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Browsing and fire decreases dominance of a resprouting shrub in woody encroached grassland

Running Head: Browsing and fire reduce shrub dominance

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Accepted Article

Abstract

North American grasslands have experienced increased relative abundance of shrubs and trees over the last 150 years. Alterations in herbivore composition, abundance and grazing pressure along with changes in fire frequency are drivers that can regulate the transition from grassland to shrubland or woodland (a process known as woody encroachment). Historically, North American grasslands had a suite of large herbivores that grazed and/or browsed (i.e. bison, elk, pronghorn, deer), as well as frequent and intense fires. In the tallgrass prairie, many large native ungulates were extirpated by the 1860's corresponding with increased homesteading (which led to decreased fire frequencies and intensities). Changes in the frequency and intensity of these two drivers (browsing and fire) has coincided with woody encroachment in tallgrass prairie. Within tallgrass prairie, woody encroachment can be categorized in to two groups: non-resprouting species that can be killed with fire, and resprouting species that cannot be killed with fire. Resprouting species require additional active management strategies to decrease abundance and eventually be removed from the ecosystem. In this study we investigated plant cover, ramet density and physiological effects of continuous simulated browsing and prescribed fire on *Cornus drummondii* C.A. Mey, a resprouting clonal native shrub species. Browsing reduced *C. drummondii* canopy cover and increased grass cover. We also observed decreased ramet density that allowed for more infilling of grasses. Photosynthetic rates between browsed and unbrowsed control shrubs did not increase in 2015 or 2016. In 2017, photosynthetic rates for browsed shrubs were higher in the unburned site than the unbrowsed control shrubs at the end of the growing season. Additionally, after the prescribed fire, browsed shrubs had ~90% decreased cover, ~50% reduced ramet density, and grass cover increased by ~80%. In the roots of browsed shrubs after the prescribed fire, non-structural carbohydrates (NSC) experienced a 2-fold reduction in glucose and a 3-fold reduction in both sucrose and starch. The combined effects of browsing and fire show strong potential as a successful management tool to decrease the abundance of clonal-resprouting woody plants in mesic grasslands and illustrate the potential significance of browsers as a key driver in this ecosystem.

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Keywords: browsing; *Cornus drummondii*; fire; Konza Prairie; mesic grasslands; nonstructural carbohydrates; resprouting/clonal; shrub encroachment; tallgrass prairie

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Introduction

Woody encroachment, the expansion of shrubs and trees into grasslands, is a global phenomenon occurring in many grasslands, savannas and steppes (Knapp et al. 2008, Saintilan and Rogers 2015, Archer et al. 2017, Stevens et al. 2017). Causes of woody encroachment are often broken down into three hierarchical scales of drivers: 1) global drivers such as elevated [CO_2]; 2) regional climate drivers (e.g. precipitation timing and amount, temporal temperature changes); and 3) local drivers such as land management history, changes in fire frequencies, land fragmentation and removal of native herbivores (Archer et al. 1995, Van Auken 2009, Wigley et al. 2010, Stevens et al. 2017, Venter et al. 2018). Each biome undergoing woody encroachment has a suite of these interacting drivers that influence the rate of woody encroachment. While global and regional drivers are important for forecasting future ecosystem patterns, identifying local drivers is paramount in the development of potential management strategies.

North American grasslands evolved with fire and a suite of herbivores (i.e. grazers, browsers and mixed feeders) that would have been comparable to modern day African grasslands (Sherow 2007, Allen and Palmer 2011, Ripple et al. 2015, Bakker et al. 2016, Flores 2016). After the mass extinction of the Pleistocene megafauna, remnant ungulate species remained in North American grasslands such as the bison (*Bos bison*, grazer), pronghorn (*Antilocapra americana*, browser), elk (*Cervus elaphus*, mixed), mule deer (*Odocoileus hemionus*, browser) and white tail deer (*Odocoileus virginianus*, browser) (Rickel 2005, Flores 2016). However, these species were nearly extirpated throughout their historic grassland ranges by the end of the 19th century through westward expansion of European settlers (Shaw and Lee 1997, Conard et al. 2006, Sherow 2007, Flores 2016). These mammalian herbivores were replaced with cattle, a grazer, which left a void in the browsing and mixed feeder niches. The loss of browsers may be a key facilitator of woody plant colonization and establishment in these grasslands. In African grasslands, it has been shown that woody plants successfully establish without browsers or mixed feeders present (Roques et al. 2001, Holdo et al. 2009, Ward 2015, Goheen et al. 2018). When cattle are present, but browser or mixed-feeder species are not, woody plant establishment may increase because of decreased herbaceous cover and increased light availability (Augustine and McNaughton 2004, Hempson et al. 2017). The top-down

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effect of browsing inhibits woody seedling establishment and decreases growth of already established woody plants.

Similar to herbivory, fire removes plant material and is a major driver of grassland structure and function. Fire is crucial for maintaining and facilitating grass dominated herbaceous communities by removing plant litter, increasing light availability, stimulating grass regeneration via belowground buds, warming soils and eliminating woody plant seedlings (Hulbert 1988, Van Auken 2000, Archibald et al. 2005, Benson and Hartnett 2006, Bond 2008, Archer et al. 2017). However, the cessation of frequent fire allows woody plant species to establish and expand, infilling grasslands and sometimes resulting in a transition to a new ecological state (Allen and Palmer 2011, Ratajczak et al. 2016, Miller et al. 2017). Many woody plants that have encroached in grasslands are capable of resprouting after disturbances, including periodic fires (Bell 2001, Bond and Midgley 2003, Lett and Knapp 2003, Hajny et al. 2011, Robertson and Hmielowski 2014). Resprouting woody plants store carbon belowground in root tissues as starch, and maintain a reserve pool of belowground buds that can then be used for regrowth after a disturbance such as herbivory or fire (Janicke and Fick 1998, Bell 2001, Schutz et al. 2011, Moreira et al. 2012, Pausas et al. 2016). This regrowth often occurs in the same growing season and corresponds with increasing stem or ramet densities (Hajny et al. 2011). Increases in woody plant cover often create positive feedbacks that further decouple the grassland from historic drivers and lead to an alternative stable state (i.e., shrubland, woodland) (Ratajczak et al. 2014a).

In the tallgrass prairie, the role of fire as a key driver of system dynamics has long been recognized (Gleason 1913, Weaver and Aldous 1935, Henderson 1982, Gibson and Hulbert 1987, Briggs et al. 2005, Allen and Palmer 2011). In this ecosystem fire frequencies >3 years (historic mean fire frequency 3.76 years (Allen and Palmer 2011)) are no longer sufficient to mitigate woody establishment because of low intensity fires, and fire is typically ineffective at removing resprouting woody plants once established (Briggs et al. 2005, Ratajczak et al. 2014b, 2017, Twidwell et al. 2016, Miller et al. 2017). If fire alone is ineffective at eliminating resprouting woody plants, then finding another ecological driver that acts in conjunction with fire may be necessary for managing woody plants in mesic temperate grasslands. We proposed to test that browsing in conjunction with fire may be a suitable prescription for the removal of resprouting woody plants from an encroached grassland.

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We specifically wanted to address three questions: 1) Does browsing a resprouting woody plant allow for increases in herbaceous understory beneath the woody plant canopy to create a buildup of fine fuel for prescribed fires? 2) Does browsing decrease carbon storage in the form of non-structural carbohydrates in resprouting woody plant roots by the end of a growing season? 3) Does the combination of browsing and fire decrease or eliminate resprouting woody plants in woody encroached grasslands? To answer these three questions, we experimentally investigated the combined importance of browsing and fire on the plant community in a woody encroached grassland as well as their effects on the demography and physiology of *Cornus drummondii* C.A. Mey. (roughleaf dogwood), a C_3 clonal resprouting shrub. *C. drummondii* and other resprouting woody plants have expanded and continue to expand into the tallgrass prairie despite a reintroduction of fire frequencies similar to presumed historic frequencies (Briggs et al. 2002, Ratajczak et al. 2014a). *C. drummondii* shrubs were selected in two locations at the Konza Prairie Biological Station (KPBS), one landscape with a 4-year fire frequency and the other with a 20-year fire frequency. We imposed a monthly simulated browsing treatment where we randomly removed 50% of new meristematic growth throughout the growing season on half of the selected *C. drummondii* shrubs for 2 years prior to a prescribed fire in the 4-year fire frequency location. The simulated browsing treatment continued for an additional year after the prescribed fire for both locations studied.

Methods

Site description

Research was conducted during the 2015 to 2017 growing seasons at the Konza Prairie Biological Station (KPBS), a 3,487-ha native C_4 dominated grassland in northeastern Kansas, USA (39°05' N, 96°35'W). KPBS is located within the Flint Hills region, one of the largest continuous expanses of unplowed tallgrass prairies left in North America. It remained unplowed due to the shallow rocky soils and steep-sided hills. The climate in the tallgrass prairie at KPBS is characteristic of mid-continental climates with high inter-annual variability in precipitation. Long-term mean annual precipitation for KPBS is 806.9 mm (1982-2017) with 79% occurring during the growing season (April-September). For research and management purposes, KPBS is divided into watershed units

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with varying fire frequencies (1, 2, 4, or 20 years). The majority of prescribed fire treatments occur during the spring (Mar-Apr).

Study design

To assess the effects of browsing and fire on resprouting woody plants we focused on *C. drummondii*, a C_3 resprouting clonal shrub that expands laterally to create shrub islands. The shrub grows through lateral rhizomes before a bud sends up a ramet. These ramets can grow upwards to be 1-2.5 m in height depending on soil profile. Due to the height of the ramets, these shrub islands reduce light to the understory which depresses herbaceous vegetation growth (Ratajczak et al. 2011). Within these shrub islands there can also be multiple woody species present (e.g., *Symphoriocarpus orbiculatus* Moench, *Gleditsia triacanthos* L., and *Prunus americana* Marshall).

In 2015, 40 randomly stratified locations were chosen with half in a 4-yr burn treatment (n = 20) and half in a 20-yr burn treatment (n = 20, last burned in spring of 2012). Hereafter this 20-yr burn treatment is referred to as 'unburned'. Each of the locations had a *C. drummondii* shrub island present that was randomly assigned to a browse treatment (browsed n = 20, unbrowsed control n = 20). The simulated browse treatment consisted of removing 50% of new meristematic growth randomly in the shrub islands through pinching or pulling off the plant tissue. All plant tissue that was removed from the shrub islands was deposited outside of the study area. The browse treatment occurred monthly through the growing season (May – September).

In the spring of 2017 *(13 April 2017)* a prescribed burn was applied to the 4-yr burn treatment. Our study area experienced a full headfire which top-killed all browsed shrub island ramets and top-killed a majority of control shrub islands. The browse treatment resumed after the prescribed fire when new growth occurred, and leaves were fully expanded.

Plant Community Composition

Each August all shrub islands were surveyed for plant community composition and cover at their center mid-point using a 10 m^2 circular plot. The circular plots did not exceed the boundary of the shrub islands. All plants within the circular plot were identified down to species level and cover was estimated using a modified Daubenmire cover scale (Bailey and Poulton 1968). The modified

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Daubenmire cover scale size classes were as follows: 0-1, 1-5, 5-25, 25-50, 50-75, 75-95, and 95-100%.

Ramet Density

At the end of each growing season, ramet density was determined by measuring the area of the *C. drummondii* shrub island and then counting each ramet within the shrub islands. Due to the irregular growth pattern of the clonal shrub islands, we calculated area of the shrub islands by dividing each clone into 1 m wide lanes centered along the island's long axis. We then measured the distance between the distalmost ramets of each lane. This distance was used to calculate the area of each lane. Shrub island area was represented by the sum of all lane areas. We selected a wide range of shrub areas with the smallest being 8.8 m^2 to the largest at 139.7 m^2. After determining the area of the shrub island, we divided the total number of ramets within the shrub islands by their respective areas. This protocol allowed us to measure the density of ramets for each individual shrub island.

Leaf Photosynthesis

We measured net photosynthesis using a LI-6400XT open gas exchange system with a red/blue light source and a CO_2 injector (LI-COR Inc., Lincoln, NE). We set the light source within the leaf chamber to 2000 μmol m^{-2} s^{-1} and the CO_2 reference level to 400 μmol mol^{-1}. Measurements were made throughout the growing season (May-August) from 1000-hr to 1500-hr on new fully expanded leaves. Two measurements were recorded per shrub island, one at the periphery of the shrub island and the second at the center of the shrub island to measure potential variation in photosynthesis within the shrub islands. Net photosynthetic rates did not differ significantly ($P > 0.05$) between the inside and outside of the shrub islands so the photosynthetic rates were treated as subsamples and averaged for each shrub island prior to statistical analysis.

Non-structural Carbohydrate Analysis

Cornus drummondii root samples were collected at the end of the growing season after leaf senescence to analyze for non-structural carbohydrates (NSC). Roots were harvested by locating three ramets at the northern, center, and southern parts of the shrub island. Soil from around the ramets was removed until fine and lateral roots were found. Once root tissues were uncovered 10 cm of root

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tissue was excised from each ramet, no rhizomes were used for analysis, and root tissue was pooled for each shrub island. We combined lateral and fine root tissues from each shrub island and placed the roots in a cooler. All roots were washed in distilled water to remove all soil particles and then microwaved for 90 seconds to halt enzymatic activity (Landhäusser et al. 2018). After microwaving, roots were oven dried at 65 °C for 72 hours. All root samples were milled to 40 mesh (400 μm) prior to ball milling (Wig-L-Bug®) and stored in glass vials in a -20 °C freezer until NSC analysis. NSC analysis was performed to extract glucose, sucrose and starch concentrations from each root sample (for a detailed methods of the NSC protocol see Appendix S1).

Because *C. drummondii* is clonal and exhibits strong responses in shrub island size following fire (Lett et al. 2004), root NSC concentrations were multiplied by their respective ramet densities for analysis and presentation. We assume that with a decrease in ramet density there will be a decrease in root density, which could result in decreased NSC concentrations. Woody plant belowground net primary production in woody encroached grasslands can be close to 50% of soil organic carbon in clay soils (Barger et al. 2011).

Statistical Analysis

All the data met the assumptions of normality for repeated measures linear mixed effects models for all response variables (plant cover, ramet density, glucose, sucrose, and starch). The fixed effects in each model were browsing treatment and year with interaction of browsing treatment by year. Our random effects for these models were shrub island nested within year to account for the variation between the different shrub islands as well as to account for the repeated measures on each shrub island. We used repeated measures mixed effects models for net photosynthetic rates. Our fixed effects were browsing treatment and date sampled with random effects of shrub island nested within year due to the repeated sampling within and between years. A fire effect (4-year or unburned) was not included in the models because of the experimental design at KPBS, where fire is prescribed at the watershed level (landscape-scale) and our experiment was nested within two watersheds. If the interaction term of browsing and date sampled was significant then a Tukey's pairwise post-hoc comparison was performed within each year or date. All analyses were done in Program R v3.4.3 (R Core Team 2012) with the "lme4" package v1.1-17 (Bates et al. 2015) for linear mixed models,

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repeated measure ANOVAs in "car" (Fox and Weisberg 2011) and figures were made with "ggplot2" v2.2.1 (Wickham 2009).

Results

Simulated browsing treatments were effective in reducing *C. drummondii* cover in both fire treatments (4-yr burn and unburned), however differences in the magnitude of the responses between the two fire treatments varied according to the measurement type and scale of inquiry.

Browsing and fire effects on community plant cover

Browsing x year were significant in the 4-yr burn for *C. drummondii* cover (browsing x year $P < 0.001$) and grass cover (browsing x year $P < 0.001$). *C. drummondii* cover in the browsed shrub islands were 20 % lower than the unbrowsed control shrub islands in the first year (2015) (Fig. 1a, $P = 0.008$). Grasses responded to the browse treatment with 43% higher cover in 2015 (Fig. 1c, $P < 0.001$). By the end of 2016, and prior to the next fire treatment, there was no additional reduction in *C. drummondii* cover, which remained 20% lower than the unbrowsed control shrub islands ($P = 0.008$). Grass cover was 67% higher in the browsed shrub islands compared to the unbrowsed control ($P < 0.001$). In the spring of 2017, the prescribed fire resulted in 100% top-kill of the browsed shrub islands and 75% top-kill of the unbrowsed control shrub islands prior to budburst. By the end of the 2017 growing season, we saw a ~90% reduction in *C. drummondii* cover in browsed shrub islands ($P < 0.001$) and grass cover was 77% higher in relation to the unbrowsed control shrub islands ($P < 0.001$).The unburned treatment experienced no statistically significant changes in shrub cover ($P = 0.096$) or grass cover ($P = 0.211$) due to browsing for any of the years sampled (Fig. 1b,d).

Ramet density in response to browsing and fire

Ramet density mimicked patterns of *C. drummondii* cover in the 4-yr burn treatment with statistically significant responses in browsing x year ($P < 0.001$ respectively). In 2015 and 2016, there was no statistically significant reduction of ramets in the browsed shrub islands compared to the unbrowsed control shrub islands (Fig. 2a). However, in 2017 after the prescribed fire, *C. drummondii* ramets increased in unbrowsed control shrub islands up to 16.7±1.4 ramets m^{-2} while in the browsed shrub islands ramets decreased to 7.4±1.0 m^{-2} ($P < 0.001$).

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We did not observe a strong browsing treatment effect on ramet density in the unburned treatment ($P = 0.225$), but we did see a browsing x year interaction (Fig. 2b; $P = 0.042$). The browsed shrub islands had higher ramet densities than the unbrowsed control shrub islands, until 2017 when there was no difference between treatments.

Photosynthetic rate response to browsing and fire

Regardless of fire frequency, net photosynthetic rates remained relatively similar in 2015 and 2016 between treatments and within fire frequencies (Fig. 3). In 2017 after the prescribed fire, browsed shrub islands had lower net photosynthetic rates compared to the unbrowsed control shrubs (Fig. 3; 4-yr burn, $P < 0.001$). Browse x date sampled was not statistically significant. While in the unburned treatment in 2017, net photosynthetic rates in the unbrowsed control shrub islands were lower compared to the browsed shrub islands by the end of the growing season (Fig. 3; Unburned, $P = 0.004$).

Non-Structural Carbohydrate (NSC) responses to browsing and fire

The effects of browsing and year on NSC varied depending on the forms of NSC measured (i.e. glucose, sucrose and starch) and the fire treatment (4-yr burn and unburned) (Fig. 4, Appendix S2: Table S1). In 2016 for the 4-yr burn treatment, we observed no effects of browsing on glucose concentration (16.6 ± 3.5 mg g^{-1}) compared to the unbrowsed control shrub islands (13.8 ± 2.4 mg g^{-1}). In 2017, glucose concentrations increased 2-fold in the unbrowsed control shrub islands and decreased by 30% in the browsed shrub islands relative to concentrations in 2016 (25.4 ± 2.2 mg g^{-1} vs 11.6 ± 1.9 mg g^{-1}; Fig. 4a, $P = 0.002$). In 2016, *C. drummondii* sucrose concentrations in the 4-yr burn treatment were not statistically significant in the browsed shrub islands (6.8 ± 1.3 mg g^{-1}) compared to unbrowsed control shrub islands (9.2 ± 3.3 mg g^{-1}). In 2017, sucrose concentrations were 3-fold higher in unbrowsed control shrub islands relative to browsed shrub islands (8.0 ± 1.6 mg g^{-1} vs 24.5 ± 5.4 mg g^{-1}, Fig. 4c, $P = 0.002$). *C. drummondii* starch concentrations in 2016 in the 4-yr burn treatment were not statistically different between the browsed shrub islands and the unbrowsed control shrub islands (400.0 ± 64.5 mg g^{-1} vs 530.7 ± 53.0 mg g^{-1}), while in 2017 starch concentrations were 3-fold higher in the control shrub islands compared to the browsed shrub islands, relative to concentrations in 2016, resulting in a significant difference between treatments (198.7 ± 45.7 mg g^{-1} vs 648.0 ± 91.9 mg g^{-1}; Fig.

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4e, $P < 0.001$). In the unburned treatment, we observed little to no difference in the amounts of glucose, sucrose and starch between the browsed and unbrowsed control shrub islands (Fig. 4b, 4d, 4f; Appendix S2: Table S1).

Discussion

Here, we provide clear evidence for the interactive role of recent fire and browsing as a strong top-down control on woody vegetation in the tallgrass prairie. As expected, simulated browsing removed enough leaf and new meristematic tissues that the typically closed canopies of *Cornus drummondii* shrub islands were opened allowing more light infiltration for grasses to increase in biomass and cover. The grasses within the shrub islands likely existed as dormant rhizomes before browsing, and changes in grass abundance were likely due to vegetative reproduction and not the germination of new seedlings (Benson and Hartnett 2006). With increased light and nutrient availability, grasses respond positively and quickly via tiller production from dormant buds (Lett and Knapp 2003, 2005, Vanderweide et al. 2014). The continuation of season-long removal of new growth over subsequent years led to decreases in *C. drummondii* ramet density and a buildup of fine fuels from grasses that, in the 4-yr burn treatment, resulted in the prescribed fire causing 100% topkill in the browsed shrub islands (personal observation). The browsed shrub island responses following fire were an even further decrease in ramet density and an 88% reduction in *C. drummondii* cover and an increase of 80% grass cover by the end of the 2017 growing season (Fig 1a, c). However, the response to fire in the unbrowsed control shrub islands in the 4-yr fire treatment was a large increase in ramet density, similar to previous studies (McCarron and Knapp 2001, Heisler et al. 2004). In the unburned treatment, browsed *C. drummondii* shrub islands gradually decreased percent cover each year with a concurrent gradual increase in grass cover (Fig 1b, d). The slower decrease in shrub cover and increase in grass cover in the unburned treatment may result from no change in ramet density among browsed shrub islands during the first 2 years of the study. To explain the dramatic differences between the 4-yr burn and unburned treatments we propose that the species composition of the woody plants present determines the efficacy of browsing (Augustine and McNaughton 2004, Ascoli et al. 2013, Roberts et al. 2014, Anderson et al. 2015). In the burned location, *C. drummondii* was the dominant woody plant on the landscape with *Rhus glabra* L (smooth sumac), another clonal resprouting shrub, mixing within the shrub islands. In the unburned location, there were more woody

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plant species that had infilled within the *C. drummondii* shrub islands (Briggs et al. 2005). Some of these woody species were not dominant at the start of the experiment, or even present, but by the end of our measurement period, significant growth of these sub-dominant species had occurred within the shrub islands. A few of these species were *Symphoriocarpus orbiculatus* Moench (coralberry), *Gleditsia triacanthos* L. (honeylocust) and *Prunus americana* Marshall (American plum), which are all resprouting and/or clonal woody plants. Thus, successful adaptive management of woody plants must focus on functional groups (i.e. clonal woody plants, resprouting woody plants, non-resprouting plants), rather than species-specific removals.

Browsing did not increase leaf-level photosynthetic rates in *C. drummondii* shrub islands throughout the growing seasons of 2015 and 2016 as expected in either the 4-yr burn or unburned treatments. In 2017 after the prescribed fire, leaf-level photosynthesis did not increase in the browsed shrub islands. However, in the unburned, unbrowsed control shrub islands leaf-level photosynthesis was lower, presumably from a pulse-drought that coincided with the July sampling (July precipitation: 2017 = 33 mm, 30-yr avg. = 100 mm; August precipitation: 2017 = 159 mm, 30-yr avg. = 107 mm). Measurements of leaf-level photosynthesis for the 4-year burn were performed in August after precipitation. Our leaf-level photosynthesis results differ from other studies that observed increases in photosynthesis following herbivory from native browsers (elk) in clonal or resprouting woody plants (Johnston et al. 2007, Rhodes et al. 2017). Generally, increases in photosynthesis from herbivory is a mechanism that plants use to compensate for loss of tissue (Pinkard et al. 2011). In 2017, after the prescribed fire, we expected to see continued increases in photosynthesis because of a release of available nitrogen and new ramet growth (Fig. 2) (Longstreth and Nobel 1980, Blair 1997). However, after the prescribed fire, only shrubs in the unbrowsed control treatments exhibited higher photosynthesis compared to previous years (Fig. 3), increasing NSC (glucose, sucrose and starch) for unbrowsed control shrubs in 2017 (Fig. 4). In contrast, browsed shrub island NSC was reduced by 200-300% following the prescribed fire (Fig. 4a), likely impacted by reduced photosynthetic rates (Fig. 4), reduced ramet density (Fig. 2) and reduced total leaf area (expressed as cover in Fig. 1). Independently, the effects of browsing or fire alone were insufficient to reduce ramet densities, photosynthesis or NSC reserves to produce large shrub ramet mortality. However, when browsing and

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fire were combined, the effects on ramet densities and root NSC were large and suggest a potential for long-term shrub mortality in this grassland.

Management Implications

Woody encroachment is one of the greatest conservation threats to grasslands worldwide. The increase in dominance of woody plants, particularly resprouting woody species, may result from changes in many drivers including land use change, urban expansion, decreased fire frequency and severity, and decreased browsing herbivore pressure. Many grasslands experience frequent disturbance and require disturbance for the maintenance of the ecosystem state. However, clonal or resprouting woody plants have developed mechanisms to increase their competitive ability with grasses and ultimately alter disturbance patterns. These strategies of clonal woody shrubs include 1) access to water deep in the soil profile (Nippert et al. 2013, Holdo et al. 2017), 2) stored energy reserves (NSC) in belowground tissues (Bond and Midgley 2003, Bond 2008), 3) stored demographic potential in belowground bud banks (Clarke et al. 2013, Vanderweide et al. 2014), and 4) utilizing rapid vertical growth which results in shading out herbaceous competitors (Bond and Midgley 2003). We have shown that of these four adaptive strategies shared by many clonal woody species, two can be negatively impacted via simulated browsing and prescribed fire. By decreasing the woody plants' abilities to adequately store energy belowground and improving the light environment for understory herbaceous species, simulated browsing decreased the dominance of the clonal woody species measured here, and promoted increased grass cover.

As land managers struggle to maintain both ecosystem function and profitability in the face of woody encroachment, finding effective tools for woody species mitigation is becoming increasingly important (Wilcox et al. 2018). Frequent disturbance of aboveground biomass to open up the canopy and increase light availability can be achieved with mechanical removal or by using browsers (Green and Newell 1982, Hart 2001, Lett and Knapp 2005). The data shown here illustrate that repeated disturbances that partially remove aboveground woody plant tissues negatively affects resprouting shrubs, while increasing grass cover. Our suggestion for land managers dealing with clonal resprouting shrubs in mesic temperate grasslands is the frequent removal of new shrub growth; total removal of aboveground biomass is not necessary. The method for removal of woody plant

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aboveground biomass can be through herd type browsers, mechanical removal, or both to increase light availability for grass growth. Once fine fuels are established, then fire can be reintroduced into the landscape for continued suppression and eventual mortality of the woody plants.

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DATA AVAILABILITY

Data are available on the LTER Network Data Portal at:
https://doi.org/10.6073/pasta/7ec1d77684c30eb707468f72db101bb0

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Figure Captions

Figure 1. Effects of browsing on *Cornus drummondii* cover and grass cover in 4-yr burn and unburned (UB) treatments from 2015 to 2017. In the 4-yr burned treatment a spring prescribed fire occurred in 2017 (red dashed line). Means are given with one SE around the mean as error bars. Significance is indicated by an asterisk ($P < 0.05$).

Figure 2. Effects of browsing on *Cornus drummondii* ramet densities in 4-yr burned and unburned (UB) treatments from 2015 to 2017. In the 4-yr burned treatment a spring prescribed fire occurred in 2017 (red dashed line). Means are given with one SE around the mean as error bars. Significance is indicated by an asterisk ($P < 0.05$).

Figure 3. Effects of browsing on the photosynthetic rates of *Cornus drummondii* in the 4-yr burned and unburned (UB) treatments. Photosynthetic rates were measured during the growing season for 3 years (2015-2017). In the 4-yr burned treatment a spring prescribed fire occurred in the spring of 2017 (red dashed line). Means are given with one SE around the mean as error bars. Significance is indicated by an asterisk ($P < 0.05$).

Figure 4. Effects of browsing on *Cornus drummondii* root glucose, sucrose and starch in 4-yr burned and unburned (UB) treatments in 2016 and 2017. In the 4-yr burned treatment a spring prescribed fire occurred in 2017 (red dashed line). Means are given with one SE around the mean as error bars. Significance is indicated by an asterisk ($P < 0.05$).

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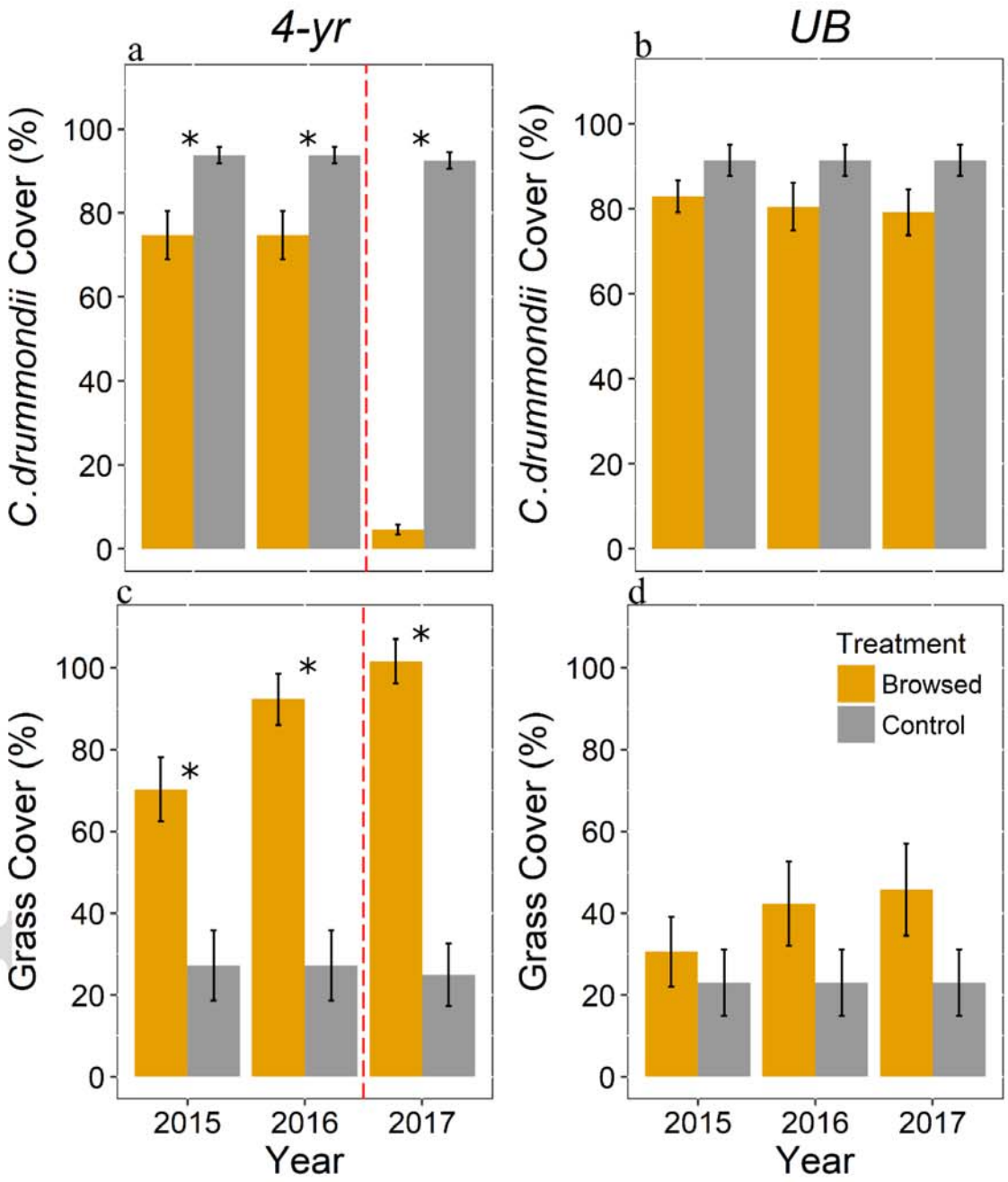

Figure 1.

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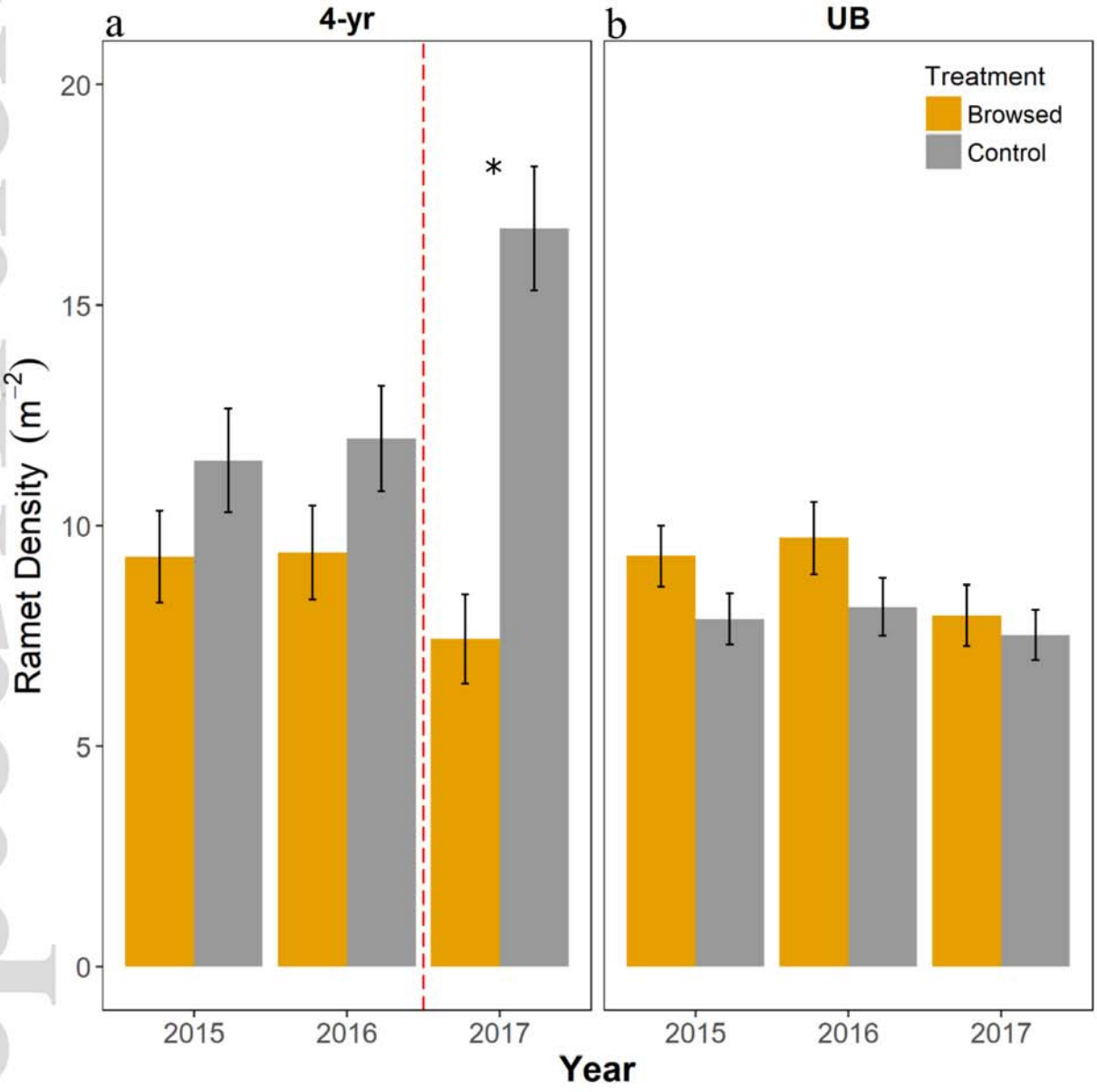

Figure 2

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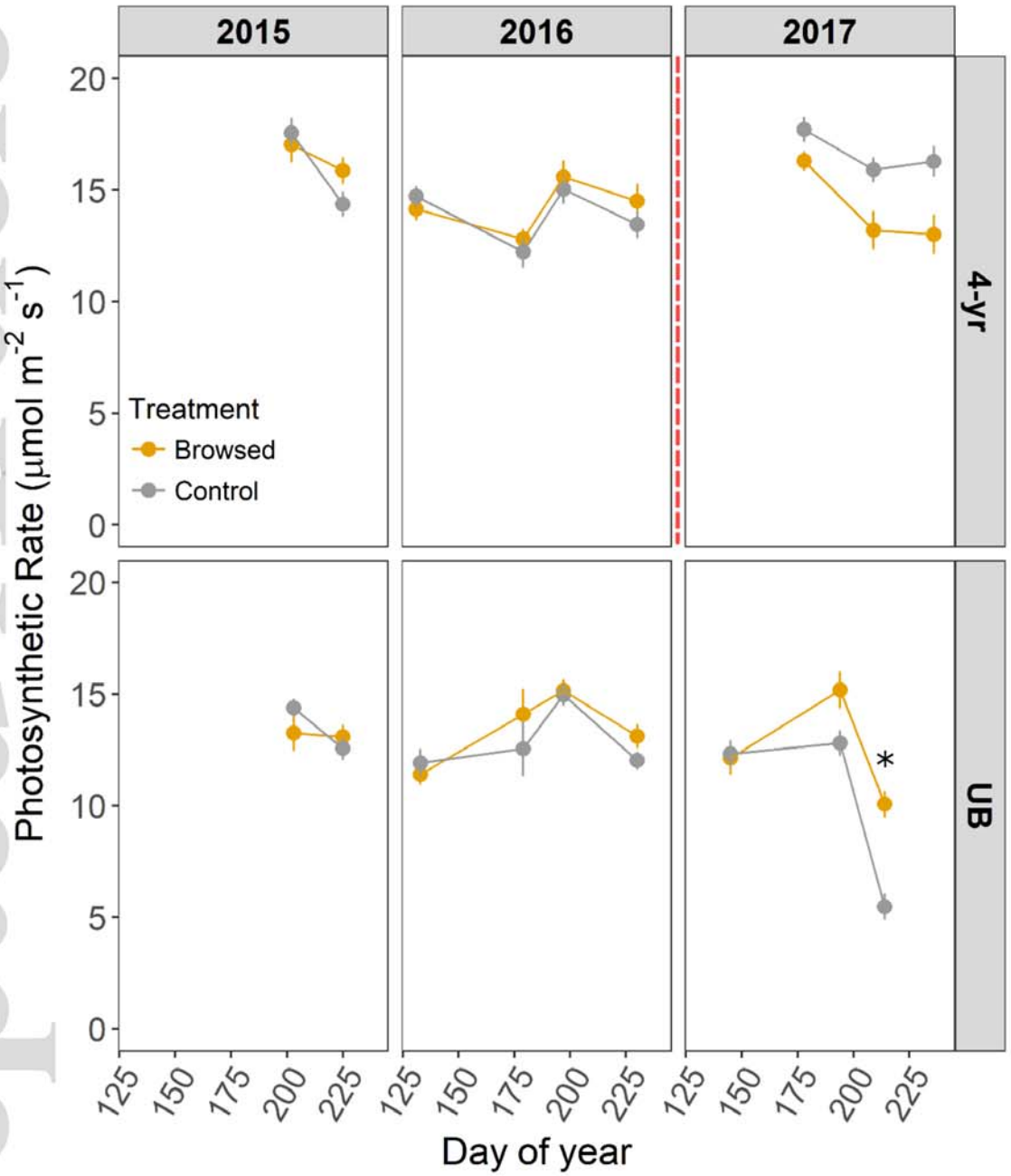

Figure 3

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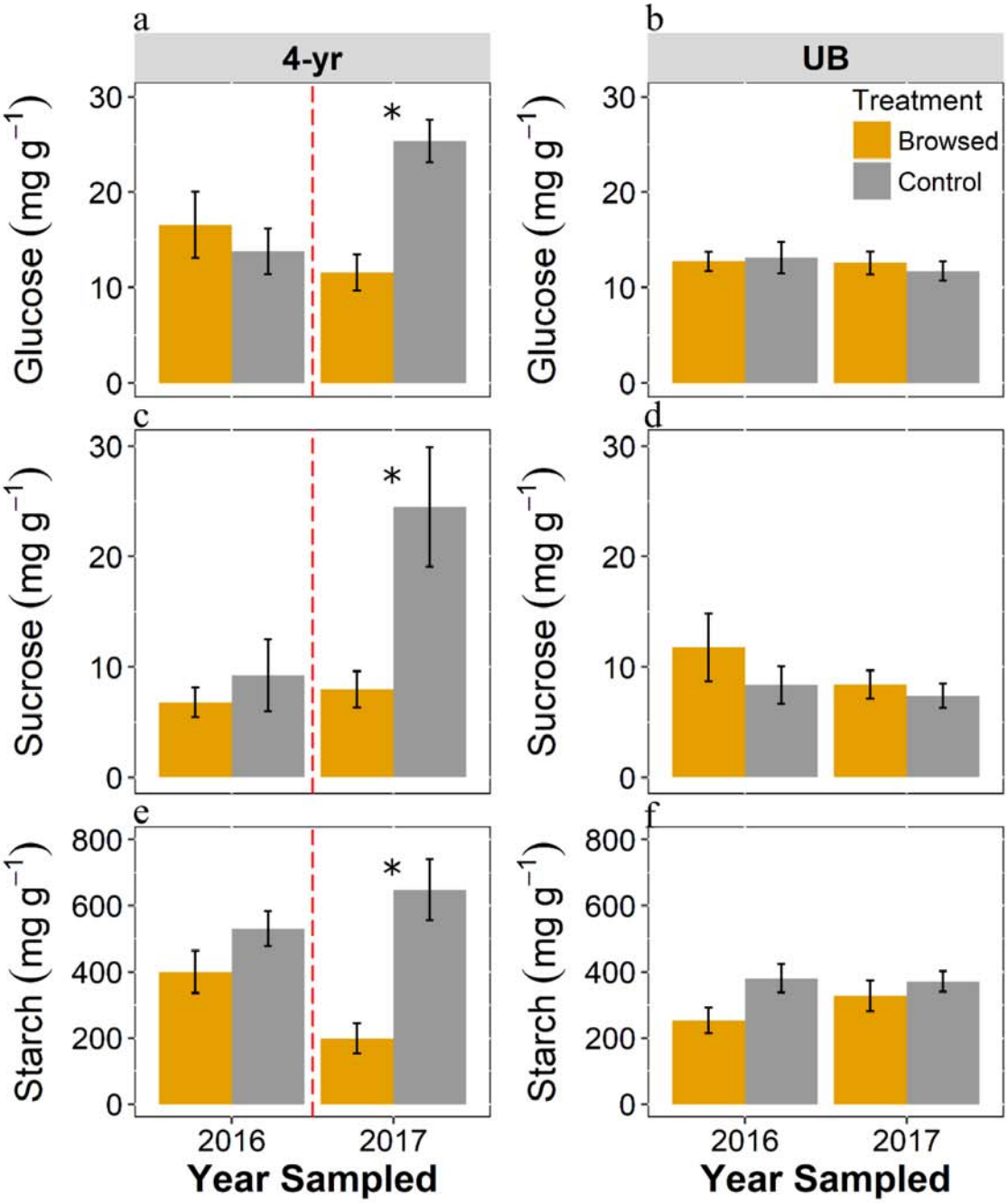

Figure 4

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