Received: 2 September 2024 | Accepted: 15 February 2025

DOI: 10.1111/1365-2664.70041

RESEARCH ARTICLE

BRITISH ECOLOGICAL SOCIETY Journal of Applied Ecology

Fire season and drought influence fire effects on invasive grasses: A meta-analysis

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Handling Editor: Cate Macinnis-Ng

Abstract

1. Fire can shape plant communities when species respond differently to fire characteristics like season and intensity. If invasive plants are more vulnerable than native species to specific aspects of fire, managers could use prescribed fires to control non-native species.
2. We conducted a meta-analysis of fire effects on six closely related Afro-Eurasian and Australian grasses (*Bothriochloa bladhii*, *B. ischaemum*, *B. pertusa*, *Dichanthium annulatum*, *D. aristatum* and *D. sericeum*, collectively 'invasive bluestems') that have invaded grasslands worldwide. Using data from 31 studies (only 3 from their native range), we evaluated whether these grasses (275 effect sizes) responded differently than native grasses (184 effect sizes) to fire season, fuel load and drought. Original data included 15 different response variables (e.g. biomass, survival) that were converted to standardized mean difference for analysis.
3. Fires in summer, fall and early winter had negative effects on invasive bluestems; no fire season had significant positive effects. Most data were for *B. ischaemum*, but the other bluestems may also be vulnerable to summer fire. Native grasses did not show significant negative responses in any month.
4. Drought (Keetch–Byram Drought Index) in the month before fire increased the negative effects of fire on invasive bluestems but not native grasses. Drought after fire led to similar negative effects on both groups.
5. Unexpectedly, fuel load (which influences fire intensity) did not significantly influence fire effects in any analysis. At the fuel loads examined (~600–10,000 kg/ha dried herbaceous biomass), fire intensity may have been too low to cause meristem mortality.
6. Between-study heterogeneity was large in all analyses ($I^2 > 80\%$), suggesting that additional factors beyond those reported in the studies influence fire effects. These factors could include plant phenology, fire behaviour, weather conditions during the fire and soil characteristics.

7. *Synthesis and applications*: Fires during summer and fall, especially during dry conditions, could harm invasive bluestems relative to native grasses, likely due to subtle differences in heat sensitivity, phenology and drought resistance. Other invasive species may have similar vulnerabilities to specific fire seasons and rainfall conditions that allow the use of fire as a control method.

KEYWORDS

burning season, exotic grasses, fire season, fuel load, grassland management, invasive grasses, Old World bluestems

1 | INTRODUCTION

Global grassland distribution is determined by climate, soils, grazing and especially fire (Bond et al., 2005). Grassland plants are adapted to specific fire regimes (characteristic fire frequency, seasonality and intensity, Gill, 1975; Keeley et al., 2011). Fire regimes can be changed by invasive plants, such as when invasive grasses increase fire frequency in semi-arid ecosystems adapted to infrequent fire (Fusco et al., 2019). However, in grasslands already adapted to frequent fire, some invasive species can be more vulnerable than native species to fire (DiTomaso et al., 2006). To control invasive plants with fire, we must understand how fire regimes (e.g. seasonality, intensity) and other disturbances (e.g. drought) affect responses in both native and invasive species, especially when the invasive and native species share life-history traits.

Seasonality and fire intensity are two important aspects of fire regimes that influence grassland plant responses to fire. Fire is more likely to harm plants when their below-ground carbohydrate reserves are low (e.g. when flowering or producing seed), while dormant plants are less vulnerable to fire (Miller et al., 2019; Mndela et al., 2023). Fire season can influence fire intensity (the energy released during a fire): fires during hot, dry seasons are more intense and consume fuel more completely (Dayamba et al., 2010). Fire intensity is also directly related to fuel load (the amount of biomass available to burn) and strongly influenced by weather conditions (Augustine et al., 2014; Fidelis et al., 2010). Plants vary in their sensitivity to heat based on meristem location (above- vs. below-ground) and meristem protection (Gagnon et al., 2012; Havill et al., 2015). Differences in phenology and heat sensitivity between native and invasive plants can be used to design prescribed fires that benefit native over invasive species (DiTomaso et al., 2006; Novak et al., 2021).

Drought can influence fire effects by changing fire behaviour and by influencing plant status. Lower fuel moisture can increase fire spread and decrease heat duration (how long tissues are exposed to lethal temperatures; Strong et al., 2013). During dry periods, plants may become dormant and less vulnerable to fire (Moore et al., 2019). While invasive C_4 grasses may be especially drought tolerant compared to other invasive plants, their advantage may be smaller in grasslands and savannas dominated by native C_4 species (e.g. South America: Baruch & Fernández, 1993; North America: Havill et al., 2015; Australia: McIvor, 2007).

To date, most research about fire effects on invasive plants has been site-scale studies, while syntheses have focused on the general effects of fire on broad functional groups (Alba et al., 2015; Mndela et al., 2023). However, to manage grasslands where the invasive plants share life-history traits with the dominant native species (e.g. C_4 bunch/tussock grasses), land managers need more detailed information about fire characteristics that benefit native over invasive species.

In this meta-analysis, we examined fire and environmental parameters (fire season, fuel load and drought) that may influence fire responses by native and invasive grasses. We used six closely related Afro-Eurasian and Australian bluestems (*Bothriochloa bladhii*, *B. ischaemum*, *B. pertusa*, *Dichanthium annulatum*, *D. aristatum* and *D. sericeum*, collectively 'invasive bluestems') as a case study because these species have invaded fire-maintained grasslands around the world, including grasslands dominated by native species in the same genera. We focused on three questions: (1) Are invasive bluestems more negatively affected than native grasses by fires during specific seasons? (2) Are invasive bluestems more vulnerable than native grasses to fires with high fuel loads? (3) Are invasive bluestems more vulnerable than native grasses to fires during drought?

2 | MATERIALS AND METHODS

2.1 | Focal species

Our focal bluestems are important components of grasslands in their native ranges (Lewis, 2006; Liu et al., 2020) but have also invaded grasslands in other regions. In their introduced range, these species have negative effects on grasslands at multiple trophic levels, including plants, arthropods, birds, mammals and reptiles (Hickman et al., 2006; Kutt & Fisher, 2011; Reed et al., 2005).

Fire has been one control strategy examined for invasive bluestems, because grasslands in their native and introduced ranges can be managed with fire. Previous studies have found that late summer or early fall fire can control some invasive bluestem species (Novak et al., 2021; Reemts et al., 2021; Simmons et al., 2007). *Bothriochloa ischaemum* has also been found to be more sensitive than native grasses to high fire intensity and drought (Havill et al., 2015). However, control of the invasive grasses varies among studies, suggesting that factors beyond fire season are important (Foster et al., 2025; Reemts et al., 2019; Twidwell et al., 2012).

2.2 | Literature search

We searched Web of Science, Agricola, Proquest and Google Scholar in July 2023 (Table S1). A separate search was conducted in each database for each of six focal species (*Bothriochloa bladhii*, *Bothriochloa ischaemum*, *Bothriochloa pertusa*, *Dichanthium annulatum*, *Dichanthium aristatum* and *Dichanthium sericeum*). The search term included scientific and common names as well as 'fire OR burn*' (Table S2; Supplement includes additional details).

Search results were stored in Rayyan (Ouzzani et al., 2016) and were screened manually by one of the authors. Studies were retained if they included burned and unburned treatments, the month or exact dates of fires, one or more focal grass species (in the native or introduced range), no additional treatments (except seeding and grazing) applied to the measured populations, and response means, sample size and measures of variation. If necessary data were missing, we attempted to contact the authors. We also conducted a forward/backward citation search (in August 2023) to locate additional papers (Figure S1).

2.3 | Data extraction

We extracted data (means, sample sizes and measures of variation for burned and unburned treatments) from tables, figures (using WebPlotDigitizer 4.6, Rohatgi, 2022), published datasets or data provided by the authors. Data included 15 different response variables: basal area, biomass, change in cover, change in frequency, cover, crown area, dead crown density, density, frequency, number of plants, number of seed heads, number of tillers, survival and stem count (Figure S16). We extracted data for focal bluestems and any native grass species. When multiple papers were published from the same study, we used the data from the most recent publication but included non-duplicate data from earlier papers.

We compiled additional information to serve as moderators (defined in Table S3) including site, latitude, species name, species range of bluestems (native vs. introduced), photosynthesis type of native grasses (C_3 and C_4 species according to Cerros-Tlatilpa et al., 2011; Osborne et al., 2014), seeding with native species (excluding focal bluestems), current grazing, study type (experimental, observational), fire type (prescribed fire, wildfire, burn box/burn barrel), time since fire, date/month of fire and response type (e.g. frequency, cover). Because we found more sites in the northern hemisphere, fire months from the southern hemisphere were adjusted by adding 6 months, making them seasonally equivalent to northern hemisphere months (e.g. 'July' is always summer). We also recorded fuel load (dried herbaceous biomass) and soil depth when available.

To examine the influence of drought on fire effects, we calculated the Keetch-Byram Drought Index (KBDI, Alexander, 1990; Keetch & Byram, 1968). KBDI represents the rainfall needed to return the soil to saturation and changes daily based on temperature and rainfall (details in Supplement). We used temperature and precipitation data from the closest weather station(s) to each study site (for the United States and Guam, National Centers for Environmental Information, 2023; for Australia, Australian Bureau of Meteorology, 2023). For studies where exact fire dates were reported, we calculated the average drought index for 2, 6 and 10 weeks before and after fire (as 6 separate variables). For studies where only the month of fire was reported, we calculated the average drought index for the month of fire and for 1 and 2 months before and after the fire (5 variables).

2.4 | Meta-analysis

Statistical analyses were conducted in R 4.3 (R Core Team, 2024). Graphs were created using the 'orchard', 'ggplot2' and 'ggpubr' packages (Kassambara, 2023; Nakagawa et al., 2023; Wickham, 2016).

The adjusted standardized mean difference (SMD, Hedges' *g*) was calculated for each pair of burned and unburned data as the effect size for meta-analysis (Hedges & Olkin, 1985). Negative SMD values indicate a negative effect of fire (e.g. lower cover in burned vs. unburned plots). SMD was calculated using the 'esc' package as $\mathrm{SMD} = (\mathrm{mean}_1 - \mathrm{mean}_2)/\surd(((N_1 - 1)^*\mathrm{sd}_1{}^2 + (N_2\text{-}1)^*\mathrm{sd}_1{}^2)/(N_1 + N_2\text{-}2))$, where N = sample size and sd = standard deviation (Ludecke, 2019). In a few cases, study data were proportions or counts, so we first calculated odds ratio or binary proportion effect sizes and then converted those into SMD using the 'esc' package.

Meta-analyses were performed using mixed-effects models ('metafor' package, Viechtbauer, 2010). Because the data include repeated measurements (i.e. multiple samples after one fire), we included random effects terms for publication and for site (some publications included multiple sites). Continuous moderators (fuel load, soil depth and the absolute value of latitude) were centred on their mean and scaled by their standard deviation across the whole dataset. The drought variables were centred on 400 (the midpoint of the Keetch-Byram Drought Index) and scaled from −1 to 1, keeping all drought variables on the same scale.

We first conducted meta-analyses with single moderators to examine overall trends, with separate models for invasive bluestems and native grasses. For some moderators, we also examined trends for subsets of the data (e.g. C_4 native grasses; Table S4).

Next, we performed model selection to identify the most important moderators using a set of predefined candidate models (Tables 1 and 2, 'MuMIn' package, Bartoń, 2023). The candidate models included fire month, three drought variables, grazing and, for the invasive bluestem dataset, species group (*B. ischaemum* vs.

TABLE 1 Model selection to predict standardized mean difference (between burned and unburned treatments) of fire effects for invasive bluestems (native and introduced range).

Model	I^2	df	Log likelihood	AICc	Delta	Weight
SpeciesGroup + Month + Grazing + Drought^{1mo-} + Drought^{mo}	95%	18	−711.87	1462.4	0	0.65
SpeciesGroup + Month + Grazing + Drought^{1mo-} + Drought^{mo} + Drought^{1mo+}	95%	19	−711.37	1463.7	1.3	0.34
Month + Grazing + Drought^{1mo-} + Drought^{mo} + Drought^{1mo+}	94%	18	−716.48	1471.6	9.22	0.01
Month + Drought^{1mo-} + Drought^{mo} + Drought^{1mo+}	92%	16	−721.16	1476.4	14.02	0.00
SpeciesGroup + Month + Drought^{1mo-} + Drought^{mo} + Drought^{1mo+}	92%	17	−720.21	1476.8	14.39	0.00
SpeciesGroup + Month + Grazing + Drought^{mo}	95%	17	−724.16	1484.7	22.29	0.00
SpeciesGroup + Month + Grazing	95%	16	−725.98	1486.1	23.65	0.00
SpeciesGroup + Month + Grazing + Drought^{mo} + Drought^{1mo+}	95%	18	−723.76	1486.2	23.77	0.00
SpeciesGroup + Grazing + Drought^{1mo-} + Drought^{mo} + Drought^{1mo+}	96%	9	−739.42	1497.5	35.11	0.00
SpeciesGroup + Month	93%	14	−736.38	1502.4	39.96	0.00
Random effects only	93%		−778.96	1563.9		

Note: The mixed models included random effects for publication and for site; a random effects only model was tested separately. SpeciesGroup = *Bothriochloa ischaemum* versus all other invasive bluestems; Month = month of fire (categorical); Grazing = ungrazed, grazed, both (data averaged across grazing levels); Drought^{1mo-} = average Keetch–Byram Drought Index (KBDI) 1 month before the month of fire; Drought^{mo} = average KBDI during the month of fire; Drought^{1mo+} = average KBDI 1 month after the month of fire.

TABLE 2 Model selection for native grasses (excluding invasive bluestems in their native range).

Model	I^2	df	Log likelihood	AICc	Delta	Weight
Month + Grazing + Drought^{mo} + Drought^{1mo+}	80%	17	−420.80	887.3	0	0.41
Month + Drought^{1mo-} + Drought^{mo} + Drought^{1mo+}	85%	16	−426.7	888.7	1.35	0.21
Month + Grazing + Drought^{mo}	77%	16	−426.9	889.1	1.81	0.17
Month + Grazing + Drought^{1mo-} + Drought^{mo} + Drought^{1mo+}	80%	18	−424.8	889.7	2.40	0.12
Month + Grazing + Drought^{1mo-} + Drought^{mo}	78%	17	−426.7	891.1	3.76	0.06
Month	84%	13	−432.8	893.8	6.53	0.02
Month + Grazing	78%	15	−430.8	894.5	7.2	0.01
Grazing + Drought^{1mo-} + Drought^{mo} + Drought^{1mo+}	75%	8	−442.14	901.1	13.8	0.00
Random effects only	83%		−447.64	901.28		

Note: See Table 1 for model descriptions and variable definitions.

all other focal bluestems; details in Supplement). Analyses of native grasses did not include a species moderator because of the large number of species ($n = 34$). For comparison, we separately tested a model with only the random effects of publication and study. We examined the influence of each moderator by calculating its sum of weights (i.e. the weights for all the models in which a moderator appears). We also calculated model-averaged coefficients for the moderators; for models in which a moderator does not appear, the coefficient was set to 0.

2.5 | Publication bias and sensitivity analyses

To test for publication bias, we used the multilevel meta-regression approach developed by Nakagawa et al. (2022). Details of this approach, additional publication bias tests and outlier/sensitivity tests are described in the Supporting Information.

3 | RESULTS

We located 31 publications that met our inclusion criteria (Figures 1 and 2). Because some theses and peer-reviewed publications described overlapping data, we used data from 27 sources (Data Sources). For invasive bluestem species (in their native and introduced ranges), we extracted 275 effect sizes distributed across 42 sites (Table S3). For native grasses (excluding invasive bluestems in their native range), we extracted 184 effect sizes from 17 publications across 17 sites (Table S3). Studies were from the United States (23), Australia (3) and Guam (1, Figure 1, Table S3). Most studies used prescribed fires (vs. wildfire or burn boxes); no studies included mid-winter fires in December (northern hemisphere) or June (southern hemisphere). For invasive bluestems, 76% of the data were for *Bothriochloa ischaemum*. Only *Dichanthium sericeum* included studies in the native range (Table S3; more details in Supplement).

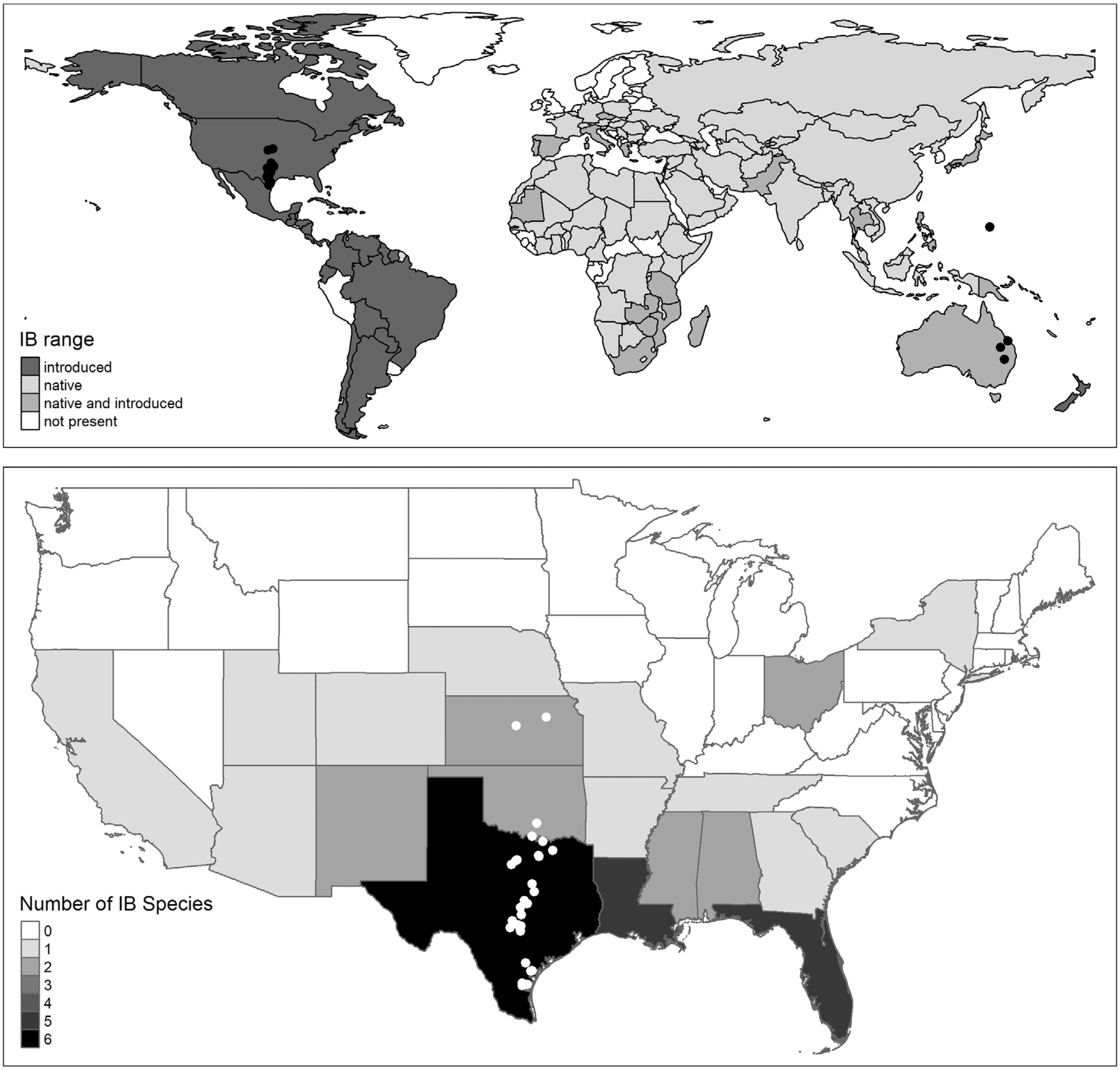

FIGURE 1 Above—Locations of all studies and presence of invasive bluestems (IB) in each country (native and introduced = country has both native and introduced bluestems; not present = not present or no data available). Below—Locations of studies in the United States and the number of invasive bluestem species present in each state.

The overall effect of fire on invasive bluestems was negative (standardized mean difference [SMD] = −0.84, 95% confidence interval = −1.28 to −0.39, Figure 2). For native grasses (excluding invasive bluestems in their native range), overall fire effects trended negative (−0.50 [−1.09–0.09], Figure 2).

3.1 | Fire responses are influenced by range, fire month, drought and grazing, but not fuel load

For invasive bluestems, studies in the introduced range found a negative effect of fire (−1.12 [−1.83 to −0.41], Figure S3, Table S4). Studies in the native range did not find negative effects of fire but included only 20 effect sizes (3 publications) for *D. sericeum* (0.20 [−1.81–2.22], Figure S3, Table S4).

Fire effects on invasive bluestems varied by month: fires in summer, fall and mid-winter had significant negative effects (specifically, northern hemisphere: June–November, January; southern hemisphere: December–May, July; Figure 3; Table S4). For *B. ischaemum* alone, fire effects remained negative for fires in the same months, with fire effects in 2 months being more negative than in the full dataset (northern/southern hemisphere: January/July and November/May; Figure S4; Table S4). For other invasive bluestem species (only in the introduced range), fire effects were

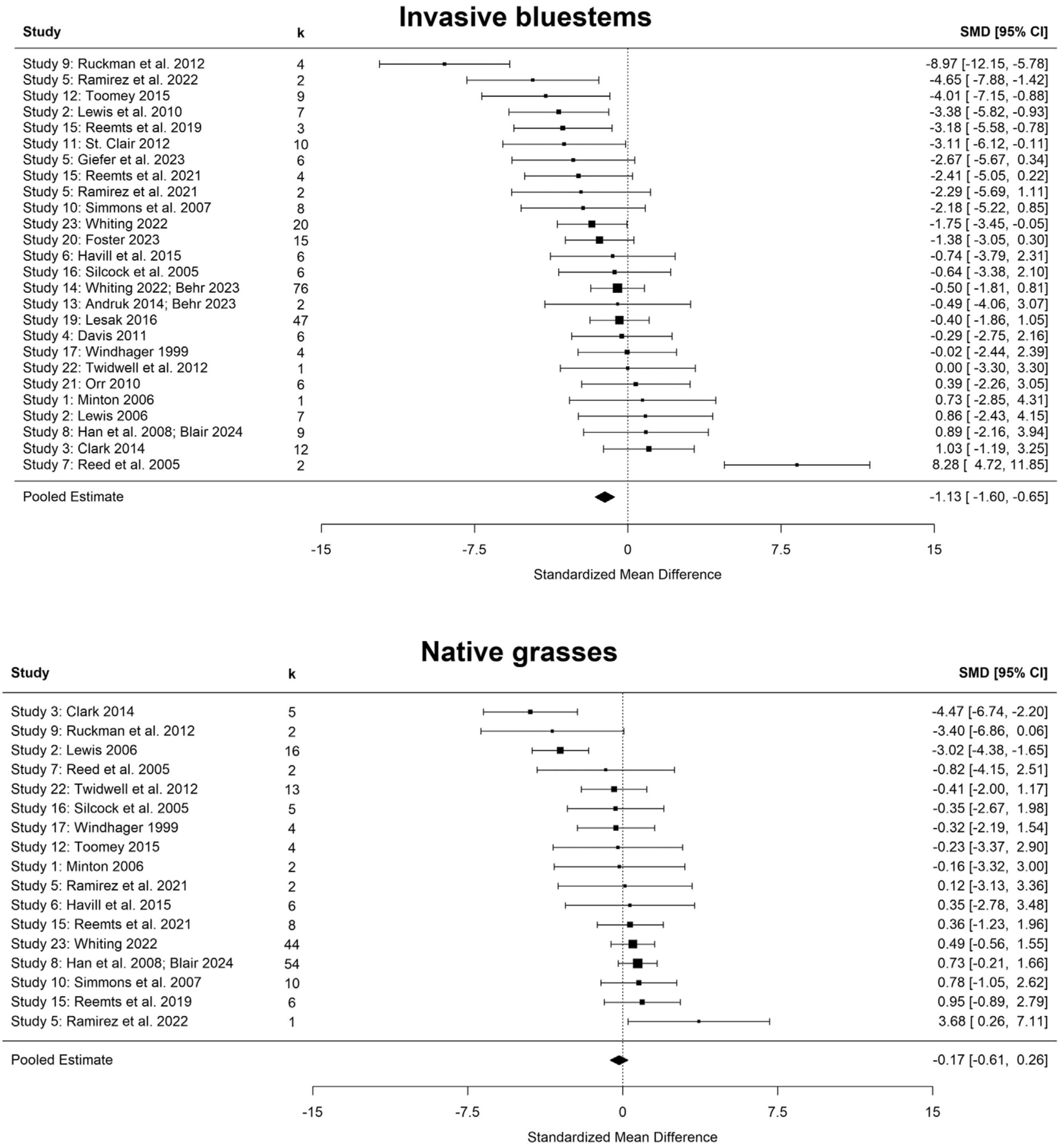

FIGURE 2 Above—Standardized mean difference (SMD) of fire effects for invasive bluestems (native and introduced range), aggregated by publication and study. Below—Fire effects from the same studies for native grasses (excluding invasive bluestems in their native range). Negative values indicate negative effects of fire. *k* = number of effect sizes.

negative only in one summer and one winter month (northern/southern hemisphere: August/February, −1.75 [−3.38 to −0.12] and November/May, −3.27 [−5.97 to −0.57]; Figure S4; Table S4). In contrast, native grasses (excluding invasive bluestems) were not significantly affected by fire in any month (Figure 3; Table S4). For native C_4 grasses (i.e. excluding C_3 grasses and invasive bluestems in their native range), fires in two winter months had significantly positive effects (northern/southern hemisphere: January/July, 1.15 [0.13–2.17] and November/May, 0.95 [0.02–1.87], Figure S5; Table S4).

Fire effects did not vary by fuel load (i.e. slopes of fitted lines were not different from 0) for invasive bluestems or for native grasses (Figure S6; Table S4). When examining only fires from summer to fall (specifically, northern hemisphere: June to October;

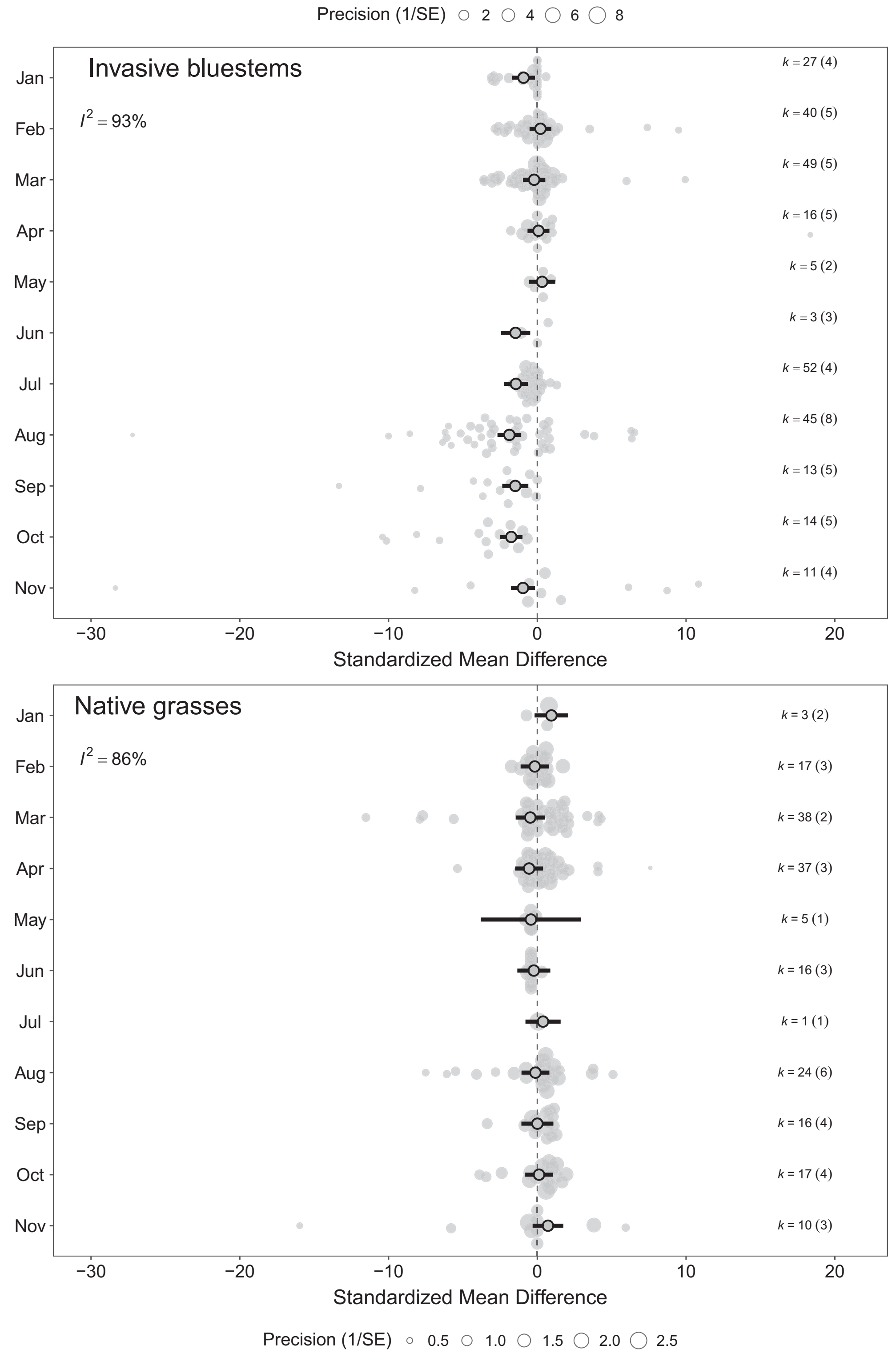

FIGURE 3 Standardized mean difference of fire effects on invasive bluestems (native and introduced range) were significantly negative in summer, fall and some winter months (northern hemisphere: June–November, January; southern hemisphere: December–May, July). Fire effects on native grasses (excluding invasive bluestems in their native range) did not differ from zero in any month. Negative values indicate a negative effect in burned versus unburned treatments. For southern hemisphere data, month was adjusted to the northern hemisphere equivalent; no studies included mid-winter fires in December (northern hemisphere) or June (southern hemisphere). Mixed models included publication and site as random effects. Points are slightly transparent to show overlap. Thick lines = 95% confidence intervals. I^2 = variability due to heterogeneity; *k* = number of effect sizes (number of publications).

southern hemisphere: December to April), fire effects still did not vary by fuel load for invasive bluestems or for only *B. ischaemum* (Table S4).

As rainfall decreased, fire effects were almost always more negative for invasive bluestems but were only sometimes negative for native grasses (Figure 4; Figures S7 and S8; Table S4). For invasive bluestems, drought occurring 1–2 months (slopes −1.3 to −1.5) or 2–10 weeks (slopes −1.2 to −1.5) before the fire had stronger negative effects than drought occurring during or after the month of fire (slopes −0.3 to −0.6). These slopes indicate that a 400-point decrease in average KBDI causes fire effects to be ~0.5 to 1.5 standard deviations more negative, a relatively large effect. In contrast, for native grasses, drought had significant (negative) effects only for the 6- and 10-week period after fire (6 weeks: slope = −0.5, 10 weeks: −0.4; Figure 4; Figures S7 and S8; Table S4).

For invasive bluestems, fire had a negative effect in ungrazed studies (−1.46 [−2.31 to −0.61]) and a positive effect in grazed studies (2.04 [0.22–3.87], Figure S10, Table S4). For native grasses, the grazing moderator did not explain significant variance (Figure S10, Table S4).

Other moderators (invasive bluestem species, seeding, study type, fire type, time since fire, soil depth, latitude and original response variable type) were highly unbalanced among levels or had no significant effects. Analyses of these moderators are described in the Supplement.

3.2 | Model selection confirms that fire timing, grazing and drought influence fire effects

For invasive bluestem data (including the native range), the two best mixed models predicting SMD of fire effects included species group, fire month, grazing and 2–3 drought moderators (Table 1 and Table S5). Drought before the month of fire (Drought^{1mo-}) appears to be the most important drought variable: the best-fitting model included both Drought^{1mo-} and drought during the month of fire but had a delta AICc of 22 compared to a similar model that excluded Drought^{1mo-} (Table 1). For native grasses (excluding invasive bluestems in their native range), the best model included fire month, grazing and 2 drought moderators (Table 2 and Table S5).

3.3 | Results are not influenced by publication bias or outliers

For both invasive bluestem and native grass data, effect size was significantly correlated with standard error, indicating that studies with more uncertainty found larger (more negative) effect sizes (invasive bluestem: slope = −1.8, 95% CI: −2.2 to −1.4; native: slope = −2.0 [−2.8 to −1.1]). However, adding sample variance as a moderator into the best-fitting model from model selection did not change the magnitude or direction of any effects, suggesting that our results are not highly sensitive to the effects of publication bias (Tables S6 and S7; details in Supplement).

4 | DISCUSSION

Our meta-analysis of 31 studies found that fire season and drought, but not fuel load, significantly influenced fire effects on invasive bluestems (*Bothriochloa* spp. and *Dichanthium* spp.). Fires in summer, fall and early winter had significant negative effects on the invasive grasses but not on native grasses. Fire effects on invasive

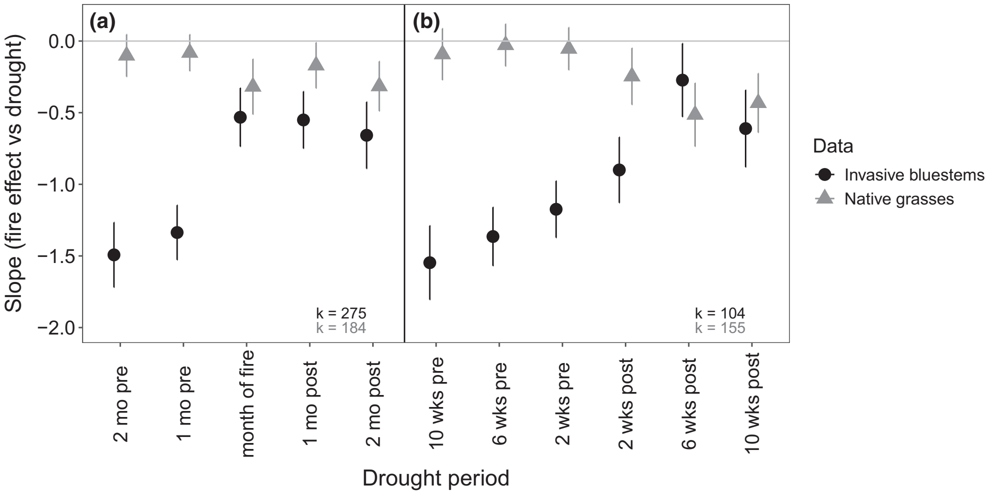

FIGURE 4 Standardized mean difference of fire effects become more negative with increasing drought for all invasive bluestem analyses (except 6 weeks post drought); for native grasses (excluding invasive bluestems in their native range), relationships are only significantly negative for 6 and 10 weeks after fire. Slope estimates (mean ± standard error) are from regressions for standardized mean difference of fire effects and drought variables, with separate models for each variable (Figures S7 and S8). (a) Slope estimates for all data; (b) slope estimates for data with exact fire dates. Daily Keetch–Byram drought index (KBDI) values were averaged for the periods listed (e.g. '2 mo pre' = 2 months before the month of fire). Drought variables were centred on 400 and scaled from −1 to 1. *k* = number of effect sizes. Mixed models included publication and site as random effects.

bluestems became more negative as rainfall in the 1–2 months before or after the fire decreased; the effect was especially strong for drought in the month before the fire. For native grasses, fire effects tended to become more negative as rainfall after the fire decreased. Surprisingly, fuel load did not influence fire effects in any analysis. Unfortunately, we found too few studies from the native range of invasive bluestems to identify differences in fire response in the native and introduced ranges. Our results suggest that that prescribed fires during dry periods in the summer or fall could favour native grasses over invasive bluestems, but that fires in any season could be used to manage grasslands for other purposes (e.g. woody plant encroachment) without consistently promoting these invasive grasses.

Previous site-scale studies had suggested that fire season could influence fire effects on *Bothriochloa ischaemum*, the most common species in our dataset (Novak et al., 2021; Reemts et al., 2021; Simmons et al., 2007), but the other invasive bluestems in our study have received less attention. Here, we found that fire during summer and fall, and likely even early winter, usually has negative effects on the invasive bluestems as a group and on *Bothriochloa ischaemum* specifically (Figure 3; Figure S4). While we lacked sufficient data to examine the effect of fire month on each of the other bluestem species individually, fires in one summer month (northern/southern hemisphere: August/February) had significant negative effects on these species as a group (Figure S4; studies included *B. bladhii* [Giefer et al., 2023], *D. annulatum* [Toomey, 2015] and *D. sericeum* [Clark, 2014]). However, individual studies included in our analysis sometimes found large positive effects after fire, even in summer and fall, suggesting that variables beyond fire season influence management outcomes. Although previous observational studies suggested that winter fires promote *B. ischaemum* (Gabbard & Fowler, 2007; Pase, 1971), we did not find a significant positive effect of fire on this species or the other invasive bluestems in any month (Figure 3; Figure S4). Our results suggest that winter fires could be used to maintain grasslands without consistently promoting these invasive grasses, while summer and fall fires could be used to reduce abundance of *B. ischaemum* and potentially other invasive bluestems.

Fire season has been used to target invasive species during vulnerable phenological stages in many grasslands. For example, some invasive annual grasses retain seeds in their inflorescences longer than native annuals, and cool season perennial grasses begin to flower while native warm-season grasses are still dormant (DiTomaso et al., 2006). Similarly, the sensitivity of *B. ischaemum*, and perhaps other invasive bluestems, to fire may be mediated by phenology. *Bothriochloa ischaemum* appears to be most vulnerable to fire when preparing to flower, possibly due to low below-ground carbohydrate reserves (Ruckman et al., 2012). Flowering is more closely related to rainfall than to season (Ruckman et al., 2012), potentially explaining the mixed outcomes from some summer fires (Figure S4). Understanding the differences in phenology between native and invasive grasses can allow fire managers to apply prescribed fires for maximum benefit.

Many dominant native grasses share life-history traits with the invasive bluestems (e.g. C_4 photosynthesis, bunch/tussock grass form) and could be vulnerable to fires at the same seasons. However, we found no significant negative effects of fire in any season on native grasses, including native C_4 grasses (Figure 3 and Figure S5). Although other studies have found that summer or fall fires can reduce the biomass and richness of warm-season grasses in the central United States (e.g. Novak et al., 2021; Weir & Scasta, 2017), our data suggest that summer and fall fires may disproportionately harm invasive grasses relative to native grasses. Similar seasonal targeting of fire has been successful for a C_3 invasive grass in a C_3-dominated grassland (Kral et al., 2018), suggesting that fire managers can leverage subtle differences between native and invasive species to design effective prescribed fires.

Grassland productivity and fire risk are linked to rainfall (Petrie et al., 2018; Verhoeven et al., 2020) but drought does not consistently change post-fire biomass, composition or diversity in fire-adapted grasslands and grasses (Koerner & Collins, 2014; Moore et al., 2019). Here, fire had more negative effects on invasive bluestems during droughts, especially drought occurring before the fire (Figure 4). While this meta-analysis lacked studies with summer burns during wet conditions, model selection highlighted the importance of drought in addition to fire season as a predictor of fire effects (Table 1). The interactive effects of fire and drought may be related to drought tolerance. *Bothriochloa ischaemum*, for example, is considered drought tolerant in its native range in China (Liu et al., 2020), but in its introduced range, its abundance decreases more quickly during drought than the abundance of native grasses (Havill et al., 2015). *Bothriochloa ischaemum* is also less likely to grow in shallow soils, suggesting water limitation (Behr et al., 2024). The other invasive bluestems likely have similar drought tolerance based on rooting depth and root biomass (Kattge et al., 2020; Zobeck et al., 2011). While fire during droughts also had negative effects on native grasses, the effects were less pronounced than for invasive bluestems (Figure 4). In native Australian grasses, drought may actually promote resprouting (Moore et al., 2019) and grasslands in South Africa are also resilient to moderate drought (Koerner & Collins, 2014). These results highlight the potential to use fire during dry conditions to favour native grasses over invasive grasses when they differ in drought tolerance.

Fuel load did not influence fire effects in any of our analyses (Figure S6). This result is surprising because *Bothriochloa ischaemum* is more vulnerable to high fire intensity than other bunchgrasses in its introduced range, perhaps because its buds are less protected from fire (Havill et al., 2015). Fuel load and fire intensity are directly related (Augustine et al., 2014; Fidelis et al., 2010), but other factors (e.g. fuel arrangement, rate of fire spread) may have more influence on heat duration and dosage (Gibson et al., 1990; Wragg et al., 2018). Heat duration may also be a more important predictor of grass mortality than measured fire temperature (Gagnon et al., 2012; Strong et al., 2013). While the range of fuel loads in our analysis was large (~600–10,000 kg/ha), even greater fuel amounts may be necessary to generate lethal intensity. For example, Gagnon et al. (2012) found that fuels of 30,000 kg/ha, but not 10,000 kg/ha, caused significant mortality for two *Schizachyrium* species. However, other studies have found lower thresholds for mortality (e.g. 4000 kg/ha for *Poa pratensis*, Kral et al., 2018). Fuel load does not appear to be a useful predictor of fire effects in grasslands.

We found significant between-study heterogeneity even in models with multiple moderators (Tables 1 and 2), suggesting that additional factors not examined here influence fire effects in grasslands. Heat duration and dosage are strongly linked to fire behaviour and weather conditions during the fire (Havill et al., 2015; Strong et al., 2013), but these variables are rarely reported (only 3 and 7 studies, respectively, in this analysis). Soil type or texture was reported for only about half of our sites, but can influence fire behaviour through changes in plant water status and fuel moisture (e.g. Dong & Ochsner, 2018). Plant phenology is influenced by factors beyond date and could also predict when plants are most vulnerable to fire (Ruckman et al., 2012). Finally, our understanding of drought effects could have been improved by having consistent reporting of fire dates (rather than just fire month).

In conclusion, our meta-analysis suggests that prescribed fires can be used to control invasive species when carefully targeted to seasons and conditions of high vulnerability. We found differences in fire effects based on fire season and drought, likely due to subtle differences in heat sensitivity, phenology and drought resistance between native and invasive grasses. Gaining this understanding required a detailed examination of fire and rainfall conditions, which will be especially important when native and invasive species share broad life-history traits. Implementing the most effective prescribed fires for invasive species control may be logistically difficult or require changes to common practices: burning during the dry summer or fall conditions that target invasive bluestems, for example, requires additional safety measures compared to cooler and wetter spring prescribed fires. However, we also identified conditions when fires had neutral effects. Such a full understanding of how prescribed fires affect invasive species will allow land managers to balance invasive species control with prescribed fire goals.

AUTHOR CONTRIBUTIONS

Charlotte M. Reemts conceived the ideas, analysed the data and led the writing of the manuscript. Charlotte M. Reemts designed with methodology with assistance from Justin C. Havird, Caroline E. Farrior, and Amelia A. Wolf. Justin C. Havird provided guidance on data analysis. Whitney L. Behr, Megan K. Clayton, Jamie L. Foster, Meagan M. Lesak and Carolyn V. Whiting contributed original data. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

We thank the many scientists and land managers whose studies were used in this analysis. We thank N. Fowler and S. Griffin for providing helpful reviews of earlier drafts and two reviewers whose comments greatly improved the manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.xpnvx0ks4 (Reemts et al., 2025).

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REFERENCES

Alba, C., Skálová, H., McGregor, K. F., D'Antonio, C., & Pyšek, P. (2015). Native and exotic plant species respond differently to wildfire and prescribed fire as revealed by meta-analysis. *Journal of Vegetation Science*, *26*(1), 102–113. https://doi.org/10.1111/jvs.12212

Alexander, M. E. (1990). Computer calculation of the Keetch-Byram drought index—Programmers beware! *Fire Management Notes*, *51*(4), 23–25.

Augustine, D. J., Derner, J. D., & Smith, D. P. (2014). Characteristics of burns conducted under modified prescriptions to mitigate limited fuels in a semi-arid grassland. *Fire Ecology*, *10*(2), Article 2. https://doi.org/10.4996/fireecology.1002036

Australian Bureau of Meteorology. (2023). Climate Data Online. http://www.bom.gov.au/climate/data/index.shtml

Bartoń, K. (2023). MuMIn: Multi-model inference (version 1.47.5) [computer software]. https://CRAN.R-project.org/package=MuMIn

Baruch, Z., & Fernández, D. S. (1993). Water relations of native and introduced C4 grasses in a neotropical savanna. *Oecologia*, *96*(2), 179–185. https://doi.org/10.1007/BF00317730

Behr, W. L., Andruk, C., Schwope, C., & Fowler, N. L. (2024). Benefits to native grasses from a summer fire still present 12 years later. *Natural Areas Journal*, *44*(3), 172–182. https://doi.org/10.3375/2162-4399-44.3.172

Bond, W. J., Woodward, F. I., & Midgley, G. F. (2005). The global distribution of ecosystems in a world without fire. *New Phytologist*, *165*(2), 525–538. https://doi.org/10.1111/j.1469-8137.2004.01252.x

Cerros-Tlatilpa, R., Columbus, J. T., & Barker, N. P. (2011). Phylogenetic relationships of Aristida and relatives (Poaceae, Aristidoideae) based on noncoding chloroplast (trnL-F, rpl16) and nuclear (ITS) DNA sequences. *American Journal of Botany*, *98*(11), 1868–1886. https://doi.org/10.3732/ajb.1100103

Clark, M. D. (2014). *Evaluating the interactive effects of seasonal prescribed fire and grazing on invasive grass abundance and woody brush encroachment* (M.S.). Texas A&M University. https://oaktrust.library.tamu.edu/handle/1969.1/154053

Dayamba, S. D., Savadogo, P., Zida, D., Sawadogo, L., Tiveau, D., & Oden, P. C. (2010). Fire temperature and residence time during dry season burning in a Sudanian savanna-woodland of West Africa with implication for seed germination. *Journal of Forestry Research*, *21*(4), 445–450. https://doi.org/10.1007/s11676-010-0095-y

DiTomaso, J. M., Brooks, M. L., Allen, E. B., Minnich, R., Rice, P. M., & Kyser, G. B. (2006). Control of invasive weeds with prescribed burning. *Weed Technology*, *20*, 535–548. https://doi.org/10.1614/wt-05-086r1.1

Dong, J., & Ochsner, T. E. (2018). Soil texture often exerts a stronger influence than precipitation on mesoscale soil moisture patterns. *Water Resources Research*, *54*(3), 2199–2211. https://doi.org/10.1002/2017WR021692

Fidelis, A., Delgado-Cartay, M. D., Blaco, C. C., Muller, S. C., Pillar, V. D., & Pfadenhauer, J. (2010). Fire intensity and severity in Braziliam campos grasslands. *Interciencia*, *35*(10), 739–745.

Foster, J. L., Clayton, M. K., Lesak, M. M., McCuistion, K., & Teinert, T. (2025). Combining management techniques for short-term reduction of introduced Old World bluestems in South Texas rangelands.

Rangeland Ecology & Management, *99*, 50–57. https://doi.org/10.1016/j.rama.2024.12.001

Fusco, E. J., Finn, J. T., Balch, J. K., Nagy, R. C., & Bradley, B. A. (2019). Invasive grasses increase fire occurrence and frequency across US ecoregions. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(47), 23594–23599. https://doi.org/10.1073/pnas.1908253116

Gabbard, B. L., & Fowler, N. L. (2007). Wide ecological amplitude of a diversity-reducing invasive grass. *Biological Invasions*, *9*, 149–160.

Gagnon, P. R., Harms, K. E., Platt, W. J., Passmore, H. A., & Myers, J. A. (2012). Small-scale variation in fuel loads differentially affects two co-dominant bunchgrasses in a species-rich pine savanna. *PLoS One*, *7*(1), e29674. https://doi.org/10.1371/journal.pone.0029674

Gibson, D. J., Hartnett, D. C., & Smith-Merrill, G. (1990). Fire temperature heterogeneity in contrasting fire-prone habitats: Kansas tallgrass prairie and Florida sandhills. *Bulletin of the Torrey Botanical Club*, *117*, 349–356.

Giefer, H., Harmoney, K., Ramirez, M., Tajchman, A., Duncan, Z., Lemmon, J., & Olson, K. (2023). Effects of late-summer prescribed fire on botanical composition, soil cover, and forage production in Caucasian bluestem-infested rangeland in the Kansas Smoky Hills: Year 4 of 5. *Kansas Agricultural Experiment Station Research Reports*, *9*(1), 1.

Gill, A. M. (1975). Fire and the Australian Flora: A review. *Australian Forestry*, *38*(1), 4–25. https://doi.org/10.1080/00049158.1975.10675618

Havill, S., Schwinning, S., & Lyons, K. G. (2015). Fire effects on invasive and native warm-season grass species in a north American grassland at a time of extreme drought. *Applied Vegetation Science*, *18*, 637–649. https://doi.org/10.1111/avsc.12171

Hedges, L. V., & Olkin, I. (1985). *Statistical methods for meta-analysis*. Academic Press.

Hickman, K. R., Farley, G. H., Channell, R., & Steier, J. E. (2006). Effects of Old World bluestem (*Bothriochloa ischaemum*) on food availability and avian community composition within the mixed-grass prairie. *The Southwestern Naturalist*, *51*, 524–530.

Kassambara, A. (2023). *Ggpubr*: *"ggplot2" based publication ready plots* (version 0.6.0) [computer software]. https://CRAN.R-project.org/package=ggpubr

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Tautenhahn, S., Werner, G. D. A., Aakala, T., Abedi, M., Acosta, A. T. R., Adamidis, G. C., Adamson, K., Aiba, M., Albert, C. H., Alcántara, J. M., Alcázar, C. C., Aleixo, I., Ali, H., … Wirth, C. (2020). TRY plant trait database—Enhanced coverage and open access. *Global Change Biology*, *26*(1), 119–188. https://doi.org/10.1111/gcb.14904

Keeley, J. E., Pausas, J. G., Rundel, P. W., Bond, W. J., & Bradstock, R. A. (2011). Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science*, *16*(8), 406–411.

Keetch, J. J., & Byram, G. M. (1968). *A drought index for forest fire control (No. Research Paper SE-38)* (p. 32 [Revised November 1988]). U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station.

Koerner, S. E., & Collins, S. L. (2014). Interactive effects of grazing, drought, and fire on grassland plant communities in North America and South Africa. *Ecology*, *95*, 98–109.

Kral, K., Limb, R., Ganguli, A., Hovick, T., & Sedivec, K. (2018). Seasonal prescribed fire variation decreases inhibitory ability of *Poa pratensis* L. and promotes native plant diversity. *Journal of Environmental Management*, *223*, 908–916. https://doi.org/10.1016/j.jenvman.2018.06.096

Kutt, A. S., & Fisher, A. (2011). Increased grazing and dominance of an exotic pasture (*Bothriochloa pertusa*) affects vertebrate fauna species composition, abundance and habitat in savanna woodland. *The Rangeland Journal*, *33*(1), 49–58. https://doi.org/10.1071/RJ10065

Lewis, T. (2006). *Management for conservation of plant diversity in native grasslands of the Moree Plains, NSW* [PhD]. University of New England. https://rune.une.edu.au/web/handle/1959.11/22183

Liu, Y., Li, P., Wang, T., Liu, Q., & Wang, W. (2020). Root respiration and belowground carbon allocation respond to drought stress in a perennial grass (*Bothriochloa ischaemum*). *Catena*, *188*, 104449. https://doi.org/10.1016/j.catena.2019.104449

Ludecke, D. (2019). *Effect size computation for meta analysis*. (version 0.5.1) [computer software] https://doi.org/10.5281/zenodo.1249218

McIvor, J. G. (2007). Pasture management in semi-arid tropical woodlands: Dynamics of perennial grasses. *The Rangeland Journal*, *29*(1), 87–100. https://doi.org/10.1071/RJ06031

Miller, R. G., Tangney, R., Enright, N. J., Fontaine, J. B., Merritt, D. J., Ooi, M. K. J., Ruthrof, K. X., & Miller, B. P. (2019). Mechanisms of fire seasonality effects on plant populations. *Trends in Ecology & Evolution*, *34*(12), 1104–1117. https://doi.org/10.1016/j.tree.2019.07.009

Mndela, M., Thamaga, H. K., & Gusha, B. (2023). A global perspective of the functional trait responses of Graminoids to the seasonality of fire. *Fire*, *6*(9), Article 9. https://doi.org/10.3390/fire6090329

Moore, N. A., Camac, J. S., & Morgan, J. W. (2019). Effects of drought and fire on resprouting capacity of 52 temperate Australian perennial native grasses. *New Phytologist*, *221*(3), 1424–1433. https://doi.org/10.1111/nph.15480

Nakagawa, S., Lagisz, M., Jennions, M. D., Koricheva, J., Noble, D. W. A., Parker, T. H., Sánchez-Tójar, A., Yang, Y., & O'Dea, R. E. (2022). Methods for testing publication bias in ecological and evolutionary meta-analyses. *Methods in Ecology and Evolution*, *13*(1), 4–21. https://doi.org/10.1111/2041-210X.13724

Nakagawa, S., Lagisz, M., O'Dea, R. E., Pottier, P., Rutkowska, J., Senior, A. M., Yang, Y., & Noble, D. W. A. (2023). orchaRd 2.0: An R package for visualizing meta-analyses with orchard plots. *EcoEvoRxiv*, *12*, 4–12. https://doi.org/10.32942/X2QC7K

National Centers for Environmental Information. (2023). Climate Data Online. https://www.ncdc.noaa.gov/cdo-web

Novak, E. N., Bertelsen, M., Davis, D., Grobert, D. M., Lyons, K. G., Martina, J. P., McCaw, W. M., O'Toole, M., & Veldman, J. W. (2021). Season of prescribed fire determines grassland restoration outcomes after fire exclusion and overgrazing. *Ecosphere*, *12*(9), e03730. https://doi.org/10.1002/ecs2.3730

Osborne, C. P., Salomaa, A., Kluyver, T. A., Visser, V., Kellogg, E. A., Morrone, O., Vorontsova, M. S., Clayton, W. D., & Simpson, D. A. (2014). A global database of C4 photosynthesis in grasses. *New Phytologist*, *204*(3), 441–446. https://doi.org/10.1111/nph.12942

Ouzzani, M., Hammady, H., Fedorowicz, Z., & Elmagarmid, A. (2016). Rayyan—A web and mobile app for systematic reviews. *Systematic Reviews*, *5*(1), 210. https://doi.org/10.1186/s13643-016-0384-4

Pase, C. P. (1971). Effect of a February burn on Lehmann lovegrass. *Journal of Range Management*, *6*(24), 454–456.

Petrie, M. D., Peters, D. P. C., Yao, J., Blair, J. M., Burruss, N. D., Collins, S. L., Derner, J. D., Gherardi, L. A., Hendrickson, J. R., Sala, O. E., Starks, P. J., & Steiner, J. L. (2018). Regional grassland productivity responses to precipitation during multiyear above- and below-average rainfall periods. *Global Change Biology*, *24*(5), 1935–1951. https://doi.org/10.1111/gcb.14024

R Core Team. (2024). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. http://www.r-project.org/

Reed, H. E., Seastedt, T. R., & Blair, J. M. (2005). Ecological consequences of C4 grass invasion of A C4 grassland: A dilemma for management. *Ecological Applications*, *15*(5), 1560–1569. https://doi.org/10.1890/04-0407

Reemts, C. M., Havird, J. C., Behr, W. L., Clayton, M. K., Foster, J. L., Lesak, M. M., Whiting, C. V., Farrior, C. E., & Wolf, A. A. (2025). Data from: Fire season and drought influence fire effects on invasive grasses: A meta-analysis. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.xpnvx0ks4

Reemts, C. M., McCaw, W. M., Greene, T. A., & Simmons, M. T. (2019). Short-term control of an invasive C4 grass with late-summer fire.

Rangeland Ecology & Management, *72*(1), 182–188. https://doi.org/10.1016/j.rama.2018.07.009

Reemts, C. M., Picinich, C., & Greene, T. A. (2021). Late-summer fire provides long-term control of the invasive Old World Bluestem (*Bothriochloa ischaemum*). *Southeastern Naturalist*, *20*(4), 589–601. https://doi.org/10.1656/058.020.0407

Rohatgi, A. (2022). *WebPlotDigitizer* (version 4.6) [computer software]. https://automeris.io/WebPlotDigitizer

Ruckman, E. M., Schwinning, S., & Lyons, K. G. (2012). Effects of phenology at burn time on post-fire recovery in an invasive C4 grass. *Restoration Ecology*, *20*(6), 756–763. https://doi.org/10.1111/j.1526-100X.2011.00830.x

Simmons, M. T., Windhager, S., Power, P., Lott, J., Lyons, R. K., & Schwope, C. (2007). Selective and non-selective control of invasive plants: The short-term effects of growing-season prescribed fire, herbicide, and mowing in two Texas prairies. *Restoration Ecology*, *15*(4), 662–669.

Strong, D. J., Ganguli, A. C., & Vermeire, L. T. (2013). Fire effects on basal area, tiller production, and mortality of the C4 bunchgrass, purple Threeawn. *Fire Ecology*, *9*(3), Article 3. https://doi.org/10.4996/fireecology.0903089

Toomey, A. E. (2015). *Effects of seasonal prescribed burning on Kleberg bluestem (Dichanthium annulatum) in south Texas* [M.S.]. Texas A&M University.

Twidwell, D., Rogers, W., McMahon, E., Thomas, B., Kreuter, U., & Blankenship, T. (2012). Prescribed extreme fire effects on richness and invasion in coastal prairie. *Invasive Plant Science and Management*, *5*, 330–340.

Verhoeven, E. M., Murray, B. R., Dickman, C. R., Wardle, G. M., & Greenville, A. C. (2020). Fire and rain are one: Extreme rainfall events predict wildfire extent in an arid grassland. *International Journal of Wildland Fire*, *29*(8), 702–711. https://doi.org/10.1071/WF19087

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, *36*, 1–48. https://doi.org/10.18637/jss.v036.i03

Weir, J. R., & Scasta, J. D. (2017). Vegetation responses to season of fire in tallgrass prairie: A 13-year case study. *Fire Ecology*, *13*(2), 137–142. https://doi.org/10.4996/fireecology.130290241

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag.

Wragg, P. D., Mielke, T., & Tilman, D. (2018). Forbs, grasses, and grassland fire behaviour. *Journal of Ecology*, *106*(5), 1983–2001. https://doi.org/10.1111/1365-2745.12980

Zobeck, T. M., Allen, V. G., Cox, J. J., & Philipp, D. (2011). Variation of soil and plant characteristics among Old World bluestem species. *Agricultural Sciences*, *02*(3), 347–356. https://doi.org/10.4236/as.2011.23046

DATA SOURCES

Andruk, C. M. (2014). *Restoration of central Texas savanna and woodland: The effects of fire, deer, and invasive species on plant community trajectories* [PhD]. University of Texas at Austin.

Behr, W. L. (2023). *The effects of prescribed fire on grasslands of the southern Great Plains* [PhD]. University of Texas at Austin.

Blair, J. M. (2024). *BGPVC plant species composition in the belowground plot experiment at Konza prairie*. Environmental Data Initiative. https://doi.org/10.6073/pasta/2199a82aedbd8e462ac9edafd915d0fc

Clark, M. D. (2014). *Evaluating the interactive effects of seasonal prescribed fire and grazing on invasive grass abundance and woody brush encroachment* [M.S.]. Texas A&M University.

Davis, F. H. (2011). *Effects of prescribed burning on King Ranch bluestem at vegetative regrowth and flowering stages* [M.S.]. Texas State University.

Foster, J. L., Clayton, M. K., Lesak, M. M., McCuistion, K., & Teinert, T. (2025). Combining management techniques for short-term reduction of introduced Old World bluestems in South Texas rangelands. *Rangeland Ecology & Management*, *99*, 50–57. https://doi.org/10.1016/j.rama.2024.12.001

Giefer, H., Harmoney, K., Ramirez, M., Tajchman, A., Duncan, Z., Lemmon, J., & Olson, K. (2023). Effects of late-summer prescribed fire on botanical composition, soil cover, and forage production in Caucasian bluestem-infested rangeland in the Kansas Smoky Hills: Year 4 of 5. *Kansas Agricultural Experiment Station Research Reports*, *9*(1), 1.

Han, X., Dendy, S. P., Garrett, K. A., Fang, L., & Smith, M. D. (2008). Comparison of damage to native and exotic tallgrass prairie plants by natural enemies. *Plant Ecology*, *198*(2), 197–210.

Havill, S., Schwinning, S., & Lyons, K. G. (2015). Fire effects on invasive and native warm-season grass species in a north American grassland at a time of extreme drought. *Applied Vegetation Science*, *18*, 637–649.

Lesak, M. M. (2016). *Management of invasive Old World bluestems to restore native grasslands* [M.S.]. Texas A&M University.

Lewis, T. (2006). *Management for conservation of plant diversity in native grasslands of the Moree Plains, NSW* [PhD]. University of New England.

Lewis, T., Reid, N., Clarke, P. J., & Whalley, R. D. B. (2010). Resilience of a high-conservation-value, semi-arid grassland on fertile clay soils to burning, mowing and ploughing. *Austral Ecology*, *35*(4), 464–481.

Minton, D. (2006). *Fire, erosion, and sedimentation in the Asan-Piti watershed and War in the Pacific NHP, Guam* (Technical Report 150). Pacific Cooperative Studies Unit, University of Hawaii at Manoa.

Orr, D. (2010). *Managing the grass-legume balance in Stylosanthes scabra cv* (p. 44). Seca pastures in central Queensland.

Ramirez, M., Tajchman, A., Duncan, Z., Lemmon, J., & Olson, K. (2021). Effects of late summer prescribed fire on botanical composition, soil cover, and forage production in Caucasian bluestem-infested rangeland in the Kansas Smoky Hills: Year 2 of 4. *Kansas Agricultural Experiment Station Research Reports*, *7*(1). https://doi.org/10.4148/2378-5977.8019

Ramirez, M., Tajchman, A., Duncan, Z., Lemmon, J., & Olson, K. (2022). Effects of late summer prescribed fire on botanical composition, soil cover, and forage production in Caucasian bluestem-infested rangeland in the Kansas Smoky Hills: Year 3 of 4. *Kansas Agricultural Experiment Station Research Reports*, *8*(1). https://doi.org/10.4148/2378-5977.8220

Reed, H. E., Seastedt, T. R., & Blair, J. M. (2005). Ecological consequences of C_4 grass invasion of A C_4 grassland: A dilemma for management. *Ecological Applications*, *15*(5), 1560–1569.

Reemts, C. M., McCaw, W. M., Greene, T. A., & Simmons, M. T. (2019). Short-term control of an invasive C_4 grass with late-summer fire. *Rangeland Ecology & Management*, *72*(1), 182–188.

Reemts, C. M., Picinich, C., & Greene, T. A. (2021). Late-summer fire provides long-term control of the invasive Old World Bluestem (*Bothriochloa ischaemum*). *Southeastern Naturalist*, *20*(4), 589–601.

Ruckman, E. M., Schwinning, S., & Lyons, K. G. (2012). Effects of phenology at burn time on post-fire recovery in an invasive C_4 grass. *Restoration Ecology*, *20*(6), 756–763.

Silcock, R. G., Jones, P., Hall, T. J., & Waters, D. K. (2005). *Enhancing pasture stability and profitability for producers in poplar box and silver-leaved ironbark woodlands*. (NAP3.208). Meat & Livestock Australia Limited.

Simmons, M. T., Windhager, S., Power, P., Lott, J., Lyons, R. K., & Schwope, C. (2007). Selective and non-selective control of invasive plants: The short-term effects of growing-season prescribed fire, herbicide, and mowing in two Texas prairies. *Restoration Ecology*, *15*(4), 662–669.

St. Clair, B. (2012). *Growing season versus dormant season fire as a control method for an invasive species, King Ranch bluestem (Bothriochloa ischaemum)* [M.S.]. Texas A&M University-Commerce.

Toomey, A. E. (2015). *Effects of seasonal prescribed burning on Kleberg bluestem (Dichanthium annulatum) in south Texas* [M.S.]. Texas A&M University.

Twidwell, D., Rogers, W., McMahon, E., Thomas, B., Kreuter, U., & Blankenship, T. (2012). Prescribed extreme fire effects on richness and invasion in coastal prairie. *Invasive Plant Science and Management*, *5*, 330–340.

Whiting, C. (2022). *Ecological relationships between invasive grasses, native grasses, and wildfire* [PhD]. University of Texas at Austin.

Windhager, S. W. (1999). *An assessment of the use of seeding, mowing, and burning in the restoration of an oldfield to tallgrass prairie in Lewisville, Texas* [Ph.D.]. University of North Texas.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Details of databases searched.

Table S2. Exact search terms used when searching the databases listed in Table 1.

Table S3. Moderator definitions.

Table S4. Model information.

Table S5. Model-averaged coefficients for invasive bluestems and native grasses.

Table S6. For invasive bluestem data, moderator estimates when including effect sizes' sample variance ("adjusted") compared to a model without that term ("unadjusted") were similar in magnitude, direction, and significance, indicating a limited effect of publication bias.

Table S7. For native grasses, moderator estimates when including effect sizes' sample variance ("adjusted") compared to a model without that term ("unadjusted") were mostly similar in magnitude, direction, and significance, indicating a somewhat limited effect of publication bias.

Figure S1. PRISMA chart for systematic search.

Figure S2. Influence of species on standardized mean difference (mean ± 95% confidence intervals) of fire effects on five focal invasive bluestem species.

Figure S3. Influence of range on standardized mean difference (mean ± 95% confidence intervals) of fire effects on five focal invasive bluestem species.

Figure S4. The influence of fire month on standardized mean difference (mean ± 95% confidence intervals) of fire effects on (above) *Bothriochloa ischaemum* and (below) other invasive bluestem species in their introduced range (i.e., excluding *Bothriochloa ischaemum*).

Figure S5. The influence of fire month on standardized mean difference (mean ± 95% confidence intervals) of fire effects on native C_4 grasses (excluding invasive bluestems in their native range).

Figure S6. Fuel load did not influence standardized mean difference (mean ± 95% confidence intervals) of fire effects on invasive bluestem species and native grasses.

Figure S7. Influence of drought variables (Keetch-Byram drought index, KBDI) on standardized mean difference of fire effects of invasive bluestems (in native and introduced ranges, left column) and native grasses (excluding invasive bluestems in their native range, right column).

Figure S8. Influence of drought variables (Keetch-Byram drought index, KBDI) on standardized mean difference of fire effects of invasive bluestems (in native and introduced ranges, left column) and native grasses (excluding invasive bluestems in their native range, right column).

Figure S9. The influence of seeding (of native species) on standardized mean difference (mean ± 95% confidence intervals) of fire effects on five focal invasive bluestem species in studies.

Figure S10. The influence of grazing on standardized mean differences (mean ± 95% confidence intervals) of fire effects on five focal invasive bluestem species and native grasses from the same studies (excluding invasive bluestems in their native range).

Figure S11. The influence of study type on standardized mean differences (mean ± 95% confidence intervals)of fire effects on (above) five focal invasive bluestem species and (below) native grasses from the same studies (excluding invasive bluestems in their native range).

Figure S12. The influence of fire type on standardized mean differences (mean ± 95% confidence intervals) of fire effects on (above) five focal invasive bluestem species and (below) native grasses from the same studies (excluding invasive bluestems in their native range).

Figure S13. The influence of time since fire on standardized mean difference of fire effects on (above) five focal invasive bluestem species and (below) native grasses (excluding invasive bluestems in their native range).

Figure S14. The influence of soil depth (to B horizon) on standardized mean difference of fire effects on (above) five focal invasive bluestem species and (below) native grasses (excluding invasive bluestems in their native range).

Figure S15. The influence of latitude (absolute value) on standardized mean difference of fire effects on (above) five focal invasive bluestem species and (below) native grasses (excluding invasive bluestems in their native range).

Figure S16. The influence of variable type of the original study on standardized mean difference (mean ± 95% confidence intervals) of fire effects on (above) five focal invasive bluestem species and (below) other native grasses (excluding invasive bluestems in their native range).

Figure S17. Sum of model weights for invasive bluestems (in their native and introduced ranges) and native grasses (excluding invasive bluestems in their native range); see Tables 1 and 2 for models tested.

How to cite this article: Reemts, C. M., Havird, J. C., Behr, W. L., Clayton, M. K., Foster, J. L., Lesak, M. M., Whiting, C. V., Farrior, C. E., & Wolf, A. A. (2025). Fire season and drought influence fire effects on invasive grasses: A meta-analysis. *Journal of Applied Ecology*, *62*, 1296–1308. https://doi.org/10.1111/1365-2664.70041