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Interactive Effects of Drought and Fire on Co-Existing Woody and Herbaceous Communities in a Temperate Mesic Grassland

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Interactive effects of drought and fire on co-existing woody and herbaceous communities in a temperate mesic grassland

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Abstract

Increased drought and woody encroachment are likely to have substantial and interactive effects on grassland carbon and water cycling in the future. However, we currently lack necessary information to accurately predict grassland responses to drought-by-fire interactions in areas experiencing woody encroachment. A more thorough understanding of these interactive effects on grass-shrub physiology would improve the effectiveness of demographic vegetation models and refine predictions of future changes in grassland ecosystem function. To this end, we constructed passive rainout shelters over mature *Cornus drummondii* shrubs and co-existing grasses in two fire treatments (1-year and 4-year burn frequency) at the Konza Prairie Biological Station (north-eastern Kansas, USA) that reduced precipitation by 50%. Plant responses to drought and fire were monitored at the leaf-level (gas exchange, predawn and midday water potential, turgor loss point) and the whole-plant level (aboveground biomass). Here, we report results from the 2020 growing season, after three years of treatment. Photosynthetic rates of *C. drummondii* and *Andropogon gerardii*, a dominant C_4 grass, were lower in drought treatments at the end of the growing season. *A. gerardii* also exhibited higher photosynthetic rates in the 4-year burn watershed, but *C. drummondii* rates were not impacted by burn frequency. Predawn and midday leaf water potential for both species, as well as turgor loss point for *C. drummondii*, were lower in the 4-year burn treatment, indicating increased water stress. This trend was more pronounced in drought shelters for *C. drummondii*. These results indicate that three years of 50% precipitation reduction has resulted in modest impacts on water stress and gas exchange in both species. Long-term studies of co-existing grasses and shrubs are useful for informing management of woody encroachment during drought and help to identify whether multiple external pressures (drought and fire) are needed to reverse grassland-to-shrubland transitions in temperate mesic grasslands.

Introduction

One of the largest threats to herbaceous ecosystems worldwide are changes in land cover associated with the expansion of woody vegetation into historically grassy areas (bush encroachment or woody encroachment), which has been well documented in mesic temperate grasslands (Briggs et al. 2005). Woody encroachment can result in a grassland-to-woodland transition (Ratajczak et al. 2014), and this shift in dominant vegetation impacts biomass allocation, ecosystem carbon and water cycling, plant productivity, and the amount of quality forage for grazing (Archer et al. 2017). Fire and climate, two of the major drivers of grassland ecosystem dynamics, both play a role in the spread or suppression of woody vegetation in grasslands (Blair et al. 2014). Frequent fire can prevent the proliferation of woody species and infrequent burning leads to a gradual grassland-to-woodland transition (Bond 2008). In many cases, once woody vegetation has become established in the absence of fire, reimplementation of frequent fire is insufficient to reverse the transition and restore grass cover (Staver et al. 2011). Climate variability, particularly the availability of soil moisture, is another major driver in grassland ecosystems (Sala et al. 1988). Variation in precipitation timing and event size impacts the amount of moisture in, and evaporation from, surface soils (Fay et al. 2003), as well as the amount of water that infiltrates to greater depths in the soil profile. Projections of global climate change predict an increase in precipitation variability in mesic grasslands, which will likely result in more frequent and severe periods of drought punctuated by larger, more intense precipitation events (Knapp et al. 2002).

Fire frequency and drought both impact aboveground net primary productivity (ANPP) of grasses and shrubs (Briggs et al. 2005). Physiological drought stress typically decreases ANPP due to stomatal closure, decreased photosynthetic rates, and decreased growth (Scott et al. 2009). Fire history can also impact the amount of aboveground biomass – frequent fire promotes grass growth and can prevent establishment of shrub seedlings, but established woody shrubs often experience low rates of stem mortality during fire (Briggs et al. 2005). In contrast, high woody biomass associated with infrequent burning is typically associated with lower aboveground grass biomass, particularly when mature woody species effectively shade out grasses (Ratajczak et al. 2011). Although C_4 grass species are typically well adapted to drought conditions, they also obtain the vast majority of their water from the top 30 cm of soil, unlike more deeply rooted C_3 shrubs and trees (Nippert and Knapp 2007). Higher evaporation rates in surface soils can result in more rapid moisture depletion during drought conditions compared to deeper portions of the soil profile. The interactive effects of drought and varying fire-frequencies on co-existing woody shrubs and grasses is not well quantified, particularly under multi-year drought conditions.

These two drivers will likely have interactive and currently unpredictable effects on grassland ecosystems experiencing woody encroachment as the climate continues to warm. Without a more detailed understanding of the eco-physiological effects of interactive fire and drought on intact woody-grass communities, grasslands will remain poorly represented in Earth System Models that predict ecosystem responses to climate warming. Due to the immense ecological and economic value of grasslands (White et al. 2000), it is vital to improve our understanding of woody-grass dynamics under different drought and land-use scenarios. In this study, we constructed passive rainout shelters over mature *Cornus drummondii* shrubs and co-existing grasses in two fire treatments (1-year and 4-year burn frequency) at the Konza Prairie Biological Station (KPBS) in a native mesic temperate grassland in north-eastern Kansas, USA. *C. drummondii* is the primary encroaching woody shrub in the tallgrass prairie region of the United States and has contributed to widespread woody encroachment at KPBS in the past several decades (Knapp et al. 2008). We monitored *C. drummondii* and *Andropogon gerardii* (a dominant C_4 grass species at KPBS) responses to drought and fire treatments at the leaf-level (gas exchange rates, water potential, and turgor loss point) and the whole-plant level (ANPP). Our overarching goal in this study is to determine how experimental changes in water availability and fire frequency impact physiological and growth traits in an encroaching woody shrub (*C. drummondii*) and a dominant grass species (*A. gerardii*) in a native mesic grassland.

Methods and Study Site

Sampling was conducted at KPBS in two neighbouring watersheds with different burn frequencies (1-year or 4-year burn frequency). In the summer of 2017, passive rainout shelters (n = 14; 6.3 x 6.3 m each) were constructed over mature *C. drummondii* and the co-existing herbaceous community. Half of the shelters were built in an annually burned watershed and half were built on a watershed with a 4-year burn frequency. Within each fire treatment, drought shelters reduced precipitation by roughly 50% and control shelters allowed ambient precipitation to reach the woody-grass community.

Leaf photosynthetic rates were measured using a Li-COR 6400 gas analyzer (Li-COR Biosciences, Lincoln, NE, USA) every 3-4 weeks throughout the 2020 growing season on two individuals per species (*C. drummondii* and *A. gerardii*) in each shelter. Predawn and midday leaf water potential were measured on the same days as leaf photosynthesis. To determine ANPP, herbaceous biomass was clipped in two 0.1 x 0.1 m frames per shelter at the end of the growing season, then dried and weighed to obtain dry mass of grasses and forbs. To avoid removing standing *C. drummondii* biomass, stem diameters were measured in one quadrant (1.5 x 1.5 m) per shelter and used to calculate aboveground woody biomass using established allometric equations (Bartmess, unpublished). Leaf osmotic potential was measured on *C. drummondii* three times during the growing season using a VAPRO-5600 vapor pressure osmometer according to the methods outlined in Bartlett et al. (2012a) and Griffin-Nolan et al. (2019). Osmotic potential was used to estimate leaf water potential at turgor loss point (π_{TLP}), a trait associated with drought tolerance (Bartlett et al. 2012b), according to established equations for woody species (Bartlett et al. 2012a).

Results

Herbaceous biomass was substantially lower in 4-year burn locations where woody and total biomass were highest. Overall, *C. drummondii* photosynthetic rates were lower and more consistent throughout the growing season compared to *A. gerardii* (Fig. 1). *A. gerardii* photosynthetic rates were significantly greater in the 1-yr burn treatment relative to the 4-yr burn treatment ($p < 0.01$), particularly for those growing under drought shelters (Fig.1). *C. drummondii* photosynthetic rates were not impacted by burn treatment ($p = 0.34$), but a drought*sampling date interaction was present ($p = 0.02$) whereby photosynthetic rates were lower in the drought shelters, but only during the last sampling period (Fig. 1). Predawn water potential values were generally lower for *C. drummondii* compared to *A. gerardii*, and both species had lower predawn water potential values in the 4-yr burn shelters toward the end of the growing season. For *C. drummondii*, this trend was more pronounced in drought shelters. *C. drummondii* midday water potential values showed a steady decline through the growing season and were slightly lower in drought shelters ($p = 0.046$) and in the 4-year burn treatment at the end of the growing season ($p < 0.01$) (Fig. 2). Turgor loss point (π_{TLP}) for *C. drummondii* declined over the course of the growing season (June through September) by roughly 0.3 MPa. π_{TLP} was lower in 4-year burn treatments and in drought shelters, particularly later in the growing season.

Discussion

Increased drought and woody encroachment are likely to have substantial and interactive effects on grassland carbon and water cycling in the future. Current demographic vegetation models lack detailed information on woody-grass dynamics in grassland ecosystems, limiting their ability to accurately predict grassland responses to future changes in climate and land-use (Pongratz et al. 2018). The goal of this long-term study is to better understand how co-existing woody-grass communities in a mesic temperate grassland respond to experimental changes in water availability and fire frequency.

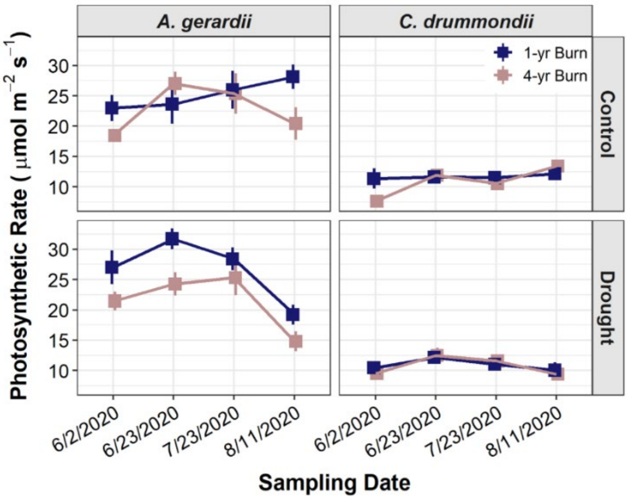

Fig. 1 Leaf photosynthetic rates measured for *A. gerardii* and *C. drummondii* in control and drought treatments throughout the 2020 growing season. Shown are mean ± 1 SEM.

Three years of 50% precipitation reduction produced small but detectable declines in soil moisture (0-30 cm; *data not shown*) compared to control shelters. For *A. gerardii*, lower photosynthetic rates in drought shelters toward the end of the growing season indicate that lower soil moisture availability was beginning to impact carbon assimilation. Similarly, lower water potential values in drought shelters toward the end of the growing season indicate an increase in water stress for both species. *A. gerardii* midday water potential did not decline as steadily over the course of the growing season as *C. drummondii*, likely due to sporadic precipitation inputs in surface soil layers where grasses are primarily accessing their water. *C. drummondii*, which primarily utilizes deeper (>30 cm depth) soil water (Ratajczak et al. 2011) has been shown to maintain remarkably stable photosynthetic rates, even during periods of low precipitation (Muench et al. 2016), which we observed in this study (Fig. 1). Declining water potential values and π_{TLP} throughout the growing season indicate that *C. drummondii* water stress was increasing, but that increased stress did not appear to impact photosynthetic rates. Plasticity in *C. drummondii* π_{TLP} indicates that *C. drummondii* was able to adjust physiologically to tolerate increasing water stress (i.e., lower midday leaf water potential) throughout the growing season.

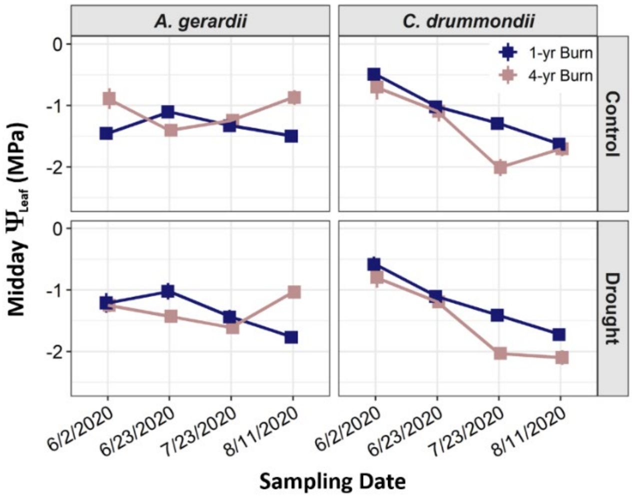

Fig. 2 Midday leaf water potential (Ψ_{Leaf}) measured for *A. gerardii* and *C. drummondii* in control and drought treatments throughout the 2020 growing season. Shown are mean ± 1 SEM.

Overall, there were stronger impacts of burn treatment on *C. drummondii* and *A. gerardii* physiology than drought. *A. gerardii* photosynthetic rates were higher in the 1-year burn treatment compared to the 4-year burn treatment, likely due to increased light availability post-burn when previous year's dead biomass is removed and increased nitrogen uptake following burning (Knapp 1985). Similarly, predawn and midday water potential for both species were generally lower in the 4-year burn treatment, indicating lower water availability, particularly later in the growing season (Fig. 2). Lower water availability in less-frequently burned watersheds could potentially be attributed to increased transpiration of woody species due to their reliance on deeper, more consistent soil water sources (Nippert and Knapp 2007) and possibly to higher infiltration rates under woody compared to grass cover (Alaoui et al. 2011). Therefore, higher woody cover could be impacting deep soil water availability and rate of soil water infiltration to deeper depths.

Results from this study indicate that three years of experimental drought has resulted in modest impacts on leaf physiology in dominant grass and woody shrub species in tallgrass prairie. Long-term studies of co-existing grass and shrub communities are useful for informing management of woody encroachment during drought, and to help identify whether multiple external pressures are needed to reverse grassland-to-shrubland transitions in temperate grasslands.

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