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ARTICLE

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Factors influencing the persistence of a fire-sensitive *Artemisia* species in a fire-dependent ecosystem

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Abstract

Fire refugia and patchiness are important to the persistence of fire-sensitive species and may facilitate biodiversity conservation in fire-dependent landscapes. Playing the role of ecosystem engineers, large herbivores alter vegetation structure and can reduce wildfire risk. However, herbivore effects on the spatial variability of fire and the persistence of fire-sensitive species are not clear. To examine the hypothesis that large herbivores support the persistence of fire-sensitive species through the creation of fire refugia in fire-prone landscapes, we examined the response of a fire-sensitive plant, Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* [Beetle & Young]) to fire and grazing in the fire-dependent mixed-grass prairie of the northern Great Plains. We carried out a controlled burn in 2010 within pre-established exclosures that allowed differential access to wild and domestic herbivores and no record of fire in the previous 75 years due to fire suppression efforts. The experiment was set up with a split-plot design to also examine potential changes in plots that were not burned. Canopy cover of big sagebrush was recorded before the burn in 2010 and again in 2011 with percent area burned recorded within 1-month post-fire in the burned plots. Percentage area burned was the greatest in ungulate exclosures (92% ± 2%) and the least in open areas (55% ± 21%), suggesting that large herbivores influenced fire behavior (e.g., reducing fire intensity and rate of spread) and are likely to increase fire patchiness through their alterations to the fuel bed. Regression analysis indicated that the proportion of sagebrush cover lost was significantly correlated with the proportion of area burned ($R^2 = 0.76$, $p = 0.05$). No differences in the non-burn plots were observed among grazing treatments or among years. Altogether, this illustrates the potential importance of large herbivores in creating biotic-driven fire refugia for fire-sensitive species to survive within the flammable fuel matrix of fire-dependent grassland ecosystems such as the mixed-grass prairie. Our findings also attest to the resiliency of the northern Great Plains to fire and herbivory and underscore the value of managing grasslands for heterogeneity with spatial and temporal variations in these historic disturbances.

KEYWORDS
Artemisia, disturbance, ecosystem engineers, fire patchiness, fire-prone ecosystems, fire refugia, fuel, Great Plains, herbivory, mixed-grass prairie, sagebrush

INTRODUCTION

Large browsers and herbivores alter resource availability and vegetation structure through the direct and indirect effects of grazing, thereby classifying them as ecosystem engineers (Cardoso et al., 2020; Jones et al., 1994). The distribution of grazing across a landscape influences the spatial heterogeneity of vegetation that affects the interspersion of vegetation types and the diversity of other consumers (Adler et al., 2001; Milchunas et al., 1988). Heterogeneity in grassland ecosystems is not driven by grazing alone but is influenced by multiple interacting forces including fire, weather, topo-edaphic features, and other ecosystem engineers such as fossorial animals (e.g., prairie dogs in the Great Plains of the USA) (Axelrod, 1985; Bond & Keeley, 2005). These disturbances have complex spatial and temporal interactions with positive and negative feedbacks that develop a shifting mosaic of patches varying in degree of disturbance and successional stage across the landscape (Fuhlendorf & Engle, 2004). A greater understanding of the complex relationships among disturbances and their implications is critical for the conservation of biodiversity as heterogeneity serves as its foundation at all levels of ecological organization (Pickett et al., 1997).

Most grassland plants evolved with and are well adapted to disturbances such as fire and grazing, but some disturbance-sensitive species persist within the vegetation matrix (Anderson, 2006). The majority of grassland plants can be top killed by disturbance but will typically resprout due to their at or belowground meristems (Bellingham & Sparrow, 2000; Bond & Midgley, 2001). Nonresprouting species, however, are readily killed by disturbances such as fire and depend solely on seeds for reproduction (Bell, 2001; Keeley & Zedler, 1978). Frequent fire in grassland ecosystems generally confines fire-sensitive species to less flammable areas or those that are difficult for fire to reach such as rocky outcrops (Burrows et al., 2008; Gill & Bradstock, 1995; Russell-Smith, 2006). However, it is important to recognize that fire is not a uniform event across a landscape due to the spatial and temporal complexity and diversity of the vegetation mosaic and its flammability (Burrows & Middleton, 2016). Furthermore, the response of fire-sensitive species depends largely on fire patchiness and intensity (Oliveira et al., 2015; Ooi et al., 2006). Increasing our understanding of the mechanisms that drive fire behavior and allow fire-sensitive species to persist in flammable ecosystems will greatly inform the management efforts that aspire to maintain or restore native biodiversity.

Big sagebrush (*Artemisia tridentata*) is a nonresprouting shrub readily killed by fire and is the dominant species of the Great Basin and sagebrush steppe ecosystems of North America (Shultz, 2006). Fire in the sagebrush steppe was historically infrequent, with estimates ranging from 50 to 240 years (Baker, 2006; Wright & Bailey, 1982). Sagebrush communities provide a habitat for several endemic wildlife species, including several declining sagebrush-obligate and specialized species of conservation concern (Rowland et al., 2006). Post-fire recovery of Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis* [Beetle & Young]) is the slowest of the big sagebrush alliance, yet it uniquely persists with a historically shorter fire-return interval in portions of the northern Great Plains mixed-grass prairie (Reid & Fuhlendorf, 2011). Fire in the mixed-grass prairie was historically variable with fire-return interval estimates ranging from 4 to 23 years across mesic and xeric regions (Umbanhowar, 1996; USDA, 2012). Fire suppression since European establishment plays a critical role in the expansion of woody species throughout the Great Plains. Woody encroachment is currently not as extensive in the northern Great Plains as it is in the South but is well documented on its edges particularly with the encroachment of eastern red cedar (*Juniperus virginiana*), rocky mountain juniper, (*Juniperus scopulorum*), western snowberry (*Symphoricarpos occidentalis*), and ponderosa pine (*Pinus ponderosa*) into native prairie landscapes (Barger et al., 2011; Grant & Murphy, 2005; Limb et al., 2018; Symstad & Leis, 2017). Woody plant encroachment is a pressing challenge for grassland management as it alters historic vegetation composition, forage availability, and habitat for grassland specialists by altering vegetation structure (Archer et al., 2017; Eldridge et al., 2011). Therefore, restoring or emulating historic fire regimes in grassland ecosystems is necessary to maintain herbaceous dominance and prevent a conversion to closed canopy woodlands or shrublands (Fuhlendorf et al., 2009; Turner, 2010).

Management guidelines for sagebrush communities often conflict with one another regarding fire, as they depend on management priorities and specific objectives, especially where livestock grazing occurs (Baker, 2006; Beck et al., 2012; Bunting et al., 1987). Conflicting arguments arise because the effects of fire on wildlife species in sagebrush communities is species dependent and highly variable according to the pattern and extent of the patchiness of burned and unburned areas (Baker, 2006; Longland & Bateman, 2002). In addition, fire suppression is generally encouraged where replacement by annual invasive grasses is possible and enhanced by fire (Baker, 2006; Hemstrom et al., 2002). Although historically sagebrush ecosystems generally did not burn often, the mixed-grass prairie is a fire-dependent ecosystem that burns frequently, yet has not lost big sagebrush from the system (Baker, 2006; Reid & Fuhlendorf, 2011). Wildfires in the sagebrush ecosystems of the mixed-grass prairie are highly variable and often retain ample unburned areas within the wildfire perimeter (Reid & Fuhlendorf, 2011), which implies spatial variation in the fuel bed.

Unburned areas and areas minimally affected by low-intensity fire are referred to as fire refugia and play a critical role in the maintenance of biodiversity by allowing fire-sensitive species to persist in the post-fire environment in unburned "islands" (Bowman & Bowman, 2000; Kolden et al., 2012; Meddens et al., 2018; Robinson et al., 2013). Fire refugia are typically associated with wetlands and topoedaphic factors (e.g., slope, aspect, soil type, exposed rock, standing water, etc.) that are abiotic in nature and affect the mechanisms that drive fire spread including local weather, fuel load, and landscape connectivity (Archibald et al., 2005). Fire spread acts as a percolation process that depends on the continuity of the fuel bed, so fire refugia can also occur where there is a break in continuity (e.g., from changes in fuel load, continuity, structure, moisture content, etc.) that prevents fire from spreading into every flammable part of the fuel complex (Beer & Enting, 1990; Caldarelli et al., 2001; Kerby et al., 2007). As ecosystem engineers that remove biomass, native and domestic large herbivores can break up fuel continuity, reduce fuel loads, and ultimately affect or even restrict the ability of fire to move across the landscape (Anderson, 2006; Cordoso et al., 2020; Davies et al., 2010; Foster et al., 2020; Hobbs et al., 1991; Kimuyu et al., 2014; Leonard et al., 2010; Starns et al., 2019; Werner et al., 2021), thereby modulating the effects of fire through the generation of biotic-driven fire refugia within the grassland matrix (Kerby et al., 2007; Werner et al., 2021). Therefore, it is plausible that large herbivores may support the persistence of fire-sensitive plants in flammable landscapes by reducing their fire event mortality through alterations in fuels and fire behavior (Werner et al., 2021).

Understanding how Wyoming big sagebrush persists in the fire-dependent mixed-grass prairie landscape will provide land managers with the ability to improve management for sagebrush-obligate species and other species of concern. Decreased mortality of non-resprouting species is correlated with increased fire patchiness, therefore we sought to quantify the effect of a gradient of herbivory on the amount of area burned and examine the corresponding response of Wyoming big sagebrush. We predicted that the presence of large herbivores would decrease the proportion of area burned, thereby creating biotic-driven fire refugia that would allow sagebrush to survive prescribed fire.

METHODS

This study was conducted on the Charles M. Russell (CMR) National Wildlife Refuge in north-central Montana, 105 km northeast of Lewistown, MT, USA (47°70′ N, 107°17′ W). The refuge extends over 200 km along the Missouri River and covers ~430,000 ha that encompass a variety of plant associations including mixed-grass prairies, sagebrush steppe, Ponderosa pine, and Douglas fir (*Pseudotsuga menziesii*) slopes, cottonwood riparian zones, and badlands (Montana Field Guide, 2020; Reid & Fuhlendorf, 2011). Native grasses western wheatgrass (*Pascopyrum smithii*) and blue grama (*Bouteloua gracilis*) dominate upland mixed-grass prairie sites along with several native shrubs including Wyoming big sagebrush, plains pricklypear (*Opuntia polycantha*), winterfat (*Krascheninnikovia lanata*), rubber rabbitbrush (*Ericameria nauseosa*), and Gardener's saltbrush (*Atriplex gardneri*) (Dullum et al., 2005; Reid & Fuhlendorf, 2011). The CMR is managed for wildlife and moderate livestock grazing by the United States Army Corps of Engineers and the United States Fish and Wildlife Service. Cattle are the only livestock grazers on the CMR, whereas native ungulate grazers include elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), pronghorn (*Antilocapra americana*), and bighorn sheep (*Ovis canadensis*).

The regional climate is characterized as temperate with cold winters and warm, dry summers. Average monthly air temperatures near Lewistown range from −4°C in January to 18°C in July and August (NOAA, 2020) when isolated dry-lightning strikes occur and regularly ignite wildfires on the CMR (Reid & Fuhlendorf, 2011). Here, ~21% of the land area of the CMR was burned by a combination of prescribed fire and wildfires between 1980 and 2008, with half of that occurring in just a 4-year span from 2004 to 2008 (Reid & Fuhlendorf, 2011). The CMR has maintained an active prescribed burn program since 1992. However, the majority of the area burned annually is from July and August wildfires, as the program has only conducted 15 prescribed burns, treating just more than 1215 ha since its initiation. One burn was conducted on 405 ha in 2008 to restore the natural fire regime, promote pyric herbivory, and enhance upland habitat, whereas the rest occurred in river bottoms, prairie dog towns, and on lakeshore to reduce Russian knapweed (*Rhaponticum repens*), enhance habitat suitability for prairie dogs or piping plovers (*Charadrius melodus*), or reduce hazardous fuels (USFWS, 2012). However, none of the plots established for this study had a previous record of fire post European settlement beyond that conducted during the experiment. Average annual precipitation in the area is 428 mm with the most precipitation occurring in May and June (72 and 78 mm, respectively; NOAA, 2020). Annual precipitation was above average in 2010 and 2011 at 130% and 131%, respectively (Figure 1; NOAA, 2020).

We used three pre-established grazing exclosures located in upland mixed-grass prairie sagebrush communities varying in topography and vegetation cover to examine the response of big sagebrush to large herbivore exclusion and fire. Two exclosures (Agate Ridge [6-ha] and Opuntia [3-ha]) were constructed in 1967 as split ungulate and livestock exclosures. The third (Bell Ridge [3-ha]) was constructed in 1984 as a livestock-only exclosure and converted into a split ungulate and livestock exclosure in 2005 to match the 1967 exclosures. Each exclosure was divided in half with one side fenced entirely with 3.3-m tall welded wire to exclude all native ungulate grazers and domestic livestock, thereby allowing only small mammal herbivory (from this point forwards "ungulate exclosure"). The second half of each exclosure was fenced on non-conjoining sides with four strands of wire to exclude domestic livestock and remain accessible to wild ungulate and small mammal herbivory (from this point forwards "livestock exclosure"). Outside the fenced exclosures, an adjoining area that was the same size as the grazer exclusion plots was designated as the control treatment (from this point forwards "Open") with the land open to all potential livestock, wild ungulate, and small mammal herbivory. These different types of exclosures alter the types of ungulates that have access but, more importantly, create a gradient that is variable in the amount of biomass removed by herbivores.

The three exclosure sites were classified as sagebrush/mixed-grass prairie ecological sites (NRCS, 2014), but the vegetation composition at each site varied with differences in topography among other factors. Sites were located north of the Missouri River and west of the UL Bend in the Missouri River Breaks with distances between exclosure sites ranging from 11 to 37 km. The Agate Ridge exclosure was established on a narrow ridgetop with steep barren dolomite clay slopes whereas gently sloping topography dominates the Bell Ridge exclosure. *Opuntia* was established on primarily flat terrain with low draws that have high forb expression.

The experimental design involved two factors (one with three levels and the other with two for a total of six treatments) and three replicates (the three exclosure sites) for a total of 18 experimental units. Factor one (herbivory) had three levels based on the exclosure design: (1) ungulate exclusion, (2) livestock exclusion, and (3) no exclusion (open; Figure 2). We superimposed a prescribed burn experiment on the existing grazing exclosures in 2010. Plots were split to add factor two (fire) at two levels: (1) no burn (from this point forwards "control") and (2) burn

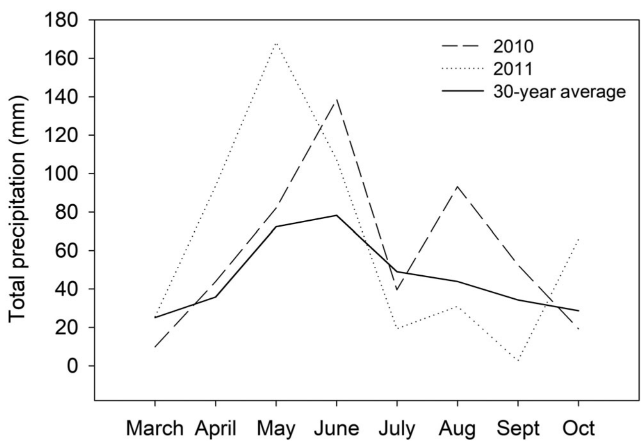

FIGURE 1 Total monthly precipitation for the 2010 and 2011 growing seasons compared with the 30-year monthly average (1981–2010). Precipitation data are from the National Oceanic and Atmospheric Administration (NOAA) weather station in Lewistown, Montana, USA (NOAA, 2020)

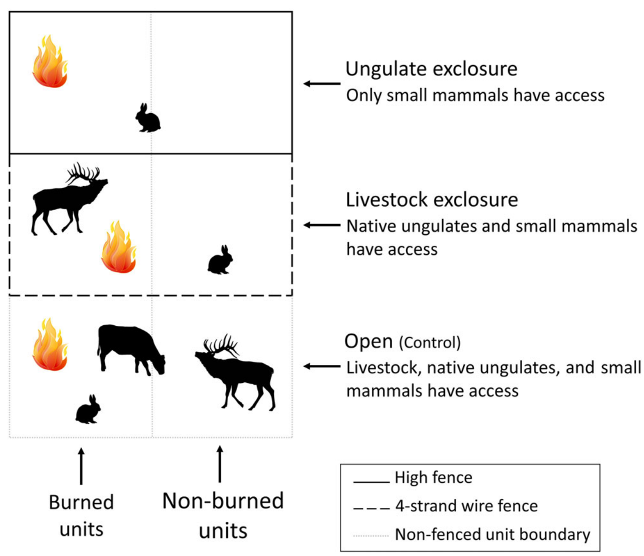

FIGURE 2 Diagram of experimental design with two factors (grazing exclusion and fire) at each of three sites in the Charles M. Russell National Wildlife Refuge (total $n = 18$). Two sites encompass 3-ha of fenced area and the third 6-ha with experimental units equal in size at each site. Here, 10 permanent sampling points were established randomly with a 5-m buffer within each experimental unit

(Figure 2). Prescribed burns were conducted on 3 August and 4 August 2010, with hourly relative humidity values ranging between 31% and 60%, air temperatures between 20–30.5°C, and winds 0–16 km h^{-1} that reflect the typical conditions of the CMR prescribed burn and wildfire season. We ignited prescribed fires with a ring-fire technique to provide the opportunity for everything within the experimental units to burn and conducted no interior ignitions. Fire rate of spread ranged from 10 to 5174 m h^{-1}, measures of fireline intensity (British Thermal Unit [BTU] m^{-1} s^{-1}) ranged from 0.3 to 2309 (BTU m^{-1} s^{-1}), and flame length (m) ranged from 0.12 to 8.35 m.

We established 10 permanent points in each experimental unit and marked them with a metal stake before sampling to record big sagebrush cover data at the same points in 2010 and 2011. The 180 points were randomly distributed with ArcGIS® 9.3 (ESRI, 2009) with a 5-m buffer to eliminate overlap in sampling at each point. At each staked point, we visually estimated the cover of Wyoming big sagebrush in a 5-m diameter circle with the stake at the center using a modified Daubenmire cover class system (1 = trace–1%, 2 = 1%–5%, 3 = 5%–25%, 4 = 25%–50%, 5 = 50%–75%, 6 = 75%–95%, 7 = 95%–100%; Daubenmire, 1959) in June of 2010 and 2011. The proportion of area burned (%) was recorded in the same 5-m circle around each stake in September 2010 following the August prescribed burn treatment. Cover classes were converted to midpoints and averaged for each experimental unit (10 points) prior to analysis.

We performed a one-way ANOVA with Tukey's b means separation on the average percentage area burned to explore differences among herbivory treatments. We also performed one-way ANOVAs to compare mean big sagebrush cover among treatments within each study year. Across year comparisons were made using independent-sample *t* tests for each treatment. To examine the degree of change in big sagebrush cover post-fire, we calculated the mean proportion of big sagebrush cover lost between years (i.e., [2010–2011 mean cover]/2010 mean cover) and omitted survey points with no pre-fire sagebrush cover and no change (i.e., increase) in 2011. We then tested for a relationship between the mean proportion of area burned and the proportion of sagebrush cover lost using regression analysis. We assessed univariate data for normality with the Shapiro–Wilk test and homogeneity of variance with Levene's test. All percent data were arcsine-square root transformed and non-transformed data are shown graphically to simplify interpretation. All results were considered significant at the 90% confidence level. IBM SPSS version 26 (IBM SPSS, Chicago, Illinois, USA) was used for all analyses.

RESULTS

Herbivore exclusion significantly affected the proportion of area burned with prescribed fire ($p = 0.06$). Areas open to all herbivores experienced the least area burned (55% ± 21%) and differed from ungulate exclusion that resulted in the most area burned (92% ± 2%, $p = 0.04$, $t = -2.55$), whereas livestock exclusion was not different from either (75% ± 12%, $p = 0.104$, $t = -1.49$; Figure 3). The linear regression indicated that the greater area burned was correlated with a larger decrease in big sagebrush cover and was significant ($R^2 = 0.76$, $p = 0.02$, $F = 25.46$; Figure 4). Big sagebrush cover was not different among grazing treatments in the non-burn treatments ($p = 0.96$, $F = 0.04$; Figure 5). However, big sagebrush cover was reduced after burning the ungulate exclosures ($p = 0.07$, $F = 4.22$) but not statistically different for any other grazing treatment ($p = 0.58$, $F = 4.22$; Figure 5).

DISCUSSION

Fire patchiness may be significant to the persistence of fire-sensitive populations in fire-prone ecosystems (Ooi et al., 2006; Whelan et al., 2002), but the mechanisms that create patchiness are poorly understood. Large herbivores remove biomass, thereby reducing fuel load and altering fuel structure that has the potential to increase

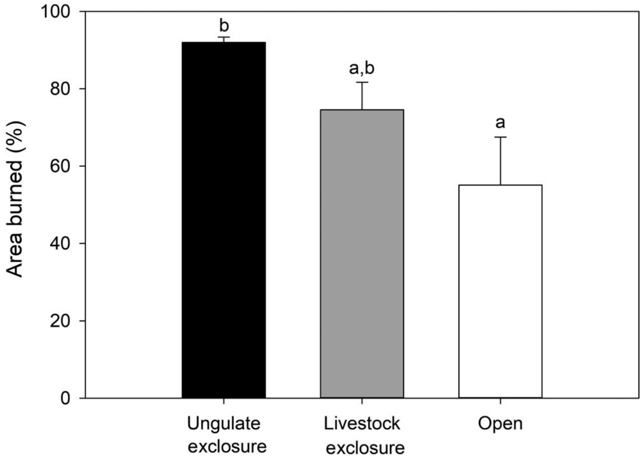

FIGURE 3 Mean proportion of area burned (%) by herbivory treatment in 2010 in the Charles M. Russell National Wildlife Refuge (non-transformed data shown). Different letters indicate statistical differences ($p < 0.10$). Error bars represent standard error of the mean. Prescribed fire burned less area in experimental units open to all potential herbivores (i.e., cattle and wild ungulates), whereas area excluded from all large ungulates burned more completely. Therefore, fires in openly grazed areas are likely to be patchier in nature

patchiness and create pockets of fire refugia within the fuel matrix. Evidence from the long-term exclosures examined in our study agrees with others in demonstrating that long-term herbivory alters fire dynamics (Kerby et al., 2007; Werner et al., 2021). Although we did not measure patchiness directly, our results are consistent in suggesting that grazed areas burn less completely than areas excluded from grazing and, therefore, experience patchier fires (Hobbs & Norton, 1996; Strand et al., 2014; Zimmerman & Neuenschwander, 1984). Our findings also suggest that within a northern fire-dependent mixed-grass prairie ecosystem, areas with patchy fire spread support greater persistence of a fire-sensitive shrub. Collectively, these data provide support for the theory that large herbivores can create refugia within a flammable fuel matrix through their alterations to fuel bed conditions and fire behavior (Kerby et al., 2007; Werner et al., 2021).

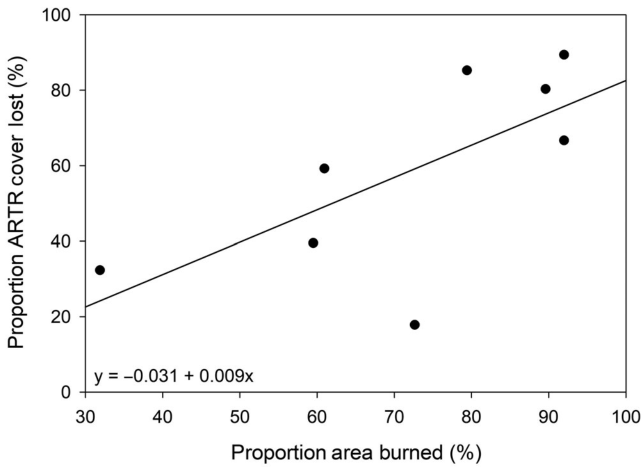

FIGURE 4 Linear regression of the relationship between the mean proportion of big sagebrush *Artemisia tridentata* (ARTR) cover lost (%) and the proportion of area burned (%) at the Charles M. Russell National Wildlife Refuge between 2010 and 2011. The regression was significant at $p = 0.05$ with arcsine-square root transformed data ($R^2 = 0.76$, $y = -0.0482 + 0.9876x$). Non-transformed data are shown. The proportion of big sagebrush cover lost due to fire increases as the proportion of area burned increases, which is correlated with herbivore access (Figure 3)

The presence of domestic and wild ungulates decreased the amount of area burned when the vegetation matrix was subjected to prescribed fire. The ability of herbivory to directly alter and reduce fuel load is recognized and applied to landscapes to reduce wildfire risk and fire intensity (Davies et al., 2010; Diamond et al., 2009; Lovreglio et al., 2014; Starns et al., 2019; Zimmerman & Neuenschwander, 1984). Trampling, trailing, defecation, and grazing by herbivores and other animals can also alter fuel bed structure and condition but the effects of these activities are less understood (Foster et al., 2020). Fuel continuity is an important component of fuel structure that affects the ability of fire to spread across a landscape as a percolation process (Caldarelli et al., 2001). Where there is enough of a break in fuel continuity to cause local extinguishment of a fire front from abiotic factors or animal activities, unburned patches can remain within a fire perimeter (Morandini & Silvani, 2010). Fires in the CMR are rarely homogeneous, leaving upward of 90% of the area unburned within prescribed fire boundaries and up to 28% with wildfires in recent history (Reid & Fuhlendorf, 2011). Average unburned area within our grazed plots ranged from 25% to 45%, whereas the areas excluded from all ungulate grazing experienced more homogeneous burns with ~8% of the area remaining

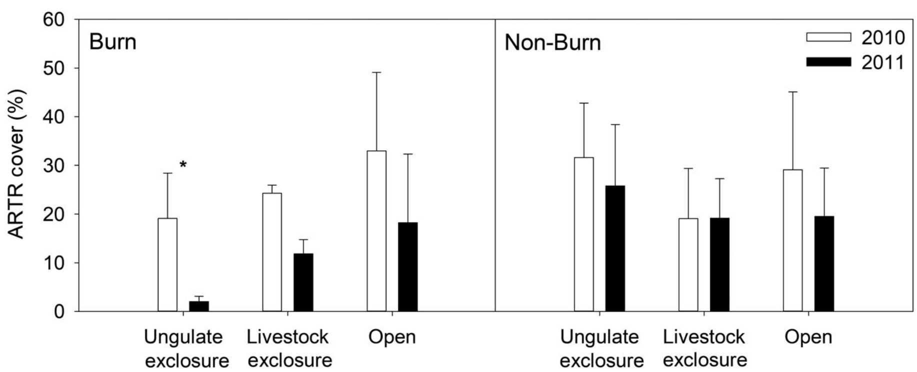

FIGURE 5 Mean big sagebrush *Artemisia tridentata* (ARTR) cover in 2010 and 2011 for burned and non-burned plots by respective herbivore exclusion treatment in the Charles M. Russell National Wildlife Refuge (non-transformed data shown). Note that 2010 burned plots represent pre-fire values as the plots were burned 1 month after data collection. Asterisks (*) represent significant *t* test results for a single treatment between years. Error bars represent standard error of the mean. There were no differences between 2010 and 2011 averages in the non-burn plots indicating a lack of an influence of yearly variation on big sagebrush cover. Therefore, the difference in cover between 2010 and 2011 in the plots open to all grazers is correlated with the prescribed fire treatment at that level of herbivory

unburned on average. It is most likely that these differences are attributed to increased fire potential due to greater fuel accumulation and height in ungrazed areas and reduced fuel continuity and fire potential in grazed areas (Davies et al., 2010; Leonard et al., 2010). Moreover, this study provides evidence that the activities of large herbivores are likely to reduce fire spread and intensity through their alterations to the fuel bed.

Exposure to fire readily kills big sagebrush plants, so its persistence within our burned plots implies the existence of refugia within the fuel matrix as expected (Ooi et al., 2006). Our study involved only a single burn during the growing season, so the response of the overall population to recurring fire warrants further investigation to fully understand its long-term persistence and population trends related to herbivory and recurring fire. It is not clear how a different fire regime, such as multiple fires over a series of growing seasons, or a longer time since fire would influence the results. Moreover, the season of the fire can influence patchiness (Price et al., 2003) and critical events in the life cycle of fire-sensitive populations may override patchiness and other factors in determining their response to fire (Bradstock et al., 1996). Studies involving multiple seasons of fire during varying life stages of Wyoming big sagebrush will be important to provide thorough management prescriptions regarding fire timing. Additionally, understanding the effects of herbivory on specific characteristics of fuels and fire behavior will reveal the mechanisms driving the reduction in percentage area burned. Generally, we argue that the response of fire-sensitive plant populations to fire is likely to be modulated by the presence of large herbivores and their ability to create heterogeneity in fuel load and structure, fire intensity, and fire patchiness.

The effects of herbivory on the proportion of area burned differed across herbivore groups. Specifically, the exclusion of all large herbivores resulted in more complete burns, whereas burns in areas open to all potential herbivores were less complete. Excluding only livestock, however, did not elicit a statistical difference in percentage area burned from areas open to all potential herbivores or areas excluded from all potential herbivores. The behavior and diet preferences of large herbivores can have contrasting effects on vegetation composition and structure that vary seasonally (Veblen & Young, 2010; Veblen et al., 2015), but may have been masked by other abiotic factors (e.g., above-average precipitation, location, soils; Davies et al., 2007; Reed et al., 2009) in our study. Regardless, others have found that cattle can serve as "surrogate wildlife" with qualitative similarities in their impacts on vegetation communities, as well as fire behavior (Veblen et al., 2016; Werner et al., 2021). Herbivore guilds utilize burned areas in different ways (Sensenig et al., 2010) and may have additive or complementary effects when examined at different scales.

When regarding livestock as "surrogate wildlife," stocking rate must be considered because it is known to influence vegetation structure. Stocking rate was not a factor examined in this study but, without accounting for wild ungulates, mixed-grass prairie plant communities are resilient and livestock grazing is slow to alter plant community composition (Limb et al., 2018). However, the long-term removal of livestock grazing (idle management) has been associated with considerable ramifications for the mixed-grass prairie, including reduced species richness, increased abundance of invasive species, and alterations in vegetation structure such as increased litter (Limb et al., 2018; Toledo et al., 2014). Furthermore, it is important to recognize that changes in grazing management often require several years to generate noticeable differences in vegetation structure and composition (Connell et al., 2018; Veblen et al., 2016), whereas exclosure ages ranged between 5 and 53 years in this study. Therefore, studies involving replicates of exclosure age and variations in livestock grazing intensity accompanied by the presence of wild ungulate grazers will provide critical information for land managers. Fine-resolution studies comparing herbivore effects on vegetation structure in sagebrush ecosystems of the mixed-grass prairie could also reveal the factors affecting differences in percentage area burned.

Woody encroachment is increasingly an issue for grassland ecosystems across the globe with an array of consequences for various ecosystem services (Archer et al., 2017; Eldridge et al., 2011). Fire suppression, increased atmospheric CO_2 and outdated land management strategies, including certain grazing regimes, promote this encroachment although its impacts threaten livestock production (Limb et al., 2014, 2016; Stevens et al., 2017). Restoring the disturbances that historically maintained grassland ecosystems (i.e., fire and grazing) has been regarded as the most appropriate avenue for controlling woody species as they are generally fire sensitive and have proliferated into grassland ecosystems due to a prolonged history of fire suppression. However, the restoration of historic fire regimes could result in a decline of more desirable, native fire-sensitive species including big sagebrush. We find that maintaining adequate levels of grazing through domesticated livestock and/or access by managed populations of wild herbivores may create sufficient refugia to support big sagebrush communities, while also aiding the control of woody invaders such as eastern red cedar, rocky mountain juniper, ponderosa pine, and western snowberry (Barger et al., 2011; Grant & Murphy, 2005; Limb et al., 2018; Symstad & Leis, 2017).

MANAGEMENT IMPLICATIONS

Our findings are limited to the short-term response of Wyoming big sagebrush communities in the northern Great Plains, but highlight the resiliency of this ecosystem to disturbance by large herbivores and fire. We found that Wyoming big sagebrush, although fire intolerant, is capable of persisting in fire-prone landscapes due to the modulating forces applied to fuels and fire behavior by large herbivores. Moreover, these findings imply that pre-fire management with herbivory has the potential to reduce the impact of wildfires on fire-sensitive species and is likely to aid in the conservation of the fauna that depend on them. Our findings also support the argument for heterogeneity as the basis for rangeland management, as it reveals that heterogeneity in fuels and fire behavior may be critical to the persistence of a keystone plant species. Increasing our understanding of the drivers of heterogeneity at all scales in grassland ecosystems and considering management practices that enhance it will further the improvement of the management of these important landscapes (Fuhlendorf & Engle, 2004).

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data (Limb et al., 2022) are available from Figshare: https://doi.org/10.6084/m9.figshare.18622880.v1.

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