FLORAL RESPONSE OF EIGHT FORB SPECIES TO PRESCRIBED FIRE IN THE SOUTHERN GREAT PLAINS (U.S.A.)

Whitney L. Behr[1]
U.S. Fish and Wildlife Service
New England Field Office
Concord, New Hampshire 03301, U.S.A.
wlbehr@gmail.com

Kyle Simpson[2]
Department of Biology
Texas A&M University
College Station, Texas 77843, U.S.A.

Elinor M. Lichtenberg[3]
Department of Biological Sciences and
Advanced Environmental Research Institute
University of North Texas
Denton, Texas 76203, U.S.A.

Kristen A. Baum[4]
Kansas Biology Survey and
Department of Ecology & Evolutionary Biology
University of Kansas
Lawrence, Kansas 66047, U.S.A.

Shalene Jha[5]
Department of Integrative Biology and
Lady Bird Johnson Wildflower Center
University of Texas at Austin
Austin, Texas 78712, U.S.A.

Norma Fowler[6]
Department of Integrative Biology
University of Texas at Austin
Austin, Texas 78712, U.S.A.

[1–6] *author sequence*

ABSTRACT

Prescribed fire is commonly used to restore and maintain grasslands, often mediating the balance between grasses, woody species, and forbs. Forbs provide the majority of plant diversity in grasslands, and the responses of forbs to fire are important to understanding and predicting the effects of fire on pollinators and on plant communities. However, much of the past research on prescribed fire effects in grasslands has focused on woody plant species and grasses, not forbs, despite the importance of their flowering dynamics to pollinators. Thus, we need to know more about the mechanisms underlying the responses of forbs to fire, especially in the understudied southern Great Plains. In this study, we asked whether the floral displays of eight native forb species in this region differed between burned and unburned plots, and, if so, whether the differences were due to plant density (plants/m^2), plant size (grams dry above-ground biomass), resource allocation to flowers (flowers/gram plant biomass), or a combination of these factors. We found that fire responses were highly species-specific. Prescribed fire increased floral display (flowers/m^2) of five of the eight species. Floral display was proportional to plant size and plant density (plants/m^2). In some species both size and density were larger in their burned plot; while other species show opposite or no patterns. The species-specific responses of forbs in this study reinforces the need to better understand and manage for increased forb diversity and overall heterogeneity to recreate or restore ecosystems that can support a wider variety of organisms and conserve biodiversity.

RESUMEN

El fuego prescrito se utiliza comúnmente para restaurar y mantener los pastizales, a menudo mediando el equilibrio entre pastos, especies leñosas y herbáceas. Las herbáceas proporcionan la mayor parte de la diversidad vegetal en los pastizales, y las respuestas de las herbáceas al fuego son importantes para comprender y predecir los efectos del fuego sobre los polinizadores y las comunidades vegetales. Sin embargo, gran parte de la investigación anterior sobre los efectos del fuego prescrito en los pastizales se ha centrado en las especies de plantas leñosas y los pastos, no en las herbáceas, a pesar de la importancia de su dinámica de floración para los polinizadores. Por lo tanto, necesitamos saber más sobre los mecanismos subyacentes a las respuestas de las herbáceas al fuego, especialmente en las Grandes Llanuras del sur, poco estudiadas. En este estudio, nos preguntamos si las exhibiciones florales de ocho especies nativas de herbáceas en esta región diferían entre las parcelas quemadas y no quemadas y, de ser así, si las diferencias se debían a la densidad de plantas (plantas/m^2), el tamaño de las plantas (gramos de biomasa seca sobre el suelo), la asignación de recursos a las flores (flores por gramo de biomasa vegetal), o una combinación de estos factores. Descubrimos que las respuestas al fuego eran altamente específicas de cada especie. El fuego prescrito aumentó la floración (flores/m^2) de cinco de las ocho especies. La floración fue proporcional al tamaño y la densidad de las plantas (plantas/m^2). En algunas especies, tanto el tamaño como la densidad fueron mayores en la parcela quemada, mientras que otras especies muestran patrones opuestos o ninguno. Las respuestas específicas de las especies de herbáceas en este estudio refuerzan la necesidad de

---

J. Bot. Res. Inst. Texas 19(3): 223–240. 2025
https://doi.org/10.17348/jbrit.v19.i3.1425

comprender y gestionar mejor la diversidad de herbáceas y la heterogeneidad general para recrear o restaurar ecosistemas que puedan sustentar una variedad más amplia de organismos y conservar la biodiversidad.

Key Words: floral display, prescribed fire, forbs, grasslands, *Chamaecrista fasciculata, Monarda punctata, Dalea multiflora, Diodia teres, Helianthus maximiliani, Ratibida columnifera, Solidago canadensis, Symphyotrichum ericoides*

INTRODUCTION

Global biodiversity loss is occurring at a rate unprecedented in humanity's history (Cardinale et al. 2012). Habitat loss is one of the leading causes of biodiversity loss in recent decades, with impacts on a wide range of taxa across local and regional scales (Horvath et al. 2019). Thus, conservation of Earth's remaining biodiversity relies, in part, on the enactment of local and regional ecological restoration efforts (Suding 2011). Despite the need, it can be challenging to design restoration projects that benefit multiple taxa in a community because of differing life histories, active periods, and resource needs. Mutualistic interactions between taxa, such as those between plants and their pollinators, can complicate the identification of broadly beneficial restoration strategies. This interaction is particularly urgent to study given global insect declines (Cardoso et al. 2020) and the critical role that pollinators play in mediating reproduction for more than 85% of all flowering plant species (Ollerton et al. 2011).

While effective restoration of plant and pollinator communities requires an understanding of both sides of the mutualistic interaction, past restoration efforts have often focused on only one side. For example, in pollinator-focused restoration efforts, vegetation sampling methods often focus only on flowers and may be insufficient to draw conclusions about the underlying effects of treatments on plant species and plant communities (Szigeti et al. 2016). Similarly, studies that focus only on plant communities often use plant species richness (total number of species present) as a metric used to measure restoration success (Towne & Kemp 2008), but this may be less relevant for pollinators, since it includes wind-pollinated plants. A bridge between plant-focused and pollinator-focused research is needed to drive restoration research that is relevant to the conservation of both plants and pollinators. Metrics that describe floral availability, such as floral display (the number of flowers available in a given area) (Cariveau et al. 2020) are more relevant for assessing pollinator resources. More flowers in a community can attract more pollinators, increase pollination success of plants, and thus increase resources available for pollinators over time in a positive feedback loop (Ghazoul 2006; Wagenius et al. 2020). Restoration strategies that increase floral display, such as prescribed fire, can utilize this positive feedback loop to benefit both plants and pollinators simultaneously.

Prescribed fire can be an effective restoration tool, particularly in ecosystems that evolved with fire, such as grasslands (Bond et al. 2005). Fire can increase plant species richness and diversity, often by increasing the number of forb species, which is the main factor underlying plant diversity in grasslands (Leach & Givnish 1999). The effect of fire on forbs is believed to be primarily driven by an indirect positive effect caused by the fire's direct negative effect on dominant grass species and the resulting release from competitive pressure for the subordinate forb species (Mulhouse et al. 2017). Thus, the effects of fire on forb species can be understood as a balance between the short-term reduction in forbs caused by a fire and the benefit from reduced competition with grass species (Briggs & Knapp 2001).

A temporary increase in flowering among forbs has been observed following fire in several systems, including California chapparal (Keeley et al. 1981), Brazilian cerrado (Fidelis et al. 2014), and grasslands of the upper Midwest (Old 1969; Wagenius et al. 2020). This increase in floral display may cause corresponding increases in insect pollinator foraging activity in burned areas (Mola & Williams 2018), benefitting both the pollinator food acquisition and plant reproduction.

Despite this potential dual benefit, the mechanisms underlying changes in floral display after fires are not clear. Floral display may increase via increased population sizes of one or more forb species (more individual plants per unit area) (Mola & Williams 2018), an increase in individual plant size that causes a proportional increase in flowers per plant (Medve 1987; Obeso 1993), or a shift in reproductive allocation (more flowers per unit biomass) (Hartnett 1991). The mechanisms are not mutually exclusive; more than one may be operating at the same time.

To understand the mechanisms driving changes in floral display after fires, we tested these potential mechanisms in forb species of the southern Great Plains of the United States, where effects of fire on grassland communities are less well-studied than those in, for example, the upper Midwest (Peoples et al. 1994; Ansley & Castellano 2007; Burton et al. 2011; Winter et al. 2013). We measured individual plant responses to prescribed fire in eight abundant native grassland forbs (Table 1) across central Texas and southern Oklahoma (Fig. 1). We tested whether the floral display (flowers/m^2) was different in a burned plot than in an unburned control plot, and if so, were the differences due to plant density (plants/m^2), plant size (grams of dry aboveground biomass), resource allocation to flowers (flowers/gram plant biomass), or a combination of these factors.

We expected to observe an increase in floral display for all or most of the species. We also expected that there would be differences between annual and perennial forb species in response to fire, with the annuals increasing floral display via plant density and the perennials via plant size.

MATERIALS AND METHODS

Field methods

This study was conducted at five sites across a 480 km (300 mi) latitudinal gradient in the Cross Timbers ecoregion of central Texas and southern Oklahoma (Fig. 1). Before the mid-1800s, this region was a mosaic of grasslands, savannas, and woodlands dominated by C_4 grass species *Schizachyrium scoparium* (Michx.) Nash (little bluestem), *Andropogon gerardi* Vitman (big bluestem), and *Sorghastrum nutans* Nash (Indian grass) with *Quercus marilandica* Münchh. (blackjack oak) and *Q. stellata* Wangenh. (post oak) as common savanna trees (Dyksterhuis 1948; Gould et al. 1960). At present, the region still contains those same characteristic species where the community has not been completely destroyed or otherwise heavily altered (Diggs et al. 1999). Fire suppression and overgrazing by cattle during the 19th and 20th century have resulted in increased occurrences of dense stands of fire-sensitive *Juniperus* species and other woody species including *Ulmus crassifolia* Nutt. (cedar elm) and *Prosopis glandulosa* Torr. (mesquite) (Diggs et al. 1999). Other current common grass species include *Nassella leucotricha* (Trin. & Rupr.) R.W. Pohl (Texas winter grass), *Bouteloua curtipendula* (Michx.) Torr. (sideoats grama), and *Aristida* species (Dyksterhuis 1948). The non-native, invasive grass *Bothriochloa ischaemum* (L.) Keng (King Ranch bluestem) is increasingly common across the region and can form dense stands in open grasslands (Gabbard & Fowler 2006).

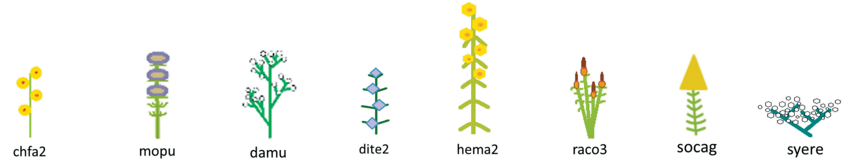
Fire has been used as a management tool in this region for centuries and continues to be utilized today (Dyksterhuis 1948; Behr 2024; Reemts 2025). Historically, the Cross Timbers ecoregion of Texas had frequent, low to medium-intensity fires with a mean fire return interval of 1–6 years (Stambaugh et al. 2014). Early written accounts describe the vegetation of the region as containing a grassy understory that was burned regularly by the Native American people during dry periods (Dyksterhuis 1948). Modern use of prescribed fire in this region is limited by legal, financial, and political constraints (Weir 2019) which results in uneven application of fire across the landscape at irregular intervals within any given site.

Present-day land use in this region includes expanding urbanization and agricultural uses, including rangeland used for cattle grazing and some limited row cropping agriculture (USDA 2017). Two of the five sites used for this study had been grazed by cattle at least once during the ten years prior to this study but all plots were fenced to exclude any grazing before this study began and remained fenced during the study.

At each of these sites, we focused our study on two plots, each 2 ha in size, where a single prescribed fire was conducted in early 2018 (January–March) at one plot, while another plot was left unburned as a control. The sites and plots were selected as part of a different landscape-scale study. Only one burned and one unburned plot of the same size was available at each site for this study, severely limiting available statistical tools for our analysis. Fires were primarily backing fires that occurred in air temperatures between 10–26°C and relative humidity between 16–56% (as in Whiting 2022).

Within each site, a forb species was selected for inclusion in this study if more than 200 plants of one forb species were present for sampling in both the burned and unburned plots during an initial site visit. The selected forb species were: *Chamaecrista fasciculata* (Michx.) Greene, *Dalea multiflora* (Nutt.) Shinners, *Diodia*

Table 1. Eight species measured as part of this study. *Symphyotrichum ericoides* was measured at two sites and all other species were measured at one site only.



species	*Chamaecrista fasciculata*	*Monarda punctata*	*Dalea multiflora*	*Diodia teres*	*Helianthus maximiliani*	*Ratibida columnifera*	*Solidago canadensis*	*Symphyotrichum ericoides*
abbreviation	chfa2	mopu	damu	dite2	hema2	raco3	socag	syere
Family	Fabaceae	Lamiaceae	Fabaceae	Rubiaceae	Asteraceae	Asteraceae	Asteraceae	Asteraceae
Duration	annual	annual	perennial	annual	perennial	perennial	perennial	perennial
Flowering period	Jun. – Oct.	May-Jul.	Jun. – Jul.	Jul-Sept.	Aug. – Nov.	May – Oct.	Aug. – Nov.	Sept. – Oct.
site(s)	Lake Whitney, TX	CrossTimbers WMA, OK	Hagerman NWR, TX	Lake Whitney, TX	Hagerman NWR, TX	Stillhouse Hollow Lake, TX	Hagerman NWR, TX	Hagerman NWR, TX Davis, OK
survey(s)	summer 2018 fall 2018	summer 2018 summer 2019	summer 2018	fall 2018	fall 2018 fall 2019	summer 2018 summer 2019	fall 2018 fall 2019	fall 2018 fall 2019
# plants measured	400	400	197	200	400	350	400	800
# plants collected	120	120	60	60	120	105	120	240

teres Walter, *Helianthus maximiliani* Schrad., *Monarda punctata* L., *Ratibida columnifera* (Nutt.) Wooton & Standl., *Solidago canadensis* L., and *Symphyotrichum ericoides* (L.) G.L. Nesom. Each selected forb species was sampled at one site each (except *S. ericoides*, which was sampled at two sites) (Table 1, Fig. 2).

For each species at each plot, 100 individuals were measured in the field and a subset were harvested (described below) during four sampling seasons, June (summer) and September (fall) of 2018 and 2019 as available and appropriate (see Table 1 for details). The center of the plot was used for other studies in this project and was avoided because this study involved removing plants from the area. A series of 100 meter transects were placed parallel to and five meters away from the boundary of this avoided central area and were unbiased relative to plant density (Fig. 2).

When a species was measured in more than one survey, the transects were in different locations within the treatment area in subsequent surveys to avoid resampling the same area. Plants of the target species were searched for along the transect within a pre-determined width (30 cm). Parallel, 100-meter transects were searched until 100 plants of the target species had been measured. To minimize bias in plant detection and correct identification, a minimum size threshold appropriate for each species was determined before sampling, based on each species' typical size distribution (including seedlings, juvenile plants, and adults) and only plants above that minimum threshold were counted.

Plant height was measured for all species, but remaining field measurements depended on the species morphology. Number of stems were counted for *Dalea multiflora* and *Ratibida columnifera*. Number of flowering stems was counted for *Monarda punctata*. The diameter of the crown of *Symphyotrichum ericoides* was measured as viewed from above. Total floral reproductive units at different phenological stages (which included visible buds, active flowers, senesced flowers, and fruits; hereafter referred to as flowers) were counted for all species except *M. punctata* and *Solidago canadensis*, for which total flower counts were estimated from a subset of collected inflorescences. For *M. punctata,* floral clusters were counted on each flowering stem. For *S. canadensis*, inflorescence height was measured and branches on the inflorescence were counted. Regressions of inflorescence measurements from field measured plants and actual flower counts from the subset of collected plants were used to estimate total flowers on the unharvested plants in the sample. For the other species, total flowers were counted and were not estimated.

At each plot, 30 of the 100 field-measured individuals were randomly selected and harvested, dried at 100 °C for at least three days, and weighed to the nearest 0.1 grams to measure the weight of the dry aboveground biomass. Regressions of biomass measurements against height of harvested individuals were used to estimate biomass of the unharvested plants in the sample for all species.

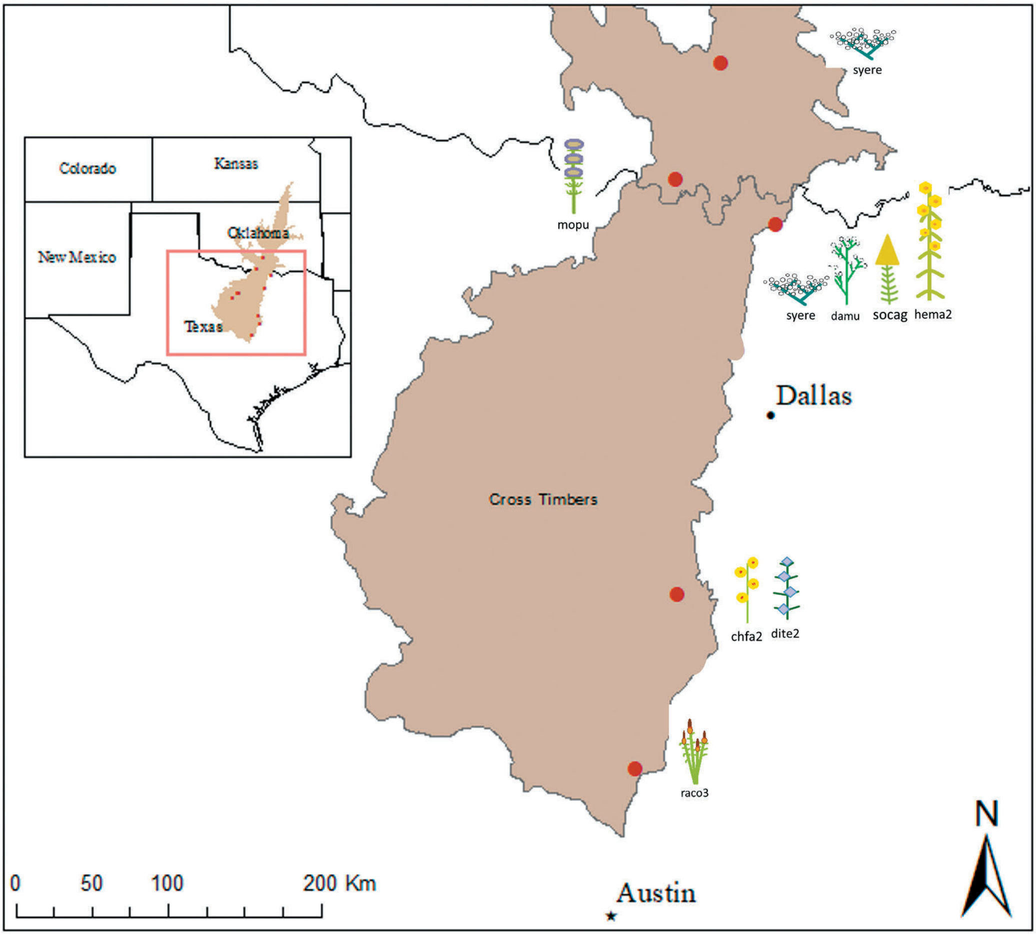


FIG. 1. Study site locations and illustrations of the species collected at each site. All study sites were in the Cross Timbers ecoregion of central Texas and southern Oklahoma.

Variable calculations

Plant density (plants/m^2) was calculated by dividing the area searched (transect length by transect width) by number of plants found in that area. Flower counts were used to calculate the flowers/plant, flowers/g plant biomass and flowers/m^2 variables used in analyses. The flowers/plant variable was calculated by dividing the total number of flowers counted on plants measured in a plot by the number of plants measured. The flowers/g plant biomass was calculated by dividing the estimated biomass of each individual plant by its number of counted or estimated flowers. The flowers/m^2 variable was calculated by dividing the area searched by the number of flowers found in that same area (Fig. 3).

Statistical analysis

We analyzed each of the eight forb species separately. This was necessary due to the extremely different morphology of each species and because, with one exception, we were unable to get samples of the same species at more than one site. Each individual plant was considered a separate observation for the analyses of plant height, estimated plant dry biomass, and flowers per plant. The fires were not applied to each individual, but rather to the whole plant community. We constructed generalized linear models using SAS PROC GLIMMIX

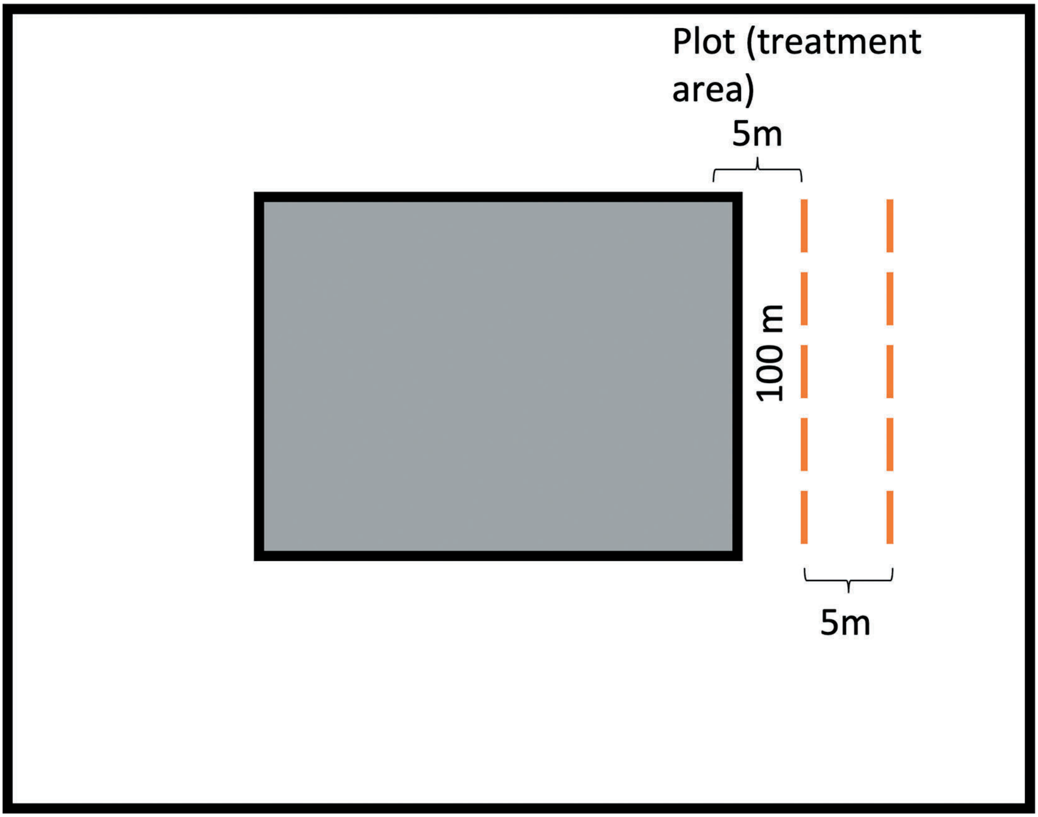


Fig. 2. Schematic of sampling methods within each plot (not to scale). We set up a series of 100 m transects (dashed black lines) parallel to but five meters outside a central 1 ha plot used for a different study (grey box). Plants of the target species above a minimum size threshold were searched for within 30 cm of the center of the transect until 100 plants of the target species had been measured, or until all individuals in that site had been surveyed, during a single sampling season. If a target species was present for more than one sampling season, an additional transect was established within the site (example indicated, dashed grey lines), also five meters outside the central plot, to avoid plant resampling.

(version 9.4, SAS Institute, Cary, North Carolina). The generalized linear models of height and dry biomass of each species used the log normal distribution. The generalized linear model of flower count of each species used the negative binomial distribution.

For each species and response variable combination, we compared all possible models. Treatment (burned vs. unburned) was always a possible predictor variable. Year, season, and site were each possible predictor variables for some species, depending on data available for the given species. For example, for *Chamaecrista fasciculata* height we compared four models: (a) treatment only, (b) season only, (c) treatment and season, and (d) treatment, season, and their interaction as predictor variables. If the response variable was flowers per plant, the possible predictor variables also included plant biomass as a covariate and associated slope comparisons. Since we analyzed each species separately, we did not include location as a possible predictor variable. We obtained the AICc (Aikake Information Criterion, corrected for small sample sizes) of every model tested. We report (Table 2), for each response variable of each species, the most parsimonious model within 2 units of the lowest AICc value for that species-response variable combination. (Results from all models tested are available from the first author).

Comparison of treatment effects on height and biomass depended on whether the best model included an interaction term. If it did not, we simply report the significance of the treatment effect. If the best model

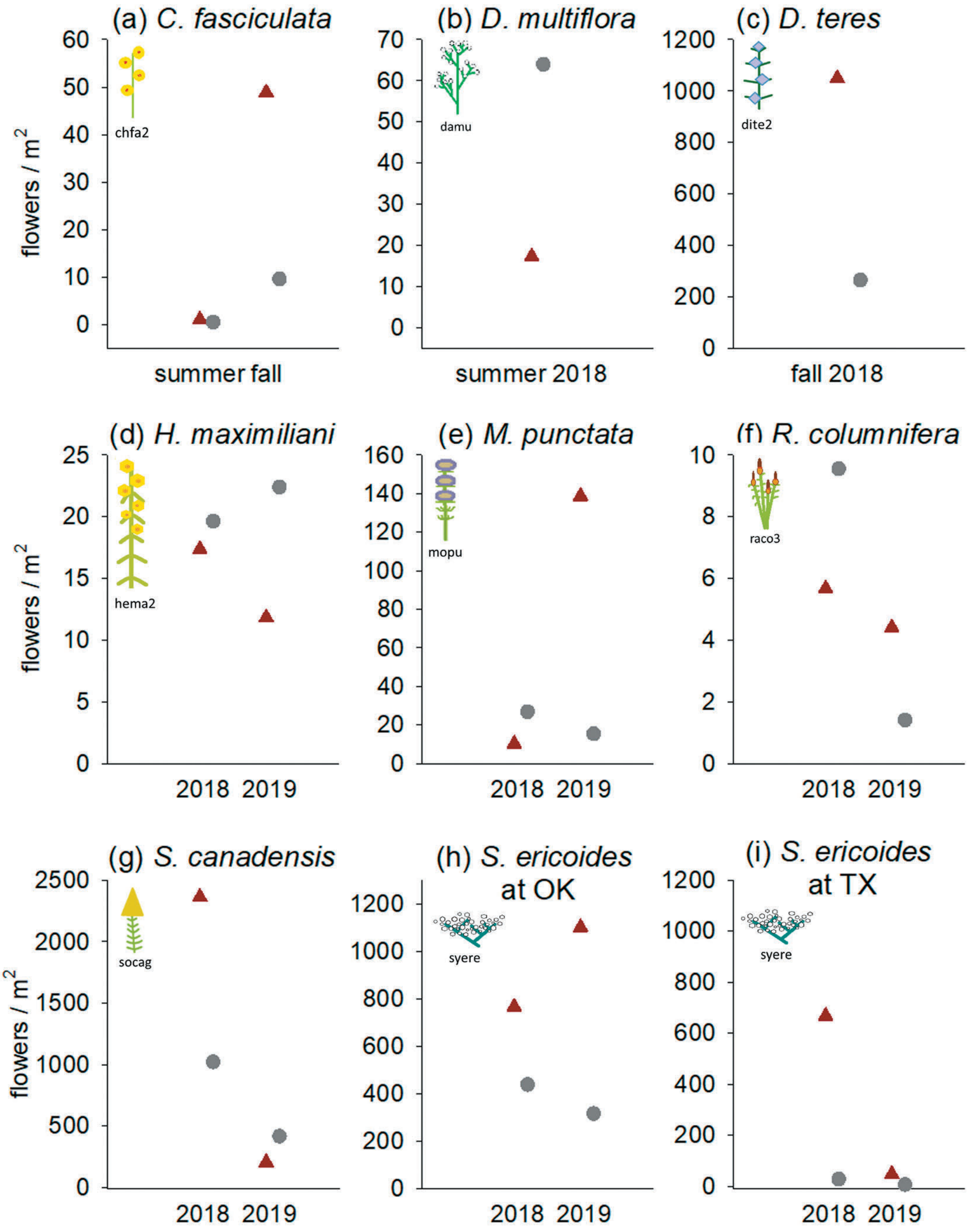
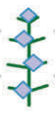


Fig. 3. Total floral display in each species as flowers per m^2 (flowers/plant × total transect area searched). Flowers/plant were calculated by dividing the total number of flowers in a plot by the number of plants measured. Transect area was calculated by multiplying the transect width (30 cm) by the transect length (the number of meters searched before finding 100 plants). **Red triangles** = burned, **gray circles** = unburned.

Table 2. Best models for each species – response variable combination. Highlighted P-values were significant ($P < 0.05$). When more than one model was within 2 AICc of the lowest value, the model with the fewest terms is reported. A complete list of all models and their AICc values is available from the first author. The variable "biomass" refers to the whole plant biomass.

species	response	predictor	df	F	P
Chamaecrista	height	treatment	1,396	0.03	0.8622
fasciculata		season	1,396	396.99	**<.0001**
 chfa2		tr × season	1,396	22.72	**<.0001**
	biomass	treatment	1,396	58.11	**<.0001**
		season	1,396	398.42	**<.0001**
	#flowers	plant biomass	1,396	83.55	**<.0001**
		treatment	1,396	6.36	**0.0121**
		season	1,396	99.14	**<.0001**
Dalea	height	treatment	1,195	1.78	0.1842
multiflora	biomass	treatment	1,195	2.71	0.1014
 damu	#flowers	plant biomass	1,193	203.83	**<.0001**
		treatment	1,193	3.09	0.0804
Diodia teres	height	treatment	1,198	61.59	**<.0001**
 dite2	biomass	treatment	1,198	91.96	**<.0001**
	#flowers	plant biomass	1,196	289.36	**<.0001**
		treatment	1,196	51.86	**<.0001**
		biomass × tr	1,196	5.08	**0.0254**
Monarda	height	treatment	1,396	45.75	**<.0001**
punctata		year	1,396	38.16	**<.0001**
 mopu		tr × year	1,396	130.38	**<.0001**
	biomass	treatment	1,396	16.1	**<.0001**
		year	1,396	3.1	0.079
		tr × year	1,396	71.33	**<.0001**
	#flowers	plant biomass	1,392	591.51	**<.0001**
		treatment	1,392	29.28	**<.0001**
		year	1,392	51.97	**<.0001**
		tr × year	1,392	65.55	**<.0001**
		biomass × tr	1,392	3.72	0.0545
		biomass × year	1,392	9.9	**0.0018**
		biomass × tr × year	1,392	26.64	**<.0001**
Ratibida	height	treatment	1,351	83.33	**<.0001**
columnifera		year	1,351	10.73	**0.0012**
 raco3		tr × year	1,351	13.01	**0.0004**
	biomass	treatment	1,352	72.45	**<.0001**
		year	1,352	102.5	**<.0001**
	#flowers	plant biomass	1,349	193.78	**<.0001**
		treatment	1,349	4.69	**0.031**
		year	1,349	6.99	**0.0086**
		biomass × tr	1,349	4.37	**0.0374**
		biomass × year	1,349	11.59	**0.0007**
Helianthus	height	treatment	1,396	6.44	**0.0116**
maximiliani		year	1,396	368.17	**<.0001**
 hema2		tr × year	1,396	79.94	**<.0001**
	biomass	treatment	1,396	4.04	**0.045**
		year	1,396	0.3	0.5816
		tr × year	1,396	26.02	**<.0001**
	#flowers	plant biomass	1,396	298.09	**<.0001**
		treatment	1,396	7.93	**0.0051**
		biomass × treatment	1,396	9.72	**0.002**
Solidago	height	treatment	1,397	6.17	**0.0134**
canadensis		year	1,397	14.66	**0.0001**
 socag	biomass	treatment	1,398	8.85	**0.0031**
	#flowers	plant biomass	1,392	145.46	**<.0001**
		treatment	1,392	3.94	**0.0477**
		year	1,392	3.06	0.0808
		tr × year	1,392	4.93	**0.027**
		biomass × tr	1,392	2.02	0.1556
		biomass × year	1,392	3.91	**0.0488**
		biomass × tr × year	1,392	1.8	0.1808
Symphyotrichum	height	treatment	1,397	100.41	**<.0001**
ericoides		year	1,397	64.47	**<.0001**
at Oklahoma		treatment × year	1,397	10.34	**0.0014**
 syere	biomass	treatment	1,399	48.3	**<.0001**
	#flowers	plant biomass	1,396	279.73	**<.0001**
		treatment	1,396	26.17	**<.0001**
		year	1,396	1.93	0.1655
		treatment × year	1,396	10.12	**0.0016**
Symphyotrichum	height	treatment	1,397	15.35	**0.0001**
ericoides		year	1,397	157.34	**<.0001**
at Texas		treatment × year	1,397	11.33	**0.0008**
 syere	biomass	treatment	1,397	75.68	**<.0001**
		year	1,397	41.4	**<.0001**
		treatment × year	1,397	17.37	**<.0001**
	#flowers	plant biomass	1,392	19.43	**<.0001**
		treatment	1,392	3.35	0.0682
		year	1,392	2.45	0.1183
		treatment × year	1,392	3.18	0.0752
		biomass × treatment	1,392	8.06	**0.0048**
		biomass × year	1,392	3.56	0.0599
		biomass × treatment × year	1,392	1.02	0.3143

contained an interaction term, we used least-squares-mean contrasts to compare treatments. For example, the best model of *Monarda punctata* height included the treatment × year term, so we contrasted height in summer 2018 in the burned plot with height in summer 2018 in the unburned plot and did the parallel contrast with the two 2019 least squares means. Note that these contrasts were part of the corresponding generalized linear model, and therefore compare log-transformed height or biomass.

We analyzed two response variables that can be thought of as measures of resource allocation, flowers/g aboveground whole plant biomass, and plant height. We were interested in plant height because it can reflect light competition. However, in our study, height was highly correlated with biomass ($r = 0.32$ to 0.93), and the results of its analyses essentially duplicated those of biomass. Species differed in the strength of the relationships between plant biomass and number of flowers per plant (Fig. 4), but in all instances the overall relationship was positive and strongly significant. Some species had significant differences between treatments in the strength of the relationship, but these differences had little effect on floral display.

Comparison of treatment effects on flowers per gram of plant (flowers per plant with plant biomass as a covariate) was similar to the analyses of height and biomass if the best model did not contain any term indicating differences in slopes of the effect of the covariate (i.e., the covariate × treatment, covariate × year, etc.

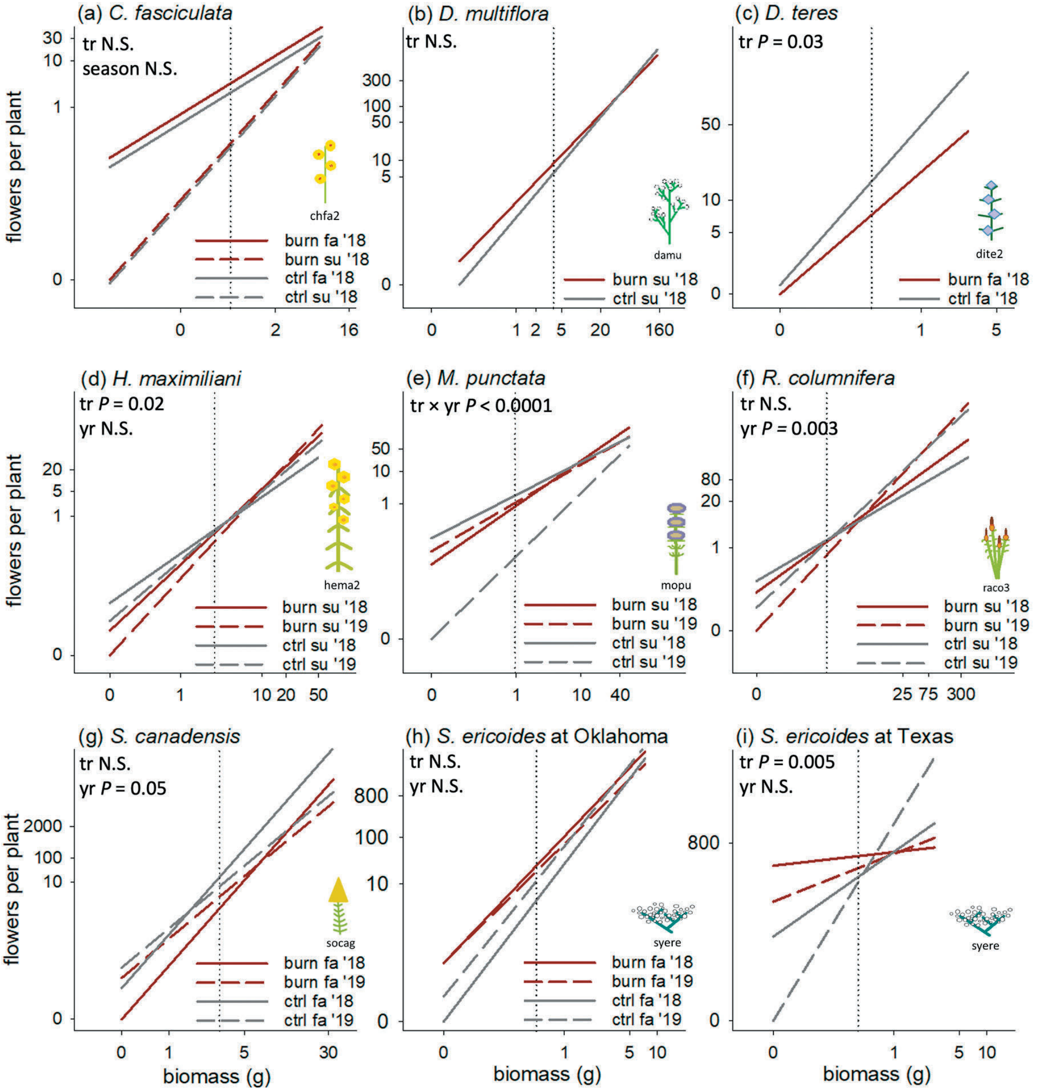


Fig. 4. Relationships between plant size and flowers per gram of biomass for each species. Dotted vertical lines represent the median biomass (g) in each species. Solid lines are from the 2018 surveys and dashed lines are from the 2019 surveys. Red lines are burned plots and gray lines are unburned plots. Treatment, season, and year abbreviations are: **burn** = burned, **ctrl** = control, **su** = summer, **fa** = fall, **'18** = 2018, and **'19** = 2019. In the initial analysis of *S. ericoides*, both the biomass × site × treatment and the biomass × site × year were significant, justifying analyzing the two sites separately (h & i).

'interaction' terms were all non-significant). If the best model contained a significant 'three-way-interaction', such as covariate × treatment × year, the contrasts were constructed to compare slopes, not means, of the two treatments in the same year (or season). If the best model did not include a significant three-way interaction but did include a significant two-way interaction, the covariate × treatment or covariate × year effect was reported.

Because for all but one species, density was only measured in one plot in each treatment (Fig. 5), we were not able to statistically compare the effects of treatment on density the way we analyzed the other response variables. However, by using the number of plants within each unit of transect length as a response variable

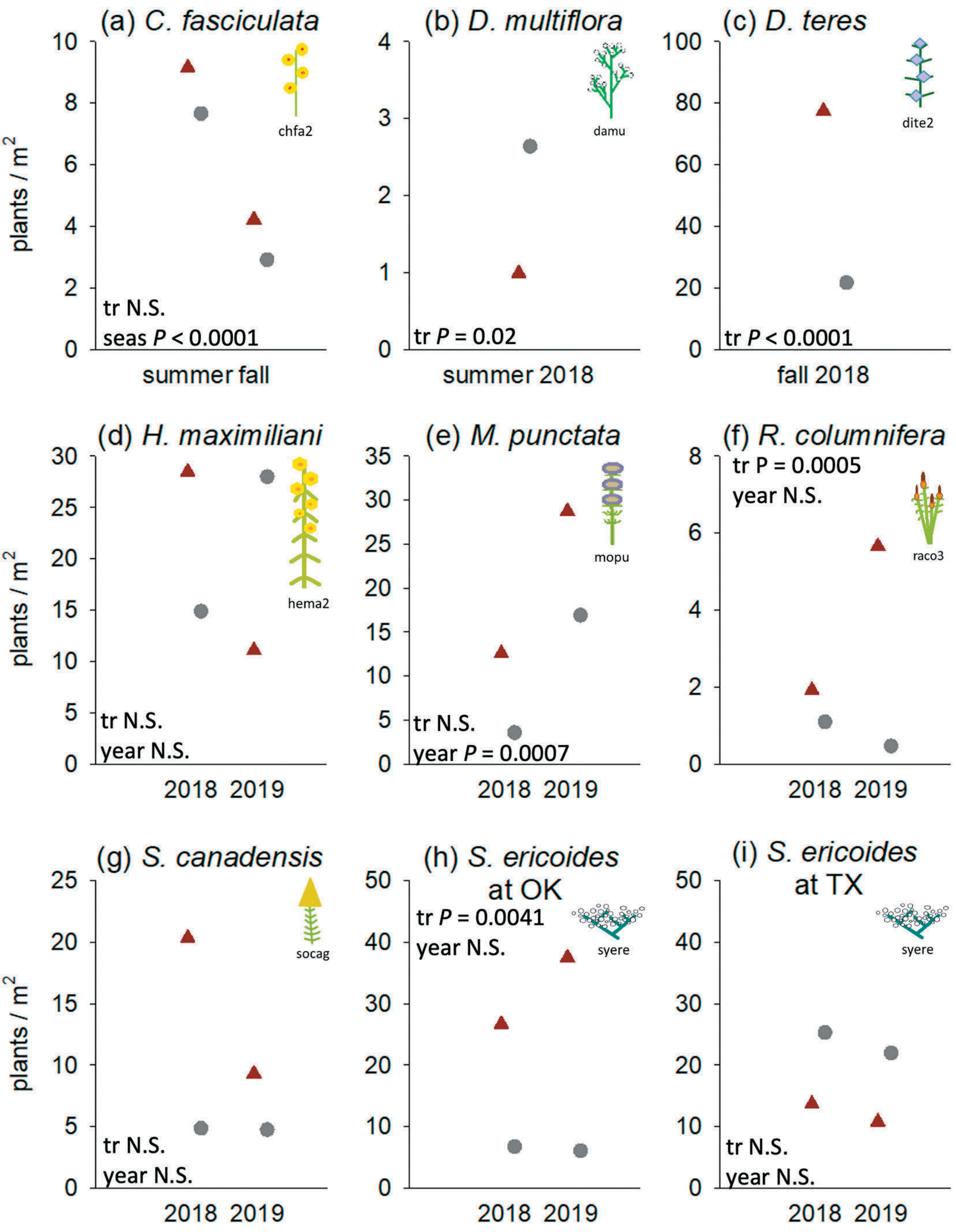


Fig. 5. Plant density of each species. Points have been slightly offset for readability. Density was calculated as the total area searched (transect length × transect width) divided by the number of plants measured during that survey (usually 100). Density models were constructed using the number of plants per unit area (1m for high density species *D. teres*, 10 m for low density species *D. multiflora* and *R. columnifera*, and 5 m for all other species) as response variable. **Red triangles** = burned, **gray circles** = unburned.

(1-meter-long units for high density species *D. teres*, 10-meter-long units for the very low density species *Dalea multiflora* and *Ratibida columnifera*, and 5-meter-long units for the other five species), we were able to estimate confidence limits on density, while recognizing that the units of a transect are not independent and therefore these confidence limits should be interpreted with caution.

RESULTS

Effects of fire on plant biomass

Plants in burned plots were on average larger than plants in the paired unburned plot in six instances (i.e., species-year-site combinations) but smaller in nine instances (Table 3). The three annual species (*Chamaecrista fasciculata*, *Diodia teres,* and *Monarda punctata*) were larger in the burned plot in three of four instances, possibly due to a reduction in thatch and shading from grasses. The five perennial species (*Dalea multiflora, D. teres, Helianthus maximiliani, Ratibida columnifera, Solidago canadensis,* and *Symphyotrichum ericoides*), in contrast, were larger in their burned plot in only 27% of instances, possibly reflecting the direct loss of biomass to the fire. There was some evidence of a lag in positive fire effects: of the six species surveyed in both years, two (*H. maximiliani* and *M. punctata*) were on average smaller in the burned plot in the first year after the fire and then larger in the burned plot the following year. However, there was no evidence of larger size post fire in *S. canadensis*, *R. columnifera*, nor in *S. ericoides* in the Oklahoma site.

Effects of fire on plant density (plants/m^2)

Like plant size, the differences in plant density between burned and unburned plots differed among species (Table 3). *Diodia teres* and *Ratibida columnifera* (in both surveys), and *Symphyotrichum ericoides* at the Oklahoma site (in both survey years) had significantly more plants/m^2 in their respective burned plot than in the unburned plot. *Chamaecrista fasciculata*, *Monarda punctata*, and *Solidago canadensis* were not significantly different in the burned plot. In contrast, *Dalea multiflora* had significantly fewer plants in the burned plot than in the unburned plot; *S. ericoides* density was not significantly different between burned and unburned plot the in the Texas site.

Floral display (flowers/m^2)

Floral display, flowers/m^2 of a given species, was greater in the burned plot than the unburned plot in eight of fifteen instances (Table 3). However, five of the eight species showed a greater floral display in the burned plot compared to the unburned plot within the second survey year– all but *Helianthus maximiliani*, *Solidago canadensis*, and *Dalea multiflora* (Fig. 3). *Chamaecrista fasciculata, Diodia teres*, and *Symphyotrichum ericoides* at both sites had more flowers per m^2 in their respective burned plots compared to unburned plots within each survey year in which they were measured. *Monarda punctata* and *Ratibida columnifera* had fewer flowers per m^2 in their burned plot in the first survey year, but more flowers per m^2 in their burned plot in the second survey year, suggesting a possible delayed positive response to fire for those two species.

Relationships among plant size, plant density and floral display

Since resource allocation (flowers per gram of plant) did not vary much between treatments (discussed below), the effects on floral display (flowers per m^2) were determined by plant size and plant density. In other words, flowers/m^2, which equaled the number of plants/m^2 × biomass/plant × flowers/biomass, was in practice largely proportional to the number of plants/m^2 × biomass/plant.

The numbers of flowers/m^2 in burned and unburned plots varied among species and survey years. Plant size and plant density differ between burned and unburned plots in only four instances. In three instances (*Chamaecrista fasciculata, Diodia teres,* and *Monarda punctata* in the second survey year), both plant size and density were higher in their respective burned plot than in their unburned plot and in one instance (*Dalea multiflora*), both plant size and density were lower in the burned plot.

In contrast, in eleven instances, plant size and density did not change in the same way (Table 3). The effects of density outweighed those of plant size in eight instances: smaller, but higher density plants leading to more flowers/m^2 in the burned plot (*Symphyotrichum ericoides* at the Oklahoma site within each of both

Table 3. Summary of the directions of fire responses in each species and survey year. Prescribed burns were conducted in Jan. to Mar. 2018 and surveys were conducted in June and September each year (see Table 1). Arrows indicate the direction of the response in the burn plot relative to the unburned plot.

Species (survey year)		plant biomass (g)	plant density (plants/m²)	floral display (flowers/m²)
annuals	*Chamaecrista* (2018)	↑	↑	↑
	Diodia (2018)	↑	↑	↑
	Monarda (2018)	↓	↑	↓
	Monarda (2019)	↑	↑	↑
perennials	*Dalea* (2018)	↓	↓	↓
	Helianthus (2018)	↓	↑	↓
	Helianthus (2019)	↑	↓	↓
	Ratibida (2018)	↓	↑	↓
	Ratibida (2019)	↓	↑	↑
	Solidago (2018)	↓	↑	↑
	Solidago (2019)	↓	↑	↓
	Symphyotrichum at OK (2018)	↓	↑	↑
	Symphyotrichum at OK (2019)	↓	↑	↑
	Symphyotrichum at TX (2018)	↑	↓	↑
	Symphyotrichum at TX (2019)	↑	↓	↑

survey years, *Ratibida columnifera* within the second survey year, and *Solidago canadensis* within the first survey year) or larger, but lower density plants leading to fewer flowers/m^2 in the burned plot (*Monarda punctata* in the first survey year, *R. columnifera* in the first survey year, *Helianthus maximilani* in the first survey year, and *S. canadensis* in the second survey year). For *S. ericoides* at the Texas site (in both survey years), plant size outweighed the effects of density: larger, but lower density plants led to more flowers/ m^2. *Symphyotrichum ericoides* had overall more flowers/m^2 in the burned plot at both sites in both survey years.

Resource allocation: height

Plant height was closely related to plant aboveground biomass in most instances, with very similar responses to fire. In other words, species that were larger in their burned plot were also taller there, with few exceptions (Figs. 6 and 7). The expected effect of fire on height, that plants in burned plots would be shorter due to less competition there, was not found.

Resource allocation: flowers/gram of plant biomass

Overall, the relationship between plant size and number of flowers per plant was positive in all species (Table 2, Fig. 5). Larger plants had more flowers than smaller plants, even though average biomass per plant differed among species by an order of magnitude, and the maxima differed even more. However, in some instances (*Diodia teres, Helianthus maximilani, Symphyotrichum ericoides* at the Texas site) this relationship differed between treatments (Figs. 5c, 5d, and 5i), and for *Monarda punctata* between treatment-survey combinations (Fig. 5e).

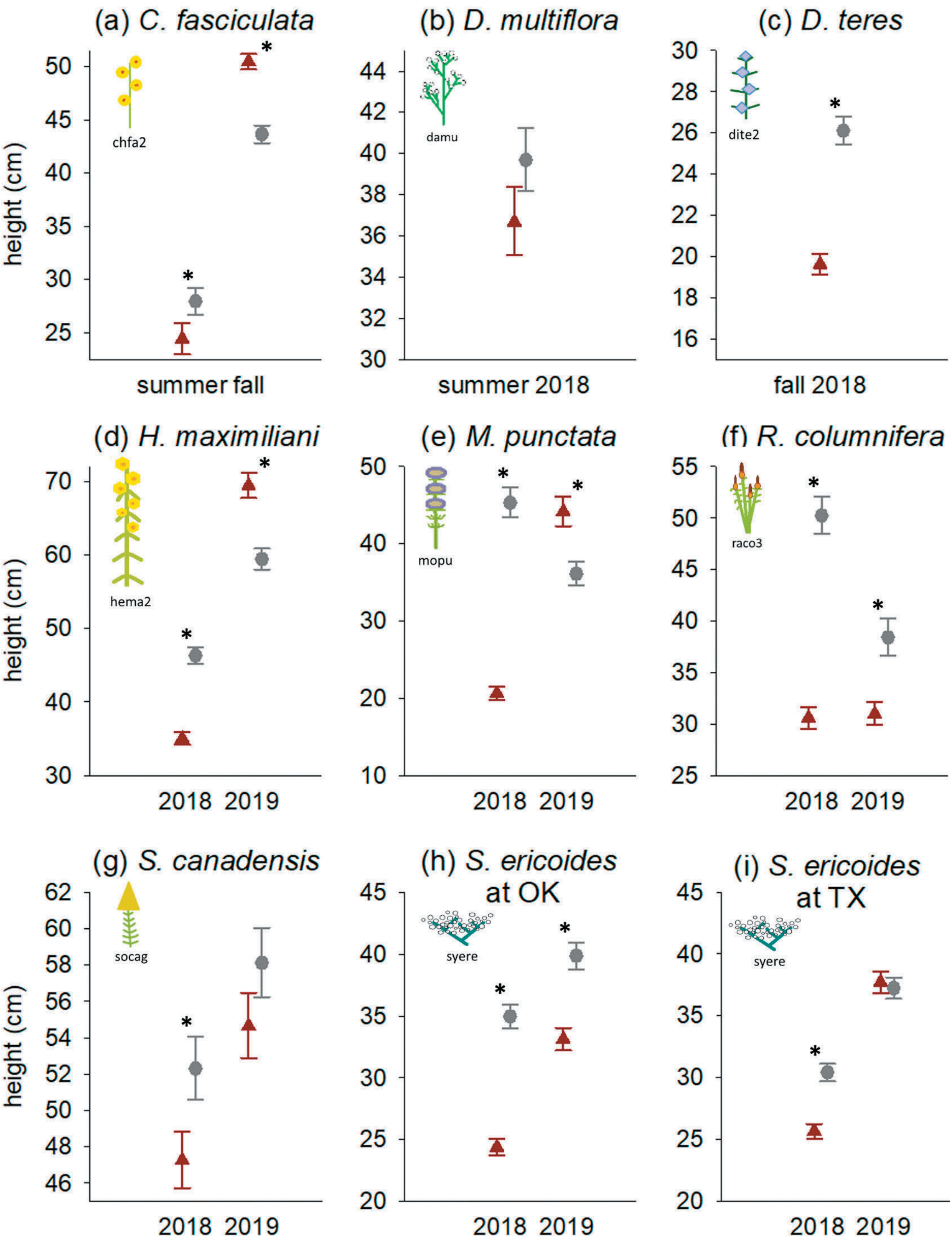


Fig. 6. Plant height back-transformed least squared means and standard error bars. Asterisks indicate a significant difference ($P < 0.05$) between the burn and control plot in the same season or year. **Red triangles** = burned, **gray circles** = unburned.

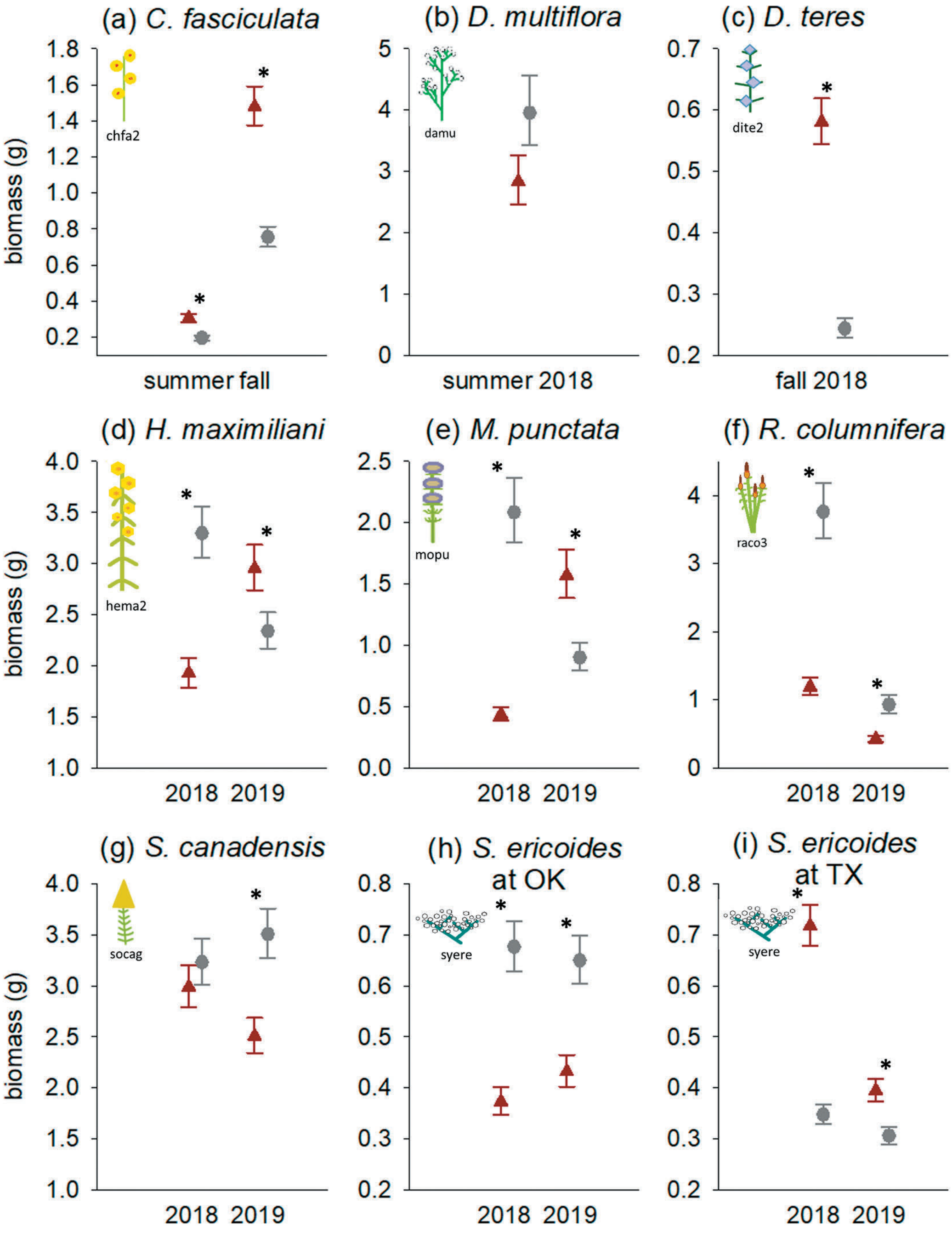


Fig. 7. Estimated dry whole-plant (including flowers) biomass back-transformed least squared means and standard error bars. Asterisks indicate a significant difference ($P < 0.05$) between the burn and control plot in the same season or year. **Red triangles** = burned, **gray circles** = unburned.

DISCUSSION

Understanding how individual forb species in the plant community respond to prescribed fires allows researchers and managers to connect the effects of fire on the plants to the effects on those plants' associated pollinator communities. Improving this understanding can help build a bridge between plant-focused and pollinator-focused research that can drive restoration strategies that are relevant to the conservation of both plants and pollinators rather than just one side of this mutualistic relationship.

In this study, we found evidence that prescribed fire had an effect on the floral display (flowers/m^2) of eight native forb species. Many of these species had a larger floral display in burned plot than in unburned plot at the same site after a single prescribed burn, especially during the second growing season. However, species followed different paths to achieve these increases in floral display. Species increased either or both plant size and plant density. Because floral display was consistently positively correlated with plant size in each species, differences in floral display between burned and unburned plots were primarily proportional to plant size and to plant density.

In four species both plant size and plant density responded to fire in the same direction within their final survey year (two years after burning). Interestingly, the three species that were both larger and more abundant in their burned plots were all three annuals: *Chamaecrista fasciculata*, *Diodia teres*, and the facultative annual *Monarda punctata* (Diggs et al. 1999). Most likely, these annuals germinated after the fire and therefore did not experience direct negative effects of the fire. The positive effects of fire on these species were likely due to release from competition from grasses (Mulhouse et al. 2017). Annual plant species often maintain a seed bank that can germinate quickly under favorable conditions and they can therefore respond quickly to the temporary release from grass competition post-fire (Mulhouse et al. 2017).

The only legume species, *Dalea multiflora*, was also the only species to have both smaller plants on average and fewer of them in its burned plot. With one survey year of data available, we cannot rule out a delayed positive effect. However, burning may have increased white-tailed deer (*Odocoileus virginianus*) herbivory in the burned plot. Deer are known to preferentially feed in recently burned areas and can reduce flowering in some grassland forb species (Anderson et al. 2017). While many legumes are well protected from herbivory by secondary compounds, *D. multiflora* is not listed as one such species (Hart et al. 2004). Alternatively, there could have been other biotic or abiotic interactions in the plots that could have influenced results.

The other four species' responses to fire were not consistent, having either smaller but more abundant plants in their burned plots two years after the burn (*Symphyotrichum ericoides* in the Oklahoma site, *Ratibida columnifera*, and *Solidago canadensis*), or larger but less abundant plants (*S. ericoides* at the Texas site, and *Helianthus maximilani*). The net effect on floral resources in the final survey years was also highly individualistic. Density outweighed plant size in *S. ericoides* in Oklahoma and *R. columnifera*, resulting in larger floral display in the burned plots, and also outweighed plant size in *H. maximilani*, resulting in a smaller overall floral display. In contrast, plant size outweighed density in *S. canadensis*, resulting in a smaller floral display in its burned plot, and in *S. ericoides* in the Texas site, resulting in a larger floral display in its burned plot.

The differences among the perennial species were likely due in part to a direct effect of fire: loss of aboveground biomass. For example, *Solidago canadensis* plants were smaller in the burned plot than in the unburned plot in both years, as were *Ratibida columnifera* plants. These results were unexpected, given that this community almost certainly burned frequently until grassland fires were suppressed less than 200 years ago (Dyksterhuis 1948). Fire is known to decrease reproduction immediately after a fire in some forb species (Rosburg 2001; Pavlovic et al. 2010), but the suppression of dominant grasses by the fire has been shown to benefit these forb species in subsequent growing seasons (Hartnett 1991; Howe 1994). The decrease in plant size was especially unexpected in *S. canadensis*. It is possible that burning in Texas in January through March, as was done in this study, was not ideal for this species. However, Towne and Kemp (2003) found that fires similarly had little effect on *S. canadensis* when they were conducted in winter or spring in Kansas. *S. canadensis* was the only clonal forb in this study; perhaps it allocated resources to new stems (which were counted as individuals in this study) rather than stem size. This is consistent with its greater plant density in the burned plot.

A direct but less lasting effect of biomass loss may explain the possible lags in the fire effects that we observed: both *Monarda punctata* (a facultative perennial) and *Helianthus maximilani* (a perennial) plants were smaller on average in the burned plot in the year of burn, but larger in the burned plot than in the unburned plot the year following the burn. However, *H. maximilani* was more abundant in the burned than in the unburned plot in the year of burn, and that pattern was reversed in the year following the burn. The delay in *M. punctata* and *H. maximilani* plant size has several possible, not mutually exclusive, explanations. It may have been due to the growth of the surviving plants, to the deaths of the smallest plants between the two survey years, to delayed germination due to dry conditions the first post-fire growing season, or to greater precipitation in the second post-fire growing season. We were limited by the financial and logistical constraints required to conduct large-scale prescribed fires across multiple sites in the Cross Timbers ecoregion, but future work should explore germination and survivorship metrics in addition to floral display, height, and biomass, and should ideally increase replication of paired burned and unburned plots within a larger number of sites.

We note that due to large differences among sites in plant community composition, only one of the eight species could be studied at more than one site. As a result, we cannot confidently rule out the possibility that some of the apparent differences between burned and unburned plots in a site were due to other environmental differences between sites and plots.

Although not all the observed differences between burned and unburned plots in plant size and in plant density were significant, and we cannot rule out other environmental differences between burned and unburned plots, the wide variety of observed relationships between plant size, plant density and floral display indicates that these relationships are highly individualistic among species and can differ substantially among years and time since fire. These differences among species may contribute to their co-existence and thereby buffer total floral display and hence pollinator resources. Forb species responding differently to fire also likely increases spatial and temporal heterogeneity within the community, which is strongly associated with greater biodiversity and ecosystem functioning (Leach & Givnish 1999; Hooper et al. 2005).

Knowing which species increase floral display after a fire and how they do so can inform decisions regarding which forb species to plant for the goal of pollinator restoration, when to burn those plant communities, and what to expect from the subsequent floral display. We did not measure the quality or quantity of the floral resources (i.e., nectar, pollen), which have also been shown to vary among forb species in response to prescribed fire (Geest & Baum 2022). Managing for different seasons and times since burn within the foraging range of pollinators may benefit the overall community by providing access to diverse floral resources. From a management perspective, these results suggests that managers cannot rely on generalizations about how forb size and density jointly act to determine floral resources for pollinators. On the other hand, highly individualistic species' responses may be a source for resilience against further land-use changes (Mori et al. 2013). The individualistic nature of the forb responses in this study reinforces the need to manage for increased forb diversity and overall heterogeneity to recreate or restore ecosystems that can support a wider variety of organisms and conserve biodiversity.

ACKNOWLEDGMENTS

We thank L. Weaver, S. Beavers, the North Texas Fire Resources, the Hagerman National Wildlife Refuge, the Oklahoma Dept. of Wildlife Conservation Cross Timbers Wildlife Management Area, and B. Reynolds for conducting the prescribed fires. We thank the U.S. Army Corps of Engineers at Stillhouse Hollow, Waco Lake, Lake Whitney, and Lewisville Lake, the Hagerman National Wildlife Refuge, the Oklahoma Dept. of Wildlife Conservation at Cross Timbers Wildlife Management Area, and several private landholders for site management history and access. We thank the staff and volunteers at the University of Texas at Austin Plant Resources Center Herbarium, especially George Yatskievych, for their help identifying, preserving, and digitizing plant specimens related to this project. We also thank R. Carden, C. Farrior, A. Green, C. Reemts, A. Wolf, K. Young, and B. Middleton for providing comments and suggestions on earlier versions of the

manuscript. We acknowledge this study took place on the traditional, ancestral, and unceded/seized territory of the following groups: Wichita, Tawakoni, Caddo, Lipan Apache, Tonkawa, Comanche, and Osage.

REFERENCES

Anderson R.C., M.R. Anderson, & E.A. Corbett. 2017. White-tailed deer (*Odocoileus virginianus*) and fire effects on flowering diversity of tallgrass prairie forbs. J. Torrey Bot. Soc. 144:243–253.

Ansley R.J. & M.J. Castellano. 2007. Prickly pear cactus responses to summer and winter fires. Rangeland Ecol. Manag. 60:244–252.

Behr, W.L. 2024. Benefits to native grasses from a summer fire still present 12 years later. Nat. Areas J. 44:172–182.

Bond, W.J., F.I. Woodward, & G.F. Midgley. 2005. The global distribution of ecosystems in a world without fire. New Phytol. 165:525–537.

Briggs, J.M. & A.K. Knapp. 2001. Determinants of C_3 forb growth and production in a C4 dominated grassland. Pl. Ecol. 152:93–100.

Burton, J.A., S.W. Hallgren, S.D. Fuhlendorf, & D.M. Leslie. 2011. Understory response to varying fire frequencies after 20 years of prescribed burning in an upland oak forest. Pl. Ecol. 212:1513–1525.

Campbell, J.W., J.H. Irvin, & J.D. Ellis. 2018. Bee contribution to partridge pea (*Chamaecrista fasciculata*) pollination in Florida. Amer. Midl. Naturalist 179:86–93.

Cardinale, B.J., J.E. Duffy, A. Gonzalez, D.U. Hooper, C. Perrings, P. Venail, A. Narwani, G.M. Mace, D. Tilman, D.A. Wardle, A.P. Kinzig, G.C. Daily, M. Loreau, J.B. Grace, A. Larigauderie, D.S. Srivastava, & S. Naeem. 2012. Biodiversity loss and its impact on humanity. Nature 486:59–67.

Cardoso, P., P.S. Barton, K. Birkhofer, F. Chichorro, C. Deacon, T. Fartmann, C.S. Fukushima, R. Gaigher, J.C. Habel, C.A. Hallmann, M.J. Hill, A. Hochkirch, M.L. Kwak, S. Mammola, J. Ari Noriega, A.B. Orfinger, F. Pedraza, J.S. Pryke, F.O. Roque, J. Settele, J.P. Simaika, N.E. Stork, F. Suhling, C. Vorster, & M.J. Samways. 2020. Scientists' warning to humanity on insect extinctions. Biol. Conserv. 242:108426.

Cariveau, D.P., B. Bruninga-Socolar, & G.L. Pardee. 2020. A review of the challenges and opportunities for restoring animal-mediated pollination of native plants. Emerging Top. Life Sci. 4:99–109.

Diggs, G.M., B. Lipscomb, & R. O'Kennon. 1999. Illustrated flora of north central Texas. Botanical Research Institute of Texas, Fort Worth, TX, U.S.A.

Dyksterhuis, E.J. 1948. The vegetation of the western cross timbers. Ecol. Monogr. 18:325–376.

Fidelis, A., C. Blanco, & J. Morgan. 2014. Does fire induce flowering in Brazilian subtropical grasslands? Appl. Veg. Sci. 17:690–699.

Gabbard, B.L. & N.L. Fowler. 2006. Wide ecological amplitude of a diversity-reducing invasive grass. Biol. Invas. 9:149–160.

Geest, E. & K. Baum. 2022. The impact of fire on nectar quality and quantity for insect pollinator communities. Amer. Midl. Naturalist 187:268–278.

Ghazoul, J. 2006. Floral diversity and the facilitation of pollination. J. Ecol. 94:295–304.

Gould, F.W., G.O. Hoffman, & C.A. Rechenthin. 1960. Vegetational areas of Texas. Texas Agricultural Extension Service Leaflet Number 492, College Station, TX, U.S.A.

Hart, C.R., T. Garland, A.C. Barr, B.B. Carpenter, & J.C. Reagor. 2004. Toxic plants of Texas. Texas Agricultural Extension Service, Texas A & M University, College Station, TX, U.S.A.

Hartnett, D.C. 1991. Effects of fire in tallgrass prairie on growth and reproduction of prairie coneflower (*Ratibida columnifera*: Asteraceae). Amer. J. Bot. 78:429–435.

Hooper, D.U., F.S. Chapin, J.J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J.H. Lawton, D.M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setala, A.J. Symstad, J. Vandermeer, & D.A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol. Monogr. 75:3–35.

Horvath, Z., R. Ptacnik, C.F. Vad, &J.M. Chase. 2019. Habitat loss over six decades accelerates regional and local biodiversity loss via changing landscape connectance. Ecol. Lett. 22:1019–1027

Howe, H.F. 1994. Response of early- and late-flowering plants to fire season in experimental prairies. Ecol. Appl. 4:121–133.

Keeley, S.C., J.E. Keeley, S.M. Hutchinson, & A.W. Johnson. 1981. Postfire succession of the herbaceous flora in southern California chaparral. Ecology 62:1608–1621.

Leach, M.K. & T.J. Givnish. 1999. Gradients in the composition, structure, and diversity of remnant oak savannas in southern Wisconsin. Ecol. Monogr. 69:353–374.

Medve, R.J. 1987. The effects of fire on resource allocation and growth of *Liatris spicata*. Amer. Midl. Naturalist 117:199–203.

Mola, J.M. & N.M. Williams. 2018. Fire-induced change in floral abundance, density, and phenology benefits bumble bee foragers. Ecosphere 9:e02056.

Mori, A.S., T. Furukawa, & T. Sasaki. 2013. Response diversity determines the resilience of ecosystems to environmental change. Biol. Rev. 88:349–364.

Mulhouse, J.M., L.M. Hallett, S.L. Collins, & V. Vandvik. 2017. The influence of seasonal precipitation and grass competition on 20 years of forb dynamics in northern Chihuahuan Desert grassland. J. Veg. Sci. 28:250–259.

Obeso, J.R. 1993. Cost of reproduction in the perennial herb *Asphodelus albus* (Liliaceae). Ecography 16:365–371.

Old, S.M. 1969. Microclimate, fire, and plant production in an Illinois prairie. Ecol. Monogr. 39:355–384.

Ollerton, J., R. Winfree, & S. Tarrant. 2011. How many flowering plants are pollinated by animals? Oikos 120:321–326.

Pavlovic, N.B., S.A. Leicht-Young, & R. Grundel. 2010. Short-term effects of burn season on flowering phenology of savanna plants. Pl. Ecolog. 212:611–625.

Peoples, A.D., R.L. Lochmiller, D.M. Leslie, & D.M. Engle. 1994. Producing northern bobwhite food on sandy soils in semiarid mixed prairies. Wildl. Soc. Bull. 22:204–211.

Reemts, C.M., J.C. Havird, W.L. Behr, M.K. Clayton, J.L. Foster, M.M. Lesak, C.V. Whiting, C.E. Farrior, & A.A. Wolf. 2025. Fire season and drought influence fire effects on invasive grasses: A meta-analysis. J. Appl. Ecol. 00:1–13.

Rosburg, T.R. 2001. Effects of late spring fires on the survival, growth, and reproduction of prairie forbs. Proceedings of the seventeenth North American Prairie Conference: seeds for the future, roots of the past, Mason City, IA, U.S.A., July 16–20, 2000 2001. North Iowa Area Community College, Mason City, IA, U.S.A.

Suding, K.N. 2011. Toward an era of restoration in ecology: successes, failures, and opportunities ahead. Ann. Rev. Ecol. Evol. Syst. 42:465–487.

Stambaugh, M.C., J.C. Sparks, & E.R. Abadir. 2014. Historical Pyrogeography of Texas, USA. Fire Ecol. 10(3):72–89.

Szigeti V., Á. Kőrösi, A. Harnos, J. Nagy, & J. Kis. 2016. Measuring floral resource availability for insect pollinators in temperate grasslands - a review. Ecol. Entomol. 41:231–240.

Towne, E.G. & K.E. Kemp. 2003. Vegetation dynamics from annually burning tallgrass prairie in different seasons. J. Range Managem. 56:185–192.

Towne, E.G. & K.E. Kemp. 2008. Long-term response patterns of tallgrass prairie to frequent summer burning. Rangeland Ecol. Managem. 61:509–520.

USDA. 2017. 2017 Census of Agriculture. USDA National Agricultural Statistics Service, Washington, DC, U.S.A.

Wagenius, S., J. Beck, & G. Kiefer. 2020. Fire synchronizes flowering and boosts reproduction in a widespread but declining prairie species. Proc. Natl. Acad. Sci. U.S.A. 117:3000–3005.

Weir, J.R., U.P. Kreuter, C.L. Wonkka, D. Twidwell, D.A. Stroman, M. Russell, & C.A. Taylor. 2019. Liability and Prescribed fire: Perception and reality. Rangeland Ecol. Managem. 72:533–538.

Whiting, C. 2022. Ecological relationships between invasive grasses, native grasses, and wildfire. Doctoral Dissertation. University of Texas at Austin, U.S.A.

Winter, S.L., K.R. Hickman, C.L. Goad, S.D. Fuhlendorf, & M.S. Gregory. 2013. Seasonal fires, bison grazing, and the tallgrass prairie forb *Arnoglossum plantagineum* Raf. Nat. Areas J. 33:327–338.