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Effects of Intermediate-Term Grazing Rest on Sagebrush Communities with Depleted Understories: Evidence of a Threshold☆,☆☆

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ABSTRACT

Millions of hectares of sagebrush (*Artemisia* L.) plant communities have been degraded by past improper management, resulting in dense sagebrush stands with depleted herbaceous understories. Rest from grazing is often applied to promote recovery. However, the effect of intermediate-term (5–10 years) rest from grazing in sagebrush communities with depleted herbaceous understories and dense sagebrush is relatively unknown. We compared well-managed, moderate grazing (grazed) with intermediate-term (5 and 6 years) rest (ungrazed) at five sites in southeastern Oregon. Sites were Wyoming big sagebrush (*Artemisia tridentata* Nutt. subsp. *wyomingensis* Beetle & Young) communities with dense sagebrush and depleted herbaceous understories. Perennial herbaceous cover was greater in ungrazed compared with grazed areas, but this was expected because herbivory removes foliar vegetation tissue (i.e., cover). Density of herbaceous vegetation, diversity, and species richness did not differ between ungrazed and grazed areas. Similarly, bare ground, litter, and biological soil crust cover did not differ between treatments. These results suggest that intermediate-term rest is unlikely to elicit recovery of the understory compared with moderate grazing in these communities. The results of this study also suggest that degraded Wyoming big sagebrush communities likely have crossed a threshold that may be difficult to reverse.

Introduction

Wyoming big sagebrush (*Artemisia tridentata* Nutt. subsp. *wyomingensis* Beetle & Young) communities are one of the most extensive plant communities in the sagebrush ecosystem that occupies > 500,000 km^2 in the Intermountain West (Küchler, 1970; Miller and Eddleman, 2000). These communities provide critical habitat for sagebrush-associated wildlife and are an important forage base for livestock production (Davies et al., 2011). However, large tracts of Wyoming big sagebrush plant communities have been degraded through historical overgrazing by sheep, cattle, and horses, resulting in communities with few large perennial bunchgrasses and perennial forbs and an increased dominance of shrubs (Davies et al., 2011; Miller and Eddleman, 2000; West, 1983). West (2000) estimated that 25% of the entire sagebrush ecosystem was composed of sagebrush plant communities with degraded herbaceous understories and increased shrub dominance. The percent of the Wyoming big sagebrush ecosystem with degraded herbaceous understories and increased shrub dominance is probably much greater than the average for the entire sagebrush ecosystem because it is less resilient to disturbance than wetter, cooler sagebrush communities (Chambers et al., 2007; Chambers et al., 2014; Davies et al., 2011). Restoration of these plant communities has become a critical management concern because of their value as wildlife habitat, as well as to provide quality livestock forage, increase resistance to exotic annual grasses, and enhance resilience to wildfire (Davies et al., 2011).

Degraded Wyoming big sagebrush communities have proven to be exceedingly difficult to restore. Using fire or mechanical methods to reduce sagebrush dominance to increase resource availability to native perennial herbaceous vegetation has generally resulted in increases in exotic annuals with little response from native perennial bunchgrasses and forbs (Beck et al., 2012; Davies et al., 2012; Pyke et al., 2014). Seeding native perennial bunchgrasses after mechanically reducing sagebrush has also been a general failure, with small increases in native bunchgrasses but large increases in exotic annual grasses and forbs (Davies and Bates, 2014). The lack of successful treatments to restore Wyoming big sagebrush plant communities may, in some ways, suggest that restoration should not be attempted. However, these plant communities historically burned in infrequent wildfires and it is likely that they will inevitably burn and then convert to exotic annuals post fire (Davies and Bates, 2014). Therefore, it is imperative to investigate methods to

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restore these communities. All the previously discussed approaches applied a disturbance that reduced or removed sagebrush in an attempt to increased native perennial understory vegetation. These treatments increased exotic annuals (Beck et al., 2012; Davies and Bates, 2014; Davies et al., 2012; Pyke et al., 2014), which are often favored by disturbances (Chambers et al., 2007; Norton et al., 2007; Seabloom et al., 2003). Therefore, a different approach is needed, likely one that does not significantly disturb the sagebrush overstory as the loss of sagebrush in these communities can increase the growth of exotics (Prevéy et al., 2010). A potential approach to promote recovery of these communities may be to exclude grazing by livestock. Rest from grazing may facilitate recovery (increases in abundance) of large native bunchgrasses and perennial forbs because defoliation may be limiting their ability to increase. Grazing can place grazed plants, through the loss of photosynthetic tissues, at a competitive disadvantage with ungrazed plants (Briske and Richards, 1995; Caldwell et al., 1987).

Rest from grazing by cattle is traditionally applied to the sagebrush steppe ecosystem to promote recovery from past grazing effects and fire (Davies et al., 2014a). Most commonly rest is applied for 1 year as part of a grazing management system and for 1 or 2 years after disturbances such as fire (Bates et al., 2009). However, longer-term grazing rest has been applied or proposed for some sagebrush plant communities. The effects of rest in sagebrush communities has mainly been long-term (>10 years) rest and in communities retaining a largely intact herbaceous understory or without a dense sagebrush overstory (Anderson and Inouye, 2001; Courtois et al., 2004; Davies et al., 2009, 2010; Manier and Hobbs, 2006; Rickard, 1985; West et al., 1984). Information on effects of intermediate-term (5–10 years) rest on sagebrush communities is rare (Davies et al., 2014a) and has been limited to sites with large native perennial bunchgrasses and forbs dominating the understory (e.g., Bates and Davies, 2014; Bates et al., 2009; Davies et al., 2014b).

Though grazing rest has been proposed by some authors (e.g., Beschta et al., 2013; Fleischner, 1994) to promote recovery from damage caused by past improper grazing practices and prevent further ecosystem degradation, it remains unclear if grazing rest conveys more ecosystem benefits than well-managed, moderate grazing. Rest from grazing is clearly advantageous over detrimental grazing practices of heavy, repeated growing season use, but moderate grazing at times may achieve similar results as grazing rest (Davies et al., 2014a). However, many grazing studies do not report grazing levels or only compare heavy, repeated defoliation during the growing season with grazing rest (Jones, 2000; Svejcar et al., 2014). Thus, information comparing effects of intermediate-term rest and well-managed, moderate grazing are lacking. This information is critical to allow for more informed land management decisions as natural resource managers attempt to restore and protect sagebrush communities.

The purpose of this research project was to determine effects of intermediate-term (5 and 6 years) rest from grazing compared with moderate grazing by cattle on Wyoming big sagebrush communities with a depleted herbaceous understory and high sagebrush cover. We predicted that intermediate-term rest would increase the density and cover of native perennial bunchgrasses and forbs, increase the cover of biological soil crusts, decrease the density and cover of annual grasses and forbs, and increase species diversity and richness. We did not expect intermediate-term grazing rest to influence sagebrush cover and density.

Materials and Methods

Study Area

This study was conducted in Wyoming big sagebrush communities in southeast Oregon between 40 and 50 km southwest of Burns, Oregon, United States. Before treatment the herbaceous understory was considered depleted and sagebrush cover was high. Large perennial bunchgrass cover and density averaged across all study sites was 1.2% and 2.4 individual$\cdot$m^{-2}, which is 7.5 to 10.2 times less cover and 4 times less dense than the average reported for relatively intact Wyoming big sagebrush communities in this region (Davies and Bates, 2010; Davies et al., 2006). Sagebrush cover averaged 19.4% across study sites, which is 1.6- to 2-fold greater than the average sagebrush cover in Wyoming big sagebrush communities with intact herbaceous understories (Davies and Bates, 2010; Davies et al., 2006). Historical livestock use of this area was heavy (>50% utilization of available forage) and often season long, but recent use was well-managed, moderate grazing (Davies et al., 2012). Well-managed, moderate grazing by cattle of native Wyoming big sagebrush plant communities is <50% utilization and alternating season of use or incorporating periods of rest to ensure that plants are only defoliated during the growing season (spring) every other year or less frequent. The depleted understory, as evident from the vast differences between our study sites and relatively intact Wyoming big sagebrush communities, was likely caused by historical heavy livestock use. These sites were not dominated by annuals as exotic annual grass cover and annual forb cover averaged < 1% and 4.4%, respectively. Sandberg bluegrass (*Poa secunda* J. Presl) and bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey) were the most common perennial grasses at study sites. Thurber's needlegrass (*Achnatherum thurberianum* [Piper] Barkworth) and/or bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve) were also found at study sites and would have likely been the dominant/codominant perennial grasses if these sites were not degraded (NRCS, 2013). Elevation of study sites was between 1263 and 1350 m, and topography was relatively flat (0−4%). Soil depths ranged from 50 to 100 cm to a duripan and were loamy and well drained. Climate was representative of the northern Great Basin with cool wet winters and hot dry summers. Long-term average annual precipitation (1981–2010) ranged from 240 to 270 mm among study sites (PRISM, 2014). Crop year (Oct. 1—Sept. 30) precipitation was 107%, 93%, 137%, 78%, 100%, and 88% of the long-term average in 2009, 2010, 2011, 2012, 2013, and 2014, respectively (PRISM, 2014).

Experimental Design and Measurements

We used a randomized complete block design with five blocks (sites) to determine the response of Wyoming big sagebrush communities to intermediate-term rest from grazing. Treatments were: 1) intermediate-term rest (ungrazed) and 2) well-managed, moderate grazing by cattle (grazed). Treatments were randomly assigned to one of two 30 × 60 m plots at each of the five sites. These five sites occurred in different grazing pastures and were on average separated by 10 km. Intermediate-term rest was applied by constructing 60 × 150 m grazing exclosures in January and February of 2009. A 30 × 60 m plot inside of each 60 × 150 m grazing exclosure was sampled to determine the effects of grazing rest. A 30 × 60 m grazed treatment plot was adjacent to each grazing exclosure with a 10-m buffer between them at each site. The grazing treatment was applied at the pasture level and pastures were > 1000 ha in size. Grazing pressure was 40% utilization of available forage, which is considered moderate use in this environment. Season of use alternated between spring use (May and June) and summer use (July and August) each year. Rotation of season of use varied among the pastures.

Vegetation, litter, bare ground, and biological soil crusts were measured in June the fifth and sixth growing seasons (2013 and 2014) after grazing exclosures were constructed. Herbaceous vegetation, litter, bare ground, and biological soil crusts were measured along four 50-m transects using 0.2-m^2 quadrats placed at 3-m intervals (starting at 3 m and ending at 45 m), resulting in 15 quadrats per transect and 60 quadrats per plot. The 50-m transects were laid out parallel to the long edge of the plot and spaced 5 m apart. Foliar cover of herbaceous vegetation by species and ground cover of litter, biological soil crust, and bare ground were visually estimated in the 0.2-m^2 quadrats using markings that divided quadrats into 1%, 5%, 10%, 25%, and 50% segments.

Herbaceous cover included both current year's and previous years' growth that was still erect. Density of herbaceous vegetation was estimated by species by counting all individuals rooted inside the 0.2-m^2 quadrats. Shrub cover by species was estimated using the line intercept method (Canfield, 1941) on each of the 50-m transects. Shrub density by species was estimated by counting all shrubs rooted in four 2 × 50 m belt transects positioned over the 50-m transects. Diversity (Shannon's Diversity Index) was calculated from density measurements. Total species richness was determined by counting all species recorded in the density measurements.

Statistical Analyses

We used repeated measures analysis of variance (ANOVA) in SAS v. 9.2 (SAS Institute, Inc., Cary, NC, USA) with the mixed models procedure to determine the effects of intermediate-term rest from grazing on plant community characteristics. Year was the repeated variable, treatment was considered a fixed variable, and block and block by treatment interactions were treated as random variables in analyses. Covariance structure was selected for each analysis using the Akaike's Information Criterion (Littell et al., 1996). Data that violated assumptions of ANOVAs were square root transformed. Nontransformed data (i.e., original data) were presented in the text and figures. In analyses, herbaceous cover and density were grouped into five groups: Sandberg bluegrass, large perennial bunchgrasses, perennial forbs, exotic annual grasses, and annual forbs. Each group was analyzed individually. Sandberg bluegrass was not grouped with the other bunchgrasses because its phenological development occurs earlier, is smaller in stature (James et al., 2008), and responds differently to disturbances (McLean and Tisdale, 1972; Yensen et al., 1992). The large perennial bunchgrass and perennial forb groups were composed solely of native species. The annual forb group was composed of native and non-native species. Desert madwort (*Alyssum desertorum* Stapf.), an exotic annual forb, comprised 74—89% of the total annual forb cover and density. Treatment means were considered different at $\alpha = 0.05$. Means were reported with standard errors (mean + S.E.).

Results

Cover of perennial herbaceous plant groups was greater in the ungrazed than grazed treatment (Fig. 1). Sandberg bluegrass cover was 1.5-fold greater in the ungrazed compared with grazed treatments (see Fig. 1; $P = 0.026$, $df = 1{,}4$). Sandberg bluegrass cover was less in 2014 than in 2013 ($P < 0.001$, $df = 1{,}8$). Large perennial bunchgrass cover was greater in the ungrazed compared with grazed treatments (see Fig. 1; $P = 0.020$, $df = 1{,}4$) but did not vary between years ($P = 0.13$, $df = 1{,}8$). Large perennial bunchgrass cover was 1.7 times greater in the ungrazed treatment compared with the grazed treatment, but both treatments had low (<2%) average large perennial bunchgrass cover. The ungrazed treatment had 1.6-fold greater perennial forb cover than the grazed treatment (see Fig. 1; $P = 0.048$, $df = 1{,}4$) but was low in both treatments. Perennial forb cover was less in 2014 compared with 2013 ($P = 0.004$, $df = 1{,}8$). Exotic annual grass cover did not differ between treatments (see Fig. 1; $P = 0.774$, $df = 1{,}4$) or between years ($P = 0.823$, $df = 1{,}8$). Cover of annual forbs was 1.4-fold greater in the grazed compared with ungrazed treatments (see Fig. 1; $P = 0.030$, $df = 1{,}4$). Annual forb cover was greater in 2014 compared with 2013 ($P < 0.001$, $df = 1{,}8$).

Total herbaceous cover did not differ between treatments (Fig. 2; $P = 0.434$, $df = 1{,}4$) but was greater in 2014 than 2013 ($P = 0.045$, $df = 1{,}8$). Bare ground did not vary between treatment (see Fig. 2; $P = 0.491$, $df = 1{,}4$) and was similar between years ($P = 0.262$, $df = 1{,}8$). Ground cover by litter did not differ between treatments (see Fig. 2; $P = 0.633$, $df = 1{,}4$) or years ($P = 0.474$, $df = 1{,}8$). Biological soil crust cover did not differ between the ungrazed and grazed treatments (see Fig. 2; $P = 0.388$, $df = 1{,}4$). Biological soil crust was less in 2014 than in 2013 ($P = 0.041$, $df = 1{,}8$). Sagebrush and total shrub cover did not differ between treatments (Fig. 2; $P = 0.556$ and 0.626, $df = 1{,}4$). Sagebrush and total shrub cover was slightly less in 2014 compared with 2013 ($P = 0.004$ and 0.004, $df = 1{,}8$).

Density of herbaceous plant functional groups did not differ between the ungrazed and grazed treatments (Fig. 3). Sandberg bluegrass density did not vary between treatments (see Fig. 3; $P = 0.8576$, $df = 1{,}4$) or years ($P = 0.712$, $df = 1{,}8$). Similarly, large perennial bunchgrass density did not differ between the ungrazed and grazed treatments (see Fig. 3; $P = 0.990$, $df = 1{,}4$) or between years ($P = 0.407$, $df = 1{,}8$). The density of perennial forbs did not statistically vary between treatments (see Fig. 3; $P = 0.090$, $df = 1{,}4$) but did differ between years ($P = 0.009$, $df = 1{,}8$). Perennial forb density was 1.3-fold greater in 2013 than in 2014. Annual grass and annual forb density did not differ between ungrazed and grazed treatments (see Fig. 3; $P = 0.787$ and 0.080, $df = 1{,}4$). Annual grass density was 1.6-fold greater in 2013 than in 2014 ($P = 0.029$, $df = 1{,}8$). Annual forb density was 1.6-fold greater in 2014 compared with 2013 ($P = 0.009$, $df = 1{,}8$). Sagebrush and total shrub densities were similar between the ungrazed and grazed treatments ($P = 0.971$ and 0.945, $df = 1{,}4$). Average sagebrush density was 0.93 ± 0.09 and 0.92 ± 0.19 plants·m^{-2} in the ungrazed and grazed treatments. Sagebrush and total shrub density was

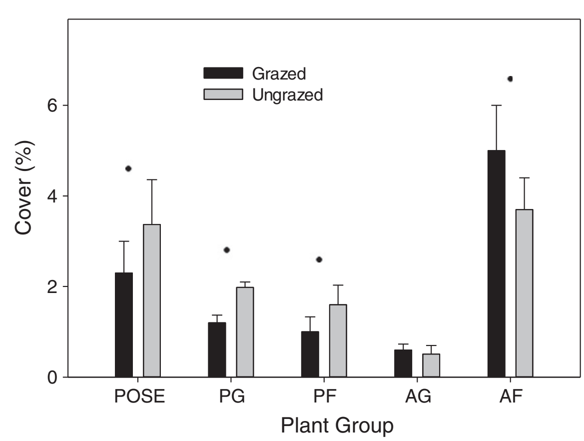

Fig. 1. Cover (mean + S.E.) of herbaceous plant groups in Wyoming big sagebrush communities that were either moderately grazed (Grazed) or intermediate-term (5–6 years) rested from grazing (Ungrazed). POSE indicates Sandberg bluegrass; PG, large perennial bunchgrasses; PF, perennial forbs; AG, exotic annual grasses; and AF, annual forbs. Asterisk (*) indicates significant difference between treatments.

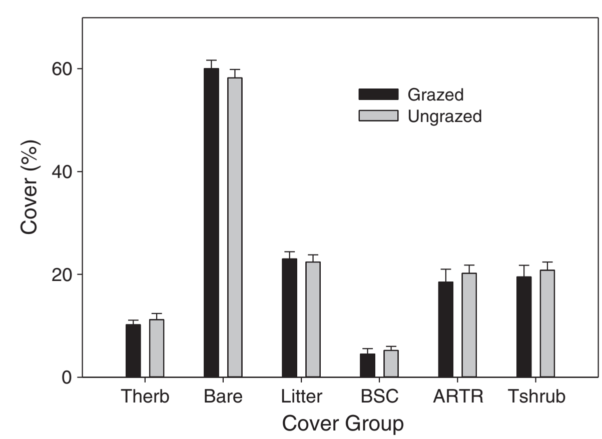

Fig. 2. Cover (mean + S.E.) of cover groups in Wyoming big sagebrush communities that were either moderately grazed (Grazed) or intermediate-term (5–6 years) rested from grazing (Ungrazed). Therb indicates total herbaceous; Bare, bare ground; Litter, ground litter; BSC, biological soil crust; ARTR, Wyoming big sagebrush; and Tshrub, total shrub. Asterisk (*) indicates significant difference between treatments.

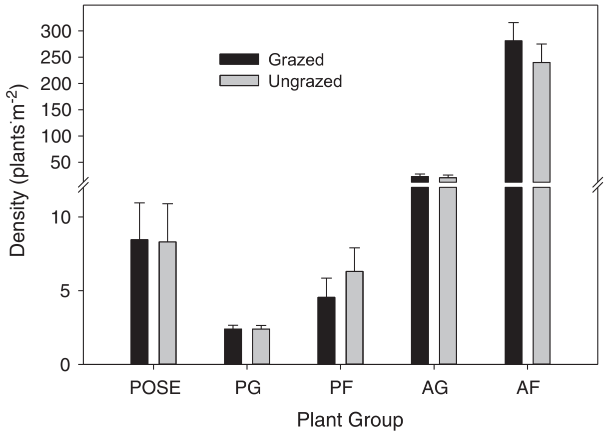

Fig. 3. Density (mean + S.E.) of herbaceous plant groups in Wyoming big sagebrush communities that were either moderately grazed (Grazed) or intermediate-term (5–6 years) rested from grazing (Ungrazed). POSE indicates Sandberg bluegrass; PG, large perennial bunchgrasses; PF, perennial forbs; AG, exotic annual grasses; and AF, annual forbs. Asterisk (*) indicates significant difference between treatments.

approximately 0.14 plants·m^{-2} less in 2014 compared with 2013 ($P =$ 0.015 and 0.010, $df = 1{,}8$).

Diversity and richness did not differ between the treatments (Fig. 4; $P = 0.256$ and 0.710, $df = 1{,}4$). Diversity was greater in 2013 than in 2014 ($P < 0.001$, $df = 1{,}8$), but richness did not vary by year ($P =$ 0.582, $df = 1{,}8$). The interaction between treatment and year was not significant for any measured response variable ($P > 0.05$, $df = 1{,}8$).

Discussion

Effects of intermediate-term (5 and 6 years) rest from grazing by cattle were mixed. As expected, cover of perennial herbaceous functional groups was greater with intermediate-term rest from grazing compared with grazed areas. Annual forb cover was also greater in the grazed area as postulated, though 5% compared with 4% annual forb cover is probably biologically insignificant. Intermediate-term rest from grazing did not influence bare ground, litter, exotic annual grass, and biological soil crust cover. More importantly, we did not find any evidence that intermediate-term rest affected the density of herbaceous plant functional groups, diversity, or species richness. Our expectation of increases in soil biological crust cover, perennial herbaceous vegetation cover and density, diversity, and species richness with intermediate-term rest was, therefore, largely unsupported.

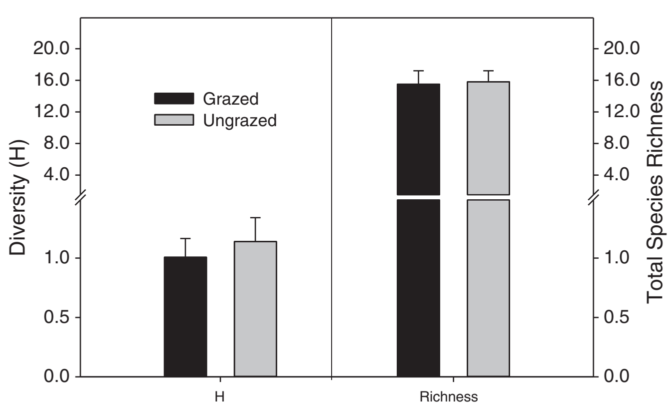

Fig. 4. Diversity (Shannon's Diversity Index) and richness (mean + S.E.) in Wyoming big sagebrush communities that were either moderately grazed (Grazed) or intermediate-term (5–6 years) rested from grazing (Ungrazed). Asterisk (*) indicates significant difference between treatments.

Perennial herbaceous vegetation cover increased with intermediate-term rest; however, this does not provide evidence that intermediate-term rest is altering plant community dynamics or that perennial herbaceous vegetation is recovering. Herbivory removes foliar tissue from plants, and therefore it is expected that ungrazed areas would have more cover because previous years' growth is intact and thereby, still providing cover. Similarly, Davies et al. (2009, 2010) and Bates and Davies (2014) found that grazing rest increased herbaceous cover in relatively intact sagebrush communities but did not influence productivity or density. Other studies (e.g., Kerns et al., 2011; Szaro and Pase, 1983) have also reported that ungrazed compared with grazed areas have greater herbaceous cover.

Our results suggest that intermediate-term rest from grazing may not promote recovery of understory vegetation in dense Wyoming big sagebrush stands. The effects of historical heavy grazing in these communities are likely exceedingly difficult to reverse; thus, a passive treatment such as removing livestock may have little effect or alternatively may take much longer than we applied. Wyoming big sagebrush communities are some of the least-resilient communities in the sagebrush biome to disturbance (Chambers et al., 2014) and therefore may not recover. It has been well documented that removing a disturbance often does not reverse the effects of the disturbance because the plant community has moved to new vegetative state that is relatively stable (Suding et al., 2004). Thus, we postulate that our results suggest that degraded Wyoming big sagebrush plant communities have shifted to a new, stable state that will be difficult and likely costly to reverse.

Three potential factors and their interactions with each other may explain the general lack of an effect of grazing exclusion. First, well-managed, moderate levels of grazing (40% utilization and altering between spring and summer use) may conceivably have negligible effects on native perennial herbaceous vegetation and therefore intermediate-term rest alone does not improve their competitiveness and ability to recruit new individuals in degraded sagebrush communities. Second, dense sagebrush stands may be limiting recovery of herbaceous understory vegetation through preemptive acquisition of available resources. Lastly, native perennial herbaceous vegetation response may be exceedingly slow. The latter two potential factors would indicate that these plant communities have shifted to an alternate vegetative state that is relatively stable.

Though grazing rest compared with detrimental grazing practices is undeniably advantageous (Davies et al., 2014a), grazing rest and well-managed, moderate grazing may produce similar results. Long-term evaluations of well-managed moderate grazing compared with grazing rest have often found few differences in plant community composition and density (Courtois et al., 2004; Davies et al., 2009; Manier and Hobbs, 2006; Rickard, 1985; West et al., 1984). These communities were either not in a state of depleted herbaceous understories with dense sagebrush when grazing rest was implemented or moderate grazing and grazing rest produced similar recovery. Well-managed, moderate grazing systems incorporate periods of no grazing, either by deferring grazing until after the growing season or short-term rest (most commonly 1 year) from grazing to allow plants to periodically complete their growth cycle without the physiological stress of herbivory (Holechek et al., 1998; Hyder and Sawyer, 1951; Ratliff et al., 1972). Modern grazing systems also limit defoliation amounts during periods of use (Holechek et al., 1998). These grazing systems are designed to maintain production potential, maintain leaf and basal area, and allow periodic seed production (Holechek et al., 1998; Hyder and Sawyer, 1951; Ratliff et al., 1972). Thus, well-managed, moderate grazing may not be limiting the ability of herbaceous plants to recovery in sagebrush communities with depleted understories and high sagebrush cover. For example, Sneva et al. (1980) reported some slight increase in perennial grass after 30 years of livestock rest, but increases were less than what occurred on adjacent moderately grazed areas.

There is also a possibility that dense sagebrush stands limit the ability of herbaceous understories to recovery. Boyd and Svejcar

(2011) reported that sagebrush dominance likely limits native perennial bunchgrass establishment. Similarly, Sneva et al. (1980) and West et al. (1984) concluded that the native herbaceous component was unlikely to recover on sites dominated by dense sagebrush. Sneva et al. (1980) concluded that sagebrush reductions would be necessary to see significant increases in native perennial grasses. However, reductions in sagebrush with mechanical methods and fire have generally not achieved desirable results in Wyoming big sagebrush plant communities with depleted herbaceous understories (Beck et al., 2012; Davies and Bates, 2014; Davies et al., 2012; Pyke et al., 2014). Davies et al. (2012) and Davies and Bates (2014) found that reducing sagebrush increased herbaceous cover and density, but increases were driven by exotic annuals and native perennial vegetation remained unchanged. Though these treatments were not successful at increasing native perennials, the increase in exotic annuals with sagebrush reduction does suggest that dense sagebrush is limiting the availability of resources to perennial herbaceous vegetation.

A slow response of native herbaceous vegetation to rest from grazing may also be a contributing factor to the lack of an effect of implementing intermediate-term rest. Native perennial bunchgrass in arid and semiarid plant communities are often relatively slow growing (Holmes and Rice, 1996; James et al., 2009). Similar to our results, densities of native perennial forb and grasses did not recover with 5 years of feral horse exclusion in mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* [Rydb.] Beetle) communities in northern Nevada (Davies et al., 2014b). Davies and Bates (2014) reduced sagebrush dominance with a mechanical treatment and then seeded native perennial bunchgrasses. Though bunchgrass density approximately doubled with this treatment, bunchgrass cover did not differ between treated and untreated plots 4 years post treatment. Bunchgrasses density also did not increase in treated areas after the first year post seeding (Davies and Bates, 2014), providing further evidence of slow recovery of native herbaceous vegetation in these communities. Sagebrush plant communities may take several decades for even partial recovery once a disturbance has ceased (Anderson and Inouye, 2001; Sneva et al., 1980; West et al., 1984). We suspect that the general lack of response of herbaceous vegetation to intermediate-term rest is likely a product of the combination of moderate grazing having limited effects on perennial vegetation, dense sagebrush stands suppressing understory vegetation, the slow response of native perennial herbaceous plants, and the interactions among these mechanisms.

The lack of an effect of intermediate-term rest on biological soil crust cover also suggests that intermediate-term rest is not promoting recovery of degraded Wyoming big sagebrush communities. Biological soil crust recovery is important because it captures resources, reduces soil erosion, and increases resistance to exotic plant invasion (Belnap, 2006; Belnap et al., 2001; Harper and Belnap, 2001). Though grazing can reduce biological soil crusts (Ponzetti and McCune, 2001), long-term grazing exclusion in sagebrush steppe communities may not increase biological soil crust cover (Muscha and Hild, 2006). Biological soil crusts are also often slow to recover after disturbance (Hilty et al., 2004). Thus, slow recovery and possibly limited impact of moderate livestock grazing on biological soil crusts likely explain why we did not detect a biological soil crust response to intermediate-term grazing rest.

Classic state and transition models for sagebrush communities generally place a threshold between degraded (or depauperated) late seral sagebrush steppe and brush and introduced annual stages (NRCS, 2015; Stringham et al., 2003). Our research suggests that this threshold may occur before the introduction annual stage in some Wyoming big sagebrush communities. This threshold is likely crossed as perennial herbaceous vegetation deceases and sagebrush increases, but exactly where the threshold exists remains unknown. Prior research (Davies and Bates, 2014; Davies et al., 2012) demonstrating the difficulty in restoring Wyoming big sagebrush communities with a degraded understory supports this assentation. This information could be used to improve state and transition models for Wyoming big sagebrush communities, but further evaluations would be valuable to more accurately predict where the threshold occurs and determine how it varies among Wyoming big sagebrush communities.

Management Implications

The lack of increases in abundance of native perennial herbaceous vegetation and cover of biological soil crusts with intermediate-term grazing rest indicates that well-managed, moderate grazing is not the mechanism limiting recovery of degraded Wyoming big communities. Determining mechanism(s) limiting native herbaceous recovery in these communities would be invaluable in developing strategies to restore these degraded communities and increase their resistance to exotic annual grasses and resilience to wildfire. Our results demonstrating that intermediate-term grazing rest did not promote recovery and the general failure of other treatments to restore the herbaceous understory in degraded Wyoming big sagebrush communities (Beck et al., 2012; Davies and Bates, 2014; Davies et al., 2012) suggest that preventing degradation from occurring should be a high priority. Clearly, restoration of these plant communities is exceedingly difficult and may be quite expensive if it requires multiple treatments to be successful. This suggests that Wyoming big sagebrush communities with a depleted herbaceous understory have likely transitioned to a new, stable state that will be difficult to reverse.

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References

Anderson, J.E., Inouye, R.S., 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. Ecol. Monogr. 71, 531–556.
Bates, J.D., Davies, K.W., 2014. Cattle grazing and vegetation succession on burned sagebrush steppe. Rangel. Ecol. Manag. 67, 412–422.
Bates, J.D., Rhodes, E.C., Davies, K.W., Sharp, R.N., 2009. Post-fire succession in big sagebrush steppe with livestock grazing. Rangel. Ecol. Manag. 61, 98–110.
Beck, J.L., Connelly, J.W., Wambolt, C.L., 2012. Consequences of treating Wyoming big sagebrush to enhance wildlife habitat. Rangel. Ecol. Manag. 65, 444–455.
Belnap, J., 2006. The potential roles of biological soil crusts in dryland hydrologic cycles. Hydrol. Process. 20, 3159–3178.
Belnap, J., Prasse, R., Harper, K.T., 2001. Influence of biological soil crusts on soil environments and vascular plants. Ecol. Stud. 150, 281–300.
Beschta, R.L., Donahue, D.L., DellaSala, D.A., Rhodes, J.J., Karr, J.R., O'Brien, M.H., Fleischner, T.L., Williams, C.D., 2013. Adapting to climate change on western public lands: addressing the ecological effects of domestic, wild, and feral ungulates. Environ. Manag. 51, 474–491.
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.
Boyd, C.S., Svejcar, T.J., 2011. The influence of plant removal on succession in Wyoming big sagebrush. J. Arid Environ. 75, 734–741.
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.
Canfield, R.H., 1941. Application of the line interception method in sampling range vegetation. J. For. 39, 388–394.
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., 2014. Resilience to stress and disturbance, and resistance to *Bromus tectorum* L. invasion in cold desert shrublands of western North America. Ecosystems 17, 360–375.
Chambers, J.C., Roundy, B.A., Blank, R.R., Meyer, S.E., Whittaker, A., 2007. What makes Great Basin sagebrush ecosystem invasible by *Bromus tectorum*? Ecol. Monogr. 77, 117–145.
Courtois, D.R., Perryman, B.L., Hussein, H.S., 2004. Vegetation change after 65 years of grazing and grazing exclusion. J. Range Manag. 57, 574–582.
Davies, K.W., Boyd, C.S., Beck, J.L., Bates, J.D., Svejcar, T.J., Gregg, M.A., 2011. Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush plant communities. Biol. Conserv. 144, 2573–2584.

Davies, K.W., Bates, J.D., 2010. Vegetation characteristics of mountain and Wyoming big sagebrush plant communities in the northern Great Basin. Rangel. Ecol. Manag. 63, 461–466.
Davies, K.W., Bates, J.D., 2014. Attempting to restore herbaceous understories in Wyoming big sagebrush communities with mowing and seeding. Restor. Ecol. 22, 608–615.
Davies, K.W., Bates, J.D., Miller, R.F., 2006. Vegetation characteristics across part of the Wyoming big sagebrush alliance. Rangel. Ecol. Manag. 59, 567–575.
Davies, K.W., Bates, J.D., Nafus, A.M., 2012. Mowing Wyoming big sagebrush communities with degraded herbaceous understories: has a threshold been crossed? Rangel. Ecol. Manag. 65, 498–505.
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. Rangel. Ecol. Manag. 63, 662–669.
Davies, K.W., Collins, G., Boyd, C.S., 2014b. Effects of feral free-roaming horses on semi-arid rangeland ecosystems: an example from the sagebrush steppe. Ecosphere 5, 127.
Davies, K.W., Svejcar, T.J., Bates, J.D., 2009. Interaction of historical and non-historical disturbances maintains native plant communities. Ecol. Appl. 19, 1536–1545.
Davies, K.W., Vavra, M., Schultz, B., Rimbey, N., 2014a. Implications of longer term rest from grazing in the sagebrush steppe. J. Rangeland Appl. 1, 14–34.
Fleischner, T.L., 1994. Ecological costs of livestock grazing in western North America. Conserv. Biol. 8, 629–644.
Harper, K.T., Belnap, J., 2001. The influence of biological soil crusts on mineral uptake by associated vascular plants. J. Arid Environ. 47, 347–357.
Hilty, J.H., Eldridge, D.J., Rosentreter, R., Wicklow-Howard, M.C., Pellant, M., 2004. Recovery of biological soil crusts following wildfire in Idaho. J. Range Manag. 57, 89–96.
Holechek, J.L., Pieper, R.D., Herbel, C.H., 1998. Range management: principles and practices. Prentice-Hall, Upper Saddle River, NJ (542 pp.).
Holmes, T.H., Rice, K.J., 1996. Patterns of growth and soil-water utilization in some exotic annuals and native perennial bunchgrasses of California. Annu. Bot. 78, 233–243.
Hyder, D.N., Sawyer, W.A., 1951. Rotation-deferred grazing as compared to season-long grazing on sagebrush-bunchgrass range in southeastern Oregon. J. Range Manag. 4, 30–34.
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.
James, J.J., Mangold, J.M., Sheley, R.L., Svejcar, T., 2009. Root plasticity of native and invasive Great Basin species in response to soil nitrogen heterogeneity. Plant Ecol. 202, 211–220.
Jones, A., 2000. Effects of cattle grazing on North American arid ecosystems: a quantitative review. West. North Am. Nat. 60, 155–164.
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.
Küchler, A.W., 1970. Potential natural vegetation. The national atlas of U.S.A. Government Printing Office, Washington, DC, USA, pp. 90–91.
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 pp.).
Manier, D.J., Hobbs, N.T., 2006. Large herbivores influence the composition and diversity of shrub-steppe communities in the Rocky Mountains, USA. Oecologia 146, 641–651.
McLean, A., Tisdale, E.W., 1972. Recovery rate of depleted range sites under protection from grazing. J. Range Manag. 25, 178–184.
Miller, R.F., Eddleman, L.L., 2000. Spatial and temporal changes of sage grouse habitat in the sagebrush biome. Technical Bulletin 151. Oregon State University, Agricultural Experiment Station, Corvallis, OR, USA (35 pp.).
Muscha, J.M., Hild, A.L., 2006. Biological soil crusts in grazed and ungrazed Wyoming sagebrush steppe. J. Arid Environ. 67, 195–207.
Norton, J.B., Monaco, T.A., Norton, U., 2007. Mediterranean annual grasses in western North America: kids in a candy store. Plant Soil 298, 1–5.
NRCS, 2013. Soil surveyAvailable at: http://websoilsurvey.nrcs.usda.gov (Accessed 12 December 2013).
NRCS, 2015. Ecological site descriptionAvailable at: https://esis.sc.egov.usda.gov/Welcome/pgReportLocation.aspx?type=ESD (Accessed 25 November 2015).
Ponzetti, J.M., McCune, B., 2001. Biotic soil crusts of Oregon's shrub steppe: community composition in relation to soil chemistry, climate, and livestock activity. Bryologist 104, 212–225.
Prevéy, J.S., Germino, M.J., Huntly, N.J., 2010. Loss of foundation species increase population growth of exotic forbs in sagebrush steppe. Ecol. Appl. 20, 1890–1902.
PRISM, 2014. PRISM data explorerAvailable at: URL http://prsimmap.nacse.org/nn/ (Accessed 19 December 2014).
Pyke, D.A., Shaff, S.E., Lindgren, A.I., Schupp, E.W., Doescher, P.S., Chambers, J.C., Burnham, J.S., Huso, M.H., 2014. Region-wide ecological responses of arid Wyoming big sagebrush communities to fuel treatments. Rangel. Ecol. Manag. 67, 455–467.
Ratliff, R.D., Reppert, J.N., McConnen, R.J., 1972. Rest-rotation at Harvey Valley: Range health, cattle gains, costs. Research Paper PSW-77. U.S. Department of Agriculture Forest Service, Berkley, CA, USA (24 pp.).
Rickard, W.H., 1985. Experimental cattle grazing in a relatively undisturbed shrubsteppe community. Northwest Sci. 59, 66–72.
Seabloom, E.W., Harpole, W.S., Reichman, O.J., Tilman, D., 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. Proc. Natl. Acad. Sci. 100, 13384–13389.
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.
Suding, K.N., Gross, K.L., Houseman, G.R., 2004. Alternative states and positive feedbacks in restoration ecology. Trends Ecol. Evol. 19, 46–53.
Svejcar, T., Boyd, C., Davies, K., Madsen, M., Bates, J., Sheley, R., Marlow, C., Bohnert, D., Borman, M., Mata-Gonzàlez, R., Buckhouse, J., Stringham, T., Perryman, B., Swanson, S., Tate, K., George, M., Ruyle, G., Roundy, B., Call, C., Jensen, K., Launchbaugh, K., Gearhart, A., Vermeire, L., Tanaka, J., Derner, J., Frasier, G., Havstad, K., 2014. Western land managers will need all available tools for adapting to climate change, including grazing: a critique of Beschta et al. Environ. Manag. 53, 1035–1038.
Stringham, T.K., Krueger, W.R., Shaver, P.L., 2003. State and transition modeling: an ecological process approach. J. Range Manag. 56, 106–113.
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. J. Range Manag. 36, 383–384.
West, N.E., 1983. Western Intermountain sagebrush steppe. In: West, N.E. (Ed.), Ecosystems of the world: temperate deserts and semideserts. Elsevier Scientific Publishing Company, Amsterdam, The Netherlands, pp. 351–374.
West, N.E., 2000. Synecology and disturbance regimes of sagebrush steppe ecosystems. In: Entwistle, P.G., DeBolt, A.M., Kaltenecker, J.H., Steenhof, K. (Eds.), Sagebrush steppe ecosystem symposium. Bureau of Land Management, Boise, ID, USA, pp. 15–26.
West, N.E., Provenza, F.D., Johnson, P.S., Owens, M.K., 1984. Vegetation change after 13 years of livestock grazing exclusion on sagebrush semidesert in west central Utah. J. Range Manag. 37, 262–264.
Yensen, E., Quinney, D.L., Johnson, K., Timmerman, K., Steenhof, K., 1992. Fire, vegetation changes, and population fluctuations of Townsend's ground squirrels. Am. Midl. Nat. 128, 299–312.