



Can Mowing Substitute for Fire in Semiarid Grassland?*

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

^a US Department of Agriculture–Agriculture Research Service, Fort Keogh Livestock and Range Research Laboratory, Miles City, MT 59301, USA

^b Wyoming Game and Fish, Cheyenne, WY 82009, USA

^c Montana State University, Bozeman, MT 59717, USA

ARTICLE INFO

Article history:

Received 16 May 2019

Received in revised form

29 July 2019

Accepted 14 August 2019

Key Words:

diversity
fire
forage quality
grazing
rangeland
soil nitrogen

ABSTRACT

Accumulating data indicate the importance of fire in rangeland systems. Mowing is a common management technique sometimes considered a surrogate for fire. However, direct comparisons of fire and mowing effects are limited. Our objective was to determine whether mowing can substitute for fire in rangeland by comparing effects on plant biomass, composition, cover, soil nutrients, and forage quality. Three disturbance treatments (nontreated control, spring mowing with clipping removal, and spring fire) were randomly assigned to 21 plots (5 × 5 m) each on silty and claypan ecological sites in a completely randomized design, with seven replications per site. Current-yr biomass was similar among control, mowed, and burned treatments (1 003, 974, 1 022 ± 64 kg ● ha⁻¹). Mowing shifted functional group composition by reducing C₃ perennial grass 12% and increasing forbs 8%. Non-native species were a larger component of mowed (12%) than control (6%) or burned plots (4%). Fire increased bare ground 35%, reduced litter 32%, and eliminated previous yrs' growth the first growing season. Plant-available soil N and S more than doubled with fire, and there was a trend for more P in burned plots. Mowing effects were limited to a trend for less soil Fe. Mowing affected 42% of the forage quality variables with a 2% average improvement across all variables. Fire affected 84% of the variables, with a 12% average improvement. Mowing increased forage P and K, whereas fire increased forage concentrations of N, K, P, S, Mg, Fe, Mn, and Cu. Total digestible nutrients increased 1.1% with mowing and 2.1% with fire. In vitro dry matter disappearance increased 2.2% with mowing and 6.7% with fire. Burned plots had greater in vitro fermentation than controls or mowed plots. Although mowing can be a useful management tool, it is not a substitute for the ecological effects of rangeland fire.

Published by Elsevier Inc. on behalf of The Society for Range Management.

Introduction

Land managers are becoming more aware of the benefits of prescribed fire. However, people are commonly hesitant to begin a burning program because they lack experience applying prescribed fire. Among the mechanisms believed to cause fire effects are nonselective biomass removal and increased light availability near

the soil surface. Therefore, it is occasionally suggested that some fire effects can be mimicked with high-intensity, short-term grazing or mowing.

Land managers in rangeland ecosystems recognize the restoration of certain ecological processes (e.g., fire, livestock grazing) as an efficient strategy for improving and maintaining rangeland plant community structure and function (Wright and Bailey, 1982; Milchunas et al., 1988). The effect of fire and grazing on rangelands varies by ecosystem, as some rangeland plant communities are more resilient to fire or grazing (Wright and Bailey, 1982). Prescribed fire and grazing have been used in tandem in tallgrass prairie to enhance forage quality, improve livestock weight gain, reduce woody encroachment, improve wildlife habitat, and increase plant diversity (Hobbs et al., 1991; Collins et al., 1998; Fuhlendorf and Engle, 2004; Joern, 2005; Scasta et al., 2016). Relative to tallgrass prairie, sagebrush steppe rangeland is more susceptible to damage from fire and grazing (Mack and Thompson, 1982; Wright and Bailey, 1982; Chambers et al., 2014). However, prescribed fire

* This work was partially supported by the US 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 US Dept of Agriculture–Agriculture Research Service (USDA-ARS), nor does it imply the approval of these products to the exclusion of others. The USDA-ARS, Plains Area, is an equal opportunity/affirmative action employer, and all agency services are available without discrimination.

* Correspondence: Lance T. Vermeire, 243 Ft Keogh Rd, US Dept of Agriculture–Agriculture Research Service, Ft Keogh Livestock and Range Research Lab, Miles City, MT 59301, USA. Tel.: +1 406 874 8200

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

and grazing may still be used in the sagebrush steppe ecosystem to maintain productive native plant communities (Davies et al., 2010; Davies et al., 2016). Whether used individually or in combination, fire and grazing are valuable land management tools that can be used to fulfill various ecosystem management objectives (Pöyry et al., 2004; Fuhlendorf et al., 2009; Pyke et al., 2010).

Fire and grazing share certain ecological characteristics; both processes remove plant biomass, convert plant material to biotic and abiotic materials, and have the potential to alter ecosystem properties, including nutrient dynamics, plant production, and diversity (Howe, 1995; Collins et al., 1998; Hart and Ashby, 1998; Wan et al., 2001; Koerner and Collins, 2014). Fire has the potential to produce direct plant mortality in certain species, particularly annuals, and improve overall forage quality of a plant community (Vermeire and Rinella, 2009; Strong et al., 2013; Dufek et al., 2014). Furthermore, fire differs from grazing in that fire does not choose what plants to “consume,” does not have nutrient requirements, removes plant biomass at a relatively uniform utilization level (Bond and Keeley, 2005), and can have direct effects on the animal community (Branson and Vermeire, 2016). In contrast, grazing may cause direct fluctuations in plant community composition and indirectly alter forage quality (Taylor et al., 1993; Vermeire et al., 2008). Hulbert (1988) suggested clipping and fire largely had similar effects in tallgrass prairie in that both increase soil temperature and increase light intensity at the soil surface. However, biomass and reproductive culm density were positively related to nitrogen addition, which is associated with fire. Therefore, while fire and grazing share similar physiognomy, both have the proclivity to set plant communities on distinct ecological trajectories.

Mechanical removal (mowing) of vegetation shares characteristics with fire and grazing (uniform utilization and incomplete vegetation removal) and has been used to test for differences between defoliation mechanisms (Cox, 1988; Moog et al., 2002; Fidelis et al., 2012). Mowing requires less planning than livestock grazing and prescribed fire and may reduce risk compared with fire. Another benefit is the relative ease of mowing applications, which makes it an attractive vegetation management alternative to livestock grazing or prescribed fire. However, as outlined previously, fire and grazing are unique ecological processes and mowing may not reasonably mimic or have the magnitude of effects that the restoration of fire or grazing could have on a rangeland ecosystem (Lodge, 1960; Prober et al., 2008; Kitchen et al., 2009; Pyke et al., 2014).

The objectives of this study were to 1) describe spring mowing and spring prescribed fire effects on plant biomass, composition, cover, soil nutrients, and forage quality; and 2) to contrast the two treatments to each other and nontreated control plots and determine whether mowing is a suitable substitute for fire in rangeland. We hypothesized that spring fire 1) reduces annual grasses and forbs, 2) reduces litter and increases bare ground, 3) increases soil nutrient availability, and 4) increases forage quality to a greater extent than spring mowing.

Methods

Study Area

Research was conducted on the Fort Keogh Livestock and Range Research Laboratory (46°23'32"N, 105°57'09"W; 809 m above sea level), near Miles City, Montana. The vegetation type is northern mixed prairie. The climate is semiarid, with 341 mm average annual precipitation, 110- to 135-d freeze-free period, and temperatures ranging from -40°C to 38°C. About 90% of annual net primary production occurs by 1 July (Vermeire et al., 2009) and is most affected by April and May precipitation (Vermeire et al., 2008). April–May precipitation was 69% (57.6 mm) and 208% (172.5 mm)

of the 78-yr median (83.1 mm) during 2015 and 2016, respectively. The study period was warmer than the 78-yr average spring (13.5°C ± 1.3°C) and summer temperatures (20.8°C ± 1.2°C), with spring temperatures of 13.9°C and 15.1°C and summer temperatures of 21.6°C and 21.1°C during 2015 and 2016, respectively.

The study sites were level uplands on Pinehill loam (fine, montmorillonitic Typic Eutroboralfs) and a complex of Gerdrum clay loam (fine, smectitic, frigid Torreritic Natrustalfs) and Creed loam (fine, smectitic, frigid Aridic Natrustalfs) soils. All three soils are deep and well drained. The Pinehill loam is classified as a silty ecological site, and the complex is classified as a claypan ecological site. Distance between sites was 1.4 km. Vegetation was dominated by C₃ perennial grasses *Pascopyrum smithii* (Rydb.) A. Löve and *Hesperostipa comata* (Trin. & Rupr.) Barkworth 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 subshrub. The most common forbs were annuals *Logfia arvensis* (L.) Holub, *Tragopogon dubius* Scop. and *Plantago patagonica* Jacq., and the perennial *Sphaeralcea coccinea* (Nutt.) Rydb.

Experimental Design

A 0.2-ha site was selected from each, a silty and claypan ecological site. Within each site, three disturbance treatments were randomly assigned to 21 plots (5 × 5 m with 1- to 3.5-m buffers) in a completely randomized design, resulting in seven replications of each disturbance treatment per site. Treatments were nontreated control, mowing, and fire. Mowing occurred 11 May 2015 with a cutting height of 6 cm, and cut material was bagged and removed from the plots. The mowing treatment was designed to remove most of the standing dead material rather than shred it and would be most representative of haying with a severe cutting height or severe flash grazing, minus animal inputs. Fires were applied 8 May 2015 with ambient temperature of 10.7°C, 44% relative humidity, and 5.5 m·s⁻¹ wind. Two K-type thermocouples (Omega Engineering, Inc., Stamford, CT) were placed in the crowns of plants in each plot, and fire temperature data were recorded each second with HOBO U12 J, K, S, T Thermocouple Data Loggers (Onset Computer Corporation, Bourne, MA) to develop time-temperature profiles and quantify heat dosage of fire treatment. Mean recorded fire variables for clayey and silty sites were maximum temperature of 202°C and 293°C ± 25°C; duration of lethal temperature of 69°C and 173 ± 13 s > 60°C; and heat dosage of 3 598°C and 13 431°C ± 1 479°C · s > 60°C, respectively.

Sampling

Plant biomass and cover were measured during mid-July of 2015 and 2016, near peak standing crop. Biomass was estimated by clipping three randomly placed 0.1-m² quadrats to ground level in each 5 × 5 m plot. Samples were dried to a constant weight at 60°C and weighed. Samples were then sorted by current-yr growth and previous yrs' growth (old dead mass) and reweighed. The point-intercept method was used to measure basal and canopy cover, with readings every 20 cm along two 4.8-m transects in each plot. Basal cover was used to estimate bare ground and litter cover and canopy, and basal hits were used to calculate species composition, richness, Simpson's diversity (1-D), and Shannon-Weiner diversity index (H'). Species data were combined to represent four functional groups—C₃ perennial grasses, C₄ perennial grasses, forbs, annual grasses—and a fifth group, non-native species across functional groups.

Soil nutrient concentrations of total nitrogen (N), nitrate (NO₃), ammonium (NH₄), phosphorus (P), potassium(K), boron (B),

calcium (Ca), copper (Cu), iron (Fe), magnesium (Mg), manganese (Mn), sulfur (S), and zinc (Zn) were estimated using cation and anion pairs of ion exchange probes (Plant Root Simulator probes [PRS probes], Western Ag Innovations, Saskatoon, Saskatchewan, Canada). Probes (containing a 17.5-cm² resin membrane) were placed vertically 2 cm below the soil surface on 20 May 2015 and extracted 15 July 2015. Three cation/anion pairs of probes were randomly placed in each plot (42 plots × 3 probe pairs × 2 probes per pair = 252 total probes). After removal, probes were cleaned with deionized water and shipped to Western Ag Innovations. Probes were analyzed colorimetrically to determine nutrient concentrations with an autoanalyzer after extraction with 0.5 M HCl.

During June and July 2015, 20 g of *P. smithii* and 20 g of *B. gracilis* current-yr growth were collected from each plot to assess forage quality (42 plots × 2 species × 2 mo = 168 total forage samples). These species were selected because they are dominant C₃ and C₄ species in the region and prominent forage species. Forage quality tests were limited to current-yr growth of the two species because treatments were expected to alter species composition and the proportion of old dead mass, both of which could have confounding effects on forage quality interpretations. Samples were transported to the laboratory in a cooler and frozen at -4°C. Frozen samples were lyophilized for 72 h and ground to pass a 2-mm sieve. Ground samples were analyzed for dry matter (DM), in vitro dry matter disappearance (IVDMD), NDF (Goering and Van Soest, 1970), in vitro neutral detergent fiber disappearance (IVNDFD), and gas production (Menke et al., 1979). In vitro gas production variables were derived from the exponential equation $G = A(1 - \exp[-k(t - \text{Lag})])$ using GraphPad Prism (GraphPad Software, San Diego, CA), where G (mL g⁻¹ OM) represents total gas production, A (mL g⁻¹ OM) represents the asymptotic (maximum) gas production (AGP), k (h⁻¹) is the fractional fermentation rate, Lag (time in h) is time between introduction of the inoculum and the onset of gas production, and t (h) is the gas reading time (France et al., 2000). Approximately 10 g of ground sample from each plot were sent to an independent commercial laboratory for analyses of crude protein (combustion method), acid detergent fiber (ADF, Ankom filter bag technique), total digestible nutrients (TDN), and net energy for maintenance (NEM). Inductively coupled plasma spectroscopy was used to determine forage P, K, B, Ca, Cu, Fe, Mg, Mn, S, and Zn.

Statistical Analysis

Analyses of variance were conducted with the mixed procedure of SAS (Littell et al., 2006) to identify fire and mowing effects. Ecological site, species, and month were included in the experimental design to broaden applicability of results rather than as variables of interest for hypothesis testing. Therefore, ecological site, species, and month were included as random variables in models of data for which they occurred. We used analysis of variance models with repeated measures (yr) containing terms for treatment, yr, and the treatment-by-yr interaction for biomass, composition, cover, and diversity data. Treatment was the fixed effect for analysis of variance models testing soil nutrients and forage quality measures. 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

Biomass and Cover

Current-yr biomass was similar among control, mowed, and burned treatments (1 003, 974, 1 022 ± 64 kg ● ha⁻¹, respectively; $P = 0.7538$). Despite the similarity in production, mowing shifted

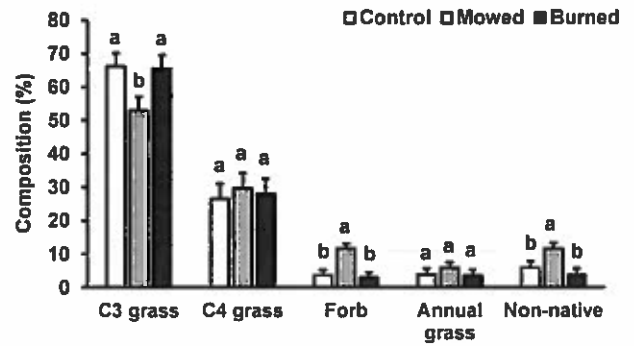


Figure 1. Functional group composition and non-native composition across functional groups and standard errors of the comparison for nontreated control, mowed, and burned plots. Samples were collected mid-July 2015 and 2016 near Miles City, Montana. Treatment means within a functional group with a common letter above bars are similar ($P > 0.05$).

functional group composition relative to control and burned plots by reducing C₃ perennial grass ($P = 0.0029$) and increasing forbs ($P < 0.0001$; Fig. 1). No differences were detected among treatments for C₄ perennial grass ($P = 0.7802$) or annual grass ($P = 0.3725$).

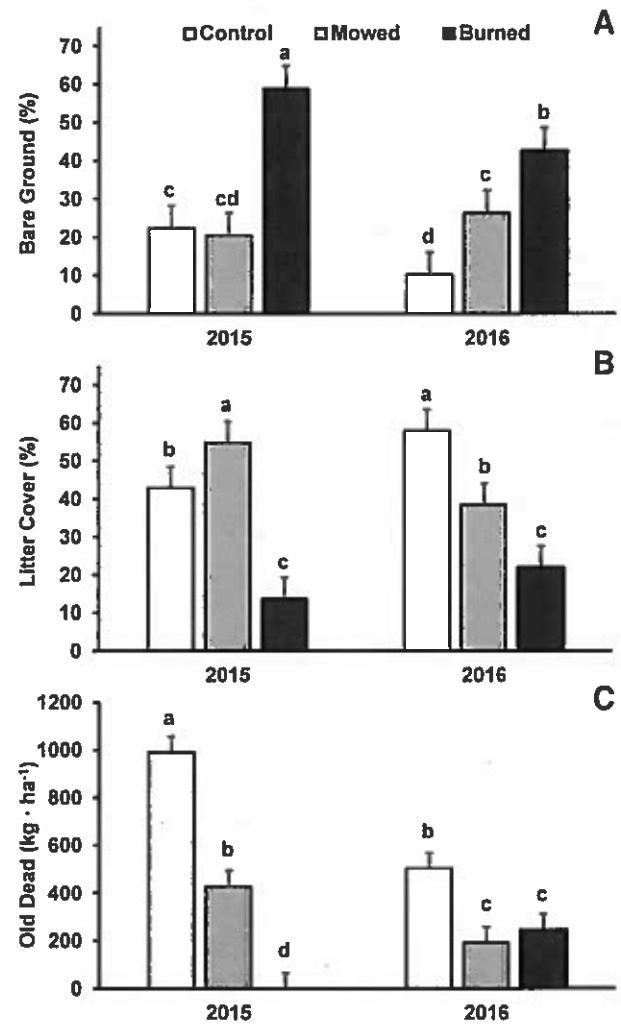


Figure 2. A, Bare ground, B, litter cover, and C, old dead mass and standard errors of the comparison for nontreated control, mowed, and burned plots by yr. Samples were collected mid-July 2015 and 2016 near Miles City, Montana. Treatment means with a common letter above bars are similar ($P > 0.05$).

Across functional groups, non-native species were also a larger component of mowed than control or burned plots ($P = 0.0002$). Driven largely by non-native species, there were trends for greater species richness (control, 5.6; mowed, 6.4; and burned, 5.6 ± 0.4 species; $P = 0.0806$) and diversity ($H' = 1.2823, 1.4174$, and 1.2685 ± 0.0730 ; $P = 0.0858$) with mowing. The most common non-native species were the annuals *Bromus japonicus*, *B. tectorum*, *Logfia arvensis*, and *Tragopogon dubius*. Considering only native species, control, mowed, and burned treatments had similar richness (4.4, 4.6, and 4.8 ± 0.3 species; $P = 0.4582$) and diversity ($H' = 1.1329, 1.1608$, and 1.1737 ± 0.0652 ; $P = 0.8151$).

Treatment interacted with yr for bare ground ($P < 0.0001$), litter cover ($P < 0.0001$), and old dead mass ($P < 0.0001$), but fire had the greatest effect on each (Fig. 2 A–C). Fire increased bare ground 35%, reduced litter 32%, and eliminated old dead mass the first growing season. Mowing did not change bare ground the first growing season, increased litter, and reduced old dead mass 59%. The second growing season after treatment, bare ground decreased for control and burned plots and was similar between yrs for mowed plots. Bare ground decreased from burned to mowed to control plots by the second growing season. The pattern for litter cover was opposite of that for bare ground, with less litter in mowed plots than controls and less in burned plots than mowed plots. Litter cover increased between yrs for controls and decreased in mowed plots, and no change was detected in burned plots. Old dead mass decreased in control and mowed plots the second growing season and increased in burned plots to a similar level as observed in mowed plots, which remained less than controls.

Soil Nutrients and Forage Quality

Fire more than doubled plant-available soil N compared with control and mowed treatments, primarily through NO_3^- (Table 1). Similarly, burned plots had more than twice the available S and there was a trend for more P in soil of burned than control or mowed plots. Evidence was lacking for fire effects on soil NH_4^+ , K, Ca, Mg, Fe, Mn, Zn, B, or Cu. There was a trend for less Fe in mowed than control or burned plots, but otherwise no mowing effects were detected for soil nutrients.

Treatment effects were much broader for forage than soils data, with mowing affecting 42% of the forage quality variables and causing an average improvement (relative to animal requirements) of 2% across all variables. Fire affected 84% of the variables, with an

Table 1

Mean plant-available soil nutrients in nontreated control, mowed, and burned plots from 20 May 2015 to 15 July 2015 (56 d) near Miles City, Montana; standard errors of the comparison (SEc); and P values for tests of treatment effects. Means within an element are similar when followed by a common letter ($P > 0.05$). Significant P values are bolded.

Element	Control	Mowed	Burned	SEc	P value
	$\mu\text{g} \bullet 10 \text{ cm}^{-2} \text{ Burial period}^{-1}$				
N	22.24 b	22.98 b	48.95 a	6.60	0.0002
NO_3^-	20.23 b	20.76 b	47.24 a	6.52	0.0002
NH_4^+	1.84 a	1.81 a	1.78 a	0.17	0.9334
P	7.23 b	7.39 b	9.89 a	1.31	0.0883
K	83.00 a	94.62 a	105.52 a	13.01	0.2369
Ca	1867.50 a	1819.79 a	1759.36 a	131.49	0.7142
Mg	507.71 a	508.79 a	488.43 a	32.35	0.7795
S	9.74 b	9.84 b	20.25 a	3.39	0.0043
Fe	6.41 a	5.16 b	6.59 a	0.68	0.0853
Mn	2.45 a	2.27 a	2.52 a	0.22	0.5126
Zn	0.60 a	0.68 a	0.85 a	0.14	0.2012
B	0.47 a	0.44 a	0.42 a	0.11	0.8976
Cu	0.16 a	0.15 a	0.19 a	0.04	0.5775

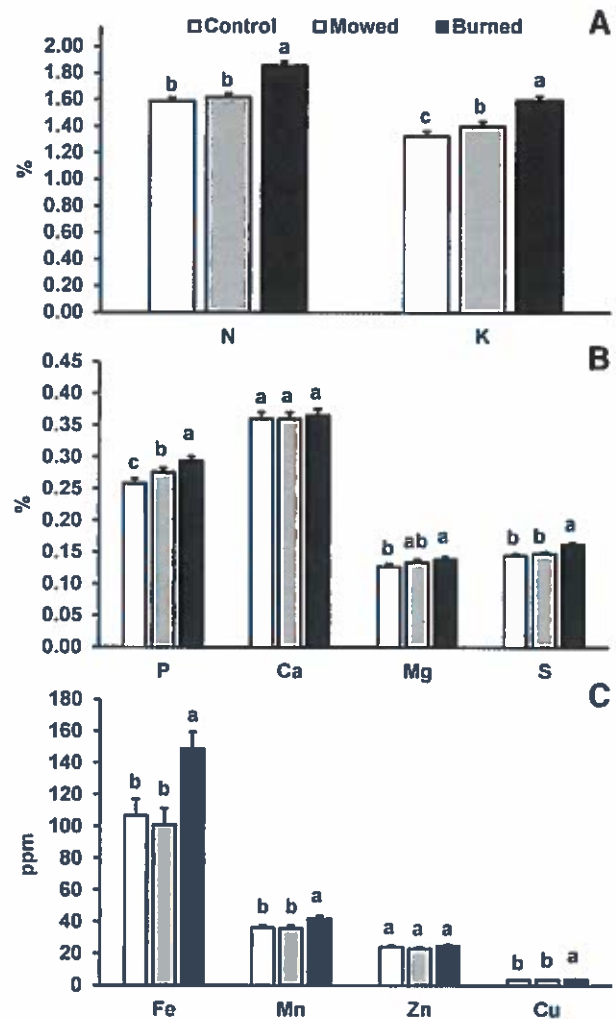


Figure 3. Forage nutrient concentration means for A, N and K; B, P, Ca, Mg, and S; and C, Fe, Mn, Zn, and Cu and standard errors of the comparison for nontreated control, mowed, and burned plots sampled June and July 2015 near Miles City, Montana. Treatment means within an element with a common letter above bars are similar ($P > 0.05$).

average improvement of 12%. Relative to controls, mowing increased P ($P < 0.0001$) and K ($P < 0.0001$) and had no detected effects on other elements (Fig. 3 A–C). Fire increased forage concentrations of N ($P < 0.0001$), K ($P < 0.0001$), P ($P < 0.0001$), S ($P < 0.0001$), Fe ($P < 0.0001$), Mn ($P = 0.0003$), and Cu ($P < 0.0001$) relative to controls and mowed plots and increased Mg ($P = 0.0346$) compared with controls. No differences were detected among treatments for Ca ($P = 0.8296$) or Zn ($P = 0.1069$). Forage nutrient concentrations were positively but not strongly correlated with 7 of the 12 respective soil nutrients, with correlation coefficients ranging from 0.31 to 0.54 (Fig. 4). For the N forms, soil NO_3^- was positively related to forage N ($r = 0.48$; $P = 0.0013$), but soil NH_4^+ was not ($r = -0.26$; $P = 0.1026$).

Mowing reduced forage ADF ($P < 0.0001$) and NDF ($P < 0.0001$) $\approx 0.9\%$ and 0.6% , and fire reduced both measures 2.0% and 2.5% (Fig. 5). In conjunction with reduced fiber fractions, treatment increased TDN ($P < 0.0001$), IVNDFD ($P < 0.0001$), and IVDMD ($P < 0.0001$), with mowing increasing each $\approx 1.1\%$, 3.0% , and 2.2% and fire increasing each 2.1% , 7.6% , and 6.7% , respectively. Net energy for maintenance was greater after mowing and greater still after fire

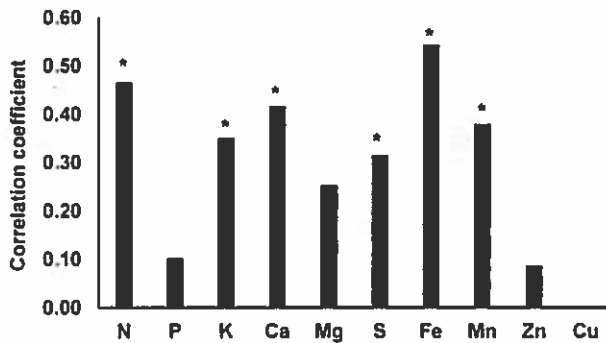


Figure 4. Coefficients for correlations between soil nutrient availability and above-ground vegetation nutrient concentration sampled June and July 2015 near Miles City, Montana. Asterisks denote P values < 0.05 .

(1.23, 1.25, and 1.28 ± 0.01 Mcal \bullet kg^{-1} ; $P < 0.0001$). Gas production data indicated greater asymptotic gas production in burned plots than controls and a greater fractional fermentation rate in burned plots than in controls or mowed plots (Table 2). No differences were detected among treatments for the lag time between introduction of inoculum and the beginning of gas production.

Discussion

Early spring mowing caused changes in functional group composition and diversity and improved some measures of forage quality, whereas spring fire did not alter functional group composition or diversity. However, fire increased bare ground through litter reduction, increased plant-available soil nutrients, and improved forage quality of current-yr growth. The hypothesis that spring fire reduces annual grasses and forbs was not supported by the data, but results supported the hypotheses that spring fire reduces litter and increases bare ground, increases soil nutrient availability, and increases forage quality to a greater extent than spring mowing, indicating mowing is not a substitute for fire.

Past work at this location showed that spring fire reduced forb biomass, annual grass frequency, and litter cover and increased basal cover of perennial C_3 grasses, perennial C_4 grasses, and native species compared with nonburned control (Vermeire and Russell, 2018). Fire and grazing effects on plant community variables can occasionally be modified by drought conditions (Vermeire et al., 2008; Vermeire et al., 2014). Summer and fall precipitation were 30% and 43% below the 82-yr average during 2014, and 2015 was the fifth driest yr overall during the same period. The extended

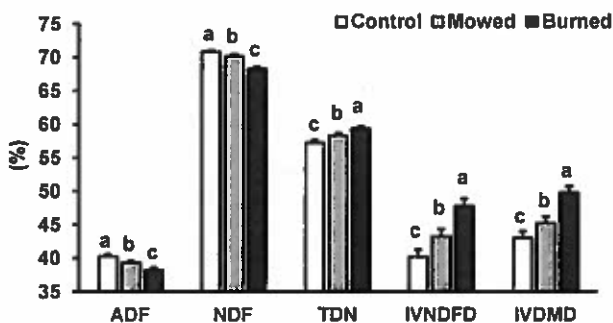


Figure 5. Mean acid detergent fiber, neutral detergent fiber, total digestible nutrients, in vitro neutral detergent fiber disappearance, and in vitro dry matter disappearance with standard errors of the comparison for nontreated control, mowed, and burned plots sampled June and July 2015 near Miles City, Montana. Treatment means within a component with a common letter above bars are similar ($P > 0.05$).

Table 2

Asymptotic gas production (AGP), fractional fermentation rate (k) and lag time means, standard errors of the comparison (SEc), and P values for tests of treatment effects among nontreated control, mowed, and burned plots. Means within a response variable are similar when followed by a common letter ($P > 0.05$). Data were collected June and July 2015 near Miles City, Montana.

Gas production variable	Control	Mowed	Burned	SEc	P value
AGP (mL \bullet g^{-1})	84.59 b	87.63 ab	89.35 a	1.57	0.0102
k (h^{-1})	0.0367 b	0.0382 b	0.0440 a	0.0010	< 0.0001
Lag (h)	1.67 a	1.72 a	1.84 a	0.09	0.1415

drought likely reduced annual grass germination in fall 2014 and spring 2015, thereby reducing overall abundance and muting treatment effects observed in previous studies. Brome abundance during an average to above-average precipitation yr would likely be greatest in mowed plots, due to increased litter (Whisenant and Uresk, 1990), and least in burned plots due to litter reduction, as well as plant and seed mortality (Vermeire and Rinella, 2009).

Forb response to fire on northern mixed-grass prairie is variable (Biondini et al., 1989; Erichsen-Arychuk et al., 2002; Vermeire and Russell, 2018). However, past research in our study area has consistently shown forb abundance decreases after fire (Vermeire et al., 2011; Strong et al., 2013; Vermeire et al., 2018), which we believe is attributable to heat damage to seeds (Vermeire and Rinella, 2009) and drier soil surface conditions after litter removal. These observations are largely based on highly ephemeral exotic annual species, such as *Logfia arvensis* and *Plantago patagonica*, that comprise the majority of the forb community. The increase in forb frequency in mowed plots could be a function of increased light availability after defoliation. A similar response to spring mowing was observed for *Melilotus officinalis* (L.) Lam. but not for sites mowed during August or November (Gates et al., 2017).

The similarity in current-yr biomass among treatments was not unusual in that past results have generally shown the same for fire effects, with shifts in species composition, but similar total biomass (Vermeire et al., 2011; Vermeire and Russell, 2018; Vermeire et al., 2018). Spring fire and mowing each increased aboveground plant production in northern mixed prairie with a history of light grazing utilization, although fire increased production more than mowing and mowing increased forbs (Gates et al., 2017). In sagebrush steppe of the Great Basin, fire caused greater shrub reduction and increased grass biomass compared with mowing (Davies et al., 2012). It appears, then, that fire has neutral to positive effects on total productivity and that fire effects tend to exceed mowing effects. Although mowing has been used to reduce invasive species (Smith et al., 2018), it commonly increases non-native species (Gibson et al., 1993; Swanson et al., 2016), as we observed. In contrast, fire can cause increases in rare species that are not observed with mowing in fire-prone systems (Weekley et al., 2011). We did not detect rare native species responding to fire, just the maintenance of fewer non-native species with fire.

Increases in plant-available soil N have been observed in semi-arid grasslands (Augustine et al., 2014; Reinhart et al., 2016). The mechanisms behind N increases after fire are complex and may include root exudation, plant mortality (e.g., root decomposition), shifts in the microbial community, and ash deposition. In our study, fire also increased S and there was a trend for increased P. Others have shown increased soil N and P after fire and no mowing effect (Prober et al., 2008). Meta-analysis indicates fire increases P in most nonconiferous systems (Butler et al., 2018). Previous research indicated plant production in semiarid northern mixed-grass prairie may be more limited by P than by N (Reinhart et al., 2016). Moreover, postfire peaks in available soil P are limited by dry conditions (Hinojosa et al., 2016) and semiarid plant communities are limited in their ability to take advantage of increased soil nutrient pools in general due to frequent drought conditions, such

as those during the study period. Fire-induced increases in soil nutrient availability did not translate to greater plant production. Changes in soil nutrient availability were also not well correlated with forage quality, as observed by others (Ben-Shahar and Coe, 1992). Taken together with the fact that there are numerous interactions among nutrients in soil-plant systems (Fageria, 2001), fire effects on soil nutrients do not appear to be good predictors for fire effects on forage quantity or quality.

Overall diet quality of a plant community depends on forage quality of individual species, animal preferences, species composition and time. Therefore, it is important to recognize observed changes in two of the dominant species because the studied system is not a comprehensive reflection of potential diet quality. However, fire in our system reduces *Opuntia polyacantha* Haw., *Aristida purpurea* Nutt., annual bromes, and standing dead mass and has neutral or positive effects on perennial grass production (Vermeire and Rinella, 2009; Vermeire and Roth, 2011; Vermeire et al., 2011; Strong et al., 2013), all of which increase forage quality or availability. In addition, past forage quality work indicates fire can shift plant nutrient concentrations in poor-quality grass species from being deficient to meeting animal requirements (Dufek et al., 2014). Reported fire effects on forage quality have been mixed, but improvement is often observed (van de Vijver et al., 1999; Raynor et al., 2015). Others reported no increases in N concentration of current-yr growth after spring fire in shortgrass steppe (Augustine et al., 2014) and no N or P increase in live tissue after fire or mowing in Inner Mongolia (Lü et al., 2012). Fire effects on forage quality likely depend on species, growing conditions, and plant phenology. Fire had a greater impact on all forage quality variables than mowing. Even during drought, fire clearly had a greater positive impact on the nutritional quality of two of the dominant native species than did mowing. Worth noting, however, is that the northern mixed-grass prairie evolved with recurrent fire and grazing. Therefore, in many respects (diversity, dominance, and annual grass abundance) fire and defoliation effects should be viewed as complementary (Vermeire et al., 2018) rather than one being a potential replacement for the other. Mowing is not a substitute for fire in northern mixed prairie.

Implications

Many rangelands evolved with recurrent fire, grazing, and variable weather. Two of the three, fire and defoliation, can be manipulated through management and both, operating in tandem, are likely required to maintain rangeland integrity. Defoliation can mimic fire in reducing standing biomass and has been successfully employed for species-specific management. However, fire effects are more complex than simply reducing standing biomass. Mowing-induced changes in functional group composition and diversity were driven by greater abundance of non-native species. Mowing increased forage quality, but fire had greater effects on forage quality in magnitude and scope. Drought likely limited annual grasses and forbs across treatments, and both functional groups are generally reduced by fire in northern mixed prairie. Taken together, results indicate that although mowing can be a useful management tool, it is not a substitute for the ecological effects of rangeland fire. Recognizing differences between fire and mowing or fire and grazing effects is important for designing land management plans and allows development of strategies that capitalize on the complementarity of both historical disturbances.

References

Augustine, D.J., Brewer, P., Blumenthal, D.M., Derner, J.D., von Fischer, J.C., 2014. Prescribed fire, soil inorganic nitrogen dynamics, and plant responses in a semiarid grassland. *Journal of Arid Environments* 104, 59–66.

- Ben-Shahar, R., Coe, M.J., 1992. The relationships between soil factors, grass nutrients and the foraging behavior of wildebeest and zebra. *Oecologia* 90, 422–428.
- Biondini, M.E., Steuter, A.A., Grygiel, C.A., 1989. Seasonal fire effects on the diversity patterns, spatial distribution, and community structure of forbs in northern mixed prairie, USA. *Vegetatio* 85, 21–31.
- Bond, W. J., and Keeley J. E. 2005. Fire as a global "herbivore": the ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution* 20:387–94.
- Branson, D.H., Vermeire, L.T., 2016. Grasshopper responses to fire and postfire grazing in the northern Great Plains vary among species. *Rangeland Ecology & Management* 66, 110–113.
- Butler, O.M., Elser, J.J., Lewis, T., Mackey, B., Chen, C., 2018. The phosphorus-rich signature of fire in the soil-plant system: a global meta-analysis. *Ecology Letters* 21, 335–344.
- Chambers, J.C., Miller, R.F., Board, D.L., Pyke, D.A., Roundy, B.A., Grace, J.B., Schupp, E.W., Tausch, R.J., 2014. Resilience and resistance of sagebrush ecosystems: Implications for state and transition models and management treatments. *Rangeland Ecology & Management* 67, 440–454.
- Collins, S.L., Knapp, A.K., Briggs, J.M., Blair, J.M., Steinauer, E.M., 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science* 280, 745–747.
- Cox, J. R. 1988. Seasonal burning and mowing impacts on *Sporobolus wrightii* grasslands. *Journal of Range Management* 41:12–15.
- Davies, K.W., Bates, J.D., Svejcar, T.J., Boyd, C.S., 2010. Effects of long-term livestock grazing on fuel characteristics in rangelands: an example from the sagebrush steppe. *Rangeland Ecology & Management* 63, 662–669.
- Davies, K.W., Bates, J.D., Nafus, A.M., 2012. Comparing burned and mowed treatments in mountain big sagebrush steppe. *Environmental Management* 50, 451–461.
- Davies, K.W., Bates, J.D., Boyd, C.S., Svejcar, T.J., 2016. Prefire grazing by cattle increases postfire resistance to exotic annual grass (*Bromus tectorum*) invasion and dominance for decades. *Ecology and Evolution* 6, 3356–3366.
- Dufek, N.A., Vermeire, L.T., Waterman, R.C., Ganguli, A.C., 2014. Fire and nitrogen addition increase forage quality of *Aristida purpurea*. *Rangeland Ecology & Management* 67, 298–306.
- Erichsen-Arychuk, C.A., Bork, E.W., Bailey, A.W., 2002. Northern dry mixed prairie responses to summer wildfire and drought. *Journal of Range Management* 55, 164–170.
- Fageria, V.D., 2001. Nutrient interactions in crop plants. *Journal of Plant Nutrition* 24, 1269–1290.
- Fidelis, A., Blanco, C.C., Müller, S.C., Pillar, V.D., Pfadenhauer, J., 2012. Short term changes caused by fire and mowing in Brazilian campos grasslands with different long-term fire histories. *Journal of Vegetation Science* 23, 552–562.
- France, J., Dijkstra, J., Dhanoa, M.S., Lopez, S., Bannink, A., 2000. Estimating the extent of degradation of ruminant feeds from a description of their gas production profiles observed in vitro: derivation of models and other mathematical considerations. *British Journal of Nutrition* 83, 143–150.
- Fuhlendorf, S.D., Engle, D.M., 2004. Application of the fire-grazing interaction to restore a shifting mosaic in tallgrass prairie. *Journal of Applied Ecology* 41, 604–614.
- Fuhlendorf, S.D., Engle, D.M., Kerby, J., Hamilton, R., 2009. Pyric herbivory: rewilding landscapes through the recoupling of fire and grazing. *Conservation Biology* 23, 588–598.
- Gates, E.A., Vermeire, L.T., Marlow, C.B., Waterman, R.C., 2017. Fire and season of postfire defoliation effects on biomass, composition, and cover in mixed-grass prairie. *Rangeland Ecology & Management* 70, 430–436.
- Gibson, D.J., Seastedt, T.R., and Briggs, J.M. 1993. Management practices in tallgrass prairie: large- and small-scale experimental effects on species composition. *Journal of Applied Ecology* 30:247–255.
- Goering, K., and Van Soest, P. J. 1970. Forage fiber analysis (apparatus, reagents, procedures and some applications). *Agriculture Handbook No. 379*, Washington, DC, USA: Agricultural Research Service, US Department of Agriculture. 20 p.
- Hart, R.H., Ashby, M.M., 1998. Grazing intensities, vegetation, and heifer gains: 55 years on shortgrass. *Journal of Range Management* 51, 392–398.
- Hinojosa, M.B., Parra, A., Laudicina, V.A., Moreno, J.M., 2016. Post-fire soil functionality and microbial community structure in a Mediterranean shrubland subjected to experimental drought. *Science of the Total Environment* 573, 1178–1189.
- Hobbs, N.T., Schimel, D.S., Owensby, C.E., Ojima, D.S., 1991. Fire and grazing in the tallgrass prairie: contingent effects on nitrogen budgets. *Ecology* 72, 1374–1382.
- Howe, H.F., 1995. Succession and fire season in experimental prairie plantings. *Ecology* 76, 1917–1925.
- Hulbert, L.C., 1988. Cause of fire effects in tallgrass prairie. *Ecology* 69, 46–58.
- Joern, A., 2005. Disturbance by fire frequency and bison grazing modulate grasshopper assemblages in tallgrass prairie. *Ecology* 86, 861–873.
- Kitchen, D.J., Blair, J.M., Callahan, M.A., 2009. Annual fire and mowing alter biomass, depth distribution, and C and N content of roots and soil in tallgrass prairie. *Plant and Soil* 323, 235–247.
- Koerner, S.E., Collins, S.L., 2014. Interactive effects of grazing, drought, and fire on grassland plant communities in North America and South Africa. *Ecology* 95, 98–109.
- Littell, R.C., Stroup, W.W., Milliken, G.A., Wolfinger, R.D., Schabenberger, O., 2006. SAS for mixed models. SAS Institute, Cary, NC, USA.
- Lodge, R.W., 1960. Effects of burning, cultivating, and mowing on the yield and consumption of crested wheatgrass. *Journal of Range Management* 13, 318–321.

- Lü, X., Lü, F., Zhou, L., Han, X., Han, X., 2012. Stoichiometric response of dominant grasses to fire and mowing in a semi-arid grassland. *Journal of Arid Environments* 78, 154–160.
- Mack, R.N., Thompson, J.N., 1982. Evolution in steppe with few large, hooved mammals. *The American Naturalist* 119, 757–773.
- Menke, K.H., Raab, L., Salewski, A., Steingass, H., Fritz, D., Schneider, W., 1979. The estimation of the digestibility and metabolizable energy content of ruminant feeding stuffs from the gas production when they are incubated with rumen liquor. *Journal of Agricultural Science* 93, 217–222.
- Milchunas, D.G., Sala, O.E., Lauenroth, W.K., 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *The American Naturalist* 132, 87–106.
- Moog, D., Poschlod, P., Kahmen, S., and Schreiber, K. F. 2002. Comparison of species composition between different grassland management treatments after 25 years. *Applied Vegetation Science* 5:99–106.
- Pöyry, J., Lindgren, S., Salminen, J., and Kuussaari, M. 2004. Restoration of butterfly and moth communities in semi-natural grasslands by cattle grazing. *Ecological Applications* 14:1656–1570.
- Prober, S. M., Lunt, I. D., and Thiele, K. R. 2008. Effects of fire frequency and mowing on a temperate, derived grassland soil in southeastern Australia. *International Journal of Wildland Fire* 17:586–594.
- Pyke, D.A., Brooks, M.L., D'Antonio, C., 2010. Fire as a restoration tool: a decision framework for predicting the control or enhancement of plants using fire. *Restoration Ecology* 18, 274–284.
- Pyke, D.A., Shaff, S.E., Lindgren, A.I., Schupp, E.W., Doescher, P.S., Chambers, J.C., Burnham, J.S., Huso, M.M., 2014. Region-wide ecological responses of arid Wyoming big sagebrush communities to fuel treatments. *Rangeland Ecology & Management* 67, 455–467.
- Raynor, E.J., Joern, A., Briggs, J.M., 2015. Bison foraging responds to fire frequency in nutritionally heterogeneous grassland. *Ecology* 96, 1586–1597.
- Reinhart, K.O., Dangi, S.R., Vermeire, L.T., 2016. The effect of fire intensity, nutrients, soil microbes, and spatial distance on grassland productivity. *Plant and Soil* 409, 203–216.
- Scasta, J., Thacker, E., Hovick, T., Engle, D., Allred, B., Fuhlendorf, S., Weir, J., 2016. Patch-burn grazing (PBG) as a livestock management alternative for fire-prone ecosystems of North America. *Renewable Agriculture and Food Systems* 31, 550–567.
- Smith, A.L., Barrett, R.L., Milner, R.N.C., 2018. Annual mowing maintains plant diversity in threatened temperate grasslands. *Applied Vegetation Science* 21, 207–218.
- Strong, D.J., Vermeire, L.T., Ganguli, A.C., 2013. Fire and nitrogen effects on purple threeawn (*Aristida purpurea*) abundance in northern mixed-grass prairie old fields. *Rangeland Ecology & Management* 66, 553–560.
- Swanson, S.R., Swanson, J.C., Murphy, P.J., McAdoo, J.K., Schultz, B., 2016. Mowing Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) cover effects across northern and central Nevada. *Rangeland Ecology & Management* 69, 360–372.
- Taylor, C. A., Brooks, T. D., and Garza, N. E. 1993. Effects of short duration and high-intensity, low-frequency grazing systems on forage production and composition. *Journal of Range Management* 46:118–121.
- Vermeire, L.T., Rinella, M.J., 2009. Fire alters emergence of invasive plant species from soil surface-deposited seeds. *Weed Science* 57, 304–310.
- Vermeire, L.T., Roth, A.D., 2011. Plains prickly pear response to fire: effects of fuel load, heat, fire weather, and donor site soil. *Rangeland Ecology & Management* 64, 404–413.
- Vermeire, L.T., Russell, M.L., 2018. Seasonal timing of fire alters biomass and species composition of northern mixed prairie. *Rangeland Ecology & Management* 71, 714–720.
- Vermeire, L.T., Heitschmidt, R.K., Haferkamp, M.R., 2008. Vegetation response to seven grazing treatments in the northern Great Plains. *Agriculture, Ecosystems and Environment* 125, 111–119.
- Vermeire, L.T., Heitschmidt, R.K., Rinella, M.J., 2009. Primary productivity and precipitation-use efficiency in mixed-grass prairie: a comparison of northern and southern US sites. *Rangeland Ecology & Management* 62, 230–239.
- Vermeire, L.T., Crowder, J.L., Wester, D.B., 2011. Plant community and soil environment response to summer fire in the northern Great Plains. *Rangeland Ecology & Management* 64, 37–46.
- Vermeire, L.T., Crowder, J.L., Wester, D.B., 2014. Semiarid rangeland is resilient to summer fire and postfire grazing utilization. *Rangeland Ecology & Management* 67, 52–60.
- Vermeire, L.T., Strong, D.J., Waterman, R.C., 2018. Grazing history effects on rangeland biomass, cover and diversity responses to fire and grazing utilization. *Rangeland Ecology & Management* 71, 770–775.
- van de Vijver, C.A.D.M., Poot, P., Prins, H.H.T., 1999. Causes of increased nutrient concentrations in post-fire regrowth in an east African savanna. *Plant and Soil* 214, 173–185.
- Wan, S., Hui, D., and Luo, Y. 2001. Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. *Ecological Applications* 11:1349–1365.
- Weekley, C.W., Menges, E.S., Berry-Greenlee, D., Rickey, M.A., Clarke, G.L., Smith, S.A., 2011. Burning more effective than mowing in restoring Florida scrub. *Ecological Restoration* 29, 357–373.
- Whisenant, S.G., Uresk, D.W., 1990. Spring burning Japanese brome in a western wheatgrass community. *Journal of Range Management* 43, 205–208.
- Wright, H.A., Bailey, A.W., 1982. *Fire ecology: United States and southern Canada*. John Wiley & Sons, New York, NY, USA, 501 p.

