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Original Research

What Is Driving the Proliferation of Exotic Annual Grasses in Sagebrush Communities? Comparing Fire with Off-Season Grazing☆

Kirk W. Davies[1,*], Chad S. Boyd[1], Jon D. Bates[1], Lauren M. Hallett[2], Madelon F. Case[2], Lauren Svejcar[1]

[1] US Department of Agriculture, Agricultural Research Service, Eastern Oregon Agricultural Research Center, Burns, OR 97720, USA
[2] University of Oregon–Institute of Ecology and Evolution, University of Oregon, Eugene, OR 97403, USA

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ABSTRACT

Exotic annual grass invasion is a pressing concern in sagebrush rangelands of the western United States. Overgrazing and fire have historically both been implicated in the rise of annual grasses, but experiments that compare the effect of grazing versus fire are lacking, particularly for contemporary grazing practices such as off-season (fall and winter) grazing. We compared 1) burned and ungrazed (burned), 2) off-season, moderately grazed and unburned (grazed), and 3) ungrazed and unburned (control) treatments at five Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* [Beetle & A. Young] S.L. Welsh) sites in southeastern Oregon for half a decade. Fire, but not off-season grazing, substantially increased exotic annual grass cover and abundance. Vegetation cover and density were generally similar between grazed and control areas. In contrast, at the end of the study exotic annual grass cover and density were over fourfold greater in burned areas. Exotic annual grass became the dominant plant group in burned areas, but not in grazed and control areas. Cover and density of annual forbs, predominately non-native species, were generally greater in the burned compared with grazed and control treatments. Fire also decreased soil biological crust cover and sagebrush cover and density compared with grazed and control treatments. This study provides strong evidence that fire is a threat to the sustainability of Wyoming big sagebrush communities at risk of exotic annual grass dominance, but that off-season, moderate grazing poses little risk. However, considering the spatial extent of our study was limited, further evaluations are needed across a larger geographic area. Given that off-season grazing can decrease the probability of fire, off-season grazing may be a valuable tool to reduce the risk of exotic annual grass dominance.

Introduction

In the western United States, exotic annual grasses (cheatgrass [*Bromus tectorum* L.], medusahead [Taeniatherum caput-medusae {L.} Nevski], and other species) are naturalized and converting native perennial rangelands to exotic annual grasslands (Davies et al. 2021c). These invasions degrade wildlife habitat, decrease native plant abundance, and exponentially reduce biodiversity (Davies 2011). Exotic annual grasses also increase highly flammable fine fuel continuity and amount (Davies and Nafus 2013), leading to increased fire frequency (D'Antonio and Vitousek 1992; Brooks et al. 2004). Exotic annual grasses are tolerant of frequent fire, but most native perennial plants are not (D'Antonio and Vitousek 1992). This facilitates the development of a positive feedback cycle between fire and exotic annual grasses (Balch et al. 2013; Bradley et al. 2018). Widespread concern over ecosystem alterations caused by exotic annual grass dominance and increased frequency and size of wildfires has resulted in researchers trying to extract the drivers of increases in exotic annual grasses (e.g., Bansal and Sheley 2016; Williamson et al. 2020). Additionally, it is important to quantify the relative influence of factors favoring exotic annual grasses compared with each other.

Fire can favor exotic annual grasses (Steward and Hull 1949; Keeley and McGinnis 2007), yet it is an integral component of the natural system that shifts dominance from woody to herbaceous vegetation and thereby promotes heterogeneity and diversity

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* Correspondence: Kirk Davies, EOARC, 67826-A Hwy 205, Burns, OR 97720, USA, 541-573-4074

E-mail address: kirk.davies@usda.gov (K.W. Davies).

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(Davies and Bates 2020). In sagebrush communities prone to exotic annual grass invasion, exotic annual grasses can fundamentally alter succession after fire, leading to a novel state dominated by exotic annual species. However, many sagebrush rangelands have also burned without converting to exotic annual grasslands (Davies et al. 2007; Rhodes et al. 2010; Ellsworth et al. 2016). Similarly, grazing by domestic livestock has also been suggested to promote exotic annual grasses (Knapp 1996; Reisner et al. 2013; Williamson et al. 2020), but the relationship between grazing and exotic annual grasses is more intricate. Studies suggesting that grazing is a driver of exotic annual grass increase often are referencing heavy and repeated growing-season grazing. In contrast, others have not found grazing to be a driver of exotic annual grass abundance (Bates and Davies 2014; Bansal and Sheley 2016). Moderate grazing even promotes resistance to postfire exotic annual grass invasion (Davies et al. 2016, 2021a). The aforementioned contrasting results of grazing are likely a result of differences in grazing management. Grazing is not binary but rather a spectrum, with its effects varying widely by intensity, duration, frequency, timing of use, and grazing animal characteristics, as well as plant community characteristics (Davies and Boyd 2020). Though increases in exotic annual grasses have been attributed to both fire and grazing, experimental comparisons of their effects are lacking, particularly in sagebrush communities at risk of exotic annual grass dominance.

Heavy, repeated growing-season grazing has, without a doubt, contributed substantially to the exotic annual grass problem in the western United States (Daubenmire 1970; Mack 1981; Knapp 1996; Davies et al. 2021c). What remains unknown is contemporary grazing management effects on exotic annual grass, in particular the effects of off-season (fall and winter) grazing. This is particularly important as off-season grazing is an increasingly common alternative to growing-season (spring and summer) grazing. Of great interest is comparing off-season grazing effects to fire effects to determine their relative contribution to the annual grass problem. Prior studies that have suggested that grazing is a major contributor to increases in exotic annual grasses have not compared grazing and fire effects, did not experimentally apply grazing treatments, and therefore, could not determine causation (e.g., Reisner et al. 2013; Williamson et al. 2020). Yet these studies have encouraged land managers to reduce or remove livestock grazing from western rangelands at risk of exotic annual grass dominance. This may prove counterproductive if fire is the major driver of increases in exotic annual grasses, as it removes a potential tool for wildfire mitigation. Moderate livestock grazing can reduce the probability of wildfire propagation by reducing fine fuel amounts and continuity and increasing fuel moisture content (Davies et al. 2010, 2015, 2017). Comparing the effects of contemporary, off-season grazing and fire on exotic annual grasses, as well as other plant community characteristics, is vital to inform land management as it faces unprecedented challenges associated with exotic annual grasses.

The objective of this study was to compare the effects of moderate, off-season grazing and fire on plant community characteristics, in particular exotic annual grass abundance and cover, in Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* [Beetle & A. Young] S.L. Welsh) communities at risk of exotic annual grass dominance. We hypothesized that 1) grazing and fire treatments would increase exotic annual grass cover and abundance and 2) exotic annual grass cover and abundance would be greater in the burned compared with grazed areas.

Methods

Study area

This study was conducted in southeast Oregon, United States near the town Diamond (43°04′N, 118°40′W) in Wyoming big sagebrush-bunchgrass dominated steppe. These communities were considered at risk of exotic annual grass dominance because they have the soil temperature and moisture regime typical of communities with low resilience and resistance to exotic annual grass invasion (Chambers et al. 2014a, 2014b). Dominant bunchgrasses were *Achnatherum thurberianum* (Piper) Barkworth (Thurber's needlegrass) and *Pseudoroegneria spicata* (Pursh) A. Löve (bluebunch wheatgrass) depending on study site. Other common bunchgrasses included *Elymus elymoides* (Raf.) Swezey (squirreltail), *Poa secunda* J. Presl (Sandberg bluegrass), and *Achnatherum hymenoides* (Roem. and Schult.) Barkworth (Indian ricegrass). Exotic annual grasses, predominantly cheatgrass, occurred in low abundance (6.6 ± 3.0 plants•m^{-2}) across the study area before study initiation. Long-term (1980–2010) average annual precipitation across the study area was 280 mm (PRISM 2020). Annual precipitation was 292, 226, 287, 180, and 336 mm in 2015, 2016, 2017, 2018, and 2019, respectively. Precipitation events occur mainly in the winter and spring, and summers are hot and dry. 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). Fire occurrence for these sagebrush steppe communities was infrequent before European settlement with fire return intervals estimated to be 50–100+ yr (Wright and Bailey 1982; Mensing et al. 2006). Study sites had no recent record of burning or any evidence of prior burning, suggesting that the sites had not experienced fire for at least +75 yr.

Experimental design and measurements

We used a randomized complete block design with five blocks and three treatments: Grazed (moderate, off-season grazing and not burned), Control (not grazed and not burned), and Burned (burned and not grazed). Treatments were applied to five different sites (blocks) that varied in site and vegetation characteristics. Site and vegetation characteristics were similar among treatments at each block. The study was initiated in the fall of 2009 by building exclosures to exclude grazing from the Burned and Control treatments. Exclosures were 60 × 100 m and had a 10-m buffer between them and other treatments. Off-season grazing by cattle was applied at the operational level in 800–1 000-ha pastures containing exclosures. Cattle were rotated through pastures between November and early April to implement the grazing treatment each year. Cattle consumed 40–60% of the available forage on the basis of biomass determined by the method described in Anderson and Curreir (1973). Cattle were fed a protein supplement to meet their nutritional needs during the study. Prescribed burns were applied in September 2014 for the Burn treatments. Air temperature ranged from 22.8°C to 27.2°C, wind speeds varied from 2 km to 20 km·h^{-1}, and relative humidity ranged from 17% to 35% during the burns. Burns were complete across each burned treatment replicate.

Vegetation characteristics were measured in June of each year from 2015 through 2019. Four, 45-m transects spaced at 5-m intervals were established in each treatment replicate for vegetation measurements. Herbaceous vegetation cover by species was visually estimated in 40 × 50 cm quadrats located at 3-m intervals on each 45-m transect (15 quadrats per transect and 60 quadrats per treatment replicate). Quadrats had markings along their sides delineating 5%, 10%, 25%, and 50% segments to aid in visual estimates of cover. Bare ground, biological soil crust, and litter cover were also estimated in the 40 × 50 cm quadrats. Herbaceous vegetation density by species was measured by counting each individual rooted in the 40 × 50 cm quadrats. Shrub cover by species was determined using the line-intercept method along the 45 m transects. Shrub density by species was measured by counting all

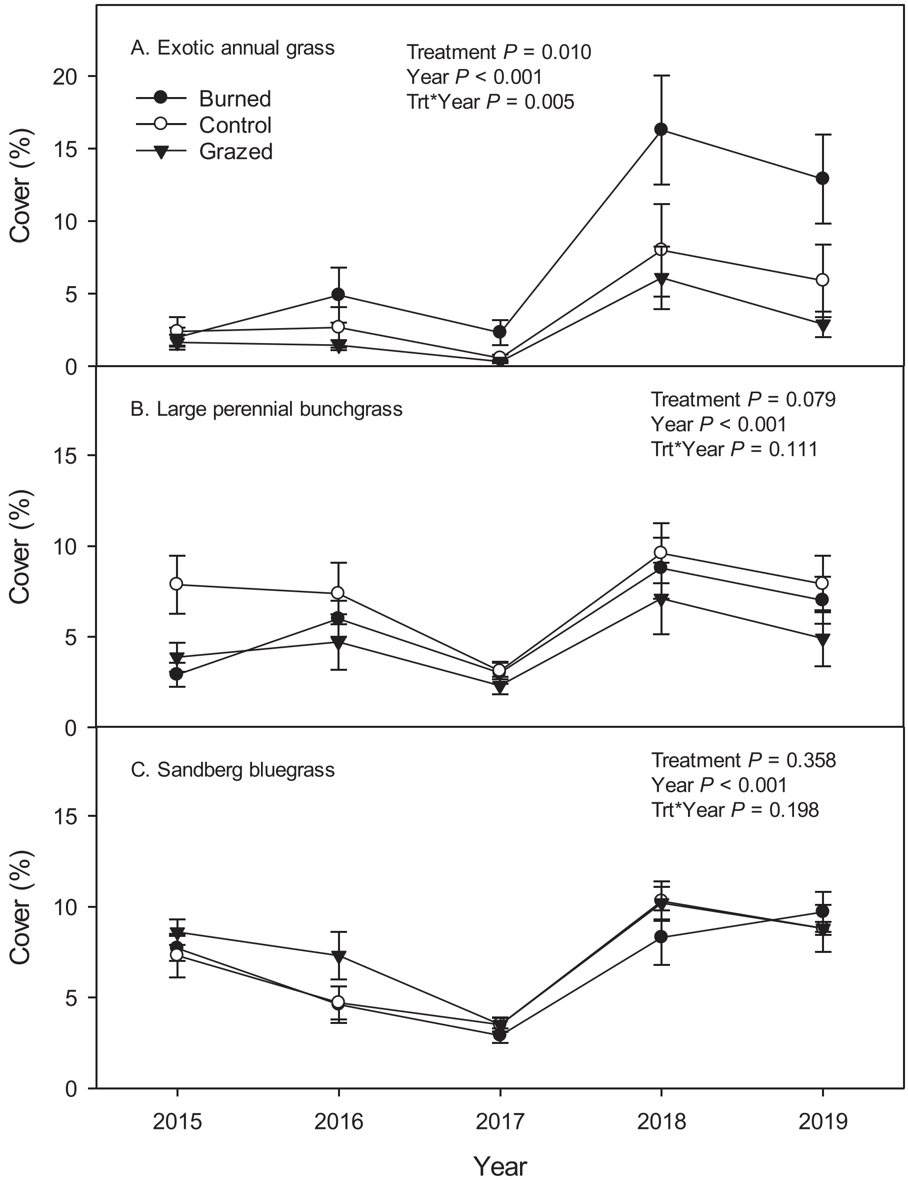

Figure 1. Cover (mean ± standard of error) of grasses in burned (burned and not grazed), control (not grazed and not burned), and off-season grazed (grazed and not burned) Wyoming big sagebrush communities from 2015 to 2019.

individuals rooted in a 2 × 45 m belt transect positioned over each 45-m transect.

Statistical analyses

We used repeated-measures analysis of variance (ANOVA) using the mixed-model procedure (SAS v. 9.4, SAS Institute, Cary, NC) to determine fire and grazing effects. Year was the repeated variable in analyses. Random variables in analyses were block and block by treatment interactions. Akaike's Information Criterion was used to select the appropriate covariance structure for analyses (Littell et al. 1996). Data that violated assumptions of ANOVA were square-root transformed. For analyses, vegetation was separated into plant functional groups: exotic annual grasses, large perennial bunchgrasses, Sandberg bluegrass, perennial forbs, annual forbs, sagebrush, and rabbitbrush. The exotic annual grass group consisted primary of cheatgrass and some medusahead. Sandberg bluegrass was analyzed separate from other bunchgrasses because it is generally smaller in stature, develops phenologically earlier, and responds differently to disturbances (McLean and Tisdale 1972; Yensen et al. 1992; Davies et al. 2021b). Sagebrush and rabbitbrush (*Chyrsothamnus viscidiflorus* [Hook.] Nutt.) were analyzed individually because rabbitbrush resprouts following fire, but sagebrush does not. The perennial grass and perennial forb groups consisted exclusively of native species. The annual forb group was largely composed of non-native species. All figures and text present original, nontransformed data. Means were separated using the least-squares function in SAS. Means were reported with standard errors in figures and text. Statistical significance was set at $P \leq 0.05$.

Results

Exotic annual grass cover was similar among treatments the first year after fire but thereafter varied among treatments (**Fig. 1A**; $P = 0.005$). Exotic annual grass cover was greater in the Burned compared with the Grazed and untreated Control ($P = 0.004$ and 0.019, respectively) but did not differ between the Grazed and Control ($P = 0.307$). At the conclusion of the study, ex-

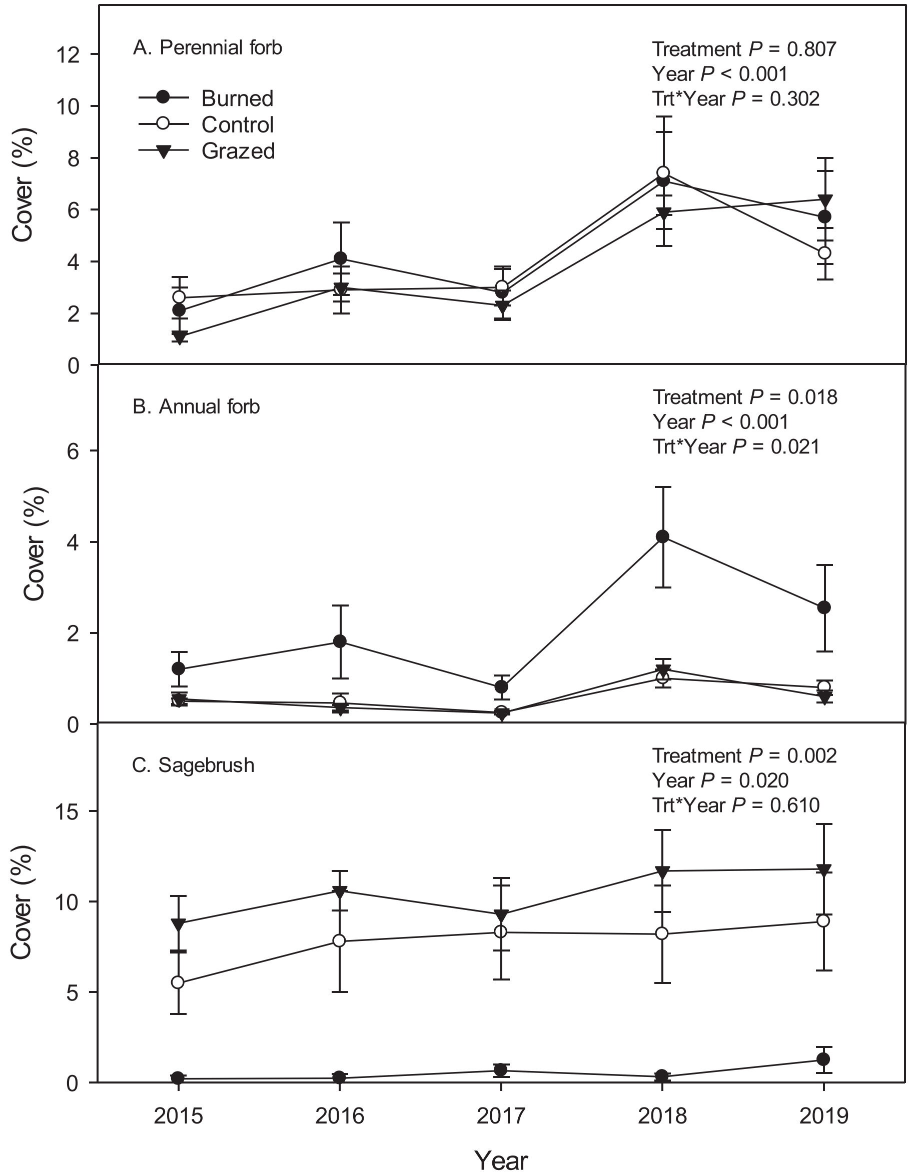

Figure 2. Cover (mean ± standard of error) of forbs and sagebrush in burned (burned and not grazed), control (not grazed and not burned), and off-season grazed (grazed and not burned) Wyoming big sagebrush communities from 2015 to 2019.

otic annual grass cover was 4.4-fold greater in the Burned compared with the Grazed. Large perennial bunchgrass cover did not vary among treatments (Fig. 1B; $P = 0.079$) but varied among years ($P < 0.001$). Sandberg bluegrass and perennial forb cover did not vary among treatments (Fig. 1C and Fig. 2A; $P = 0.358$ and 0.807, respectively) but varied among years ($P < 0.001$). The magnitude of difference in annual forb cover varied among treatments across years (Fig. 2B; $P = 0.021$). Annual forb cover was greater in the Burned compared with the Grazed and the Control ($P = 0.012$ and 0.012) but did not differ between the Grazed and Control ($P = 0.989$). Sagebrush cover varied among treatments (Fig. 2C; $P = 0.002$) and across years ($P = 0.020$). Sagebrush cover was less in the Burned compared with the Grazed and Control ($P < 0.001$ and 0.006, respectively) but did not differ between the Grazed and Control ($P = 0.194$). Rabbitbrush cover did not vary among treatments or across years (data not shown; $P = 0.385$ and 0.696, respectively). Bare ground was initially greater in the Burned, but over time it became less in the Burned compared with the other treatments (**Fig. 3A**; $P < 0.001$). In general, bare ground was greater in the Grazed compared with the Burned and Control ($P = 0.037$ and 0.016, respectively). In the final sampling year, bare ground was 1.3-fold greater in the Grazed compared with the Control. Litter was initially less in the Burned compared with the other treatments but became similar among treatments over time (Fig. 3B; $P = 0.001$). Biological soil crust cover varied among treatments (Fig. 3C; $P = 0.017$) and across years ($P < 0.001$). Biological soil crust cover was less in the Burned compared with the Grazed and Control ($P = 0.021$ and 0.008, respectively) but was similar between the Grazed and Control ($P = 0.531$).

Exotic annual grass density was similar among treatments the first year after fire but differed among treatments in subsequent years (**Fig. 4A;** $P = 0.026$). Exotic annual grass density was greater in the Burned compared with the Grazed and Control ($P = 0.002$ and 0.015, respectively) but was similar between the Grazed and Control ($P = 0.213$). In the final year of the study, exotic annual grass density was 4.3- and 2.6-fold greater in the Burned compared with the Grazed and Control, respectively. Large perennial bunchgrass density did not vary among treatments (Fig. 4B; $P = 0.347$)

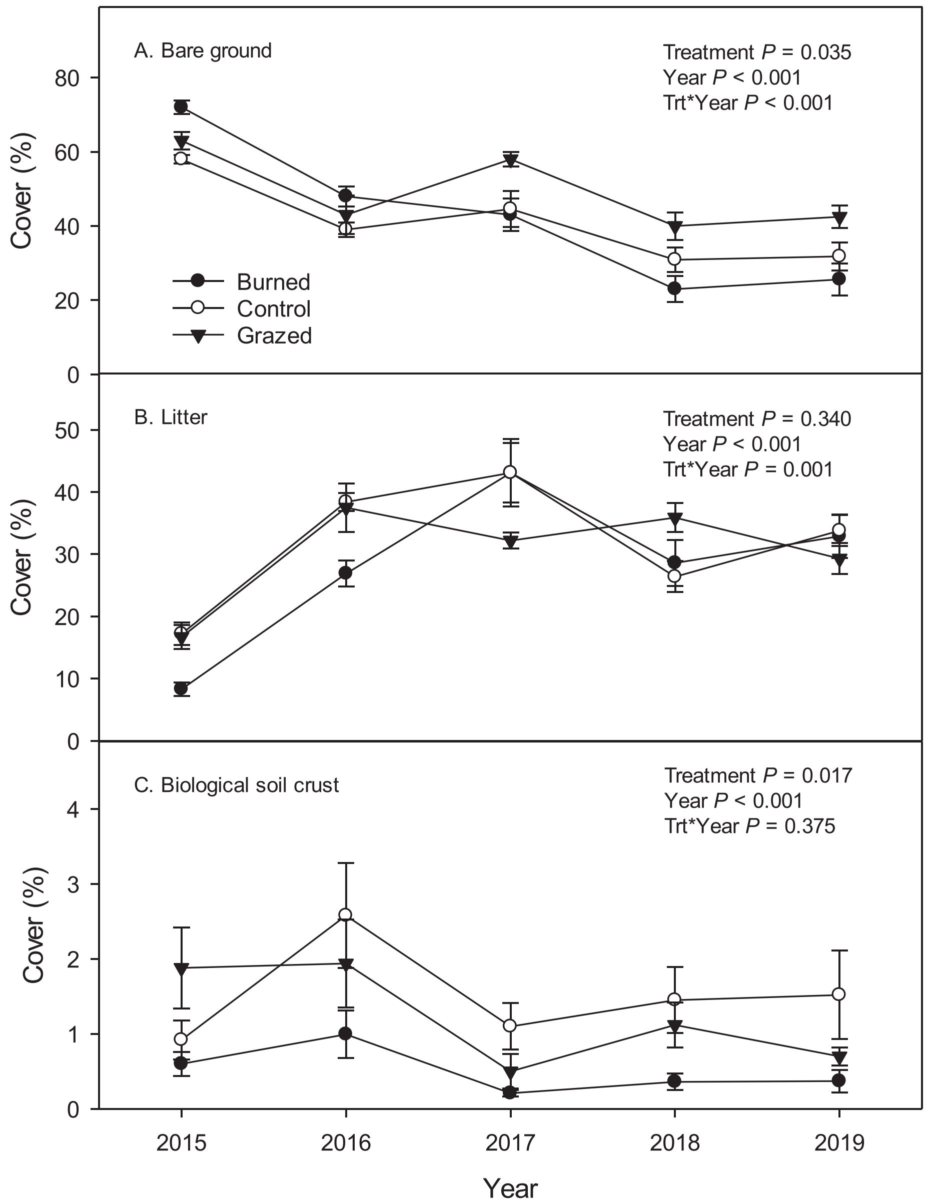

Figure 3. Bare ground, litter, and biological soil crust cover (mean ± standard of error) in burned (burned and not grazed), control (not grazed and not burned), and off-season grazed (grazed and not burned) Wyoming big sagebrush communities from 2015 to 2019.

but varied among years ($P = 0.028$). Density of Sandberg bluegrass was influenced by the interaction between treatment and year (Fig. 4C; $P = 0.021$). Sandberg bluegrass density was similar between the Burned and Grazed treatment the first year after fire, but thereafter it was greater in the Grazed compared with the Burned and Control ($P < 0.001$ and 0.001, respectively). Perennial forb density did not vary among treatments (**Fig. 5A;** $P = 0.560$) but varied across years ($P < 0.001$). Annual forb density was similar among treatments the first yr post fire, but after that it was generally greater in the Burned compared with the other treatments (Fig. 5B; $P < 0.001$). At the conclusion of the study, annual forb density was 2.9- and 3.1-fold greater in the Burned compared with the Grazed and Control, respectively. Sagebrush density varied among treatments (Fig. 5C; $P = 0.007$) but not across years ($P = 0.296$). Sagebrush density was greater in the Grazed and the Control compared with the Burned ($P = 0.002$ and 0.039, respectively) but was similar between the Grazed and the Control ($P = 0.890$). Rabbitbrush density was similar among treatments (data not shown; $P = 0.322$) but varied across years ($P = 0.003$).

Discussion

While annual grass invasion has frequently been attributed to fire (e.g., Steward and Hull 1949; Keeley and McGinnis 2007) and grazing (e.g., Knapp 1996; Reisner et al. 2013; Williamson et al. 2020), our study provides one of the first experimental tests to compare their relative effect. We assumed that off-season grazing and fire would increase the abundance and cover of exotic annual grasses compared with an ungrazed, unburned control; however, exotic annual grasses only increased with burning. Fire, as predicted, resulted in greater exotic annual grass cover and abundance compared with the off-season grazed treatment. Contrary to expectations, exotic annual grass cover and abundance were similar between the grazed and control treatments even though these treatments had been applied for a decade. When comparing just off-season grazed and ungrazed areas (without a burned treatment), off-season grazing decreased exotic annual grasses (Davies et al., 2022). This discrepancy with our current results is because fire has such a large effect that it masks the effects of off-season

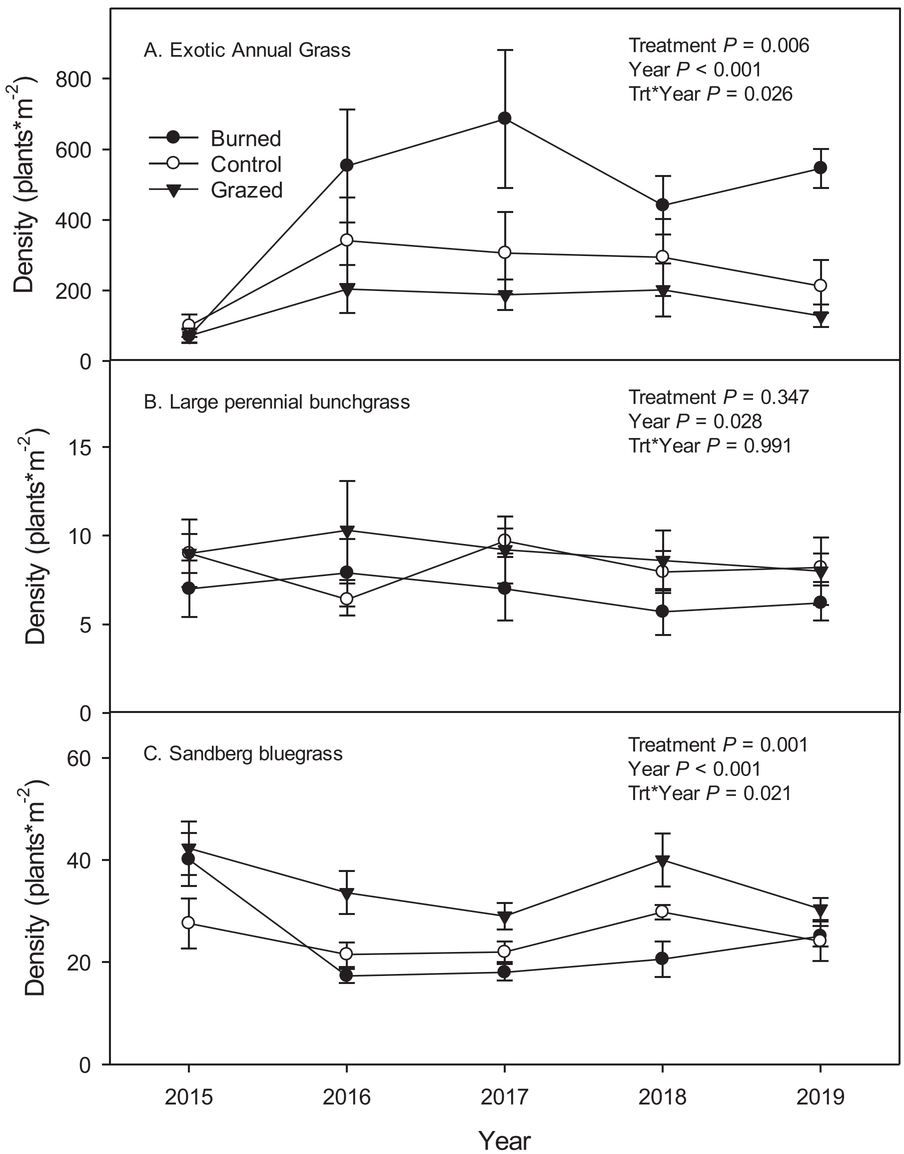

Figure 4. Density (mean ± standard of error) of grasses in burned (burned and not grazed), control (not grazed and not burned), and off-season grazed (grazed and not burned) Wyoming big sagebrush communities from 2015 to 2019.

grazing. Fire appears to be a major driver of the proliferation of exotic annual grasses in sagebrush communities with low resilience and resistance. In agreement, many others have correlated fire with greater occurrence and prevalence of cheatgrass in the central Great Basin (e.g., Stewart and Hull 1949; Chambers et al. 2007; Williamson et al. 2020). In contrast to fire, off-season, moderate grazing by cattle did not favor exotic annual grasses in this study.

Historic, repeated grazing during the growing season by sheep, horse, and cattle decreased perennial herbaceous vegetation and facilitated exotic annual grass invasion (Knapp 1996), likely creating a dogma that all grazing increases exotic annual grass invasion. Treating grazing as a binary disturbance (grazed or not grazed) is all too common, and contemporary grazing management is not similar to historic grazing practices (Davies and Boyd 2020). Contemporary grazing practices have been hard to study, as many years are likely needed to have a robust study, and this has led to attempts to investigate grazing effects using observational studies (e.g., Reisner et al. 2013; Bansal and Sheley 2016; Williamson et al. 2020) that struggle to separate historic and contemporary grazing effects. Thus, it is not surprising that with an experimental test of off-season grazing, we found that grazing did not favor exotic annual grasses, counter to reports of grazing increasing annual grasses (e.g., Reisner et al. 2013; Williamson et al. 2020). In their observation study, Williamson et al. (2020) found that grazing and the proportion of years grazed were positively correlated with exotic annual grass occurrence and prevalence in unburned plots, though they also noted an opposite pattern in burned plots, where prevalence of exotic annual grass decreased as the proportion of years grazed increased. Similarly, heavy, repeated growing season use was correlated with increased abundance of exotic annual grass in sagebrush communities (Reisner et al. 2013). The discrepancy between our results and these two studies could be caused by a couple of factors. First, correlations between exotic annual grass and grazing found in these studies could be the result of livestock being attracted to increased abundance of forage (exotic annual grass) or management increasing livestock use in response to greater abundance of exotic annual grasses. The invasion of cheatgrass in many rangeland communities increased livestock forage production by an order of magnitude (Young and Clements 2007). Since Reisner et al. (2013) and Williamson et al. (2020) were

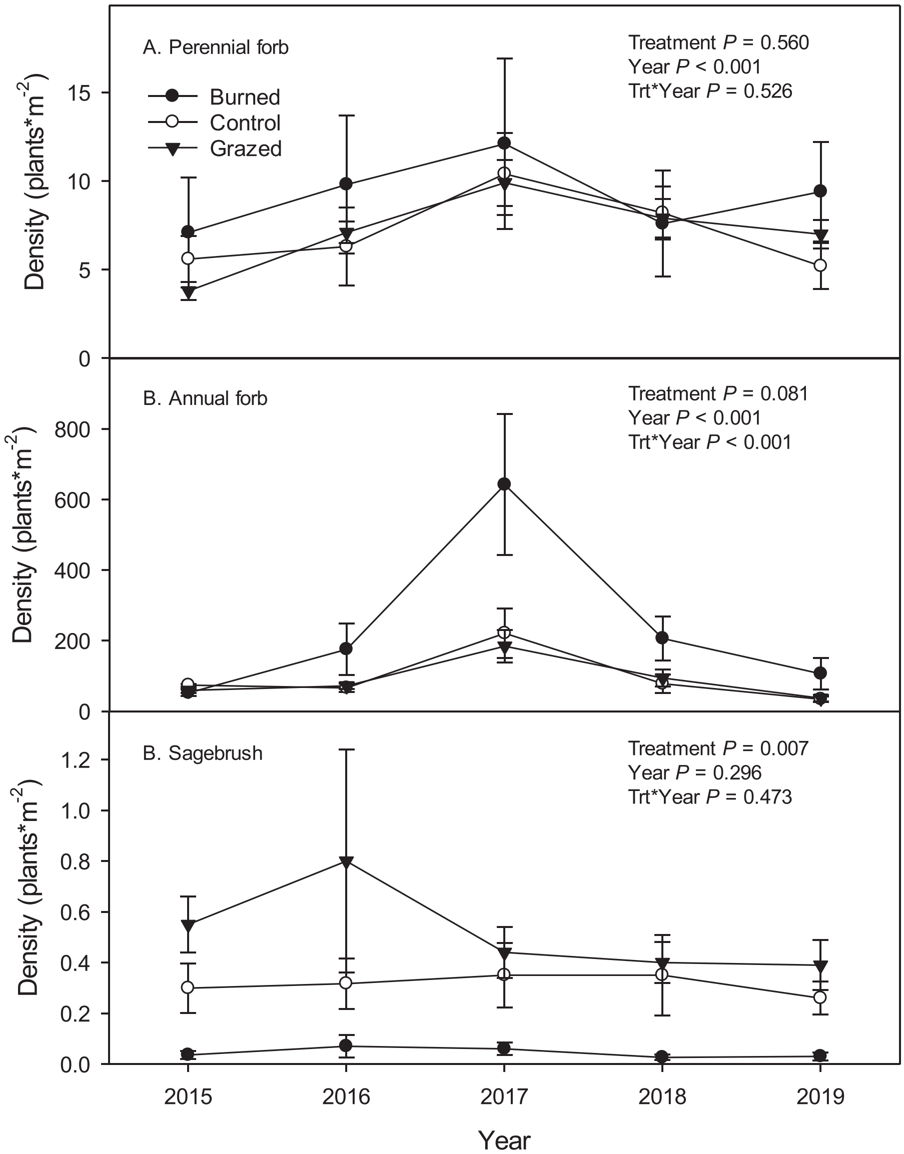

Figure 5. Density (mean ± standard of error) of forbs and sagebrush in burned (burned and not grazed), control (not grazed and not burned), and off-season grazed (grazed and not burned) Wyoming big sagebrush communities from 2015 to 2019.

observation studies, it cannot be determined if grazing caused increased exotic annual grass or if greater annual grass resulted in increased grazing. By contrast, our study was an empirical experiment that could determine causation. Second, the grazing suggested to promote increases in exotic annual grasses was heavy and repeated growing season use (Reisner et al. 2013; Williamson et al. 2020), which is widely known to negatively impact native bunchgrasses and favor exotic annuals (Davies et al. 2014). However, this is not representative of active, modern management practices and we found that moderate grazing by livestock in the off season did not promote exotic annual grasses. Contrasting results between our study and Reisner et al (2013) and Williamson et al. (2020) reaffirm that timing, intensity, and frequency of grazing are critical to determining the risk it poses to exotic species proliferation and provides land managers with options for creating sustainable grazing management plans.

The results of our study provide strong evidence that fire is a major driver of increases in exotic annual grass abundance and cover, though further evaluations are needed across different plant communities and across a larger geographic area. Exotic annual grass was a relatively minor component of the Grazed and Control treatments, where its cover was 2.9% and 5.9% at the end of the study, respectively. However, in the Burned treatment, annual grass cover was 12.9%, almost double the large perennial grass value, at the end of the study. With burning, exotic annual grasses became the dominant plant group in these sagebrush communities, whereas in the Grazed and Control treatments, exotic annual grass cover was 59% and 75% of large perennial bunchgrass cover at the end of the study, respectively. This indicates that fire can shift dominance to exotic annual grasses. Exotic annual grasses have increased substantially with wildfire and prescribed burning in other sagebrush communities (Stewart and Hull 1949; Chambers et al. 2007; St. Clair and Bishop 2019). Our results, combined with prior studies, suggest that fire can cause an acute and likely persistent increase in exotic annual grass cover and abundance.

The proliferation of exotic annual grasses with burning was likely caused by increased soil nutrient availability and decreased competition with the loss of sagebrush. Fire in sagebrush communities increase soil nutrient concentrations, particularly nitrogen, one of the most limiting soil resources after water (Davies et al.

2007). Decreases in sagebrush often favor exotic annual grasses and other exotic plants (Prevéy et al. 2010; Davies et al. 2012; Chambers et al. 2014b). The loss of sagebrush with fire increases safe sites, nutrient concentrations, and soil water, and this often leads to proliferation of exotic annual grasses (Roundy et al. 2014, 2018). Excess resources generally favor exotic species, especially annual species, as they are better adapted to rapidly respond to increases and pulses in resources compared with slower-growing perennial species (Mata-González et al. 2007; Vasquez et al. 2008). Fire in sagebrush communities likely favors the faster growing exotic annuals that can take advantage of the excess in resources it creates.

The postfire increase in exotic annual grasses suggests that fire may be driving these communities toward a new state dominated by exotic annuals. In agreement with this, annual forbs, predominantly exotic species, also increased with burning. The substantial increase in exotic annual grasses raises the probability of more frequent fire and development of an exotic annual grass-fire cycle where native perennial vegetation declines and exotic annuals increase with each subsequent fire (Balch et al. 2013; Bradley et al. 2018). Thus, the postfire increase in exotic annual grasses could be the inception of a transition to an exotic annual grassland.

Fire, but not off-season grazing, substantially reduced biological soil crust cover. Decreases in biological soil crust are concerning because they capture soil resources, decrease soil erosion, and increase invasion resistance in semiarid and arid ecosystems (Belnap et al. 2001; Harper and Belnap 2001; Belnap 2006). Similar to our results, fire has been repeatedly demonstrated to decrease biological soil crust (Hilty et al. 2004; Dettweiler-Robinson 2013a; Root et al. 2017; Bates et al. 2020). Biological soil crust cover is also inversely related to the cover of exotic annual grasses (Ponzetti et al. 2007; Dettweiler-Robinson et al. 2013b). Thus fire, and consequent increase in exotic annual grasses, reduced biological soil crust cover to 24% of the Control treatment by the end of the study. In contrast, biological soil crust cover was similar between the Grazed and Control treatments. This result is in contrast with other studies that found grazing decreases biological soil crust cover (Kleiner and Harper 1977; Jeffries and Klopatek 1987; Memmott et al. 1998; Root et al. 2020). However, similar to our results, biological soil crust cover did not differ between grazing exclosures and grazed areas in the northern sagebrush steppe in Wyoming (Muscha and Hild 2006). Grazing in the winter may decrease the likelihood that biological soil crusts are damaged because the soil is frozen or wet (Memmott et al. 1998), as crust may be more susceptible to damage when dry (Anderson et al. 1982). Timing and intensity of grazing are likely a factor in these differences of grazing effects on biological soil crusts. However, it also appears that grazing effects on biological soil crust may be less in cooler sagebrush steppe communities compared with hotter and drier communities. Our study and Muscha and Hild (2006) occurred in cooler Wyoming big sagebrush communities, whereas studies reporting negative effects of grazing on biological soils crust generally occurred in lower elevation, hotter, drier communities (e.g., Kleiner and Harper 1977; Jeffries and Klopatek 1987; Root et at al. 2020). Fire effects, compared with moderate, off-season grazing effects, on biological soil crust provide additional evidence that suggests that fire is a major driver of ecosystem dynamics in these sagebrush communities.

Here we saw that burning dramatically reduced sagebrush, whereas off-season grazing did not alter sagebrush densities. Furthermore, other studies have found that grazing decreases the probability of fire by modifying fuels (Davies et al. 2015, 2017) and, therefore, may ultimately be a useful tool in protecting sagebrush-obligate wildlife habitat, in particular preventing the loss of sagebrush from burning. Also in support of this, other important habitat elements, large perennial bunchgrass and perennial forb cover and density, were also similar between off-season grazed and control areas. These results imply that off-season, moderate grazing can be compatible with management goals for sagebrush communities, including maintaining native perennial dominance, limiting exotic annual grasses, and providing habitat for sagebrush-associated wildlife.

Management Implications

Fire and historic grazing practices have played a major role in the abundance and spread of exotic annual grasses in sagebrush plant communities. Compared with moderate grazing during the off season, however, our data indicate that fire results in increased abundance and cover of exotic annual grasses. This suggests that ameliorating the exotic annual grass problem will involve minimizing fire, but that decreasing or eliminating off-season moderate grazing would not produce a concomitant reduction in annual grasses. In fact, reducing or eliminating grazing may exacerbate the exotic annual grass problem by increasing fine fuel amount and continuity, resulting in increased probability of fire ignition and spread and greater fire severity (Davies et al. 2015, 2016, 2017), all of which collectively amplify fire-associated increases in exotic annual grasses. Increases in exotic annual grasses and annual forbs and a decline is biological soil crust with fire are concerning as they suggest that these communities may transition from native perennial dominance toward exotic annual dominance. Though fire was historically an important ecological event associated with transient shifts from shrub to native herbaceous vegetation dominance (Wright and Bailey 1982), exotic annual grass invasion has supplanted native vegetation postfire succession and fundamentally altered the ecological role of fire in low resistant and resilient Wyoming big sagebrush communities. However, fire is still critical to limit conifer expansion in higher-elevation sagebrush communities that have a lower risk of exotic annual grass dominance (Davies et al. 2019). Dissimilar to fire, moderate grazing during the off season appears compatible with the sustainability of Wyoming big sagebrush communities with low resilience and resistance and the ecological goods and services they provide. Divergent from off-season moderate grazing, mismanaged grazing can negatively impact these communities by depleting the native perennial understory and facilitating an increase in exotic annual grasses (Daubenmire 1970; Mack 1981; Knapp 1996). This reaffirms prior assertions (e.g., Davies and Boyd 2020) that grazing is not simply grazed or not grazed, but its effects vary by timing, duration, intensity, frequency and other factors. Grazing management based on the best available science will be critical for the conservation of sagebrush communities and the species that inhabit them. That being acknowledged, fire is a growing threat to sagebrush communities prone to exotic annual grass invasion and efforts should likely focus on decreasing their likelihood of burning to limit exotic annual grass expansion and dominance.

Declaration of Competing Interest

We do not have any conflict of interest to declare.

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References

Anderson, E.W., Curreir, W.F, 1973. Evaluating zones of utilization. Journal of Range Management 26, 87–91.
Anderson, D.C., Harper, K.T., Holmgren, R.C, 1982. Factors influencing development of cryptogamic crusts in Utah deserts. Journal of Range Management 35, 180–185.
Balch, J.K., Bradley, B.A., D'Antonio, C.M., 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980-2009). Global Change Biology 19, 173–183.
Bansal, S., Sheley, R.L, 2016. Annual grass invasion in sagebrush steppe: the relative importance of climate, soil properties and biotic interactions. Oecologia 181, 543–557.
Bates, J.D., Boyd, C.S., Davies, K.W, 2020. Longer-term post-fire succession on Wyoming big sagebrush steppe. International Journal of Wildland Fire 29, 229–239.
Bates, J.D., Davies, K.W, 2014. Cattle grazing and vegetation succession in burned sagebrush steppe. Rangeland Ecology & Management 67, 412–422.
Belnap, J., 2006. The potential roles of biological soil crusts in dryland hydrologic cycles. Hydrological Processes 20, 3159–3178.
Belnap, J., Prasse, R., Harper, K.T, 2001. Influence of biological soil crusts on soil environments and vascular plants. Ecological Studies 150, 281–300.
Bradley, B.A., Curtis, C.A., Fusco, E.J., Abatzoglou, J.T., Balch, J.K., Dadashi, S., Tuanmu, M., 2018. Cheatgrass *(Bromus tectorum)* distribution in the intermountain Western United States and its relationship to fire frequency, seasonality, and ignitions. Biological Invasion 20, 1493–1506.
Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., DiTomaso, J.M., Hobbs, R.J., Pellant, M., Pyke, D., 2004. Effects of invasive alien plants on fire regimes. Bioscience 54, 677–688.
Chambers, J.C., Bradley, B.A., Brown, C.S., D'Antonio, C., Germino, M.J., Grace, J.B., Hardegree, S.P., Miller, R.F., Pyke, D.A, 2014a. Resilience to stress and disturbance and reistance to *Bromus tectorum* L. invasion in cold desert shrublands of western North America. Ecosystems 17, 360–375.
Chambers, J.C., Miller, R.F., Board, D.I., Pyke, D.A., Rundy, B.A., Brace, J.B., Schupp, E.W., Tausch, R.J, 2014b. Resilience and resistance of sagebrush ecosystems: implications for state and transition models and management treatments. Rangeland Ecology & Management 67, 440–454.
Chambers, J.C., Roundy, B.A., Blank, R.R., Meyer, S.E., Whittaker, A., 2007. What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum?*. Ecological Monographs 77, 117–145.
D'Antonio, C.M., Vitousek, P.M, 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23, 63–87.
Daubenmire, R., 1970. Steppe vegetation of Washington. Washington Agricultural Experiment Station Technical Bulletin 62, 131.
Davies, K.W., 2011. Plant community diversity and native plant abundance decline with increasing abundance of an exotic annual grass. Oecologia 167, 481–491.
Davies, K.W., Bates, J.D, 2020. Re-introducing fire in sagebrush-steppe experiencing decreased fire frequency: does burning promote spatial and temporal heterogeneity? International Journal of Wildland Fire 29, 686–695.
Davies, K.W., Bates, J.D., Boyd, C.S., Copeland, S.M., O'Connor, R, 2021a. Dormant season grazing pre-fire maintains diversity and reduces exotic grass response post–fire in imperiled *Artemisia* steppe. Rangeland Ecology & Management 79, 91–99.
Davies, K.W., Bates, J.D., Boyd, C.S., Svejcar, T.J, 2016. Prefire grazing by cattle increases postfire resistance to exotic annual grass *(Bromus tectorum)* invasion and dominance for decades. Ecology and Evolution 6, 3356–3366.
Davies, K.W., Bates, J.D., Miller, R.F, 2007. Short-term effects of burning Wyoming big sagebrush steppe in southeast Oregon. Rangeland Ecology & Management 60, 515–522.
Davies, K.W., Bates, J.D., Nafus, A.M, 2012. Mowing Wyoming big sagebrush communities with degraded herbaceous understories: has a threshold been crossed? Rangeland Ecology & Management 65, 498–505.
Davies, K.W., Bates, J.D., Perryman, B., Arispe, S., 2021b. Fall-winter grazing after fire in annual grass-invaded sagebrush steppe reduced annuals and increased a native bunchgrass. Rangeland Ecology & Management 77, 1–8.
Davies, K.W., Bates, J.D., Svejcar, T.J., Boyd, C.S, 2010. Effects of long-term livestock grazing on fuel characteristics in rangelands: an example from the sagebrush steppe. Rangeland Ecology & Management 63, 662–669.
Davies, K.W., Boyd, C.S, 2020. Grazing is not binomial (i.e., grazed or not grazed): a reply to Herman. BioScience 70, 6–7.
Davies, K.W., Boyd, C.S., Bates, J.D., Hulet, A., 2015. Dormant-season grazing may decrease wildfire probability by increasing fuel moisture and reducing fuel amount and continuity. International Journal of Wildland Fire 24, 849–856.
Davies, K.W., Boyd, C.S., Copeland, S.M., Bates, J.D., 2022. Moderate grazing during the off-season (fall-winter) reduces exotic annual grasses in sagebrush-bunchgrass steppe. Rangeland Ecology & Management.
Davies, K.W., Gearhart, A., Boyd, C.S., Bates, J.D, 2017. Fall and spring grazing influence fire ignitability and initial spread in shrub steppe communities. International Journal of Wildland Fire 26, 485–490.
Davies, K.W., Leger, E.A., Boyd, C.S., Hallett, L.M, 2021c. Living with exotic annual grasses in the sagebrush ecosystem. Journal of Environmental Management 288, 112417.
Davies, K.W., Nafus, A.M, 2013. Exotic annual grass invasion alters fuel amounts, continuity and moisture content. International Journal of Wildland Fire 22, 353–358.
Davies, K.W., Rios, R.C., Bates, J.D., Johnson, D.D., Kerby, J., Boyd, C.S., 2019. To burn or not to burn: comparing re-introducing fire with cutting an encroaching conifer for conservation of an imperiled shrub-steppe. Ecology and Evolution 9, 9137–9148.
Davies, K.W., Vavra, M., Schultz, B., Rimbey, N., 2014. Implications of longer-term rest from grazing in the sagebrush steppe. Journal of Rangeland Applications 1, 14–34.
Dettweiler-Robinson, E., Bakker, J., Grace, J.B, 2013b. Controls of biological soil crust cover and composition shift with succession in sagebrush shrub-steppe. Journal of Arid Environments 94, 96–104.
Dettweiler-Robinson, E., Ponzetti, J., Bakker, J., 2013a. Long-term changes in biological soil crust cover and composition. Ecological Processes 2, 5.
Ellsworth, L.M., Wrobleski, D.W., Kauffman, J.B., Reis, S.A, 2016. Ecosystem resilience is evident 17 years after fire in Wyoming big sagebrush ecosystems. Ecosphere 7, e01618.
Harper, K.T., Belnap, J., 2001. The influence of biological soil crusts on mineral uptake by associated vascular plants. Journal of Arid Environments 47, 347–357.
Hilty, J.H., Eldridge, D.J., Rosentreter, R., Wiclow-Howard, M.C., Pellant, M., 2004. Recovery of biological soil crusts following wildfire in Idaho. Rangeland Ecology & Management 57, 89–96.
Jeffries, D.L., Klopatek, J.M, 1987. Effects of grazing on the vegetation of the blackbrush association. Journal of Range Management 40, 390–392.
Keeley, J.E., McGinnis, T.W, 2007. Impact of prescribed fire and other factors on cheatgrass persistence in Sierra Nevada ponderosa pine forest. International Journal of Wildland Fire 16, 96–106.
Kleiner, E.F., Harper, K.T, 1977. Occurrence of four major perennial grasses in relation to edaphic factors in a pristine community. Journal of Range Management 30, 286–289.
Knapp, P.A., 1996. Cheatgrass (*Bromus tectorum* L.) dominance in the Great Basin Desert: history, persistence, and influences to human activities. Global Environmental Change 6, 37–52.
Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D, 1996. SAS System for Mixed Models. SAS Institute Inc. 633 p, Cary, NC, USA.
Mack, R.N., 1981. Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. Agro-Ecosystems 7, 145–165.
Mata-González, R., Hunter, R.G., Coldren, C.L., McLendon, T., Paschke, M.W, 2007. Modelling plant growth dynamics in sagebrush steppe communities affected by fire. Journal of Arid Environments 69, 144–157.
McLean, A., Tisdale, E.W, 1972. Recovery rate of depleted range sites under protection from grazing. Journal of Range Management 25, 178–184.
Memmott, K.L., Anderson, V.J., Monsen, S.B, 1998. Seasonal grazing impacts on cryptogamic crusts in a cold desert ecosystem. Journal of Range Management 51, 547–550.
Mensing, S., Livingston, S., Barker, P., 2006. Long-term fire history in Great Basin sagebrush reconstructed from macroscopic charcoal in spring sediments, Newark Valley, Nevada. Western North American Naturalist 66, 64–77.
Muscha, J.M., Hild, A.L, 2006. Biological soil crust in grazed and ungrazed Wyoming sagebrush steppe. Journal of Arid Environments 67, 195–207.
NRCS [Natural Resource Conservation Service]. 2013. Web soil survey. Available at: http://websoilsurvey.sc.egov.usda.gov/App/WebSoilSurvey.aspx. Accessed December 1, 2013.
Prevéy, J.S., Germino, M.J., Huntly, N.J, 2010. Loss of foundation species increases population growth of exotic forbs in sagebrush steppe. Ecological Applications 20, 1890–1902.
Ponzetti, J.M., McCune, B., Pyke, D.A, 2007. Biotic soil crusts in relation to topography, cheatgrass and fire in the Columbia Basin, Washington. The Bryologist 110, 706–722.
PRISM. 2020. PRISM Climatic Group. Available at: http://prism.nacse.org/explorer/. Accessed December 19, 2020.
Reisner, M.D., Grace, J.B., Pyke, D.A., Doescher, P.S, 2013. Conditions favouring *Bromus tectorum* dominance of endangered sagebrush steppe ecosystems. Journal of Applied Ecology 50, 1039–1049.
Rhodes, E.C., Bates, J.D., Sharp, R.N., Davies, K.W, 2010. Fire effects on cover and dietary resources of sage-grouse habitat. Journal of Wildlife Management 74, 755–764.
Root, H.T., Brinda, J.C., Dodson, E.K, 2017. Recovery of biological soil crust richness and over 12-16 years after wildfires in Idaho, USA. Biogeosciences 14, 3957–3969.
Root, H.T., Miller, J.E.D., Rosentreter, R., 2020. Grazing disturbance promotes exotic annual grasses by degrading soil biocrust communities. Ecological Applications 30, e02016.
Roundy, B.A., Young, K., Cline, N., Hulet, A., Miller, R.R., Tausch, R.J., Chambers, J.C., Rau, B., 2014. Piñon-juniper reduction increases soil water availability of the resource growth pool. Rangeland Ecology & Management 67, 495–505.
Roundy, B.A., Chambers, J.C., Pyke, D.A., Miller, R.F., Tausch, R.J., Schupp, E.W., Rau, B., Gruell, T., 2018. Resilience and resistance in sagebrush ecosystems are associated with seasonal soil temperature and water availability. Ecosphere 9, 02417.
Stewart, G., Hull, A.C, 1949. Cheatgrass (*Bromus tectorum* L.)—an ecologic intruder in southern Idaho. Ecology 30, 58–74.
St. Clair, S.B., Bishop, T.B.B., 2019. Loss of biotic resistance and high propagule pressure promote invasive grass-fire cycles. Journal of Ecology 107, 1995–2005.
Vasquez, E., Sheley, R., Svejcar, T., 2008. Nitrogen enhances the competitive ability of cheatgrass *(Bromus tectorum)* relative to native grasses. Invasive Plant Science & Management 1, 287–295.

Williamson, M.A., Fleishman, E., MacNally, R.C., Chambers, J.C., Bradley, B.A., Dobkin, D.S., Board, D.I., Fogarty, F.A., Horning, N., Leu, M., Zillig, M.W, 2020. Fire, livestock grazing, topography, and precipitation affect occurrence and prevalence of cheatgrass *(Bromus tectorum)* in the central Great Basin, USA. Biological Invasions 22, 663–680.

Wright, H.A., Bailey, A.W., 1982. Fire ecology: United States and Southern Canada. John Wiley & Sons, Inc., New York, NY, USA, p. 496.

Yensen, E., Quinney, D.L., Johnson, K., Timmerman, K., Steenhof, K., 1992. Fire, vegetation changes, and population fluctuations of Townsend's ground squirrels. American Midland Naturalist 128, 299–312.

Young, J.A., Clements, C.D., 2007. Cheatgrass and grazing rangelands. Rangelands 29, 15–20.