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Original Research

Plant Community Composition After 75 Yr of Sustained Grazing Intensity Treatments in Shortgrass Steppe[☆]Lauren M. Porensky^{a,*}, Justin D. Derner^b, David J. Augustine^a, Daniel G. Milchunas^{c,1}^a Research Ecologist, US Department of Agriculture (USDA)—Agricultural Research Service (ARS) Rangeland Resources Research Unit, Fort Collins, CO 80526, USA^b Rangeland Scientist and Research Leader, USDA-ARS Rangeland Resources Research Unit, Cheyenne, WY 82009, USA^c Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80526, USA

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ABSTRACT

Plant community responses to livestock grazing lack conformity across studies, even those conducted within similar ecosystems. Variability in outcomes can often be traced back to short-term or mid-term weather patterns, differences in grazing timing or intensity, or interactive effects of management and weather. Long-term experimental data are needed to determine how grazing intensity affects plant community composition in semi-arid ecosystems where precipitation is low and highly variable. However, long-term grazing intensity experiments, particularly experiments with more than two grazing intensity treatment levels, are quite rare. We capitalized on one of the longest-term grazing studies, with 75 yr of sustained stocking rate treatments (none, light, moderate, and heavy), to identify long-term effects of livestock grazing on plant community composition in shortgrass steppe. Plant community composition was similar between moderately and heavily grazed pastures after 75 yr of continuous, season-long (May to October) grazing treatments, and heavy grazing did not extirpate cool-season perennial graminoids. These findings support the long-term sustainability of livestock grazing in the shortgrass steppe, which has high resistance to season-long heavy grazing. Conversely, ungrazed and lightly grazed pastures experienced relatively large shifts in plant community composition, especially in the past 25 yr. Light or no grazing was associated with increased abundance of cool-season perennial graminoids, as well as several weedy and invasive species. Moreover, across most grazing treatments, several aspects of plant community composition have been shifting directionally during the past 25 yr, which recent experiments in this grassland suggest may be a response to increasing atmospheric (CO₂). The shortgrass steppe is not only tolerant of fairly high grazing intensities but also likely requires some level of grazing to resist invasion by weedy annuals and to maintain cover of blue grama, a highly drought-tolerant species.

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Introduction

A fundamental goal of rangeland ecology and management is to understand how large herbivore grazing influences plant community composition. Decades of livestock grazing research in rangeland ecosystems worldwide have yielded system-level, specific information, as well as synthetic relationships (Milchunas et al., 1988; Milchunas and Lauenroth, 1993; Carmel and Kadmon, 1999; Diaz et al., 2007; Davies et al., 2015; Khishigbayar et al., 2015; van Rooyen et al., 2015; Sanderson et al., 2016). Theoretical models suggest that precipitation or aboveground primary production and evolutionary history of grazing are key drivers of differences in vegetation response to grazing

(Milchunas et al., 1988), and analyses of compositional responses to grazing have identified considerable variation among plant communities in their direction and magnitude of response based on these variables (Milchunas and Lauenroth, 1993).

In semiarid rangelands, livestock grazing can induce transitions to alternative stable states (Courtois et al., 2004; Briske et al., 2005; Cingolani et al., 2005; Miller et al., 2011; Kachergis et al., 2012), but can also induce gradual and reversible vegetation shifts that occur over time scales of decades or longer (Fuhlendorf et al., 2001; Valone et al., 2002; Milchunas, 2011; Bestelmeyer et al., 2013; Khishigbayar et al., 2015; van Rooyen et al., 2015; Porensky et al., 2016). In order to maximize rangeland productivity and sustainability, it is critical to understand when and where a given management action is likely to cause a threshold shift versus gradual, reversible change. What drives differences in plant community responses to grazing? Some differences are likely related to landscape context (e.g., topography, site potential, Milchunas et al., 1989; Carmel and Kadmon, 1999; Chambers et al., 2007; Khishigbayar et al., 2015) and evolutionary history of grazing (Milchunas et al., 1988; Sternberg et al., 2015). However, variation

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* Correspondence: Lauren Porensky, USDA-ARS Rangeland Resources Research Unit, 1701 Centre Ave, Fort Collins, CO 80526, USA. Tel.: +1 970 492 7139.

E-mail address: lauren.porensky@ars.usda.gov (L.M. Porensky).

¹ Current address: Daniel G. Milchunas, retired, PO Box 943, LaPorte, CO 80535, USA.

among studies can also be driven by weather patterns and differing levels of grazing intensity or management.

Due to the low and variable precipitation regimes that characterize semiarid rangeland ecosystems, short-term (seasonal to annual) to longer-term (semi-decadal to decadal) precipitation patterns can strongly influence plant community composition and production (Weaver and Albertson, 1936; Lauenroth and Sala, 1992; Milchunas et al., 1994; Derner and Hart, 2007; Porensky et al., 2013; O'Connor, 2015; van Rooyen et al., 2015). For example, rangelands impacted by both herbivory and drought can experience faster or larger community changes than rangelands impacted by a singular stress (Albertson and Weaver, 1944; Fuhlendorf and Smeins, 1997; Loeser et al., 2007; Stubbendieck and Tunnell, 2008; Dreber and Esler, 2011; Bagchi et al., 2012). Moreover, shifts in weather can be temporally confounded with shifts in grazing management (Davies et al., 2015; Morris et al., 2016), making it difficult for short- and mid-term studies to disentangle grazing effects from weather effects or weather by grazing interactions. In many cases, results are presented relative to specific weather contexts (wet yr vs. dry yr; Milchunas et al., 1989; Milchunas et al., 1990; Dreber and Esler, 2011; Porensky et al., 2013). Longer-term data are needed to determine the sensitivity of rangeland ecosystems to sustained grazing management treatments while minimizing or accounting for weather-related bias (Morris et al., 2016).

Furthermore, most long-term manipulative experiments involving livestock grazing compare only two levels of grazing intensity (grazed vs. ungrazed or low vs. high stocking rate; Milchunas and Lauenroth, 1993; Sanderson et al., 2016), but see (Derner and Hart, 2007; Smart et al., 2010; Sternberg et al., 2015). Manipulative studies measuring plant community responses for > 30 yr across a range of grazing intensities are especially rare (in addition to this study's focal experiment, examples include Manley et al., 1997; Hart and Ashby, 1998; Fuhlendorf et al., 2001; Porensky et al., 2016). This makes it difficult to make long-term predictions about a range of livestock grazing intensities, which is the reality faced by most rangeland decision makers (Ritten et al., 2010; Khishigbayar et al., 2015).

Here, we examine plant community compositional responses to long-term grazing intensity in the shortgrass steppe rangeland ecosystem of the western North American Great Plains. This semiarid ecosystem has a long evolutionary history of grazing (Milchunas et al., 1988) and is well known for being extremely resistant to livestock grazing (Holechek et al., 2006; Milchunas et al., 2008). In 1939, the US Department of Agriculture–Agricultural Research Service (USDA-ARS) implemented four levels of grazing intensity (none, light, moderate, and heavy) on 129.5-ha pastures, and these treatments have been continuously maintained for 75 yr. Reports from the first 50 yr of the study indicated only minor effects of grazing on plant community composition (Klippel and Costello, 1960; Hyder et al., 1966; Moir and Trlica, 1976; Milchunas et al., 1989; Milchunas et al., 1990). After 53 yr, heavy grazing had increased dominance of warm-season (C_4) perennial grasses and reduced relative abundance of cool-season (C_3) perennial graminoids (Hart and Ashby, 1998), but livestock grazing effects on shortgrass plant communities were still modest compared with other semiarid and mesic grasslands around the world (Milchunas et al., 2008). It is unclear whether the effects of grazing continued to get stronger over time during yr 55–75 of the experiment.

We asked 1) how 75 yr of livestock grazing at four different levels of sustained grazing intensity treatments affected plant community composition and 2) whether stocking rate treatments were associated with ongoing divergence or convergence in plant community composition during yr 65–75 of the study.

Methods

Site Description

This grazing intensity experiment was initiated in 1939 (Klippel and Costello, 1960; Hart and Ashby, 1998) at the USDA-ARS Central Plains

Experimental Range, a Long-Term Agro-ecosystem Research (LTAR) network site located in north-central Colorado, United States (40°49'N, 107°46'W). The primary climate-soil-plant community classification is Loamy Plains (Ecological Site ID: R067BY002CO, see <https://esis.sc.egov.usda.gov/>). Long-term mean annual precipitation at the site is 340 mm. From 2003 to 2014, mean annual precipitation was 342 ± 59 mm (mean \pm SD) and substantial droughts occurred in 2006 and 2012. The complete record of annual and spring precipitation from 1939 to 2014 is shown in Fig. S1 (available online at <http://dx.doi.org/10.1016/j.rama.2016.12.001>). Mean annual air temperature is 8.4°C, ranging from -2.6°C in December to 21.2°C in July.

Vegetation at the site is dominated by the perennial warm-season (C_4) grass species blue grama (*Bouteloua gracilis* [Willd. ex Kunth] Lag. ex Griffiths), with buffalograss (*B. dactyloides* [Nutt.] J.T. Columbus) and plains pricklypear cactus (*Opuntia polyacantha* Haw.) as subdominants. Important perennial cool-season (C_3) graminoids include western wheatgrass (*Pascopyrum smithii* [Rydb.] Á. Löve), needle-and-thread (*Hesperostipa comata* [Trin. & Rupr.] Barkworth), and needle-leaf sedge (*Carex duriuscula* C.A. Mey.). Scarlet globemallow (*Sphaeralcea coccinea* [Nutt.] Rydb.) is the most important forb, and fringed sagewort (*Artemisia frigida* Willd.) the most important subshrub. Annual grasses consist almost entirely of six-weeks fescue (*Vulpia octoflora* [Walter] Rydb.).

Experimental Design

Three 129.5-ha pastures were randomly assigned to three grazing intensity treatments (one replicate per treatment, Hart and Ashby, 1998). These pastures represent the single remaining block (the “upland grama-buffalograss” block, located within a 2425×3200 m area) of the original experiment, which was a randomized complete block design with four replicates per treatment (Klippel and Costello, 1960). Grazing intensity treatments included light grazing (9.3 Animal Unit Days (AUD)/ha, targeted for 20% utilization of peak growing season biomass), moderate grazing (12.5 AUD/ha, 40% utilization), and heavy grazing (18.6 AUD/ha, 60% utilization) (Irisarri et al., 2016). An ungrazed enclosure (2 ha, 1600 m long \times 12 m wide) was also maintained for the duration of the experiment. A similar range of topographic variation was represented within each of the three pastures, as well as the enclosure (Milchunas et al., 1989). Each grazed pasture was managed using growing-season-long continuous grazing, with grazing beginning in mid-May and ending in early to mid-October. Grazing animals were British breed yearlings. Before the start of the experiment, the site had experienced extreme drought conditions in the 1930s.

Vegetation Sampling

From 2003 to 2014, plant community composition was sampled annually in late July or early August. In each of the four pastures, sixty 0.1-m² (20 \times 50 cm) quadrats were sampled each yr. Quadrats were evenly spaced throughout each pasture. From 1 yr to the next, exact quadrat locations changed slightly (5–10 m in a random cardinal direction). Within each quadrat, basal plant cover of each species was visually estimated using modified Daubenmire (1959) cover classes (<1, 1–5, 5–15, 15–25, 25–40, 40–60, or 60–100%). For portions of the quadrat with no basal plant cover, cover of litter, dung, lichen + moss, and bare ground were estimated using the same classes. Midpoints of cover classes were used to calculate abundance of each species (c.f. Hickman and Derner, 2007), and data were standardized so that basal cover for each quadrat totaled 100%.

Statistical Analysis

To determine whether grazing intensity was associated with community-level differences, we used a partial canonical correspondence analysis (CCA) ordination where yr was included as a covariable (Lepš and Šmilauer, 2003). This approach allows investigators to identify

treatment and treatment by time effects while controlling for annual shifts in plant community composition. Results include sample and species scores along a set of constrained CCA axes that relate plant community composition to treatments and time by treatment interactions. We performed CCA using the vegan library (Oksanen et al., 2013) in R (version 3.0.1).

To prepare data for CCA analysis, we calculated the relative cover of each species as its percent of total plant cover within each quadrat. We averaged data across the 60 quadrats (subplots) within each pasture to generate pasture-scale relative cover values ($N = 44$; 4 pastures over 11 yr). We excluded plant species that occurred in $< 5\%$ of the 44 samples (i.e., only 1 or 2 samples, sensu Harrison et al., 2010; Alday et al., 2013). This reduced the dataset from 83 taxa (82 species and 1 multispecies group) to 60 taxa (59 species and 1 multispecies group; Table S1, available online at <http://dx.doi.org/10.1016/j.rama.2016.12.001>).

We identified the constrained CCA axes (hereafter simply called CCA axes) that, when summed, explained at least 80% of treatment-related sample variance. Data transformations (e.g., Wisconsin square root transform) did not qualitatively affect our results but reduced the percent variance explained by CCA axes. To maximize the amount of variance addressed with these and subsequent analyses, we present results from ordinations on untransformed data. Because our ordination included repeated measures (11 yr of data per pasture) and no replication within each level of grazing intensity (one pasture per grazing intensity treatment), we did not perform multivariate statistical tests on the ordination results. However, we extracted the CCA axis scores in order to examine them using more rigorous statistical methods (see later). At the community level, we also calculated Whittaker's index of association values comparing each grazed pasture to the ungrazed pasture within each yr. Hereafter, Community Similarity = Whittaker's Index of Community Association as defined by Whittaker (1952).

We used linear mixed models (LMMs) to evaluate the effects of grazing intensity, experiment duration (yr of study during yr 65–75), and spring weather covariates on 1) extracted CCA axis scores, 2) Community Similarity values, 3) relative cover of different functional groups (as defined in Table S1, available online at <http://dx.doi.org/10.1016/j.rama.2016.12.001>), and 4) species diversity (Shannon–Weiner index calculated from pasture-scale relative cover values for all 83 taxa) (Shannon, 1948). For some but not all treatments, data were also available for yr 64 of the study; these data were included in analyses whenever possible.

For all response variables, we first decided whether to include only a linear or also a quadratic term for grazing intensity in the LMM. To make this decision, we averaged responses over time and then ran a simple regression of the average response values on grazing intensity. If a quadratic relationship fit the data better than a linear relationship (i.e., had a higher R^2_{adj} value), we included the quadratic term and its associated interactions in the more complex LMM.

For each response variable, we ran an LMM in which fixed factors included grazing intensity (treated as a continuous variable with 4 levels), (grazing intensity)² if appropriate, experiment duration (yr 65–75 of experiment, continuous), spring precipitation (April–June total), spring temperature (April–June average daily), and two-way interactions between grazing intensity terms and other factors. Spring weather and its effects were not the central focus of this paper, but both spring temperature and spring precipitation can strongly impact primary and secondary production in this system (Derner and Hart, 2007; Derner et al., 2008; Reeves et al., 2013) and were therefore included as covariates in mixed models. Most weather results are summarized in Fig. S2, (available online at <http://dx.doi.org/10.1016/j.rama.2016.12.001>). We checked for collinearity among model predictors and determined that grazing intensity and experiment duration were not correlated with one another or with either of the spring weather terms ($-0.10 < r < 0.10$). To account for repeated measurements within the same pastures, we included pasture as a random factor and used a compound symmetry covariance structure. Responses were transformed when necessary to meet model assumptions. Results are reported as means \pm 1 SE. LMM analyses were performed in JMP, Version

11 (SAS Institute, Inc., Cary, North Carolina, 1989–2007). Due to the low replication of this experiment, we report all results as significant at the 0.10 P value level (Peterman, 1990).

Historical Trends

One goal of this study was to compare current trends to data from previous reports on this experiment (Klipple and Costello, 1960; Moir and Trlica, 1976; Milchunas et al., 1989; Hart and Ashby, 1998; Milchunas et al., 2008). The Community Similarity method was employed by several past studies and we therefore used this method to make direct comparisons at the community scale. We also calculated the basal and foliar relative percent cover of three plant taxa for which we have reliable historical data. These included blue grama + buffalograss (which were lumped in several early studies), western wheatgrass, and needle-and-thread grass. Together, these species make up $> 70\%$ of basal plant cover. Due to differences in data collection methodologies, replication, and data availability among studies, we did not attempt to conduct statistical analyses of the 75-yr trends. However, visual summaries provide important historical context for this study.

Results

Plant Community Composition

Partial CCA ordination results indicated that from 2003 to 2014, annual variability explained 36% of the overall variance in the plant community data, while grazing intensity treatment and time by treatment explained 40% of the overall variance. Of this 40%, CCA Axis 1 explained 45%, Axis 2 explained 35%, and other axes explained the remaining 20%. Axes 1 and 2 each explained more of the variation in species level data than would be expected by chance (anova.cca $P < 0.005$). When sample scores were plotted along Axes 1 and 2, the enclosure and lightly grazed pasture were clearly separated from the moderately and heavily grazed pastures (Fig. 1A).

Relative cover of blue grama had a strong negative correlation ($r < -0.4$) with CCA Axis 1 (Table 1, Fig. 1B). Species with strong positive correlations ($r > 0.4$) included virtually all of the cool-season perennial graminoids (western wheatgrass, needle-and-thread, needle-leaf sedge, and bottlebrush squirreltail, or *Elymus elymoides* [Raf.] Swezey), as well as a few perennial forbs (slimflower scurfpea, or *Psoraleidium tenuiflorum* [Pursh] Rydb., and hairy false goldenaster, or *Heterotheca villosa* [Pursh] Shinnars) and weedy annuals (Canadian horsetweed, or *Conyza canadensis* [L.] Cronquist, prairie sunflower, or *Helianthus petiolaris* Nutt., and cheatgrass, or *Bromus tectorum* L.; see Table 1, Fig. 1B). Higher grazing intensities were associated with lower scores along Axis 1 (Fig. 2A; stocking rate [SR] $P = 0.02$, $SR^2 P = 0.04$), reflecting higher relative cover of blue grama and lower relative cover of cool-season graminoids, perennial forbs, and weedy annuals with increased grazing intensity. Canadian horsetweed, prairie sunflower, and the invasive annual cheatgrass were all more than 10 times as abundant in the enclosure as in grazed pastures (Table S1, available online at <http://dx.doi.org/10.1016/j.rama.2016.12.001>). Axis 1 did not provide any evidence for divergence or convergence among treatments during yr 65–75 of the experiment ($yr \times SR P = 0.5$, $yr \times SR^2 P = 0.6$).

CCA Axis 2 separated stiff greenthread (*Thelesperma filifolium* [Hook.] A. Gray), sand dropseed (*Sporobolus cryptandrus* [Torr.] A. Gray), and needle-and-thread (negative correlations) from woolly plantain (*Plantago patagonica* Jacq.) and buffalograss (positive correlations; see Table 1, Fig. 1B). Axis 2 scores appeared to be associated with compositional characteristics separating the lightly grazed pasture (low scores, more cover of stiff greenthread and sand dropseed) from the heavily grazed pasture (high scores, more cover of buffalograss and woolly plantain; see Fig. 2A). Grazing intensity was associated with temporal trajectory on Axis 2, with Axis 2 scores declining more rapidly over time in lightly grazed pastures (Fig. 2B; $yr \times SR P = 0.2$, $yr \times SR^2$

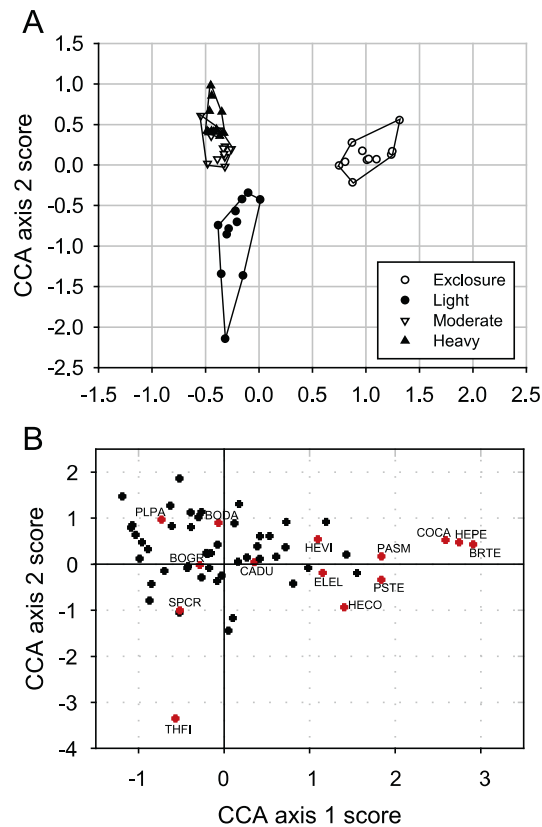


Figure 1. A, Scores along canonical correspondence analysis (CCA) axes 1 and 2 for different stocking rate treatments. Multiple markers per stocking rate reflect data from different yrs. B, Species scores along CCA axes 1 and 2. Species with correlations coefficients > 0.40 are labeled and highlighted in red. BODA, *Bouteloua dactyloides*; BOGR, *Bouteloua gracilis*; BRTE, *Bromus tectorum*; CADU, *Carex duriuscula*; COCA, *Conyza canadensis*; ELEM, *Elymus elymoides*; HECO, *Hesperostipa comata*; HEPI, *Helianthus petiolaris*; HEVI, *Heterotheca villosa*; PASM, *Pascopyrum smithii*; PLPA, *Plantago patagonica*; PSTE, *Psoralea tenuiflora*; SPCR, *Sporobolus cryptandrus*; THFI, *Thelesperma filifolium*. Data for both figures are from yrs 65–75 of a long-term grazing experiment in the shortgrass steppe of northeastern Colorado, United States.

$P = 0.05$). This result is at least partially driven by a dramatic increase in stiff greenhead cover in the lightly grazed pasture during yr 65–75 of the experiment (6% relative cover in 2003 and 22% in 2014).

During yr 65–75 of the experiment, Community Similarity values comparing grazed pastures with the ungrazed pasture ranged from 0.58 to 0.75 and did not differ significantly among grazing treatments ($SR P = 0.4$, $SR^2 P = 0.6$). However, temporal trends did differ among grazing intensity treatments (Fig. 3; $yr \times SR P = 0.01$, $yr \times SR^2 P = 0.11$). During yr 65–75, the lightly grazed pasture became more similar to the ungrazed pasture, while the heavily and moderately grazed pastures became less similar to the ungrazed pasture (see Fig. 3). Community Similarity values were sensitive to spring precipitation, with differences between grazed and ungrazed pastures becoming more pronounced in wet yr ($P = 0.09$).

Functional Groups

Grazing intensity treatments had clear effects on the cover of different plant functional groups. Absolute cover displayed patterns similar to relative cover (Fig. S3, available online at <http://dx.doi.org/10.1016/j.rama.2016.12.001>). We present relative cover here because it is more directly comparable with ordination results.

Relative cover of warm-season perennial grasses increased with grazing intensity (Fig. 4A; $SR P = 0.02$), while cover of cool-season perennial graminoids declined (see Fig. 4A; $SR P = 0.05$, $SR^2 P = 0.12$). On average, warm-season perennial grass relative cover increased by about

Table 1

Pair-wise correlations between canonical correspondence analysis axis 1 and 2 scores and the relative cover of individual plant species. Only correlations significant at the $P < 0.10$ level are displayed. Correlations with coefficients > 0.40 are bolded

CCA axis	Species	Correlation coefficient	95% CI low	95% CI high	P value
CCA1	<i>Bouteloua gracilis</i>	−0.66	−0.80	−0.46	<.0001
CCA1	<i>Talinum parviflorum</i>	−0.34	−0.58	−0.05	0.0242
CCA1	<i>Sporobolus cryptandrus</i>	−0.33	−0.57	−0.03	0.0301
CCA1	<i>Plantago patagonica</i>	−0.30	−0.55	−0.01	0.0455
CCA1	<i>Lygodesmia juncea</i>	−0.27	−0.53	0.03	0.0732
CCA1	<i>Cryptantha minima</i>	−0.25	−0.51	0.05	0.0966
CCA1	<i>Liatris punctata</i>	0.26	−0.04	0.51	0.0920
CCA1	<i>Astragalus/Oxytropis</i> spp.	0.33	0.04	0.57	0.0289
CCA1	<i>Helianthus petiolaris</i>	0.44	0.17	0.65	0.0027
CCA1	<i>Bromus tectorum</i>	0.46	0.19	0.66	0.0017
CCA1	<i>Elymus elymoides</i>	0.50	0.23	0.69	0.0006
CCA1	<i>Conyza canadensis</i>	0.53	0.27	0.71	0.0002
CCA1	<i>Carex duriuscula</i>	0.53	0.28	0.71	0.0002
CCA1	<i>Heterotheca villosa</i>	0.55	0.30	0.73	0.0001
CCA1	<i>Psoralea tenuiflora</i>	0.65	0.44	0.79	<.0001
CCA1	<i>Hesperostipa comata</i>	0.76	0.60	0.86	<.0001
CCA1	<i>Pascopyrum smithii</i>	0.95	0.92	0.97	<.0001
CCA2	<i>Thelesperma filifolium</i>	−0.82	−0.90	−0.69	<.0001
CCA2	<i>Sporobolus cryptandrus</i>	−0.55	−0.73	−0.30	0.0001
CCA2	<i>Hesperostipa comata</i>	−0.42	−0.63	−0.14	0.0050
CCA2	<i>Ericameria nauseosa</i>	−0.32	−0.56	−0.02	0.0370
CCA2	<i>Eriogonum effusum</i>	−0.31	−0.55	−0.01	0.0419
CCA2	<i>Lepidium densiflorum</i>	−0.30	−0.55	0.00	0.0483
CCA2	<i>Opuntia polyacantha</i>	−0.26	−0.51	0.04	0.0939
CCA2	<i>Evolvulus nuttallianus</i>	0.27	−0.03	0.53	0.0742
CCA2	<i>Talinum parviflorum</i>	0.28	−0.02	0.53	0.0667
CCA2	<i>Ipomopsis laxiflora</i>	0.30	0.01	0.55	0.0448
CCA2	<i>Tragopogon dubius</i>	0.31	0.01	0.55	0.0439
CCA2	<i>Lappula redowskii</i>	0.31	0.01	0.55	0.0416
CCA2	<i>Haplopappus spinulosus</i>	0.38	0.10	0.61	0.0103
CCA2	<i>Plantago patagonica</i>	0.41	0.13	0.63	0.0061
CCA2	<i>Bouteloua dactyloides</i>	0.64	0.43	0.79	<.0001

6% over the past decade (see Fig. 4C; $P = 0.009$), while cool-season perennial graminoid relative cover declined by about 5% over the same time period (see Fig. 4C; $P = 0.005$). Effects of grazing intensity did not depend on experiment duration during yr 65–75 (all interaction $P > 0.17$). Annual grasses did not display any significant relationships with yr, grazing intensity, or their interaction ($P > 0.10$).

Taken together, cactus + forb + subshrub relative cover was highest at intermediate grazing intensity (see Fig. 4B; $SR P = 0.3$, $SR^2 P = 0.07$) and declined by about 6% over time (see Fig. 4C; $P = 0.08$). When forbs and cactus + subshrubs were examined separately, hump-shaped responses to grazing intensity were apparent but not significant ($P > 0.15$). Nongrassoid functional groups did not display any other significant relationships with yr, grazing intensity, or their interaction ($P > 0.10$).

Bare ground and lichen + moss cover both increased with increasing grazing intensity (Fig. 5A; bare $SR P = 0.02$, $SR^2 P = 0.08$; lichen + moss $SR P = 0.001$, $SR^2 P = 0.03$) and declined over time from 2003 to 2014 (Fig. 5B; bare $P = 0.10$; lichen + moss $P = 0.02$). Conversely, litter cover declined with increasing grazing intensity (see Fig. 5A; $SR P = 0.07$, $SR^2 P = 0.3$) and increased by 40% over time from 2003 to 2014 (see Fig. 5B; $P < 0.0001$). Total plant cover declined from 2003 to 2014 (see Fig. 5B; $P = 0.004$). Bare ground, litter, lichen + moss, and total plant cover did not display any other significant relationships with yr, grazing intensity, or their interaction ($P > 0.10$).

Diversity

Shannon–Weiner diversity index values declined by 18% as grazing intensity increased from no grazing to heavy grazing (Fig. 4D; $SR P = 0.03$, $SR^2 P = 0.15$) and also declined by 24% from 2003 to 2014 (2003: 2.28 ± 0.11 , 2014: 1.73 ± 0.18 ; $P < 0.0001$). Effects of grazing intensity did not depend on experiment duration during yr 65–75 of the experiment ($P > 0.25$).

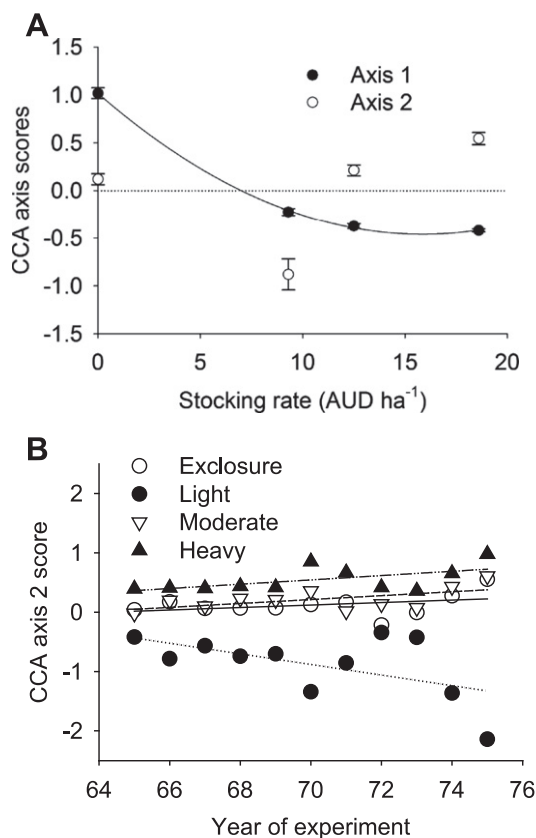


Figure 2. A, Canonical correspondence analysis (CCA) axes regressed on stocking rate. B, Annual variation in CCA axis 2 scores during yrs 65–75 of a long-term grazing experiment in the shortgrass steppe of northeastern Colorado, United States. Curves joining points indicate significant relationships.

Historical Trends

Both community-level metrics and species-level cover data suggest that it took > 50 yr for grazing intensity treatments to substantially alter plant community composition. Community Similarity values comparing grazed and ungrazed plant communities were consistently > 0.8 during the first 50 yr of the study (before 1989) and < 0.8 after yr 50 (Fig. 6). Similarly, inspection of basal and foliar cover values for two of the most dominant plant taxa (blue grama/buffalograss and western wheatgrass) suggested that ungrazed and lightly grazed pastures began to diverge strongly from the heavily grazed pasture after yr 50 of

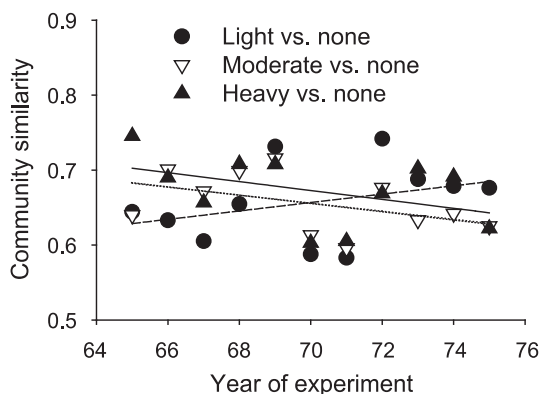


Figure 3. Variation in community similarity between grazed and ungrazed pastures during yrs 65–75 of a long-term grazing experiment in the shortgrass steppe of northeastern Colorado, United States.

the study (Fig. 7A–D). Basal cover of needle-and-thread followed the same pattern (Fig. 7E). Foliar cover of needle-and-thread increased linearly in ungrazed pastures between yrs 1 and 53 and then remained relatively stable in ungrazed pastures during yrs 53–75 (Fig. 7F). In the lightly grazed pasture, foliar cover of needle-and-thread remained low until yr 53 of the experiment (see Fig. 7F).

In addition to these treatment effects, historical data suggest some overall temporal trends. In particular, relative cover of blue grama and buffalograss has declined across treatments, while cover of western wheatgrass has increased across all except the heavily grazed treatment (see Fig. 7A–D).

Discussion

Managers in semiarid rangelands often lack data on the timescales of plant community change and the limits of system resilience in response to grazing intensity (Porensky et al., 2016). This study, one of a precious few manipulative grazing intensity experiments in which more than two grazing intensity levels have been monitored for > 50 yr (see also Fuhlendorf et al., 2001), helps to fill the information gap. Trajectories of plant community change over the 75 yr provide strong evidence of the value of such long-term efforts (see also Sanderson et al., 2016). Data taken during the first 47 yr of this study (when it was already well-known as a rare, long-term experiment) suggested that grazing intensity had very minor effects on plant community composition (see Figs. 6 and 7; Klipple and Costello, 1960; Hyder et al., 1966; Moir and Trlica, 1976; Milchunas et al., 1989; Milchunas et al., 1990). However, plant communities subjected to different grazing treatments began to diverge sometime between yrs 48 and 53 (Hart and Ashby, 1998), and our results indicate that differences among treatments have become stronger over the subsequent 2 decades (see Figs. 2 and 7). Although this study's level of replication declined over time since 1939, we have several reasons to believe that our findings are defensible or even conservative. First, previously reported data from yrs 32–53 were also based on the single remaining block, and those studies continued to show little community change relative to baseline conditions. Second, the remaining block was more heavily dominated by warm-season grasses than the other blocks (Klipple and Costello, 1960), which would make it more difficult to observe an increase in cool-season grass abundance merely by chance or due to the loss of other replicates. Finally, our statistical approach avoids pseudoreplication by treating stocking rate as a continuous predictor and accounting for temporal autocorrelation.

Enclosures and lightly grazed pastures experienced relatively large shifts in plant community composition between yrs 47 and 75, while community composition remained more stable in moderately and heavily grazed pastures (Figs. 2 and 7). It is unclear whether these changes are reversible or represent a more permanent state shift (Scheffer et al., 2001; Kachergis et al., 2014), but recent reports from Great Plains grasslands, including our field site, suggest that major compositional shifts are reversible on decadal timescales (Milchunas, 2011; Augustine et al., 2014; Porensky et al., 2016).

Heavily grazed pastures had similar plant community composition as moderately grazed pastures, even after 75 yr of continuous, season-long grazing at a stocking rate 50% above the rate recommended by the National Resource Conservation Service (see Fig. 1A). This result supports previous characterizations of this grassland ecosystem as one of the world's most grazing-tolerant rangelands (Milchunas et al., 2008). In contrast to their similarity to one another, the moderately and heavily grazed pastures differed substantially from the lightly grazed and ungrazed pastures (see Fig. 1A). A breakpoint in plant community composition trajectories between lightly and moderately grazed pastures has also been highlighted in other long-term grazing studies in semiarid rangelands with long evolutionary histories of grazing (Porensky et al., 2016; Veblen et al., 2016). Our data support previous work suggesting that in shortgrass steppe, the absence of grazing is a

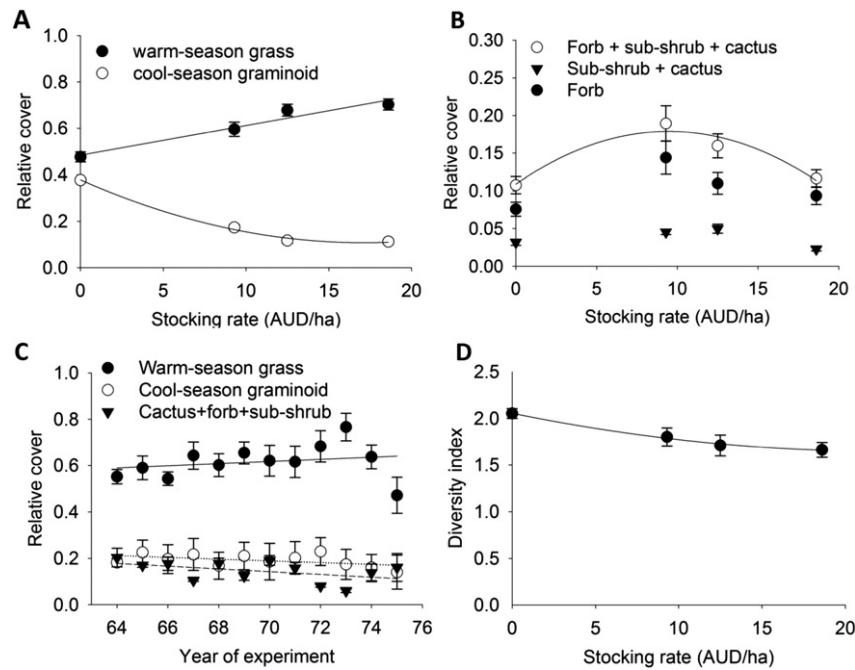


Figure 4. Relationships among **A**, stocking rate and relative cover of perennial graminoids, **B**, stocking rate and relative cover of other plant functional groups, **C**, experiment duration and relative cover of different functional groups, and **D**, stocking rate and Shannon-Weiner diversity index values during yrs 64–75 of a long-term grazing experiment in the shortgrass steppe of northeastern Colorado, United States. Curves joining points indicate significant relationships.

larger perturbation than heavy grazing (Milchunas et al., 1990), as we observed that several weedy and non-native annual species were nearly absent from all the grazed pastures and more abundant in the grazing enclosure (see Fig. 1B, Table S1, available online at <http://dx.doi.org/10.1016/j.rama.2016.12.001>).

Previous experimental work in this system suggests a causal link between the loss of dominant grasses and invasion by weedy species (Milchunas et al., 1992).

During the past 10 yr of this experiment, plant community composition has remained relatively stable over time in the ungrazed, moderately grazed, and heavily grazed pastures. In contrast, community-level metrics changed over this time period in the light-grazing pasture. Inspection of ordination results (see Fig. 1B) and species-level data (Table S1, available online at <http://dx.doi.org/10.1016/j.rama.2016.12.001>) suggests that this result reflects shifts in the relative abundance of forbs (e.g., stiff green thread) and subdominant grasses (e.g., sand dropseed and needle-and-thread), rather than the more dominant species (e.g., blue grama/buffalograss or western wheatgrass). According to Similarity Index data, this pasture may be becoming more similar to the long-term enclosure at a whole-plant-community scale (see Fig. 3). Continued monitoring will be necessary to determine whether these

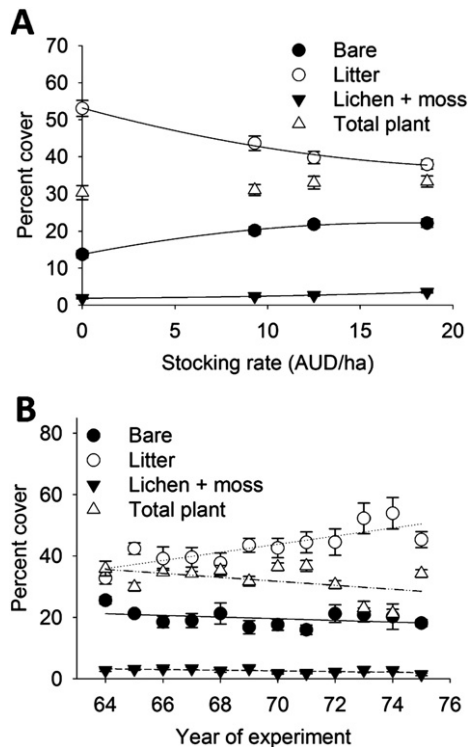


Figure 5. Relationships among **A**, stocking rate and bare ground or cover of litter, lichen + moss and total plants, and **B**, experiment duration and bare ground or cover of litter, lichen + moss, and total plants during yrs 64–75 of a long-term grazing experiment in the shortgrass steppe of northeastern Colorado, United States. Curves joining points indicate significant relationships.

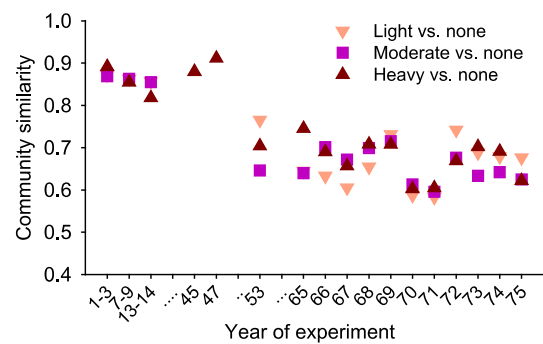


Figure 6. Effects of experiment duration on community similarity values comparing the ungrazed pasture to the heavily, moderately, and lightly grazed pastures. Values before yr 65 are copied from Milchunas et al., (2008). Before yr 45, data were averaged across four replicates of each grazing treatment; values from yr 45 onwards are from the single remaining replicate of the experiment. Due to methodological differences among studies, association values were calculated using foliar cover data in yrs 1–13, density data in yrs 45–47, frequency data in yr 53, and basal cover data in yrs 65–75.

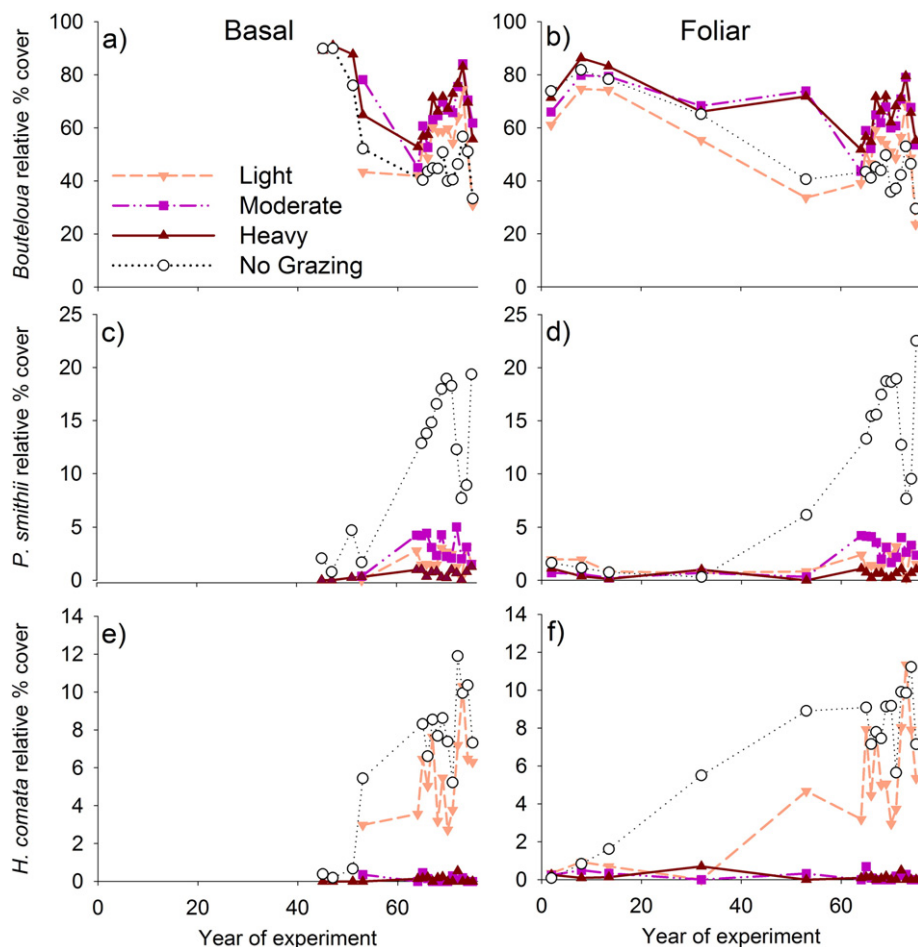


Figure 7. Effects of experiment duration on relative basal (a, c, e) and foliar (b, d, f) cover of *Bouteloua* spp. (a and b), western wheatgrass (c and d), and needle-and-thread (e and f). Historical data were obtained from multiple previous studies (Klippel and Costello, 1960; Moir and Trlica, 1976; Milchunas et al., 1989; Hart and Ashby, 1998) and also include previously unpublished data for yr 51. Before yr 32, data were averaged across four replicates of each grazing treatment; values from yr 32 onwards are from the single remaining replicate of the experiment. Locations sampled for the “no grazing” treatment vary among studies, but all grazing exclosures were established in 1939.

trends are temporary (e.g., driven by recent weather) or if they reflect long-term shifts in the lightly grazed pasture.

Community-level patterns were paralleled by the responses of different functional groups. In agreement with previous reports from this experiment (Klippel and Costello, 1960; Moir and Trlica, 1976; Milchunas et al., 1989; Hart and Ashby, 1998) and other, similar experiments in the Great Plains (Fuhlendorf et al., 2001; Porensky et al., 2016; Sanderson et al., 2016), we found that higher grazing intensities were associated with more warm-season perennial grass cover, less cool-season perennial graminoid cover, more bare ground, and less litter (see Figs. 4 and 5). While warm-season perennial grass cover increased linearly with grazing intensity, cool-season perennial graminoid cover declined exponentially (see also Irisarri et al., 2016).

It is notable that even after 75 yr of continuous, season-long heavy grazing, desirable perennial cool-season graminoids were not extirpated. This result does not match the current predictions of a state-and-transition model for this site (USDA NRCS, 2007). In heavily grazed pastures, recovery potential of the more productive perennial cool-season graminoids and subsequent community composition reversal may be of limited value for managers operating on subdecadal timescales, but it could be relevant in the context of longer-term planning or payments for ecosystem services (Porensky et al., 2016).

For nongrass species, our data suggested that cover is highest in lightly and moderately grazed pastures, which may indicate that lightly or moderately grazed pastures can support a larger diversity of wildlife species, including pollinators and mixed-feeding ungulates, than heavily grazed or ungrazed pastures. Along the same lines, and as predicted in

conceptual models (Milchunas et al., 1988), we found a slight decline in plant species diversity as grazing intensity increased.

Our estimate of “spring precipitation” (April–June rainfall) was not a strong predictor of annual differences in community composition or diversity (Fig. S2, available online at <http://dx.doi.org/10.1016/j.rama.2016.12.001>). However, Dissimilarity Index results show that differences among pastures were more pronounced in yrs with wet springs. This result matches previous reports from ungrazed shortgrass steppe indicating that a wet yr had greater richness than a dry yr (Milchunas et al., 1989). Cool, wet springs were associated with more forb and total plant cover (Fig. S2, available online at <http://dx.doi.org/10.1016/j.rama.2016.12.001>) and greater aboveground net primary production (Milchunas et al., 1994), which likely accentuated species-level differences among pastures and grazing treatments.

Finally, cover of western wheatgrass, the dominant perennial cool-season (C_3) grass, has increased during the past 25 yr in all treatments other than heavy grazing (see Fig. 7C–D). While this may result from a delayed response of this species to the grazing treatments, or delayed recovery from the severe 1930s drought, other factors may also be interacting with experimental treatments. In particular, atmospheric CO_2 has increased from approximately $315 \text{ } \mu\text{mol mol}^{-1}$ in 1960 to $400 \text{ } \mu\text{mol mol}^{-1}$ today, which represents a range over which photosynthesis of C_3 plant species is unsaturated (Stitt, 1991). Recent experimental field studies conducted in the western Great Plains, including our field site, have shown that elevated CO_2 benefits growth of cool-season perennials (Morgan et al., 2001; Morgan et al., 2007; Mueller et al., 2016). We suggest that the effect of rising atmospheric CO_2 is

one possible explanation for our finding that western wheatgrass has increased across most treatments, including the moderate grazing intensity treatment, in the most recent 25 yr of the experiment. The lack of any increase in the heavy grazing treatment suggests that past management may influence the ability of cool-season species to respond to elevated CO₂. Similarly, increased needle-and-thread cover in the lightly grazed and ungrazed pastures over the past 25 yr (see Fig. 7E–F) may be at least partially driven by interactions between elevated CO₂ and grazing treatments.

Implications

In grazing-resistant, semiarid ecosystems, substantial uncertainty surrounds the long-term (generational-scale) outcomes of different grazing management practices. Long-term pressures may erode ecosystem resilience and eventually lead to catastrophic shifts in structure and function (Carpenter et al., 2015; Scheffer et al., 2015). This study is one of few long-term manipulative experiments that subjected plant communities to a range of grazing intensities for more than half a century. In general, our results suggest that shortgrass steppe is indeed highly resistant to season-long heavy grazing. One or several years of heavy grazing are unlikely to push the system over a threshold, or indeed have any major impacts on plant community composition. Pastures stocked at light rates over the long-term can maintain relatively high cover of non-dominant species, including cool-season perennial graminoids that have substantial ecological and economic value in the region (Derner et al., 2009; Dunn et al., 2010) and, in yrs with sufficient spring moisture, are taller and substantially more productive than the co-occurring C₄ shortgrasses (Milchunas et al., 1994). To increase desirable cool-season perennial graminoids in pastures where these species are rare, land managers may need to consider grazing strategies including rest, deferment, and lighter or variable stocking rates linked with spring precipitation variability. Recovery of cool-season perennial graminoids in such pastures will likely be slow (taking at least a decade), even under continuous light stocking (Milchunas, 2011; Porensky et al., 2016). Long-term exclusion of grazing in this rangeland ecosystem is not desirable as weedy and invasive species become problematic, and the loss of blue grama may reduce ecosystem-level drought tolerance (Morgan et al., 1998). The shortgrass steppe is not only tolerant of fairly high grazing intensities but also likely requires some level of grazing to maintain key functions (e.g., drought tolerance and invasion resistance) over the long term.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.rama.2016.12.001>.

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