



Combined effects of fire and drought are not sufficient to slow shrub encroachment in tallgrass prairie

R. M. Keen¹ · S. Bachle^{1,2} · M. Bartmess³ · J. B. Nippert¹

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Abstract

Woody encroachment—the spread of woody vegetation in open ecosystems—is a common threat to grasslands worldwide. Reversing encroachment can be exceedingly difficult once shrubs become established, particularly clonal species that resprout following disturbance. Single stressors are unlikely to reverse woody encroachment, but using multiple stressors in tandem could be successful in slowing or reversing encroachment. We explored whether increasing fire frequency in conjunction with multi-year drought could reduce growth and survival of encroaching shrubs in a tallgrass prairie in northeastern Kansas, USA. Passive rainout shelters (~50% rainfall reduction) were constructed over mature clonal shrubs (*Cornus drummondii*) and co-existing C₄ grasses in two fire treatments (1-year and 4-year burn frequency). Leaf- and whole-plant level physiological responses to drought and fire frequency were monitored in shrubs and grasses from 2019 to 2022. Shrub biomass and stem density following fire were unaffected by five years of consecutive drought treatment, regardless of fire frequency. The drought treatment had more negative effects on grass leaf water potential and photosynthetic rates compared to shrubs. Shrub photosynthetic rates were remarkably stable across each growing season. Overall, we found that five consecutive years of moderate drought in combination with fire was not sufficient to reduce biomass production or stem density in an encroaching clonal shrub (*C. drummondii*). These results suggest that moderate but chronic press-drought events do not sufficiently stress encroaching clonal shrubs to negatively impact their resilience following fire events, even when fire frequency is high.

Keywords Tallgrass prairie · Woody encroachment · Drought · Fire frequency · Interacting drivers

Introduction

Woody encroachment—the spread of woody shrubs and trees into historically grass-dominated systems—is a primary threat to grassland ecosystems worldwide (Van Auken 2000; Gibbens et al. 2005; Knapp et al. 2008; Brandt et al. 2013; Formica et al. 2014; Ratajczak et al. 2014a, b; Stevens et al. 2017). This process leads to lower plant biodiversity (Ratajczak et al. 2012; Eldridge et al. 2011), reduced forage for grazing livestock (Anadón et al. 2014), shifts in carbon

and nutrient cycling (Knapp et al. 2008; Mureva et al. 2018; Connell et al. 2020), and potentially negative impacts on water yield (Viglizzo et al. 2015; Acharya et al. 2018; Zou et al. 2018). In mesic grasslands, the primary local driver of woody encroachment is fire (Briggs et al. 2005; Twidwell et al. 2013; Ratajczak et al. 2014b). While frequent fire maintains open grasslands, reducing fire frequency by only 3–4 years leads to rapid shrub expansion and a transition to an alternative shrub-dominated state (Ratajczak et al. 2014b). Recent evidence shows that this ecosystem transition exhibits hysteresis, where reducing fire frequency results in a grassland-to-shrubland transition, but restoring frequent fire to an encroached grassland is not sufficient to reverse that transition once woody vegetation is established (Ratajczak et al. 2014b; Collins et al. 2021).

In addition to these shifts in land cover, which are largely influenced by local management strategies (i.e., frequency of prescribed fire), increasing precipitation variability and frequency of extreme events—including drought—are projected as a result of climate change (Dai 2013; Wehner

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✉ R. M. Keen
rlease@ksu.edu

¹ Division of Biology, Kansas State University, Manhattan, KS, USA

² LI-COR Biosciences, Lincoln, NE 68504, USA

³ United States Department of Agriculture, Natural Resource Conservation Service, Pottawatomie County, KS, USA

et al. 2017; Jones 2019; IPCC 2021) and have already been observed in the midwestern United States (Ford et al. 2021). In mesic grasslands, including the tallgrass prairie ecoregion of the Great Plains (central USA), increased precipitation variability is expected to lead to longer drought periods punctuated by fewer, but larger, rainfall events (Easterling et al. 2000; Jones 2019). Independent shifts in land-management (prescribed fire frequency) and climate (drought) have been shown to impact grassland productivity and community composition (Collins 1992; Fay et al. 2002, 2003; Hoover et al. 2014a, 2014b), but the interactive effects of these drivers are not well understood in tallgrass prairie, particularly in the context of woody encroachment.

Grass-dominated systems typically exhibit reduced aboveground net primary productivity (ANPP) in response to drought (Carroll et al. 2021; Knapp et al. 2015), and the severity of these impacts depends in part on the length and intensity of the drought event (i.e., press vs. pulse droughts; Hoover and Rogers 2016; Luo et al. 2020; Carroll et al. 2021). However, grassland ecosystems are known to show high resilience even to severe drought events (Hoover et al. 2014b; Isbell et al. 2015; Wilcox et al. 2020; Slette et al. 2022). The C_4 grasses that dominate much of the Great Plains are well adapted to drought—high fine root biomass in surface soils allows grasses to access and absorb water quickly when it is available, and the ability to tolerate and adjust to low water availability allows for continued carbon fixation under low soil moisture conditions (Knapp 1984, 1985; Nippert et al. 2009). However, the impact of drought on encroaching shrub growth and physiology is not well understood, making it difficult to predict responses of woody-encroached grassland ecosystems to future climate conditions.

Understanding the combined effects of drought and fire on encroached communities could also provide additional management tools for slowing or reversing the process of woody encroachment. For many mesic grasslands, prescribed fires occur in the spring prior to the onset of vegetation growth. This fire strategy removes previous-year dead biomass, results in faster surface soil warming, and favors the growth of grasses with the C_4 photosynthetic pathway (Reichma 1987; Knapp and Medina 1999). Additionally, frequent spring burning prohibits the establishment of woody shrubs with the C_3 photosynthetic pathway (Briggs et al. 2005). Once established, removal of woody vegetation (particularly clonal shrubs) typically requires extreme mechanical intervention, often with the addition of herbicide treatment (Engle et al. 2006; Nelson et al. 2006). High intensity fires have been reported as an effective short-term strategy for shrub encroachment (Twidwell et al. 2016), but long-term monitoring suggests that high-intensity fires may be ineffective over the long term (Nippert et al. 2021; Strydom et al. 2023).

Previous work in tallgrass prairie has begun to explore whether combinations of external pressures can be employed to address shrub encroachment. Browsing in combination with fire, for example, has shown success in stressing rough-leaf dogwood (*Cornus drummondii*, encroaching clonal shrub) sufficiently to reduce nonstructural carbohydrate (NSC) reserves and growth over time (O'Connor et al. 2020). The combination of drought and frequent fire has not been explored to the same degree but could potentially produce similar results if shrubs can be sufficiently drought stressed (i.e., reduced carbon capture and growth, declines in NSC storage; McDowell et al. 2008; McDowell 2011) prior to burning. If successful, burning during or following future drought events could be leveraged as a management strategy for woody encroachment in tallgrass prairie.

Here, our primary goal was to assess the combined impacts of multi-year drought and fire frequency on shrub and grass physiology to (a) improve predictions of grassland ecosystem responses to changing climate conditions and (b) inform land managers as to whether burning during drought conditions could be an effective strategy for reducing or slowing the spread of shrub cover in rangelands. To this end, we constructed passive rainout shelters (50% reduction) over intact *C. drummondii* shrubs and co-existing herbaceous communities (Fig. 1). Shelters were placed on watersheds with a 1-year or 4-year burn interval to assess the interactive effects of drought and fire frequency. Treatments began in 2018 and data were collected during the 2019–2022 growing seasons. Our questions include: (1) How do co-existing grasses and shrubs physiologically respond to multiple consecutive years of drought, and how are these responses mediated by fire history? (2) Does 50% precipitation reduction lead to differences in aboveground biomass production in grasses or shrubs? (3) Does multi-year drought impact the survival or recovery of encroaching shrubs following fire events?

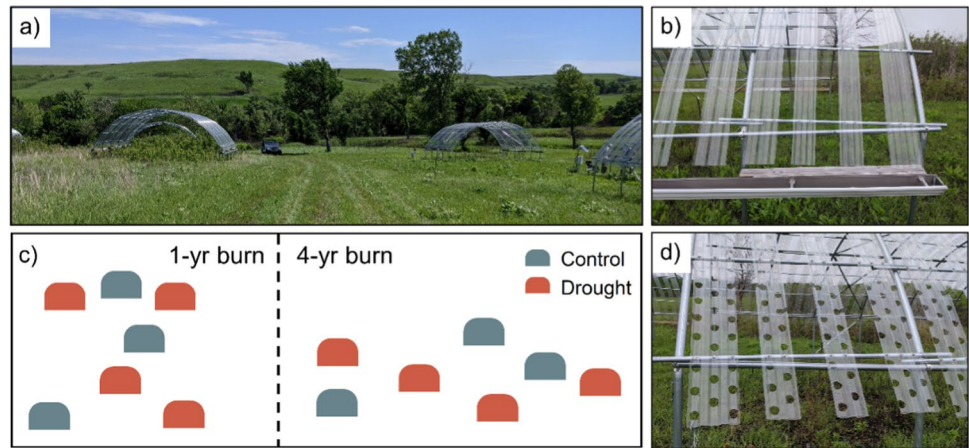
Materials and methods

Site description and experimental design

Konza Prairie Biological Station (KPBS)

KPBS is a 3,487-ha tallgrass prairie site near Manhattan Kansas, USA (39.1°N, 96.9°W). The site is characterized by hillslopes of alternating limestone and shale layers, resulting in an underlying merokarst geology as these layers weather at different rates (Vero et al. 2017; Sullivan et al. 2020). Upland soils are shallow and rocky, while lowland soils are deeper (> 2 m) and classified as silty-clay loams (Ransom et al. 1998). KPBS is a Long-Term Ecological Research (LTER) site that is split into replicated experimental

Fig. 1 Experimental design and layout of the ShRaMPs experimental site. **a** ShRaMPs experimental site at KPBS and **c** diagram of drought (red) and control (blue) shelter locations on a 1-yr and 4-yr burn watershed. **b** Drought shelters excluded ~50% of precipitation using plastic roofing, gutter systems, and flashing to reduce overland flow. **d** Control shelters allowed ambient precipitation to reach vegetation



watersheds with varying grazing and fire treatments. The site is dominated by C_4 grasses, including *Andropogon gerardii*, *Panicum virgatum*, *Sorghastrum nutans*, and *Schizachyrium scoparium*, but supports high plant biodiversity (Collins and Calabrese 2012). Historically, this region was open and grassy, with limited shrub cover and tree cover isolated in stream corridors (Abrams 1986). Available evidence indicates that the historical (i.e., pre-European settlement) fire frequency in tallgrass prairie was ~2.5–4 years on average but likely ranged from 2 to 10 years (Desantis et al. 2010; Allen and Palmer 2011; Stambaugh et al. 2013). Over the last century, particularly in the last 2–3 decades, woody cover has increased drastically in areas with fire return intervals > ~3 years (Briggs et al. 2005; Ratajczak et al. 2014b, 2016).

ShRaMPs experimental design

Shrub Rainout Manipulation Plots (ShRaMPs) are a drought x fire experiment located in adjacent watersheds K01B (1-year burn frequency, un-grazed) and K04A (4-year burn frequency, un-grazed) at KPBS (Fig. 1a,b). Watershed K01B has been annually burned for 12 years (2011 to 2022) but was previously burned every 4 years (1980 to 2008), which allowed for the limited establishment of *C. drummondii* shrubs before annual burning was implemented. K04A has been burned every 4 years since 1980. K01B was burned in the spring (March or April) each year of the experiment (2018–2022). K04A was burned in the spring of 2017 (prior to the start of this experiment) and again in the spring of 2021. In lowland positions on both watersheds, seven passive rainout shelters (6 × 6 m; three control shelters and four drought shelters per watershed) were constructed over intact *C. drummondii* shrubs and their surrounding herbaceous communities. Shelters were built in the summer of 2017 and the drought treatment was implemented in 2018.

Shelter design was modeled after the long-term Rainout Manipulation Plots (RaMPs) experiment, also at KPBS

(Fay et al. 2002, 2003; <http://www.konza.ksu.edu/ramps/>). Drought shelters were designed to exclude ~50% of incoming precipitation using polyethylene roofing panels and gutter systems that route blocked precipitation away from the plots (Fig. 1c). The sides and ends (north and south) of the shelters were left open to maximize airflow and minimize changes in relative humidity and temperature in the plots. Drought plots were trenched, and metal flashing was installed to a depth of 15 cm to reduce lateral water flow into the plots at the soil surface and through surficial soils. In 2021, we added (1) additional paneling to the south side of each drought shelter to reduce blow-in from rainstorms approaching from the south-west and (2) additional flashing on the south side of drought shelters that were on a slope to reduce any overland flow that might occur during heavy rain events. Polyethylene roofs were also added to control shelters, but control roofs had small circular holes cut in the polyethylene panels to allow ambient precipitation to reach the underlying plant communities (Fig. 1d). As such, control shelter roofs mimic any microclimatic effects without the rainfall exclusion. Shelter roofs were removed for roughly 1 month during the vegetative dormant period (typically mid-February to mid-March) when watersheds were burned, but otherwise remained intact year-round. Each watershed contained four drought shelters and three control shelters for a total of 14 shelters (Fig. 1b). Each shelter was divided into four equal subplots—one subplot was reserved for species composition and shrub stem measurements (no destructive sampling and minimal foot traffic), and the other three were reserved for gas exchange, water potential, and herbaceous biomass collection.

Each shelter was equipped with 30 cm time-domain reflectometry (TDR) probes (Campbell Scientific) at soil depths of 10, 15, and 30 cm. Soil moisture data were recorded at 30-min intervals on Campbell Scientific data loggers (CR1000X). A weather station was constructed on-site to measure photosynthetically active radiation (PAR), relative humidity, and air temperature throughout the study

period. Weather station data were recorded at 30-min intervals on a Campbell Scientific data logger (CR1000). Daily precipitation data were collected at KPBS headquarters, ~5 km away from the study site, using an Ott Pluvio2 rain gauge (Nippert 2023).

Focal species

Andropogon gerardii and *Cornus drummondii* were sampled in this study to characterize dominant grass and shrub responses to drought and fire frequency. *A. gerardii* is one of the most abundant C₄ grasses in tallgrass prairie (Knapp 1984). This species is known for high intraspecific trait variability, facilitating a broad range throughout the Great Plains and central North America (Bachle et al. 2018). Physiological characteristics including high photosynthetic capacity and water use efficiency (Knapp 1985; Nippert et al. 2007), osmotic adjustment (Knapp 1984, 1985), and extensive fine root systems that allow for rapid water uptake in surface soils (Nippert and Knapp 2007; Nippert et al. 2012) give *A. gerardii* high tolerance to drought conditions (Knapp 1985; Nippert et al. 2009; Hoover et al. 2014b).

Cornus drummondii is a C₃ shrub species that is rapidly encroaching in many portions of the eastern Great Plains (Briggs et al. 2002). This species is clonal, and individual shrubs primarily reproduce asexually through belowground buds and rhizomes that produce new, inter-connected stems referred to as *ramets*. As individual shrubs produce ramets, they form monospecific stands called ‘islands’ that can grow to be multiple meters in diameter in the absence of fire (Ratajczak et al. 2011). This clonal growth form and the ability to resprout make this species extremely resilient to disturbance, including fire and browsing (Ratajczak et al. 2011; Liu et al. 2016; Ott et al. 2019). In addition, *C. drummondii* canopies can reach leaf area index (LAI) values of ~8—higher than LAI values of many temperate deciduous forest ecosystems—and reduce light availability by roughly 97% below the canopy (Tooley et al. 2022). As *C. drummondii* shrub islands establish and expand, they shade out understory grass and forb species which reduces fine fuels and buffers the shrubs against future fires (Ratajczak et al. 2011).

Data collection

Gas exchange

To assess how changes in water availability and fire frequency impacted rates of gas exchange, net photosynthetic rates (A_{net}) for *C. drummondii* and *A. gerardii* were measured every 3–4 weeks throughout each growing season (2019–2022) using an LI-COR 6400XT or 6800 infrared gas analyzer (LI-COR Inc., Lincoln, NE, USA). In

two subplots per shelter, one individual per species was selected for gas exchange measurements. This yielded a total of two individuals per species in each shelter. Reference CO₂ concentration was set to 400 $\mu\text{mol mol}^{-1}$, PAR was set to 2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, and relative humidity was maintained between 50 and 65% during measurements to approximate ambient conditions at this site. Measurements were taken between the hours of 10:00 and 13:00 on clear, sunny days.

Water potential

Predawn and midday leaf water potential (Ψ_{PD} and Ψ_{MD} , respectively) measurements were taken every 3–4 weeks throughout each growing season to assess the impacts of water availability and fire frequency on leaf water status of both species. Measurements were taken using a Scholander pressure chamber (PMS Instrument Company, Albany, OR, USA). For *A. gerardii*, the youngest fully expanded leaf was collected for measurement. For *C. drummondii*, the youngest, most distal leaves at the top of a ramet were collected for measurement. For both species, three replicates (one from each of three subplots) were collected in each shelter during each sampling round. After collection, leaves were immediately placed in sealed plastic bags with high [CO₂] and a moist paper towel, and bags were placed in a dark cooler to encourage stomatal closure and minimize transpiration. Samples were allowed to equilibrate for 1–1.5 h prior to measurement (Rodriguez-Dominguez et al. 2022). Midday samples were collected between the hours of 12:00 and 13:00 on the same days as gas exchange measurements were performed. Predawn measurements were taken approximately 1 h before dawn either on the same day as midday measurements, or on the following morning. No rainfall occurred overnight when predawn measurements were taken on the following morning.

Herbaceous aboveground net primary productivity

Peak biomass for herbaceous vegetation was collected toward the end of each growing season (late August or early September). Biomass was collected in 0.1 m² frames in two subplots per shelter. The same subplots were used for herbaceous biomass collection during all 4 years of the study. For annually burned shelters, samples were sorted into graminoid and forb biomass each year. For shelters burned every 4 years, samples were sorted into live graminoid, live forb, and previous years’ dead biomass. Sorted biomass was dried at 60 °C for at least 72 h, and then dried live biomass was weighed to determine herbaceous aboveground net primary productivity (ANPP).

Woody aboveground biomass

Shrub aboveground biomass was not harvested to allow for perennial aboveground growth of woody stems. Instead, *C. drummondii* stems were counted and stem basal diameters were measured in one subplot of each shelter during the fall or winter following each growing season. In each shelter, the same subplot was measured each year so that stem densities and woody biomass could be directly compared year-to-year. Stem density (number of stems per m² ground area) was recorded for each shelter. *C. drummondii* aboveground biomass was estimated from stem counts and diameters using the following allometric equation from KPBS (see Appendix 1 for more detail):

$$\sum_{i=1}^n [(a * \ln(d_i)) - b],$$

where a and b are constants ($a = 2.53099$, $b = 1.29768$), d_i is diameter of stem i , and n is the total number of live stems in a given shelter.

Data analysis

Mixed effects models were performed for each response variable using the *lmer* function from the *lmerTest* package (Kuznetsova et al. 2017) and the *Anova* function from the *car* package (Fox and Weisberg 2019) in R version 4.1.0 (R Core Team 2021). Tukey's HSD adjustment was used for pairwise comparisons when necessary using the *emmeans* package (Lenth 2020).

Water availability and stress

Differences in VWC between drought and control treatments were assessed using mixed-effects models. Separate models were performed for each soil depth (10, 15, and 30 cm). VWC was included as the response variable, drought treatment was included as a fixed effect, and random effects included shelter and day of year nested within year. We used the longest continuous time period in which we had VWC measurements, which was 5/1/2020 to 8/10/2022.

To assess intra-annual changes in predawn and midday water potential (Ψ_{PD} and Ψ_{MD}), separate mixed-effects models were performed for each year (2019–2022). In these models, fixed effects included drought treatment, burn treatment, day of year, and their interactions. Replicate nested within shelter was included as a random effect to account for pseudoreplication within shelters. Separate models were constructed for each species (*A. gerardii* and

C. drummondii). Predawn water potential (Ψ_{PD}) was log-transformed to meet model assumptions of normality.

Carbon assimilation and biomass production

Changes in net photosynthetic rates (A_{net}) were assessed in the same way as Ψ_{PD} and Ψ_{MD} . Separate mixed-effects models were performed for each species (*A. gerardii* and *C. drummondii*) and year of study (2019–2022). Fixed effects included drought treatment, burn treatment, day of year, and their interactions, while replicate nested within shelter was included as a random effect.

Mixed effects models for herbaceous ANPP, shrub biomass, and stem density were performed separately. Fixed effects included burn treatment, drought treatment, year, and their interactions. For shrub biomass and stem density, shelter was included as a random effect. For herbaceous ANPP, replicate nested within shelter was included as a random effect to account for pseudoreplication within each shelter.

Results

Water availability and stress

Precipitation and soil moisture

The first year of the study (2019) had higher total annual precipitation (970.8 mm) compared to the long-term average for this site (832.9 mm; 1982–2022 average; Fig. 2). 2020 and 2022 were both near-average years (832.8 and 825.7 mm, respectively), but 2021 was drier than the long-term average (632.2 mm). Dormant season precipitation was similar across all 4 years (222.7 mm \pm 17.3 mm; long-term average, 228.0 mm), but growing season precipitation was above-average in 2019 (724.2 mm; long-term average, 604.9 mm) and below-average in 2021 (423.6 mm). Differences in soil volumetric water content (VWC) between drought and control shelters were observed at 10 cm ($p = 0.048$; 19.1% reduction) and 15 cm ($p = 0.081$; 16% reduction) depths, where drought shelters had lower VWC than control shelters (Table S1). At the 30 cm depth, the drought effect was not significant ($p = 0.261$; 16% reduction), but the same trend was present (Fig. 3). In addition, VWC was generally lower, and the difference in VWC between control and drought treatments was larger, in the 4-year burn compared to the 1-year burn treatment. Across all soil depths, VWC was reduced by ~23% in the 4-year burn treatment, and by ~12% in the 1-year burn treatment (Table S1). Sensor malfunctions due to rodent damage resulted in multiple periods without available VWC data, primarily in 2019 and the end of 2022. Continuous VWC data were available from May 2020 to August 2022 (Fig. 3).

Fig. 2 Cumulative precipitation (top) and daily precipitation (bottom) measured at KPBS headquarters from 2019 to 2022. Dashed black line represents the long-term (1982–2022) mean annual precipitation for KPBS (832.9 mm). Black lines represent precipitation occurring during the growing season (April–September) and gray lines represent precipitation occurring during the dormant season (October–March)

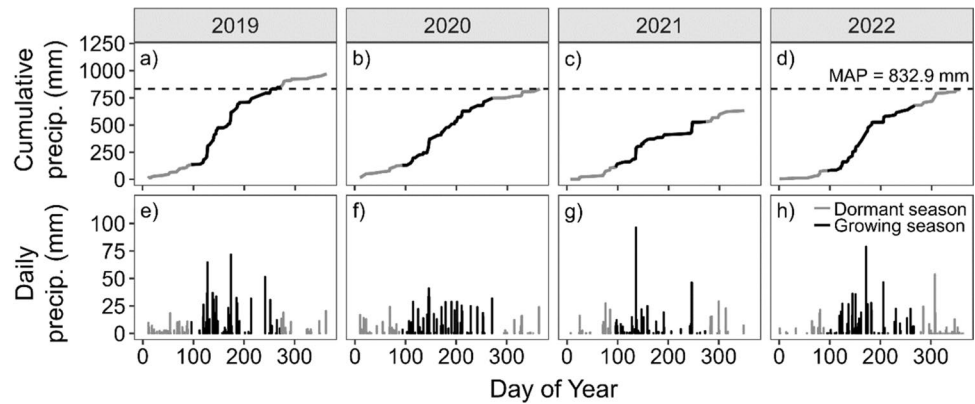
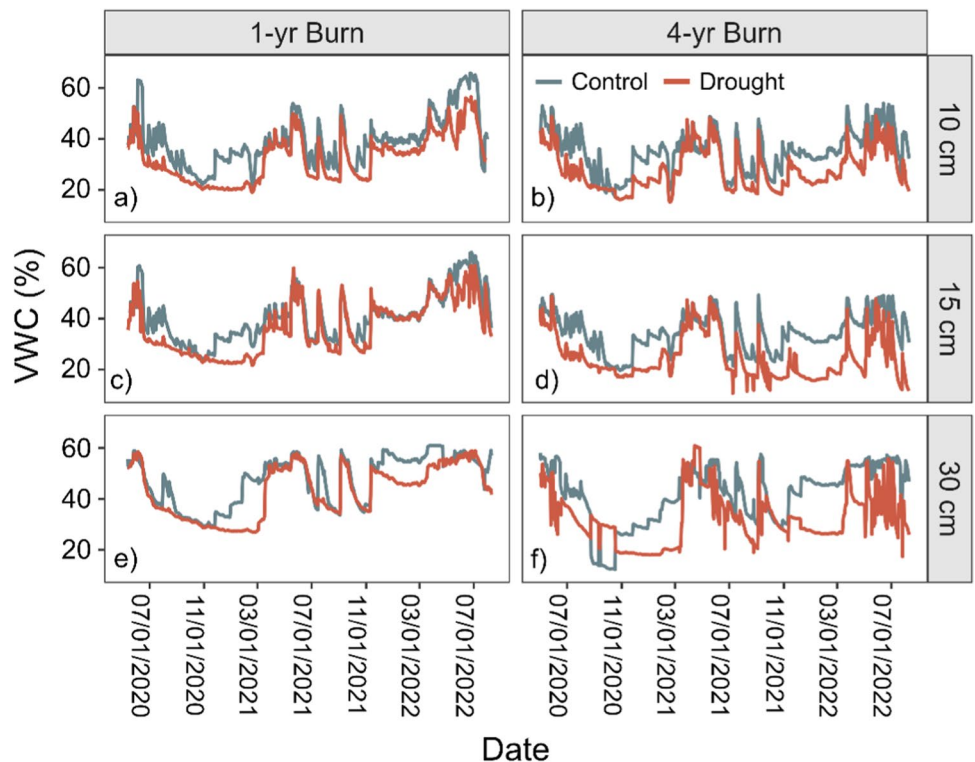


Fig. 3 Volumetric water content (VWC) at three depths (10, 15, and 30 cm) in each shelter at ShRaMPs from 5/1/2020 to 8/10/2022. Drought treatment is shown in blue (control) and red (drought)



Water potential

Substantial variability in predawn leaf water potential (Ψ_{PD}) values occurred within individual growing seasons for both species (Fig. 4a). On average, Ψ_{PD} values were significantly lower in 2021 compared to the other 3 years of study (47.41% and 24.5% lower for *A. gerardii* and *C. drummondii*, respectively; Table 1). Intra-annual changes in Ψ_{PD} for both species generally tracked precipitation inputs during the growing season (Fig. 2, Fig. 4a). *A. gerardii* Ψ_{PD} values were lower in the 4-year burn treatment (Table 1; Fig. 4a) where surface soil moisture was often lower than in the 1-year burn treatment, particularly in 2021 (24.2% lower) and 2022 (86.7% lower Fig. 3). *C. drummondii* Ψ_{PD}

values were also lower in the 4-year burn treatment during portions of each growing season, but the burn effect was less pronounced compared to *A. gerardii* (Table 1; Fig. 4a).

Midday water potential (Ψ_{MD}) values for both species declined across each individual growing season (Fig. 4b). Significant drought effects—where Ψ_{MD} values were lower in drought shelters compared to control shelters—occurred during at least one time point each year, typically in the mid-to-late-growing season (DOY 200–240; Table S5). These effects were most pronounced in 2021 when conditions were driest overall (Fig. 4b; Table 2). In 2021, the driest year of the study, both species saw significant declines in Ψ_{MD} in

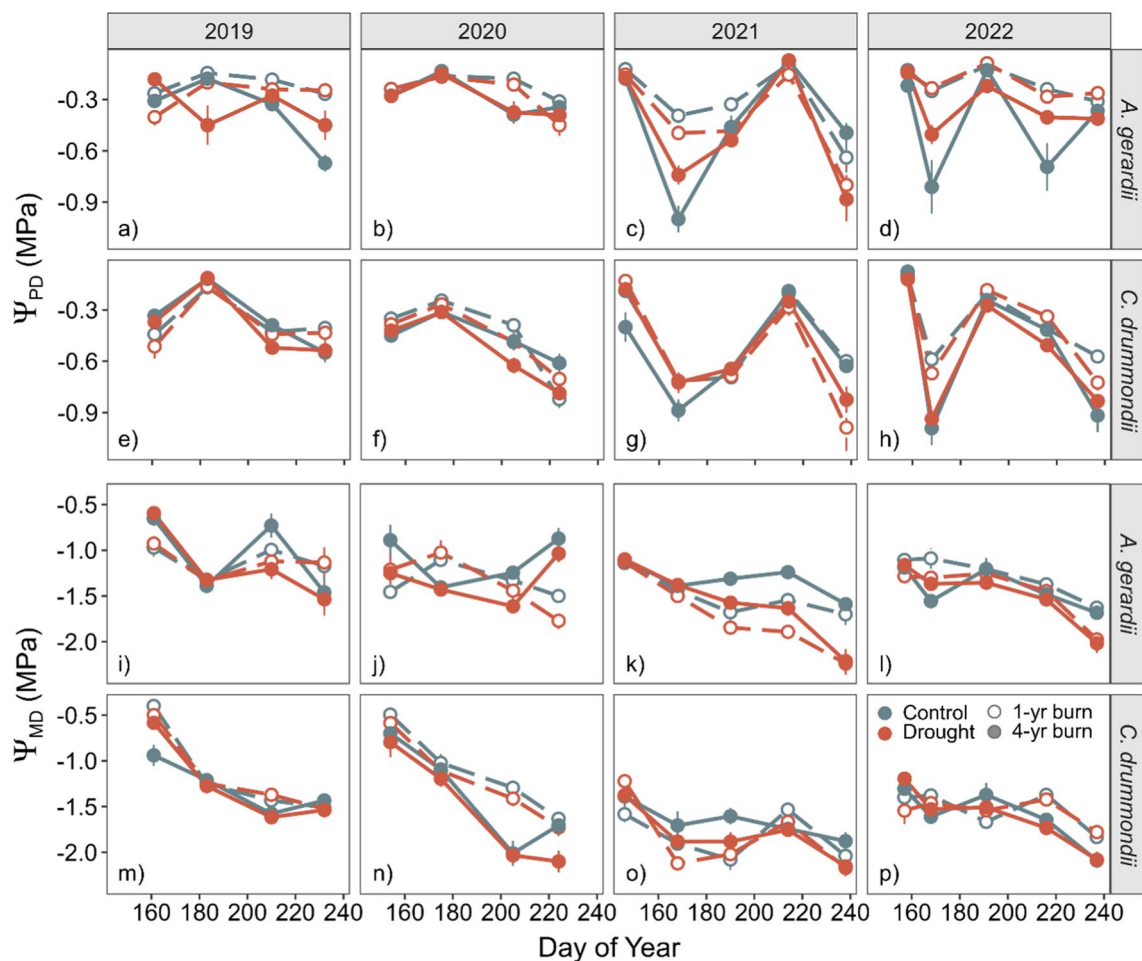


Fig. 4 Predawn leaf water potential (Ψ_{PD}) values for *Andropogon gerardii* (C_4 grass; **a–d**) and *Cornus drummondii* (C_3 shrub; **e–h**) throughout the 2019–2022 growing seasons, and midday leaf water potential (Ψ_{MD}) values for *A. gerardii* (**i–l**) and *C. drummondii* (**m–p**) throughout the 2019–2022 growing seasons. Points are mean Ψ_{PD} or

Ψ_{MD} values ± 1 SE. Burn treatment is shown using open (1-year burn) and closed (4-year burn) circles, and drought treatment is shown in blue (control) and red (drought). Tables S4 and S5 contains p values for pairwise comparisons for significant interactions for Ψ_{PD} and Ψ_{MD} , respectively

Table 1 P values for predawn water potential (Ψ_{PD}) mixed-effects models

Predictor	<i>A. gerardii</i> Ψ_{PD}				<i>C. drummondii</i> Ψ_{PD}			
	2019	2020	2021	2022	2019	2020	2021	2022
Drought	0.643	0.287	<0.001*	0.373	0.610	0.030*	0.645	0.333
Burn	0.001*	0.009*	0.017*	<0.001*	0.096 ⁺	0.002*	0.030*	<0.001*
DOY	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*
Drought*Burn	0.009*	0.306	0.032*	0.798	0.610	0.477	0.167	0.231
Drought*DOY	0.003*	0.589	0.174	0.102	0.757	0.122	<0.001*	0.295
Burn*DOY	<0.001*	<0.001*	<0.001*	0.005*	0.013*	0.031*	<0.001*	0.008*
Drought*Burn*DOY	0.014*	0.533	0.053 ⁺	0.002*	0.635	0.072 ⁺	0.755	0.009*

* denotes significant values ($p < 0.05$) and (+) denotes marginally significant values ($p < 0.10$)

July and August, particularly in the 4-year burn treatment (Fig. 4b; Table 2; Table S5).

Carbon assimilation and biomass production

Photosynthetic rates

Intra-annual variability in A_{net} was higher for *A. gerardii* than *C. drummondii* in all 4 years (Fig. 5; Table S2). In all years except for 2021, A_{net} was higher in the 1-year

burn compared to the 4-year burn treatment for *A. gerardii* (Table 3; Fig. 5)—these differences were most pronounced in 2020 (16.5% difference) and 2022 (19% difference). Drought effects were seen in 2020 and 2021 for *A. gerardii* (Table 3)—in 2021, drought shelters had consistently lower A_{net} compared to control shelters, but in 2020, A_{net} values were actually highest in the 1-year burn drought shelters (Fig. 5; Table 3). The burn treatment only impacted *C. drummondii* A_{net} in 2019 (Table 3), where values were 15.3% higher in the 1-year burn treatment compared to the

Table 2 P values for midday water potential (Ψ_{MD}) mixed-effects models

Predictor	<i>A. gerardii</i> Ψ_{MD}				<i>C. drummondii</i> Ψ_{MD}			
	2019	2020	2021	2022	2019	2020	2021	2022
Drought	0.280	0.022*	<0.001*	<0.001*	0.708	0.0046*	0.059 ⁺	0.712
Burn	0.858	0.010*	<0.001*	0.007*	0.001*	<0.001*	0.020*	0.051 ⁺
DOY	<0.001*	0.036*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*
Drought*Burn	0.391	0.044*	0.670	0.104	0.500	0.662	0.115	0.828
Drought*DOY	0.745	0.223	<0.001*	0.007*	0.196	0.648	0.012*	0.921
Burn*DOY	<0.001*	<0.001*	0.023*	0.041*	<0.001*	0.001*	0.001*	<0.001*
Drought*Burn*DOY	0.553	0.118	0.948	0.082 ⁺	0.005*	0.604	0.192	0.130

* denotes significant values ($p < 0.05$) and (+) denotes marginally significant values ($p < 0.10$)

Fig. 5 Net photosynthetic rates (A_{net}) for *A. gerardii* (C_4 grass; a-d) and *C. drummondii* (C_3 shrub; e-h) throughout the 2019–2022 growing seasons. Points represent mean A_{net} values \pm 1 SE. Burn treatments are shown using open (1-year burn) and filled (4-year burn) circles, and drought treatments are shown in blue (control) and red (drought). Table S6 contains p values for pairwise comparisons

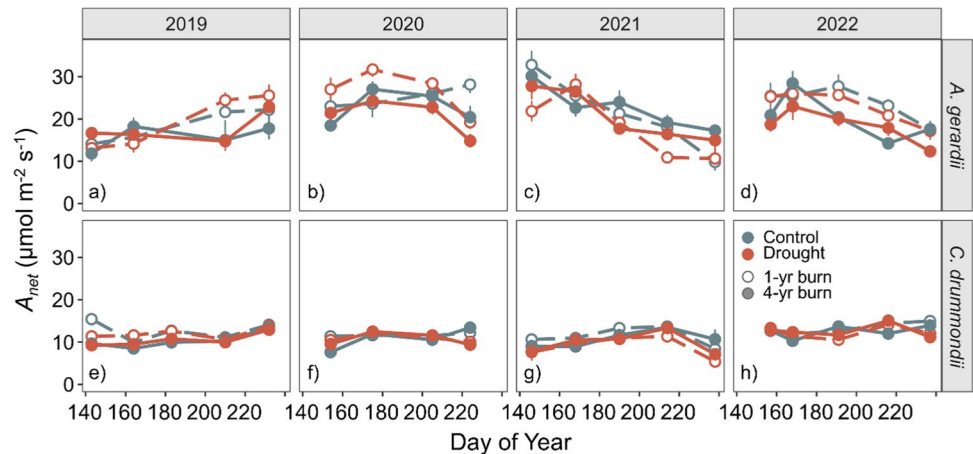


Table 3 P values for photosynthetic rates (A_{net}) mixed-effects models

Predictor	<i>A. gerardii</i> A_{net}				<i>C. drummondii</i> A_{net}			
	2019	2020	2021	2022	2019	2020	2021	2022
Drought	0.260	0.785	0.023*	0.248	0.554	0.446	0.003*	0.218
Burn	0.093 ⁺	<0.001*	0.110	<0.001*	<0.001*	0.340	0.801	0.534
DOY	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	0.007*	<0.001*	0.001*
Drought*Burn	0.713	0.131	0.558	0.680	0.365	0.551	0.155	0.142
Drought*DOY	0.319	0.002*	0.027*	0.758	0.086 ⁺	0.019*	0.392	0.001*
Burn*DOY	0.007*	0.566	0.187	0.107	0.093 ⁺	0.181	0.354	0.434
Drought*Burn*DOY	0.537	0.136	0.309	0.214	0.481	0.326	0.895	0.370

* denotes significant values ($p < 0.05$) and (+) denotes marginally significant values ($p < 0.10$)

4-year burn treatment. Small, but significant, drought effects occurred in all years except for 2019 for *C. drummondii*, but overall variability in A_{net} values for this species was impressively low (Table 3; Fig. 5; Table S2). The largest drought treatment effect for *C. drummondii* was in 2021, where A_{net} values were 14.3% lower in the drought treatment compared to the control treatment.

Aboveground biomass and stem density

In 2021, the 4-year burn frequency watershed was burned, and the *C. drummondii* shrub islands in all but two shelters experienced complete top-kill (no surviving ramets following the fire). A significant burn*year interaction occurred for shrub (*C. drummondii*) biomass ($p < 0.001$), where shrub biomass was significantly higher in the 4-year burn compared to the 1-year burn treatment in 2020 (65.5% difference) and 2022 (61.1% difference) (Fig. 6). This trend was also present in 2019, but the difference was not significant (Table S3, S7). Following the burn in 2021, both shrub biomass and herbaceous biomass were similar between the 1-year and 4-year burn treatments. A significant burn*year interaction also occurred for herbaceous biomass ($p = 0.03$)—herbaceous biomass was higher in the 1-year burn compared to 4-year burn treatment in 2019 (76.0% difference), 2020 (79.0% difference), and 2022 (62.4% difference), but not in 2021 when the 4-year burn treatment had its prescribed burn (Fig. 6; Table S7). No drought effects were observed for herbaceous biomass ($p = 0.112$), shrub biomass ($p = 0.954$), or shrub stem density ($p = 0.915$) during these 4 years. Shrubs stem density was generally higher in the 1-year burn treatment in 2019 and 2020, but the differences were

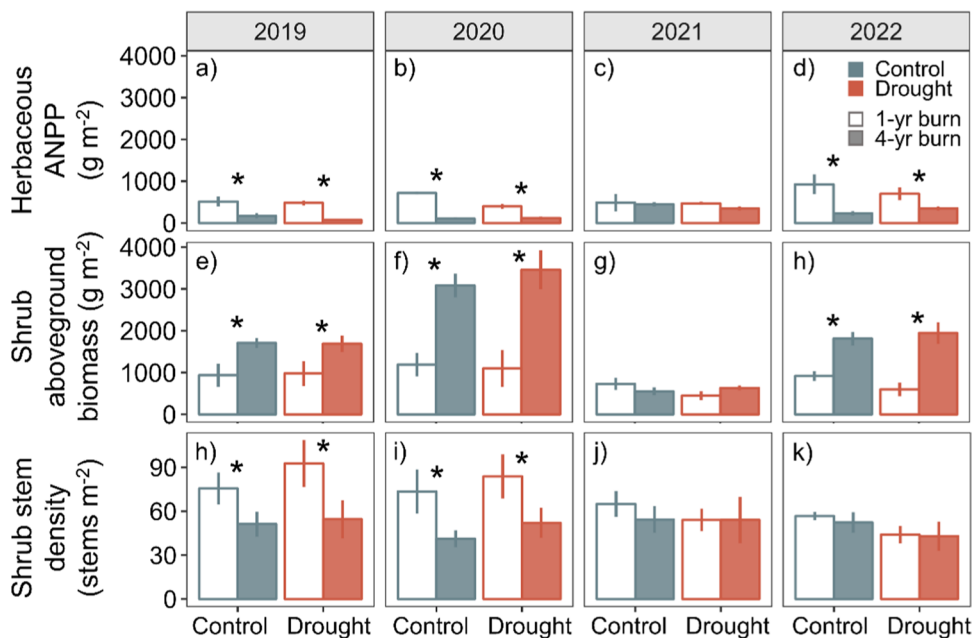
not significant (Fig. 6; Table S3). In 2021 and 2022, there were no observed effects of burn treatment on stem density (Table S3).

Discussion

In this study, we assessed the interactive effects of fire and multi-year drought on woody-encroached communities in tallgrass prairie to determine whether this combination of drivers would result in greater declines in shrub growth or biomass production than either driver on its own. Previous work has found that other driver combinations—particularly browsing and frequent fire—have been successful in slowing the spread of clonal shrubs in tallgrass prairie (O’Connor et al. 2020; Wedel et al. 2021a, 2021b). Although drought does not typically result in the loss of live aboveground tissue during the growing season like browsing, drought stress that leads to stomatal closure and reductions in photosynthetic rates can decrease carbon capture, productivity, and potentially deplete NSC reserves (McDowell 2011). We hypothesized that these consequences of physiological drought stress—if experienced by *C. drummondii* during drought—would diminish the resilience of these shrubs to future fire events, particularly after multiple consecutive years of drought, leading to reduced growth and survival.

However, after five years of drought treatment (50% precipitation reduction), we saw very few impacts of drought on the growth or survival of *C. drummondii* shrub islands, even in conjunction with annual burning (Fig. 6). The 2021 fire in the 4-year burn treatment—which

Fig. 6 a–d) Herbaceous above-ground net primary productivity (ANPP), e–h) shrub (*C. drummondii*) aboveground biomass, and h–k) shrub stem density from 2019 to 2022. Colors represent drought treatments (control = blue, drought = red). Open bars represent the 1-year burn treatment and filled bars represent the 4-year burn treatment. Bars show mean values ± 1 SE, and asterisks represent significant differences between burn treatments ($p < 0.05$). Tables S3 and S7 contain p values for main effects and pairwise comparisons



occurred during the year with the lowest ambient precipitation (Fig. 2) and resulted in complete top-kill of all but two *C. drummondii* shrub islands—essentially ‘reset’ the 4-year burn watershed, knocking shrub biomass back to levels similar to the 1-year burn and allowing for a concurrent increase in herbaceous biomass in 4-year burn shelters (Fig. 6). Contrary to expectations, the drought treatment did not impact shrub recovery (i.e., biomass production or stem density) following the 2021 fire (Fig. 6), indicating that the magnitude of drought stress experienced by these shrubs was insufficient to impact growth via reductions in carbon fixation or storage of NSCs (O’Connor et al. 2020). In addition, both aboveground shrub biomass and shrub cover rebounded nearly to pre-fire levels within one-to-two growing seasons (Fig. 6, Figure S1).

Although drought did not impact overall aboveground production, we did see physiological effects of drought during individual sampling periods, particularly in 2021. Ψ_{MD} values were lower during much of the 2021 growing season for both species, but especially for *A. gerardii* in late July and August (Fig. 4b). Drought had less of an impact on *C. drummondii* Ψ_{MD} , even in 2021. Rather, the burn treatment had a greater influence on shrub Ψ_{MD} , with shrubs in the 4-year burn having lower Ψ_{MD} values overall compared to those in the 1-year burn treatment (Fig. 4b). The 4-year burn treatment did tend to have lower overall soil VWC compared to the 1-year burn (Fig. 3), likely due to higher shrub cover (Figure S1). Increased shrub cover in tallgrass prairie leads to increased leaf area, largely due to the dense canopies and high leaf area index of *C. drummondii* (Tooley et al. 2022), which likely leads to an increase in canopy interception of rainfall (although, this has not been studied for *C. drummondii*). Higher shrub biomass also results in increased water loss via transpiration as grasses are replaced by shrubs with higher canopy transpiration rates and access to deeper soil moisture when surface soils are dry (O’Keefe et al. 2020; Keen et al. 2022).

Increased evapotranspiration driven by higher shrub cover is more pronounced during years with lower annual precipitation (Logan and Brunsell 2015), so we expected to see greater drought effects in the 4-year burn treatment, where soil moisture should be the lowest. We primarily saw drought treatment effects on *A. gerardii* Ψ_{MD} (especially in 2021), but the burn treatment impacted *C. drummondii* Ψ_{MD} to a greater degree than drought (Fig. 4b). This is likely an artifact of the differences in depth of water uptake between grasses and shrubs. It is well documented that *C. drummondii* can access deeper soil water sources compared to co-existing grasses (Nippert and Knapp 2007; Ratajczak et al. 2011; O’Keefe and Nippert 2017), although it is assumed that these shrubs are capable of substantial plasticity in depth of water uptake within individual growing seasons (Keen et al. 2022). In previous studies, it has been

hypothesized that this access to deeper soil moisture essentially decouples *C. drummondii* from climate and environmental variability (Nippert et al. 2013; Brunsell et al. 2014), while grasses rely on surface soil moisture and are highly responsive to precipitation inputs (Nippert and Knapp 2007; Fay et al. 2008).

In line with that hypothesis, *C. drummondii* had remarkably low variability in A_{net} throughout the study, both within and across growing seasons (Fig. 5; Table S2), despite substantial variability in leaf water potential and inter- and intra-annual precipitation amounts and timing (Fig. 2; Fig. 4a-b). This consistency in gas exchange rates in *C. drummondii*, regardless of environmental conditions, has been observed in the previous studies (Muench et al. 2016; Wedel et al. 2021a), but never over multiple consecutive years of drought. These results suggest that grassland communities with high woody cover may experience faster reductions in soil moisture compared to areas with lower woody cover if climate conditions become drier in the future. This trend (gradual declines in deep soil moisture in shrub-encroached areas) has been documented to a degree in tallgrass prairie (Craine and Nippert 2014), and eddy covariance data have shown that ET can outpace precipitation inputs in grasslands with higher shrub cover during drier years (Logan and Brunsell 2015).

Overall, grassland communities are generally considered to be highly resilient to drought, with the ability to recover aboveground (Isbell et al. 2015; Wilcox et al. 2020) and belowground (Slette et al. 2022) biomass following even extreme drought events. However, in this study, we also saw impressive *resistance* to a multi-year drought treatment, particularly in *C. drummondii*. Many drought-related studies in grassland systems have focused on extreme, short-term drought events (Hoover et al. 2018) rather than press-droughts, which are chronic but less intense reductions in moisture availability (Hoover and Rogers 2016). These drought types have been shown to elicit different responses in grassland productivity and carbon cycling (Hoover and Rogers 2016; Luo et al. 2020; Carroll et al. 2021). Extreme pulse droughts typically have greater immediate impacts on productivity, carbon cycling, and community composition (Hoover and Rogers 2016; Carroll et al. 2021), but chronic reductions in precipitation could reduce ecosystem resilience to future disturbances (Hoover and Rogers 2016). Longer term press-droughts can be a result of direct decreases in precipitation or increased temperatures and/or aridity that result in lower soil moisture (Dai 2013). Climate change projections for many grassland regions include increased precipitation variability, which enhances the probability of extreme pulse-drought events, but also of increased aridity overall, which could function as a more chronic reduction in available water (Christensen et al. 2007; Dai 2013; Cook et al. 2015).

Results from this study suggest that moderate but chronic press-drought events do not stress encroaching clonal shrubs enough to negatively impact their resilience to fire events, even when fire frequency is high (i.e., annual fire). Longer and/or more extreme drought events would likely be necessary to reduce deep soil moisture and sufficiently stress these clonal shrubs due to their access to deep soil water below the grass rooting zone (Nippert and Knapp 2007; Ratajczak et al. 2011; O’Keefe and Nippert 2017). Implementation of more novel fire management strategies (such as high-intensity fires, multiple prescribed fires per year, or burning during hot summer droughts) in combination with other drivers or physiological stressors (e.g., browsing or mechanical cutting) may be required to mitigate or reverse shrub encroachment in tallgrass prairie. As changing climate conditions continue to occur concurrently with woody encroachment, understanding the interactive effects of drought and increased woody cover (driven by reductions in fire frequency) is vital to predicting future grassland ecosystem function in the face of climate and land-cover change.

Appendix 1

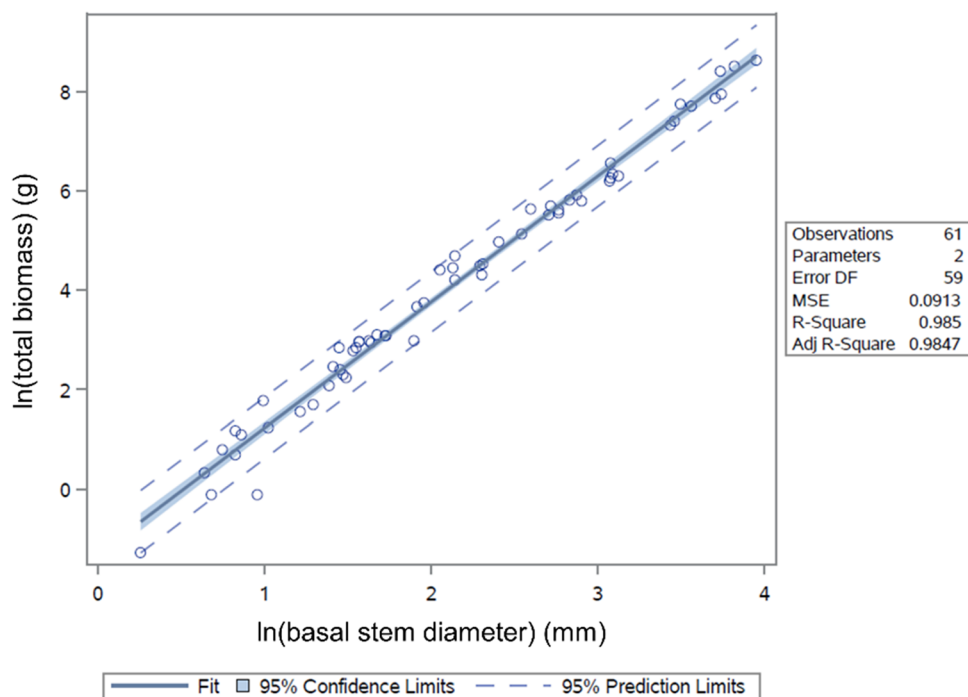
Combined effects of fire and drought are not sufficient to slow shrub encroachment in tallgrass prairie.

Cornus drummondii Allometric Equations

Allometric equations were developed to estimate *C. drummondii* aboveground biomass based on stem counts and measurement of basal stem diameters. This method is non-destructive and prevents the removal of perennial aboveground shrub biomass, allowing for the measurement of year-to-year changes in shrub biomass. A previous study by Lett et al. (2004) developed similar equations for *C. drummondii* in northeastern Kansas and found strong relationships between stem basal area and both leaf and woody biomass. These additional equations were developed (by M. Bartmess) to span a wider range of stem diameters than those included in Lett et al. 2004, making them appropriate to use in larger, well-established *C. drummondii* shrub islands (Figs. 7, 8, 9).

To develop these allometric equations, *C. drummondii* stems were collected in July of 2019 (the estimated time of peak foliar biomass for *C. drummondii*). A total of 62 stems with a range of 1–55 mm basal diameter were harvested near ground-level using bypass pruners and

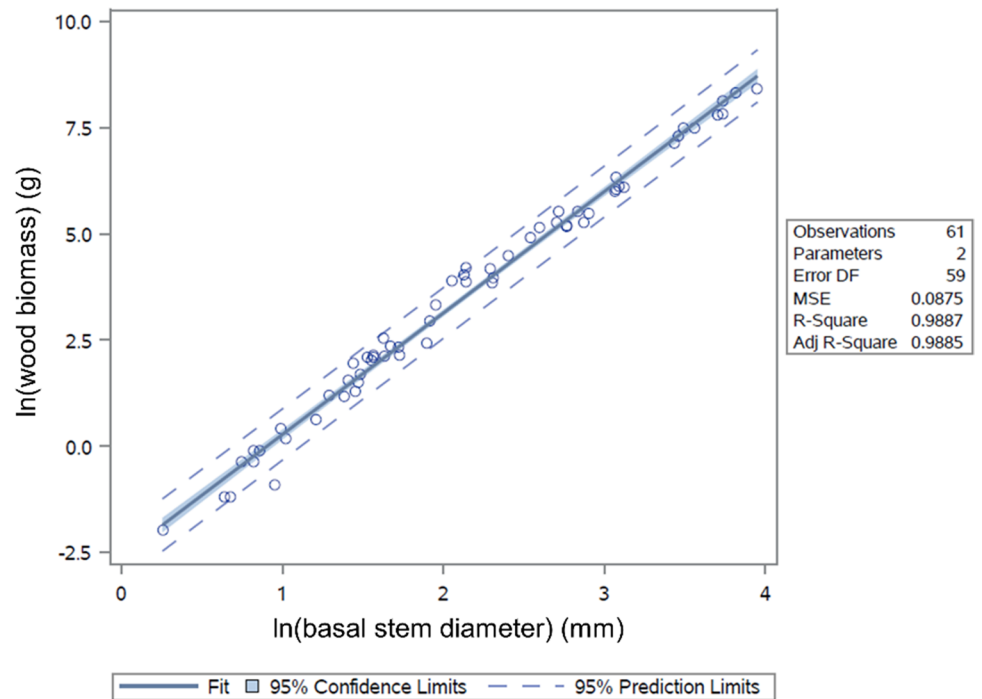
Fig. 7 Allometric regression for the natural log of *C. drummondii* total biomass (leaves + stems) and the natural log of *C. drummondii* basal stem diameter



$$\ln(\text{total mass}, g) = 2.53099 \ln(\text{basal diameter}, mm) - 1.29768$$

$$\text{Adjusted } R^2 = 0.9847$$

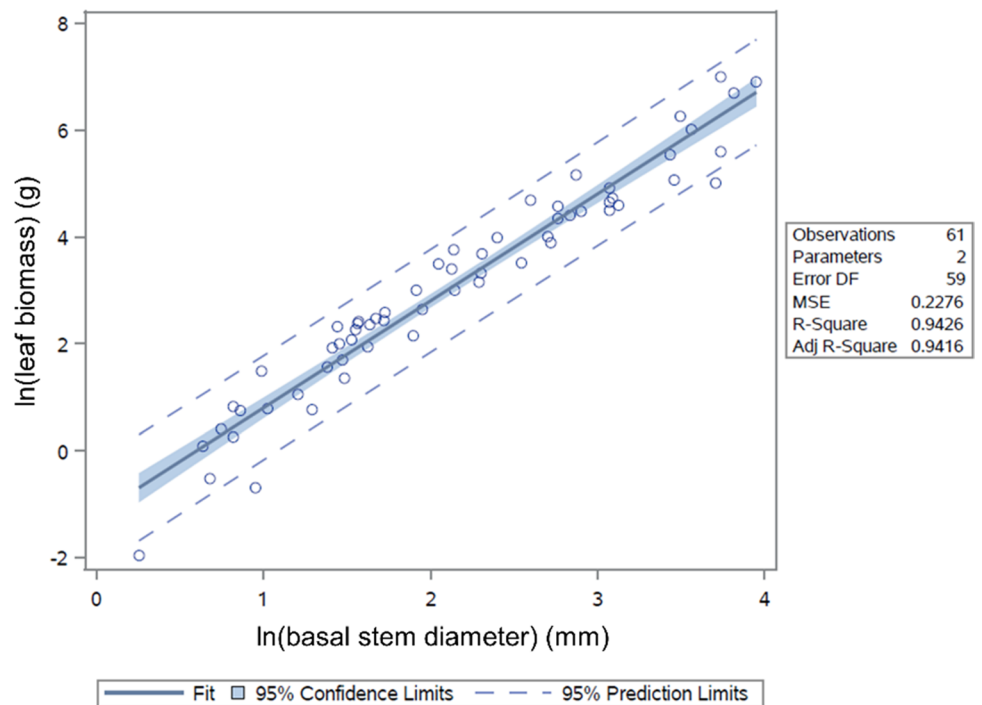
Fig. 8 Allometric regression for the natural log of *C. drummondii* woody biomass (stems) and the natural log of *C. drummondii* basal stem diameter



$$\ln(\text{wood mass}, g) = 2.85849 \ln(\text{basal diameter}, mm) - 2.58203$$

$$\text{Adjusted } R^2 = 0.9885$$

Fig. 9 Allometric regression for the natural log of *C. drummondii* leaf biomass and the natural log of *C. drummondii* basal stem diameter



$$\ln(\text{leaf biomass}, g) = 2.00047 \ln(\text{basal diameter}, mm) - 1.00047$$

$$\text{Adjusted } R^2 = 0.9416$$

a pruning saw. All individual stems were then labelled, basal diameter was measured at each cut end, and leaves were removed. Leaves and stems were dried at 60 °C for roughly five days, or until the mass of each sample stabilized between measurements. The mass of each stem and associated leaf biomass was weighed after drying was complete. Least-squares regressions were performed for total biomass (leaves + stems), leaves only, and stems only. In all models, $\ln(\text{mass})$ (where ‘mass’ is the mass of stems, leaves, or stems + leaves) was included as the response variable and $\ln(\text{basal stem diameter})$ was included as the independent variable. The natural log transformation was selected based on the curve shape of the linear plotted data. Developed equations for total biomass (leaves + stems; Fig. 1), leaves only (Fig. 2), and stems only (Fig. 3) can be found below.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00442-024-05526-x>.

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Author contribution statement JBN established the experimental design at ShRaMPs. Data collection was led by RMK, with assistance from JBN and SB. MB developed the allometric equations necessary to estimate shrub biomass. Data analysis and writing were led by RMK, with substantial input from JBN, SB, and MB. All authors critically examined and edited the manuscript and gave final approval before publication.

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Data availability Data will be made available through the Konza Prairie Biological Station (KPBS) Long-Term Ecological Research (LTER) website (<http://lter.konza.ksu.edu/data>) (Keen and Nippert 2024).

Code availability Not applicable.

Declarations

Conflict of interest The author declare that they have no conflict of interest.

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

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