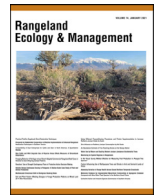


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Dormant-Season Moderate Grazing Prefire Maintains Diversity and Reduces Exotic Annual Grass Response Postfire in Imperiled *Artemisia* Steppe[☆]



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ABSTRACT

Grazing and fire are both independently important drivers of plant community dynamics; however, their interactive effects may be even more influential. Little is known about prefire grazing effects on postfire plant community dynamics. We investigated the effects of dormant-season, moderate prefire grazing by cattle on postfire plant community response in the imperiled *Artemisia* (sagebrush) steppe. Treatments were moderately grazed or not grazed by cattle for 5 yr before fire. The first yr post fire, shrub density was 4 × greater in grazed areas, demonstrating fire-induced mortality was reduced with grazing. This further suggested that grazing reduced fire severity and postfire large bunchgrass biomass was greater in grazed compared with ungrazed areas. Biomass and abundance of the exotic annual grass, *Bromus tectorum* L., were substantially greater and plant diversity was lower in ungrazed compared with grazed areas post fire. Five years post fire, perennial herbaceous vegetation still dominated prefire-grazed areas, but ungrazed areas were dominated by *B. tectorum*, suggesting that a novel ecosystem state had developed. Substantial increases in *B. tectorum* are concerning because it prevents recruitment of native perennial plants and increases fire frequency, which would further decrease diversity and reinforce an exotic annual-dominated state. Lower diversity in ungrazed areas post fire is concerning because diversity can be important for plant community stability. The importance of livestock as ecological engineers through their influence on fire has largely been overlooked but is clearly substantial and needs to be integrated into conservation and management plans.

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Introduction

Grazing and fire are powerful ecological forces that shape and define plant communities. Though both grazing and fire independently influence ecological processes in many terrestrial ecosystems, their interactive effects are probably more important than their independent effects. A copious amount of research has investigated recoupling fire and grazing (e.g., Fuhlendorf and Engle 2004; Fuhlendorf et al. 2006; Kerby et al. 2007; Koerner and Collins 2014; Starns et al. 2019). This fire-grazing interaction can promote diversity and heterogeneity (Pillbury et al. 2011; Winter et al. 2012), maintain grasslands and savannahs (Capozzelli et al. 2020), and modify future fire risk and behavior (Starns et al. 2019). Postfire grazing is undoubtedly a major driver of ecosystem processes and services in many ecosystems. Grazing, however, also occurs before fire and likely influences plant community postfire dynamics.

Effects of prefire grazing, with a few exceptions, on plant community response to fire have been overlooked or are confounded with postfire grazing effects. Livestock grazing can modify the amount, continuity, structure, and composition of fuels (Davies et al. 2010, 2015; Bernardi et al. 2019; Foster et al. 2020). Though grazing may produce positive and negative effects on flammability (Blackhall et al. 2017), most of these livestock-induced changes to fuel characteristics decrease incidents of fire (Blackhall et al. 2017; Bernardi et al. 2019; Foster et al. 2020) and alter fire behavior and severity (Davies et al. 2016a; Foster et al. 2020). Grazing-induced effects on fire severity, through fuel modification, could be a major determinant of postfire plant community assembly and future trajectory.

In western North America, cattle, an introduced herbivore, and infrequent fire are nearly ubiquitous across the *Artemisia* (sagebrush) ecosystem. Fire is a periodic disturbance in this ecosystem with historical fire return intervals varying from over a century to around a quarter century in drier and more mesic *Artemisia* communities, respectively (Wright and Bailey 1982; Mensing et al. 2006). *Artemisia tridentata* Nutt. subsp. *wyomingensis* Beetle and A. Young (Wyoming big sagebrush) is dominant in drier environments

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of the *Artemisia* steppe, and these communities are generally less resilient to disturbance (Davies et al. 2011; Chambers et al. 2014). Historically, fires shifted dominance from *Artemisia* to herbaceous vegetation and, as time since fire increased, *Artemisia* would re-dominate these sites until the next fire (Wright and Bailey 1982). However, vegetation succession has been greatly modified by exotic annual grass invasion of some *A. t.* subsp. *wyomingensis* communities after fire.

Exotic annual grasses are of great concern across the western United States. *Bromus tectorum* L. (cheatgrass) is one of the most problematic exotic annual grasses in the *Artemisia* ecosystem, where it has invaded tens of millions of hectares (Bradley and Mustard 2005; Meinke et al. 2009). Invasion by *B. tectorum* can represent a fundamental shift in the plant community to a novel state, an exotic annual grassland. Fire frequency is often substantially increased with *B. tectorum* invasion (Stewart and Hull 1949; D'Antonio and Vitousek 1992; Balch et al. 2013) because it increases highly flammable fine fuels that dry out earlier than native vegetation (Davies and Nafus 2013). More frequent fire is an ecosystem alteration that promotes further invasion and perpetuates exotic annual grass dominance—in other words, the development of an exotic annual grass–fire cycle (D'Antonio and Vitousek 1992). As *B. tectorum* or other exotic annual grass species increase, the capacity to return to a native perennial-dominated plant community is depleted because native vegetation is unlikely to establish in exotic annual grass–dominated communities and frequent fire associated with these invasions further reduces native perennial vegetation that are not adapted to this novel fire regime (D'Antonio and Vitousek 1992).

The effects of the interaction between grazing and fire on *Artemisia* communities are not clear and likely vary by grazing management. Both fire and long-term heavy, repeated growing season grazing (hereafter referred to as heavy grazing) by livestock, independently, have been linked to *B. tectorum* and other exotic annual grass invasions in *Artemisia* communities (Mack and Thompson 1982; Chambers et al. 2007; Chambers et al. 2014). The combination of fire and heavy grazing decreases the resistance of *Artemisia* communities to *B. tectorum* by reducing native perennial bunchgrasses (Condon and Pyke 2018). Heavy grazing decreases large perennial bunchgrasses in interspaces between shrub canopies, resulting in remaining large perennial bunchgrasses clustered under shrub canopies (Reisner 2010), where they are much more susceptible to fire-induced mortality because woody fuels burn hotter and longer (Boyd et al. 2015; Davies et al. 2016a). Decreases in large perennial bunchgrasses are concerning because they are the dominant herbaceous plant functional group (Davies et al. 2006) and are critical to limiting exotic annual grasses in these communities (Chambers et al. 2007). Undoubtedly, heavy grazing can deplete the native understory, but this information does little to illuminate the effects of other types of grazing.

Contemporary, moderate grazing, especially dormant-season grazing, effects on *Artemisia* communities are less clear. Moderate grazing is 40–60% utilization of available forage that is either alternated between the growing season and dormant season or occurs entirely in the dormant season. Moderate grazing generally has minor if any effects on the composition or density of vegetation in *Artemisia* steppe (West et al. 1984; Courtois et al. 2004; Davies et al. 2009; Copeland et al. 2021) but can alter fuel characteristics (Davies et al. 2010, 2015, 2018) and subsequently fire intensity and severity (Davies et al. 2016a). Consequently, it seems reasonable that moderate grazing could modify plant community response to fire through its influence on prefire fuel characteristics. In support of this idea, one study, with a limited sample size ($n=3$), found that long-term (+50 yr) grazing exclusion compared with moderate grazing decreases postfire exotic annual grasses response and maintains perennial dominance (Davies et al. 2009). Further tests

of moderate grazing effects on postfire plant community dynamics are needed in general and, in particular, evaluations of dormant-season grazing effects.

The purpose of this study was to investigate the influence of dormant-season moderate prefire grazing by cattle on postfire plant community dynamics. In our study ecosystem, substantial postfire increases in *B. tectorum* and declines in perennial vegetation, especially large perennial bunchgrasses, can lead to the development of a novel ecosystem state. We hypothesized that prefire grazing maintains perennial dominance in these communities by modifying fuel characteristics, leading to reduced fire severity and associated declines in native perennial vegetation and risk of conversion to an exotic annual grass-dominated state. Specifically, we expected that after fire, prefire moderately grazed areas compared with ungrazed areas would have 1) lower *B. tectorum* abundance and biomass, 2) greater large perennial bunchgrass abundance and biomass, 3) greater shrub abundance, and 4) greater diversity and species richness.

Materials and Methods

Study area

This study was implemented on sagebrush rangelands near the Diamond Craters in southeastern Oregon (43°04'N, 118°40'W). Plant communities were shrub-bunchgrass–dominated steppe with *Artemisia tridentata* subsp. *wyomingensis* being the dominant shrub across all study sites. Other shrubs included *Artemisia arbuscula* Nutt. (low sagebrush), *Ericameria* Nutt. (rabbitbrush sp.), and *Tetradymia* DC. (horsebrush sp.). The dominant bunchgrass was *Achnatherum thurberianum* [Piper] Barkworth (Thurber's needlegrass) or *A. thurberianum* was codominant with *Pseudoroegneria spicata* [Pursh] A. Löve (bluebunch wheatgrass) depending on the study site. Other common bunchgrasses included *Poa secunda* J. Presl (Sandberg bluegrass), *Elymus elymoides* [Raf.] Swezey (squirreltail), and *Achnatherum hymenoides* [Roem. and Schult.] Barkworth (Indian ricegrass). *B. tectorum* occurred in low abundance across the study area before treatment application. Long-term (1980–2010) average annual precipitation at the study area was 280 mm (PRISM 2020). The majority of precipitation events occur in the winter and spring, and summers are typically dry and hot. Crop year (October–September) precipitation was below average in the immediate years before burning and near average in the 3 yr following burning (Fig. 1). Study sites were relatively flat and elevation was approximately 1 450 m. Study sites occurred on two ecological sites: Sandy Loam 10–12 PZ (R023XY213OR) and Droughty Loam 11–13 PZ (R023XY316OR) Ecological Sites (NRCS 2013). The wildfire season generally spans from July to mid to late September depending on interannual climate (Davies and Nafus 2013; NIFC 2021). Fire occurrence was infrequent before European settlement for these *Artemisia* communities with fire return intervals estimated to be 50–100+ yr (Wright and Bailey 1982; Mensing et al. 2006).

Experimental design

We evaluated the effect of prefire, dormant-season moderate grazing on postfire vegetation response using a randomized complete block design with five blocks. We selected blocks that occurred in winter-grazed pastures, were sagebrush-bunchgrass–dominated communities, and were large enough for treatment plots to occur on the same site characteristics. The five blocks varied in site (soil, aspect, and slope) and vegetation characteristics, but treatment plots within blocks did not differ in site or vegetation characteristics before treatment applications (Davies et al. 2015, 2016c). Each block consisted of one grazed and ungrazed

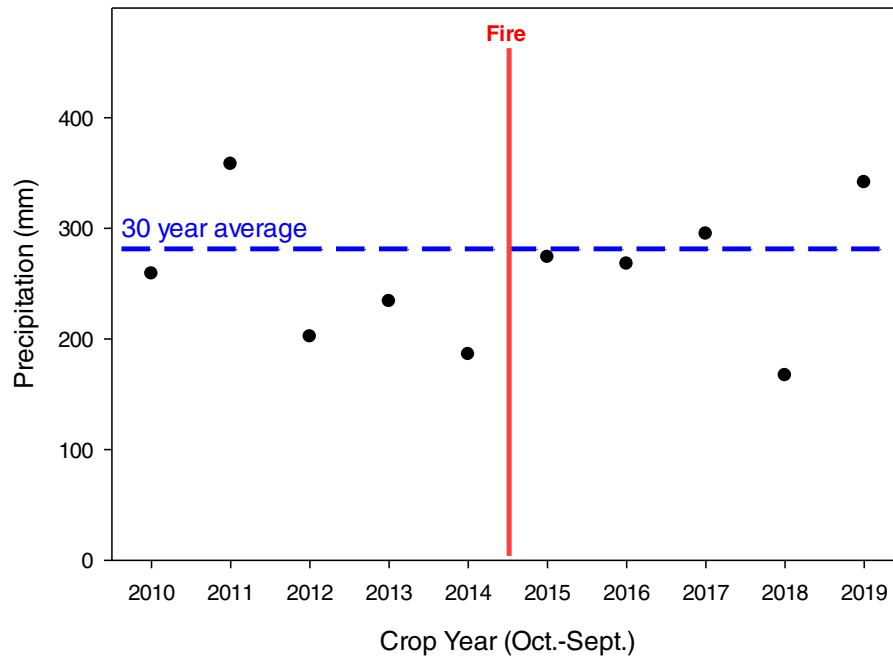


Figure 1. Crop year (October–September) precipitation (PRISM 2020) before and after prescribed fire (red line) with the 30-yr (1980–2010) annual average (blue dashed line) at the study area near Diamond Craters in southeastern Oregon.

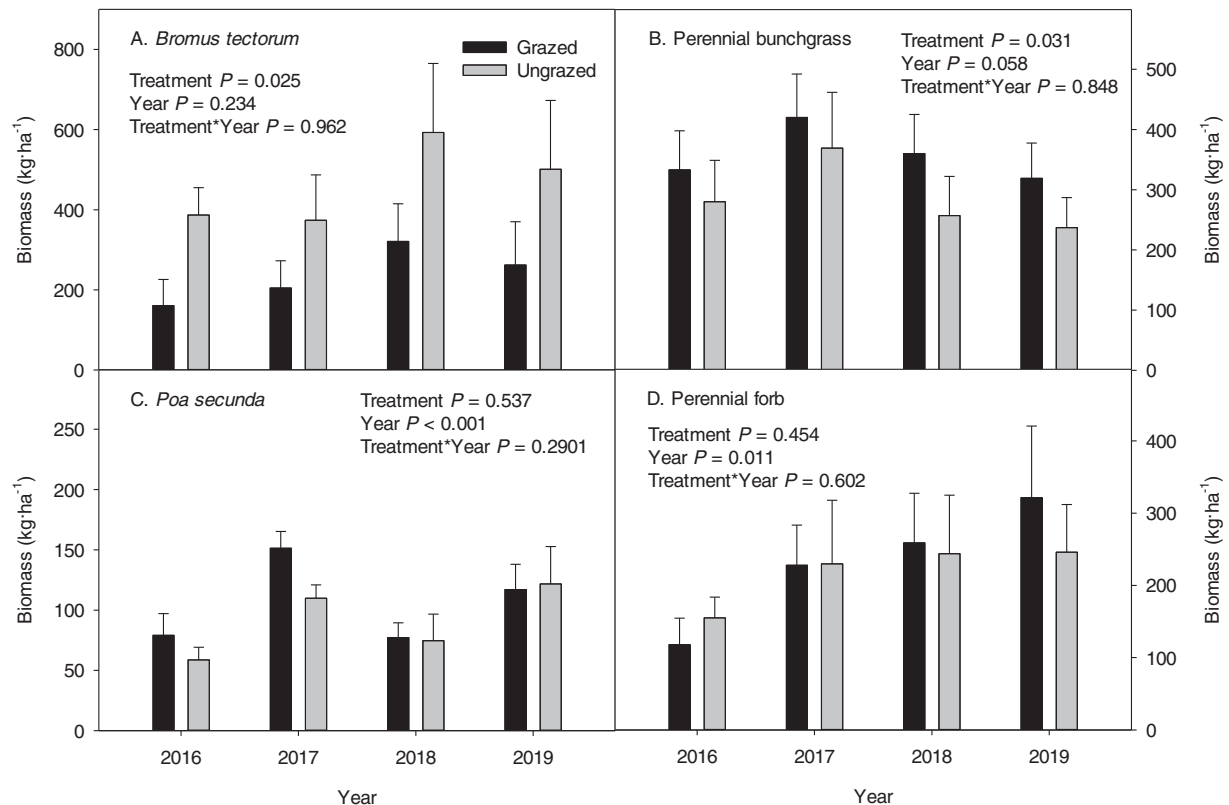


Figure 2. A–D, Annual biomass (mean + standard error) for plant functional groups in prefire grazed and ungrazed areas for 2–5 yr post fire (2016–2019).

treatment plot. Treatments were randomly assigned to 50 × 50 m plots per block that were separated by a 10-m buffer. Treatments (prefire moderately grazed or ungrazed) were applied for 5 yr before being burned. Before burning, sagebrush cover averaged 11% (Davies et al. 2016a). Before burning, total herbaceous biomass was 361 and 632 kg·ha⁻¹, litter biomass was 141 and 420

kg·ha⁻¹, and sagebrush biomass was 3 660 and 3 860 kg·ha⁻¹ in grazed and ungrazed treatments, respectively (Davies et al. 2016a). Large perennial bunchgrass and exotic annual grass density and annual production were similar between grazed and ungrazed areas (Davies et al. 2016c). The ungrazed treatment was applied by establishing 60 × 100 m enclosures inside of large (~800–1 000 ha)

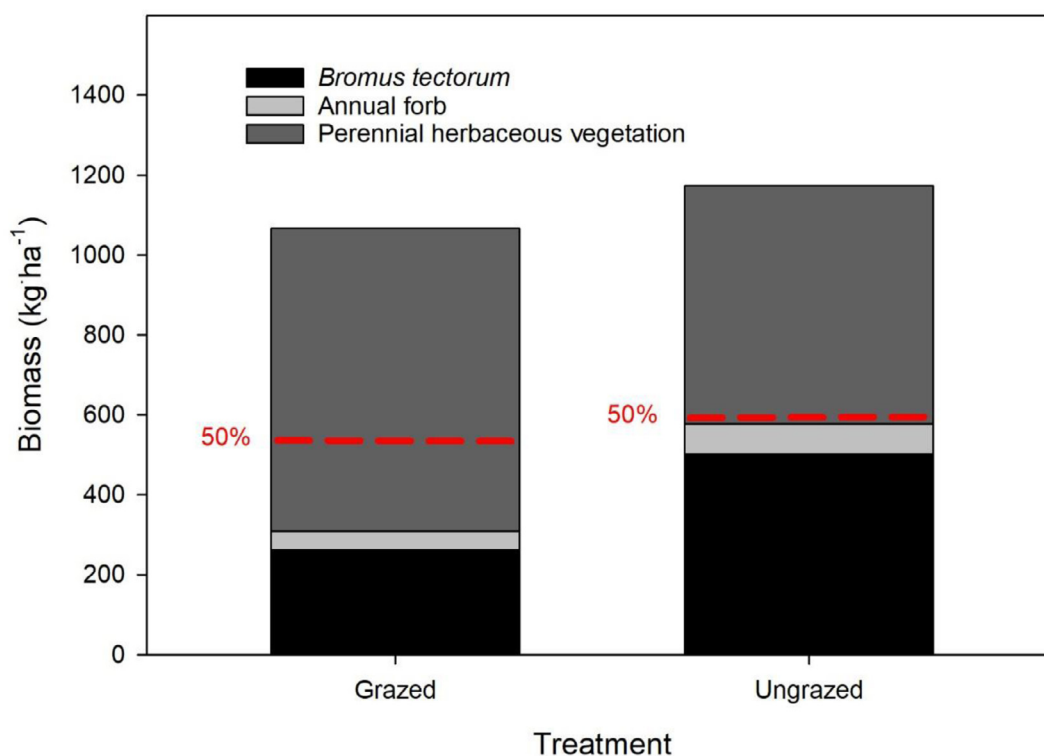


Figure 3. Biomass contributions from annual (annual forb and *Bromus tectorum*) and perennial herbaceous vegetation in prefire grazed and ungrazed areas in the final yr (5 yr post fire) of the study (2019). Red dashed line marks 50% of the total biomass in each treatment.

management units. Grazing by cattle was applied at the management unit level to ensure that results were reflective of and applicable to land management scenarios. Grazing rotation varied across years, between November and early April (predominantly the dormant season), in accordance with the grazing schedule for the larger management unit. Utilization (forage consumption) by cattle was between 40% and 60% based on biomass in each grazed plot, quantified using the method describe in Anderson and Curreir (1973). Prescribed burns were applied at the end of the wild-fire season on September 23, 2014 (Davies et al. 2016a). Both treatments in a block were burned simultaneously and were applied as head fires using drip torches for ignition. During prescribed burns, wind speed ranged from 2.4 to 20.4 km•h⁻¹, relative humidity was between 17 and 35%, and air temperature ranged between 22.8°C and 27.2°C (Davies et al. 2016a). After prescribed burning, grazing was ceased for the remainder of the study to prevent postfire grazing effects from confounding prefire grazing effects.

Fire intensity and severity differed between treatments because of differences in fuel characteristics induced by grazing (Davies et al. 2015, 2016a). Prefire grazing reduced maximum temperature and heat load experienced at the meristematic crowns of perennial bunchgrasses during burning compared with ungrazed areas (Davies et al. 2016a). Maximum fire temperature was approximately 100°C greater in ungrazed compared with grazed areas (Davies et al. 2016a). Shrub fuel consumption during fires was greater in the ungrazed compared with the grazed treatment (Davies et al. 2016b). Shrub biomass remaining post fire was 1 183 kg•ha⁻¹ less in ungrazed compared with grazed areas (Davies et al. 2016b). These results suggest that fires were more severe and intense in ungrazed compared with grazed areas.

Measurements

Vegetation characteristics were measured in June of each yr from 2015 to 2019. Biomass was not sampled in 2015 because we

did not want to add extra stress to plants that were recovering from burning. Herbaceous biomass was measured by clipping 15 randomly located 1-m² quadrats in each treatment plot. If a randomly located 1-m² quadrat occurred on an already clipped area, that quadrat was moved 5 m to the east. Biomass was clipped by plant functional groups: *B. tectorum* (the only exotic annual grass), large perennial bunchgrass, *P. secunda*, perennial forb, and annual forb. Harvested biomass was oven-dried at 50°C for 72 h, separated into current and prior years' growth, and weighed. Four, 45-m transects spaced at 5-m intervals were established in each plot for vegetation density measurements. Herbaceous vegetation density by species was measured in 40 × 50 cm quadrats located at 3-m intervals on each 45-m transect, resulting in 15 quadrats per transect and 60 quadrats per plot. Perennial bunchgrasses were considered individuals if > 3 cm existed between clumps. Shrub density was measured by counting all individuals rooted in a 2 × 45-m belt transect positioned over each 45-m transect. Diversity was calculated from species density measurements summarized at the plot level using the Shannon Diversity Index (Krebs 1998). Species richness was determined by counting all species found in a plot during density sampling.

Statistical analysis

Repeated-measure analysis of variance (ANOVA) using the mixed-models procedure (Proc Mixed SAS v. 9.4, SAS Institute, Cary, NC) was used to determine the effects of prefire grazing on postfire vegetation response. Random variables in models were block and block-by-treatment interactions. Year was the repeated variable and treatment was considered the fixed variable. Akaike's Information Criterion was used to select the appropriate covariance structure for repeated-measures ANOVA (Littell et al. 1996). For all analyses, vegetation measurements were summarized to the plot level. For analyses, vegetation was separated into six plant functional groups: *B. tectorum*, *P. secunda*, large perennial bunchgrasses,

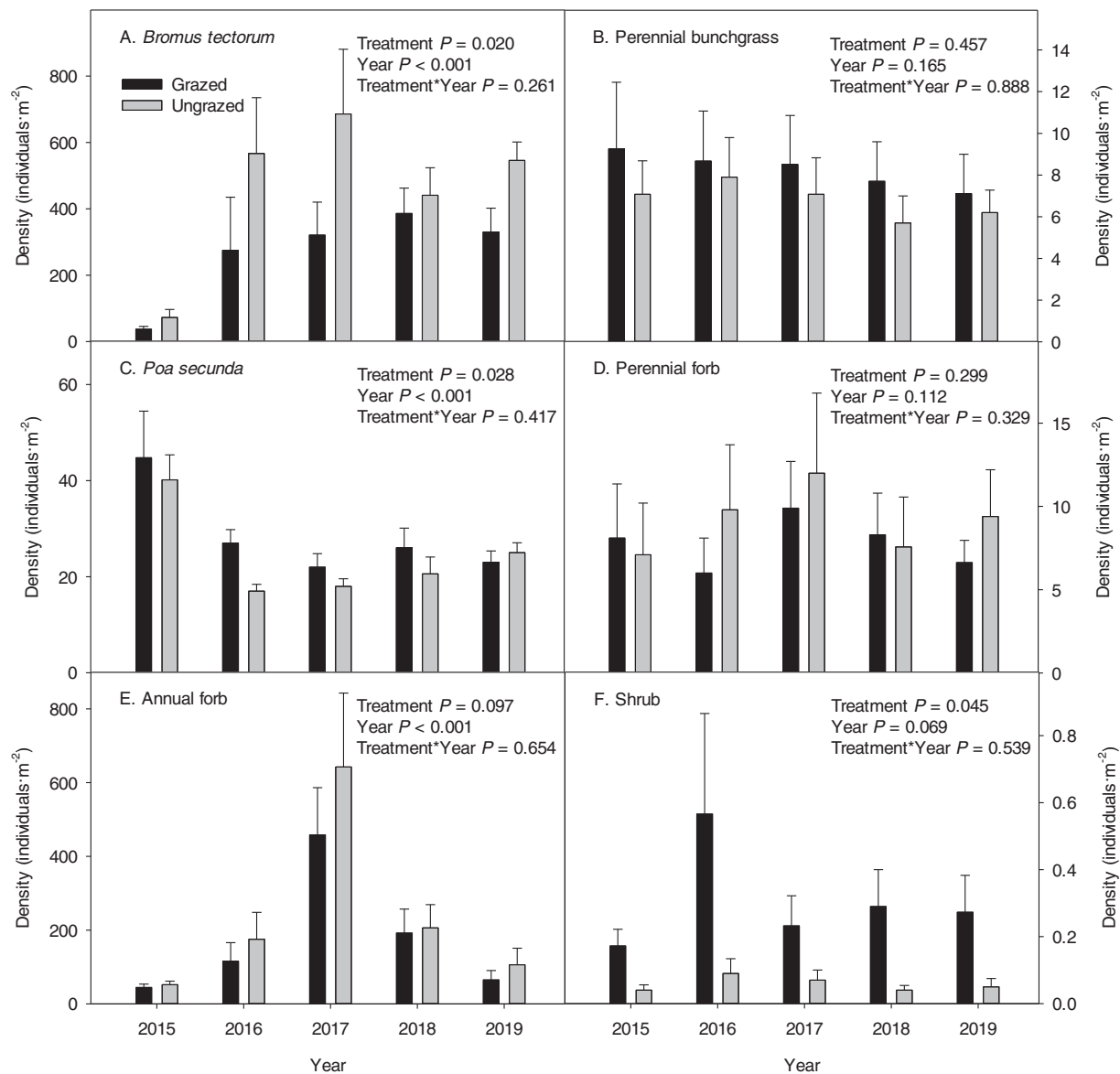


Figure 4. Density (mean + standard error) for plant functional groups in prefire grazed and ungrazed areas for 1–5 yr post fire (2015–2019).

perennial forbs, annual forbs, and shrubs. *P. secunda* was separated from other bunchgrasses because it is generally smaller in stature, develops phenologically earlier, and responds differently to grazing and fire (McLean & Tisdale 1972; Yensen et al. 1992). Data that did not meet assumptions of ANOVA were square-root transformed. All figures and text present original, nontransformed data. Means were reported with standard errors in figures and text. Statistical significance was set at $P \leq 0.05$.

Results

Biomass

B. tectorum biomass was greater in ungrazed compared with grazed areas post fire (Fig. 2A; $P=0.025$). Averaged across post-fire sample years, *B. tectorum* biomass in ungrazed areas was twice that of grazed areas. *B. tectorum* biomass did not vary among years ($P=0.234$). In contrast to the *B. tectorum* response, biomass of large perennial bunchgrass was greater in grazed compared with ungrazed areas (see Fig. 2B; $P=0.031$). At the end of the

study, bunchgrass biomass was 35% greater in grazed compared with ungrazed areas. We found limited evidence that bunchgrass biomass varied among years ($P=0.058$). *P. secunda* and perennial forb biomass did not differ between treatments (see Fig. 2C and 2D; $P=0.537$ and 0.454) but varied among years ($P < 0.001$ and 0.011). *P. secunda* biomass fluctuated from year to year, but perennial forb biomass appeared to increase with time since fire. Biomass of annual forbs did not differ between treatments or vary among years ($P=0.415$ and 0.372). Annual forb biomass averaged $84 \pm 17 \text{ kg} \cdot \text{ha}^{-1}$ and $128 \pm 39 \text{ kg} \cdot \text{ha}^{-1}$ in grazed and ungrazed areas, respectively. At the end of the study, annual vegetation (largely *B. tectorum*) contributed ~50% of the total herbaceous biomass in ungrazed areas but only ~30% in grazed areas (Fig. 3).

Density and diversity

Density of *B. tectorum* differed between treatments and varied among years (Fig. 4A; $P=0.020$ and < 0.001). *B. tectorum* density was 1.7-fold greater in ungrazed compared with grazed areas at the conclusion of the study. *B. tectorum* density was low-

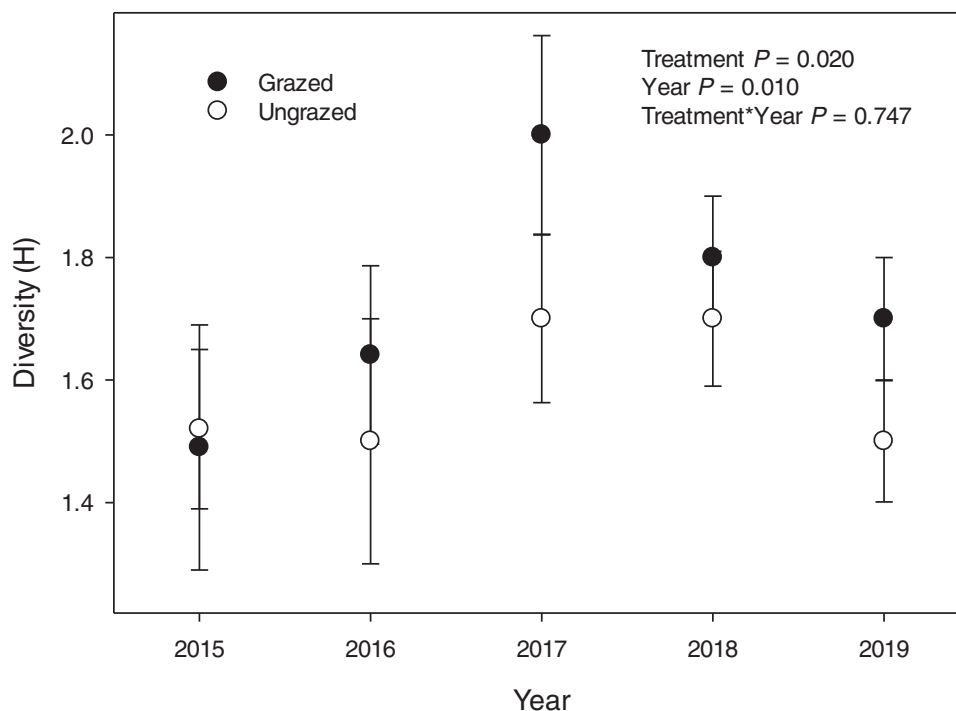


Figure 5. Shannon diversity index (H) (mean \pm standard error) after fire in prefire grazed and ungrazed areas from 2015 to 2019.

est the first postfire year and then appeared to fluctuate with interannual climatic conditions. Large perennial bunchgrass density did not differ between treatments or vary among years (see Fig. 4B; $P=0.457$ and 0.165). Density of *P. secunda* differed between treatments and varied among years (see Fig. 4C; $P=0.028$ and < 0.001). *P. secunda* density was generally greater in grazed compared with ungrazed areas, but the difference was small. Perennial forb density was not influenced by treatment and did not vary among years (see Fig. 4D; $P=0.299$ and 0.112). Annual forb density did not differ between grazed and ungrazed areas (see Fig. 4E; $P=0.097$) but did vary among years ($P < 0.001$). Annual forb density was lowest in the first year post fire and then varied with interannual climatic conditions. Density of shrubs was greater in grazed compared with ungrazed areas (see Fig. 4F; $P=0.045$) but did not vary among years ($P=0.069$). The first year post fire, shrub density was 4.3-fold greater in grazed compared with ungrazed areas. At the end of the study, shrub density was 5.5-fold greater in grazed compared with ungrazed areas.

Diversity was generally greater in grazed compared with ungrazed areas (Fig. 5; $P=0.020$) and varied among years ($P=0.010$). Species richness did not differ between grazed (24.44 ± 0.95 species \cdot plot $^{-1}$) and ungrazed areas (23.28 ± 0.83 species \cdot plot $^{-1}$) ($P=0.401$). Species richness varied among years ($P < 0.001$), but no clear pattern emerged.

Discussion

Grazing and fire have an interactive role that has a strong top-down influence on plant communities. In support of our hypothesis, dormant-season moderate prefire grazing helped maintain perennial vegetation dominance in sagebrush communities at risk of conversion to exotic annual grasslands. In contrast, in ungrazed areas, exotic annual grasses increased substantially post fire. These results are similar to results reported in Davies et al. (2009). Dissimilar to Davies et al. (2009), grazing was excluded for a much shorter period of time in the ungrazed treatment and grazing was only applied during the dormant season in the grazed treatment.

The results are also important because prefire grazing effects were reaffirmed in another location, in a different year, and with different fire conditions. Livestock in this scenario acted as ecological engineers that strongly influenced the postfire response of these plant communities. This was achieved through grazing effects on fuels and, consequently, fuel effects on fire severity.

Fires were more severe in prefire ungrazed areas compared with prefire moderately grazed areas. Before burning, ungrazed areas had more than double the biomass of fine fuels because of accumulations of prior years' growth (Davies et al. 2015). Similarly, grazing exclusion resulted in $5 \times$ as much prior years' growth in rangelands in eastern Montana (Vermeire et al. 2018). The accumulation of fuel in our system was especially noticeable on meristematic crowns of large perennial bunchgrasses where fine fuel biomass was $2.5 \times$ greater in ungrazed compared with grazed areas (Davies et al. 2015). Consequently, when ungrazed areas burned, maximum fire temperature and heat load (degree seconds $\geq 60^\circ\text{C}$) at bunchgrass crowns were approximately 100°C and 1.7 to $2.2 \times$ greater, respectively (Davies et al. 2016a). Greater fire temperatures and longer periods of elevated temperatures increase the likelihood of fire-induced mortality of perennial vegetation (Wright and Klemmedson 1965; Odion and Davis 2000; Pelaez et al. 2001; Vermeire and Roth 2011). This was observed in our study where more intense fires in ungrazed compared to grazed areas resulted in less perennial vegetation abundance; most noticeably, when examining the response of dominant plant functional groups, i.e. shrubs and large perennial bunchgrasses. Shrub density was $4 \times$ greater in grazed compared with ungrazed areas in the first growing season following fire, providing strong evidence that fire-induced mortality was substantially greater in ungrazed areas. In the first postfire year, shrub density was 37.5% and 13.3% of prefire shrub density in the grazed and ungrazed areas, respectively (Davies et al. 2016c). It also appears that greater portions of large perennial bunchgrass crowns suffered mortality in ungrazed areas as evidenced by less postfire biomass production; however, complete mortality of large bunchgrasses did not appear to differ between grazed and ungrazed areas as large bunch-

grasses densities were not statistically different between treatments. Fire-induced reductions in perennial grass crown area result in decreased biomass production (Strong et al. 2013). Davies et al. (2009) similarly observed that long-term ungrazed areas had lower large perennial bunchgrass biomass after fire compared with grazed areas; however, they also found that bunchgrass density was ~50% less in ungrazed compared with grazed areas. This suggested that accumulations and characteristics of fuels in ungrazed areas lead to substantially greater fire-induced mortality of large perennial bunchgrasses (Davies et al. 2009). Half a century of grazing exclusion in Davies et al. (2009) may have led to substantial fire-induced, whole-plant mortality of bunchgrasses because of even greater fuel accumulation and structural changes (Davies et al. 2018) than found in our current study. Differences in fire conditions may have also limited the mortality observed in our current study compared with Davies et al. (2009). However, fire conditions were not measured in Davies et al. (2009). Similar to our current study, prefire grazing in an African savanna also reduced fire severity (Kimuyu et al. 2014). Prefire grazing can clearly reduce fire severity in the *Artemisia* ecosystem and likely other ecosystems.

Greater reductions in dominant perennial vegetation after fire in ungrazed areas likely increased resources for *B. tectorum*; hence, its biomass was approximately twice as great in ungrazed compared with grazed areas. Dominant perennial vegetation, particularly perennial bunchgrasses, compete heavily with exotic annual grasses for resources in this ecosystem (James et al. 2008). Reductions in these plant functional groups result in exponential increases in *B. tectorum*, especially when coupled with fire (Chambers et al. 2007). The greater reductions in dominant perennial vegetation in ungrazed areas after fire opened the plant community to substantial *B. tectorum* invasion. In contrast, relative maintenance of these groups after fire in grazed areas reduced opportunities for *B. tectorum*.

Dormant-season moderate, prefire grazing maintained the perennial dominance of these communities by reducing postfire exotic annual grass invasion. Ungrazed areas, in contrast, had shifted from a large perennial bunchgrass– to an exotic annual grass–dominated system after fire (Figs. 2 and 3). At the conclusion of the study in ungrazed areas, herbaceous biomass contributed by annuals and perennials were equal with *B. tectorum* contributing the most of any plant functional group, but in grazed areas, native perennials dominated the community and comprised > 70% of the herbaceous biomass (see Fig. 3). The substantial increase in *B. tectorum* in ungrazed areas appears to create a novel ecosystem state that would probably be maintained by a new set of biotic and abiotic legacies, assuming these areas were landscape scale instead of experimental plots. In this situation, competition from *B. tectorum* would likely limit recruitment of native perennial species (Aguirre and Johnson 1991; Rafferty and Young 2002) and frequent fire, as a result of *B. tectorum* contributing more flammable and continuous fine fuels (Davies and Nafus 2013), would maintain and further exacerbate exotic annual dominance (Stewart and Hull 1949; D'Antonio and Vitousek 1992; Balch et al. 2013). In other ecosystems with depleted native plant communities, novel states can also develop after disturbance and then are reinforced by a new set of legacies (Scheffer et al. 2001; Williams and Jackson 2007; Bowman et al. 2015).

Less diversity in ungrazed compared with grazed areas post fire provides further evidence that grazing exclusion can have concerning impacts. Similar to our study, diversity was greater in grazed compared with nongrazed areas in a grazing-effects-on-response-to-fire study in the Great Plains (Vermeire et al. 2018). Plant diversity is important because it influences community stability and higher trophic levels (Tilman et al. 1997; Knops et al. 1999; Tilman 1999; Haddad et al. 2001). Less plant diversity in ungrazed areas after fire also suggests that these areas may be less resilient to fu-

ture disturbances. Diverse plant communities are often more resilient to disturbances (Frank and McNaughton 1991; Tilman and Downing 1994; Mulder et al. 2001); however, the relationship is complex (Lavorel 1999). Species richness did not differ between treatments, even though it was numerically greater in grazed compared with ungrazed areas post fire. However, repeated fires associated with substantial *B. tectorum* invasion have been shown to decrease richness (Mahood and Balch 2019). The decline in diversity, combined with the shift in communities from perennial to annual codominated, is compelling evidence, even without a change in richness, that a novel state has developed in ungrazed areas after fire.

Though this research provides evidence that moderate, prefire grazing by cattle can reduce postfire exotic annual grass invasion compared with ungrazed areas and thereby maintain native perennial dominance of the plant community, it should not be misinterpreted to suggest that all types of grazing will achieve similar results. Grazing is clearly not as simple as grazed or not grazed (Davies and Boyd 2020). In contrast to our study where dormant-season moderate grazing was applied, long-term heavy, repeated growing-season grazing can decrease perennial bunchgrasses, resulting in increases in exotic annual grasses (Stewart and Hull 1949; Reisner et al. 2013; Condon and Pyke 2018). Hence, improper grazing can deplete the native perennial understory and promote the development of novel states. Grazing management should be implemented in such a manner as to limit undesirable compositional changes (e.g., decreases in large bunchgrasses in this ecosystem) and yet yield desirable outcomes (e.g., fuel reduction).

Implications

Livestock effects on fire impacts imply that they are ecological engineers. Our current results and prior work (Davies et al. 2009) provide strong evidence that moderate livestock grazing before fire can determine postfire plant community dynamics in fire-prone *Artemisia* communities at risk of exotic annual grass invasion. Further supporting that livestock are ecological engineers because of their effect on fire, other research has demonstrated that grazing significantly modifies fire regimes around the world (Bernardi et al. 2019; Foster et al. 2020). Livestock and other large ungulates can also be ecological engineers via their affinity for recently burned areas, which can increase habitat diversity among other effects (Pillsbury et al. 2011; McGranahan et al. 2012; Donaldson et al. 2018). The management of livestock as ecological engineers is crucial to achieve desired ecological outcomes. This is important as most models predict wildfire frequency and severity will increase in the future (Fried et al. 2004; Fulé 2008; Yue et al. 2013).

Though other research has clearly shown the influence of grazing after fire on ecosystem function and services (Fuhlendorf and Engle 2004; Pillsbury et al. 2011; McGranahan et al. 2012; Winter et al. 2012), our current research is novel as it suggests that effects of grazing before fire can be just as important because of its influence on postfire plant community dynamics. It is highly probable that modification of fuels by herbivores before fire is a major driver of postfire plant community composition and dynamics. In agreement with this, browsing before prescribed fire was shown to improve control of an encroaching shrub in mesic grasslands (O'Connor et al. 2020). Herbivory effects on fire likely extend beyond the plant community and influence higher trophic levels through direct effects of the fire, as well as indirectly through habitat modifications. For example, survivorship of ants in fires increased with prefire herbivory (Kimuyu et al. 2014). Maintenance of grasslands with prefire browsing of encroaching shrubs (O'Connor et al. 2020) can benefit grassland-obligate wildlife (Fulbright et al. 2018). The interaction between prefire herbivory and fire needs to be accounted for in restoration,

conservation, and general management of ecosystems. To facilitate accomplishing this task, prefire grazing influence on postfire plant community dynamics after fire will need to be explored in grazed ecosystems around the world.

Declaration of Competing Interest

We have not declaration of interest.

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