Oecologia (2021) 196:1039–1048
https://doi.org/10.1007/s00442-021-04980-1

POPULATION ECOLOGY – ORIGINAL RESEARCH

Fire and browsing interact to alter intra-clonal stem dynamics of an encroaching shrub in tallgrass prairie

Emily R. Wedel[1] · **Jesse B. Nippert**[1] · **David C. Hartnett**[1]

Received: 12 May 2020 / Accepted: 28 June 2021 / Published online: 6 July 2021

Abstract

The expansion of woody species into grasslands has altered community structure and ecosystem function of grasslands worldwide. In tallgrass prairie of the Central Great Plains, USA, decreased fire frequency and intensity have increased the cover and abundance of woody species. In particular, clonal shrub cover has increased at accelerated rates due to vegetative reproduction and resprouting after disturbance. We measured the intra-clonal stem demography and relative growth rates (estimated change in woody biomass) of the shrub *Cornus drummondii* in response to fire frequency (4 vs 20 year burn intervals) and simulated browsing during the 2018 and 2019 growing seasons at Konza Prairie Biological Station (Manhattan, Kansas). Overall, infrequent fire (4 year burn interval) increased intra-clonal stem relative growth rates and shrub relative growth rates. Intra-clonal stem relative growth rates were reduced in unbrowsed clones in 2018 due to drought and simulated browsing reduced intra-clonal stem relative growth rates in 2019. Additionally, simulated browsing nearly eliminated flower production within clones but did not affect intra-clonal stem mortality or recruitment within a growing season. Fire in conjunction with simulated browsing reduced estimated relative growth rates for entire shrub clones. Browsed shrubs that experienced prescribed fire in 2017 had reduced intra-clonal stem densities compared to unbrowsed shrubs and stem densities of browsed shrubs did not recover in 2018 or 2019. These results illustrate that infrequent fire alone promotes the expansion of clonal shrubs in tallgrass prairie and multiple interacting disturbances (e.g., fire and browsing) are required to control the spread of clonal shrubs into grasslands.

Keywords Clonal shrub · *Cornus drummondii* · Growth · Stem demography · Woody encroachment

Introduction

The increased cover and abundance of woody species in grasslands, referred to as woody encroachment, has altered ecosystem structure and function in grasslands worldwide (Roques et al. 2001; Briggs et al. 2005; Van Auken 2009; Stevens et al. 2017). Woody encroachment has resulted in decreased floristic diversity and graminoid productivity (Briggs et al. 2002a; Lett and Knapp 2005; Ratajczak et al. 2012), increased above-ground biomass (Hughes et al. 2006; Knapp et al. 2008), altered nutrient dynamics (Hughes et al. 2006; Knapp et al. 2008; Barger et al. 2011; Ward et al. 2018), and decreased forage for livestock (Anadón et al. 2014). These alterations typically manifest as nonlinear state transitions in response to shifts in a number of drivers at the global, regional, and local level. These drivers may include increased atmospheric CO_2 and N deposition (global), altered precipitation patterns (regional), and changes in land-use management (local) such as fire suppression and increased grazing intensity (Van Auken 2009; D'Odorico et al. 2012; Ratajczak et al. 2014; Devine et al. 2017).

In mesic grasslands and savannas, which receive enough precipitation to support woody species, woody cover is limited by frequent disturbances including fire and browsing (Higgins et al. 2000; Sankaran et al. 2005). Frequent fire and browsing create demographic bottlenecks preventing the establishment of trees and shrubs and their transition into larger browsing- and fire-resistant size classes. This maintenance of shoots in vulnerable small size classes is commonly referred to as the fire and browse trap (Higgins et al. 2000; Sankaran et al. 2005; Briggs et al. 2005; Staver

Communicated by Brian J. Wilsey.

✉ Emily R. Wedel
erwedel@ksu.edu

[1] Division of Biology, Kansas State University, 116 Ackert Hall, Manhattan, KS 66506, USA

et al. 2009; Midgley et al. 2010; Ratajczak et al. 2011). The sapling stage is the most vulnerable, and once woody plants have outgrown the bottlenecks (reached a threshold minimum height and diameter that can survive surface fires), they are more resistant and resilient to the effects of fire and browsing.

The effects of fire and browsing are most impactful when experienced in combination, resulting in a longer period of time spent in the fire and browse trap (Midgley and Bond 2001; Staver et al. 2009; LaMalfa et al. 2018). Fire and browsing may reduce seed production as recovering stems experience trade-off among growth, defense, and reproductive fitness (Goheen et al. 2007; Fornara and Du Toit 2007; Young and Augustine 2007). Browsing can alter plant growth by causing increased branching and reduced vertical growth in trees and shrubs (Augustine and McNaughton 2004; Midgley et al. 2010; Staver and Bond 2014) and induce compensatory growth by increasing investment in shoot growth to compensate for lost tissue (McNaughton 1983; du Toit et al. 1990).

In the tallgrass prairie of the Central Great Plains of the USA, fire frequency and intensity are the primary determinants of the amount of woody cover in the system (Bragg and Hulbert 1976; Briggs et al. 2002b). It is well understood that changes in land use have reduced fire frequency and intensity, aiding in woody encroachment. Fire frequencies of every 1–3 years are required to maintain a grassland state, while suppression of fire for just 4 years in tallgrass prairie allows establishment and growth of clonal shrubs which can quickly grow to a size resistant to fire (Ratajczak et al. 2014). Additionally, browsing pressure on woody shrubs has been greatly reduced in the Central Great Plains since European settlement (mid-1800s) due to the decline in the diversity and abundance of large browsers, such as elk and pronghorn (Conard et al. 2006; Flores 2016). Historically, large populations of browsers may have interacted with fire to aid in the suppression of woody plants across the landscape. The effects of browsing on encroaching shrubs in tallgrass prairie are unclear and largely understudied compared to other disturbances.

For many regions of this ecosystem, the primary encroaching shrub species is *Cornus drummondii* C.A. Mey (rough-leaf dogwood), a clonal shrub native to tallgrass prairie but historically at low abundance. Clonal shrubs spread vegetatively via rhizomes and resprout after disturbance from below-ground basal and rhizomatous buds. These clonal traits make shrubs highly successful in disturbance prone systems like the tallgrass prairie, which experiences frequent fire, drought, and herbivory. Following colonization of a clonal shrub by a seed, expansion of *C. drummondii* and other clonal shrubs in tallgrass prairie is primarily due to lateral rhizomatous spread (Ratajczak et al. 2014). Clonal, resprouting shrubs are more resilient to fire and browsing than non-resprouting shrubs and are typically more likely to survive after disturbance via regrowth after top kill due to established root systems, below-ground perennating storage organs, and bud banks (Clarke et al. 2013; Dietze et al. 2014). Post-burn resprouting shrubs tend to regenerate rapidly from basal and below-ground buds resulting in increased stem densities and growth rates compared to shrubs that are infrequently burned (Heisler et al. 2004, 2007; Lett et al. 2004).

In this study, we assessed the effects of fire and browsing on intra-clonal stem demography and growth of discrete *C. drummondii* shrub clones in tallgrass prairie. Studying intra-clonal stem dynamics is uncommon and can provide detailed insight into the growth strategies clonal shrubs use to recover from disturbance such as fire and browsing and the effectiveness of these disturbances on suppressing woody growth. To understand the interactive effects of fire and browsing on intra-clonal stem dynamics, we used an existing simulated browsing experiment in tallgrass prairie (O'Connor et al. 2020) and tracked the mortality, recruitment, and flower production of stems within distinct shrub clones. To assess the effects of fire frequency, we compared shrub clones within a landscape burned at a 4 year interval to clones within a 20 year burn interval. Additionally, we quantified intra-clonal stem relative growth rates (RGR; estimated woody biomass) and estimated RGR of entire shrub clones. We hypothesized shrubs clones within the 4 year burn interval would have increased intra-clonal stem densities and stem RGR and decreased flower production, as clones invest in stem production and growth to recover after disturbance (Heisler et al. 2004; Lett et al. 2004). We also hypothesized that simulated browsing would reduce intra-clonal stem RGR and flower production and increase intra-clonal stem mortality, because the frequent removal of above-ground tissue would deplete below-ground growth reserves from repeated investment in above-ground growth (O'Conner et al. 2020). Finally, we hypothesized that the effects of browsing would be largest in conjunction with fire, with larger differences in RGR and intra-clonal stem mortality and recruitment between simulated browsed and unbrowsed shrubs in the 4 year burn interval than in the 20 year burn interval.

Materials and methods

Study site

Data were collected at Konza Prairie Biological Station (KPBS; 39°05′ N, 96°35′ W) located 15 km south of Kansas State University in Manhattan, Kansas, USA. The Konza Prairie is a 3487-hectare native tallgrass prairie characterized by uplands with shallow limestone soils and lowlands with deep silty-clay loams separated by rocky hillslopes. The elevation varies from 320 to 444 m above sea level. The site is divided into watershed units, each assigned to a specific fire frequency (1, 2, 4, or 20 year intervals) and grazing treatment (bison, cattle, or no large mammalian grazers). Mean annual precipitation (1982–2019) is 842 mm, with approximately 73% of annual precipitation falling during the growing season (April–September). Sampling was done during an extremely dry year (2018) and wet year (2019). In 2018, only 55% (283 mm) of growing season precipitation fell before or during the sampling period. In contrast, growing season precipitation in 2019 was approximately 49% higher (915 mm) than the long-term average (614 ± 26 mm from 1982 to 2019; all data reported as mean ± SEM). Temperature means (1982–2019) range from a low of − 1.2 °C in January to a high of 26.1 °C in July. C_4 warm-season grasses (*Andropogon gerardii* Vitman*, Panicum virgatum* L.*, Sorghastrum nutans* L. Nash*,* and *Schyzachyrium scoparium* Michx.) dominate the plant cover and annual productivity in portions of the site that are frequently burned (1–2 year burn intervals). Areas subject to infrequent burns (prescribed fire every 4 or more years) are encroached primarily by the clonal woody shrubs *C. drummondii* and *Rhus glabra* L. In areas of KPBS with 20 year burn frequencies, *Juniperus virginiana* var. virginiana L. (an evergreen tree) is abundant.

Study design

We conducted this research in the summers of 2018 and 2019 on two ungrazed experimental watersheds at KPBS which included 4 year (last burned in 2017) and 20 year (last burned in 2012) burn frequencies. Prescribed burning occurs during the spring (March–April; Knapp and Seastedt 1998). We used the widespread clonal shrub *C. drummondii* to assess the effects of fire and simulated browsing on intra-clonal stem growth, reproduction, density, and demography. *C. drummondii* reproduces vegetatively via rhizomes and produces new stems from basal or below-ground buds, resulting in the formation of discrete multi-stemmed shrubs ("genets" or "clones") made up of genetically identical stems. *C. drummondii* often resprouts from several basal buds located at the base of ramets that were killed by disturbance such as fire. *C. drummondii* shrub clones usually produce flowers in June and set fruit in July (Great Plains Flora Association 1986).

Simulated browsing experiment

Stems within shrub clones in the 4 year and 20 year burn intervals were subjected to simulated browsing to understand the impacts of fire, browsing, and their interaction on intra-clonal stem demography and RGR. These shrubs were a part of a simulated browsing experiment established in 2015 (described in O'Connor et al. 2020). In 2015, 40 isolated shrub clones were randomly selected in the lowlands of the 4 year and 20 year burn interval watersheds ($n = 20$ shrubs in each burn treatment; Table 1). While true replication of treatments was not possible in this watershed-level study, the watersheds contain similar silty-clay soils, had similar land-use history prior to initiation of the different fire return interval treatments, and have received consistent fire treatments for nearly 40 years. Half of the shrubs were randomly selected for a simulated browsing treatment ($n = 10$ browsed shrubs and 10 unbrowsed shrubs in each watersheds). Browsing was simulated by stripping 50% of current year shoot growth by hand from each stem within a given shrub clone each month throughout the growing season (May–September). The 'browsed' tissues were removed from the site. Simulated browsing occurred every growing season from 2015 to 2019.

Sampling

We established a 0.25 m-wide transect that spanned through the longest axis of each shrub clone. In May 2018, we tagged each stem, including all stems originating from basal buds at the soil surface and from rhizomatous buds, within each transect using an insulated copper wire ring around the shoot base. We recorded the number of living stems. Stems were counted again in September and the number of dead (with tag) and new stems (no tag) was recorded. Many of the small stems were easily identifiable as basal resprouts and we could be confident we did not include seedlings in intra-clonal stem counts. Stem densities were calculated as the number of live stems within the transect of each shrub clone at the end of the growing season divided by the area (m^2) of the transect. Flower production was estimated as the number of flowering stems within each transect during peak flowering in June. We estimated flowering effort by counting the number of inflorescence clusters on five stems on the periphery and five stems in the center of each shrub clone. Measurements were repeated in May and September of 2019.

Table 1 Burn interval, years since last burn, if shrub clones were subject to simulated browsing (*N* No, *Y* Yes), and the number of shrub clones for each treatment

Burn interval (years)	Years since last burn		Simulated browsing	*n*
	2018	2019		
20	6	7	N	10
20	6	7	Y	10
4	1	2	N	10
4	1	2	Y	10

We used five center and five peripheral stems to measure stem height (to the nearest 1 mm) and basal diameter (to the nearest 0.5 mm) in June (May in 2019) and August. Height was measured to the last leaf-bearing node on the tallest shoot axis. Height and diameter of stems within shrub clones were used to estimate woody stem biomass using published allometric equations (Heilser et al. 2004). Intra-clonal stem RGR (g g^{-1} wk^{-1}) was calculated as

$$\frac{\ln\left(\text{biomass}_2\right) - \ln\left(\text{biomass}_1\right)}{t_2 - t_1},$$

where biomass_1 and biomass_2 are estimated stem dry weight (g) at timepoints t_1 and t_2 (# of weeks). When diameter or height were larger at the beginning than end of the growing season, final measurements were set to equal initial measurements and calculated as zero growth. Negative RGR were assumed to be zero growth, such as simulated browsed stems with reduced height at the end of the season due to no growth after removal of browsed tissues. We used allometric relationships for woody biomass and excluded herbaceous tissues as any shifts in allometry due to simulated browsing would likely impact herbaceous tissue more than woody tissue.

The area of each shrub clone was calculated using an ellipse area equation by measuring the maximum horizontal length and perpendicular width of each clone at the end of each growing season. Clones ranged from approximately 14 to 162 m^2. To estimate the total number of stems per clone, we multiplied clone area by the end of season intra-clonal stem density of each shrub clone. We then estimated the RGR of a shrub clone by multiplying the number of stems per clone by the average intra-clonal stem RGR of each clone. Additionally, we compared leaf size among treatments. We measured leaf area (cm^2) of four randomly selected leaves from each shrub clone using LEAFSCAN smartphone application (leafscanapp.com).

Statistical analysis

All analyses were conducted using the statistical software R V3.6.0 (R Core Team 2019). Stem RGR and leaf area were averaged for each shrub clone before analysis. We used repeated-measures ANOVA to test for differences in end of season intra-clonal stem densities, intra-clonal stem RGR, and estimated clone RGR among treatments using the lme4 (Bates et al. 2015) and car package (Fox and Weisberg 2019). Estimated clone RGR were log transformed to meet the assumptions of normality and homogeneity of variance. The effects of fire, simulated browsing, and year on the number of stems producing flowers within each clone as well as intra-clonal stem recruitment and mortality were tested using generalized linear mixed effects models with a logit link using the lme4 package (Bates et al. 2015). Fixed effects for all models included simulated browsing treatment, burn interval, sampling year, and their interaction. Shrub ID was included as a random effect to account for repeated measures. For mixed models, we report X^2 values with associated P values to assess the effects of the fixed factors. We used pairwise comparisons where necessary to determine the difference between treatments using the emmeans package (Lenth 2019) with Tukey's HSD adjustment.

Results

Intra-clonal stem densities

More frequent fire increased intra-clonal stem densities in unbrowsed shrub clones. On average, unbrowsed clones in the 4 year burn interval had greater stem densities than clones in the 20 year burn interval (Table 2). While fire alone increased intra-clonal stem densities, fire in conjunction with simulated browsing significantly reduced stem densities (Table 2; Fire and simulated browsing interaction: $X^2 = 5.87$, df = 1, $P = 0.015$). This difference in intra-clonal stem densities between simulated browsed and unbrowsed clones in the 4 year burn interval was only significant in 2018 ($P = 0.004$). Unbrowsed clones in the 4 year burn interval had significantly higher mortality in 2019 (12.83 ± 0.93% of stems) than in 2018 (4.73 ± 0.89% of stems; $P < 0.001$) and reduced differences in stem densities between the simulated browsed and unbrowsed clones (Table 2; $P = 0.25$).

Stem relative growth rates

The effects of fire and simulated browsing on intra-clonal stem RGR varied by year (Table S2; three-way interaction: $X^2 = 4.99$, df = 1, $P = 0.025$). Intra-clonal stem RGR did not differ among fire or simulated browsing treatments during the 2018 drought but simulated browsing significantly reduced intra-clonal stem RGR in 2019 (Fig. 1; $P < 0.001$). In 2019, unbrowsed stems in the 4 year burn interval had significantly higher RGR than all other treatments ($P < 0.001$).

Flower production

Simulated browsing nearly eliminated flower production (only 1 stem of 1 shrub clone flowered in 2018 and 2019; Fig. 2). For this reason, we removed the browsed treatment from analysis for differences in flower production among treatments. Flower production showed a significant interaction between fire and year (Table S3; $X^2 = 158.74$, df = 1, $P < 0.001$). Fire reduced flower production as clones in the 20 year burn interval had significantly higher proportion of flowering stems than clones in the 4 year burn interval

Table 2 Mean clone area (m^2), initial and final intra-clonal stem densities (m^{-2}), estimated number of stems within a clone, and estimated relative clone growth rates ($g\ g^{-1}\ wk^{-1}$) for *Cornus drummondii* shrubs in fire and simulated browsing treatments

Year	Burn interval (years)	Simulated browsing	Clone area (m^2)	Initial stem density (m^{-2})	Final stem density (m^{-2})	# of stems	Clone relative growth rates ($g\ g^{-1}\ wk^{-1}$)
2018	20	N	49.2 ± 6.5	15.1 ± 2.0^{a}	17.3 ± 2.4^{a}	839.3 ± 154.4	7.3 ± 1.5^{a}
	20	Y	43.0 ± 8.6	18.1 ± 2.2^{a}	19.0 ± 3.0^{a}	750.9 ± 132.1	8.1 ± 1.8^{a}
	4	N	102.4 ± 11.7	36.7 ± 2.5^{b}	37.7 ± 2.6^{b}	3791.0 ± 475.5	50.5 ± 6.8^{b}
	4	Y	42.4 ± 11.8	22.3 ± 3.7^{a}	23.1 ± 3.7^{a}	901.0 ± 195.3	10.4 ± 2.8^{a}
2019	20	N	55.1 ± 6.4	17.2 ± 2.8^{a}	17.9 ± 2.6^{a}	987.0 ± 167.4	28.3 ± 7.3^{b}
	20	Y	46.4 ± 8.5	18.8 ± 2.6^{a}	20.0 ± 2.8^{a}	866.3 ± 144.7	6.1 ± 1.4^{a}
	4	N	105.2 ± 11.8	34.0 ± 1.3^{b}	31.4 ± 1.3^{b}	3381.3 ± 210.5	148.7 ± 21.4^{c}
	4	Y	45.8 ± 12.5	23.7 ± 3.5^{a}	23.9 ± 3.3^{ab}	1027.2 ± 210.5	10.2 ± 2.3^{a}

All values are means ± 1 SE. Different letters indicate significant differences among treatments within years ($P < 0.05$) based on pairwise comparisons with Tukey's HSD adjustment

(Fig. 2; $P < 0.001$). Clones the 4 year burn interval had more flowering stems in 2019 (2 years since fire) than 2018 (1 year since fire; $P < 0.001$). Fire also reduced the number of inflorescences per stem within clones (Table S4). In 2018 and 2019, clones in the 20 year burn interval had 31.33 ± 5.07 and 30.68 ± 5.02 inflorescences per stem, respectively. Shrubs in the 4 year burn interval had 0.83 ± 0.50 inflorescences per stem in 2018 and this increased to 4.95 ± 1.29 in 2019 (Table S4).

Stem mortality and recruitment

Fire and simulated browsing had minimal effects on intra-clonal stem mortality and recruitment within a growing season (Fig. 2). Intra-clonal stem mortality showed a significant interaction between simulated browsing and year (Table S3; $X^2 = 9.73$, df = 1, $P = 0.002$). Intra-clonal stem mortality did not differ among treatments in 2018 or 2019 (Fig. 2; $P > 0.05$), but unbrowsed clones in the 4 year burn interval had higher mortality in 2019 (12.8 ± 0.01% of stems) than 2018 (4.73 ± 0.01% of stems; $P < 0.001$).

Intra-clonal stem recruitment showed a significant interaction between fire and simulated browsing (Table S3; $X^2 = 4.18$, df = 1; $P = 0.041$). Unbrowsed clones within the 4 year burn interval had significantly lower intra-clonal stem recruitment than unbrowsed clones in the 20 year burn interval in 2018 and 2019 (Fig. 2; $P = 0.001$ and $P = 0.005$, respectively). There were no differences in intra-clonal stem recruitment between years for any treatment (Table S3; main effect of year: $X^2 = 0.08$, df = 1, $P = 0.77$).

Clone relative growth rates

Differences in relative growth rates ($g\ g^{-1}\ wk^{-}1$) for entire shrub clones varied by year (Table S5; interaction between simulated browsing and year: $X^2 = 19.77$, df = 1, $P < 0.001$). Overall, fire increased clone RGR in unbrowsed shrub clones, while simulated browsing tended to reduce clone RGR (Table 2). Unbrowsed clones in the 4 year burn interval had higher growth rates than all other treatments in both years ($P < 0.001$). In 2018, there was no difference in clone RGR between simulated browsed and unbrowsed clones in the 20 year burn interval ($P > 0.99$), but in 2019, unbrowsed clones had significantly higher clone RGR than simulated browsed clones (Table 2; $P = 0.002$).

Leaf area

Simulated browsing reduced average leaf size (cm^2) of shrub clones (Table S6; $P < 0.001$). On average, browsed shrubs had 86.91% smaller leaves than unbrowsed shrubs in 2018

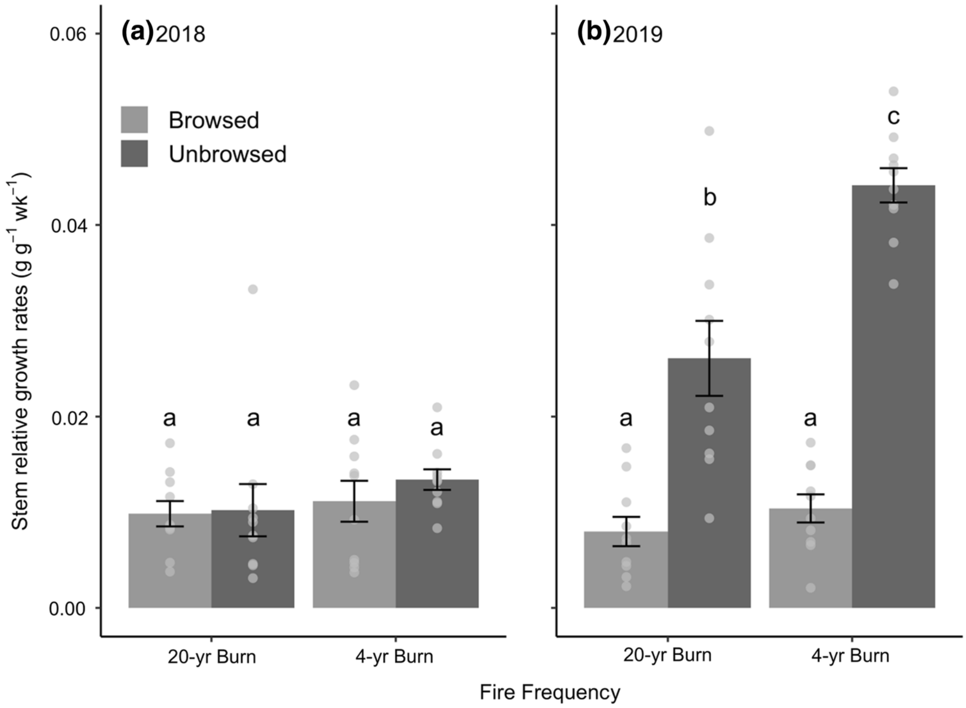

Fig. 1 Barplot of *Cornus drummondii* stem relative growth rates (g g^{-1} wk^{-1}, means ± 1SE) for fire and simulated browsing treatments in **a** 2018 and **b** 2019. Units can be interpreted as biomass per unit existing biomass per week. Grey points represent the data points. Different letters indicate significant differences within and among years ($P < 0.05$) based on pairwise comparisons with Tukey's HSD adjustment

and 51.05% smaller leaves in 2019 (Fig. 3). Fire frequency did not affect leaf size.

Discussion

The data shown here illustrate that intra-clonal stem dynamics of *C. drummondii* vary in response to multiple top–down drivers, with the greatest reduction in shrub growth rates when fire and simulated browsing interact. Simulated browsing in conjunction with fire reduced the RGR of both intra-clonal stems and entire shrub clones, while infrequent fire alone (4 year burn interval) had the opposite effect, resulting in increased woody growth. Overall, unbrowsed shrubs in the 4 year burn interval had greater intra-clonal stem densities, stem RGR, and clone RGR than the other fire and simulated browsing treatments. Increased stem densities in response to 4 year burn frequencies agree with the previous research that showed fire stimulates growth of rhizomatous and basal buds after top kill (Heisler et al. 2004; Lett et al. 2004). Stem densities at the beginning and end of the season tended to be similar (Table 2) due to low stem mortality and the complete replacement of any stems that died during the growing season (Fig. 2). This is similar to intra-clonal dynamics of another major encroaching species in tallgrass prairie, *Rhus glabra*. Hajny et al. (2011) found stable stem densities of *R. glabra* due to complete replacement of stems after fire. Additionally, population growth in *R. glabra* was higher in burned than unburned sites (Hajny et al. 2011). In this study, unbrowsed clones in the 4 year burn interval had the greatest RGR of both intra-clonal stems (2019) and entire shrub clones (2018 and 2019). These results illustrate that woody growth rates are greater in infrequently burned areas (4 year burn interval) even in years without fire.

Fire in conjunction with simulated browsing interacted to alter intra-clonal stem densities and RGR. Stem densities of browsed shrub clones were significantly reduced after the fire in 2017 due to reduced vegetative resprouting (O'Connor et al. 2020). Here, we show even 1–2 years after fire, stem densities of browsed clones have not recovered. Additionally, simulated browsing reduced intra-clonal stem RGR in the 4 year and 20 year burn intervals in 2019, suggesting that shrub clones did not show compensatory stem growth after 4 and 5 years of simulated browsing. Compensatory growth is a common plant response to herbivory (McNaughton 1983). For example, simulated winter browsing tended to increase shoot growth during the following growing season in *Acacia* species, attributed to release from intraspecific competition for light (du Toit et al. 1990; Gadd et al. 2001; Rooke et al. 2004). Clonal shrubs that experience simulated browsing may invest in production of new stems and basal resprouts to compensate for lost tissue rather than increase growth of existing stems. Shrub clones that experienced simulated browsing had to repeatedly invest in growth and resprouting to recover lost tissues. This growth strategy reduces below-ground nonstructural carbohydrates (NSC) stores (O'Connor et al. 2020). Depleted NSC stores potentially reduce the clones' ability to recover from fire or invest in growth the following growing season. In 2018, there was no difference in intra-clonal stem RGR between fire or simulated browsing treatments and stem RGR were low in all treatments likely due to the summer drought.

Fire alone decreased flower production as unbrowsed clones in the 4 year burn interval had lower flower production than clones in the 20 year burn interval. Clonal and resprouting plants in frequently disturbed areas tend to have lower sexual reproduction due to allocation of resources to below-ground storage, maintenance of bud banks, lateral vegetative growth, and resprouting to recover from disturbance (Hoffman 1998; Bond and Midgley 2001; Lamont and Weins 2003; Herben et al. 2015). In addition, *C. drummondii* flowers relatively early in the growing season (May and June), which reduces root NSC stores (Janicke and Fick 1998) and suggests the amount of carbon gained the previous year may influence flower production the next year (Keeley 1977). Decreased flower production of unbrowsed shrubs in the 20 year burn interval in 2019 may be explained by reduced carbon gain during the 2018 drought. In contrast, unbrowsed shrubs in the 4 year burn interval likely

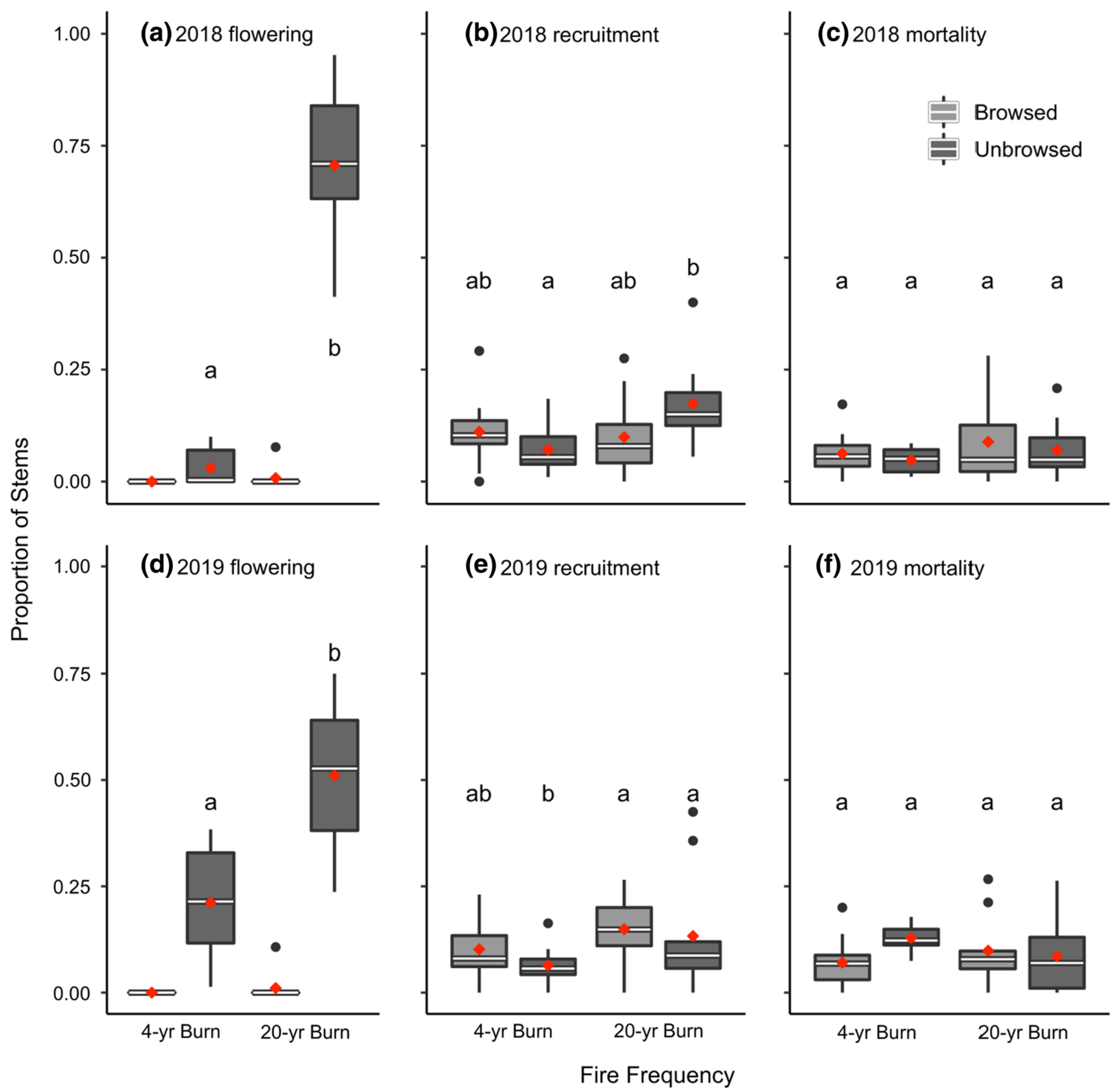

Fig. 2 Boxplot of the proportion of *Cornus drummondii* stems within the transects that produced flowers (flowering), are new (recruitment), or died (mortality) for fire and simulated browsing treatments in **a–c** 2018 and **d–f** 2019. Proportions were calculated as: (1) flowering = # of flowering stems within transect/# of live stems at the beginning of the season; (2) mortality = # of dead stems at the end of the season/# of live stems at the beginning of the season; (3) recruitment = # of new stems at the end of the season/the total # of stems at the end of the season. Red diamonds represent the means for each treatment. Different letters indicate significant differences within years ($P < 0.05$) based on pairwise comparisons with Tukey's HSD adjustment. Simulated browsed shrub clones were removed from flower production analysis and do not have letters to indicate significant differences

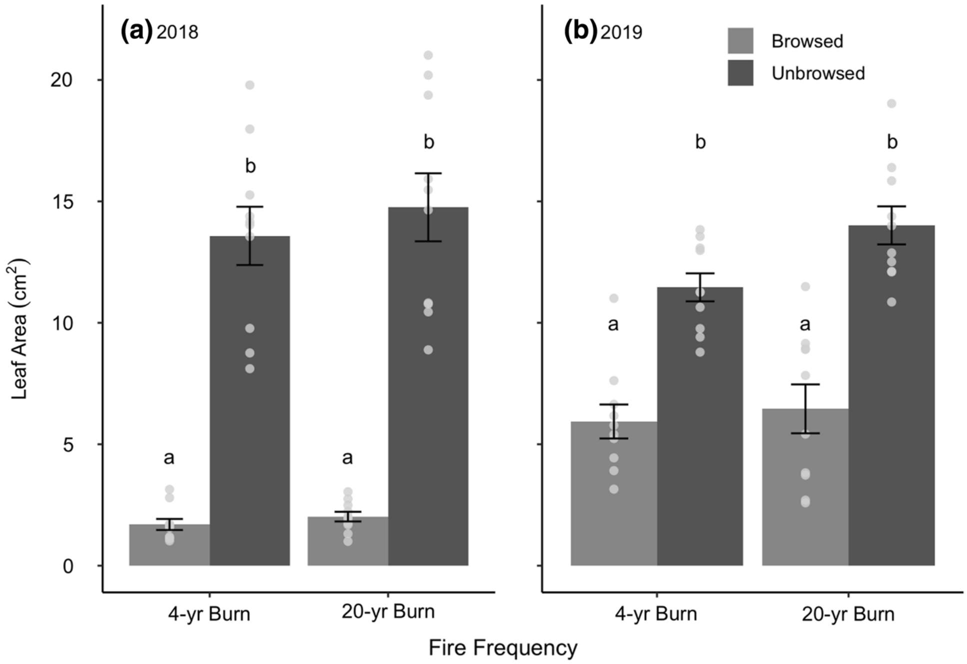

Fig. 3 Barplot of *Cornus drummondii* leaf area (cm^2, means ± 1SE) for fire and simulated browsing treatments in **a** 2018 and **b** 2019. Grey points represent the data points. Different letters indicate significant differences within and among years ($P < 0.05$) based on pairwise comparisons with Tukey's HSD adjustment

recovered to pre-fire sizes in 2019, resulting in increased a flower production. Thus, precipitation and time since fire may have interactive effects on flower and seed production. However, it is important to note that little is known about seed production and seedling establishment and survival of *C. drummondii* in tallgrass prairie and further work at the meta-population level is needed to fully understand tradeoffs between vegetative and sexual reproduction in response to disturbance.

Contrary to our hypothesis, simulated browsing did not result in increased intra-clonal stem mortality. This was surprising as these clones faced an extremely dry year in 2018 and repeated simulated browsing throughout the growing season. Stems that died within shrubs throughout the growing season were replaced by new recruits. The low stem mortality and ability of these shrubs to recruit new stems during the 2018 drought in combination with the simulated browsing treatment emphasize the persistence of clonal shrubs and the significance of below-ground NSC and bud banks for stabilizing clonal plant population dynamics (Ott et al. 2019). Stem turnover was primarily due to mortality and recruitment of small basal resprouting stems rather than turnover of larger, established stems (personal observation). The difference in intra-clonal stem densities between unbrowsed and simulated browsed shrubs experiencing a 4 year burn interval, despite no difference in single-year stem mortality or recruitment indicates that fire and browsing have longer-term cumulative effects on stem population dynamics that were not detected within one or two growing seasons. Additionally, there was a similar increase in shrub clone size from 2018 to 2019 without a shift in stem densities suggesting lateral expansion during the 2019 growing season.

Browsed shrubs tended to be shorter and smaller than unbrowsed shrubs in both the 4 year burn and 20 year burn watersheds (data not shown) and browsed clones had decreased shrub cover and increased grass cover (O'Connor et al. 2020). Leaves on browsed shrubs were on average ~ 86% smaller than unbrowsed shrubs in 2018 and ~ 50% smaller in 2019. Browsed shrubs may reduce leaf size to invest in more leaves and fill out the canopy faster than investing in fewer large leaves (Hartnett et al. 2012). Other studies of simulated browsing have shown increased leaf area (Rooke et al. 2004). However, these studies either implemented browsing during the winter or browsed less frequently than our study. Additionally, we hypothesize that reduced leaf size may reduce the damage from future browsing by reducing the amount of tissue lost per bite (Rhodes et al. 2017).

Conclusions

We assessed the intra-clonal stem demography and RGR for the most important encroaching woody species in the Kansas tallgrass prairie region, *C. drummondii*, in response to simulated browsing and fire. The study shows the persistence of established clonal shrubs despite multiple disturbances in tallgrass prairie and emphasizes that infrequent fire alone (4 year burn interval) promotes, not controls, the growth of shrub clones. In addition, concentrated and repeated browsing during the growing season in conjunction with fire may be an effective management technique to suppress shrub growth and reduce clone size. Simulated browsing during the growing season was an effective control for shrub flower and seed production. An investment in shrub removal strategies (brush cutting, herding browsers, herbicides) is likely to prevent or minimize contributions to the seed bank. Drought may reduce growth rates, but does not appear to affect shrub survival in the short term. Future research should focus on the mechanisms of establishment and impact of disturbance on the growth and persistence of juvenile shrubs.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00442-021-04980-1.

Acknowledgements The authors thank Jeff Taylor for leading the simulated browsing of dogwood shrubs each month and the undergraduate students who helped with browsing and field work. We also thank Rory O'Connor, Caitlin Broderick, Marissa Zaricor, Sammi Grieger, and Mark Sandwick for their help with data collection and analysis. Funding was provided by the Konza Prairie Long Term Ecological Research program (NSF DEB-1440484).

Author contribution statement ERW, JBN, and DCH conceived and designed the experiment. ERW conducted fieldwork and analyzed the data. ERW, JBN, and DCH wrote the manuscript.

Funding Funding was provided by the Konza Prairie Long Term Ecological Research program (NSF DEB-1440484).

Data availability The data were deposited in the Environmental Data Initiative Portal https://portal.edirepository.org/nis/home.jsp.

Declarations

Conflict of interest We have no conflicts of interest to disclose.

Ethical approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

References

Anadón JD, Sala OE, Turner BL, Bennett EM (2014) Effect of woody-plant encroachment on livestock production in North and South America. Proc Natl Acad Sci 111:12948–12953. https://doi.org/10.1073/pnas.1320585111

Augustine DJ, McNaughton SJ (2004) Regulation of shrub dynamics by native browsing ungulates on East African rangeland. J Appl Ecol 41:45–58. https://doi.org/10.1111/j.1365-2664.2004.00864.x

Barger NN, Archer SR, Campbell JL, Huang C, Morton JA, Knapp AK (2011) Woody plant proliferation in North American drylands: a synthesis of impacts on ecosystem carbon balance. J Geophys Res. https://doi.org/10.1029/2010JG001506

Bates D, Maechler B, Bolker B, Walker S (2015) Fitting linear mixed effects models using lme4. J Stat Softw 67:1–48. https://doi.org/10.18637/jss.v067.i01

Bond WJ, Midgley JJ (2001) Ecology of sprouting in woody plants: the persistence niche. Trends Ecol Evol 16:45–51. https://doi.org/10.1016/S0169-5347(00)02033-4

Bragg TB, Hulbert LC (1976) Woody plant invasion of unburned kansas bluestem prairie. J Range Manag 29:19–24. https://doi.org/10.2307/3897682

Briggs JM, Hoch GA, Johnson LC (2002a) Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. Ecosystems 5:578–586. https://doi.org/10.1007/s10021-002-0187-4

Briggs JM, Knapp AK, Brock BL (2002b) Expansion of woody plants in tallgrass prairie: a fifteen-year study of fire and fire-grazing interactions. Am Midl Nat 147:287–294. https://doi.org/10.1674/0003-0031(2002)147[0287:EOWPIT]2.0.CO;2

Briggs JM, Knapp AK, Blair JM et al (2005) An ecosystem in transition: causes and consequences of the conversion of mesic grassland to shrubland. Bioscience 55:243. https://doi.org/10.1641/0006-3568(2005)055[0243:AEITCA]2.0.CO;2

Clarke PJ, Lawes MJ, Midgley JJ et al (2013) Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. New Phytol 197:19–35. https://doi.org/10.1111/nph.12001

Conard JM, Gipson PS, Peek M (2006) Historical and current status of elk in Kansas. Springer JT, Springer EC (eds) In: Proceedings of the 20th North American prairie conference in Kearny, Nebraska. University of Nebraska at Kearney, Kearney, pp 307–312

D'Odorico P, Okin GS, Bestelmeyer BT (2012) A synthetic review of feedbacks and drivers of shrub encroachment in arid grasslands. Ecohydrology 5:520–530. https://doi.org/10.1002/eco.259

Devine AP, McDonald RA, Quaife T, Maclean IMD (2017) Determinants of woody encroachment and cover in African savannas. Oecologia 183:939–951. https://doi.org/10.1007/s00442-017-3807-6

Dietze MC, Sala A, Carbone MS et al (2014) Nonstructural carbon in woody plants. Annu Rev Plant Biol 65:667–687. https://doi.org/10.1146/annurev-arplant-050213-040054

du Toit JT, Bryant JP, Frisby K (1990) Regrowth and palatability of *Acacia* shoots following pruning by African savanna browsers. Ecology 71:149–154. https://doi.org/10.2307/1940255

Flores DL (2016) American Serengeti: the last big animals of the Great Plains. University Press of Kansas, Lawrence

Fornara DA, Toit JTD (2007) Browsing lawns? Responses of *Acacia nigrescens* to ungulate browsing in an African aavanna. Ecology 88:200–209. https://doi.org/10.1890/0012-9658(2007)88[200:BLROAN]2.0.CO;2

Fox J, Weisberg S (2019) An R companion to applied regression, 3rd edn. Sage, Thousand Oaks

Gadd ME, Young TP, Palmer TM (2001) Effects of simulated shoot and leaf herbivory on vegetative growth and plant defense in *Acacia drepanolobium*. Oikos 92:515–521. https://doi.org/10.1034/j.1600-0706.2001.920312.x

Goheen JR, Young TP, Keesing F, Palmer TM (2007) Consequences of herbivory by native ungulates for the reproduction of a savanna tree. J Ecol 95:129–138. https://doi.org/10.1111/j.1365-2745.2006.01196.x

Hajny KM, Hartnett DC, Wilson GWT (2011) *Rhus glabra* response to season and intensity of fire in tallgrass prairie. Int J Wildland Fire 20:709–720. https://doi.org/10.1071/WF09127

Hartnett DC, Ott JP, Sebes K, Ditlhogo MK (2012) Coping with herbivory at the juvenile stage: responses to defoliation and stem browsing in the African savanna tree *Colophospermum mopane*. J Trop Ecol 28:161–169. https://doi.org/10.1017/S0266467412000028

Heisler JL, Briggs JM, Knapp AK et al (2004) Direct and indirect effects of fire on shrub density and aboveground productivity in a mesic grassland. Ecology 85:2245–2257. https://doi.org/10.1890/03-0574

Heisler JL, Knapp AK, Briggs JM (2007) Fire and resource availability influence carbon and water relations of the C3 shrub roughleaf dogwood in a mesic grassland. Masters RE, Galley KEM (eds) Proceedings of the 23rd tall timbers fire ecology conference: fire in grassland and shrubland ecosystems, Tallahassee, pp 86–93

Herben T, Šerá B, Klimešová J (2015) Clonal growth and sexual reproduction: tradeoffs and environmental constraints. Oikos 124:469–476. https://doi.org/10.1111/oik.01692

Higgins SI, Bond WJ, Trollope WSW (2000) Fire, resprouting and variability: a recipe for grass–tree coexistence in savanna. J Ecol 88:213–229. https://doi.org/10.1046/j.1365-2745.2000.00435.x

Hoffmann WA (1998) Post-burn reproduction of woody plants in a neotropical savanna: the relative importance of sexual and vegetative reproduction. J Appl Ecol 35:422–433. https://doi.org/10.1046/j.1365-2664.1998.00321.x

Hughes RF, Archer SR, Asner GP et al (2006) Changes in aboveground primary production and carbon and nitrogen pools accompanying woody plant encroachment in a temperate savanna. Glob Change Biol 12:1733–1747. https://doi.org/10.1111/j.1365-2486.2006.01210.x

Janicke GL, Fick WH (1998) Prescribed burning effects on total nonstructural carbohydrates of roughleaf dogwood. Trans Kans Acad Sci 101:39. https://doi.org/10.2307/3628175

Keeley JE (1977) Seed production, seed populations in soil, and seedling production after fire for two congeneric pairs of sprouting and nonsprouting chaparal shrubs. Ecology 58:820–829. https://doi.org/10.2307/1936217

Knapp AK, Seastedt TR (1998) Introduction: grasslands, konza prairie, and long-term ecological research. In: Knapp AK, Briggs JM, Hartnett DC, Collins SL (eds) Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, New York

Knapp AK, Briggs JM, Collins SL et al (2008) Shrub encroachment in North American grasslands: shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. Glob Change Biol 14:615–623. https://doi.org/10.1111/j.1365-2486.2007.01512.x

LaMalfa EM, Kimuyu DM, Sensenig RL, Young TP, Riginos C, Veblen KE (2018) Tree resprout dynamics following fire depend on herbivory by wild ungulate herbivores. J Ecol. https://doi.org/10.1111/1365-2745.13186

Lamont BB, Wiens D (2003) Are seed set and speciation rates always low among species that resprout after fire, and why? Evol Ecol 17:277–292. https://doi.org/10.1023/A:1025535223021

Lenth R (2019) Emmeans: estimated marginal means, aka least-squares means. R Package Version 1(3):4

Lett MS, Knapp AK (2005) Woody plant encroachment and removal in mesic grassland: production and composition responses of herbaceous vegetation. Am Midl Nat 153:217–231. https://doi.org/10.1674/0003-0031(2005)153[0217:WPEARI]2.0.CO;2

Lett MS, Knapp AK, Briggs JM, Blair JM (2004) Influence of shrub encroachment on aboveground net primary productivity and carbon and nitrogen pools in a mesic grassland. Can J Bot 82:1363–1370. https://doi.org/10.1139/b04-088

McNaughton SJ (1983) Compensatory plant growth as a response to herbivory. Oikos 40:329–336. https://doi.org/10.2307/3544305

Midgley JJ, Bond WJ (2001) A synthesis of the demography of African *Acacias*. J Trop Ecol 17:871–886. https://doi.org/10.1017/S026646740100164X

Midgley JJ, Lawes MJ, Chamaillé-Jammes S (2010) Savanna woody plant dynamics: the role of fire and herbivory, separately and synergistically. Aust J Bot 58:1–11. https://doi.org/10.1071/BT09034

O'Connor RC, Taylor JH, Nippert JB (2020) Browsing and fire decreases dominance of a resprouting shrub in woody encroached grassland. Ecology. https://doi.org/10.1002/ecy.2935

Ott JP, Klimešová J, Hartnett DC (2019) The ecology and significance of below-ground bud banks in plants. Ann Bot 123:1099–1118. https://doi.org/10.1093/aob/mcz051

R Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria

Ratajczak Z, Nippert JB, Hartman JC, Ocheltree TW (2011) Positive feedbacks amplify rates of woody encroachment in mesic tallgrass prairie. Ecosphere. https://doi.org/10.1890/ES11-00212.1

Ratajczak Z, Nippert JB, Collins SL (2012) Woody encroachment decreases diversity across North American grasslands and savannas. Ecology 93:697–703. https://doi.org/10.1890/11-1199.1

Ratajczak Z, Nippert JB, Ocheltree TW (2014) Abrupt transition of mesic grassland to shrubland: evidence for thresholds, alternative attractors, and regime shifts. Ecology 95:2633–2645. https://doi.org/10.1890/13-1369

Rhodes AC, Anderson V, St Clair SB (2017) Ungulate herbivory alters leaf functional traits and recruitment of regenerating aspen. Tree Physiol 37:402–413. https://doi.org/10.1093/treephys/tpx015

Rooke T, Bergström R, Skarpe C, Danell K (2004) Morphological responses of woody species to simulated twig-browsing in Botswana. J Trop Ecol 20:281–289. https://doi.org/10.1017/S0266467403001226

Roques KG, O'Connor TG, Watkinson AR (2001) Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. J Appl Ecol 38:268–280. https://doi.org/10.1046/j.1365-2664.2001.00567.x

Sankaran M, Hanan NP, Scholes RJ et al (2005) Determinants of woody cover in African savannas. Nature 438:846–849. https://doi.org/10.1038/nature04070

Staver AC, Bond WJ (2014) Is there a 'browse trap'? Dynamics of herbivore impacts on trees and grasses in an African savanna. J Ecol 102:595–602. https://doi.org/10.1111/1365-2745.12230

Staver AC, Bond WJ, Stock WD et al (2009) Browsing and fire interact to suppress tree density in an African savanna. Ecol Appl 19:1909–1919. https://doi.org/10.1890/08-1907.1

Stevens N, Lehmann CER, Murphy BP, Durigan G (2017) Savanna woody encroachment is widespread across three continents. Glob Change Biol 23:235–244. https://doi.org/10.1111/gcb.13409

Van Auken OW (2009) Causes and consequences of woody plant encroachment into western North American grasslands. J Environ Manage 90:2931–2942. https://doi.org/10.1016/j.jenvman.2009.04.023

Ward D, Trinogga J, Wiegand K et al (2018) Large shrubs increase soil nutrients in a semi-arid savanna. Geoderma 310:153–162. https://doi.org/10.1016/j.geoderma.2017.09.023

Young TP, Augustine DJ (2007) Interspecific variation in the reproductive response of *Acacia* species to protection from large mammalian herbivores. Biotropica 39:559–561. https://doi.org/10.1111/j.1744-7429.2007.00281.x