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Grazing History Effects on Rangeland Biomass, Cover and Diversity Responses to Fire and Grazing Utilization[☆]

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ABSTRACT

Exclusion of large grazers from rangelands that evolved with significant grazing pressure can alter natural processes and may have legacy effects by changing magnitude or direction of community responses to subsequent disturbance. Three moderately grazed pastures were paired with 12-ha areas with 15 yr of livestock exclusion. Six treatments were assigned to each in a 2 × 3 factorial arrangement of fire (fall fire or no fire) and grazing utilization (0%, 50%, or 75% biomass removal) to determine grazing history effects on rangeland response to subsequent disturbance. Livestock exclusion increased C₃ perennial grass (1 232 vs. 980 ± 50 kg · ha⁻¹) and forbs (173 vs. 62 ± 19 kg · ha⁻¹) and reduced C₄ perennial grass (36 vs. 180 ± 25 kg · ha⁻¹) with no effect on total current-year biomass. Diversity was greater in pastures than exclosures (H' = 1.5400 vs. 1.3823 ± 0.0431). Every biomass, cover, and diversity measure, except subshrub biomass, was affected by fire, grazing utilization, or both. Contrary to expectations, grazing history only interacted with fire effects for old standing dead material and interactions with grazing utilization were limited to old dead, bare ground, richness and dominance. Fire by grazing utilization interaction was limited to bare ground. Fire reduced annual grass (64 vs. 137 ± 29 kg · ha⁻¹), forbs (84 vs. 133 ± 29 kg · ha⁻¹), and diversity (H' = 1.3260 vs. 1.5005 ± 0.0537) with no difference in total current-year biomass (1 557 vs. 1 594 ± 66 kg · ha⁻¹). Grazing to 75% utilization reduced total current-year biomass (1 467 vs. 1 656 ± 66 kg · ha⁻¹) and dominance (0.4824 vs. 0.5584 ± 0.0279). Grazing history affected starting points for most variables, but changes caused by grazing utilization or fire were similar between pastures and exclosures, indicating management decisions can be made based on independent knowledge of grazing or fire effects.

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Introduction

Ecosystem response to a particular disturbance event may be affected by prior disturbance history. For example, grazing history has interacted with recent management to affect soil fauna, diversity of plant dispersal traits, and plant functional group composition (Villenave et al., 2011; Purschke et al., 2014; Vandewalle et al., 2014). Identifying such legacy effects can help explain responses to past and present management or disturbances. The magnitude of these responses likely increases as the kind, frequency, or intensity of disturbance differs from the historical disturbance regime. In grasslands, particularly the Great Plains, precipitation, grazing, and fire are the main ecological forces.

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Understanding the interactions between fire and grazing is important because they are factors for which we can exert some control in affecting grassland structure and function.

Native grasslands that evolved under grazing pressure generally respond positively or neutrally to moderate grazing (Reeder and Schuman, 2002; Derner et al., 2007; Havstad et al., 2007). However, grazing effects on some grassland properties, such as productivity, may appear erratic (Biondini et al., 1998; McNaughton et al., 1998; Skinner et al., 2002; Koerner and Collins, 2014) and suggest that other factors, including precipitation patterns and site history, play an important role in the responses. Exclusion of large grazers is often recommended for grassland preservation and recovery, but represents a large deviation from historical disturbance in the Great Plains. Accumulation of litter in the absence of grazing can lead to light limitations and elevated growing points that are then more susceptible to damage. Long-term cessation of grazing by large herbivores and prevention of fire alter the structure and function of grassland systems and may make them less resistant or less resilient to future disturbances (Davies et al., 2009). In the northern Great Basin, grazing history affected how production and cover responded to fire such that fire

increased perennial grass production on grazed sites and increased the invasive annual, cheatgrass (*Bromus tectorum* L.), on nongrazed sites (Davies et al., 2009).

Fire can manipulate the distribution of grazing animals, reduce fuel loads, shift nutrient dynamics, alter plant diversity, mitigate shrub and tree encroachment, and reduce the impact of invasive species (Wright and Bailey, 1982; Vermeire et al., 2004; Fuhlendorf et al., 2009; Vermeire and Rinella, 2009; Ansley et al., 2010). Within the northern Great Plains, prescribed fire had a positive or neutral effect on the native herbaceous community, reduced the impact of exotic annual grasses, and improved the palatability of plants typically avoided by livestock (Vermeire et al., 2011; Dufek et al., 2014). Heat dosage and duration of lethal temperatures increase with fuel load, which is affected by grazing history, and both are positively related to fire damage to seeds, buds, and whole plants (Vermeire and Rinella, 2009; Vermeire and Roth, 2011; Russell et al., 2013; Strong et al., 2013).

Northern Great Plains plant communities are highly resilient to moderate livestock grazing after fire during below- or above-average precipitation (Vermeire et al., 2014; Gates et al., 2017), but effects of longer-term fire or grazing history on rangeland response to subsequent fire or grazing are not well known. In tallgrass prairie, reintroduction of fire to nonburned sites quickly made the plant community resemble those of frequently burned sites, but removal of fire did not approximate long nonburned sites in the near term (Spasojevic et al., 2010). In a paired study in Konza Prairie, Kansas and Kruger National Park, South Africa fire history affected how production and diversity responded to drought and defoliation (Koerner and Collins, 2014). For example, drought reduced production on infrequently burned sites, but not on frequently burned sites. Effectively maintaining and improving rangeland structure and function requires understanding the combined effects of disturbance events and disturbance history on ecosystem processes.

The objective of this research was to determine how grazing history affects grassland biomass, cover and diversity responses to future disturbances (fire and grazing utilization), and whether management history affects post-disturbance trajectory of the plant community. We hypothesized that long-term livestock exclusion reduces grassland stability in response to fire and grazing. We expected changes in grazing utilization to have greater effects in exclosures than in pastures because differences between utilization levels (0%, 50%, 75%) and historical utilization (0%, 50%) would be greater for exclosures than moderately grazed pastures. We expected fire to reduce diversity in pastures and increase diversity in exclosures because much of the diversity in the region comes from ruderal species that are fire-sensitive and more abundant in grazed sites, whereas fire could reduce dominance in exclosures and temporarily open niches for less competitive species.

Methods

Study Area

Research was conducted near Miles City, Montana on the Fort Keogh Livestock and Range Research Laboratory (46°82'40"N, 105°85'60"W; 815 m above sea level). The area is semiarid, northern mixed prairie with a freeze-free period of 110 to 135 d and temperatures from 38°C during summer to -40°C during winter. Average annual precipitation is 341 mm, with 75% occurring in April through September. Precipitation effects on current-year biomass and standing crop are generally greatest during April and May (Vermeire et al., 2008), with about 90% of annual net primary production occurring by 1 July (Vermeire et al., 2009). April–May precipitation was 71% (58.4 mm), 221% (183.3 mm), and 349% (289.0 mm) of the 75-yr median (82.8 mm) during 2009, 2010, and 2011, respectively, with 2011 being the wettest on record. Generally dry periods occurred during the winters of 2009 and 2010 and summer 2011 (Fig. 1). The study period was consistently cooler

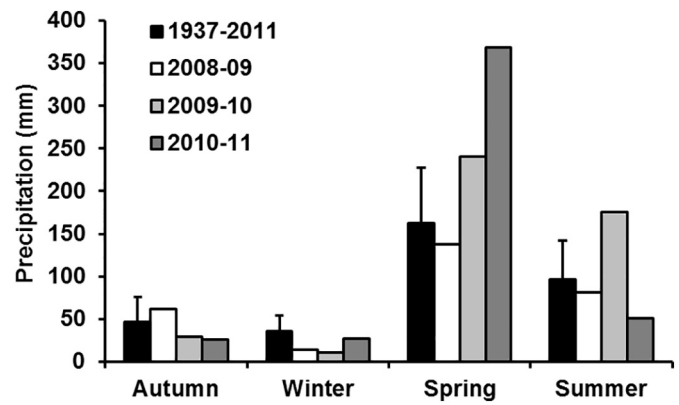


Figure 1. Autumn (October–December), winter (January–March), spring (April–June), and summer (July–September), 75-yr mean seasonal precipitation (\pm SD) and precipitation for each year of study based on an October to September water year.

than the 75-yr average spring temperature (13.4°C), with April–June temperatures of 12.6 °C, 13.0 °C, and 11.3°C.

The study sites were level uplands on Pinehill loam (Fine, montmorillonitic Typic Eutroboralfs), Eapa loam (Fine-loamy, mixed, superactive, frigid Aridic Argiustolls), and Sonnett loam (Fine, smectitic, frigid Aridic Haplustalfs) soils. All three soils were deep and well drained and classified as Silty ecological sites. Distances between sites were 14, 12, and 11 km. Vegetation was dominated by C3 perennial graminoids *Hesperostipa comata* (Trin. & Rupr.) Barkworth, *Pascopyrum smithii* (Rydb.) A. Löve, *Carex filifolia* Nutt., and *Poa secunda* J. Presl and the C4 perennial grass *Bouteloua gracilis* (Willd. Ex Kunth) Lag. ex Griffiths. Annual grasses were *Bromus japonicus* Thunb., *B. tectorum* L., and *Vulpia octoflora* (Walter) Rydb. *Artemisia frigida* Willd. was the primary sub-shrub. The most common forbs were annuals *Plantago patagonica* Jacq., *Logfia arvensis* (L.) Holub, and *Tragopogon dubius* Scop. and perennial *Sphaeralcea coccinea* (Nutt.) Rydb.

Experimental Design

Three permanent 12-ha exclosures were fenced during 1994 to exclude livestock grazing within three larger pastures. Exclosures were paired with adjacent grazed pasture to examine differences between long-term moderate grazing (1 animal unit month \cdot ha⁻¹) and livestock exclusion. During 2009, six 12.25 x 12.25-m plots were fenced using wire cattle panels within each exclosure and pasture. Plots were randomly assigned to six levels of disturbance within each exclosure and grazed pasture in a 2 x 3 factorial arrangement of fire (fall fire or no fire) and grazing utilization (0%, 50%, or 75% biomass removal) to determine grazing history effects on rangeland response to subsequent disturbance (3 sites, 2 grazing histories, 6 fire x grazing utilization treatments = 36 plots). Plots were each grazed to the prescribed utilization in 1 or 2 days during early July 2009 and 2010 using 8 to 12 sheep per plot. Fire treatments were applied 23 October 2009 (14°C ambient temperature, 39% relative humidity, 16.7 km \cdot hr⁻¹ wind). Burned plots were not grazed during 2009, before fire, and had grazing treatments applied during 2010. The Livestock and Range Research Laboratory Institutional Animal Care and Use Committee considered the use of sheep in this study as a standard management practice requiring no official approval for handling and experimental procedures.

Sampling

Plant biomass and cover were measured the day before grazing each year such that 2009 measurements represented grazing history effects before fire and grazing utilization treatments and 2010 and 2011 measurements reflected previous year's disturbance treatment effects. Biomass was estimated by clipping five randomly placed 0.25-m²

quadrats to ground level by functional group (C₃ perennial grass, C₄ perennial grass, annual grass, forbs, and sub-shrubs) in each plot. Clipped samples were dried to a constant weight at 60°C, then weighed, sorted by current-year growth and previous years' growth (old dead) and reweighed. Basal and canopy cover were determined using the point-intercept method with two 10-m transects in each plot and readings at 20-cm intervals. Basal cover was used to estimate bare ground and litter cover and canopy and basal hits were used to calculate richness, Simpson's diversity (1-D), Shannon-Weiner diversity index (H'), and Berger-Parker dominance ($N_{\max} \cdot N^{-1}$).

Statistical Analysis

We used analysis of variance models with repeated measures containing terms for grazing history, fire, grazing utilization, year (2009–2011), and all interactions to test for grazing history effects and grazing history interactions. Response variables were biomass of old dead material, current-year vegetation, C₃ perennial grass, C₄ perennial grass, annual grass, forbs, and subshrubs, bare ground, litter cover, richness, Simpson's diversity, Shannon-Weiner diversity index, and Berger-Parker dominance. Analyses of variance were conducted with the mixed procedure of SAS, using site as a random variable (Littell et al., 2006), with the primary interest in identifying grazing history effects and grazing history interactions with subsequent disturbances. Models were then tested without grazing history terms, using initial 2009 values as covariates when significant, to test effects of fire, grazing, year (2010–2011), and all interactions. Analyses of covariance were planned to follow analyses of variance to assess fire and grazing utilization effects after accounting for expected pretreatment differences due to grazing history. Statistical significance of tests was declared at $\alpha = 0.05$, and interactions were followed by tests of simple effects. Tests generating *P* values between 0.05 and 0.10 were reported and discussed as trends.

Results

No differences were detected between pastures and exclosures for total current-year biomass ($P = 0.7050$) or litter cover ($P = 0.1176$; Table 1). However, all other measures were affected by grazing history. Pastures had more C₄ perennial grass ($P < 0.0001$) and subshrub biomass ($P = 0.0457$) and greater diversity (1-D, $P = 0.0015$; H', $P = 0.0004$) than exclosures. Exclosures had more C₃ perennial grass ($P < 0.0001$) and forb biomass ($P < 0.0001$) than pastures.

Old standing dead had the most complex response to experimental manipulations, with two 3-way interactions, grazing history by grazing

Table 1
Biomass, cover, and diversity means and standard errors by grazing history (pastures and exclosures).

| Response variable | Grazing history | | |
|--|----------------------|-----------|--------|
| | Pasture | Exclosure | SE |
| Old dead (kg · ha ⁻¹) | 95 * ¹ | 235 | 15 |
| Current-yr (kg · ha ⁻¹) | 1 515 a ² | 1 534 a | 50 |
| C ₃ per. grass (kg · ha ⁻¹) | 980 b | 1232 a | 50 |
| C ₄ per. grass (kg · ha ⁻¹) | 180 a | 36 b | 25 |
| Ann. grass (kg · ha ⁻¹) | 211 * | 38 | 26 |
| Forbs (kg · ha ⁻¹) | 62 b | 173 a | 19 |
| Subshrubs (kg · ha ⁻¹) | 84 a | 54 b | 15 |
| Bare ground (%) | 42 * | 36 | 2 |
| Litter cover (%) | 41 a | 45 a | 3 |
| Richness (spp.) | 10 * | 10 | 0.3 |
| Simpson's diversity (1-D) | 0.6769 a | 0.6234 b | 0.0163 |
| Shannon-Weiner (H') | 1.5400 a | 1.3823 b | 0.0431 |
| Berger-Parker Dominance | 0.4762 * | 0.5377 | 0.0179 |

¹ Asterisk indicates a higher-order interaction exists.

² Means within response variable are similar when followed by a common letter ($P > 0.05$).

Table 2

Old dead mass (kg · ha⁻¹) means and standard errors for the grazing history by grazing utilization by year interaction and the grazing history by fire by year interaction.

| Trt factor | Trt level | 2009 | | 2010 | | 2011 | |
|------------|-----------|-------------|-----------|-------------------|-----------|---------|-----------|
| | | Pasture | Exclosure | Pasture | Exclosure | Pasture | Exclosure |
| | | Utilization | 0% | 63 b ¹ | 302 a | 142 ab | 227 a |
| | 50% | 72 b | 388 a | 35 c | 136 b | 118 b | 152 b |
| | 75% | 64 b | 352 a | 26 c | 76 bc | 188 b | 103 b |
| | SE | 44 | 44 | 44 | 44 | 44 | 44 |
| Fire | No Fire | 64 b | 363 a | 135 b | 293 a | 182 ab | 215 a |
| | Fire | 69 b | 332 a | 0 c | 0 c | 121 b | 207 a |
| | SE | 36 | 36 | 36 | 36 | 36 | 36 |

Abbreviation: Trt, treatment.

¹ Means within treatment factor and year are similar when followed by a common letter ($P > 0.05$).

utilization by year ($P = 0.0011$), and grazing history by fire by year ($P = 0.0162$). Initially, exclosures had about five times the old dead as grazed pastures (Table 2). In 2010, grazing reduced old dead compared with no utilization in pastures and exclosures. Old dead was similar between pastures and exclosures when utilization was 0% or 75%, but greater in exclosures than pastures when grazed at 50% utilization. During 2011, exclosures with no utilization had more old dead than all other treatment combinations.

For the grazing history by fire by year interaction, initial differences were limited to exclosures having more, old dead material than pastures (Table 2). Fire eliminated old dead during 2010 and nonburned exclosures still had more old dead than nonburned pastures that year, but the magnitude of the difference was smaller than during 2009. Differences were not detected between burned and nonburned exclosures during 2011. Burned pasture had less old dead than exclosure sites of either fire treatment, and no differences were detected between nonburned pasture and any other treatment combination.

Grazing history and grazing utilization interacted in their effects on bare ground ($P = 0.0145$), richness ($P = 0.0172$), and dominance ($P = 0.0004$; Table 3). Bare ground was similar between grazing histories when the grazing regime was continued (50% utilization in pastures and no utilization in exclosures). Bare ground was more abundant in pastures grazed to 75% than 50% utilization, and exclosures grazed to 50% utilization had more bare ground than nongrazed exclosures. Pastures had more bare ground than exclosures when they had been grazed to 75% utilization or not grazed, whereas no differences were detected between pastures and exclosures that were grazed to 50% utilization. Absence of grazing in pastures reduced species richness compared with nongrazed exclosures and pasture grazed at 50% or 75% utilization. Grazed pasture had less dominance than grazed exclosures and nongrazed pasture. However, grazing to 50% utilization increased dominance compared with nongrazed plots in exclosures.

Grazing history did not interact with grazing utilization for any of the current-year biomass components, nor for litter, Simpson's diversity, or the Shannon-Weiner diversity index ($P > 0.05$). With the exception of the grazing history by fire by year interaction for old dead, fire

Table 3

Bare ground, species richness, and Berger-Parker dominance means and standard errors for the grazing utilization by grazing history interactions.

| Utilization | Bare ground (%) | | Richness | | Dominance | |
|-------------|--------------------|-----------|----------|-----------|-----------|-----------|
| | Pasture | Exclosure | Pasture | Exclosure | Pasture | Exclosure |
| 0% | 43 ab ¹ | 32 c | 9.1 b | 10.3 a | 0.5327 ab | 0.4905 bc |
| 50% | 36 bc | 40 ab | 10.7 a | 9.8 ab | 0.4667 c | 0.5746 a |
| 75% | 48 a | 37 bc | 10.7 a | 10.1 ab | 0.4292 c | 0.5482 ab |
| SE | 4 | 4 | 0.6 | 0.6 | 0.0310 | 0.0310 |

¹ Means within a response variable are similar when followed by a common letter ($P > 0.05$).

Table 4

Annual grass biomass (kg · ha⁻¹) and species richness means and standard errors for the year by grazing history interactions.

| Year | Annual grass | | Richness | |
|------|--------------------|-----------|----------|-----------|
| | Pasture | Exclosure | Pasture | Exclosure |
| 2009 | 290 a ¹ | 54 b | 9.4 c | 10.9 ab |
| 2010 | 255 a | 37 b | 11.2 a | 9.6 c |
| 2011 | 86 b | 23 b | 9.9 bc | 9.8 bc |
| SE | 45 | 45 | 0.6 | 0.6 |

¹ Means within a response variable are similar when followed by a common letter ($P > 0.05$).

did not interact with grazing history for any of the response variables ($P > 0.05$).

Grazing history effects varied by year for annual grass biomass ($P = 0.0151$) and species richness ($P = 0.0010$; Table 4). Annual grasses were about six times as abundant in pastures as they were in exclosures during 2009 and 2010. No differences in annual grass biomass were detected between pastures and exclosures during 2011. Species richness was greater in exclosures than pastures during 2009 then greater in pastures than exclosures during 2010. Richness was similar between pastures and exclosures during 2011.

The preponderance of grazing history effects and lack of grazing history interactions with fire or grazing utilization indicated pre-existing differences likely limited statistical power and control for assessing fire and grazing utilization effects. Following results are fire and grazing effects after accounting for initial (2009) differences with analysis of covariance and can be interpreted as main and interaction effects after controlling for grazing history. Initial variable values were significant covariates for all variables except forb biomass and species richness. No differences were detected between nonburned and burned sites for total current-year biomass ($P = 0.5766$), C₃ perennial grass ($P = 0.6344$), C₄ perennial grass ($P = 0.8815$), or subshrub biomass ($P = 0.7880$; Table 5). Fire reduced annual grasses more than 50% ($P = 0.0132$) and trended toward a reduction in forb biomass ($P = 0.0911$). Fire reduced litter cover to about half of that on nonburned sites ($P = 0.0172$). Fire reduced species richness ($P = 0.0034$), Simpson's diversity ($P = 0.0028$), and Shannon-Weiner index ($P = 0.0019$) as well and increased dominance ($P < 0.0001$). Reduced diversity and increased dominance was due, at least in part, to the reduction of non-native species composition with fire (6.9 vs. $10.1 \pm 1.6\%$; $P = 0.0465$).

There was a trend for reduced total current-year biomass with 75% utilization compared with no grazing utilization ($P = 0.0634$; Table 5). Grazing at 50% or 75% utilization reduced C₃ perennial grass biomass ($P = 0.0016$) and increased annual grass biomass ($P = 0.0189$). C₄ perennial grass trended ($P = 0.0753$) toward greater biomass with 50% than 75% utilization, and biomass was intermediate with no grazing.

Table 5

Biomass, cover, and diversity means and standard errors for the main effects of fire and grazing utilization treatments across grazing histories (pastures and exclosures). Individual biomass components do not sum to group totals because some means were adjusted using pre-treatment measures as covariates.

| Response variable | Fire treatment | | | Grazing utilization | | | |
|--|----------------------|----------|--------|---------------------|-----------|----------|--------|
| | No fire | Fire | SE | 0% | 50% | 75% | SE |
| Current-yr (kg · ha ⁻¹) | 1 594 a ¹ | 1 557 a | 66 | 1 656 a | 1 602 ab | 1 467 b | 87 |
| C ₃ per. grass (kg · ha ⁻¹) | 1 161 a | 1 189 a | 59 | 1 325 a | 1 155 b | 1 046 b | 79 |
| C ₄ per. grass (kg · ha ⁻¹) | 117 a | 120 a | 24 | 103 ab | 158 a | 94 b | 30 |
| Ann. grass (kg · ha ⁻¹) | 137 a | 64 b | 29 | 42 b | 118 a | 141 a | 35 |
| Forbs (kg · ha ⁻¹) | 133 a | 84 b | 29 | 90 a | 117 a | 119 a | 35 |
| Subshrubs (kg · ha ⁻¹) | 70 a | 75 a | 19 | 63 a | 84 a | 71 a | 25 |
| Bare ground (%) | 45 ^{*2} | 62 | 3 | 49 * | 54 | 57 | 4 |
| Litter cover (%) | 41 a | 22 b | 3 | 37 a | 26 b | 32 ab | 4 |
| Richness (spp.) | 10.8 a | 9.4 b | 0.4 | 9.7 a | 10.3 a | 10.4 a | 0.5 |
| Simpson's diversity (1-D) | 0.6667 a | 0.6005 b | 0.0212 | 0.5628 * | 0.6493 | 0.6886 | 0.0263 |
| Shannon-Weiner (H') | 1.5005 a | 1.3260 b | 0.0537 | 1.2296 * | 1.4482 | 1.5618 | 0.0661 |
| Berger-Parker Dominance | 0.4685 b | 0.5701 a | 0.0229 | 0.5584 a | 0.5171 ab | 0.4824 b | 0.0279 |

¹ Means within response variable and fire treatment or utilization are similar when followed by a common letter ($P > 0.05$).

² Asterisk indicates a higher-order interaction exists.

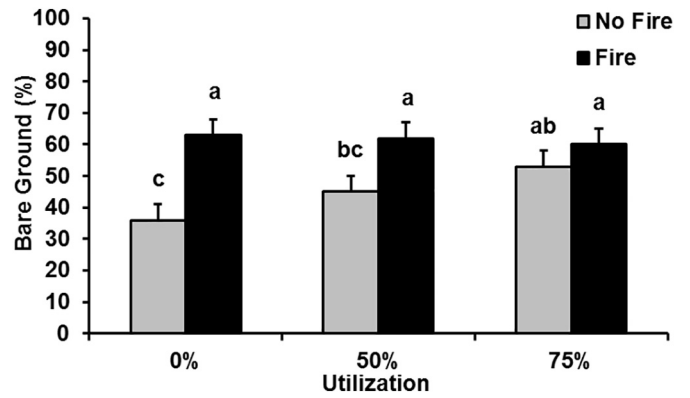


Figure 2. Bare ground (%) by fire and grazing utilization treatment with standard error bars for the fire by grazing utilization interaction. Means with a common letter above bars are similar ($P > 0.05$).

Table 6

Simpson's diversity and Shannon-Weiner index means and standard errors for the year by grazing utilization interactions across grazing histories (pastures and exclosures).

| Utilization | Simpson's Diversity | | Shannon-Weiner (H') | |
|-------------|-----------------------|----------|---------------------|----------|
| | 2010 | 2011 | 2010 | 2011 |
| 0% | 0.6208 b ¹ | 0.5048 c | 1.3909 b | 1.0684 d |
| 50% | 0.6680 ab | 0.6306 b | 1.5386 ab | 1.3578 c |
| 75% | 0.6743 ab | 0.7029 a | 1.5448 ab | 1.5788 a |
| SE | 0.0365 | 0.0365 | 0.0933 | 0.0933 |

¹ Means within a response variable are similar when followed by a common letter ($P > 0.05$).

No grazing utilization effects were detected for forb ($P = 0.6544$) or sub-shrub biomass ($P = 0.7093$). Litter cover was reduced by 50% utilization compared with no grazing and no differences were observed between these treatments and 75% utilization ($P = 0.0319$). Grazing to 75% utilization reduced dominance, compared with no grazing, and dominance was intermediate with 50% utilization ($P = 0.0328$).

Fire and grazing utilization had interacting effects on bare ground ($P = 0.0258$; Fig. 2). Without fire, bare ground increased with increasing grazing utilization. No differences in bare ground were detected among utilization levels on burned sites. Bare ground was more abundant on burned than nonburned sites when plots were not grazed or grazed to 50% utilization. During 2010, no differences in Simpson's or Shannon-Weiner diversity were observed, but both measures of diversity increased with increasing grazing utilization during 2011 ($P = 0.0236$, $P = 0.0285$; Table 6). Simpson's diversity decreased between years with no grazing, and Shannon-Weiner index decreased between

years with no grazing and 50% utilization. Unlike fire effects on diversity, no differences in non-native species composition were detected among grazing utilization levels (8.9, 7.8, $8.9 \pm 1.9\%$ for 0%, 50%, and 75% utilization, respectively; $P = 0.7802$).

Discussion

Interactions between grazing history and recent grazing utilization or fire were limited and did not support expectations that long-term livestock exclusion would reduce rangeland stability in response to fire and grazing. Instead, grazing history, grazing utilization, and fire effects were largely independent of one another. Grazing history affected biomass of all functional groups and the various measures of diversity, so the rarity of interactions was not due to the lack of effects. Fire and grazing utilization also affected composition and measures of diversity. Grazing history interacted with grazing utilization only for old dead material, bare ground, richness, and dominance. In the case of bare ground, the interaction was likely explained by 50% utilization pasture plots having less initial bare ground. Otherwise, pasture had more bare ground than exclosures and when initial measurements were used as a covariate, bare ground increased with utilization. Considered along with the lack of grazing history interactions with fire, data indicate that 15 yr of livestock exclusion had little effect on rangeland response to subsequent grazing utilization or fire.

Grazing History

A primary effect of livestock exclusion is often the accumulation of litter and standing dead material. Litter has been noted to sometimes increase productivity in northern mixed prairie (Willms et al., 2002; Hilger and Lamb, 2017). However, litter also reduces diversity (Foster and Gross, 1998; Berendse, 1999; Ruprecht et al., 2010; Letts et al., 2015; Mariotte et al., 2017) and promotes exotic and invasive species in numerous systems (Whisenant and Uresk, 1990; Coleman and Levine, 2006; Eppinga et al., 2011; Mariotte et al., 2017). We expected fire and grazing utilization to interact strongly with grazing history because of these known effects of litter and old dead, and because both should be sensitive to fire and grazing. Fire and grazing utilization each interacted with grazing history in their effects on old dead, but that did not translate into changes in biomass or composition with respect to those interactions. More abundant old dead in burned exclosures than burned pasture during 2011 cannot be readily explained because there was no grazing history by fire by year interaction for any of the biomass components. Richness was slightly reduced with the removal of grazing in pastures, as may be expected with an accumulation of more old dead and litter, but there was no corresponding increase in richness when exclosures were grazed.

Throughout the study period, litter cover was similar between exclosures and pastures. Litter depth was not measured. Old dead was more abundant in exclosures before treatment, but the magnitude of that difference was reduced over time with respect to grazing treatments and was only reduced by fire the first growing season after fire. Differences between old dead in pastures and exclosures were potentially less than required to have measurable effects on the plant community or soil environment during the generally wet period. Although we observed pre-study years with sufficient litter to support aboveground rodent tunnels in the exclosures, it is common that only a small fraction of old dead remains by the middle of the next growing season. Therefore, it is not clear that litter can be consistently accumulated to impactful levels or that the abundance of litter would necessarily increase with longer livestock exclusion.

Exclosures maintained more C_3 perennial grass and forbs whereas pastures maintained more C_4 perennial grass and subshrubs and greater diversity across time and treatments. Despite differences in composition, current-year biomass was similar between pastures and exclosures. Our results are in partial agreement with those of a 70-yr

exclosure study in northern mixed prairie with the same dominant species (Willms et al., 2002) in that livestock exclusion increased C_3 perennial grass and reduced C_4 perennial grass. However, no differences in forbs, subshrubs, or diversity were detected by Willms et al. (2002), and they reported greater current-year biomass for exclosures on one soil type and no difference on another. Shortgrass steppe diversity was also greater with long-term moderate grazing compared with 55 yr of livestock exclusion (Hart, 2001).

The annual grass response to grazing history is more complex than our study period data reveal. The dominant annual grasses, cheatgrass and Japanese brome, are somewhat erratic in the northern Great Plains (Ashton et al., 2016). Japanese brome has been more abundant in the exclosures than pastures in the years preceding this study (data not reported) and is known to be favored by litter and fall precipitation (Whisenant and Uresk, 1990; Haferkamp et al., 1993). Cheatgrass was the dominant annual grass during the study period and is less predictable, but tends to occur on drier sites with greater direct sun exposure. A history of grazing was more conducive to cheatgrass establishment during the first 2 yr of the study than livestock exclusion. The reduction of cheatgrass in pastures during the third yr is indicative of cheatgrass' ephemeral nature in the Great Plains and contrasts with its tendency for persistence in the Great Basin (Mack, 1981; Knapp, 1996).

Fire and Grazing Utilization

Fire and grazing collectively affected all response variables except subshrub biomass after adjusting for pre-existing differences due to grazing history. Bare ground was the only variable for which fire and grazing had interacting effects and those effects were simple in that bare ground was consistent across utilization levels following fire whereas bare ground increased with increasing utilization without fire. Fire effects on biomass mirrored those reported following late summer fire (Vermeire et al., 2011, 2014), with reductions in annual grasses and forbs and no differences in current-year biomass. Fire effects on grassland diversity are conditional and variable (Harrison et al., 2003). The reduction in diversity and greater dominance we observed following fire was driven by a reduction of non-native species composition.

The reduction of C_3 perennial grasses and increase in annual grasses with grazing indicate some changes from long-term livestock exclusion can be quickly reversed. No differences in current-year biomass were detected between moderately grazed pastures and exclosures after 15 yr of treatment, but 75% utilization led to an 11% reduction in 1 or 2 yr. The negative trend for C_4 perennial grasses as utilization increased from 50% to 75% is noteworthy and indicates that even short-duration 75% utilization can be detrimental because the dominant C_4 grass, blue grama, is generally considered grazing tolerant (Milchunas et al., 1990; Manley et al., 1997; Hart and Ashby, 1998). Rangelands have been observed to be resilient to grazing effects at the study location during generally dry periods (Eneboe et al., 2002; Vermeire et al., 2008), but grazing effects often vary with precipitation (Milchunas et al., 1994; Porensky et al., 2013). Diversity was not initially responsive to utilization, but increased with increasing utilization after 2 yr of grazing. These results provide evidence that diversity can be effectively manipulated by altering grazing utilization as suggested by Lwiwski et al. (2015).

Implications

Interactions between grazing history and recent grazing utilization or fire were limited and did not support expectations that long-term livestock exclusion would reduce rangeland stability in response to fire and grazing. Instead, grazing history, grazing utilization, and fire effects were largely independent of one another. Previous work has shown the region to be resistant to grazing effects in the short term and resilient to grazing in the longer term (Vermeire et al., 2008). Similarly, the dominant perennial grasses have neutral to positive responses

to fire and moderate grazing after fire (Vermeire et al., 2011, 2014; Gates et al., 2017). Limited interactions between grazing history and grazing utilization or fire suggest moderate grazing and livestock exclusion differ little in their effects on rangeland stability in terms of species composition and productivity. Conditions causing greater differences than we observed between grazed and nongrazed sites could lead to more interacting effects between disturbance and disturbance history. For example, an influx of grazing- or fire-sensitive species, or accumulation of fuel with livestock exclusion could be expected to reduce community resistance to disturbance by increasing the proportion of the community susceptible to disturbance in the first case or by increasing the severity of the disturbance in the second case. Without respect to grazing history, fire and grazing utilization effects on annual grasses, diversity, and dominance were in direct opposition to each other, indicating one factor is a good candidate for reversing effects of the other. Fire reduced annual grasses, forbs, and non-native species composition while maintaining total current-year biomass. Grazing history may affect the starting point, but the magnitude and direction of change with grazing utilization or fire were similar between pastures and enclosures for most variables. The independence of grazing history, grazing utilization, and fire should facilitate management decisions.

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