growth grasslands, have such poor colonization potential (Buisson et al. 2019) that even nearby remnant populations of old-growth species may contribute little to community recovery (e.g., Turley et al. 2017). In our study, the experimental sites are isolated from the nearest old-growth grasslands and seeds of conservative grassland species would have to disperse long distances. Despite the failure of prescribed fire to restore species composition, we found that prescribed fire is able to reduce woody encroachment, and that fire season was important to restoring local-scale species richness and limiting invasive grass cover.

Season of burn influenced local-scale species richness and the characteristic plant functional types in the experimental sites. Summer burning was the only fire treatment that resulted in local-scale (1 m^2) species richness that was both greater than unburned sites and equivalent to old-growth grasslands (Fig. 3b). Because summer burns controlled both woody plants and invasive grasses (Figs. 4-6), we suggest reduced competition as a mechanism for high local-scale species richness (e.g., Myers and Harms 2009). Indeed, several previous studies in North American grasslands found summer burns to promote forb richness by controlling woody encroachment and limiting the abundances of dominant grasses (Engle et al. 1998, Towne and Kemp 2008, Howe 2011). Such effects on richness did not extend to the plot scale (1000 m^2; Fig. 3a): all treatments, including unburned sites, supported herbaceous-layer plant diversity that was equivalent to old-growth grasslands (Appendix S1: Fig. S4). Although richness within plots was similar, community composition and characteristic plant functional types were quite different.

Old-growth grasslands were characterized by perennial C_4 grasses such as *Bouteloua curtipendula, Bouteloua rigidiseta, Schizachyrium scoparium*, and *Sorghastrum nutans*, whereas experimental fire sites were characterized by the C_3 grasses *Nassella leucotricha* and *Sphenopholis interrrupta* (Fig. 1b). Certain long-lived forbs with underground storage organs (Zaloumis and Bond 2011), such as *Liatris mucronata* (corm) and *Stillingia texana* (woody taproot and rhizomes), only occurred in old-growth grasslands (Fig. 1b, Appendix S1: Table S1). Experimental sites sorted along an apparent fire-intensity gradient of light-demanding herbaceous species in summer burn sites to shade-tolerant woody species in unburned sites, with fall and winter sites intermediate in composition (Fig. 1b,c). Such sorting of species by fire- and shade-tolerance is well-documented across other grassland-woodland boundaries (e.g., Cavender-Bares and Reich 2012). The importance of C_3 grass species at the summer burn end of NMDS axis-1 (Fig. 1c) is reminiscent of other seasonal prescribed fire studies, which indicate summer fires promote C_3 grasses by limiting the dominance of C_4 grasses (Howe 1994, Engle et al. 1998, Howe 2011).

Prescribed fire in any season limited woody encroachment, but summer and winter burns most consistently maintained the vegetation structure of old-growth grasslands. As in many studies on the use of prescribed fire to restore vegetation structure (e.g., Ruth et al. 2007, Scott et al. 2012, Bassett et al. 2020), our results show that fire in any season produces herbaceous cover and canopy cover similar to old-growth grasslands, while fire exclusion (i.e., unburned treatment) resulted in woody dominance and reduced herbaceous cover (Fig. 4). For tree basal area and small stem density, only summer burns maintained these two structural attributes at the low levels of old-growth grasslands and significantly lower than unburned sites (Fig. 4c,d). Some prior studies on seasonal burning for control of woody species have found summer burns to be more effective than winter burns (Taylor et al. 2012), while other studies show no difference in season (Cronan et al. 2015). We found that like summer burns, winter (late cool season) burns also maintained canopy cover and tree basal area at the levels of old-growth grasslands (Fig. 4b,c). Although ambient temperatures during winter burns are much lower than during summer burns, fuel moisture tends to be uniformly low in the winter due to little live (green) fine fuel in the herbaceous layer. High fire intensity, which is strongly related to ambient temperatures and fuel moisture content (Twidwell et al. 2009, Rissi et al. 2017), would explain why both summer (high temperatures) and winter burns (cool temperatures but low fuel moisture) reliably maintained low canopy cover and tree basal area, whereas the combined cool temperatures and higher moisture conditions of fall burns did not (see differences in ranges, Fig. 4). In addition to higher temperatures, several authors propose that spring and summer burns decrease post-fire resprouting by top-killing trees when belowground carbohydrate reserves are low (Drewa 2003, DiTomaso et al. 2006). This hypothesis offers a plausible explanation for why summer burns in our experiment, but not winter or fall burns, maintained small stem density at levels that were significantly lower than unburned sites (Fig. 4d).

We found that prescribed fires in the summer simultaneously maintained low woody canopy cover and controlled invasion by an exotic invasive grass, *Bothriochloa ischaemum* (Fig. 4-6). In general, *B. ischaemum* invasion is constrained by canopy cover (Fig. 6; Gabbard and Fowler 2007), which means that when prescribed fire limits woody plants, it also produces sunny conditions suitable for invasion. Thus, *B. ischaemum*, like other invasive fire-adapted C_4 grasses (e.g., Reed et al. 2005), poses a major challenge to the use of prescribed fire to restore communities of fire-dependent native grasses and forbs (Buisson et al. 2019). Previous short-term studies showed that a single late summer fire (September and October) could reduce *B.*

ischaemum by 10 to 88% (Simmons et al. 2007, Reemts et al. 2018). Menke and Trlica (1981) and Ruckman et al. (2012) proposed that summer burns decrease *B. ischaemum* populations because fires occur at a time when belowground carbohydrate stores are low and aboveground biomass investment is high (i.e., during periods of flowering). High fire intensity offers another explanation for why *B. ischaemum* is limited by summer fires. Havill et al. (2015) found that *B. ischaemum* rose to higher internal temperatures and had greater sensitivity to increased soil temperatures at a shallower depth than the native C_4 bunch grass, *S. scoparium*. Whatever the mechanism may be**,** our study offers the first long-term experimental evidence that summer burns can control *B. ischaemum* while maintaining the vegetation structure of old-growth grasslands. By analyzing the relationship between woody canopy cover and invasive grass cover at both the 1000 m^2 and 1 m^2 scales, we confirmed that low mean *B. ischaemum* cover in summer sites (Fig. 5) was not merely an artifact of mean canopy cover at the plot-scale (Fig. 6), but due to reduced probability of dense invasive grass cover at the local-scale at which tree-grass interactions occur (Table 1, Hoffmann et al. 2012).

Although our results point toward the benefits of summer fires, future research on grassland restoration in central Texas should also consider spring burns. Prescribed fires in late March through May would correspond with a seasonal transition period of high precipitation, frequent lightning, and ample quantities of dead fine fuel (Appendix S1: Fig. S1; Noss et al. 2015). Unfortunately, where C_4 bunchgrass abundance is low, due to overgrazing and woody encroachment, grasslands often lack the dead fine fuel needed to carry a spring fire through a fuel bed of green C_3 graminoids and forbs. Thus, active restoration of C_4 grasses appears to be a prerequisite for spring prescribed fires. Once fuels permit, we should expect spring fires to have seasonal effects on restoration of community compositions that are distinct from the summer, fall, and winter fires tested in this experiment. For example, restoration studies in other North American grasslands found that spring fires increase the abundance of C_4 grass species (Howe 1994, Howe 2011), whereas summer fires increase the abundance of cool-season C_3 grasses and forbs (Engle et al. 1998). Consistent with this pattern, our summer burn sites were characterized by two C_3 grasses (Fig. 1c) and with limited invasion by an exotic C_4 grass (Fig. 5). If future research shows spring fires can help restore community composition of old-growth grasslands, it may be necessary to intersperse occasional summer burns to control invasive grasses.

CONCLUSION

Our results show that after 18 years and seven prescribed fires in historically fire-excluded and overgrazed grasslands of central Texas, burning in different seasons (i.e., summer, fall, winter) produced different herbaceous-layer plant communities, and resulted in different levels of control of woody plants and invasive grasses. Of the seasons tested, summer burns restored vegetation structure, local-scale species richness, and invasive grass abundance to levels that closely approximated old-growth grasslands. Because interactions between fire season and plant phenology differ among ecosystems, we view our results not as an endorsement of summer fires *per se*, but as a demonstration that the strategic use of fire in particular seasons can benefit restoration. Nonetheless, it is notable that the timing of our summer burns corresponded with the lightning season, and thus the fire season under which old-growth grassland species would have evolved (Noss et al. 2015). In addition to the importance of fire season, our results underscore the conservation value of old-growth grassland plant communities: even after cessation of grazing and reintroduction of fire over 18 years, the historically overgrazed and fire-excluded grasslands in this study did not recover their former species composition. Efforts to restore plant community composition in grasslands of Central Texas, like many other tropical and subtropical grasslands globally, will need to combine prescribed fire with sowing of native perennial C_4 grasses and long-lived forbs (Buisson et al. 2019). As such efforts proceed, we recommend that ecologists and land managers give appropriate consideration to fire season and that environmental policymakers recognize the critical role prescribed fire plays in grassland conservation and restoration.

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SUPPORTING INFORMATION

Additional supporting information may be found online at:

http://onlinelibrary.wiley.com/doi/10.1002/ecs2.XXXX/full

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository at:

https://doi.org/10.5061/dryad.mcvdnck06.

TABLES

TABLE 1. Results of logistic regressions that modeled the probability of high local-scale invasive grass cover (i.e., *Bothriochloa ischaemum* cover ≥25% in 1-m^2 subplots) as a function of canopy cover (trees and shrubs ≥1.3 m measured above each 1-m^2 subplot) in the prescribed fire experiment. For each fire treatment, there were $n = 6$ sites per treatment and 10 subplots per site. In the models, we treated site ($n = 6$) as a random effect, enabling us to focus on local-scale relationships between grass invasion and woody canopy cover. To describe the range of inference of these models, the minimum (min) and maximum (max) values for canopy cover and invasive grass cover are listed for the 60 subplots (in $n = 6$ sites) per model.

	Model Parameters		Range of values in $N = 60$, 1-m^2 subplots	
	Woody canopy cover	Intercept	Woody canopy cover (%, min – max)	Invasive grass cover (%, min – max)
Logistic Model:				
Summer	-0.176	-2.389**	0 – 97	0 – 87
Fall	-0.059*	-0.145	0 – 97	0 – 97
Winter	-0.108**	1.602	0 – 92	0 – 99
Unburned	-0.064**	0.069	0 – 98	0 – 90

Note: *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$

FIGURE CAPTIONS

FIG. 1. Non-metric multidimensional scaling (NMDS, $k = 3$ dimensions, stress = 0.091) of plant communities in an 18-yr prescribed fire experiment and old-growth grasslands ($n = 6$ sites per treatment). (a) Ordination of sites based on herbaceous layer species composition; ellipses depict 95% confidence for treatment centroids. (b) Characteristic taxa, with significant species factors (i.e., $p < 0.001$ based on 999 permutations), plotted to show their relationships to the sites in each treatment; see (a) for symbols. (c) Characteristic taxa classified by duration and functional type; for comparison to treatments, the 95% confidence ellipses are repeated from (a).

FIG. 2. Compositional similarity (i.e., 1 – Bray Curtis Dissimilarity) between herbaceous layer plant communities in the prescribed fire experiment and old-growth grasslands ($n = 6$, 1000-m^2 sites per treatment). For reference, data is also plotted for mean similarity of each of old-growth site ($n = 6$) to the other five old-growth sites. Boxplots display quartiles. Letters indicate significant differences in means at $p < 0.05$ (ANOVA and Tukey's HSD pairwise comparisons).

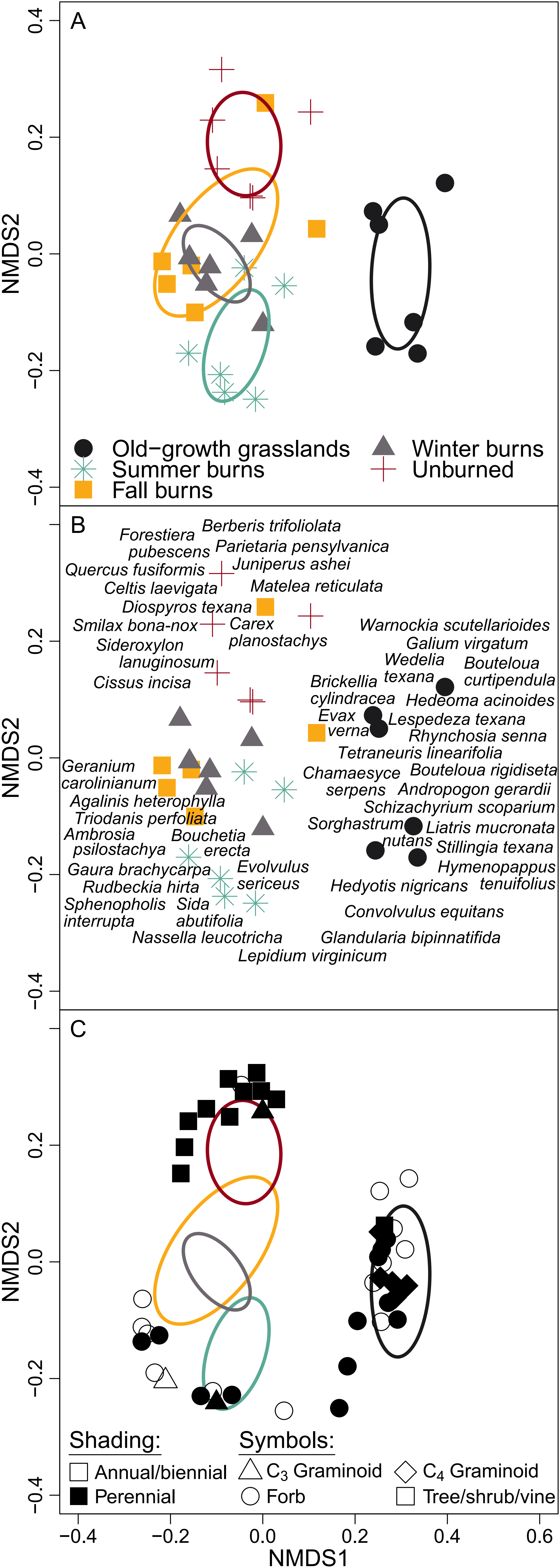
FIG. 3. Herbaceous-layer plant species richness in the prescribed fire experiment and old-growth grasslands ($n = 6$ per treatment) at the (a) 1000-m^2 and (b) 1-m^2 scales. Boxplots display quartiles. Letters indicate significant differences in means at $p < 0.05$ (ANOVA and Tukey's HSD).

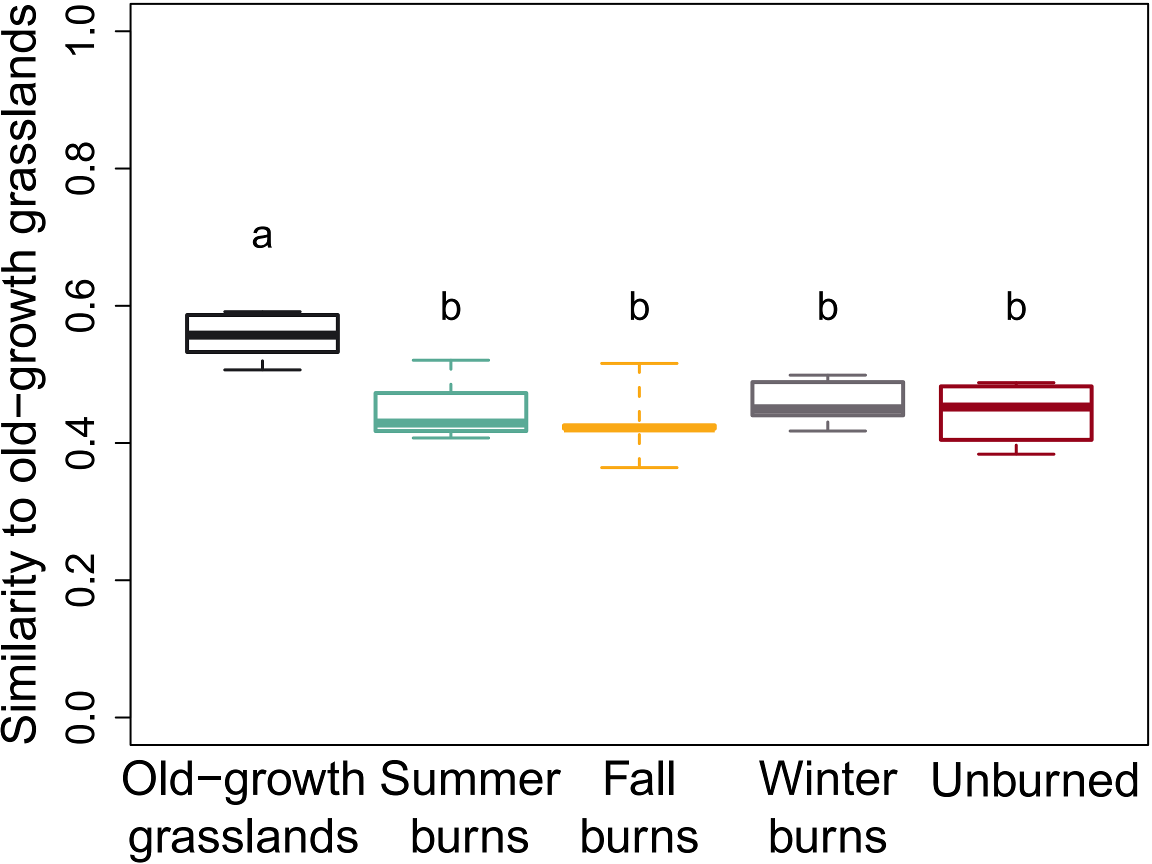
FIG. 4. Vegetation structure in the prescribed fire experiment and old-growth grasslands ($n = 6$ per treatment). (a) Mean cover of herbaceous plants (graminoids and forbs). (b). Mean woody canopy cover (trees and shrubs ≥ 1.3 m). (c) Mean tree basal area (≥ 5 cm diameter). (d) Mean small stem density (woody plants ≥ 1.3 m tall and < 5 cm diameter). Boxplots represent

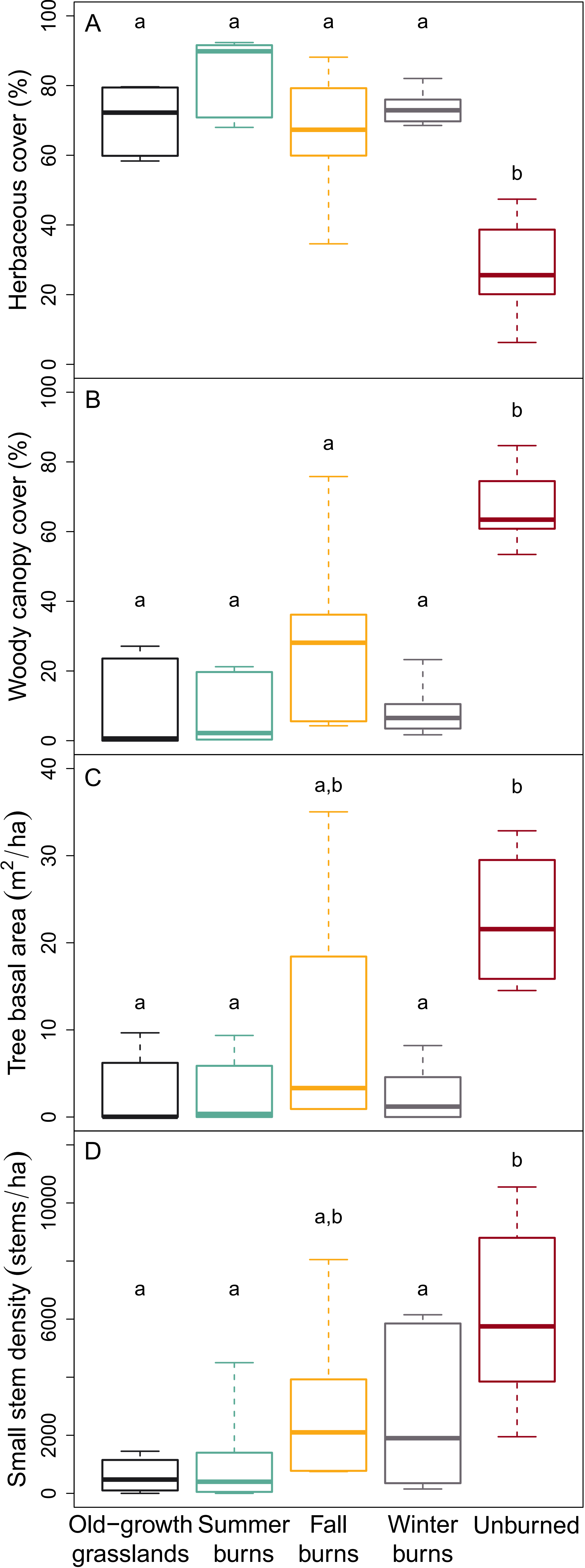
quartiles. Letters indicate significant differences in means at $p < 0.05$ (ANOVA and Tukey's HSD).

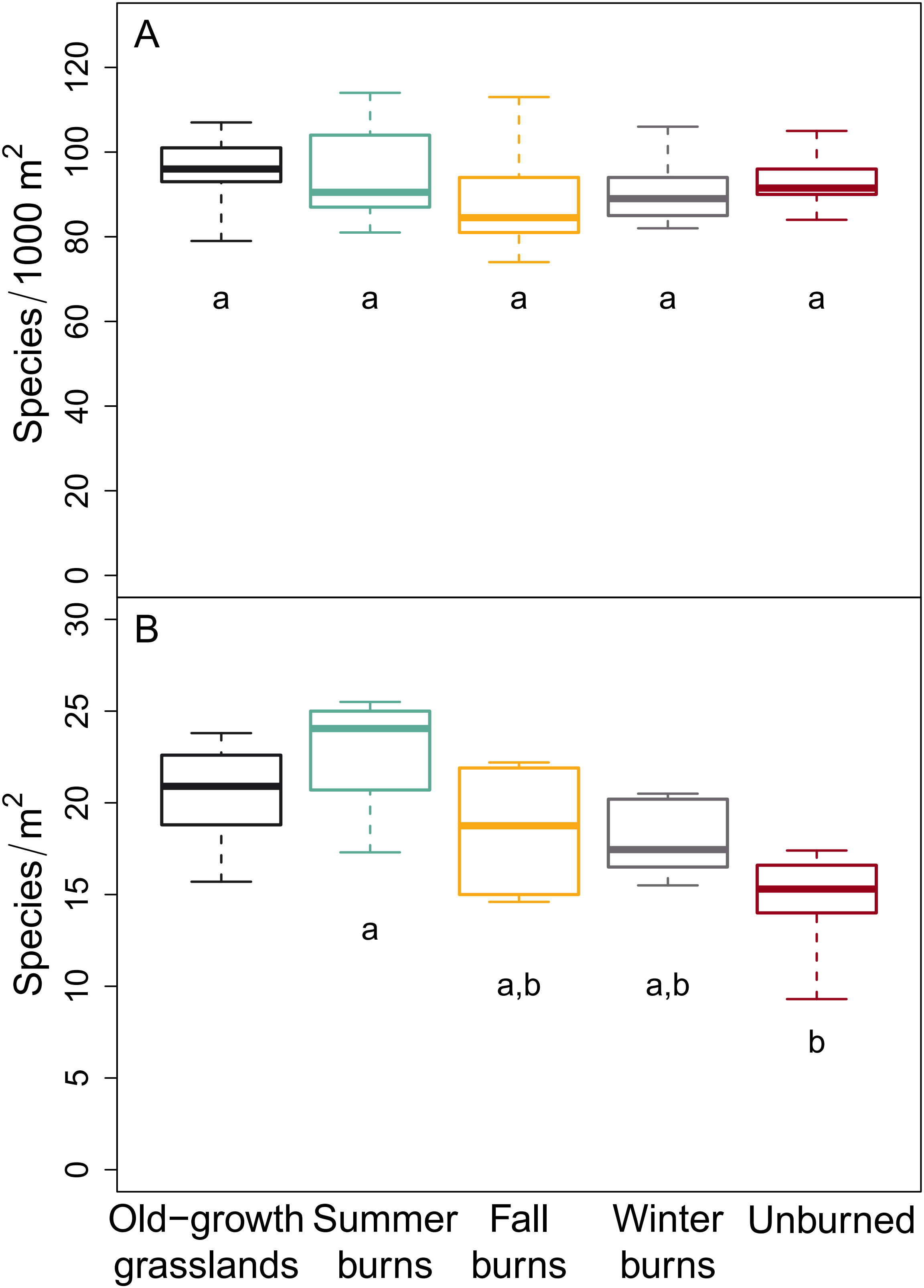
FIG. 5. Cover of the invasive grass, *Bothriochloa ischaemum,* in the prescribed fire experiment and old-growth grasslands ($n = 6$ sites per treatment). Boxplots represent quartiles and letters indicate differences in means at $p < 0.05$ (ANOVA, Tukey's HSD).

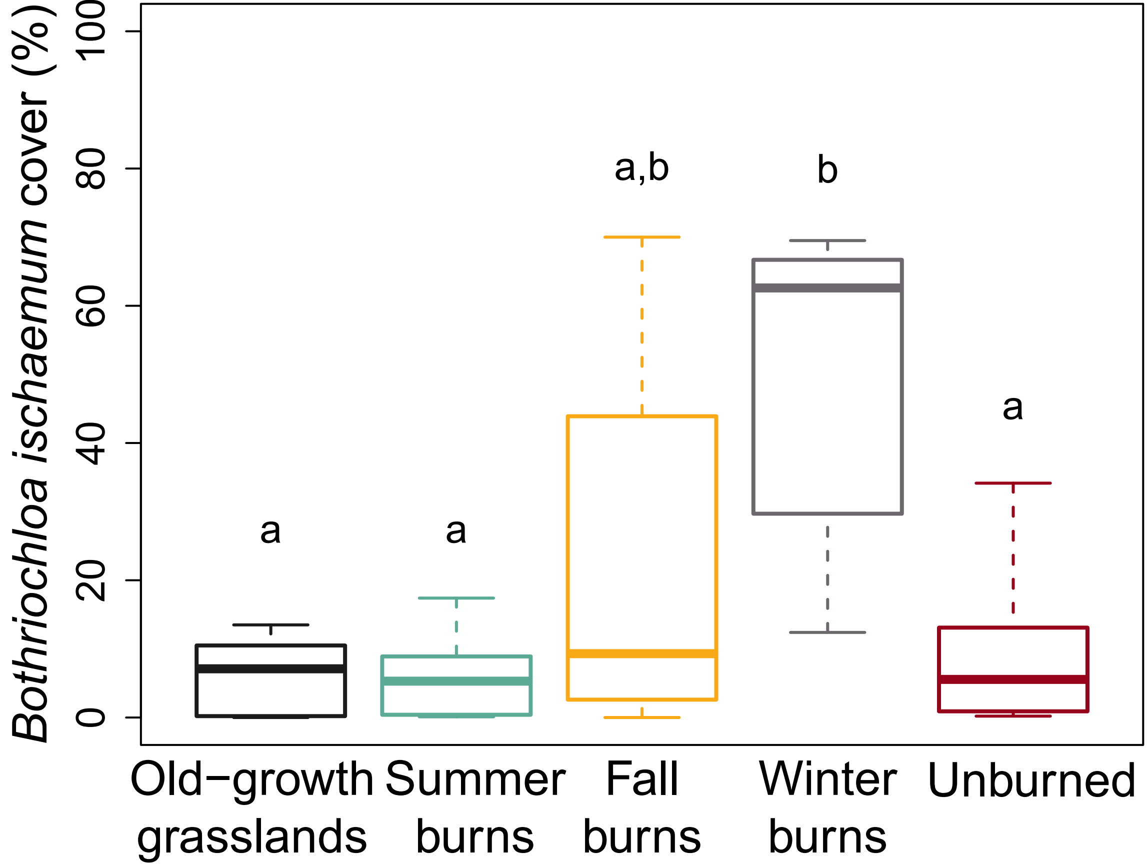
FIG. 6. Relationship between cover of the invasive grass, *Bothriochloa ischaemum*, and woody canopy cover (trees and shrubs ≥1.3 m) in the prescribed fire experiment ($n = 6$ sites per treatment). Displayed as a dashed black line, the regression equation for all four treatments combined was: *B. ischaemum* cover = -0.37(canopy cover) + 32.77, $n = 24$, $r^2 = 0.17$, $p = 0.046$. Excluding the summer treatment (non-significant trend line, $n = 6$) and displayed as a solid black line, the regression equation for the fall, winter, and unburned sites combined was: *B. ischaemum* cover = -0.64(canopy cover) + 50.10, $n = 18$, $r^2 = 0.47$, $p = 0.0017$.

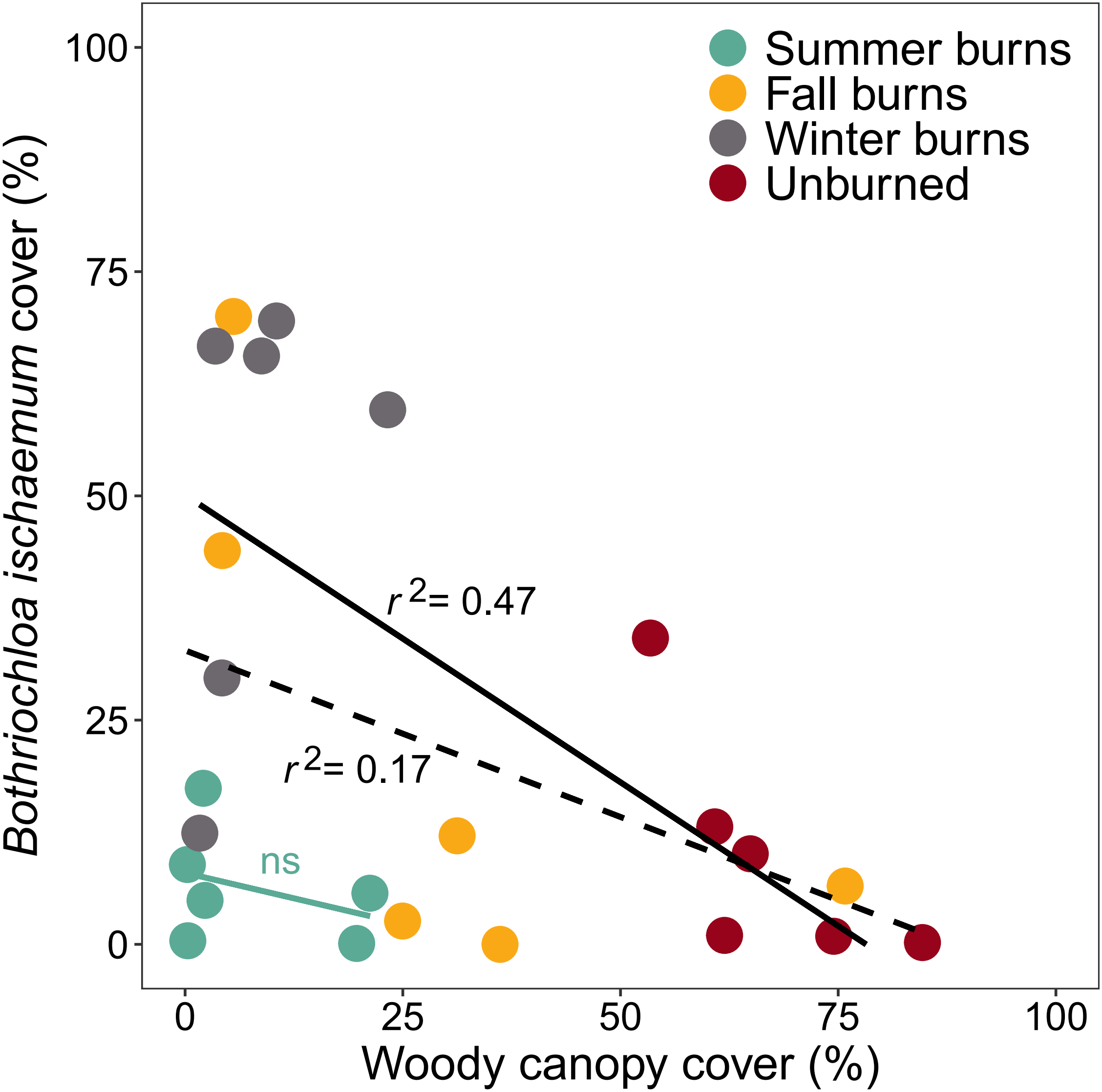

A
0.4
0.2
0.0
−0.2
−0.4
NMDS2
Old−growth grasslands
Summer burns
Fall burns
Winter burns
Unburned
B
Forestiera pubescens
Berberis trifoliolata
Parietaria pensylvanica
Quercus fusiformis
Juniperus ashei
Celtis laevigata
Matelea reticulata
Diospyros texana
Smilax bona-nox
Carex planostachys
Sideroxylon lanuginosum
Cissus incisa
Warnockia scutellarioides
Galium virgatum
Wedelia texana
Bouteloua curtipendula
Brickellia cylindracea
Hedeoma acinoides
Evax verna
Lespedeza texana
Rhynchosia senna
Tetraneuris linearifolia
Chamaesyce serpens
Bouteloua rigidiseta
Andropogon gerardii
Schizachyrium scoparium
Sorghastrum nutans
Liatris mucronata
Stillingia texana
Hymenopappus tenuifolius
Hedyotis nigricans
Convolvulus equitans
Glandularia bipinnatifida
Lepidium virginicum
Geranium carolinianum
Agalinis heterophylla
Triodanis perfoliata
Ambrosia psilostachya
Bouchetia erecta
Gaura brachycarpa
Evolvulus sericeus
Rudbeckia hirta
Sphenopholis interrupta
Sida abutifolia
Nassella leucotricha
C
Shading:
Annual/biennial
Perennial
Symbols:
C3 Graminoid
C4 Graminoid
Forb
Tree/shrub/vine
−0.4
−0.2
0.0
0.2
0.4
0.6
NMDS1


Similarity to old−growth grasslands
0.0
0.2
0.4
0.6
0.8
1.0
a
b
b
b
b
Old−growth grasslands
Summer burns
Fall burns
Winter burns
Unburned


A
Herbaceous cover (%)
0
20
40
60
80
100
a
a
a
a
b
B
Woody canopy cover (%)
0
20
40
60
80
100
b
a
a
a
a
C
Tree basal area (m^2/ha)
0
10
20
30
40
a,b
b
a
a
a
D
Small stem density (stems/ha)
0
2000
6000
10000
b
a,b
a
a
a
Old−growth grasslands
Summer burns
Fall burns
Winter burns
Unburned


A
Species / 1000 m^2
0
20
40
60
80
100
120
a
a
a
a
a
B
Species / m^2
0
5
10
15
20
25
30
a
a,b
a,b
b
Old−growth grasslands
Summer burns
Fall burns
Winter burns
Unburned


Bothriochloa ischaemum cover (%)
0
20
40
60
80
100
a
a
a,b
b
a
Old−growth grasslands
Summer burns
Fall burns
Winter burns
Unburned


Summer burns
Fall burns
Winter burns
Unburned
r^2= 0.47
r^2= 0.17
ns
Bothriochloa ischaemum cover (%)
Woody canopy cover (%)
0
25
50
75
100
0
25
50
75
100

Supporting Information

Novak, E.N., M. Bertelsen, D. Davis, D.M. Grobert, K.G. Lyons, J.P. Martina, W.M. McCaw, M. O'Toole, and J.W. Veldman. Season of prescribed fire determines grassland restoration outcomes after fire exclusion and overgrazing. Ecosphere.

Appendix S1

This file contains supporting figures (Fig. S1-S4) that we cited in the methods and results sections of the main text. It also provides a comprehensive species list (Table S1) of all taxa that we observed during sampling of herbaceous-layer plant communities.

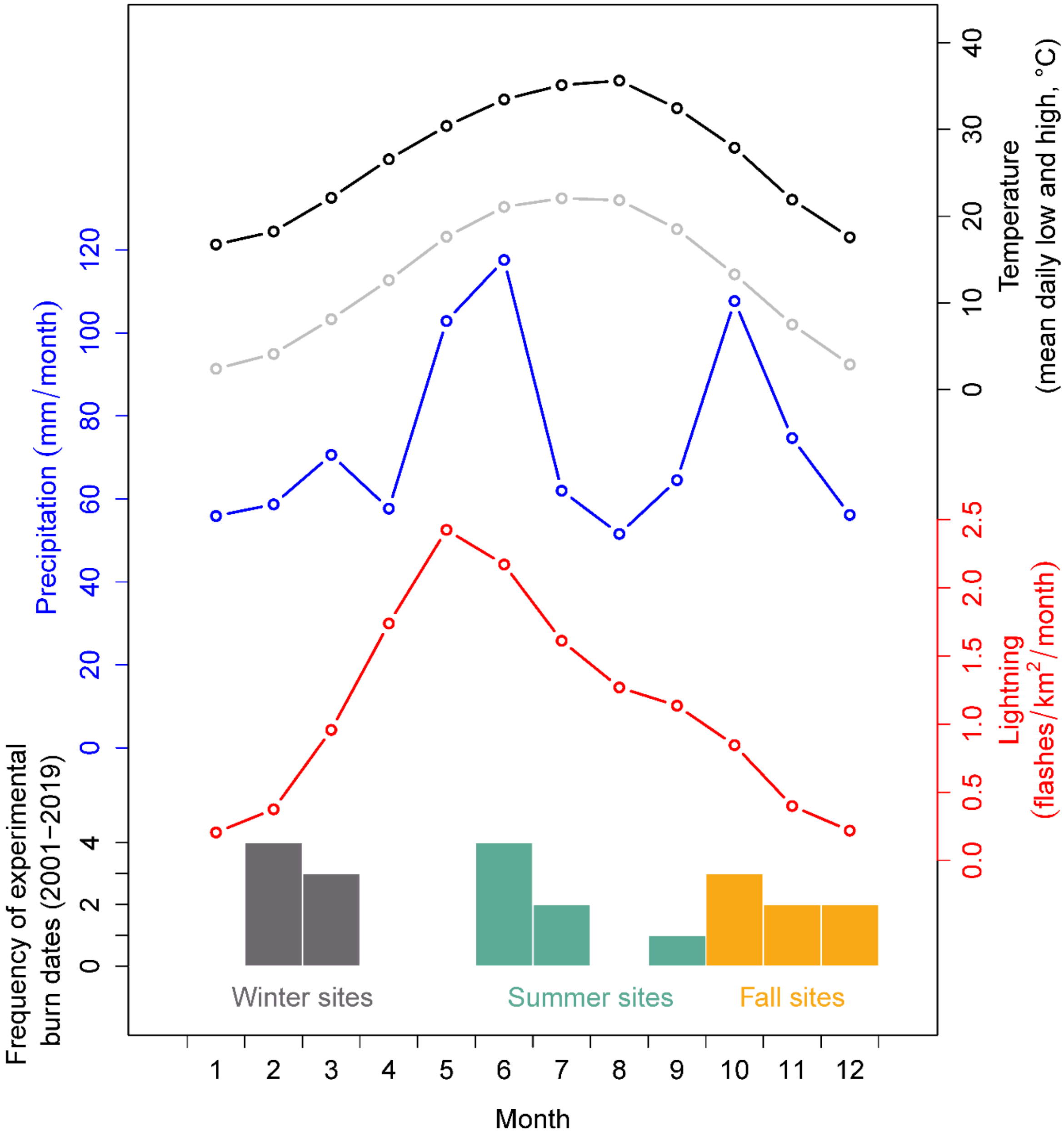


Figure S1. Season of experimental prescribed fire treatments in relation to climatic variables for central Texas grasslands. Temperature: monthly mean daily high (black) and low (gray) temperatures for Austin-Bergstrom Airport, Texas (NWS, 1981-2010). Precipitation: mean monthly precipitation (blue) for Austin-Bergstrom Airport, Texas (NWS, 1981-2010). Lightning: mean monthly lightning flash density for the Blackland Prairie and Edwards Plateau ecoregions of Texas (1998-2013, Albrecht et al. 2016). Frequency of experimental burn dates: the distribution by month of prescribed fires conducted in the summer, fall, and winter burn sites at the Lady Bird Johnson Wildflower Center. From 2001 to 2019, sites of each seasonal treatment burned seven times, with a mean fire return interval of 2.8 yr (range 1-5 yr).

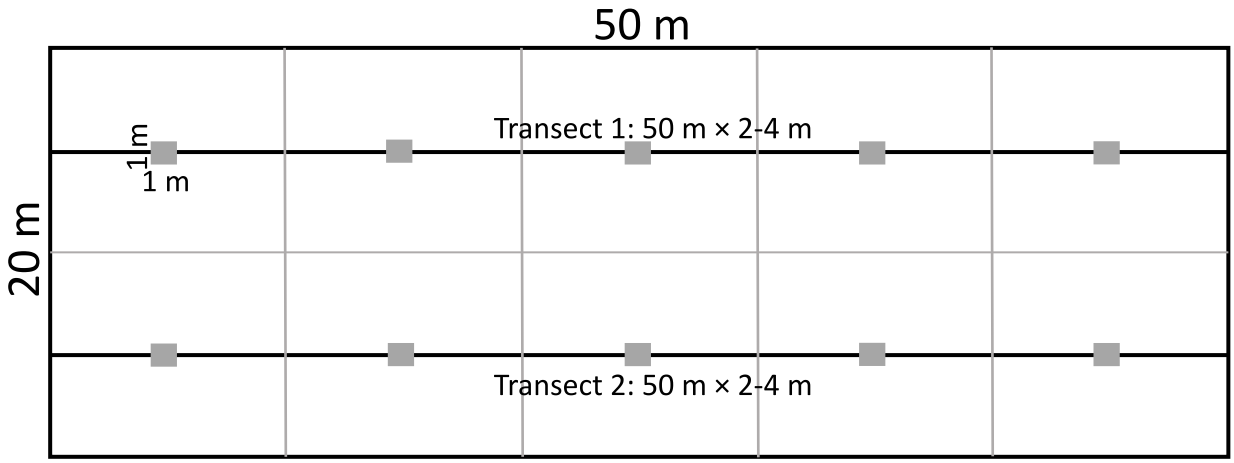


Figure S2. Diagram of the sampling design, showing the 1000-m^2 plot, with ten 1-m^2 subplots and two 50-m transects spaced 10 m apart (modified from Peet et al. 1998).

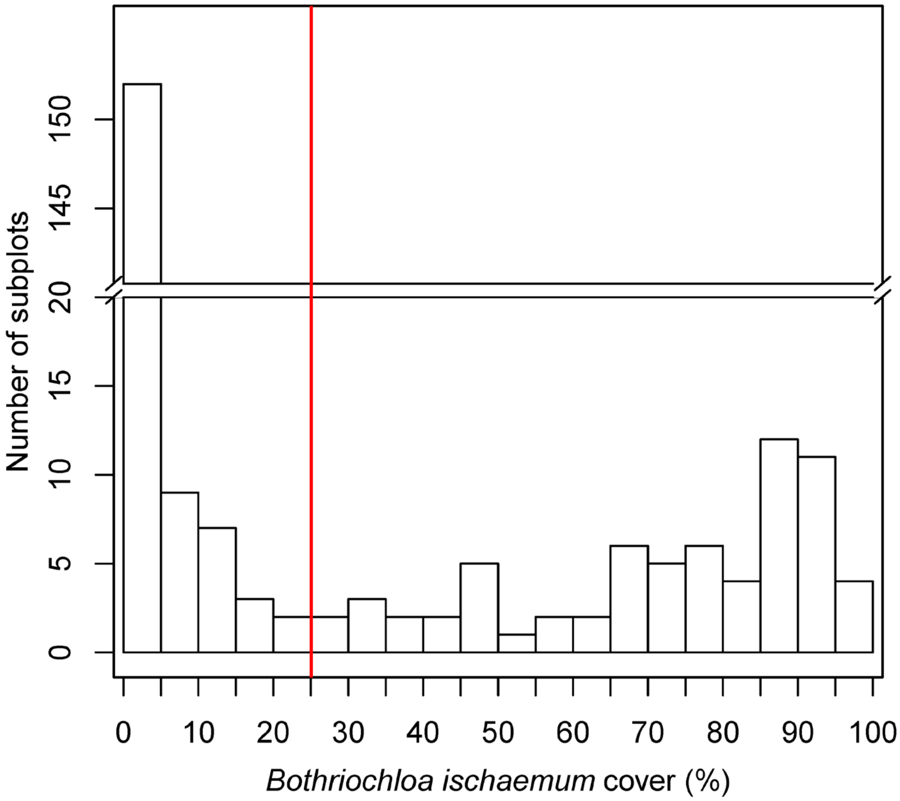


Figure S3. Frequency histogram of *Bothriochloa ischaemum* cover in all 1-m^2 subplots (N = 240) of the experimental prescribed fire sites (10 subplots per site, n = 6 sites per treatment). The vertical red line indicates the cutoff we used to define subplots with high cover (≥25%) versus those with low cover or absence (<25%) for the logistic regression (Table 1). Note the break in the y-axis from 20 to 140.

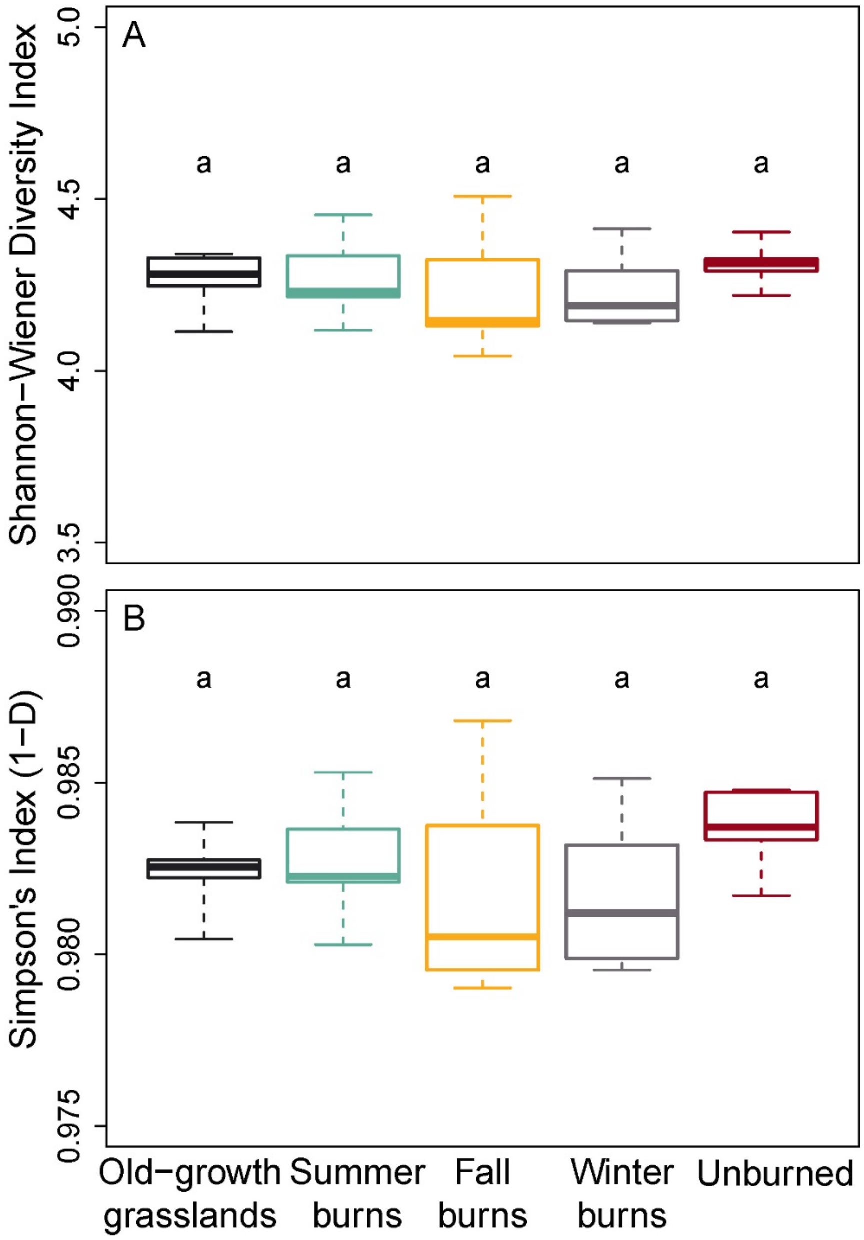


Figure S4. Herbaceous layer plant species diversity in the prescribed fire experiment (*n* = 6) and old-growth grasslands (*n* = 6) at the 1000-m^2 scale. For the Shannon-Wiener (a) and Simpson's (b) diversity indices, we used the within–plot frequency scores (0-11) of each species to represent abundances (see *Methods*). Boxplots display quartiles. Means of treatments did not differ at $p < 0.05$ (ANOVA and Tukey's HSD).

Table S1. Taxa recorded in old-growth grasslands (City of Austin Water Quality Protection Lands, $n = 6$) and experimental prescribed fire sites (Lady Bird Johnson Wildflower Center, $n = 6$ per treatment), ordered alphabetically by family and species. Column values in bold are the frequency of occurrence (0-6) at the 1000-m^2 scale. Colum values in italics are the mean within-plot frequencies (0 to 11, calculated as the frequency in ten 1-m^2 subplots plus presence in the 1000-m^2 plot, see Methods). Nomenclature for grasses (Poaceae) followed Gould (1975) and for all other families Diggs (et al. 1999). When nomenclature in Gould (1975) or Diggs et al. (1999) differ from the currently accepted names in The Plant List (2013), we list the accepted names as synonyms. Taxa in bold font were associated with old-growth grasslands and had significant species factors ($p <$ 0.001 based on 999 permutations) in the non-metric multidimensional scaling (Fig. 1).

Family	Species	Old-growth grasslands		Summer Burns		Fall Burns		Winter Burns		Unburned	
Acanthaceae	*Dyschoriste linearis* (Torr. & A.Gray) Kuntze	**3**	*1.0*	**1**	*0.3*	**1**	*0.5*	**0**	*0.0*	**1**	*0.2*
	Ruellia nudiflora (Engelm. & A.Gray) Urb.	**1**	*0.2*	**3**	*0.5*	**2**	*0.7*	**3**	*1.7*	**3**	*0.8*
Agavaceae (Asparagaceae)$^+$	*Yucca rupicola* Scheele	**2**	*0.8*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
Anacardiaceae	*Rhus lanceolata*(A. Gray) Britton	**3**	*0.5*	**3**	*0.7*	**1**	*0.2*	**5**	*1.2*	**3**	*0.8*
	Rhus trilobata Nutt.	**3**	*0.5*	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*	**2**	*0.5*
	Toxicodendron radicans (L.) Kuntze	**0**	*0.0*	**3**	*0.7*	**4**	*1.2*	**3**	*0.7*	**4**	*1.2*
Apiaceae	*Chaerophyllum tainturieri* Hook. & Arn.	**6**	*5.0*	**4**	*2.8*	**5**	*3.0*	**6**	*4.8*	**6**	*4.2*
	Daucus pusillus Michx.	**4**	*1.2*	**5**	*3.7*	**6**	*2.3*	**5**	*1.8*	**3**	*0.5*
	Polytaenia texana (J.M. Coult. & Rose) Mathias & Constance	**0**	*0.0*	**3**	*0.7*	**3**	*2.8*	**3**	*2.7*	**5**	*0.8*
	Spermolepis inermis (Nutt. ex DC.) Mathias & Constance	**6**	*7.0*	**6**	*7.0*	**6**	*5.5*	**6**	*6.2*	**4**	*2.2*
	Torilis arvensis (Huds.) Link	**5**	*1.2*	**5**	*2.5*	**6**	*4.2*	**6**	*2.2*	**6**	*2.3*
Aquifoliaceae	*Ilex decidua* Walter	**0**	*0.0*	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*	**1**	*0.5*

Family	Species	Old-growth grasslands		Summer Burns		Fall Burns		Winter Burns		Unburned	
	Ilex vomitoria Aiton	**3**	*0.7*	**1**	*0.2*	**3**	*0.5*	**4**	*0.8*	**4**	*0.7*
Asclepiadaceae (Apocynaceae)+	*Asclepias asperula* (Decne.) Woodson	**4**	*0.8*	**6**	*1.8*	**5**	*1.0*	**6**	*1.5*	**5**	*0.8*
	Asclepias oenotheroides Schltdl. & Cham.	**1**	*0.2*	**2**	*0.3*	**0**	*0.0*	**1**	*0.2*	**0**	*0.0*
	Matelea biflora (Raf.) Woodson	**2**	*0.3*	**3**	*0.8*	**3**	*0.5*	**2**	*0.5*	**1**	*0.2*
	Matelea reticulata (Engelm. ex A.Gray) Woodson	**4**	*0.7*	**3**	*0.5*	**4**	*1.0*	**1**	*0.2*	**6**	*2.2*
Asteraceae (Compositae)+	*Achillea millefolium* L.	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**1**	*0.2*	**1**	*0.2*
	Ambrosia psilostachya DC.	**2**	*0.5*	**6**	*4.0*	**5**	*5.5*	**6**	*3.7*	**4**	*1.2*
	Artemisia ludoviciana Nutt.	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Aster ericoides L., synonym of *Symphyotrichum ericoides* (L.) G.L.Nesom	**3**	*1.3*	**5**	*2.0*	**4**	*1.7*	**6**	*2.8*	**5**	*1.2*
	***Brickellia cylindracea* A.Gray ex A.Gray & Engelm.**	**4**	*0.8*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Calyptocarpus vialis Less.	**1**	*0.2*	**1**	*0.2*	**2**	*0.8*	**1**	*0.3*	**3**	*0.8*
	Centaurea melitensis L.	**0**	*0.0*	**3**	*1.5*	**3**	*0.7*	**0**	*0.0*	**0**	*0.0*
	Centaurium texense (Griseb.) Fernald, unresolved name, probable synonym of *Zeltnera texensis* (Griseb.) G. Mans. ex J.S. Pringle	**1**	*0.2*	**3**	*0.5*	**1**	*0.2*	**1**	*0.2*	**3**	*0.7*
	Chaetopappa asteroides (Nutt.) Nutt. ex DC.	**1**	*0.5*	**3**	*3.0*	**2**	*0.8*	**1**	*0.3*	**3**	*0.5*
	Cirsium texanum Buckley	**6**	*3.5*	**6**	*3.3*	**6**	*2.2*	**6**	*2.3*	**6**	*1.7*

Family	Species	Old-growth grasslands	Summer Burns	Fall Burns	Winter Burns	Unburned
	Conyza canadensis (L.) Cronquist, synonym of *Erigeron canadensis* L.	**5** *1.0*	**1** *0.3*	**2** *0.7*	**4** *1.0*	**4** *0.8*
	Coreopsis tinctoria Nutt.	**1** *0.3*	**0** *0.0*	**0** *0.0*	**0** *0.0*	**0** *0.0*
	Engelmannia peristenia (Raf.) Goodman & C.A.Lawson	**0** *0.0*	**2** *0.5*	**0** *0.0*	**0** *0.0*	**0** *0.0*
	Erigeron tenuis Torr. & A.Gray	**0** *0.0*	**0** *0.0*	**0** *0.0*	**2** *0.3*	**2** *0.5*
	Eupatorium incarnatum Walter, synonym of *Fleischmannia incarnata* (Walter) R.M.King & H.Rob.	**0** *0.0*	**0** *0.0*	**1** *0.2*	**2** *0.7*	**3** *0.7*
	Evax prolifera Nutt. ex DC., synonym of *Diaperia prolifera* (Nutt. ex DC.) Nutt.	**0** *0.0*	**0** *0.0*	**0** *0.0*	**0** *0.0*	**1** *0.2*
	***Evax verna* Raf., synonym of *Diaperia verna* (Raf.) Morefield**	**6** *2.8*	**0** *0.0*	**2** *0.7*	**0** *0.0*	**0** *0.0*
	Gaillardia pulchella Foug.	**2** *1.8*	**6** *3.8*	**6** *4.5*	**6** *4.5*	**6** *4.7*
	Gamochaeta pensylvanica (Willd.) Cabrera, synonym of *Gnaphalium pensylvanicum* Willd.	**0** *0.0*	**4** *2.0*	**6** *2.5*	**6** *2.3*	**3** *1.0*
	Grindelia squarrosa (Pursh) Dunal	**1** *0.2*	**0** *0.0*	**0** *0.0*	**0** *0.0*	**0** *0.0*
	Gutierrezia texana (DC.) Torr. & A.Gray	**5** *5.7*	**5** *2.0*	**6** *4.5*	**4** *1.3*	**6** *1.7*
	Helenium amarum (Raf.) H.Rock, unresolved name, possible synonym of *Helenium tenuifolium* Nutt.	**0** *0.0*	**3** *0.5*	**2** *0.3*	**0** *0.0*	**0** *0.0*
	Helianthus annuus L.	**1** *0.2*	**0** *0.0*	**1** *0.3*	**2** *0.3*	**0** *0.0*
	Heterotheca subaxillaris (Lam.) Britton & Rusby	**2** *0.3*	**0** *0.0*	**0** *0.0*	**0** *0.0*	**0** *0.0*
	***Hymenopappus tenuifolius* Pursh**	**5** *2.7*	**1** *0.2*	**0** *0.0*	**0** *0.0*	**1** *0.2*

Family	Species	Old-growth grasslands		Summer Burns		Fall Burns		Winter Burns		Unburned	
	Krigia cespitosa (Raf.) K.L.Chambers	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Lactuca ludoviciana (Nutt.) Riddell	**2**	*0.7*	**0**	*0.0*	**4**	*1.5*	**2**	*0.5*	**4**	*1.0*
	***Liatris mucronata* DC.**	**4**	*2.5*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Lindheimera texana A.Gray & Engelm.	**4**	*1.3*	**1**	*0.3*	**2**	*0.5*	**1**	*0.2*	**3**	*0.7*
	Lygodesmia texana (Torr. & A.Gray) Greene ex Small	**5**	*1.3*	**3**	*1.7*	**3**	*1.2*	**2**	*0.3*	**2**	*0.7*
	Pinaropappus roseus (Less.) Less.	**4**	*1.3*	**0**	*0.0*	**0**	*0.0*	**1**	*0.2*	**2**	*0.5*
	Pyrrhopappus carolinianus (Walter) DC.	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**1**	*0.2*	**0**	*0.0*
	Pyrrhopappus pauciflorus (D.Don) DC.	**3**	*1.2*	**1**	*0.2*	**2**	*0.5*	**3**	*0.5*	**2**	*0.7*
	Ratibida columnifera (Nutt.) Wooton & Standl.	**1**	*0.2*	**3**	*0.7*	**1**	*0.2*	**3**	*1.7*	**4**	*1.2*
	Rudbeckia hirta L.	**6**	*5.2*	**6**	*10.7*	**6**	*9.0*	**6**	*9.0*	**6**	*4.5*
	Solidago canadensis L.	**0**	*0.0*	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*	**2**	*0.3*
	Solidago nemoralis Aiton	**1**	*0.3*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Sonchus asper (L.) Hill	**2**	*0.5*	**2**	*0.8*	**2**	*0.5*	**3**	*0.7*	**0**	*0.0*
	Sonchus oleraceus (L.) L.	**2**	*0.8*	**0**	*0.0*	**1**	*0.3*	**0**	*0.0*	**0**	*0.0*
	***Tetraneuris linearifolia* (Hook.) Greene**	**5**	*1.7*	**1**	*0.5*	**1**	*0.7*	**0**	*0.0*	**1**	*0.2*
	Verbesina virginica L.	**1**	*0.2*	**1**	*0.2*	**0**	*0.0*	**1**	*0.2*	**2**	*0.5*
	***Wedelia texana* (A.Gray) B.L.Turner**	**6**	*4.2*	**5**	*1.5*	**2**	*0.3*	**3**	*0.7*	**5**	*1.0*

Family	Species	Old-growth grasslands		Summer Burns		Fall Burns		Winter Burns		Unburned	
Berberidaceae	*Berberis trifoliolata* Moric., unresolved name, probable synonym of *Mahonia trifoliolata* (Moric.) Fedde	**4**	*1.0*	**4**	*0.7*	**6**	*2.2*	**4**	*0.7*	**6**	*3.8*
	Nandina domestica Thunb.	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**1**	*0.2*
Brassicaceae	*Arabis petiolaris* (A.Gray) A.Gray	**1**	*0.2*	**3**	*0.8*	**4**	*0.7*	**4**	*0.8*	**2**	*0.5*
	Draba cuneifolia Nutt.	**1**	*0.3*	**0**	*0.0*	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*
	Lepidium virginicum L.	**5**	*1.7*	**4**	*2.8*	**3**	*1.0*	**3**	*1.3*	**0**	*0.0*
	Lesquerella recurvata (Engelm. ex A. Gray) S. Watson, synonym of *Physaria recurvata* (Engelm. ex A. Gray) O'Kane & Al-Shehbaz	**5**	*2.0*	**5**	*3.0*	**2**	*0.8*	**1**	*0.7*	**3**	*1.0*
Cactaceae	*Echinocereus reichenbachii* (Terscheck) J.N.Haage	**1**	*0.2*	**0**	*0.0*	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*
	Opuntia engelmannii Salm-Dyck ex Engelm.	**4**	*1.2*	**3**	*0.7*	**3**	*1.0*	**5**	*1.5*	**6**	*1.7*
	Opuntia leptocaulis DC., synonym of *Cylindropuntia leptocaulis* (DC.) F.M.Knuth	**0**	*0.0*	**0**	*0.0*	**3**	*0.5*	**1**	*0.2*	**4**	*0.8*
	Opuntia macrorhiza Engelm.	**5**	*1.0*	**6**	*2.2*	**4**	*1.7*	**5**	*2.0*	**6**	*2.0*
Campanulaceae	*Triodanis coloradoensis* (Buckley) McVaugh	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Triodanis perfoliata (L.) Nieuwl.	**5**	*2.7*	**6**	*5.8*	**6**	*6.3*	**6**	*7.2*	**6**	*2.3*
Caryophyllaceae	*Arenaria benthamii* Fenzl ex Torr. & A.Gray	**1**	*0.5*	**1**	*0.3*	**2**	*1.0*	**0**	*0.0*	**0**	*0.0*
	Silene antirrhina L.	**0**	*0.0*	**1**	*0.3*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
Cistaceae	*Lechea tenuifolia* Michx.	**3**	*1.2*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Commelina erecta L.	**1**	*0.2*	**4**	*1.2*	**3**	*1.0*	**2**	*0.7*	**3**	*0.7*

Family	Species	Old-growth grasslands		Summer Burns		Fall Burns		Winter Burns		Unburned	
Commelinaceae	*Tradescantia hirsutiflora* Bush	**0**	*0.0*	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Tradescantia subacaulis Bush	**0**	*0.0*	**0**	*0.0*	**1**	*0.2*	**1**	*0.2*	**0**	*0.0*
Convolvulaceae	***Convolvulus equitans*** **Benth**.	**6**	*3.8*	**6**	*3.3*	**4**	*1.3*	**3**	*0.7*	**3**	*0.7*
	Dichondra recurvata Tharp & M.C. Johnst.	**3**	*2.2*	**6**	*3.8*	**4**	*1.3*	**4**	*1.5*	**5**	*1.7*
	Evolvulus sericeus Sw.	**3**	*2.5*	**6**	*8.8*	**6**	*4.5*	**6**	*4.7*	**5**	*3.0*
Crassulaceae	*Sedum nuttallianum* Raf., unresolved name, possible synonym of *Sedum nuttallii* Torr. & E.James ex Eaton	**0**	*0.0*	**0**	*0.0*	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*
Cucurbitaceae	*Cucurbita foetidissima* Kunth	**0**	*0.0*	**1**	*0.2*	**1**	*0.2*	**1**	*0.2*	**0**	*0.0*
	Ibervillea lindheimeri (A.Gray) Greene	**1**	*0.2*	**3**	*1.0*	**4**	*0.8*	**2**	*0.5*	**6**	*1.3*
Cupressaceae	*Juniperus ashei* J.Buchholz	**2**	*0.5*	**2**	*0.5*	**4**	*1.7*	**3**	*0.7*	**6**	*3.3*
Cyperaceae	*Carex austrina* Mack.	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Carex muehlenbergii Willd.	**0**	*0.0*	**1**	*0.3*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Carex planostachys Kunze	**2**	*0.7*	**3**	*0.7*	**3**	*2.2*	**2**	*0.8*	**6**	*3.8*
	Cyperus retrorsus Chapm.	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**1**	*0.2*
	Cyperus strigosus L.	**1**	*0.3*	**1**	*0.2*	**0**	*0.0*	**1**	*0.2*	**0**	*0.0*
	Scleria oligantha Michx.	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
Ebenaceae	*Diospyros texana* Scheele	**6**	*1.3*	**6**	*1.7*	**6**	*2.0*	**5**	*1.2*	**5**	*2.2*
Euphorbiaceae	*Acalypha phleiodes* Cav.	**0**	*0.0*	**0**	*0.0*	**3**	*1.2*	**1**	*0.5*	**0**	*0.0*

Family	Species	Old-growth grasslands		Summer Burns		Fall Burns		Winter Burns		Unburned	
	***Chamaesyce serpens* (Kunth) Small, synonym of *Euphorbia serpens* Kunth**	**4**	*1.5*	**1**	*0.3*	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*
	Croton fruticulosus Torr.	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Croton monanthogynus Michx.	**6**	*7.3*	**6**	*7.5*	**6**	*6.5*	**6**	*6.0*	**6**	*5.2*
	Ditaxis humilis (Engelm. & A.Gray) Pax	**5**	*3.0*	**4**	*2.5*	**5**	*1.8*	**6**	*3.2*	**5**	*2.0*
	Ditaxis mercurialina (Nutt.) J.M.Coult.	**0**	*0.0*	**1**	*0.2*	**1**	*0.3*	**0**	*0.0*	**1**	*0.2*
	Euphorbia cyathophora Murray	**3**	*1.3*	**1**	*0.2*	**2**	*0.8*	**3**	*1.2*	**4**	*1.7*
	Euphorbia dentata Michx.	**1**	*0.2*	**1**	*0.3*	**0**	*0.0*	**3**	*1.0*	**2**	*0.5*
	Euphorbia marginata Pursh	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**3**	*0.7*	**0**	*0.0*
	Euphorbia roemeriana Scheele	**3**	*1.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Euphorbia spathulata Lam.	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**3**	*0.7*
	Phyllanthus polygonoides Nutt. ex Spreng.	**6**	*3.2*	**2**	*0.7*	**3**	*1.5*	**4**	*1.5*	**2**	*0.8*
	***Stillingia texana* I.M. Johnst**.	**5**	*4.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Tragia brevispica Engelm. & A.Gray	**2**	*0.5*	**2**	*1.2*	**4**	*2.5*	**5**	*3.3*	**4**	*2.5*
	Tragia ramosa Torr.	**5**	*5.3*	**6**	*4.3*	**5**	*3.3*	**6**	*5.0*	**5**	*2.5*
Fabaceae (Leguminosae)+	*Astragalus nuttallianus* DC.	**0**	*0.0*	**5**	*2.7*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Dalea aurea C.Fraser	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Desmanthus acuminatus Benth.	**4**	*4.5*	**6**	*7.3*	**5**	*2.2*	**6**	*5.0*	**5**	*2.0*

Family	Species	Old-growth grasslands		Summer Burns		Fall Burns		Winter Burns		Unburned	
	Desmanthus velutinus Scheele	**1**	*0.7*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Desmodium psilophyllum Schltdl.	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Eysenhardtia texana Scheele	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Indigofera miniata Ortega	**2**	*1.2*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	***Lespedeza texana* Britton**	**5**	*2.5*	**0**	*0.0*	**1**	*0.3*	**0**	*0.0*	**1**	*0.2*
	Lupinus texensis Hook.	**2**	*0.7*	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Medicago lupulina L.	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Medicago minima (L.) L.	**2**	*0.5*	**4**	*3.7*	**5**	*2.3*	**0**	*0.0*	**1**	*0.3*
	Melia azedarach L.	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**1**	*0.2*	**0**	*0.0*
	Mimosa nuttallii (DC.) B.L. Turner	**5**	*2.2*	**3**	*0.5*	**4**	*1.0*	**5**	*0.8*	**6**	*1.7*
	Pediomelum rhombifolium (Torr. & A.Gray) Rydb., synonym of *Psoralea rhombifolia* Torr. & A.Gray	**0**	*0.0*	**2**	*0.5*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Prosopis glandulosa Torr.	**4**	*0.7*	**5**	*0.8*	**3**	*0.5*	**6**	*1.0*	**3**	*0.5*
	***Rhynchosia senna* Hook.**	**5**	*2.3*	**0**	*0.0*	**1**	*0.3*	**0**	*0.0*	**0**	*0.0*
	Senna lindheimeriana (Scheele) H.S.Irwin & Barneby	**5**	*1.2*	**3**	*1.2*	**2**	*0.5*	**2**	*0.7*	**1**	*0.2*
	Vicia ludoviciana Nutt.	**6**	*5.3*	**6**	*5.5*	**6**	*4.8*	**6**	*6.7*	**6**	*3.3*
Fagaceae	*Quercus buckleyi* Nixon & Dorr	**1**	*0.3*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**2**	*0.3*
	Quercus fusiformis Small	**5**	*1.3*	**6**	*1.8*	**5**	*1.8*	**5**	*1.3*	**6**	*4.3*

Family	Species	Old-growth grasslands		Summer Burns		Fall Burns		Winter Burns		Unburned	
	Quercus marilandica (L.) Münchh.	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**1**	*0.2*
	Quercus stellata Wangenh.	**0**	*0.0*	**0**	*0.0*	**1**	*0.2*	**2**	*0.5*	**4**	*1.2*
Geraniaceae	*Erodium texanum* A. Gray	**0**	*0.0*	**3**	*1.3*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Geranium carolinianum L.	**2**	*1.2*	**6**	*5.8*	**6**	*4.3*	**6**	*4.8*	**5**	*2.8*
Hydrophyllaceae (Boraginaceae)+	*Nama jamaicense* L., possible synonym of *Nama jamaicensis* L.	**0**	*0.0*	**1**	*0.3*	**1**	*0.3*	**1**	*0.2*	**0**	*0.0*
	Phacelia congesta Hook.	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
Iridaceae	*Herbertia lahue* (Molina) Goldblatt	**0**	*0.0*	**1**	*0.3*	**2**	*0.5*	**2**	*0.5*	**1**	*0.3*
	Nemastylis geminiflora Nutt.	**3**	*2.2*	**1**	*0.5*	**2**	*0.7*	**5**	*1.3*	**2**	*0.5*
	Sisyrinchium angustifolium Mill.	**1**	*0.3*	**1**	*0.3*	**2**	*0.3*	**1**	*0.5*	**0**	*0.0*
	Sisyrinchium minus Engelm. & A.Gray	**0**	*0.0*	**0**	*0.0*	**1**	*0.3*	**0**	*0.0*	**0**	*0.0*
Juncaceae	*Juncus dudleyi* Wiegand	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**1**	*0.2*
Krameriaceae	*Krameria lanceolata* Torr.	**3**	*0.7*	**2**	*0.3*	**0**	*0.0*	**1**	*0.2*	**2**	*0.3*
Lamiaceae	***Hedeoma acinoides* Scheele**	**6**	*10.2*	**6**	*5.5*	**6**	*4.2*	**5**	*4.2*	**6**	*5.7*
	Marrubium vulgare L.	**0**	*0.0*	**0**	*0.0*	**1**	*0.3*	**0**	*0.0*	**0**	*0.0*
	Monarda citriodora Cerv. ex Lag.	**3**	*2.5*	**5**	*5.7*	**5**	*3.2*	**5**	*3.5*	**5**	*2.5*
	Salvia farinacea Benth.	**2**	*0.7*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Scutellaria drummondii Benth.	**5**	*2.2*	**5**	*3.5*	**3**	*1.8*	**6**	*2.0*	**5**	*1.8*

Family	Species	Old-growth grasslands		Summer Burns		Fall Burns		Winter Burns		Unburned	
	Stachys crenata Raf., synonym of *Stachys agraria* Schltdl. & Cham.	**2**	*0.5*	**3**	*1.0*	**2**	*0.7*	**2**	*0.7*	**0**	*0.0*
	Warnockia scutellarioides **(Engelm. & A.Gray) M.W.Turner**	**6**	*9.2*	**4**	*2.2*	**3**	*1.8*	**3**	*1.5*	**6**	*4.5*
Liliaceae (Amaryllidaceae)+	*Allium canadense* L.	**2**	*0.8*	**2**	*0.7*	**2**	*0.3*	**1**	*0.2*	**3**	*0.5*
	Allium drummondii Regel	**1**	*0.2*	**3**	*2.7*	**1**	*0.3*	**2**	*0.3*	**1**	*0.2*
	Cooperia pedunculata Herb., synonym of *Zephyranthes drummondii* D.Don	**3**	*0.7*	**4**	*1.0*	**3**	*0.5*	**5**	*2.0*	**4**	*0.8*
	Habranthus tubispathus (L'Hér.) Traub	**0**	*0.0*	**1**	*0.2*	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*
	Nothoscordum bivalve (L.) Britton	**3**	*0.8*	**2**	*0.7*	**0**	*0.0*	**4**	*1.2*	**2**	*0.7*
Linaceae	*Linum hudsonioides* Planch.	**0**	*0.0*	**3**	*2.2*	**2**	*0.5*	**1**	*0.2*	**3**	*0.8*
Malvaceae	*Abutilon fruticosum* Guill. & Perr.	**2**	*0.3*	**2**	*0.3*	**1**	*0.2*	**1**	*0.2*	**0**	*0.0*
	Allowissadula holosericea (Scheele) D.M.Bates*	**0**	*0.0*	**1**	*0.2*	**0**	*0.0*	**1**	*0.2*	**0**	*0.0*
	Callirhoe pedata (Nutt. ex Hook.) A.Gray	**2**	*0.8*	**2**	*0.3*	**1**	*0.3*	**2**	*0.3*	**2**	*0.3*
	Modiola caroliniana (L.) G.Don	**1**	*0.2*	**0**	*0.0*	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*
	Sida abutifolia Mill.	**5**	*3.3*	**6**	*8.5*	**6**	*5.8*	**5**	*3.0*	**5**	*2.2*
Menispermaceae	*Cocculus carolinus* (L.) DC.	**1**	*0.2*	**3**	*2.0*	**6**	*2.7*	**5**	*2.2*	**6**	*2.7*
Nyctaginaceae	*Mirabilis albida* (Walter) Heimerl	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**2**	*0.5*	**0**	*0.0*
	Mirabilis linearis (Pursh) Heimerl	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*

Family	Species	Old-growth grasslands		Summer Burns		Fall Burns		Winter Burns		Unburned	
	Mirabilis nyctaginea (Michx.) MacMill., synonym of *Oxybaphus nyctagineus* (Michx.) Sweet	**1**	*0.2*	**1**	*0.2*	**2**	*0.3*	**0**	*0.0*	**1**	*0.2*
Oleaceae	*Forestiera pubescens* Nutt.	**1**	*0.3*	**3**	*0.8*	**6**	*3.5*	**4**	*1.3*	**6**	*6.3*
	Fraxinus texensis (A.Gray) Sarg.	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
Onagraceae	*Gaura brachycarpa* Small	**0**	*0.0*	**6**	*5.3*	**3**	*1.2*	**5**	*1.2*	**3**	*0.7*
	Gaura sinuata Nutt. ex Ser.	**4**	*1.7*	**1**	*0.3*	**1**	*0.2*	**1**	*0.8*	**0**	*0.0*
	Oenothera laciniata Hill	**0**	*0.0*	**1**	*0.3*	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*
	Oenothera speciosa Nutt.	**0**	*0.0*	**3**	*0.7*	**3**	*0.7*	**4**	*1.5*	**1**	*0.2*
Oxalidaceae	*Oxalis drummondii* A. Gray	**1**	*0.3*	**2**	*1.0*	**2**	*0.7*	**1**	*0.3*	**2**	*0.8*
	Oxalis stricta L., possible synonym of *Oxalis dillenii* Jacq.	**6**	*5.3*	**6**	*6.5*	**6**	*7.2*	**6**	*4.7*	**6**	*5.5*
Papaveraceae	*Argemone aurantiaca* Ownbey	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
Passifloraceae	*Passiflora affinis* Engelm.	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Passiflora lutea L.	**1**	*0.2*	**3**	*0.7*	**3**	*0.7*	**2**	*0.3*	**3**	*0.7*
Phytolaccaceae	*Phytolacca americana* L.	**0**	*0.0*	**1**	*0.2*	**0**	*0.0*	**2**	*0.3*	**0**	*0.0*
	Plantago helleri Small	**0**	*0.0*	**1**	*0.3*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
Plantaginaceae	*Plantago rhodosperma* Decne.	**5**	*3.7*	**6**	*4.0*	**5**	*2.8*	**6**	*2.8*	**6**	*2.7*
Poaceae	***Andropogon gerardii* Vitman**	**6**	*2.2*	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Aristida oligantha Michx.	**1**	*0.3*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Aristida purpurea Nutt.	**6**	*2.5*	**5**	*1.3*	**4**	*1.8*	**4**	*1.5*	**6**	*1.5*

Family	Species	Old-growth grasslands		Summer Burns		Fall Burns		Winter Burns		Unburned	
	Bothriochloa ischaemum (L.) Keng	**5**	*4.3*	**6**	*4.8*	**5**	*4.8*	**6**	*9.5*	**6**	*5.2*
	Bothriochloa laguroides (DC.) Herter	**5**	*4.5*	**6**	*2.2*	**6**	*4.2*	**6**	*6.8*	**6**	*2.2*
	Bouteloua curtipendula **(Michx.) Torr.**	**6**	*4.2*	**5**	*1.0*	**5**	*1.5*	**5**	*1.5*	**5**	*1.7*
	Bouteloua hirsuta Lag., synonym of *Chondrosum hirsutum* (Lag.) Sweet	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Bouteloua rigidiseta **(Steud.) Hitchc.**	**6**	*1.8*	**1**	*0.2*	**3**	*0.7*	**1**	*0.2*	**0**	*0.0*
	Bromus catharticus Vahl	**0**	*0.0*	**1**	*0.3*	**2**	*1.0*	**0**	*0.0*	**1**	*0.2*
	Bromus japonicus Thunb.	**2**	*0.3*	**3**	*0.8*	**3**	*1.0*	**3**	*0.7*	**3**	*0.8*
	Buchloe dactyloides (Nutt.) Engelm.	**0**	*0.0*	**3**	*1.2*	**1**	*0.3*	**1**	*0.3*	**1**	*0.2*
	Desmazeria rigida (L.) Tutin, synonym of *Catapodium rigidum* (L.) C.E.Hubb.	**0**	*0.0*	**1**	*0.3*	**2**	*0.5*	**0**	*0.0*	**2**	*0.7*
	Dichanthelium oligosanthes (Schult.) Gould, synonym of *Panicum oligosanthes* Schult.	**6**	*3.8*	**6**	*4.8*	**6**	*5.8*	**6**	*7.7*	**6**	*5.2*
	Dichanthium sericeum (R.Br.) A.Camus	**5**	*2.3*	**5**	*2.5*	**2**	*0.8*	**4**	*0.8*	**2**	*0.3*
	Digitaria cognata (Schult.) Pilg.	**3**	*1.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**1**	*0.2*
	Elymus canadensis L.	**2**	*0.3*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**2**	*0.8*
	Eragrostis curtipedicellata Buckley	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Eragrostis intermedia Hitchc.	**3**	*2.0*	**6**	*2.8*	**4**	*1.5*	**6**	*1.7*	**3**	*0.8*
	Eriochloa sericea (Scheele) Munro ex Vasey	**3**	*2.3*	**0**	*0.0*	**1**	*0.2*	**1**	*0.3*	**1**	*0.2*

Family	Species	Old-growth grasslands		Summer Burns		Fall Burns		Winter Burns		Unburned	
	Festuca versuta Beal	**2**	*0.3*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Hilaria belangeri (Steud.) Nash	**4**	*1.5*	**4**	*1.3*	**2**	*0.7*	**1**	*0.2*	**3**	*1.2*
	Hordeum pusillum Nutt.	**0**	*0.0*	**1**	*0.3*	**1**	*0.3*	**1**	*0.3*	**2**	*0.3*
	Leptochloa dubia (Kunth) Nees	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Limnodea arkansana (Nutt.) Dewey	**6**	*9.2*	**6**	*8.2*	**6**	*3.7*	**6**	*7.3*	**6**	*3.8*
	Lolium perenne L.	**0**	*0.0*	**0**	*0.0*	**2**	*0.5*	**0**	*0.0*	**0**	*0.0*
	Mnesithea cylindrica (Michx.) de Koning & Sosef, synonym of *Coelorachis cylindrica* (Michx.) Nash	**0**	*0.0*	**0**	*0.0*	**1**	*0.2*	**1**	*0.3*	**1**	*0.2*
	Nassella leucotricha (Trin. & Rupr.) R.W.Pohl	**6**	*5.3*	**6**	*9.5*	**6**	*7.0*	**6**	*5.7*	**6**	*4.3*
	Panicum coloratum L.	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**1**	*0.2*	**0**	*0.0*
	Panicum hallii Vasey	**6**	*2.0*	**5**	*3.7*	**0**	*0.0*	**0**	*0.0*	**1**	*0.3*
	Paspalum dilatatum Poir.	**1**	*0.5*	**0**	*0.0*	**1**	*0.2*	**1**	*0.2*	**1**	*0.2*
	Paspalum setaceum Michx.	**0**	*0.0*	**1**	*0.7*	**1**	*0.2*	**0**	*0.0*	**1**	*0.2*
	Phalaris caroliniana Walter	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**1**	*0.2*
	***Schizachyrium scoparium* (Michx.) Nash**	**6**	*7.3*	**1**	*0.3*	**1**	*0.7*	**0**	*0.0*	**3**	*0.5*
	***Sorghastrum nutans* (L.) Nash**	**6**	*4.7*	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Sorghum halepense (L.) Pers.	**0**	*0.0*	**3**	*0.5*	**2**	*1.3*	**6**	*1.3*	**0**	*0.0*
	Sphenopholis interrupta (Buckley) Scribn.	**0**	*0.0*	**5**	*6.3*	**4**	*3.7*	**6**	*3.7*	**4**	*1.3*

Family	Species	Old-growth grasslands		Summer Burns		Fall Burns		Winter Burns		Unburned	
	Sporobolus compositus (Poir.) Merr.	**5**	*3.2*	**1**	*0.2*	**4**	*1.2*	**4**	*1.7*	**6**	*1.7*
	Vulpia octoflora (Walter) Rydb.	**0**	*0.0*	**4**	*2.3*	**3**	*0.5*	**2**	*0.5*	**2**	*0.7*
Polemoniaceae	*Gilia incisa* Benth., synonym of *Giliastrum incisum* (Benth.) J.M.Porter	**1**	*0.5*	**1**	*0.3*	**0**	*0.0*	**0**	*0.0*	**1**	*0.3*
	Phlox cuspidata Scheele	**0**	*0.0*	**0**	*0.0*	**1**	*0.3*	**0**	*0.0*	**0**	*0.0*
	Phlox roemeriana Scheele	**1**	*0.8*	**1**	*0.5*	**1**	*0.7*	**0**	*0.0*	**2**	*0.5*
Ranunculaceae	*Anemone berlandieri* Pritz.	**1**	*0.3*	**0**	*0.0*	**2**	*1.0*	**3**	*1.0*	**3**	*1.0*
	Clematis drummondii Torr. & A.Gray	**1**	*0.3*	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Delphinium carolinianum Walter	**0**	*0.0*	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*	**2**	*0.3*
Rosaceae	*Prunus mexicana* S. Watson	**0**	*0.0*	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Rubus trivialis Michx.	**6**	*4.0*	**6**	*3.7*	**6**	*3.3*	**6**	*4.7*	**5**	*1.8*
Rubiaceae	*Galium aparine* L.	**0**	*0.0*	**0**	*0.0*	**1**	*0.3*	**3**	*0.7*	**1**	*0.5*
	Galium texense A.Gray	**3**	*1.2*	**2**	*1.0*	**3**	*2.0*	**1**	*0.3*	**3**	*1.3*
	***Galium virgatum* Nutt.**	**6**	*7.7*	**6**	*3.7*	**6**	*3.8*	**6**	*4.5*	**6**	*4.0*
	***Hedyotis nigricans* (Lam.) Fosberg, synonym of *Stenaria nigricans* (Lam.) Terrell**	**5**	*4.2*	**0**	*0.0*	**1**	*0.3*	**2**	*0.3*	**1**	*0.2*
	Richardia tricocca (Torr. & A.Gray) Standl.	**0**	*0.0*	**2**	*1.2*	**1**	*0.3*	**1**	*0.5*	**0**	*0.0*
Rutaceae	*Zanthoxylum hirsutum* Buckley, synonym of *Zanthoxylum clava-herculis* subsp. *fruticosum* (A. Gray) Reynel	**3**	*0.5*	**3**	*0.5*	**0**	*0.0*	**2**	*0.3*	**1**	*0.3*

Family	Species	Old-growth grasslands		Summer Burns		Fall Burns		Winter Burns		Unburned	
Sapotaceae	*Sideroxylon lanuginosum* Michx.	**6**	*1.0*	**6**	*1.8*	**6**	*2.2*	**6**	*2.7*	**6**	*3.2*
Scrophulariaceae (Orobanchaceae)+	*Agalinis heterophylla* (Nutt.) Small ex Britton	**2**	*0.5*	**6**	*7.0*	**6**	*6.0*	**6**	*4.5*	**6**	*3.7*
	Castilleja indivisa Engelm.	**0**	*0.0*	**2**	*0.3*	**0**	*0.0*	**1**	*0.2*	**0**	*0.0*
Scrophulariaceae (Plantaginaceae)+	*Nuttallanthus texanus* (Scheele) D.A. Sutton	**2**	*0.7*	**4**	*2.2*	**3**	*1.2*	**0**	*0.0*	**1**	*0.3*
Smilacaceae	*Smilax bona-nox* L.	**6**	*2.3*	**6**	*2.8*	**6**	*5.2*	**6**	*4.8*	**6**	*6.7*
Solanaceae	*Bouchetia erecta* DC. ex Dunal	**4**	*1.7*	**6**	*7.7*	**6**	*5.0*	**6**	*4.8*	**6**	*3.0*
	Physalis cinerascens (Dunal) Hitchc.	**5**	*1.3*	**6**	*2.7*	**5**	*2.3*	**6**	*2.0*	**6**	*2.2*
	Solanum dimidiatum Raf.	**1**	*0.3*	**1**	*0.3*	**1**	*0.2*	**2**	*0.7*	**0**	*0.0*
	Solanum elaeagnifolium Cav.	**0**	*0.0*	**3**	*1.0*	**1**	*0.3*	**0**	*0.0*	**0**	*0.0*
	Solanum rostratum Dunal	**1**	*0.5*	**1**	*0.2*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
Ulmaceae (Cannabaceae)+	*Celtis laevigata* Willd.	**6**	*1.5*	**5**	*1.3*	**6**	*2.5*	**6**	*2.0*	**6**	*3.3*
Ulmaceae	*Ulmus crassifolia* Nutt.	**4**	*1.2*	**6**	*2.5*	**5**	*3.0*	**6**	*2.3*	**5**	*5.5*
Urticaceae	*Parietaria pensylvanica* Muhl. ex Willd.	**5**	*3.8*	**5**	*2.2*	**5**	*5.0*	**6**	*4.0*	**6**	*7.5*
Valerianaceae (Caprifoliaceae)+	*Valerianella amarella* (Lindl. ex A. Gray) Krok	**3**	*0.8*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*
	Valerianella radiata Dufr.	**0**	*0.0*	**6**	*3.8*	**3**	*2.2*	**5**	*2.8*	**4**	*1.7*
Verbenaceae	***Glandularia bipinnatifida* (Schauer) Nutt.**	**5**	*5.2*	**5**	*3.5*	**5**	*1.5*	**6**	*1.2*	**4**	*0.8*

Family	Species	Old-growth grasslands		Summer Burns		Fall Burns		Winter Burns		Unburned	
	Lantana urticoides Hayek	**0**	*0.0*	**3**	*0.5*	**0**	*0.0*	**0**	*0.0*	**1**	*0.2*
	Verbena halei Small	**3**	*0.5*	**3**	*0.7*	**4**	*1.0*	**5**	*1.5*	**3**	*0.5*
	Verbena xutha Lehm.	**0**	*0.0*	**2**	*0.5*	**1**	*0.5*	**0**	*0.0*	**0**	*0.0*
Violaceae	*Hybanthus verticillatus* (Ortega) Baill.	**0**	*0.0*	**1**	*0.2*	**0**	*0.0*	**1**	*0.2*	**0**	*0.0*
Vitaceae	*Cissus incisa* (Nutt.) Des Moul. ex S.Watson	**4**	*1.3*	**6**	*2.5*	**6**	*2.8*	**6**	*2.3*	**6**	*2.5*
	Parthenocissus heptaphylla (Buckley) Britton ex Small, synonym of *Parthenocissus quinquefolia* (L.) Planch.	**3**	*0.7*	**1**	*0.2*	**5**	*1.2*	**5**	*1.2*	**4**	*0.8*
	Parthenocissus quinquefolia (L.) Planch.	**3**	*0.7*	**4**	*0.7*	**5**	*0.8*	**4**	*1.0*	**3**	*0.7*
	Vitis cinerea (Engelm.) Engelm. ex Millardet	**0**	*0.0*	**2**	*0.5*	**0**	*0.0*	**0**	*0.0*	**2**	*0.7*
	Vitis monticola Buckley	**1**	*0.3*	**1**	*0.2*	**2**	*0.3*	**3**	*0.7*	**5**	*2.3*
	Vitis mustangensis Buckley	**4**	*1.0*	**3**	*0.7*	**3**	*1.0*	**6**	*1.2*	**3**	*0.7*
	Vitis vulpina L.	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**0**	*0.0*	**1**	*0.3*

[+] Family name from (The Plant List, 2013).

*Species absent from *Diggs et al. (1999);* identity confirmed against specimens at the S.M. Tracy Herbarium, Texas A&M University.

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