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Original Research

Eighty Years of Grazing by Cattle Modifies Sagebrush and Bunchgrass Structure☆

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ABSTRACT

Grazing by cattle is ubiquitous across the sagebrush steppe; however, little is known about its effects on sagebrush and native bunchgrass structure. Understanding the effects of long-term grazing on sagebrush and bunchgrass structure is important because sagebrush is a keystone species and bunchgrasses are the dominant herbaceous functional group in these communities. To investigate the effects of long-term grazing on sagebrush and bunchgrass structure, we compared nine grazing exclosures with nine adjacent rangelands that were grazed by cattle in southeast Oregon. Grazing was moderate utilization (30 – 45%) with altering season of use and infrequent rest. Long-term grazing by cattle altered some structural aspects of bunchgrasses and sagebrush. Ungrazed bunchgrasses had larger dead centers in their crowns, as well as greater dead fuel depths below and above the crown level compared with grazed bunchgrasses. This accumulation of dry fuel near the meristematic tissue may increase the probability of fire-induced mortality during a wildfire. Bunchgrasses in the ungrazed treatment had more reproductive stems than those in the long-term grazed treatment. This suggests that seed production of bunchgrasses may be greater in ungrazed areas. Sagebrush height and longest canopy diameter were 15% and 20% greater in the ungrazed compared with the grazed treatment, respectively. However, the bottom of the sagebrush canopy was closer to the ground in the grazed compared with the ungrazed treatment, which may provide better hiding cover for ground-nesting avian species. Sagebrush basal stem diameter, number of stems, amount of dead material in the canopy, canopy gap size, and number of canopy gaps did not differ between ungrazed and grazed treatments. Moderate grazing does not appear to alter the competitive relationship between a generally unpalatable shrub and palatable bunchgrasses. Long-term, moderate grazing appears to have minimal effects to the structure of bunchgrasses and sagebrush, other than reducing the risk of bunchgrass mortality during a fire event.

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Introduction

Grazing by livestock in sagebrush steppe communities of the Great Basin can be controversial. This is largely because these communities historically experienced limited grazing pressure from large ungulates (Mack and Thompson, 1982) and because of resource damage from widespread overuse by sheep, cattle, and horses following initial European settlement (Mack, 1981; Young and Allen, 1997; Chambers et al., 2007). Examples of glaring mismanagement, particularly in riparian areas (Beschta et al., 2014; Batchelor et al., 2015), have led many to assume that all grazing negatively affects sagebrush steppe ecosystems. However, ungrazed rangelands and moderate grazed rangelands have repeatedly been demonstrated to be similar in production, native species composition and abundance, and exotic annual grass abundance (Sneva et al., 1980; Courtois et al., 2004; Davies et al., 2009; Davies et al., 2014). Moderate grazing is utilization levels of 30%–45% of available forage (Holechek et al., 1999) with season of use altering between growing season and dormant season use. In contrast, overgrazing (greater utilization and often repeated growing season use) of sagebrush (*Artemisia* L.) steppe communities reduces native perennial grasses and promotes exotic annual grass invasion (Laycock, 1967; Mack, 1981; Young and Allen, 1997; Reisner et al., 2013).

Moderate grazing, however, does alter some plant community characteristics. Grazed areas generally have less herbaceous cover than ungrazed areas (Szaro and Pase, 1983; Davies et al., 2010; Kerns et al., 2011; Bates and Davies, 2014). There may also be some shifts in competition that favor plants not grazed compared with grazed plants because of the loss of photosynthetic tissues (Caldwell et al., 1987; Briske and Richards, 1995). Grazed plant communities can have greater fine fuel moisture content than ungrazed plant communities (Davies et al., 2015, 2016, 2017). Ungrazed rangelands also have an accumulation of fuels, particularly standing-dead fine fuels (Davies et al., 2010,

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2017). Ungrazed rangelands, because of an accumulation of dry fine fuels, are at a greater risk of fire propagation (Davies et al., 2017) and more likely to experience a more intense and severe fire than moderate grazed rangelands (Davies et al., 2009, 2016).

However, little is known about the effects of cattle grazing on many structural characteristics of sagebrush communities. Grazing by sheep has been demonstrated to reduce sagebrush cover, especially with fall grazing (Laycock, 1967; Bork et al., 1998), which likely translates to smaller sagebrush canopies. Sheep consume more browse than cattle and therefore results from sheep studies should not be extrapolated to cattle. Shrub cover was similar in cattle grazed compared with ungrazed sagebrush steppe (Davies et al., 2010), but response of sagebrush was not evaluated on an individual plant basis. However, grazing of riparian areas by cattle during the summer can alter the structure of other shrubs such as willows (*Salix* sp.) (Schultz and Leininger, 1990). Livestock grazing alterations to woody vegetation structure can also influence fire intensity and frequency in forested ecosystems (Zimmerman and Neuenschwander, 1984).

Cattle influence the structure of vegetation they consume, but vegetation's long-term structural response to grazing is generally unknown. Even less is known about the influence of cattle on the structure of vegetation they generally do not consume. Of particular interest in sagebrush steppe communities would be the structural response of sagebrush and large perennial bunchgrasses to long-term, moderate grazing. Sagebrush is a keystone species that provides vital habitat to sagebrush obligate wildlife species (Connelly et al., 2000; Prevéy et al., 2010). Alterations to sagebrush structure may influence wildlife that use sagebrush for hiding and nesting cover. For example, greater sage-grouse *(Centrocercus urophasianus)* mostly nest under sagebrush, and sagebrush structure often determines preference (Sveum et al., 1998). Though cattle generally consume very little, if any, sagebrush (Krysl et al., 1984), they may physically damage sagebrush as they graze herbaceous vegetation between and underneath sagebrush canopies. Large perennial bunchgrasses are vital because they are the most important plant functional group to preventing exotic annual grass invasion (Chambers et al., 2007; Davies, 2008) and, subsequently, the development of an exotic annual grass — fire cycle (D'Antonio and Vitousek, 1992). Alteration to bunchgrass structure through grazing, such as reducing fuel accumulations on their crowns, may influence their sensitivity to disturbances (Davies et al., 2009). Perennial bunchgrasses also provide important hiding cover for wildlife (Sveum et al., 1998; Connelly et al., 2000). Considering that cattle grazing is extensive across the sagebrush steppe (Davies et al., 2014), it is critical to understand the influence of long-term grazing by cattle on sagebrush and perennial bunchgrass structure.

The purpose of this study was to evaluate the effects of long-term (80 yr) grazing compared with no grazing by cattle on sagebrush and perennial bunchgrass structure. We hypothesized that grazing by cattle would alter sagebrush and native bunchgrass structure. Specificity, we expected that sagebrush canopies would be smaller with long-term grazing by cattle because of physical damage. In addition, we hypothesized that grazing by cattle would reduce dead fuels in the center of bunchgrasses.

Methods

Study Area

The study was conducted in southeastern Oregon approximately 50 — 60 km west of Burns, Oregon, at the Northern Great Basin Experimental Range (NGBER) (lat 43°29′N, long 119°43′W). Climate at the NGBER is typical of the northern Great Basin with cool, wet winters and hot, dry summers. The headquarters of the NGBER received on average 300 mm of precipitation annually during the past 50 yr (1956 — 2005). Elevation at the study sites ranges from approximately 1 300 to 1 500 m above sea level, and the topography is flat (slopes 0° — 3°) to 15° with aspects from south to north. Soils at the study sites are Aridisols, Mollisols, and Andisols with varying soil depths (Lentz and Simonson, 1986). Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* [Beetle and A. Young] S. L. Welsh) and mountain big sagebrush (*A. t.* spp. *vaseyana* [Rydb.] Beetle) were the dominant shrubs with dominant bunchgrass species varying by study site. Thurber's needlegrass (*Achnatherum thurberianum* [Piper] Barkworth), Idaho fescue (*Festuca idahoensis* Elmer), prairie junegrass (*Koeleria macrantha* [Ledeb.] J. A. Schultes), bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve), needle and thread (*Hesperostipa comata* [Trin. and Rupr.] Barkworth), and bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey) were common large perennial bunchgrasses at the study sites. Plant communities were dominated by native perennial vegetation (sagebrush and bunchgrasses) with very limited abundance of exotic annual grasses (< 4% cover). Plant community composition and plant functional group densities were similar between exclosures and grazed areas (Bates et al., unpublished data). The plant communities at the study sites are common in the northern Great Basin (Daubenmire, 1970; Davies et al., 2006; Davies and Bates, 2010). These plant communities are not believed to have recently evolved with high numbers of large ungulates (Mack and Thompson, 1982), but they have evolved with periodic fire (Wright and Bailey, 1982; Miller and Rose, 1999; Mensing et al., 2006; Miller and Heyerdahl, 2008).

Experimental Design

We used a randomized complete block design with two treatments. Treatments were long-term, moderate grazing (grazed), and long-term grazing exclusion (ungrazed) and were applied to nine different sites with varying vegetation, soils, and topography. The ungrazed treatments were 2-ha livestock exclosures established in 1936. The grazed treatments were concurrently established adjacent to the livestock exclosures and were similar in site characteristics (soil, topography, etc.) and vegetation composition. Thus, the experiment consisted of nine grazed and nine ungrazed areas. We considered moderate grazing to be utilization between 30% and 45% (Holechek et al., 1999) and season of use altering between growing season and dormant season use (deferred rotation). In 1937, density was similar among treatments for large perennial bunchgrasses, Sandberg bluegrass, perennial forbs, annual forbs, and annual grass ($P > 0.05$). Grazed treatments were grazed by cattle through 2015. Grazing pressure by cattle was moderate, 30 — 45% use of the available forage. From 1938 to 1949 cattle use was rotation grazing with stocking rates determined from range surveys conducted in 1938 and 1944. From 1949 to 2015, the grazing program was a deferred-rotational system with an occasional year of complete rest. Stocking rates ranged between 0.15 and 0.36 animal unit months (AUMs) per ha with an average of 0.22 AUMs per ha. In 2016, no grazing occurred before sampling. Grazed treatments were in nine fenced rangeland pastures ranging in size from 65 to 810 ha. Wildlife were not excluded from the grazed or ungrazed treatments.

Measurements

Bunchgrass and sagebrush structure was measured in late June through July 2016. Fifty native perennial bunchgrasses, excluding Sandberg bluegrass (*Poa secunda* J. Presl), were randomly selected in each treatment replication. Sandberg bluegrass was excluded from measurements because it is smaller in stature, develops phenologically earlier (James et al., 2008), and differs in its response to disturbances compared with larger native bunchgrasses (McLean and Tisdale, 1972; Yensen et al., 1992). Total crown diameter (live and dead), dead crown center diameter, crown height, and depth of fuel in dead center above and below crown level were measured on each selected bunchgrass. Crown height was measured as the distance between the surrounding soil surface and the crown. Depth of fuel below the crown level was measured by excavating a small hole in the center of the dead materials at the center of each plant until soil was contacted. Number of reproductive stems, reproductive stem height, and droop height were also measured on 50 previously selected bunchgrasses.

Fifty sagebrush plants were randomly selected in each treatment replication. Height, widest canopy diameter, diameter perpendicular to widest diameter, basal trunk diameter, and number of basal stems were measured on each selected sagebrush. Number of gaps > 10 cm and length of gaps in the canopy were also measured on each sagebrush. Height of the bottom of the sagebrush canopy was measured at the dripline and halfway between the dripline and the trunk (50% of dripline) on each sagebrush.

Statistical Analyses

We used analysis of variance (ANOVA) with the PROC MIXED procedure in SAS v. 9.4 (SAS Institute, Cary, NC) to evaluate perennial bunchgrass and sagebrush structural responses to long-term grazing. Treatment (grazed, ungrazed) was considered a fixed variable, and block and block-by-treatment interaction were considered random variables in the models. The appropriate covariance structure, compound symmetry, was selecting using Akaike's Information Criterion (Littell et al., 1996). Data that violated assumptions of ANOVAs were square root transformed to better meet assumptions. Original data (i.e., nontransformed) were presented in the figures and text. Means were considered different at $\alpha \leq 0.05$. Means were reported with standard errors in the text and figures.

Results

Perennial bunchgrass total crown diameter (live and dead) was 20% greater in the ungrazed compared with the grazed treatment (Fig. 1; $P = 0.005$). The diameter of the bunchgrass crown that was dead was 1.3 times greater in the ungrazed than grazed treatment (see Fig. 1; $P = 0.017$). Crown height above the soil surface did not differ between treatments (see Fig. 1; $P = 0.093$). Depth of the fuel in dead center of the crown above the crown level was 1.6 times greater in the ungrazed compared with the grazed treatment (Fig. 2; $P = 0.006$). Depth of fuel in the dead center of the crown below the crown level was 40% greater in the ungrazed compared with grazed treatment (see Fig. 2; $P = 0.014$). Number of reproductive stems per bunchgrass was 1.7 times greater in the ungrazed compared with the grazed treatment (Fig. 3; $P = 0.012$). Height of reproductive stems was 1.2 times greater in the ungrazed compared with the grazed treatment (see Fig. 3; $P = 0.001$).

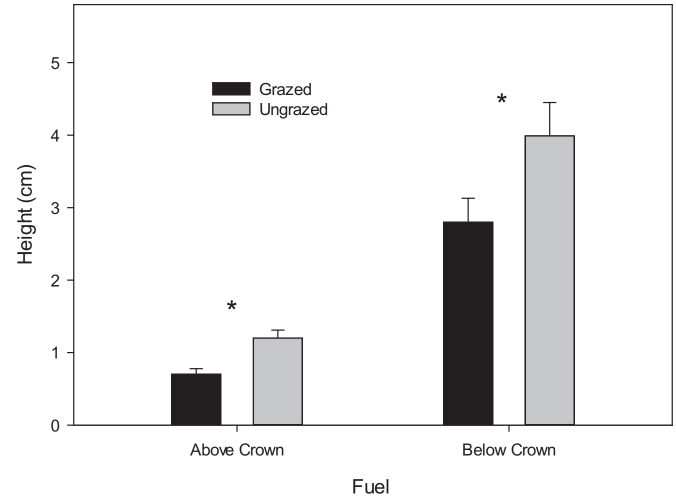

Figure 2. Fuel heights above and below bunchgrass crown level (mean + S.E.) in long-term grazed and ungrazed sagebrush steppe communities. Asterisks (*) indicate difference between treatment means ($P \leq 0.05$).

The droop height of bunchgrasses was 1.3 times greater in the ungrazed compared with the grazed treatment (see Fig. 3; $P = 0.006$).

Sagebrush height differed between treatments (Fig. 4; $P = 0.022$) and was 15% greater in the ungrazed compared with the grazed treatment. The longest diameter of the sagebrush canopy was 1.2 times greater in the ungrazed compared with the grazed treatment (see Fig. 4; $P = 0.039$); however, the diameter perpendicular to the longest diameter did not differ between treatments (see Fig. 4; $P = 0.140$). Dripline height of the bottom of the sagebrush canopy did not differ between treatments (see Fig. 4; $P = 0.149$). Height of the bottom of the canopy at 50% of the dripline was 1.3 times greater in the ungrazed compared with the grazed treatment (see Fig. 4; $P = 0.007$). Number of basal stems did not differ between the ungrazed and grazed treatment (Grazed = 2.60 ± 0.20 stems·plant^{-1}, Ungrazed = 2.63 ± 0.15 stems·plant^{-1}; $P = 0.847$). Basal diameter of sagebrush was similar between treatments (Grazed = 11.92 ± 1.29 cm, Ungrazed = 13.04 ± 1.12 cm; $P = 0.177$). The percent of dead in the sagebrush canopy did not differ between the ungrazed and grazed treatments (Grazed = 30.18 ± 7.75%, Ungrazed = 27.25 ± 8.98%; $P = 0.609$). The number of gaps (Grazed = 0.55 ± 0.08 gaps·plant^{-1}, Ungrazed = 0.50 ± 0.05 gaps·plant^{-1}) and the length of the gaps

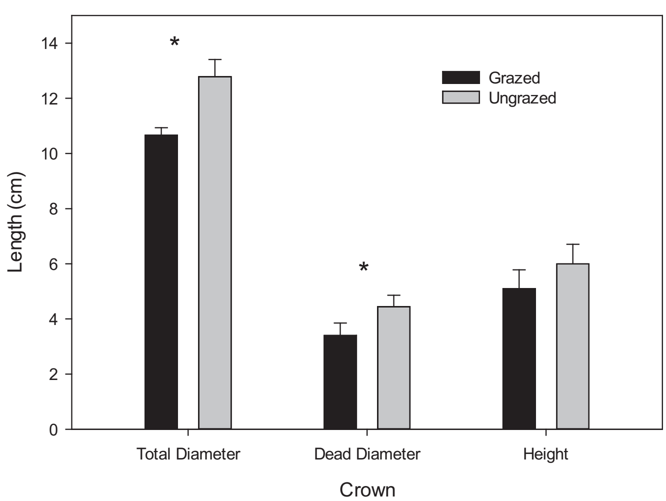

Figure 1. Bunchgrass crown total diameter (live + dead), dead diameter, and height above soil surface (mean + S.E.) in long-term grazed and ungrazed sagebrush steppe communities. Asterisks (*) indicate difference between treatment means ($P \leq 0.05$).

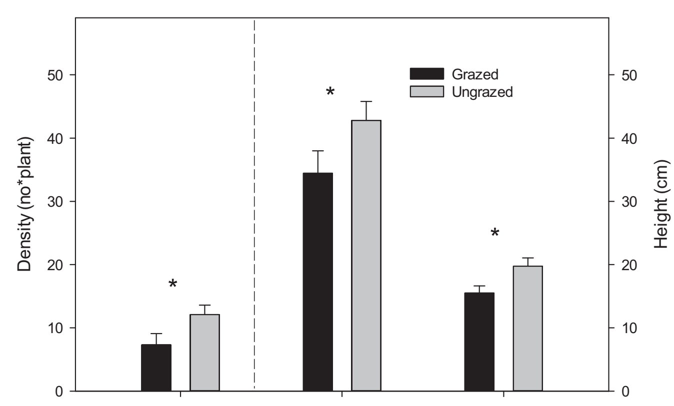

Figure 3. Bunchgrass reproductive stem density (left panel) and reproductive stem and droop height (right panel) (mean + S.E.) in long-term grazed and ungrazed sagebrush steppe communities. Asterisks (*) indicate difference between treatment means ($P \leq 0.05$).

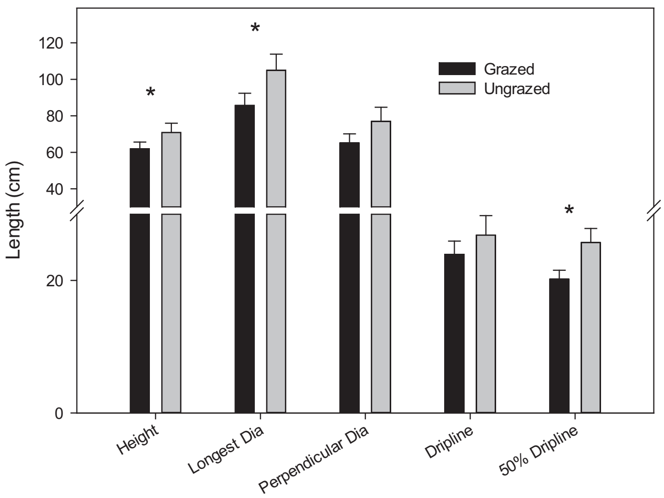

Figure 4. Sagebrush height, longest canopy diameter, diameter perpendicular to longest diameter, and canopy height aboveground at dripline and at 50% of dripline (mean + S.E.) in long-term grazed and ungrazed sagebrush steppe communities. Asterisks (*) indicate difference between treatment means ($P \leq 0.05$).

(Grazed = 26.82 ± 2.04 cm, Ungrazed = 28.43 ± 1.78 cm) in the sagebrush canopy did not differ between treatments ($P = 0.500$ and 0.440, respectively).

Discussion

Long-term, moderate grazing by cattle influenced the structure of native perennial bunchgrasses and sagebrush. These effects likely have both positive and negative consequences to the persistence of sagebrush steppe communities, as well as associated wildlife. However, many grazing-induced structural changes were negligible and therefore their ecological impact may be limited. Structural changes to bunchgrasses may be an exception when coupled with fire as ungrazed plants could be more susceptible to fire-induced mortality. Interestingly, moderate grazing influenced structure of sagebrush, a generally unpalatable shrub to cattle (Krysl et al., 1984). However, it was not the product of altering resource competition as might be expected when an unpalatable shrub grows with palatable grasses. If grazing altered the competitive relationship by consuming grasses, we would have expected greater sagebrush size in the grazed areas, but we found the inverse. Further, supporting our conclusion that moderate grazing was not affecting the competitive relationship between grasses and sagebrush, Bates et al. (unpublished data) found similar densities of sagebrush and bunchgrasses between the grazed and ungrazed areas. Sagebrush structure was likely altered by physical effects of livestock traversing between shrubs.

Long-term grazing-induced changes to bunchgrasses may influence their risk of fire-induced mortality. In ungrazed areas, the larger centers of dead materials in the crowns of perennial bunchgrasses combined with a greater depth of fuel in this center below and above the meristematic tissues increase the risk that these bunchgrasses will experience lethal temperatures during a fire. Accumulations of dry fuels elevate fire temperature and elongate the time temperatures are elevated (Byram, 1959; Kimuyu et al., 2014; Davies et al., 2016). The probability of fire-induced mortality of perennial bunchgrasses increases with longer duration of elevated temperatures during fires (Wright and Klemmedson, 1965; Wright, 1970; Odion and Davis, 2000; Hulet et al., 2015). This structural change to perennial bunchgrasses likely explains why Davies et al. (2009) observed a 50% reduction in perennial bunchgrass density after fire in ungrazed compared with grazed rangelands. Increased perennial bunchgrass mortality is concerning because bunchgrasses are the dominant herbaceous functional group in sagebrush steppe communities (Davies et al., 2006; Davies and Bates, 2010) and are critical to limiting exotic annual grass invasion and dominance (Chambers et al., 2007; Davies, 2008). Long-term, moderate grazing, by altering the structure of perennial bunchgrasses, is likely reducing the probability that bunchgrasses will suffer mortality during a fire and, thereby, helping to maintain resistance to exotic annual grass invasion. This should not be interpreted to be suggesting that all grazing promotes resistance to exotic annual grass invasion. Improper grazing can decrease the resistance of the plant community to exotic annual grass invasion by decreasing bunchgrasses (Daubenmire, 1970; Reisner et al., 2013).

Significant postfire invasion of exotic annual grasses, especially cheatgrass (*Bromus tectorum* L.), is particularly concerning. Exotic annual grasses dry out earlier than native perennial vegetation (Davies and Nafus, 2013) and can promote frequent wildfires that are detrimental to native vegetation (D'Antonio and Vitousek, 1992). Cheatgrass and other exotic annual grass invasion is a great management challenge as there are no cost-effective methods to control cheatgrass across the vast areas it has invaded (Stohlgren and Schnase, 2006), let alone restore these areas.

The lower number of reproductive stems per bunchgrass with long-term grazing may be of concern. Fewer reproductive stems may indicate lower seed produced per plant, which could mean that fewer seeds are available to occupy safe sites and populate the seed bank. However, we cannot definitively conclude that fewer seeds were produced in grazed areas because we did not measure seed production. Even if fewer seeds were produced in the grazed areas, it appears that seeds were plentiful enough to recruit sufficient individuals to offset mortality, as perennial bunchgrasses are relatively short-lived (Svejcar et al., 2014). However, additional research is warranted to determine the effects of long-term grazing on seed production and fitness and seedling vigor of perennial bunchgrasses.

Decreases in perennial bunchgrass and sagebrush heights with long-term grazing were likely not biologically significant. Similar to our current study, Davies et al. (2010) found that long-term ungrazed bunchgrasses were 1.3-fold taller than long-term grazed bunchgrasses, even though annual production of bunchgrasses was the same. Sagebrush heights were only 9 cm taller in the ungrazed compared with the grazed treatments, which likely has little influence on its value to wildlife. For example, sagebrush in both the grazed and ungrazed treatments exceed the sagebrush height requirements for productive sage-grouse habitat (Connelly et al., 2000), though the ubiquitous application of these guidelines is ill-advised (Davies et al., 2006).

The longest diameter and height of the bottom of the sagebrush canopy may influence its value to wildlife. For example, sage-grouse generally nest under sagebrush with larger canopies (Sveum et al., 1998). The longer canopy diameter results in a larger under-canopy area for hiding cover, particularly for nesting, in the ungrazed compared with the grazed treatments, especially since amount of dead, number of gaps, and gap size in canopies were similar between treatments. However, the height of the bottom of sagebrush canopy may have the opposite effect on under-canopy hiding cover in the ungrazed treatment. Less distance between the ground and the bottom of the sagebrush canopy at 50% of dripline in the grazed compared with the ungrazed may provide important hiding cover in the grazed treatments. Sage-grouse often select sagebrush for nesting with less distance between the canopy and the ground (Fischer, 1994; Sveum et al., 1998; Holloran, 1999). Less distance between the sagebrush canopy and the ground at the 50% dripline was surprising as we expected that cattle grazing under the shrubs would likely break off lower branches, resulting in more distance between the bottom of the canopy and the ground. Cattle, however, often avoid grazing under sagebrush plants until total utilization exceeds 40% of available forage (France et al., 2008). Considering that both treatments may have opposing effects on hiding cover under sagebrush, it is likely that long-term grazing effects are minor. Furthermore, to conclude with any certainty that either of these structural differences influences nest success and wildlife population demographics would requiring measuring wildlife response to these treatments (Fulbright et al. 2018).

Moderate, long-term grazing by cattle appears to have little effect in the interior of the sagebrush canopy. Number of gaps, gap size, and amount of dead in the canopy were similar between grazed and ungrazed treatments. The numbers of basal stems and basal diameter were not influenced by long-term grazing, further suggesting that the interior of sagebrush plants was not influenced by grazing by cattle. Therefore grazing by cattle, as conducted in this study, largely influences the exterior of the canopy, likely through physical damage as cattle traverse between sagebrush plants. Alterations to canopy size are likely caused by physical damage as cattle generally do not consume big sagebrush unless grazing pressure is heavy and even then it generally constitutes < 5% of their diet (Krysl et al., 1984). Grazing pressure in this study was moderate and during the spring and summer; therefore, sagebrush consumption by cattle was probably minimal.

Management Implications

Long-term grazing by cattle influences the structure of plants they readily consume (bunchgrasses) and plants they generally avoid consuming (big sagebrush). The effects of moderate grazing, particularly on bunchgrasses, likely influences the persistence of some sagebrush communities. Most likely, moderate grazing is decreasing the probability of fire-induced mortality of native bunchgrasses by reducing the amount of dry fuel in and on top of bunchgrass crown and thereby decreasing the risk of postfire dominance by exotic annual grasses. However, reduced bunchgrass reproductive effort with grazing should be further investigated. Grazing reduces the size of sagebrush plants, but what effect this has on sagebrush communities and associated wildlife is unclear. The reductions in sagebrush height and canopy diameter were small and may be biologically insignificant. Grazing, however, does modify plant structure and with improper management (e.g., greater grazing pressures than used in this study) may have undesirable effects on structure. Nevertheless, our data provides compelling evidence that the effects of long-term, moderate grazing on bunchgrass and sagebrush structure likely has limited effects and may contribute to the persistence of these communities.

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References

Batchelor, J.L., Ripple, W.J., Wilson, T.M., Painter, L.E., 2015. Restoration of riparian areas following the removal of cattle in the northwestern Great Basin. Environmental Management 55, 930–942.

Bates, J.D., unpublished data. Long-term grazing exclusion compared to moderate grazing dataset. Eastern Oregon Agricultural Research Center, Burns, OR..

Bates, J.D., Davies, K.W., 2014. Cattle grazing and vegetation succession on burned sagebrush steppe. Rangeland Ecology & Management 67, 412–422.

Beschta, R.L., Kauffman, J.B., Dobkin, D.S., Ellsworth, L.M., 2014. Long-term livestock grazing alters aspen age structure in the northwestern Great Basin. Forest Ecology Management 329, 30–36.

Bork, E.W., West, N.E., Walker, J.W., 1998. Cover components of long-term seasonal sheep grazing treatments in three-tip sagebrush steppe. Journal of Range Management 51, 293–300.

Briske, D.D., Richards, J.H., 1995. Plant responses to defoliation: a physiological, morphological and demographic evaluation. In: Bedunah, D.J., Sosebee, R.E. (Eds.), Wildland plants: physiological ecology and developmental morphology. Society for Range Management, Denver, CO, USA, pp. 635–710.

Byram, B.M., 1959. Combustion of forest fuels. In: Davis, K.P. (Ed.), Forest fire: control and use. McGraw Hill, New York, NY, USA, pp. 61–89.

Caldwell, M.M., Richards, J.H., Manwaring, J.H., Eissenstat, D.M., 1987. Rapid shifts in phosphate acquisition show direct competition between neighboring plants. Nature 327, 615–616.

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*? Ecology Monograph 77, 117–145.

Connelly, J.W., Schroeder, M.A., Sands, A.R., Braun, C.E., 2000. Guidelines to manage sage-grouse populations and their habitat. Wildlife Society Bulletin 28, 967–985.

Courtois, D.R., Perryman, B.L., Hussein, H.S., 2004. Vegetation change after 65 years of grazing and grazing exclusion. Journal of Range Management 57, 574–582.

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 Evolution Systems 23, 63–87.

Daubenmire, R., 1970. Steppe vegetation of Washington. Washington Agricultural Experiment Station Technical Bulletin 62 131 p..

Davies, K.W., 2008. Medusahead dispersal and establishment in sagebrush steppe plant communities. Rangeland Ecology & Management 61, 110–115.

Davies, K.W., Bates, J.D., 2010. Vegetation characteristics of mountain and Wyoming big sagebrush plant communities in the northern Great Basin. Rangeland Ecology & Management 63, 461–466.

Davies, K.W., Bates, J.D., Miller, R.F., 2006. Vegetation characteristics across part of the Wyoming big sagebrush alliance. Rangeland Ecology & Management 59, 567–575.

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., 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., Bates, J.D., Hulet, A., 2016. Winter grazing can reduce wildfire size, intensity and behaviour in a shrub-grassland. International Journal Wildland Fire 25, 191–199.

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 Wildland Fire 26, 485–490.

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., Svejcar, T.J., Bates, J.D., 2009. Interaction of historical and non-historical disturbances maintains native plant communities. Ecology Application 19, 1536–1545.

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, 1434.

Fischer, R.A., 1994. The effects of prescribed fire on the ecology of migratory sage grouse in southeastern Idaho [dissertation]. University of Idaho, Moscow, ID, USA, p. 150.

France, K.A., Ganskopp, D.C., Boyd, C.S., 2008. Interspace/undercanopy foraging patterns of beef cattle in sagebrush habitats. Rangeland Ecology & Management 61, 389–393.

Fulbright, T.E., Davies, K.W., Archer, S.R., 2018. Wildlife response to brush management: a contemporary evaluation. Rangeland Ecology & Management 71, 35–44.

Holechek, J.L., Gomez, H., Molinar, F., Galt, D., 1999. Grazing studies: what we've learned. Rangelands 22, 12–16.

Holloran, M.J., 1999. Sage grouse *(Centrocercus urophasianus)* seasonal habitat use near Casper, Wyoming [thesis]. University of Wyoming, Laramie, WY, USA, p. 123.

Hulet, A., Boyd, C.S., Davies, K.W., Svejcar, T.J., 2015. Prefire (preemptive) management to decrease and reduce reliance on post-fire seeding. Rangeland Ecology & Management 68, 437–444.

James, J.J., Davies, K.W., Sheley, R.L., Aanderud, Z.T., 2008. Linking nitrogen partitioning and species abundance to invasion resistance in the Great Basin. Oecologia 156, 637–648.

Kerns, B.K., Buonopane, M., Thies, W.G., Niwa, C., 2011. Reintroducing fire into a ponderosa pine forest with and without cattle grazing: understory vegetation response. Ecosphere 2, 59.

Kimuyu, D.M., Sensenig, R.L., Riginos, C., Veblen, K.E., Young, T.P., 2014. Native and domestic browsers and grazers reduce fuels, fire temperature, and acacia ant mortality in an African savanna. Ecology Applications 24, 741–749.

Krysl, L.J., Hubbert, M.E., Sowell, B.F., Plumb, G.E., Jewett, T.K., Smith, M.A., Waggoner, J.W., 1984. Horses and cattle grazing the Wyoming Red Desert, I Food habits and dietary overlap. Journal of Range Management 37, 72–76.

Laycock, W.A., 1967. How heavy grazing and protection affect sagebrush-grass ranges. Journal of Range Management 20, 206–213.

Lentz, R.D., Simonson, G.H., 1986. A detailed soil inventory and associated vegetation of Squaw Butte Range Experiment Station. Oregon Agricultural Experiment Station Special Report 760. Oregon State University, Corvallis, OR, USA 184 p.

Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., 1996. SAS system for mixed models. SAS Institute Inc., Cary, NC, USA 633 p.

Mack, R.N., 1981. Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. Agro-Ecosystems 7, 145–165.

Mack, R.N., Thompson, J.N., 1982. Evolution in steppe with few large, hooved mammals. The American Naturalist 119, 757–773.

McLean, A., Tisdale, E.W., 1972. Recovery rate of depleted range sites under protection from grazing. Journal of Range Management 25, 178–184.

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 Nature 66, 64–77.

Miller, R.F., Heyerdahl, E.K., 2008. Fine-scale variation of historical fire regimes in sagebrush-steppe and juniper woodland: an example from California, USA. International Journal of Wildland Fire 17, 245–254.

Miller, R.F., Rose, J.A., 1999. Fire history and western juniper encroachment in sagebrush steppe. Journal of Range Management 52, 550–559.

Odion, D.C., Davis, F.W., 2000. Fire, soil heating, and the formation of vegetation patterns in chaparral. Ecology Monographs 70, 149–169.

Prevéy, J.S., Germino, M.J., Huntly, N.J., 2010. Loss of foundation species increases population growth of exotic forbs in sagebrush steppe. Ecology Applications 20, 1890–1902.

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.

Schultz, T.T., Leininger, W.C., 1990. Differences in riparian vegetation structure between grazed areas and exclosures. Journal of Range Management 43, 295–299.

Sneva, F.A., Rittenhouse, L.R., Tueller, P.T., 1980. Forty years—inside and out. Research in rangeland management. Special Report No. 586. Oregon State University, Oregon Agricultural Experiment Station, Corvallis, OR, USA, pp. 10–12.

Stohlgren, T.J., Schnase, J.L., 2006. Risk analysis for biological hazards; what we need to know about invasive species. Risk Analysis 26, 163–173.

Svejcar, T., James, J., Hardegree, S., Sheley, R., 2014. Incorporating plant mortality and recruitment into rangeland management and assessment. Rangeland Ecology & Management 67, 603–613.

Sveum, C.M., Edge, W.D., Crawford, J.A., 1998. Nesting habitat selection by sage grouse in south-central Washington. Journal of Range Management 51, 265–269.

Szaro, R.C., Pase, C.P., 1983. Short-term changes in a cottonwood-ash-willow association on a grazed and an ungrazed portion of Little Ash Creek in central Arizona. Journal of Range Management 36, 383–384.

Wright, H.A., 1970. A method to determine heat-caused mortality in bunchgrasses. Ecology 51, 582–587.

Wright, H.A., Bailey, A.W., 1982. Fire ecology: United States and Southern Canada. John Wiley & Sons, New York, NY, USA 528 p.

Wright, H.A., Klemmedson, J.O., 1965. Effect of fire on bunchgrasses of the sagebrush-grass region in southern Idaho. Ecology 46, 680–688.

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 Nature 128, 299–312.

Young, J.A., Allen, F.A., 1997. Cheatgrass and range science: 1930-1950. Journal of Range Management 50, 530–535.

Zimmerman, G.T., Neuenschwander, L.F., 1984. Livestock grazing influences on community structure, fire intensity, and fire frequency within the Douglas-fire/ninebark habitat type. Journal of Range Management 37, 104–110.