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Source: Rangeland Ecology and Management, 78(1) : 117-126

Published By: Society for Range Management

URL: <https://doi.org/10.1016/j.rama.2021.06.004>

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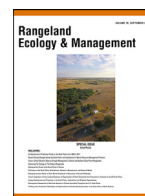
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Rangeland Ecology & Management

journal homepage: www.elsevier.com/locate/rama

Influence of Grazing Season, Residual Herbage, and Precipitation on Rumen Extrusa Diet Quality^{☆,☆☆}

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ARTICLE INFO

Article history:

Received 12 January 2021

Revised 25 May 2021

Accepted 9 June 2021

Key Words:

fall grazing
fiber
grassland
micromineral
protein
ruminant

ABSTRACT

While considerable research has quantified effects of grazing management and precipitation on plant communities, less is known about how seasonal effects influence extrusa diet quality selected by grazing ruminants. We tested effects of cattle grazing to two residual herbage (600 kg [moderate] or 300 kg [low] animal unit mo [AUM]/ha) and two grazing seasons (summer and fall) on 20 indicators of ruminant extrusa diet quality over a 6-yr period. We found no effect of residual herbage on 13 indicators of diet extrusa quality ($P \geq 0.13$) and no effect of season on 4 indicators of extrusa diet quality ($P \geq 0.0773$). We did, however, detect effects of yr on extrusa diet quality metrics and nutrients, likely due to variation in annual precipitation, which ranged from 63.9% to 138.6% of the long-term average. Most noticeably, the mineral Mn in extrusa was substantially lower in yrs with higher precipitation ($P < 0.0001$). While grazing intensity had divergent effects on forage quality in the summer versus fall, annual precipitation was often important. Crude protein was lowest in fall of 2013 (6.5%) and 2018 (7.78%), two high-precipitation yrs, but it was also low in fall of 2015 (7.30%), a low-precipitation yr ($P < 0.0001$). Forage extrusa Cu, an important catalyst in ruminant metabolism, exhibited a yr \times season interaction. Copper in fall of 2018 was greater compared with all other yrs and seasons in the study ($P < 0.0001$), 35.7% greater than summer of 2018, a high-precipitation yr, and 82.9% and 43.5% greater than summer and fall of 2013, another high-precipitation yr. Seasonal variation in diet nutrients and quality indicators were complex and complicated by yr effects, which sometimes related to precipitation amounts.

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Introduction

Precipitation is the greatest controlling factor for rangeland productivity in terms of both short-term fluctuation (weather) or long-term shifts (climate). Short-term weather and its interacting effects with management are of significant interest because these relatively short pulses of precipitation cause rapid changes in rangeland productivity and are experienced most often (Lauenroth and Sala 1992). More specific to the northern Great Plains, about 90% of annual primary productivity occurs by 1 July (Vermeire et al. 2009) and biomass production is strongly correlated with to-

tal precipitation occurring in April and May (Heitschmidt and Vermeire 2005). Regionally, 80% of the wet or dry periods ($\pm 25\%$ of the median) are short duration and last 1 or 2 consecutive yr (Vermeire, unpublished data). During the past 80 yr, the longest period of consecutive spring drought was 4 yr (1949–1952: unpublished data). Recently, concern about long-term climate change has increased. Shifts in precipitation along with more extreme weather events (e.g., deluge, drought) are projected (Shafer et al. 2014; Derner et al. 2018). Scientists have also observed that growing seasons have lengthened over the past 100 yr (Dunnell and Travers 2011). A concern is that recent historical records of weather and rangeland production data are not enough to accurately assess plant and animal responses to long-term changes in precipitation.

Rangeland management practices may also influence the quantity and quality of grazeable forages. Most research on grazing effects has focused on periods of plant growth, partially because this may be when plants are most sensitive to grazing. Less is known about effects of grazing while rangeland plants are dormant (McGeough et al. 2017; Wyffels et al. 2019). Smart et al. (2012) tested effects of clipping during the growing and dormant seasons and observed clipping in winter versus summer did not

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<https://doi.org/10.1016/j.rama.2021.06.004>

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affect plant species composition, suggesting that land managers and livestock producers may improve harvest efficiency (utilization of available biomass) by grazing during the dormant season. However, the quality of forages ingested by ruminants tends to be greater when plants are actively growing than when senescent (Adams and Short 1988; Johnson et al. 1998; Grings et al. 2005). Senescent vegetation is less susceptible to defoliation by livestock due to increased lignification (Vallentine 1990). While much is known about how to sustainably manage rangelands during the growing season, research is needed to better understand how to use rangelands during seasons of dormancy.

Developing strategies for greater dormant-season utilization demands identifying maximum thresholds for the plant communities and how those thresholds may be affected by interactions with short-term and long-term changes in precipitation. Cattle growth varies dramatically from yr to yr, and factors responsible for this variation are not fully elucidated (Nardone et al. 2010; Derner et al. 2018). Data describing how weather (or climate) interacts with management practices and other disturbances are essential to fully understand these interactions. Some climate change forecasts predict improved livestock productivity in northern latitudes resulting from increased quantity and quality of primary production with increases in both temperature and precipitation (Baker et al. 1993; Bolortsetseg and Tuvaansuren 1996), while others have detected decreases in forage quality (Craine et al. 2010; Craine et al. 2017; Brookshire et al. 2020).

To better understand the effects of grazing management and precipitation on indicators of forage quality and animal productivity, we conducted a 6-yr field experiment (2013–2018). The experiment tested the effects of grazing to leave residual herbage of 600 kg/ha (moderate) or 300 kg/ha (low) and season (June [summer], October/November [fall]) on diet extrusa nutrient composition (defined as extrusa diet quality at the time of turnout with five treatment replications). We hypothesized that extrusa diet quality would be greater in summer than fall and greater in wet compared to dry yr. The low residual biomass treatment may increase grazing-tolerant plant species and possibly increase the abundance of forages that are less susceptible to defoliation by ruminants or may just increase herbaceous consumption of present vegetation. However, less is known about whether stocking effects lead to compositional shifts with divergent forage quality (Porensky et al. 2017).

Methods

Study area

This study was conducted August 2013 through October 2018 at the Fort Keogh Livestock and Range Research Laboratory located approximately 1.6 km west of Miles City, Montana (46°22'N, 105°5'W). The lab's Institutional Animal Care and Use Committee approved all animal handling and experimental procedures used in the present study (22719-5). The experimental site was a calcareous grassland consisting of Pinehill loam soil (Fine, montmorillonitic Typic Eutroboralfs). The most abundant graminoids were needle-and-thread (*Hesperostipa comata* [Trin. & Rupr.] Barkworth, 31%); western wheatgrass (*Pascopyrum smithii* [Rydb.] A. Löve, 17%); blue grama (*Bouteloua gracilis* [Willd. ex Kunth] Lag. ex Griffiths, 12%); and threadleaf sedge (*Carex filifolia* Nutt, 12%; Reinhart et al. [2019]). Fringed sage (*Artemisia frigida* Willd) and prickly-pear cactus (*Opuntia polyacantha* Haw) were frequent. Fringed sage comprised < 3% of the biomass. Forbs generally comprised < 8% of total biomass.

Average temperatures range from −10°C in January to 24°C in July. Average 81-yr annual precipitation is 33.75 cm with most of the precipitation occurring from April through September (Fig. 1).

Experimental design and analysis

The experiment consisted of two residual herbage treatments (moderate, low) factorially combined with two grazing seasons (June [summer], October/November [fall]) arranged in a randomized complete block design with five replications (2 grazing residuals × 2 grazing seasons × 5 replications). Each paddock was 60 × 30 m (20 total paddocks). Ruminally cannulated cows (*Bos taurus*) with calves in June and without calves in October/November grazed paddocks at moderate (1 AUM/ha) and low (1.5 AUM/ha) residual herbage, until 600 and 300 kg/ha of standing biomass remained, respectively.

To estimate extrusa diet quality, extrusa samples were obtained from ruminally cannulated cows (two per paddock). Samples were collected on 9 August and 28 October 2013, 20 June and 24 October 2014, 22 June and 2 November 2015, 20 June and 24 October 2016, 16 June and 27 October 2017, and 25 June and 15 October 2018 on the first day of grazing.

On the day of extrusa sampling, ruminally cannulated cows were gathered and rumen contents were evacuated and stored in 208-L plastic containers. Ruminant walls were sponge-dried to remove any residual moisture as described by Lesperance et al. (1960). Cows were then released into paddocks and allowed to graze for 45–60 min. After the grazing bout, extrusa was removed from the rumen and thoroughly mixed. An aliquot (filled gallon-sized Ziplock bag) was saved for analysis, and original ruminal contents were replaced back into the rumen.

Extrusa samples were frozen at −20°C, lyophilized, ground to pass a 2-mm screen in a Willey Mill, and stored until analysis for dry matter (DM), organic matter (OM: [AOAC 1990]), and neutral detergent fiber (NDF [Goering and Van Soest 1970]). Subsamples of ground extrusa were analyzed by an independent laboratory (Midwest Laboratories, Omaha, NE) to estimate crude protein (CP), acid detergent fiber (ADF), total digestible nutrients (TDN), net energy (MJ/kg) for lactation (NEI), maintenance (NEm), and growth (NEg), along with macromineral (Ca, K, Mg, Na, P, and S) and micromineral (Cu, Mn, and Zn) content.

To estimate diet digestibility, ground extrusa samples (5 g) were placed in duplicate Dacron bags (10 × 20 cm; pore size = 53 ± 10 µm; Ankom Technology Corp., Fairport, NY). Duplicate bags containing ground extrusa and empty sealed Dacron bags (i.e., blanks) were placed into 60 × 60 cm zippered laundry bags with an attached cord in two separate rumen cannulated cows grazing a common crested wheatgrass (*Agropyron cristatum* [L.] Gaertn) pasture. Dacron bags (4/cow) containing ground extrusa samples and a blank empty bag (1/cow) were placed into the rumen at specific times to allow for 96, 48, 24, and 0 h of incubation. Amount of residue in the blank Dacron bag was subtracted from each sample bag collected at the same incubation time to correct for influx of particles during incubation. Upon removal from the rumen, at 0 h, bags were subjected to an initial rinse by submerging bags three times in a 19-L container. The 19-L container was filled with cold water to stop fermentation (0-h bags were not inserted into the rumen but were subjected to the rinsing in the 19-L container) and stored in plastic zippered bags before being frozen at −20°C for further analysis. Once thawed, bags were individually rinsed in cold tap water until the effluent was clear, after which bags were frozen (−20°C), lyophilized, and weighed. Residue remaining in the bag was analyzed for DM, OM, and NDF, and in-situ NDF disappearance (ISNDFD) was calculated.

Statistical analysis

Forage nutritional composition and mineral data were analyzed using the MIXED procedure of SAS (Littell et al. 2006) with paddock as the experimental unit. Residual herbage (moderate and

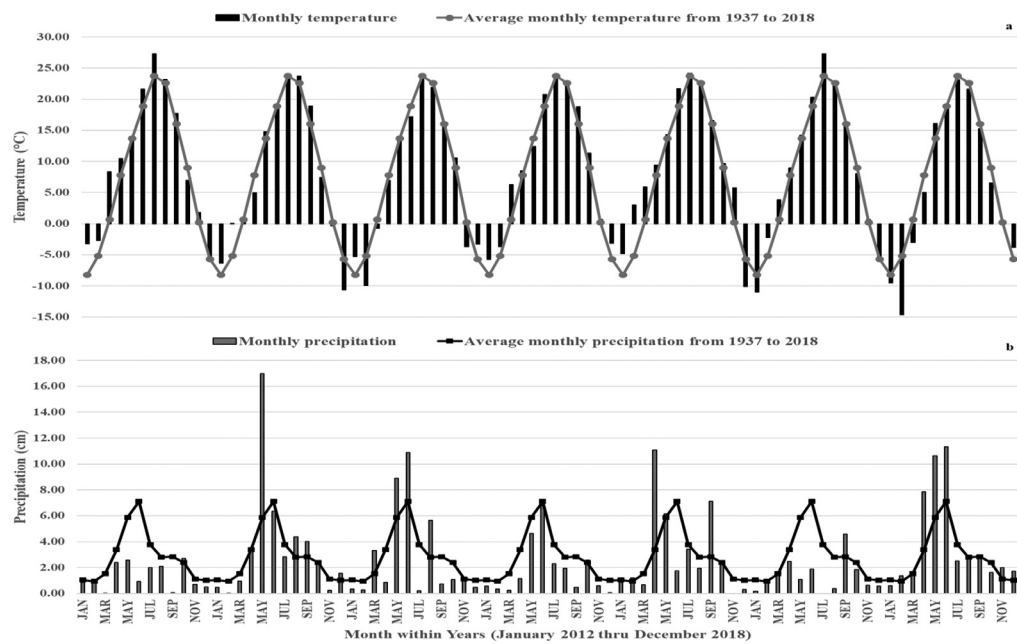


Fig. 1. Monthly temperature (a, °C) and precipitation (b, cm) from January 2012 to December 2018 and their corresponding 81-yr averages for Miles City, Montana. Annual precipitation was 15.65, 43.46, 33.76, 21.59, 36.96, 16.08, and 46.76 cm, respectively for 2012, 2013, 2014, 2015, 2016, 2017, and 2018 with a 81-yr average of 33.75 cm. Weather data were obtained from Western Regional Climate Center (WRCC 2020).

low, 600 and 300 kg/ha of postgrazing residual standing biomass, respectively); season of sampling (summer or fall); yr of study (2013–2018), which also corresponds to the interannual fluctuations in precipitation; and their interactions were included in the model. The REPEATED statement included yr, with paddock within season as the subject, and compound symmetry was used as the covariance structure. When significant ($P \leq 0.05$), main effect means were separated using LSMEANS. Mean separations were carried out using PDMIX800 (Saxton 1998).

Results

Precipitation variation

Annual precipitation was below the 81-yr average of 33.75 cm, the yr preceding (2012; 46.4% of average) and for 2 yr during the experiment (2015 and 2017; 63.9% and 46.8% of average, respectively). Precipitation was at or slightly above average for 2 yr (2014 and 2016; 100.8% and 109.5% of average, respectively) and above average for 2 yr (2013 and 2018; 128.8% and 138.6% of average, respectively) with only slight deviations from average temperature across all study yr (see Fig. 1).

Residual herbage, season, and year main effects

We found no main effects of residual herbage ($P \geq 0.15$) on extrusa diet quality for 13 indicators (Table 1). In addition, there was no detection that grazing season influence ($P \geq 0.0773$) for four indicators of extrusa diet quality (Table 2), thereby suggesting that some extrusa diet quality properties do not vary consistently, at least for initial turn out diet selection by livestock, in summer versus fall. Three indicators of extrusa diet quality were influenced by yr. The first indicator was 48 h DM ISNDFD, which was greater in 2017, a yr with low precipitation, and lowest in 2014, a yr with average precipitation, with all other yrs being intermediate ($P=0.0001$; Table 3). Likewise, 48 h OM ISNDFD was greater in 2016, an average-precipitation yr, and did not differ for all other yrs. The micromineral Mn was greatly reduced in high-

precipitation yrs (2013 and 2018) by 185.6% and 180.8% compared with 2017, a low-precipitation yr ($P < 0.0001$; see Table 3).

Interactive effects on forage quality properties

We detected a significant ($\alpha=0.05$) interactive effect of yr and season on 12 metrics of extrusa quality (Table 4). Effects including yr can be complex. Specifically, forage extrusa DM was lowest, first yr of the study, in 2013 when precipitation was above-average precipitation for both summer and fall (yr \times season; $P < 0.0001$). The highest DM occurred in fall of 2015, and DM was intermediate for both summer and fall in 2017, both in a low-precipitation yr. Forage extrusa OM was lowest for summer 2014, an average-precipitation yr, compared with summer 2017, a low-precipitation yr, that yielded the highest percent OM and contributed to the yr \times season differences observed ($P < 0.0001$), whereas OM was intermediate for fall 2013, a high-precipitation yr. Livestock production is reliant on both quality and quantity of available forage. More important is the ability of livestock to capture and use the available energy for growth, maintenance, and ultimately reproduction. Typically, rangeland forages increase in NDF during growth and disappearance of that fiber decreases as forages senesce. Changes in forage extrusa NDF on both a DM and OM were greater for summer and fall measures in 2015. Compared with summer and fall measures observed in 2017, this decrease in NDF was 22.1% and 22.5%, respectively, for DM and OM ($P < 0.0001$; see Table 4).

Forage extrusa ADF resulted in a yr \times season interaction with fall having greater ADF in 2014, an average-precipitation yr, and lowest in summer of 2017, a low-precipitation yr. Also, ADF in the fall of 2014 was greater than any ADF measured in the summer across all yrs ($P=0.0029$; see Table 4).

A residual herbage \times season \times yr interaction for 24-h ISNDFD on a dry matter basis ($P=0.0407$) and on an organic matter basis ($P=0.0534$; Fig. 2) was observed. The first 24 h for ISNDFD is typically the most rapid period for NDF disappearance. Differences in 24 h ISNDFD, on dry matter basis, occurred between 2014, an average yr for precipitation, and 2017, a low-precipitation yr, where

Table 1

Least square means (\pm standard error of the mean [SEM]) for extrusa diet quality indicators of rumen extrusa samples by residual herbage.

Extrusa diet quality metric ¹	Residual herbage ²		SEM	P value
	Moderate	Low		
DM, %	93.23	93.27	0.06	0.6197
OM, %	87.25	87.53	0.22	0.3786
ADF, % DM	38.01	38.13	0.28	0.7505
NDF, % DM	61.99	62.91	0.55	0.2357
NDF, % OM	62.57	63.54	0.57	0.2320
0h ISNDFD, % DM	13.64	14.02	0.50	0.5892
0h ISNDFD, %OM	18.47	18.48	0.54	0.9873
24h ISNDFD, % DM	50.81	53.41	0.86	0.0346
24h ISNDFD, %OM	51.14	53.52	0.95	0.0786
48h ISNDFD, % DM	67.71	69.37	0.78	0.1325
48h ISNDFD, % OM	67.85	69.44	0.84	0.1835
96h ISNDFD, % DM	77.82	78.44	0.50	0.3834
96h ISNDFD, % OM	77.07	78.21	0.56	0.1535
CP, %	9.58	9.76	0.15	0.3656
TDN, %	56.81	56.65	0.31	0.7235
NEI, MJ/kg	5.34	5.33	0.033	0.6785
NEm, MJ/kg	5.10	5.08	0.035	0.7230
NEg, MJ/kg	2.93	2.92	0.026	0.8352

¹ DM indicates dry matter; OM, organic matter; ADF, acid detergent fiber; NDF, neutral detergent fiber; ISNDFD, in-situ neutral detergent fiber disappearance; CP, crude protein; TDN, total digestible nutrients; NEI, net energy for lactation; NEm, net energy for maintenance; MJ, megajoule; Neg, net energy for gain.

² Grazed paddocks at moderate 600 kg/ha and low 300 kg/ha residual herbage.

Table 2

Least square means (\pm standard error of the mean) for extrusa diet quality metrics and nutrients from rumen extrusa samples by season of collection.

Extrusa diet quality metric ¹	Grazing season		SEM	P value
	Summer	Fall		
DM, %	93.21	93.29	0.06	0.3570
OM, %	86.87	97.91	0.002	0.0012
ADF, %DM	35.89	40.25	0.29	< 0.0001
NDF, %DM	52.52	62.38	0.55	0.8550
NDF, %OM	62.95	63.16	0.57	0.7941
0h ISNDFD, % DM	8.89	18.78	0.50	< 0.0001
0h ISNDFD, % OM	14.54	22.41	0.54	< 0.0001
24h ISNDFD, % DM	53.38	50.84	0.86	0.0385
24h ISNDFD, % OM	54.06	50.60	0.95	0.0115
48h ISNDFD, % DM	68.65	68.44	0.78	0.8437
48h ISNDFD, % OM	69.35	67.93	0.84	0.2325
96h ISNDFD, % DM	77.76	78.49	0.50	0.3076
96h ISNDFD, % OM	77.55	77.73	0.56	0.8193
CP, %	10.44	8.90	0.14	< 0.0001
TDN, %	59.05	54.41	0.31	< 0.0001
NEI, MJ/kg	5.57	5.10	.033	< 0.0001
NEm, MJ/kg	5.36	4.85	0.04	< 0.0001
NEg, MJ/kg	3.09	2.77	0.03	< 0.0001
Ca, %	0.6034	0.6077	0.0245	0.9007
K, %	1.3016	0.7367	0.0306	< 0.0001
Mg, %	0.1624	0.1487	0.0055	0.0829
Na, %	1.6857	1.5050	0.0320	0.0001
P, %	0.3368	0.3095	0.0056	0.0009
S, %	0.1470	0.1328	0.0018	< 0.0001
Cu, ppm	16.41	21.86	0.88	< 0.0001
Fe, ppm	312.1	414.7	57.4	0.2094
Mn, ppm	41.0	46.4	2.1	0.0773
Zn, ppm	22.77	20.14	0.59	0.0022

¹ DM indicates dry matter; OM, organic matter; ADF, acid detergent fiber; NDF, neutral detergent fiber; ISNDFD, in-situ neutral detergent fiber disappearance; CP, crude protein; TDN, total digestible nutrients; NEI, net energy for lactation; MJ, megajoule; NEm, net energy for maintenance; Neg, net energy for gain.

24-h ISNDFD was higher for 2017 summer low and moderate residual herbage and fall low residual herbage compared with 2014 summer moderate and fall moderate and low residual herbage (see Fig. 2a). A difference in 24-h ISNDFD, on an organic matter basis, was measured between 2015, a low-precipitation yr, and 2016, an average-precipitation yr, where in 2015 24-h ISNDFD for fall moderate residual herbage was 33.82% lower than 2016 fall

low residual herbage (see Fig. 2b). Furthermore, 2016 summer low residual herbage and 2018 fall moderate residual herbage were also lower in 24-h ISNDFD compared with 2017 fall low residual herbage.

A 96-h ISNDFD residual herbage \times season effect indicated that for moderate residual herbage paddocks, extent of disappearance for 96-h ISNDFD decreased from summer to fall, whereas

Table 3Least square means (\pm standard error of the mean) for extrusa diet quality metrics and nutrients of rumen extrusa samples by yr. Row means with different letters differ ($P < 0.05$).

Extrusa diet quality metric ¹	Yr ²						SEM	P value
	2013	2014	2015	2016	2017	2018		
DM, %	90.55c	94.03a	94.26a	93.80a	92.67b	94.18a	0.10	< 0.0001
OM, %	87.12c	82.57d	89.15ab	87.75bc	89.81a	87.94abc	0.004	< 0.0001
ADF, %dm	39.65ab	40.58a	39.95a	37.47bc	34.17d	36.59c	0.49	< 0.0001
NDF, %dm	65.97ab	61.61bc	68.16a	61.14c	58.42c	59.40c	0.95	< 0.0001
NDF, %om	65.96ab	62.26bc	68.55a	62.36bc	58.86c	60.34c	0.99	< 0.0001
0h ISNDFD, % DM	16.07aab	11.94bc	11.17c	14.78abc	10.86c	18.20a	0.87	< 0.0001
0h ISNDFD, % OM	16.08b	18.64b	11.57c	28.07a	.	18.02b	0.84	< 0.0001
24h ISNDFD, % DM	50.90b	43.33c	50.04bc	51.04bc	62.24a	55.11ab	1.49	< 0.0001
24h ISNDFD, % OM	50.85ab	48.35b	49.71b	49.71b	.	55.23ab	1.50	0.0001
48h ISNDFD, % DM	67.11b	58.51c	68.63b	71.02b	77.90a	68.08b	1.38	0.0001
48h ISNDFD, % OM	67.32b	63.41b	68.45b	75.25a	.	68.78b	1.35	< 0.0001
96h ISNDFD, % DM	77.18b	75.51b	79.66b	79.68b	87.06a	69.67c	0.89	< 0.0001
96h ISNDFD, % OM	76.94b	78.57b	79.63ab	82.93a	.	70.12c	0.90	< 0.0001
CP, %	6.85c	9.78b	9.40b	11.59a	11.66a	8.73b	0.24	< 0.0001
TDN, %	47.65d	57.45bc	57.00c	59.83b	63.59a	54.85c	0.54	< 0.0001
NEI, MJ/kg	4.44d	5.39bc	5.36c	5.64b	6.03a	5.16c	0.06	< 0.0001
NEm, MJ/kg	4.19d	5.15bc	5.10c	5.42b	5.83a	4.94c	0.06	< 0.0001
NEg, MJ/kg	2.34d	2.97bc	2.94bc	3.11b	3.44a	2.79c	0.05	< 0.0001
Ca, %	0.5195bc	0.6913ab	0.5340bc	0.5908bc	0.4695c	0.8285a	0.0424	< 0.0001
K, %	0.7235d	1.1385ab	0.8778cd	1.3000a	1.0678abc	1.0073bc	0.0530	< 0.0001
Mg, %	0.1315b	0.1590b	0.1183b	0.1555b	0.1358b	0.2333a	0.0096	< 0.0001
Na, %	1.1568b	1.6408a	1.6835a	1.6218a	1.8605a	1.6088a	0.0554	< 0.0001
P, %	0.2222c	0.3695a	0.3478ab	0.3178b	0.3275ab	0.3540ab	0.0097	< 0.0001
S, %	0.1033c	0.1395b	0.1520ab	0.1603a	0.1395b	0.1450ab	0.0032	< 0.001
Fe, ppm	252.9	452.81	351.45	454.55	421.35	247.43	99.49	0.4724
Cu, ppm	37.98b	3.94c	3.94c	4.13c	3.81c	61.00a	1.53	< 0.0001
Mn, ppm	2.86c	65.09ab	52.94b	61.04ab	76.47a	3.85c	3.69	< 0.0001
Zn, ppm	17.18a	21.19ab	23.89a	23.32a	24.01a	19.15ab	1.03	< 0.0001

¹ DM indicates dry matter; OM, organic matter; ADF, acid detergent fiber; NDF, neutral detergent fiber; ISNDFD, in-situ neutral detergent fiber disappearance; CP, crude protein; TDN, total digestible nutrients; NEI, net energy for lactation; MJ, megajoule; NEm, net energy for maintenance; NEg, net energy for gain.² Organic matter was not determined in 2017 for ISNDFD.**Table 4**Least square means \pm standard error of the mean for forage characteristics from rumen extrusa samples by yr \times season. Characteristic with different letters differ ($P < 0.05$).

Extrusa diet quality metric	Grazing season	Yr ²						SEM	P value
		2013	2014	2015	2016	2017	2018		
DM, %	Summer	90.55d	93.89b	93.76b	93.77b	92.96c	94.32ab	0.14	< 0.0001
	Fall	90.55d	94.16ab	94.75a	93.83c	92.37c	94.05ab		
OM, %	Summer	88.17abc	76.85d	89.33ab	88.29abc	90.53a	88.04abc	53.92	< 0.0001
	Fall	86.06c	88.29abc	88.96abc	87.21bc	89.09ab	87.85abc		
ADF, %	Summer	39.24bcd	37.80cdef	38.14bcde	34.36efg	31.64g	34.15fg	0.69	0.0029
	Fall	40.07abcd	43.36a	41.76ab	40.59abc	36.71def	39.04bcd		
NDF, % DM	Summer	67.88ab	57.69de	67.19ab	59.02cde	61.44bcde	61.91abcdde	1.34	< 0.0001
	Fall	64.06abcd	65.56abc	69.15a	63.27abcd	55.39e	56.89de		
NDF, % OM	Summer	67.88ab	58.17de	66.97abc	60.05cde	61.76bcde	62.87abcde	1.40	< 0.0001
	Fall	64.04abcd	66.34abc	70.14a	64.68abcd	55.95e	57.81de		
96h ISNDFD, % DM	Summer	76.46bcd	77.36bcd	77.67bc	77.56bc	86.67a	70.86de	1.22	0.0063
	Fall	77.91bc	73.65cde	81.66ab	81.79ab	87.45a	68.48e		
96h ISNDFD, % OM	Summer	76.46bc	81.06ab	77.60bc	81.14ab	.	71.48cd	1.32	0.0013
	Fall	77.42bc	76.08bc	81.67ab	84.72a	.	68.76d		
CP, %	Summer	7.15de	11.04ab	11.51a	12.11a	11.14ab	9.68bc	0.33	< 0.0001
	Fall	6.55e	8.52cd	7.30de	11.07ab	12.18a	7.78de		
TDN, %	Summer	48.13gh	59.45bcd	59.06cde	63.39ab	66.48a	57.78cde	0.76	0.0025
	Fall	47.18h	55.46def	54.94ef	56.27de	60.70bc	51.92fg		
NEI, MJ/kg	Summer	4.48gh	5.59bcd	5.56bcde	5.99ab	6.31a	5.43cde	0.08	0.0055
	Fall	4.37h	5.17def	5.14ef	5.26def	5.72bc	4.86fg		
NEm, MJ/kg	Summer	4.23gh	5.36bcd	5.31cde	5.80ab	6.14a	5.24cde	0.08	0.0037
	Fall	4.12h	4.92def	4.87ef	5.01def	5.50bc	4.61fg		
NEg, MJ/kg	Summer	2.38f	3.09bcd	3.09bcd	3.31b	3.66a	2.98bcd	0.06	0.0535
	Fall	2.29f	2.83de	2.78de	2.90cde	3.20bc	2.59ef		

¹DM indicates dry matter; OM, organic matter; ADF, acid detergent fiber; NDF, neutral detergent fiber; ISNDFD, in-situ neutral detergent fiber disappearance; CP, crude protein; TDN, total digestible nutrients; NEI, net energy for lactation; MJ, megajoule; NEm, net energy for maintenance; NEg, net energy for gain.² Organic matter was not determined in 2017.

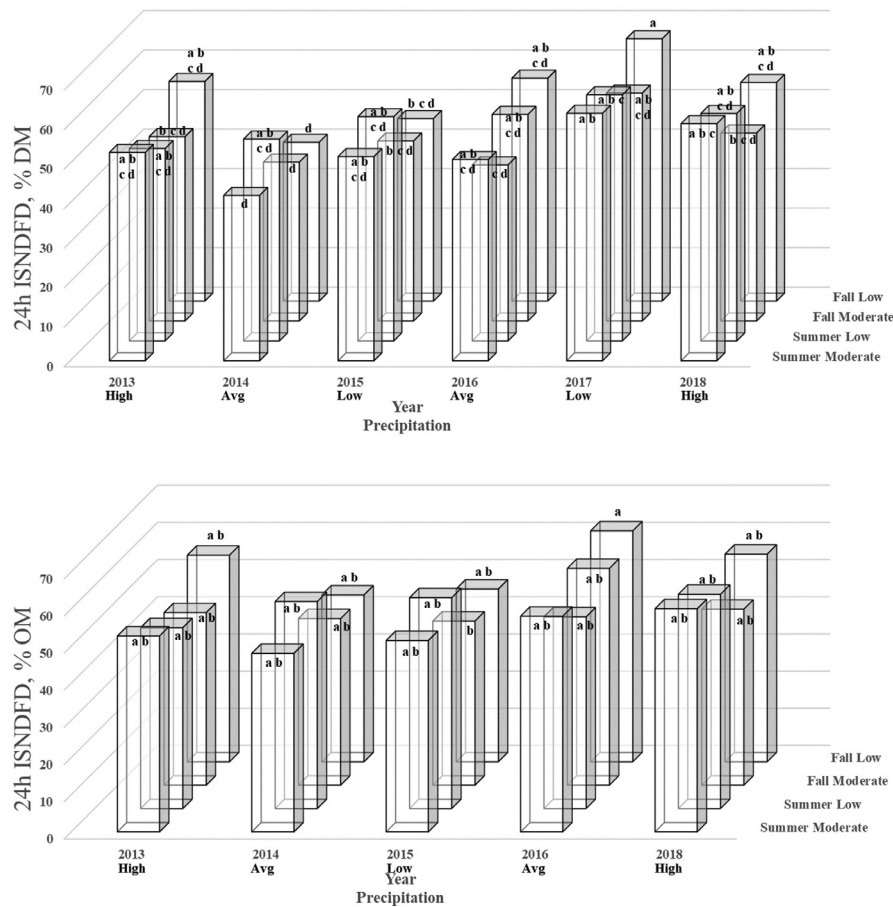


Fig. 2. Least square means \pm standard error of the mean for 24-h in-situ neutral detergent fiber disappearance (ISNDFD) on a dry matter basis (**A**, $P=0.0407 \pm 2.97$) and on an organic matter basis (**B**, $P=0.0534 \pm 2.99$) from rumen extrusa samples by yr \times season \times residual herbage. Year also refers to low, average (Avg) or high annual precipitation. Disappearance percentages with different letters differ ($P < 0.05$). Organic matter was not determined in 2017.

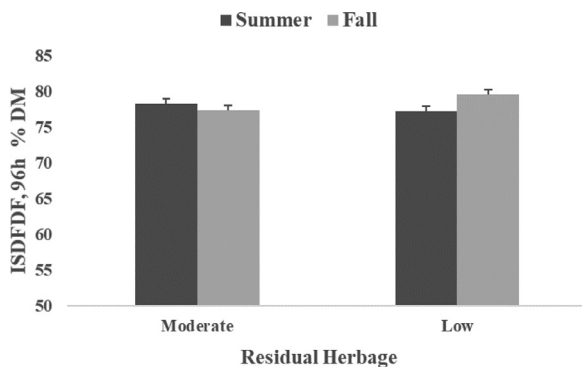


Fig. 3. Least square means \pm standard error of the mean for 96h DM in-situ neutral detergent fiber disappearance (ISNDFD; $P=0.0268 \pm 0.7192$) from rumen extrusa samples by season \times residual herbage.

disappearance increased from summer to fall in low residual herbage paddocks ($P=0.0268$; Fig. 3). A tendency ($P=0.0964$) for a yr \times residual herbage effect at 96 h (i.e., extent) ISNDFD suggests that prolonged prescribed grazing may have slight effects on fiber disappearance. However, precipitation may influence plant structure and how fiber is broken down in the rumen. In 2017, when precipitation was below normal, which may relate to slower plant growth and fiber development, fiber may have disappeared more readily compared with 2018, when precipitation was above normal

and plant growth most likely went into stem growth and fiber disappearance was diminished (Table 5).

In addition, a yr \times season effect for 96-h DM ISNDFD was greater in 2017 than 2018, which corresponded with low- and high-precipitation yrs, respectively. This indicated that plants accumulate fiber differently depending on available precipitation. For fall 96-h DM ISNDFD in 2016, a yr with average precipitation, disappearance of NDF was 20.8% greater than fall of 2018, a high-precipitation yr ($P=0.0013$; see Table 4).

Forage extrusa CP was influenced by a yr \times season interaction with greater CP concentrations in the summer 2014, 2015, 2016, and 2017 and fall of 2016 and 2017 ($P < 0.0001$; see Table 4) compared with other summer of 2018 and fall of 2013, 2014, 2015, and 2018 concentrations of CP. Lowest measures of CP were in fall of 2013 and 2018, both of which were high-precipitation yrs, and in fall of 2015, which was a low-precipitation yr. Forage extrusa TDN was greatest in summer of 2017 and like concentrations observed in summer of 2016 ($P=0.0025$; see Table 4). A 34% difference between summer 2017 and fall of 2013 was observed for TDN concentrations.

Interactive effects on forage minerals

There were 10 indicators from extrusa samples that interacted with measured minerals. A residual herbage \times season \times yr interaction for extrusa P concentrations was observed ($P=0.0086$; see Fig. 4). In 2013, a high-precipitation yr, extrusa P con-

Table 5

Least square means \pm standard error of the mean (SEM) for forage in-situ neutral detergent fiber disappearance (ISNDFD) from rumen extrusa samples by yr \times residual herbage. Characteristic with different letters differ ($P < 0.10$).

Extrusa diet quality metric	Residual	Yr						SEM	P value
	Herbage ¹	2013	2014	2015	2016	2017	2018		
96h ISNDFD, % DM	Moderate	77.13cd	76.22cd	77.90cd	80.20bc	87.67a	67.78e	1.29	0.0964
	Low	77.23cd	74.80cd	81.43abc	79.16c	86.45ab	71.56de		

¹ Grazed paddocks at moderate 600 kg/ha and low 300 kg/ha residual herbage.

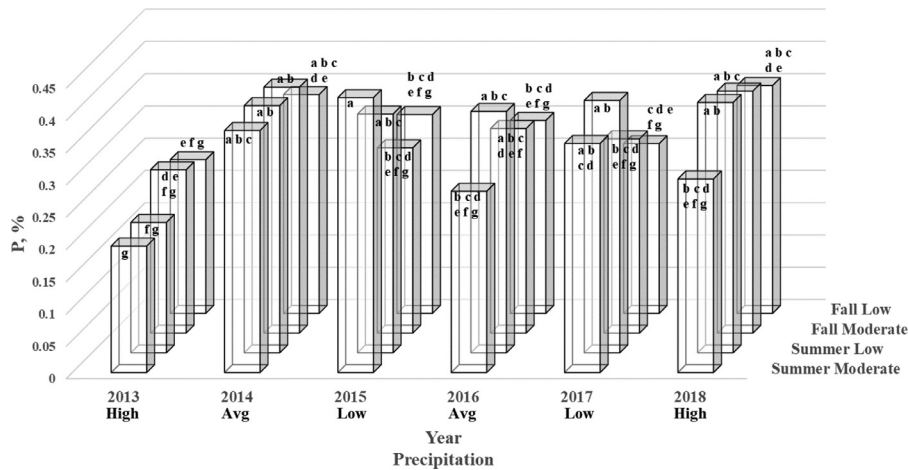


Fig. 4. Least square means \pm standard error of the mean for macromineral P concentration ($P = 0.0086 \pm 0.019$) from rumen extrusa samples by yr \times season \times residual herbage. Year also refers to low, average (Avg), or high annual precipitation. Mineral percentages with different letters differ ($P < 0.05$).

Table 6

Least square means \pm standard error of the mean (SEM) for forage macrominerals and microminerals from rumen extrusa samples by yr \times season. Mineral characteristics with different letters differ ($P < 0.05$).

Extrusa diet quality metric	Yr	Yr						SEM	P value
		2013	2014	2015	2016	2017	2018		
S, %	Summer	0.10f	0.15bcd	0.18a	0.17ab	0.15bcde	0.13cde	0.004	< 0.0001
	Fall	0.10f	0.13de	0.12ef	0.15bcd	0.13de	0.16abc		
K, %	Summer	0.84def	1.49ab	1.32abc	1.67a	1.17bcd	1.33abc	0.075	< 0.0001
	Fall	0.61ef	0.79def	0.44f	0.93cde	0.97cde	0.69ef		
Mg, %	Summer	0.14bc	0.19b	0.14bc	0.19b	0.15bc	0.17b	0.014	< 0.0001
	Fall	0.13bc	0.13bc	0.09c	0.12bc	0.12bc	0.29a		
Ca, %	Summer	0.48b	0.77ab	0.58b	0.66b	0.50b	0.63b	0.06	< 0.0001
	Fall	0.56b	0.61b	0.49b	0.53b	0.44b	1.02a		
Na, %	Summer	1.15e	1.53bcde	1.95ab	1.96a	1.94ab	1.57abcde	0.08	< 0.0001
	Fall	1.16e	1.75abc	1.42cde	1.28de	1.78abc	1.64abcd		
Cu, ppm	Summer	29.74c	4.79d	5.10d	4.84d	3.87d	50.13b	2.16	< 0.0001
	Fall	46.21b	3.10d	2.79d	3.43d	3.75d	71.88a		
Zn, ppm	Summer	15.13c	22.51abc	28.99a	24.45ab	25.17ab	20.38bc	1.45	< 0.0001
	Fall	19.24bc	19.88bc	18.79bc	22.19abc	22.84abc	17.92bc		

sistently remained low regardless of residual herbage or season compared with other yrs, but in 2018, another high-precipitation yr, P did not follow a similar trend. In 2015, a low-precipitation yr, P had the greatest concentration in the summer moderate-grazed treatment and was 34.7% greater than the summer moderate-grazed treatment in 2013, a high-precipitation yr.

Forage extrusa S was 57.1% greater in summer 2015, a low-precipitation yr, than the lowest S in 2013 for both summer and fall ($P < 0.0001$; Table 6). Forage extrusa K was 116.6% greater in summer of 2016, an average-precipitation yr, than K in the fall of 2015, a low-precipitation yr. Across all yrs, K decreased from summer to fall each yr except in 2017, a low-precipitation yr, where concentrations remained did not differ between summer and fall. Forage extrusa Mg was 105.3% greater in fall 2018, a high-precipitation yr, than fall of 2015, a low-precipitation yr, while Mg concentrations did not differ across all other yrs and seasons ($P < 0.0001$; see Table 6).

Forage extrusa Ca was 75.5% greater in fall 2018, a high-precipitation yr, than the lowest Ca that occurred in the fall of 2017, a low-precipitation yr, which did not differ from all other yrs and season Ca concentrations ($P < 0.0001$; see Table 6). Forage extrusa Na was 52.1% greater in summer of 2016, an average-precipitation yr, than summer and fall of 2013, a high-precipitation yr ($P < 0.0001$; see Table 6).

Micromineral forage extrusa Cu was 35.7% greater in fall 2018 than for summer of 2018, a high-precipitation yr, and 82.9 and 43.5% greater than summer and fall of 2013, another high-precipitation yr. Furthermore, both high-precipitation yrs (2013 and 2018) had greater Cu concentrations compared with all other yrs and seasons in the study and increased from summer to fall ($P < 0.0001$; see Table 6). Forage extrusa Zn was 62.8% greater in summer 2015, a low-precipitation yr, than summer of 2013, a high-precipitation yr ($P < 0.0001$; see Table 6).

No main effects ($P > 0.05$) of residual herbage were observed for S, K, Ca, Na, Fe, Cu, Mn, and Zn (Table 7). However, extrusa Mg

Table 7Least square means \pm standard error of the mean (SEM) for forage macrominerals and microminerals of rumen extrusa samples by residual herbage.

Extrusa diet quality metric	Residual herbage ¹		SEM	P value
	Moderate	Low		
S, %	0.1391	0.1407	0.0018	0.5192
K, %	1.0416	0.9967	0.0306	0.3023
Mg, %	0.1647	0.1463	0.0056	0.0210
Ca, %	0.6226	0.5886	0.0245	0.3287
P, %	0.3206	0.3257	0.0056	0.5229
Na, %	1.6002	1.5905	0.032	0.8314
Fe, ppm	370.81	356.02	57.44	0.8560
Cu, ppm	19.7583	18.5083	0.88	0.3192
Mn, ppm	44.2358	43.1792	2.13	0.7266
Zn, ppm	21.8858	21.0242	0.59	0.3060

¹ Grazed paddocks at moderate (1 animal unit day [AUD]/ha) and low (1.5 AUD/ha) residual herbage, until a 600 kg/ha and 300 kg/ha of postgrazing residual standing biomass was achieved, respectively.

was 11.8% greater for moderate-grazed treatments compared with low-grazed treatments ($P=0.0210$).

Discussion

Rangelands in the northern Great Plains are considered to be resilient, and they have the ability to adapt to herbivory, fire, and drought (Hoover et al. 2014; Vermeire et al. 2014; Sanderson et al. 2015; Arterburn et al. 2018; Reeves et al. 2020). The interannual variability of precipitation that occurs in the northern Great Plains rangelands is a major factor behind forage quality and quantity. Livestock producers must constantly adjust in their management strategies to best accommodate current conditions. We reported 97.6% difference in ambient annual precipitation between the highest and lowest precipitation yrs within the current study with a mean of 33.1 ± 4.94 cm (range 16.07–46.76 cm).

Rangelands in the northern Great Plains are physiologically adapted to maximize water-use efficiency and adapt to variations in precipitation (Smoliak 1986; Sala et al. 1988; Lauenroth and Sala 1992; Ponce-Campos et al. 2013; Stuart-Haëntjens et al. 2018). In addition, forages in the northern Great Plains are responsive to soil moisture, especially when temperatures are suitable for growth (Patton et al. 2007). There is evidence of southern Great Plains rangelands experiencing a reduction in perennial grass production resulting from decreases in precipitation and increasing temperatures as well (McIntosh et al. 2019).

Impacts of grazing on rangelands can influence forage availability and species composition and in long-term studies have shown that a high level of herbivory can reduce forage production, yet low and moderate levels can enhance forage production compared with nongrazed enclosures (Patton et al. 2007; Porensky et al. 2017). Also, timing or season of herbivory can influence forage production on the northern Great Plains. While there is a plethora of research evaluating grazing impacts during the growing season in the northern Great Plains, there is limited research evaluating dormant-season grazing.

Fiber disappearance had a disappearance of 40% or greater after 24 hours of incubation regardless of season. Fiber disappearance is a measure of available energy for rumen microbial synthesis and ultimately the energy source for the host ruminant. After 24 hours no differences in NDF disappearance between seasons or residual herbage were observed, but the greatest disappearance occurred in a yr with the lowest annual precipitation. This was also observed in the extent of disappearance (96-h) ISNDFD for yr \times residual herbage, indicating that yrs of lower precipitation generate highly digestible forage of higher quality, though forage

quantity is lower. Typically, as forages senesce, NDF disappearance declines, resulting in lower energy available to meet grazing ruminant requirements (Johnson et al. 1998; Waterman et al. 2007).

It is well documented that the factors that determine range livestock productivity include nutrients available in diets being consumed, the quantity of forage available, and how well the nutrient requirements of the herbivore are being met (Adams and Short 1988). As forages senesce, the fiber portion of the forage becomes more lignified and microbial degradation of fiber slows. Range livestock managers, in order to optimize utilization of the fiber, often supplement protein to enhance microbial breakdown of the fiber and capture as much of the energy in the forage as possible.

In the current study CP concentrations met or exceeded range livestock requirements in most yrs of low to average ambient precipitation (NRC 2016); however, in yrs of above-average precipitation, CP concentration marginally met or did not meet requirements of range livestock. This phenomenon is not novel and is often observed in forages with rapid active growth and put a lot of nutrients toward shoot growth, which is often recognized as the nitrogen dilution effect (Grant et al. 2014). CP concentrations in the present study were similar to those previously reported for the northern Great Plains (Adams and Short 1988; Johnson et al. 1998; Waterman et al. 2007; Waterman and Vermeire 2011).

While fiber (energy) and CP are two of the most common nutrients evaluated in rumen diets, macrominerals and microminerals can become deficient and reduce animal performance (Grings et al. 1996). Nutrient concentrations in forages can fluctuate depending on soil fertility, plant species composition, plant growth stage, and water availability (Greene et al. 1987; Schlegel et al. 2016).

Here, P concentrations generally met or exceeded requirements required by grazing ruminants (NRC 2016) with the exception of summer of 2013, when concentrations were below 0.20%. Phosphorus concentrations changed depending on residual herbage, season, and yr but were similar to those reported previously for clipped plant material (Grings et al. 1996). A targeted 1.5 to 2.0:1 Ca:P is ideal for cattle grazing rangelands (NRC 2016), and Ca:P averaged approximately 1.8:1 in the current study. From summer to fall, Ca increased in wet yrs (2013 and 2018) and decreased in drier yrs (2014–2017).

Sodium concentrations exceeded (NRC 2016) the recommended requirements for grazing livestock (0.08%) and may have included some salivary Na from the collecting cannulated cow contributing to these values. Pinchak et al. (1990) cautions that esophageal extrusa may contain salivary Na and thereby overestimate Na coming from the forage. As Na concentrations in the present study were 20 \times greater than the recommended requirements, we believe

salivary contamination occurred, especially as previously measured Na concentrations have been considerably less in our system (Grings et al. 1996).

Potassium concentrations were similar to those reported previously in the northern Great Plains (Grings et al. 1996). Potassium concentrations were more sporadic across yrs but consistently decreased from summer to fall in extrusa samples. Similarly, extrusa S concentrations differed across yrs and tended to be more similar between seasons.

The maximum tolerable concentration for Fe is 500 ppm, and the requirement is 50 ppm (NRC 2016). In the current study extrusa concentrations averaged 300 ppm but were not influenced by residual herbage, season, or yr.

Copper (Cu) and manganese (Mn) tend to vary by yr and precipitation amount. Interestingly, extrusa Cu concentrations increased 16-fold in yrs (2013 and 2018) with above-average precipitation and increased from summer to fall and exceeded ruminant requirements of 10 ppm (NRC 2016). In drier yrs (2014–2017) Cu concentrations were similar to previous reports (Grings et al. 1996) and extrusa Cu was below the recommended requirement for ruminants (NRC 2016). This suggests that in yrs with above-average precipitation, changes in soil moisture alter the plants' ability to take up Cu, making it more available in forages to livestock. Conversely, extrusa Mn was lowered by 19-fold in yrs (2013 and 2018) with above-average precipitation compared with all other yrs. The nutritional requirement for Mn is 20 ppm and yrs of low or average precipitation extrusa met this requirement. However, yrs of above-average precipitation were substantially below nutritional requirements. The mechanisms that allow for more Cu uptake and less Mn in yrs of above-average precipitation are not fully understood. Extrusa zinc concentrations were more consistent across yrs and seasons and had no grazing treatment effects. However, zinc concentrations at no time met the nutritional requirement for range cattle (NRC 2016) and were similar to concentrations previously reported (Grings et al. 1996).

In conclusion, the present research over 6 yr of differing ambient precipitation nutritional composition of diets were altered by season of grazing and grazing pressure imposed on paddocks used in the study. The authors caution that findings may not directly correlate to larger pasture setting as these were 60 × 30 m paddocks under high-intensity, short-duration grazing management. This study focused on longer-term residual herbage effects along with repeated seasonal grazing on diet extrusa quality. Rumen cannulated animals were collected on the first day that grazing occurred and likely consumed the most favorable diet available in each paddock. Effects of residual herbage are likely more strongly expressed at the end of grazing periods.

Management Implications

Interannual variation in precipitation, annual primary forage production, residual herbage, and season of herbivory are all factors considered by land managers and livestock producers when developing grazing plans. Results from this study imply that precipitation can influence plant characteristics such as energy, protein, and mineral values of rangeland forages and that season of use and grazing pressure also contribute to forage nutritive quality. Although studies have shown the N depletion affects forages when above-average precipitation occurs, this study identifies that supplementation of protein to meet animal requirements may still be necessary when there is an abundance of grazable forage with a lot of shoot mass. Furthermore, mineral incorporation into plant biomass is greatly influenced by precipitation. Mineral infiltrations to translocate minerals to roots requires moisture, and the abundance of or inadequate precipitation influences the availability of soil minerals to be used by range plants. This was especially ob-

served for microminerals such as Cu and Mn, which have an important role in metabolism of range livestock and are important in reproductive performance.

Declaration of Competing Interest

The authors report no declarations of interest.

Acknowledgments

The authors appreciate Susan Reil, Dustin Strong, Whisper Kelly, Brad Eik, Bern Garber, Lindsey Voigt Cook, Brooke Shipp, Emily Gates, Jeremiah Jansen, Jackcee Idland, Amanda Williams, Cole Ryan, Megan Markeson, Megan VanEmon, Doug Armstrong, Dana Dale Jansen, Hayden Nelson Vandenberg, Aly Christians Robins, Kailley Toderoff Smidt, Alexis Shipp, Gavin Herzog, Tory Ogelin, Merina Sweet, Katy Stoecklein, Abby Zezeski, Susan Bellows, Amber Eskew Rath, Elise Anderson, Jennifer Muscha, Lindsey Miller, Scott Crevier, Beau Huft, Tom Kunesch, Mike Landers, Dennis Logan, Tom Mott, and Riley Messman for their assistance with treatment implementation, cattle handling/hauling, and data collection.

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