



Reconsidering rest following fire: Northern mixed-grass prairie is resilient to grazing following spring wildfire



Emily A. Gates^a, Lance T. Vermeire^{b,*}, Clayton B. Marlow^a, Richard C. Waterman^b

^a Montana State University, Bozeman, MT, United States

^b USDA-ARS Fort Keogh Livestock and Range Research Laboratory, Miles City, MT, United States

ARTICLE INFO

Article history:

Received 27 June 2016

Received in revised form 27 December 2016

Accepted 3 January 2017

Available online xxx

Keywords:

Grassland

Grazing management

Land management

Post-fire grazing

Rangeland

Wildfire

ABSTRACT

Current federal post-fire land management recommendations in the United States suggest that rangelands be rested from grazing for two growing seasons following fire to allow for proper recovery, despite the lack of empirical literature supporting this recommendation. This project was designed to determine if grazing the first growing season following a spring wildfire alters subsequent productivity and species composition of northern mixed-grass prairie. Following the April 2013 Pautre wildfire in northwestern South Dakota, 100 m² exclosures were erected in three burned pastures to simulate two growing seasons of rest. Grazing exclosures were paired with sites grazed both the first and second growing seasons following the fire and replicated across loamy and sandy ecological sites. Prior to grazing the second growing season, five 2 m² cages were placed at each grazed site to assess first-year grazing effects. Following the second growing season, productivity and species composition were determined for exclosures and cages. Productivity was greater for loamy than sandy ecological sites (loamy = 2764 kg ha⁻¹, sandy = 2356 kg ha⁻¹; $P = 0.0271$), but was similar between grazing treatments (rested = 2556 kg ha⁻¹, grazed = 2564 kg ha⁻¹; $P = 0.9550$). Ecological site strongly determined species composition. Loamy sites consistently contained more *Pascopyrum smithii*, *Bouteloua gracilis* and *Carex duriuscula* than sandy sites (30 v 0%, 18 v 8%, 4 v 1%; $P = 0.0004$, 0.0457 and 0.0382 respectively). The effects of grazing exclusion were limited to *Hesperostipa comata* and the non-native *Agropyron cristatum* composition. *H. comata* was more prevalent on rested sites (22 v 15%, $P = 0.0096$). *A. cristatum* experienced a grazing treatment by ecological site interaction as it was reduced by grazing on sandy sites, but was not affected on loamy sites ($P = 0.0226$). Results do not support the notion that a two growing season rest period following fire is required in the northern mixed-grass prairie.

Published by Elsevier B.V.

1. Introduction

Current federal land management recommendations in the United States decouple the historic disturbances of fire and grazing in North American prairies. Natural disturbances and the regimes in which they occur, far from being stressors as the nomenclature might imply, are integral ecological processes essential to long term ecosystem stability (Sousa, 1984). Scholars agree that prairies evolved under a tight, fire-grazing linkage, termed pyric herbivory, with herbivores being attracted to recently burned areas when given the freedom of selection (Anderson, 2006; Fuhlendorf et al., 2009). Recent literature suggests that not only are prairies well adapted to fire and post-fire grazing, but that the combination of

these disturbance may be necessary for the maintenance of ecological processes in these grasslands (Collins and Barber, 1986). However, current federal recommendations suggest that rangelands should be rested from grazing following fire. Although this recommendation may be beneficial on some rangelands, it may be unnecessary or inappropriate when applied to all rangelands due to the large variety of rangeland ecosystems with individual disturbance regimes.

United States Forest Service (USFS) recommendations state, "Revegetated areas and areas that have been burned but not revegetated will be closed to livestock grazing for at least two growing seasons following the season in which the wildfire occurred to promote recovery of burned perennial plants and/or facilitate the establishment of seeded species. Livestock closures for less than two growing seasons may be justified, on a case-by-case basis, based on sound resource data and experience" (Blaisdell et al., 1982). The Bureau of Land Management utilizes an

* Corresponding author.

E-mail address: lance.vermeire@ars.usda.gov (L.T. Vermeire).

essentially identical recommendation (Bureau of Land Management, 2007). The rationale for these policies relies on several assumptions. First, it is assumed that fire will reduce plant vigor and productivity, rendering plants less capable of surviving a grazing event. However, literature indicates that plants may respond negatively, neutrally or positively to fire (Engle and Bidwell, 2001; Knapp et al., 2009; Russell et al., 2015). Additionally, it is assumed that fire will result in appreciable plant mortality, requiring the recruitment of new seedlings for recovery. There are examples of fire actually increasing germination and seedling accumulation of native species (Maret and Wilson, 2000) and reducing emergence of non-native species (Vermeire and Rinella, 2009). However, literature indicates that the plants of some ecoregions experience little mortality following fire (Benson and Hartnett, 2006; Haile, 2011) and that ecosystem recovery does not rely on seedling recruitment (Benson and Hartnett, 2006). Lastly, this recommendation assumes an increased risk of soil erosion following fire due to bare ground resulting from litter combustion and plant mortality, indicating that burned sites should be protected from the increased erosion that can result from grazing (Naeth et al., 1991). Conversely, ground litter and detritus can actually build up to detrimental levels, limiting productivity, in under-disturbed prairies (Knapp and Seastedt, 1986). Empirical evidence to support the recommendation for rest across the whole geographic region to which it is applied is sparse.

The few available references indicating that there may be a need for rest following fire originate primarily from the Great Basin and specifically assess the effects of fire and post-fire defoliation on caespitose grasses, primarily *Pseudoroegneria spicata* (Pursh) Á. Löve and *Festuca idahoensis* Elmer. Clipping following fire additively increased the mortality experienced by these species when compared to unclipped plants (Jirik and Bunting, 1994). These studies suggest that rest from grazing for 1–3 years following fire will allow for plant vigor and seed production of these caespitose grasses to return to pre-fire levels while avoiding additive mortality from defoliation (Patton et al., 1988; Bunting et al., 1998). The rest interval also allows newly recruited seedlings to become sufficiently established to withstand a grazing event without mortality being inevitable, as recommended by the theory of rest-rotation grazing management (Hormay, 1970). Within the Great Basin, recent research has questioned the need for post-fire rest (Bates et al., 2009; Roselle et al., 2010), but the response of the rhizomatous and caespitose species of the northern mixed-grass prairie is not widely documented.

Research in the northern mixed-grass prairie indicates that vigor and productivity generally remain unaffected or are enhanced by fire (White and Currie, 1983; Vermeire et al., 2014) with few, if any, plants experiencing mortality (Haile, 2011). Furthermore, many northern mixed-grass species have a rhizomatous or stoloniferous, rather than caespitose, habit (e.g. *Pascopyrum smithii* (Rydb.) Á. Löve, *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths, *Bouteloua dactyloides* (Nutt.) J.T. Columbus, etc.) (Wakimoto et al., 2005). A recent study indicates that, while neither the caespitose *Hesperostipa comata* (Trin. & Rupr.) Barkworth nor the rhizomatous *P. smithii* mixed-prairie grasses experience immediate mortality following fire, rhizomatous grasses are overall less susceptible than caespitose grasses (Russell et al., 2015). Rhizomatous grasses are also less reliant on the regular recruitment of seedlings for propagation (Cheplick, 1998). Additionally, in the neighboring tallgrass prairie, composed of similar growth forms and subjected to similar disturbances as the northern mixed-grass prairie, Benson and Hartnett (2006) indicate that community recovery does not rely on germination of seed, but rather on tillering by surviving plants. Seasonality of fire further influences whether fire effects are negative, neutral or positive. In shortgrass prairie, dormant season fire may have no effect on plant vigor or

survival, with effects essentially limited to the removal of litter, while fire during the peak of the summer growing season may limit productivity (Brockway et al., 2002). However, the evolutionary history of North American prairies indicates that most naturally ignited wildfires occurred during summer (Higgins, 1984), suggesting that prairies should be well adapted to fire even in the most damaging season. Species-specific or plant functional group responses can vary with fire factors, such as seasonality and intensity (Knapp et al., 2009). As such, it is important to identify how fire variables may affect species composition and how those changes can affect or be further altered by subsequent ecological processes, including herbivory. Adaptations to deal with the effects of fire should be equally apparent in soil quality as they are in the vegetation.

Canopy and litter cover have been shown to moderate soil moisture and quality (Hulbert, 1969) and reduce erosive potentials (Benkobi et al., 1993). Fire will readily consume existing litter whereas grazing reduces litter via biomass removal and trampling (Naeth et al., 1991), indicating that either fire, grazing or post-fire grazing could reduce soil moisture or quality and increase erosion. However, Knapp and Seastedt (1986) indicate that, in tallgrass prairie, litter can accumulate to such a degree that it will inhibit productivity. Furthermore, in moisture limited systems, decomposition of litter occurs at limited rates, necessitating augmented recycling of litter through fire or grazing to maintain sustainable nutrient cycling (Brockway et al., 2002).

Taking this all into account, it is probable that individual rangelands have the capacity to respond disparately to the same disturbance regimes. Additionally, responses within one rangeland system can be expected to differ as annual precipitation and ecological site change across the landscape. Precipitation patterns, not management regimes, have been shown to account for the majority of yearly variation in productivity on northern mixed-grass prairie (Derner and Hart, 2007). Furthermore, ecological sites have been shown to maintain individuality unless severely or frequently disturbed (Gibson and Hulbert, 1987). Thus, post-fire grazing considerations likely need to be based upon the type of rangeland as well as the yearly and topographical variations within each rangeland type, indicating that the responses of Great Basin caespitose grasses may not be reflective of the adaptive capacity of the northern mixed-grass prairie to respond to fire and grazing.

Though North American rangelands, particularly the northern mixed-grass prairie, are specifically addressed in this work, post-fire land management with respect to grazing is far from an issue unique to the United States or North America. In Norway, Vandvik et al. (2005) indicate that post-fire grazing in heathland systems should not be considered equivalent to the sum of the effects of fire and grazing applied individually. Kutt and Woinarski (2007) suggest that the effects of grazing immediately following fire in Australian tropical savanna woodlands are not well understood despite this being the most common management practice.

Given the limited empirical support for current management recommendations, we evaluated the effects of grazing and rest following spring wildfire on two ecological sites within the northern mixed-grass prairie. The objective of this study was to quantify the effects of moderate post-fire grazing versus rest on productivity, community composition and basal cover. White and Currie (1983) found no negative impact of fire on post-fire productivity and Vermeire et al. (2011 [Vermeire et al., 2014]2014) found no negative effects of summer fire or post-fire grazing on productivity. Vermeire et al. (2014) found minimal effects on community composition and Bates et al. (2009) found none when comparing grazed and rested sites following fire. Vermeire et al. (2014) observed that moderate post-fire grazing may reduce litter mass and Bates et al. (2009) suggested that litter frequency under post-fire grazing will recover to levels comparable to rested sites

within two years. Therefore, we hypothesized that 1) grazing following a spring wildfire would have little effect on productivity the year following fire; 2) post-fire grazing would have no effect on plant community composition the year after fire; and 3) litter cover and bare ground would each be similar between grazed and rested sites the second growing season following spring wildfire.

2. Methods

2.1. Wildfire & study sites

The Pautre fire (31 km southwest of Lemmon, SD), occurred on 3 April 2013 and was contained on 7 April 2013, burning a 4322 ha mosaic of Grand River Cooperative Grazing Association, Grand River National Grassland and private lands. This study was conducted on the Dyson grazing allotment located within the Grand River National Grassland portion of the burn (lat 45° 51' 20" N long 102° 28' 35" W). The Dyson allotment burned in its entirety and is comprised of North (143 ha), Southeast (74 ha) and Southwest (41 ha) pastures. Pastures were dominated by the C3 grasses *H. comata*, *Agropyron cristatum* (L.) Gaertn. and *P. smithii*, with lesser a component of the C4 grasses *B. gracilis* and *Aristida purpurea* Nutt. *Psoralidium lanceolatum* (Pursh) Rydb., *Artemisia biennis* Willd. and *Artemisia ludoviciana* Nutt. were the most common forbs. *Artemisia frigida* Willd., the only woody shrub present, was rare. A complete list of species and their frequency by ecological site and grazing treatment are provided in Supplementary Table 1.

Following the wildfire, six 10 × 10 m grazing exclosures were erected, with two exclosures located in each pasture. Within each pasture, one exclosure was built on a loamy ecological site (Reeder-Lantry loams: Fine-loamy, mixed, superactive, frigid Typic Argiustolls and Fine-silty, mixed, superactive, calcareous, frigid Typic Ustorthents; 2–9% slopes) and the second on a sandy ecological site (Vebar-Cohagen fine sandy loams: Coarse-loamy, mixed, superactive, frigid Typic Haplustolls and Loamy, mixed, superactive, calcareous, frigid, shallow Typic Ustorthents; 6–25% slopes) (Soil Survey Staff USDA-NRCS, 2008). The median distance between any two exclosures was 209 m (23–861 m).

Precipitation averages 413 mm in Lodgepole, SD (approximately 12 km northeast of the study site) and 453 mm in Lemmon, SD with most occurring from April to September (National Climate Data Center, 2015). During the study period from 2013 to 2014, precipitation was above average. Precipitation was 710 and 863 mm (190 and 172% of average) during 2013 and 474 and 457 mm (101 and 114% of average) during 2014 in Lodgepole and Lemmon, respectively.

2.2. Post-fire grazing

Moderate grazing, following the USFS recommended stocking rates, was applied to pastures the first and second growing season following fire. Grazing occurred from 17 June to 31 October 2013 using 78 cow-calf pairs and 6 bulls (1.43 animal unit months [AUM] ha⁻¹) and from 22 June to 30 September 2014 using 78 cow-calf pairs and 3 bulls (1.14 AUM ha⁻¹). Prior to the 2014 grazing season, five 2 × 1-m grazing exclosure cages were paired with each exclosure to prevent further grazing during the 2014 season and measure the effects of grazing during the 2013 growing season.

2.3. Sampling

At the end of the first growing season following the fire, August 2013, grazing utilization was measured by clipping eight quadrats within each exclosure and eight quadrats from the grazed sites paired with each exclosure. The difference in standing biomass

from within and outside of the exclosures was assumed to represent grazing utilization during 2013 and used to further quantify grazing treatment along with stocking rate. In August 2014, at the conclusion of the second growing season following the fire, standing biomass, community composition and basal cover were sampled. Ten quadrats were clipped from each exclosure and two quadrats were clipped from beneath each cage. All quadrats were 0.1 m² (20 × 50 cm). Community composition was measured via the point-intercept method (Caratti, 2006). Ten randomly distributed points were measured beneath each exclosure cage while fifty randomly distributed points were measured within each exclosure. Observations at each point were used to calculate canopy and basal cover. Differences between the exclosures ("rested sites") and the cages ("grazed sites") were assumed to represent the effects of grazing the first growing season after fire.

Biomass samples were dried at 60 °C until loss in weight was no longer observed. Total standing biomass weights were recorded. Two samples from each exclosure and set of exclosure cages were then sorted and reweighed with respect to current-year production and old (previous years) standing dead biomass.

2.4. Statistical analysis

The SAS MIXED procedure was used to perform analysis of variance using the 10 × 10 m exclosures (n=6) and grazed sites (n=6) as the experimental units (Littell et al., 2006). Response variables for the mixed linear models included total standing biomass, old dead, current-year productivity, canopy composition by species and functional group (functional group refers to plants with similar life strategies; groups used were cool season (C3) grasses, warm season (C4) grasses, annual grasses, sedges and forbs), total canopy cover, basal cover composition, species richness and Shannon's diversity index (calculated using canopy frequency "hits" from the line-intercept transect). When necessary, effects on composition were compared against raw frequency data to determine if changes represented shifts in actual or relative abundance. Where outlier values were suspected, they were verified using the Generalized Extreme Studentized Deviate Test and removed from further analysis. Ecological site and grazing treatment were used as fixed-effect explanatory variables with pasture included as a random-effect variable. An α of 0.05 was used to identify significant effects and interactions while an α between 0.05 and 0.1 was used to identify trends or tendencies. Mean separations using the PDIF option in SAS were used when significant interactions between ecological site and grazing treatment were found.

3. Results

3.1. Biomass

In 2013, at the conclusion of the first growing season following the fire, grazing utilization was 35% on average with a median of 47%. Median grazing utilization likely represents a more accurate utilization estimate as biomass data in 2013 were markedly left-skewed. Grazed sites had less standing biomass when compared to rested sites at the end of the grazing period (Fig. 1A; $P=0.0307$). Standing biomass was similar between loamy and sandy ecological sites the first growing season after fire (Fig. 1B; $P=0.7409$).

In 2014, following the second post-fire grazing season, total standing biomass was 1.2 times greater on rested sites than grazed sites (Fig. 1A; $P=0.0381$). However, current-year productivity was similar between grazed and rested sites (Fig. 1A; $P=0.7966$) with old dead, which was greater on rested sites, accounting for the difference in total standing biomass (Fig. 1A; $P<0.0001$). Standing biomass and current-year productivity were, respectively, 1.20 and

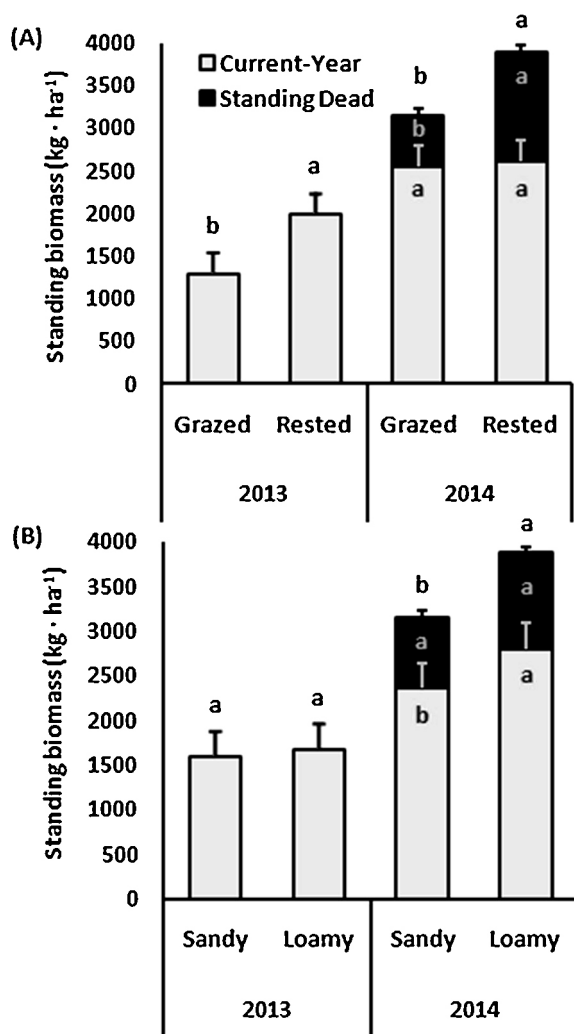


Fig. 1. Current-year and old standing dead and total biomass + standard errors of the means for (A) grazed and rested sites and (B) sandy and loamy ecological sites. Means within a component and year with common letters do not differ $P > 0.05$.

1.17 times greater on loamy sites than sandy sites (Fig. 1 B; $P = 0.0259$ and 0.0271 , respectively). Total canopy cover tended to be less on grazed sites (98%) than on rested sites (100%) ($P = 0.0603$).

3.2. Canopy composition

With respect to canopy community composition (Table 1), only *A. cristatum* (Fig. 2) and *H. comata* were sensitive to grazing. Grazing and site effects interacted in effects on *A. cristatum* with grazing causing a reduction on sandy sites and no effect on loamy sites where *A. cristatum* was uncommon (Fig. 2). *H. comata* was the only species ubiquitously reduced by grazing (Table 1). C4 grasses increased in relative composition under grazing. Forbs trended toward greater abundance on grazed sites. Total species richness was lower on rested sites. Grazing and site effects interacted with respect to Shannon's Diversity Index, with grazing increasing the index on sandy sites with no apparent effect on loamy sites (Fig. 3). *P. smithii*, *B. gracilis* and *Carex* spp. (*Carex duriuscula* C.A. Mey. and *Carex filifolia* Nutt.) composition percentages were greater on loamy than sandy ecological sites and *Koeleria macrantha* (Ledeb.) Schult. followed a similar trend (Table 2). Other C4 perennial grasses, primarily *Schizachyrium scoparium* (Michx.) Nash, were more abundant on the sandy ecological site.

Table 1

Canopy cover composition (%), species richness (No. species per 50 random points), ground cover (%) and standard errors for sites grazed or rested across ecological sites following spring wildfire near Lemmon, SD, USA. Results from a mixed model analysis of variance with ecological site and grazing treatment as fixed-effect explanatory variables and pasture included as a random-effect variable are displayed for the main effect of grazing treatment. Species comprising functional groups are described in Supplementary Table 1.

Component	Grazed	Rested	SE	P-value
<i>Hesperostipa comata</i>	15.0	22.4	3.2	0.0096
<i>Pascopyrum smithii</i>	14.4	15.6	4.0	0.7820
<i>Koeleria macrantha</i>	2.8	3.1	1.0	0.8317
Other C3 per. grass	2.0	0.0	0.9	0.1647
<i>Carex</i> spp.	5.4	8.5	3.7	0.5727
<i>Bouteloua gracilis</i>	16.5	9.0	4.2	0.1017
<i>Aristida purpurea</i>	5.8	4.1	2.5	0.3617
Other C4 per. grass	3.1	0.8	1.2	0.1729
Annual grass	2.1	1.6	0.9	0.7363
Forbs	12.2	2.9	3.5	0.0878
All C3 per. grass	34.2	41.1	3.7	0.2331
All C4 per. grass	25.4	13.9	3.5	0.0268
Richness	10	8	1.2	0.0247
Litter	20.7	12.3	5.7	0.3205
Bare ground	30.0	47.3	12.1	0.3194

Significant P-values are in bold font.

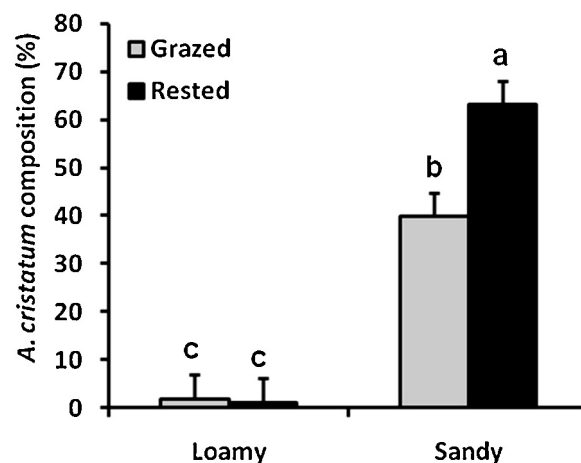


Fig. 2. *Agropyron cristatum* canopy cover composition + standard errors of the means by ecological site and post-fire grazing treatment. Means with a common letter do not differ ($P > 0.05$) within the ecological site by grazing treatment interaction ($P = 0.0226$).

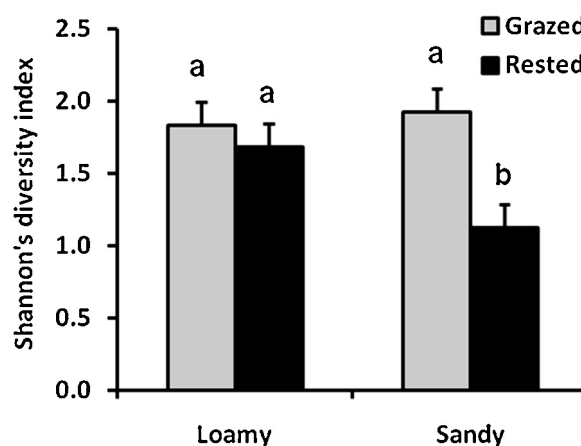


Fig. 3. Shannon's diversity index + standard errors of the mean by ecological site and post-fire grazing treatment. Means with a common letter do not differ ($P > 0.05$) within the ecological site by grazing treatment interaction ($P = 0.0344$).

Table 2

Canopy cover composition (%), ground cover (%) and standard errors for Loamy and Sandy ecological sites across grazed and rested treatments following spring wildfire near Lemmon, SD, USA. Results from a mixed model analysis of variance with ecological site and grazing treatment as fixed-effect explanatory variables and pasture included as a random-effect variable are displayed for the main effect of ecological site. Species comprising functional groups are described in Supplementary Table 1.

Component	Loamy	Sandy	SE	P-value
<i>Hesperostipa comata</i>	20.0	17.3	3.2	0.2229
<i>Pascopyrum smithii</i>	29.8	0.3	4.0	0.0004
<i>Koeleria macrantha</i>	4.3	1.5	1.0	0.0985
Other C3 per. grass	1.2	0.8	0.9	0.7794
<i>Carex</i> spp.	13.0	0.8	3.7	0.0571
<i>Bouteloua gracilis</i>	17.7	7.9	4.2	0.0457
<i>Aristida purpurea</i>	3.6	6.4	2.5	0.1545
Other C4 per. grass	0.0	3.9	1.2	0.0401
Annual grass	2.0	1.6	0.9	0.7872
Forbs	7.0	8.0	3.5	0.8360
All C3 per. grass	55.3	19.9	3.7	0.0005
All C4 per. grass	21.2	18.1	3.5	0.4607
Litter	18.7	14.3	5.7	0.5938
Bare ground	21.7	55.7	12.1	0.0773
Fecal	0.7	1.0	0.5	0.6349

Significant P-values are in bold font.

3.3. Basal cover

Litter cover and bare ground were each similar between grazed and rested treatments (Table 1). Fecal cover appeared only on grazed sites (1.7 vs $0.0 \pm 0.5\%$; $P=0.0465$). Litter and bare ground were similar across grazed and rested sites. Basal cover composition differed between ecological sites across grazing treatments with respect to three species. *A. cristatum* appeared only on sandy sites (5.6 vs $0.0 \pm 0.9\%$; $P=0.0022$) and *A. purpurea* provided greater basal coverage on sandy sites (4.0 vs $0.7 \pm 1.2\%$; $P=0.0092$). Loamy sites exhibited greater *B. gracilis* basal coverage than sandy sites (25.7 vs $5.7 \pm 1.2\%$; $P=0.0426$).

4. Discussion

Results support the hypothesis that moderate grazing during the first year following fire will not alter subsequent-year community productivity. At the end of the first and second growing seasons, grazing the first growing season after fire predictably reduced standing biomass by 35 and 19%, respectively. At the conclusion of the first growing season, we can account for this reduction as actual use. At the conclusion of the second growing season, standing-dead from the previous year accounted for the deficit in total standing biomass. Rested sites had 691 kg ha^{-1} (53%) more old dead material than grazed sites while current-year productivity remained similar across the grazed and rested sites. This finding agrees with observations of post-fire grazing in other areas of the northern mixed-grass prairie as well as sagebrush steppe that report no difference in current-year productivity (Bates et al., 2009; Vermeire et al., 2014). Greater than average precipitation during the study period almost certainly affected productivity and may have affected species composition. Given that this experiment studied grazing effects following wildfire and was not repeated with different weather conditions, the data cannot predict whether post-fire grazing effects would vary with drier conditions. However, rangeland productivity and composition responses to grazing following summer fire were consistent across dry and wet growing conditions and effects on productivity were similar whether biomass utilization was 0, 17, 34, or 50% (Vermeire et al., 2014). Had conditions been drier, it is likely that the magnitude of the difference in old dead material would have been smaller because the absolute difference in

residual mass between grazed and nongrazed sites shrinks as forage production decreases.

Contrary to the hypothesis, community composition, as measured by canopy cover, shifted slightly under moderate post-fire grazing. On an individual species basis, only *A. cristatum* and *H. comata* were found to be sensitive to grazing. C4 grasses were 11.5% more prominent after grazing. These changes were primarily attributable to the dynamics of *A. cristatum* and *H. comata*. C3 grasses are not only of a greater nutritional quality, but dominate the canopy over the relatively short statured C4 species found at the site, ultimately causing C3 grasses to be preferred by grazers (Vinton et al., 1993; Coleman et al., 2004). Changes in community composition, including the reduction of *H. comata* is not unprecedented following fire or grazing nor is the shift in the C3:C4 ratio necessarily undesirable. A C3:C4 ratio closer to 1:1 can extend forage quality by ensuring that active growth of high quality forage occurs during both cool and warm seasons (Doll et al., 2011).

The observed increase in Shannon's diversity index on grazed, sandy sites can be accounted for by the concurrent trend toward increased abundance of forbs on grazed sites. This agrees with the observations of Collins and Barber (1986) in which diversity was increased with the combined disturbances of fire and bison grazing when compared to fire alone, as predicted by the intermediate disturbance hypothesis. It is not unprecedented that this effect was only found on sandy sites as Gibson and Hulbert (1987) report a similar soil type by fire interaction.

As a species especially resistant to disturbances such as grazing (Looman and Heinrichs, 1973) and drought that can form persistent monocultures (Rogler and Lorenz, 1983), the observed reduction in *A. cristatum* composition is somewhat unique. While valued by some producers as an early-season forage and as a competitor of more invasive species, some range managers and conservationists also struggle to reduce *A. cristatum* in attempts to restore native species (Cook and Harris, 1952; Sedivec et al., 2010; Fansler and Mangold, 2011). Managing *A. cristatum* for either maintenance or reductions was not the primary goal of this research. However, results suggest that the role of post-fire grazing in maintaining or reducing *A. cristatum* stands warrants future consideration. The difference in *A. cristatum* response to post-fire grazing between ecological sites was likely driven by its abundance on sandy sites and limited occurrence on loamy sites.

The observed reduction in *H. comata* closely mimics the response observed by Vermeire et al. (2014) following summer fire with 50% post fire utilization. This correspondence of results suggests that *H. comata* may be more sensitive to post-fire grazing than the other dominant mixed-prairie grasses. Russell et al. (2015) found that spring burns reduced the bud bank of *H. comata* the second growing season following spring fire. Additionally, *H. comata* has been reported to decrease under grazing pressure (Dormaar et al., 1994), suggesting that the reduction seen here may be a compound effect of fire and grazing. The results of this study and others imply that, while northern mixed-grass prairie may be generally resilient to fire and post-fire grazing, northern mixed-grass ranges dominated by *H. comata* may be less resistant.

We suspect that the observed reductions in *H. comata* and *A. cristatum* may be transient because observed reductions were based on measurements of the canopy. Neither the basal coverage of *H. comata* nor *A. cristatum* was found to change after one application of post-fire grazing. As basal cover is more resistant to change than canopy cover and is not affected by current defoliation, it may provide a more reliable indication of longer term vegetative trends (Cosgrove et al., 2001). Thus, the reductions in canopy cover indicate that these two species are susceptible to the immediate effect of post-fire grazing while the lack of change in basal cover indicates that the longer-term position of these species in the community may be stable. However, repeated

moderate grazing can result in rangelands dominated by unselected, unpalatable species (Westoby et al., 1989). If the reductions in canopy cover of these two species resulted from selective grazing, decreases in basal cover may result from prolonged selective overuse. As the results of this study are indicative only of one year of grazing following fire, it is unclear what a pattern of successive burning and grazing events might have on the plant community composition, specifically with respect to basal cover.

The results of this study support the hypothesis that grazing the first growing season following fire will not affect the basal composition of the burned community. Neither litter, bare ground nor any other basal cover metric with the exception of fecal cover, differed between grazed or rested sites by the second growing season following the fire, indicating that grazing did not adversely affect the recovery of ground cover. The only observed impact, fecal cover, obviously results from the presence of animals versus the absence. While Bates et al. (2009) also found that litter had recovered similarly between grazed and rested post-fire treatments, the results of this study seemingly contrast with those of Vermeire et al. (2014) which indicated that post-fire grazing depressed litter mass. However, the estimate of litter obtained through the point-intercept method indicates the frequency at which litter was encountered, providing no estimate of the thickness or density of the litter layer. While results indicate that litter provides the same amount of cover on grazed or rested sites within two growing seasons following fire, rested sites may have a thicker or denser litter layer due to the greater availability of old standing dead material. Litter in prairies has been observed to be positively related to the retention of soil moisture, indicating that depressed litter production via the removal of biomass by grazers could impact soil quality (Hulbert, 1969). However, Vermeire et al. (2011) determined that a reduced litter layer following fire did not cause appreciable reductions in soil moisture.

By the second growing season following fire, ecological site had a greater impact than grazing treatment on productivity, community composition on an individual species basis and basal cover composition than did grazing treatment. Gibson and Hulbert (1987) indicate that ecological site has a stronger deterministic effect on community composition than disturbance unless disturbance is severe or frequent. The results of this study suggest that fire combined with one post-fire grazing event does not represent a disturbance severe enough to override the effects of ecological site. Although the sandy and loamy sites tested at the Pautre fire had retained their individuality after post-fire grazing, the responses of the two sites, in most cases, were similar in direction and magnitude, indicating that grazing can be managed similarly across these ecological sites following fire.

5. Conclusions

The results of this study indicate that moderate post-fire grazing rendered few impacts on northern mixed-grass prairie vegetation and was positive with regard to diversity. Although post-fire rest from grazing may be desirable in some situations, the results of this study and growing evidence from other research (Bates et al., 2009; Vermeire et al., 2014) indicate that rest is not required to maintain plant productivity or ground cover. The observed reduction in total standing biomass, resulting from the loss of old dead vegetation, will minimally reduce desirable forage in moderately stocked pastures. However, the combustion of old standing dead herbage represents a temporary reduction in total forage availability, potentially requiring adjustments in stocking rate. Grazing after fire shifted canopy composition away from *H. comata* and the non-native *A. cristatum*, indicating that rangelands dominated by caespitose grasses known to be sensitive to fire or

grazing may require more consideration for post-fire grazing management. Similarity of bare ground and litter between the grazed and rested treatments suggests that post-fire grazing will neither reduce subsequent-year soil moisture retention nor increase erosive potential. While the results of this study represent one year of grazing rather than annually repeated grazing as might take place in a livestock production setting, the limited and generally non-negative impacts of post-fire grazing provided no support for northern mixed-grass prairie requiring two growing seasons of rest following fire.

Funding

This work was supported by the United States Forest Service [13-IA-11011800-012]. Mention of any trade name or proprietary product does not constitute a guarantee or warranty by the authors or USDA-ARS, nor does it imply the approval of these products to the exclusion of others.

The USDA-ARS, Northern Plains Area, is an equal opportunity/affirmative action employer, and all agency services are available without discrimination.

Acknowledgements

The authors would like to thank the United States Forest Service, particularly Chad Prosser, David Hodges and Paul Drayton, for their funding, support and feedback. The authors would like to also acknowledge Dustin Strong and the Fort Keogh summer range crews for sampling and logistical support.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2017.01.001>.

References

- Anderson, R.C., 2006. Evolution and origin of the central grassland of North America: climate, fire, and mammalian grazers. *J. Torrey Bot. Soc.* 133, 626–647.
- Bates, J.D., Rhodes, E.C., Davies, K.W., Sharp, R., 2009. Postfire succession in big sagebrush steppe with livestock grazing. *Rangel. Ecol. Manag.* 62, 98–110.
- Benkobi, L., Trlica, M., Smith, J.L., 1993. Soil loss as affected by different combinations of surface litter and rock. *J. Environ. Qual.* 22, 657–661.
- Benson, E.J., Hartnett, D.C., 2006. The role of seed and vegetative reproduction in plant recruitment and demography in tallgrass prairie. *Plant Ecol.* 187, 163–178.
- Blaisdell, J.P., Murray, R.B., McArthur, E.D., 1982. Managing intermountain rangelands. USDA For. Serv. Gen. Tech. Rep. INT-134. Intermountain Forest & Range Experiment Station, Ogden, Utah.
- Brockway, D.G., Gatewood, R.G., Paris, R.B., 2002. Restoring fire as an ecological process in shortgrass prairie ecosystems: initial effects of prescribed burning during the dormant and growing seasons. *J. Environ. Manag.* 65, 135–152.
- Bunting, S., Robberecht, R., Defosse, G., 1998. Length and timing of grazing on postburn productivity of two bunchgrasses in an Idaho experimental range. *Int. J. Wildland Fire* 8, 15–20.
- Bureau of Land Management, 2007. H-1742-1 Burned Area Emergency Stabilization and Rehabilitation Handbook. In: D.o.t. Interior (Ed.), .
- Caratti, J., 2006. Point Intercept (PO) Sampling Method, vol. 2006. Rocky Mountain Forest Research Station Report number RMRS-GTR-164-CD.
- Cheplick, G.P., 1998. Population Biology of Grasses. Cambridge University Press.
- Coleman, S., Moore, J.E., Wilson, J.R., 2004. Quality and utilization. Warm-season (C4) grasses. *Agron. Ser.* 45, 267–308 (8).
- Collins, S.L., Barber, S.C., 1986. Effects of disturbance on diversity in mixed-grass prairie. *Vegetatio* 64, 87–94.
- Cook, C.W., Harris, L.E., 1952. Nutritive value of cheatgrass and crested wheatgrass on spring ranges of Utah. *J. Range Manag.* 5, 331–337.
- Cosgrove, D., Undersander, D., Cropper, J., 2001. Guide to Pasture Condition Scoring. .
- Derner, J.D., Hart, R.H., 2007. Grazing-induced modifications to peak standing crop in northern mixed-grass prairie. *Rangel. Ecol. Manag.* 60, 270–276.
- Doll, J.E., Haubensak, K.A., Bouressa, E.L., Jackson, R.D., 2011. Testing disturbance, seeding time, and soil amendments for establishing native warm-season grasses in non-native cool-season pasture. *Restor. Ecol.* 19, 1–8.
- Dormaar, J.F., Adams, B.W., Willms, W.D., 1994. Effect of grazing and abandoned cultivation on a *Stipa-Bouteloua* community. *J. Range Manag.* 47, 28–32.
- Engle, D.M., Bidwell, T.G., 2001. Viewpoint: the response of central North American prairies to seasonal fire. *J. Range Manag.* 54, 2–10.

- Fansler, V.A., Mangold, J.M., 2011. Restoring native plants to crested wheatgrass stands. *Restor. Ecol.* 19, 16–23.
- Fuhlendorf, S.D., Engle, D.M., Kerby, J., Hamilton, R., 2009. Pyric herbivory: rewilding landscapes through the recoupling of fire and grazing. *Conserv. Biol.* 23, 588–598.
- Gibson, D.J., Hulbert, L.C., 1987. Effects of fire, topography and year-to-year climatic variation on species composition in tallgrass prairie. *Vegetatio* 72, 175–185.
- Haile, K.F., 2011. Fuel Load and Heat Effects on Northern Mixed Prairie and Four Prominent Rangeland Graminoids [Life Sciences & Earth Sciences]. Montana State University, Bozeman, MT (71 p.).
- Higgins, K.F., 1984. Lightning fires in North Dakota grasslands and in pine-savanna lands of South Dakota and Montana. *J. Range Manag.* 37, 100–103.
- Hormay, A.L., 1970. Principles of Rest-Rotation Grazing and Multiple-Use Land Management. US Department of the Interior, Bureau of Land Management.
- Hulbert, L.C., 1969. Fire and litter effects in undisturbed bluestem prairie in Kansas. *Ecology* 50, 874–877.
- Jirik, S., Bunting, S., 1994. Postfire defoliation response of *Agropyron spicatum* and *Sitanion hystrix*. *Int. J. Wildland Fire* 4, 77–82.
- Knapp, A.K., Seastedt, T.R., 1986. Detritus accumulation limits productivity of tallgrass prairie. *BioScience* 36, 662–668.
- Knapp, E.E., Estes, B.L., Skinner, C.N., 2009. Ecological effects of prescribed fire season: a literature review and synthesis for managers. General Technical Report PSW-GTR-224. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA 80 p.
- Kutt, A.S., Woinarski, J.C.Z., 2007. The effects of grazing and fire on vegetation and the vertebrate assemblage in a tropical savanna woodland in north-eastern Australia. *J. Trop. Ecol.* 23, 95–106.
- Littell, R.C., Stroup, W.W., Milliken, G.A., Wolfinger, R.D., Schabenberger, O., 2006. SAS for Mixed Models. SAS institute.
- Looman, J., Heinrichs, D.H., 1973. Stability of crested wheatgrass pastures under long-term pasture use. *Can. J. Plant Sci.* 53, 501–506.
- Maret, M.P., Wilson, M.V., 2000. Fire and seedling population dynamics in western Oregon prairies. *J. Veg. Sci.* 11, 307–314.
- Naeth, M.A., Bailey, A.W., Pluth, D.J., Chanasyk, D.S., Hardin, R.T., 1991. Grazing impacts on litter and soil organic-matter in mixed prairie and fescue grassland ecosystems of Alberta. *J. Range Manag.* 44, 7–12.
- National Climate Data Center, 2015. Available at: <https://www.ncdc.noaa.gov/cdo-web/2015>.
- Patton, B.D., Hironaka, M., Bunting, S.C., 1988. Effect of burning on seed production of bluebunch wheatgrass, Idaho fescue, and Columbia needlegrass. *J. Range Manag.* 41, 232–234.
- Rogler, G.A., Lorenz, R.J., 1983. Crested wheatgrass – early history in the United-States. *J. Range Manag.* 36, 91–93.
- Roselle, L., Seefeldt, S.S., Launchbaugh, K., 2010. Delaying sheep grazing after wildfire in sagebrush steppe may not affect vegetation recovery. *Int. J. Wildland Fire* 19, 115–122.
- Russell, M.L., Vermeire, L.T., Ganguli, A.C., Hendrickson, J.R., 2015. Season of fire manipulates bud bank dynamics in northern mixed-grass prairie. *Plant Ecol.* 216, 835–846.
- Sedivec, K.K., Tober, D.A., Duckwitz, W.L., 2010. Grasses for the Northern Plains: growth patterns, forage characteristics and wildlife values. *Cool Season*, vol. 1. . Soil Survey Staff USDA-NRCS, 2008. Official Soil Series Descriptions. . Available at: <http://soils.usda.gov/technical/classification/osd/index.html>.
- Sousa, W.P., 1984. The role of disturbance in natural communities. *Annu. Rev. Ecol. Syst.* 15, 353–391.
- Vandvik, V.E., Heegaard, I.E., Maren, Aarestad, P.A., 2005. Managing heterogeneity: the importance of grazing and environmental variation on post-fire succession in heathlands. *J. Appl. Ecol.* 42, 139–149.
- Vermeire, L.T., Rinella, M.J., 2009. Fire alters emergence of invasive plant species from soil surface-deposited seeds. *Weed Sci.* 57, 304–310.
- Vermeire, L.T., Crowder, J.L., Wester, D.B., 2011. Plant community and soil environment response to summer fire in the northern Great Plains. *Rangel. Ecol. Manag.* 64, 37–46.
- Vermeire, L.T., Crowder, J.L., Wester, D.B., 2014. Semiarid rangeland is resilient to summer fire and postfire grazing utilization. *Rangel. Ecol. Manag.* 67, 52–60.
- Vinton, M.A., Hartnett, D.C., Finck, E.J., Briggs, J.M., 1993. Interactive effects of fire, bison (*Bison bison*) grazing and plant community composition in tallgrass prairie. *Am. Midl. Nat.* 129, 10–18.
- Wakimoto, R.H., Willard, E.E., Hedrich, M., Reid, B., 2005. Historic Fire Regimes and Change Since European Settlement on the Northern Mixed Prairie: Effect on Ecosystem Function and Fire Behavior. Joint Fire Science Program. University of Montana, Missoula, MT.
- Westoby, M., Walker, B., Noy-Meir, I., 1989. Opportunistic management for rangelands not at equilibrium. *J. Range Manag.* 42, 266–274.
- White, R.S., Currie, P.O., 1983. Prescribed Burning in the Northern Great Plains – Yield and cover responses of 3 forage species in the mixed grass prairie. *J. Range Manag.* 36, 179–183.