

Recoupling fire and grazing reduces wildland fuel loads on rangelands

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Citation: Starns, H. D., S. D. Fuhlendorf, R. D. Elmore, D. Twidwell, E. T. Thacker, T. J. Hovick, and B. Luttbeg. 2019. Recoupling fire and grazing reduces wildland fuel loads on rangelands. *Ecosphere* 10(1):e02578. 10.1002/ecs2.2578

Abstract. Fire suppression and exclusion, the historically dominant paradigm of fire management, has resulted in major modifications of fire-dependent ecosystems worldwide. These changes are partially credited with a recent increase in wildfire number and extent, as well as more extreme fire behavior. Fire and herbivory historically interacted, and research has shown that the interaction creates a unique mosaic of vegetation heterogeneity that each disturbance alone does not create. Because fire and grazing have largely been decoupled in modern times, the degree to which the interaction affects fuels and fire regimes has not yet been quantified. We evaluated effects of fire-only and pyric herbivory on rangeland fuels and fire behavior simulated using BehavePlus at four sites across the southern Great Plains. We predicted patches managed via pyric herbivory would maintain lower fuel loads, and less intense simulated fire behavior than fire alone. We found that time since fire was a significant predictor of fuel loads and simulated fire behavior characteristics at all sites. Fuel loads and simulated fire behavior characteristics (flame length and rate of spread) increased with increasing time since fire in all simulated weather scenarios. Pyric herbivory mediated fuel accumulation at all sites. Mean fuel loads in fire-only treatments exceeded 5000 kg/ha within 24 months, but pyric herbivory treatments remained below 5000 kg/ha for approximately 36 months. Simulated flame lengths in fire-only treatments were consistently higher (up to 3 ×) than in pyric herbivory treatments. Similarly, fire spread rates were higher in fire-only than in pyric herbivory treatments in all simulated weather conditions. Although all sites had potential to burn in the most extreme weather conditions, pyric herbivory reduced fuel accumulations, flame lengths, and rates of spread across all weather patterns simulated. These reductions extended the amount of time standard wildland firefighting techniques remain effective. Therefore, incorporating pyric herbivory into fuel management practices, in areas of high herbaceous productivity, increases the effectiveness of fuel treatments.

Key words: BehavePlus; coastal prairie; fire behavior; fire weather; fuels reduction; grazing; Great Plains; patch-burning; pyric herbivory; rangelands; tallgrass prairie; wildland fire.

Received 27 November 2018; accepted 3 December 2018. Corresponding Editor: Debra P. C. Peters.

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INTRODUCTION

Fire and grazing have occurred on every vegetated continent for millions of years and are two

of the primary factors that influence most aspects of the dominant ecosystems of the world (Bond and Keeley 2005, Bowman 2005, Archibald et al. 2013). Historically, these disturbances interacted

with one another, and in addition to weather and climate, shaped grassland and savanna landscapes worldwide (Fuhlendorf and Engle 2001, van Langevelde et al. 2003, Bond and Keeley 2005, Anderson 2006). The fire–grazing interaction, termed “pyric herbivory,” created a shifting mosaic of vegetation types, including vegetation that varied in amount and type of grazing as well as frequency and intensity of fire (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2009). Pyric herbivory and its effects were undoubtedly influenced by climate, which determined how rapidly fuels accumulated (Govender et al. 2006, Fule et al. 2012) in addition to the structure (e.g., canopy cover, species composition, height) of those fuels (Lane et al. 2000). Weather not only influences fuel accumulation via precipitation (Harcombe et al. 1993, Hsu and Adler 2014), but also impacts fire occurrence and intensity (e.g., flame length and rate of spread) through parameters such as relative humidity and wind speed (Ellair and Platt 2013, Platt et al. 2015).

Prior to European settlement, the interaction between fire and grazing in the North American Great Plains was critical to landscape structure and function (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2009). When European explorers first encountered the Great Plains, they reported the indigenous peoples frequently used fire to attract grazing animals such as American bison (*Bison bison*) and elk (*Cervus canadensis*), among other reasons (Pyne 2010). Management of North American rangelands during the late nineteenth and early twentieth centuries centered on practices that encouraged fire prevention and suppression (Fuhlendorf and Engle 2001, 2004). As grazing pressure from domestic livestock increased, fine fuels decreased, limiting the frequency and/or intensity of fires (Briggs et al. 2005, Van Auken 2009). Moreover, as permanent settlement increased, fire suppression efforts increased, effectively leading to exclusion of fire from the landscape. Subsequent decades of fire exclusion, coupled with heavy uniform grazing by domestic livestock, in addition to a host of other environmental and anthropogenic factors, contributed to extensive transformation of grasslands into shrublands and woodlands (Archer et al. 2017). This transition, primarily caused by the decoupling of fire and grazing (Fuhlendorf et al. 2009), shifted fuel structure allowing large, catastrophic wildfires.

Since 1985, wildfire activity in the Great Plains has increased, both in number of fires and in total area burned (Donovan et al. 2017). Over the past 15 years alone (2002–2016), wildfires have burned more than 41 million hectares in the southern Great Plains (NIFC 2017). In addition to loss of property and human life, wildfires can affect plant and animal community dynamics and contribute to invasions of non-native species as well as extinctions (Foxcroft et al. 2010, Abom et al. 2016, Potvin et al. 2017). This increasing frequency of wildfires emphasizes the need for implementation of effective fuel management techniques. Fuel management treatments are aimed at reducing wildland fire intensity, which has direct implications on the success of standard wildland firefighting techniques (NWCG 2014). Fire severity has also been linked to recovery of ecosystems after the occurrence of a fire (Gonzalez et al. 2015).

After burning, it is often the policy of federal and state agency managers to remove grazing animals for two years to allow recovery of the vegetative community (USDI-BLM 2014). However, recent research has demonstrated that an extended recovery period is not necessary (Augustine et al. 2010, Gates et al. 2017, Clark et al. 2018) and is clearly a departure from how fire and grazing historically interacted (Fuhlendorf et al. 2012). This significant departure from disturbance patterns under which Great Plains flora and fauna developed is a concern for biodiversity, perhaps most notably that of grassland birds (Holcomb et al. 2014, Hovick et al. 2014). Moreover, due to rapid recovery of herbaceous biomass in the southern Great Plains, deferral of grazing after fire may limit utility of prescribed fire as a fuels reduction treatment unless annual treatment of large areas is performed. However, such treatment frequency tends to reduce landscape heterogeneity inherent in this region, with an added consequence of reducing biodiversity (Fuhlendorf et al. 2006, 2017).

An alternative rangeland management paradigm that focuses on the interaction of fire and grazing, termed pyric herbivory, has recently been demonstrated as a method of maintaining or restoring heterogeneity of vegetation both temporally and spatially (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2012). Pyric herbivory creates a shifting mosaic of vegetation structure and

composition across a landscape as a result of the interaction between fire and grazing that is unique from the effects of fire or grazing in isolation (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2009). Large herbivores (e.g., bison, cattle) preferentially forage in the most recently burned patches on a landscape when such selection is allowed (Allred et al. 2011, 2013). Intense localized selective herbivory maintains these patches in a state of short vegetative regrowth and limits the accumulation of biomass and fine dead material necessary to fuel a fire. Surrounding areas of greater time since fire are only sparsely grazed; thus, fuels for subsequent fires accumulate. The pyric herbivory process is analogous to the interaction that occurred between fire and grazing prior to European settlement (Fuhlendorf and Engle 2001, 2004, Fuhlendorf et al. 2009, 2017, Allred et al. 2011). Furthermore, it has been shown to maintain or improve biodiversity of vegetation (Collins and Smith 2006, Collins and Calabrese 2012), invertebrates (Cook and Holt 2006, Engle et al. 2008), and a host of vertebrate assemblages (Danley et al. 2004, Coppedge et al. 2008, Fuhlendorf et al. 2010, Green et al. 2015, Hovick et al. 2015). In addition to the numerous reported conservation benefits, pyric herbivory benefits livestock production (Limb et al. 2011, Polito 2012, Allred et al. 2014, Scasta et al. 2015).

Our goal was to determine how the restoration of the complex fire–grazing interaction, which can maintain grazing productivity and biodiversity (Fuhlendorf et al. 2009), affects fuel management across highly variable climatic conditions. We developed a large-scale experiment capable of comparing fire-only treatments (ungrazed) to pyric herbivory treatments across four sites throughout the southern Great Plains and used these data to conduct modeling experiments with BehavePlus 5.0 (Heinsch and Andrews 2010). Our objectives were to (1) determine how time since fire and the fire–grazing interaction affect rangeland fuel accumulation in pyric herbivory vs fire-only treatments; (2) evaluate the effect of pyric herbivory on simulated fire behavior characteristics that impact suppression capabilities; and (3) determine whether pyric herbivory increases the length of time standard wildland firefighting techniques are effective compared to fire-only treatments across

variable weather patterns. Our findings document the potential benefits to fuel management using pyric herbivory compared to fire-only management.

STUDY SITES AND METHODS

Study sites and design

Our study was conducted at four sites across the southern Great Plains (Table 1). All sites were managed using fire to promote spatial and temporal heterogeneity across the landscape. Sites were chosen on the basis of having an active prescribed fire program, with preference for those already incorporating pyric herbivory into the management regime. Sites included the Tallgrass Prairie Preserve and Packsaddle Wildlife Management Area (WMA) in Oklahoma, and the Aransas National Wildlife Refuge (NWR) and the Attwater's Prairie-Chicken NWR in Texas (Table 1). Tallgrass Prairie Preserve, owned by The Nature Conservancy, consists of 16,000 ha dominated by tallgrass prairie species, with approximately one-third burned annually. Packsaddle WMA is comprised of 7900 ha and is owned by the Oklahoma Department of Wildlife Conservation. The site is dominated by shinnery oak (*Quercus havardii*) and mixed-grass species in the eastern portion, with the western portion consisting of sand sagebrush (*Artemisia filifolia*) and mixed-grass species, and approximately 2500 ha is burned annually. Attwater's Prairie-Chicken NWR is owned by U.S. Fish & Wildlife Service and comprised of 4200 ha of coastal prairie dominated by tallgrass species, with about one-fourth burned annually. Aransas NWR is comprised of 46,000 ha of coastal prairie dominated by gulf cordgrass (*Spartina spartinae*) interspersed with areas of live oak (*Quercus virginiana*). Approximately 4300 ha of Aransas NWR are burned annually. Burns were planned and executed by management personnel at each site according to each location's management goals and occurred in dormant and growing seasons. In pyric herbivory treatments, cattle (*Bos taurus*) were allowed unrestricted access to areas with varying times since fire. All sites included patches of fire-only and pyric herbivory treatments, except for Aransas National Wildlife Refuge, which was entirely fire-only. Our study region consists primarily of vegetation that likely

Table 1. Summary description of study sites (fuel model) sorted by plant community, grazing species, climate (growing season length; GS), mean annual precipitation (MAP), and physical characteristics (size, ownership; owner).

Site (fuel model) by plant community	Size (ha)	State	Owner	Grazers	MAP (cm)	GS (d)	Dominant herbaceous vegetation	Dominant woody vegetation	Refs
Gulf coastal prairie									
Aransas NWR (gr9)	46,000	TX	USFWS	None	105	338	<i>Schizachyrium scoparium</i> , <i>Sorghastrum nutans</i> , <i>Spartina spartinae</i>	<i>Prosopis glandulosa</i> , <i>Quercus virginiana</i>	USFWS (2010a)
Attwater's Prairie-Chicken NWR (gr9)	4200	TX	USFWS	<i>Bos taurus</i>	111	251	<i>Schizachyrium scoparium</i> , <i>Sorghastrum nutans</i> , <i>Panicum virgatum</i>	NA	USFWS (2010b)
Shinnery oak									
Packsaddle WMA (gs2)	7900	OK	ODWC	<i>Bos taurus</i>	66	198	<i>Schizachyrium scoparium</i> , <i>Andropogon gerardii</i> , <i>Bouteloua curtipendula</i>	<i>Quercus havardii</i>	Carroll et al. (2017)
Sand sagebrush									
Packsaddle WMA (gs2)	7900	OK	ODWC	<i>Bos taurus</i>	66	198	<i>Schizachyrium scoparium</i> , <i>Andropogon gerardii</i> , <i>Bouteloua curtipendula</i>	<i>Artemisia filifolia</i>	Carroll et al. (2017)
Tallgrass prairie									
Tallgrass Prairie Preserve (gr9)	16,000	OK	TNC	<i>Bos taurus</i> , <i>Bison bison</i>	117	203	<i>Andropogon gerardii</i> , <i>Schizachyrium scoparium</i> , <i>Sorghastrum nutans</i>	<i>Quercus marilandica</i> , <i>Q. stellata</i>	Hamilton (2007)

Note: NWR, National Wildlife Refuge; ODWC, Oklahoma Department of Wildlife Conservation; TNC, The Nature Conservancy; USFWS, U.S. Fish & Wildlife Service; WMA, Wildlife Management Area.

co-evolved with fire and grazing since the end of the last glacial period (Fuhlendorf and Engle 2001, Anderson 2006). Vegetation ranged from tallgrass prairie in the east to mixed-grass and mixed-grass shrub vegetation further west. Climate ranged from humid subtropical into temperate, and from mesic, highly productive systems in the east to semi-arid in the west. Historically, the southern Great Plains most likely had a mean fire return interval of less than 6 yr due to the interaction of climate, herbivory, topography, vegetation type, and Native American influences (Frost 1998, Guyette et al. 2012).

Sampling was performed from June 2014 through August 2016, at post-fire intervals between 0 and 43 months since fire (MSF). Transects were randomly placed in both pyric herbivory and fire-only patches, with an attempt to collect data at each study site from patches of similar time since fire in both treatments. To ensure that data collected were relevant to the study objectives, sampling was limited to patches comprised primarily of native vegetation. Eight fixed transects were randomly placed

in each patch within each study site. In an effort to avoid differences caused by variability in fire intensity resulting from differences between headfires, backfires, and flank-fires (Bidwell et al. 1990), transects were >50 m from patch perimeters, roads, or natural fire breaks. Vegetation measurements were recorded at 5-m intervals in 0.25-m² plots along each transect to quantify fuel properties within each patch. Fuels measurements included aboveground biomass (fuel load in g), fuel bed depth (cm), percent cover of 1-h (diameter <6.4 mm, including dormant/dead fine herbaceous), 10-h woody (diameter 6.4–25.4 mm), and 100-h (diameter 25.4–76.2 mm) woody fuels, litter, and bare ground. To measure aboveground biomass, vegetation along each transect was clipped and oven-dried at 45°C to a stable weight. Woody fuels in the 10-h and 100-h class were hand-separated and weighed apart from 1-h fuels and litter. To avoid artificially altering future vegetation measurements along transects, clippings were taken from five 0.25-m² plots parallel to each transect at a distance of 10 m away.

Fire simulations

Using fuels data collected from each study site to simulate fire behavior in the BehavePlus 5.0 fire modeling software program (Heinsch and Andrews 2010), we were able to accomplish two objectives. First, we evaluated the impacts of pyric herbivory on the relationship between time since fire and simulated fire behavior characteristics. Additionally, we examined the potential for pyric herbivory to extend the time period in which standard wildland firefighting techniques remain effective for fire suppression versus fire-only treatments. BehavePlus allows users to model fire behavior characteristics resulting from user-defined fuel and environmental parameters. Surface fire behavior characteristics (flame length, rate of spread) are calculated by the SURFACE module in BehavePlus using Rothermel's (1972) fire spread model. The SURFACE module allows users to select from 53 distinct fuel models representing different vegetation types (Scott and Burgan 2005). Users can also customize models to reflect site-specific fuel characteristics.

Following the approach of Twidwell et al. (2016), we customized dynamic fuel models to simulate fire behavior in BehavePlus. Dynamic fuel models characterize predictable changes in fuel properties resulting from changes in environmental conditions and transition live vegetation into available fuel using fuel curing scenarios. To develop fuel models for simulation of fires at our study sites, we used the fuel model most similar to each study site to initialize pre-defined inputs. Fuels data (e.g., fuel load, fuel bed depth) from field measurements were used in place of pre-defined values before running each model (Scott and Burgan 2005). To capture the range of variation inherent in southern Great Plains fuels, we simulated scenarios for each transect ($n = 638$) sampled at each study site. Simulations included a variety of weather scenarios ranging from extreme to mild fire weather. Weather scenarios included fuel moisture values from 5% to 35%, and low (16 km per h) and high (40 km per h) wind speeds, for a total of 8932 simulations. Inputs for surface area/volume ratio and fuel heat content used the pre-defined values for the fuel model. Flame length and rate of spread output were compiled, and temporal changes in these characteristics for pyric herbivory and fire-only treatments were analyzed. To establish thresholds

of fire suppression effectiveness, we used values determined by the National Wildfire Coordinating Group to be relevant to standard firefighting techniques (NWCG 2014). These techniques include heavy equipment as well as aerial methods and become ineffective when flame lengths reach more than 3.4 meters. Lower critical thresholds of effectiveness are also recognized—at 1.4 m flame lengths, hand tools become ineffective; at 2.4 m flame lengths, control efforts at the head of the fire become ineffective (NWCG 2014). In areas where fuels reduction treatments have been implemented, prescribed fire has been used more than other treatments (e.g., thinning, mastication), and federal agencies indicate that prescribed fire will be a dominant fuel management option in this region (USDI-BLM 2014).

Analyses

Due to the unbalanced nature of our data, we used a linear mixed-effects model (using lme4 in the R statistical environment) to measure how fire and grazing treatments affected biomass (Bates et al. 2013, R Core Team 2016). Mixed-effect models allow the evaluation of multi-level nested designs including unbalanced data and account for autocorrelation. Random effects included transect nested within patch within site in addition to collection year. Explanatory variables of interest were number of months since fire (MSF), presence/absence of grazing (Grazing), and the interaction between the two (MSF \times Grazing). For similar reasons, we used linear mixed-effects models to measure how time since fire, presence/absence of grazing, and their interaction affected BehavePlus simulation outputs of flame lengths and spread rates. Because biomass and other variables we measured were input directly into our custom fuel models, which treat these as drivers of fire simulations, we did not include them as potential predictors of BehavePlus output. Grazing intensity was categorized as light relative to the potential vegetation production at each study site, so grazing was recorded as presence/absence rather than continuous.

RESULTS

Preliminary analysis of response variables at each study site suggested minimal differences

among sites, so data from all sites were combined. Time since fire was a significant predictor of biomass and 1-h fuel loads across study sites, and when grazing interacted with fires, the fuel management lasted longer than when grazing was excluded. Months since fire was a significant predictor of biomass, which increased with MSF ($\beta = 2.19$, $\sigma = 0.088$, $P < 0.001$). The fire–grazing interaction was also a significant predictor, with a negative effect on biomass ($\beta = -0.51$, $\sigma = 0.106$, $P < 0.001$), suggesting that pyric herbivory reduced the influence of MSF. Biomass was higher and accumulated more rapidly in fire-only than in pyric herbivory patches (Fig. 1). Months since fire was also a significant predictor of percent cover of 1-h fuel ($\beta = 0.110$, $\sigma = 0.013$, $P < 0.001$), which was greater in fire-only than pyric herbivory patches for up to 18 months after fire (Fig. 2).

Following a trend similar to that of biomass and 1-h fuels, simulated flame lengths differed between treatments (Fig. 3). Months since fire was a significant predictor of flame length output for all simulated weather conditions (Table 2). Presence of grazing failed to significantly predict flame length in all except one weather scenario (low wind, 5% fuel moisture; Table 2). The fire–grazing

interaction was a significant predictor of flame length across all fuel moistures at high (40 km per h) wind speeds, but not significant at fuel moistures $\geq 20\%$ at low wind speeds (16 km per h). When simulating extreme weather conditions (wind speed = 40 km per h, 5% fuel moisture), flame lengths in pyric herbivory treatments did not cross the 3.4 m threshold until approximately 8–9 MSF, compared to 3–4 months for fire-only (Fig. 3). Under slightly less extreme weather conditions (wind speed = 16 km per h, and 5% fuel moisture), pyric herbivory maintained flame lengths below 3.4 m for approximately 18 months compared to 6 months for fire-only treatments (Fig. 3).

In both scenarios, simulated flame lengths in pyric herbivory treatments remained lower than in fire-only patches. An even more drastic decrease in flame lengths occurred as a result of a shift in fire weather conditions typical of diurnal shifts in wind speed and moisture (reduction in wind speed from 40 to 16 km per h paired with an increase in fuel moisture from 5% to 10%). Moreover, this was most prominent in the pyric herbivory treatments, as flame lengths in fire-only treatments rose above 3.4 m at 6 months post-fire (Fig. 4). Overall, flame lengths

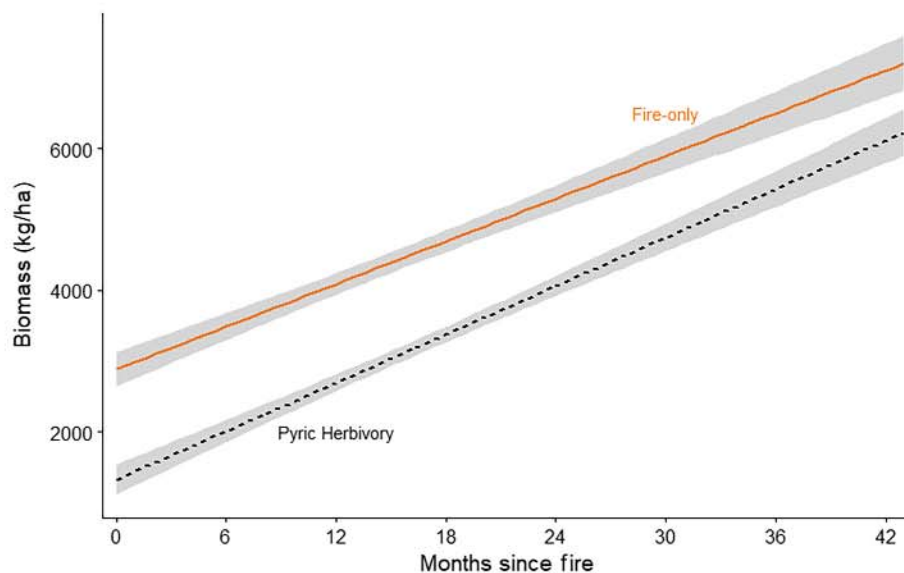


Fig. 1. Mean aboveground biomass (kg per ha) with increasing months since fire across four sites in the southern Great Plains (2014–2016) for fire-only (solid orange line) and pyric herbivory (dashed black line) treatments. Shaded areas indicate 95% confidence intervals ($n = 3190$).

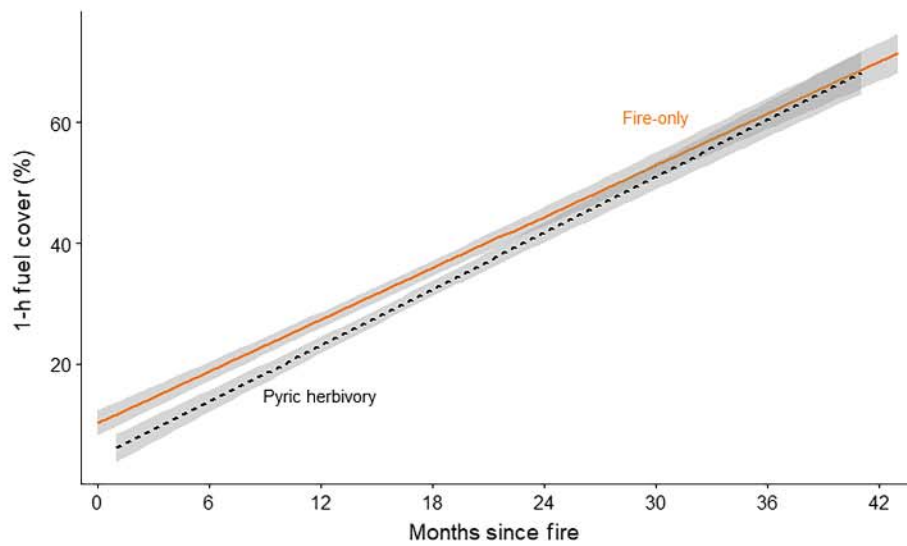


Fig. 2. Mean cover of 1-h fuels (%) with increasing months since fire across four sites in the southern Great Plains (2014–2016) for fire-only (solid orange) and pyric herbivory (dashed black) treatments. Shaded areas indicate 95% confidence intervals ($n = 3190$).

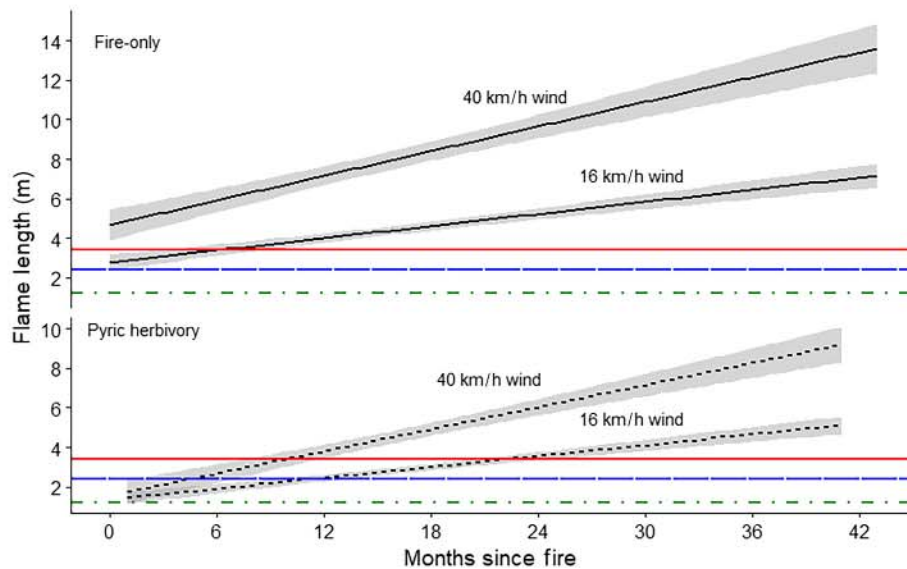


Fig. 3. Mean simulated flame length (m) with increasing months since fire across four sites in the southern Great Plains (2014–2017) for fire-only (top) and pyric herbivory (bottom) treatments. The green (dot-dash) horizontal line indicates the maximum threshold (1.4 m) at which hand tools are effective for fighting wildland fires. The blue (long dash) horizontal line indicates flame length at which aerial and heavy equipment effectiveness diminishes (2.4 m). The red (solid) horizontal line indicates the threshold at which all standard wildland fire-fighting techniques become ineffective (3.4 m). Top panel depicts mean flame length at high (40 km per h) and low (16 km per h) wind speed scenarios at 5% fuel moisture for fire-only treatments ($n = 336$). Bottom panel depicts mean flame length at high (40 km per h) and low (16 km per h) wind speed scenarios at 5% fuel moisture for pyric herbivory treatments ($n = 302$).

Table 2. Beta coefficients, standard errors, and *P*-values for main effects of time since fire (MSF), grazing (presence/absence), and their interaction given different wind speeds and dead fuel moisture content (FMC).

Variable		Interaction effects (MSF × Grazing)			Main effects (MSF)			Main effects (Grazing)		
Wind (km per h)	FMC (%)	β	σ	<i>P</i>	β	σ	<i>P</i>	β	σ	<i>P</i>
Flame Length										
40	5	-0.097	0.035	<0.01	0.406	0.024	<0.001	-2.166	1.325	0.11
	10	-0.085	0.029	<0.01	0.333	0.021	<0.001	-1.723	1.090	0.12
	15	-0.080	0.026	<0.01	0.030	0.018	<0.001	-1.466	0.969	0.13
	20	-0.077	0.024	<0.01	0.276	0.017	<0.001	-1.344	0.903	0.15
	25	-0.072	0.023	<0.01	0.253	0.016	<0.001	-1.233	0.836	0.15
	30	-0.073	0.020	<0.001	0.219	0.014	<0.001	-0.825	0.725	0.26
	35	-0.064	0.013	<0.001	0.150	0.009	<0.001	-0.273	0.490	0.58
16	5	-0.039	0.017	<0.05	0.196	0.013	<0.001	-1.064	0.657	<0.05
	10	-0.029	0.014	<0.05	0.160	0.011	<0.001	-0.914	0.543	0.1
	15	-0.026	0.013	<0.05	0.142	0.009	<0.001	-0.821	0.483	0.1
	20	-0.011	0.015	0.06	0.132	0.009	<0.001	-0.800	0.452	0.09
	25	-0.020	0.011	0.08	0.121	0.008	<0.001	-0.750	0.423	0.08
	30	-0.016	0.010	0.11	0.102	0.007	<0.001	-0.658	0.365	0.08
	35	-0.010	0.007	0.15	0.073	0.005	<0.001	-0.522	0.271	0.06
Rate of Spread										
40	5	-0.006	0.020	0.78	0.147	0.016	<0.001	-1.868	0.641	<0.01
	10	-0.013	0.016	0.43	0.118	0.012	<0.001	-1.371	0.502	<0.05
	15	-0.014	0.013	0.29	0.099	0.010	<0.001	-1.098	0.414	<0.05
	20	-0.014	0.012	0.24	0.088	0.008	<0.001	-0.953	0.367	<0.05
	25	-0.011	0.010	0.28	0.073	0.007	<0.001	-0.802	0.309	<0.05
	30	-0.019	0.008	<0.05	0.062	0.006	<0.001	-0.489	0.244	0.052
	35	-0.018	0.004	<0.001	0.038	0.003	<0.001	-0.124	0.135	0.36
16	5	0.002	0.006	0.76	0.023	0.004	<0.001	-0.301	0.148	<0.05
	10	0.005	0.004	0.21	0.019	0.003	<0.001	-0.337	0.110	<0.01
	15	0.004	0.003	0.2	0.016	0.002	<0.001	-0.286	0.090	<0.01
	20	0.004	0.003	0.19	0.014	0.002	<0.001	-0.258	0.079	<0.01
	25	0.004	0.003	0.11	0.012	0.002	<0.001	-0.240	0.073	<0.01
	30	0.003	0.002	0.23	0.011	0.002	<0.001	-0.189	0.060	<0.01
	35	0.002	0.001	0.13	0.008	0.001	<0.001	-0.151	0.043	<0.01

Note: Bold text indicates significant results.

in pyric herbivory treatments were consistently lower than in fire-only treatments with a similar MSF. Pyric herbivory also influenced how flame lengths responded to simulated changes in weather conditions. In extreme (40 km per h winds and 5% fuel moisture) scenarios, 58% of pyric herbivory simulations and 79% of fire-only simulations yielded flame lengths greater than 3.4 m. In low wind speed (16 km per h)–10% fuel moisture simulations, the percentage of flame lengths above 3.4 m were reduced to 20% and 55% in pyric herbivory and fire-only, respectively (Fig. 5).

As with flame lengths, MSF was a significant predictor of spread rates for all simulations (Table 2). In contrast, the fire–grazing interaction

was only significant for two fuel moisture scenarios, both at high wind speed. Presence of grazing was a significant predictor of spread rate in all scenarios except these two (Table 2). Spread rates also differed between treatments, overall lower in pyric herbivory than in fire-only treatments with similar MSF (Fig. 6). Spread rates in fire-only treatments reached 3 meters per second after approximately 6–8 MSF in our most extreme simulated weather conditions, while spread rates in pyric herbivory treatments did not reach 3 m per second until approximately 30 MSF. These results also underscore the importance of weather conditions on fire behavior, and that large, fast-moving fires may occur in any fuels during extreme fire weather events.

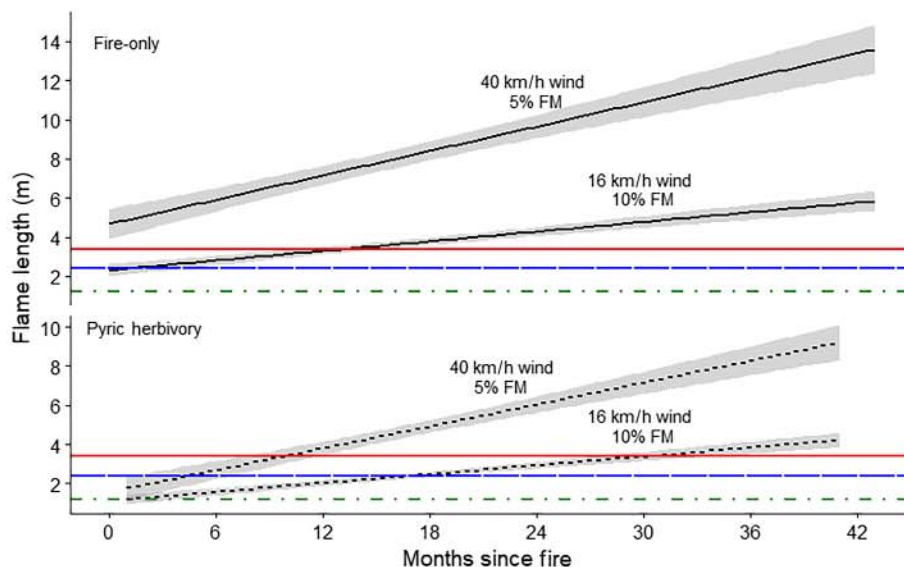


Fig. 4. Changes in fire suppression capabilities in fire-only (top, $n = 336$) and pyric herbivory (bottom, $n = 302$) treatments with increasing months since fire across four sites in the southern Great Plains (2014–2017). Upper line for each treatment represents mean flame length simulated using extreme (40 km per h and 5% fuel moisture) daytime conditions. Lower line for each treatment represents less extreme (16 km per h and 10% fuel moisture) overnight conditions characteristic of the SGP. The green (dot-dash) horizontal line indicates the maximum threshold (1.4 m) at which hand tools are effective for fighting wildland fires. The blue (long dash) horizontal line indicates flame length at which aerial and heavy equipment effectiveness diminishes (2.4 m). The red (solid) horizontal line indicates the threshold at which all standard wildland firefighting techniques become ineffective (3.4 m). Shaded areas represent 95% confidence intervals. Changes in simulated weather conditions reflect typical changes associated with nightfall in the southern Great Plains.

DISCUSSION

We sought to determine the effect of pyric herbivory on grassland fuel management across a wide range of weather conditions. We found that pyric herbivory reduced fuel loads and simulated fire behavior characteristics in all weather conditions simulated. While all fuel loads were susceptible to fire in the most extreme weather events, simulated fire behavior in patches treated with pyric herbivory was less extreme than in fire-only patches. Less extreme fire behavior not only improves effectiveness of suppression tactics, but also decreases fire severity. Therefore, incorporating pyric herbivory into rangeland management practices has potential to reduce the occurrence and impacts of high-severity wildfires which can cause changes in dominant vegetation types, sometimes allowing increases in exotic species (Forrestel et al. 2011, McDonald

and McPherson 2011, Ghermandi et al. 2013, Guthrie et al. 2016). Our data address a knowledge gap described by Limb et al. (2016), specifically that few fire studies consider how time since fire affects the systems being studied, and even fewer look at impacts of the pyric herbivory interaction (Fuhlendorf et al. 2011, Limb et al. 2016).

We found that fuel loads increased rapidly with increasing MSF, but total fuel accumulation and rate of accumulation were mediated by pyric herbivory. Our results are consistent with findings that time since fire was a determinant of fuel loads in African savannas, and that increasing time since fire increased fire risk, which was related to biomass and fuel moisture content (Govender et al. 2006, Fernandes et al. 2012). Additionally, recent work has determined that biomass in grazing exclosures in African savanna returned to pre-fire levels within a single

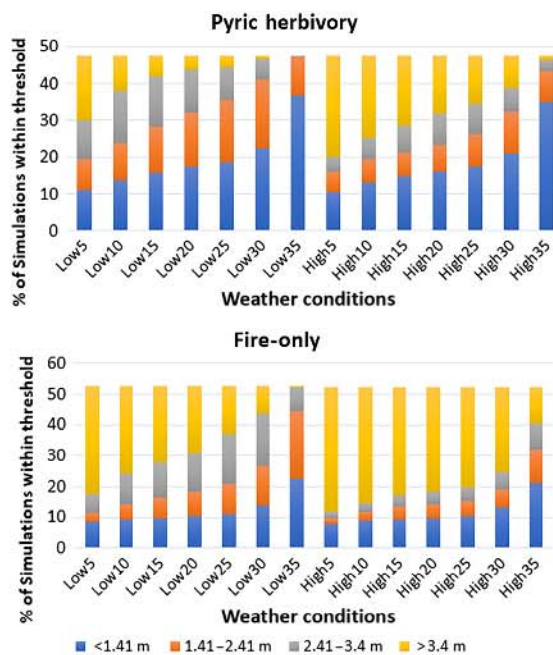


Fig. 5. Percentages of fire simulations within each critical threshold associated with effectiveness of wildland firefighting techniques for fire-only and pyric herbivory treatments across four sites in the southern Great Plains (2014–2017). Weather conditions simulated were wind speeds 16 km per h (Low) and 40 km per h (High), and fuel moistures from 5% to 35%, MSF 0–43.

growing season (Donaldson et al. 2018). Our results indicate pyric herbivory regulates the rate of accumulation of biomass compared to fire-only treatments. This reduced rate of accumulation helps to achieve fuel management objectives by extending the amount of time standard wildland firefighting techniques remain effective. The importance of the fire–grazing interaction is highlighted by its role in determining rate of fuel accumulation. In pyric herbivory treatments, simulated fire behavior was such that standard techniques remained effective for at least six months longer than fire-only treatments and up to 36 months post-fire, depending on weather conditions. In our fire simulations, pyric herbivory treatments consistently produced lower flame lengths and rates of spread than fire-only treatments. Rates of spread increased rapidly during the first 12 months post-fire along the same pattern as biomass and flame lengths, regardless of simulated weather

conditions. Our work supports the suggestion that effectiveness of fuels reduction via fire-only can be short-term (Fernandes and Botelho 2003) and that extreme fire weather can overwhelm effects of fuel treatments (McCarthy and Tolhurst 2001).

The differences we found between treatments varied with simulated wind and fuel moisture conditions. Fire behavior characteristics produced by our most extreme wind and fuel moisture conditions illustrate that uncontrollable fires are possible during periods of extreme fire weather regardless of treatments. However, slight changes in weather conditions can significantly improve effectiveness of suppression efforts in areas treated using pyric herbivory. Similar interactions between weather and time since fire were reported in a study of fuel treatment effects on wildfire severity, where fuels reduction treatments showed the greatest benefit in evening and overnight (Tolhurst and McCarthy 2016).

Fuels reduction burning (fire-only) has been suggested as an effective method to reduce the occurrence of wildfires (Butry 2009, North et al. 2012, Ager et al. 2014). However, much current literature regarding effectiveness of fuel treatments focuses on forested systems. Annual burning reduces fuels, but also leads to simplification of grasslands (Fuhlendorf et al. 2006). In addition to fuels reduction burning, targeted herbivory (grazing-only) has been considered as a fuels reduction treatment (Taylor 2006, Leonard et al. 2010). However, grazing-only treatment was reported to have mixed utility depending on grass morphology (Leonard et al. 2010) and may also promote growth of unpalatable plants (Kirkpatrick and Bridle 2016). Our study demonstrates that restoration of the complex interaction between fire and grazing benefits fuel management objectives in addition to benefits to biodiversity reported by others (O'Reilly et al. 2006, Fuhlendorf et al. 2010, Hovick et al. 2014) and livestock production (Limb et al. 2011, Scasta et al. 2016). We re-emphasize the importance of the fire–grazing interaction and time since fire in determining herbaceous biomass accumulation (van Langevelde et al. 2003).

We assert that differences in the application of fire or grazing will change the impacts of pyric herbivory, altering the magnitude of differences observed. For example, increased grazing

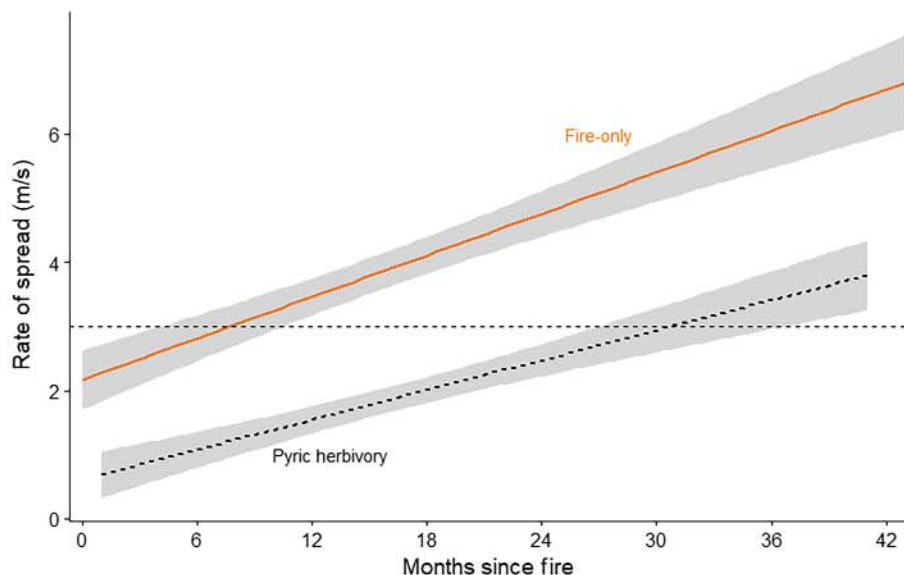


Fig. 6. Simulated rate of spread (m per s) for fire-only (solid orange) and pyric herbivory (dashed black) treatments under extreme (40 km per h and 5% fuel moisture) conditions across four sites in the southern Great Plains (2014–2017). Shaded areas indicate 95% confidence intervals ($n = 638$). Dashed horizontal line represents rate of spread of 3.0 m per second.

pressure could further reduce fire behavior, but could also reduce the benefits to biodiversity (Fuhlendorf et al. 2009). Increased grazing pressure could also decrease the effect of fire on grazing patterns (McGranahan et al. 2012, Augustine and Derner 2014). It is also important to note that dynamic fuel models convert live green vegetation to available fuels as a function of grass curing scenarios built into the software (Scott and Burgan 2005). These models assume homogeneity and continuity of fuels, which may lead to an overestimation of rates of spread (Parsons et al. 2011). However, the prediction of our models that ungrazed areas could support fire in <12 months is consistent with a previous report that a similar grassland community sustained fire spread as few as six months after fire, even in a period of below average rainfall (Bragg 1982). While we did not directly evaluate probability of ignition, our models may have overestimated this parameter given the presumed greenness of a recently burned area. However, recent studies have shown high variability, including relatively rapid decreases within a year, in live fuel moisture (Jurdao et al. 2012, Ellsworth et al. 2013). Also, due to the heterogeneous nature of burns

at our sites, some transects may have measured herbaceous vegetation that failed to burn due to lack of fuel continuity or properties of the vegetation itself. Because information regarding such vegetation properties is lacking in primary literature, avoidance of such areas would require first-hand experience executing the fires, which was not feasible in our study.

CONCLUSIONS

It is clear from our data that pyric herbivory significantly benefits fuel management goals by extending the effects of fuels reduction beyond those of fire alone. Incorporating pyric herbivory—which has repeatedly been reported to increase biodiversity—has potential to reduce the occurrence and impacts of large and severe wildfires. To achieve maximum benefit for fuel reduction and conservation goals, managers could incorporate pyric herbivory at spatial and temporal patterns most suitable to their needs depending on landscape features.

Fire managers and researchers can use our results applied across landscapes to decrease the size or occurrence of catastrophic wildfires.

Incorporating pyric herbivory into fuel management treatments will increase their utility by extending the amount of time treatments remain effective at preventing ignitions or reducing fire behavior characteristics. Additionally, managers can compare our data with fuels data specific to other sites of interest to identify priority areas to implement pyric herbivory where current management techniques fail to maintain fuels at levels below which fire suppression tactics can be carried out safely and successfully. Finally, assuming readily accessible management records, wildfire responders may be able to improve personnel safety by prioritizing resources to areas most recently treated with pyric herbivory.

ACKNOWLEDGMENTS

This research was funded by Joint Fire Sciences Program, project 13-1-06-8. The authors would like to thank the personnel at all study sites for logistical support and for providing burn history data. The authors also appreciate the contributions of two anonymous reviewers.

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